33

Diet and foraging behaviour of Macaroni and Chinstrap Penguins at Bouvetøya, South Atlantic Ocean

by

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"The penguins swam within a foot of the bottom (it was only four or five foot deep in that little embayment), travelling at a high rate of speed and resembling torpedoes going through the water ... one could observe their heads darting from time to time to the left and to the right, evidently picking out euphausians as they moved. In fact, their necks were jerking out and their beaks going just about as fast as a barn-yard fowl feeds on grain thrown on the floor"

Sir Douglas Mawson
Antarctic Explorer

[cited in Zusi 1975]

Declaration

This thesis documents original research, carried out at the Percy FitzPatrick Institute of African Ornithology (University of Cape Town) as part of the requirements for the degree of MSc Conservation Biology. The work has not been submitted in whole or in part for a degree at any other university. All assistance that I have received has been fully acknowledged.

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Onno Huyser
September 2000

Table of Contents

Abstract

Huyser, O.A.W. 2000. Diet and foraging behaviour of Macaroni and Chinstrap Penguins at Bouvetøya, South Atlantic Ocean. Unpublished MSc (Cons Biol) thesis. Cape Town, South Africa: University of Cape Town. 164 pp. with 3 appendices.

Bouvetøya (Bouvet Island; 54°25'S, 3°21'E) is an isolated island situated in the South Atlantic Ocean. Little biological research has been conducted at this globally important breeding site for seabirds. I aimed to improve our understanding of the foraging ecology of two important consumers of marine resources breeding at Bouvetøya, Macaroni *Eudyptes chrysolophus* and Chinstrap *Pygoscelis antarctica* Penguins, during visits in December–February 1996/97 and 1998/99. I studied the diets and foraging behaviour of these species to gain a better understanding of resource use and variability at Bouvetøya, to assess how extrinsic and intrinsic factors influence community organization in this depauperate community of marine predators, to determine the limits to foraging in a specialist consumer of Antarctic krill *Euphausia superba*, and to satisfy long-term monitoring (and ultimately conservation) objectives. Macaroni Penguin diets were dominated by three prey in both years: the myctophid fish *Krefftichthys anderssoni*, krill and another euphausiid *Thysanoessa macrura*. Seasonal effects were strong: above-average representation of *K. anderssoni*, krill and *T. macrura* occurred in diets from the first, second and final third of the chick-rearing period, respectively. Mean foraging depth of Macaroni Penguins in 1999 was 38.7 ± 27.7 m, but foraging was focused at two depth modes (5-15 m & 50-70 m; assessed with time-depth recorders), strongly suggesting that euphausiids were eaten during shallow dives, and fish during deeper dives. Adult body condition explained a significant amount of variation in mean sample mass and number of prey, and was positively related to chick condition. Thus parents in better condition may be able to invest more in their offspring. Female Macaroni Penguins adjusted their behaviour at sea to demands from the chick by conducting shorter trips and diving deeper when chicks were small. This probably allowed them to return lipid-rich fish to the chick and limited their horizontal searching, but may be a more costly foraging strategy than feeding on krill alone. Chinstrap Penguins ate mainly krill in both years, dived shallower (mean maximum depth 25.5 ± 17.9 m) than Macaroni Penguins, and spent a disproportionately greater amount of time at 20–35 m depths, suggesting a focus of feeding activity and hence krill presence. Both species dived less and to shallower depths at night, but conducted the deepest feeding dives at sunrise and sunset. This may result from rapid vertical migration of prey, which may cause disruption of anti-predator aggregating behaviour, or from penguins maximising short-term rates of prey intake in a rapidly changing light regime. Deep diving in Macaroni Penguins may be ultimately limited by light, but most day-time dives are not light limited, probably because penguins have light levels at, or above which, they prefer to forage, but can surpass if necessary. Four dive bout types were recognised in Chinstrap Penguins; types were distinguished by length, period since the last dive, bottom time, descending vertical velocity, and mean maximum depth. Type I bouts probably constituted unsuccessful searching behaviour. Type II bouts appeared to be terminated proximately by penguin satiation, and ultimately by prey patch quality. Type III bouts appeared to occur after a long resting or travelling phase at sea. Type IV bouts appeared to be terminated by declining prey capture rates (resource depression), probably resulting from krill escape behaviour. Physiological limitation of diving did not appear to take place, which is inconsistent with the finding that 36.4% of dives exceeded the Theoretical Aerobic Dive Limit, but suggests that Chinstrap Penguins might possess compensating mechanisms that allow them to maximise the amount of serial time underwater over long intervals. This accords with the finding that Chinstrap Penguins search a comparatively small volume of water for prey, yet have a comparatively short fledging period, and accumulate energy rapidly for the brood at Bouvetøya. Inter-bout intervals indicate that Chinstrap Penguins searched for prey at an average spacing of ca. 320 m, but encountered prey at an average spacing of ca. 400 m. Thus penguins can serve as environmental monitors to gauge the dispersion and patch quality of a variable prey resource. This is important, because existing monitoring programmes that are concerned with impacts of krill shortages on predator performance primarily use land-based measures to assess predator performance at sea. Increased investment in direct monitoring of behaviour at sea will enhance our understanding of predator-prey relationships. The three main diving predators at Bouvetøya (including Antarctic Fur Seals *Arctocephalus gazella*) are ecologically segregated, with some niche overlap. Chinstrap Penguins are predominantly shallow-diving, inshore-feeding, krill specialists; Macaroni Penguins shallow- and deep-diving, offshore, mixed krill and fish generalists; fur seals shallow-diving, offshore, krill specialists. These niches closely resemble those at other sites, including those where greater numbers of sympatric species occur. Interference competition and aggressive interactions on land between fur seals and penguins indicates that intrinsic community interactions do influence community structure at Bouvetøya (primarily penguin demography), but there is little evidence that interactions at sea (predation or competition) structure realised foraging niches. The ecological segregation observed might be an outcome of adaptations by each species to conditions experienced in the centre of their respective ranges. Inferred large-scale environmental variability in marine resources did not exist during the study, but small differences in trip length, prey size distributions and digestion show that small-scale environmental differences did exist.

General Acknowledgements

I am deeply indebted to my supervisors Rory Wilson and Peter Ryan for their support and guidance throughout the completion of this thesis. Rory is awash with great ideas, enthusiasm and a love for his work that is rare and exhilarating to experience. Peter has given me space to follow my own path, yet with his keen insight corrected my course whenever it was required, especially during the write-up. John Cooper has been a source of constant enthusiasm, friendship and information. Thank you John for your selfless efforts in organizing the expeditions to Bouvetøya, without which none of my work would have been possible. John and Peter have also both dragged me towards a tighter style of writing.

Many people have encouraged and assisted me throughout, both in the field and at home. Bruce Dyer, Ross Wanless, Kjell Isaksen, Greg Hofmeyr, Steve Kirkman, Alf Næstvold and Wendy Wilson were capable and supportive team mates at Bouvetøya. Bruce is thanked in particular for his Herculean efforts at sorting and identifying (smelly) prey from numerous penguin diet samples. I am grateful to Steve for making his unpublished data available to me at short notice and for directing me to pertinent literature on fur seals, and to Ross for criticisms on the Synthesis. I am also grateful to my coauthors on Appendices B & C for their labours in collecting, analysing and writing up the data, and for permitting me to append the reports.

The following people have all provided valued comments or help at various stages during the evolution of this thesis: Ian Boyd, Andrew Brierley, Yves Cherel, Rob Crawford, John Croxall, Bruce Dyer, David Gremillet, Phil Hockey, Kjell Isaksen, Steve Kirkman, Norbert Klages, Denis Lepage, Paul Martin, Fridtjof Mehlum, Denzil Miller, Deon Nel, Gerrit Peters, Daniel Polakow, Lorenzo Prendini, Keith Reid, Eugene Sabourenkov, Les Underhill, Ross Wanless, Tony (A.J.) Williams and Anton Wolfaardt. Lionel Mansfield and Chris Tobler provided sterling technical support at home, and Jochim Lage was always ready to assist when I had problems with software.

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All research at Bouvetøya was conducted under the aegis of the Norwegian Polar Institute; Fridtjof Mehlum, Kjell Isaksen, Jan-Erling Haugland, Ian Gjertz and Vidar Bakken are thanked in particular for co-ordinating logistics in Norway. No doubt I have omitted the names of some that deserve thanks. This is not intentional, and I hope I cause no offence.

Finally, without Colleen's support, gentle encouragement, and patience during the long periods apart, this would all have been so less joyless. Thank you Coll; I hope I can reciprocate when your turn comes.

Introduction

Most of our knowledge about the lives of land-based marine predators in the Southern Ocean comes from studies performed on land. Yet a quick glance at any map reveals the vast expanse that is the Southern Ocean, and where many seals and seabirds spend the majority of their time; not on land but at sea. Throughout the region the few outposts of land are heavily utilised by breeding seals and birds, chiefly during the summer, when the comparatively lenient weather permits breeding. Such an outpost is Bouvetøya (Bouvet Island), the most isolated island in the world, situated in the mid South Atlantic Ocean (Fig. 1).

The biological value of Bouvetøya is best appreciated in the globally significant numbers of breeding seabirds (penguins and volant birds) and seals the island supports (Appendix A). But this has not always been so. Early landings at the island were made to take seal skins and blubber. When the island was annexed in 1928, the hope was that it could serve as a staging post for whaling expeditions to higher latitudes (Christensen 1935). With so little land in the South Atlantic, the island received renewed attention in the 1950s and 60s for its potential as a weather station, but, as with the earlier plans, this never materialised (Crawford 1982). The few biological expeditions that visited Bouvetøya did not remain for long, until 1996/97 and 1998/99 when two expeditions visited for approximately three months each. The primary goal of these expeditions was to conduct monitoring of important penguin and fur seal predator populations at the island for conservation purposes; Isaksen et al. (1997a) review the circumstances fully.

Bouvetøya is a small island of volcanic origin, situated approximately 500 km south of the Antarctic Polar Frontal Zone but north of the Marginal Ice Zone (MIZ). The island is thus unusual (together with South Georgia) in that, while large concentrations of Antarctic krill *Euphausia superba* (hereafter krill) are not commonly found in the MIZ situated to the south, krill occurs in the surrounding waters of the island (e.g. Fevolden 1980). The bathymetry drops off rapidly around the island, and the extent of shallow inshore waters is consequently small (Norsk Polarinstitutt 1981). Most of Bouvetøya (93%) is permanently covered by ice (Orheim 1981), and pack ice from the Weddell Sea is also present occasionally. The island is bounded by steep, ice-free cliffs with narrow boulderine beaches on the north, west and south coasts, and has a sloping ice shelf leading down from Olavtoppen (780 m a.s.l.) to shingle beaches on the east coast (Fig. 1). The study site at Bouvetøya is situated at Nryøysa, on the western side of the island (Fig. 1). Details on the biota, climate and breeding schedules of penguins at Bouvetøya are provided in Isaksen et al. (1997b) and Appendices A, B & C.

Nyrøysa has an interesting history. It consists of a raised and unstable (Appendix C) rubble platform, bordered by large beaches at the southern and northern ends. Nyrøysa was created during the late 1950s (Fig. 1), and is a major focus of activity for seabird and Antarctic Fur Seal *Arctocephalus gazella* populations breeding at the island. Nyrøysa now holds 95% or more of the entire Bouvetøya fur seal population (Bakken 1991; Isaksen et al. 1997b; Kirkman et al. in press), and numbers are currently the highest ever recorded (Fig. 2). This is likely to be at least partly attributable to the availability of land where previously none accessible to fur seals existed. This increase is also consistent with the post-exploitation recovery phase seen at other sites in the Southern Ocean (SCAR 1992; Boyd 1993; Hofmeyr et al. 1997). The extent of sealing activities at Bouvetøya is not known in detail, but the harvest was probably substantial (Holdgate et al. 1968). A final factor possibly promoting increased seal numbers throughout the Southern Ocean is the great reduction in numbers of baleen whales, leading to greater availability of krill, the main prey of Antarctic Fur Seals (Laws 1984; Croxall et al. 1988; Jouventin & Weimerskirch 1990; Croxall 1992; Reid & Arnould 1996).

Nyrøysa also holds large numbers of breeding Macaroni *Eudyptes chrysolophus* and Chinstrap *Pygoscelis antarctica* Penguins (Fig. 1). Penguins outnumbered fur seals at Nyrøysa in the early 1980s, but since then have decreased substantially (Fig. 2). Chinstrap Penguins have fared the worse of the two species, and their long-term persistence at Nyrøysa must be in doubt. Some of these decreases can be attributed to interference competition for breeding sites, and aggressive interactions with fur seals (Synthesis; Appendix C; unpubl. data). Much of the inland portion of Nyrøysa is sparsely occupied by loafing fur seals, breeding Pintado Petrels *Daption capense* and Subantarctic Skuas *Catharacta antarctica lonnbergi*, thus it is surprising that disputes for breeding space between penguins and fur seals occur as frequently as they do. Evidence of declines at other penguin colonies on Bouvetøya is circumstantial, and should be treated with caution (Appendix A).

The visits to Nyrøysa enabled me to study the diet and foraging ecology of Macaroni and Chinstrap Penguins, two important consumers of marine resources in the Southern Ocean (Croxall 1984; Croxall et al. 1984; Brown 1989). These species are the two most numerous penguins in the Southern Ocean (Marchant & Higgins 1990; Woehler 1993; Ellis et al. 1998). Macaroni Penguin numbers are decreasing both globally (Ellis et al. 1998), and at Nyrøysa (Bakken 1991; Isaksen et al. 1997b; Appendix A; Fig. 2). Long-term monitoring from the South Georgia colonies suggest a halving of numbers since the late 1970s (Ellis et al. 1998), and Macaroni Penguins thus warrant conservation attention (BirdLife International 2000).

Aspects of the diet and foraging ecology of both Macaroni and Chinstrap Penguins are reasonably well known from other sites in the Southern Ocean (reviewed in Williams 1995), but our knowledge from Bouvetøya is poor. This needs to be redressed if we seek to understand the potential impacts of expanding commercial krill (mainly *Euphausia superba*) fisheries on their populations, their conservation status, and their role in local ecosystem processes. In my study I address this lack of knowledge about the diet and diving behaviour of the Macaroni Penguin at Bouvetøya, and contrast its foraging ecology with populations elsewhere, as well as that of the Chinstrap Penguin at Bouvetøya.

Penguins are one of the most well-studied of avian families, and occur across environmental gradients stretching from the fast-ice of the high Antarctic latitudes to equatorial South America (Williams 1995). They are thus unique among birds in both their marine specialization and their capacity to tolerate environmental extremes. The family is distributed throughout the Southern Ocean, with some sites holding up to five sympatric breeding species (Wilson 1983; Woehler 1993). Penguins thus offer excellent opportunities to study mechanisms permitting ecological segregation of potential competitors. Such studies have focused on Antarctic communities (e.g. Volkman et al. 1980; Lishman 1985; Trivelpiece et al. 1986; Wilson 1995), and the sub-Antarctic communities at the Prince Edward Islands (Adams & Brown 1989) and the Crozet Islands (Ridoux et al. 1988; Ridoux 1994). Bouvetøya possesses a comparatively depauperate penguin community, with only two regularly breeding species (Bakken 1991; Appendix A). It is thus a relatively simple system compared to other sites where studies have been conducted, and is suitable for assessing the extent to which extrinsic and intrinsic factors influence community organization.

It is widely appreciated that no community is truly discrete and closed. In fact, communities are open systems with respect to the flow of energy, materials, and species composition (Brown 1987). Species composition varies little over time in systems that are nearly closed (e.g. tropical primates; Terborgh & Van Schaik 1987), but greatly in those that are almost open (Brown 1987). With their high levels of biotic and physical flux across an arbitrarily-defined boundary, oceanic islands and the surrounding marine environment are good exemplars of open systems. Extrinsic (abiotic) factors are thought to be more important in determining community organization in open systems (Brown 1987). Communities are also influenced by intrinsic interactions among the constituent species. Amongst others, intrinsic interactions can take the form of competition for limiting resources (food, mates, breeding sites), or predation.

The krill resource at Bouvetøya is known to be temporally variable, as is the case elsewhere in South Atlantic (Brierley et al. 1997; Croxall et al. 1999), and is suspected to originate from elsewhere (Fevolden 1980). I thus expected to find variability in marine resources at Bouvetøya over the two year study period, and that this would be reflected in the diets of the breeding penguins. Since the predator component of the system is also comparatively depauperate, I expected that intrinsic factors at sea would be less important in structuring realised foraging niches, and that physical variability in the prey component of the community would be a dominant process.

The key questions I address are, therefore:

1. What is the diet of breeding Macaroni and Chinstrap Penguins at Bouvetøya?
2. How does this vary seasonally and inter-annually, and how does this relate to our current understanding of marine resource variability in the Southern Ocean?
3. How does the diving behaviour of breeding penguins at Bouvetøya relate to their diet, and how is behaviour at-sea adjusted with increasing demands from the brood as the season progresses?

4. What are the realised niches of penguins at Bouvetøya, and how does this compare with studies conducted at comparatively species-rich sites?
5. Are intrinsic interactions important determinants of these realised niches?
6. What limits successful foraging in a specialist consumer of krill at Bouvetøya, and can the foraging behaviour of this specialist yield useful information on prey abundance and dispersion?
7. Finally, are conservation ends best served with current monitoring schemes, or are improvements, that take greater account of the behaviour of predators at sea, feasible?

Outline

Chapter 1 : I present information on the diet of breeding Macaroni Penguins at Bouvetøya, and discuss variation in diet composition, and how seasonal, inter-annual and sex differences account for this. I also compare the diet with that of Macaroni Penguins elsewhere, and consider whether intrinsic community interactions at sea (competition) influence the diet of breeding female Macaroni Penguins.

Chapter 2 : I link the most important findings of Chapter 1 with information on diving and foraging behaviour of female Macaroni Penguins, and consider how females adjust their behaviour at sea when they are the sole provisioners of the chick.

Chapter 3 : I discuss inter-annual variation in diet, foraging rhythms and diving behaviour of Chinstrap Penguins at Bouvetøya. I compare the niche occupied by Chinstrap Penguins with that occupied elsewhere, and with that occupied by Macaroni Penguins at Bouvetøya. I also consider the evidence for the realised niche of Chinstrap Penguins being limited by competitive interactions with other consumers of krill.

Chapter 4 : I consider how the foraging behaviour of Chinstrap Penguins, specialist consumers of krill, is limited by one (or more) of four hypothesised factors: krill presence, krill abundance and density, penguin satiation, or physiological limitation. I also show that temporal patterns in penguin foraging activity yields information on prey spatial distribution, which can be a useful tool for monitoring programmes.

Chapter 5 : I discuss shortcomings of the CCAMLR Ecosystem Monitoring Programme (CEMP), which seeks to understand the relationship between krill availability and the performance of dependent land-based predators. I propose increased investment in the direct monitoring of penguin behaviour at sea, to better understand predator-prey relationships.

The chapters are written as stand-alone papers, and include Abstract and Reference sections. None have been submitted for publication, yet. I also provide as an aid to the reader the text of three background references that are frequently cited, but not widely available. These are contained in the three appendices. I am the sole author of the first, a junior co-author on the second, and a senior co-author on the third. In the *Synthesis* I do not substantiate statements that are substantiated elsewhere in the thesis.

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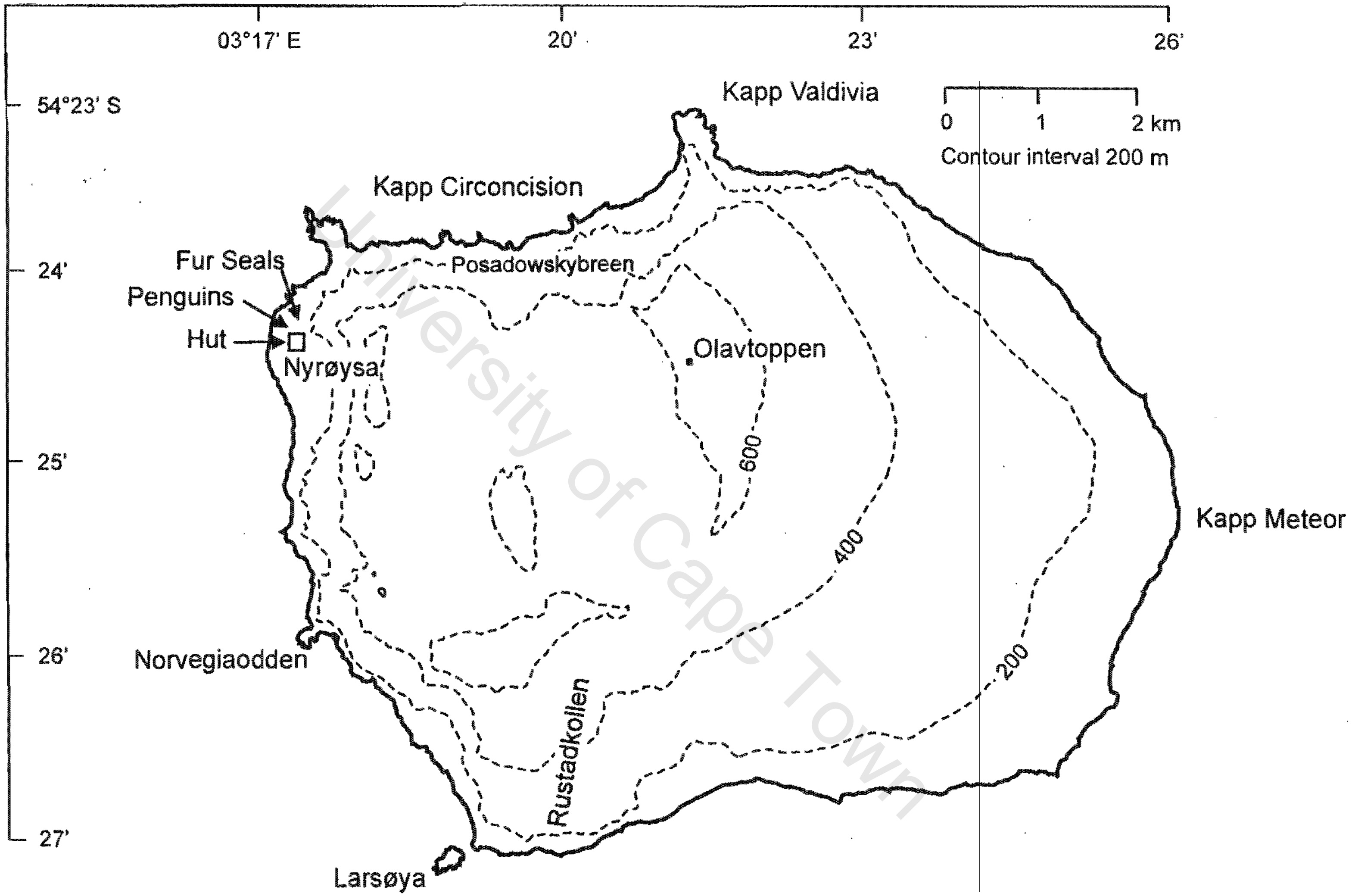
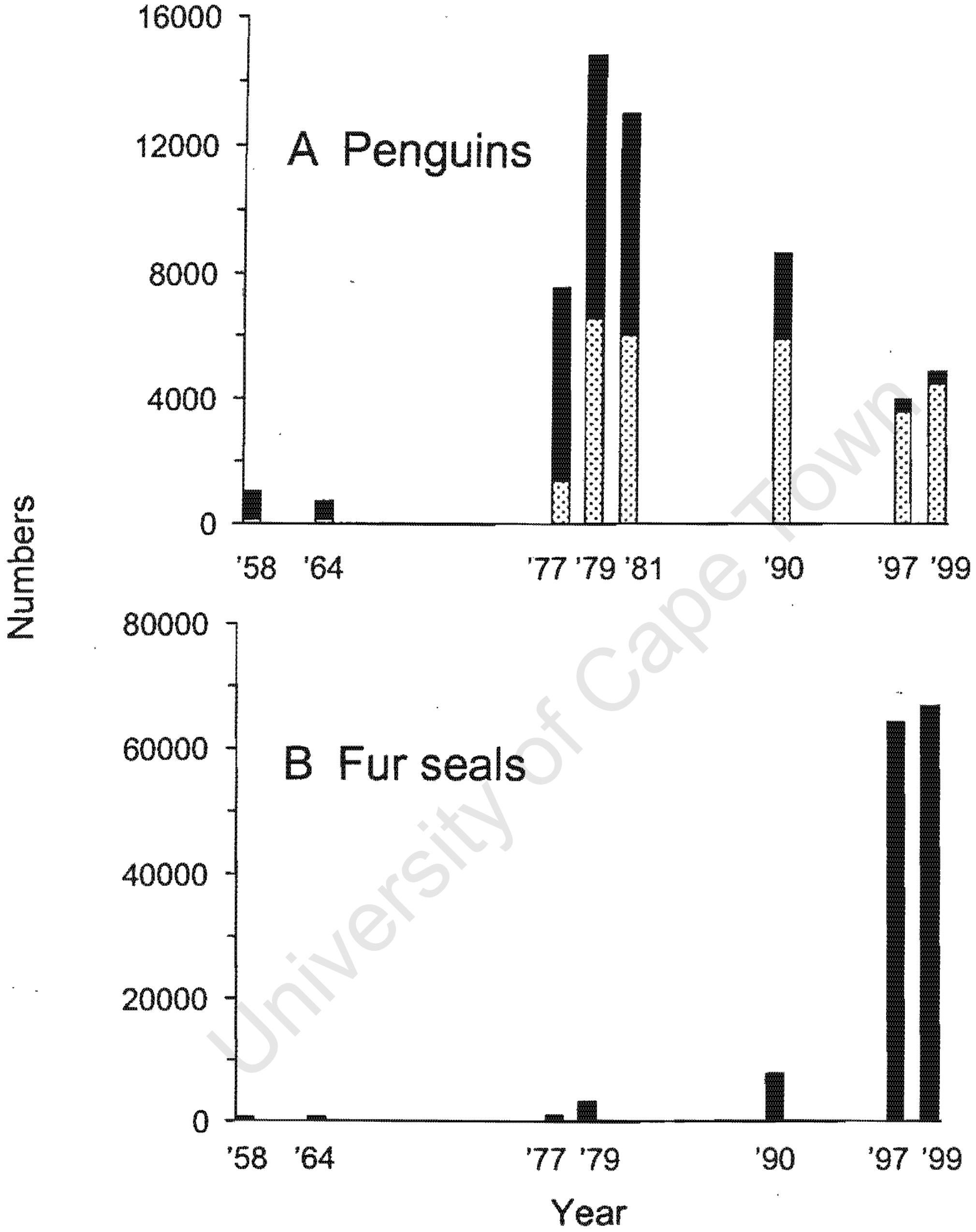


Introduction: Figure 1. Bouvetøya. The Nyrøysa platform on the west side of the island was formed sometime between 1955 and 1958, probably by a large landslide (Prestvik & Winsnes 1981). The platform is ca. 700 m long with an average height of between 25 and 40 m a.s.l. The CEMP station is situated at the northern end of the platform, adjacent to the slopes holding the penguin colonies, which lead down to the large Nordstrand beach holding the breeding population of Antarctic Fur Seals.



Introduction: Figure 2. Population sizes (adults) of Chinstrap Penguins *Pygoscelis antarctica* (solid bars) and Macaroni Penguins *Eudyptes chrysolophus* (stippled bars) (Panel A), and Antarctic Fur Seals *Arctocephalus gazella* (Panel B) at Nyrøysa, Bouvetøya. References for data as follows: 1958: Winsnes (1966), Solyanik (1964); 1964: Holdgate et al. (1968); 1977: Fevolden & Sømme (1977); 1979: Haftorn et al. (1981); 1981: Watkins (1981); 1990: Bakken (1991); 1997: Isaksen et al. (1997a); 1999: Appendix C. Note different scales on y-axes.

Chapter 1

Seasonal, inter-annual and inter-sexual variability in the diet of Macaroni Penguins *Eudyptes chrysolophus* at Bouvetøya

Abstract

I studied the diet of breeding Macaroni Penguins *Eudyptes chrysolophus* at Bouvetøya during the breeding seasons of 1996/97 and 1998/99. I report the relationship between adult and chick body condition, and mass and abundance of prey returned to shore, as well as seasonal, inter-annual and inter-sexual variation in diet. Three prey taxa predominated in both years: the myctophid *Krefftichthys anderssoni*, and the euphausiids *Euphausia superba* (krill) and *Thysanoessa macrura*. Overall, though, diets contained more prey taxa than at other sites south of the Antarctic Polar Frontal Zone, and were unlike the diet of Macaroni Penguins from sites in the western South Atlantic. Adult body condition explained a significant amount of variation in mean sample mass and number of prey, and was weakly positively related to chick condition. Thus parents in better condition may be able to invest more in their offspring. Samples were less digested and mean sample mass was higher in 1999 than 1997, although mean number of prey did not differ. Penguins might thus have been foraging closer to the island in 1999, suggesting small-scale inter-annual variation in distribution of prey. In both years fish dominated diets by mass at the beginning of chick-rearing, but subsequently declined to equivalence with euphausiids. This decrease in fish representation is contrary to other penguin studies, possibly because lipid-rich pelagic myctophid resources suitable for small chicks might be more readily available close to Bouvetøya during summer than at other sites. In both seasons, above-average representation of *K. anderssoni*, *E. superba* and *T. macrura* occurred in samples from the first, second and final third of the chick-rearing period, respectively. Inter-annual differences in diet species composition were insignificant, sex had a weak effect, and seasonal effects were systematic and strong. The large ENSO event of 1997/98 might have been expected to influence prey abundance at the island in 1999, and has been implicated in Antarctic krill shortages elsewhere in the western South Atlantic. Thus, the diet of an important predator indicates that while consistent small-scale environmental differences existed between 1997 and 1999 at Bouvetøya, large-scale differences did not.

Introduction

Knowledge about the impact predators have upon marine resources is necessary to understand their role in local ecological processes, how this role differs from populations elsewhere, and ultimately for conservation objectives. The Macaroni Penguin *Eudyptes chrysolophus* is the most numerous penguin species in the world (Woehler 1993), with a population of ca. 9-11.8 million breeding pairs (Woehler 1993; Ellis et al. 1998), distributed throughout the sub-Antarctic and Antarctic regions (Marchant & Higgins 1990; Woehler 1993; Williams 1995). Macaroni Penguins are important consumers of euphausiid crustaceans and myctophid fish at many sites in the Southern Ocean (Marchant & Higgins 1990; Williams 1995; Hull 1999), and this is of some concern since important prey species such as Antarctic krill *Euphausia superba* (hereafter krill) are attracting increasing attention from commercial fisheries (e.g. CCAMLR 1999). Little information has been presented before on the biology of Macaroni Penguins at Bouvetøya (Cooper et al. 1984; Bakken 1991; Isaksen et al. 1997a; Mehlum et al. 1998; Appendices B & C), an important predator species at this island (Bakken 1991; Appendix A).

Inter-annual variation in the availability of seabird prey has been inferred from changes in predator diet at various sites throughout the Southern Ocean, perhaps most conspicuously at South Georgia (Boyd et al. 1994; Croxall et al. 1999). Here, and commonly elsewhere in the region, this involves variability in the availability of krill (e.g. Croxall et al. 1988; Priddle et al. 1988; Boyd et al. 1994; Brierley et al. 1997,1999; Croxall et al. 1999; Reid et al. 1999). The large-scale oceanographic El Nino–Southern Oscillation (ENSO) anomaly has been implicated in shortages of krill, which tend to lag the anomaly by about one year (Croxall et al. 1988; Priddle et al. 1988; SC-CAMLR 1998). Krill is a key species in the Southern Ocean food web (Everson 1984; Murphy et al. 1988; Croxall et al. 1997), and shortages can therefore depress reproduction and survival of predators (Boyd et al. 1994; Croxall et al. 1988, 1999). Given this baseline of variability in the region, I studied the diet of breeding Macaroni Penguins at Bouvetøya over two seasons, and was fortunate that the study straddled a year in which one of the largest ENSO events of the century occurred (ENSO Monitor 2000).

I also expected that the seasonally-influenced changing availability of prey (small-scale environmental change), coupled with increasing demands from growing offspring, would cause changes in diet over the course of the breeding period. This could be compounded by effects from adult quality, with adults in poor physical condition possibly unable to satisfy fully the nutritional demands of their offspring. Macaroni Penguins have a marked division in provisioning labour. During approximately the first three weeks of chick-rearing, the female alone provides for the chick while the male remains ashore brooding, or regaining body condition at sea during his first post-fast trip (Williams 1995; Mehlum et al. 1998; unpubl. data). I expected that this might also, in conjunction with the sexual dimorphism of this species, lead to inter-sexual differences in diet.

In this study, I (1) describe the diet of breeding Macaroni Penguins at Bouvetøya, (2) investigate the relationship between adult and chick condition, and mass and abundance of prey returned to shore, and (3) discuss seasonal, inter-annual and inter-sexual patterns in diet.

Methods

For details on the Nyrøysa study site, and biota and climate of Bouvetøya, see the Introduction, Isaksen et al. (1997a,b), and Appendices A, B & C.

Diet sampling

In 1997 and 1999 stomach contents were collected from adult birds newly arrived ashore from foraging, and that had not yet fed their chick. Macaroni Penguins lay two eggs, but the first seldom hatches (Williams 1995; unpubl. data). In 1997 returning penguins (identified by their wet plumage, pinkish tinge to the under-flippers and distended stomachs) were captured at walkways close to the beach and the colony. In 1999 penguins were captured at the nest by hand or with a hoop-net. This enabled identification of the returning bird's chick, which was captured and weighed using a 3- or 10-kg spring balance before feeding occurred. Only penguins which had not commenced feeding their chick were sampled.

Stomach contents were collected using a modified water-offloading technique (Wilson 1984). In both years samples were collected by an experienced operator, usually assisted by two helpers. In 1997 birds were flushed once or twice, and in 1999 birds were flushed until the water was clean, which was mostly twice. For experienced operators this is usually sufficient to collect most, if not all, of the stomach contents (B.M. Dyer pers. comm.; pers. obs.).

Penguins were sexed visually before stomach sampling, males having on average longer and deeper bills than females (Marchant & Higgins 1990; Williams 1995; CCAMLR 1997). In 1999, sex was confirmed by measuring bill depth at gonys and bill length (CCAMLR 1997). All measures were made to the nearest 0.1 mm using Vernier calipers. Adult mass (± 0.1 kg) was also taken before stomach sampling using a 10-kg spring balance, and flipper length - the perpendicular straight line distance from the distal end of the horizontally extended flipper to the point anterior to the point of attachment on the body - was recorded using a tape measure (± 1 mm).

In both years stomach contents were collected after peak hatching had passed. Mean hatching date was 30 December in 1996/97 (Isaksen et al. 1997a), and 31 December in 1998/99 (Appendix C). Sampling commenced on 10 January 1997 and 1999, and took place invariantly every five days, ending on 19 February, shortly before fledging commenced. Five samples were collected on each sample day providing a total of 45 samples per season. All samples were collected between 18h00 and 21h20 (GMT+1).

Diet analysis

All samples were frozen, and returned to South Africa for analysis. Samples were thawed and drained, and the wet mass recorded (± 0.1 g) with an electronic mass balance. The material was sorted into crustacean, fish and cephalopod (squid) components and each component weighed separately. The state of digestion (SDig) of the components (SDig = 1: fresh, 2: semi-digested, 3: well digested) was then recorded, with the component portions searched for identifiable prey items, most of which were identifiable to species level. Fish were identified from otoliths using keys in Hecht (1987), Gon & Heemstra (1990), and reference material at Marine and Coastal Management, Cape Town, and the Port Elizabeth

Museum. Crustaceans were identified from the same reference collections. Some fish were only identifiable to genus level, owing to developmental immaturity or the advanced state of digestion. Some amphipods and all squid beaks were identified to order level only. It was only possible to weigh the crustacean component; other taxa typically were too digested to separate out.

The total numbers of each species occurring in the sample were recorded, either by counting total left or right otoliths (fish), or whole individuals or carapaces (crustaceans). Otoliths were sorted, separated into left and right otoliths, and measured to the nearest 0.1 mm with a microscope and graticule if not eroded by digestion.

Statistical analysis

Dietary data are presented in two forms: standardised (%) frequency of occurrence (proportion of samples where that prey taxon was present), and whole wet mass. Reconstituted mass was not employed because digestion precluded accurate measurements of most crustaceans, amphipods and many fish otoliths. Also, the mean length of dominant fish prey (as calculated from lengths of otoliths in good condition) did not change significantly with time over the season (regression ANOVAs; all $p > 0.05$). Therefore changes in numerical frequency can also be interpreted as changes in mass.

Adult body size was calculated as the first order principle component (PC1) combining morphometric measurements bill length, bill depth (gonys), and flipper length. The effect of size was first removed by regressing body mass against PC1, the resulting residual taken to be an index of body condition (e.g. Lorentsen 1996). To test the influence of adult body condition on chick body condition (measured as mass corrected for age), the mean chick and adult condition (food provisioner only) for each sample day was calculated, and residual values for pairs of chicks and parents correlated. Most correlations were thus between females and their chick, since males do not feed the chick during the guard period (Williams 1995). To do this I had to assume that all chicks on a sample day were the same age. Although this was not the case, Macaroni Penguin hatching at Bouvetøya is highly synchronous (Williams 1995; Isaksen et al. 1997a; unpubl. data) and no systematic bias should therefore exist. Sample sizes vary in these analyses because it was not always possible to capture and weigh the chicks, and collect all mensural measurements from all adults.

All data were tested for normality using Shapiro-Wilkes W tests (Zar 1996), and if non-normal either transformed (proportional data arcsine-transformed) or non-parametric procedures employed. Analyses were conducted using Statistica 5.5 (StatSoft, Inc. 1999). All summary statistics are quoted as mean ± standard deviation (SD).

Multivariate analyses

It was necessary to use a number of techniques to resolve multivariate patterns in diet composition, since no single approach that does this satisfactorily exists. I conducted a hierarchical cluster analysis of the dietary data from both seasons using PRIMER software (Clarke & Warwick 1994a,b), which calculated Bray-Curtis similarity between each sample, using the standardised transformed (square-root) numerical frequencies of prey occurrence per sample.

Penguins returning to shore at the same time might have been foraging in groups together, and thus have similar diets. This was investigated by testing whether samples collected on the same day tended to cluster into the major groups. Serial correlations of sample identification values (n), numbered sequentially from the beginning of 1997 to the end of 1999, and neighbouring values ($n_{k+1,k-1...}$) were calculated. I reasoned that, if samples were more similar to neighbouring samples collected in time (indicative of birds foraging together), this would be reflected in the cluster analysis as a significant positive correlation between n and a, where $a = (n_{k+1} + n_{k-1})/2$.

Since the assumptions of a MANOVA were not met, an Analysis of Similarities (ANOSIM) was conducted using PRIMER. ANOSIM is built upon a simple non-parametric permutation procedure, applied to the rank pairwise similarity matrix underlying the classification of samples (Clarke & Green 1988; Clarke & Warwick 1994b), and employs Monte Carlo randomizations (Hope 1968; Clarke & Warwick 1994b). Two-way nested ANOSIM designs were employed (e.g. Clarke 1993).

Covariate biplot ordinations were conducted to provide visual insight into the cluster analysis. This ordination was a modified version of that used by Berruti et al. (1993). The standardised transformed (square root) frequency of occurrence of each prey species recorded for each diet, and supplementary points representing the independent variables (prey species), were projected on to the ordination to show which species were responsible for the majority of the variability (see references and Appendix in Berruti et al. 1993, and Croxall et al. 1997). For visual convenience, each sampling season was divided into thirds; I refer to these as the first, second and final periods.

Results

Based on comparison with measurements and using information from South Georgia (Williams & Croxall 1991) visual sexing of Macaroni Penguins in 1999 was accurate in 43/45 cases (> 95%), thus I am confident of my assignment of sex for the birds sampled in 1997. In 1997 samples were taken from 33 females, 11 males and 1 unsexed bird, and in 1999 from 35 females and 10 males.

Diet composition

Euphausiids and fish occurred most frequently in diet samples, with amphipods and cephalopods occurring relatively infrequently. In 1997 a minimum of 18 prey species was recovered from 45 samples, and in 1999 12 species from 45 samples (Table 1.1). Over both years, a total of 20 prey species was recorded (Table 1.1).

Fish dominated by mass in both years (1997: 73%; 1999: 78% mean sample mass), followed by euphausiids (1997: 28%; 1999: 22% mean sample mass) (Appendix 1.1). Numerically *Krefftichthys anderssoni* dominated, with smaller contributions from *Electrona carlsbergi* and *Notolepis coatsi* (12% and 3%, respectively; Table 1.2).

More *K. anderssoni* individuals were recovered in 1999 than 1997. This is undoubtedly at least partly a consequence of samples being heavier in the latter season (see below). In 1997 *K. anderssoni* of around 45-mm total length were most frequently eaten, but there was a pronounced bimodality in the 1999 samples with individuals of both ca. 45-mm and 30-mm being consumed, the latter class less often (Fig. 1.1). This explains why the *K. anderssoni* consumed in 1997 were longer than in 1999 (1997: 44.8 ± 6.3 mm, 1999: 38.2 ± 8.2 mm; Kolomogorov-Smirnov test; $p < 0.001$).

Although more *E. carlsbergi* individuals were recovered in 1999 (Fig. 1.2), individuals were very slightly larger in 1997 (1997: 83.5 ± 4.3 mm; 1999: 82.1 ± 3.8 mm) (t-test; $p < 0.001$).

Numerically, the euphausiids *Thysanoessa macrura* and krill dominated the crustacean component of the samples from both years (Table 1.2). *Thysanoessa macrura* was particularly abundant in 1997 (90% of all crustaceans), but by mass krill was more important (Appendix 1.1).

Sample mass, total number of prey and state of digestion

Average sample mass was significantly greater in 1999 (232 ± 107 g) than in 1997 (150 ± 81 g) (t-test; $p < 0.001$) (Table 1.3), but was not significantly influenced by sex in either year (t-test; ns; Table 1.3) or both years together (Table 1.4). There was no difference between the seasons in the mean number of prey items per sample (1997: 505 ± 987, 1999: 358 ± 312; t-test; ns), but variability within seasons was large (Table 1.3). Year was the most important variable in structuring patterns in sample mass (best-subset GLM; Table 1.4). Overall the pattern was for sample mass and number of prey to increase with sample date in both years (but non-significantly so; linear regressions).

The number of prey items per sample was not correlated with sample mass in 1997, but the two were correlated in 1999 ($r = 0.46$; $p = 0.001$). This could be a consequence of the state of digestion of samples: prey were more digested in 1997 than in 1999 (mean prey item SDig, 1997: 2.78 ± 0.43; SDig 1999: 2.58 ± 0.50; Mann Whitney, $U = 6345$; $p < 0.001$), but this parameter is not a refined measurement so this small difference (8%) should be interpreted conservatively.

A combination of adult body condition, sample date, and the interaction between sex and size predicted sample mass in 1999 (Table 1.5). Similarly, adult body condition, along with sex and three interaction terms, significantly explained the number of prey items (Table 1.5).

Effects of adult body condition on chick condition

The mean body condition of chicks provisioned by adults with the best body condition (i.e. top 50%), was significantly greater (2700 ± 1221 g) than that of chicks of adults in poor condition (1615 ± 1221 g) (t-test; df = 38; p = 0.008). However, adult body condition was also significantly positively related to date ($r = 0.361$; $p < 0.05$; df = 38), suggesting that the relationship between adult and chick body condition might be an artefact of seasonal patterns in adult body condition. I therefore controlled for date by regressing the residual chick body condition on residual body condition of adults (effect of size already removed) for each sample day. Once date was corrected for, the relationship between adult and chick body condition approached significance ($r = 0.289$; df = 38; $p = 0.07$) (Fig. 1.3).

Patterns in prey community

The Bray-Curtis similarity cluster analysis revealed 11 major meaningful groupings identifiable at the 72.5% similarity level (Fig. 1.4).

Collection identification numbers were normally distributed across the major clusters ($W = 0.981$; $p < 0.972$). There was also no relationship between identification values *n* and neighbouring values (correlation; ns). These both indicate that individual penguins that arrived back to shore at similar times had not been foraging on the same prey, and strongly suggests they had been foraging in different areas.

The ANOSIM revealed that prey composition did not differ between sexes within years, and that there was no overall difference between years ($R < 0.02$; ns). However, samples differed markedly across periods within each year ($R = 0.12$; $p < 0.001$). No males were sampled during the first sampling period of both years (they remain at the nest at this stage) (Williams 1995; Mehlum et al. 1998), and I thus suspected the strong effect of collection period might be confounded by sex. An ANOSIM for sexes within years (but only for the period starting with the appearance of the first male in the sampling log) was reconducted. In this case there was a weak effect of sex within years ($R = 0.05$; $p = 0.14$), and differences between years were non-existent ($R < 0.01$; $p = 1.0$).

The covariate biplot projection (Fig. 1.5) captured 76.2% of total variability in prey composition. Adding a third dimension added 11.1% but was non-informative, since it stemmed from the action of a single highly variable, but overall numerically unimportant, prey species. Three prey species dominated the prey communities: *K. anderssoni*, krill and *T. macrura* (Fig. 1.5). The remaining species had relatively little influence in separating the samples, and thus aggregate close to the origin. Diets tended to be dominated by one of the three major prey species, as indicated by the high degree of overall scatter, with few samples situated close to the origin (where samples with average numbers of all three major prey species would occur).

When considering 1997 and 1999 together, the sector (1) containing samples with above-average representation of *K. anderssoni,* tends to be dominated by samples from the first third of both seasons, the sector (2) with above-average representation of krill, by samples from the middle of the seasons, and sector (3) with above-average representation of *T. macrura,* by samples from the end of the seasons (Table 1.6, Fig. 1.5). This can be interpreted as a pattern of sequential seasonal dominance of, first, *K. anderssoni*, followed by the two euphausiid crustacean species, and was also clear in each season, when considered separately.

Since mean length of *K. anderssoni* did not change significantly over the course of either season (linear regressions; both years ns) this numerical decline in importance of fish was matched by a decrease in its representation by mass and an increase in representation by mass of euphausiids (Fig. 1.6; % fish: $p = 0.005$; % euphausiids: $p = 0.005$).

When males were excluded (to control for inter-sexual differences), the same marked pattern of movement from sector (1) to (2) is evident, with a weak dominance in sectors (2) and (3) of second-period and third-period samples, respectively (Fig. 1.7, Table 1.6). No patterns were visible when samples were plotted by year, indicating that seasonal effects were more prominent than inter-annual effects.

Discussion

Macaroni Penguins at Bouvetøya have a diverse diet. Crested penguins (*Eudyptes*) generally forage on a broad range of crustacean, fish and cephalopod taxa (reviewed by Cooper et al. 1990), but at most localities prefer planktonic crustacean prey (Cooper et al. 1990; Ridoux 1994). Macaroni Penguins at Bouvetøya depart noticeably from this pattern. In both seasons fish markedly dominated the samples by mass, even though crustaceans outnumbered fish (this owing to samples containing large numbers of the small *T. macrura*). If sample masses were reconstituted (as was done by Cooper et al. 1990), fish would likely dominate even more. The findings of this study are in keeping with the results of previous studies at Bouvetøya (Cooper et al. 1984; Bakken 1991).

Macaroni Penguins are widely distributed in the Southern Ocean, with major populations occurring in true Antarctic waters, the Antarctic Polar Frontal Zone (APFZ) and still farther north in the waters of the Subantarctic Zone (Marchant & Higgins 1990). The APFZ, consisting of the area between the southerly Antarctic Polar Front (APF) and the northerly Subantarctic Front (SAF), exerts an important influence upon diets of crested penguin populations (Cooper et al. 1990). Eddies and meanders are generated along the length of the APF (Gordon 1988), and these features are thought to be sites of enhanced productivity due to the mixing of nutrients, with prey found either in higher concentrations or closer to the surface (Lutjeharms et al. 1985; Rodhouse et al. 1996; Hull 1999). Physical gradients (e.g. temperature; Fischer & Hureau 1985) over the APFZ are also pronounced (Deacon 1982) and, combined with eddy features, have large-scale influences upon biological productivity and prey species distributions south and north of the APFZ.

In the western South Atlantic, south of the APFZ, Macaroni Penguins display relative uniformity in their prey preference (Table 1.7). At Bird Island, South Georgia, krill is the main prey, except in anomalous years when *Themisto gaudichaudii* and/or *T. macrura* occur more frequently in stomachs (Croxall et al. 1993). Elsewhere in the region, limited information indicates that euphausiid crustaceans are also the predominant prey (Table 1.7). Further east, euphausiids have likewise predominated in two studies at Heard Island (Klages et al. 1989; Green et al. 1998), but with differences between years in the constituent species. In both studies *K. anderssoni* dominated the fish fraction (Klages et al. 1989; Green et al. 1998), with the number of euphausiids in 1993 declining with the progression of the breeding season until the diets were composed almost completely of *K. anderssoni* (Green et al. 1998). The diet of the closely-related Royal Penguin *E. schlegeli* (Williams 1995; Woehler 1995) at Macquarie Island, situated near the APFZ, largely resembles that of Macaroni Penguins (Table 1.7), but fish appear to be better represented than at most sites where Macaroni Penguins occur.

North of the APFZ, Macaroni Penguins occur in large numbers at the Prince Edward Islands (Marion Island) and the Crozet Islands (Marchant & Higgins 1990). At both island groups, crustaceans have dominated in all sample years (Table 1.7), but in some years at Marion Island one or more taxa are largely or even entirely absent (Brown et al. 1990). Marked seasonal variation in both species composition and relative proportions of prey type also occurs here (Brown et al. 1990).

At sites north of the APFZ euphausiids generally (and krill in particular) tend to be less dominant than in the western South Atlantic, and are replaced by a greater diversity of crustacean species with no alternative single species dominating the micronektonic community to the same extent (Ridoux 1994; Prince et al. 1999). Thus, the species representation in Macaroni Penguin diets from Marion Island and Possession Island (Crozet Islands), is an average 35 species per site, but from sites south of the APFZ (Bird Island, Heard Island, South Shetlands) an average 11 species per site (calculated from Cooper et al. (1990), but possible effects from sampling intensity cannot be discounted). Macaroni Penguins at Bouvetøya therefore possess the most speciose diets of birds breeding south of the APFZ (where sufficient data exist), with at least 21 species recorded so far (Cooper et al. 1984; Bakken 1991; this study).

Most prey species taken by breeding Macaroni Penguins at Bouvetøya do not appear to be particularly important, when considered by mass representation in the diet. This implies that they either occur in low densities, fall outside the range of, or are avoided by foraging penguins. Their presence is suggestive of either temporal or spatial resource variability at Bouvetøya. Spatial variability could be related to the paucity of shelf waters, thereby making open pelagic waters and an overall greater diversity of prey more accessible to foraging penguins than is the case elsewhere in the South Atlantic.

Distributions and behaviour of prey

In the only recent survey of Bouvetøya waters, Fevolden (1980) recorded the euphausiids *E. frigida* and *T. macrura*, and krill. This study adds no new records to his results. The shallow-water species *T. macrura* (Nemoto 1966; Dzik & Jazdzewski 1978) occurs commonly in diet samples from sites to the south of the APFZ, but less so to the north (cf. Table 1.7 and references therein) which mirrors current knowledge about its distribution pattern (Nemoto 1966; Dzik & Jazdzewski 1978; Fischer & Hureau 1985). Although *E. frigida* only occurs south of the APFZ (Dzik & Jazdzewski 1978; Fischer & Hureau 1985), it appears to be relatively unimportant for land-based marine predators at Bouvetøya (Klages et al. 1999; Kirkman et al. in press; Chapter 3; unpubl. data).

Fevolden (1980) found that krill dominated in horizontal trawls off Bouvetøya, but that it was the only species for which no larvae were recorded, and suggested that the specimens were immigrants to the island. Everson (1976, Fig. 8) describes Bouvetøya waters to be of high krill density, but the lack of surveys hampers our understanding of the extent to which local stocks are consistently present or abundant. In both 1997 and 1999 gravid krill were recorded in Macaroni and Chinstrap Penguin *Pygoscelis antarctica* stomach samples. This might not indicate, though, that successful recruitment of krill occurs at Bouvetøya, since this requires specific ecological conditions (reviewed in Miller & Hampton 1989) considered to be absent at the island (D. Miller, pers. comm.).

Factors other than recruitment, such as oceanographic concentrating mechanisms, could also support krill stocks. Areas of high current shear (i.e. in frontal zones, meanders and eddies, and where the bathymetry is irregular) support high biomasses of krill in the western South Atlantic (Witek et al. 1982; Miller & Hampton 1989). Large-scale features to the south of

Bouvetøya such as the Weddell Gyre and Weddell Polynya (Gordon 1988), and the eastward flowing Weddell Drift, where a generally high abundance of post- and late-stage krill larvae has been recorded (Miller & Hampton 1989), are also possible influences on stocks near the island. Further surveys of marine resources, coupled with long-term research of predator populations at Bouvetøya, are required to understand the dynamics of krill at Bouvetøya and, if the pronounced shortages common to sites in the western South Atlantic occur (Croxall et al. 1988), what impact this has on predators (Croxall et al. 1999). I discuss this further in Chapter 3.

The mesopelagic myctophid *K. anderssoni* is a cosmopolitan, broadly Antarctic species associated principally with the APFZ but which occurs as far north as the Subtropical Convergence (Hulley 1981, 1985; McGinnis 1982). The predominance of *K. anderssoni* in the diet of Macaroni Penguins suggests that dense shoals must occur frequently in the vicinity of Bouvetøya (cf. Adams & Klages 1987), probably consisting of different age cohorts (Fig. 1.2). At the Kerguelen Islands, *K. anderssoni* exhibit diurnal vertical migration from the upper layers (down to 250 m) in the day where it is one of three common fish species, to deeper layers (deeper than 100 m) at night (Duhamel 1998; Duhamel et al. 2000). Like many mesopelagic myctophids, it also shoals densely (Sabourenkov 1991), and its vertical distribution falls well within the diving capabilities of penguins and fur seals breeding at Bouvetøya (Isaksen et al. 1997a; Chapters 2 & 3). That they are not commonly taken by other predators at Bouvetøya (Isaksen et al. 1997a; Klages et al. 1999; Kirkman et al. in press; Chapter 3; unpubl. data), but are common prey for Macaroni Penguins at other islands (Heard, Possession and Marion Islands) suggests that they could be selectively targeted. Most other predators at Bouvetøya eat krill (Klages et al. 1999; Kirkman et al. in press; Chapter 3), and an alternative explanation is that this could also represent niche differentiation mediated through competition at sea. This would permit ecological segregation from the other two air-breathing divers at the island, Chinstrap Penguins and fur seals. This seems unlikely, however, and is explored more fully in Chapter 2.

Other myctophids eaten by Macaroni Penguins at Bouvetøya were *Electrona carlsbergi, E. antarctica*, *Protomyctophum choriodon* and *Gymnoscopelus braueri*. Both *Electrona* spp. occur in the upper 100 m in the vicinity of the APF and are distributed circumpolarly (Hulley

1990). At the Kerguelen Islands, *E antarctica* has a pronounced diel migration, occurring frequently in shallower waters of 50 m at night, but seldom above 200 m during the day (Duhamel et al. 2000). Since it is considered to be the most common myctophid south of the APF (Hulley 1990) and falls within the depth range of diving Macaroni Penguins, it is not surprising that it is well represented in their diet at Bouvetøya. Also at the Kerguelen Islands, *E. carlsbergi* is found mostly in deeper waters (> 200 m) (Duhamel et al. 2000), which is out of the known diving range of Macaroni Penguins at Bouvetøya (Chapter 2).

The paralepid fish *Notolepis coatsi*, *Arctozenus risso* and *Magnisudis prionosa* are all mesopelagic to bathypelagic (Post 1986, 1990). Both *M. prionosa* and *Notolepis* sp. have been recorded as prey of Macaroni Penguins at one site each before, and *A. risso* is a new prey record for this penguin (see Cooper et al. 1990).

Other interesting records include the benthopelagic notothenid *Nototheniops larseni*, the benthic/epibenthic notothenid *Trematomus* sp., and other smaller notothenid fish too young to identify unambiguously. This group is considered to be largely benthic (DeWitt et al. 1990), and should therefore fall outside the foraging range of Macaroni Penguins, although early stages of benthic notothenids have been recovered from trawls in the upper layer at Kerguelen (Duhamel et al. 2000).

The *Trematomus* and *Bathylagus* spp. (Bathylagidae) records are both new for Macaroni penguins (see Cooper et al. 1990). Of the nine fish species found in Macaroni Penguin diets at Bouvetøya, five (*N. coatsi*, *M. prionosa*, *A. risso*, *E. carlsbergi* and *P. choriodon*) are new distributional records for the immediate waters of the island (cf. McGinnis 1982; Gon & Heemstra 1990; FishBase 1996).

One crustacean, the hyperiid amphipod *Hyperia macrocephala*, is previously unknown from other Macaroni Penguin diets (cf. Cooper et al. 1990), but is probably widespread and abundant in the region, being a common pelagic crustacean in the South Shetland Islands area (Jazdzewski 1982). The pelagic hyperiid *T. gaudichaudii* has a subantarctic distribution pattern (Kane 1966), and is regarded as the commonest and most abundant amphipod in the Southern Ocean (Jazdzewski, 1982). It is found in the upper layer (50 m) day and night

(Duhamel et al. 2000) and thus, not surprisingly, occurs frequently in crested penguin diets (cf. Cooper et al. 1990).

Effects of adult condition on chick condition

In 1999 the body condition of chicks was positively related to parental condition. Adult condition also improved during the chick rearing period. If female penguins in better condition laid earlier in the season (cf. Moreno et al. 1997,1998), their chicks should be older (and therefore heavier) during the diet sampling period. However, hatching in Macaroni Penguins was highly synchronous in both years, so I believe that this effect would be apparent only early in the season, and that chicks of poor providers would rapidly lose any 'advantage' gained from being older (relative to other birds in the study) provided that growth and condition is not solely heritable. Certainly, adult body condition appeared to be the most consistently important factor in explaining variance during 1999 in sample mass and number of prey returned to the nest.

Body condition could be influenced by age (Burger et al. 1996), or experience (Nager & Van Noordwijk 1995). The linkage between adult and chick condition in Macaroni Penguins suggests that adults in better condition may be able to allocate more resources to chicks. It is unclear whether this is because of active decision-making *per se*, or if this is because investment varies directly and proportionally with condition. The exact mechanism - varying provisioning rates or quality of food - is also unknown and merits further investigation. This linkage has been observed in other studies of seabirds (e.g. Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994; Lorentsen 1996; Erikstad et al. 1997; Tveraa et al. 1998), and penguins are known to be sensitive to large-scale changes in prey density, suffering low breeding success in years of low prey availability (e.g. Croxall et al. 1988, 1999; Irvine et al. in press).

During the incubation and guard stages Macaroni Penguins spend long periods ashore fasting. This is undoubtedly stressful, leading to marked changes in body mass (see Croxall 1995) and condition. In 1999, while males were excluded from sampling during the brood stage, the body condition of females improved. This indicates that the brood stage may not have been as costly for females as the latter stages of incubation, where the lengthy relief schedules probably lead to loss of condition (cf. Croxall 1995).

Intra-annual patterns in diet

The composition of diets during 1997 and 1999 was not influenced by year or related by proximity in time to other samples, but was strongly influenced by sampling period and sex, with period exerting perhaps the most influence. Fish dominated (numerically and by mass) during the first part of the season, and krill and *T. macrura* in the middle and latter parts respectively. This pattern was similar and systematic during both years.

Seasonal changes in diet have been observed elsewhere (e.g. Croxall & Prince 1980; Brown & Klages 1987; Ridoux 1994; Green et al. 1998; Hull 1999), but in all these cases the tendency has been for fish to increase proportionally with time (although the strength of the effect varied considerably). This is the first study where penguin diets have demonstrated a contrary and markedly systematic pattern of fish becoming less important over the course of the breeding season. There are three possible reasons for this.

Firstly, this pattern might be a consequence of small-scale natural fluctuations in abundance of prey around the island. This implies consistent patterns of oceanographic change occurred in both years, which seems unlikely.

Second, penguins may have been were targeting specific prey at certain times. Preying selectively upon fish early in the season could be advantageous to penguins with small chicks. Myctophid fish are lipid-rich, with *K. anderssoni* proving to be the most nutritious (8.1 kJ.g^{-1} wet mass) of three fish and one squid species preyed upon by king penguins *Aptenodytes patagonicus* at Possession Island (Cherel & Ridoux 1992). Heath & Randall (1985) showed that the type of prey consumed, and their lipid and caloric content, influences the growth of penguin chicks, with birds consuming fish growing faster than those consuming squid. Similarly, Van Heezik & Davis (1990) demonstrated lower growth rates and higher chick mortality when the diet of Yellow-eyed penguin *Megadyptes antipodes* chicks switched from lipid-rich to lipid-poor prey. Thus, if myctophid resources close to Bouvetøya are abundant during breeding, adults might be expected to target such prey. Small fish are also digested more rapidly than larger fish and crustacean prey at Bouvetøya (pers. obs.). Regurgitation of semi-digested food might thus lower digestion costs for smaller chicks, which require frequent small meals.

Brown & Klages (1987) considered it likely that the increasing foraging ranges of birds with larger chicks were responsible for bringing them into the open waters favoured by pelagic myctophids. If this is the case, the relative paucity of neritic waters at Bouvetøya could favour pelagic foraging and a prey delivery pattern that is favourable from the outset for the development of chicks. This might also suggest that birds should tend to return with smaller meals when feeding small chicks, and this was indeed the case for both seasons. However, why adult penguins should return less fish to shore later in the season is not clear. Perhaps the deeper-dwelling myctophids are more costly to capture than shallower krill (Fevolden 1980; Miller & Hampton 1989; unpubl. data), and Macaroni Penguins balance this cost with the needs of the chick.

Third, competitive interactions at sea with other krill consumers at Bouvetøya could force Macaroni Penguins to prey upon fish, rather than krill. This assumes that krill is a limiting resource at Bouvetøya (cf. Wiens 1989), for which there is no evidence. This is considered further in Chapters 2 and 3.

Inter-sexual differences in diet, as this study suggests might occur, have been observed in other studies. Clarke et al. (1998) found differences in diet in Adélie Penguins *P. adeliae*, as well as differences in foraging range. In another pygoscelid, the Gentoo *P. papua*, Volkman et al. (1980) also recorded differences in diet. Sexual segregation of foraging areas has been demonstrated in Wandering Albatrosses *Diomedea exulans* (Shaffer et al. 2000), which is thought to be a result of this species' sexual dimorphism. The marked sexual dimorphism of Macaroni Penguins, and their unusual breeding chronology, might therefore favour different patterns of spatial and depth usage, and consequently diet.

Finally, systematic differences in prey specificity of individual penguins might, at least partly, explain why very few diet samples contained average numbers of the three principal prey. When diets are dominated by one species, as is frequently observed (B. Dyer pers. comm.;

pers. obs.), it is often attributed to penguins encountering a patch of this species, and returning to shore having completed feeding in the patch. But the same pattern could also result if individuals specialised in targeting certain prey. Repeat sampling of individually marked birds would be required to test this.

Inter-annual patterns in diet

Macaroni Penguin diets differed very little between the two sample years. In 1999 samples were heavier and were less digested, but had the same number of prey and a composition indistinguishable from 1997. Differences in sampling technique seem likely, given the big differences in sample mass between the years (Tables 1.3 & 1.4); two-flush sampling is therefore recommended for Bouvetøya. However, I fail to see how this can account for differences in digestion, lack of differences in number of prey, and similarity in diet composition. Digestion differences alone suggest that in 1999 small-scale natural variability in prey abundance meant foraging penguins conducted shorter foraging trips (cf. Chapter 2), thereby returning fresher food to the nest.

Croxall et al. (1988) and Priddle et al. (1988) suggested the possible connection between ENSO events and shortages of krill in the western South Atlantic, a phenomenon which is not well understood. During 1978 and 1984 predators did poorly at Bird Island with both seasons lagging behind strong (massive in 1983) ENSO events. Recently, SC-CAMLR (1998) found krill abundance at South Georgia to be associated with both the summer Southern Oscillation Index and regional sea ice extent, and identified an 8 month maximum lagged cross-correlation in sea surface temperature (SST) anomalies between the Southeast Pacific and South Georgia. This is consistent with the migration of anomalous conditions with the Antarctic Circumpolar Wave (ACW) (Murphy et al. 1995; White & Peterson 1996) which is a circumpolar anomaly precession associated mainly with the Antarctic Circumpolar Current (ACC). Bouvetøya lies close to the ACC, and at the rate of travel reported by White & Peterson (1996), might be expected to have encountered anomalous conditions from the very strong 1997/98 ENSO event (ENSO Monitor 2000) during the 1998/99 season. However, this was not detected in the diets or breeding success of either Macaroni or Chinstrap penguins (Appendix C; Chapter 3; unpubl. data), or the diets of fur seals (Klages et al. 1999;

Kirkman et al. in press). Certainly, as is the case elsewhere in the region, local factors such as cycles in distribution and extent of sea ice (e.g. Priddle et al. 1988; Brierley et al. 1997; SC-CAMLR 1998; Reid et al. 1999) could also be important determinants of krill resources which require both recruitment and transport to be abundant at Bouvetøya and have been shown to be variable in the short-term in the past (Fevolden 1980).

During December - January 1998/99 acoustic estimates of krill at South Georgia revealed abundances that, while not abnormally low (11-12 $g.m^{-2}$) (Brierley & Goss 1999), were well below the long-term average for the region (44.3 $g.m^{-2}$) (Brierley et al. 1999). How predators performed at South Georgia at this time is not yet openly documented, but elsewhere in the Southern Ocean, at Béchervaise Island, Adélie penguins experienced high levels of chick mortality, caused by adults spending longer at sea foraging than in normal years (Irvine et al. in press).

Further work at Bouvetøya will help us understand patterns in environmental variability occurring throughout the South Atlantic Ocean.

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Chapter 1: Tables

Table 1.1 Frequency of occurrence (%) of identified prey species in Macaroni Penguin diet samples, Bouvetøya, 1997 and 1999.

Prey		Year	
		1997	1999
Euphausiids		100	87
	Euphausia superba	93	73
	Thysanoessa macrura	89	76
	Nematoscelis megalops	13	0
	E. frigida	2	4
Amphipods		9	0
	Hyperia macrocephala	2	0
	Themisto gaudichaudii	2	0
Cephalopods		2	9
Fish		93	98
	Krefftichthys anderssoni	64	82
	Electrona carlsbergi	53	84
	Notolepis coatsi	40	40
	E. antarctica	13	9
	Nototheniops larseni	0	11
	Arctozenus risso	4	0
	Magnisudis prionosa	2	0
	Protomyctophum choriodon	2	2
	Gymnoscopelus braueri	0	4
	Notothenia sp.[1]	9	0
	Notolepis sp.	2	0
	Trematomus sp. ?	2	0
	Bathylagus sp. ?	0	2
Minimum total prey taxa recorded		18[2]	12[3]

[1] All *Notothenia* sp. fish are juveniles, and thought likely to be *N. rossi*.

[2] Including a minimum of one additional species of amphipod, and a minimum of one species of cephalopod (both unidentifiable).

[3] Including a minimum of one (unidentifiable) species of cephalopod.

Prey items not identified to genus or further:

1. 1997: amphipods: 2 individuals; cephalopods: 1 individual; fish: 11 individuals (7 larval fish);
2. 1999: amphipods: no items; cephalopods: 4 individuals; fish: 1 individual.

Table 1.2 Total numbers (and proportions) of individuals of the most important fish and crustacean prey species recovered from the diets of Macaroni Penguins, Bouvetøya, 1997 and 1999.

	1997	1999	Both seasons
Fish			
Krefftichthys anderssoni	1732 (84)	5278 (86)	7010 (86)
Electrona carlsbergi	212 (10)	704 (12)	916 (11)
Notolepis coatsi	51 (3)	77 (1)	128 (2)
Other species	71 (3)	63 (1)	134 (2)
Total fish (n species[1])	2066 (11)	6122 (9)	8188 (14)
Crustaceans			
Euphausia superba	1975 (10)	2151 (22)	4126 (14)
Thysanoessa macrura	18220 (90)	7809 (78)	26029 (86)
Other species	131 (1)	3 (< 0.1)	134 (< 1)
Total crustaceans (n species[1])	20326 (7)	9963 (3)	30289 (7)

[1] Minimum total prey taxa.

Table 1.3 Mean ± SD minimum number of prey items recovered in each diet sample, and mean sample mass (g), of male and female Macaroni Penguins at Bouvetøya, 1997 and 1999.

	Male	Female	Both sexes
1997			
Number of prey	705 ± 1210	438 ± 913	505 ± 987
Sample mass	130 ± 76	156 ± 83	150 ± 81
1999			
Number of prey	312 ± 268	370 ± 326	358 ± 312
Sample mass	242 ± 90	229 ± 113	232 ± 107

Table 1.4 Results of a General Linear Model (best-subset approach) for Macaroni Penguin sample masses, Bouvetøya, 1997 and 1999. The variables sex, year, date and time and all interactions were considered. The model which explained the most variation is presented ($F_{5,83} = 5.841$; $p < 0.001$; adjusted $r^2 = 0.216$). One penguin was excluded because of uncertain sex.

	Parameter		
Factor	df	F	p
Year	1	9.610	0.002
Year*Sample time	1	8.796	0.004
Sample date	1	2.486	0.119
Year*Sex	1	2.208	0.141
Year*Sex*Sample time	1	2.132	0.148

Table 1.5 Results of General Linear Models (best-subset approach) of sample mass and number of prey per sample, for Macaroni Penguins at Bouvetøya in 1999. In both models the variables sex, adult body condition and size, sample date and all interactions were entered into the best-subset model. The model which explained the most variation is presented. The model for sample mass is significant ($F_{5,36}$ = 3.79; $p = 0.007$; adjusted $r^2 = 0.253$), as is the model for number of prey per sample ($F_{5,36}$ = 6.477; $p < 0.001$; adjusted $r^2 = 0.400$).

Factor	Parameter df	F	p
dependent variable: sample mass			
Adult body condition	1	6.10	0.02
Sample date	1	5.17	0.03
Sex*Adult size	1	5.99	0.02
Sex*Adult size*Adult body condition	1	2.38	0.13
Sex*Adult size*Adult body condition*Sample date	1	3.07	0.09
dependent variable: number of prey per sample			
Sex	1	13.26	< 0.001
Adult body condition	1	14.42	< 0.001
Sex*Adult body condition	1	6.13	0.02
Sex*Sample date	1	11.27	< 0.01
Adult size*Sample date	1	4.48	0.04

Table 1.6 Numbers and attributes (*n* & sector %) of Macaroni Penguin diet samples (1997 and 1999) falling into each one of the three prey sectors identified by covariate biplot analysis (see Figs. 1.5 & 1.7).

	Prey species sector								
Figure	*K. anderssoni*			*E. superba*			*T. macrura*		
6	O	□	Δ	O	□	Δ	O	□	Δ
	19 (61)	9 (29)	3 (10)	3 (11)	14 (52)	10 (37)	8 (25)	7 (22)	17 (53)
8	O	□	Δ	O	□	Δ	O	□	Δ
	19 (68)	7 (25)	2 (7)	3 (16)	9 (47)	7 (37)	8 (36)	4 (18)	10 (46)

Table 1.7 Comparison of the diets (by mass) of other populations of Macaroni Penguins, and the closely-related Royal Penguin.

Species	Site	Diet	Reference(s)
Macaroni Penguin			
	Bird Island, South Georgia	*E. superba* > 90% , fish < 5%	Croxall & Prince 1980; Croxall et al. 1988,1993
		T. gaudichaudii 67%, *E. superba* 13%, fish 15%[1]	Croxall et al. 1999
	Elephant Island, South Shetland Islands	*E. superba* 37%, *T. macrura* 38%, fish 25%	Croxall & Furse 1980; Croxall & Lishman 1987
	King George Island, South Shetland Islands	Crustaceans 96%, fish 4%	Jablonski 1985
	Heard Island	Crustaceans 77% (mostly *T. macrura*); fish 23%	Klages et al. 1989
		Crustaceans 59% (mostly *T. gaudichaudii*); fish 41%	Green et al. 1998
	Bouvet Island	Crustaceans 28% & 22%, fish 72% & 78%	this study
	Crozet Islands	Crustaceans 61% (mostly *E. vallentini*), fish 29%	Ridoux 1994
	Marion Island	Crustaceans 100% (*E. vallentini*, *T. macrura*)	Williams & Laycock 1981
		Crustaceans > 83% (*Nauticaris marionis*, *E. vallentini*, *T. vicina*), fish < 16%	Brown & Klages 1987; Brown et al. 1990
		Crustaceans 56-99%, fish bulk of remainder	R.J.M. Crawford (MCM), unpubl. data
Royal Penguin			
	Macquarie Island	26% & 3% euphausiids, 62% & 54% fish	Horne 1985
		51% euphausiids, 24% fish (*K. anderssoni*)	Hindell 1988
		50% euphausiids, 30% fish	Hull 1999

[1] 1994: an anomalous year (cf. Croxall et al. 1999)

Figure legends

Fig. 1. Length frequencies of *Krefftichthys anderssoni* fish recovered from diets of Macaroni Penguins in 1997 and 1999.

Fig. 2. Length frequencies of *Electrona carlsbergi* fish recovered from the diets of Macaroni Penguins in 1997 and 1999.

Fig. 3. Chick condition regressed against adult condition (both grams). Both condition indices calculated as residuals from means for that sample day; effect of size first removed from adult condition index by regressing against PC1 (see Methods).

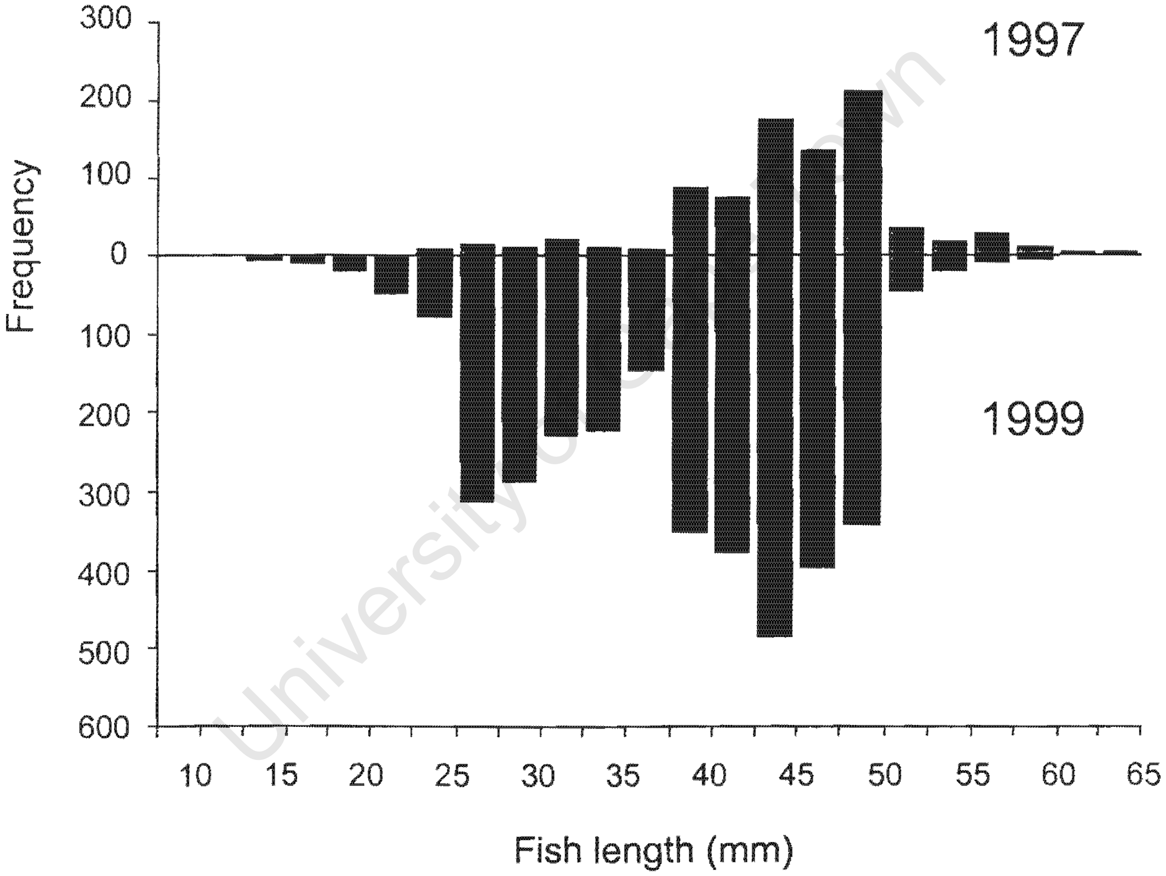
Fig. 4. Cluster analysis of all diet samples (90) from Macaroni Penguins collected in 1997 and 1999. Column A shows sample identification numbers, and column B the major groups identified at the 72.5% similarity level (dashed line, see Methods). Sample numbering: 1997: 1-45, 1999: 46-90. Within each year the numbering is sequential through the periods when samples were taken (5 per day).

Fig. 5. Covariate biplot of all Macaroni Penguin diet samples collected in 1997 and 1999. Samples are displayed according to which third of the season they were collected in. Three prey species exert the greatest influence upon the diets: krill and *Thysanoessa macrura*, and the myctiphorm fish *Krefftichthys anderssoni*. They are indicated, as well as the remaining prey species which congregrate close to the origin and are therefore less influential. The diets are divided into three sectors (dashed lines) with samples containing above-average representation of the dominant prey species in that sector. There are similar numbers of samples contained in each sector (Table 1.6). The large arrows indicate the temporal sequence of events: from the *K. anderssoni* sector (dominated proportionally by samples collected in the first third of the season, circles) to the krill sector (samples collected in the second part of the season, squares), to the *T. macrura* sector (samples collected in the final third of the season, triangles) (Table 1.6). This movement is mimicked by the motion of the centroids (shown

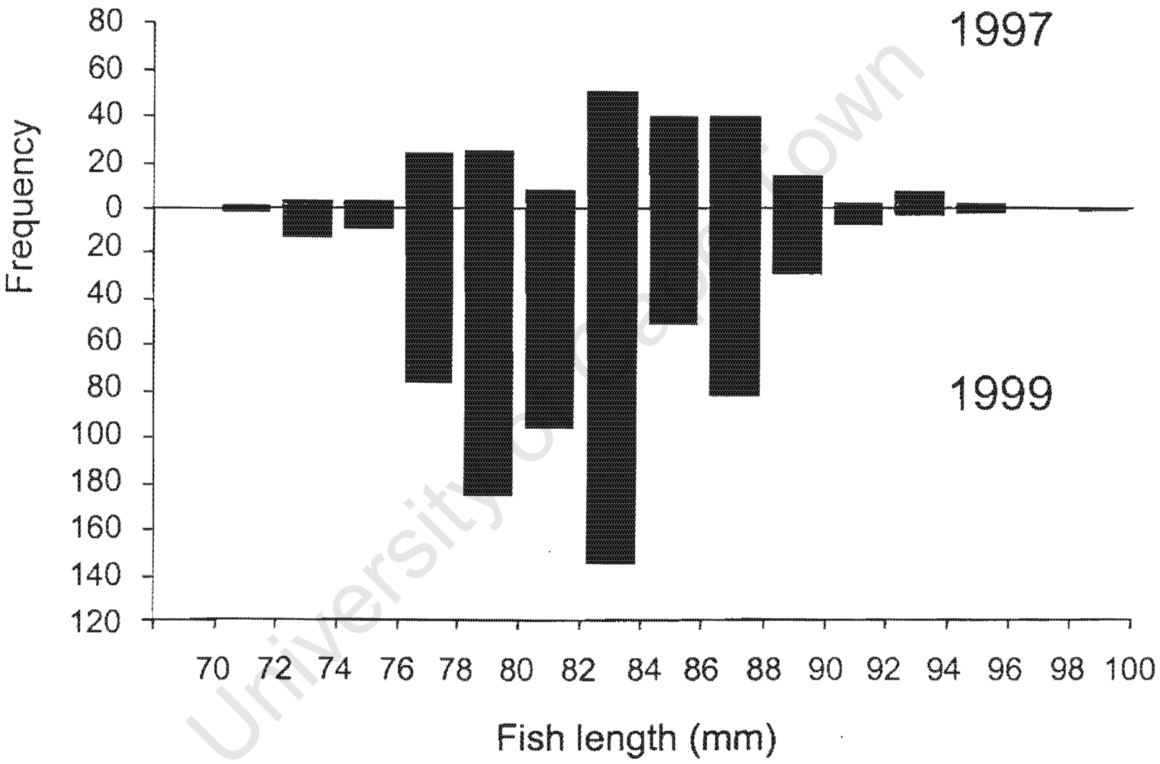
shaded, the centre of the median convex hole calculated for the samples from that period) for each of the sample periods.

Fig. 6. Mean sample masses of all fish and euphausiid components in Macaroni Penguin diets, 1997 and 1999 together.

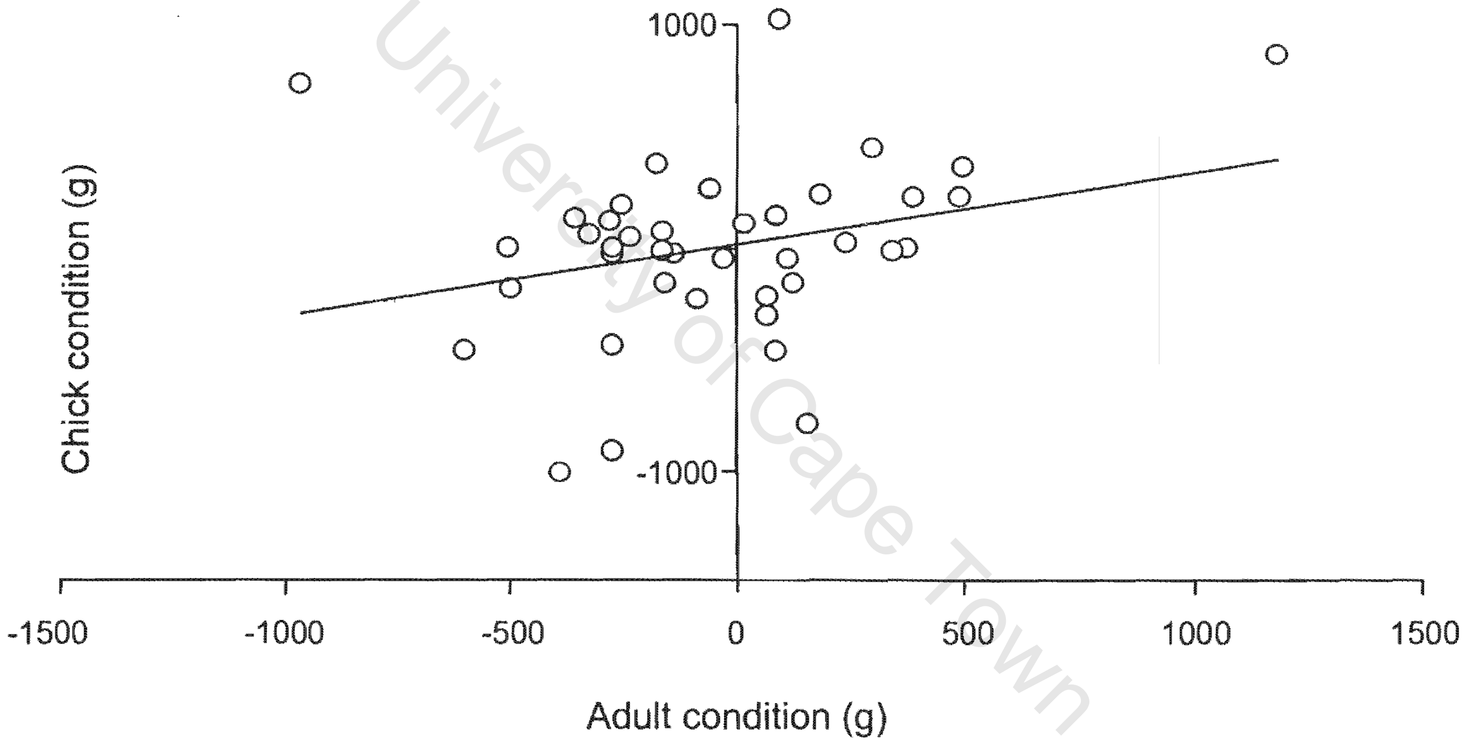
Fig. 7. Covariate biplot of female Macaroni Penguin diet samples, from 1997 and 1999. Samples are displayed according to which third of the season they were collected in. As before (Fig. 1.6), three prey species are responsible for separating the diets, and the diets with above-average representation of that principle prey item are separated (dashed lines) into three sectors. There are similar numbers of samples contained in each sector (Table 1.6).



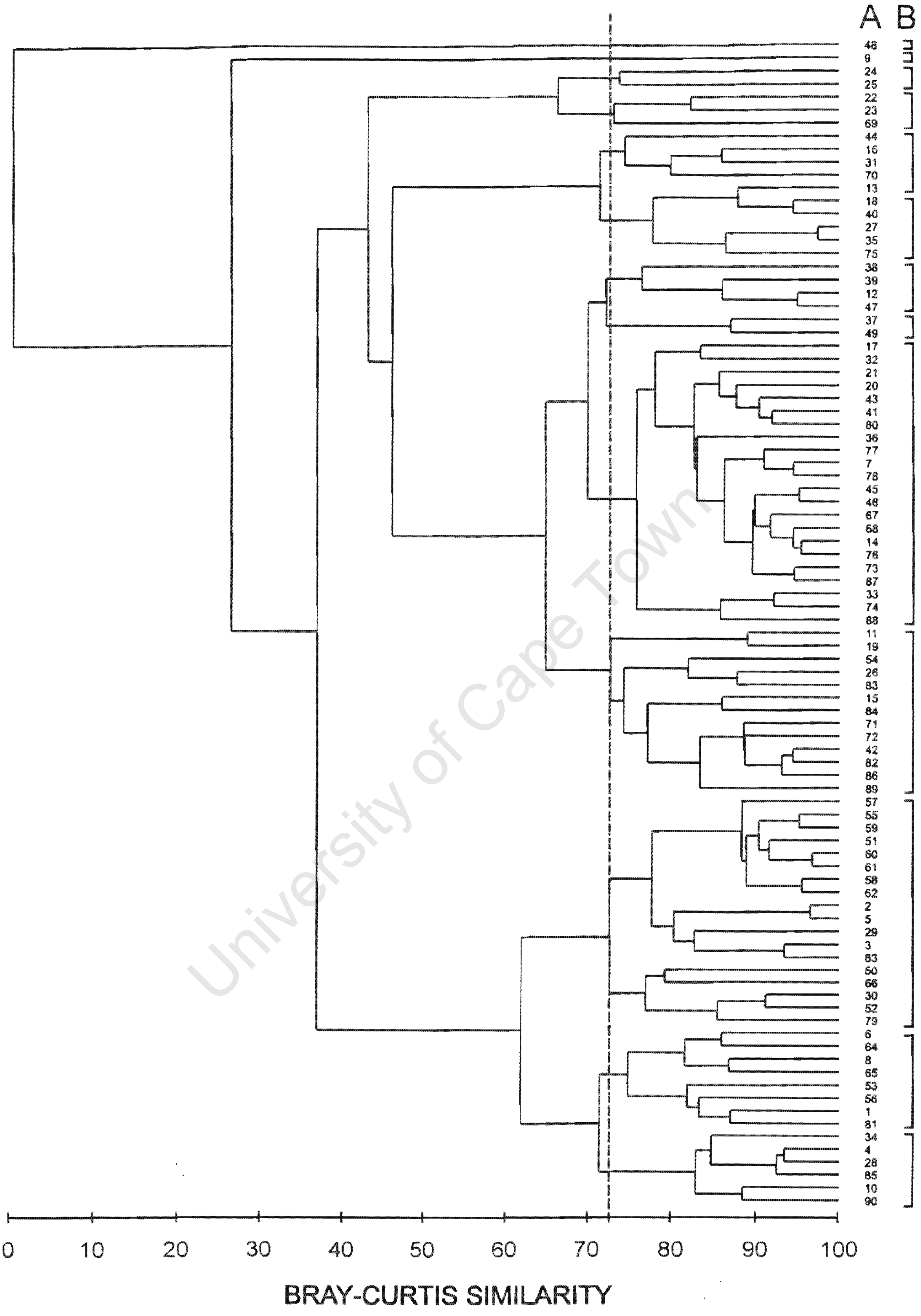
Chapter 1: Figure 1. Length frequencies of *Krefftichthys anderssoni* fish recovered from diets of Macaroni Penguins in 1997 and 1999.



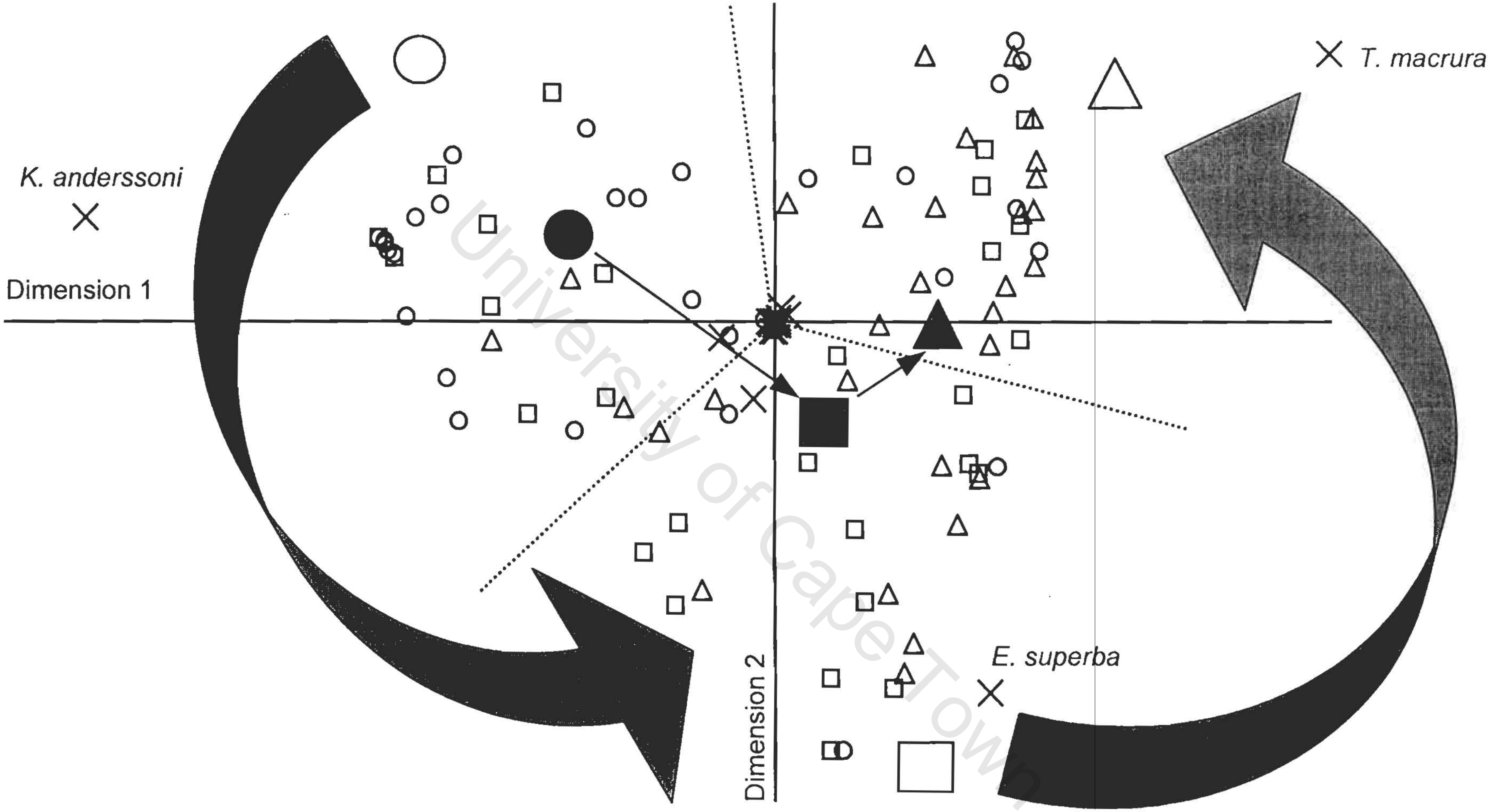
Chapter 1: Figure 2. Length frequencies of *Electrona carlsbergi* fish recovered from the diets of Macaroni Penguins in 1997 and 1999.



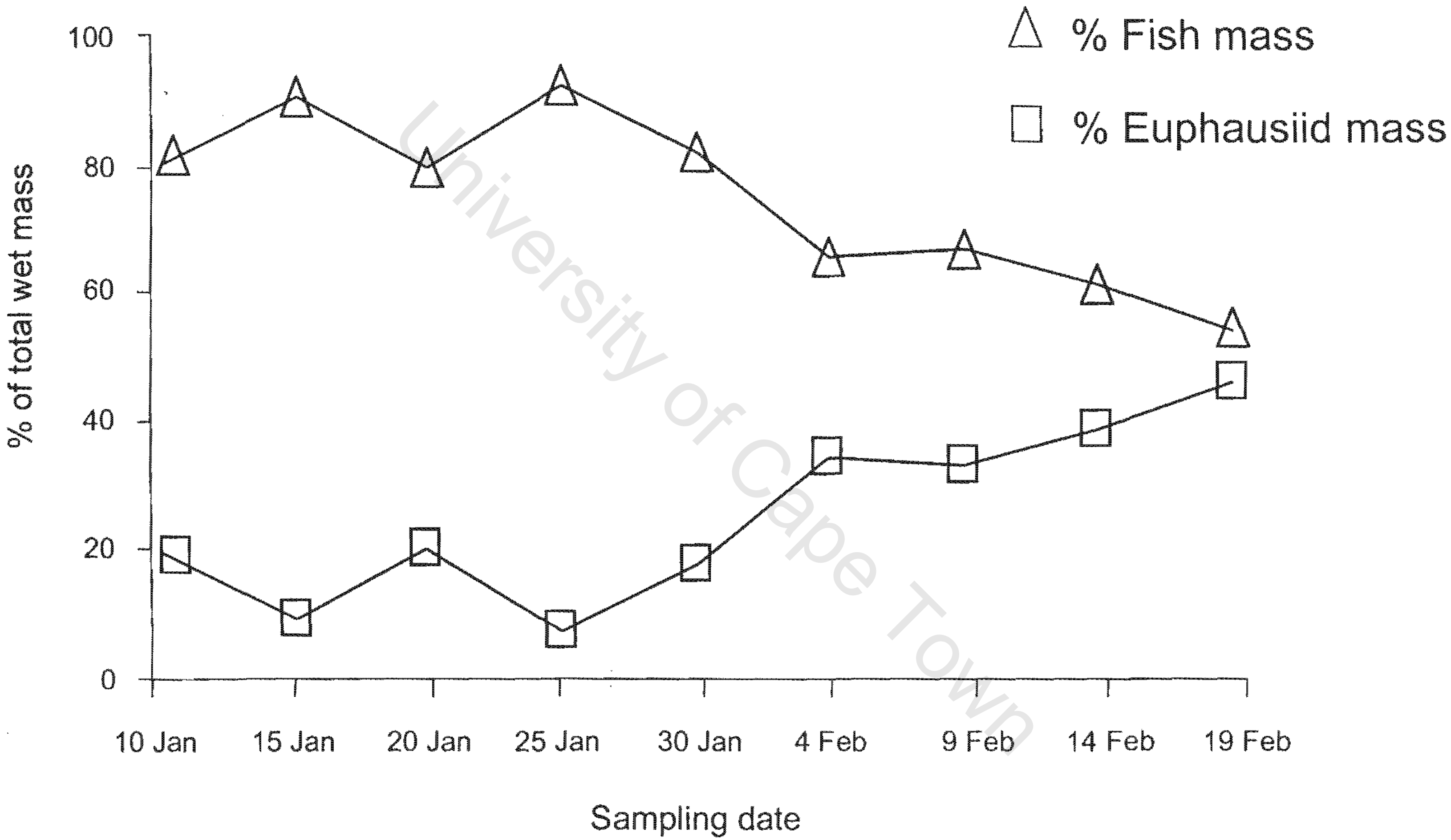
Chapter 1: Figure 3. The relationship between chick condition and adult condition (both grams). Both condition indices calculated as residuals from means for that sample day; effect of size first removed from adult condition index by regressing against PC1 (see Methods).



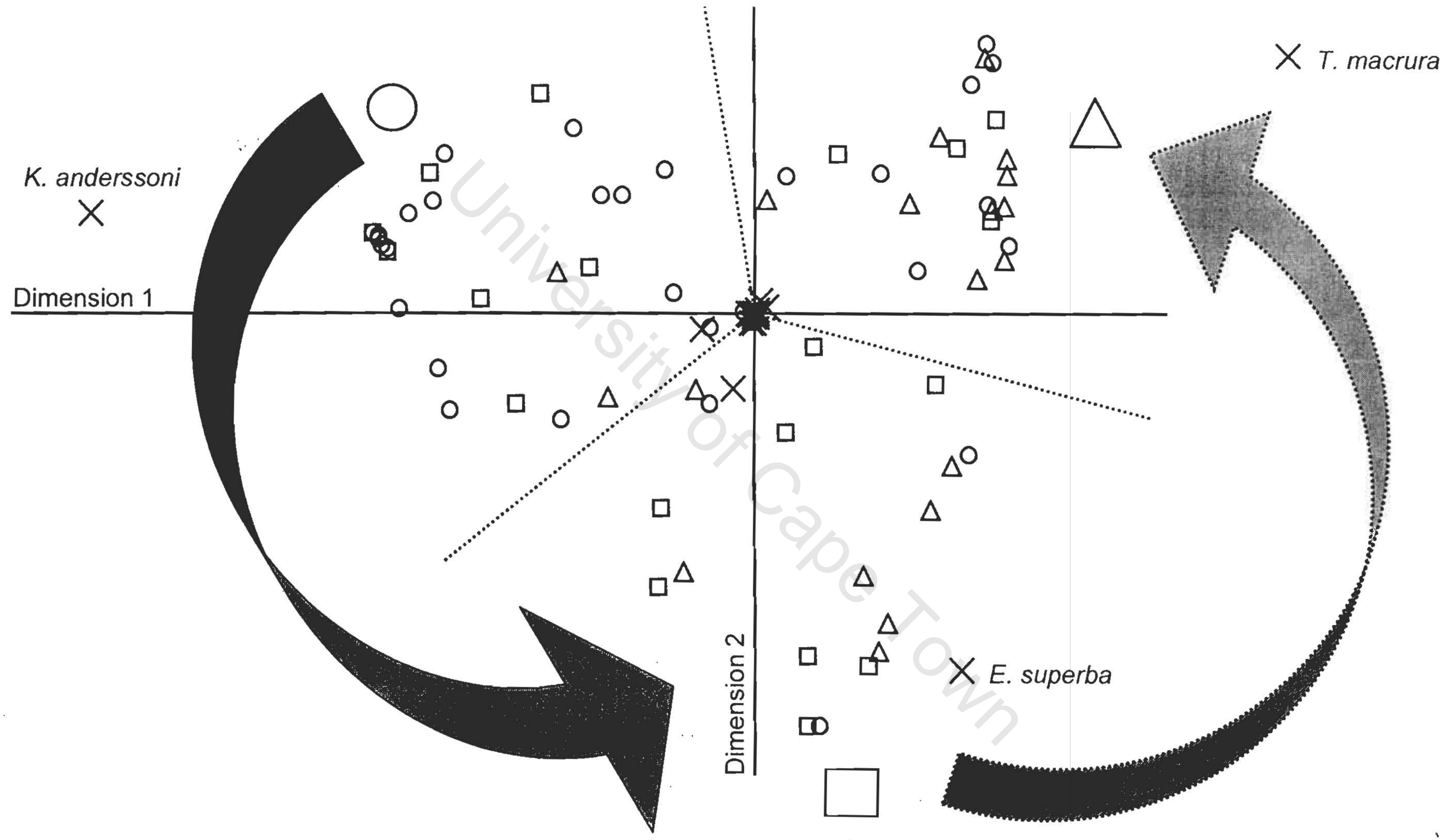
Chapter 1: Figure 4. Cluster analysis of all diet samples (90) collected from Macaroni Penguins in 1997 and 1999. Column A shows sample identification numbers, and column B the major groups identified at the 72.5% similarity level (dashed line, see Methods). Sample numbering: 1997: 1-45, 1999: 46-90. Within each year the numbering is sequential through the periods when samples were taken (5 per day).



Chapter 1: Figure 5. Covariate biplot of all Macaroni Penguin diet samples, 1997 and 1999. Samples are displayed according to which third of the season they were collected in. Three prey species exert the greatest influence upon the diets: krill and *Thysanoessa macrura*, and the myctophid *Krefftichthys anderssoni*. They are indicated, as well as the remaining prey species which congregrate close to the origin and are therefore less influential. The diets are divided into three sectors (dashed lines) with samples containing above-average representation of the dominant prey species in that sector. There are similar numbers of samples contained in each sector (Table 1.6). The large arrows indicate the temporal sequence of events: from the *K. anderssoni* sector (dominated proportionally by samples collected in the first third of the season, circles) to the krill sector (samples collected in the second part of the season, squares), to the *T. macrura* sector (samples collected in the final third of the season, triangles) (Table 1.6). This movement is mimicked by the motion of the centroids (shown shaded, the centre of the median convex hole calculated for the samples from that period) for each of the sample periods.



Chapter 1: Figure 6. Mean sample masses of all fish and euphausiid components in Macaroni Penguin diets, 1997 and 1999 combined.



Chapter 1: Figure 7. Covariate biplot of female Macaroni Penguin diet samples, from 1997 and 1999. Samples are displayed according to which third of the season they were collected in. As before (Fig. 1.5), three prey species are responsible for separating the diets, and the diets with above-average representation of that principle prey item are separated (dashed lines) into three sectors. There are similar numbers of samples contained in each sector (Table 1.6).

Appendix 1.1 Mean sample mass (and proportion of total mass) of components in Macaroni Penguin diets, Bouvetøya, 1997 and 1999. Fish component species not weighed separately (see Methods), and therefore not presented.

Taxa	1997	1999
Euphausiids		
Euphausia superba	28	43
Thysanoessa macrura	13	8
Nematoscelis megalops	0.1	0
E. frigida	< 0.1	< 0.1
Mean euphausiids (%)	41 (28)	50 (22)
Amphipods		
Hyperia macrocephala	< 0.1	0
Parathemisto gaudichaudii	< 0.1	0
Mean amphipods (%)	< 0.1 (< 0.1)	0 (0)
Total crustaceans (%)	41 (27)	50 (22)
Mean cephalopods (%)	0 (0)	< 0.1 (< 0.1)
Mean fish (%)	109 (73)	182 (78)

Chapter 2

Diving behaviour of female Macaroni Penguins *Eudyptes chrysolophus* at Bouvetøya

Abstract

While a great deal is known about the diet of breeding Macaroni Penguins *Eudyptes chrysolophus*, comparatively little is known about the diving behaviour of this, the most numerous, penguin species. I conducted a study on the diving behaviour of 17 female Macaroni Penguins in two years (1997 & 1998/99) at Bouvetøya, shortly before hatching and during the first month of chick rearing. I wished to know if the depth usage of females reflected their mixed diet, if temporal patterns in depth usage existed, and if females, who are the sole providers of the chick in the early part of chick rearing, adjust their behaviour at sea as food demands from the chick increase. A total of 15542 dives was recorded in both years, of which 12263 (78.9%) contained a bottom phase, interpreted as signifying successful foraging. Dive depths were bimodal, with most dives recorded at 5–15 m, and a second mode at 50–70 m. In conjunction with information on diet, this suggests that penguins fed on euphausiids (chiefly Antarctic krill *Euphausia superba* and *Thysanoessa macrura*) during shallow dives, and myctophid fish (chiefly *Krefftichthys anderssoni*) during deeper dives. Penguins dived at all times of the day, but less at night, to shallower depths, and less successfully. There were two intriguing patterns in diurnal depth usage, dissimilar to those recorded elsewhere: (1) deepest dives were at sunrise and sunset, and (2) penguins tended to dive shallowly in the first part of the morning, and deeper from late morning through until evening. The first is hypothesised to result from rapid vertical migration of prey, which may cause disruption of anti-predator aggregating behaviour, or penguins maximising short-term rates of prey intake in a rapidly changing light regime. Thus while Macaroni Penguins may be ultimately limited by light in their foraging, most day-time dives are not light limited, probably because penguins have light levels at, or above which, they prefer to forage, but can surpass if necessary. The second pattern suggests that penguins fed mainly on euphausiids in the morning, and on fish from late morning through to evening. Female penguins adjusted their behaviour at sea by decreasing trip length and diving deeper when chicks were small. This may result from greater vertical searching closer to the island, enabling penguins to conduct shorter foraging trips, and provide lipid-rich fish suitable for small chicks. There is little evidence that competitive exclusion at sea by other air-breathing diving krill predators at Bouvetøya, Antarctic fur seals *Arctocephalus gazella* and Chinstrap Penguins *Pygoscelis antarctica*, forces Macaroni Penguins to eat fish instead of krill.

Introduction

The Macaroni Penguin *Eudyptes chrysolophus* is the most abundant penguin species in the world (Woehler 1993), with a population of ca. 9–11.8 million breeding pairs (Woehler 1993; Ellis et al. 1998), distributed throughout the sub-Antarctic and Antarctic regions (Marchant & Higgins 1990; Woehler 1993; Williams 1995). It must therefore be considered an important consumer of marine resources in the Southern Ocean (Brown 1989). Macaroni Penguins are dietary generalists (Chapter 1), and their impact on resources is thus also expected to vary from site to site. Despite this, few studies have been conducted on the diving and foraging behaviour of this penguin, with our knowledge based on findings from South Georgia (Croxall et al. 1988, 1993) and Heard Island (Green et al. 1998). The diving and foraging behaviour of one eudyptid penguin (there are six species in the genus) is well known, namely that of the Rockhopper Penguin *E. chrysocome* (e.g. Wilson et al. 1997; Tremblay & Cherel 1999a,b; Cherel et al. 1999).

At South Georgia, Macaroni Penguins eat Antarctic krill (*Euphausia superba*, hereafter krill), except in years of low krill availability, and dive to shallow depths (25–30 m) (Croxall et al. 1988, 1993, 1999). At Heard Island penguins dive deeper and eat euphausiids and fish, with the latter increasing in dominance through the course of the breeding season (Green et al. 1998). Patterns in diet are yet more complex at Bouvetøya (Chapter 1), an isolated island situated in the mid South Atlantic Ocean, and which supports large populations of two other air-breathing diving predators of krill: Antarctic fur seals *Arctocephalus gazella*, and Chinstrap Penguins *Pygoscelis antarctica*. This community of marine predators is relatively species-poor, and thus offers a good opportunity to understand whether the realised niche of Macaroni Penguins is a consequence of intrinsic community interactions (e.g. competition) or extrinsic (physical) factors.

At Bouvetøya the diet of Macaroni Penguins is dominated by mesopelagic (Hulley 1985, 1990; Duhamel et al. 2000) myctophid fish (mainly *Krefftichthys anderssoni*), especially in the first period of chick rearing when the female is the sole provider for the single chick (Williams 1995; Chapter 1). Prey of lesser importance consumed during this period are shallow-dwelling krill and another euphausiid *Thysanoessa macrura* (Chapter 1).

These and other findings prompted me to ask if the depth usage of female Macaroni Penguins reflects their mixed diet and, if so, what temporal patterns in depth usage existed. I also wished to test whether female Macaroni Penguins adjust their behaviour at sea as food demands from the chick increase. Females could do this in four ways, by: (1) conducting longer trips, (2) shortening turn-around time in the colony, (3) increasing the proportion of time spent underwater, and (4) changing depth usage. Finally, I tested the hypothesis that fish are delivered preferentially to small chicks (Chapter 1), by comparing the depth usage of chick-rearing females with that of birds before hatching.

Methods

Details on the biota and climate of Bouvetøya, and breeding schedules of penguins at Nyrøysa, are provided in the Introduction, Isaksen et al. (1997a,b) and Appendices A,B & C.

Logger recording devices (DK 602 series; Driesen and Kern GmBH, Bad Bramstedt, Germany) were deployed in 1997 (3–28 January) and 1998/99 (30 December–18 January) at Bouvetøya. Loggers measured 143 x 64 x 22 m (150 g = ca. 48 g in water) in 1997, and 105 x 55 x 21 mm (110 g = ca. 35 g in water) in 1999. Breeding female Macaroni Penguins were captured by hand at the nest and restrained (Wilson 1997), and the logger attached to the lower back above the tail following suggestions in Bannasch et al. (1994) using layered Tesa ™ adhesive tape. Birds were sexed following methods in Chapter 1. Equipment failure prevented males from being instrumented in both years. Equipping birds seldom took longer than five minutes. In both years all but two equipped birds were in the early stage of chick rearing. These two birds (1998/99) were at sea on the last relief before hatching (ca. 10 days; Williams 1995) and were thus, at least temporarily, migratory.

The loggers recorded temperature (± 0.2°C) and pressure (± 0.01 m) with 16-bit resolution, and were set at 2- and 5-second recording intervals which is sufficiently frequent to avoid errors in interpreting the dive record identified by Boyd (1993) and Wilson et al. (1995). Upon return to shore, birds were recaptured, the logger retrieved and the data downloaded to a portable computer.

Sunrise and sunset were calculated by using a US National Oceanic and Atmospheric Administration (NOAA) Surface Radiation Research Branch sunset - sunrise calculator, available at http://www.srrb.noaa.gov/highlights/sunrise/gen.html. During the study sunrise occurred between 04:26 and 05:13 (mean 04:47) and sunset between 20:50 and 21:19 (mean 21:08). Times are given as local times (GMT +1).

Dive records were analysed with MultiTrace software (Jensen Software Systems, Laboe, Germany). Descents to less than 5m were omitted (e.g. Bengston et al. 1993), because it is difficult to separate shallow foraging dives from commuting. Inspection of the dive record shows periods in the dive where the otherwise smooth ascent and descent of the bird was interrupted, usually for a sustained period. These irregularities were interpreted as prey capture events (e.g. Bengston et al. 1993; Chappell et al. 1993; Wilson 1995; Wilson & Peters 1999), and termed bottom time since they mostly occurred at the deepest phase of the dive (Fig. 2.1). I assume that the length of bottom time in the dive is proportional to the success (total prey captured) of the dive; this has not been validated but is logical since the bottom phase of the dive is commonly considered to be where prey capture takes place (e.g. Bengston et al. 1993; Chappell et al. 1993; Wilson 1995; Wilson & Peters 1999). MultiTrace recorded dive start time, maximum depth, mean depth of bottom time, total dive duration and total bottom time.

Foraging trip durations were interpreted by simultaneous inspection of pressure (depth) and temperature records: entering and exiting the water was usually accompanied by a marked (> 4°C) and rapid (< 30 s) change in temperature. Statistical analyses were performed using Statistica 5.5 (StatSoft, Inc. 1999). All summary statistics are quoted as mean ± standard deviation (SD).

Results

A total of 6009 dives was recorded from six penguins in 1997, and 9536 dives from nine chick-rearing, and two pre-hatching, penguins in 1998/99. Of the total 15542 dives recorded in both years, 12263 (78.9 %) contained a bottom phase, interpreted as successful foraging. Only two forms of dive were apparent: those without bottom time (typified by smooth rates of ascending and descending vertical velocity), and those with irregular bottom phases (Fig. 2.1). This is contrary to the dive forms recognised for Macaroni Penguins at South Georgia (Croxall et al. 1993), and Heard Island (Green et al. 1998). Diving was divided into distinct bouts, interspersed with long resting phases, with some rests lasting longer than one hour. The ambient temperature would frequently climb to a maximum of ca. 4°C during long rests. Deep diving (> 50 m) was initiated soon after re-entering the water after a few rests. This suggested that penguins might have been resting on icebergs.

The depths of dives with a bottom phase were bimodally distributed, with most recorded at 5–15 m (shallow), and the second mode at 50–70 m (deep) (Fig. 2.2). Dives with bottom time were shallower (28 ± 22.3 m) in 1997 than 1999 (38.7 ± 27.7 m) (Mann Whitney, $U = 6253843$; $p < 0.0001$).

The deepest feeding dives reached 115 m, and the deepest dive recorded in both seasons was 162 m. Penguins dived at all times of the day and night, but more frequently during the day (day: mean 4.8% of all dives performed.hr^{-1}; night: mean 2.9% of all dives performed.hr^{-1}; $n = 15542$ dives) (Fig. 2.3). There was a lull in diving activity shortly before dawn (Fig. 2.3). Most dives fell within 10% of the depth of the previous dive, indicating that penguins were systematic in the sequencing of their diving (Fig. 2.4).

The pattern of depth usage with time of day revealed that night dives were shallower (17.5 ± 19.0 m) than day dives (39.3 ± 26.1 m) in both years, and that the deepest dives recorded were conducted at sunrise and sunset (Fig. 2.5). After the pre-sunrise lull in activity, there was a rapid increase in the number of dives performed and the depths reached (Figs. 2.3 & 2.5). Penguins tended to dive shallowly (< 20 m) in the morning, but from late morning started to dive deep (> 60 m) (Fig. 2.5). Apart from sunrise and sunset dives, dives were at their deepest at noon (ca. 70 m), and subsequently became shallower, reaching intermediate depths (ca. 30 m) in the evening (Fig. 2.5). Relatively few dives ended at intermediate depths during the day, and relatively few shallow dives were made from late morning onwards (Fig. 2.5). Fewer dives at night were successful (77.3% successful) than day dives (79.4%), judging by the proportion of dives with a bottom phase ($\chi2 = 6.5$; $df = 1$; $p < 0.025$).

Twenty-eight complete foraging trips were recorded in both years, and portions from a further six trips. Most (79%, n = 34) birds went to sea between 04:00–07:00, with the remaining trips initiated later in the morning and in the afternoon. Only one trip was started after sunset. Most penguins returned to shore again between noon and 22:00 (89%, n = 28), with a peak (32%) between 19:00 and 22:00. Mean trip length was 25.7 ± 12.0 hrs, and did not differ significantly between years (t-test; ns).

For females with chicks, trip length was positively related to chick age ($r = 0.439$; $df = 25$; $p < 0.025$). Females pre-hatching also dived significantly shallower (30.1 ± 20.0 m) than females with chicks (both years: 35.3 ± 27.1 m) (Mann Whitney, $U = 3088769$; $p < 0.0001$) (Fig. 2.6). This was not because females with chicks dived more often during the day, though ($\chi 2 = 0.11$; ns). The mean depth of the bottom phase decreased significantly with chick age in both years (combined $r = 0.145$; $df > 10\,000$; $p < 0.0005$). Neither the proportion of total time at sea spent underwater, nor the turn-around time the colony, was related to chick age (linear regression; both ns).

Discussion

Logger recorders are known to disrupt hydrodynamic effectiveness, and so increase the costs of transport (e.g. Wilson et al. 1986; effects reviewed by Wilson 1995). Given the remarkably low drag coefficients of penguins (Wilson 1995), it is hard to see that the devices used in this study did not affect diving to some extent. This is strongly suggested by the shallower diving depths in 1997, when differences in diet between the years were small (Chapter 1). Although all loggers used in both years were tapered anteriorly, vertically compressed, and attached in such a way to minimise drag (Bannasch et al. 1994), the 1999 loggers were smaller and concave, and thus fitted the penguin better. This difference, while seemingly small to the naïve, appears to have influenced the dive depths of birds markedly, but systematically. I therefore consider both seasons together, since the level of the analysis presented here is not unduly complex, and I have verified that all other inter-annual differences in diving behaviour are minor.

Depth usage

The patterns in depth usage of Macaroni Penguins at Bouvetøya are consistent with their diet. Krill are largely restricted to shallow oxygen rich waters (< 150 m), and at many sites migrate to the surface at night (e.g. South Georgia, Croxall et al. 1985; reviewed by Miller & Hampton 1989). The euphausiid *T. macrura* is also shallow-dwelling (Nemoto 1966; Dzik & Jazdzewski 1978). Diel migration occurs in many myctophid fish including *Electrona carlsbergi* and, probably, *Notolepis coatsi* (Hulley 1985, 1990; Duhamel et al. 2000), but *K. anderssoni* is unusual in that it is available in surface waters (shallower than 250 m) during the day, and moves to waters deeper than 100 m at night (Duhamel et al. 2000). The bimodal depth usage of Macaroni Penguins at Bouvetøya is likely to be a consequence of birds feeding on deeper fish (probably *K. anderssoni*) and shallower euphausiids during the day, and shallow euphausiids, and possibly fish other than *K. anderssoni*, at night.

In the western South Atlantic euphausiids generally (and krill in particular) tend to dominate the micronektonic community (Ridoux 1994; Prince et al. 1999), and this is reflected in the diets of Macaroni Penguins (Chapter 1; reviewed by Williams 1995) and other predators in the region (e.g. Croxall et al. 1988, 1997, 1999). Krill is similarly an important resource for breeding seabirds and seals at Bouvetøya (Chapter 3). Since it, and other prey of Macaroni Penguins, occurs closer to the surface at night, and diving is energetically costly, requiring unprofitable transit to depths were prey are situated, foraging at night should offer clear advantages to Macaroni Penguins, as Croxall et al. (1985) argue is the case for fur seals. Despite this, at South Georgia, Heard Island, and Bouvetøya, Macaroni Penguins conduct the bulk of their diving during the day (Croxall et al. 1988, 1993; Green et al. 1998). Fur seals are unlikely to employ the same predatory techniques as penguins, and vision may also differ. They may therefore be better suited to night-time diving. Certainly, while Macaroni Penguins at Bouvetøya do dive at night, most trips end before nightfall and start at dawn, and night dives appear to be less successful. This is consistent with the observations of Wilson et al. (1993) on Adélie Penguins *P. adeliae*, where diving continued through the night, but resulted in far fewer prey being caught. Macaroni Penguins may therefore be limited ultimately by light in their foraging.

Two unusual patterns in depth usage were identified in this study. First, the deepest dives were consistently performed at sunrise and sunset. Second, penguins tended to dive shallowly in the first part of the morning, but then switched to deeper diving in late morning through until evening. To the best of my knowledge, neither of these patterns has been observed before in any species of penguin, and the first is in direct contrast to that exhibited by Macaroni Penguins at South Georgia (Croxall et al. 1993).

Generally, most penguin species dive deepest at noon, when light penetrates the water column the furthest, and shallowest at night (e.g. Wilson et al. 1993; Kirkwood & Robertson 1997a,b; Luna-Jorquera & Culik 1999; Wilson & Peters 1999). Thus it is thought that penguins are limited by light in their patterns of depth usage (Wilson et al. 1993; Wilson 1995). The bulk of dives of Macaroni Penguins at Bouvetøya mirror this, with the notable exception of dives at sunrise and sunset. Chinstrap Penguins, which feed almost solely on krill at Bouvetøya, also exhibit this pattern (Chapter 3). This appears, at first, to be difficult to reconcile with the evidence that foraging is light limited.

The deep dives of Macaroni Penguins all had bottom time, indicating that feeding occurred, so deep diving is unlikely to constitute unsuccessful searching behaviour. There are two further possible explanations, which are not necessarily exclusive. First, rapid vertical migration of krill may play a role. If rapidly changing light levels (i.e. sunrise and sunset) are cues for vertical movement, and this is achieved rapidly, anti-predator aggregating behaviour (O'Brien 1987) may diminish, so favouring the penguin. Second, if prey vertical migration is a response to predation pressure (cf. Wilson et al. 1993), penguins could be diving deeper rather than searching horizontally, to reach more predictably encountered prey, and so maximise their rate of prey capture over the short period where prey dispersion is rapidly changing. Penguins would thus be responding to hunger stimulus in the morning, and rapidly diminishing light levels in the evening.

For these hypotheses to be consistent with the evidence that Macaroni Penguins are light limited, the majority of day dives cannot be proximately light limited. Other penguins (e.g. Emperor *Aptenodytes forsteri* and King *A. patagonicus*) regularly exceed 300 m and 200 m depths, respectively (Kooyman et al. 1992; Kirkwood & Robertson 1997a,b). Barring major differences in vision, Macaroni Penguins should encounter sufficient light at 150 m depths. As ambient light levels decrease, both spatial resolution (Snyder et al. 1977) and the probability of a penguin pursuing a fish decrease, at first linearly until an asymptote is reached (Cannell & Cullen 1998). This implies that penguins have preferred light intensities at which they will forage, and only when prey are unavailable at that depth and intensity will they search elsewhere, either at the same intensity, or occasionally at greater depths where light intensity is less but where they can still perceive prey.

In the absence of surveys of zooplankton at Bouvetøya and information on Macaroni Penguins diet in the morning, I speculate that changing patterns in diurnal depth usage are a consequence of penguins feeding on euphausiids in the morning, and fish from late morning through until evening. This systematic difference is consistent with the sequencing of dives to similar depth, and the tendency for diets to be dominated by a single prey species (Chapter 1). Once having encountered prey, birds dive upon it repeatedly. These patterns in behaviour clearly warrant further investigation.

Adjustment of behaviour to increased chick food demands

Female Macaroni Penguins cope with increasing food demands at the nest by adjusting their behaviour at sea. Females with chicks stay at sea longer (and hence accumulate more bottom time), dive deeper at first and, as the chick grows older, dive shallower. Deeper diving at hatching has also been observed at Heard Island (Green et al. 1998). Fish dominate the diets of Macaroni Penguins at Bouvetøya, especially during the first third of chick rearing (Chapter 1), when this dive study was conducted. Deeper diving at hatching and soon thereafter may thus be a behavioural adjustment that favours provisioning of small chicks.

Deeper dwelling fish are thought to be more scattered than dense aggregations of krill, where densities can exceed 10^2 g.m^{-3} (Miller & Hampton 1989). This, coupled with both the extra costs of diving to greater depths, and the shallower dive depths of pre-hatching females, suggests that penguins might preferentially return krill to the nest, as they do at South Georgia (Croxall et al. 1988, 1993). However, myctophid fish are lipid-rich and twice as nutritious as krill (*K. anderssoni* = 8.1 kJ.g^{-1}, vs krill = 4.6 kJ.g^{-1}; Cherel & Ridoux 1992;

Clarke 1984). Small chicks require frequent meals rather than large meals, and deeper diving that targets fish could be an adaptive strategy if fish are sufficiently abundant close to the island (Chapter 1). By adjusting their vertical, rather than horizontal, searching, females effectively reduce the duration of their return period to the nest and return with the most nutritious food available.

Another possibility is that this pattern is enforced by competition with other krill consumers at the island, such as Chinstrap Penguins which feed inshore (Chapter 3). However, this does not seem likely since Macaroni Penguin trip length in the first two weeks after hatching (21.5 ± 12.2 hrs) is still roughly double the length of an average Chinstrap Penguin trip (Chapter 3), suggesting spatial overlap between the two species is not great. Fur seals are also significant consumers of krill at Bouvetøya during the breeding season (Kirkman et al. in press), but dive shallower and have longer trips than Macaroni Penguins (Isaksen et al. 1997a; Chapter 3; S. Kirkman unpubl. data) suggesting limited spatial overlap, and are in fact less abundant at the island during January (G. Hofmeyr unpubl. data) when fish are eaten by penguins. This is discussed further in Chapter 3. In sum, there is little evidence to suggest that exploitation of fish by Macaroni Penguins is driven by competition.

The positive relationship between increased trip length and chick age has been documented for other penguins (e.g. Gentoo Penguin *Pygoscelis papua*; Williams & Rothery 1990). Bigger chicks should possess better fasting capabilities than smaller chicks, so longer trips in female Macaroni Penguins may serve their own ends in that it enables them more time to recover condition lost earlier in the breeding season. Macaroni Penguins have long relief schedules during breeding (see Williams 1995) and this is reflected in large changes in body mass (Croxall 1995). Certainly, the body condition of female Macaroni Penguins at Bouvetøya improved during chick rearing (Chapter 1), suggesting that the pre-hatching period or very early part of chick rearing might have been stressful and so caused their condition to deteriorate.

In conclusion, the depth usage of female Macaroni Penguins at Bouvetøya is consistent with their mixed diet. This is achieved by segregated diurnal depth usage, and diving at night. Diving is performed less often at night, and is less successful. While this suggests that foraging of Macaroni Penguins are ultimately limited by light, most day-time diving activity is probably not limited by light. Females adjust their behaviour at sea to cope with demands from the chick, by shortening trip length and diving deeper when chicks are small. The deeper dives enable bird to return lipid-rich fish to the chick, and appears to be adaptive, and not a consequence of competitive exclusion from krill resources by other air-breathing divers at the island. This indicates that, in the relatively species-poor community of air-breathing divers at Bouvetøya, the realised niche of Macaroni Penguins is not strongly defined by intrinsic community interactions such as competition.

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Figure legends

Fig. 1. Anecdotal example of a sequence of successful dives from a Macaroni Penguin, Bouvetøya 1999. The bottom phase in each dive, were prey are captured, is denoted by the dotted lines.

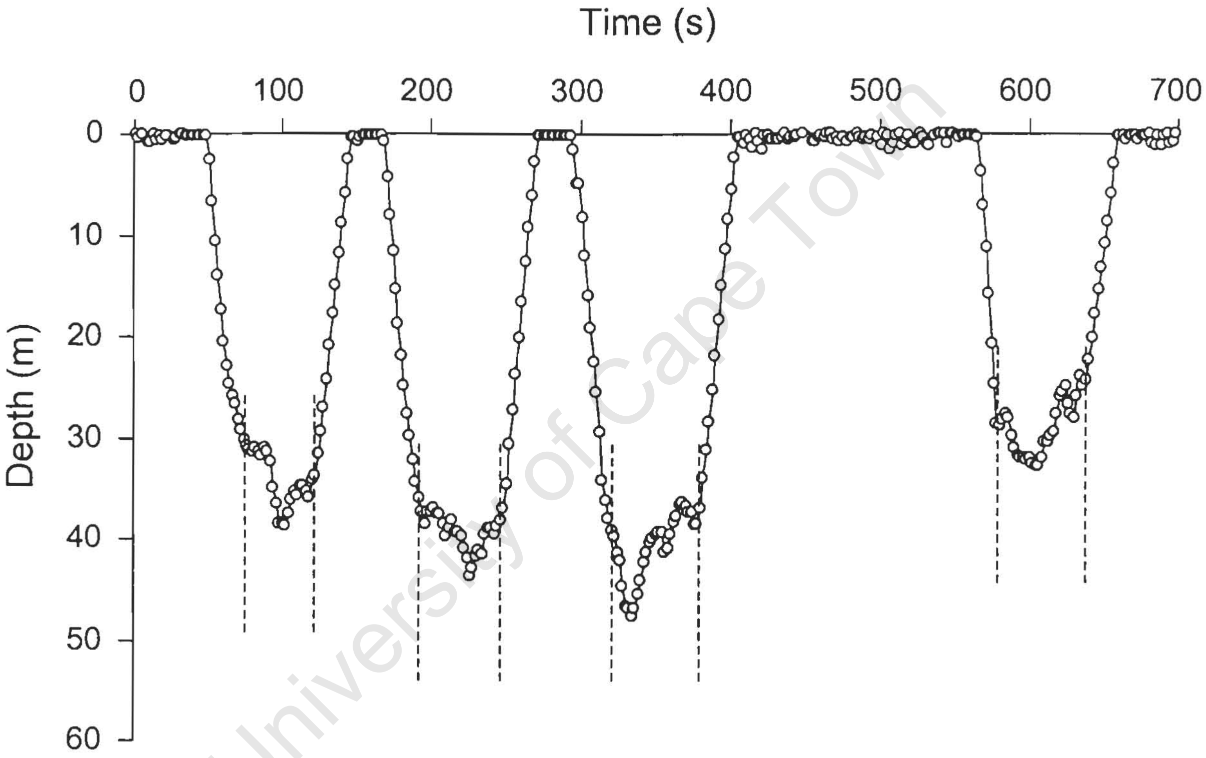
Fig. 2. Depth histogram of dives with bottom time (i.e. feeding dives) of Macaroni Penguins, Bouvetøya 1997 and 1999.

Fig. 3. Number of dives with bottom time initiated per hour, Macaroni Penguins, Bouvetøya 1997 and 1999. The lull in activity before sunrise is indicated.

Fig. 4. The deviation (%) of dive depth from the depth of the previous dive, all dives of Macaroni Penguins, Bouvetøya 1997 and 1999. Most dives return to within 5% of the depth reached during the previous dive.

Fig. 5. Scatterplot of all dives with bottom time (i.e. feeding dives) of Macaroni Penguins, Bouvetøya 1997 and 1999. Dives initiated during the day are indicated with small circles, those initiated at night with open squares. The density of points is proportional to the amount of dives to that depth.

Fig. 6. Depth histograms of dives with bottom time (i.e. feeding dives) of pre-hatching females (hatched bars), and chick-rearing (solid bars) female Macaroni Penguins, Bouvetøya 1997 and 1999.



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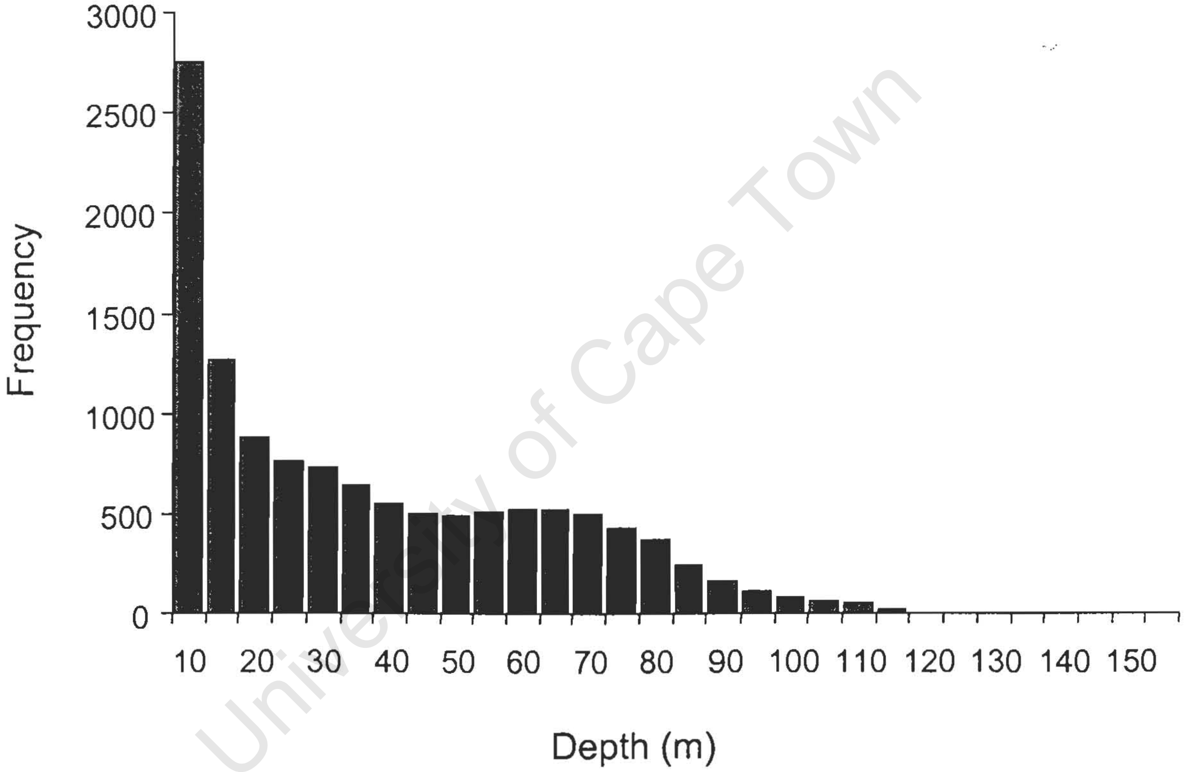

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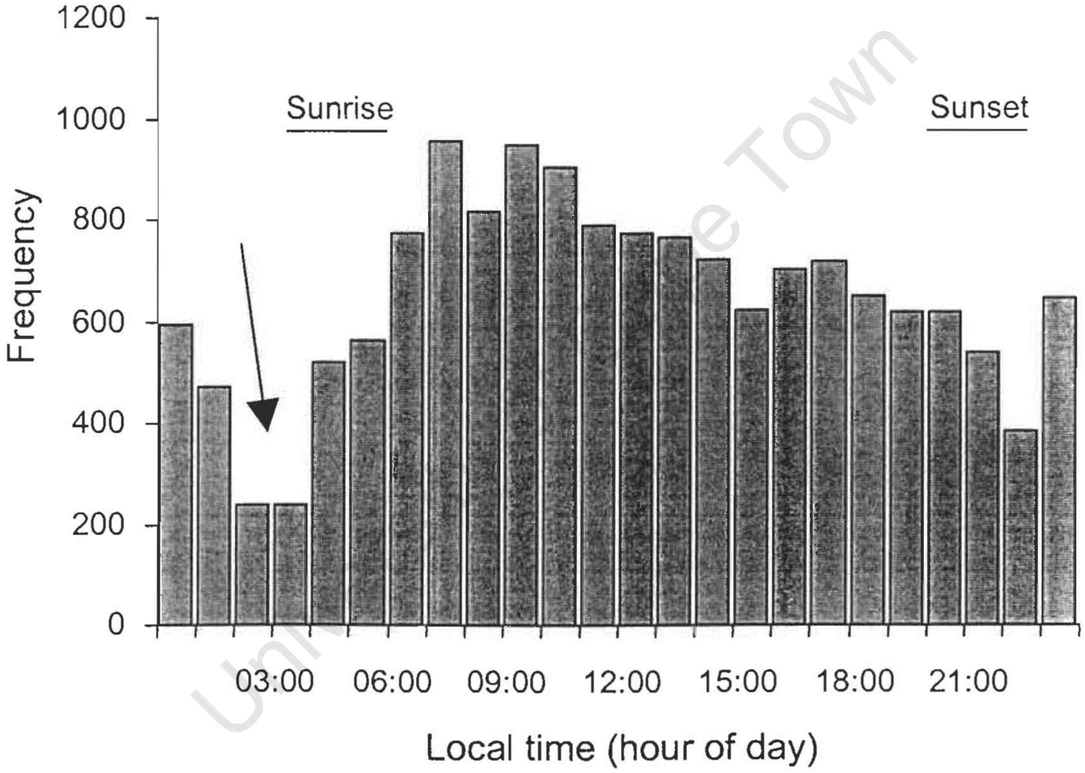

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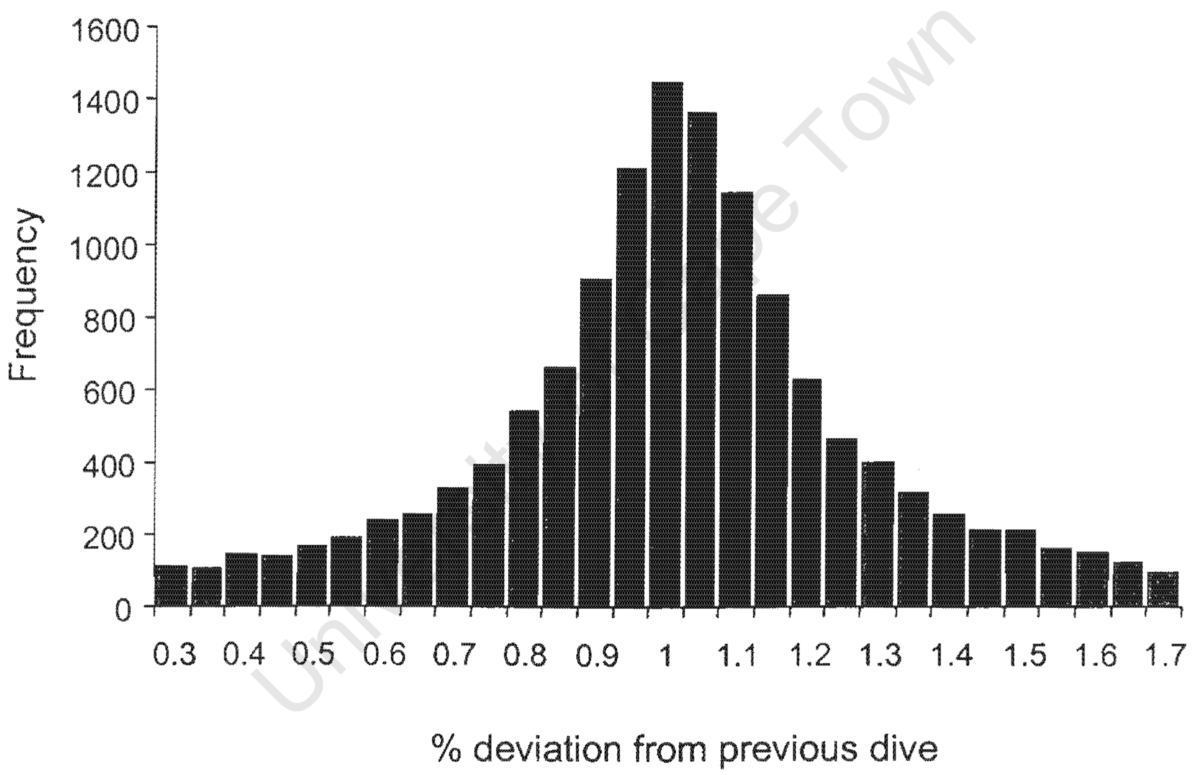

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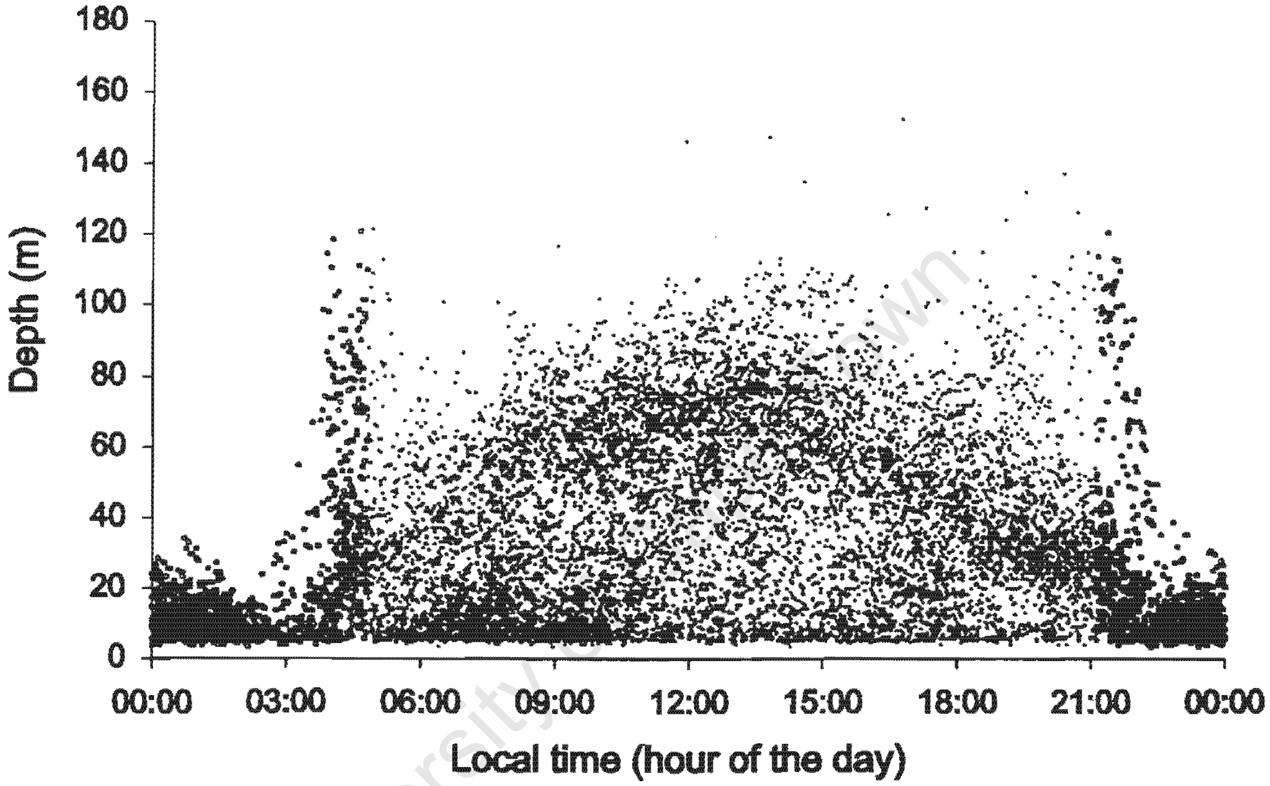
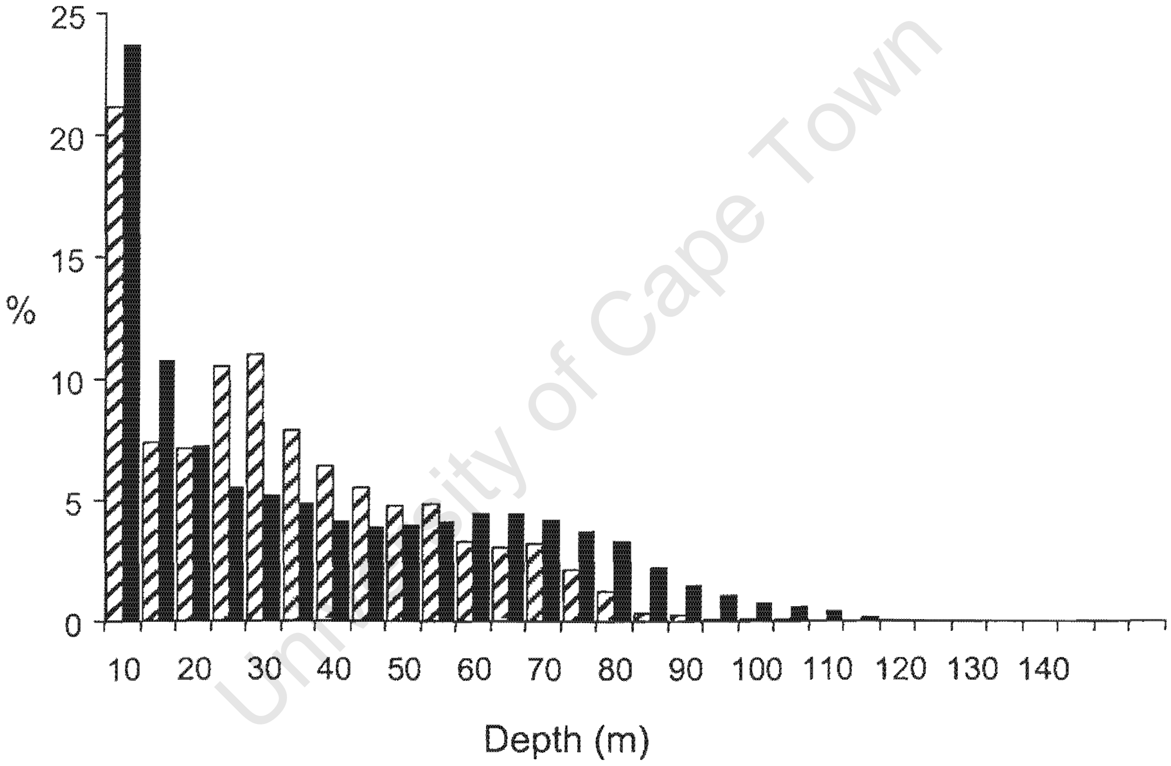


Chapter 2: Figure 5. Scatterplot of all dives with bottom time (i.e. feeding dives) of female Macaroni Penguins, Bouvetøya, 1997 and 1999. Dives initiated during the day are indicated with small circles, those initiated at night with open squares. The density of points is proportional to the amount of dives to that depth.



Chapter 2: Figure 6. Depth histograms of dives with bottom time (i.e. feeding dives) of pre-hatching (hatched bars, 1999), and chick-rearing (solid bars, 1997 & 1999) female Macaroni Penguins, Bouvetøya.

Chapter 3

Diet, diving behaviour, and niche of Chinstrap Penguins *Pygoscelis antarctica* at Bouvetøya

Abstract

The diet of breeding Chinstrap Penguins *Pygoscelis antarctica* was studied over two seasons, and diving behaviour over one season, at Bouvetøya. Diet was dominated by Antarctic krill *Euphausia superba* in both years, as is the case at most other breeding sites. Most krill eaten were large (50-60 mm total length), but some smaller krill (30–40 mm) were taken in 1997. This inter-annual difference is consistent with evidence of inter-annual variation in krill demography at other sites in the South Atlantic. Penguins conducted short foraging trips (9.2 ± 6.2 hrs), which suggests that most foraging effort is concentrated within 15-20 km of the island. The diving behaviour of seven chick-rearing penguins, equipped with depth loggers, was characterised by high inter-individual variation in depth usage. However, there were consistently high levels of diving activity in the morning, and fewer, shallower dives at night. Foraging effort decreased with increasing depth, except at 20–35 m where penguins spent a disproportionately greater amount of time. Mean maximum depth was 25.5 ± 17.9 m (maximum dive = 114.3 m), with 96% of all foraging effort shallower than 60 m. Differences in diet, depth and spatial usage, and peak breeding food demands suggests that while there is ecological segregation of the three main diving predators at Bouvetøya, there is also some niche overlap. The niche of Chinstrap Penguins at Bouvetøya is predominantly that of a shallow-diving, inshore-feeding, krill specialist, as is the case at most other sites. There is little evidence to suggest that ecological segregation between Chinstrap Penguins and another krill-consuming penguin at Bouvetøya, the Macaroni Penguin *Eudyptes chrysolophus*, is as a result of competition at sea. Thus intrinsic community interactions at sea may not be important determinants of community structure at Bouvetøya, and the ecological segregation observed might be an outcome of adaptations by each species to conditions experienced in the centre of their respective ranges.

Introduction

Penguins are important top predators in the Southern Ocean food web (Croxall & Lishman 1987; Adams et al. 1993; Wilson 1995; Woehler 1995) and, by virtue of their biomass (Woehler 1993) and high metabolic rates, impact substantially on populations of forage prey species, especially around breeding islands (Croxall 1984; Wilson 1995). Antarctic Krill *Euphausia superba* (hereafter krill) is a keystone component of the Southern Ocean food web, and an important prey species for most top predators in the Southern Ocean including many penguin species. Variation in its abundance has been linked to variation in predator performance (e.g. Boyd et al. 1994; Croxall et al. 1988a, 1999).

Chinstrap Penguins *Pygoscelis antarctica* are specialist consumers of krill (Marchant & Higgins 1990; Williams 1995), and number ca. 7.5 million breeding pairs, or approximately 26% of all penguins in the Southern Ocean (Woehler 1993). Neither their diet nor foraging ecology is well understood at Bouvetøya (Bouvet Island), a small island of volcanic origin situated in the mid South-Atlantic Ocean (54°25'S, 03°21'E), and an important breeding site for land-based marine predators (Appendix A). Bouvetøya is the northernmost breeding site for the Chinstrap Penguin (Marchant & Higgins 1990; Williams 1995; Woehler 1995). The community of air-breathing diving predators at this island (Chinstrap Penguins, Macaroni Penguins *Eudyptes chrysolophus*, and Antarctic fur seals *Arctocephalus gazella*) is unusually depauperate, and thus offers a simple system for studying interactions among species which are all known to consume krill (Isaksen et al. 1997a; Chapter 1).

Cooper et al. (1984), Bakken (1991) and Isaksen et al. (1997a; Appendix B) present information on the diets of breeding Chinstrap Penguins at Bouvetøya, and Isaksen et al. (1997a) present information on foraging behaviour (diving and trip duration). These accounts are limited by the small number of samples, though, and I seek to redress this here. Foraging of Chinstrap Penguins has been studied in detail elsewhere in the Southern Ocean at the South Shetland and South Orkney Islands (e.g. Lishman & Croxall 1983; Lishman 1985; Trivelpiece et al. 1986, 1987; Bengston et al. 1993; Wilson & Peters 1999), but not at Bouvetøya. Recent technical developments in miniaturised recording devices permits unprecedented insight into aspects of foraging not previously possible, including mechanisms allowing sympatric diving predators to co-exist.

Here I present information on the diet of breeding Chinstrap Penguins at Bouvetøya, describe patterns in foraging behaviour, specifically timing of dives and foraging trips, trip length, and depth usage, and discuss ecological segregation between other consumers of krill at the island.

Methods

For details on the Nyrøysa study site, and biota and climate of Bouvetøya, see the Introduction, Isaksen et al. (1997a,b), and Appendices A, B & C.

Diet sampling

Adult penguins newly arrived ashore (identified by wet plumage, pinkish tinge to the underflippers and distended stomachs) were captured at walkways close to the beach and in the colony in 1997 and 1999. Stomach contents were only collected from birds that had not yet fed their chick(s), using a modified water-offloading technique (Wilson 1984). Penguins were flushed once in 1997, and until the water was clean in 1999, which was mostly twice. In both years diets were collected after peak hatching (mean hatching dates: 28 December 1996; 31 December 1998) (Isaksen et al. 1997a; Appendix C). Diet sampling commenced on 5 January 1997 and 10 January 1999, and took place every five days (Table 3.1), with two samples collected every sampling day.

Samples were preserved in 60% ethanol, but frozen if fish remains were present. All samples were returned to South Africa for analysis, where they were thawed, drained, and wet mass measured (± 0.1g) with an electronic mass balance. The material was sorted into crustacean and fish components. Each component was weighed separately and prey items were used to identify, as far as possible, the prey to species level. Fish were identified from keys to otoliths in Hecht

(1987), Gon & Heemstra (1990), and reference material at Marine and Coastal Management, Cape Town, and the Port Elizabeth Museum. Some fish could only be identified to genus, owing to developmental immaturity or the advanced state of digestion. Crustaceans were identified and sexed (males, females, gravid females) from the same reference collections. Total numbers of each species occurring in the sample were recorded, either by counting total left or right otoliths (fish), or whole individuals or carapaces (crustaceans). Whole intact carapace length (CL) (Morris et al. 1988; Hill 1990) of fresh crustaceans was measured (nearest 0.1 mm) with a microscope and graticule, and total length (AT; Morris et al. 1988) estimated from the α-model regressions of Morris et al. (1988).

Diving behaviour

Logger recording devices (DK 602 series; Driesen and Kern GmBH, Bad Bramstedt, Germany) were deployed in January 1999. The loggers were the smaller, better fitting models also used on Macaroni Penguins in 1999 (Chapter 2). Penguins were captured by hand at the nest, and restrained following Wilson (1997). The loggers were tapered anteriorly, vertically compressed (Chapter 2), and attached to the lower back above the tail following suggestions in Bannasch et al. (1994) using layered Tesa ™ adhesive tape. Equipping birds seldom took longer than five minutes. Loggers recorded temperature (± 0.2°C) and pressure (± 0.01 m) with 16-bit resolution, and were set at 2- and 5-second recording intervals, which is sufficiently frequent to avoid errors in interpreting the dive record identified by Boyd (1993) and Wilson et al. (1995). Upon return to shore, birds were recaptured, the logger retrieved and the data downloaded to a portable computer. Four birds were also stomach sampled to recover the entire diet for comparison with the dive record. No sexing of birds was possible, owing to difficulties with validating measurements that could discriminate between the sexes, and were repeatable.

Sunrise and sunset were calculated by using a US National Oceanic and Atmospheric Administration (NOAA) Surface Radiation Research Branch sunset - sunrise calculator, available at http://www.srrb.noaa.gov/highlights/sunrise/gen.html. Over the month of sampling, sunrise occurred between 04:26 and 05:13 (mean 04:47) and sunset between 20:50 and 21:19 (mean

21:08). Times are given as local times (GMT +1). Foraging trip durations were interpreted by simultaneous inspection of pressure (depth) and temperature records: entering and exiting the water was usually accompanied by a marked (> 4°C) change in temperature.

Dive records were analysed with MultiTrace software (Jensen Software Systems, Laboe, Germany). Descents to less than 5m were omitted (e.g. Bengston et al. 1993), as it is difficult to separate shallow foraging dives from commuting. Inspection of the dive record shows periods in the dive where the otherwise smooth ascent and descent of the bird was interrupted, usually for a sustained period. These irregularities were interpreted as prey capture events, and termed bottom time (e.g. Bengston et al. 1993; Chappell et al. 1993; Wilson 1995; Wilson & Peters 1999) since they mostly occurred at the deepest phase of the dive (cf. Figs. 2.1 & 4.1). I assume that the length of bottom time in the dive is proportional to the success (total prey captured) of the dive; this has not been validated but is logical. MultiTrace recorded dive start time, maximum depth, mean depth of bottom time, total duration and bottom time, and preceding surface interval.

Bouts were identified for each foraging trip by calculating the bout criterion interval (Martin & Bateson 1986). This interval was calculated from breakpoint regressions (Statistica 5.5; StatSoft, Inc. 1999) fitted to log-frequency plots of inter-dive durations, enabling the λ_{fast} and λ_{slow} parameters of a two-process Poisson model (Slater & Lester 1982; Sibly et al. 1990) to be estimated using equation 4 from Slater & Lester (1982). Separate bout criterion intervals were calculated for each foraging trip; these were then used to identify bouts with MultiTrace. The programme searched for the first dive, and if the following dive fell within the bout criterion interval it was assigned to the same bout. This continued until two consecutive dives were separated by an interval greater than the bout criterion. When this happened a new bout began.

Data on diet and aspects of diving behaviour of Macaroni Penguins at Bouvetøya in 1997 and 1999 (cf. Chapters 1 & 2) are also presented here for purposes of comparison. Unless otherwise stated, all summary statistics are quoted as mean ± standard deviation (SD).

Results

Diet

In both years euphausiids dominated diet samples, principally krill which occurred in all samples (Table 3.1), constituting a mean 99.6% of whole wet sample mass in 1997, and 99.9% in 1999 (Table 3.2). No cephalopods were recovered in either season, fish only in 1997, and amphipods only in 1999 (Table 3.1). Four prey species were recovered from 20 diet samples in 1997, and three species from 18 diet samples in 1999 (Table 3.1). In 1999, diet samples were heavier, and contained more krill than in 1997 (t-test, whole wet mass; $p = 0.05$) (Table 3.2).

In 1997, neither number of prey individuals per sample, nor sample mass, was significantly related to either time or date of sampling (forward stepwise multiple regressions; all ns). The result was the same for 1999, although date was significantly related to sample mass (forward stepwise multiple regression, time of day removed; date: $\beta = 0.47$, $t = 2.15$, $p = 0.05$; overall: $F = 4.61$, $p = 0.05$). Date (i.e. chick mass) and sample mass were also positively related at King George Island (Trivelpiece et al. 1987), as a consequence of increasing demands from the growing offspring. It also suggests that, at Bouvetøya in 1997, single flush stomach sampling failed to recover the whole sample.

Mean krill lengths recovered from diet samples were 51.4 ± 4.4 mm in 1997, and 52.7 ± 5.0 mm in 1999. Both seasons had modes at 56 mm, but overall length frequency distributions differed significantly (Kolmogorov-Smirnov two-sample test; $p < 0.01$), with krill in 1997 having a weak bimodal distribution and a second mode at 38 mm (Fig. 3.1). This could indicate the presence of two age classes of krill at sea (cf. Fevolden 1980), but it is difficult to know if they correspond to the classes 2 and 3 at South Georgia (Reid et al. 1999), because information on growth of krill at Bouvetøya is lacking.

Length frequencies of krill recovered from another krill consumer at Bouvetøya, the Macaroni Penguin *Eudyptes chrysolophus*, differed significantly from those of Chinstrap Penguins, but only in 1997 (1997 mean Macaroni 46.5 ± 3.6 mm; Kolmogorov-Smirnov two-sample test; $p < 0.01$). In both seasons there was a pronounced bias in the sex of krill recovered from Chinstrap Penguins (1997: males 4.9%; 1999: 1.7%), but the proportion per sample did not change significantly over the course of either season (linear regressions; both ns). This is contrary to the pattern recorded by Fevolden from surveys at sea (1980). In 1997, krill mean length did not change over the course of the season, although it increased significantly with date in 1999 (linear regression; $r = 0.181$, $df = 957$, $p < 0.0005$).

Diving

Data for 15 complete foraging trips were obtained from seven adult penguins in 1999, all raising chicks (Table 3.3). A total of 3319 dives was performed during these trips, averaging 221 ± 129 dives per trip.

The logger-equipped penguins conducted trips with a mean length of 9.2 ± 6.2 hrs in 1999. Total number of dives was significantly positively related to trip length in 1999 (Spearman $R = 0.82$, $p < 0.001$). Most trips were short, between 3 and 9 hours long (mean 6.9 ± 1.8 hrs), except for two when the penguin remained at sea overnight. These long trips lasted 21.3 and 25.9 hrs. Trip length did not change significantly over the course of the breeding season (all trips, and short trips only; linear regression; both ns). With the exception of one penguin (#7), all penguins conducted only one trip per day, even if the first trip was short and the chicks were old enough to creche without adult attention (Table 3.3).

Penguins began diving an average 17 ± 9 mins after leaving shore. Assuming birds travel at 4.5 ± 0.4 $km.h^{-1}$ (Trivelpiece et al. 1986), this is equivalent to initiation of foraging within 1.3 ± 0.7 km of the shore. Mean maximum depth for all dives was 25.5 ± 17.9 m, and the deepest dive recorded was 114.3 m. In 1997 mean maximum dive depth was 22.5 m (maximum 92m; $n = 2$ birds) for Chinstrap Penguins, 34.7 m (maximum 122 m; $n = 2$ birds) for Macaroni Penguins, and for fur seals approximately 18 m (maximum 102 m; $n = 3$ animals) (Isaksen et al. 1997a). In 1999 Macaroni Penguins also dived deeper (41.1 ± 31.1 m; $n = 9536$ dives) than

Chinstrap Penguins (Chapter 2).

Birds differed significantly from each other in mean maximum dive depth (depths log-transformed; one-way ANOVA, $F = 63.3$, $p < 0.005$). There was no significant relationship between trip length, total number of dives, total number of dives with bottom time, total time underwater, or total bottom time with date, chick mass, or number of krill recovered in the diet sample (Spearman R; all ns). Adult mass and chick mass were also not correlated with mean maximum depth (Spearman R; both ns).

Diving took place at all times of day and night (Fig. 3.2). Most diving was performed during the day and the greater part conducted in the morning, when most birds went to sea (Fig. 3.3). Daytime dives were significantly deeper than those at night (Mann Whitney, $U = 512990$, $p < 0.0001$; Fig. 3.3), but the deepest dives with bottom time were recorded at sunrise and sunset in two consecutive bouts each time, by one penguin (# 4; Table 3.3) (Fig. 3.4). Overall, mean maximum dive depth and depth of dives with bottom time increased markedly with the onset of sunrise, and decreased at sunset (Figs. 3.3 & 3.4). There was a lull in diving activity in the early afternoon, but activity increased in the late afternoon and evening, although not to morning levels (Figs. 3.3 & 3.4). Only three penguins (#s 1,3 & 4) made more than 20 dives at night, and most (89%) were made by the two penguins that made long trips, and thus remained at sea throughout the night.

The proportion of total time spent at different depths decreased evenly, and an exponential model fit the data well ($r = 0.90$; $df = 20$; $p < 0.001$). By comparison, the proportion of bottom (foraging) time spent at depth decreased steeply over the 10–20 m depth range, and flattened out at the 20-35 m depth range (Fig. 3.5), suggesting that this depth range was a focus of foraging activity. Mean trip depth of the bottom phase (22.2 m; Table 3.3) falls within this range. Most bottom time (77.1 %) occurred within the 5-35 m depth range, and hardly any foraging occurred deeper than 60 m (4.1%) (Fig. 3.5).

The mean bout criterion interval was 176 s (2.9 min) but varied greatly from bird to bird and between trips (Table 3.3). A total of 274 bouts was identified, lasting 20.6 ± 45.1 min. Bouts were initiated at all times of the day, except from 23:30 - 02:00, but the majority (64%) commenced in the morning (04:30 - 12:00), mirroring the pattern seen in dive frequency (Fig. 3.3). The bout criterion interval for each foraging trip was strongly positively correlated to date ($r = 0.729$; $df = 13$; $p < 0.0005$).

Discussion

Diet

Breeding Chinstrap Penguins at Bouvetøya are specialist krill consumers. Krill has been recorded as the predominant diet in most other populations (e.g. Croxall & Furse 1980; Lishman 1985; Croxall & Lishman 1987; Trivelpiece et al. 1987; Marchant & Higgins 1990; Williams 1995), with only one study at King George Island being notably different, where large amounts of fish were eaten (Jablonski 1985, but see Volkman et al. 1980). All fish eaten at Bouvetøya were notothenids, a mainly bottom-dwelling group (Fischer & Hureau 1985; DeWitt et al. 1990). Notothenids are present in small numbers in diets of other fish-eating predators at the island: Antarctic Fur Seals (Klages et al. 1999; Kirkman et al. in press), and Macaroni Penguins (Chapter 1). This suggests either that all predators can forage demersally, or that notothenids at Bouvetøya are not solely demersal. The latter appears more likely, given that demersal foraging is not known to occur in penguins (Wilson 1995).

Chinstrap Penguins rarely occur north of the Antarctic Polar Frontal Zone (APFZ) (Marchant & Higgins 1990; Williams 1995), the northerly limit of krill (Everson 1976; Priddle et al. 1988). Bouvetøya is approximately 500 km south of the APFZ, and is the northernmost breeding site for this penguin (Marchant & Higgins 1990; Woehler 1993; Williams 1995). Krill dynamics at Bouvetøya are poorly understood, but the historical presence of Chinstrap Penguins (Olstad 1929; Solyanik 1964; Lunde 1965; Müller et al. 1967; Holdgate et al. 1968; Fevolden & Sømme 1977; Haftorn et al. 1981; Watkins 1981; Bakken 1991; Isaksen et al. 1997a) and previous surveys of penguin diets (Cooper et al. 1984; Bakken 1991) suggest long-term availability of krill resources at the island. In the only zooplankton survey of Bouvetøya waters, Fevolden (1980) recovered no larvae of krill, suggesting that adults were immigrants from another region. If this is the case, oceanographic concentrating mechanisms (Witek et al. 1982; Miller & Hampton 1989a) might be responsible for the Bouvetøya stock, which could be derived from the eastward flowing cyclonic arm of the Weddell Gyre (Gordon 1988) known as the Weddell Drift, where a generally high abundance of post- and late-stage krill larvae has been recorded (Miller & Hampton 1989a).

Length frequency distributions of krill collected from predator diet samples show marked long-term inter-annual variation at South Georgia (Reid et al. 1999; Croxall et al. 1999), and this has been linked to changes in krill availability (Brierley et al. 1997) and, ultimately, predator performance (Croxall et al. 1999). Inter-annual differences in krill size recorded at Bouvetøya in this study, while statistically significant, are small compared to some of the variation recorded at South Georgia (cf. "good" and "bad" years; Croxall et al. 1999). All together, the penguins at Bouvetøya consumed larger krill (mode = 52 mm) in 1997 (few measurable krill from Macaroni Penguins in 1999) than at South Georgia (mode = 44 mm; Reid et al. 1999), suggesting that krill at Bouvetøya might be from an older class (Priddle et al. 1988; Reid et al. 1999), and that the two stocks are not necessarily directly linked.

High within-year variability in krill size has also been linked to low krill abundance at South Georgia, with low years typified by replacement of large krill in early summer with small krill towards the end of summer (Reid et al. 1999). Although no trend existed in 1997, a small increase in size of krill eaten by Chinstrap Penguins was recorded in 1999. This was also recorded for krill eaten by fur seals by Kirkman et al. (in press), who attributed the increase to krill growth during summer. Interpreted in light of the experience of South Georgia, these findings suggest that neither 1997 nor 1999 were poor krill years at Bouvetøya. Other indices of predator performance at the island, including penguin breeding success and chick growth (Isaksen et al. 1997a; Appendix C; unpubl. data), support this conclusion. This is interesting when it is considered that in 1997/98 one of the strongest El Nino–Southern Oscillation (ENSO) events of the century occurred (ENSO Monitor 2000). ENSO anomalies have been implicated in shortages of krill in the western South Atlantic, which tend to lag the anomaly by about one year (Croxall et al. 1988a; Priddle et al. 1988; SC-CAMLR 1998).

Diving behaviour

Loggers are known to disrupt the hydrodynamic effectiveness of penguins (e.g. Wilson et al. 1986; Croxall et al. 1988b; Croll et al. 1991; Kooyman et al. 1992; Bengston et al. 1993; Wilson 1995; Wilson & Peters 1999). Given their remarkably low drag coefficients (Wilson 1995), it is hard to see that the devices used in this study did not affect the foraging of penguins to some extent (cf. Chapter 2). One bird (penguin #3) lost 500 g between device deployment and retrieval; in this case I cannot be sure that the penguin had not fed its chicks before retrieval because it was caught at the nest, and was already partly dry. Other than this case, behaviour at the nest, adult body condition, provisioning of offspring and diving parameters all appeared to be within expected ranges, suggesting that device effects in this study were acceptable. This aspect should not be overlooked however, especially when considering finer patterns of diving behaviour.

Diving in Chinstrap Penguins is reasonably well known from the South Orkney Islands (Lishman & Croxall 1983) and South Shetland Islands (Trivelpiece et al. 1986,1987; Bengston et al. 1993; Wilson 1995; Wilson & Peters 1999). Five main points emerge from this study at Bouvetøya. Firstly, there is considerable inter-individual variation in depth usage. Second, most diving activity including initiation of foraging trips and bouts takes place in the morning. Third, diving occurs at all times of the day, with the shallowest dives at night and the deepest at sunrise and sunset. Fourth, penguins appear to focus foraging effort in the 20–35 m depth zone. Finally, most foraging trips are short (< 9 hrs).

Why inter-individual variation in depth usage should be so great is perplexing. In a comparable study, Bengston et al. (1993) did not detect such variation. Generally the spatial distribution of krill is random (and hence unpredictable) (Miller & Hampton 1989b), and three-dimensionally patchy even at small scales (Zamon et al. 1996). Limited evidence from Bouvetøya suggests krill may also be temporally unpredictable (Fevolden 1980). Thus natural krill dynamics could account for the variation, since my study was performed on relatively few animals, spaced over four weeks. Changing krill dispersion could also account for the increase in bout criterion intervals with date. If krill became less patchy and patch quality decreased, the time between successive dives might be expected to increase owing to penguins searching more for prey, and having to dive deeper once it was encountered. This could lead to a higher bout criterion interval. There is no direct evidence that krill dispersion changes at Bouvetøya, and only limited evidence that abundance changes (see Fevolden 1980), however, therefore this merits further investigation. Wilson et al. (1991) detected similar inter-individual variation in breeding Adélie Penguins *P. adeliae*. Their findings that changes in depth usage were related to chick age do not pertain here, but I cannot discount effects from the small sample size.

Similarly, assessing trip 'success' crudely by relating foraging parameters (trip length, total number of dives with bottom time, total time spent underwater etc.) with number of krill returned to shore is compromised by sample size. The error might also result from assuming that the amount of prey returned to shore relates directly to foraging parameters that summarise information at the scale of the entire foraging trip (Peters 1997a, in press). Penguins appear to modify digestion at sea at will, and have two broad states of gastric activity, the first where food is digested for self early in the trip, and a second 'fasting' state where gastric action is reduced to bring food back for offspring (Peters 1997a,b). This is sometimes evident from diet samples where prey are in one of two sharply separated states of digestion (G. Peters, pers. comm.). Sampling of krill returned to shore therefore relates chiefly to this second state. This is supported by Moreno & Sanz (1996) who calculated that foraging Chinstrap Penguins needed ca. 1670 g of krill per foraging trip to meet their and their brood's energetic needs. This is considerably greater than the largest meal size recorded in my study (538 g).

Foraging penguins are thought to be limited ultimately by light (Wilson et al. 1993; Wilson 1995; Wilson & Peters 1999; but see Croxall et al. 1985; Kooyman et al. 1992; Chapter 2). Sunrise and sunset appear to be important events in foraging of Chinstrap Penguins at Bouvetøya, and could support this contention. If this is so, diurnal patterns in diving activity are probably driven by hunger (leading to initiation of most bouts in the morning), which combined with the short trips produces a midday lull in activity when most birds have returned to shore.

It is a little more difficult to understand patterns in deep dives, and indeed why night diving occurs at all, since Bouvetøya does not have as favourable a summer light regime as more southerly sites (Bengston et al. 1993; Wilson 1995; Wilson & Peters 1999). Wilson (1995) hypothesised that night diving of Chinstrap Penguins at King George Island might be favoured by a visual system better adapted than that of sympatric congenerics to lower light levels, but little is known for certain about the visual capabilities of this species. Similar patterns in depth usage are also exhibited by Macaroni Penguins at Bouvetøya (Chapter 2). The possible interpretations I discuss there are also germane here. However, it should be borne in mind that, without knowledge of the patterns of vertical migration of krill at Bouvetøya (generally variable; reviewed by Miller & Hampton 1989a), it remains difficult to interpret diel changes in dive depth and foraging activity as driven either by prey dispersion or light limitation (see discussion in Bengston et al. 1993). Two factors that would seem to argue that light is not proximately limiting for Chinstrap Penguins, though, are the deeper depths attained by Macaroni Penguins at Bouvetøya at the same time (Chapter 2), and the depths (> 200 m) reached by Emperor *Aptenodytes forsteri* and King *A. patagonicus* Penguins at other sites (Kooyman et al. 1992; Kirkwood & Robertson 1997a,b).

Depth usage by Chinstrap Penguins at Bouvetøya is largely in accord with that of other studies, confirming this penguin's status as a relatively shallow diver. This suggests that krill at Bouvetøya conform to depth distributions noted elsewhere, where they occur mostly in well oxygenated waters above 150 m (reviewed in Miller & Hampton 1989a).

Ecological segregation of predators at Bouvetøya

Most land-based predators at Bouvetøya consume krill. These include penguins (Isaksen et al. 1997a; Appendix C; Chapter 1) and fur seals (Klages et al. 1999; Kirkman et al. in press) which collectively number in the hundreds of thousands (Marchant & Higgins 1990; Kirkman et al. in press; Appendices A & C), and volant seabirds such as Pintado Petrels *Daption capense* (Huyser et al. 1997), Southern Fulmars *Fulmarus glacialoides*, and prions *Pachyptila* spp. (unpubl. data). Fur seals alone consume a minimum estimated 14 365 tons of krill during December–February (Kirkman et al. in press). Evolutionary pressures to lessen competition for this important resource would therefore be expected to be strong, especially where species are foraging in sympatry as do the three divers. What differences, then, exist in the foraging niches of the three air-breathing diving predators at Bouvetøya, and what can this tell us about factors promoting ecological segregation?

Chinstrap Penguins ate larger krill than Macaroni Penguins in 1997, and fur seals in 1999 (51.0 ± 3.0 mm; Kirkman et al. in press). Assuming equivalent methods, differences in size of krill eaten by penguins and fur seals at Bouvetøya in 1999 could reflect small differences in size selectivity, or different depth usage since there is evidence that vertical separation of krill with size can exist if the water is strongly stratified (Loeb & Shulenberger 1987; other evidence reviewed in Miller & Hampton 1989a). Penguins also appear to select for size and sex when feeding on krill (Hill et al. 1996), although potentially different escape responses of particular classes of krill cannot be discounted. Neither selectivity nor different depth usage seem to result in great differences in the size of krill eaten, though; the overlap in size distribution across the three species is broad.

Macaroni Penguins generally dive deeper than both Chinstrap Penguins and fur seals at Bouvetøya (Isaksen et al. 1997a; Chapter 2). This probably enables them to capture the deeper-dwelling myctophid fish that dominate their diet, and may be advantageous during the early stage of chick rearing (Chapters 1 & 2).

Chinstrap Penguins undertook relatively short trips in 1997 (Isaksen et al. 1997a) and 1999. The longer trips of female (1997: 27.9± 12.5 hrs; 1999: 25.7 ± 12.0 hrs) and male (1997: 30.0 ± 6.9 hrs) Macaroni Penguins, and fur seal mothers (1997: 69.6 ± 43.2 hrs) (Isaksen et al. 1997a; Mehlum et al. 1998; Chapter 2) strongly suggests that Chinstrap Penguins feed closest to the island of the three predators. Generally, penguins and fur seals travel greater distances and move further away from the colony during longer trips (Wilson 1995; Boyd 1999; Bonadonna et al. 2000; but see caveats in Wilson 1995). I estimate the mean maximum foraging range of Chinstrap Penguins to have been 15 km in 1997, and 20 km in 1999 (calculated at an average travelling speed of 4.5 $km.h^{-1}$; cf. Trivelpiece et al. 1986). Assuming an average travelling speed of 4.3 $km.h^{-1}$ for Macaroni Penguins (Wilson 1995), and 6.5 $km.h^{-1}$ for fur seals (Boyd 1996), I estimate the mean maximum foraging range of Macaroni Penguins to be ca. 56–65 km, and that of fur seals 230 km. The inferred at-sea overlap between Chinstrap Penguins and Macaroni Penguins therefore appears to be small: the Chinstrap Penguin with the longest mean trip length in 1997 was 0.43 of the duration of the Macaroni Penguin with the shortest mean trip length (Isaksen et al. 1997a). Chinstrap Penguins almost always initiated foraging within 2 km of the island.

Estimated peak fur seal pupping at Bouvetøya is approximately 25 days earlier than peak penguin hatching (Kerley 1983; Doidge et al. 1986; Isaksen et al. 1997a; Appendix C), but lactation probably extends through to mid-March (Doidge et al. 1986), by which time most penguin chicks probably have fledged (see Williams 1995 for details on breeding biology). Both penguin species have similar breeding chronologies (Isaksen et al. 1997a; Appendix C). Peak food demands for all three predators thus largely conincide.

It is striking how Chinstrap Penguins at Bouvetøya return large meals to their brood (often two chicks; Isaksen et al. 1997a; unpubl. data) frequently, when they spend comparatively little time at sea, search a comparatively small volume of water for their prey, and have a comparatively short fledging period (Croxall & Davis 1999). Chinstrap Penguins are considerably faster swimming than other penguins of similar body size (Wilson 1995; Wilson & Peters 1999) which may be related to their dietary specialisation. In Chapter 4 I speculate that they might possess compensating mechanisms, enabling them to dive serially upon prey aggregations for long periods. Support for this is that Chinstrap Penguins have comparable rates of daily energy delivery (ca. 1200 $kJ.day^{-1}.adult^{-1}$), and energy acquisition at sea for the brood (average of ca. 130 $kJ.hr^{-1}$, calculated from Tables 3.2 & 3.3; energy density of krill = 4.6 $kJ.g^{-1}$; Clarke 1984) to populations elsewhere, and other species (see Williams 1995).

This crude analysis of diet, depth and spatial usage, and food demands, indicates that the niches of the three diving predators at Bouvetøya are as follows: Chinstrap Penguin- inshore-feeding, shallow-diving, krill specialist; Macaroni Penguin- offshore-feeding, shallow- and deep-diving, mixed krill and fish generalist; Antarctic fur seal- offshore-feeding, shallow-diving, krill specialist. These predators are clearly ecologically segregated, but it is also true that limited niche overlap also exists between them. Overlapping resource utilisation, inferred parapatric (or limited sympatric) distributions at sea, and partially segregated depth usage, are the strongest circumstantial evidence suggesting that competition might shape predator niches at Bouvetøya. Is this really the case, or are the realised niches of predators at Bouvetøya influenced by other factors?

Factors responsible for ecological segregation

Studies of ecological segregation in sympatric penguins have focused mainly on pygoscelid (Chinstrap, Adélie, and Gentoo *P. papua*) penguins in the true Antarctic (e.g. Volkman et al. 1980; Lishman 1985; Trivelpiece et al. 1986; Wilson 1995), and penguin communities at sub-Antarctic sites (Adams & Brown 1989; Ridoux et al. 1988). Lishman (1985) and Volkman et al. (1980) recorded broad overlap in krill size between Chinstrap Penguins and their congeners. Trivelpiece et al. (1987) found that breeding chronology, depth and spatial use differed among the three sympatric pygoscelids at King George Island, and that this favoured co-existence but was not a product of competition at sea. Adams & Brown (1989) observed similar patterns in ecological segregation at Marion Island, and reached similar conclusions to Trivelpiece et al. (1987).

Also at King George Island, but at a different time and site (Ardley Island), Wilson (1995) observed that spatial and depth usage could not solely account for ecological segregation of the three pygoscelids. Here temporal separation of foraging was important, with Chinstrap Penguins tending to forage more often at night, possibly advantaged by superior vision. Chinstrap Penguins at Ardley Island also foraged inshore (< 25 km; Wilson 1995), like at Bouvetøya and Seal Island (Bengston et al. 1993), but unlike elsewhere at King George Island (Trivelpiece et al.

1987) and Signy Island, South Orkney Islands (Lishman 1985). As discussed above, depth usage was very similar at all sites.

Chinstrap Penguins at Bouvetøya occupy a niche very similar to that occupied elsewhere. Most differences across sites and studies are in trip length (spatial usage), which could be a consequence of variability in krill availability. Unlike elsewhere, though, they are exempt from potential competition with congenerics at Bouvetøya. If competition defined the niches of sympatric penguins at King George Island, one might expect the absence of congeneric competition at Bouvetøya to allow the realised niche of Chinstrap Penguins to expand (even slightly) to something closer to the fundamental niche. This does not seem to occur, and offers indirect evidence for lack of competition at sea, at both King George Island and Bouvetøya. Wiens (1989) provides cogent arguments why evidence from parapatry (or limited sympatry), and niche-overlap patterns, cannot constitute strong evidence for competition. This difficulty is especially acute when information on resource limitation is scarce. A fundamental condition for competition to occur is that resources shared by competitors, in this case chiefly krill, are limiting in the sense that rates of energy acquisition are significantly lessened in the presence of a competitor. There is no evidence that this is the case at Bouvetøya; krill surveys are required to address this fully.

Macaroni Penguins probably outnumber Chinstrap Penguins at Bouvetøya (Haftorn et al. 1981; Bakken 1991), and there is no great difference in body mass between the two (cf. Williams 1995), implying from rules of allometry (Wilson 1995) that both have similar diving abilities. This suggests that persistent asymmetrical competition between the two species, excluding Macaroni Penguins from foraging inshore, does not exist. Rather, the life history, foraging behaviour and generalist diet of Macaroni Penguins may predispose them to favour dispersion and densities of prey that are more frequently encountered offshore, as appears to be the case at Marion Island (Brown 1987; Adams & Brown 1989), South Georgia (Croxall & Prince 1980; Trathan et al. 1998) and Heard Island (Green et al. 1998) (cf. Chapter 2).

Lishman (1985) stated that a species is likely to be adapted to the environment experienced at the centre of its distribution. Trivelpiece et al. (1987) explored this further and suggested the ecological segregation they observed in pygoscelids at King George Island was an outcome of this. This conclusion implies species' responses are largely invariable across their distributions, and is supported by evidence from Bouvetøya. Macaroni Penguins have a catholic diet across their entire distribution (Chapter 1) with dietary specialisation occurring chiefly in the comparatively krill-rich waters of the western South Atlantic. At other sites they also forage offshore, and have similar diel diving patterns although depth usage does appear to vary with diet (Croxall et al. 1988b, 1993; Green et al. 1998; Chapter 2).

In conclusion, while the three main air-breathing divers are ecologically segregated at Bouvetøya, there is little evidence that this is a consequence of competitive interactions at sea. Perhaps a more intriguing question is why Gentoo Penguins, which have been recorded visiting Bouvetøya (Appendix C), and Adélie Penguins, which have previously bred at the island but never in great numbers (Haftorn et al. 1981), do not breed there. On the surface of it, conditions on land (nesting space is not limiting at Nyrøysa) and at sea appear suitable for both of these species at Bouvetøya, but their niches remain vacant (see Synthesis). In general, understanding large-scale variation in population responses will become increasingly important for understanding the limits to species' ranges, and how they might fare under conditions of environmental change.

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Table 3.1 Frequency of occurrence (%) of identified prey species in Chinstrap Penguin *Pygoscelis antarctica* diet samples, Bouvetøya, 1997 (5 January - 19 February) and 1999 (10 January - 19 February). "Other fish" constitutes fish identified to genus level only.

Prey		Year	
		1997 (n = 20)	1999 (n = 18)
Euphausiids		100	100
	Euphausia superba	100	100
	Thysanoessa macrura	5	11
Amphipods		0	11
	Hyperia macrocephala	0	11
Fish		30	0
	Nototheniops larseni	10	0
	Notothenia sp.[1]	20	0
Total prey taxa recovered[2]		4	3

1. All *Notothenia* sp. fish are juveniles, and thought likely to be *N. rossi*.
2. Unidentified fish prey; 1997: 11 individuals (8 larval fish).

Table 3.2 Mean (± SD) number of prey items and krill (*Euphausia superba*) recovered per sample, and mean sample mass (g) and krill mass (g), for diets of Chinstrap Penguins breeding at Bouvetøya, 1997 and 1999.

	1997	1999
Mean number of prey	194.1 ± 93.6	242.8 ± 145.1
Mean number of krill per sample	193.3 ± 93.3	241.8 ± 146.0
Mean mass of krill	221.8 ± 105.0	261.3 ± 172.2
Mean sample mass	222.7 ± 105.6	261.4 ± 172.1

Table 3.3 Characteristics of foraging trips conducted by Chinstrap Penguins at Bouvetøya, 1999.

Penguin	Chicks	Dates	Mass (g)		Trip	Trip length (hrs)	No of dives	No of dives with bottom phase	Mean ± SD depth in bottom phase (m)	Bout length criterion (s)	No of bouts
			Start	End							
1	2	02-03.01.99	4600	4600	1	21.3	508	232	19.8 ± 16.7	143	40
2	1	11.01.99	4150	5300	1	7.80	147	102	17.3 ± 7.8	83	18
		12.01.99			2	4.95	143	88	18.8 ± 7.4	94	7
		13.01.99			3	5.37	126	91	27.7 ± 9.2	180	7
3	2	15.01.99	4400	3900	1	8.03	221	128	20.8 ± 12.0	87	29
		16.01.99			2	6.22	159	86	6.7 ± 1.9	151	28
		17.01.99			3	9.07	193	121	34.8 ± 15.0	208	20
4	1	20-21.01.99	4800	5750	1	25.93	547	457	35.3 ± 21.2	111	46
5	1	24.01.99	5400	-	1	5.92	184	132	11.6 ± 5.5	129	15
		25.01.99			2	8.53	148	121	30.4 ± 14.6	242	8
6	1	27.01.99	4475	4900	1	7.37	184	122	25.2 ± 11.8	110	29
		28.01.99			2	6.32	172	118	24.6 ± 15.1	253	5
		29.01.99			3	9.03	227	168	27.1 ± 11.0	305	8
7	2	31.01.99	-	5150	1	8.16	235	156	23.6 ± 15.6	224	11
		31.01.99			2	3.28	125	94	8.6 ± 3.2	315	3

Figure legends

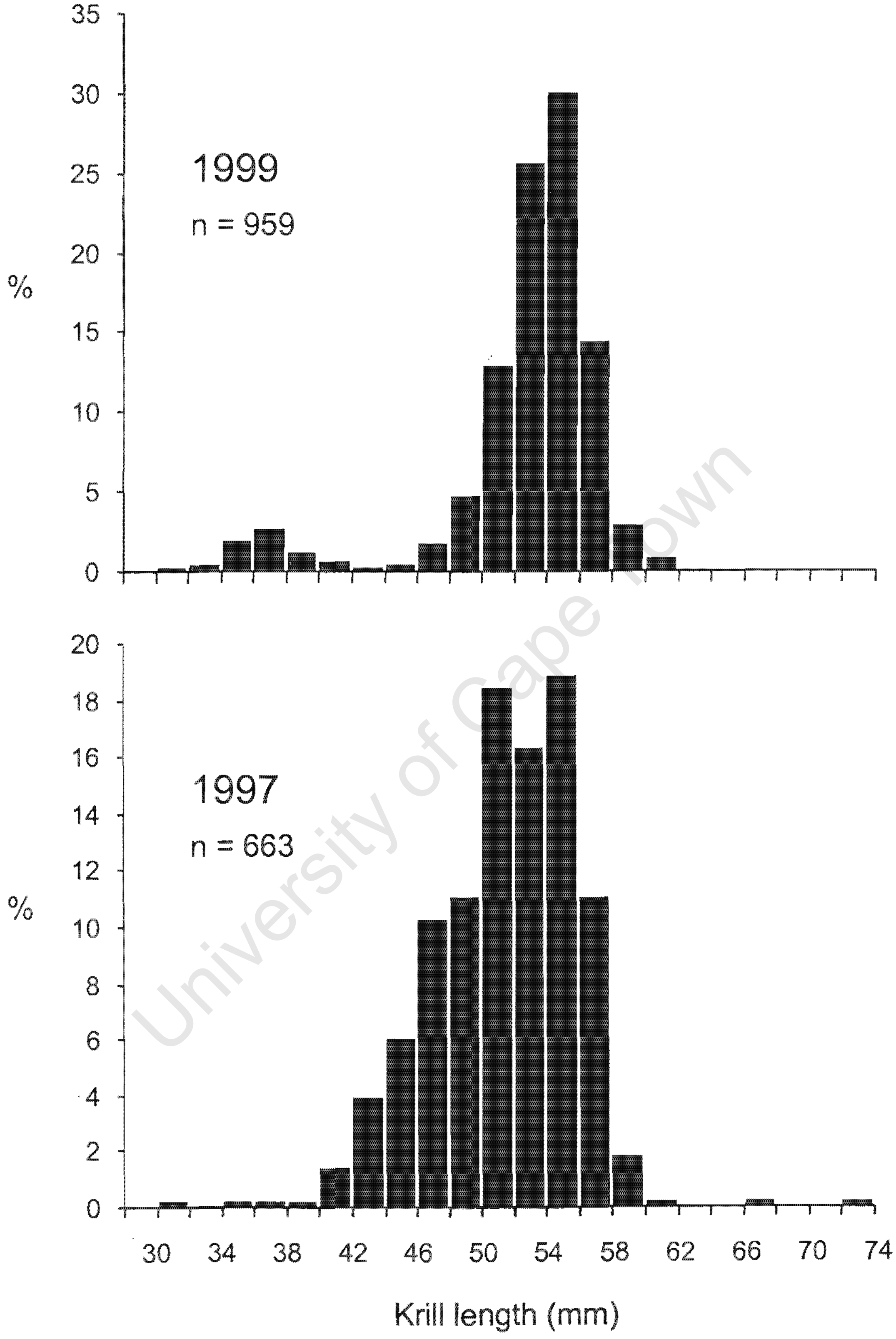
Fig. 1. Length frequencies of Antarctic krill recovered from diet samples of Chinstrap Penguins breeding at Bouvetøya, 1997 and 1999.

Fig. 2. Example of a time-compressed dive record from a Chinstrap Penguin, Bouvetøya 1999, conducting a long trip. Diving is organised into distinct bouts, and is conducted day and night. Sunset on January 20 1999, and sunrise on January 21 are indicated with arrows.

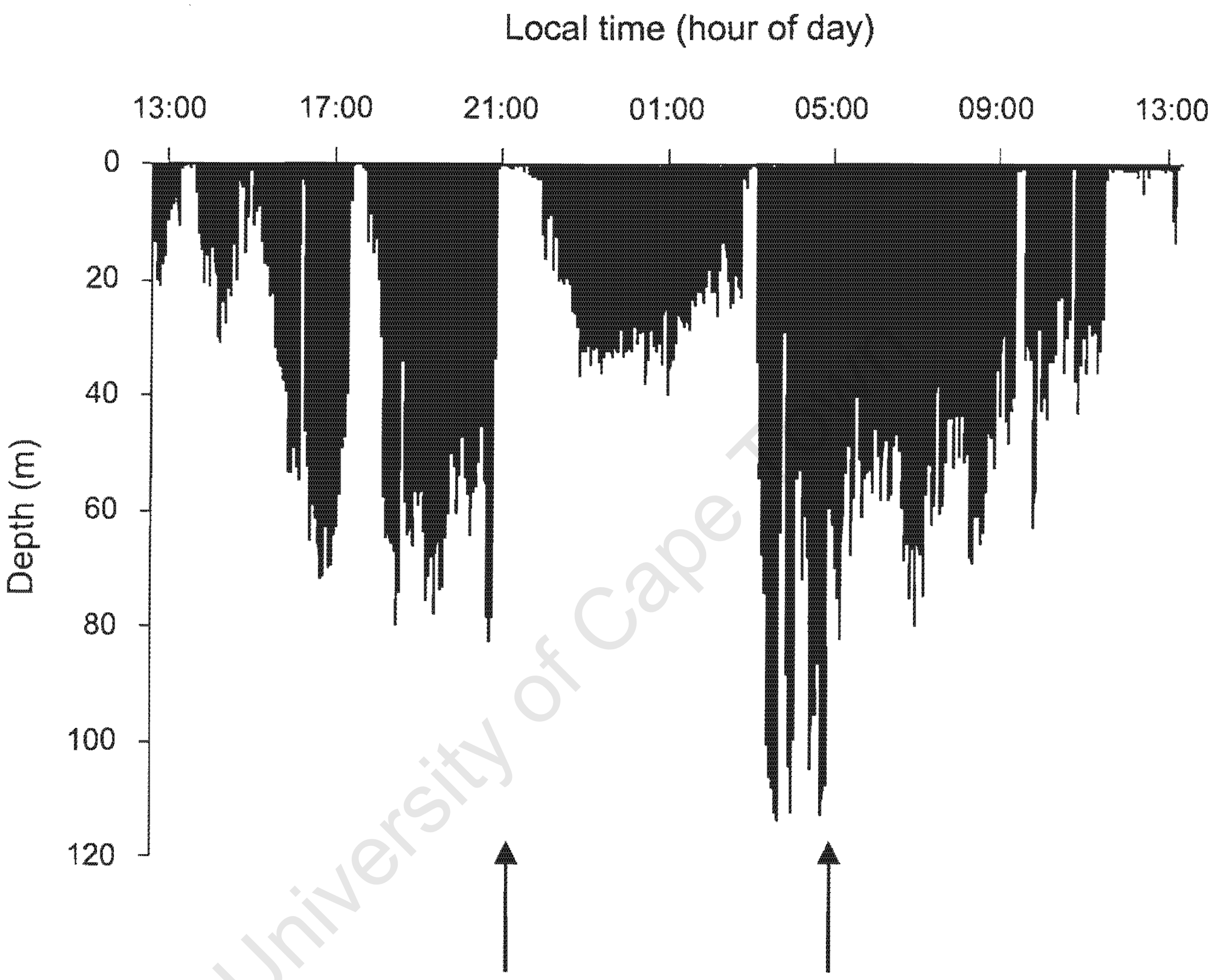
Fig. 3. Mean (± SD) maximum dive depth, number of dives and frequency of foraging trips initiated per hour local time (GMT +1) for Chinstrap Penguins, Bouvetøya 1999. The shaded portion represents nighttime (sunset-sunrise). The solid line shows maximum dive depth recorded (all dive records) for that hour.

Fig. 4. Mean depth of bottom time for all dives with bottom time made by Chinstrap Penguins, Bouvetøya 1999. Circles indicate dives conducted at night (initiated before sunrise, or after sunset), and crosses dives made during the day. The deep dives at sunrise and sunset were made by the same penguin (# 4).

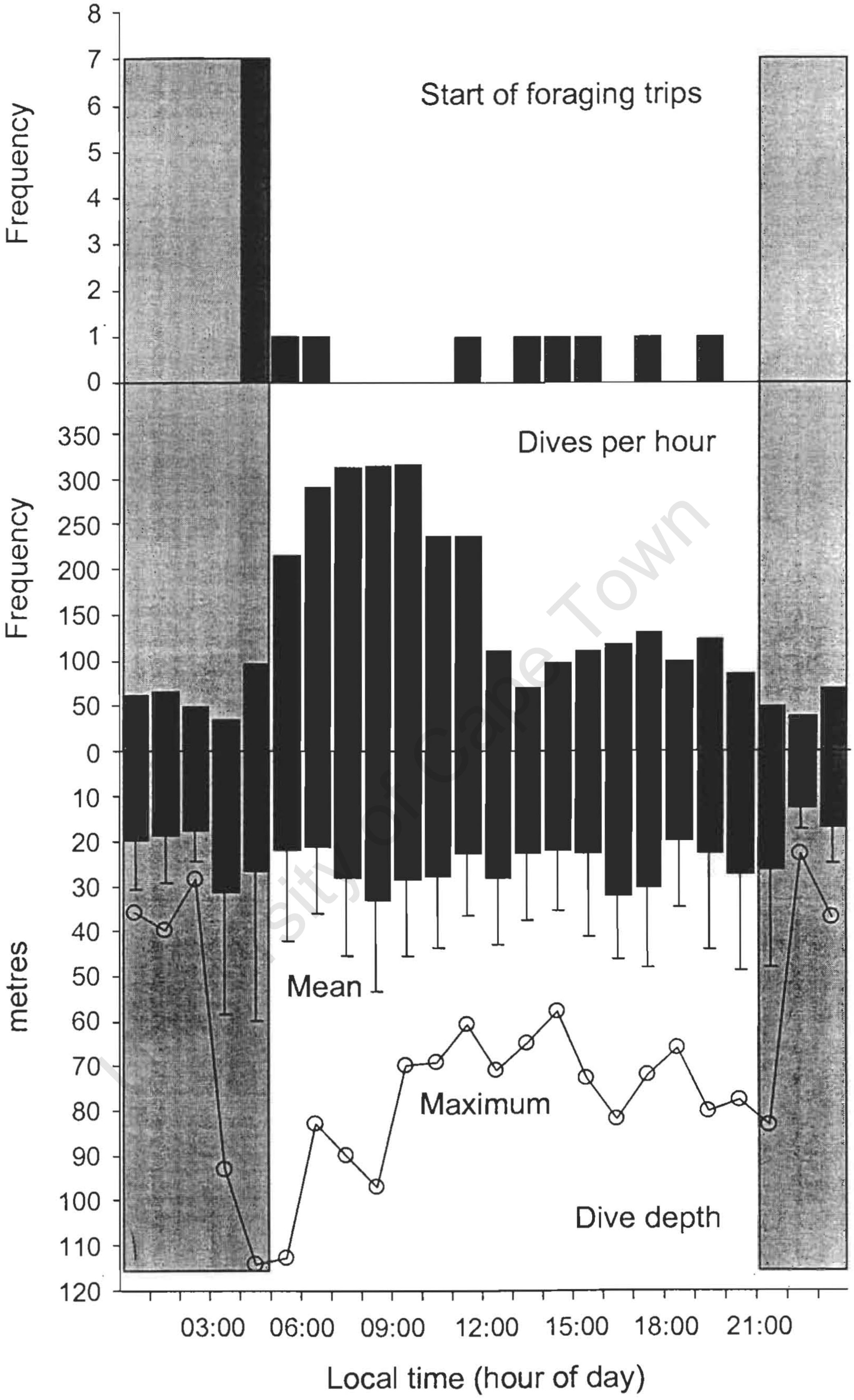
Fig. 5. Mean (± SE) proportion of total time (circles) and bottom (i.e. foraging) time (squares) spent at decreasing depth by Chinstrap Penguins, Bouvetøya 1999. Note that the first depth class (0-5 m) is omitted for scaling purposes and to make distinction between subsequent classes clearer: no bottom time occurs in this class, but the majority (63.1%) of transit time does.



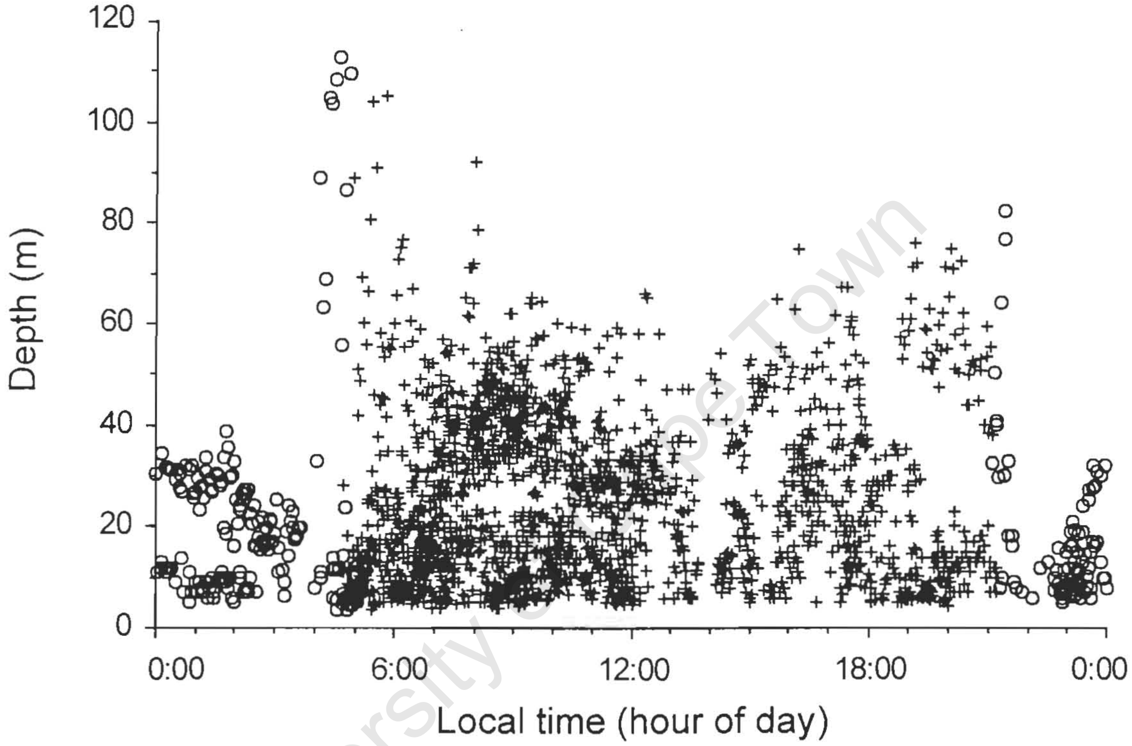
Chapter 3: Figure 1. Length frequencies of Antarctic krill recovered from diet samples of Chinstrap Penguins breeding at Bouvetøya, 1997 and 1999.



Chapter 3: Figure 2. Example of a time-compressed dive record from a Chinstrap Penguin, Bouvetøya 1999, conducting a long trip. Diving is organized into distinct bouts, and is conducted day and night. Sunset on January 20 1999 and sunrise on January 21 are indicated with arrows.



Chapter 3: Figure 3. Mean (± SD) maximum dive depth, number of dives and frequency of foraging trips initiated per hour local time (GMT +1) for Chinstrap Penguins, Bouvetøya 1999. The shaded portion represents nighttime (sunset-sunrise). The solid line shows maximum dive depth recorded (all dive records) for that hour.



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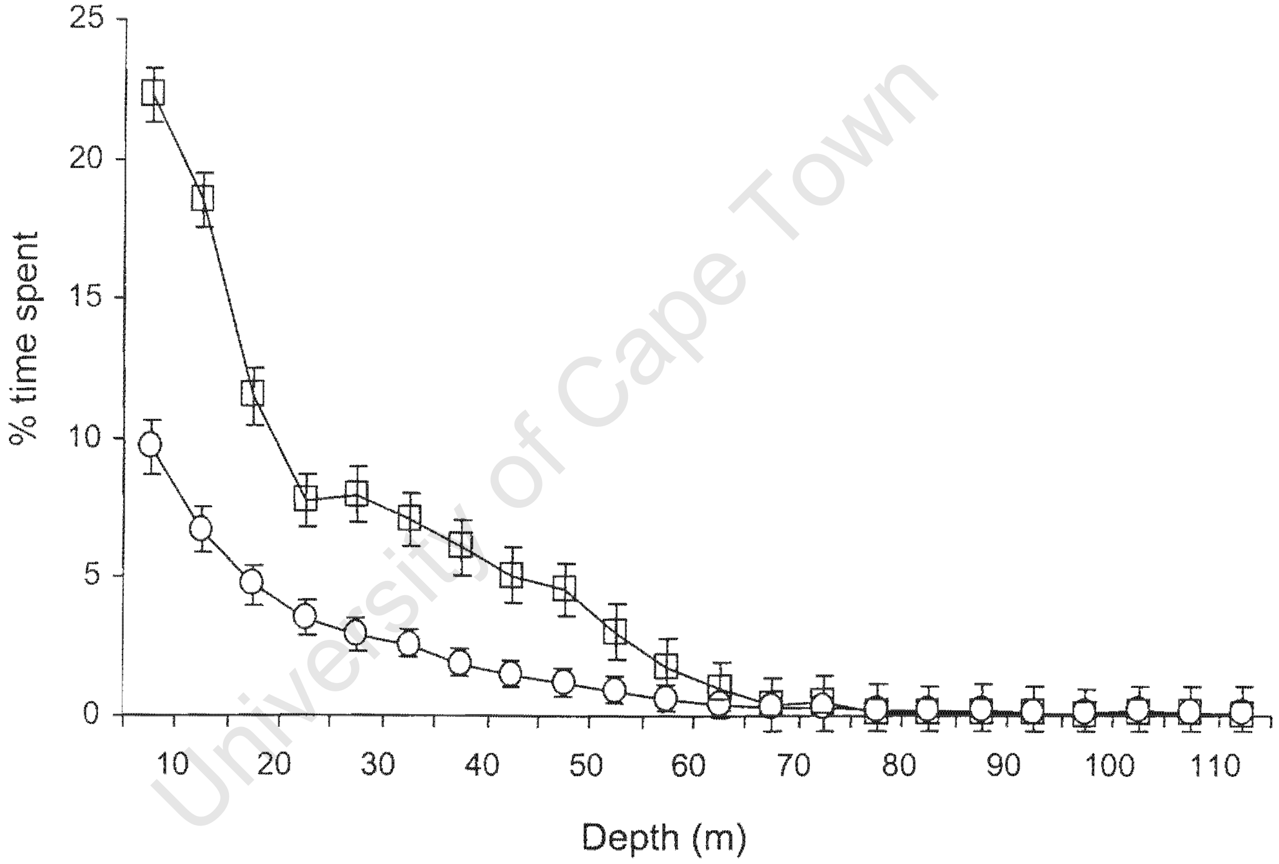

Chapter 3: Figure 5. Mean (± SE) proportion of total time (circles) and bottom (i.e. foraging) time (squares) spent at decreasing depth by Chinstrap Penguins, Bouvetøya 1999. Note that the first depth class (0-5 m) is omitted for scaling purposes and to make distinction between subsequent classes clearer: no bottom time occurs in this class, but the majority (63.1%) of transit time does.

Chapter 4

Dive bouts and foraging behaviour of the Chinstrap Penguin *Pygoscelis antarctica*

Abstract

The dive bouts of air-breathing predators can be terminated because of factors related to either the prey or the predator, and can thus, together with the temporal arrangement during the foraging trip, potentially yield information on predator - prey relationships and prey dispersion. I studied the organization of dive bouts in seven breeding Chinstrap Penguins *Pygoscelis antarctica*, an important predator in the southern Ocean. A total of 3319 dives was recorded from 15 foraging trips, with 13.4% of all dives exceeding the Theoretical Aerobic Dive Limit (TADL). A total of 269 bouts was recognised; these bouts were assigned to one of four types with a clustering procedure: *Unsuccessful* (n = 57), *Deep* (n = 102), *Slow* (n = 17), and *Shallow* (n = 93). Bout types were distinguished by differences in length, period since the last dive, bottom time, descending vertical velocity, and mean maximum depth. *Unsuccessful* bouts were short and with little bottom time, and probably constituted unsuccessful searching behaviour. *Deep* bouts were longer and deeper, with proportionally high amount of bottom time which was negatively correlated to total number of dives in bout. This suggests that bouts were terminated proximately by penguin satiation, and ultimately by prey patch quality. *Shallow* bouts were short and shallow, with proportionally little bottom time which was positively correlated to the total number of dives in the bout. This suggests that declining prey capture rates (resource depression), probably resulting from prey (Antarctic krill *Euphausia superba*) escape behaviour, terminated the bouts. Physiological limitation of diving did not appear to exist, which is inconsistent with the high number of dives that exceeded the TADL. This suggests that Chinstrap Penguins may have compensating mechanisms that allow them to maximise the amount of serial time underwater over long intervals. Finally, inter-bout intervals indicate that penguins searched for prey at an average spacing of approximately 320 m, but encountered prey at an average spacing of approximately 400 m. This accords well with the results of other studies, and is important since it allows us to use penguins as environmental monitors to gauge the dispersion and patch quality of a variable prey resource.

Introduction

Central-place foragers must optimise the time they spend travelling between patches of food, and the time spent within that patch when other potentially more profitable patches might be exploited (reviewed in Stephens & Krebs 1986). Land-based air-breathing divers such as penguins are central-place foragers in two senses: they must leave the shore to find often patchily distributed food and, once this has been located, must dive to capture it. Since they are physiologically prevented from spending unlimited time underwater (Kooyman 1989; Williams 1995), they will dive serially upon a prey patch when it is encountered. These sequences of dives are known as dive bouts. It is widely recognised that penguins and many other air-breathing marine predators (e.g. fur seals; Boyd 1996) concentrate most of their foraging effort into bouts (reviewed by Wilson 1995).

Most work on penguin foraging behaviour has focused on one of two scales: that of the foraging trip (patterns in spatial and depth usage, and temporal activity) (e.g. Wilson et al. 1994; Bost et al. 1997; Kirkwood & Robertson 1997; Clarke et al. 1998; Wilson et al. 1998, Wilson & Peters 1999) and theoretical and empirical investigations of the dive cycle (e.g. Houston & Carbone 1992; Chappell et al. 1993; Wilson et al. 1996; Mori 1999; Wilson & Peters 1999). Relatively little attention has been directed towards a third, intermediate, scale of behaviour, which is the dive bout (cf. Naito et al. 1990; Williams et al. 1992; Mori 1997). Bouts are thought to terminate when prey disperse or are consumed to the point when capture rate becomes unprofitable, or when physical (light, depth) or physiological limits set it. Bouts are therefore an important behaviour which can contribute to our understanding of the relationships between predators and prey abundance and dispersion (e.g. Le Maho et al. 1993; Boyd et al. 1994; Boyd 1996, 1997a), and predator foraging behaviour which is, at least theoretically, optimal (e.g. Mori 1998).

In the only detailed study of dive bouts in a penguin, Mori (1997) showed that in the Chinstrap Penguin *Pygoscelis antarctica* two bout types existed, which were terminated depending on whether prey were encountered (searching dives), or when foraging efficiency decreased to a threshold of diminishing returns. Mori's study was conducted on two birds that varied considerably, with no rigorous definition of bout types, and disregarded prey capture events within dives. Wilson & Peters (1999) observed that Chinstrap Penguins dive continuously while at sea, with no inter-bout periods, which contrasts with Mori (1997). These results prompt a re-evaluation of dive bouts in the Chinstrap Penguin, an important predator of Antarctic krill (*Euphausia superba*, hereafter krill) in the Southern Ocean numbering an estimated 7.5 million breeding pairs, or ca. 26% of the total penguin numbers in the region (Woehler 1993).

In this study I consider which of four hypothesised factors limit the termination of dive bouts in Chinstrap Penguins: prey presence or absence, prey abundance and density, penguin satiation, or physiological limitation. I also show that temporal patterns in penguin foraging activity yields information on prey dispersion.

Methods

Logger recording devices (DK 602 series; Driesen and Kern GmBH, Bad Bramstedt, Germany) were deployed from 2–31 January 1999 at Nyrøysa, Bouvetøya. Details on the biota, climate and penguin breeding schedules at the study site are provided in the Introduction, Isaksen et al. (1997a,b) and Appendices B & C.

Breeding Chinstrap Penguins were captured by hand at the nest and restrained (Wilson 1997), and the logger attached to the lower back above the tail following suggestions in Bannasch et al. (1994) using layered Tesa ™ adhesive tape. Equipping birds seldom took longer than five minutes. The loggers recorded temperature (± 0.2°C) and pressure (± 0.01 m) with 16-bit resolution, and were set at 2- and 5-second recording intervals which is sufficiently frequent to avoid errors in interpreting the dive record identified by Boyd (1993) and Wilson et al. (1995). Upon return to shore, birds were recaptured, the logger retrieved and the data downloaded to a portable computer.

Sunrise and sunset were calculated by using a US National Oceanic and Atmospheric Administration (NOAA) Surface Radiation Research Branch sunset - sunrise calculator, available at http://www.srrb.noaa.gov/highlights/sunrise/gen.html. During the study sunrise occurred between 04:26 and 05:13 (mean 04:47) and sunset between 20:50 and 21:19 (mean

21:08). Times are given as local times (GMT +1).

Dive records were analysed with MultiTrace software (Jensen Software Systems, Laboe, Germany). Descents to less than 5m were omitted (e.g. Bengston et al. 1993), because it is difficult to separate shallow foraging dives from commuting. Inspection of the dive record shows periods in the dive where the otherwise smooth ascent and descent of the bird was interrupted, usually for a sustained period. These irregularities were interpreted as prey capture events (e.g. Bengston et al. 1993; Chappell et al. 1993; Wilson 1995; Wilson & Peters 1999), and termed bottom time since they mostly occurred at the deepest phase of the dive (Fig. 4.1A). I assume that the length of bottom time in the dive is proportional to the success (total prey captured) of the dive; this has not been validated but is logical. MultiTrace recorded dive start time, maximum depth, mean depth of bottom time, total duration, descending time and vertical velocity, bottom time and vertical velocity, mean ascending time and vertical velocity, and preceding surface interval.

The Theoretical Aerobic Dive Limit (TADL; Boyd & Croxall 1996) of a Chinstrap Penguin was calculated as follows. The basal metabolic rate (BMR) of Chinstrap Penguins is an estimated 1152 $kJ.day^{-1}$ (Ellis 1984) and, assuming a mass of 4.7 kg (mean mass of chick-rearing Chinstrap Penguins at Bouvetøya; n = 24; unpubl. data) and a field metabolic rate (FMR) of 3762 $kJ.d^{-1}$ (Nagy et al. 1999). Total body oxygen stores were taken to be 46 $mlO_2.kg^{-1}$ (Kooyman 1989), converted to kJ using a factor of 20.1 $kJ.l^{-1}O_2$ (Schmidt-Nielsen 1983), and the Theoretical Aerobic Dive Limit (TADL) was therefore calculated as 100 s (1.67 min).

Foraging trip durations were interpreted by simultaneous inspection of pressure (depth) and temperature records: entering and exiting the water was usually accompanied by a marked (> 4°C) change in temperature. Bouts were identified for each foraging trip by calculating the bout criterion interval (Martin & Bateson 1986). This interval was calculated from breakpoint regressions (Statistica 5.5; StatSoft, Inc. 1999) fitted to log-frequency plots of inter-dive durations, enabling the λ_{fast} and λ_{slow} parameters of a two-process Poisson model (Slater & Lester 1982; Sibly et al. 1990) to be estimated using equation 4 from Slater & Lester (1982). Separate bout criterion intervals were calculated for each foraging trip; these were then used to identify bouts with MultiTrace. The programme searched for the first dive, and if the following dive fell within the bout criterion interval it was assigned to the same bout. This continued until two consecutive dives were separated by an interval greater than the bout criterion. When this happened a new bout began. Once the bout start and end times had been identified, the dives (previously analysed) were placed within the correct bout which was uniquely numbered.

Bouts were categorised into types using a k-means cluster analysis procedure (Statistica 5.5). This involves selecting the number of clusters you wish produced, with the clustering procedure performing a one-way ANOVA-like analysis where error and group variances are quoted for each discriminatory variable. The bout means of the following variables were selected to discriminate bout types in the cluster analysis: start time, length, number of dives, period since last dive, dive duration, bottom time, descending vertical velocity, and maximum depth.

Two clusters appeared to explain the greatest amount of variation per cluster (Fig. 4.2), and inspection showed that they were distinguished chiefly by length and amount of bottom time. This suggested that they constituted unsuccessful and successful foraging. Since the purpose of the study was also to understand what limited successful foraging, I selected four clusters (Fig. 4.2) as bout types, and conducted further analyses on these. All summary statistics are quoted as mean ± standard deviation (SD).

Results

Dives

Data for 15 complete foraging trips were obtained from seven adult penguins, all raising chicks. A total of 3319 dives was performed during these trips, averaging 221 ± 129 dives per trip. Mean maximum depth for all dives was 25.5 ± 17.9 m, and the deepest dive recorded was 114.3 m. Depth usage, and timing of dives and bouts receives fuller treatment elsewhere (Chapter 3). Stomach samples from other breeding penguins during the study indicated that the diet consisted almost wholly of krill (Chapter 3).

Mean dive duration was 70.1 ± 26.0 s, with the longest dive lasting 164 s (2.73 min). Distribution of dive length frequencies was unimodal (Fig. 4.3), but significantly positively skewed (Shapiro-Wilkes $W = 0.98$, $p < 0.0001$) (Zar 1996) as would be expected where relatively more shallow dives are performed (Chapter 3). The TADL was calculated as 100 s (1.67 min), thus 446 dives (13.4%) exceeded the TADL.

The following dive parameters were all significantly related to mean maximum dive depth (all $df = 144$; all $p < 0.001$): dive duration ($\text{duration} = 30.98 \times \ln(\text{depth}) - 25.02$; $r = 0.88$), total dive cycle time ($\text{dive cycle time} = 1.73 \times \text{depth} + 62.77$; $r = 0.81$), bottom time ($\text{bottom time} = 6.33 \times \ln(\text{depth}) - 2.07$; $r = 0.46$), and descending vertical velocity ($\text{descending vv} = 0.016 \times \text{depth} + 0.52$; $r = 0.78$) (Fig. 4.4). Correlation between depth and other parts of the dive cycle is a general pattern exhibited by penguins (reviewed in Wilson 1995). Significantly, the rate of increase in bottom time decreased with increasing depth (Fig. 4.4C). Total dive cycle time increased with increasing dive duration, as duration and the preceding surface interval were significantly correlated ($\text{preceding surface interval} = 0.17 \times \text{dive duration} + 25.57$; $r = 0.21$; $df = 146$; $p < 0.01$) (Fig. 4.5). Dive angle is correlated with dive depth (Wilson 1995) which suggests that penguins start a dive with a pre-determined depth in mind (Wilson & Peters 1999). This means that the preceding surface interval (and not the post-dive recovery period) is the relevant parameter with respect to the preparation required by the penguin before starting an anticipated dive.

Dive bouts

A total of 269 bouts was identified, representing a mean 17.9 ± 13.6 bouts per foraging trip. Trip length and the number of bouts performed were significantly correlated ($r = 0.78$; $p < 0.0005$).

The four main bout types recognised were discriminated by bout length, period since last dive, bottom time, descending vertical velocity, and depth (Table 4.1). Start time did not differ between bout types (Table 4.1). Bout length was a covariate of number of dives, and dive duration a covariate of depth (Fig. 4.4A).

Most bouts belonged to one of two types (II and IV), and Type III bouts occurred infrequently. Bouts of Type I were typically short, usually consisting of only a single shallow dive (median, modal number of dives = 1) which had little bottom time, and intermediate descending vertical velocity and depth (Fig. 4.1B; Table 4.1). These bouts correspond to the single dives of Mori (1997) who suggested they constitute unsuccessful searching behaviour. This bout type was therefore named *Unsuccessful*. Bouts of Type III were distinguished on the basis of the length of the period since the last dive. They had bottom time and were of intermediate length, suggesting foraging behaviour occurred. The typical period for these bouts was nearly 10x than for other bout types (Table 4.1), and this type was therefore named *Slow*.

Bouts of Type II were deep, long (mean 20.6 ± 36.7 dives) and had a high proportion of underwater time in the bottom phase (Fig. 4.6; Table 4.1). This bout type was named *Deep*. The fourth bout type was shallow, of intermediate length (mean 8.3 ± 12.2 dives) and bottom time, and with a relatively high rate of descending vertical velocity (akin to dives of ca. 20 m; unpubl. data) (Table 4.1). It was named *Shallow* in contrast to *Deep* bouts. These bouts are the main foraging bouts, and are discussed further.

The time budgets of birds in *Deep* and *Shallow* bouts differed quite markedly. The mean total amount of bottom time accumulated in *Deep* bouts was greater (630 ± 810 s) than in *Shallow* bouts (110 ± 143 s). In *Deep* bouts birds spent a higher proportion of time underwater (67.8 ± 8.8 %) than in *Shallow* bouts (60.5 ± 12.9 %), and also proportionally more time in the bottom phase of the dive (*Deep* 21.7 ± 6.5 %; *Shallow* 11.3 ± 5.4 %) (Mann-Whitney U; all $p < 0.001$).

The proportion of bottom time in underwater time was negatively correlated to total number of dives in the bout for *Deep* bouts ($r = 0.31$; df = 71; $p < 0.01$), and was weakly positively correlated to total number of dives in bout for *Shallow* bouts ($r = 0.22$; df = 65; $p = 0.08$). Dive cycle duration, mean maximum dive depth, and the proportion of time spent underwater did not correlate to number of dives in bout for either bout type (linear regression; both ns). The total energetic cost per dive cycle (calculations as in Mori 1997, swimming metabolic rate = 13 W.kg^{-1}; Culik & Wilson 1991; Culik et al. 1991) was also not related to the number of dives in the bout in either bout type (linear regression; ns).

Deep and *Shallow* bouts did not differ in their frequencies of occurrence at day or night (χ^2; ns) or relative position in the foraging trip (Kolmogorov-Smirnov two-sample test; ns) (Fig. 4.7). Penguins differed significantly from each other in the frequency of occurrence of each bout type (Table 4.2). Most of these differences came from penguins three and four, and bout types *Deep* and *Shallow*.

The distribution of inter-bout durations (Fig. 4.8) was strongly positively skewed. Median and average inter-bout durations were 4.23 mins and 7.70 ± 11.68 mins (all bouts; Fig. 4.8A). Very long inter-bout durations are more likely to be resting phases at sea rather than unsuccessful travelling and prospecting. Assuming a constant and directional (cf. Wilson 1995) travelling speed of 4.5 km.h^{-1} (Trivelpiece et al. 1986), the median inter-bout duration indicates penguins spaced their searching at an approximate average interval of 320 m. When *Unsuccessful* bouts are excluded, the median (5.20 mins) and mean (9.60 ± 13.23 mins) inter-bout duration is significantly longer (Fig. 4.8B; Mann Whitney U = 23393; $p = 0.03$). This indicates that prey patches were only encountered by penguins at an approximate average spacing of 400 m.

Discussion

This study of dive bouts in Chinstrap Penguins shows that they have different types of foraging behaviour. Bouts are distinguished by length, bottom time, depth and the length of the period since the last dive.

A similar clustering procedure (but different bout definition procedure) was used by Boyd et al. (1994) for Antarctic fur seals *Arctocephalus gazella*. Four bout types were also recognised for this krill-consuming predator at South Georgia. The main findings were that the frequency of bouts differed among individuals, varied between night and day (fur-seals dive extensively at night; Croxall et al. 1985) and between years of high and low krill abundance. Two of these results are relevant to this study.

Inter-individual variation occurred in bout type frequency of Chinstrap Penguins and, like fur seals (Boyd et al. 1994), this was mostly the case for *Deep* and *Shallow* bouts. Many factors could be responsible for this: inter-sexual differences (e.g. Clarke et al. 1998), differing vertical distributions of prey, differing foraging areas, or differing individual specialisation. Judging by the mass gains of chicks when their parents returned to shore, all penguins in this study returned with food so it appears that this variation does not affect foraging in a large way. Chinstrap Penguins should serve as good models for investigating this further because they are dietary specialists, conduct short foraging trips, and their general biology and that of their prey is well understood. This simplifies interpretation of their behaviour at sea.

Chinstrap Penguins at Bouvetøya dive throughout the day and night, but most diving is conducted between dawn and noon (Chapter 3). Bout types did not vary in either their start time or diel occurrence, suggesting that they are not a direct response to the diel vertical migration habits of krill (e.g. Croxall et al. 1985; Miller & Hampton 1989) but rather an outcome of a searching predator encountering prey which is patchily distributed (e.g. Zamon et al. 1996) and varies temporally in vertical and horizontal distribution.

Shortcomings of the study

Categorising bouts aids analysis and is therefore appealing. However, a shortcoming of this is that it is more likely that a continuum of behaviour exists (e.g. Boyd et al. 1994). More divisions (clusters) will capture more of this natural variability, but ultimately fail to help us understand the causes of behavioural variation. There is also no independent means of verifying the classification outcome produced here, and the biological validity of the results should thus be carefully considered. Nevertheless, this study shows differences between bout types which reflect different behavioural patters, and thus carry genuine biological meaning.

Logger recorders are known to disrupt hydrodynamic effectiveness, and so increase the costs of transport (e.g. Wilson et al. 1986; effects reviewed by Wilson 1995). Given the remarkably low drag coefficients of penguins (Wilson 1995), it is hard to see that the devices used in this study did not affect diving to some extent. The recorders I used were tapered anteriorly, vertically compressed, and attached in such a way to minimise drag (Bannasch et al. 1994). Behaviour at the nest (no desertions in 17 deployments at Bouvetøya), adult body condition, diet masses, trip lengths and diving behaviour (unpubl. data) all fell within expected ranges, suggesting that device effects in this study were reasonably small.

Why are bouts terminated?

A number of factors, not necessarily exclusive, might cause birds to halt diving and thus terminate a bout: prey presence, prey abundance and density, penguin satiation or physiological limitation (e.g. Mori 1997). This study suggests that foraging by Chinstrap Penguins was influenced by at least three of these (prey presence or absence, satiation, and prey abundance and/or density), although it should be borne in mind that interpretation is hindered by the generally variable aggregating behaviour of krill (reviewed by Miller & Hampton 1989), and the lack of zooplankton surveys at Bouvetøya.

Unsuccessful bouts were short (mostly only a single dive) and had little bottom time, suggesting a pattern of unsuccessful searching. Penguins would then move to another area and resume prospecting. Penguins dive in such a way to maximise their vertical and horizontal acuity in the water column (Wilson et al. 1996), and Chinstrap Penguins have been observed swimming slowly with their heads underwater and looking downward (Zamon et al. 1996), presumably prospecting for krill which can occur close to the surface (Miller & Hampton 1989; Zamon et al. 1996). Thus travelling, combined with prospecting dives, enables a bird to gauge the potential returns of a large volume of water.

Provided prey dispersion does not vary, shallow prey should be energetically less costly to capture than deeper prey. This is because transit times increase with dive depth, resulting in less bottom time being available as a proportion of total dive and dive cycle time. This occurred in Chinstrap Penguins (Figs. 4.4C & 4.5), thus penguins should also be expected to prospect at the intermediate (or shallow) depths of most *Unsuccessful* bouts (Table 4.1; Fig. 4.7). Most, if not all, bouts should start with *Unsuccessful* dives, since birds are expected to be unsure of finding prey in the first dive at any area. Having located prey, this *Unsuccessful* bout then continues as a successful one (i.e. *Deep*, *Slow* or *Shallow*).

Deep bouts were typically deep and long, and with a relatively high proportion of time (compared to other foraging bouts) in the bottom phase. The number of dives in the bout did not appear to be limited by the proportion of time spent underwater or the energetic costs of the dive cycle. Thus physiological limitation (from accumulation of lactic acid, a byproduct of anaerobic metabolism; Kooyman 1989) did not appear to constrain further diving. Rather, there was evidence that satiation limited diving proximately, since the amount of bottom time was negatively related to the number of dives (suggesting that if birds were more successful and caught more prey i.e. had a greater amount of bottom time, diving would be terminated sooner). This is an expected outcome where poor patch quality (i.e. low krill density) will cause birds to forage longer before satiation is achieved, and *vice versa*. This suggests that penguins might have been diving on krill in deeper, scattered aggregations or layers (Miller & Hampton 1989) which are usually less dense (ca. 10^1 $g.m^{-3}$) than swarms.

Zamon et al. (1996) used acoustic methods to visualise krill abundance in a survey grid and observed Chinstrap Penguins simultaneously. They recorded the highest correlation between krill aggregations and penguin numbers at 30–40 m depths, although krill occurred at all depths. Krill were most abundant, but also most patchy in the 10–20 m layer, suggesting that penguins dived past shallower prey to target more homogeneously distributed prey offering higher encounter probabilities per unit volume searched. This accords with this study, and suggests that *Deep* bouts may offer the greatest net energetic returns for feeding penguins than other bout types.

Shallow bouts were typically shallow, short, with high rates of descending vertical velocity, little total time under water, and a relatively low proportion of time spent in the bottom phase. Again, the proportion of time spent underwater was not related to the number of dives in the bout, suggesting together with the short bout length that diving was not terminated for physiological reasons.

The proportion of time spent in the bottom phase of *Shallow* bouts was positively correlated to the number of dives. This is predicted to occur when foraging is limited by prey abundance or density. This suggests that penguins encountered small aggregations (probably swarms) of shallow krill, and dived serially with relatively steep dive angles (and hence high rates of descending vertical velocity) until the prey either (1) dispersed or moved off, or (2) was consumed. This second option seems unlikely given the generally high concentrations of swarms (10^2 g.m^{-3}) in which most krill occur (Miller & Hampton 1989). Swarming krill exhibit many behavioural reactions to predatory threats including moving off (swimming at ca. 0.2 m.s^{-1}), flash-expanding, splitting and dispersing (O'Brien 1987; reviewed in Miller & Hampton 1989). Thus it appears that declining prey capture rates (i.e. resource depression; Krebs & Davies 1993) resulting from krill behavioural responses to the presence of the penguin caused termination of *Shallow* bouts. This is consistent with Mori (1997), who suggested decreasing capture rates limited dive bout lengths in Chinstrap Penguins, and also with Wilson et al. (1993) who suggest that prey diel migration and dispersion patterns are a response to pressure from predators. It does not seem likely that the *Shallow* bouts identified by Boyd et al. (1994) for fur seals, which were also short but occurred seldom and took place mainly at night, fulfil the same function in Chinstrap Penguins.

Slow bouts do not differ much from *Shallow* bouts, except in the period since the last dive. These bouts occurred at all times during the foraging trip (Fig. 4.7), and were not particularly associated with fewer birds (Table 4.2). This indicates that they might have been the first bout after a long resting or travelling phase at sea. These phases are well know from penguins (e.g. Wilson 1995), and if they are a consequence of resting after previous feeding, would be consistent with the interpretation of *Deep* bouts.

Physiological limitation

Since Chinstrap Penguins forage predominantly on an aggregated prey which are mostly close to the surface, but can move off when threatened, the total serial underwater time available to access this resource should be maximised when the prey are encountered. Thus dive cycles with short surface intervals and low anaerobic debt build-up would be expected to take place, otherwise physiological limitation might set in before prey capture rates declined or the penguin reached satiation. This prediction matches the finding that relatively few (approximately only 13%) of dives of Chinstrap Penguins at Bouvetøya exceed the TADL, thus most dives do not appear to incur the costs of anaerobic debt build-up.

Diving penguins commonly exceed their TADL, and why this should be is a perennial debate (e.g. Kooyman 1989; Williams 1995; Boyd & Croxall 1996; Boyd 1997b). A number of possible compensating mechanisms have been suggested; these are reviewed by Boyd & Croxall (1996), and Boyd (1997b). Overestimated costs of transport (cf. Wilson 1995), inaccurate estimates of body oxygen stores (cf. Boyd & Croxall 1996) and metabolic depression (e.g. Handrich et al. 1997; Le Maho 1999) will cause errors in estimation of the metabolic costs of diving, and hence estimation of the TADL. Penguins also appear to possess physiological methods to deal with lactic acid accumulation and blood acidosis (e.g. Lenfant et al. 1969; Williams 1995), when dives are truly anaerobic.

Chinstrap Penguins are smaller than most of their sympatric diving competitors. Following general rules of allometry, this means their maximum dive depth is also less (cf. Wilson 1995; Wilson & Peters 1999) and consequently the volume of water they can search for prey is smaller. Wilson & Peters (1999) interpreted the continuous day and night diving of Chinstrap Penguins at Ardley Island, Antarctica, to be a behavioural mechanism permitting ecological segregation from competing Gentoo *P. papua* and Adélie *P. adeliae* Penguins. This explanation cannot apply to Bouvetøya, since Chinstrap Penguins dive less at night (Chapter 3), and not continuously. Another possibility, which applies to both studies, is that Chinstrap Penguins possess compensating mechanisms which allow them to maximise their total time underwater over long time intervals. This is consistent with the results of this study and Mori (1997), who concluded that physiological mechanisms did not terminate diving of Chinstrap Penguins at Seal Island, South Shetland Islands. Here, diving ceased when the rate of prey capture declined to some value indicative of the animal's perception of marginal value of maximal foraging efficiency (Charnov 1976).

Prey distribution at sea

Predators can reveal information about the dispersion, as well as the quality, of prey patches, because they are sensitive to variation in both of these factors. This is exemplified by the foraging behaviour of fur seals at South Georgia, where the inter-bout durations revealed that krill were clumped at the fine-scale, but more evenly dispersed at the meso-scale level (Boyd 1996). In one year of low krill abundance, fur seal behaviour suggested that poorer performance was not as a result of fewer prey patches, but rather a result of poorer patch quality (Boyd 1996).

Judging by inter-bout durations, Chinstrap Penguins at Bouvetøya searched for prey at finer scales (ca. 320 m) than they encountered them (ca. 400 m). Diving unsuccessfully is energetically costly and wastes time which could be better spent feeding. Penguins would be exepected to trade this cost off against the risk of missing ("overshooting") a krill aggregation, and should therefore search at spatial scales similar to that which their prey occur at. The spacing of krill aggregations detected in this study accords well with the results of other studies. At South Georgia fur seals encounter krill at 180–270 m spacing (Boyd 1996), which is similar to that suggested by acoustic surveys (100–300 m) (Miller et al. 1993) in the same region. Further work on inter-annual variation in spacing of krill aggregations at Bouvetøya should prove an interesting comparison to the variability experienced at South Georgia (Boyd 1996).

Unlike fur seals, Chinstrap Penguins do not conduct long foraging trips (Doidge et al. 1986; Isaksen et al. 1997a; McCafferty et al. 1998) and have unimodal inter-bout durations, indicating most foraging activity was conducted at fine spatial scales. They therefore cannot provide information on meso-scale (1–10 km) krill spacing. Nevertheless, Chinstrap Penguins appear to be suitable environmental monitors (Le Maho et al. 1993; Wilson et al. 1994) and, combined with other measures of performance, can elucidate important trophic interactions.

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Chapter 4: Tables

Table 4.1 Mean (± 95% confidence limits) parameters for cluster analysis of Chinstrap Penguin foraging bouts, Bouvetøya, 1999. Highlighted values are those that discriminate that bout type from other types.

Bout types	Start time (24 hr clock)	Length (mins)	No of dives	Period since last dive (s)	Dive duration (s)	Bottom time (s)	Descending vertical velocity ($m.s^{-1}$)	Maximum depth (m)
Type I *"Unsuccessful"* n =57	11:42 (10:35-12:48)	2.75 (1.85-3.67)	2.12 (1.62-2.62)	283 (232-334)	54.5 (48.0-61.0)	0.1 (-0.01-0.21)	0.57 (0.50-0.63)	15.95 (12.45-19.44)
Type II *"Deep"* n = 102	10:20 (9:22-11:18)	38.88 (25.88-51.87)	20.58 (14.04-27.11)	377 (277-477)	77.85 (73.7-82.0)	25.0 (23.5-26.5)	0.99 (0.93-1.06)	27.76 (24.74-30.78)
Type III *"Slow"* n = 17	9:58 (7:00-12:57)	9.00 (0-21.68)	5.06 (-0.64-10.76)	2777 (1806-3747)	50.4 (38.4-62.3)	6.3 (2.2- 0.4)	0.53 (0.39-0.66)	13.65 (7.58-19.71)
Type IV *"Shallow"* n = 93	9:50 (8:57-10:43)	11.52 (8.45-14.60)	8.32 (6.03-10.62)	318 (275-362)	51.2 (47.6-54.8)	9.9 (9.1-10.7)	0.71 (0.67-0.76)	15.21 (13.12-17.29)

Table 4.2 Individual variation in occurrence of the four recognised bout types. Table gives χ^2 values of frequency per penguin of the bout type. Major contributions to the total χ^2 value are shaded.

Penguin	Bout type				
	Unsuccessful	*Deep*	*Slow*	*Shallow*	Total χ^2
1	0.91	0.97	0.12	0.02	2.02
2	0.07	1.15	0.64	2.78	4.64
3	0.75	3.10	0.18	7.30	11.33
4	0.31	12.15	0.00	10.47	22.93
5	1.69	0.01	0.21	0.53	2.44
6	2.41	0.31	0.92	0.05	3.69
7	0.02	1.74	0.04	1.40	3.20
Total χ^2	6.16	19.43	2.11	22.55	50.25

Figure legends

Fig. 1. Examples from dive records (penguins 3 & 6) of dive types of Chinstrap Penguins at Bouvetøya, 1999. Dives have either a broken descent and ascent (A), or a smooth ascent and descent (B). The irregular phase in dives with broken ascents and descents is known as the bottom phase, and the duration is bottom time (A). Type I dive bouts (B) were typified by having few dives, and little bottom time.

Fig. 2. The proportion of total variation acounted for by the number of clusters chosen. This proportion was calculated as the mean of the variance for each of the discriminatory variables. Four clusters were chosen as a suitable compromise between explaining maximal amounts of variance, and preserving some biological realism.

Fig. 3. Frequency histogram of total dive duration (n = 3319) from seven Chinstrap Penguins, Bouvetøya, 1999. The mean dive duration and the Theoretical Aerobic Dive Limit (TADL) are indicated; an estimated 36% of dives exceed the TADL.

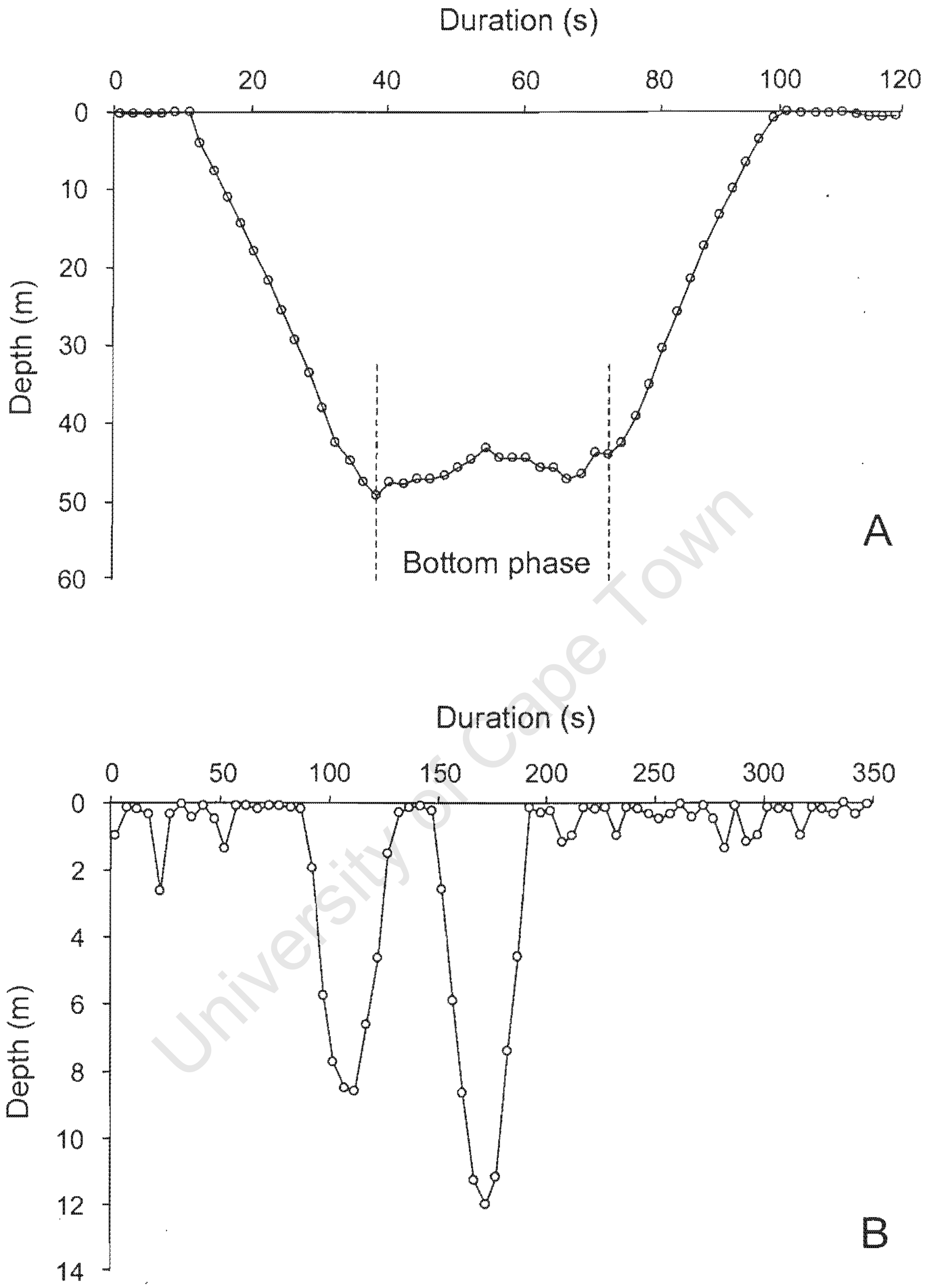
Fig. 4. Relationships between bout mean maximum dive depth and (A) dive duration, (B) total dive cycle time, (C) bottom time, and (D) descending vertical velocity. All foraging bouts (i.e. with bottom time, bout types *Deep*, *Slow* and *Shallow*) and with > 2 dives (n = 146) were included. Regression relationships are significant, equations are in the text.

Fig. 5. Relationship between bout mean dive duration and preceding surface interval (combined as the total dive cycle time). All bouts with bottom time (i.e. bout types *Deep*, *Slow* and *Shallow*) and with > 2 dives (n = 146) were included.

Fig. 6. Example from the dive record (penguin 6) of a *Deep* bout. The penguin accumulates a relatively high proportion of bottom time (cf. Fig. 1) throughout the bout.

Fig. 7. Relative position and mean maximum depth of each bout (classified according to type, n = 269) within the foraging trip. Fifteen trips, from seven birds, were recorded.

Fig. 8. Frequency histograms of inter-bout durations from seven Chinstrap Penguins, Bouvetøya, 1999. Panel A shows inter-bout durations of all bout types (n = 259), and Panel B inter-bout durations of foraging bouts only (i.e. excluding *Unsuccessful* bouts; n = 204).



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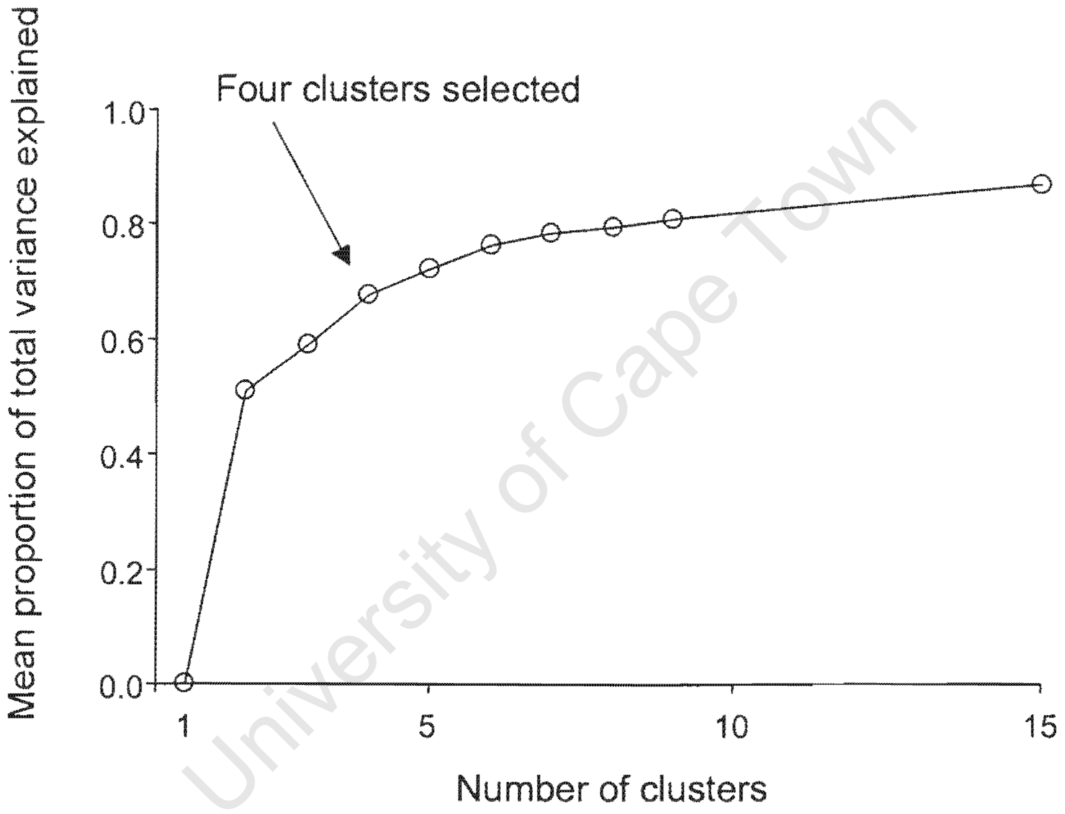

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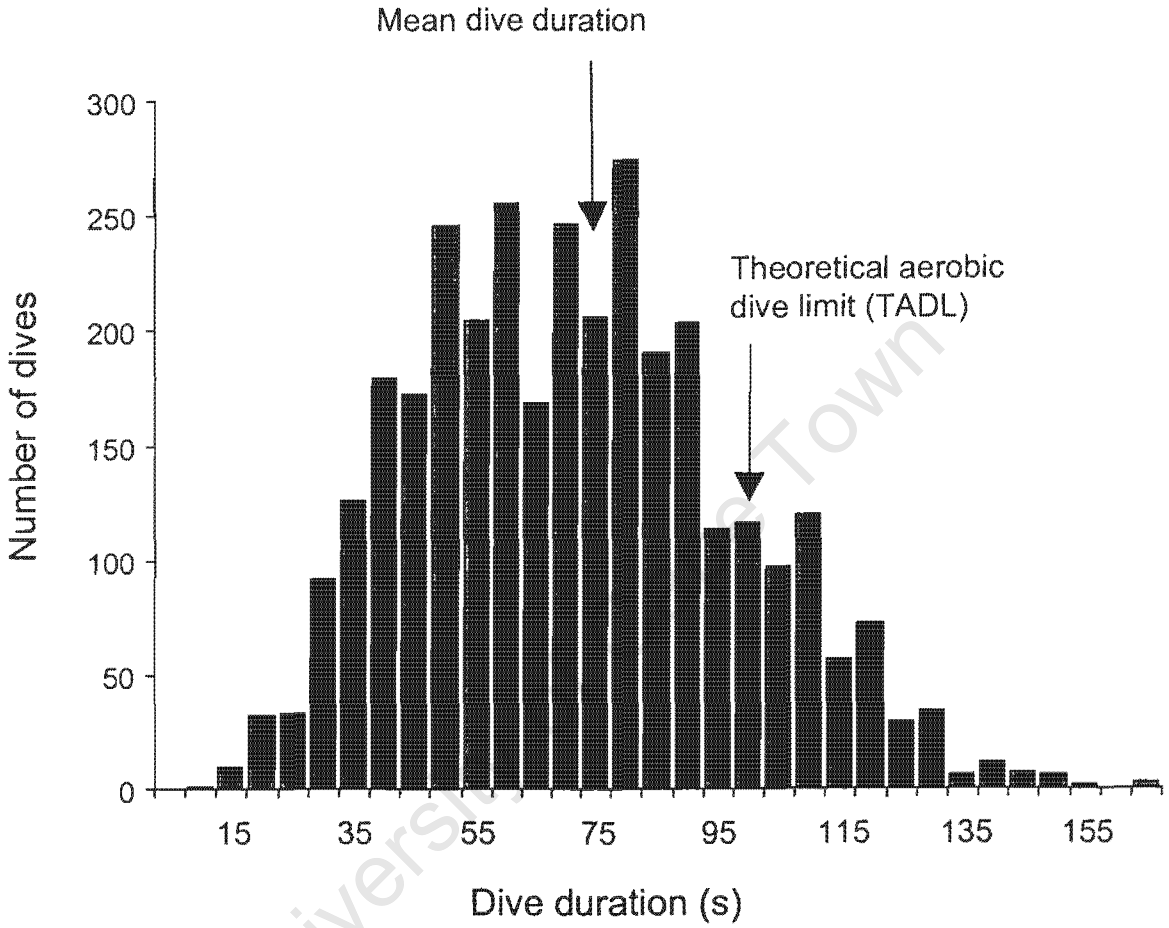

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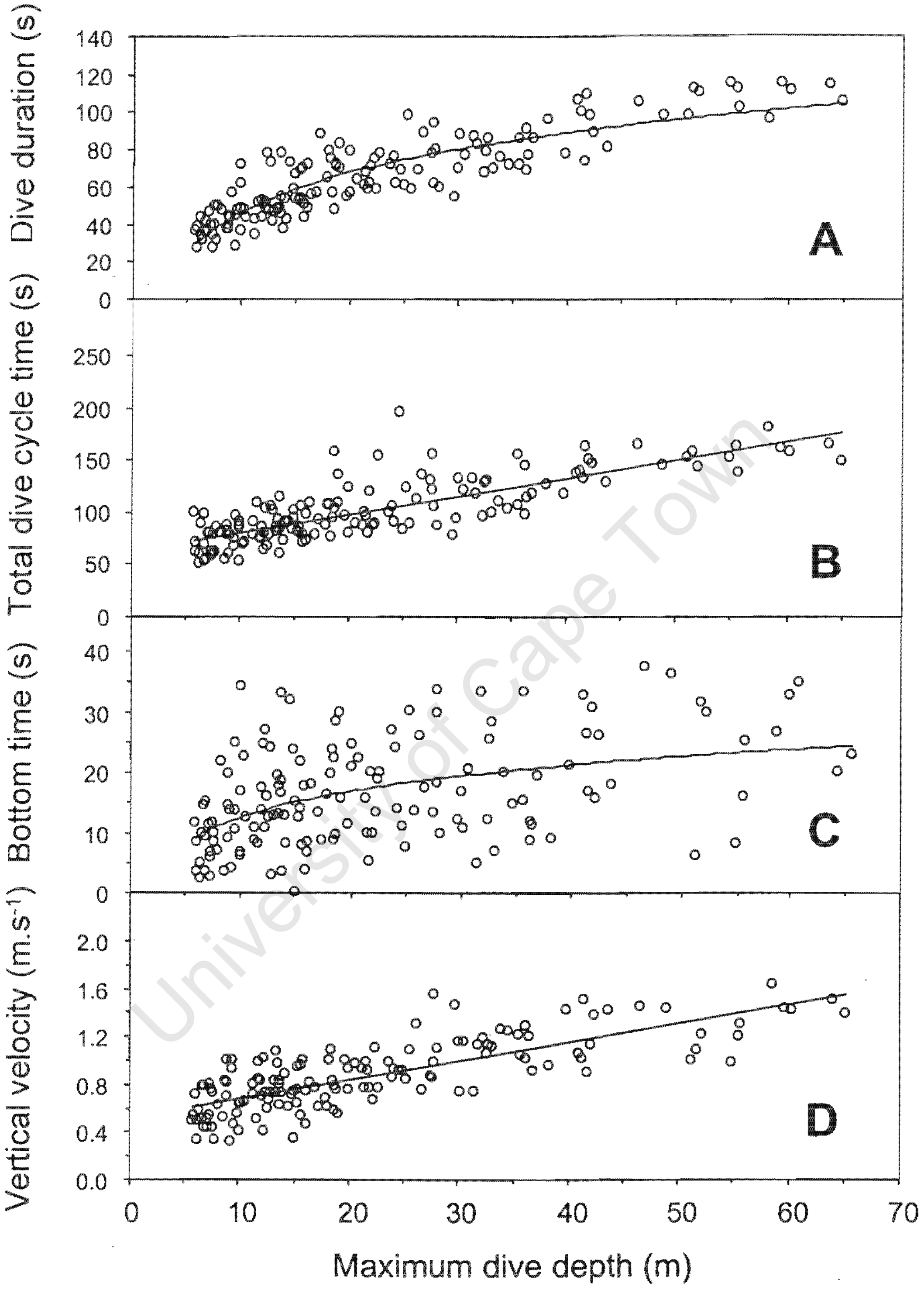

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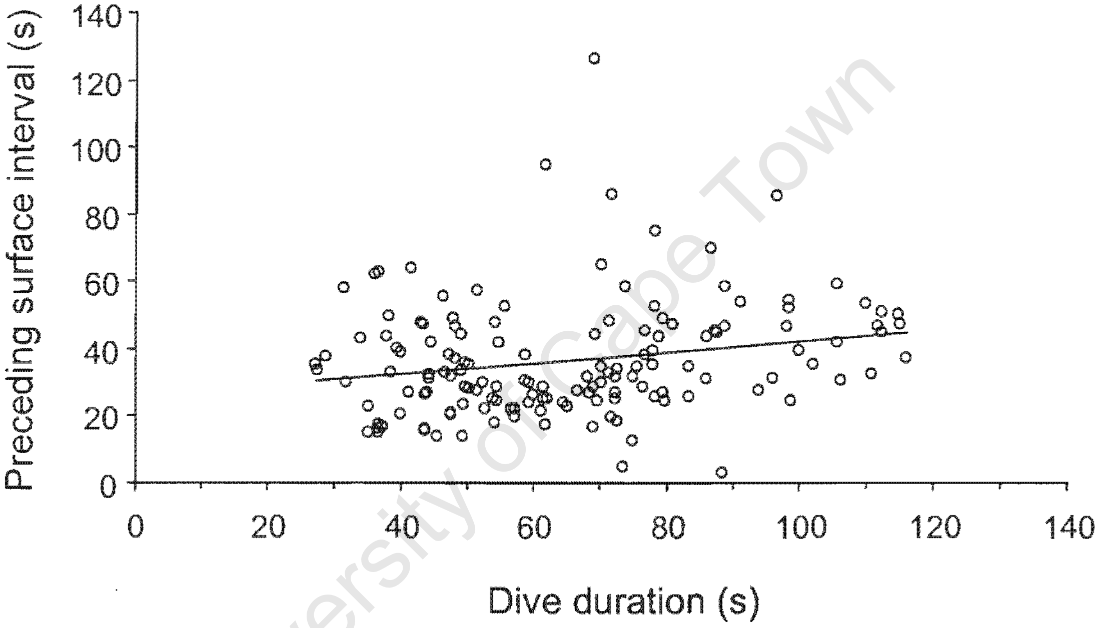

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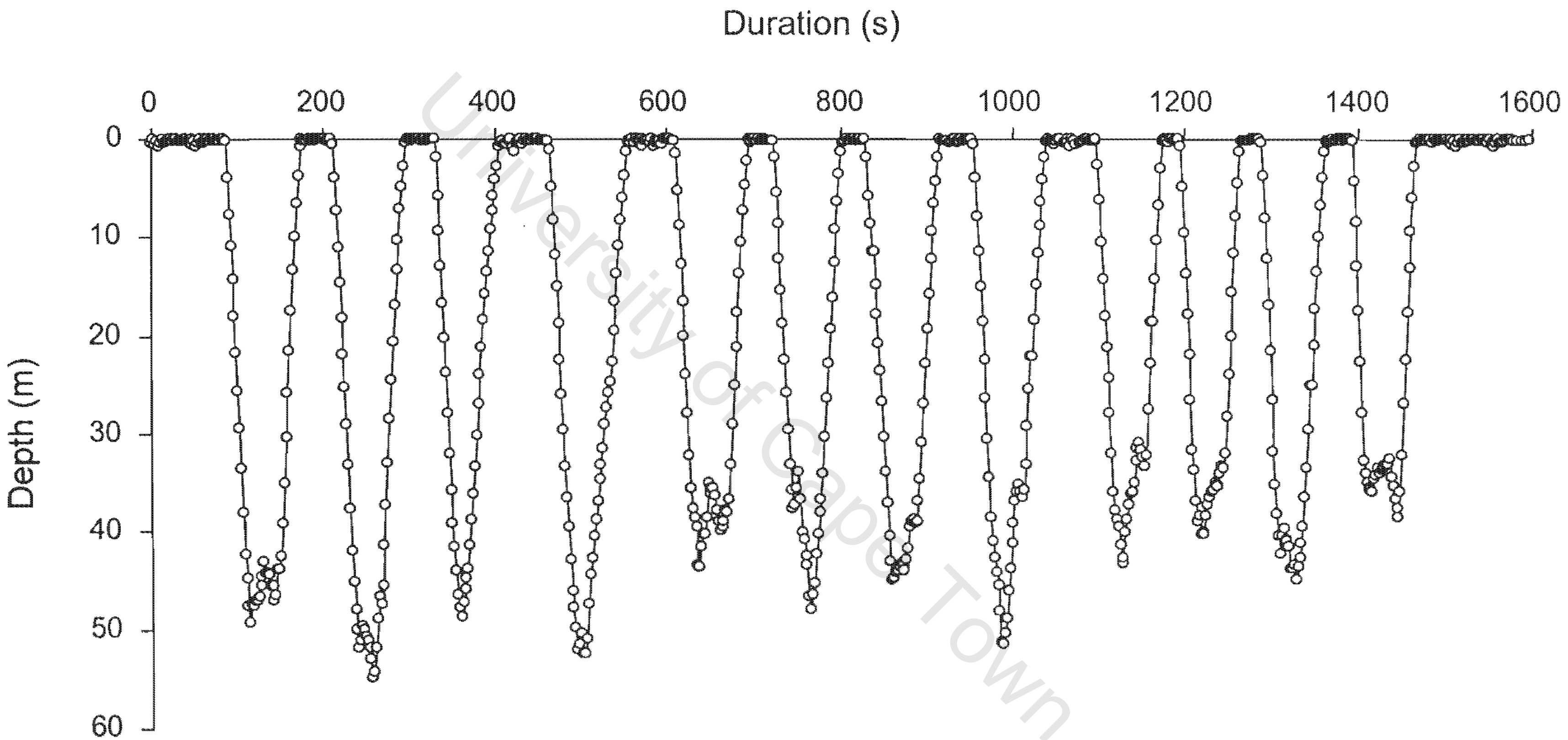

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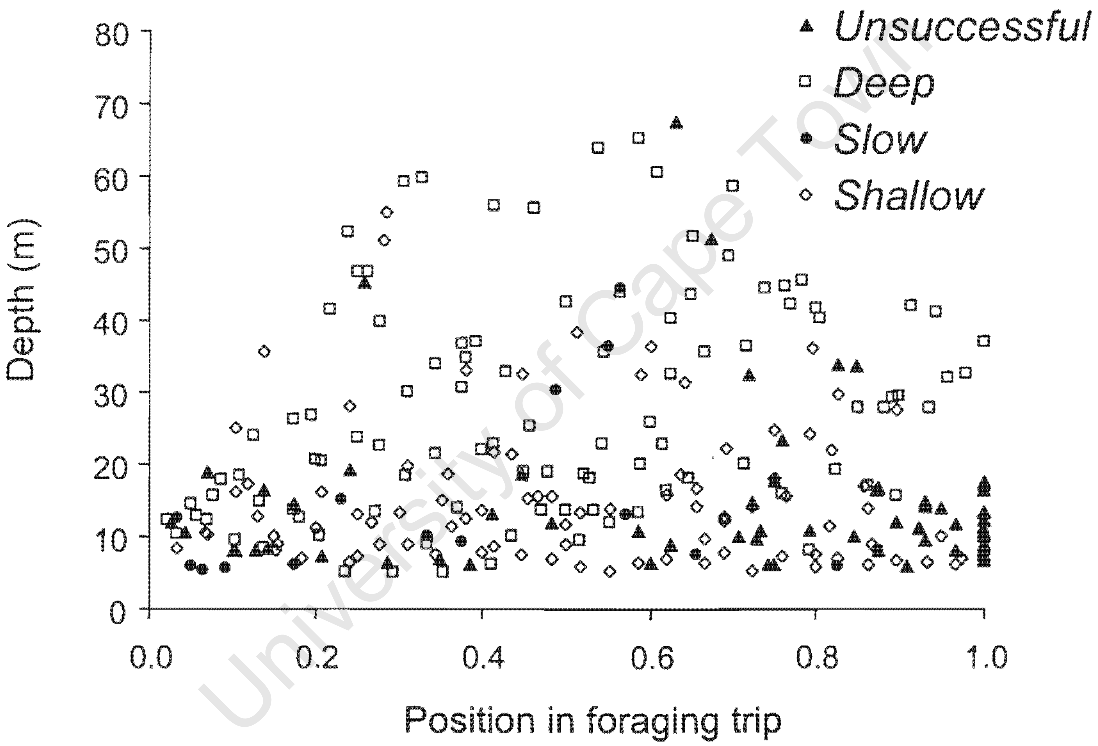

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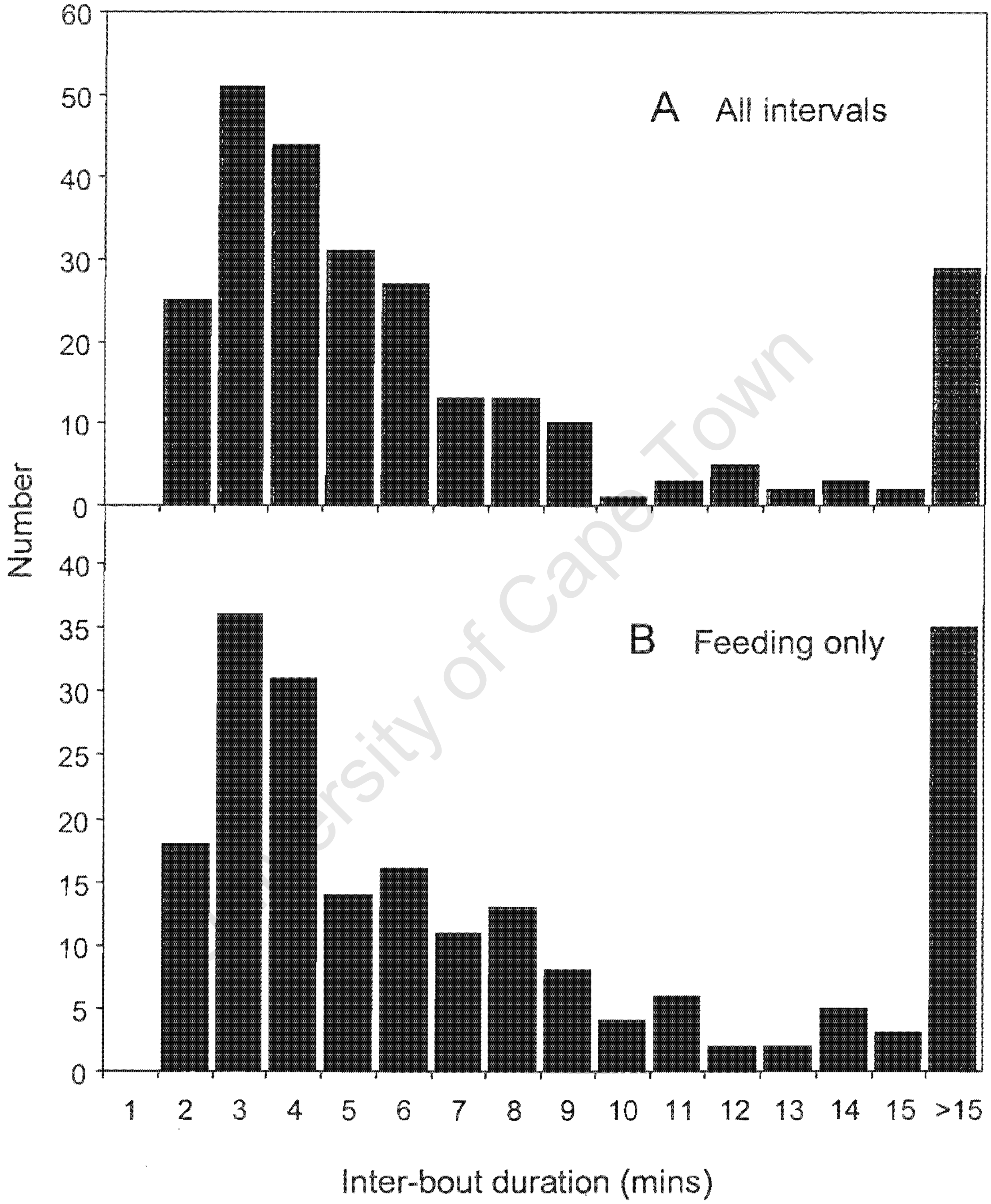

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Chapter 5

Is monitoring the at-sea behaviour of penguins a valid option for ecosystem monitoring programmes?

Abstract

The goals of the CCAMLR Ecosystem Monitoring Programme (CEMP) are sound, but theoretical as well as practical evidence from the Bouvetøya CEMP suggests that many of the land-based indices of predator performance are too integrative, and are confounded by biological and physical factors unrelated to food. This might be overcome by improving our system of monitoring the at-sea foraging behaviour of penguins and other important top predators in the region. Parameters derived from overlap of predators and fisheries, and the organization of dive bouts, appear to be of the greatest immediate use. These include: the FFO (foraging-fishery overlap) index (Agnew & Phegan 1995), the interval between consecutive successful bouts, the proportion of successful to unsuccessful bouts, and the average length of bouts that are not terminated by satiation or physiological limitation of the predator. Increased quantitative effort to validate the usefulness of these, and other parameters derived from foraging behaviour conducted at the level of the entire foraging trip and individual dive cycle, will be required before we can proceed. Technical impediments such as observer disturbance and handling stress, device effects, and the costs of long-term device deployment will also need to be addressed before device-assisted studies of at-sea behaviour of penguins can proceed as a monitoring tool.

CCAMLR, and the Ecosystem Monitoring Programme (CEMP)

The Convention on the Conservation of Antarctic Marine Living Resources is perhaps unique as a piece of international conservation legislation owing to the vast size of the Southern Ocean, the complexity of political and commercial interests in the region, and the adoption of a "whole ecosystem" conservation approach. The affairs of the Convention are managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which receives input from the Scientific Committee (SC-CAMLR), further served by a number of permanent scientific working groups.

An important management objective of CCAMLR is to ensure that exploitation of natural resources is not detrimental to natural consumers (Croxall 1989). This obligation has led to the establishment of, along with the Fish Stock Assessment Working Group, the Ecosystem Monitoring and Management Working Group (WG-EMM). Through the WG-EMM, CCAMLR has established an Ecosystem Monitoring Programme (CEMP) aimed at long-term monitoring of vertebrate predators that satisfy certain criteria (see Croxall et al. 1988a; Croxall 1989). Amongst others, these are that the predator must specialise on prey species also of commercial interest (at present only Antarctic krill *Euphausia superba,* hereafter krill), the species should be widely distributed, be tractable for intensive study, and have a basic biology that is already reasonably well known. With time, squid- and fish-stock systems might also be monitored, but practicalities exclude monitoring of all species. The penguin species that CEMP monitors are the Gentoo *Pygoscelis papua*, Adélie *P. adeliae*, Chinstrap *P. antarctica* and Macaroni *Eudyptes chrysolophus* Penguins. These penguins are important consumers of krill in the region, and are widespread and abundant (Woehler 1993, 1995).

This whole-ecosystem management approach is a notable departure from single-species management, which, through lack of ecological realism, has probably contributed significantly to the parlous state of many of the world's fisheries. It is also noteworthy as it actively incorporates the conservation of non-target species into management objectives, and embodies a precautionary approach to environmental risk.

From the outset, CEMP has aimed to detect and record significant changes in critical ecosystem components in an effort to distinguish between changes caused by harvesting of commercial prey species, and changes caused by environmental variability, both physical and biological (SC-CAMLR-IV, paragraph 7.2). The programme has developed methods for measuring ecologically-oriented indices (parameters) of predator performance, known as CEMP Standard Methods (CCAMLR 1997a), which contributing member states are requested to follow as closely as possible. Standard methods for monitoring relevant physical environmental variables (e.g. sea ice extent, sea surface temperature etc.), and populations of harvested species are also included. The Standard Methods and analytical treatment of the various indices that result evolve constantly as new needs appear (see e.g. CCAMLR 1988, 1992, 1997a; CCAMLR 1995, 1996, 1997b, 1998, 1999), and baseline information accumulates (e.g. Agnew et al. 1996). Further details of CEMP can be found in Croxall et al. (1988a), Croxall (1989) and CCAMLR (1997a).

Indices of predator performance

For monitoring predators, CEMP has identified parameters that are biologically relevant, easy to measure, and that should be informative when contrasted with environmental or prey indices (Table 5.1). Large sample sizes (within and among years) are required to render sufficient statistical power, as well as indices capable of integrating ecological information over short periods (i.e. are highly sensitive) (CCAMLR 1997a). Intra- and inter-annual variability both influence parameter sensitivity. Low intra-annual variability increases power, but low inter-annual variability indicates the parameter might be non-responsive. Since high inter-annual variability reduces long-term statistical power, the middle road - moderate variability - is generally most desirable (cf. Croxall et al. 1988a; Croxall 1989).

Because competition between commercial and natural consumers of food is of concern, knowledge about at-sea behaviour of CEMP predators is invaluable. Diet, spatial and temporal overlap with commercial fisheries, rate of energetic gain, and rate of energetic delivery to offspring by parents are all of interest. A summary of the CEMP parameters for penguins (Table 5.1), indicates that only two (A5 and A8) directly measure activities at sea, and only one (A1) estimates conditions during the non-breeding period. Most of the parameters also integrate information over a relatively long period (e.g. A3, A4, A6, A7), thereby reducing their sensitivity. There are good reasons for measuring these parameters, not least of which is that monitoring methods should be simple and cheap which land-based measures are. Nevertheless, indices which could quantify aspects of the marine ecosystem directly, are scalable (i.e. can integrate information from small to large scales) and have the required sensitivity would at least theoretically be an improvement. Yet are such methods available, and are they practical?

Firstly, we should consider factors other than food that could influence predator performance. Predator performance undoubtedly can be influenced by food (e.g. Croxall et al. 1988a, 1999; Montevecchi et al. 1988; Monaghan et al. 1989), but other factors can also be influential. This influence is likely to vary with species and site, which will limit the interpretability of standard predator indices. In this chapter I consider shortcomings of CEMP, and suggest possible ways to improve its effectiveness.

Bouvetøya CEMP

At Nyrøysa, Macaroni and Chinstrap Penguin numbers have decreased in recent years, whereas Antarctic fur seal *Arctocephalus gazella* numbers have increased substantially (Bakken 1991; Isaksen et al. 1997; Appendix A & C) (Introduction, Fig. 2).

Fur seals dominate in competition for breeding space at Nyrøysa, causing near-total breeding failure of both penguin species in the lower sections of the penguin colony (unpubl. data), which overlaps with the expanding fur seal colony. Aggressive interactions between territory-holding male fur seals and incubating or brooding penguins frequently lead to serious or even fatal injuries to penguins and consequent failure of the breeding attempt (Appendix C; unpubl. data). Eggs and chicks are also lost when penguins are forced off nesting sites (unpubl. data). These interactions on land are not predatory, but active predation takes place at sea (Synthesis). With burgeoning numbers of fur seals, competition at sea for food might also occur since fur seals and both penguin species consume krill (Klages et al. 1999; Kirkman et al. in press; Chapters 1 & 3), although there is no strong evidence that this is currently the case. Finally, disintegration of the seaward margin of the

Nyrøysa platform is eroding penguin breeding space. This process is ongoing (Appendix C), forcing many birds to relocate each season.

Direct interactions with fur seals almost certainly influences penguin numbers at Nyrøysa. Although population estimates are limited (Introduction, Fig. 2), changes in prey abundance cannot explain why penguin populations are decreasing while fur seal numbers are increasing, because krill is consumed by both groups. Other parameters (e.g. breeding success and chronology, juvenile and adult survival) should also be influenced by interactions with fur seals, ultimately compromising the long-term value of the CEMP information from penguins.

Dynamics of predator populations elsewhere might also be driven by their own unique set of variables. Some support for this is in Agnew et al. (1996), who, with an eight-year dataset from Seal Island, South Shetland Islands, found markedly different relationships between predator parameters (Macaroni and Chinstrap penguins, and fur seals) and local environmental and prey parameters.

Speculation aside, common sense is needed when interpreting any index, regardless of provenance. CCAMLR (e.g. SC-CAMLR-XVII, paragraph 6.16) has recognised this, but the salient point is that with each caveat the value of an integrative, or surrogate, index is lessened. Surrogate indices are widely used in ecological research and monitoring. While they have obvious attractions, over-integrated indices might obscure important relationships and trends. Thus, while CEMP indices can distinguish between normal and anomalous years, it is not certain that impacts from moderate (yet locally influential) commercial removal of krill are detectable with the existing indices.

One remedy might be to measure aspects of foraging performance of predators such as penguins as directly as possible.

At-sea monitoring of foraging performance

When CEMP was established, research into at-sea behaviour of penguins was in its infancy. Great technological advances in the last decade have made it possible to equip many seabirds and all penguins with miniaturized recorders (e.g. Time-Depth Recorders, TDRs) that measure variables such as depth, light, activity, ambient (water or air) temperature, swimming speed, core temperature, heart rate, prey ingestion events, and compass heading while the bird is at sea (reviewed by Wilson 1995). Sensor accuracy, device size and streamlining, memory, power requirements and sampling frequency are all rapidly improving.

Croxall (1995) discusses how technology has revolutionised the study of marine top predators. The at-sea behaviour of predators has the potential to provide information about the physical and biological environment, as well as prey dispersion and abundance and the scale thereof (Boyd 1996a, 1997). This information aids understanding of the variability in predator reproductive performance (Boyd 1997).

CCAMLR has recognised this potential boon, and Boyd (1996b, 1997) discusses the treatment of data returned by fur seals for development of indices of at-sea behaviour. However, the at-sea behaviour of fur seals and penguins is unlikely to be so similar that an index developed for one is easily applied to the other. Fur seals appear to maximise rates of energy delivery to offspring over appreciably longer cycles than do most penguins (Boyd 1999). Thus we must renew our efforts to follow the performance of penguins at sea; only by so doing can we resolve the intermediate links in the chain of causation from marine conditions to changes in fitness measured on land.

Overlap with fisheries

Four measures of overlap have been reviewed by the CCAMLR Secretariat (see e.g. WG-EMM-99/11; SC-CAMLR-XVIII/3, paragraphs 6.9-6.12), all of which require data about behaviour at sea.

Only in the last few years have sufficient baseline data on predator performance existed to test whether commercial krill fisheries might influence predator populations. Testing whether harvesting of krill explains any residual variation in performance of Chinstrap Penguins at Seal Island, South Orkney Islands, Agnew et al. (1996) show that neither the current nor past season's catches were significant. Ichii et al. (1996) and Croll & Tershy (1998) considered the potential for competition between fisheries and predators at the South Shetland Islands, but reached different conclusions as to its significance. Better information regarding foraging patterns of predators is needed to resolve whether competition between fisheries and predators is taking place. Agnew & Phegan (1995) demonstrated this when they found the existing CCAMLR index of fisheries catches taken during critical breeding periods, when penguins are restricted close to the colonies (the critical period-distance index), to be inadequate. By comparison, their refined model of overlap between predators and fisheries (the foraging-fishery overlap, or FFO, index), is sensitive to foraging distance and bearing from the colony, but this detailed information is lacking for most sites.

Position-determining devices suitable for addressing the problem of spatial overlap exist (e.g. Wilson et al. 1994). Dead-reckoners (Wilson et al. 1991a,1992a), geolocational loggers (Hill 1994), and satellite transmitters are all available commercially and have been used successfully on penguins (e.g. Wilson et al. 1994; Pütz et al. 1999). In the near future we can expect GPS and GPS-satellite hybrid devices to become useful. Given the position of the bird, it is possible to calculate time spent per unit area, and correlate this with positional data returned from the fishery. This would result in an index of spatial and temporal overlap which is east to interpret. Dead-reckoning devices offer the greatest resolution, and are thus the most scalable. Combined with depth sensors, drawing inferences on the extent to which birds are foraging in a given area is also possible, permitting catch per unit time or effort (CPUE) calculations (see below) (Wilson 1995).

Although this approach would be easiest during the breeding season, satellite transmitters could also yield valuable information during winter, when considerable commercial fishing for krill takes place (SC-CAMLR-XVIII/3, paragraph 6.11). Since satellite transmitters are costly, an improvement might be to attach geolocational loggers to adult birds of known history, with a combination of tape, glue and a cable-linked neoprene foot band. This has been performed successfully on Magellanic Penguins *Spheniscus magellanicus*, for up to two years with no noticeable detrimental effect on the birds (Wilson et al. unpubl. data).

Foraging behaviour

The analysis of foraging behaviour is also feasible and can be informative. Boyd (1997) recognises three widely distinct scales at which this can be conducted: at the level of entire foraging trips, dive bouts, and individual dives. No CEMP methods exist for analysis of individual dives or dive bouts, but a simple measure at the scale of the foraging trip (trip length) exists (Standard Method A5; Table 5.1).

Foraging trip

Although easy to measure, trip length for penguins is difficult to interpret (Croxall et al. 1988a) because it tends to be highly variable (Williams & Rothery 1990; Agnew et al. 1996) and relatively insensitive to decreased abundance of prey at sea (cf. Croxall et al. 1999). It is therefore being reassessed as a monitoring tool (WG-EMM-95, paragraphs 5.17-5.19).

Trip length is more informative for fur seal mothers, who increase their foraging trip duration, and time spent ashore, in years of reduced food availability (Croxall et al. 1988a; McCafferty et al. 1998; Boyd 1999). For penguins, measures likely to be more informative and that deserve consideration include: total time spent resting and underwater at sea, the proportion of time spent underwater where prey was captured (cf. Wilson et al. 1992b; Wilson et al. 1993; Pütz & Bost 1994), depth usage (e.g. Wilson et al. 1991b; Charrassin et al. 1999), and time spent foraging for self and for offspring, as indicated by gastric activity (Peters 1997a,b). Much research remains to be done here, but a device-assisted experimental approach where foraging costs are manipulated (e.g. Boyd et al. 1997) will be valuable.

Dive bouts

Diving in marine predators typically is arranged into bouts, thought to represent serial diving on prey which continues until the prey disperse or are consumed to the point when capture rate becomes unprofitable, or when physical (light, depth) or physiological limits set in (Chapter 4). Inter-bout periods reflect resting, or travel and searching until spatially unpredictable prey (Miller & Hampton 1989) are encountered again (e.g. Boyd 1996a). Thus information about both bouts and inter-bout periods can provide information on conditions in the environment, as research on fur seals at South Georgia, and Chinstrap Penguins at Bouvetøya, has demonstrated (Boyd et al. 1994; Boyd 1996a; Chapter 4).

Defining bout lengths is difficult, because there is no widely accepted method to define a bout (Boyd 1997). Boyd's (Boyd et al. 1994; Boyd 1996a) method for determining bout lengths has not been applied to penguins. Traditional methods (Slater & Lester 1982; Martin & Bateson 1986; Sibly et al. 1990) have proved useful (e.g. Mori 1997; Chapter 4) for penguins, however, and technical problems therefore appear less of an impediment than was earlier thought. Some indices worth considering are: the mean interval between consecutive successful bouts, the proportion of successful to unsuccessful bouts, and the average length of bouts that are not terminated by satiation or physiological limitation. Again, more research is needed.

Dive categorisation

Classification of individual dives into dive types has been a feature of penguin dive analysis (e.g. Green et al. 1998), probably inherited from elephant seal *Mirounga* research (e.g. Le Boeuf et al. 1987). Elephant seals are substantially larger than penguins, and were therefore one of the first marine predators to be instrumented. Dive typing suffers from the difficulty that dive types may not possess unique biological properties. Summaries of predator behaviour drawn from frequencies of dives of certain types should therefore be treated with caution. Unfortunately little effort has been made to go beyond simple dive categorisation, and much potential exists to interrogate dive profiles further.

Perhaps the most contentious aspect of analysis at the level of the individual dive is whether food is ingested, and if so how much. Currently the only means of assessing whether food is consumed in a dive is with stomach-temperature devices (EATLs; Wilson et al. 1992b). This method is not successful when large amounts of small prey are consumed (R.P. Wilson, pers. comm.), because the stomach contents increasingly buffer the sensor from temperature changes from newly-ingested prey. It may be possible to correlate ingestion events with underwater behaviour, though. For instance, sudden changes in swimming speed, direction and depth may all indicate prey capture events. Light intensity, a measure of water turbidity, might also assist since it is predicted that when penguins encounter schooling prey such as swarms of krill, turbidity will increase. Highly sensitive light meters with high sampling resolution might even enable detection of encounter rate of bio-luminescent prey groups (e.g. krill swarms, myctophid fish schools).

Data analysis and interpretation

Clearly, a great many options for monitoring aspects of at-sea behaviour of penguins exist. Many of these offer sensitive measures of short-term prey availability. If integrated over a breeding season, they offer a sensitive means of resolving how changing prey conditions influence the predator's fitness as measured on land. The two sets of indices that appear to be of the greatest immediate value are predator foraging ranges (predator-fisheries overlap), and organization of dive bouts.

We are still hampered by an incomplete understanding of the various relationships, but this can be overcome with focused experimental efforts incorporating zooplankton surveys and metabolic studies. As with the pioneering research at Bird Island, South Georgia, on which CEMP was based, detailed studies of penguin foraging performance and the convergence with existing land-based parameters will be needed to proceed. Quantitative research of at-sea behaviour of fur seals has borne fruit (e.g. Croxall et al. 1985; Boyd et al. 1994; Boyd 1996a,1999; McCafferty et al. 1998). Boyd (1996b, 1997) considers the possibility of employing at-sea measures of predator behaviour, and focuses on indices derived from fur seal behaviour.

No doubt some parameters will be found to be inadequate (see above, desirable characteristics of parameters), but I contend many will add value to our monitoring objectives. There are two advantages worth mentioning. Most proposed parameters appear to be statistically tractable, which is of considerable practical importance. Secondly, the widely different scales of the proposed indices should afford the models similar scalability.

Technical constraints

CCAMLR already has an approved procedure for collecting data on diving behaviour (CCAMLR 1997a). It should aim to standardise future monitoring efforts, including directing standard methodology, statistical analyses, and interpretation of the data in conjunction with other information.

There are a number of technical problems with routine use of devices. Participants may use different devices and analysis software, and consequently produce non-standard analyses. If CCAMLR approves certain models of devices for CEMP work, one option might be for participants to submit virgin logger files directly to CCAMLR for analysis. Three further disadvantages are the technical difficulties of deploying some devices (e.g. heart rate monitors), the cost of devices, and device effects. The first is partly remedied through experience and improved techniques as researchers become more familiar with the issues. The second remains problematic, but scale of economy suggests that increasing demand will bring prices down. Some manufacturers already produce devices with long life expectancies (years).

Perhaps the most troubling issue is device effects. Clearly, for any CEMP technique to be appropriate, disturbance to the monitored species should be minimal. Device effects have been widely considered (e.g. Wilson et al. 1986; Croxall et al. 1988b; Croll et al. 1991; Kooyman et al. 1992; Bengston et al. 1993; Wilson 1995). Devices disrupt hydrodynamic effectiveness of the predator, so increasing transport costs. This can have knock-on effects reducing dive depth and time and ultimately foraging performance. Given the remarkable streamlining of penguins (Wilson 1995) it is hard to see how devices cannot depress their foraging performance. The good news though, is that properly controlled studies permit estimation of the costs of device attachment (e.g. Boyd et al. 1997) and if the bias is consistent, but small, throughout, the overall impact on the monitoring programme can be minimal.

Conclusions

Existing monitoring must continue, but to understand what extent factors at sea (as measured by the birds themselves) are contributing to trends on land, the behaviour of penguins at sea requires greater quantitative attention. A number of parameters appear to have potential, especially those related to overlap of fisheries and predators, and organization of dive bouts at sea. Future studies should aim to test the validity of these and other potential parameters explicitly.

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Table 5.1 The CEMP Standard Methods A1-9 (CCAMLR 1997a) for monitoring penguins. CCAMLR (1997a) also includes methods for monitoring flying birds and fur seals, and for monitoring environmental parameters. Methods vary greatly with respect to the period over which the index integrates information (for further details see Croxall et al. 1988a).

Method	Procedure	Technique	Integration period
A1	Adult weight upon arrival at breeding colony	Weigh individuals upon arrival over arrival period	Months (whole pre-breeding period)
A2	Duration of the first incubation shift	Monitor randomly selected nests	Days-weeks
A3	Breeding population size	Standard censuses of certain colonies	Years
A4	Age-specific annual survival and recruitment	Banding of adults and chicks	Years
A5	Foraging trip duration	VHF-device cycle monitoring	Days
A6	Breeding success	Standard censuses of certain colonies	Months
A7	Chick weight at fledging	Weigh fledglings over fledging period	Months
A8	Chick diet	Sample diet returned by adults over chick period	Days
A9	Breeding chronology	Regular monitoring of randomly selected nests	Uncertain

Synthesis

Although aspects of the diet and foraging ecology of Macaroni *Eudyptes chrysolophus* and Chinstrap *Pygoscelis antarctica* Penguins are reasonably well known from a number of sites in the Southern Ocean, this is not the case for Bouvetøya, an important breeding site for seabirds that has received little attention from biologists. In this thesis, I aimed to rectify this deficiency in our knowledge of the foraging ecology of these two penguin species at Bouvetøya, in order to gain a better understanding of resource use and variability for monitoring (and ultimately conservation) objectives (Chapters 1,2,3 & 5), to assess how extrinsic and intrinsic factors influence community organization (Chapters 2 & 3), to determine the limits to foraging in a specialist consumer of Antarctic krill (*Euphausia superba*, hereafter krill) (Chapter 4), and to use this information to improve existing long-term monitoring programmes (Chapter 5).

Variability in diets and marine resources

The diet of breeding Macaroni Penguins was diverse in both 1997 and 1999, but dominated overall by three prey taxa: the myctophid fish *Krefftichthys anderssoni*, krill, and another euphausiid *Thysanoessa macrura*. Chinstrap Penguins displayed trivial inter-annual differences in their diet, eating almost only krill (and taking even fewer alternative species of euphausiids than Macaroni Penguins), which is consistent with their accepted position as dietary specialists. Macaroni Penguin diets displayed greater variability with sex and sampling period than with year. This result was contrary to my initial expectations, and the evidence largely suggested that what variability existed was not a consequence of changing resource availability *per se*.

Firstly, female Macaroni Penguins appeared to benefit by providing fish to small chicks, since it limited their horizontal searching and allowed delivery of food with high energetic content to the chick. I interpret this as a behavioural adjustment to cope with the unique demands placed upon female Macaroni Penguins, who are the sole providers for the duration of the brood period. Second, other studies on penguins and volant seabirds have shown that sexes can be ecologically segregated; I suggest that in Macaroni Penguins this might be related to sexual dimorphism, and the long relief schedules which lead to marked swings in condition throughout the breeding season. Thus birds that are recovering condition after a lengthy fast ashore (during either incubation or guarding) will become temporarily migratory, resulting in temporal and spatial segregation of resource use.

There was, however, some evidence from both penguin species that suggested that small levels of inter-annual variability in resources existed. I found small differences in size distributions of myctophid fish and krill, and differences in trip length and digestion of prey returned by Macaroni Penguins to the chick. Differences in depth usage by Macaroni Penguins probably resulted from the use of larger loggers in the first year. This emphasises the need to exercise care when interpreting the diving behaviour of penguins equipped with devices. Perhaps researchers should consider effects from devices as a null model where large differences in diving behaviour are observed across studies with similarly large differences in device hydrodynamic impact.

Two parts of the pattern in diet switching exhibited by Macaroni Penguins that are difficult to explain are (1) the switch away from fish, while female body condition improved, and (2) the subsequent switch from krill to *T. macrura*. This latter effect was weaker than the former, but was seen in both years, and might reflect differing availability of these resources with the progression of the season. The switch away from fish could stem from the higher costs of diving required to capture deeper-dwelling myctophids. This is at odds with the improvement in body condition over the same period, however. Nevertheless, adult body condition correlated with chick body condition, suggesting that foraging was a costly exercise and that adults that were better foragers invested more in their offspring. This tradeoff has been observed before in long-lived seabirds. Both of these patterns warrant further work. An improved understanding of the availability and habits of the important prey of penguins at Bouvetøya is also required urgently; too little is known at present. This is a major shortcoming of my study and, I think fair to say, common to many studies of seabird foraging ecology.

Diving behaviour

Surveys of the vertical migration habits of prey will also aid the interpretation of the patterns in depth usage I recorded. Macaroni Penguins predominantly fed at 5-15 m depths, but a second mode existed at 50-70 m. This depth usage is consistent with their mixed diet. Information from zooplankton surveys conducted elsewhere indicate that Macaroni Penguins probably fed on euphausiids during shallower dives, and fish during deeper dives. Chinstrap Penguins also dived shallowly (mostly < 35 m) but with a disproportionately greater amount of time spent at 20-35 m, consistent with the near-surface distribution of krill. Whereas Macaroni Penguins conducted longer trips than Chinstrap Penguins in both years, both species exhibited similar foraging rhythms with the majority of diving conducted in the morning. Both species dived at night, but less often and to shallower depths.

An intriguing pattern, observed in both species, was that the deepest feeding dives were conducted at sunrise and sunset. I suggest that this may result from rapid vertical migration of prey, which may cause disruption of anti-predator aggregating behaviour, or from penguins maximising short-term rates of prey intake in a rapidly changing light regime. Chinstrap Penguins are probably not limited proximately by light or physiological limits in their foraging, but krill presence or absence, penguin satiation (and hence ultimately prey patch quality), declining prey capture rates (resource depression, probably resulting from krill escape behaviour), all terminate dive bouts. Similarly, while diving by Macaroni Penguins may be ultimately limited by light, most day-time dives are not light limited, probably because penguins have light levels at, or above which, they prefer to forage, but can surpass if necessary. This is partly in agreement with Wilson et al. (1993), who showed that Adélie Penguins *P. adeliae* foraging at night captured substantially less prey than they did during the day. Diving in this species appeared to be limited exclusively by light availability, however (Wilson et al. 1993). The interpretation that penguins were foraging at preferred light levels, thus balancing the horizontal and vertical components of their searching in some optimal way, cannot be excluded as an explanation for the pattern observed in Adélie Penguins.

Realised foraging niches of penguins at Bouvetøya, and controlling factors

The differences in diet, depth and spatial usage, when considered together, indicate that the two penguin species at Bouvetøya are largely ecologically segregated, with some niche overlap. Chinstrap Penguins are predominantly shallow-diving, inshore-feeding, krill specialists. Macaroni Penguins are predominantly shallow- and deep-diving, offshore-feeding, mixed krill and fish generalists. Their realised niches at Bouvetøya accord largely with what has been recorded elsewhere, and there is little evidence of niche expansion in the relatively species-poor predator community at Bouvetøya.

Perhaps the most intriguing aspect of community organization at Bouvetøya is why it is depauperate. Specifically, the scarcity of Adélie Penguins *P. adeliae*, and absence of Gentoo Penguins *P. papua* and representatives of the cormorant genus *Phalacrocorax* is anomalous. Breeding *Phalacrocorax* cormorants occur from the Antarctic Peninsula and islands of the Scotia Arc to the coast of southern South America, and further north and east of Bouvetøya at islands in the Kerguelen Province (Marchant & Higgins 1990). One Gentoo Penguin has been recorded visiting Bouvetøya, suggesting that isolation alone is insufficient to explain why this species has not been recorded breeding at the island. One reason may be that, with the exception of Nyrøysa, which was only created in the late 1950s, much of the island that is ice-free is steep and rocky, and therefore probably unsuitable for nesting Gentoo Penguins (Williams 1995). A second factor hampering colonisation by Gentoo Penguins, and probably also cormorants, is the paucity of shallow (< 100 m) shelf waters at Bouvetøya (Norsk Polarinstitutt 1981). Elsewhere, Gentoo Penguin numbers correlate with the area of continental shelf which is their preferred foraging area (Robertson 1986; Bost & Jouventin 1990). Southern Ocean *Phalacrocorax* cormorants also forage inshore, and mainly demersally (Espitalier-Noel et al. 1988; Marchant & Higgins 1990). Bouvetøya is considered the most northerly breeding site for Adélie Penguins, but they are uncommon at the island and have not been recorded breeding since 1981 (Bakken 1991). They have a similar diet to Chinstrap Penguins (reviewed in Williams 1995) thus it is hard to see how availability of preferred food constrains them from being more numerous at Bouvetøya. Perhaps the shortage of sea ice in summer at Bouvetøya is an impediment to colonisation. This awaits further work.

Competition and predation at sea by Antarctic Fur Seals *Arctocephalus gazella* are two forms of intrinsic interactions that could potentially influence the realised foraging niches of penguins at Bouvetøya. There is circumstantial evidence that this occurs: (1) overlapping resource utilisation, (2) inferred parapatric (or limited sympatric) distributions, and (3) partially segregated depth usage. However, since there is no evidence that krill availability is a limiting resource at Bouvetøya, none of these three arguments can be considered strong. I cannot discount that intrinsic interactions are important; merely that there is currently little good evidence for it, following principles of parsimony and the falsificationist philosophy embodied in null models of community analysis (Brady 1979; Strong et al. 1979; Wiens 1989; Gotelli & Graves 1996). Stronger evidence that neither competition nor predation define the foraging niches of penguins at Bouvetøya is that these niches are very similar to those occupied elsewhere. This includes sites with greater numbers of sympatric species, and sites where fur seals either do not occur, or do so in comparatively small numbers. The absence of niche expansion at Bouvetøya might therefore indicate that the ecological segregation observed between the three main air-breathing divers is an outcome of adaptations by each species to conditions experienced in the centre of their respective distributions.

Predation upon penguins at sea by fur seals occurs at Bouvetøya (Appendix C; unpubl. data), as is the case at many other sites in the Southern Ocean (e.g. Bonner & Hunter 1982; Todd 1988; Hofmeyr & Bester 1993; Williams 1995; S. Kirkman pers. comm.). Twenty-two fur seal scats and regurgitants containing penguin feathers were found at Nyrøysa in 1999 (unpubl. data; S. Kirkman pers. comm). This is a very small proportion of the total number of scats and regurgitants searched (S. Kirkman pers. comm.). Assuming that each scat or regurgitant equates to one bird taken at sea, this corresponds to predation of 0.45% of the total adult penguin population at Nyrøysa in 1999 (Appendix C). Given that fur seals outnumber penguins substantially at Nyrøysa (but probably not at Bouvetøya), predation might have important consequences for the demography of penguins at Bouvetøya. This requires further quantitative study, and modelling exercises should prove fruitful in this regard.

Intrinsic interactions on land appear important in defining community structure at Bouvetøya. Interference competition for breeding sites, and aggressive interactions between fur seals and penguins, is almost certainly the cause of decreasing penguin numbers at Nyrøysa. Such interactions are well documented from elsewhere, and are not restricted to penguins (e.g. Crawford et al. 1989; Croxall et al. 1990; Williams 1995; Lewis Smith 1997). In 1997 at Nyrøysa, 30 penguins (0.8% of the estimated total population) were either killed, or injured so severely by fur seals that they probably died as a consequence. More regular surveys in 1999 revealed that 56 penguins (1.2%) were either killed or severely injured. A further 62 penguins (1.3%) were either lightly injured, or were recovering from injuries. Many nest sites were abandoned after disturbance by fur seals, and crushed eggs and chicks were also observed (pers. obs.). One male fur seal was watched chasing penguins unsuccessfully in the water at the main landing beach in 1999 (S. Kirkman pers. comm.), but most injuries appear to have occurred on land (unpubl. data).

Penguins are long-lived, hence populations are expected to be sensitive to changes in adult survival (Croxall & Davis 1999; Croxall & Sæther 1999). Thus, interactions on land, coupled with predation at sea, probably have important implications for the demography of penguins at Nyrøysa. For example, Chinstrap Penguins overlap spatially less with fur seals at sea, and are faster swimming than Macaroni Penguins, yet have decreased substantially more than Macaroni Penguins at Nyrøysa since the early 1980s (Haftorn et al. 1981; Introduction, Fig. 1). This is probably because the major part of their preferred breeding habitat at Nyrøysa has been invaded by fur seals (see Haftorn et al. 1981). This has two important implications.

Firstly, it demonstrates a weakness in the current CCAMLR Ecosystem Monitoring Programme philosophy. Populations are not only sensitive to food abundance; unique interactions that accompany each community at each site can distort indices of predator performance. At Nyrøysa penguin breeding population size, breeding success and chronology, and adult and juvenile survival are all influenced by fur seals. These difficulties might be alleviated by monitoring the behaviour of penguins directly at sea. Direct measures of overlap between commercial krill fisheries and predators are the easiest data to obtain, and foraging behaviour at the level of the dive bout (prey patch quality and spacing) appears also to hold potential. Ideally, we require focused studies to validate the monitoring indices of interest before proceeding with confidence.

Second, intrinsic interactions do shape the predator community at Bouvetøya. Contrary to my original expectations, these occur chiefly on land and modify demography rather than realised foraging niches. This is interesting. At one scale population processes are being influenced by horizontal interactions with a dominant species, but at another scale individual decisions (foraging behaviour) appear not to be. Normally the two would be expected to be linked, since population biology is an emergent property of decisions made by individuals. In this case the spatial separation of the influences (sea and land) means the two are decoupled.

Finally, krill is the most important marine resource at Bouvetøya for land-based predators, who are restricted in time and space during the breeding season in their access to it. Current knowledge also suggests that the island receives krill passively 'downstream' from sources further south. The diet, historical presence of Chinstrap and Macaroni Penguins (this and previous studies), and indices of general breeding performance, indicate that inter-annual variability in marine resources at the island were small. Thus, extrinsic factors may be less important than was originally hypothesised in regulating this system.

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Appendix A

Bouvetøya, an Important Bird Area

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Bouvetøya (Bouvet Island) Nature Reserve	54°25'S, 03°20'E
Antarctic/Maritime Antarctic Island	ca. 5000 ha
Fully protected	
Global IBA (A4ii, iii)	

Site Description

Bouvetøya (Bouvet Island; 54°25'S, 03°20'E) is a small (ca. 50 km^2), uninhabited island situated in the south Atlantic Ocean, ca. 2600 km from South Africa and 1600 km from the Antarctic Continent. This isolated island, 9.5 km long and 7 km wide, is the southernmost island on the extensive Mid-Atlantic Ridge, and is thus of volcanic origin. Although Bouvetøya was discovered in 1739, the island was only sporadically visited, mainly by sealers, during the following two centuries. The *Norvegia* expedition of 1927/28 claimed Bouvetøya for Norway, and in 1930 the island officially became a Norwegian dependency by law.

Bouvetøya rises to 780 m a.s.l. (Olavtoppen; Chapter 1, Fig. 1), and is bounded by steep slopes on the northern, western and south western sides, with narrow beaches. Permanent ice covers 93% of the island, leaving only a few ice-free areas along the coast. The largest such area is Nyrøysa, which was formed between 1955 and 1958, probably by a large landslide. The Nyrøysa platform is ca. 700 m long with an average height of between 25 and 40 m a.s.l. The surface is irregular, consisting of jumbled boulders, lava blocks and gravel. Inland the platform is bounded by scree slopes created by rockfalls from the high (150 to 350 m) cliffs, and at the southern and northern ends by the shingle beaches of Westwindstranda. Abrasion by the action of the sea on the seaward cliff of Nyrøysa above Westwindstranda is pronounced and ongoing, with an estimated 50-100 m lost from 1966-1979, and 6-9 m disappearing in places from 1996/97-1998/99. All recent research expeditions to Bouvetøya have been based at Nyrøysa, since it is the most accessible part of the island and supports breeding populations of seabirds and seals.

Bouvetøya is positioned in the cold waters south of the Antarctic Polar Frontal Zone. With a mean annual air temperature range at sea level of -2.7 – 1.6°C, the polar marine climate of the island is characterised by small daily and seasonal temperature variations. An automatic weather station has been in place at Nyrøysa since 1977.

The vegetation of Bouvetøya is entirely non-vascular, and consists of ascomycetes and lichens (Fungi), and mosses and liverworts (Bryophyta). Algae are also represented. Engelskjøn (1981) classifies the vegetation of Bouvetøya into 20 communities, including those of snow algae on glaciers and two of marine algae in the littoral zone. It is of typical maritime Antarctic composition and structure, and bears phytogeographical relations to the vegetation of more westerly peri-Antarctic archipelagos like the South Sandwich and South Shetland

Islands. Owing to the extensive ice covering of Bouvetøya, the vegetation is largely restricted to the coastal cliffs, capes and boulderine beaches, and the few ice-free nunatak ridges and sections of summit plateau. However most ice-free areas are so steep and exposed to avalanches that only crustose lichen and algal formations are able to persist. Five moss species, five lichen species, one fungus species, and 20 algal species have been recorded occurring at Nyrøysa. Here the manuring from seabirds and seals promotes development of algal *Prasiola* and *Ulothrix* communities, but where trampling from penguins and seals occurs, no macro-vegetation is able to exist.

Only seven species of free-living terrestrial arthropods have been recorded at Bouvetøya. Three of these species belong to Collembola (springtails), and four to Acari (mites). Oligochaet worms (Annelida) are common under rocks in the Nyrøysa Antarctic Fur Seal *Arctocephalus gazella* colony.

Birds

To date 12 bird species - all seabirds - have been recorded breeding at Bouvetøya (Table 1). The Slenderbilled Prion *P. belcheri* is currently suspected of breeding at Nyrøysa, and earlier authors suspected breeding by the Kelp Gull *Larus dominicanus*. There has been no recent confirmation of breeding by Southern Giant Petrel *Macronectes giganteus*, Adélie Penguin *Pygoscelis adeliae*, Antarctic Tern *Sterna vittata* and Snow Petrel *Pagodroma nivea*. The infrequency of surveys makes it possible that these species continue to breed at the island, and also hampers estimation of whole-island population numbers for confirmed breeding species. In the summer seasons of 1996/97 and 1998/99 Southern Giant Petrels were common at Nyrøysa, and Antarctic Terns and Snow Petrels were less frequently seen. In 1998/99 Adélie Penguins were recorded at Nyrøysa.

Excepting those species suspected of breeding, 19 species have been recorded as summer visitors to the island and its nearby waters: King Penguin *Aptenodytes patagonicus* (moulters), Wandering Albatross *Diomedea exulans*, Lightmantled Albatross *Phoebetria palpebrata*, Sooty Albatross *P. fusca*, Blackbrowed Albatross *Thalassarche melanophris*, Greyheaded Albatross *T. chrysostoma*, Yellownosed Albatross *T. chlororhynchos*, Northern Giant Petrel *M. halli*, Antarctic Petrel *Thalassoica antarctica*, Blue Petrel *Halobaena caerulea*, Fairy Prion *P. turtur*, Softplumaged Petrel *Pterodroma mollis*, Kerguelen Petrel, *P. brevirostris*, Whiteheaded Petrel *P. lessonii*, Whitechinned Petrel *Procellaria aequinoctialis*, Great Shearwater *Puffinus gravis*, Common Diving Petrel *Pelecanoides urinatrix*, South Polar Skua *Catharacta maccormicki*, and Arctic Skua *Stercorarius parasiticus*.

The island holds globally significant numbers of Southern Fulmars *Fulmarus glacialoides* (an estimated 10^4-10^5 individuals), breeding on the cliffs in large numbers at especially Kapp Valdivia, Kapp Circoncision, Nyrøysa, and the southwest part of the island from Norvegiaodden to Rustadkollen. Nyrøysa alone possibly also supports globally significant numbers of breeding Blackbellied Storm Petrels *Fregetta tropica* (an estimated 10^2-10^3 individuals).

Other than Nyrøysa, the major penguin colonies at Bouvetøya are situated at Posadowskybreen, Kapp Circoncision, Norvegiaodden and Larsøya (a small rocky offshore islet situated to the southwest of Bouvetøya) (Fig. 1). The Kapp Circoncision colony is the largest, with an estimated 25 000 individuals recorded in 1989/90. In 1978/79 there were an estimated 117 000 penguins at Bouvetøya, the majority being Macaroni Penguins *Eudyptes chrysolophus*, with Chinstrap Penguins *P. antarctica* making up the bulk of the remainder. An estimated total 62 125 individuals were recorded in 1989/90. Owing to the infrequency of the surveys, and because the methods may not be directly comparable, an inferred annual whole-island decline of 5.6% over the 11 years from 1979/80 to 1989/90 should be treated with extreme caution. However, over the same period, more detailed surveys at Nyrøysa indicate a decline of 4.8% p.a. in penguin numbers. Subsequent data from the 1990s suggest an accelerated rate of decline since 1989/90 at Nyrøysa. Aerial surveys also suggest that declines may have continued elsewhere at the island in the 1990s, but not necessarily for the same reasons. Over the same period numbers of Antarctic Fur Seals have increased substantially at Nyrøysa.

Other threatened/endemic wildlife

No recognised globally endangered (IUCN) or endemic animal taxa occur at Bouvetøya, but at least three endemic ascomycetes species have been recorded, and three lichen species including an endemic genus *Bouvetiella*. Other plant and invertebrate species are restricted to a few other Antarctic sites (e.g. South Georgia, South Orkney Islands) and thus can be considered near-endemics.

Based on population declines elsewhere, but mirrored to some extent at Bouvetøya, the Macaroni Penguin is included in *Threatened birds of the World* (BirdLife International 2000) as Vulnerable. Using IUCN criteria, Ellis et al. (1998) include both the Chinstrap and Adélie Penguin as Lower Risk.

Breeding by Southern Elephant Seals *Mirounga leonina* at Bouvetøya was reconfirmed in 1998/99 for the first time in many years; 88 weaned pups were counted at Nyrøysa on 11 December 1998. In January 1999 there were an estimated 13 010 live fur seal pups (15 665 including dead pups) at Nyrøysa, slightly more than the estimated 12 528 present in January 1997. After global near-extinction earlier this century, fur seal numbers are currently stable or increasing at other sites throughout the Antarctic and sub-Antarctic. Humpback Whales *Megaptera novaeangliae* were frequently sighted from Nyrøysa in the summers of 1996/97 and 1998/99, and Killer Whales *Orcinus orca* have been recorded previously.

Conservation Issues

The Norwegian Polar Institute is the environmental administrative authority for Bouvetøya. The island and surrounding territorial waters of four nautical miles was declared a Nature Reserve by Royal Decree in 1971. The pertinent regulations protect the landscape of the reserve from physical encroachment and disturbance, and protect the flora and fauna against unnecessary disturbance (although fur seals have been protected since 1935). Additionally, species alien to the Reserve are not to be introduced, terrestrial and airborne landings are prohibited without permission, and disposal of waste at the island is prohibited.

As of 1997, Nyrøysa (incorporating the platform and northern and southern beaches of Westwindstranda) has been declared a CEMP (CCAMLR Ecosystem Monitoring Programme) site. A draft management plan exists but is not yet in force. The designation of Nyrøysa as a CEMP site supports the objectives of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) to establish a network of sites throughout the Southern Ocean for conducting long-term monitoring of the foraging ecology, demography and population trends of vertebrate predator populations. Norwegian and South African biologists have co-operated in two CEMP expeditions to date, in 1996/97 and 1998/9, where monitoring of Macaroni and Chinstrap Penguins and Antarctic Fur Seals was undertaken.

A source of unprecedented concern for seabird populations throughout the Southern Ocean is the current expansion of commercial longline fisheries. CCAMLR approved a New Longline Fishery for toothfish *Dissostichus spp.* in CCAMLR Statistical Subarea 48.6, into which Bouvetøya falls, in 1997. The catch limit for *D. eleginoides* was set at 888 tons for the area north of 65°S, but no catches were reported to CCAMLR for the period July 1997 - June 1999. There is no information on unregulated fishing. Although the island is not known to support breeding populations of species likely to incur incidental mortality from longline activities (mainly albatross and large petrel species) with the possible exception of Southern Giant Petrels, birds visiting the waters will be at risk unless suitable mitigation measures are employed, and fishing gear that is improperly disposed of will be an entanglement hazard for fur seals.

A contributing factor to the declines in recent years of penguin numbers at Nyrøysa has been the expanding fur seal population. Fur seals impact upon penguins in at least three ways: interference competition on land for breeding territories, incidental injury and mortality in disputes over breeding territories, and predation at sea. However, inferred long-term declines elsewhere at the island, where fur seals do not breed, suggests that larger-scale impacts such as oceanographic change or competition for food may be important contributory factors, although there is no evidence to support either. Expansion of the fur seal colony at Nyrøysa has also resulted in destruction of *Brachythecium* moss hummocks, and the cessation of breeding by Southern Giant Petrels.

With Nyrøysa being one of the most important areas for breeding birds at Bouvetøya, the ongoing loss of the seaward cliff is of concern. Should the platform retreat until nothing but the inland scree slope remains, it is conceivable that most, if not all, breeding by Macaroni and Chinstrap Penguin, Blackbellied and Wilson's Storm Petrel, Subantarctic Skua, and Antarctic and Slenderbilled Prion will cease at Nyrøysa.

There are no records of introduced flora or fauna occurring at Bouvetøya. With the island being only slightly modified and remaining in essentially a natural state, the conservation value of Bouvetøya is high.

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Table 1. Birds breeding at Nyrøysa, Bouvetøya.

Species		Estimated active breeding population (pairs unless otherwise stated)[a]
Possibly 1% or more of global population		
Blackbellied Storm Petrel	*Fregetta tropica*	10^2–10^3 (individuals)
Other important populations[b]		
Macaroni Penguin	*Eudyptes chrysolophus*	1670
Chinstrap Penguin	*Pygoscelis antarctica*	220
Southern Fulmar	*Fulmarus glacialoides*	5720[c]
Pintado Petrel	*Daption capense*	380[d]
Antarctic Prion	*Pachyptila desolata*	10^2–10^3 (individuals)
Slenderbilled Prion	*P. belcheri*	suspected breeding at Nyrøysa
Wilson's Storm Petrel	*Oceanites oceanicus*	10^1
Subantarctic Skua	*Catharacta antarctica lonnbergi*	38

[a] Data from 1996/97 and 1998/99

[b] The following species do not breed at Nyrøysa, but are suspected of breeding elsewhere at the island: Southern Giant Petrel *Macronectes giganteus*, Snow Petrel *Pagodroma nivea*, and Antarctic Tern *Sterna vittata*

[c] Only ca. 55 pairs on Nyrøysa itself, remainder on cliffs at southern and northern end of Nyrøysa

[d] Figure given is for the platform only. An estimated additional 100 pairs breed elsewhere on the cliffs surrounding Nyrøysa

Appendix B

Studies of seabirds and seals at Bouvetøya 1996/97

Isaksen, K., Hofmeyr, G.J.G., Dyer, B.M., Huyser, O. & Næstvold, A. 1997. Studies of seabirds and seals at Bouvetøya 1996/97. In: Report of the Norwegian Antarctic Research Expedition 1996/97. J-G Winther (Ed.). Norsk Polarinst. Medd. 148. Oslo: Norsk Polarinstitutt. pp. 21-29.

Introduction

The early history of harvesting of biological resources in the Antarctic was dominated by over-exploitation. Several species of baleen whales and fur seals were especially targeted. The *Convention on the Conservation of Antarctic Marine Living Resources* (CCAMLR) was established in 1980 to control the harvest of marine living resources in the Antarctic. The increasing interest in krill fisheries (mainly Antarctic krill *Euphausia superba*) at that time was of particular concern. Krill is a key species in the Antarctic marine ecosystem and many species of penguins, seals and whales rely on a high availability of krill for food. A significant harvest of krill by humans may thus have negative effects on species preying on krill.

To obtain information on the harvest of both krill and fish, and the effects of this harvest on other species in the ecosystem, the *CCAMLR Ecosystem Monitoring Program* (CEMP) was instituted. Monitoring of several species of seabirds and seals that prey predominantly on krill are important parts of the CEMP-program today. Several aspects of the biology of these species that are thought to be sensitive to changes in the availability of food are included in the program. Monitoring programs following standard CCAMLR methods have been implemented by a number of Antarctic Treaty states at sites throughout the treaty area.

Bouvetøya is the only land within a considerable portion of the South Atlantic. Large numbers of seabirds and seals aggregate on the island to breed during summer. The dynamics of these populations have been little studied. To gain more information concerning penguins and fur seals and to be able to assess the effects of future krill fisheries in the ocean around the island, the Norwegian Ministry of the Environment decided to start a CEMP monitoring program at Bouvetøya in the 1996/97 field season. The responsibility for carrying out the monitoring program was given to the Norwegian Polar Institute.

The expedition ship R/V *Polar Queen* arrived at Bouvetøya on 9 December 1996. The five members of the expedition to the island were Bruce M. Dyer, Onno Huyser (both South Africa), Greg Hofmeyr (Norway/South Africa), Kjell Isaksen and Alf Næstvold (both Norway). The *Polar Queen* returned to Bouvetøya on 22 February 1997 to collect the team.

A more thorough presentation of the monitoring program at Bouvetøya and preliminary results from the 1996/97 season can be found in Isaksen et al. (1997a,b).

Objectives

The objective of the project was to establish a monitoring program (CEMP) for penguins and fur seals on Bouvetøya. This was to be the first of a number of seasons during which populations on the island would be monitored. In addition to the CEMP program other work on seabirds and seals was to be carried out.

A research station was to be built at the study site to accommodate the researchers working on the monitoring program.

Study area

Bouvetøya is a small (10x7 km), isolated island in the South Atlantic (54°25'S, 3°20'E). It is of volcanic origin, situated on the Mid-Atlantic Ridge. Most of the island (93%) has permanent ice cover (Orheim 1981), but some ice-free areas exist along the coast, especially in the western parts of the island. The wildlife on the island is concentrated in these areas.

Twelve species of seabirds have thus far been recorded breeding on the island. Among the most numerous are Chinstrap Penguins (*Pygoscelis antarctica*), Macaroni Penguins (*Eudyptes chrysolophus*), Southern Fulmars (*Fulmarus glacialoides*), Pintado Petrels (*Daption capense*), Blackbellied Storm Petrels (*Fregetta tropica*), Antarctic Prions (*Pachyptila desolata*) and Subantarctic Skuas (*Catharacta antarctica lonnbergi*). Antarctic Fur Seals (*Arctocephalus gazella*) maintain a large breeding population on the island. Southern Elephant Seals (*Mirounga leonina*) are common on some beaches of the island during summer moult, but it is not known whether they breed on the island at present. Few studies, apart from a number of counts of birds and seals made during earlier visits to the island, have been completed.

A large landslide between 1955 and 1958 formed a new area of relatively flat land on the western side of the island (Prestvik & Winsnes 1981). The new beach, Westwindstranda, together with the plateau Nyrøysa, comprise almost the only relatively flat, ice-free areas on Bouvetøya. Westwindstranda/Nyrøysa also provides the only suitable camp site on the island. Westwindstranda and Nyrøysa were quickly colonised by penguins and fur seals, and these areas now constitute suitable sites for studying these species.

Erection of the field station

After the arrival of the R/V *Polar Queen* at Bouvetoya on 9 December 1996, a group of people were transported to Nyrøysa by helicopter to find the best site to erect the field station. This was duly selected 60 m from the coastline and close to a small hill. The main penguin colonies and seal breeding areas on Nyrøysa were situated nearby, on the other side of the hill. These areas were therefore out of sight of the station and well protected from noise and other direct disturbance from the station area.

The work on the main lodging unit started early the next day when all equipment was transported to Nyrøysa. The completed hut consists of seven prefabricated sections of steel mounted on a frame with eight legs. It measures three by nine meters and has a total weight of six tons. It contains beds for four persons, a small office section with two desks, and a kitchen section. A smaller container for a generator was placed at some distance from the main hut. A 10 kW diesel generator supplies electricity for lighting, heating, office equipment and a deep freezer for storing scientific samples. Communication with the rest of the world was established by satellite (phone, telefax and e-mail) as well as with HF-radio. In addition to the main hut, tents were erected to provide space for storage of equipment and additional room for working and sleeping.

The purpose of the station will be to provide accommodation and working facilities for personnel engaged in CEMP-related work. It accommodated five people and served its purpose very well during the 2½ month stay in 1996/97.

Field work and preliminary results

The first period on the island after arrival on 10 December was devoted to carrying out practical work required to set up the station, after which the scientific work started. The field work was terminated on 22 February 1997 when the ship returned to pick up the expedition members.

Standard methods have been developed by CCAMLR to be used at all sites participating in the CEMP-program (CCAMLR 1992). The monitoring program at Bouvetøya follows these methods. For Chinstrap and Macaroni Penguins the program involves monitoring six different biological parameters, whereas only two are monitored for Antarctic Fur Seals.

CEMP-work on penguins

Breeding population size (CEMP Standard Method A3)

The breeding colonies of Chinstrap and Macaroni Penguins at Nyrøysa were sectioned into separate plots. For each plot the number of incubated nests, the number of occupied (but not incubated) nests, and the total number of birds were counted separately at least three times. The monitoring included all breeding penguins at Nyrøysa, but none in other areas of the island.

The resulting numbers were considerably lower than previous counts from the late 1970s to the early 1990s (Haftorn et al. 1981, Watkins 1981, Bakken 1991), especially for Chinstrap Penguins.

Age-specific annual survival and recruitment (A4)

A relatively small number of Chinstrap (54 breeding adults and 50 chicks) and Macaroni Penguins (100 breeding adults and 50 chicks) were banded with flipper bands for a long-term study of individual survival. Few individuals were banded due to uncertainty about the suitability of the flipper bands.

Duration of foraging trips (A5)

VHF radio transmitters (Advanced Telemetry Systems) were attached to 40 Chinstrap and 40 Macaroni Penguins with chicks. The transmitters were attached to the backs of the birds with fast-setting epoxy. The presence of these penguins in the breeding colony at Nyrøysa was monitored by a VHF-receiver/data-logger system (RX-900, Televilt Int.) during parts of January and February 1997 at 10–30 minute intervals.

A preliminary analysis of some of the data shows that Chinstrap Penguins making foraging trips departed from the colony in the morning and generally returned in the evening the same day. Macaroni Penguins made foraging trips of longer duration, often lasting more than 24 h. This was especially so for the first major foraging trip made by male Macaroni Penguins during the chick-rearing period; these trips lasted for several days.

Breeding success (A6)

The number of chicks and adults in the colonies at Nyrøysa was counted in the period 4–7 February. At least three separate counts were made in the same plots that were used to determine breeding population size. The breeding success of the Macaroni Penguins seemed to be very low in the northern parts of the colony, probably due to interactions with fur seals, whereas the breeding success of the Chinstrap Penguins generally seemed to be high.

Chick diet (A8)

Food samples from two Chinstrap and five Macaroni Penguin adults were collected every five days during the chick period. The low number of Chinstrap Penguins sampled was due to the low number of breeding pairs of this species on Nyrøysa. The food was sampled by stomach pumping (Wilson 1984) adults when they arrived at the colony from the sea to feed their chicks. All samples were collected between 1800 and 1930 h 'local time' (GMT+1h). Samples were preserved in alcohol (Chinstrap Penguins) or frozen (Macaroni Penguins).

The Chinstrap Penguins had taken almost exclusively *E. superba* as prey. Macaroni Penguins on the other hand fed mostly on fish, with *E. superba* constituting an important part of the diet for some birds in some periods.

Breeding chronology (A9)

The timing of important breeding events (*e.g.* egg-laying and hatching) may vary from year to year depending on snow melt, ice conditions and other environmental factors. Information on the timing of breeding is important for interpreting the results of other monitoring parameters, for instance breeding population size.

About 50 Chinstrap Penguin and 100 Macaroni Penguin nests were marked and checked every other day. The presence of eggs or young was noted for each nest, as well as whether the chicks were guarded by an adult or not. The mean hatching dates of both Chinstrap and Macaroni Penguins were at the very end of December. The Macaroni Penguins generally hatched later and were more synchronous than the Chinstrap Penguins.

CEMP-work on Antarctic fur seals

Duration of adult female foraging/attendance cycles (C1)

Forty-five adult females, seen to be suckling pups, were captured, either with a choker pole or hoop net (David & Meyer 1990). VHF radio transmitters (Advanced Telemetry Systems) were attached midway between the shoulders of each animal with fast-setting epoxy. The seals were then tagged with flipper tags and released. The presence of the instrumented females on shore was recorded by the automatic VHF-receiver/data-logger system (RX-900, Televilt Int.) over 39 days from 12 January to 19 February. The station searched for each frequency at 10-30 minute intervals. The data from 36 VHF transmitters yielded the durations of 223 complete foraging trips and 223 complete shore attendance periods.

Pup growth (C2)

Two methods were used. (1) Pups (77 ind.) were caught, marked and weighed at birth. Throughout the season, animals from this group were opportunistically recaptured and re-weighed. (2) Random samples of 100 pups each were weighed at 30, 60 and 74 days after mean pupping date. Mean weights for each sex were calculated using both methods. The results obtained from the two procedures for measuring pup growth rates differ. Procedure 1 is usually the more accurate of the two as it requires repeated sampling of individual pups, whereas procedure 2 does not. In the case of the Bouvetøya study, however, its accuracy was compromised because of the timing of birth of the sampled pups; they were born at the end of the season. Timing does not impact on procedure 2 as the samples of pups are weighed on specific dates.

Additional projects

In addition to the monitoring program other work on seabirds and seals was carried out during the stay on the island. Some of this work is listed below.

General registration of the wildlife on the island

Records were kept of sightings of less common birds and mammals. Antarctic Prion and Wilson's Storm Petrel (*Oceanites oceanicus*) were confirmed breeding on the island for the first time (see Bakken 1991 for breeding of unidentified prions). Subantarctic Fur Seal, *A. tropicalis*, was recorded on the island for the first time. Humpback Whale (*Megaptera* *novaeangliae*), Wandering Albatross (*Diomedea exulans*) and Light-mantled Sooty Albatross (*Phoebetria palpebrata*) were regularly seen from Nyrøysa. Several King Penguins (*Aptenodytes patagonicus*) stayed at Westwindstranda to moult.

Breeding biology of seabirds

Investigations of breeding biology of Southern Fulmars, Pintado Petrels, Blackbellied Storm Petrels and Subantarctic Skuas were carried out. For all species a number of nests were monitored and hatching dates, chick growth, breeding success and causes of failure recorded. See Huyser et al. (1997) for results of the work on Pintado Petrels.

Seabird and fur seal diets

Stomach samples were collected from breeding Southern Fulmars, Pintado Petrels, Antarctic Prions and Blackbellied Storm Petrels for analysis of prey composition. Diets from Southern Fulmars and Pintado Petrels were sampled from adults, using a modified water-offloading technique similar to that used on penguins, when they returned to feed their chicks. Following CEMP procedures five samples were collected every five days over the chick-rearing period for Pintado Petrels. Only five diet samples were obtained from Southern Fulmars due to the low number of accessible nests and few pairs still breeding at that stage. Diets from Antarctic Prions and Blackbellied Storm Petrels were obtained from birds caught in mist nets. They were induced to regurgitate and the samples collected and frozen. Krill was an important part of the diets of all these species, with other prey (fish and other euphausiids) less important.

Pellets from Subantarctic Skuas were collected for analysis of predation rates, and for analysis of ingestion of plastic particles by Blackbellied Storm Petrels.

Ninety Antarctic Fur Seal scats were collected. Most of the scats contained krill and 17 yielded the remains of fish, as yet unidentified. Two scats contained feathers (possibly from penguins).

Diving Behaviour of Penguins

Two types of devices were used to study the foraging behaviour of penguins. Time-depth recorders (Wildlife Computers Mk5-type microprocessor-controlled TDR) were fitted to four Chinstrap and four Macaroni Penguins rearing chicks. The instruments weighed 50 g and were glued onto the lower back of the penguins with fast-setting epoxy. Depth and temperature were sampled every five seconds. The instruments were removed from the penguins to download the data after 5 to 14 days. The depth resolution of the instruments was 2 m. Only dives deeper than 4 m were included in the analysis in order to exclude travelling dives (cf. Bengtson et al. 1993).

Data-logger time-depth-recorders (TDRs) (Driesen and Kern, Bad Bramstedt, Germany) were fitted to both Chinstrap and Macaroni Penguins. The data loggers were set to record water/air temperature, light intensity, depth, swim speed and three-dimensional compass readings, but the swim speed and compass sensors all failed. A total of 18 complete foraging trips from eight female Macaroni Penguins were logged, and four incomplete foraging trips from two Chinstrap Penguins.

Preliminary results from the first type of devices show that Macaroni Penguins generally made deeper dives and dives of longer duration than Chinstrap Penguins. This is probably a consequence of the different diets of the two species.

Diving behaviour of fur seals

Wildlife Computers (Redmond, USA) Mk5-type microprocessor-controlled Time-Depth Recorders were deployed on three adult female Antarctic Fur Seals nursing pups between 8 January and 12 February 1997. The animals were caught and restrained using a hoop net and the TDR applied directly to the fur midway between the shoulders using a fast-setting epoxy. The animals were then tagged and released after 10 minutes. Data was downloaded onto a computer either in the field while restraining the animal with the hoop net or after removal of the device from the animal. The TDR sampled depth at five second intervals, and temperature and light level at 60 second intervals. Only dives that achieved a depth of five metres or more were analysed.

Diving behaviour of the three study animals was recorded over 12, 14 and 21 days, giving a total of 47 days of data. During this time 8003 dives of a depth of five or more metres were recorded from 13 complete and 2 partial foraging trips.

Ringing and tagging

Antarctic Prions, Blackbellied Storm Petrels (adults) and Subantarctic Skuas (adults and chicks) were captured and ringed for estimation of survival rates. Recaptures of Antarctic Prions will be used to estimate local population size at Nyrøysa.

In total, 193 adult female, 1 subadult and 478 pup Antarctic Fur Seals were tagged to provide supplementary data on attendance patterns and as part of a long-term project on survival rates and dispersal.

Morphometric analysis

Extensive morphological measurements (body mass, wing length, tarsus length, head length and several measurements of bill morphology) were taken from a sample of the birds captured for ringing. Measurements of eggs of all species of seabirds accessible on Nyrøysa were taken.

One Southern Elephant Seal skull and approximately 80 Antarctic Fur Seal skulls were collected for morphometric analysis.

Collection of material for analysis of genetics and pollutants

Fifty-one blood samples were obtained from several species of seabirds. The species sampled were Chinstrap Penguin, Macaroni Penguin, Southern Fulmar, Pintado Petrel, Antarctic Prion, Wilson's Storm Petrel, Blackbellied Storm Petrel and Subantarctic Skua. Blood samples were also taken from Antarctic Fur Seals. In addition, genetic material in the form of biopsy samples from fur seals, and skin samples from Southern Elephant Seals were taken.

Milk and blood samples from nursing adult female Antarctic Fur Seals, and blood samples from their pups, were taken for studies on pollutants.

Estimation of pup production

A mark-recapture experiment was conducted to determine the number of Antarctic Fur Seal pups on Nyrøysa. A total of 1669 pups distributed evenly throughout the colony were marked with paint, and the proportion of marked and unmarked pups recorded at two later counts in the colony.

Counts of Southern Elephant Seals

Weekly counts of Southern Elephant Seals were completed. The maximum number hauled out (on the 6 January) was 171 adult females, 71 sub-adult males, 1 sub-adult female, 101 sub-adults of undetermined sex, and 6 yearlings.

Recordings of vocalisations

Vocalisations of Antarctic Fur Seal adult males, and adult female-pup pairs, were recorded for comparison with other populations. Recordings were also made of calls of several seabird species.

Marine debris

Surveys of beached marine debris were conducted according to guidelines approved by CCAMLR. In addition, records were kept of seals (and seabirds) entangled in man-made material (such as nets).

Collection of seaweed

Seaweed washed up on the beach was collected to investigate which species of seaweed and seaweed epiphytes are found around the island.

Conclusion

The field work at Bouvetøya was very successful. The planned work on the monitoring project on penguins and fur seals were completed, as well as most of the additional work that was planned. The field station was successfully erected during the first days of the stay at the island, and the logistics at the station also functioned very well. The island proved to be a promising site for further studies of seabirds and seals.

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Appendix C

Studies of seabirds and seals at Bouvetøya 1998/99

Isaksen, K., Huyser, O., Kirkman, S., Wanless, R. & Wilson, W. 2000. Studies of seabirds and seals on Bouvetøya 1998/99. Norsk Polarinst. Internrapp. 2. Tromsø: Norsk Polarinstitutt.

Summary

Field studies were carried out at Bouvetøya from 9 December 1998 to 27 February 1999. The main objective for the 1998/99 expedition was to continue the CEMP-monitoring work initiated in 1996/97. The species monitored were Chinstrap Penguin (*Pygoscelis antarctica*), Macaroni Penguin (*Eudyptes chrysolophus*) and Antarctic Fur Seal (*Arctocephalus gazella*). In addition to the CEMP-work, other work on seabirds and seals was carried out, including diving behaviour of penguins, and studies of diet and pup production of fur seals. The following CEMP-parameters were studied in Chinstrap Penguin and Macaroni Penguin: breeding population size (A3), age-specific annual survival and recruitment (A4), duration of foraging trips (A5), breeding success (A6), chick diet (A8), and breeding chronology (A9). For Antarctic Fur Seals, data were collected on the duration of adult female foraging/attendance cycles (C1) and pup growth (C2).

Introduction

Bouvetøya (54°25'S, 3°20'E) is a small island situated in an isolated part of the South Atlantic. Although large numbers of seabirds and seals aggregate on the island to breed during summer, the dynamics of these populations have been little studied to date. To obtain more information about the populations of penguins and fur seals and to better assess the potential impacts of possible krill fisheries around the island, a suite of monitoring programmes was initiated during the NARE 1996/97 field season. These programmes are part of the *CCAMLR Ecosystem Monitoring Programme* (CEMP), following standard monitoring procedures agreed upon within the framework of the *Convention on the Conservation of Antarctic Marine Living Resources* (CCAMLR). Monitoring following the standard methods is carried out at a number of other sites in the Antarctic (see Agnew 1997). The Norwegian Polar Institute is responsible for carrying out the monitoring at Bouvetøya, in cooperation with the FitzPatrick Institute of African Ornithology of the University of Cape Town and the University of Pretoria.

A more detailed description of the study site and the monitoring programme has been given by Isaksen et al. (1997a,b). Preliminary results from the 1996/97 field season have been presented by Hofmeyr et al. (1997), Huyser et al. (1997), Isaksen et al. (1997a,c), and Mehlum et al. (1998).

The main objective for the 1998/99 expedition to Bouvetøya was to continue the CEMP-monitoring work initiated in 1996/97. The species monitored were Chinstrap Penguin (*Pygoscelis antarctica*), Macaroni Penguin (*Eudyptes chrysolophus*) and Antarctic Fur Seal (*Arctocephalus gazella*). In addition to the CEMP-work, other work on seabirds and seals was carried out.

The South African expedition vessel MV *SA Agulhas* arrived at Bouvetøya on 8 December 1998. Due to strong winds helicopter flights to the island were delayed until the morning of

9 December. The five members of the Bouvetøya team were then flown to Nyrøysa, situated on the western side of the island, in a South African Air Force Oryx helicopter. The helicopter flights were stopped before all the field equipment had been transferred to the island due to increasing winds at the ship's position at the eastern side of the island. The rest of the equipment was transferred the following day when the ship moved to the western side of the island. The expedition team stayed at the field station at Nyrøysa, which was erected during the 1996/97 expedition (see Isaksen et al. 1997a,b). Additional space for sleeping and storage of food and equipment was provided through tents and South African Department of Environmental Affairs and Tourism (DEAT) storage containers. The MV *SA Agulhas* returned to Bouvetøya on 27 February 1999. The transfer of expedition members and equipment from Bouvetøya to the ship was carried out without delay the same day.

Field work and preliminary results

Monitoring of penguins

The monitoring of Chinstrap and Macaroni Penguins at Nyrøysa follows the standard methods that have been developed for the CEMP (CCAMLR 1997). Six different biological parameters are monitored.

Breeding population size (CEMP Standard Method A3)

The monitoring includes all breeding penguins at Nyrøysa, but none occurring elsewhere at the island. The number of incubated nests and the number of occupied (but not incubated) nests were counted separately at least three times on 17 December 1998. Following the CEMP procedure, birds that appeared to be incubating were not disturbed to verify the nest contents.

For Macaroni Penguins the number of incubated nests counted in 1998/99 (1344) was higher than the number from 1996/97 (1047), whereas the number of incubated Chinstrap Penguin nests was lower in 1998/99 (192 compared to 205).

According to the CEMP Standard Methods the censuses are to be performed one week after peak egg-laying. This was not possible in 1996/97 or 1998/99 because of the expedition team's arrival at the island, well after peak egg-laying. Censuses performed late in the season will give lower numbers of incubated nests than censuses performed early in the season as the number of incubated nests will decline as the season progresses. This trend will be particularly pronounced at Nyrøysa as interactions with seals result in a substantial number of failures during incubation. The census in 1996/97 was made about nine days later than in 1998/99. It is therefore likely that some of the increase in the number of incubated Macaroni Penguin nests is a consequence of the different census dates. Similarly, the decline in the number of incubated Chinstrap Penguin nests between the two seasons may be larger than indicated by the survey data. A census of the number of incubated Chinstrap Penguin nests on 30 December 1998 gave approximately 159 nest, a decline of 17% over the 13 days from 17 December.

There are often difficulties classifying nests into the three categories of incubated nests, occupied nests and unoccupied nests. The distinction between the two latter especially becomes increasingly difficult and subjective as the breeding season progresses. The number of occupied nests probably also varies considerably with time during the day and over the course of the season. These factors are likely to account for a large difference between the 1996/97 and 1998/99 census in the number of occupied Macaroni Penguin nests.

The penguin breeding colonies at Nyrøysa are situated on slopes leading up from the large Antarctic Fur Seal colony, bordering the sea. From 6 to 9 metres of the cliff area upon which the colonies are situated have been washed away by the sea since 1996/97 (measured at three points assumed to be representative for the colony). The trend of penguins being displaced by fur seals, especially at the periphery of the breeding colonies, has also continued since 1996/97. Several sub-colonies have fewer breeding pairs, have disappeared altogether, or are becoming progressively fragmented through male fur seals holding breeding territories in the more accessible, flatter parts. In some places little affected by seals, the Chinstrap Penguins (and to a lesser degree also Macaroni Penguins) have expanded their breeding area inland or settled in new areas.

Age-specific annual survival and recruitment (A4)

A relatively small number of penguins was banded with S-series flipper bands (Lambournes Ltd.) in 1996/97 for a long-term study of individual survival. In total, 104 Chinstrap Penguins (54 adults and 50 chicks) and 150 Macaroni Penguins (100 adults and 50 chicks) were banded. The low number of individuals banded was due to uncertainty about the suitability of the flipper bands. Observations in 1996/97 and 1998/99 indicated that an unacceptably high proportion of these bands had opened somewhat on the flipper and/or caused feather abrasion to the birds wearing them. An unknown proportion of the banded birds had lost their bands (one band was found on the ground in the Macaroni Penguin colony).

Lambournes now produces flipper bands made of stronger metal and with improved design. Bands of this type (A-series) were used to band 99 adult and 100 young Macaroni Penguins in 1998/99. Based on experience with banding African Penguins (*Spheniscus demersus*) in South Africa, it is hoped that the A-series bands will not have a significant impact on penguin survival, and that they will have improved longevity compared to the previous S-series bands.

Duration of foraging trips (A5)

VHF radio transmitters (Advanced Telemetry Systems) were attached to both females and males in 19 Macaroni Penguin pairs with chicks. Similarly, both members of 19 Chinstrap

Penguin pairs and one additional male were instrumented. Fast-setting epoxy was used to attach the instruments to the lower backs of the Macaroni Penguins, whereas Tesa tape was used on the Chinstrap Penguins. The tape attachments were made using a modified version of Method 3 described by Wilson et al. (1997), without using glue. The Tesa tape functioned equally well or in some respects even better than the epoxy over the 36–50 days the tape attachments lasted. The presence of the instrumented penguins in the breeding colony at Nyrøysa was monitored by a VHF-receiver/data-logger system (RX-900, Televilt Int.) during most of January and February 1999 at 10-minute intervals. One of the instrumented Macaroni Penguin females was killed by a fur seal. Another was seen seriously wounded from a bite and probably died later as a result of the injuries. One Macaroni Penguin female lost its transmitter and was subsequently refitted with a new instrument. Of the 39 instruments attached to Macaroni Penguins, 37 were retrieved at the end of the season. Thirty of 39 Chinstrap Penguin instruments were retrieved.

Breeding success (A6)

The number of penguin chicks at Nyrøysa was counted on 7–8 February 1999. The number of Macaroni Penguin chicks in 1998/99 was similar to that in 1996/97 (824 compared to 812). Chinstrap Penguins produced fewer chicks in 1998/99 than in 1996/97 (157 compared to 247). A considerable portion of the area occupied by breeding Chinstrap Penguins in 1996/97 was eroded by the sea by 1998/99, and some of the new areas that the penguins had started to use were quite steep. This has probably resulted in a higher rate of loss of eggs and young chicks. It may also have made them more susceptible to disturbances from human activities (e.g. helicopter flights and research activity).

Counts of chicks do not have the same sources of error as described above for counts of adults/nests. These numbers are therefore easier to compare between seasons. Chick production is, however, influenced not only by the number of breeding pairs, but also by food availability, mortality from predation etc.

Chick diet (A8)

Food samples from two Chinstrap and five Macaroni Penguin adults were collected every five days during the chick rearing period (10 January - 19 February). The number of Chinstrap Penguins sampled was low because the breeding population at Nyrøysa was small. Diet samples were collected by stomach pumping (Wilson 1984) adults of both sexes when they arrived at the colony from the sea to feed their chicks. The birds were weighed before sampling, and measured. All samples were collected between ca. 18h30 and 21h30 local time (GMT+1). Samples were preserved in alcohol (Chinstrap Penguins) or frozen (Macaroni Penguins).

Chinstrap Penguins took exclusively crustacean prey items, with Antarctic Krill (*Euphausia superba*) forming the bulk. Macaroni Penguins on the other hand fed mostly on fish, with *E. superba* constituting an important part of the diet in some periods.

Breeding chronology (A9)

Forty Chinstrap Penguin and 101 Macaroni Penguin nests were checked every other day from before hatching until creching. The presence of eggs or young was noted for each nest, as well as whether or not the chicks were guarded by an adult. The mean hatching date (of the first egg) was 31 December for both Chinstrap (range 22 December - 8 January) and Macaroni Penguins (range 20 December - 13 January). This is three days later for Chinstrap Penguins and one day later for Macaroni Penguins compared to the 1996/97 season.

Macaroni Penguin chicks were guarded by at least one of the parents for a mean period of 25 days after hatching (range 18–34 days). The first chick not being guarded was seen on 22 January, and by 3 February all the monitored chicks had been seen unguarded one or more times. The mean date for the cessation of brooding was 25 January. There was no marked termination of the brooding period for Chinstrap Penguins. The chicks seemed to be guarded more by the adults and were left unattended less regularly than Macaroni Penguin chicks.

Monitoring of Antarctic Fur Seals

The monitoring programme for Antarctic Fur Seals at Nyrøysa follows the CEMP standard methods (CCAMLR 1997). Two biological parameters are monitored.

Duration of adult female foraging/attendance cycles (C1)

Forty VHF radio transmitters (Advanced Telemetry Systems) were attached with quick setting epoxy, midway between the shoulders of lactating Antarctic Fur Seal females that were captured with a hoop net. The females were tagged in each foreflipper, and their pups were weighed and marked (with a bleach mark and a single tag). The pups were re-weighed throughout the season, and their growth was compared to control pups, the mothers of which were not fitted with transmitters. An attempt was made to record the first foraging trip of as many females as possible, but as capture and deployment occurred well after the peak of the breeding season (6 December for the South Georgia population), and older and heavier females are known to give birth earlier in the season (Boyd et al. 1990), it is likely that the results of this experiment are not representative of the population as a whole. It is also not as easy to gauge the health of newborn pups as it is for older pups. The newborn pups of 12 instrumented mothers out of 24 died before or during the first foraging trip, and another died some weeks later. All transmitters were retrieved from failed deployments, and redeployed as soon as possible on females whose pups were by that stage more established. Thus, in total, 54 females carried transmitters during the season.

The presence of the instrumented females on shore was recorded by the automatic VHF-receiver/data-logger system (RX-900, Televilt Int.) from 16 December to 26 February. The system searched for each frequency at 10-minute intervals. Thirty of the 40 transmitters were retrieved at the end of the season, and 31 females that had carried transmitters were weighed upon retrieval, in order to investigate the effects of maternal mass on foraging trip length and pup growth.

One female never returned after deployment, but the other 39 transmitters rendered good data. However, one transmitter picked up interference from an old transmitter that had been moulted off in the region of the VHF tower after the 1996/97 expedition, a problem which was only solved in the middle of the season, while another transmitter had been mistakenly deactivated, and only functioned for the last month.

Pup growth (C2)

Two methods were used. (1) Pups were caught, marked (with a bleach mark and a single tag) and weighed at birth, and opportunistically recaptured and re-weighed throughout the season. Eighty-two newborn pups were initially captured, but 24 of these were of VHF mothers. Of the remainder, mortality and tag-loss further reduced the sample size. (2) Random samples of 100 pups each were weighed at 30, 60 and 74 days after the estimated mean pupping date. Mean weights for each sex were calculated using both methods.

Procedure 1 is usually the more accurate of the two as it requires repeated sampling of individual pups, whereas procedure 2 does not. In the case of the Bouvetøya study, however, the accuracy of procedure 1 was compromised (a) because the sampled pups were born near the end of the season, and (b) because sampling of newborns was of necessity biased toward the perimeter of the colony. Temporal and spatial prejudices do not have such an effect on procedure 2, which is also far less disturbing.

Additional projects

In addition to the monitoring programme other work on seabirds and seals was carried out during the stay on the island. Some of this work is listed below.

General registration of the wildlife on the island

Records were kept of sightings of less common birds and mammals. A Gentoo Penguin (*Pygoscelis papua ellsworthi*) was observed at the island for the first time. Several Adélie Penguins (*Pygoscelis adeliae*) and one adult male Subantarctic Fur Seal (*Arctocephalus tropicalis*) were also observed. Several King Penguins (*Aptenodytes patagonicus*) stayed at Nyrøysa to moult. Humpback Whales (*Megaptera novaeangliae*) were seen less regularly and in smaller numbers than in the 1996/97 season.

Breeding biology of seabirds

Investigations of breeding biology of Southern Fulmars (*Fulmarus glacialoides*), Pintado Petrels (*Daption capense*), Blackbellied Storm Petrels (*Fregetta tropica*) and Subantarctic Skuas (*Catharacta antarctica lonnbergi*) were carried out. For all species nests were monitored and hatching dates, breeding success and causes of failure were recorded. Growth of skua and storm petrel chicks was also recorded in 1998/99.

Seabird and fur seal diets

Stomach samples were collected from breeding Antarctic Prions (*Pachyptila desolata*) and Blackbellied Storm Petrels for analysis of prey composition. In 1998/99 few diets from Antarctic Prions and Blackbellied Storm Petrels were obtained from birds caught in mist nets, compared to 1996/97.

Pellets from Subantarctic Skuas were collected for analysis of predation rates on Blackbellied Storm Petrels, and for analysis of ingestion of plastic particles by the storm petrels.

One hundred and twenty three scat samples and 90 regurgitation samples of Antarctic Fur Seals were collected. Most of the scats and regurgitants consisted almost exclusively of krill, although remains of fish and squid were found in a few samples. The samples have yet to be sorted and analysed. A number of scats containing penguin feathers were found, especially on the beach on the southern part of Nyrøysa (Sørstrand), which is predominantly populated by sub-adult and adult male fur seals. The presence of penguin feathers in fur seal scats strongly suggests predation by fur seals on penguins at sea. Thus there are three known impacts at Bouvetøya of fur seals on penguins, the other two being interference competition for nest sites, and incidental mortality and injuries from bites incurred during competition for breeding territories. Ten fur seal carcasses were dissected shortly after death, in order to search for gut parasites and food remains. No food remains were found in any of the stomachs, but nematodes and larval cestodes were found in two stomachs, and adult cestodes were found in several scats.

Diving behaviour of penguins

Two types of devices were used to study the diving behaviour of penguins. Wildlife Computers Mk5-type microprocessor-controlled TDRs were fitted to six Chinstrap (both members of two pairs and one female and one male from two other pairs) and seven Macaroni Penguins (two males during their first long foraging trip and five females) rearing chicks. The instruments weighed 50 g and were glued onto the lower back of the penguins with fast-setting epoxy. Depth was sampled every two or five seconds. Temperature and light were sampled at four or six seconds intervals on some deployments. The instruments were removed from the penguins to download the data after 5 to 19 days (most deployments lasted 5 to 9 days).

Data-logger time-depth-recorders (TDRs) (Driesen and Kern, Bad Bramstedt, Germany) were fitted to both Chinstrap and Macaroni Penguins. The data loggers were set to record water/air temperature, light intensity, depth, swim speed and three-dimensional compass heading. However, sensor failure sabotaged device deployments, and little compass and swim speed data was eventually collected.

Ringing and tagging

Antarctic Prions and Blackbellied Storm Petrels were trapped in mist nets at night and ringed at 10-day intervals between 19 December 1998 and 17 February 1999, as well as during some additional trapping sessions. Breeding and non-breeding Subantarctic Skuas at Nyrøysa were ringed with a standard steel metal ring and a yellow plastic alphanumeric colour ring. Retrapped birds from the 1996/97 season were also colour-ringed. All skua chicks fledged at Nyrøysa were ringed with a standard steel metal ring and a red plastic alphanumeric colour ring. This study investigates survival and recruitment rates of Subantarctic Skuas at Nyrøysa. Southern Fulmars and Pintado Petrels were ringed as part of breeding biology studies started in 1996/97. Some Pintado Petrels were ringed with a red plastic alphanumeric colour ring in addition to the metal ring. The number of each species ringed is summarised in Table 1.

Table 1. Birds ringed at Nyrøysa in 1998/99. Numbers in parentheses are number of colour-ringed birds.

Species	Juv.	Adults	Total
Macaroni Penguin *Eudyptes chrysolophus*	100	99	199
Southern Fulmar *Fulmarus glacialoides*	0	8	8
Pintado Petrel *Daption capense*	0	70 (19)	70 (19)
Antarctic Prion *Pachyptila desolata*	0	84	84
Wilson's Storm Petrel *Oceanites oceanicus*	0	1	1
Blackbellied Storm Petrel *Fregetta tropica*	0	67	67
Subantarctic Skua *Catharacta antarctica lonnbergi*	21 (21)	33 (47)	54 (68)

One colour-ringed Northern Giant Petrel (*Macronectes halli*) was observed at Nyrøysa on 2 February. The bird (a male) was ringed as a chick at Marion Island (Prince Edward Islands) on 29 January 1991. It bred in 1998/99 and was last seen at the breeding site at Marion Island with a fledging chick on 12 January 1999 (D. Nel, pers. comm.). The bird was thus on its post-breeding migration. One Southern Giant Petrel (*Macronectes giganteus*) with a metal ring was also observed at Nyrøysa in February 1999, but was not identified. No giant petrels have ever been ringed at Bouvetøya. These birds are the first records from Bouvetøya of birds of any species ringed elsewhere.

A total of 67 adult female Antarctic Fur Seals were double-tagged, and 144 pups were tagged with only a single tag to minimize the chance of infection. As single-tagged animals have little value in long-term monitoring studies, most of these tags were removed at the end of the study. No foreign tags or brands were observed on fur seals or Southern Elephant Seals (*Mirounga leonina*).

Morphometric data

Morphological measurements were taken from a sample of the birds captured for ringing. Approximately 60 Antarctic Fur Seal skulls were collected for morphometric analysis, 30 for Marthan Bester, University of Pretoria, and 30 for Øystein Wiig, Zoological Museum in Oslo. About 2/3 of the skulls were from intact carcasses of animals that had died recently. The skulls are in storage at Marine and Coastal Management (previously Sea Fisheries Research Institute) in Cape Town. A total of 25 fur seal baculi was collected, together with teeth for ageing them, for Marthan Bester, University of Pretoria.

Collection of material for analysis of genetics and pollutants

Samples of muscle and liver for analysis of contaminants were taken from three Chinstrap and 14 Macaroni Penguins killed by a landslide. Blood samples were taken from 16 Antarctic Prions for genetic analyses.

Estimation of pup production

A mark-recapture experiment was conducted to determine the number of Antarctic Fur Seal pups at Nyrøysa. A total of 1800 pups distributed evenly throughout the colony at the northern beach at Nyrøysa (Nordstrand) were marked with a bleach spot on the head between 5 and 8 January. The proportion of marked and unmarked pups was subsequently recorded during eight replicate counts in the colony from 12 to 15 January. The total estimate for Nordstrand was 12 645 ± 523 (S.E.). Four separate replicate counts were done along the narrow beach south of Nordstrand, giving an estimate of 366 ± 9.8 (S.E.). The total estimate of live pups at this time was thus 13 010, very similar to the figure arrived at two years ago of 12 528. An effort was also made to count dead pups throughout Nyrøysa, in the period 18–20 January. The count was facilitated by marking counted pup carcasses or groups of counted pup carcasses. A total of 2655 dead pups were counted. This count is very much an underestimate, considering the numbers of carcasses which were likely washed away or buried beneath rubble. Adding the two totals gives a figure of 15 665 (a minimum estimate of total pup production) of which 16.9% were dead (a minimum estimate of mortality) by mid-January.

Counts of Southern Elephant Seals

Weekly counts of Southern Elephant Seals were completed. The maximum number counted was 383 individuals on 6/7 January, including 217 adult females, 151 subadults, 14 yearlings and 1 weaned pup. Some 88 weaned pups were counted during the first census after arrival (11 December). Slide photographs were taken of some pups. The highest number of adult females (241) was counted on 14 January.

Recordings of plumage and vocalisations

In addition to recording morphological and plumage characteristics from individuals of the very variable population of Antarctic Prions breeding at Nyrøysa, recordings of vocalisations were made.

Marine debris

Surveys of beached marine debris were conducted according to guidelines approved by CCAMLR. In addition, records were kept of seals entangled in man-made material (such as nets and straps). Out of 27 sightings of entangled seals, all Antarctic Fur Seals, entangling material was removed from 24 seals. Thirteen cases were adjudged to be severe or very severe.

Focal attendance patterns

Eighteen Antarctic Fur Seal mother-pup pairs, as well as additional pups, were marked at a small isolated rookery ("the Rope") on the narrow beach in the middle part of Nyrøysa. Focal studies of attendance were done twice daily for over a month, with opportunistic re-weighing of pups. The aim was to compare pup growth and shore visit duration (using the VHF-based study recordings that coincided with the focals) between this small colony and the large Nordstrand colony, to see whether colony size and density affected attendance patterns.

Conclusion

The planned work on the monitoring project on penguins and fur seals was completed successfully. Because of the late and cold season storm petrels and prions bred late and probably a large proportion of the population (compared to 1996/97) skipped breeding. Some of the planned work on these species therefore had to be cancelled. The field station and the logistics at the station functioned very well.

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