

**The comparative foraging ecology of Royal *Eudyptes schlegeli* and  
Rockhopper *E. chrysocome* Penguins**

by

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BEd, BSc (Hons.)


A thesis submitted in fulfilment of the requirements for the degree of Doctor of  
Philosophy in the Science Faculty, Zoology Department

UNIVERSITY OF TASMANIA

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### **Declaration**

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgment is made in the text of the thesis.

A handwritten signature in cursive script, reading "Cindy Hull".

Cindy Hull

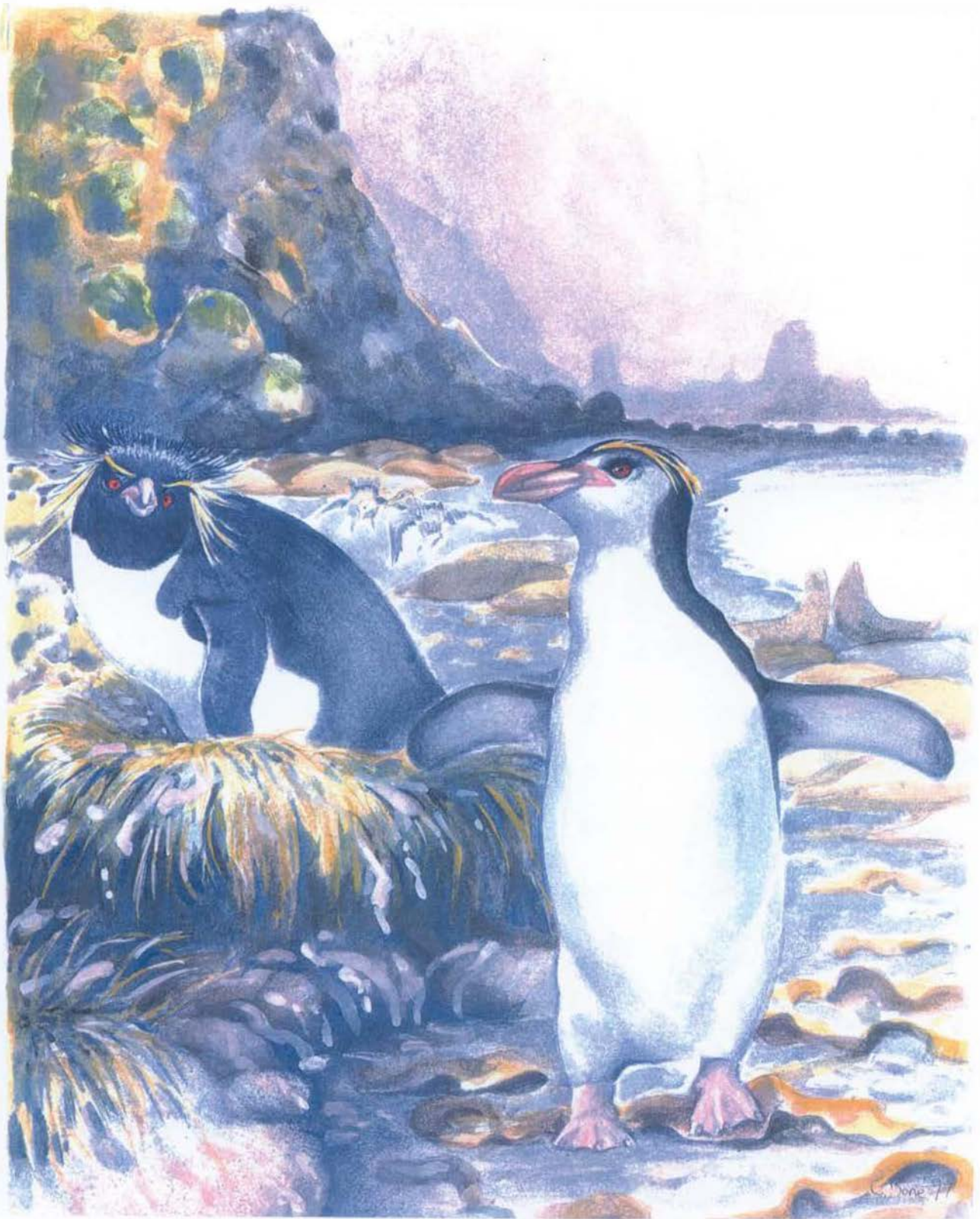
### **Authority**

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## **Frontispiece**

Watercolour inspired by Royal and Rockhopper Penguins at Macquarie Island.

Catherine Bone, May 1997



## Abstract

Penguins are well adapted to the marine environment, spending the majority of their time at sea. Whilst their ecology is intrinsically linked to this environment, details of how they interact with biotic and abiotic aspects of it are not well known for most species. The majority of penguins have a limited breeding season, and commitments at the nest necessitate that their foraging ranges are restricted, presumably placing pressure on prey resources around nesting colonies. Sympatrically breeding species are thought to compete for these resources, and their co-existence is thought possible by the segregation of aspects of their ecologies, in particular foraging zones, diet or the asynchrony in breeding timetables. Royal and Rockhopper Penguins both belong to the *Eudyptes* genus, are ecologically very similar, and breed sympatrically on Macquarie Island. This similarity provides the opportunity to explore the issue of ecological segregation in these two species. The purpose of this study was to describe the foraging ecology of Royal and Rockhopper Penguins and to determine the degree of overlap in resource use. It was undertaken over three years (1993/4, 1994/5 and 1995/6) to examine inter-annual variability.

The thesis is divided into two parts, the first dealing with methodological aspects. Morphometric indices were determined for externally sexing birds in the field. Bill length and depth were found to be reliable measures for sexing individuals of both species. Experiments assessing the impact of investigators on breeding success found no significant effects, provided care was taken when working in the colony. The

deployment of external devices (transmitters and Time Depth Recorders, TDRs) was an integral part of data collection in the study, and the impact of these on Royal Penguins was examined. No effects were found in birds carrying the small, streamlined VHF transmitters, but the attachment of the larger, unstreamlined TDRs decreased the likelihood that penguins would return from a foraging trip, increased foraging trip duration, increased water influx rates, and decreased accumulated fat levels. The different impacts of the devices was related to their size and streamlining most likely affecting drag. Some aspects of the foraging ecology of penguins carrying TDRs were therefore not entirely representative of unencumbered birds.

The second part of the thesis examined the foraging ecology and degree of overlap in resource use in Royal and Rockhopper Penguins. Aspects examined were: foraging zones (using satellite telemetry, TDRs which estimated positions using geolocation, sea surface temperature, and foraging trip durations); diving behaviour; diet; and breeding biology.

Both species foraged offshore, to the southeast of Macquarie Island in the polar frontal zone, further than had previously been estimated (Royal Penguins 600 km and Rockhopper Penguins 480 km). Foraging zones changed with stage in the breeding season, with their extent being related to foraging trip durations, determined by commitments at the nest. The sea surface temperatures in which both species travelled were the same (6.8 - 10.8° C), and constant between years and stages in the breeding season. The position of the polar frontal zone changed during this period, suggesting

that the species targeted a specific part of the zone.

Royal and Rockhopper Penguins were predominantly diurnal foragers, with most diving between the hours of 04:00 and 21:00. They spent 38.9% and 36.6% of a 24 hour period respectively, diving. Both species were capable of diving to over 100 m, but spent the majority of their time at depths less than 60 m in dives of less than 2 minutes duration. This emphasis on shallow, short dives probably maximised foraging efficiency by reducing the degree of anaerobic metabolism, with its associated cost of removing respiratory byproducts, and reduced time spent descending and ascending in the water column, which is presumably less profitable foraging time.

The diet of both species was dominated by small, gregarious pelagic prey, particularly euphausiids (dominated by *Euphausia vallentini*), and myctophid fish (dominated by *Krefftichthys anderssoni*). Diet varied between years, but was constant across the breeding season, although fewer taxa were consumed before, compared to after, the hatching of chicks.

The breeding biology of both species was similar and synchronous between individuals and years of the study, which is most likely related to the limited temporal window these species have in which to breed. The investment in clutches was low (6.3% in Royal Penguins and 7.0% in Rockhopper Penguins), and breeding success was constant between species and years (on average 53.3% in Royal Penguins and 47.3% in Rockhopper Penguins). Most breeding failures occurred during incubation, with

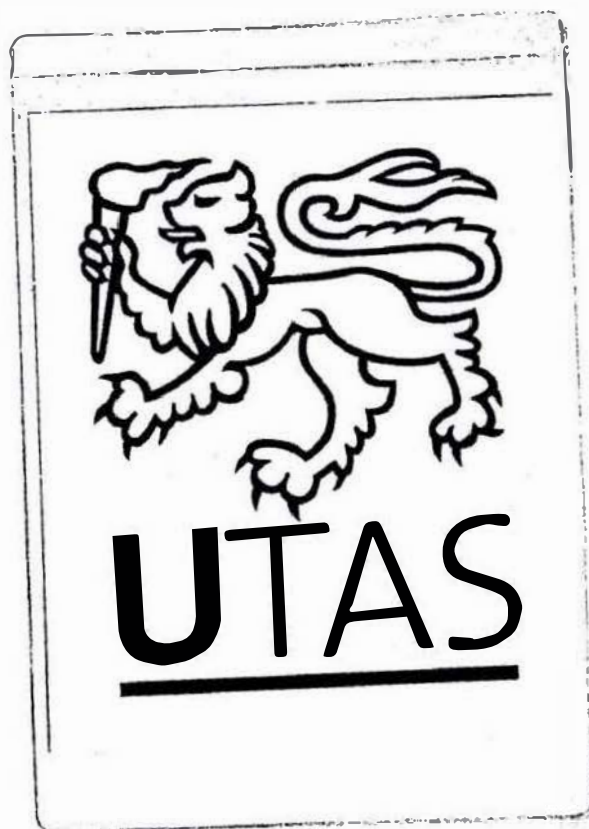
failures in Royal Penguins due to the late return of mates from foraging trips, and in Rockhopper Penguins, predation by skuas. It was speculated that the two species differed in the degree of being "capital" versus "income" breeders.

Inter-annual differences were only found in diet, and Rockhopper Penguin fledging masses, but foraging behaviour of both species was constant, suggesting that prey resources were variable and the species opportunistically consumed those which are encountered. The consistently high breeding success during the study suggests that these years were probably all "good" years in terms of the abundance and accessibility of prey.

Although Royal and Rockhopper Penguins exhibited many similarities in their foraging ecology, the overlap in resource use was not high. The mechanisms (particularly in combination with each other) minimising overlap were differences in: (1) Foraging zones (taking into account the three week asynchrony in the breeding timetables of the two species); (2) Diet, with Royal Penguins consuming larger and more myctophid fish, and fewer euphausiids than Rockhopper Penguins. Further, differences in the degree of digestion of prey suggested that the species foraged on different prey cohorts; (3) Asynchrony in the breeding season, reducing the overlap in peak food demands and the duration of foraging trips (which determined the extent of foraging zones).

This study determined that the foraging ecology of Royal and Rockhopper Penguins was intrinsically linked to the polar frontal zone and regulated by commitments at the nest.

Although these species were similar in aspects of their ecology, the overlap in resource use was less than has been suggested previously.





## **Acknowledgments**

The opportunity to work on Royal and Rockhopper Penguins at Macquarie Island was provided by Mark Hindell, for which I am grateful. Macquarie Island is one of the more fascinating and exciting places in which I have been fortunate to spend considerable amounts of time. The choice of the Sandy Bay site was fortuitous, being arguably one of the more beautiful bays on the east coast. The milder, albeit slightly, climate on the east coast made the long hours working outside easier, and the site abounds with examples of most fauna and flora of the island. Sandy Bay and all Macquarie Island were a constant source of interest as there were also new things to explore and observe. The hut at Sandy Bay was an aircraft engine packing crate established as a field hut in the 1950's. After the initial shock at its small size and basic commodities, and with the help of a number of people to improve the comfort factor, it became home. Its character and charm will always remain with me and it is sad to consider that it is now out of service. Working on Royal and Rockhopper Penguins was another delightful aspect of this project. They are both fascinating and immensely comical species which were a delight to simply observe. Long hours of observation during the project provided the opportunity to watch the antics of these and other species, which provided a great deal of pleasure.

Whilst I have made specific acknowledgments at the end of each chapter, there are some I wish to reiterate. Field assistance during the three years of the project was provided by Mary-Anne Lea, Jane Wilson, Kirsten Le Mar and Paul Scofield. I am grateful to

each of these people who spent extended times at Macquarie Island, being dragged out on those unbearably windy and wild days that Macquarie is capable of. They all showed great tenacity and tolerance. I would particularly like to thank Jane Wilson who spent one and a half seasons on the island for the project. She was great support during the numerous equipment breakdowns and glitches in the project, a great friend and constant source of fun and entertainment.

A number of people assisted in a myriad of ways, from helping carry back the copious quantities of penguin vomit that I collected, to bringing emergency supplies of food, assisting with observations, or fixing things in the hut. I thank the following: Don (Scone face) Hudspeth who will carry anything if bribed with enough cakes, Lance (Larnce) Biddle who can lift anything, Noel Carmichael who will pack anything in a plastic bag, Terry Reid, Scobie Pye, Peter Mantel (Elwood), Catherine Bone, Joan Russell, Sue Robinson, Louise Wynen, Alan Wiltshire, Ken Barrett, Richard Warner, Matt Brading and Graham MacKenzie (Kiwi).

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biological projects, instilled an interest in all the community which made for a cohesive and co-operative summer station. I am grateful to them all for their help and enthusiasm.

A number of people in Tasmania assisted with parts of the program which I greatly appreciate. Rod Ledingham from the Australian Antarctic Division always had great ideas for solving some of the logistic difficulties and was always generous and helpful when lending equipment. Don Reid was forever helpful and supportive, as was Warren Papworth. Assistance with identifications was provided by Steve Nichol, Graham Hosie, Dick Williams and Dave Slip, all of whom I thank.

From the Zoology Department, University of Tasmania, Richard Holmes adeptly built a number of pieces of equipment including the nets and some of the dummy packs, and Barry Rumbold handled the purchasing and management of accounts. Alan Dumphy was always helpful when finding and lending microscopes and various other pieces of laboratory equipment, and Sherrin Bowden was her usual incredibly efficient, helpful and reliable self in the department. Kit Williams was a wonderful source of help preparing electronic equipment for the vagaries of the Macquarie Island climate, and repairing numerous things after each field season. He also rescued me on a number of occasions from computers and programs that seized, for which I am grateful. Thanks to them all.

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## Chapter 1

### General Introduction

#### 1.1 Background

As a group, seabirds have a number of features in common, reflecting adaptations to the requirements of feeding in the oceans and breeding on land, which separates them from other avian groups. Seabirds generally have long life spans, but produce few, relatively large offspring, allocating less energy to annual reproduction than to adult maintenance (Ashmole 1971). These reproductive characteristics are thought to have arisen due to the difficulty that breeding birds have in bringing sufficient food from remote feeding grounds to the colony in order to successfully raise young (Ashmole 1971). This particularly applies to the pelagic feeders which rely on a distant, limited or ephemeral food supply (Ashmole 1971).

Penguins (order Sphenisciformes) are seabirds that are well-adapted to the marine environment, and are ecologically and taxonomically remote from other birds (Stonehouse 1967). All are flightless in air and, except for the Galapagos Penguin *Spheniscus mendiculus*, are restricted to the Southern Ocean. Their distribution is circumpolar in the antarctic and subantarctic region, ranging north to the southern coasts of Africa, Australasia and South America (Stonehouse 1967). Penguins constitute 60-70% of total avian biomass in the antarctic marine environment, highlighting the significance of this group of animals as marine consumers (Prevost 1981).

Until the recent development of devices such as satellite transmitters and time depth recorders, the majority of research on penguins had focused on their activities on land, particularly aspects of their breeding biology. However, as penguins spend the majority of their time at sea an understanding of key aspects of their ecology, such as how they interact with the abiotic and biotic components of the marine ecosystem remained unknown. The information on behaviour at sea is now increasing (eg. Croxall *et al.* 1993, Ancel *et al.* 1992, Jouventin *et al.* 1994, Kerry *et al.* 1995, Davis *et al.* 1996, Bost *et al.* 1997), but there are still many species for which little or nothing is known.

#### *Ecological segregation in penguin communities*

Like all seabirds, penguins need to come ashore to breed. Hence, their distribution during the breeding season is limited to suitable sites either within, or in close proximity to, feeding areas (Ashmole 1971). As prey are obtained from the marine environment, foraging and breeding grounds are separated. Further, as penguins are flightless they have limited dispersal capabilities during the breeding season due to commitments at the nest. These constraints have led to the assumption that the demand for food resources around colonies during the breeding season is high (Ashmole 1971). Due to the highly seasonal climatic conditions, the breeding season for subantarctic seabirds is more restricted than it is for tropical species, resulting in a potential increase in competition for resources by sympatrically breeding species (Croxall & Prince 1980a, Furness & Birkhead 1984). In particular, this is speculated to be the case when two or more ecologically similar species breed sympatrically (in antarctic and subantarctic penguins see Croxall & Prince 1980a, Trivelpiece *et al.* 1987, Adams & Brown 1989,

Klages *et al.* 1989, Cooper *et al.* 1990, Ridoux 1994, Hindell *et al.* 1995)

These various factors have lead to speculation that interspecific competition (Gause 1934, Elton & Miller 1954, Hutchinson 1957) is, or was, a fundamental structuring mechanism in penguin communities and that species must segregate some aspect of their ecology to avoid competition for what are assumed to be limited resources (eg. Croxall & Prince 1980a, Cooper *et al.* 1990, Hindell *et al.* 1995). The co-existence of species is thought possible only if some aspects of their ecologies differ. The hypothesised proximate mechanisms resulting in ecological segregation are: the type and size of prey taken; foraging ranges or depths; and/or the timing of breeding (Croxall & Prince 1980a, Brown & Klages 1987, Cooper *et al.* 1990, Ridoux 1994, Hindell *et al.* 1995).

This project tests the hypothesis that closely related, sympatrically breeding species segregate aspects of their ecology when peaks in resource demands occur, during the breeding season (see Hindell *et al.* 1995). Four species of penguins breed at subantarctic Macquarie Island, Royal *Eudyptes schlegeli*, Rockhopper *E. chrysocome*, King *Aptenodytes patagonicus* and Gentoo *Pygoscelis papua* Penguins. Royal and Rockhopper Penguins are both crested (eudyptid) penguins, so named for the presence of a yellow crest on their heads. Of the four species of penguins on Macquarie Island they are the most closely related and ecologically similar, and therefore were appropriate species in which to examine this issue. Ecological segregation has been examined to some extent in other members of the crested penguin group, Macaroni *E.*



*chrysolophus* and Rockhopper *E. chrysocone* Penguins at Marion and the Crozet Islands (Adams & Brown 1989, Klages *et al.* 1989, Ridoux 1994). However, these studies have only assessed overlap in diet and not compared other aspects of foraging ecology such as zones of the ocean used, or diving behaviour.

Previous work on Royal and Rockhopper Penguins at Macquarie Island had predominantly focused on aspects of breeding biology. Other than three single-season studies examining diet (Horne 1985, Hindell 1988a, b), no work has been undertaken on the foraging ecology of Royal and Rockhopper Penguins.

#### *Objectives of the study*

The objectives of this study were to examine a poorly understood aspect of Royal and Rockhopper Penguins' ecology, foraging behaviour at sea, and to investigate the degree of overlap in resource use. The project was undertaken during the breeding season when the demand for resources is presumably high due to the increased food requirements of breeding and restricted foraging ranges due to commitments at the nest. It was carried out over three years in order to quantify inter-annual differences.

In order to examine the foraging ecology and comparative resource use of these species, the following questions were addressed, and assessed seasonally and inter-annually:

1. What are the foraging zones of Royal and Rockhopper Penguins during the breeding season; what are the characteristics of the marine environment utilised by each species;

and to what extent do they overlap?

2. What is the diving behaviour of Royal and Rockhopper Penguins; which parts of the water column are utilised; is it similar between the species?

3. What is the diet of Royal and Rockhopper Penguins; do the species consume the same taxa and size classes of prey in the same proportions?

4. What are the breeding systems of the two species? Does the three week asynchrony in breeding timetables contribute to a segregation in prey resources or foraging behaviour utilised by both species?

5. How do the foraging ecology variables inter-relate and what effect do they have on aspects of breeding biology? What is the overlap in resource use between Royal and Rockhopper Penguins?

## **1.2 The study species and site**

Of the 18 currently recognised species of penguin (IUCN/SSC 1996), six are categorised as eudyptid penguins. They breed between 38 - 62° S, with Rockhopper Penguins being the most widespread and found in the greatest variety of latitudes (Stonehouse 1967, Warham 1975). The eudyptid penguins differ from other species of penguin, and seabirds generally, in that of the two eggs that are laid it is the second which is larger. Almost invariably it is this egg which produces the one surviving chick

(Warham 1975, St Clair *et al.* 1995). Further, unlike other species of penguin, it is the female which undertakes the first incubation shift once the eggs are laid (Warham 1975).

Royal and Rockhopper Penguins are migratory, departing the island during the winter, non-breeding period and return to the island to breed in September/October each year. Their foraging grounds outside the breeding season are unknown, although there have been sightings from Tasmania (40- 44° S) to 65° S (Woehler 1992, Reid *et al.* in press). Royal Penguins return to the island in September each year, and Rockhopper Penguins return in October. Males of both species return first to the island, with the females arriving 6 - 10 days later (Carrick 1972, Warham 1963, 1975).

The breeding system of the two species is asynchronous, with Royal Penguins beginning their breeding season one month earlier than Rockhopper Penguins (Warham 1971, Carrick 1972) (Fig. 1.1). Royal Penguin chicks fledge in early February, and Rockhopper Penguins chicks fledge in mid to late February (Warham 1971, Carrick 1972).

### *Royal Penguins*

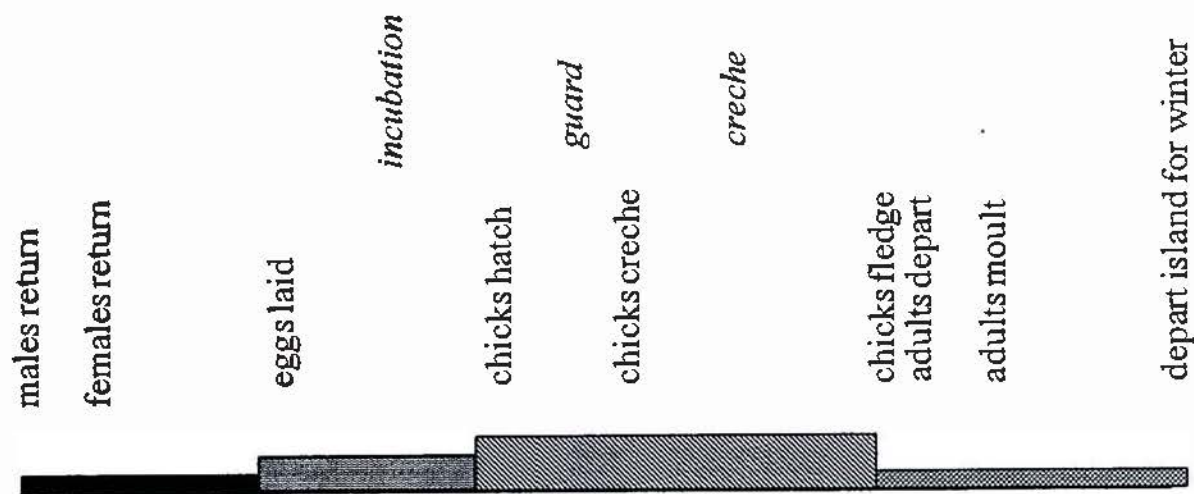
Royal Penguins were once considered a sub-species of the slightly smaller Macaroni Penguin but recent phylogenetic work has confirmed their specific status (Edge 1996). They are a medium-sized penguin, but one of the largest eudyptid penguins with a mass of 5 - 6 kg and a height of 65 - 75 cm (Marchant & Higgins 1990). Sexes are similar

in appearance, although males are slightly larger. They are endemic to Macquarie Island, and were exploited for their oil from 1873 - 1918 (Cumpston 1968). There are currently an estimated 850,000 breeding pairs in 46 colonies around Macquarie Island (Copson & Rounsevell 1987). They nest in large colonies of 75,000 - 160,000 pairs on the shore, slopes, or on the hills behind the shore, with some colonies 1.6 km inland (Warham 1971,

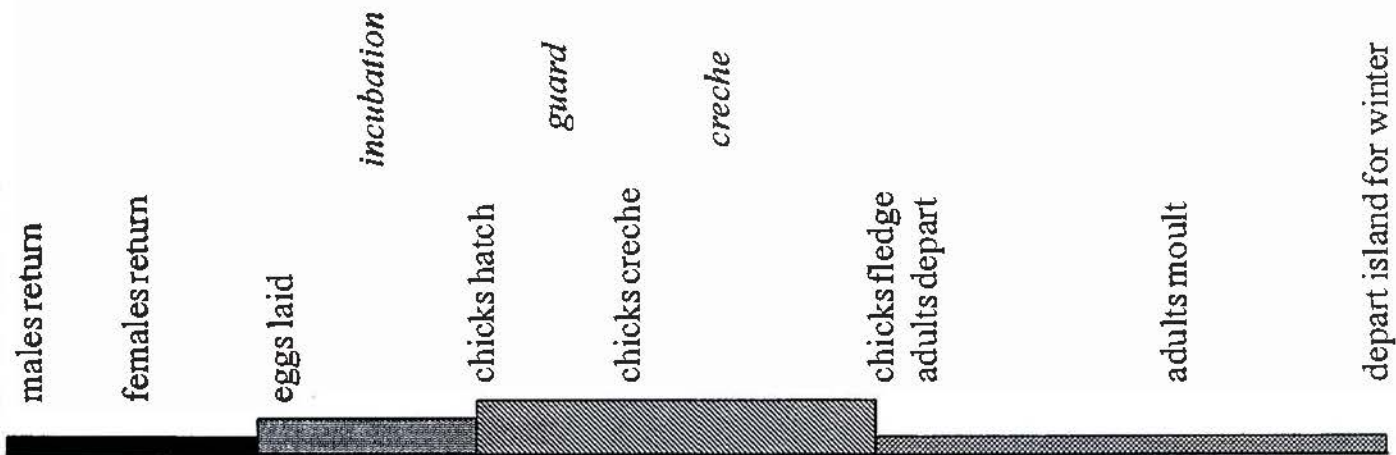
**Fig. 1.1** The breeding timetables of Royal and Rockhopper Penguins



# NOCKHUPPEL PENGUINS



# KOYAL PENGUINS



September

October

November

December

January

February

March

April

Copson & Rounsevell 1987). Nests are in open areas with no vegetation, and are made up of collections of small stones and bones of dead chicks. Two eggs are laid 3 - 4 days apart in mid to late October. The first (A) egg is smaller than the second (B) egg. The B egg is the sole egg that is incubated with the A egg being rejected or lost (Warham 1975, St Clair *et al.* 1995). This behaviour remains unexplained because the egg is fertile and rejection of the first egg prior to the laying of the B egg provides no form of insurance if the B egg is lost (St Clair *et al.* 1995).

Royal penguins are highly synchronous in their breeding timetables, with strong site and mate fidelity (Carrick 1972, Warham 1975). Extra-pair parentage is amongst the lowest for colonial birds (St Clair *et al.* 1995).

Female Royal Penguins undertake the first incubation shift, as males go to sea to forage after having fasted ashore for up to 5 weeks. The first foraging trip of males lasts 17 - 18 days, depending on the location of the colony (Carrick 1972). Upon the return of the male, the female leaves for a ten day foraging trip, during which the male incubates the egg. The female returns as the egg hatches, after a total incubation period of 35 days (Carrick 1972). The chick remains guarded by the male for another 2 - 3 weeks (guard stage), whilst the female provides food for the chick. Once the chick moves into a creche, both parents forage to feed the chick. Parents cease providing food for the chick at 55 - 60 days of age, when it fledges and departs the island (Warham 1975).

Breeding success is between 25 - 50%, and is positively correlated with experience and

age (Carrick 1972). The earliest age at which Royal Penguins breed is five years, but rarely are 5 - 6 year olds successful in their breeding attempts (Carrick 1972). All individuals are breeding by 11 years of age (Carrick 1972). Once chicks have fledged, adults return to the sea for approximately four weeks to replenish body stores and prepare for the moult and associated fast, which they undertake in March for approximately four weeks (Carrick 1972, Warham 1975).

### *Rockhopper Penguins*

Rockhopper Penguins are a circumpolar species, with three recognised sub-species: *E. c. filholi* (eastern) found on Marion, Crozet, Kerguelen, Heard, Macquarie, Campbell, Auckland and Antipodes Islands; *E. c. chrysocome* (southern) found on Falkland Island and off Cape Horn; and *E. c. moseleyi* (northern) found at Tristan da Cunha, Iles Amsterdam and St. Paul (Marchant & Higgins 1990). There is some doubt about the taxonomy of this species, with some of the sub-species perhaps deserving species status (SCAR sub-Committee on Bird Biology), however until phylogenetic work is undertaken, they remain a single species.

Rockhopper Penguins have a mass of 2.3 - 2.7 kg and a height of 45 - 58 cm (Marchant & Higgins 1990). Sexes are similar, with males slightly larger than females. The size of the population at Macquarie Island is unknown, but estimates range from 100,000 - 500,000 pairs (Warham, 1963, Rounsevell & Brothers 1984, G. Copson in Scott 1994). They nest in small caves and crevices associated with rocky outcrops, sometimes in *Poa* spp. tussocks, and often in large colonies of several thousand birds (Warham 1963).

Nests consist of a scrape in the ground lined with stones and sometimes vegetation. Two eggs (the first, A egg, being the smaller of the two) are laid four days apart, both of which are incubated. Incubation begins once the second egg is laid (Warham 1963, 1975). It is unusual for more than one chick of a pair to fledge, with the smaller chick usually dying 2 -5 days after hatching (Warham 1963).

The breeding schedule is the same as that for Royal Penguins, with females undertaking the first incubation shift, and all the foraging trips during guard stage. However, foraging trips are of a shorter duration in Rockhopper Penguins than Royal Penguins (Warham 1963). At 19 - 23 days of age chicks move into creches, and then depart the island when parents cease to bring food at 67 - 71 days of age (Warham 1963). Rockhopper Penguins leave for the pre-moult foraging trips in April, moult for approximately four weeks and then depart the island in May (Warham 1963).

Rockhopper Penguins, like Royal Penguins, are synchronous in their breeding timetables and exhibit strong nest site and mate fidelity (Warham 1963).

#### *The study site, Macquarie Island*

Macquarie Island is a small (37 km long and 5 km wide, 12,785 ha, Scott 1994), subantarctic island in the Australian sector of the Southern Ocean. Located at 54° 30' S, 158° 57' E, 1466 km south-east of Tasmania, 1100 km south-west of New Zealand, and 1294 km north of Antarctica (Fig. 1.2), it is one of only eight islands categorised as subantarctic. Subantarctic islands are defined by their proximity to the antarctic polar

frontal zone, with no trees, predominantly herbaceous vegetation, and a mean temperature of between 1- 5° C (Clark & Dingwall 1985).

Macquarie Island is an exposed section of uplifted ocean crust, situated on the Macquarie Ridge complex. The ridge is shallow, less than 1000 m in depth, and dissected in a number of places by deep passes (Selkirk *et al.* 1990). On the western side of the island the ridge gently slopes to the ocean basin, but on the east coast the gradient is much steeper, dropping into the 5000 m deep Macquarie Trench (Selkirk *et al.* 1990) (Fig. 1.3). The climate on the island is cool, wet and windy, with a mean annual precipitation of 895 mm (Bureau of Meteorology). The vegetation on the island predominantly comprises tussock grasslands, herbs and sedges and areas of peat bog (Davis, B.W. 1988).

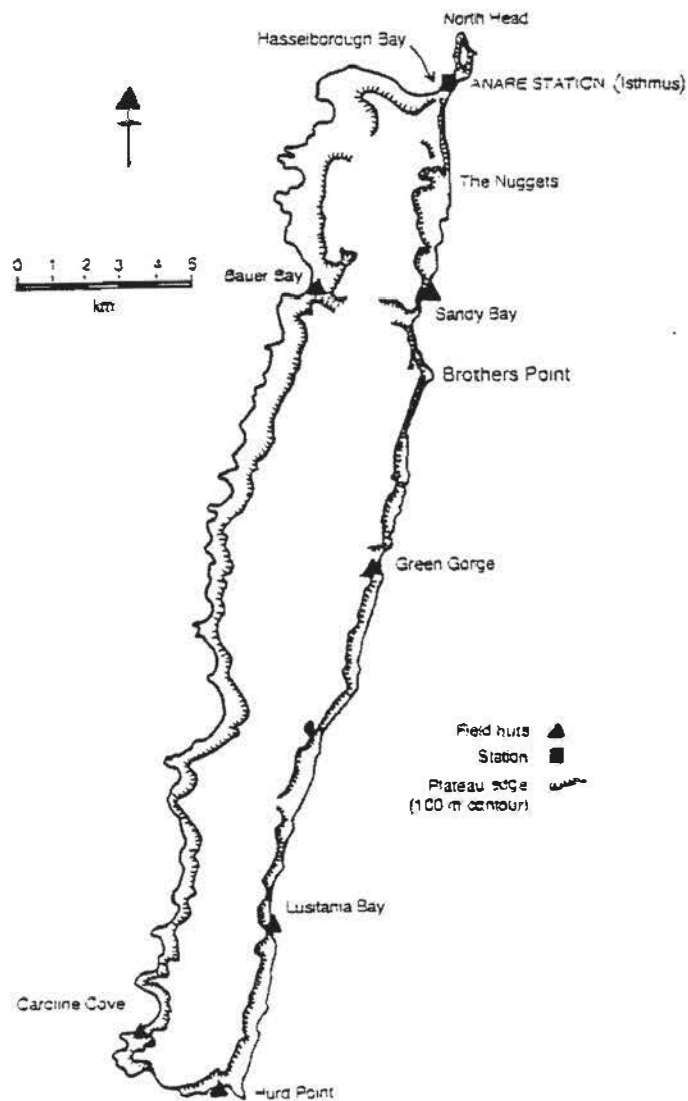
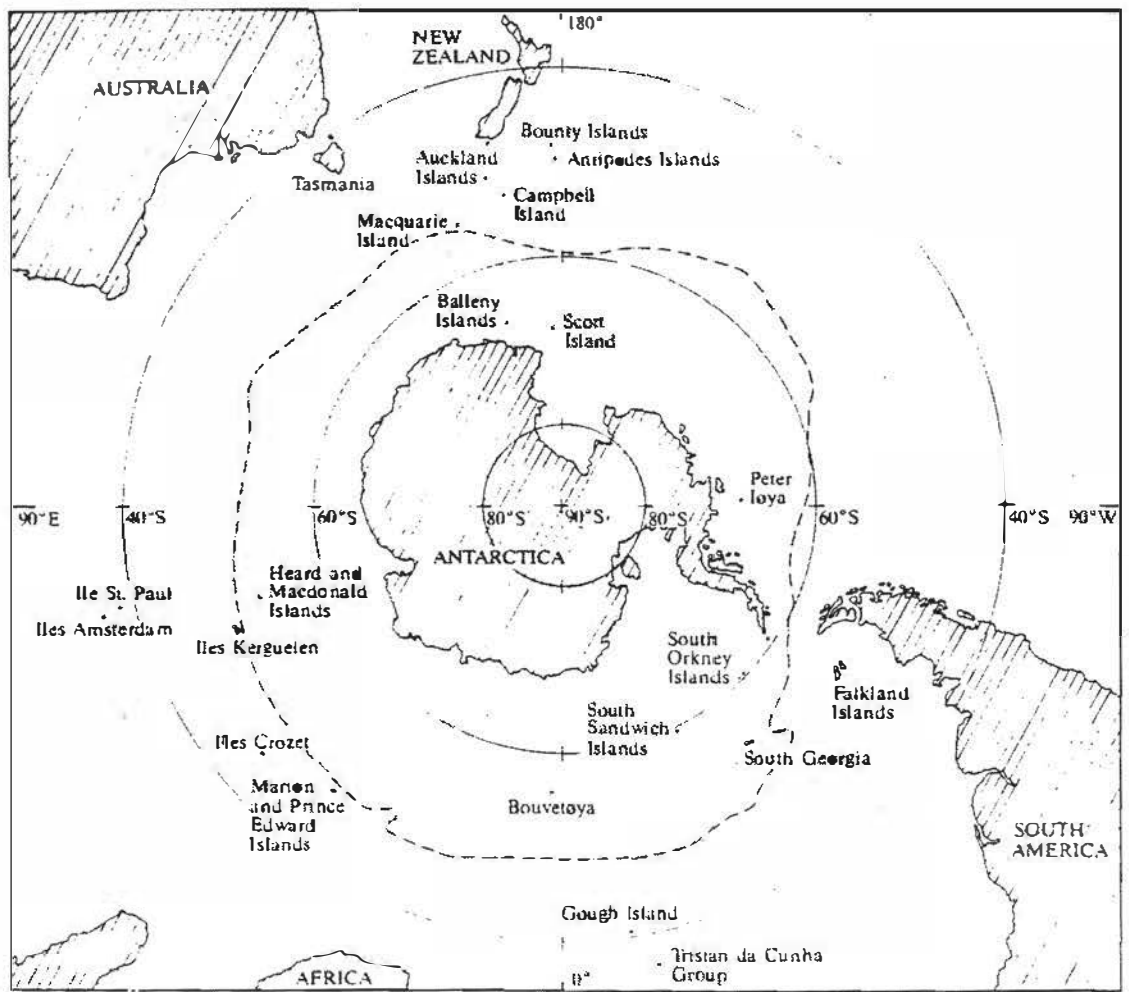
Aside from the four species of penguin, other vertebrates breeding on the island include 16 species of seabird, three species of fur seal, and the Southern Elephant Seal *Mirounga leonina*. The introduced species on the island are Feral Cats *Felis catus*, Rabbits *Oryctolagus cuniculus*, House Mice *Mus musculus* and Black Rats *Rattus rattus* (Selkirk *et al.* 1990). Self-introduced species include the Common Starling *Sturnus vulgaris*, Redpoll *Acanthis flammea* and Mallard *Anas platyrhynchos* (Selkirk *et al.* 1990).



**Fig. 1.2** Macquarie Island and its location in the Southern Ocean.

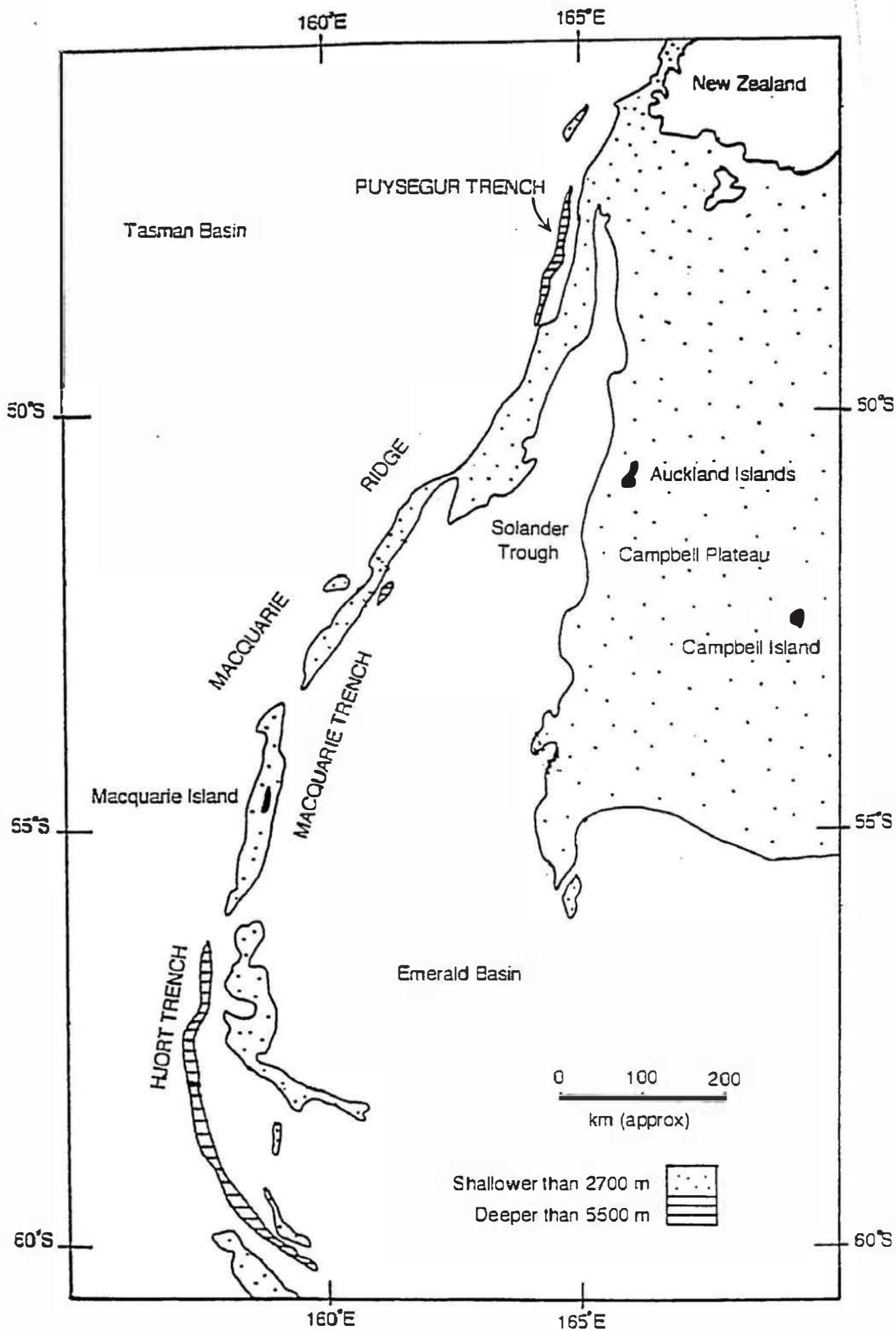
- - - - - polar frontal zone

(Sources: Division of Mapping, Australia 1978 and Department of Environment and Land Management, Tasmania 1991)



**Fig. 1.3** Bathymetry surrounding Macquarie Island, and the Macquarie Ridge.

(Source: Selkirk *et al.* 1990)



map 1042

The island is located in the region of the Polar Frontal Zone (PFZ), which is comprised of the subantarctic and polar fronts (Fig. 1.2). These fronts form the northern and southern boundaries between the warmer, less-dense subantarctic, and cold, dense antarctic waters (Tchernia 1980). The PFZ is an important oceanographic feature, generating eddies along its entire length (Lutjeharms & Baker 1980), which are thought to be sites of enhanced productivity (Haney & McGillivray 1985, Haney 1986). Another important oceanographic feature in this region is the Antarctic Circumpolar Current (ACC), which dominates circulation in the Southern Ocean (Deacon 1982).

### *Field work*

All field work was carried out at Sandy Bay (54° 33' 51" S, 158° 54' 11" E) on the east coast of Macquarie Island, eight km south of the ANARE (Australian National Antarctic Research Expedition) base (Figs. 1.2 and 1.4). This site has two Royal Penguin colonies, an upper and a lower, and one Rockhopper Penguin colony at Brothers Point, at the southern end of Sandy Bay.

The upper Royal Penguin (c. 5,000 breeding pairs) and the Brothers Point Rockhopper (c. 2,000 breeding pairs) colonies were used for all field work (Fig. 1.4). The Sandy Bay site was selected because of the close proximity of the Royal and Rockhopper Penguin colonies to each other, giving the opportunity to explore the degree of overlap in resource use between the species foraging in similar sections of the marine environment. Field work was carried out from August/September to late February/March during each of the three years of the study.

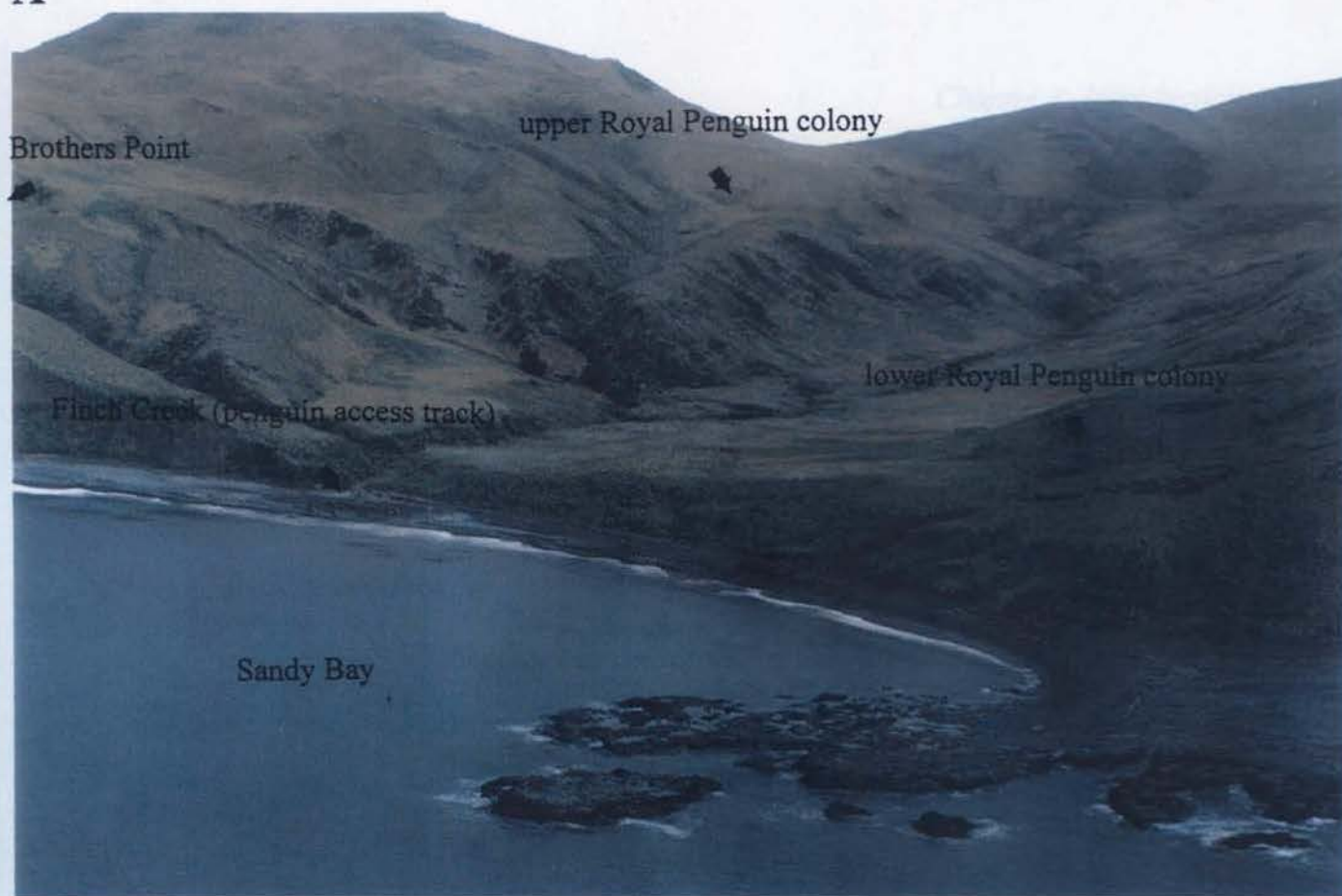


**Fig. 1.4** The study colonies at Macquarie Island.

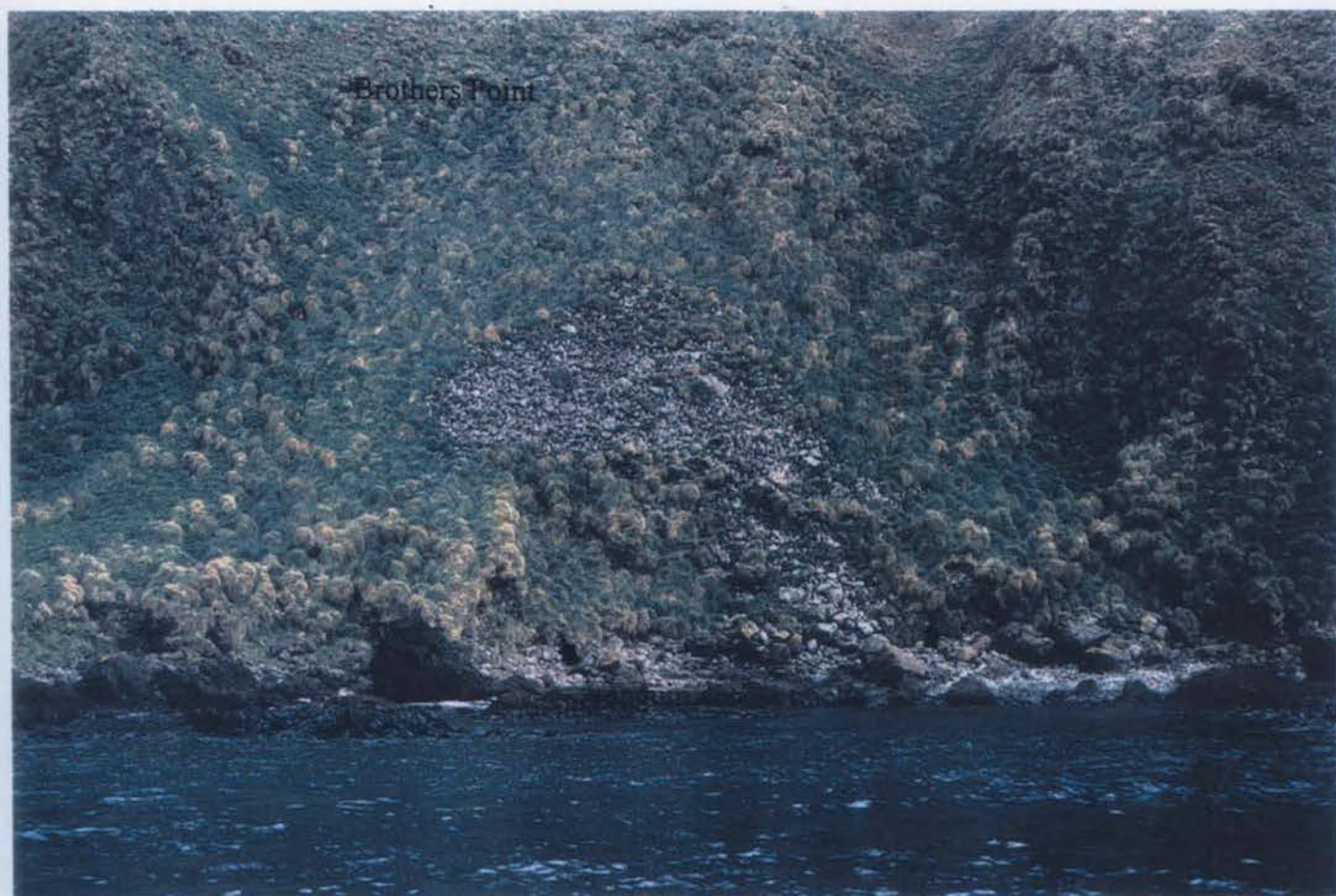
**A** Sandy Bay with the two Royal Penguin colonies, Brothers Point and penguin access to the colony (Finch Creek) marked

**B** Rockhopper Penguin colony at Brothers Point with penguin access tracks shown

A



B



### 1.3 Organisation of the thesis

The thesis comprises two sections. Section A covers methodological aspects which have not been previously studied in these species. Morphometric indices for externally sexing adult Royal and Rockhopper Penguins were determined in Chapter 2, allowing the fast identification of the gender of individuals in the field. These results provide the foundation for the majority of the determination of sex of penguins studied in all other chapters. Chapter 3 assessed the effect of investigators on the breeding biology of the two species. The purpose was to determine if the presence of investigators sufficiently disturbed the penguins to affect breeding success. Determining the impact of investigators also allowed an estimation of how representative the data were of penguins under normal conditions. Techniques established for working in the colonies are discussed in this section and applied throughout the study. Chapter 4 determined the effect of instruments on Royal Penguins. Much concern has been raised about the impact to penguins of carrying devices, and as devices were an integral part of the data collection in much of this thesis, the impacts were measured. The results give an indication of the accuracy of the data obtained from penguins carrying devices.

Section B contains chapters examining the comparative foraging ecology and overlap in resource use between Royal and Rockhopper Penguins. The foraging zones of both species were investigated in Chapters 5 and 6. As different techniques were employed to measure the foraging grounds of the species, this chapter was divided into two chapters: satellite tracking of Royal Penguins (Chapter 5), and foraging zones of both species using a variety of techniques (Chapter 6). Chapter 7 examined the diving



behaviour of both species, Chapter 8 dietary overlap, and Chapter 9 breeding biology. Chapter 10 is the general discussion where all aspects of the foraging ecology of these two species are discussed, and final conclusions on the at-sea foraging behaviour and degree of overlap in resource use between the species are drawn.

All chapters are self-contained and written as papers. As a result there is at times some repetition of information, particularly in the methods sections. Some chapters (2, 3, 4, and 5) have been accepted for publication, the details of which are given at the start of the chapter. These chapters have been presented as they were published, although the references have been removed and compiled into one reference list at the end of the thesis.

## **Section A**

### **Methodological aspects**



## Chapter 2

### **Morphometric indices for sexing adult Royal and Rockhopper Penguins at Macquarie Island**

*Published as: Hull, C.L. In press. Morphometric indices for sexing adult Royal Eudyptes schlegeli and Rockhopper E. chrysocome Penguins at Macquarie Island. Marine Ornithology 24.*

#### **2.1 Introduction**

Studies of the ecology of avian species often require the identification of the sexes of individuals. In penguins there are no reliable plumage differences that can be used to distinguish the sex of individuals visually (Davis & Spiers 1990, Marchant & Higgins 1990). In order to avoid destructive or invasive techniques, the use of external morphometrics to sex animals reliably is of great value. Whereas penguins are dimorphic in body mass, this measure is unreliable due to its variability across animals within and between years (Warham 1975, Davis & Spiers 1990, Groscolas 1990).

External morphometric indices are used widely to assist in the sexing of penguins (Scolaro 1987, Gales 1988a, Kerry *et al.* 1992, Amat *et al.* 1993, Agnew & Kerry 1995, Woehler 1995). However, there are no published data on the morphometrics of Rockhopper Penguins (*Eudyptes chrysocome filholi*) from Macquarie Island, and the

few data for Royal Penguins *E. schlegeli* indicate a need for further statistical analysis of morphometric characters (Woehler 1995).

Sexual dimorphism has been noted in all species of penguins, with males always larger than females (Livezey 1989). The degree of dimorphism, however, varies between groups of penguins. Using skin measurements Livezey (1989) found eudyptid (crested) penguins to be the most dimorphic, but they were only moderately dimorphic when compared using skeletal measurements.

The purpose of this paper is to provide data on the morphometric indices for identifying the sex of individual Royal and Rockhopper Penguins, and to thus determine the most reliable means of sexing birds in the field. These data are then compared to previous studies on Royal and Macaroni *E. chrysolophus* Penguins.

## **2.2 Materials and methods**

The study was carried out at Macquarie Island (54° 30' S , 158° 57' E) during the 1993/4 and 1994/5 breeding seasons. Royal Penguins were measured at Sandy Bay, and Rockhopper Penguins at Brothers Point, at the southern end of Sandy Bay. Measurements (to 0.1 mm) were made with Vernier calipers of bill depth (at a point proximal to the tip of triangular inter-ramal feather patch), bill width (maximum width of the culminicorn), bill length (length of exposed culmen) (as per Warham 1972, 1975) and head length (maximum length from the dorsal brain case to tip of the beak) of penguins of presumed sex as determined by breeding behaviour. Breeding behaviour

included date of return to the island (males return at least one week earlier than females), incubation shift (females carry out the first incubation shift), and guard-stage foraging shifts (undertaken by females) (Warham 1963, Smith 1970, Warham 1971, Carrick 1972, Warham 1972, Marchant & Higgins 1990). As there is no published, or observed, evidence of reverse-role behaviours in these species this technique was deemed to be reliable. Individuals were marked with permanent metal flipper bands and were observed at least once per week throughout the breeding season, enabling further confirmation of the sex of an individual (Hull & Wilson 1996a, also Chapter 3). During the 1993/4 season, 50 pairs of breeding Royal and 50 pairs of breeding Rockhopper Penguins were measured. Pairs on nests were selected haphazardly from three transects in the Royal Penguin colony and two in the Rockhopper Penguin colony (see Hull & Wilson 1996a, also Chapter 3). All birds were measured while on the nest to minimise disturbance (Hull & Wilson 1996a, also Chapter 3). During the subsequent season, previously unbanded breeders on the transects were measured. Therefore, a total of 138 Royal (67 males, 71 females), and 117 Rockhopper (60 males, 57 females) Penguins were measured.

Comparison of morphometric data between the sexes were made using *t*-tests. Discriminant Function Analyses (DFA) were used to determine the accuracy of assigning penguins to a sex using these morphometric data, and to determine the most reliable measurements. A jackknife analysis was then used to cross-check the accuracy of the DFA (Tabachnick & Fidell 1989). From these results, discriminant formulae were derived to assign a sex to individuals for future studies. In addition, a Bill Shape

Index (BSI) was calculated from the multiplication of bill depth, bill width and bill length, and divided by 10 (see Warham 1975) for the purpose of comparisons to Woehler's (1995) study. A Mean Dimorphism Index (MD), a Separation Index (S), and a Bill Surface Area (BSA) were also calculated for each of the characters for comparison to other studies (see Agnew & Kerry 1995). These indices were defined as follows:

$$MD = \frac{200 (x_m - x_f)}{(x_m + x_f)} (\%)$$

where  $x_m$  is the mean of the male character and  $x_f$  is the mean of the female character

$$S = 1 - p$$

where  $p$  is the proportion of individuals that are misclassified by a single factor discriminant analysis

$$BSA = \sqrt{\pi r l}$$

where  $l$  is bill length and  $r$  is (= half bill depth) (the formula is the shape of a cone)

## 2.3 Results

### *Sexing penguins by morphometric indices*

All mean measurements in this study were significantly different between the sexes in both species ( $t$ -tests  $P < 0.05$ ), with males being larger (Table 2.1). The mean

difference ranged from 73.8% (BSI) to 94.1% (bill width) in Royal Penguins, and 74.9% (BSI) to 94.7% (head length) in Rockhopper Penguins (Table 2.1).

In Royal Penguins the canonical loadings from the DFA determined that bill length was the most reliable predictor of sex, and in Rockhopper Penguins, bill depth (Table 2.2). Lower loadings for bill width and head length in both species indicated a lesser contribution of these measurements to the accurate assignment of sex to a penguin. Using the four variables, the DFA accurately assessed 95.5% of males, and 97.2% of females in Royal Penguins (96.4% overall), and 93.3% of males and 93.0% of females in Rockhopper Penguins (93.2% overall) (Table 2.2). However, removing bill width and head length increased the accuracy of the DFA to 97.0% males, 97.2% females in Royal Penguins (97.1% overall), and 93.3 of males, 93.0% of females (93.2% overall). Cross-validation of these two variables using a jackknife analysis found that 97% of males and 97.0% of females in Royal Penguins (97.1% overall), and 93.0% of males, and 93.0% of females in Rockhopper Penguins (93.2% overall) were accurately assigned a sex. The DFA produced the following formulae for the determination of sex in these penguins:

#### Royal Penguins

$$D = -919.9 + (13.45 \text{ BD}) + (8.24 \text{ BL})$$

#### Rockhopper Penguins

$$D = -739.3 + (21.97 \text{ BD}) + (6.86 \text{ BL})$$



Where  $BD$  = Bill Depth,  $BL$  = Bill Length, and  $D$  is the discriminant function. Using these formulae, individual penguins that fall above zero are male and those that fall below are female.

**Table 2.1.** Morphometric indices in mm (mean  $\pm$  standard deviation) of Royal and Rockhopper Penguins from Macquarie Island.All significantly different,  $P < 0.05$ .

<i>Species</i>	<i>Sex</i>	<i>Bill depth</i>	<i>Bill width</i>	<i>Bill length</i>	<i>Head length</i>	<i>BSI *</i>
Royal Penguin	male (67)	30.4 $\pm$ 1.57	14.1 $\pm$ 1.23	68.7 $\pm$ 2.85	143.5 $\pm$ 4.72	2954.3 $\pm$ 373.1
	female (71)	26.8 $\pm$ 1.27	13.3 $\pm$ 1.15	61.1 $\pm$ 2.63	133.8 $\pm$ 4.34	2181.6 $\pm$ 246.8
	<i>t</i> values	14.6	4.1	16.2	12.5	14.3
	% difference between sexes	88.3	94.1	88.9	93.3	73.8
Rockhopper Penguin	male (60)	21.0 $\pm$ 0.99	10.8 $\pm$ 0.81	46.4 $\pm$ 2.05	115.6 $\pm$ 2.98	1051.8 $\pm$ 114.6
	female (57)	18.7 $\pm$ 0.85	10.0 $\pm$ 0.85	41.9 $\pm$ 2.13	109.6 $\pm$ 3.63	788.2 $\pm$ 116.4
	<i>t</i> values	13.8	4.9	11.6	9.8	12.3
	% difference between sexes	88.7	92.9	90.3	94.7	74.9

\* Bill Shape Index

Removing data that overlap between the sexes in each species, the non-overlapping ranges for bill depths and lengths for each of the sexes (mm) are given in Table 2.3.

#### *Inter-population comparisons*

All Royal Penguin measurements obtained in this study were compared with those of Woehler (1995). Bill depth of males, and female and male bill length were found to be significantly different, with bill depth being less, and bill length being greater in this study compared to Woehler's (1995) (two-tailed  $t$ -test,  $P < 0.05$ ) (Table 2.4). BSI differed in opposite directions for males and females. Bill depth, bill width, bill length, and BSI were also compared between Macaroni Penguins from Heard Island (Woehler 1995) and Royal Penguins (this study). Significant differences were found in all measurements, with Royal Penguins being larger in both sexes (two-tailed  $t$ -test,  $P < 0.05$ ) (Table 2.4).

MD and S values for all measurements are given in Table 2.5. Both the S values and the canonical loadings values given in Table 2.2 confirm that bill depth and bill length are the most reliable measurements in both species. As it was not possible to compare the MD and S values on BSI between this study and that of Agnew & Kerry (1995) and Woehler (1995), these were not calculated.

**Table 2.2.** Canonical loadings of morphometric indices for Royal and Rockhopper Penguins from the discriminant function analyses.

<i>Variable</i>	<i>Royal Penguins</i>	<i>Rockhopper Penguins</i>
Bill depth	0.743	-0.883
Bill width	0.207	-0.318
Bill length	0.818	-0.749
Head length	0.633	-0.637

Group Classification function coefficients:

<i>Variable</i>	<i>Males</i>	<i>Females</i>	<i>Males</i>	<i>Females</i>
Bill depth	46.1	34.3	76.3	53.6
Bill width	125.2	121.3	73.9	75.7
Bill length	35.3	27.9	-20.6	-27.9
Head length	59.3	58.0	101.6	101.9

**Table 2.3.** Non-overlapping ranges for bill depth and length in Royal and Rockhopper Penguins (mm). The figures in parentheses represent the proportion of animals that can be sexed using these ranges.

<i>Species</i>	<i>Sex</i>	<i>Bill depth</i>	<i>Bill length</i>
Royal Penguins	Males	29.3 - 33.5 (77.6%)	67.0 - 73.8 (73.1%)
	Females	24.3 - 27.7 (73.2%)	55.8 - 62.7 (77.5%)
Rockhopper Penguins	Males	20.3 - 23.3 (75%)	46.2 - 51.2 (60%)
	Females	16.7 - 18.8 (49%)	38.5 - 42.2 (63%)

**Table 2.4.** Mean  $\pm$  SD (mm) for morphometric indices of Royal and Macaroni Penguins at Macquarie and Heard Islands (\*  $P < 0.05$ )

<i>Measurement</i>	<i>Sex</i>	<i>Royal Penguins Macquarie Is. This study 1</i>	<i>Royal Penguins Macquarie Is. Woehler (1995) 2</i>	<i>Macaroni Penguins Heard Is. Woehler (1995) 3</i>	<i>1 X 2 Significance (% difference to 1)</i>	<i>1 X 3 Significance (% difference to 1)</i>
Bill Depth	M	30.4 $\pm$ 1.57	32.9 $\pm$ 1.87	27.5 $\pm$ 0.82	* (92.51)	* (110.62)
	F	26.8 $\pm$ 1.27	27.6 $\pm$ 2.42	24.0 $\pm$ 1.02	ns (97.24)	* (111.69)
Bill Width	M	14.1 $\pm$ 1.23	14.7 $\pm$ 1.06	12.9 $\pm$ 0.87	ns (95.99)	* (109.37)
	F	13.3 $\pm$ 1.15	13.1 $\pm$ 0.85	11.1 $\pm$ 0.41	ns (101.84)	* (119.30)
Bill Length	M	68.7 $\pm$ 2.85	64.8 $\pm$ 3.78	61.4 $\pm$ 1.68	* (106.04)	* (111.90)
	F	61.1 $\pm$ 2.63	57.3 $\pm$ 3.34	53.7 $\pm$ 2.07	* (106.69)	* (113.68)
BSI	M	2954.3 $\pm$ 373.1	3136.6 $\pm$ 391.2	2166.2 $\pm$ 186.5	ns (94.19)	* (136.38)
	F	2181.6 $\pm$ 246.8	2078.4 $\pm$ 370.0	1439.9 $\pm$ 95.7	ns (104.96)	* (151.51)
sample size	M	67	10	10		
	F	71	10	10		



**Table 2.5.** Mean Dimorphism index (MD) and Separation index (S) for Royal and Rockhopper Penguins

<i>Measurement</i>	<i>Royal Penguins</i>	<i>Rockhopper Penguins</i>
Bill depth	12.47 (91.30)	11.78 (92.31)
Bill width	6.06 (60.14)	7.31 (67.52)
Bill length	11.67 (92.75)	10.17 (88.03)
Head length	6.96 (85.50)	5.38 (86.33)
BSA	12.07 (96.38)	10.96 (93.16)

## 2.4 Discussion

### *Sexing penguins by morphometric indices*

The significant differences found in bill depth, bill width, bill length and head length between the sexes of Royal and Rockhopper Penguins on Macquarie Island are of little surprise. The dimorphic nature of penguins is well documented (eg. Warham 1975, Gales 1988a, Livezey 1989, Davis & Spiers 1990, Murie *et al.* 1991, Agnew & Kerry 1995), although the extent of the difference in the Macquarie Island populations was previously unknown for Rockhopper Penguins, and less well known for Royal Penguins. More importantly, it is now possible to determine the sex of individual penguins of these species without invasive techniques.

Discriminant function analyses indicated that the use of only two of the measurements is sufficient to accurately assign the sex to individuals of Royal and Rockhopper Penguins on average 97.1% and 93.2% of the time, respectively. This rate is higher

than that of other species subjected to the same procedure, such as the Adélie Penguin *Pygoscelis adeliae*, in which a 85% success rate was recorded, the latter being less dimorphic than the crested penguins in these measurements (Kerry *et al.* 1992).

The results from both the DFA and S (Single factor discriminant analyses) values further confirm that the most reliable single morphometric measure for assessing sex was bill length in Royal Penguins, and bill depth in Rockhopper Penguins. The S values (Table 2.5) indicate the percentage of individuals which did not overlap. Bill width was the least reliable measure, with only 60.1% of measurements and 67.5% of measurements not overlapping, and BSA the most reliable at 96.4% and 93.2% of measurements not overlapping in Royal and Rockhopper Penguins, respectively. The non-overlapping ranges of bill depth or bill length given above, or preferably BSI, can therefore be used in the field to sex these species of penguin. Measurements from individuals that fall outside the ranges given, should be applied to the discriminant formulae presented above. The derived discriminant formulae cannot be applied to chicks or juveniles, which in this and other species, have smaller bills than adults (Warham 1972, Scolaro 1987, Gales 1988a).

Both Royal and Rockhopper Penguins from this study fall within the range of the mean dimorphism indices of the other species of crested penguins given by Agnew & Kerry (1995). Rockhopper Penguins from this study were smaller in mean bill depth and mean bill length than in the other studies listed by Agnew & Kerry (1995). It has not been possible to compare data from this and other studies further statistically. However,

using these morphometric indices (but not using other skeletal measurements, Livezey 1989), Royal and Rockhopper Penguins are, like all the crested penguins, among the most dimorphic, and can be sexed reliably in the field using these characters.

### *Inter-population comparisons*

Comparisons of the Royal Penguin data presented in this study and those in Woehler's (1995) Macquarie Island study indicate significant differences in bill depth for males, and bill length for both sexes. In this study, male bill depth, male bill length and female bill length were 92.5%, 106.0%, 106.7% the size of individuals measured in Woehler's (1995) study, respectively. Woehler's (1995) study was carried out at a different colony than this study, and whilst one cannot discount the possibility that there are morphological differences between the various colonies on the island, the most likely cause is differences in measurements taken between various workers (eg. Barrett *et al.* 1989, Lorentsen & Røv 1994). Whereas this study and that of Woehler's (1995) followed the techniques of Warham (1975), there were subtle differences in the interpretation of precisely where on the bill measurements should be taken. This indicates that bill length, and to an extent bill depth, were more variable between workers than some other measurements, with BSI being the most reliable measure. Although BSI is a derived index, the differences between measurers of these variables deviates in different directions, resulting in a masking of inconsistencies. The results also suggest differences in all measurements between Royal (this study) and Macaroni Penguins (Woehler 1995). Due to the above difficulties these differences have to be viewed tentatively. Therefore, comparative studies with data derived by different

workers should be conducted with caution, particularly studies describing inter-population variation within species. These findings confirm the work of Barrett *et al.* (1989) who suggest that all workers should measure the same birds to resolve differences in techniques, or a number of samples from various measurers be taken in all cases.

## 2.5 Summary

Four measurements were taken from a sample of known-sex Royal *Eudyptes schlegeli* and Rockhopper *E. chrysocome* Penguins at Macquarie Island. Significant differences were found between sexes in all measurements. Bill depth and bill length were the most reliable measures for assigning sex and, when these were applied to a discriminant function analysis accurately assessed 97.0% males, 97.2% females in Royal Penguins (97.1% overall), and 93.3% males, 93.0% females in Rockhopper Penguins (93.2% overall). Cross-validation using jackknife analysis accurately assigned the sex of 97% of males, 97% of females in Royal Penguins (97.1% overall), and 93% males, and 93% females in Rockhopper Penguins (93.2% overall), indicating the validity of using these measurements. The non-overlapping ranges (mm) were: in Royal Penguins bill depth, males - 29.3 - 33.5, females - 24.3 - 27.7; bill length, males 67.0 - 73.8, females 55.8 - 62.7; in Rockhopper Penguins bill depth, males - 20.3 - 23.3, females - 16.7 - 18.8; bill length: males - 46.2 - 51.2, females - 38.5 - 42.2. These ranges should be used to assign sex in the field. For penguins that fall outside these ranges bill depth and length should be applied to the derived discriminant formulae. Some significant morphometric differences were found between Royal Penguins in this and a previous study on

Macquarie Island, indicating the difficulty of comparing studies involving different workers. Methods for overcoming these difficulties are discussed.

## **2.6 Acknowledgments**

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## Chapter 3

### **The effect of investigators on the breeding success of Royal and Rockhopper Penguins at Macquarie Island**

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#### **3.1 Introduction**

Many investigators examining evolutionary and ecological questions in birds have begun to question the effect of their studies on the subjects (eg. Wilson *et al.* 1989b). The premise behind this examination is the need to assess the accuracy of results, and to develop techniques which ensure birds are treated appropriately during experiments.

Much of the research into the effects of experimenter activity on study animals has involved species of penguins. The response by penguins to humans includes an increase in heart rate (Culik *et al.* 1990, Nimon *et al.* 1995), increased stress hormone levels (Axelrod & Reisine 1984), body temperature, and thus energetic costs (Wilson *et al.* 1989b, Culik 1994), and a reduction in breeding success, recruitment rates or the size of the overall breeding population (Culik *et al.* 1990, Wilson *et al.* 1991c, Woehler *et al.* 1994). An increase in heart rate in Adélie Penguins *Pygoscelis adeliae* begins when a human is 30 m away (Culik *et al.* 1990). The close proximity (< 3 m) of a human to

birds, and the handling of birds, induced the highest level of anxiety in line with the "fight" or "flight" response (Perry 1973), and is likely to have the greatest potential effect on the breeding success of birds, because chicks are more vulnerable to predation and hypothermia (Culik *et al.* 1990, Cooper *et al.* 1993).

Royal, *Eudyptes schlegeli*, and Rockhopper, *E. chrysocome*, Penguin species are abundant in the sub-Antarctic. As part of a inter-annual breeding biology study (Chapter 9) individuals of both species were, initially, handled to take morphometric measurements and banded with metal flipper bands, then were exposed to twice weekly nest checks during the incubation phase, and once weekly chick weighings following hatching. The data collected for the breeding biology study were used to establish growth curves for chicks, ascertain breeding success and determine the proximal factors that affect these parameters. The majority of work was carried out by two investigators operating in the colony together. In the study reported here we examined the effects on reproductive success of carrying out this breeding biology work on these two species of penguin at Macquarie Island.

### 3.2 Materials and methods

The study was carried out at two colonies on Macquarie Island (54° 30' S, 158° 57' E) during the 1994/5 breeding season. Royal Penguins were studied at Sandy Bay (upper colony). Three transect lines with a total of fifty nests used for the breeding biology study (experimental) sampled the upper, middle and lower sections of the colony. The number of nests in the experimental transect lines were as follows: 25 in the lower, 14

in the middle and 11 in the upper. Three corresponding lines (control) as per the experimental lines were sited three metres (therefore, outside the "close" criteria as given by Culik *et al.* 1990) above or below the experimental lines.

Rockhopper Penguins were studied at the Brothers Point colony (at the southern end of Sandy Bay). Two experimental transect lines with fifty nests each were placed in the upper and lower sections of the colony, with two corresponding control lines with fifty nests three metres from the experimental lines (25 nests were in each of the transect lines). Only four transects were used in this colony, as it is smaller than the Royal Penguin colony.

Only active nests were examined, and these were defined as nests that contained a pair that attempted to breed and produced an egg (those that did not produce an egg were not included). Potential nest sites in the control and experimental transects were marked prior to the return of penguins to Macquarie Island, from their winter absence at sea. Experimental nest sites were marked during the previous (1993/4) season, with the markers being left in place for the 1994/5 season. Control nest sites were placed in identical locations within the colonies in transects alongside (approximately three metres away, either above or below) the experimental ones. Active nests closest to the markers were examined.

Nests were marked with metal stakes 600 mm long with small ( $2\text{ cm}^2$ ), aluminium labels embossed with numbers in the Royal Penguin colony, and labels (as above) were attached to rocks adjacent to nests in the Rockhopper Penguin colony.

The breeding status of penguins in the control nests was observed from the experimental lines. In the control nests, the presence of adults, eggs and chicks was recorded. Both the experimental work and the observation of the control nests continued until the chicks entered the creche stage (Royal Penguins: 20 December 1994, and Rockhopper Penguins: 11 January 1995). During the creche stage chicks left the nest site, making it impossible to follow the fate of unmarked birds.

Particular care was taken, such as moving slowly, when working in the colonies. If there was any indication that birds were leaving their nests because of our actions, we found it helpful to stop and crouch down. When handling birds, adults were left on the nest and their eyes either covered with a hood, or an investigator's hands. Chicks and eggs were removed for measurement by covering the adults eyes in the above manner, and gently raising the bird up a little to obtain and return the young. Removal of adults from nests was avoided at all times.

### **3.3 Results and discussion**

The number of active nests in the experimental and control lines decreased significantly in both species over the breeding season (repeated measure ANOVA, Royal Penguins  $F_{11, 44} = 8.7$ ,  $P < 0.001$ ; Rockhopper Penguins  $F_{11, 22} = 15.3$ ,  $P < 0.001$ ). However, there

was no significant difference in the number of active nests between the control and experimental transects across the season for either Royal ( $F_{1,4} = 0.005$ ,  $P > 0.05$ ) or Rockhopper ( $F_{1,2} = 1.8$ ,  $P > 0.05$ ) Penguins (Table 3.1). Therefore, the breeding success for both species up to creche stage, was not significantly affected by the investigators' actions. (The large standard deviation shown in number of active Royal Penguin nests in the early stage of the breeding season is a function of the different number of nests in the three transect lines).

Royal and Rockhopper Penguins, like many other penguin species, have a strong affinity to their nests and are reluctant to leave even when a human approaches. We found that only after extreme disturbance would a Royal or Rockhopper Penguin leave its nest, and if it did, would return within seconds once the disturbance abated. If there was a substantial stress induced by our presence, it appears that the bond between adults and the nest was greater than any stress experienced by the birds.

As we entered the colony only twice weekly, it is unlikely that the birds acclimatised to our presence, as has been found with more frequent contact in other species (Jones & Faure 1981, Fowler 1993). Hence, a probable stress response initiated by our presence, such as an elevated heart rate, would probably remain unchanged over the breeding season.



**Table 3.1.** Mean number  $\pm$  standard deviation of active nests in both control and experimental transects in Royal (3 replicates) and Rockhopper Penguins (2 replicates)

<i>Week</i>	<i>Stage</i>	<i>Royal</i>	<i>Penguins</i>	<i>Rockhopper</i>	<i>Penguins</i>
		<i>Experimental</i>	<i>Control</i>	<i>Experimental</i>	<i>Control</i>
1	incubation	16.0 $\pm$ 7.21	16.3 $\pm$ 7.52	24.0 $\pm$ 0.0	24.0 $\pm$ 0.0
1.5	incubation	15.7 $\pm$ 7.37	16.3 $\pm$ 7.57	24.0 $\pm$ 0.0	24.0 $\pm$ 0.0
2	incubation	14.7 $\pm$ 7.37	15.0 $\pm$ 8.18	24.0 $\pm$ 0.0	21.5 $\pm$ 0.71
2.5	incubation	14.7 $\pm$ 7.37	15.0 $\pm$ 8.18	23.0 $\pm$ 0.0	20.0 $\pm$ 2.83
3	incubation	12.7 $\pm$ 5.03	14.3 $\pm$ 7.09	20.5 $\pm$ 2.12	18.5 $\pm$ 3.54
3.5	incubation	11.3 $\pm$ 3.05	12.3 $\pm$ 4.04	19.5 $\pm$ 2.12	17.0 $\pm$ 4.24
4	incubation	10.3 $\pm$ 3.51	10.7 $\pm$ 4.04	18.5 $\pm$ 2.12	16.0 $\pm$ 4.24
4.5	incubation	10.3 $\pm$ 3.51	10.7 $\pm$ 4.04	16.5 $\pm$ 2.12	14.0 $\pm$ 1.41
5	guard	10.3 $\pm$ 3.51	10.0 $\pm$ 3.0	16.0 $\pm$ 2.83	13.5 $\pm$ 0.71
5.5	guard	10.3 $\pm$ 3.51	10.0 $\pm$ 3.0	15.5 $\pm$ 2.12	13.0 $\pm$ 1.41
6	guard	10.3 $\pm$ 3.51	9.7 $\pm$ 3.51	14.5 $\pm$ 2.12	11.5 $\pm$ 0.71
7	guard	9.0 $\pm$ 3.61	9.0 $\pm$ 3.61	13.5 $\pm$ 0.71	10.0 $\pm$ 1.41

It appears that the use of flipper bands on experimental birds has not contributed to a decrease in breeding success of these birds. Previous studies have found that flipper bands can increase mortality in birds, particularly during the moult stage (Ainley *et al.* 1983). However, Hindell *et al.* (1996) found no effect on breeding success in Royal Penguins wearing flipper bands.

It is most likely that the techniques employed when working in a colony are important in minimising the impact of investigators. Moving slowly, crouching and not removing birds from nests appear to be key factors. The benefit of moving slowly through a colony reinforces the findings of Ball & Amlaner (1980) and Culik *et al.* (1990) in Herring Gulls *Larus argentatus* and Adélie Penguins respectively. Crouching most likely reduces the "looming quality" of intruders, as described by Jones *et al.* (1981). Capture and handling has been found to induce the highest stress response, with 270% increases in heart rate when birds were placed in bags to be weighed (Culik *et al.* 1990).

In conclusion, this study indicates that regular visits and handling of Royal and Rockhopper Penguins has had no short term (one season) effect on their breeding success, provided that an investigator approaches the birds in a manner similar to that described here. It also indicates that the breeding biology data collected, over one season at least, are from birds exhibiting normal behaviour. Although the effect on recruitment rates is unknown one can assume at this stage that the effect of this form of investigation has had no measurable effect on the survival of Royal and Rockhopper Penguins on Macquarie Island.

### **3.4 Summary**

The impact on reproductive success of investigators studying the breeding biology of Royal and Rockhopper Penguins was assessed. Control and experimental transects were established in a colony of each species and the number of active nests, from egg laying to creche stage, were compared. Experimental nests were those used in breeding biology work, where birds were measured and banded, and nest checks were carried out at least once per week. Control nests were in equivalent locations but birds were not handled, and no contact was made with the nests once breeding had begun. There were no significant differences in the number of active nests between the control and experimental transects (and, therefore, breeding success) in either species. It is concluded that, provided care is taken when working with these species, no impacts on the short term (up to creche stage, in one breeding season) breeding success of these populations will occur.

### **3.5 Acknowledgments**

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## Chapter 4

### The effect of carrying devices on breeding Royal Penguins

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#### 4.1 Introduction

Studies of the foraging ecology of penguins often use data loggers and/or transmitters to record aspects of their behaviour. However, the behavioural, reproductive and energetic effects on penguins equipped with such devices have recently been scrutinised (Obrecht *et al.* 1988, Croll *et al.* 1991, Culik & Wilson 1991). Deleterious effects range from increased foraging trip durations, reduced swimming speed, reduced food intake, increased energy expenditure, and impaired movement (Wilson *et al.* 1986, Gales *et al.* 1990, Culik & Wilson 1991). Generally, different species of penguin compensate for devices in one of two ways: (1) reducing their speed, foraging range, and mass gain, or (2) increasing the duration of foraging trips (Culik & Wilson 1991), or a combination of the two.

As part of a study of the foraging ecology and breeding biology of Royal Penguins *Eudyptes schlegeli* on Macquarie Island, Time Depth Recorders (TDRs) and VHF radio transmitters were deployed on birds throughout the breeding cycle. In the current study the effects of carrying these devices were quantified by comparing return rates, foraging

trip length, changes in mass, water influx, and body composition of instrumented birds to those of control birds without devices.

#### 4.1 Methods

Royal Penguins from the upper Sandy Bay colony, Macquarie Island (54° 30' S, 158° 57' E) were studied at four stages of the 1993-1994 and 1994-1995 breeding seasons. These stages were: male incubation (end of October), female incubation (mid-November), guard (mid-December), and early creche (early January). Departing adults were captured on the beach to reduce human disturbance in the colony (Hull & Wilson 1996a, also Chapter 3) and to ensure that the birds were undertaking a foraging trip. Breeding adults were selected on the basis of plumage characteristics (Warham 1971) and by the presence of a brood patch. Birds were sexed using bill morphometrics (Hull in press, also Chapter 2).

The penguins were allocated to one of three treatments (Table 4.1): (1) Controls (no device;  $n = 45$ ), (2) Transmitters ( $n = 26$ ), or (3) TDRs ( $n = 38$ ). The transmitters were an exact model of two-stage VHF radio transmitters, packaged in black, hydrodynamic waterproof housings (Faunatech, Eltham Victoria). They measured 47 x 25 x 11 mm (frontal cross-sectional area: 0.36 cm<sup>2</sup>, 0.24% cross-sectional area of a Royal Penguin), weighed 9 g, had a 20 cm flexible antenna, were neutrally buoyant and streamlined to reduce drag. The antenna was a multistrand, nylon-coated stainless steel wire, 1.0 mm in diameter. The TDRs were clear, perspex models of the Mark V Wildlife Computers TDRs, 62 x 38 x 12 mm, weighing 50 g, with a frontal cross-sectional area of 4.6 cm<sup>2</sup>



(2.3% cross-sectional area of a Royal Penguin), and no streamlining. Other than the allocation to different groups, all penguins were handled in the same manner. A temporary velcro band with an unique number was secured on the right flipper of all penguins to identify individuals.

TDRs and transmitters were attached to the lower medial portion of the back of unanaesthetised penguins using a cyanoacrylate adhesive (Loctite 401) which bonds quickly with the feathers of the bird. The loss of some devices from birds during the experiment resulted in unequal numbers of individuals in different stages of the breeding season. Transmitters were not deployed on male Royal Penguins during the incubation stage, and only on females during the guard stage as males do not undertake foraging trips at this time. Daylight observations were made from a hide on the beach so that birds could be recaptured when returning from a foraging trip. All devices and velcro bands were removed when penguins returned to the beach.

#### *Water influx and body composition*

Water influx and body composition were measured during the male and female incubation trips only. A 2 mL sample of blood was taken from the brachial vein (Samour & Jones 1983) to measure background levels of tritium in all birds. One mL (5 mCi/mL activity) of tritium, in physiological saline solution, was then injected intraperitoneally. The birds were left in an enclosure for 2 hr to allow the tritium to equilibrate with the body fluids (Green & Gales 1990). An additional 2 mL of blood was then taken and the bird released. When the penguins returned from a foraging trip



they were re-weighed, a 2 mL sample of blood taken, a second injection of tritium made, and then left for 2 hours to re-equilibrate. The birds were then re-bled and released. This process was repeated on return from a foraging trip because of a greater than 10% change in mass, and consequently water pool sizes, during their time at sea (Green & Gales 1990).

Blood samples were frozen at  $-20^{\circ}\text{C}$  until analysis back in Hobart a few months later. Water was extracted from whole blood using vacuum distillation (Nagy 1983). Fifty  $\mu\text{l}$  of extracted water was added to 3 mL of PCS scintillation fluid and counts of tritium made in a liquid scintillation counter (Beckman LS 5801). Water influx was measured from the decline in specific activity of the isotope between the initial equilibration and the recaptured equilibration, using equation four of Nagy & Costa (1980). Individuals with isotope levels were less than four times the background levels (Gales 1989) following return from the foraging trip were deleted from analyses due to the inaccuracy of these flux estimates (Nagy 1980). Total body water was calculated from tritium dilution, and body composition (body fat content) by comparing total body water, which is the inverse of body fat content (Groscolas *et al.* 1991), before and after a foraging trip.

An additional trial was carried out during the male incubation period to assess the effect of the tritium injection, and handling time during the experiment. For this, 15 birds were banded with individually-marked velcro bands, weighed, then released. Their return rate, foraging trip duration, and mass change were recorded upon their return.

The likelihood of penguins returning to continue the breeding attempt was assessed using  $\chi^2$  analysis. Mass changes, foraging trip duration, water influx, and body composition were analysed using independent, two-tailed  $t$ -tests, two-way ANOVAs (stages and devices), and post-hoc Tukey tests. Mass change data were arcsine transformed. Data presented are mean  $\pm$  standard deviation (SD).

### 4.3 Results

There were no differences in return rate ( $\chi^2_1 = 1.5$ ,  $P > 0.05$ ), foraging trip duration ( $t_{13} = 0.1$ ,  $P > 0.05$ ), or mass gained ( $t_{14} = 0.3$ ,  $P > 0.05$ ) between birds with tritium and no device ( $n = 7$ ), and birds with no tritium and no device ( $n = 9$ ), indicating no adverse effect from the injection and handling. These two groups were subsequently combined to form the control group ( $n = 16$ ) in further analyses.

Overall, 51 of the 122 (42%) penguins used during the experiment were not re-caught. Of these, 41 (76%) returned to the colony at some stage later in the season, but as failed breeders.

**Table 4.1.** The number of Royal Penguins used in each stage of the trials

<i>Stage</i>	<i>Device</i>	<i>No. deployed (returned)</i>
Male incubation trip	control	15 (7)
	control 2*	15 (9)
	TDRs	12 (7)
	transmitters	not tested
Female incubation trip	control	10 (9)
	transmitters	10 (8)
	TDRs	10 (8)
Guard (females)	control	10 (4)
	transmitters	10 (6)
	TDRs	10 (2)
Creche (male)	control	5 (4)
	transmitters	3 (3)
	TDRs	3 (1)
Creche (female)	control	5 (2)
	transmitters	3 (1)
	TDRs	3 (0)
Total		122 (71)

\* No tritiated water.

### *Transmitters*

Deployment of transmitters produced no discernible effects on any variables examined. Penguins with transmitters were equally likely to return from a foraging trip as control birds ( $\chi^2_3 = 13.6$ ,  $P > 0.05$ ) (Table 4.1). There were also no differences in foraging trip duration ( $F_{1,33} = 0.4$ ,  $P > 0.05$ ), mass gained ( $F_{1,31} = 0.03$ ,  $P > 0.05$ ), water influx ( $F_{2,16} = 0.2$ ,  $P > 0.05$ ), or body composition change (Tukey test,  $P > 0.05$ ) (Table 4.2).

### *TDRs*

In contrast, penguins carrying TDRs were less likely to return from a foraging trip during any stage ( $\chi^2_3 = 13.6$ ,  $P < 0.003$ ), and had longer foraging trips during the incubation stage (males:  $24.9 \pm 2.5$  days; females:  $20.1 \pm 4.3$  days) than control birds (males:  $22.9 \pm 1.7$  days; females:  $15.9 \pm 2.6$  days;  $F_{1,47} = 8.7$ ,  $P < 0.005$ ). Significant differences were also found in water influx in males ( $148.0 \pm 19.8$  ml kg<sup>-1</sup> day<sup>-1</sup>, or 191% greater water influx,  $t_5 = 7.6$ ,  $P < 0.001$ ) than controls ( $77.4 \pm 7.0$  ml kg<sup>-1</sup> day<sup>-1</sup>), but not in females ( $F_{2,16} = 0.2$ ,  $P > 0.05$ ). Females with TDRs gained less fat than did control birds following their incubation trip ( $F_{2,16} = 15.0$ ,  $P < 0.001$ ), but males with TDRs did not differ from controls ( $t_8 = 1.2$ ,  $P > 0.05$ ) (Table 4.2). Mass gain was not significantly different for birds carrying TDRs at any stage ( $F_{1,47} = 0.7$ ,  $P > 0.05$ ) (Table 4.2).

**Table 4.2.** Mean  $\pm$  SD of variables assessing the effect of transmitters and TDRs on Royal Penguins\* Significant to controls,  $P < 0.05$ .

<i>Variable</i>	<i>Treatment</i>	<i>Stage 1 (male incubation)</i>	<i>n</i>	<i>Stage 2 (female incubation)</i>	<i>n</i>	<i>Stage 3 (guard/creche)</i>	<i>n</i>
Foraging trip duration (days)	Control	22.9 $\pm$ 1.7	16	15.9 $\pm$ 2.6	9	3.9 $\pm$ 2.4	10
	Transmitters	-	-	15.5 $\pm$ 2.8	8	3.3 $\pm$ 1.8	10
	TDRs	24.9 $\pm$ 2.5*	7	20.1 $\pm$ 4.3*	8	5.0 $\pm$ 2.0	3
Mass gained (% of body weight)	Control	46.0 $\pm$ 9.1	15	33.3 $\pm$ 10.2	9	10.6 $\pm$ 5.2	10
	Transmitters	-	-	36.2 $\pm$ 8.0	8	8.0 $\pm$ 9.0	10
	TDRs	32.4 $\pm$ 11.9	7	31.9 $\pm$ 11.2	8	15.9 $\pm$ 3.2	3
Water influx (ml kg <sup>-1</sup> day <sup>-1</sup> )	Control	77.4 $\pm$ 7.0	6	191.4 $\pm$ 45.4	7	-	-
	Transmitters	-	-	194.4 $\pm$ 16.7	5	-	-
	TDRs	148.0 $\pm$ 19.8*	5	201.1 $\pm$ 28.1	7	-	-
Body composition (% difference of water before and after foraging)	Control	4.5 $\pm$ 2.1	6	4.2 $\pm$ 3.8	7	-	-
	Transmitters	-	-	5.7 $\pm$ 3.6	5	-	-
	TDRs	2.9 $\pm$ 2.3	5	-4.9 $\pm$ 3.9*	7	-	-

#### 4.4 Discussion

The attachment of devices to penguins has been previously found to cause an increase in drag, and impact on foraging behaviour and/or foraging success (Wilson *et al.* 1986, Culik & Wilson 1991). However, the effects of devices on Royal Penguins and other closely related species was not known, although these or similar devices have been used in previous studies (Brown 1987). The long foraging trips undertaken by Royal Penguins also enabled the assessment of instrument effects over extended periods.

##### *Effect of tritiated water experiments*

Injection of tritium alone did not influence return rate, foraging trip duration or mass gained in Royal Penguins, indicating that injected birds were representative of the behaviour of Royal Penguins at this time of year. Previous studies have found a decrease in body mass when penguins were injected in the pectoralis muscle with isotopes (Nagy & Obst 1992, Culik & Wilson 1992), perhaps due to an effect on foraging behaviour caused by obstruction of this muscle (Nagy *et al.* 1984). In the current study penguins were injected intra-peritoneally using small quantities of physiological saline solution (Culik 1994), probably reducing any impact.

Water influx, estimated by a decline in the specific activity of tritium during a trip to sea, measures water intake from food, drinking and metabolism (Green & Gales 1990). In free-living birds, the most effective way of ascertaining the contribution of metabolism is to use  $^{22}\text{Na}$  and  $^{18}\text{O}$ , the known sodium and water content of prey, and the assimilation efficiency of the penguin species, and then extract the contribution of food



and drinking (Green & Gales 1990). Measurement of these factors was beyond the scope of this study. The intake of water from drinking usually is assumed to be minimal and less than 5% of water influx rates (Robertson *et al.* 1988). Hence, the water influx values described here represent the contributions from the three factors (but, primarily food and metabolic water) and not free-living energetics alone.

### *Effects of devices*

Previous studies have found that the effects of devices are minimised if they are small, neutrally buoyant, streamlined, and attached as far caudally as possible (Bannasch *et al.* 1994, Culik *et al.* 1994). They should be placed exactly on the midline to prevent a rudder effect which forces penguins to alter their swimming course to compensate (Culik & Wilson 1991). Despite using as many of these recommendations as possible when deploying the devices during this study, there were still effects from the attachment of TDRs.

The addition of TDRs resulted in increased foraging trip durations during the incubation period. The TDRs used had a relatively large cross-sectional area, which presumably resulted in an increase in drag (Bannasch *et al.* 1994), causing increased energy expenditure (Culik & Wilson 1991). Even small devices that are approximately 2% of the cross-sectional area of a penguin decreased swimming speed measurably in flow tanks (Culik & Wilson 1991). Further, the TDRs in this study were not streamlined. The penguin body is particularly well streamlined and the addition of any device disrupts the flow geometry around the bird (Bannasch *et al.* 1994). The TDRs probably

affected swimming speed and therefore foraging success. Incubation period foraging trips are no doubt important for penguins to regain lost condition following the prolonged fast during the early part of the breeding season. The addition of a TDR, with its associated extra drag, may make it more difficult for penguins to regain condition, thereby increasing the duration of foraging trips.

Furthermore, the attachment of TDRs decreased the probability that penguins would continue the breeding attempt. This probably occurred due to the increased drag from the device on swimming speed and foraging success. This would reduce the penguins' ability to regain condition and/or obtain sufficient food for chicks, forcing an abandonment of the breeding attempt. The inability to regain condition after fasting causes the abandonment of a breeding attempt in Adélie Penguins *Pygoscelis adeliae* (Davis & Miller 1992).

The effects of TDRs on body composition and water influx varied with the stage in the breeding season and/or the sex of the penguin. Differences in fat accumulation, indicated by body composition, were found in females carrying TDRs, but not males. The quantity of fat acquired by females with TDRs was substantially less than controls (7.8% less, see Table 4.2). Conversely, males exhibited a considerable increase in water influx (191%), whereas females only showed a small, non-significant increase. This may reflect a size (although unlikely due to the magnitude of difference in this variable) or physiological difference between the sexes, an ecological difference as females provide the first meal for chicks when they return from this foraging trip, or

different ingestion rates between the sexes. The effect on body composition and water influx rates most likely arose, again, because of reduced foraging success, resulting in either the inability to acquire as much condition, or an increase in energy expenditure to obtain a given quantity of food. Although not measured, the effect is likely to be similar or greater during guard and creche stage due to the dual requirements of chick and adult maintenance (Gales *et al.* 1990).

By contrast, there was no effect on any of the variables tested for penguins carrying transmitters, corresponding with previous work on Chinstrap Penguins *P. antarctica* where effects were found only if devices were greater than 0.9% the cross-sectional area of the penguin (Croll *et al.* 1996). The transmitters used during the current study were streamlined with a very small cross-sectional area. The drag of an earlier, slightly larger model of this transmitter has been estimated at less than 17% for a 1 kg Little Penguin *Eudyptula minor* (Weavers 1992), with 70% of the drag due to the antenna. It is assumed that the effect on drag to Royal Penguins would be less than 17%, due to this penguins' larger size (approximately 5 kg). Although antennae have been previously found to increase drag and interfere with steering, causing serious behavioural disturbances when swimming (Fraser & Trivelpiece 1993), the lack of effect from the transmitters in this study suggests that the increase in drag is sufficiently small for these penguins to compensate.

The addition of devices did not affect mass, in contrast to previous studies (Wilson *et al.* 1986, Gales *et al.* 1990, Davis & Miller 1992). The effect was probably not found

in the current study because Royal Penguins either compensated in other ways, or mass is not a sufficiently sensitive indicator of the impact of devices (Gales *et al.* 1990).

This study has found that the impact of devices is related to their design. Effects were only detected in the larger, un-streamlined TDRs, confirming suggestions that device design should be made in relation to the animal's girth and frontal area, and be streamlined (Bannasch *et al.* 1994, Croll *et al.* 1996). The attachment of TDRs to penguins had several effects which differed with stage in the breeding season and sex, indicating that the impact of devices is complex. The increase in drag from TDRs probably affects swimming ability and foraging success, therefore, it can be assumed that return rates, duration of foraging trips, water influx, and body composition of Royal Penguins equipped with TDRs will not be representative of natural behaviour. Nor will studies in which these devices are used to measure swimming speed and foraging behaviour, such as diving, probably be entirely representative of penguins under natural conditions. Satellite transmitters are now being deployed on penguins, and are generally larger than TDRs. Until the impact of these is measured empirically it can only be assumed that it probably is significant. Researchers should minimise the effects by using appropriate device design until new technology is available.

#### 4.5 Summary

The impact of Time Depth Recorders (TDRs) and VHF transmitters, deployed on Royal Penguins (*Eudyptes schlegeli*) to examine foraging behavior, was assessed during all stages of the breeding season. Models of the devices were attached to penguins and

compared to control birds with no devices. There were no impacts from transmitters on probability of return from a foraging trip, foraging trip duration, mass gained, water influx, or body composition, but substantial impacts from the TDRs. Attachment of TDRs (1) reduced the likelihood that penguins would continue the breeding attempt, (2) increased foraging trip duration, (3) increased water influx, and (4) decreased fat levels. The effects varied with sex and stage in the breeding season, which appeared to relate to the energetic demands of the stage in the breeding season. TDRs probably increased drag, affecting swimming speed and foraging success. The differential impact of the devices is most likely related to their cross-sectional area and streamlining, with TDRs being larger and less streamlined than transmitters.

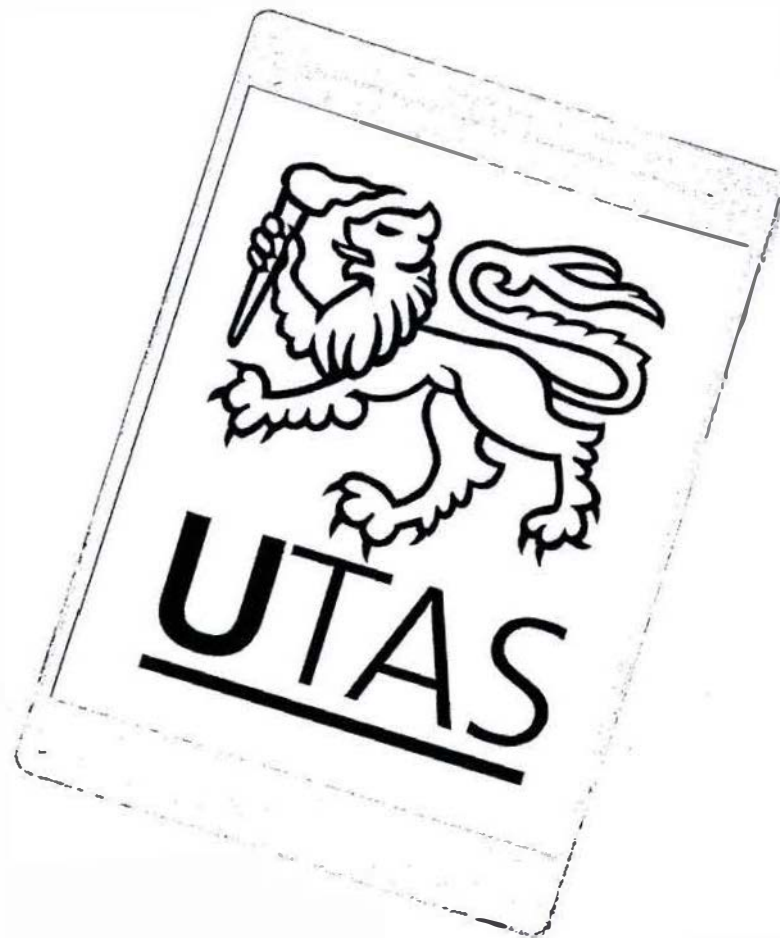
#### **4.6 Acknowledgments**

This work was generously supported by the Antarctic Scientific Advisory Committee, and SeaWorld Research and Rescue Foundation grants. I would like to thank Mary-Anne Lea and Jane Wilson for assistance in the field, Keith Newgrain for analysing the blood, and Mark Hindell, Leon Barmuta, Melissa Geise, Gerry Kooyman, and an anonymous referee for comments on the manuscript. Work was carried out under MI/34/94 and MI/3/95 Tasmanian National Parks and Wildlife permits.



## **Section B**

### **Foraging ecology**





## Chapter 5

### **The foraging zones of Royal Penguins during the breeding season, and their association with oceanographic features**

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#### **5.1 Introduction**

Penguins are important consumers of marine resources (Croxall & Lishman 1987), but for most species little is known about how they interact with the biotic and abiotic components of the marine system. It is postulated that the foraging zones of penguins, like other seabirds, are influenced by: (1) oceanographic processes acting at several spatial scales (Hunt & Schneider 1987); (2) the constraints placed on them during the breeding season, such as relieving incubating partners and feeding chicks (Wilson *et al.* 1995); and (3) prey distribution (Hunt 1990).

The limited data on penguins at sea suggest that they are not randomly distributed (Veit *et al.* 1993), but patchy, like many other species of seabird (Hunt 1988). Patchiness in seabird distribution can often be related to aspects of the physical (and biological) environment. For example, correlations have been demonstrated between seabird distribution and oceanic fronts (Ainley & Jacobs 1981, Abrams 1985, Schneider 1990),

and eddies (Haney & McGillivray 1985, Abrams & Miller 1986, Haney 1986). Distribution can be described at a variety of temporal and spatial scales: *mega* scales (greater than 3000 km) relate to biogeographical regions; *macro* scales (1000 - 3000 km) to regions of higher or lower productivity within them; *meso* scales (100 - 1000 km) to the interactions between larger scale features; coarse scales to the borders of these features with each other and with land or ice; and fine scales to interactions with prey (Hunt & Schneider 1987). The advent of telemetric and/or data logging devices has now allowed the examination of these relationships in species of penguin (Ancel *et al.* 1992, Jouventin *et al.* 1994, Wilson *et al.* 1995, Davis *et al.* 1996, Bost *et al.* 1997).

Royal Penguins *Eudyptes schlegeli* are the only endemic species of penguin on Macquarie Island, with an estimated 850,000 breeding pairs (Copson & Rounsevell 1987). Whilst some aspects of their biology have been investigated, such as breeding (Warham 1971, Carrick 1972) and diet (Horne 1985, Hindell 1988a), details of their foraging ecology are unknown. Estimates of foraging ranges have been made from foraging trip durations and assumed swimming speeds (Horne 1985, Croxall & Lishman 1987), and extrapolations from the closely related Macaroni Penguin *E. chrysolophus* (Scott 1994). Some records of Royal Penguins at sea have also been obtained during voyages (Woehler *et al.* 1990, Reid *et al.* in press), but the age and breeding status of these individuals is generally unknown.

The purpose of the current study was to assess the meso-scale interaction between Royal

Penguins and the oceanographic environment. Foraging zones were investigated throughout the breeding season and compared to oceanographic and productivity features of the local environment. Where possible any travelling behaviours were characterised.

## 5.2 Materials and methods

### *Deployments*

Royal Penguins from Sandy Bay (upper colony) east coast of Macquarie Island ( $54^{\circ} 33' 51''$  S,  $158^{\circ} 54' 11''$  E) were used in this study. Known breeding birds were selected, sexed by measurements of bill length and depth (Hull in press, also Chapter 2) and marked with a coloured velcro flipper band, which was removed when the birds returned to the colony (banding of penguins allowed the confirmation of the return of a bird when a satellite transmitter was lost). Telonics ST-10 satellite transmitters (932E Impala Ave Mesa, Arizona, USA) were attached to the lower medial part of each penguin's back (to minimise drag, Bannasch *et al.* 1994) using a cyanoacrylate adhesive (Loctite 401), with cable ties passed through the birds' feathers and locked around the device. The transmitters were affixed to the birds at the nest site using the techniques described by Hull & Wilson (1996a, also Chapter 3).

The satellite transmitters had saltwater switches (to transmit only when the penguins were on the surface, thereby saving power), were embedded in resin (for protection against high pressure when the penguins were diving), and then potted in black, waterproof housings (Sirtrack, Private Bag 1404, Havelock North, New Zealand). Four

such transmitters were deployed during the 1994/5 and 1995/6 breeding seasons. The devices were 95 x 42 x 20 mm (representing approximately 4% of the frontal cross-sectional area of Royal Penguins), weighed 80 g and were streamlined to reduce drag (Wilson *et al.* 1986). A total of ten deployments was made as follows (number of deployments is shown in parentheses): first male trip during incubation (2); first female trip during incubation (3); guard stage (2 females undertaking 2 trips each, only females forage at this time); and creche stage (1 male).

#### *Preliminary analysis/filtering*

Data were extracted, edited and validated from the dispose and diagnostic files using SATPAK software (Wildlife Computers, 16150 NE 85th St, Redmond WA, USA). The accuracy of each location class was estimated from the error at a known position on land (using a Global Positioning System receiver, with an accuracy of 70 m or better). All locations were filtered to remove aberrant data using the technique described by McConnell *et al.* (1992) and assuming a maximum swimming speed of 10 km/hr, calculated from the most reliable location classes (1, 2 and 3) and from published swimming speeds for Macaroni Penguins (Clarke & Bemis 1979, Brown 1987, Wilson *et al.* 1989a).

Rates of travel, comprising all activities from resting to porpoising and diving, between consecutive locations for the filtered data were calculated and log-transformed (due to lack of normality). These data were compared across stages of the breeding season using a nested ANOVA (individuals nested in stages), and across days of the foraging

trip by categorising days into three groups: (1) days one and two (outgoing leg); (2) middle of the trip, (3) last two days (return leg), and analysing with a repeated measures ANOVA. Similarly, rates of travel during different hours of the day were compared by categorising the day into four, six-hour blocks: (1) 0:00 - 6:00; (2) 7:00 - 12:00; (3) 13:00 - 18:00; (4) 19:00 - 24:00 and analysed with a repeated measures ANOVA.

A Foraging Zone Coefficient (FZC) was calculated as the maximum distance travelled (km) divided by the area of the foraging zone ( $\text{km}^2$ ) (derived from home range analysis, see below). A meander coefficient, representing the degree of non-linear swimming (an indication of foraging activity), was calculated by determining the deviation of points from the  $45^\circ$  regression line of speed x distance on filtered locations. This was carried out on locations between one and two hours apart. Coarser temporal resolutions could not be used due to the inaccurate representation of rates of travel (see Results). Locations less than one hour apart were not used because it was felt that the error margins inherent in the ARGOS estimation of location (Table 5.1) would mask some of the meandering behaviour over this limited time period. Although this meant that there was an underestimate of rates of travel compared to locations less than one hour apart, it was felt this temporal resolution was the most suitable way to describe meandering behaviour. Data were log-transformed, due to lack of normality, and analysis was carried out in the same manner as for rates of travel, using a nested ANOVA to compare stages in the breeding season, and repeated measures ANOVAs to compare day of the foraging trip and time of the day.



trip by categorising days into three groups: (1) days one and two (outgoing leg); (2) middle of the trip; (3) last two days (return leg), and analysing with a repeated measures ANOVA. Similarly, rates of travel during different hours of the day were compared by categorising the day into four, six-hour blocks: (1) 0:00 - 6:00; (2) 7:00 - 12:00; (3) 13:00 - 18:00; (4) 19:00 - 24:00 and analysed with a repeated measures ANOVA.

A Foraging Zone Coefficient (FZC) was calculated as the maximum distance travelled (km) divided by the area of the foraging zone ( $\text{km}^2$ ) (derived from home range analysis, see below). A meander coefficient, representing the degree of non-linear swimming (an indication of foraging activity), was calculated by determining the deviation of points from the 45° regression line of speed x distance on filtered locations. This was carried out on locations between one and two hours apart. Coarser temporal resolutions could not be used due to the inaccurate representation of rates of travel (see Results). Locations less than one hour apart were not used because it was felt that the error margins inherent in the ARGOS estimation of location (Table 5.1) would mask some of the meandering behaviour over this limited time period. Although this meant that there was an underestimate of rates of travel compared to locations less than one hour apart, it was felt this temporal resolution was the most suitable way to describe meandering behaviour. Data were log-transformed, due to lack of normality, and analysis was carried out in the same manner as for rates of travel, using a nested ANOVA to compare stages in the breeding season, and repeated measures ANOVAs to compare day of the foraging trip and time of the day.



### *Foraging zones*

Home range analysis was used to assess clusters of locations (CL), the area of foraging zones, as well as the degree of overlap between zones. As the probability of a penguin being at any position in the zone (the utilisation distribution) was not of interest, the temporal spacing of locations and issues of autocorrelation did not apply (White & Garrott 1990). Locations were converted to cartesian co-ordinates using CALHOME (CALifornia HOME Range, US Forest Service, Pacific SW Research Station, CA, USA), and home range analysis was performed using a fixed Kernel Analysis from Ranges V (Kenward & Hodder, Institute of Terrestrial Ecology, Dorset, UK), incorporating an objective smoothing factor and 85% isopleths, to describe the foraging zones. CL were used as an indication of presumed increased foraging activity. As reduced rates of travel in King *Aptenodytes patagonicus* and Emperor *A. forsteri* Penguins coincide with a higher local density of satellite locations, and are positively associated with feeding bouts (Ancel *et al.* 1992, Bost *et al.* 1997), CL were considered an appropriate indicator. CL were determined using 40% isopleths (from home range analysis), as these described core areas in the zone. Core areas were defined using the technique of Wray *et al.* (1992). This involves calculating the area of a range from successive isopleths, and using the isopleth which results in the greatest increase in area.

Incremental analysis was used to determine the number of locations required to accurately represent a foraging zone (Ford & Krumme 1979). This was performed by randomly selecting locations from a complete track (representative female during

incubation stage). It was not possible to undertake this analysis on the other individuals, as they had either incomplete tracks, trips of short duration, or non-representative data (the aberrant female, see below). The following number of locations were used: 10, 20, 30, 40, 50, 60, 70 and 80, with ten replicates of each randomly selected. The area of the derived foraging zone was then plotted and the point of the areal asymptote indicated the minimum number of locations required (Ford & Krumme 1979).

### *Oceanographic influence*

There are scant data available on the oceanographic conditions around Macquarie Island (see Gordon 1972), and none on prey resources. Therefore, assessment of the abiotic and biotic features of zones in which Royal Penguins were recorded foraging had to be evaluated using satellite data. Contemporaneous, weekly sea surface temperatures at a spatial scale of 19 x 19 km (NASA PO.DAAC data) were used to describe oceanographic features. There were no contemporaneous data on productivity levels available, therefore an indicator of productivity was derived from phytoplankton pigment concentration composite data at a spatial resolution of 1 km x 1 km, for the period 1978-1986 (NASA CZCS data). Productivity levels, as signified by phytoplankton pigment concentrations, during both periods (October to December - incubation stage; January to March - chick provisioning) ranged from less than 80 to 160 counts. A count is described by the following formula:  $\text{count} = (\log(\text{pigment}) + 1.4)/0.012$  (NASA PO.DAAC). Bathymetric data were obtained from the Australian Antarctic Division.

Mean values  $\pm$  standard deviation are used throughout.

### 5.3 Results

#### *Satellite tracking data*

An average of 13 locations was received per 24 hour period (pre-filtering) (Table 5.1), with marginally fewer locations received during the 1994/5 (average  $13.0 \pm 3.5$  per day) than the 1995/6 season (average  $14.1 \pm 3.5$  per day). There was a bimodal distribution in the number of locations received during a 24 hour period, with none available around midday (local time) (Fig. 5.1). The absence of signals was longer (four hours) in the 1994/5 season than the 1995/6 season (two hours). The number of locations retained after filtering also varied between seasons. During the 1994/5 season only 160 (22.2%) were retained, whilst 757 (54.8%) were retained during the 1995/6 season.

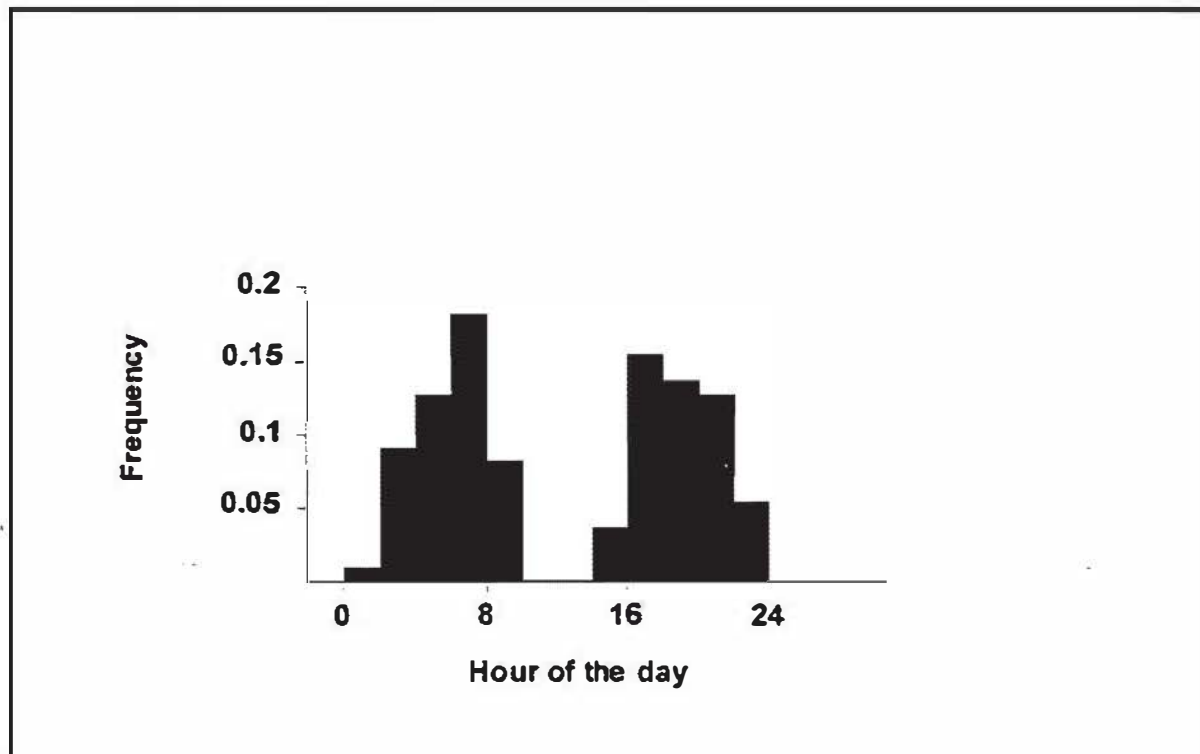
Successive locations were separated by between three minutes and 67 hours (average 3.8 hours). Aside from the reduction in locations around midday, the frequency of locations varied with time of day ( $F_{22,878} = 2.6$ ,  $P < 0.001$ ), with 1500 hours (local time, GMT + 10) having the most locations. Regressions of speed and distance calculated from locations less than one hour, 1 - 2 hours, 2 - 3 hours, and 3 - 4 hours apart were significantly different (ANCOVA,  $F_{3,295} = 1840.7$ ,  $P < 0.001$ ) (Fig. 5.2). This indicated that rates of travel estimated from locations separated by different times periods were not constant, and that greater separations led to more severe underestimates of rates of travel. All further analyses refer to filtered data, and rates of travel are calculated from locations less than one hour apart.

**Fig. 5.1** Number of locations (unfiltered) received over a 24 hour period during each season of the study.

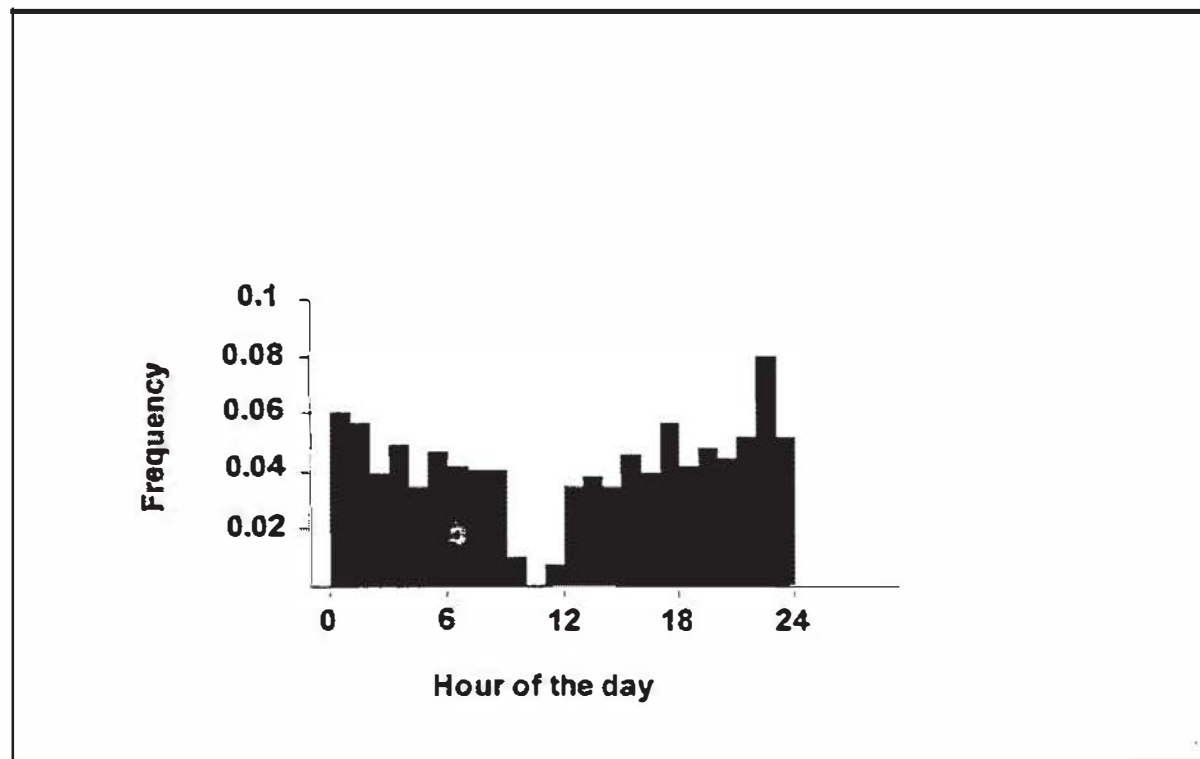
A. 1994/5

B. 1995/6

A



B



**Table 5.1.** Percentage of locations received and calculated errors (km) when penguins were at a known location on land, in each location class

<i>Location class</i>	<i>Locations received 1994/5 (%)</i>	<i>Locations received 1995/6 (%)</i>	<i>Latitudinal error: average (range)</i>	<i>Longitudinal error: average (range)</i>	<i>n</i>
3	0.5	1.0	1.0 (0.5 - 1.5)	0.6 (0.1-1.1)	8
2	1.3	1.9	1.0 (0.2 - 1.5)	0.9 (0.1 - 1.4)	20
1	6.6	20.0	1.0 (0.1 - 1.7)	1.0 (0.0 - 4.1)	43
Total 1, 2, 3	8.4	22.9			
0	56.4	51.0	7.0 (0.1 - 89.2)	8.7 (0.1 - 100.8)	65
A	16.2	11.6	9.0 (0.1 - 40.2)	14.9 (0.2 - 145.3)	20
B	11.6	14.4	4.0 (0.3 - 6.1)	4.6 (0.1 - 14.7)	9
Z	7.4	0.1	29.0 (6.6 - 63.7)	44.2 (1.2 - 112.8)	5
Total 0, A, B, Z	91.6	77.1			

### *Travelling behaviour*

Rates of travel were constant across the breeding season ( $F_{3,4} = 0.7$ ,  $P > 0.05$ ) (Table 5.2), days of the foraging trip ( $F_{6,6} = 0.4$ ,  $P > 0.05$ ), and time of day ( $F_{2,10} = 0.4$ ,  $P > 0.05$ ).



**Fig. 5.2** Regressions of rate of travel and distance between consecutive locations of different temporal resolutions.

The 45° line through the origin represents when animals were swimming in a straight line. Points below the line, therefore, represent an underestimate of rate of travel, with the further locations were apart the greater the error.

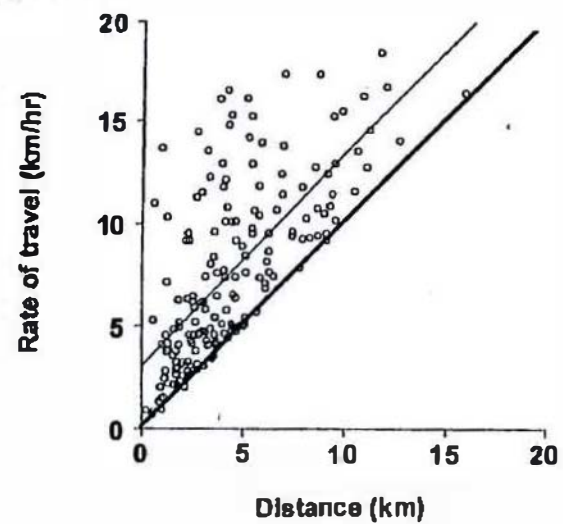
A < one hour

B 1 - 2 hours

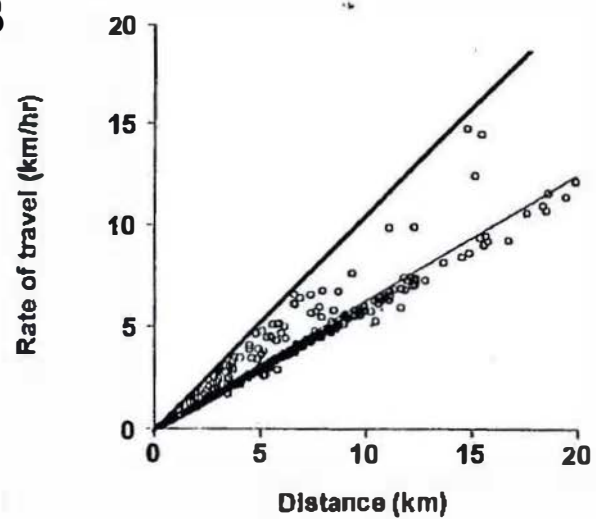
C 2 - 3 hours

D 3 - 4 hours

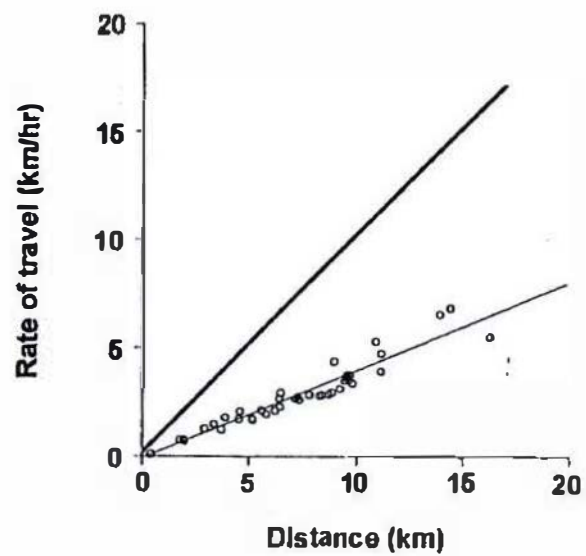
A



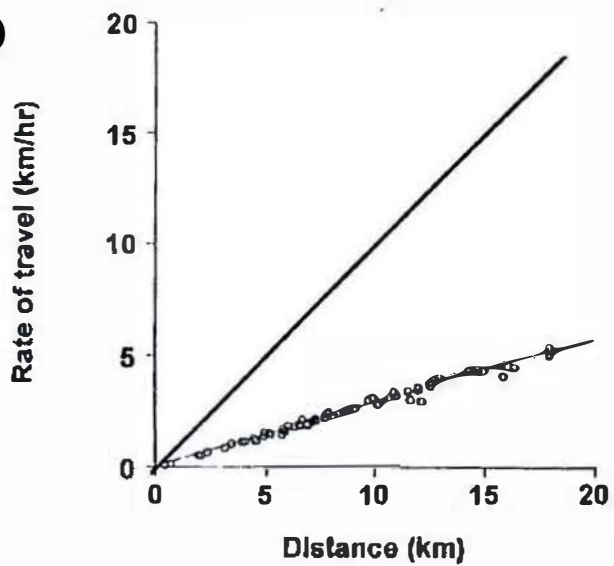
B



C



D



**Table 5.2.** Estimated rate of travel (km/hr) by Royal Penguins (mean  $\pm$  standard deviation). (Locations less than one hour apart)

<i>Stage</i>	<i>Mean rate of travel</i>	<i>Number of estimates</i>
Males during incubation	6.1 $\pm$ 5.4	27
Females during incubation	7.8 $\pm$ 4.5	132
Guard	4.6 $\pm$ 3.4	13
Creche	5.0 $\pm$ 3.8	25
Combined	7.0 $\pm$ 4.6	197

The meander coefficients varied from 0.0 to -11.95 (mean  $-2.16 \pm 1.8$ ), where 0.0 represented swimming in a straight line and increased negative coefficients indicated a greater degree of meandering. There were no significant differences in the degree of meandering between stage in the breeding season ( $F_{1,2} = 1.8$ ,  $P > 0.05$ ). Degree of meandering was constant across day of the foraging trip ( $F_{2,12} = 1.3$ ,  $P > 0.05$ ), but varied significantly with hour of the day ( $F_{3,18} = 6.7$ ,  $P < 0.007$ ). The greatest degree of meandering occurred between 07:00 and 18:00 hours.

#### *Home range analysis*

The number of locations per individual, after filtering, used to define foraging areas ranged from 24 to 378. The incremental analysis determined that a minimum of 20 locations were required to represent the foraging range of Royal Penguins during the breeding season.

The area of foraging zones and the FZC are given only for complete tracks. Of the ten foraging zones obtained, four were incomplete due to: (1) loss of a device from a male during incubation, therefore the return leg of the foraging trip was not complete (the bird did return to the colony, however); (2) a female during incubation not returning from her foraging trip; (3) another female during incubation remaining absent from the colony for two months, becoming a failed breeder and whose behaviour was subsequently regarded as aberrant; and (4) damage of the antenna on a device deployed on the male during creche stage, hence not transmitting signals in the last stage of the foraging trip.

All foraging activity occurred offshore, to the south-east of Macquarie Island and south of the Campbell Plateau in the Emerald Basin (Figs. 5.3 - 5.6). The water in this region is 4000 - 5000 m deep. A maximum distance of over 600 km and minimum distance of 68 km was travelled from the colony, with the distance covered varying with stage in the breeding season (Table 5.3). There was a significant relationship between the duration of the foraging trip and the maximum distance travelled ( $r^2 = 0.5$ ,  $F_1 = 6.3$ ,  $P < 0.04$ ). The relationship between duration of the foraging trip and area of the foraging zone was even stronger ( $r^2 = 0.8$ ,  $F_1 = 20.7$ ,  $P < 0.006$ ).

**Fig. 5.3** Tracks of male Royal Penguins during the incubation stage.

● male 1 (incomplete track)

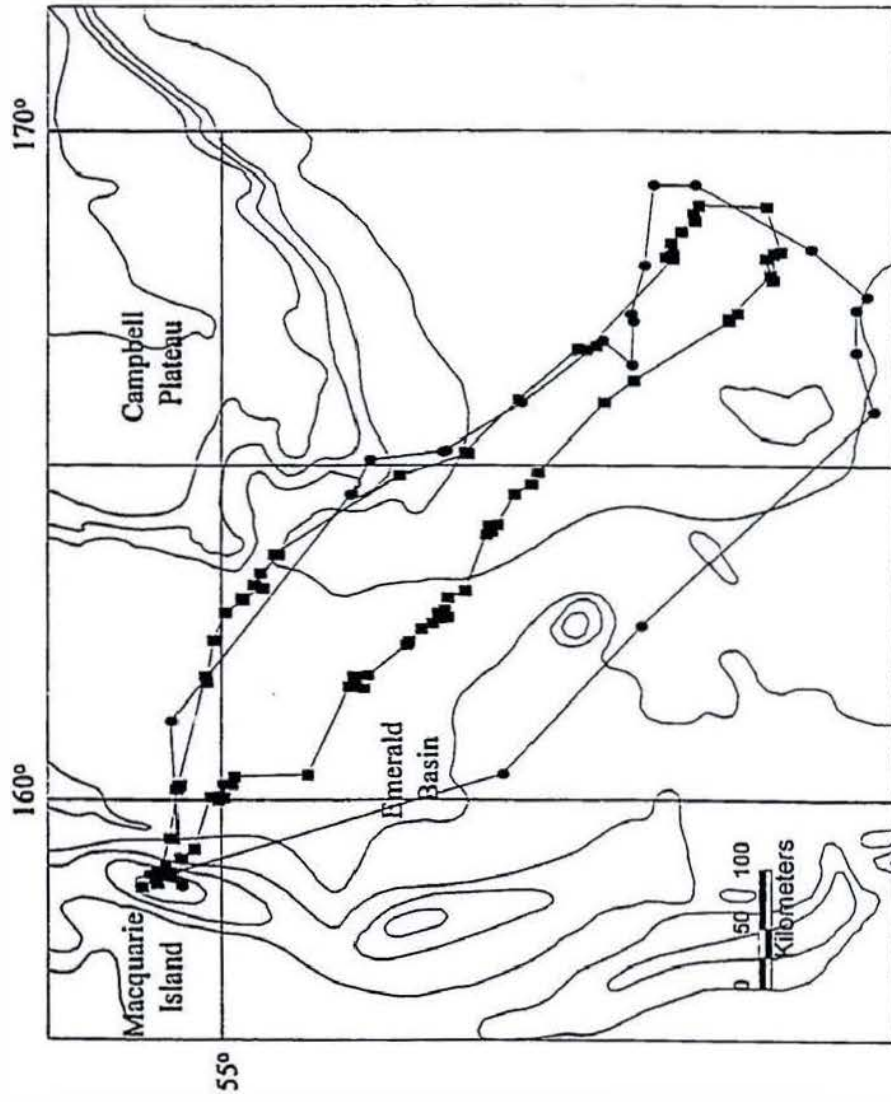
■ male 2

A. showing 1000 m bathymetry lines

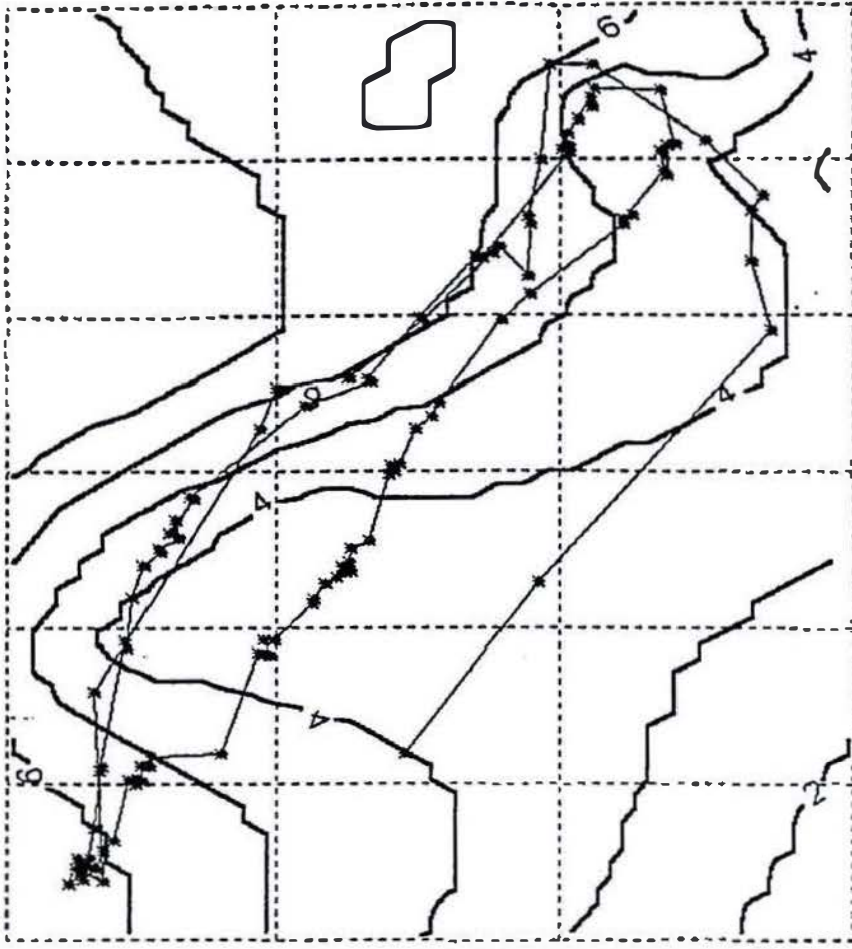
B. showing contemporaneous sea surface temperatures ( $^{\circ}\text{C}$ )

(NASA PO.DAAC data)

A



B





**Fig. 5.4** Tracks of female Royal Penguins during the incubation stage.

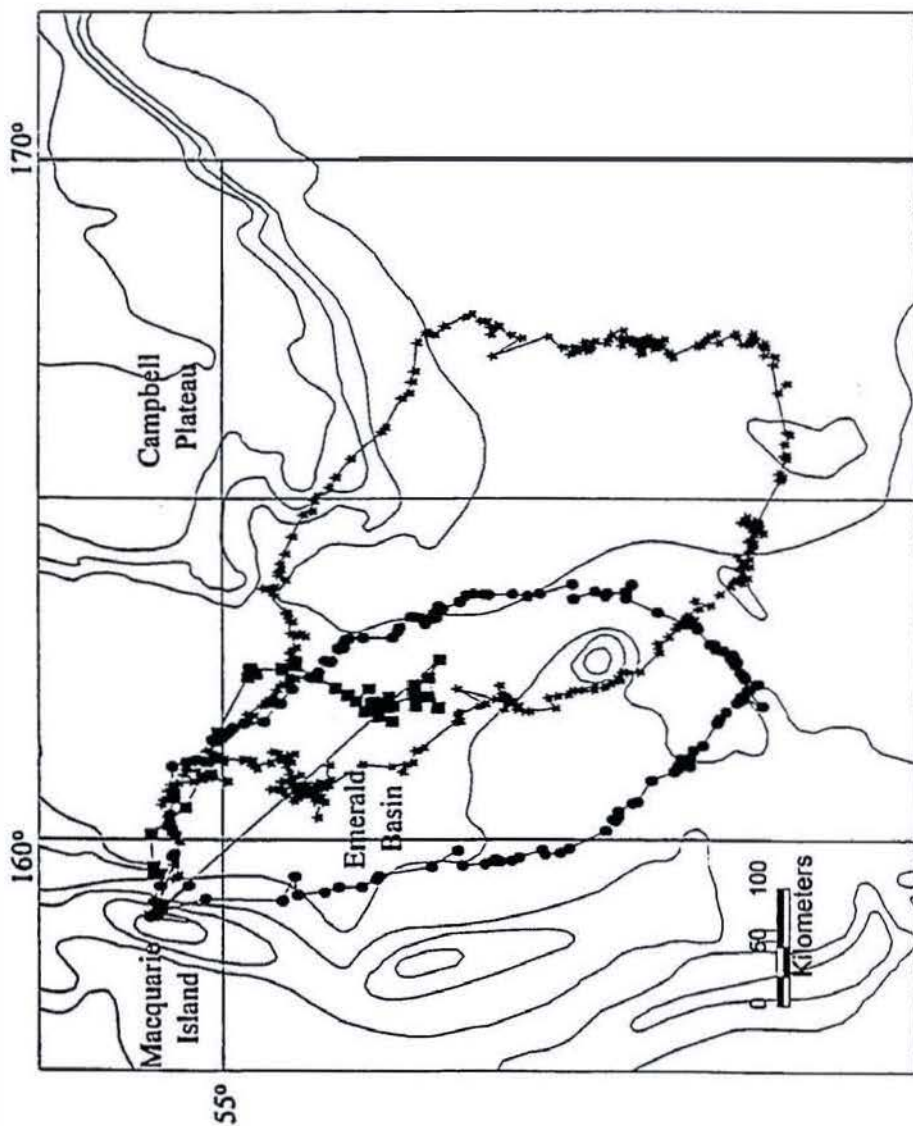
- female 1
- female 2 (incomplete track)
- ★ female 3 (aberrant)

A. showing 1000 m bathymetry lines

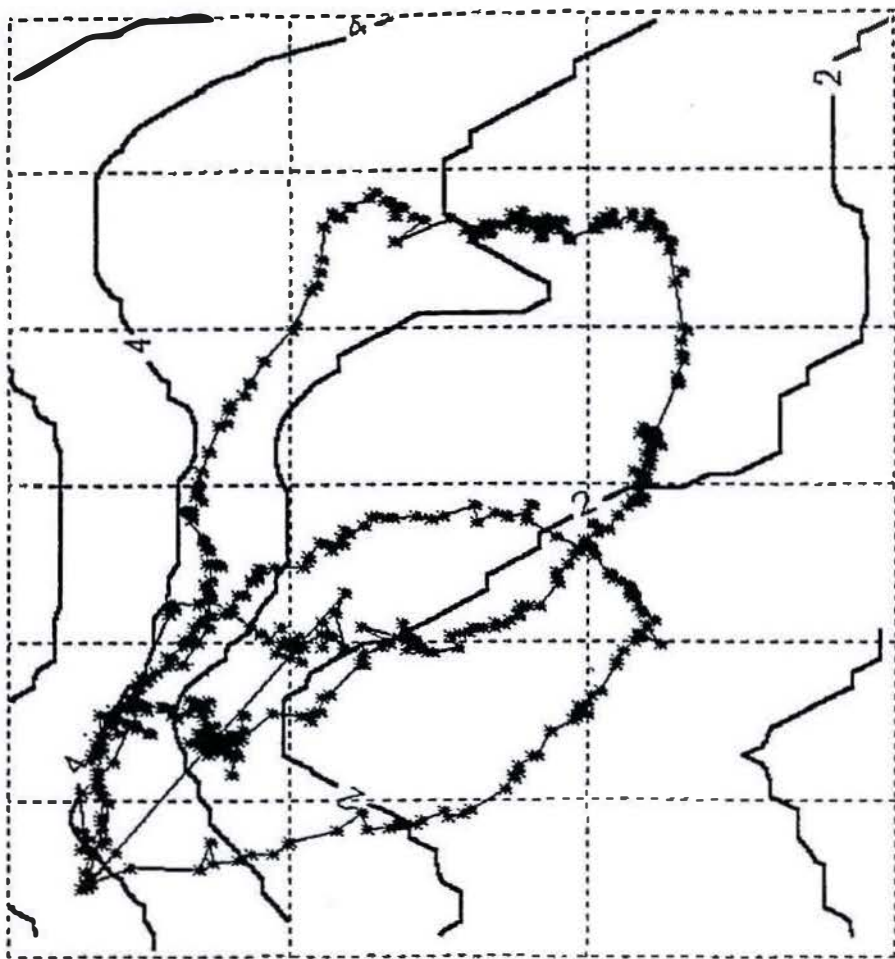
B. showing contemporaneous sea surface temperatures ( $^{\circ}$  C)

(NASA PO.DAAC data)

A



B



**Fig. 5.5** Tracks of females during guard stage.

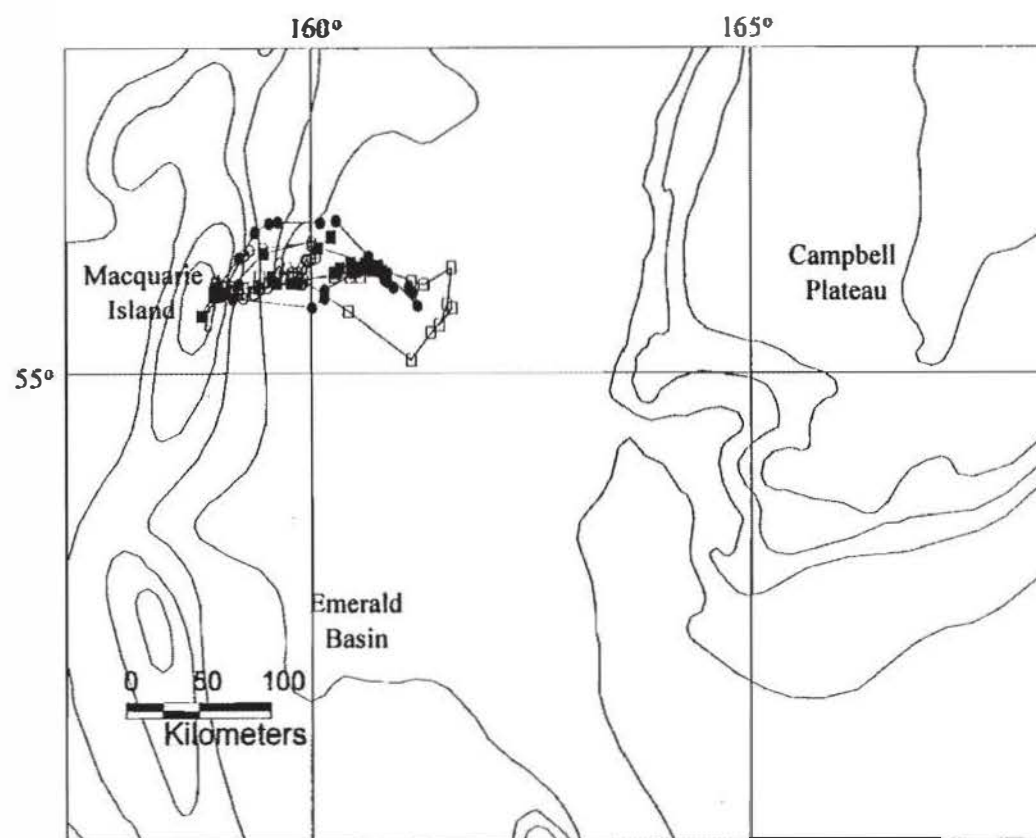
- female 1, first trip
- female 1, second trip
- female 2, first trip
- female 2, second trip

A. showing 1000 m bathymetry lines

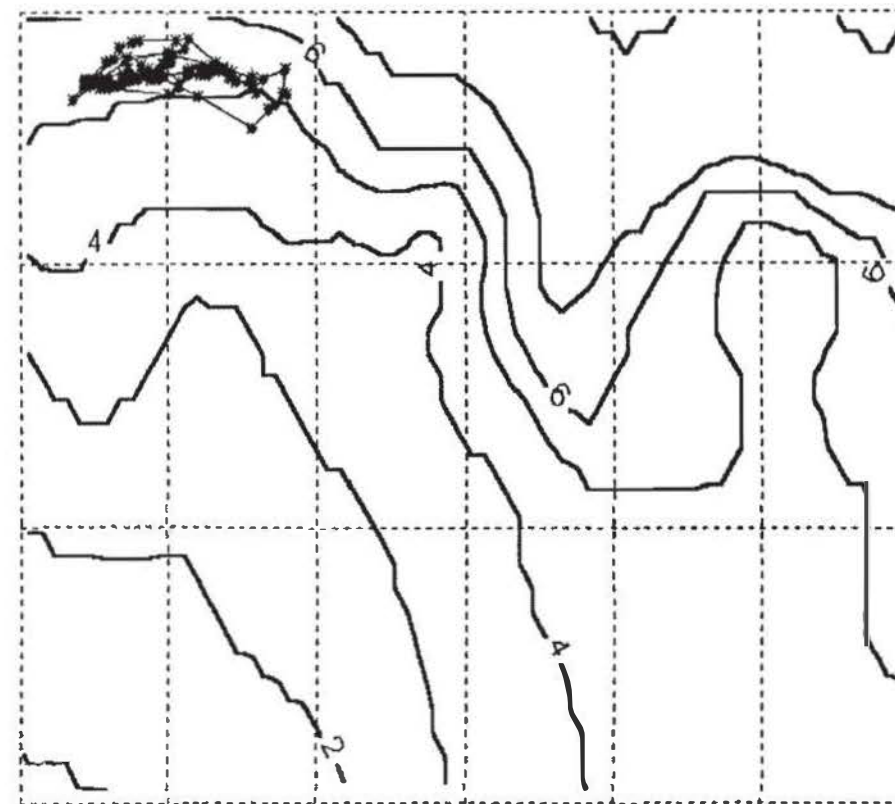
B. showing contemporaneous sea surface temperatures ( $^{\circ}$  C)

(NASA PO.DAAC data)

A



B



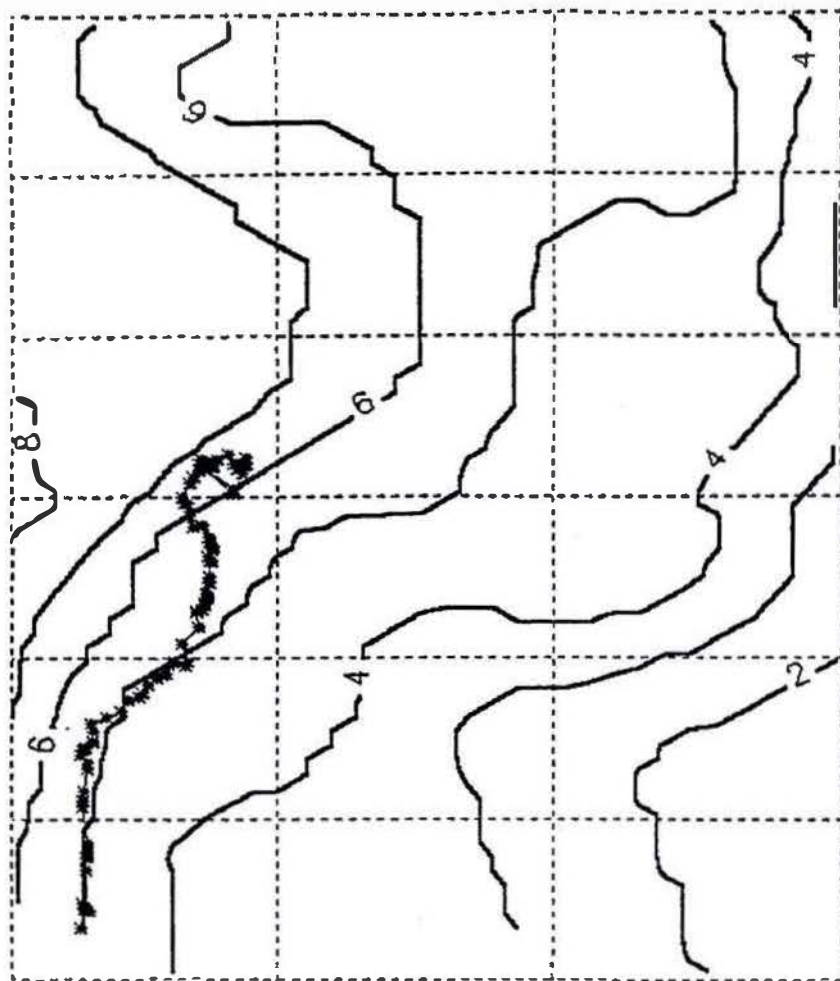
**Fig. 5.6** Track of male during creche stage

A. showing 1000 m bathymetry lines

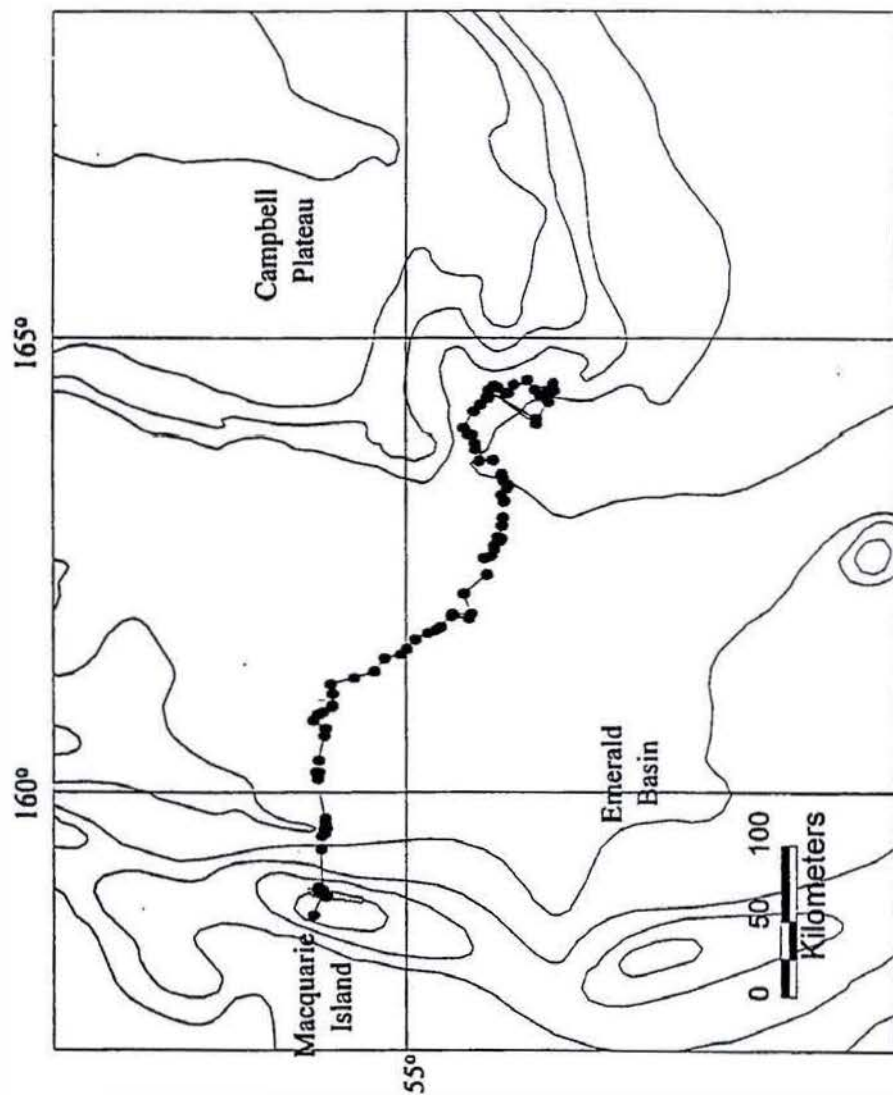
B. showing contemporaneous sea surface temperatures ( $^{\circ}\text{C}$ )

(NASA PO.DAAC data)

B



A





All penguins left Macquarie Island and travelled due east before heading south-east, returning to the island in a clockwise path. The FZC increased as the season progressed (Table 5.4). During the incubation stage both male and female birds undertook "circular" tracks (as defined by Jouventin *et al.* 1994) with large areas being covered. However, during the chick provisioning stage (guard and creche) the tracks were "direct" (as defined by Jouventin *et al.* 1994) to specific areas of the foraging zones.

**Table 5.3.** Maximum distance travelled, average distance per day (km) and duration of foraging trips by Royal Penguins during each stage of the breeding season

<i>Individual and stage</i>	<i>Maximum distance (km)</i>	<i>Average distance per day (km)</i>	<i>Duration of trip (days)</i>
1. Male during incubation	654.9	28.5	23
2. Male during incubation	664.2	31.6 *	21
3. Female during incubation	269.2	*	*
4. Female during incubation	415.7	29.7	14
5. Female during incubation+	587.7	18.4	68
6. Guard 1 (female)	68.6	23.0	3
7. Guard 1 second trip	131.0	43.7	3
8. Guard 2 (female)	109.1	36.3	3
9. Guard 2 second trip	153.5	51.2	3
10. Creche (male)	330.4	47.1 *	7

\* incomplete trips

+ aberrant

The degree of overlap of foraging zones for stages was low (average 22.4%) (Table 5.5), indicating discrete foraging zones across the breeding season. Of the 90 comparisons only 11 had a degree of overlap greater than 50%. These overlaps were between the incomplete male trip during incubation and most other trips, the aberrant female and guard stage trips, and within guard stage (Table 5.5). The results of the incomplete track of the male during incubation and the aberrant female must be viewed with caution as neither of these tracks may be representative.

**Table 5.4.** The area, centre of activity and Foraging Zone Coefficients (FZC) of Royal Penguin foraging zones (using 85% isopleths). Only complete trips are given

<i>Stage</i>	<i>Deployment</i>	<i>Centre (distance from colony, km)</i>	<i>Area (HA)</i>	<i>FZC</i>	<i>Number of locations</i>
Male (Incubation)	1	626.3	1330	0.49	24
Female	2	473.5	1720	0.24	151
(Incubation)	3	162.6	2620	0.22	378
Guard	1	65.0	200	0.34	29
	1a	108.8	100	1.31	28
	2	92.9	50	2.18	31
	2a	20.2	120	1.28	30

"a" denotes second trip by the same individual

**Table 5.5.** Degree of overlap between each Royal Penguin foraging trip (%) derived from home range analysis

<i>Trip</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>10</i>
1	-	34.6	0.6	4.0	26.8	1.1	1.3	1.6	4.0	2.7
2	17.4	-	3.6	24.8	56.0	1.3	1.8	1.9	3.7	18.7
3	6.7	100	-	30.9	90.4	6.8	0.0	3.4	9.4	30.5
4	3.1	39.0	1.7	-	20.9	0.9	0.8	0.8	2.9	13.0
5	12.6	53.1	3.1	12.5	-	0.0	1.0	0.7	1.2	12.9
6	37.4	100	21.9	47.4	0.0	-	2.4	21.2	74.7	0.0
7	33.6	93.9	0.0	28.6	57.9	1.9	-	45.8	47.3	8.9
8	35.9	95.0	6.0	25.5	38.1	12.1	38.2	-	64.7	0.2
9	48.0	92.2	4.5	7.9	45.1	30.4	20.3	19.3	-	4.5
10	4.7	63.3	3.6	26.8	46.0	0.0	0.5	0.1	0.6	-

Trip:

1 male during incubation

2 male during incubation

3 female during incubation

4 female during incubation

5 female during incubation

6 guard 1

7 guard 1a

8 guard 2

9 guard 2a

10 creche

### *Oceanographic influence*

Sea surface temperature data indicated that all foraging took place in the Polar Frontal Zone (PFZ) (Figs. 5.3 - 5.6), in water that ranged between 2 - 6° C (PFZ defined by Burling 1961). The reliance on this zone was consistent throughout the breeding season, although the locations of females during incubation were in slightly cooler water. The PFZ moved further south during the summer period, and there were no indications of any features such as eddies or gyres in this region at this time (NASA PO.DAAC data, Figs. 5.3 - 5.6).

Productivity was variable in the region and whilst CL of the penguins overlapped to some extent with regions of highest productivity it was not confined to these areas (Fig. 5.7).

## **5.4 Discussion**

### *ARGOS data*

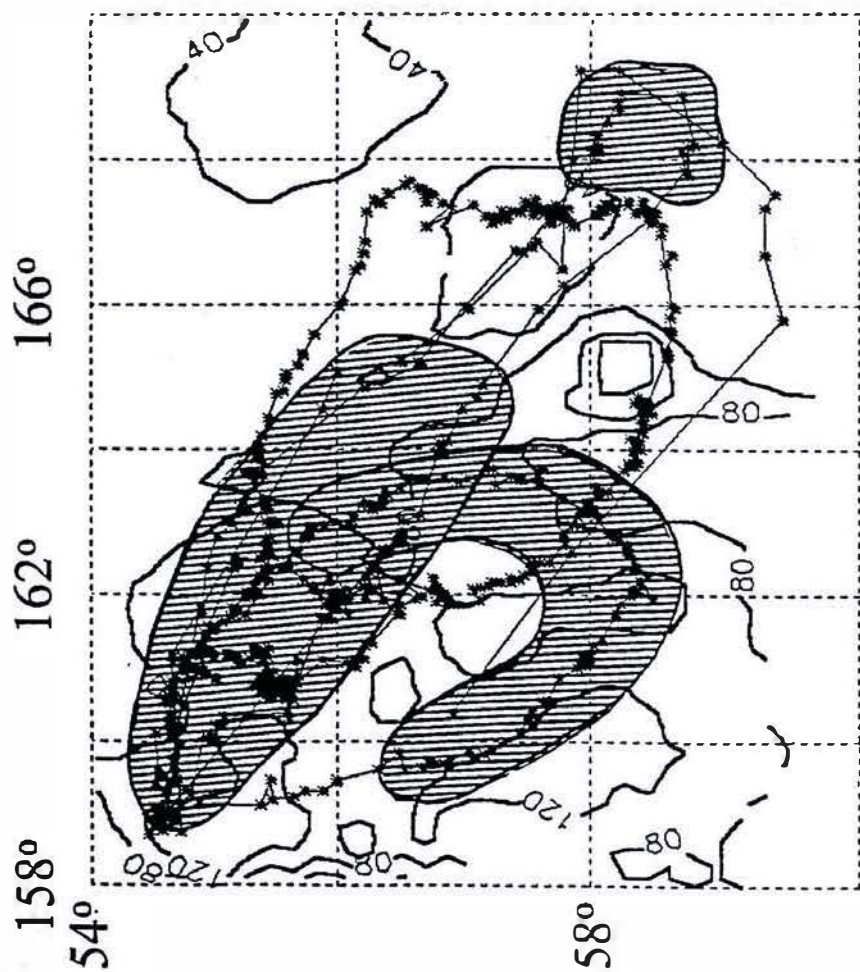
The NOAA satellites pass on average 16 times per day at the latitude of Macquarie Island (ARGOS manual) therefore in this study, locations were received during 81% of satellite passes. The difference in the number and quality of locations received between the 1994/5 to 1995/6 seasons is due to the commissioning of the NOAA J satellite by ARGOS in early 1995, which resulted in a reduction in non-standard and skipped (low class) locations (ARGOS manual). For this reason, more locations were filtered due to

**Fig. 5.7** Penguin tracks with 40% isopleths showing clusters of locations overlaying productivity indicator. Productivity indicator derived from phytoplankton pigment counts, which have a logarithmic relationship to pigment concentrations (NASA CZCZ 1978-86 composite data sets)

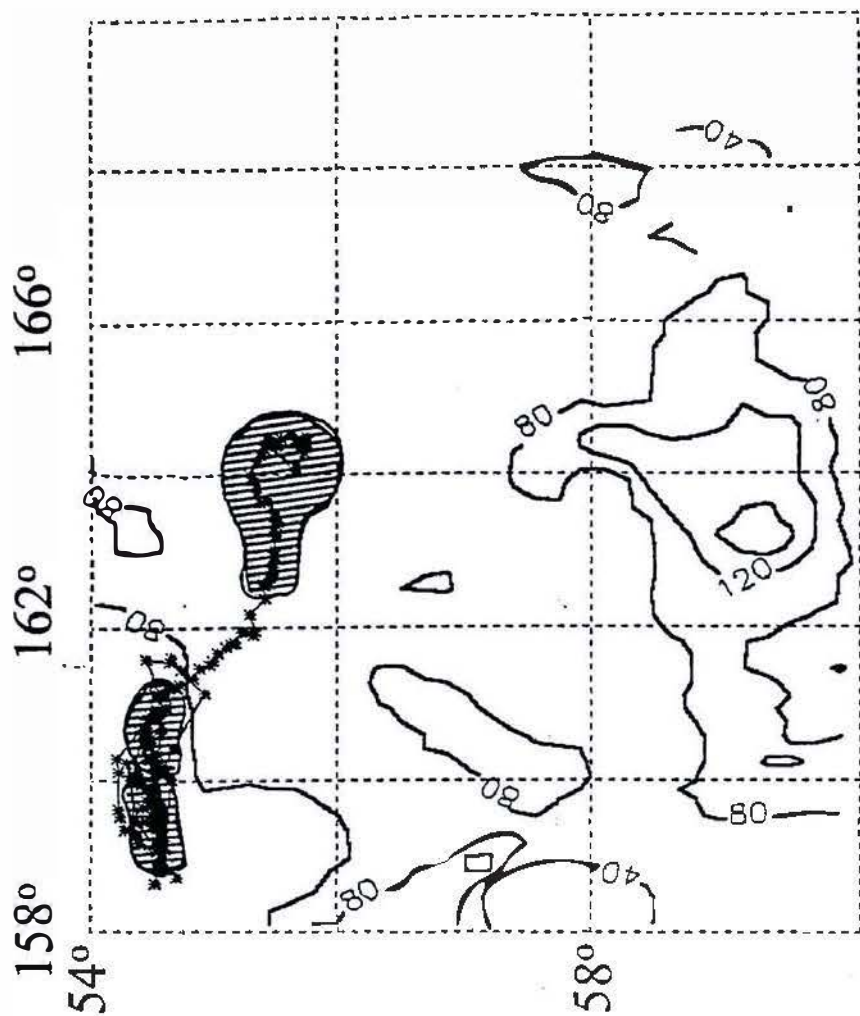
A. October - December average with incubation stage tracks

B. January - March average with guard and creche stage tracks

A



B





their aberrant nature in the 1994/5 season (77.8%), compared to the 1995/6 season (45.2%).

The error margins of all location classes calculated in this study were greater than those cited by ARGOS, and other studies (McConnell *et al.* 1992, Jouventin *et al.* 1994, Stewart & DeLong 1995). This is probably due to the characteristics of the transmitters (size, insulation, power output, antenna type and oscillator stability which is influenced by thermal conditions, Stewart *et al.* 1989), and/or the latitude at which the signals were transmitted.

The temporal spacing of locations significantly affected estimates of rates of travel (Fig. 5.2), as has also been shown by Walker *et al.* (1995). This arises because travel between consecutive locations is assumed to be a straight line. The further locations are apart in time, the more incorrect this assumption is, because birds rarely travel in straight lines when searching for prey (Walker *et al.* 1995). Estimates of rates of travel are best derived from locations as closely spaced as possible.

### *Effects of devices*

It is likely that the foraging behaviour of Royal Penguins is affected to some extent by the satellite transmitters, as effects have been recorded when similar-sized time depth recorders were deployed on this species (Hull 1997, also Chapter 4). However, we hope to have minimised effects by streamlining the transmitters to reduce drag (Bannasch *et al.* 1994). The antenna may have limited some of the advantage gained by streamlining;

as Weavers (1992) estimated that 70% of the induced drag was due to the antenna in VHF transmitters. Other models of satellite transmitters resulted in increased foraging trip durations and changes in diving effort when attached to King Penguins (Bost *et al.* 1997), and increased foraging trip durations and reduced mass gain when attached to Adélie Penguins *Pygoscelis adeliae* (Kerry *et al.* 1995). Aside from the aberrant female and the creche male, the foraging trip durations of all Royal Penguins in this study were the same as birds without transmitters (Chapter 9). This suggests that the impact from the transmitters was probably only marginal, as foraging trip durations were one of the variables significantly affected by the addition of large, unstreamlined devices (Hull 1997, also Chapter 4). The foraging duration of the creche male was longer than those recorded for this time of year (Chapter 4) suggesting that this track may not be representative of birds in this stage. Aside from this trip, it is assumed that the foraging zones of Royal Penguins were not significantly affected by the attachment of these devices (c.f. Bost *et al.* 1997), although this does not discount the possibility that other aspects of Royal Penguin behaviour may have been altered by the transmitters.

### *Travelling behaviour*

Although speed was not measured directly, the average rates of travel ( $7.0 \pm 4.6$  km/hr) were comparable with that of 7.5 km/hr measured in Macaroni Penguins (Brown 1987). No patterns in rates of travel were detected in this study, probably because many fine scale foraging patterns cannot be discerned from satellite tracking data. Higher rates of travel on return legs of trips have been described previously for a number of penguin

species (Williams & Siegfried 1980, Croxall & Lishman 1987, Kerry *et al.* 1995, Wilson *et al.* 1995, Bost *et al.* 1997). Increases in speed on both the outward and return trips to foraging grounds, compared to lower speeds in the feeding area, have also been described (Croxall & Lishman 1987, Heath & Randall 1989, Croxall & Davis 1990).

The meandering coefficient indicated diurnal patterns, suggesting increased foraging activity during the hours of 7:00 to 18:00. This is consistent with diurnal foraging patterns described in previous studies of penguins (Williams & Siegfried 1980, Wilson *et al.* 1989a, Croxall *et al.* 1993, Bost *et al.* 1997, Green *et al.* submitted). It suggests that the meandering coefficient is a better indicator of foraging activity than rates of travel derived from satellite tracking data.

#### *Foraging zones and oceanographic influence*

The distances travelled during the incubation stage (over 600 km) make Royal, along with King Penguins (Jouventin *et al.* 1994), the most pelagic species of penguin studied to date. The data derived from this study also indicate that they are: (1) offshore feeders (Croxall & Lishman 1987); (2) that foraging zones are not constant across the breeding season; and (3) that they travel further than previously assumed from extrapolations of studies at other localities (Horne 1985, Scott 1994).

All foraging was undertaken in a quadrant to the south-east of Macquarie Island, bounded by 54° 30' to 60° S and 158° 54' to 165° E, indicating a non-random use of the ocean, as exhibited by other seabirds (Baum 1987, Hunt *et al.* 1986, Bost *et al.* 1997).

The few observations of Royal Penguins at sea have not recorded them this far south, nor east (Woehler *et al.* 1990, Reid *et al.* in press), but this is probably a function of the lack of visits by ships to the eastern side of Macquarie Island. The penguins were foraging predominantly in water 4000 - 5000 m deep which accords with observations at sea (Reid *et al.* in press) and confirms the pelagic foraging habit of this species (Hindell 1988a).

Foraging ranges tended to lie within the PFZ, predominantly near the northern boundary of the zone, probably in the sub-Antarctic Front (defined by water 5 - 9° C, Burling 1961). The Antarctic Circumpolar Current (ACC) is a dominant feature of the PFZ, flowing in an easterly direction (Radok 1966, Gordon 1972). As the ACC approaches the Macquarie Ridge it is diverted southward and then loops north into the Emerald Basin forcing relatively cooler water further north and causing mixing (Gordon 1972). Like most frontal zones, the PFZ is believed to restore nutrients to the region and enhance productivity (Ainley & Jacobs 1981, Foster 1984, Abrams 1985, Lutjeharms *et al.* 1985, Schneider 1990). Seabirds have demonstrated associations with frontal zones (Haney & McGillivray 1985) presumably due to the increases in productivity. This study shows that Royal Penguins, like King Penguins around the Crozet Archipelago (Bost *et al.* 1997), exhibit an affinity with frontal zones.

Whilst myctophid fish and some cephalopods have a broad Antarctic/sub-Antarctic distribution, they are found closer to the surface and in higher concentrations in the PFZ (Hulley 1981, Gon & Heemstra 1990). The diet of Royal Penguins 400 to 600 km from

the colony is not known, but assumed to be the same as that brought ashore, where it is dominated by euphausiids and myctophid fish, with some cephalopods taken (Hindell 1988a). Presumably the PFZ near Macquarie Island exhibits high densities of prey, providing an abundant and/or predictable source of prey for these penguins.

Although average prey densities in the PFZ are purportedly higher and more predictable than other sectors of the Southern Ocean, prey are still regarded as patchy in distribution (Bost *et al.* 1997). CL within the foraging zones of Royal Penguins also suggested a patchiness in prey distribution. Foraging patterns (meander coefficient and FZC) also suggested a difference in the availability of resources before and after the hatching of chicks. Foraging zones during the incubation period were circular with lower FZC compared to the guard stage. Circular tracks are thought to be related to unpredictable and patchy food resources in penguins (Jouventin *et al.* 1994, Wilson *et al.* 1995), and imply a "systematic randomness" in foraging between patches as defined by Baum (1987) for other seabirds. After chicks hatched the tracks of the penguins were direct, with a higher FZC. This suggests more predictable resources in the sector, and a more systematic rather than random foraging behaviour (c.f. Baum 1987), linked with the constraints of foraging trip durations during the breeding season due to the demands of chicks.

During the incubation stage, CL occurred generally throughout the foraging zone, whereas it tended to be clumped following the hatching of chicks (Fig. 5.7). However, CL did not correspond strongly to regions of increased standing stocks of



phytoplankton. This discrepancy suggests that phytoplankton pigment concentrations may not be a good indicator of increased abundance of prey consumed by the penguins, because there is not a direct trophic link between phytoplankton and penguins; or that the penguins were not recorded foraging in regions of the highest prey abundance.

Aside from guard stage and non-representative trips, overlap between foraging zones was generally low. The separate foraging zones used during different stages of the breeding season may represent either changes in the prey resources available in separate parts of the ocean during different times of year, or different food requirements of the penguins across the season (with different prey items being caught in different sectors of the ocean). Overriding any of these effects would be the activities at the nest which would constrain the duration of foraging trips.

Foraging trip duration, distance travelled and foraging area were all highly correlated, similar to the situation found with King Penguins (Adams 1987). The duration of foraging trips was greatest during the incubation stage, which also concurs with other studies (Warham 1971, Carrick 1972, Croxall & Prince 1980a, Wilson *et al.* 1995). The major objective of foraging trips may also differ across the breeding season. The long foraging trips after an incubation shift, which involves a fast of up to five weeks in Royal Penguins (Carrick 1972, Chapter 8), are probably required to restore body condition, whilst those carried out once chicks hatch may predominantly be to provide food for chicks. In contrast to the incubation stage, adults lose mass when foraging during chick rearing (Adams 1987, Brown 1987), suggesting a greater focus on



acquiring food for chicks than replenishing adult condition.

Royal Penguins departing Macquarie Island followed a latitude of 54° 33' S until 161° E longitude, with tracks in a clockwise direction. The consistent latitude used when departing the colony may indicate that the birds are taking advantage of the Antarctic Circumpolar Current, as has been proposed for other species (with other currents) (Randall *et al.* 1981). The ACC moves at a maximum speed of 15-20 cm/sec, and is very broad and deep, transporting water two to three times the rate of the Gulf Stream (Foster 1984). On return to Macquarie Island penguins may avoid the major flow of the current by approaching the island in a north-westerly direction.

### *Conclusion*

This study has located the foraging grounds of Royal Penguins, and demonstrated that they are much larger and more variable across the breeding season than has been assumed. Like King Penguins (Jouventin *et al.* 1994), the foraging patterns of Royal Penguins appear to be intrinsically linked with the PFZ, and probably the availability of their prey. The changes in foraging patterns and behaviour of Royal Penguins are also strongly linked with the breeding biology of the species.

### **5.5 Summary**

Satellite transmitters were deployed on breeding Royal Penguins at Macquarie Island during four stages (first male foraging trip during incubation [ $n = 2$ ], first female foraging trip during incubation [ $n = 3$ ], guard [ $n = 4$ ], and early creche [ $n = 1$ ]) of the

1994/5 and 1995/6 breeding seasons. From these data, foraging zones, oceanographic features of the zones, and travelling behaviours were determined. Foraging trip length, area of foraging zone, and distance travelled were strongly correlated and were greatest during incubation. The estimated rate of travel was constant across individuals and stages in the breeding season. No diurnal patterns in rates of travel were detected, nor any patterns on different days of a foraging trip. A meander coefficient (the degree of linear travel, to give an indication of foraging activity) was constant between stages in the breeding season, and day of the foraging trip, but was greater from 7:00 - 18:00 hours, suggesting increased foraging activity. Foraging during all stages of the breeding season was offshore, in deep water (greater than 2000 m) and in the polar frontal zone. During incubation stage the foraging zones were circular, with a low Foraging Zone Coefficient (FZC: maximum distance from the colony divided by area of the foraging zone), but more direct with a higher FZC after chicks hatched. These different patterns are thought to be associated with prey resources in the region. It is concluded that the foraging behaviour of Royal Penguins is closely linked to the polar frontal zone, their prey, and the constraints of the breeding season.

## 5.6 Acknowledgments

We would like to thank Jane Wilson, Kirsten Le Mar and Paul Scofield for assistance in the field, Al Rooke for downloading and relaying ARGOS data to us in the field, and Roger Hansworth and Dale Main for changing batteries on the devices. Funds were generously provided by the Charles A. and Anne Morrow Lindbergh Fund, the Japanese Penguin Fund, SeaWorld Research and Rescue Foundation, and the Antarctic Scientific

Advisory Committee for various aspects of the work. The sea surface temperature and phytoplankton pigment concentration data were obtained from the NASA Physical Oceanography Distributed Active Archive Centre at the Jet Propulsion Laboratory, California Institute of Technology, to whom we are grateful. Work was carried out under Macquarie Island special permits MI/3/95 and MI/13/96.

## Chapter 6

### **The foraging zones of breeding Royal and Rockhopper Penguins: a species comparison and assessment of techniques**

#### **6.1 Introduction**

Royal *Eudyptes schlegeli* and Rockhopper *E. chrysocome* Penguins breed sympatrically on Macquarie Island, where the former species is endemic. These species are ecologically and taxonomically very similar, raising questions as to the degree of overlap in resource use, particularly at sea (Croxall & Lishman 1987, Hindell *et al.* 1995). Overlap in resource use is potentially greatest during the breeding season due to the increased demands of breeding, and because commitments at the nest restrict the duration of foraging trips and therefore the extent of foraging zones. It is speculated that sympatrically breeding, ecologically similar species must differ in some aspects of their foraging ecologies in order to co-exist. One aspect that may differ is the spatial use of the marine environment either through different foraging zones, or different depths (Croxall & Prince 1980a, Cooper *et al.* 1990, Hindell *et al.* 1995). Another is that the asynchrony in breeding season between sympatrically breeding penguins assists with the segregation of resource use by offsetting peak demands for food (Brown and Klages 1987).

Whilst aspects of the breeding biology, behaviour on land (Warham 1963, 1972, Carrick 1972), and diet (Horne 1985, Hindell 1988a, b) have been investigated to some extent

in both species, the foraging zones are not known, although recent satellite tracking work on Royal Penguins has made some progress in redressing this (Hull *et al.* in press, also Chapter 5). The only site where the foraging zones of Rockhopper Penguins has been examined is Marion Island, where swimming speed meters and foraging trip lengths have been used to estimate foraging zones (Brown 1987). Therefore, the foraging zones of Rockhopper Penguins at almost all sites, including Macquarie Island, remains unknown. Consequently, it is not presently possible to understand this aspect of Rockhopper Penguin behaviour at sea, nor make direct comparisons to the closely related and ecologically similar Royal Penguin, in order to explore the issue of ecological segregation of foraging zones.

The techniques currently available for estimating foraging zones in penguins are: (1) VHF transmitters with telemetry from land, air or sea (see Trivelpiece *et al.* 1986, Heath & Randall 1989, Weavers 1992); (2) satellite telemetry (see Ancel *et al.* 1992, Jouventin *et al.* 1994, Davis *et al.* 1996, Bost *et al.* 1997); (3) light sensors to estimate locations, either with Time Depth Recorders (TDRs) with the geolocation option enabled (see Green *et al.* submitted), or with Global Location Sensors (GLS) (see Wilson *et al.* 1995); (4) Sea Surface Temperature (SST) data collected by TDRs and then related to known SST in the region (C. Guinet unpubl. data); and (5) velocity meters in conjunction with foraging trip durations (Brown 1987, Gales *et al.* 1990). Some of these various techniques were trialed to define the foraging zones of Royal and Rockhopper Penguins.

This study had three principal aims: (1) to trial a variety of techniques to ascertain the most appropriate for determining the foraging zones in these species; (2) to determine the foraging zones of Royal and Rockhopper Penguins during the breeding season ; (3) to determine the degree of overlap in foraging zones of both species.

## 6.2 Materials and methods

### *Techniques for measuring foraging zones*

#### 1. VHF telemetry

VHF transmitters were deployed on ten male Royal Penguins during the long incubation foraging trip. Two-stage VHF radio transmitters (Microlite GP1, Titley Electronics, NSW) packaged in black, hydrodynamic housings (Faunatech, Victoria, Australia) with 160 mm flexible, whip aerials were deployed on the penguins. The devices weighed 9 g, measured 47.1 x 25.5 x 11.4 mm and streamlined to reduce drag (c.f. Bannasch *et al.* 1994). Devices were attached with a cyanoacrylate adhesive (Loctite 401) to the lower medial portion of the penguins' backs to further minimise drag (c.f. Bannasch *et al.* 1994).

Three receiving stations were established along the east coast of the island, at Sandy Bay, the Nuggets and North Head (Fig. 6.1). At each station a telonics receiver powered by a 12 volt battery was used to scan for frequency transmissions. Two metre antennae were used to detect signals. Each frequency was scanned for five minutes and tracking continued for three days during daylight hours (5:00 - 18:00 hours, see Fig. 6.2).



2. Satellite telemetry. Satellite transmitters have been successfully deployed on Royal Penguins (Hull *et al.* in press, also Chapter 5), but the same models were considered too large for Rockhopper Penguins. The devices were over 5% the cross-sectional area of Rockhopper Penguins, which was likely to decrease swimming speed and increase energy expenditure (Culik & Wilson 1991). There were smaller satellite devices available, but these could not withstand the pressures experienced at depths greater than 50 m, to which Rockhopper Penguins regularly dive (Chapter 7).

3. Time Depth Recorders, with geolocation (TDRs). TDRs are currently smaller than satellite transmitters (2.3% cross-sectional area of Royal Penguins; 2.9% of Rockhopper Penguins) and were deployed on both species during this study. Geolocation data are known to be much less precise, to within 1° at best, than satellite telemetry (Hill 1994, Hull *et al.* in press, also Chapter 5). However, the deployment of TDRs on both species allowed comparisons of foraging zones using data derived from the same technique.

In order to determine the accuracy of locations calculated using geolocation, trials were carried out by deploying TDRs on penguins known to be in the colonies. The location of the colonies was determined using a geopositioning system (error of approximately 70 m). It was assumed that the sources of errors from the TDRs on land were the same as those at sea.

4. Sea Surface Temperature (SST). SST data were collected by the TDRs in order to determine the water bodies each species travelled in during foraging trips. These data

were compared to contemporaneous NASA PO.DAAC data, allowing an estimation of the latitudinal location of foraging zones.

5. Foraging trip durations. Foraging trip durations were recorded on penguins from the initiation to cessation of diving, to assist with estimations of the longitudinal extent of foraging zones. As the reported swimming speeds of Rockhopper and Macaroni Penguins *E. chrysolophus* were the same (Brown 1987), and the latter are closely related and a similar size to Royal Penguins, it was assumed that Royal and Rockhopper Penguins also swam at the same speed. Maximum distances travelled from the island were therefore estimated from trip durations, with the amount of movement each day assumed to be the same as that found in Royal Penguin satellite tracking studies (Hull *et al.* in press, also Chapter 5).

#### *Deployment of devices*

Randomly selected breeding Royal Penguins from Sandy Bay (upper colony), and Rockhopper Penguins from Brothers Point, southern end of Sandy Bay (east coast 54° 33' 51" S, 158° 54' 11" E) were used during this study. Sex was determined by bill length and depth (Hull in press, also Chapter 2), and each bird individually marked with a coloured velcro flipper band. Mark V TDRs (Wildlife Computers, Redmond, USA) measuring 62 x 38 x 12 mm, with a mass of 50 g, were deployed 61 times during the 1994/5 and 1995/6 breeding seasons (Table 6.1). Devices were attached to the lower medial part of the penguins' backs using Loctite 401. All attachments were undertaken in the colony at the nest using the techniques described by Hull & Wilson (1996a, also

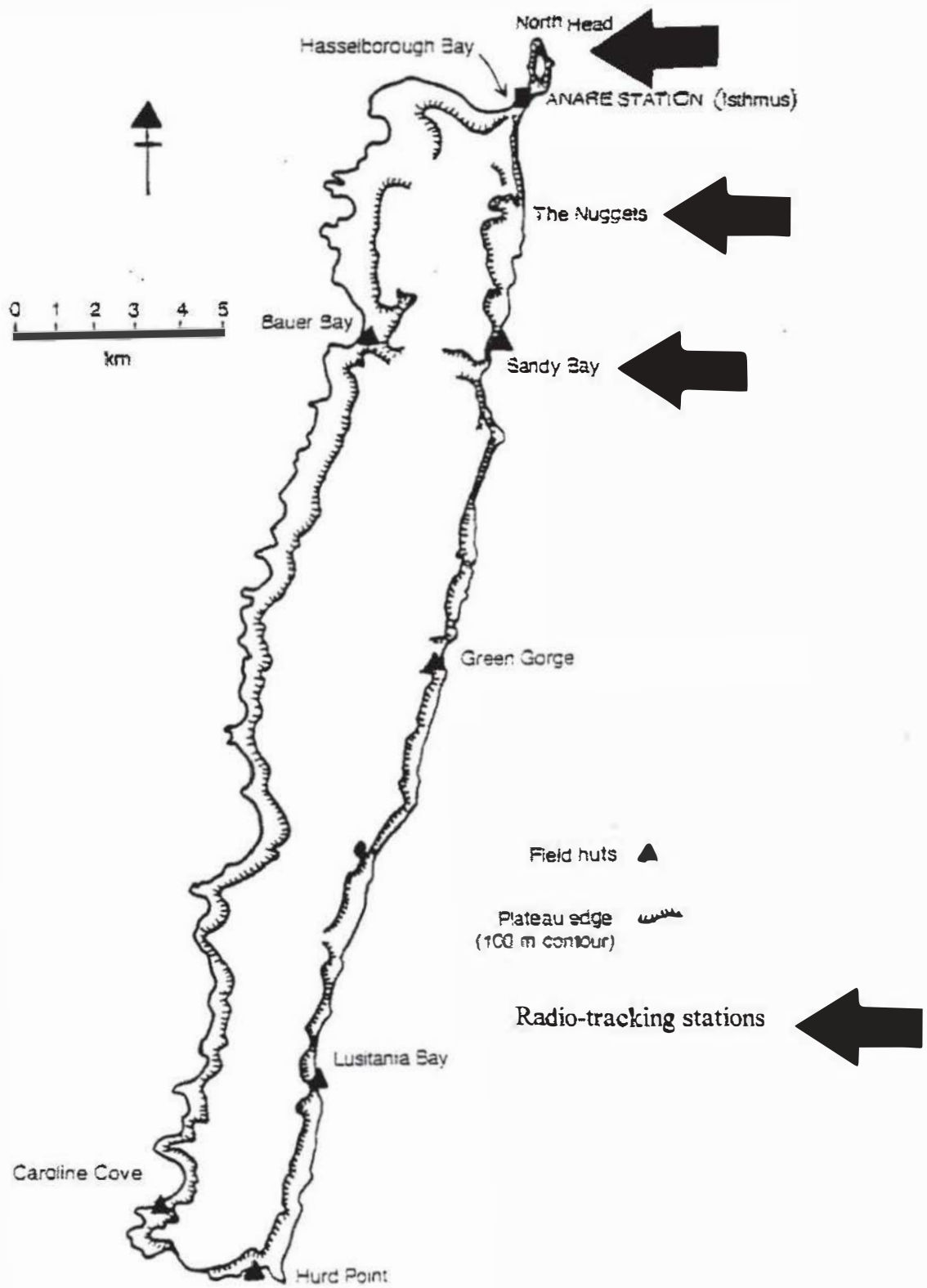
Chapter 3). Devices and velcro bands were removed when the penguins returned from one foraging trip.

Deployments were made at the nest during four stages of the 1994/5 and 1995/6 breeding seasons: (1) male first foraging trip during incubation; (2) female first foraging trip during incubation; (3) guard; and (4) creche from one foraging trip (Table 6.1, Fig. 6.2). During the long foraging trips during incubation (two to three weeks, Warham 1971, Carrick 1972), TDRs were duty-cycled at one day on, two days off to ensure data collection for the entire trip. Foraging trips during guard and creche stages trips are generally less than seven days (Warham 1971, Carrick 1972), so duty-cycling was not required.

#### *Data extraction and analysis*

Daily locations were estimated using light-levels, with longitude being calculated from local midday, and latitude calculated from day length (Hill 1994). Locations were corrected by adding the mean error determined from device trials on land during each stage in the breeding season. Data were also filtered to remove aberrant locations, with locations greater than 200 km from that of the preceding or succeeding day being deleted. Two hundred km was greater than either species could be expected to travel per day (assuming a maximum mean rate of travel of  $7.8 \text{ km hour}^{-1}$ , Hull *et al.* in press, also Chapter 5).

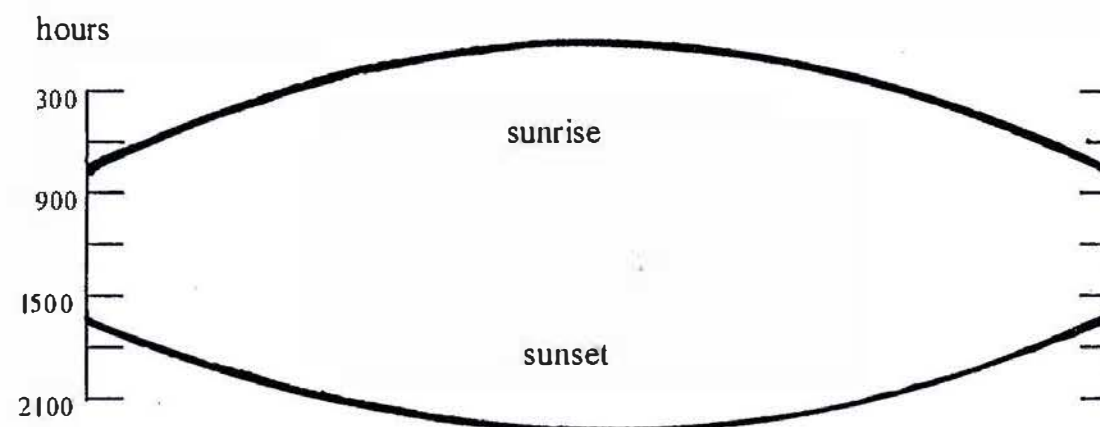
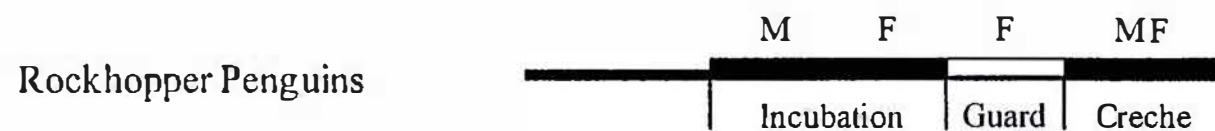
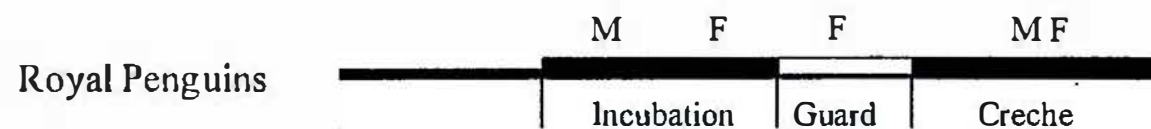
**Fig. 6.1** Sites where radio-tracking towers were established on the east coast of Macquarie Island.



**Fig. 6.2** The stages in the breeding season of Royal and Rockhopper Penguins. The times of sunrise and sunset are shown (derived from Selkirk *et al.* 1990).



September	October	November	December	January	February
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Sea Surface Temperature (SST) data were extracted from the geolocation files using the program 'lightex' (Wildlife Computers), on birds known to be in the water (indicated by diving activity). Only records during the night (hours of 22:00 to 03:00 local time, Fig. 6.2) were analysed. Both species undertake few dives below 6 m at night (Chapter 7), and data were only used from these times to minimise the possibility of influencing the SST readings by delays in the equilibration of the TDRs' temperature sensors following deep diving.

Analyses were carried out using nested Analysis of Variance (ANOVAs) (individuals within each year, species or stage in the breeding season) and Tukey tests. Data are presented as mean  $\pm$  standard deviations.

### 6.3 Results

#### 1. VHF telemetry

The radio-tracking trial conducted on Royal Penguins provided few reliable positions, with the majority of signals being detected by the station at Sandy Bay. A combination of the large distances these penguins travelled (Hull *et al.* in press, Chapter 5), the sea conditions, and the inability to track penguins from aircraft or boats were assumed to result in this technique failing. As it was not possible to derive three signals for a given penguin, and hence not be able to triangulate to estimate locations, radio-tracking was abandoned.

## 2. TDRs

Of the 61 deployments, 37 provided data for geolocation analysis and SST (18 Royal Penguins and 19 Rockhopper Penguins) (Table 6.1). Of the other deployments: twelve birds either returned to the colony without the device; or did not return during the breeding season; four were failed breeders; and the remaining eight did not record data for the entire trip.

### *Geolocation*

A total of 192 locations was obtained from the TDRs. A location was not always calculated for each penguin on every day of a foraging trip. This would have arisen because light measurement did not provide clear indications of dawn and dusk, which was no doubt exacerbated by animals diving at these times (Hill 1994, Chapter 7).

### *Errors*

Seventy-nine locations were calculated when the penguins were at known positions. The average errors were: latitude  $27.6 \pm 472.8$  km (median 106.7 km); and longitude  $37.3 \pm 266.7$  km (median 26.1 km) (Table 6.2). The errors in locations were significantly different across the stages in the breeding season, but not between species (Table 6.2).

**Table 6.1.** Number of deployments of time depth recorders, foraging trip durations

and number of locations calculated from light levels (mean  $\pm$  sd). \* Duty cycled at one day on, two days off

<i>Species</i>	<i>Stage in breeding season</i>	<i>Sex</i>	<i>Deployments (available for analysis)</i>	<i>Foraging trip duration (days)</i>	<i>Number of locations per penguin</i>
Royal	Incubation *	Male	9 (6)	19.5 $\pm$ 1.2	9.8 $\pm$ 4.2
Penguin	Incubation *	Female	7 (2)	19.0 $\pm$ 7.1	4.8 $\pm$ 3.8
	Guard	Female	9 (6)	4.6 $\pm$ 1.3	4.1 $\pm$ 3.4
	Creche	both	7 (5)	6.2 $\pm$ 3.5	6.0 $\pm$ 4.2
Rockhopper	Incubation *	Male	8 (7)	10.5 $\pm$ 3.5	4.4 $\pm$ 1.1
Penguin	Incubation *	Female	7 (4)	13.7 $\pm$ 4.0	4.8 $\pm$ 2.5
	Guard	Female	7 (6)	7.0	8.3 $\pm$ 9.5
	Creche	both	7 (1)	7.3 $\pm$ 5.8	3.5 $\pm$ 0.7
Total			61 (37)		192

**Table 6.2** Latitudinal and longitudinal errors (km) in geolocation calculations when penguins were at a known location. Statistical comparisons between species and stages are given. **Significant cases in bold**

<i>Stage in breeding season</i>	<i>Latitudinal error</i>	<i>Longitudinal error</i>
Incubation - males	367.0 ± 701	8.5 ± 294
Incubation - females	77.8 ± 322	32.6 ± 176
Guard	122.3 ± 267	12.4 ± 242
Creche	451.5 ± 311	254.5 ± 320
Comparisons - stages	<b><math>F_{3,71} = 11.32, P &lt; 0.001</math></b>	<b><math>F_{3,71} = 9.22, P &lt; 0.001</math></b>
Comparisons - species	$F_{1,71} = 3.56, P > 0.05$	$F_{1,71} = 2.29, P > 0.05$

The direction of errors was northwesterly during guard stage, but southeasterly during the other three stages. These mean latitudinal and longitudinal errors were applied to the locations for each species during each stage of the breeding season to correct at-sea locations.

#### *Locations from geolocation*

Corrected and filtered locations for both species were predominantly in an area bounded by 158 - 160° E and 54 - 56° S (Fig. 6.3). This is in the region of the Emerald Basin and the Campbell Plateau, where water depths range from 2,000 - 5,000 m. Due to the magnitude of the errors it was not possible to use geolocation to accurately determine whether foraging zones differed between the species and stages in the breeding season.

## 2. Sea surface temperature

Both species travelled in waters with mean SST ranging between 6.8 - 10.8° C, which corresponds to the northern section of the polar frontal zone (Burling 1961). The changes in the SST recorded across foraging trips are illustrated in Fig. 6.4, and indicate birds moved over water bodies of different temperatures in a single foraging trip. The differences between SST encountered by penguins departing and returning to the island during some stages arose either because of short-term changes in the temperature of water close to the island, or more likely because the data were an amalgam of a number of individuals, which exhibited a high variance and difference in foraging trip durations (see Table 6.1).

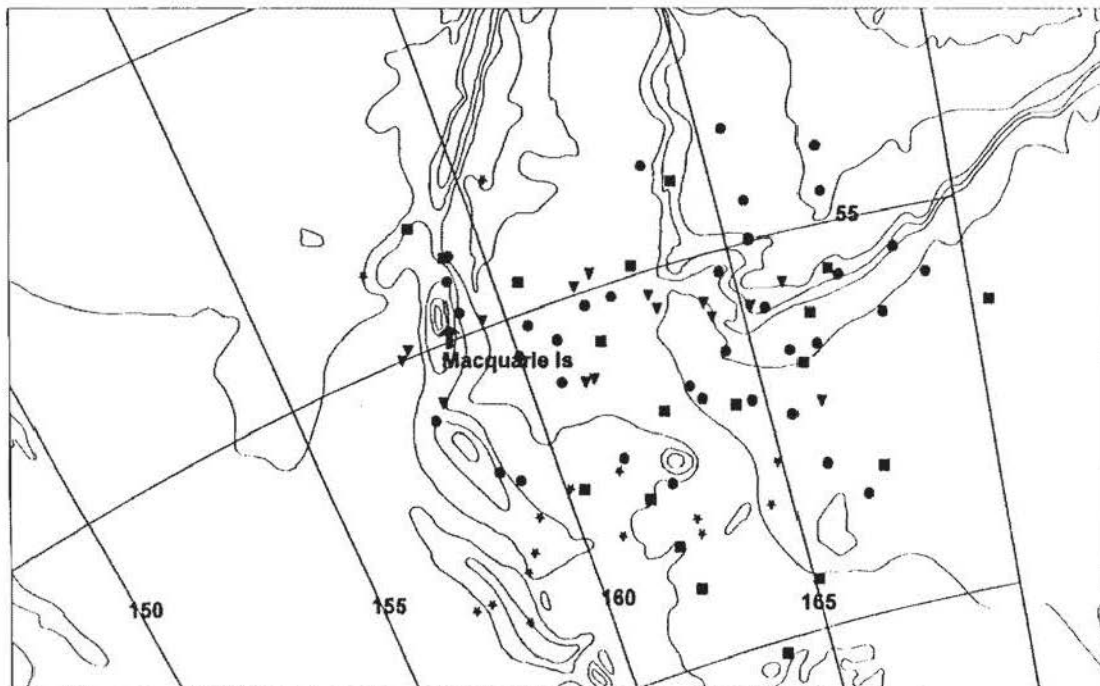
There were no inter-annual differences in the SST in which Royal Penguins travelled at any stage in the breeding season (male incubation  $F_{1,4} = 0.8$ ,  $P > 0.05$ ; guard  $F_{1,4} = 5.8$ ,  $P > 0.05$ ; creche  $F_{1,3} = 0.6$ ,  $P > 0.05$ ). Nor was there a difference in waters in which Rockhopper Penguins travelled during any stage (male incubation  $F_{1,5} = 0.1$ ,  $P > 0.05$ ; female incubation:  $F_{1,2} = 0.8$ ,  $P > 0.05$ ; guard =  $F_{1,4} = 1.9$ ,  $P > 0.05$ ) (Table 6.3). Given the variability in the data, a significant difference between the species would not have been detected unless the mean temperature of the waters used by each species differed by 6° C (e.g.  $\leq 4^\circ\text{C}$  or  $\geq 10^\circ\text{C}$ ).



**Fig. 6.3** The locations of Royal and Rockhopper Penguins derived from geolocation analysis during the four stages of the breeding season (locations corrected and filtered).

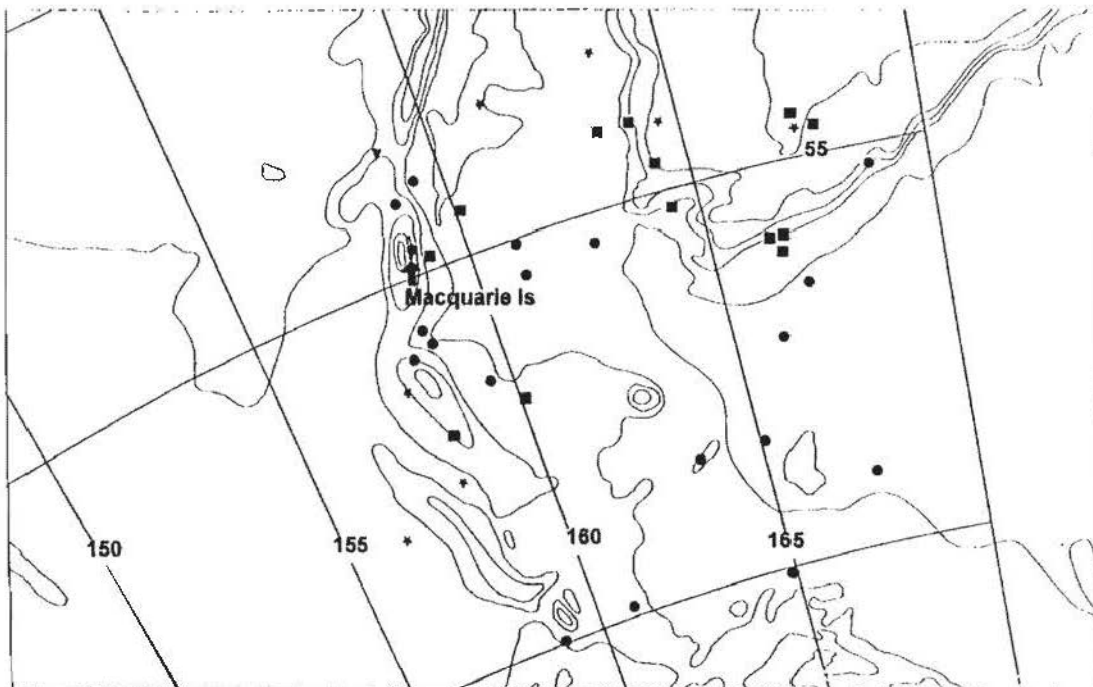
**Fig. 6.4** Sea surface temperatures in which Royal and Rockhopper Penguins used during each stage in the breeding season.

Dashed lines during incubation indicate that devices were duty-cycled at one day on, two days off.



## Royal Penguins

- Incubation - males
- Incubation - females
- ★ Guard
- ▼ Creche



## Rockhopper Penguins

Royal Penguins travelled in water with the same SST during all stages of the breeding season (1994/5  $F_{2,5} = 0.8$ ,  $P > 0.05$ ; 1995/6  $F_{1,1} = 2.3$ ,  $P > 0.05$ ), as did Rockhopper Penguins during 1994/5 ( $F_{2,9} = 0.2$ ,  $P > 0.05$ ). However, SST used by Rockhopper Penguins varied with stage during 1995/6 ( $F_{2,1} = 597096.5$ ,  $P < 0.001$ ), with males in significantly cooler water ( $7^{\circ}\text{C}$ ) during their incubation foraging trip than at other times of the breeding season ( $10^{\circ}\text{C}$ ) (Table 6.3).

There were no significant differences in the temperature of water used by Royal and Rockhopper Penguins during any stage of the breeding season (male incubation  $F_{1,5} = 0.4$ ,  $P > 0.05$ ; female incubation  $F_{1,4} = 0.0$ ,  $P > 0.05$ ; guard  $F_{1,10} = 0.3$ ,  $P > 0.05$ ; creche  $F_{1,4} = 0.9$ ,  $P > 0.05$ ) (Table 6.2).

Male and female Royal Penguins did not differ significantly in the SST utilised during creche stage ( $F_{1,3} = 0.04$ ,  $P > 0.05$ ). It was not possible to compare the use of the water masses between the sexes in Rockhopper Penguins during creche stage due to insufficient samples.

**Table 6.3** Mean  $\pm$  standard deviation of sea surface temperature ( $^{\circ}$  C) in which Royal and Rockhopper Penguins travelled during foraging trips. **Bold signifies significant difference** ( $P < 0.05$ ) to other stages in that species and year

<i>Species</i>	<i>Stage</i>	<i>Year</i>	<i>Mean</i>	<i>Median</i>	<i>Minimum</i>	<i>n</i> ( <i>days</i> )
Royal Penguin	1. male incubation	1994/5	8.1 $\pm$ 4.5	6.5	2.9	387
		1995/6	7.2 $\pm$ 3.0	7.2	1.7	310
	2. female incubation	1994/5	8.5 $\pm$ 3.6	7.4	4.8	174
		1995/6	-	-	-	-
	3. guard	1994/5	8.6 $\pm$ 3.5	7.6	5.0	293
		1995/6	10.3 $\pm$ 3.4	9.4	6.2	168
	4. creche	1994/5	9.2 $\pm$ 5.0	7	4.4	95
		1995/6	8.7 $\pm$ 4.4	7.5	4.1	284
Rockhopper Penguin	1. male incubation	1994/5	7.2 $\pm$ 4.2	5.6	2.4	234
		<b>1995/6</b>	<b>7.1 <math>\pm</math> 3.3</b>	6.3	3.5	104
	2. female incubation	1994/5	7.9 $\pm$ 3.0	7.8	2.8	282
		1995/6	10.3 $\pm$ 3.8	8	6.5	58
	3. guard	1994/5	7.6 $\pm$ 3.4	6.6	3.9	704
		1995/6	10.8 $\pm$ 3.7	9.7	6.8	101
	4. creche	1994/5	6.8 $\pm$ 1.1	6.9	5.0	108
		1995/6	-	-	-	-

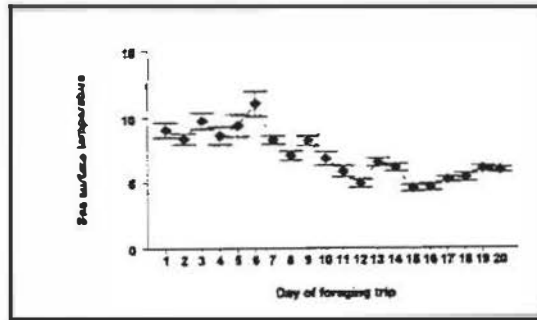
**Fig. 6.4** Sea surface temperatures in which Royal and Rockhopper Penguins used during each stage in the breeding season.

Dashed lines during incubation indicate that devices were duty-cycled at one day on, two days off.

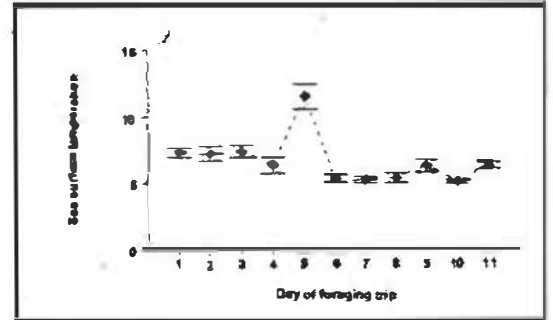


## Royal Penguins

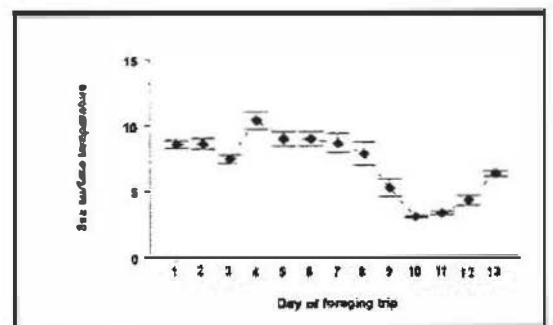
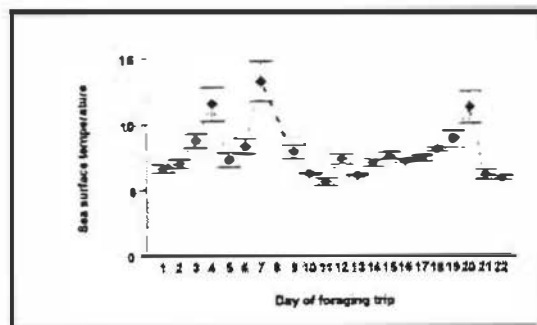
### Incubation - males



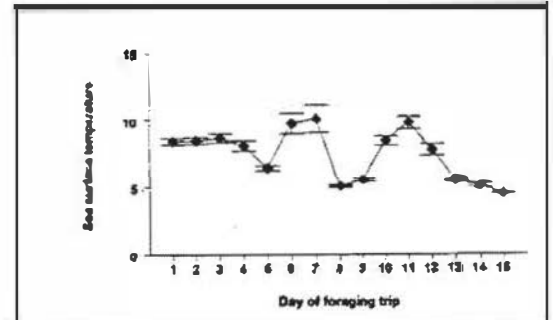
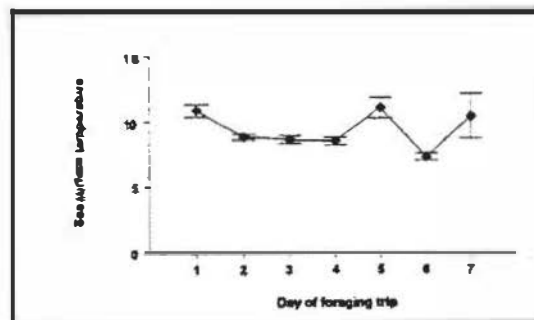
## Rockhopper Penguins



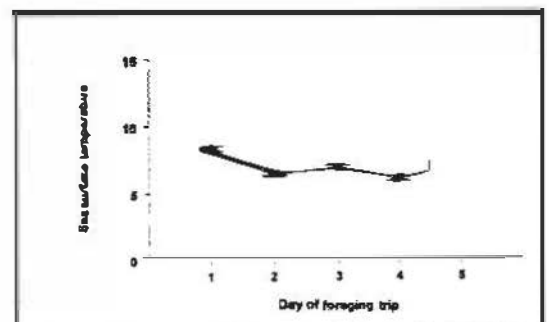
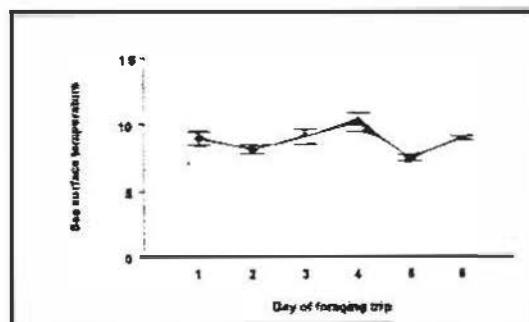
### Incubation - females



### Guard



### Creche



### 3. Foraging trip durations

Accurate foraging trip durations were determined for 47 individuals from the TDRs (33 Royal Penguins and 14 Rockhopper Penguins). These durations were significantly different between species ( $F_{1,47} = 18.8$ ,  $P < 0.0001$ ) and between stages ( $F_{3,47} = 30.2$ ,  $P < 0.0001$ ) (Table 6.1). Trip durations were on average 14% longer in Royal Penguins and 17% longer in Rockhopper Penguins than for penguins not carrying TDRs (Chapter 9), indicating an adverse impact from the devices (Hull 1997, also Chapter 4). This impact may have been greater for Rockhopper Penguins. As the effect of these devices has not been measured in Rockhopper Penguins, it is not possible to determine the difference in impact between the species.

Due to the longer foraging trips in this study, maximum distances travelled on foraging trips were estimated from trip durations of birds without devices (Chapter 9), assuming that the distances travelled to forage were constant between penguins with and without devices. It was beyond the scope of this study to determine if there was a differential impact of the TDRs on Royal and Rockhopper Penguins. It was assumed that the foraging zones described were generally representative, and that any effect from the devices was relatively constant between the species.

Rockhopper Penguins foraging trips were on average 76% the duration of Royal Penguins (Chapter 9). A conservative estimate of the maximum distances travelled are given in Table 6.4. Possible foraging zones have estimated by marking the regions of the ocean where SST (NASA PODAAC data) of the same average temperature that the

penguins used (Figs. 6.5 and 6.6). Note that the maps of SST given are from 1994/5, and hence do not show inter-annual variability in SST. This explains some of the variance between SST and the temperatures the penguins were located.

**Table 6.4** The estimated maximum distance travelled by Royal and Rockhopper Penguins (km), based on foraging trip durations and extrapolated from satellite tracking studies of Royal Penguins (Hull *et al.* in press, also Chapter 5).

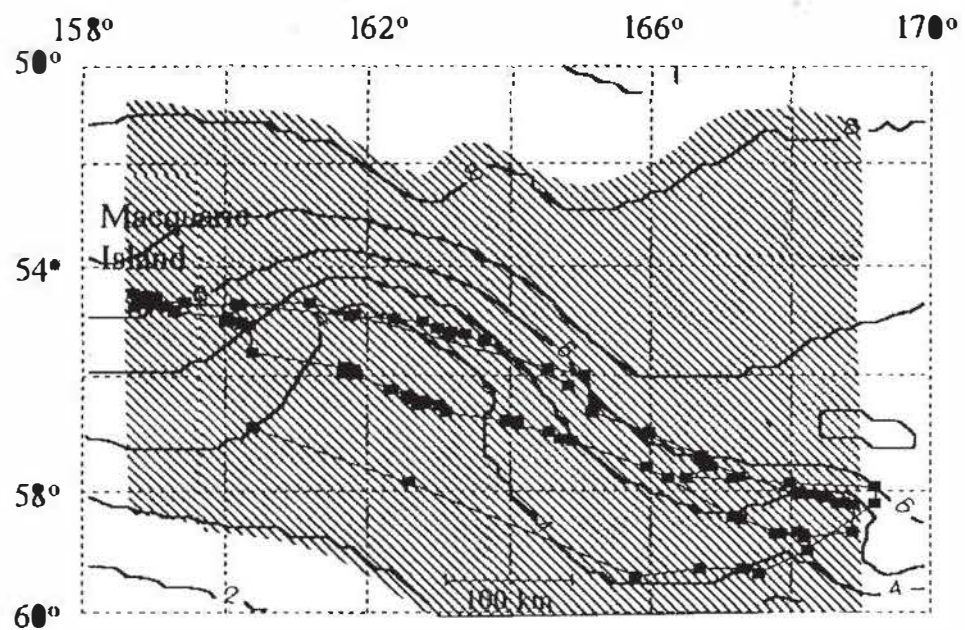
<i>Species</i>	<i>Incubation - males</i>	<i>Incubation - females</i>	<i>Guard</i>	<i>Creche</i>
Royal	650	415	116	201
Rockhopper	410	270	104	173

#### *Overlap in foraging zones*

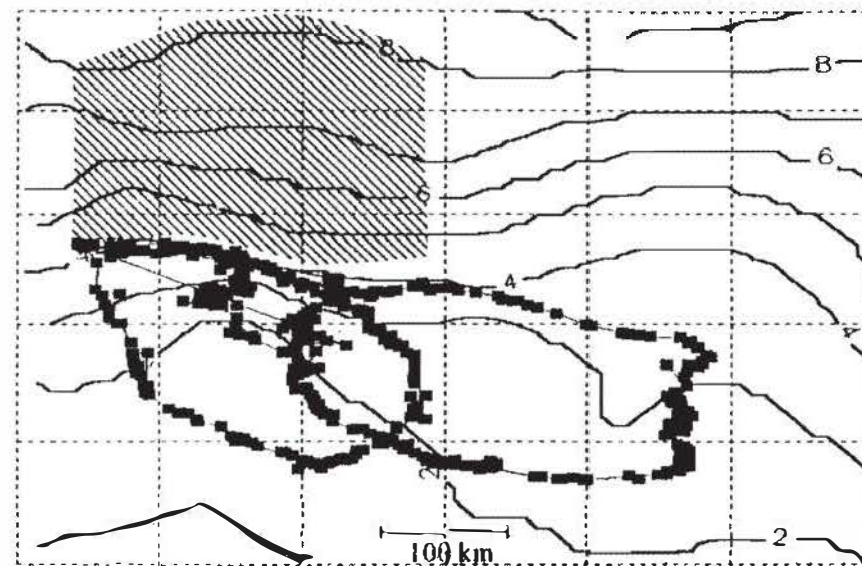
In order to examine the hypothesis that the three week asynchrony in the breeding season of Royal and Rockhopper Penguins (Chapter 9) assisted with the segregation of resource use (Brown & Klages 1987), the estimated degree of overlap (derived from geolocation, SST and foraging trip durations) was compared between stages on a contemporaneous basis. Therefore, Rockhopper Penguin male incubation stage was compared to Royal Penguin female incubation, Rockhopper female incubation to Royal guard, and Rockhopper guard to Royal Penguin creche stage (Fig. 6.7).

**Fig. 6.5** Estimated foraging zones (hatched areas) of Royal Penguins from SST recorded on TDRs, and in relation to the maximum distance penguins were expected to travel, determined from foraging trip durations of unencumbered birds. These are overlaid on sea surface temperatures from 1994/5 (NASA PO.DAAC data), along with satellite tracks (Chapter 5).

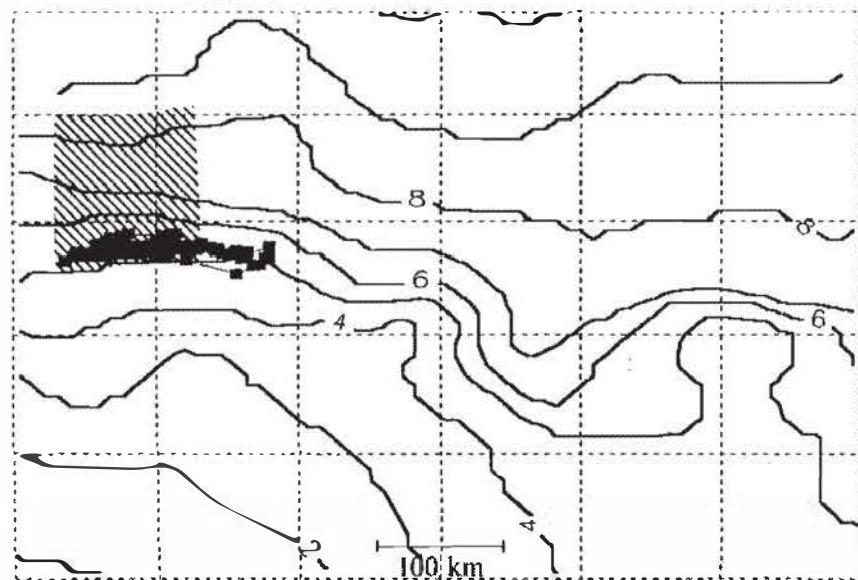
Incubation - males



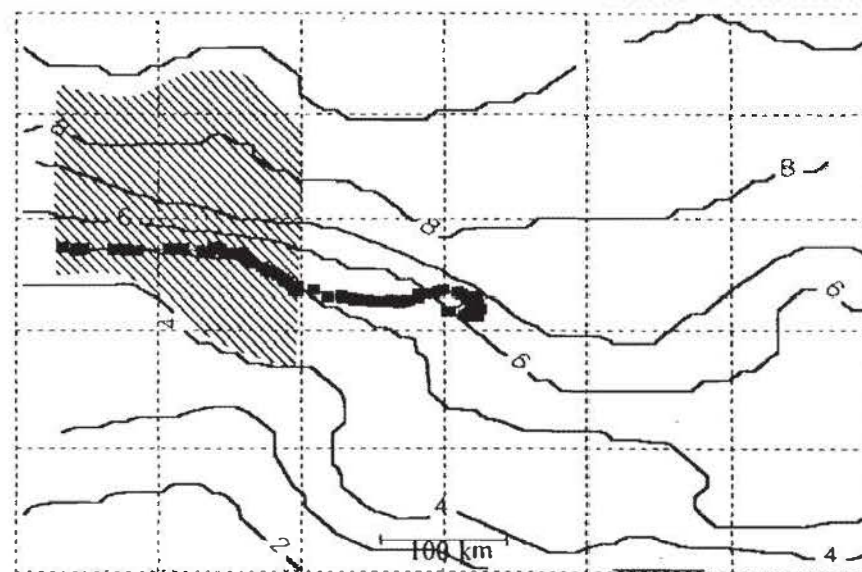
Incubation - females



Guard



Creche

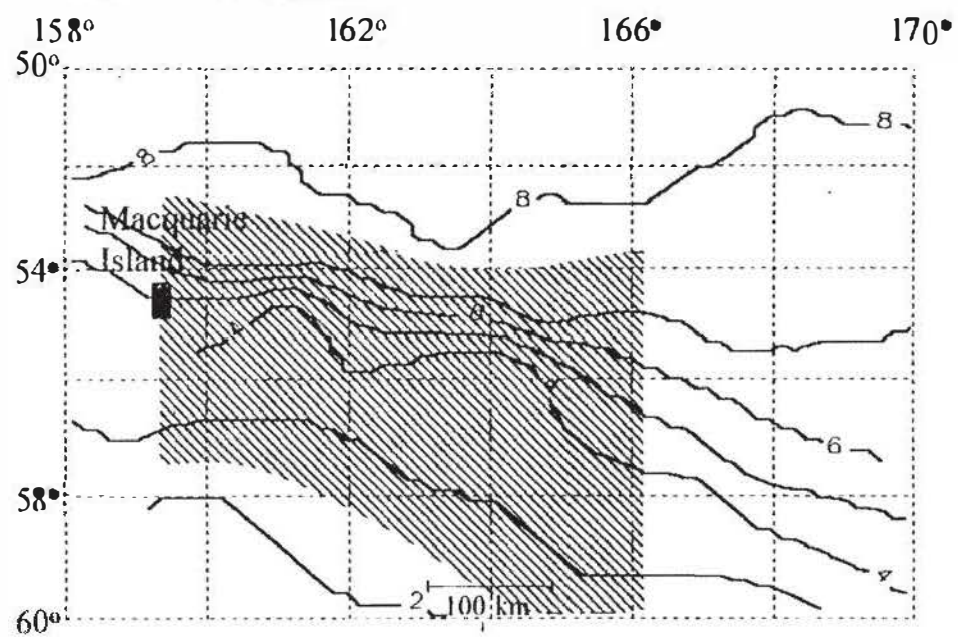




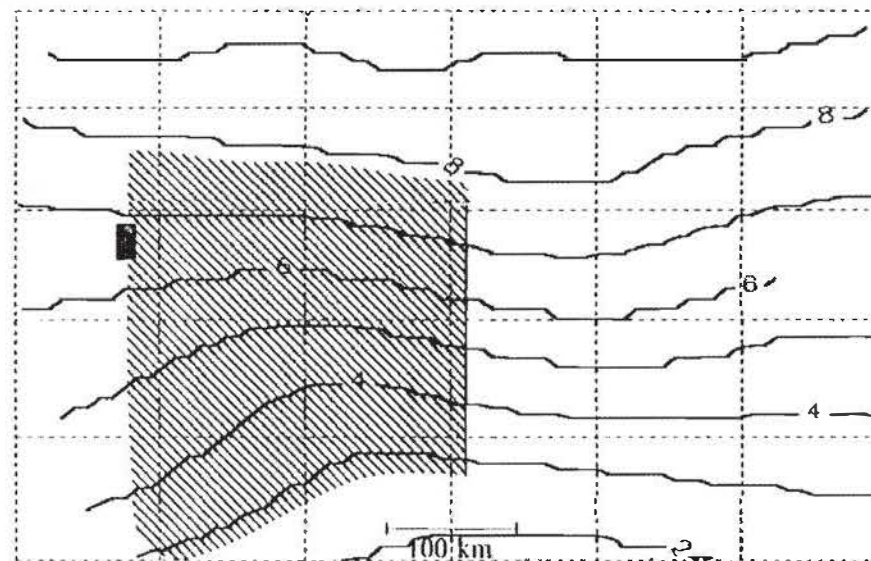
**Fig. 6.6** Estimated foraging zones of Rockhopper Penguins (hatched areas) from SST recorded on TDRs, and in relation to the maximum distance penguins were expected to travel, determined from foraging trip durations of unencumbered birds. These are overlaid on sea surface temperatures from 1994/5 (NASA PO.DAAC data).



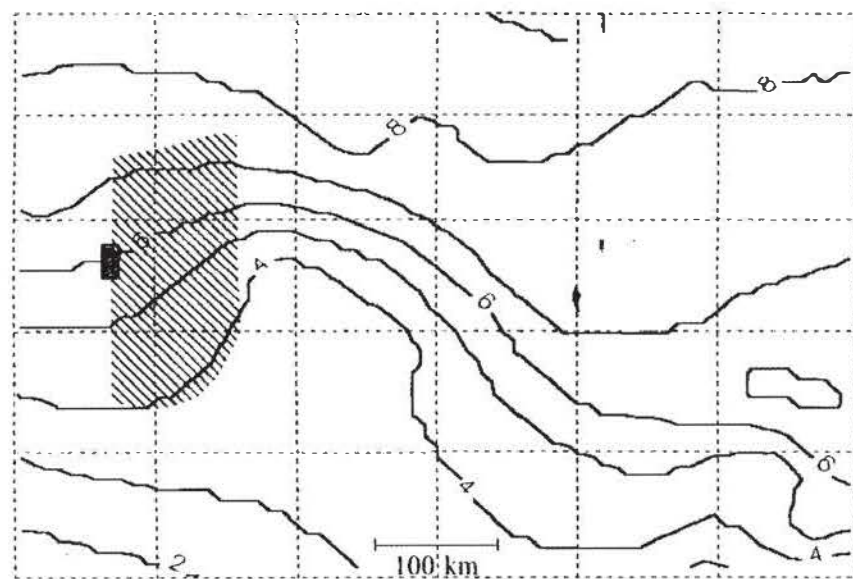
Incubation - males



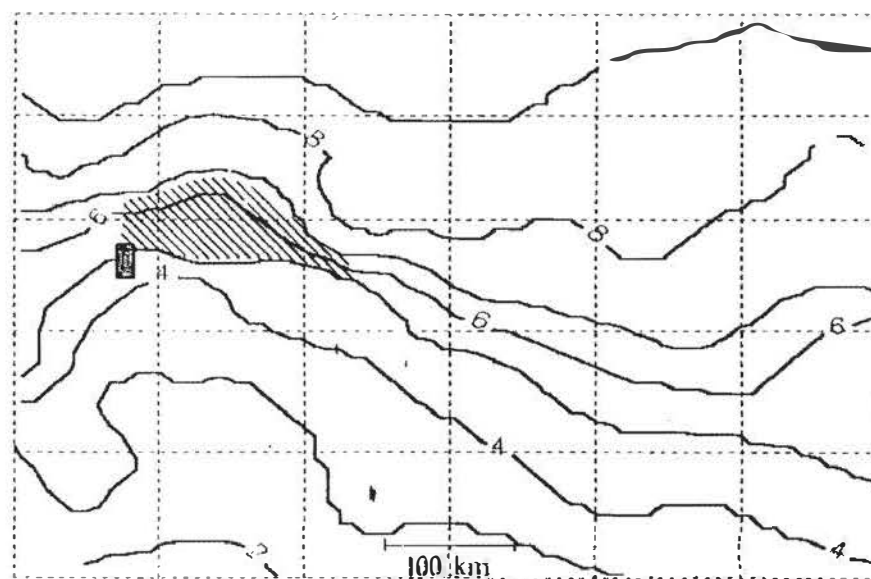
Incubation - females



Guard



Creche



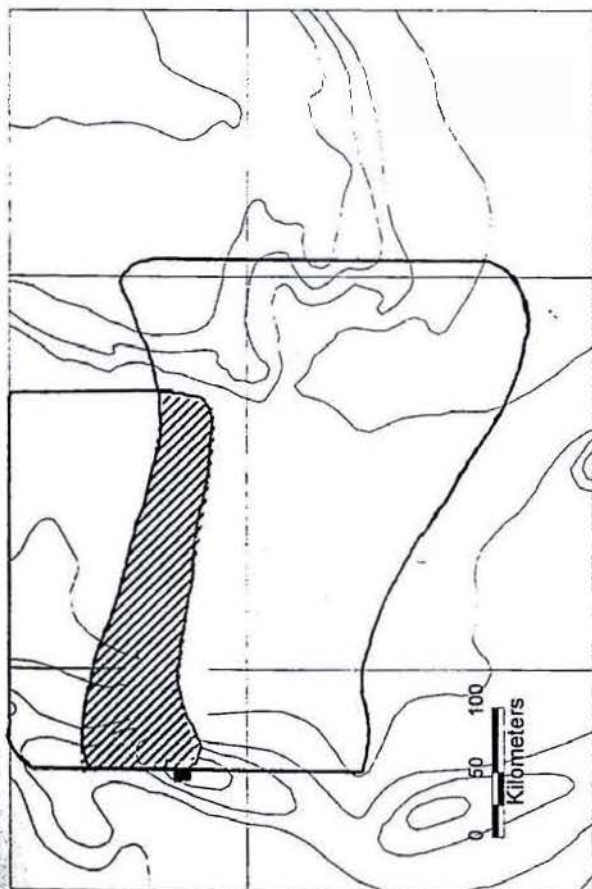
**Fig. 6.7** Estimated overlap in contemporaneous foraging zones of Royal and Rockhopper Penguins (see also Figs. 6.5 and 6.6).

A Rockhopper Penguin male incubation/Royal Penguin female incubation

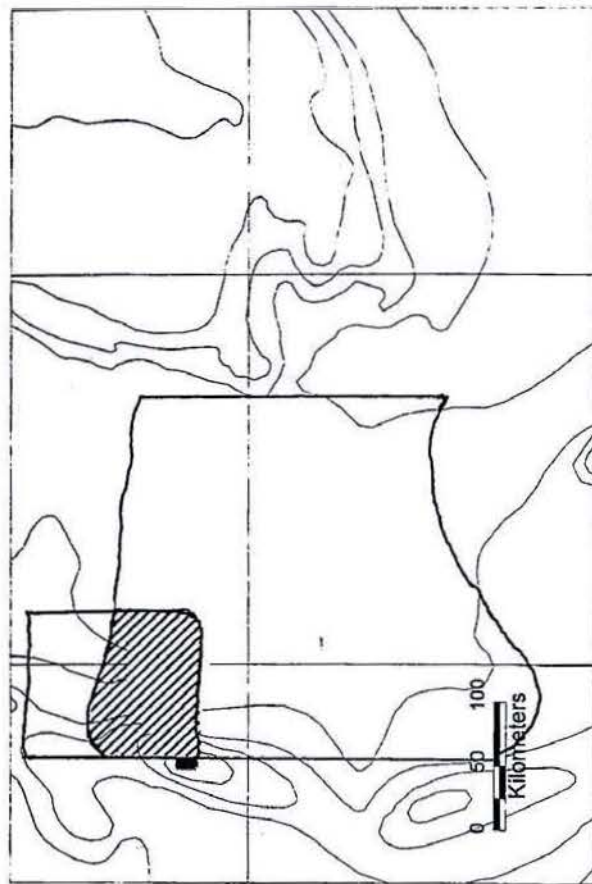
B Rockhopper Penguin female incubation/Royal Penguin guard

C Rockhopper Penguin guard/Royal Penguin creche

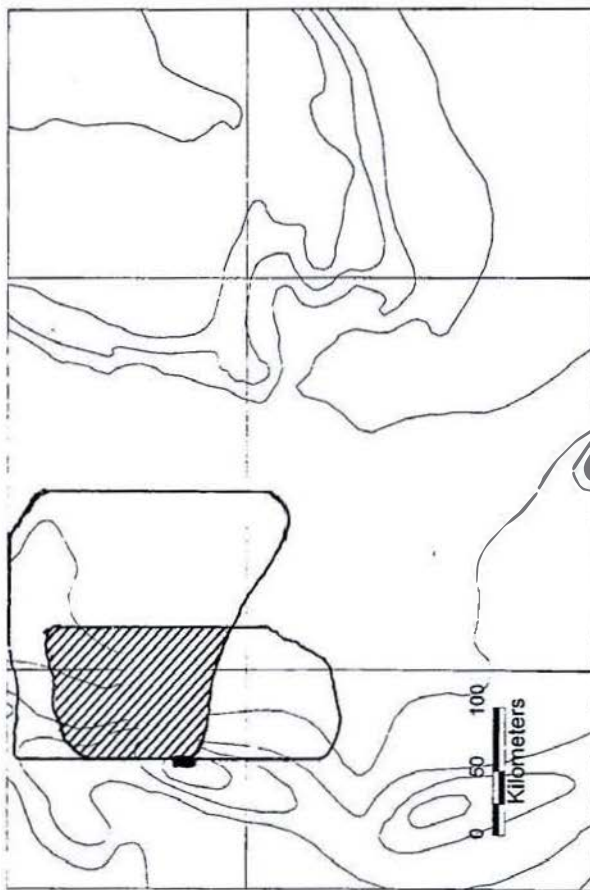
A



B



C



## 6.4 Discussion

### *Assessment of techniques*

#### Geolocation

The latitudinal and longitudinal errors from geolocation analysis (latitude:  $27.6 \pm 472.8$  km; longitude:  $37.3 \pm 266.7$  km) were less than that estimated by Wildlife Computers of  $\pm 60$  nautical miles (111.2 km) under good conditions, but were still too large to determine precise foraging zones for Royal and Rockhopper Penguins, particularly during creche stage. The differences in error across the breeding season were probably related to the time of year (day length) and/or greater mobility of the penguins following the cessation of incubation. The penguins would also be less often in a prone position during this stage as they were no longer incubating eggs or young chicks.

It is possible that the errors on land were not the same as those at sea, or that the greater errors experienced later in the season were primarily due to the penguins' behaviour on land, which differed from that at sea. However, it is impossible to determine from this study if locations at sea were more or less accurate than those on land. The use of geolocation on these species has provided only a coarse approximation of foraging zones, and errors of this magnitude make it impossible to compare species and stages in the breeding season.

#### Sea Surface Temperature

The SST data derived from the TDRs indicated that the penguins were located in waters ranging from 2 - 15° C. This range is substantial, limiting the value of this technique



in estimating foraging zones. The variability in the data is probably a function of the coarseness of the NASA data set, which may not detect localised areas of SST, but generalises across a 19 x 19 km block. Comparisons between foraging zones estimated from SST and satellite tracking indicate moderate compliance during most stages (apart from females during incubation) (Figs. 6.5 and 6.6).

Although there was substantial variability in the range of SST used by these penguins, mean and median values suggest that both species probably utilised the Polar Frontal Zone (PFZ) during all stages in the breeding season. This is consistent with satellite tracking studies of Royal Penguins and dietary studies (Hull *et al.* in press, also Chapter 5 and 8).

#### Foraging trip durations

Foraging trip durations allowed an estimate of the longitudinal extent of foraging zones. Whilst the information necessitated a number of assumptions, it provided the first indicator of the foraging zones of Rockhopper Penguins, and evidence of the potential overlap in foraging zones between the species.

The foraging trip durations of Royal Penguins during chick rearing were shorter than those of Macaroni Penguins at Marion Island (Brown 1987), yet the estimation of maximal foraging ranges are greater in the former (Table 6.4). This discrepancy is most likely due to different foraging patterns at the two sites, as satellite tracking studies found that foraging zones of Royal Penguins are further offshore than those estimated

for Macaroni Penguins at Marion Island and Heard Island (Brown 1987, Hull *et al.* in press, also Chapter 5, Green *et al.* submitted)

Conversely, Rockhopper Penguins in this study had longer foraging trips than those on Marion Island (Brown 1987). The estimated foraging zones of this species on Macquarie Island is further offshore than that estimated for Marion Island. This is probably related to the unique oceanic conditions, and possibly prey resources, around Macquarie Island compared to other localities (Hindell 1988a), resulting in these species of penguin foraging further offshore.

#### *Foraging zones of Royal and Rockhopper Penguins*

The estimated foraging zones of Royal and Rockhopper Penguins indicated that both species were moving further offshore than has been previously assumed (Horne 1985, Scott 1994). Estimated locations of both species indicated a reliance on the PFZ, which has abundant and/or predictable food resources, particularly myctophid fish (Bost *et al.* 1997), which are an important component of both Royal and Rockhopper Penguins diets (Hindell 1988a, 1988b, Chapter 8). Prey species are found closer to the surface and in higher concentrations in this region (Hulley 1981, Brown & Klages 1987, Gon & Heemstra 1990), no doubt making them more accessible to these species of penguin (See Chapter 7). This abundance in prey resources is presumably linked to high productivity levels in the zone due to the action of the Antarctic Circumpolar Current which causes the mixing of warm and cool water, restoring nutrients (Radok 1966, Ainley & Jacobs 1981, Foster 1984, Abrams 1985, Lutjeharms *et al.* 1985, Schneider



1990).

During the 1995/6 season, female Rockhopper Penguins utilised warmer water during incubation and guard stages than did males during incubation. Aside from this, both species foraged in water of the same temperatures throughout the breeding season, suggesting they may have targeted a specific part of the PFZ, even though the frontal zone moved further south as the summer progressed (Jouventin *et al.* 1994, NASA PO.DAAC data, Figs. 6.5 and 6.6). Whilst the same section of the PFZ targeted, the extent of foraging zones was not constant across the breeding season. The difference in foraging zones would be dictated by commitments at the nest, with those during chick provisioning being shorter in order to regularly supply growing chicks with food.

#### *Overlap in foraging zones between the species*

The SST of the water masses used by both species indicated an overlap in the general regions of the PFZ utilised. However, the differences in estimated maximum foraging distances show some potential for segregation of foraging zones, although not a complete segregation. As Royal Penguins foraged throughout a trip (Hull *et al.* in press, also Chapter 5), presumably individuals in this study behaved similarly.

The three week asynchrony in the breeding season of Royal and Rockhopper Penguins has been postulated to assist with the segregation of food resources, as it would result in peaks in food demands occurring at different times (Brown & Klages 1987). Fig 6.7 takes this asynchrony into account, and shows that the degree of overlap in estimated

foraging zones may assist with the segregation of foraging zones to an extent. Peaks in food demand occur during creche stage (Chapter 8) when both adults are providing food for the chick and for their own maintenance. There is some overlap (see Fig. 6.2) in creche stages of these species, therefore in the peak demand period. However, the segregation of foraging zones, as indicated by this study, suggest that this overlap in food demands may be offset by the use of different sectors of the marine environment. Further studies are required to accurately determine the locations of Rockhopper Penguins during the breeding season which would allow examination of the suggestion that there are differences in the foraging zones of Royal and Rockhopper Penguins. This would confirm that one of the mechanisms for reducing the overlap in resource use between sympatrically breeding penguins is differential foraging zones (Croxall & Prince 1980a, Ridoux 1994, Hindell *et al.* 1995).

## 6.5 Summary

This study used a number of techniques to describe the foraging zones of Royal and Rockhopper Penguins, and to determine the degree of overlap in zones between the species. VHF telemetry was trialed but proved to be inadequate for determining locations at sea. Satellite telemetry could not be used due to the size of the devices in relation to that of Rockhopper Penguins, instead geolocation and sea surface temperature recorded by Time Depth Recorders with geolocation (TDRs), and foraging trip durations were used. TDRs were deployed 61 times across the four stages of the breeding season (males during incubation, females during incubation, guard and creche) during 1994/5 and 1995/6 austral summers, 37 of these provided data for analysis. The

errors inherent in geolocation made it impossible to determine precise foraging zones and differences between the species. However, sea surface temperature data and foraging trip durations provided better estimates of foraging zones. Both species foraged in waters of the same temperature (6.8 - 10.8° C), representing the same regions of the polar frontal zone. The water bodies used were constant across the breeding season in both species, except during one year in which Rockhopper Penguins travelled in cooler water early in the breeding season. It was estimated that Rockhopper Penguins did not travel as far as Royal Penguins, providing a small degree of segregation in foraging zones. When the data were assessed contemporaneously, to take into account the three week asynchrony in the breeding season of the species, the overlap in foraging zones was small. It was concluded that the overlap in foraging zones of these species was probably small and therefore may be an important mechanism for reducing the overlap in resource use between the species. Until smaller satellite transmitters are available, sea surface temperature and foraging trip durations can approximate foraging zones in these and other small species of penguin, but conclusions on the degree of overlap between Royal and Rockhopper Penguins can only be tentative.

## 6.6 Acknowledgments

Thanks go to Jane Wilson, Mary-Anne Lea, Kirsten Le Mar and Paul Scofield for assistance in the field. Roger Hansworth fixed problematical devices in the field, for which I thank him. I also would like to thank Mark Hindell, Di Moyle and Christophe Guinet for comments on drafts of the manuscript. Funding was generously provided by the Antarctic Science Advisory Committee, SeaWorld Research and Rescue Foundation,

and the M.A. Ingram Trust, for which I am grateful. Work was carried out under Macquarie Island special permits MI/3/95, and MI/3/96.

## Chapter 7

### Aspects of the diving behaviour of Royal and Rockhopper Penguins: a comparative examination of use of the water column

#### 7.1 Introduction

Penguins spend the majority of their time at sea and their ecology is closely linked with this environment. Quantitative description of the spatial use of the water column is therefore fundamental to understanding their foraging ecology. The development of remote recorders has allowed the description of foraging behaviour; however for a number penguins this has only been examined briefly, and in some cases, not at all.

The crested (eudyptid) penguins constitute a group of six species, including the most abundant species, Macaroni Penguin *Eudyptes chrysolophus* (Croxall *et al.* 1993). Diving behaviour, however, has only been described in two species, Macaroni and Rockhopper *E. chrysocome* Penguins, at a limited number of sites. Macaroni Penguins have been studied to some extent at South Georgia (during guard and creche stages) and at Heard Island (across the breeding season) (Croxall *et al.* 1988, 1993, Green *et al.* submitted).

There are three subspecies of Rockhopper Penguin (*E. c. chrysocome*, *E. c. filholi* and *E. c. moseleyi*), and preliminary dive analysis has been undertaken on two of these, *E. c. moseleyi* at Amsterdam Island using maximum depth recorders (Tremblay *et al.*

1997), and on one individual *E. c. filholi* at Possession Island, Crozet Archipelago (Wilson *et al.* 1997). Both studies on Rockhopper Penguins were conducted only during the creche stage.

Two species of crested penguin breed on Macquarie Island, Royal *E. schlegeli* which is endemic, and Rockhopper *E. c. filholi* Penguins, but no diving studies have been undertaken on either. A comparison of the diving behaviour and regions of the vertical water column used by these penguins is of interest as they are ecologically and taxonomically very similar, and therefore overlap in the use of resources (Cooper *et al.* 1990, Hindell *et al.* 1995). In order for these species to co-exist presumably they must partition some aspects of their habitat in order to avoid competition (Croxall & Prince 1980a, Cooper *et al.* 1990, Hindell *et al.* 1995). A number of mechanisms have been hypothesised which would result in different use of habitats and therefore resources, one being the depth in the water column that the species obtain prey (Croxall & Prince 1980a, Cooper *et al.* 1990, Hindell *et al.* 1995).

The purpose of this study was to (1) Describe aspects of the diving behaviour of Royal and Rockhopper Penguins, and (2) Examine the hypothesis that these species exploit different parts of the water column, thereby minimising an overlap in resource use.

## 7.2 Materials and methods

Diving data were collected using Mark V Time Depth Recorders (TDRs) (Wildlife Computers, Redmond, USA). Each device was 62 x 38 x 12 mm (2.3% cross-sectional



area of Royal and 2.9% of Rockhopper Penguins [frontal cross-sectional area of Rockhopper Penguins from C. Brown pers. comm. ]), and had a mass of 50 g. A total of 89 deployments was made on different individuals during the 1993/4, 1994/5 and 1995/6 breeding seasons. Breeding Royal Penguins were randomly selected from the upper colony at Sandy Bay, and breeding Rockhopper Penguins from Brothers Point, Sandy Bay (east coast 54° 33' 51" S, 158° 54' 11" E). The sex of the penguins was determined by bill length and depth (Hull in press, also Chapter 2).

TDRs were attached to the lower, medial portion of the back of the penguins (to minimise drag, Bannasch *et al.* 1994), using a cyanoacrylate adhesive (Loctite 401), and a coloured velcro band was attached to the right flipper to identify individuals. No device was left on a bird for more than one foraging trip, and all attachments were made in the colony using the techniques of Hull & Wilson (1996a, also Chapter 3). Mass was not measured at deployment due to the increased risk of birds abandoning the nest (Hull & Wilson 1996a, also Chapter 3). Both the TDR and velcro band were removed when the penguins returned from a foraging trip.

Deployments were made during four stages of the breeding season each year: male first foraging trip during incubation; female first foraging trip during incubation; guard; and creche. TDRs were duty-cycled at one day on, two days off during the long foraging trips in the incubation period to maximise data collection (Warham 1971, Carrick 1972).

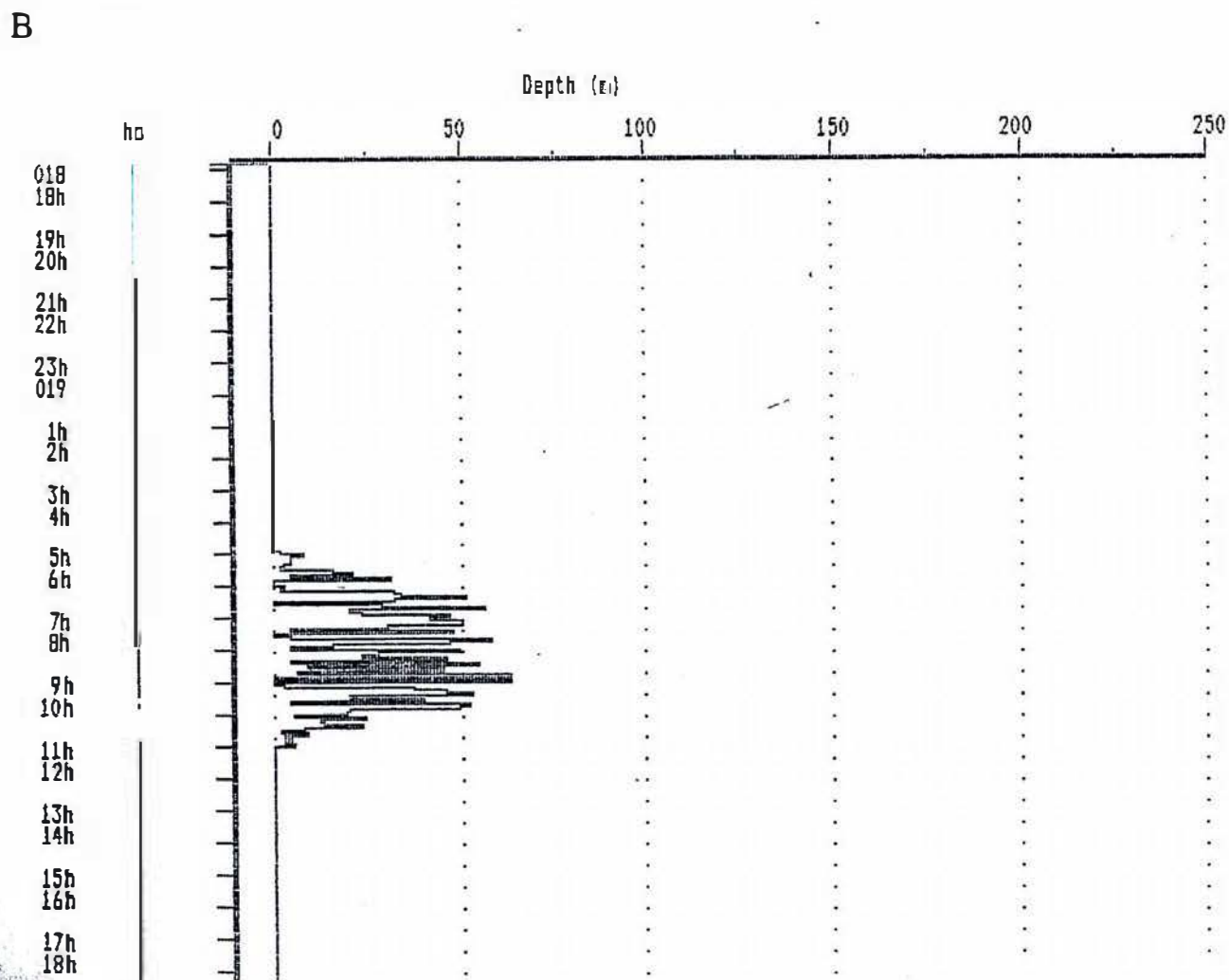
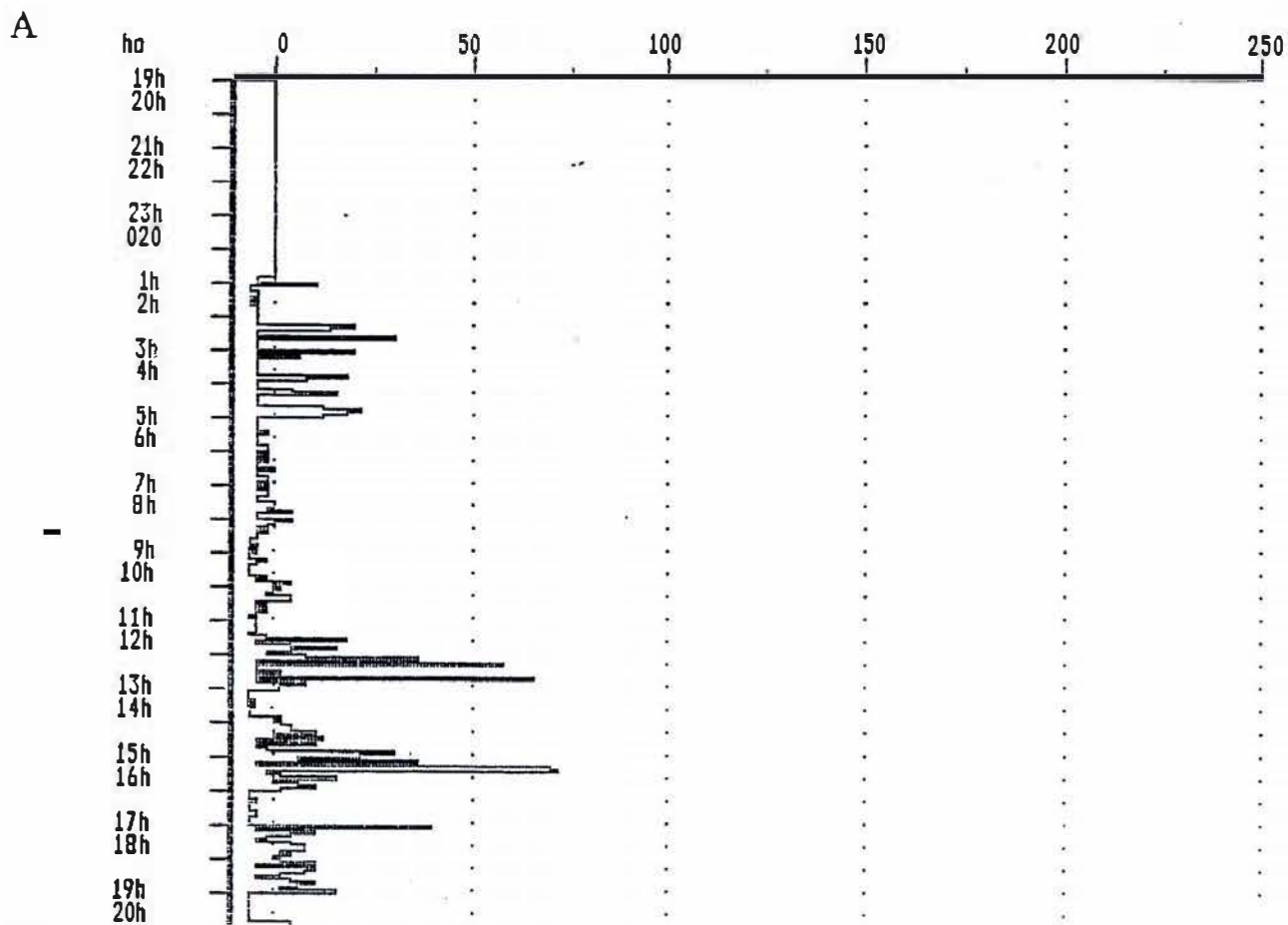
TDRs were programmed to collect dive data every two seconds, in order to detect fine

scale patterns (c.f. Boyd 1993). The memory of the TDRs were either 1.3 or 5.2 Kbytes, with the majority of deployments being devices with the smaller memory. Data were processed with Zero Offset Correction software (Wildlife Computers, Redmond WA, USA) in order to make adjustments for drifting of the zero-depth reading. Diving information was processed with Dive Analysis software (Wildlife Computers, Redmond WA, USA). A depth resolution of 2 m was used, and only records greater than 6 m in depth were regarded as potential foraging dives and used in the analyses, with those less than 6 m being assumed to be surface noise or travelling dives. Examples of dive profiles of each species are given in Fig. 7.1.

### 1. Description of diving behaviour

Inter-annual and species comparisons were made by quantifying the following variables: rate of diving; maximum depth of dives; duration of dives; time spent submerged; bottom time; wiggles; descent and ascent rates. Descent rates were the average rate of descent from the commencement of a dive to the beginning of bottom time, and ascent rates the average rate from the end of bottom time to the end of the dive. Bottom time was based on 85% of the maximum depth. The presence of wiggles in dives was used as an indication of feeding behaviour (c.f. Kirkwood & Robertson 1997). The data were analysed using nested Analysis of Variance (ANOVAs) when the entire data set was used (the majority of analyses), and one and two-way ANOVAs when the means of individuals (number of dives) were used. Diving behaviour was also examined across the breeding season, foraging trip and hour of the day using the same methodology.

**Fig. 7.1** Examples of dive profiles of Royal (A) and Rockhopper (B)  
Penguins



## 2. Use of the water column

To compare the use of the water column between the species regressions between depth and duration of dives, depth and bottom time, depth and wiggles, depth and ascent rates, depth and descent rates were compared using Analysis of CoVariance (ANCOVAs).

The percentage of time spent submerged at different depths was also used to give an indication of sections of the water column used. The time spent submerged and number of dives performed at various depths were compared between the species by grouping dives into the following categories: 6 - 20 m, 21 - 40 m, 41 - 60 m, 61 - 80 m, and > 81 m. The number of dives and time spent in each dive category were then compared using  $\chi^2$  analysis.

Data are presented as mean  $\pm$  standard deviations.

## **7.3 Results**

Of the 89 deployments of TDRs, 58 were available for analysis (Table 7.1). Twelve devices were lost during the course of the study, with penguins either returning without the device, or not returning during the breeding season. The data from two units were corrupted due to low battery voltage, and the remaining seventeen data sets were from birds that were failed breeders. As the focus of this study was on the diving behaviour of successful breeders, those that failed were not regarded as representative.

A total of 99,512 dives (42,382 Royal Penguins and 57,130 Rockhopper Penguin) were

analysed from these 58 files, from a total of 398 days of diving. Details of the diving behaviour of all individuals are given in Appendix 7.1.

**Table 7.1** The number of penguins from which dive data were successfully obtained during each stage of the breeding cycle each year

	1993/4	1994/5	1995/6	1993/4	1994/5	1995/6	
<i>Stage</i>	<i>Royal</i>		<i>Penguins</i>	<i>Rockhopper</i>		<i>Penguins</i>	<i>Total</i>
Incubation	0	5	2	0	6	1	14
- males							
- females	5	2	1	2	4	2	16
Guard	0	5	3	1	4	2	15
Creche-males	1	1	2	3	1	1	9
- females	0	1	1	2	0	0	4

### *Foraging trip durations*

Foraging trip durations were determined when birds were observed leaving and returning to the colony, and therefore precisely known ( $n = 47$ , Table 7.2). Foraging trip durations were not significantly different between the species ( $F_{1,47} = 18.8$ ,  $P < 0.0001$ ) and between stages ( $F_{3,47} = 30.2$ ,  $P < 0.0001$ ), with trips during the incubation period being longer than during chick provisioning (guard and creche stages) (Table 7.2).



**Table 7.2** Foraging trip durations (days) of penguins equipped with time depth recorders

Stage	Royal Penguins	n	Rockhopper Penguins	n
Incubation - males	19.5 ± 1.2	6	10.5 ± 3.5	6
Incubation - females	19.0 ± 7.1	7	13.7 ± 4.0	3
Guard	4.6 ± 1.3	5	7.0	2
Creche	6.2 ± 3.5	5	7.3 ± 5.8	3

### 1. Diving behaviour

#### *Daily diving activity*

Both species were diurnal in their diving activity, with dives made predominantly between the hours of 04:00 - 21:00 (local time) during all stages of the breeding season. This diurnal pattern was reflected in both the number (Fig. 7.2) and depth of dives (Royal Penguins: male incubation  $F_{23, 95} = 5.6$ ,  $P < 0.0001$ , female incubation  $F_{23, 48} = 2.1$ ,  $P < 0.01$ , guard  $F_{23, 168} = 13.9$ ,  $P < 0.0001$ , creche  $F_{23, 120} = 7.2$ ,  $P < 0.0001$ . Rockhopper Penguins: male incubation  $F_{23, 144} = 10.0$ ,  $P < 0.0001$ , female incubation  $F_{23, 71} = 4.9$ ,  $P < 0.0001$ , guard  $F_{23, 72} = 5.9$ ,  $P < 0.0001$ , creche  $F_{23, 120} = 6.3$ ,  $P < 0.0001$ ) (Fig. 7.3, Table 7.3).

#### *Rate of diving*

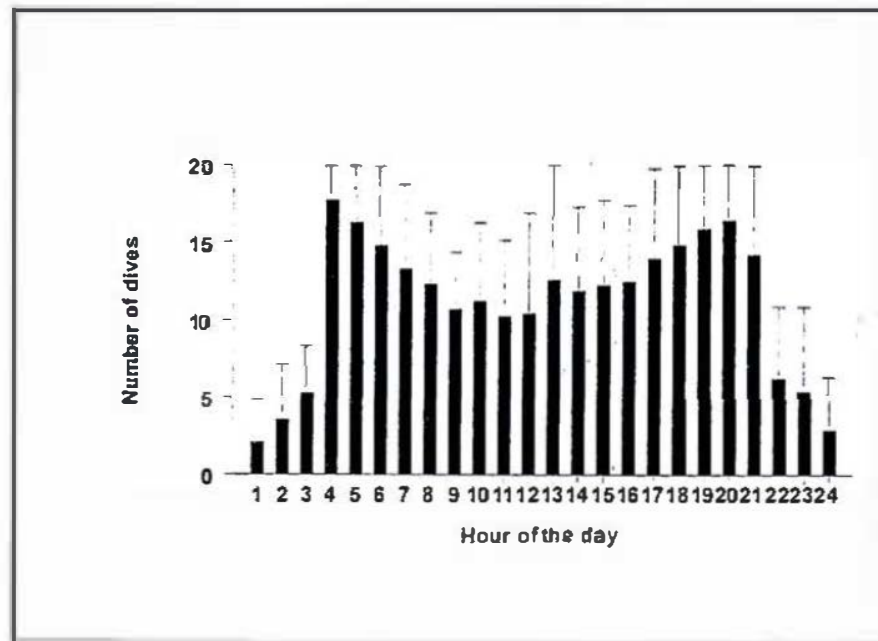
Royal Penguins made on average  $11.1 \pm 6.9$  dives per hour, and Rockhopper Penguins  $14.8 \pm 9.4$  dives per hour. Rockhopper Penguins undertook more dives per day (355.4

$\pm 175.1$ ) than Royal Penguins did ( $262.7 \pm 125.0$ ). The differences between the species was significant ( $F_{1, 27} = 15.5$ ,  $P < 0.001$ ) (Fig. 7.2).

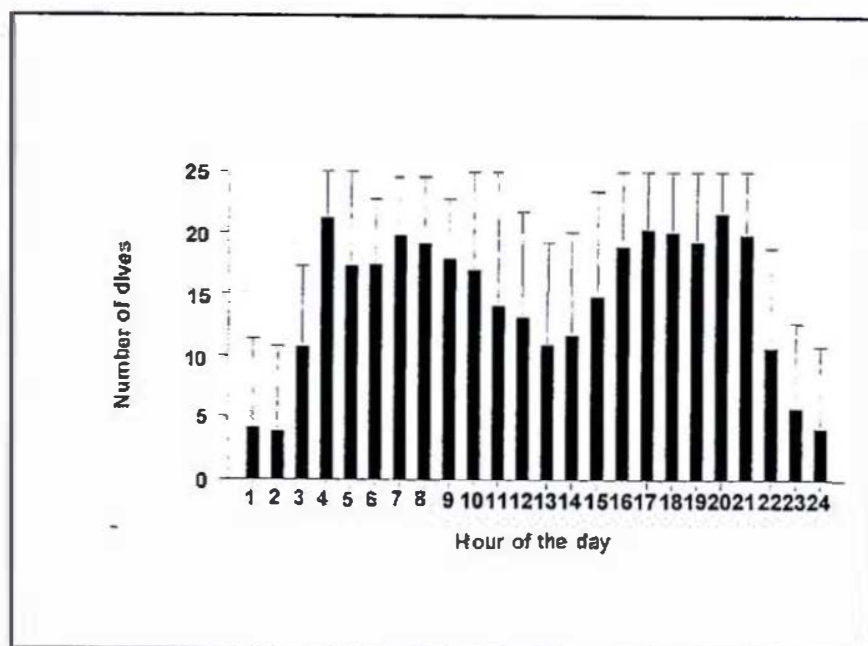
The rate of diving did not change significantly across the breeding season in either species (Royal Penguins  $F_{3, 11} = 0.3$ ,  $P > 0.05$ , Rockhopper Penguins  $F_{3, 17} = 2.4$ ,  $P > 0.05$ ). Rate of diving was also constant between years in both species (Royal Penguins  $F_{2, 19} = 1.6$ ,  $P > 0.05$ , Rockhopper Penguins  $F_{2, 26} = 1.4$ ,  $P > 0.05$ ).

**Fig. 7.2** Rate of diving by Royal and Rockhopper Penguins  
across a 24 hour period

## Royal Penguins

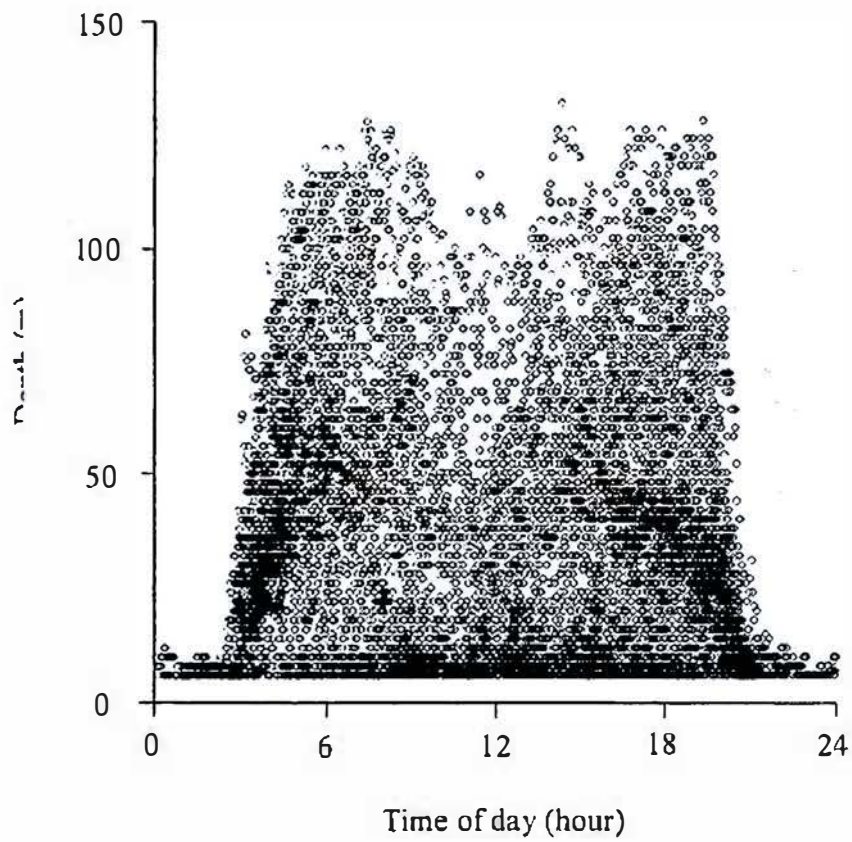


## Rockhopper Penguins

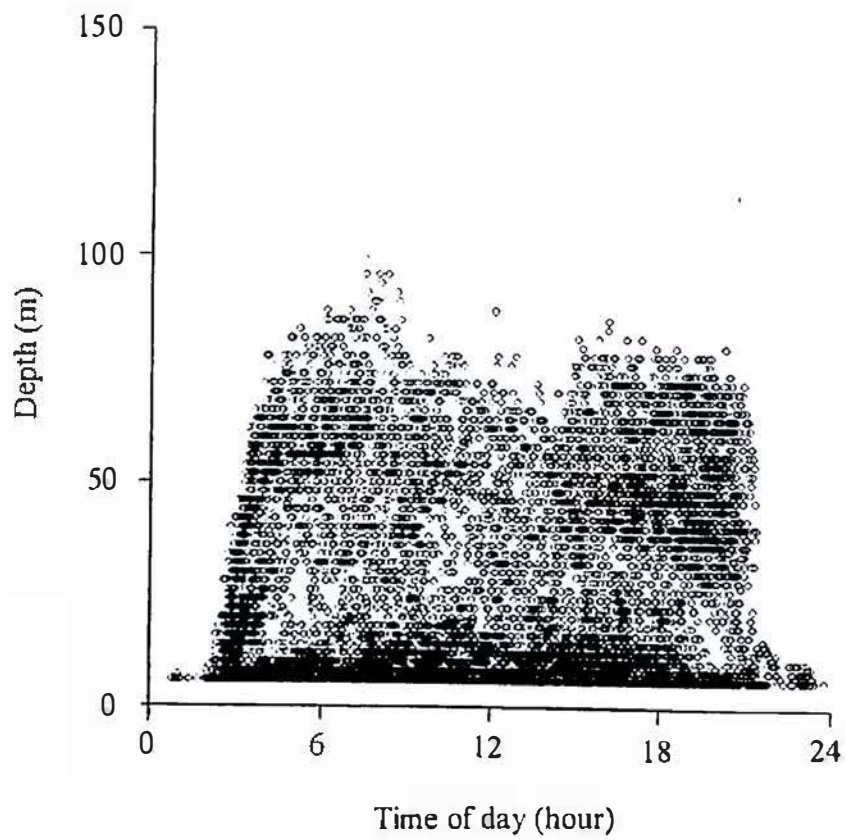


**Fig. 7.3** The depth of dives of Royal (A) and Rockhopper (B) Penguins across a 24 hour period

A



B





**Table 7.3** Depth of dives (mean  $\pm$  standard deviation) of all Royal ( $n = 29$ ) and Rockhopper Penguins ( $n = 29$ ) during each hour of the day

<i>Hour</i>	<i>Royal Penguins</i>	<i>Rockhopper Penguins</i>
1	6.0 $\pm$ 3.4	6.0 $\pm$ 3.1
2	6.3 $\pm$ 3.7	6.0 $\pm$ 3.2
3	10.1 $\pm$ 4.4	11.1 $\pm$ 5.5
4	24.1 $\pm$ 8.4	21.5 $\pm$ 9.4
5	41.6 $\pm$ 14.7	29.5 $\pm$ 13.8
6	45.3 $\pm$ 17.7	31.9 $\pm$ 12.5
7	40.5 $\pm$ 18.8	31.8 $\pm$ 12.5
8	44.5 $\pm$ 17.7	32.0 $\pm$ 12.2
9	41.8 $\pm$ 13.5	29.2 $\pm$ 11.5
10	36.1 $\pm$ 14.6	28.5 $\pm$ 13.0
11	40.5 $\pm$ 18.3	28.8 $\pm$ 13.4
12	32.5 $\pm$ 16.8	26.9 $\pm$ 13.1
13	34.4 $\pm$ 17.4	28.0 $\pm$ 15.8
14	34.8 $\pm$ 13.1	28.8 $\pm$ 15.9
15	39.9 $\pm$ 13.9	29.8 $\pm$ 14.6
16	40.0 $\pm$ 15.5	33.3 $\pm$ 11.9
17	44.4 $\pm$ 15.8	35.8 $\pm$ 12.2
18	42.5 $\pm$ 16.5	35.6 $\pm$ 12.3
19	41.1 $\pm$ 16.2	34.0 $\pm$ 12.4
20	35.6 $\pm$ 15.4	33.6 $\pm$ 12.3
21	22.3 $\pm$ 9.7	25.8 $\pm$ 13.0
22	10.6 $\pm$ 7.0	12.6 $\pm$ 9.4
23	6.9 $\pm$ 4.2	6.0 $\pm$ 4.2
24	5.2 $\pm$ 3.2	6.0 $\pm$ 3.5

*Time spent submerged*

Royal Penguins spent  $38.9 \pm 8.9$  % of a 24 hour period diving, and Rockhopper Penguins  $36.6 \pm 9.3$  % (Table 7.4, Appendix 7.1). These times were not significantly different between the species, nor between years or stages in the breeding season (species:  $F_{1,38} = 0.5$ ,  $P > 0.05$ ; years:  $F_{2,43} = 0.6$ ,  $P > 0.05$ ; stages  $F_{3,38} = 2.6$ ,  $P > 0.05$ ).

*Diving depths*

The deepest dive of a Royal Penguin was 226 m, and a Rockhopper Penguin 104 m. The depth of 226 m attained by one Royal Penguin was unusual, and aside from this record, the maximum depth was 132 m (Fig. 7.4, Appendix 7.1). The mean depth of dives was 32.9 m in Royal Penguins and 27.3 m in Rockhopper Penguins. Individuals of both species exhibited a great deal of variability in the depth of dives (Appendix 7.1). There were no significant differences between Royal and Rockhopper Penguins in the depth of dives (Table 7.5, Appendix 7.1).

The depths that Royal Penguins dived to did not differ between years (male incubation  $F_{1,5} = 1.0$ ,  $P > 0.05$ ; female incubation  $F_{2,5} = 1.0$ ,  $P > 0.05$ ; guard  $F_{1,6} = 1.3$ ,  $P > 0.05$ ; creche  $F_{2,3} = 5.0$ ,  $P > 0.05$ ). But they did in Rockhopper Penguins during male incubation ( $F_{1,5} = 9.1$ ,  $P < 0.03$ ), with deeper dives undertaken during 1994/5 than 1995/6. The depth of dives did not differ between years in the other stages in the breeding season (female incubation  $F_{2,5} = 0.2$ ,  $P > 0.05$ ; guard  $F_{2,4} = 0.7$ ,  $P > 0.05$ , creche  $F_{2,4} = 2.2$ ,  $P > 0.05$ ).

Diving depths were constant across the breeding season in Royal (1993/4  $F_{1,4} = 0.1$ ,  $P > 0.05$ ; 1994/5  $F_{3,10} = 1.3$ ,  $P > 0.05$ ; 1995/6  $F_{3,5} = 3.3$ ,  $P > 0.05$ ) and Rockhopper Penguins (1993/4  $F_{2,4} = 4.8$ ,  $P > 0.05$ ; 1994/5  $F_{3,11} = 1.6$ ,  $P > 0.05$ ; 1995/6  $F_{3,2} = 1.6$ ,  $P > 0.05$ ).

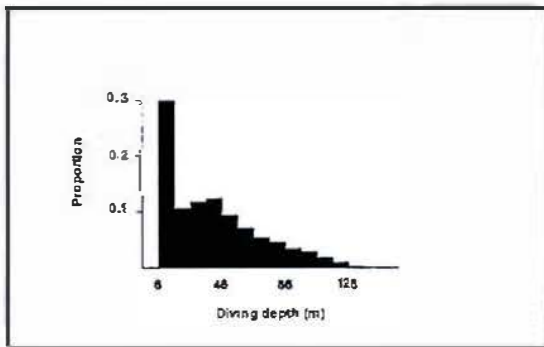
Wiggles suggested that feeding activity occurred primarily during dives 30 - 50 m in both species (Fig. 7.5).

**Table 7.4** Duration of dives in each depth class (% minutes) and number of dives (%) undertaken by Royal and Rockhopper Penguins

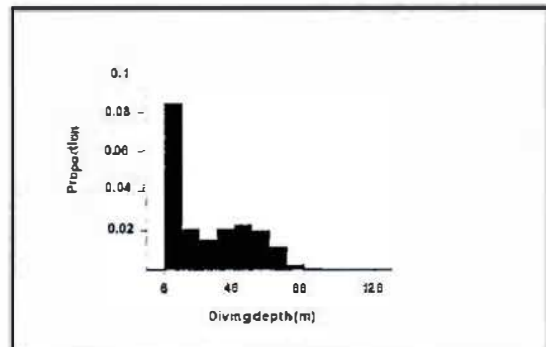
<i>Depth (m)</i>	<i>Variable</i>	<i>Incubation - males</i>		<i>Incubation - females</i>		<i>Guard</i>		<i>Creche</i>		<i>Total</i>	
		<i>Royal</i>	<i>Rockhopper</i>	<i>Royal</i>	<i>Rockhopper</i>	<i>Royal</i>	<i>Rockhopper</i>	<i>Royal</i>	<i>Rockhopper</i>	<i>Royal</i>	<i>Rockhopper</i>
6 - 20	time	19.2	32.4	27.8	42.7	26.1	26.9	28.0	18.8	25.2	28.7
21 - 40		24.4	20.1	22.8	30.9	25.7	25.1	22.4	21.0	23.8	24.1
41 - 60		22.9	28.8	19.4	20.9	25.8	38.1	27.6	38.2	23.6	32.9
61 - 80		15.7	17.8	17.1	5.1	15.8	9.7	14.7	19.7	15.9	13.3
> 81		17.8	0.9	12.9	0.4	6.6	0.2	7.3	2.3	11.5	1.0
6 - 20	number dives	35.0	49.5	45.2	58.1	42.2	45.1	43.5	35.0	41.5	46.5
21 - 40		23.7	17.4	20.2	25.0	23.9	21.8	20.6	20.0	22.0	21.2
41 - 60		18.7	21.2	14.6	13.6	19.4	26.7	21.2	29.7	18.2	23.3
61 - 80		11.3	11.4	11.9	3.1	10.4	6.3	10.0	13.8	11.0	8.4
> 81		11.3	0.5	8.1	0.2	4.1	0.1	4.7	1.5	7.3	0.6

**Fig. 7.4** Diving depths of Royal and Rockhopper Penguins  
during each stage of the breeding season

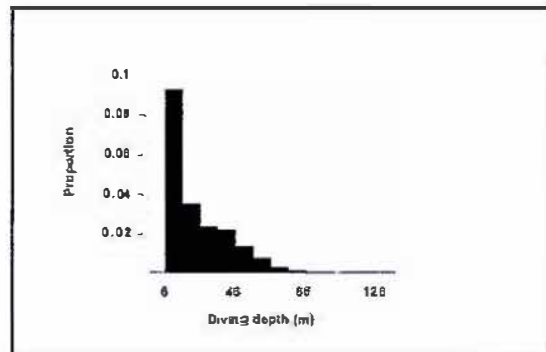
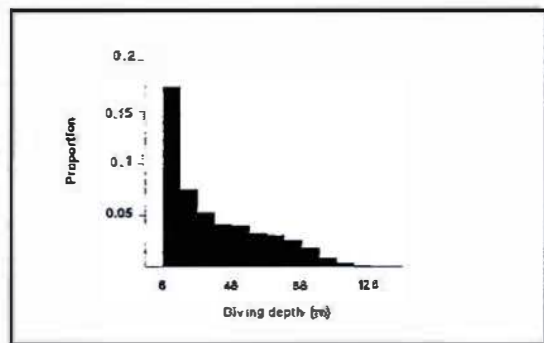
## Royal Penguins Males during incubation



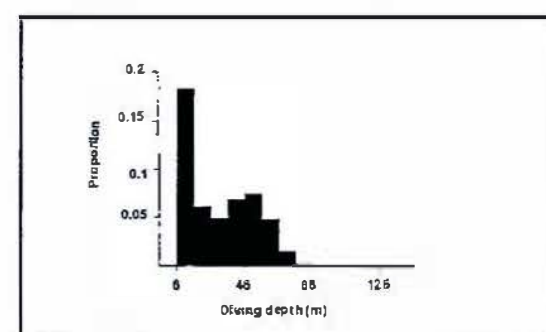
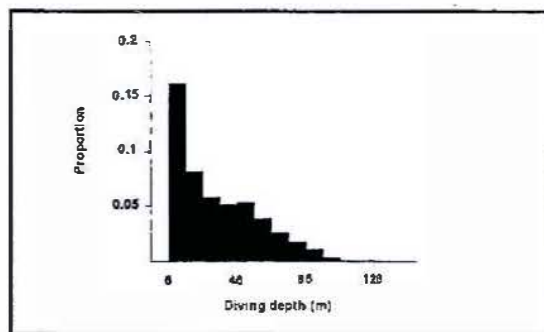
## Rockhopper Penguins



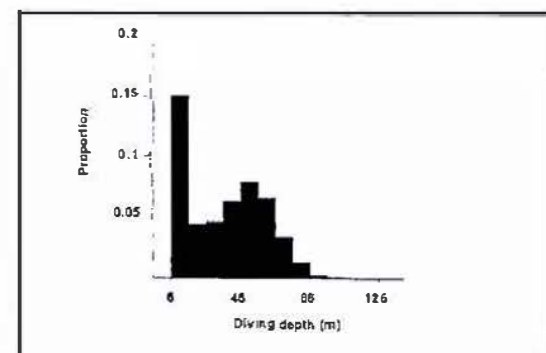
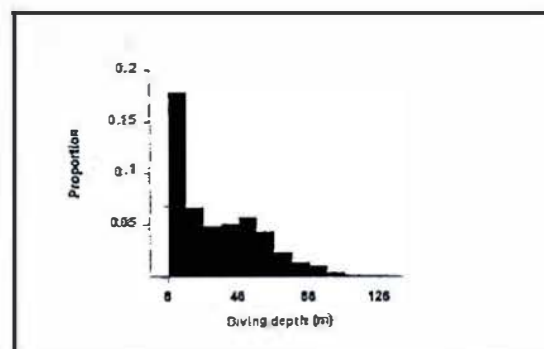
## Females during incubation



## Guard



## Creche





**Table 7.5** Comparisons of the depth and duration of dives during between Royal and Rockhopper Penguins during each year of the study and stage in the breeding season. **Significant cases in bold.** Stage 1: Incubation - males

Stage 2: Incubation - females

Stage 3: Guard

Stage 4: Creche

<i>Year</i>	<i>Stage</i>	<i>Depth</i>		<i>Duration</i>	
		<i>F value</i>	<i>Significance</i>	<i>F value</i>	<i>Significance</i>
1993/4	2	$F_{1,5} = 3.6$	$P > 0.05$	<b><math>F_{1,5} = 15.9</math></b>	<b><math>P &lt; 0.01</math></b>
1993/4	4	$F_{1,4} = 0.1$	$P > 0.05$	$F_{1,4} = 1.3$	$P > 0.05$
1994/5	1	$F_{1,9} = 1.4$	$P > 0.05$	<b><math>F_{1,9} = 10.9</math></b>	<b><math>P &lt; 0.009</math></b>
1994/5	2	$F_{1,4} = 3.0$	$P > 0.05$	$F_{1,4} = 4.4$	$P > 0.05$
1994/5	3	$F_{1,7} = 0.5$	$P > 0.05$	<b><math>F_{1,7} = 15.0</math></b>	<b><math>P &lt; 0.006</math></b>
1994/5	4	$F_{1,1} = 39.4$	$P > 0.05$	$F_{1,1} = 0.2$	$P > 0.05$
1995/6	1	$F_{1,1} = 63.4$	$P > 0.05$	$F_{1,1} = 12.7$	$P > 0.05$
1995/6	2	$F_{1,1} = 0.01$	$P > 0.05$	$F_{1,1} = 1.1$	$P > 0.05$
1995/6	3	$F_{1,3} = 0.08$	$P > 0.05$	$F_{1,3} = 3.1$	$P > 0.05$
1995/6	4	$F_{1,2} = 3.4$	$P > 0.05$	$F_{1,2} = 8.2$	$P > 0.05$

*Diving durations*

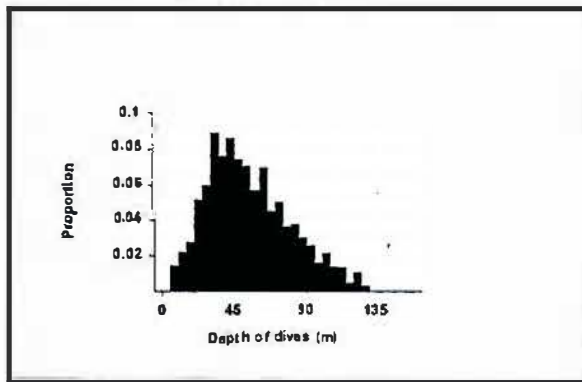
The maximum duration of dives was 7.5 minutes by a Royal Penguin and 11.0 minutes by a Rockhopper Penguin. Dives of these durations, however, were rare with Royal Penguins undertaking dives of 1.7 minutes on average, and Rockhopper Penguins 1.2 minutes (see Table 7.5). Significant differences were found in dive durations between the species during female incubation stage in 1993/4, male incubation in 1994/5, and guard in 1994/5 (Table 7.5). The remaining stages and years did not differ significantly between the species (Table 7.5).

The duration of dives was constant between years in Royal Penguins (male incubation  $F_{1,5} = 1.5$ ,  $P > 0.05$ ; female incubation  $F_{2,5} = 3.4$ ,  $P > 0.05$ ; guard  $F_{1,6} = 0.6$ ,  $P > 0.05$ ; creche  $F_{2,3} = 5.0$ ,  $P > 0.05$ ) and Rockhopper Penguins (male incubation  $F_{1,5} = 2.8$ ,  $P > 0.05$ ; female incubation  $F_{2,6} = 1.6$ ,  $P > 0.05$ ; guard  $F_{2,4} = 0.3$ ,  $P > 0.05$ ; creche  $F_{2,4} = 2.9$ ,  $P > 0.05$ ).

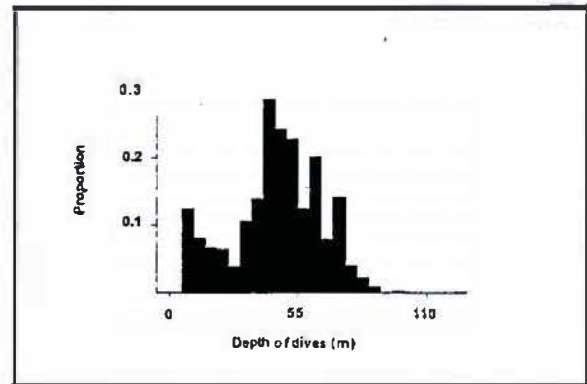
The duration of dives was also constant across the breeding season in both species (Royal Penguins: 1993/4  $F_{1,4} = 0.3$ ,  $P > 0.05$ ; 1994/5  $F_{3,10} = 3.7$ ,  $P > 0.05$ ; 1995/6  $F_{3,5} = 3.3$ ,  $P > 0.05$ ; Rockhopper Penguins (1993/4  $F_{2,4} = 2.7$ ,  $P > 0.05$ ; 1994/5  $F_{3,11} = 0.9$ ,  $P > 0.05$ ; 1995/6  $F_{3,2} = 1.6$ ,  $P > 0.05$ ).

**Fig 7.5** The depths at which wiggles were performed by  
Royal and Rockhopper Penguins

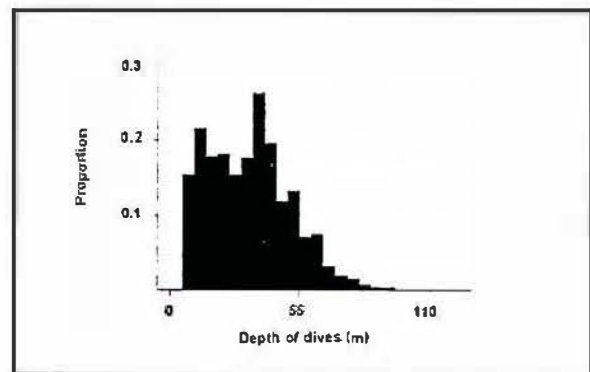
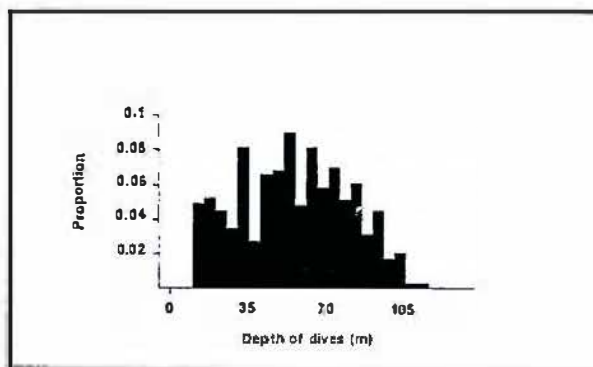
## Royal Penguins Males during incubation



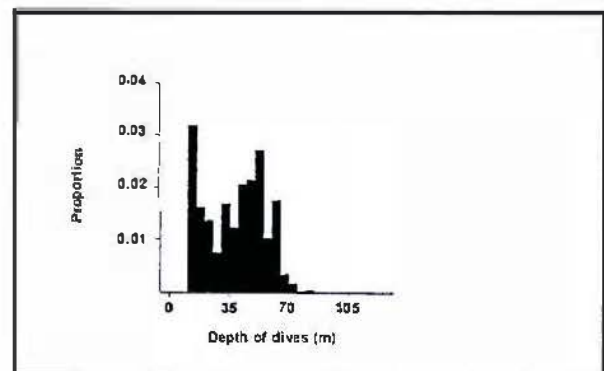
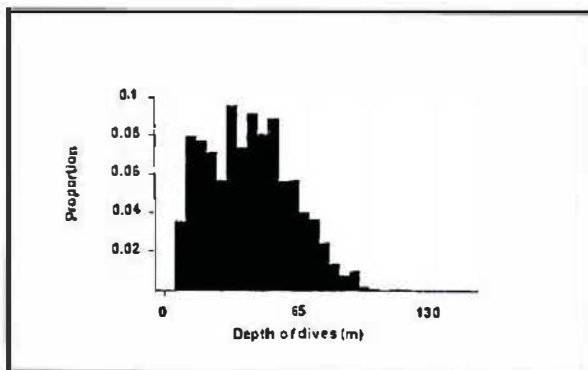
## Rockhopper Penguins



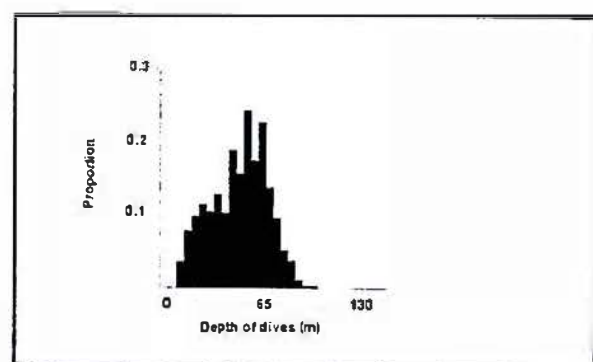
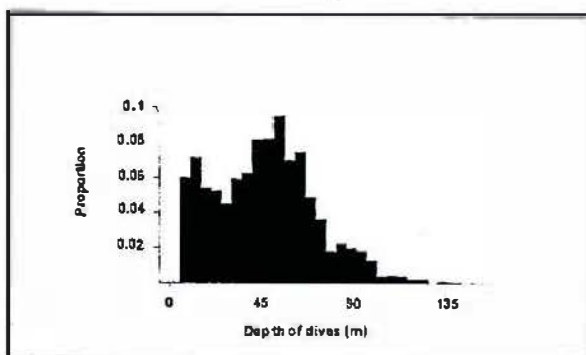
## Females during incubation



## Guard



## Creche



*Ascent and descent rates*

Descent rates in Royal Penguins were 1.0 m/sec and 1.1 m/sec in Rockhopper Penguins, with ascent rates 1.0 m/sec in both species (Table 7.6). Only the descent rates during guard stage in 1994/5 were significantly faster in Rockhopper Penguins than Royal Penguins, in all other stages and years, descent rates of the species were comparable (Table 7.6).

**Table 7.6** Ascent and descent rates of Royal and Rockhopper (RH) Penguins (m/sec) ( $P > 0.05$ ). **Significantly different between the species in bold**

Year	Stage	Royal	RH	F value	Royal	RH	F value
		Descent	rates		Ascent	rates	
1993/4	2	1.0 ± 0.5	0.9 ± 0.5	$F_{1,5} = 0.8$	0.9 ± 0.5	0.9 ± 0.4	$F_{1,5} = 0.7$
	3	-	1.5 ± 0.6	-	-	1.1 ± 0.5	-
	4	1.0 ± 0.5	1.2 ± 0.5	$F_{1,4} = 0.9$	1.1 ± 0.6	1.0 ± 0.5	$F_{1,4} = 0.01$
1994/5	1	1.0 ± 0.5	1.2 ± 0.4	$F_{1,9} = 3.0$	1.0 ± 0.6	1.1 ± 0.6	$F_{1,9} = 0.1$
	2	1.1 ± 0.5	0.9 ± 0.5	$F_{1,4} = 1.6$	1.0 ± 0.6	0.9 ± 0.4	$F_{1,4} = 4.1$
	3	1.0 ± 0.5	1.3 ± 0.4	<b><math>F_{1,7} = 6.2</math></b>	0.9 ± 0.6	1.2 ± 0.5	$F_{1,7} = 1.3$
	4	0.9 ± 0.4	1.3 ± 0.4	$F_{1,1} = 31.1$	0.9 ± 0.6	1.0 ± 0.6	$F_{1,1} = 0.9$
1995/6	1	1.0 ± 0.5	0.8 ± 0.4	$F_{1,1} = 5.9$	1.0 ± 0.6	0.8 ± 0.4	$F_{1,1} = 2.1$
	2	0.8 ± 0.5	1.2 ± 0.5	$F_{1,1} = 24.6$	0.9 ± 0.9	1.3 ± 0.9	$F_{1,1} = 0.5$
	3	0.9 ± 0.5	1.4 ± 0.4	$F_{1,3} = 6.6$	1.1 ± 1.2	1.0 ± 0.5	$F_{1,3} = 6.6$
	4	1.0 ± 0.5	0.9 ± 0.3	$F_{1,2} = 0.1$	0.9 ± 0.5	0.8 ± 0.3	$F_{1,2} = 0.8$

*Diving activity across a foraging trip*Royal Penguins

Royal Penguins made significantly fewer dives on the first and fourth day of foraging trips during incubation (males) ( $F_{7,36} = 2.9$ ,  $P < 0.01$ ), guard ( $F_{6,29} = 8.8$ ,  $P < 0.0001$ ), and creche stages ( $F_{11,23} = 3.5$ ,  $P < 0.006$ ) (Fig. 7.5). Diving activity was constant across trips during the incubation (females) stage ( $F_{11,6} = 1.8$ ,  $P > 0.05$ ) (Fig. 7.6).

Although the rate of diving by Royal Penguins changed across foraging trips in some stages in the breeding season, the depth and duration of dives did not (male incubation: depth  $F_{7,36} = 1.5$ ,  $P > 0.05$ , duration  $F_{7,36} = 1.1$ ,  $P > 0.05$ ; female incubation: depth  $F_{11,6} = 2.7$ ,  $P > 0.05$ , duration  $F_{11,6} = 2.5$ ,  $P > 0.05$ ; guard: depth  $F_{6,29} = 1.2$ ,  $P > 0.05$ , duration  $F_{6,29} = 1.6$ ,  $P > 0.05$ ; creche: depth  $F_{11,23} = 1.6$ ,  $P > 0.05$ , duration  $F_{11,23} = 0.9$ ,  $P > 0.05$ ).

Rockhopper Penguins

Rockhopper Penguin diving activity was constant across foraging trips during all stages of the breeding season (Fig. 7.6), except in males during incubation (male incubation  $F_{5,23} = 3.3$ ,  $P < 0.02$ ; female incubation  $F_{6,14} = 0.4$ ,  $P > 0.05$ ; guard  $F_{15,26} = 1.7$ ,  $P > 0.05$ ; creche  $F_{14,36} = 0.8$ ,  $P > 0.05$ ). Males during incubation also undertook significantly deeper and longer dives on the first three days of a foraging trip compared to the last three days (depth  $F_{5,23} = 11.2$ ,  $P < 0.0001$ , duration  $F_{5,23} = 8.3$ ,  $P < 0.0001$ ). Again, this difference was not found during the other stages of the breeding season (female incubation: depth  $F_{6,14} = 0.8$ ,  $P > 0.05$ , duration  $F_{6,14} = 0.8$ ,  $P > 0.05$ ; guard:



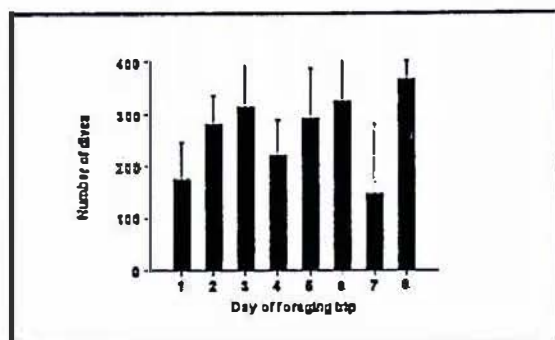
depth  $F_{3,4} = 3.1$ ,  $P > 0.05$ , duration  $F_{3,4} = 2.2$ ,  $P > 0.05$ ; creche: depth  $F_{14,31} = 0.5$ ,  $P > 0.05$ , duration  $F_{14,31} = 0.4$ ,  $P > 0.05$ ).

*Differences between the sexes during creche stage*

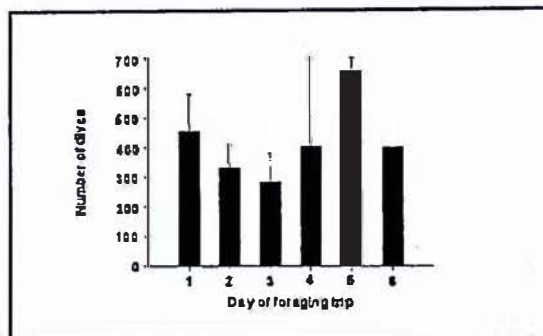
There were no significant differences between the sexes of each species in the rate of diving (Royal penguins:  $F_{1,4} = 0.3$ ,  $P > 0.05$ ; Rockhopper Penguins  $F_{1,5} = 1.7$ ,  $P > 0.05$ ), nor the maximum depth or duration of dives (Royal Penguins: depth  $F_{1,6} = 0.02$ ,  $P > 0.05$ ; duration  $F_{1,6} = 0.06$ ,  $P > 0.05$ . Rockhopper Penguins: depth  $F_{1,5} = 1.1$ ,  $P > 0.05$ ; duration  $F_{1,5} = 3.5$ ,  $P > 0.05$ ).

**Fig. 7.6** Rate of diving over a foraging trip in Royal and Rockhopper Penguins

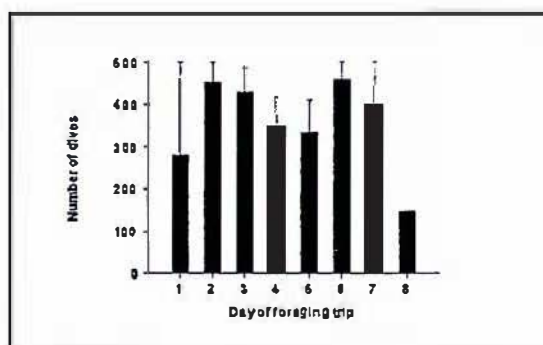
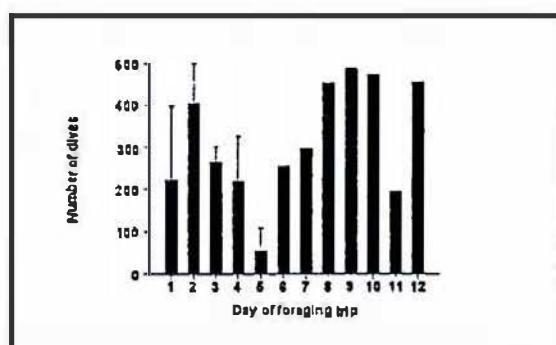
## Royal Penguins Males during incubation



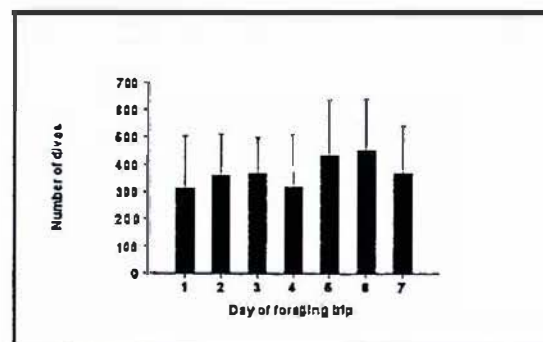
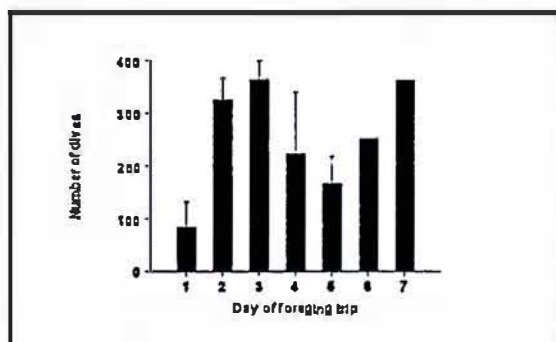
## Rockhopper Penguins



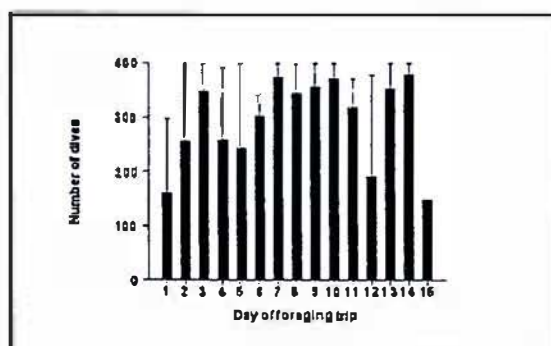
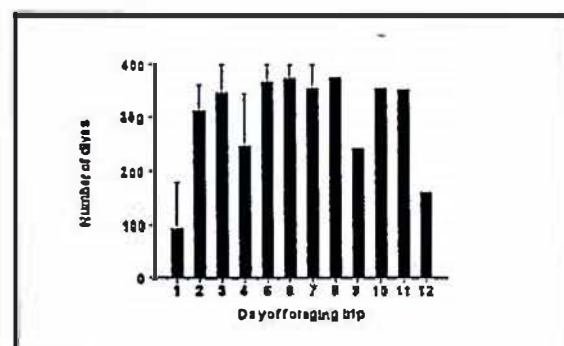
## Females during incubation



## Guard



## Creche



## 2. Use of the water column

There were significant differences between the species in the time spent at different depths (time spent at various depths  $\chi^2_4 = 8117.4$ ,  $P < 0.0001$ ; number of dives  $\chi^2_4 = 3806.9$ ,  $P < 0.0001$ ), with Royal Penguins undertaking more dives and spending more time at greater depths than Rockhopper Penguins (Table 7.4). This difference in use of the water column was also apparent in regressions of dive depth and duration of dives ( $F_{1, 53} = 12.1$ ,  $P < 0.001$ ), with Royal Penguins undertaking longer dives at greater depths (Fig. 7.8), and depth against bottom time ( $F_{1, 53} = 7.7$ ,  $P < 0.008$ ), and longer bottom times at greater depths (Fig. 7.8). Rockhopper Penguins ascended at a faster rate than Royal Penguins ( $F_{1, 52} = 5.4$ ,  $P < 0.02$ ) (Fig. 7.8). However, no differences were found in regressions of depth against number of wiggles ( $F_{1, 53} = 1.6$ ,  $P > 0.05$ ), nor depth against descent rates ( $F_{1, 53} = 0.002$ ,  $P > 0.05$ ).

Significant differences between the species were also found in the depth of dives against day of a foraging trip during male incubation stage ( $F_{1, 70} = 4.1$ ,  $P < 0.04$ ), indicating that Royal Penguins undertook deeper dives later in a foraging trip than did Rockhopper Penguins (female incubation:  $F_{1, 35} = 1.7$ ,  $P > 0.05$ ; guard  $F_{1, 40} = 0.1$ ,  $P > 0.05$ ; creche  $F_{1, 77} = 0.2$ ,  $P > 0.05$ ) (Fig. 7.7).

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Time spent at different depths in both species varied significantly over the breeding season (time spent at various depths: Royal Penguins  $\chi^2_{12} = 2057.2$ ,  $P < 0.0001$ , Rockhopper Penguins  $\chi^2_{12} = 6018.3$ ,  $P < 0.0001$ ; number of dives: Royal Penguins  $\chi^2_{12} = 852.0$ ,  $P < 0.0001$ , Rockhopper Penguins  $\chi^2_{12} = 3429.4$ ,  $P < 0.0001$ ) (Table 7.4).

These differences, however, were not reflected in regressions of dive variables (Royal Penguins: depth and duration  $F_{3,21} = 1.2$ ,  $P > 0.05$ ; depth and wiggles  $F_{3,21} = 0.6$ ,  $P > 0.05$ ; depth and bottom time  $F_{3,21} = 1.5$ ,  $P > 0.05$ . Rockhopper Penguins: depth and duration  $F_{3,20} = 0.3$ ,  $P > 0.05$ ; depth and wiggles  $F_{3,20} = 0.8$ ,  $P > 0.05$ ; depth and bottom time  $F_{3,20} = 2.1$ ,  $P > 0.05$ ).

Regions of the water column used by both species was constant across years (Royal Penguins: depth and duration  $F_{1,16} = 0.02$ ,  $P > 0.05$ ; depth and wiggles  $F_{1,16} = 0.003$ ,  $P > 0.05$ ; bottom time  $F_{1,16} = 0.05$ ,  $P > 0.05$ . Rockhopper Penguins: depth and duration  $F_{1,18} = 0.01$ ,  $P > 0.05$ ; depth and wiggles  $F_{1,18} = 0.5$ ,  $P > 0.05$ ; depth and bottom time  $F_{1,18} = 1.4$ ,  $P > 0.05$ ).

Further, there were no differences in the relationship between pairs of variables in the sexes of Royal Penguins, indicating they used the same regions of the water column (depth and duration  $F_{1,2} = 5.0$ ,  $P > 0.05$ ; depth and bottom time  $F_{1,2} = 1.4$ ,  $P > 0.05$ ; depth and number of wiggles  $F_{1,2} = 2.9$ ,  $P > 0.05$ ). Nor were any differences found between the sexes in Rockhopper Penguins in depth and duration ( $F_{1,3} = 1.4$ ,  $P > 0.05$ ), depth and bottom time ( $F_{1,3} = 0.7$ ,  $P > 0.05$ ), although there was in depth and number of wiggles ( $F_{1,3} = 43.2$ ,  $P < 0.007$ ). Female Rockhopper Penguins performed more wiggles, and at a shallower depth than males.

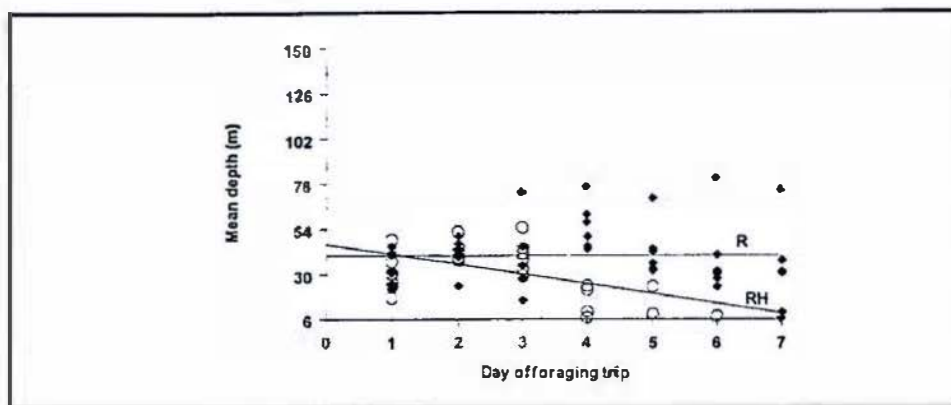
**Fig. 7.7** Regressions of the depth of dives against day of foraging trip during each stage of the breeding season

◆ R = Royal Penguins

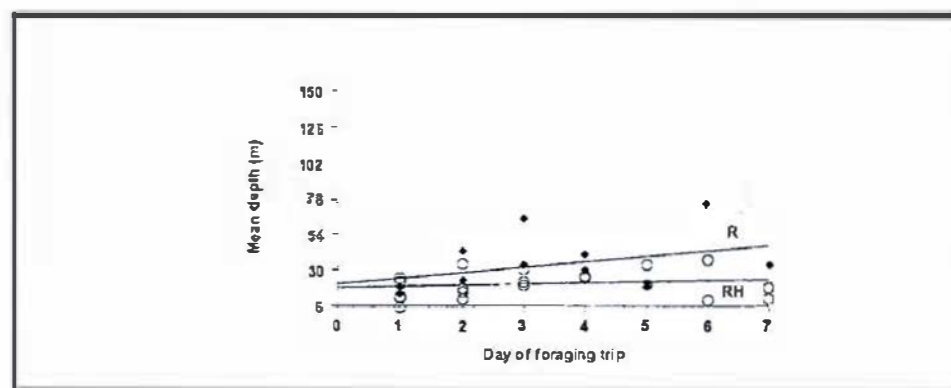
○ RH = Rockhopper Penguins



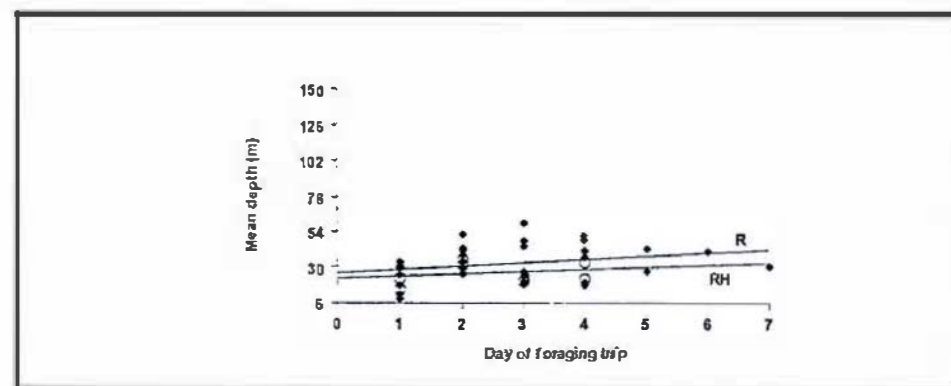
## Males during incubation



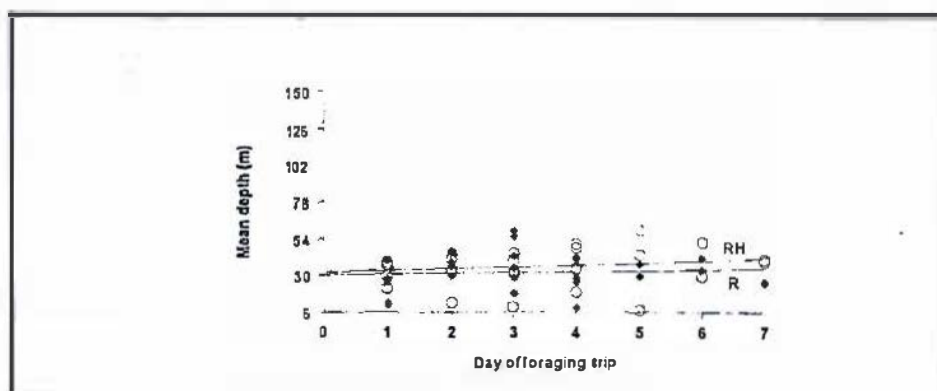
## Females during incubation



## Guard



## Creche

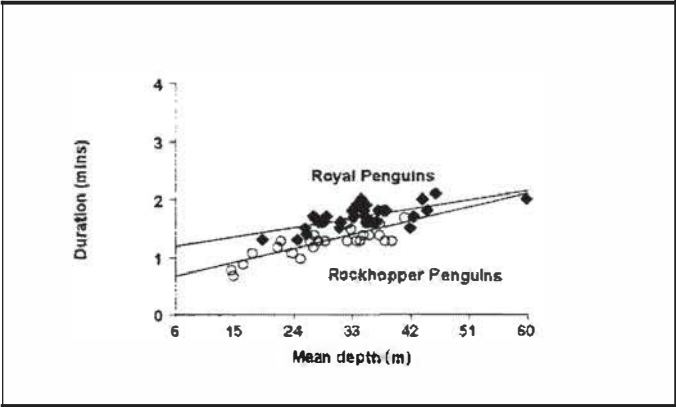


**Fig. 7.8** Comparisons between Royal and Rockhopper Penguins  
of depth against duration, bottom time and ascent rates

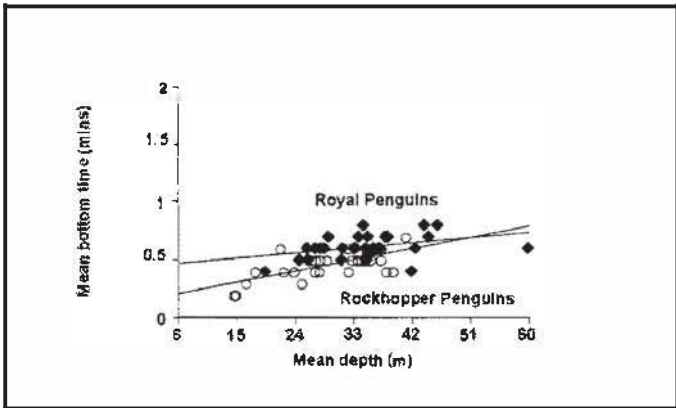
◆ R = Royal Penguins

○ RH = Rockhopper Penguins

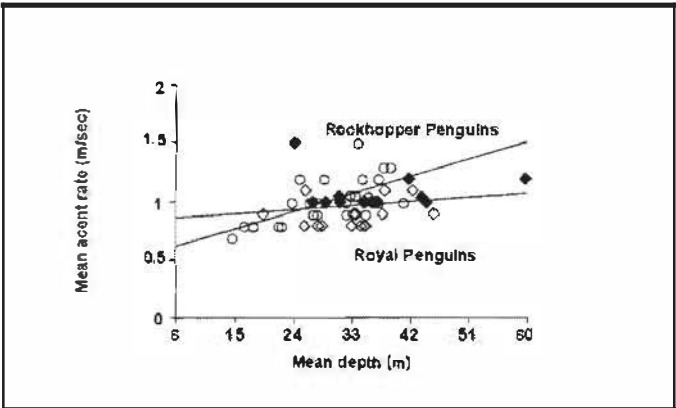
Depth versus duration



Depth versus bottom time



Depth versus ascent rates



## 7.4 Discussion

### *Effects of devices*

The deployment of TDRs is presently the most common means of obtaining details of the diving behaviour of penguins. However, it is likely that the behaviour recorded in this study was not representative of birds under natural conditions as the devices used increased drag, affecting swimming speed and possibly foraging success (Croll *et al.* 1991, Bannasch *et al.* 1994, Hull 1997, also Chapter 4). Whilst there is some understanding of the impact of TDRs on aspects of penguins' foraging behaviour, such as foraging trip durations, body composition and the probability of continuing the breeding attempt (Hull 1997, also Chapter 4), the impact on diving behaviour is unknown.

The depths of dives, and ascent and descent rates may be affected due to the increased drag of the TDRs (c.f. Wilson & Peters submitted). Diving depths of Rockhopper Penguins derived from this study were substantially less than those of northern Rockhopper Penguins (*E. c. moseleyi*) which were equipped with capillary tubes rather than TDRs (Tremblay *et al.* 1997). However, it is impossible to determine whether these differences represented an effect of the devices, differences between the subspecies, or specific diving patterns of the subspecies related to characteristics of the local environment.

Foraging trip durations in this study were longer than for birds without devices (Table 7.2, Chapter 9), hence it is likely there was some impact from the TDRs. Therefore, the

data collected on diving must be regarded as a conservative estimate and not necessarily representative of birds without devices.

### 1. General diving behaviour

There was a great deal of individual variability in the diving behaviour of both species (see Appendix 7.1). This variability has been found in other species of penguin, and is associated either with different abilities or strategies of the birds, or that prey are patchy in distribution and individuals respond opportunistically to the prey patches they encounter (Wilson *et al.* 1991a, b, Wilson *et al.* 1996, Kirkwood & Robertson 1997).

Both species of penguin showed distinct diurnal patterns in their diving behaviour, with little activity below 6 m during the night. Diurnal foraging patterns in other penguin species has been attributed either to penguins being visual predators and cannot forage efficiently in the dark (Croxall *et al.* 1993, Wilson *et al.* 1993, Cannell 1994), or that they follow the diel migrations of prey that rise to shallower depths at night (Croxall *et al.* 1988, 1993). The prey species of Royal and Rockhopper Penguins are primarily myctophid fish and euphausiids (Chapter 8). Both these groups rise to the top 20 - 50 m in the water column during the night, although there may also be seasonal differences in the position in the water column in which they are located (Perissinotto & McQuaid 1992). However, few wiggles were performed by either Royal or Rockhopper Penguins during shallow dives, suggesting it was unlikely that foraging took place during these hours, supporting the contention that these species, like most penguins, are predominantly visual predators, foraging more efficiently during daylight.

Daylight hours at Macquarie Island extend from 05:00 to 17:30 during the early part of the breeding season, and 03:00 - 20:30 in the early to mid creche in Rockhopper and Royal Penguins, respectively. Diving activity in both species occurred between the hours of 04:00 and 21:00, hence early in the breeding season (during male foraging trips in the incubation period) some diving would have been at night. This confirms that the reasons prompting diurnal foraging in penguins may not be quite so simplistic as merely being visual predators (Croxall *et al.* 1993). Nor is it probably constant across all species, as King Penguin *Aptenodytes patagonicus* for example, dive to depths where light is diminished and hence foraging is not completely dictated by the availability of light (Pütz & Bost 1994). Therefore, whilst foraging may be more efficient during daylight, other factors such as the bioluminescence of prey may allow a small amount of foraging at night during some stages in the breeding season.

It is probable that both species moved locations at night. Rates of travel determined from satellite tracking studies of Royal Penguins (Hull *et al.* in press, also Chapter 5), suggested that this species travelled at the same rate at night as during the day. Royal, and possibly Rockhopper, Penguins may not necessarily rest on the surface at night, as has been previously contended (Wilson *et al.* 1993), but instead undertake some travelling, but little foraging.

The degree of diving activity (indicated by amount of diving over a 24 hour period) remained constant across the breeding season in both species. Other penguin species may extend foraging activity in relation to day length, as a means of increasing the



quantity of food that can be obtained for chicks (Croxall *et al.* 1993). As this did not occur in Royal and Rockhopper Penguins it suggests that either sufficient food was obtained during the hours in which dives were performed, or that the penguins were diving at a near maximum rate (for example due to the physiological constraints of removing lactic acid from anaerobic diving) and could not increase diving activity. The former implies that prey resources are not limiting which is unlikely, hence, the latter explanation is more plausible.

The diving patterns of both species indicated a daily bimodal peak, with a reduction in diving activity around midday. A reduction in the ingestion of prey around midday has been found in a number of other species of penguin (Wilson *et al.* 1993, Wilson & Wilson 1995, Pütz 1994), which has been attributed to either prey migrating down the water column during the middle of the day and becoming inaccessible to penguins, or the penguins dive less in order to digest food caught during the morning foraging (Wilson & Peters submitted). However, as penguins in this study dived throughout the day this latter explanation seems unlikely. A reduction in diving during the middle of the day may be related to an inability of these penguins to make continuous long dives due to physiological constraints.

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Both Royal and Rockhopper Penguins had the capacity to dive over 100 m and for up to 11 minutes in duration. The diving capabilities of penguins is related to their body mass due to mass-specific metabolic rates, with smaller animals reaching aerobic limits faster than larger ones (Kooyman *et al.* 1992, Kooyman & Kooyman 1995 and

references therein). Based on the formula of Wilson (1995), Royal Penguins can potentially dive to 145 m and southern Rockhopper Penguins to 111 m. However, both species rarely dived to these depths or undertook dives of long duration (less than two minutes on average). Royal and Rockhopper Penguins spent 72% and 86% of their respective time at depths less than 60 m. The depth of dives would not be limited by the proximity of the sea floor, as the waters to the eastern side of Macquarie Island where these penguins forage are over 2000 m in depth, with a steep shelf area (Selkirk *et al.* 1990, Chapters 5 and 6).

Like Royal and Rockhopper Penguins, other penguins dived substantially above attainable depths, and their theoretical maximum capacity. This is thought to be linked with maximising foraging efficiency (Kooyman 1989, Croll *et al.* 1992, Chappell *et al.* 1993). By diving predominantly to shallow depths penguins would limit the need for anaerobic respiration and the associated cost of removing lactic acid (Chappell *et al.* 1993). Penguin muscles are thought to be better adapted to aerobic rather than anaerobic respiration (Baldwin *et al.* 1984) and the cost of removing lactic acid due to anaerobic metabolism is high (Chappell *et al.* 1993).

Shallow dives also involve less time in the descent and ascent phases and therefore have a greater proportion of bottom time. The descent and ascent phases of a dive are probably not profitable in terms of foraging, hence shallower dives allow greater foraging time (Boyd *et al.* 1995). The ability to selectively dive to shallower depths relies on the presence of prey at these depths. It appears, therefore, that diving

behaviour in these species is linked more to the location of prey and maximising foraging efficiency than to the penguins' physiological constraints (Lishman & Croxall 1983).

The rare deeper dives undertaken by species of penguins may be of some value as a means of searching for prey (Lishman & Croxall 1983, Williams *et al.* 1992), or if large prey are caught (Burger 1990). As deep dives in this study also involved wiggles it is probable that the searching component was less important than the consumption of prey. An alternate explanation for deep dives is postulated for Emperor Penguins *Aptenodytes forsteri*, where its role is thought to be linked with obtaining gastric stones and assisting with navigation (Kooyman & Kooyman 1995, Kirkwood & Robertson 1997). As both Royal and Rockhopper Penguins foraged in waters greater than 2000 m in depth (Hull *et al.* in press, also Chapters 5 and 6), this explanation is highly unlikely in these species. It is possible that some deep dives may be to avoid predators.

#### *Diving in relation to prey species*

The prey species of Royal and Rockhopper Penguins undergo diel migrations to 300 - 400 m during the day (Perissinotto & McQuaid 1992), making them potentially beyond the diving depth of these penguins. Both Royal and Rockhopper Penguins undertook the majority of dives and wiggles at depths from 30 - 50 m. As both species are obviously successfully obtaining these prey during dives (Chapter 8), either the descriptions of the diel migration and dispersion patterns of prey for some sites do not apply to Macquarie Island, or prey are closer to the surface in the polar frontal zone,

where these species forage (Hulley 1981, Gon & Heemstra 1990).

Deeper dives were made by Royal Penguins closer inshore during chick provisioning than during incubation. Foraging trip durations are far more restricted in their duration during guard and creche stages due to the need to regularly feed chicks, therefore, the availability of prey relatively close to the colonies at these times is important. As long foraging trips do not result in an overall increase in energy expenditure (Croxall & Davis 1990), presumably moving further offshore early in the breeding season when there is not the need to return to feed chicks, before beginning foraging has advantages such as a greater abundance or predictability of prey resources. Alternatively, prey may also not be available in close to colonies early in the breeding season.

The amount of diving activity did not change from guard to creche stage in either species. It might be expected that once both parents begin foraging for food to provision chicks (creche stage) that less diving would be required per individual (c.f. Croxall *et al.* 1993). As this did not occur it suggests that other demands dictated the degree of diving activity. The increased food requirements of chicks later in the breeding season, and the opportunity for parents to replenish lost body condition following guard stage, which is the most taxing period during the breeding season (Chapter 9), were probably important.

Diving behaviour of the penguins was constant across years, suggesting that either prey resources were located at similar depths and locations, or that the foraging behaviour

of these penguins is relatively fixed and that they opportunistically take prey which is encountered. The differences in diet found across the years (Chapter 8) suggests that the species are opportunistic in the prey taken, and that the interplay of prey availability and accessibility, maximising foraging efficiency during diving and the commitments at the nest are all important factors dictating the diving behaviour of these penguin species.

#### *Differences in use of the water column by Royal and Rockhopper Penguins*

A number of differences were found between Royal and Rockhopper Penguins some of which were probably linked to differing physiological capacities of these penguins. Rockhopper Penguins made more dives, spent a greater proportion of time at shallower depths, and ascended through the water column at a faster rate from shallower depths than did Royal Penguins. However, the time spent submerged was constant between the species, indicating that the two species have different diving strategies, but which result in the same time spent underwater. Being smaller, Rockhopper Penguins presumably have lower aerobic capacity and therefore undertake more, shorter dives than Royal Penguins, in order to minimise anaerobic respiration and its associated costs (c.f. Kooyman *et al.* 1992).

The parts of the water column used by both species overlapped, but the regions in which foraging apparently took place differed. Further, the region of the water column used by both species changed across the breeding season, but in a different manner. Royal Penguins foraged in progressively shallower water, and Rockhopper Penguins in



progressively deeper water as the season progressed.

The changes in foraging patterns detected across days of a foraging trip in Royal Penguins confirm that they are feeding further offshore than Rockhopper Penguins (Chapter 8). These differential foraging zones and the different use of the water column all indicate that these species are not overlapping greatly in the use of prey resources.

#### *Comparisons to Macaroni and Rockhopper Penguins at other sites*

Few comparisons can be made between Royal Penguin diving behaviour from this study and that of Macaroni Penguins, due to methodological differences between the studies. The two studies conducted at South Georgia (Croxall *et al.* 1988, 1993) examined diving only during creche stage, and all dives rather than just potential foraging dives. Hence, the observation that Royal Penguins undertook less dives per hour than Macaroni Penguins (Croxall *et al.* 1993) may be a function of data analysis.

The general diving patterns of both species were similar in the propensity for short and shallow dives, but a number of differences are apparent. Changes in diving behaviour across the breeding season have been found in Macaroni Penguins. At Heard Island penguins dived deeper as the breeding season progressed, and at South Georgia undertook less dives in creche stage (Croxall *et al.* 1988, 1993, Green *et al.* submitted). The increase in dive depth across the breeding season has been correlated with the quantity of euphausiids consumed, suggesting this behaviour is driven by the availability of prey (Green *et al.* submitted), whilst the reduction in dives during creche



stage has been attributed to both parents foraging and hence less food having to be caught by each member of a pair (Croxall *et al.* 1988, 1993).

Royal Penguins did not exhibit seasonal changes in diving activity throughout the breeding season, although they did in the parts of the water column used. Presumably, the diving behaviour of these species is governed to a large extent by the availability of prey in the local environment. As Royal Penguins only have two incubation shifts compared to three in Macaroni Penguins at South Georgia (Williams & Croxall 1991) they are able to undertake longer foraging trips and therefore exploit larger areas of ocean (Hull *et al.* in press, also Chapter 5 and 6).

Comparisons between the two previous Rockhopper Penguin studies and the current one can only be cursory due to methodological differences. Both previous studies were of short duration (Tremblay *et al.* 1997, Wilson *et al.* 1997), and different devices were used in the Amsterdam Island study (Tremblay *et al.* 1997). Changes in the depths varied between early and late creche stage at Amsterdam Island which was thought to be linked with diet changes during this period (Tremblay *et al.* 1997). Such changes were not detected in this study, or in diet studies of this species at Macquarie Island (Chapter 8). Again local conditions and prey resources are probably very important in determining the foraging ecology of these subspecies of Rockhopper Penguins at various localities.

In conclusion, the diving behaviour of Royal and Rockhopper Penguins during the

breeding season is dictated by the availability of prey and is also related to attempting to maximise foraging efficiency. Differences to other species or subspecies of crested penguins at other sites is most likely related to biotic and abiotic features of the local environment.

## 7.5 Summary

The diving behaviour and use of the water column was assessed in Royal and Rockhopper Penguins at Macquarie Island during the 1993/4, 1994/5 and 1995/6 breeding seasons. A total of 89 deployments of time depth recorders were made, from which 58 were used for analysis. The diving variables that were assessed were depth and duration of dives, time spent submerged, bottom time, wiggles and descent and ascent rates. Both species dived predominantly during daylight hours (4:00 - 21:00), which was probably related to them being visual predators. There was a bimodal pattern in diving, with less dives undertaken around midday. Both species dived to over 100 m and the longest durations of dives was 11 minutes. However, they rarely dived to these depths instead spending 72% and 86% respectively of their time at depths of less than 60 m, and in dives of short duration. This preponderance for shallow and short dives was most likely related to maximising foraging efficiency, as less anaerobic diving would occur, with its associated cost of removing lactic acid, and it would allow more time in the bottom part of a dive, which is probably more profitable foraging time. Differences were found between the species in the parts of the water column in which diving took place, with Royal Penguins spending more time at greater depths. Rockhopper Penguins undertook more dives than Royal Penguins, but spent a similar

amount of time underwater, which was probably related to their smaller size and lower aerobic capacity. It is concluded that whilst there was overlap in the regions of the water column used by both species, there was some segregation of this aspect of this part of the marine environment.

## **7.6 Acknowledgments**

I would like to thank Mary-Anne Lea, Jane Wilson, Kirsten Le Mar and Paul Scofield for assistance in the field, and Roger Hansworth for repairing devices. Thanks also to Mark Hindell for comments on a draft of the manuscript and to Leon Barmuta for statistical advice. Work was carried out under Macquarie Island special permits MI/34/94, MI/3/95 and MI/13/96.

# Appendix 7.1 Basic statistics of diving behaviour in Royal and Rockhopper Penguin individuals.

Stage 1: Incubation - males

Stage 2: Incubation - females

Stage 3: Guard

Stage 4: Creche

<i>Species</i>	<i>Stage</i>	<i>Duration of trip (days)</i>	<i>Depth mean (m)</i>	<i>Depth median (range)</i>	<i>Duration mean (mins.)</i>	<i>Duration median (range)</i>	<i>Time since last dive mean (mins.)</i>	<i>Time since last dive median (range)</i>	<i>Submerged time (% 24 hours)</i>	<i>n dives</i>
Royal	1	1	41.6	41 (6 - 103)	1.5	1.3 (0.4 - 3.0)	3.5	1.1 (0.03 - 103.4)	-	136
Penguin	1	7	44.5	41 (6 - 125)	1.8	1.9 (0.2 - 3.5)	1.7	0.8 (0.07 - 298.5)	39	1690
	1	8	37.0	34 (6 - 122)	1.8	1.8 (0.07 - 3.8)	1.7	0.8 (0.03 - 153.8)	42	2042
	1	7	59.8	68 (6 - 128)	2.0	2.2 (0.03 - 3.7)	2.7	0.9 (0.03 - 217.9)	32	1605
	1	8	31.2	26 (6 - 132)	1.6	1.6 (0.03 - 3.9)	2.0	0.8 (0.03 - 367.7)	31	2392
	1	7	33.3	31 (6 - 102)	1.7	1.6 (0.1 - 3.01)	3.0	0.6 (0.03 - 450.6)	26	1644
	1	7	31	28 (6 - 110)	1.5	1.6 (0.03 - 7.3)	2.6	0.8 (0.03 - 458.5)	28	1956
	2	17	42.4	34 (6 - 120)	1.7	1.9 (0.1 - 3.4)	1.0	0.8 (0.08 - 44.3)	-	1656
	2	17	34.8	24 (6 - 104)	1.8	1.8 (0.03 - 9.8)	1.2	0.7 (0.08 - 46.4)	-	1145
	2	17	35.0	28 (6 - 118)	1.7	1.8 (0.08 - 3.9)	1.2	0.7 (0.08 - 44.9)	-	1385

<i>Species</i>	<i>Stage</i>	<i>Duration of trip (days)</i>	<i>Depth mean (m)</i>	<i>Depth median (range)</i>	<i>Duration mean (mins.)</i>	<i>Duration median (range)</i>	<i>Time since last dive mean (mins.)</i>	<i>Time since last dive median (range)</i>	<i>Submerged time (% 24 hours)</i>	<i>n dives</i>
	2	13	35.2	26 (6 - 98)	1.6	1.7 (0.08 - 3.3)	0.9	0.7 (0.08 - 43.5)	-	954
	2	20	25.7	20 (6 - 96)	1.5	1.6 (0.08 - 3.2)	0.8	0.6 (0.08 - 17.5)	-	2007
	2	5	36.7	26 (6 - 104)	1.6	1.7 (0.03 - 3.1)	2.3	0.8 (0.03 - 226.5)	35	1005
	2	12	36.0	28 (6 - 130)	1.6	1.6 (0.03 - 3.4)	1.7	0.6 (0.03 - 320.2)	36	3722
	2	1	19.3	12 (6 - 80)	1.3	1.2 (0.03 - 2.7)	1.5	0.7 (0.03 - 108.9)	-	420
	3	4	43.8	40 (6 - 118)	2.0	2.1 (0.03 - 3.4)	1.8	0.6 (0.03 - 376.8)	51	1129
	3	7	35.1	31 (6 - 121)	1.9	1.9 (0.1 - 4.0)	2.8	0.5 (0.03 - 656.9)	42	1926
	3	5	29.0	22 (6 - 116)	1.7	1.7 (0.03 - 3.6)	2.8	0.6 (0.03 - 427.3)	38	1116
	3	4	28.4	22 (6 - 86)	1.6	1.6 (0.07 - 3.6)	1.4	0.5 (0.07 - 300.9)	57	1400
	3	4	33.8	32 (6 - 100)	1.9	2.0 (0.03 - 3.3)	2.6	0.7 (0.03 - 610.7)	37	1019
	3	4	27.0	20 (6 - 98)	1.7	1.8 (0.03 - 3.9)	2.4	0.6 (0.03 - 332.3)	45	868
	3	4	24.5	12 (6 - 128)	1.3	1.4 (0.03 - 3.1)	4.4	0.8 (0.03 - 329.4)	24	671
	3	4	34.4	32 (6 - 111)	2.0	2.1 (0.2 - 7.1)	3.0	0.7 (0.1 - 684.4)	41	788
	4	4	38.2	40 (6 - 104)	1.8	1.8 (0.03 - 3.1)	3.5	0.7 (0.2 - 504.1)	30	819
	4	4	26.0	20 (6 - 106)	1.4	1.5 (0.03 - 3.2)	2.4	0.7 (0.03 - 575.4)	36	1179



<i>Species</i>	<i>Stage</i>	<i>Duration of trip (days)</i>	<i>Depth mean (m)</i>	<i>Depth median (range)</i>	<i>Duration mean (mins.)</i>	<i>Duration median (range)</i>	<i>Time since last dive mean (mins.)</i>	<i>Time since last dive median (range)</i>	<i>Submerged time (% 24 hours)</i>	<i>n dives</i>
	4	12	27.8	19 (6 - 125)	1.6	1.5 (0.03 - 4.0)	2.8	0.6 (0.03 - 307.9)	36	3699
	4	4	45.8	48 (6 - 226)	2.1	2.4 (0.2 - 3.6)	2.0	0.7 (0.03 - 237.5)	55	807
	4	4	33.0	29 (6 - 101)	1.8	1.8 (0.2 - 3.3)	1.9	0.6 (0.07 - 345.5)	51	1234
	4	7	37.8	36 (6 - 130)	1.8	1.9 (0.1 - 7.5)	2.9	0.7 (0.03 - 1372.7)	42	1938
Rockhopper	1	5	33.6	30 (6 - 86)	1.3	1.4 (0.03 - 2.8)	1.3	0.5 (0.03 - 311.3)	33	1883
Penguin	1	4	32.8	30 (6 - 100)	1.5	1.6 (0.03 - 2.6)	1.4	0.7 (0.03 - 260.3)	31	1463
	1	3	39.2	46 (6 - 86)	1.3	1.5 (0.03 - 2.5)	1.4	0.7 (0.03 - 340.3)	43	1278
	1	3	34.7	40 (6 - 78)	1.4	1.5 (0.03 - 2.6)	2.7	0.7 (0.03 - 450.8)	29	846
	1	6	23.8	10 (6 - 78)	1.1	0.9 (0.03 - 2.6)	1.8	0.6 (0.03 - 411.6)	29	2205
	1	3	38.0	38 (6 - 88)	1.3	1.3 (0.03 - 2.6)	1.3	0.6 (0.03 - 167.3)	33	1242
	1	5	17.8	11 (6 - 69)	1.1	1.0 (0.2 - 2.6)	1.2	0.3 (0.03 - 261.6)	40	2539
	2	10	21.7	16 (6 - 94)	1.2	1.2 (0.2 - 2.6)	1.0	0.5 (0.08 - 41.8)	-	1285
	2	18	27.1	20 (6 - 80)	1.4	1.3 (0.03 - 5.5)	0.9	0.5 (0.08 - 22.2)	-	1391
	2	7	16.4	13 (6 - 51)	0.9	0.9 (0.2 - 5.7)	1.2	0.4 (0.03 - 128.7)	34	3853
	2	2	27.7	21 (6 - 73)	1.3	1.2 (0.2 - 3.4)	1.9	0.5 (0.03 - 149.0)	-	703



<i>Species</i>	<i>Stage</i>	<i>Duration of trip (days)</i>	<i>Depth mean (m)</i>	<i>Depth median (range)</i>	<i>Duration mean (mins.)</i>	<i>Duration median (range)</i>	<i>Time since last dive mean (mins.)</i>	<i>Time since last dive median (range)</i>	<i>Submerged time (% 24 hours)</i>	<i>n dives</i>
	2	8	32.2	30 (6 - 91)	1.3	1.3 (0.1 - 4.8)	2.7	0.6 (0.07 - 702.5)	34	2388
	2	7	22.2	16 (6 - 64)	1.3	1.2 (0.2 - 3.0)	3.1	0.5 (0.03 - 906.4)	33	2088
	2	1	14.9	10 (6 - 50)	0.7	0.7 (0.03 - 1.8)	2.0	0.4 (0.03 - 101.8)	-	787
	2	2	25.0	20 (6 - 68)	1.0	1.1 (0.07 - 2.0)	1.8	0.6 (0.03 - 218.0)	22	1028
	3	3	39.8	44 (6 - 70)	1.6	1.9 (0.03 - 2.4)	5.0	0.8 (0.02 - 1087.1)	-	492
	3	7	35.6	40 (6 - 76)	1.4	1.6 (0.07 - 2.5)	1.7	0.5 (0.03 - 895.3)	12	2614
	3	4	35.2	38 (6 - 76)	1.6	1.8 (0.03 - 2.5)	1.8	0.6 (0.03 - 514.4)	46	1374
	3	7	27.8	20 (6 - 94)	1.3	1.1 (0.03 - 2.6)	1.1	0.4 (0.03 - 287.6)	50	3700
	3	16	27.0	20 (6 - 82)	1.2	1.2 (0.07 - 9.7)	1.9	0.5 (0.03 - 819.5)	52	6930
	3	4	28.8	30 (6 - 68)	1.3	1.5 (0.03 - 4.4)	2.5	0.5 (0.03 - 439.1)	40	1109
	3	4	26.5	24 (6 - 64)	1.3	1.3 (0.03 - 3.5)	1.8	0.4 (0.03 - 309.1)	38	1365
	4	4	36.4	38 (6 - 86)	1.6	1.7 (0.03 - 2.4)	2.1	0.6 (0.03 - 631.0)	45	1301
	4	4	34.2	38 (6 - 80)	1.3	1.5 (0.03 - 2.5)	2.2	0.8 (0.03 - 374.4)	34	1245
	4	14	32.2	28 (6 - 90)	1.5	1.5 (0.03 - 11.1)	3.3	0.5 (0.03 - 1200.4)	31	3987
	4	15	37.2	40 (6 - 104)	1.6	1.8 (0.1 - 8.9)	2.8	0.7 (0.03 - 1194.1)	36	4732

<i>Species</i>	<i>Stage</i>	<i>Duration of trip (days)</i>	<i>Depth mean (m)</i>	<i>Depth median (range)</i>	<i>Duration mean (mins.)</i>	<i>Duration median (range)</i>	<i>Time since last dive mean (mins.)</i>	<i>Time since last dive median (range)</i>	<i>Submerged time (% 24 hours)</i>	<i>n dives</i>
	4	4	41.0	46 (6 - 96)	1.7	1.9 (0.03 - 3.0)	1.7	0.6 (0.1 - 478.6)	51	1487
	4	5	37.3	40 (6 - 86)	1.4	1.6 (0.03 - 2.5)	3.0	0.5 (0.03 - 1977.2)	37	1539
	4	5	14.6	11 (6 - 45)	0.8	0.7 (0.03 - 1.8)	28.9	0.5 (0.03 - 2411.2)	4.2	245

## Chapter 8

### **The diet of Royal and Rockhopper Penguins during the breeding season: a species and inter-annual comparison**

#### **8.1 Introduction**

Penguins are the most abundant seabird in the Southern Ocean, and are therefore important components of the marine ecosystem (Prevost 1981). Determining how they interact with biotic and abiotic aspects of this environment is essential to understanding their ecology. An integral part of such an examination is determining their diet.

Of particular interest in diet studies is the issue of overlap in resource use by sympatrically breeding species. It is generally assumed that food resources are limited around colonies, particularly during the breeding season when demand for these resources is presumably higher due to the requirements of chicks, and foraging ranges restricted by commitments at the nest (Ashmole 1971, Croxall & Prince 1980a, Furness & Birkhead 1984). This demand may be further elevated when two or more ecologically similar species breed sympatrically.

The co-existence of sympatrically breeding species may require the partitioning of food resources to avoid competition between species (Croxall & Prince 1980a, Cooper *et al.* 1990, Hindell *et al.* 1995). The issue of overlap in resource use has been explored to some degree in some groups of penguins, one being the crested or eudyptid penguins

(Croxall & Prince 1980a, Adams & Brown 1989, Klages *et al.* 1989, Cooper *et al.* 1990, Hindell *et al.* 1995).

The crested penguin group comprises six species, with Macaroni Penguins *Eudyptes chrysolophus* arguably the most numerically abundant species in the subantarctic region (Wilson 1983). Diet of the subantarctic crested penguins has been examined at Marion Island, Crozet, South Georgia, Heard and Macquarie Islands, with the major prey items being euphausiids, myctophid fish and crustaceans (Ealey 1954, Croxall & Prince 1980b, Williams & Laycock 1981, Horne 1985, Brown & Klages 1987, Hindell 1988a, b, Ridoux 1988, Adams & Brown 1989, Klages *et al.* 1989, Brown *et al.* 1990, Adams *et al.* 1993, Green 1993, Ridoux 1994).

Royal *E. schlegeli* and Rockhopper *E. chrysocome* Penguins, breed sympatrically on Macquarie Island. Royal Penguins are closely-related to Macaroni Penguins and are endemic to Macquarie Island, where they are the most abundant species of penguin, with approximately 850,000 breeding pairs (Copson & Rounsevell 1987). Royal and Rockhopper Penguins are taxonomically and ecologically very similar, and often found nesting in close proximity to each other.

The diet of these species has been examined conducted in three separate, single-year studies (Horne 1985, Hindell 1988a, b). Two of these (Hindell 1988a, b), covered one entire breeding season, but the third was carried out only during late creche stage (Horne 1985). Therefore, a multi-year study comparing the variability in diet between

these species at one site on Macquarie Island has not been undertaken. Nor has a direct comparison been made of the diet of individuals from spatially close colonies. Such an examination would allow a determination of the degree of dietary difference in species accessing the same sector of ocean. The purpose of this study was to compare the diet of Royal and Rockhopper Penguins from colonies in close proximity to each other. The study was conducted over three years in order to detect inter-annual variability.

## 8.2 Materials and methods

### *Diet sampling*

The diet of Royal and Rockhopper Penguins was assessed during the 1993/4, 1994/5 and 1995/6 breeding seasons (Chapter 9) using stomach flushing (lavaging, or water-offloading) (c.f. Wilson 1984). Royal Penguins were sampled at Sandy Bay (54° 33' S 158°, 54' E) and Rockhopper Penguins at Brothers Point, the southern end of Sandy Bay (0.75 km away). Penguins were captured by hand on the beach as they returned from a foraging trip, weighed, allocated to sex using bill depth and length (Hull in press, also Chapter 2), and flushed.

A flexible 5 mm diameter catheter was inserted into the stomach to within approximately one cm of the bottom, and the bird's stomach slowly filled with freshwater using a hand pump. All water was heated to 20°C to minimise the potential thermal load of introducing cold water into the bird's body core (Wilson & Culik 1991). Once full, the bird was inverted and its abdomen and throat massaged until all water and food was removed. Flushing was repeated until clean water was returned from the bird.

During the incubation period this usually required one flush, and during the chick feeding stage, four to five flushes. Samples were sieved through a 0.5 mm mesh in the field to remove excess water, and then frozen at -20 °C until analysis. No bird was sampled more than once during a breeding season; flushed individuals were recognised by marking the breast feathers with a small circle of paint, which remained until the feathers were moulted at the end of the breeding season.

Sampling was undertaken during the four main stages in the breeding season (male foraging trip during incubation, female foraging trip during incubation, guard and creche) (Table 8.1). The sampling regime was reduced slightly in the 1995/6 season with only one sampling session during guard, and two during creche stage, in an attempt to reduce the number of penguins that were flushed. No samples were collected from female Rockhopper Penguins when they returned from their incubation foraging trip in the 1995/6 season.

Only breeding birds were sampled. Non-breeding Royal Penguins do not return to the island until late November, whilst non-breeding Rockhopper Penguins return early December each year (Warham 1963, Carrick 1972). After this, breeding birds were identified by the presence of a brood patch, and by their full stomachs (c.f. Robertson *et al.* 1994a). Penguins that contained no food during the chick provisioning stages were excluded from the data set, as they were most likely non-breeders.



**Table 8.1.** The number of Royal and Rockhopper (RH) Penguins from which diet samples were collected (\* only females forage at this time. See Chapter 9 for description of breeding timetable). Those marked with a line (-) not sampled

Stage	1993/4	1993/4	1994/5	1994/5	1995/6	1995/6
	Royals	RH	Royals	RH	Royals	RH
Male return	17	3	17	5	10	5
Female return	13	13	13	12	10	13
Male incubation	5	3	8	3	8	9
Female incubation	5	5	5	5	9	-
Early guard *	15	10	17	13	10	9
Late guard *	10	6	16	8	-	-
Early creche	20	15	18	11	10	9
Mid creche	10	16	10	18	-	-
Late creche	19	20	19	16	10	9
Total (540)	114	91	123	91	67	54

#### *Identification of prey items*

The complete samples were sorted into hard and soft parts by elutriation until the hard parts remained at the bottom of the container. The supernatant was then sieved through a 0.5 mm sieve, allowed to sit until water ceased to drip from it, and then wet-weighted on a top-loading balance (to 0.1 g). Both the hard and soft parts of the sample were sorted into taxonomic groups, and each item identified to the lowest taxonomic level possible.

### *Crustaceans*

Identification of crustaceans was made using collections held at the Australian Antarctic Division and Kirkwood (1982). Whole crustacean bodies, where present, and pairs of eyes in digested samples, were counted to determine the number of individuals consumed. Total lengths of any undigested crustaceans were measured using a compound microscope fitted with a graticule (magnification 16x), which was later calibrated to mm. Eyes were not used to determine standard length as they were always ruptured.

### *Cephalopods*

Squid were identified from whole bodies using Fisher & Hureau (1985b), or from lower beaks, which were present in the samples as loose beaks (free) or in buccal masses, using Clarke (1986). Numbers of squid were determined by counting lower beaks. The mantle lengths and masses of individuals were calculated from mantle lengths of whole squid (Fisher & Hureau 1985b), or regressions of mantle lengths from the Lower Rostral Lengths (LRL) of beaks (measured on a microscope, as above) (Clarke 1986, Rodhouse *et al.* 1990). Beaks were categorised according to their degree of erosion using the following criteria:

1. Removed from the buccal mass
2. Free in the sample, with no evidence of erosion, wings and all components undamaged
3. Free in the sample, with some evidence of erosion (the margins of wings and lateral walls showing some damage)

4. Free in the sample, with severe erosion (wings, hood or lateral walls lost, most distinguishing features destroyed).

Cephalopod beaks have been found to accumulate in the gut of seabirds (e.g. for up to 50 days in Shy Albatrosses *Diomedea cauta*, Furness *et al.* 1984), creating a problem of over-estimating the number of squid when re-constructing diet (Furness *et al.* 1984, Gales 1988b). Over-estimation of squid was minimised in this study by estimating the percentage number and percentage mass of squid only using beaks of erosion category one and two.

### *Fish*

Fish were identified from whole bodies and otoliths (Fisher & Hureau 1985a, Williams & McEldowney 1990). Jaw bones were not used as they were less commonly found in the samples than otoliths. The number of individuals was determined by counting pairs of otoliths. Each otolith was categorised according to the following erosion criteria (Robertson *et al.* 1994a):

1. Removed from the fish skull
2. No evidence of erosion
3. Some erosion evident, but all major features intact
4. Clear signs of erosion, identification becoming difficult
5. Featureless disk, very difficult to identify.

Standard lengths of fish were determined by measuring the length of whole, undigested

fish, or from regressions of otolith length (Williams & McEldowney 1990) of otoliths from erosion categories one and two. One to two hours of digestion of fish erodes otoliths sufficiently in Little Penguins *Eudyptula minor* to result in an under-estimate of the size of fish (Gales 1988b). The otoliths that were measured were predominantly taken from the skull of fish, as free otoliths in the samples were rarely in a sufficiently uneroded condition for measurement.

### *Composition of diet*

Diet was described in terms of frequency of occurrence, percentage by number and percentage by mass, to allow for the various biases of each of these techniques (Hyslop 1980, Duffy & Jackson 1986). When a sample was too digested to directly measure and weigh components, it was reconstructed from the number and size of otoliths, cephalopod beaks of erosion category one and two, and numbers of crustaceans. As otoliths were rarely found in samples that had no fleshy parts, it is likely that they were digested quickly (within four hours in African Penguins *Spheniscus demersus* [Davies 1956], 12 hours in Little Penguins [Gales 1988b], and 24 hours in Yellow-eyed Penguins *Megadyptes antipodes* depending on the size of the otolith and activity of the penguin [van Heezik & Seddon 1989]) and did not accumulate as squid beaks do. Therefore, the reconstruction of the fish component of the diet was made from otoliths of all erosion categories (although estimates of fish lengths were only made from otoliths of erosion category one and two). When a direct measure of the size and/or mass of a prey item could not be made, it was extrapolated from the average size and mass found in undigested samples collected at the same time.

*Degree of digestion of samples*

Soft tissue in each sample was scored for its degree of digestion, using an index of digestion based on Robertson *et al.* (1994a):

1. Heavily digested - samples finely textured, few lumps
2. Moderately digested - samples more fibrous, bones and flesh apparent
3. Lightly digested - coarsely textured, fish and/or squid and/or euphausiid parts evident, otoliths visible in food mass.

Degree of digestion was only assessed during the stages from female incubation trip to the end of creche, as little food was brought ashore before chicks hatch (see below).

The two major prey components, fish and euphausiids, were assessed separately as they appeared digested to different extents.

*Statistical analyses*

Degree of digestion between species, years and stages in the breeding season was assessed using Chi-squared ( $\chi^2$ ) analysis. Due to small samples sizes and the risk of biased  $\chi^2$  (Zar 1984), weekly categories with less than 5 counts (fish in 1995/6, and euphausiids in 1994/5 and 1995/6) were grouped into two larger categories comprising early (weeks 1 - 3), and late in chick provisioning (weeks 4 - 6).

The quantity of food brought ashore as a percentage of body mass minus food (arcsine transformed) was compared between species and stages, using two-way ANOVAs; and across the years within each species and stage using one-way ANOVAs. Sexual

differences were examined during creche stage using two-tailed *t*-tests.

Dietary overlap between species, stages and years was assessed using percentage by mass, as frequency of occurrence over-estimates overlaps in diet (Hartley 1948). Mass was also a preferable measure due to the different size classes found in a number of prey species (see below) (Duffy & Jackson 1986). The data were separated into pre- and post-hatching as the quantity of food brought ashore during the two periods differed substantially (see below).

Overlap in diet between species, years and stages in the breeding season was assessed using an analysis of similarity. This analysis is similar to ANOVA, but the test statistics use a Monte-Carlo type randomisation and a symmetric association matrix (Clark & Green 1988). The advantage of this form of analysis over previous techniques such as version of Morisita's Index (see Diamond 1983) is that it allows a statistical comparison of the differences and does not just rely on trends (Diamond 1983).

For both pre- and post-hatching diets the data were categorised into groups according to species, year and flushing session (i.e. stage in breeding season). This resulted in 18 groups in pre-hatching diet, and 31 groups in post-hatching diet. The variability between these groups was compared using an analysis of similarity with 1000 randomisations, based on a Bray-Curtis association matrix. To determine where the differences lay between groups, a cluster analysis was performed. Multi-dimensional scaling was used to represent these points in space and their relationship to one another.



The dietary items that significantly contributed to the clusters were determined from the correlation coefficients derived from the analysis of similarity.

### 8.3 Results

#### *Quantity of food brought ashore*

The maximum food brought ashore by a Royal Penguin was 980 g, and by a Rockhopper Penguin 485 g. The average quantity of food varied with stage in the breeding season (Table 8.2).

There were some significant differences in the quantity of food brought ashore between the years (Table 8.2), with Royal Penguins bringing more food ashore in the 1994/5 season during male incubation, and less during early guard and late creche than the other seasons. Rockhopper Penguins brought more food ashore during the 1993/4 season in late guard and early creche than the other seasons (Table 8.2).

Significant differences in food as a percentage of body mass were found between the species during 1993/4 but not during the other years (1993/4  $F_{1,197} = 22.0$ ,  $P < 0.0001$ ; 1994/5  $F_{1,187} = 0.3$ ,  $P > 0.05$ ; 1995/6  $F_{1,99} = 13.1$ ,  $P < 0.0001$ ), with Rockhopper Penguins bringing less food ashore than Royal Penguins during 1993/4 (Table 8.2).

**Table 8.2** Quantity of food (g) (mean  $\pm$  standard deviation) brought ashore by Royal and Rockhopper Penguins during each stage and year.Food as a percentage of body mass in parentheses. *F*, *t* and *P* values are given. **Significant differences between years in bold**

Stage	Royal Penguins				Rockhopper Penguins			
	1993/4	1994/5	1995/6	Statistical comparisons	1993/4	1994/5	1995/6	Statistical comparisons
Male return	1.5 $\pm$ 3.6 (0.03 $\pm$ 0.07)	<b>2.8 <math>\pm</math> 8.0</b> (0.05 $\pm$ 0.1)	11.5 $\pm$ 16.4 (0.2 $\pm$ 0.3)	<b>F<sub>2,41</sub> = 3.7</b> <b>P &lt; 0.03</b>	2.7 $\pm$ 4.7 (0.08 $\pm$ 0.1)	18.0 $\pm$ 23.3 (0.5 $\pm$ 0.7)	4.1 $\pm$ 5.0 (0.1 $\pm$ 0.1)	F <sub>2,10</sub> = 1.3 P > 0.05
Female return	4.1 $\pm$ 8.6 (0.08 $\pm$ 0.2)	0.6 $\pm$ 1.2 (0.01 $\pm$ 0.02)	2.4 $\pm$ 4.4 (0.04 $\pm$ 0.08)	F <sub>2,33</sub> = 1.4 P > 0.05	12.5 $\pm$ 14.9 (0.4 $\pm$ 0.4)	1.6 $\pm$ 2.5 (0.04 $\pm$ 0.7)	10.2 $\pm$ 10.6 (0.3 $\pm$ 0.3)	<b>F<sub>2,35</sub> = 3.5</b> <b>P &lt; 0.04</b>
Incubation - males	4.5 $\pm$ 1.0 (0.001 $\pm$ 0.002)	35.1 $\pm$ 39.4 (0.6 $\pm$ 0.6)	9.1 $\pm$ 10.0 (0.2 $\pm$ 0.2)	F <sub>2,18</sub> = 3.6 P > 0.05	25.0 $\pm$ 32.3 (0.6 $\pm$ 0.8)	3.5 $\pm$ 6.1 (0.08 $\pm$ 0.1)	1.5 $\pm$ 3.3 (0.04 $\pm$ 0.08)	F <sub>2,12</sub> = 3.6 P > 0.05
Incubation - females	67.3 $\pm$ 51.3 (1.3 $\pm$ 1.0)	71.0 $\pm$ 55.9 (1.3 $\pm$ 1.1)	104.2 $\pm$ 52.7 (2.0 $\pm$ 1.0)	F <sub>2,16</sub> = 0.8 P > 0.05	42.5 $\pm$ 14.1 (1.5 $\pm$ 0.4)	34.4 $\pm$ 21.1 (1.05 $\pm$ 0.6)	-	F <sub>1,8</sub> = 1.3 P > 0.05
Guard - early	288.7 $\pm$ 150.3 (6.7 $\pm$ 3.6)	193.0 $\pm$ 110.5 (4.2 $\pm$ 2.5)	269.1 $\pm$ 98.5 (6.4 $\pm$ 2.5)	F <sub>2,39</sub> = 3.1 P > 0.05	151.3 $\pm$ 54.5 (5.7 $\pm$ 2.0)	138.1 $\pm$ 65.4 (4.8 $\pm$ 2.4)	150.5 $\pm$ 79.0 (5.2 $\pm$ 2.9)	F <sub>2,29</sub> = 0.4 P > 0.05
Guard - late	487.6 $\pm$ 204.8 (11.3 $\pm$ 5.2)	422.2 $\pm$ 131.6 (9.2 $\pm$ 2.8)	-	F <sub>1,24</sub> = 1.9 P > 0.05	309.6 $\pm$ 117.3 (13.2 $\pm$ 5.3)	144.7 $\pm$ 72.8 (5.9 $\pm$ 3.0)	-	<b>F<sub>1,12</sub> = 10.7</b> <b>P &lt; 0.007</b>
Creche - early	501.0 $\pm$ 291.2 (10.9 $\pm$ 6.4)	437.7 $\pm$ 126.8 (8.9 $\pm$ 2.8)	381.7 $\pm$ 90.2 (7.9 $\pm$ 1.9)	F <sub>2,45</sub> = 1.8 P > 0.05	263.9 $\pm$ 113.1 (11.4 $\pm$ 5.2)	151.1 $\pm$ 101.6 (5.8 $\pm$ 4.2)	116.0 $\pm$ 76.9 (4.2 $\pm$ 2.7)	<b>F<sub>2,32</sub> = 9.5</b> <b>P &lt; 0.001</b>
Creche - mid	492.4 $\pm$ 84.4 (10.0 $\pm$ 1.6)	587.5 $\pm$ 120.2 (11.9 $\pm$ 2.7)	-	F <sub>1,19</sub> = 4.0 P > 0.05	233.2 $\pm$ 152.3 (9.3 $\pm$ 7.0)	156.3 $\pm$ 67.4 (5.5 $\pm$ 2.6)	-	<b>F<sub>1,32</sub> = 4.5</b> <b>P &lt; 0.03</b>
Creche - late	544.2 $\pm$ 135.7 (11.1 $\pm$ 2.7)	410.8 $\pm$ 131.6 (8.4 $\pm$ 2.9)	468.8 $\pm$ 89.8 (9.4 $\pm$ 2.0)	<b>F<sub>2,44</sub> = 5.1</b> <b>P &lt; 0.01</b>	141.3 $\pm$ 86.7 (5.7 $\pm$ 3.4)	161.3 $\pm$ 67.6 (5.5 $\pm$ 2.2)	166.6 $\pm$ 126.3 (5.6 $\pm$ 4.3)	F <sub>2,42</sub> = 0.01 P > 0.05

Extrapolating from the quantity of food brought ashore during each stage of the breeding season and assuming 22 foraging trips for female Royal Penguins, the average penguin brought ashore 8458.2 g of food in a season, male Royal Penguins (12 foraging trips) 4870.5 g, female Rockhopper Penguins 3676.1 g, and male Rockhopper Penguins 1778.8 g.

There were no significant differences in the quantity of food brought ashore during creche stage between males and females in either species (early creche: Royal Penguins  $t = 1.7$ ,  $P > 0.05$ , Rockhopper Penguins  $t = 0.09$ ,  $P > 0.05$ ; mid-creche: Royal Penguins  $t = 1.0$ ,  $P > 0.05$ , Rockhopper Penguins  $t = 1.1$ ,  $P > 0.05$ ; late creche: Royal Penguins  $t = 0.4$ ,  $P > 0.05$ , Rockhopper Penguins  $t = 1.6$ ,  $P > 0.05$ ).

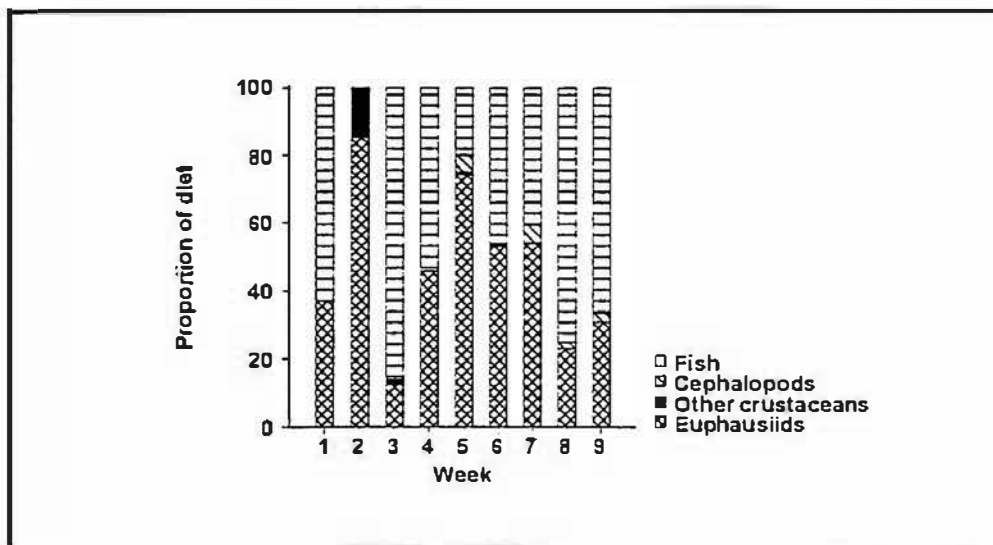
### *Diet*

A total of 553,981 prey items from 38 taxa (species or species group) were recorded during this study. They consisted of: 3 taxa of euphausiids, 7 taxa of crustaceans other than euphausiids, 16 squid taxa, and 12 fish taxa. The frequency of occurrence of prey items is given in Appendix 8.1, percentage by mass and percentage by number of prey are given in Appendix 8.2, and a summary in Table 8.3. The same prey taxa were taken across the breeding season, but pre-hatching diet consisted of fewer prey items and a lower diversity of taxa (18) than did post-hatching diet (29) (Appendices 8.1 and 8.2).

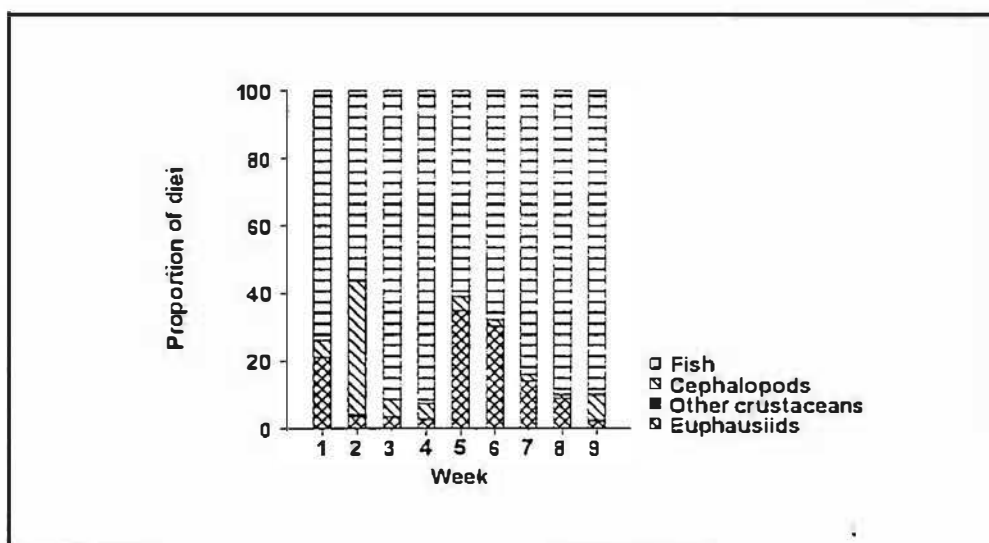
The proportions of prey items consumed, although variable across the season (Figs. 8.1 and 8.2), did not differ significantly (see dietary overlap).

**Fig. 8.1** The proportion of major prey groups consumed by Royal Penguins across the breeding season

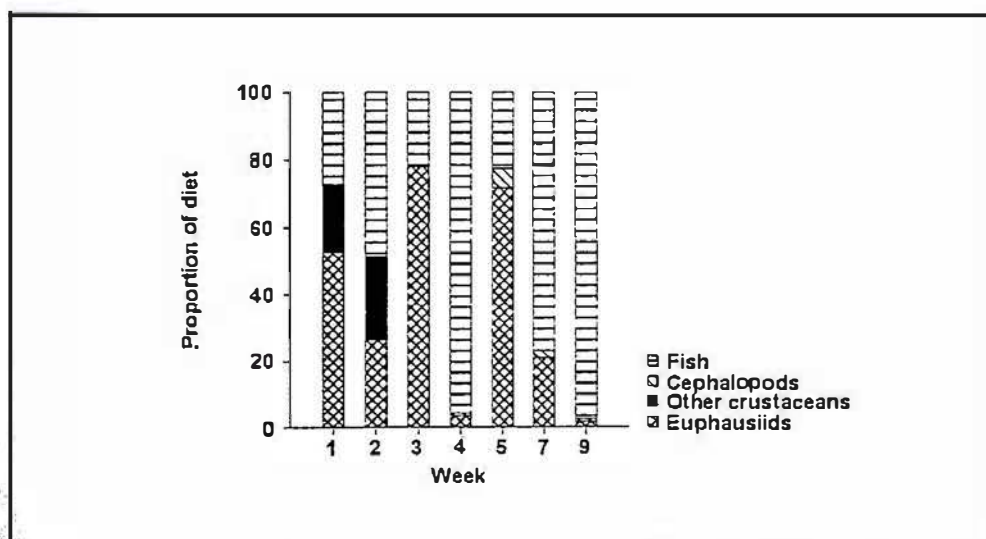
1993/4



1994/5



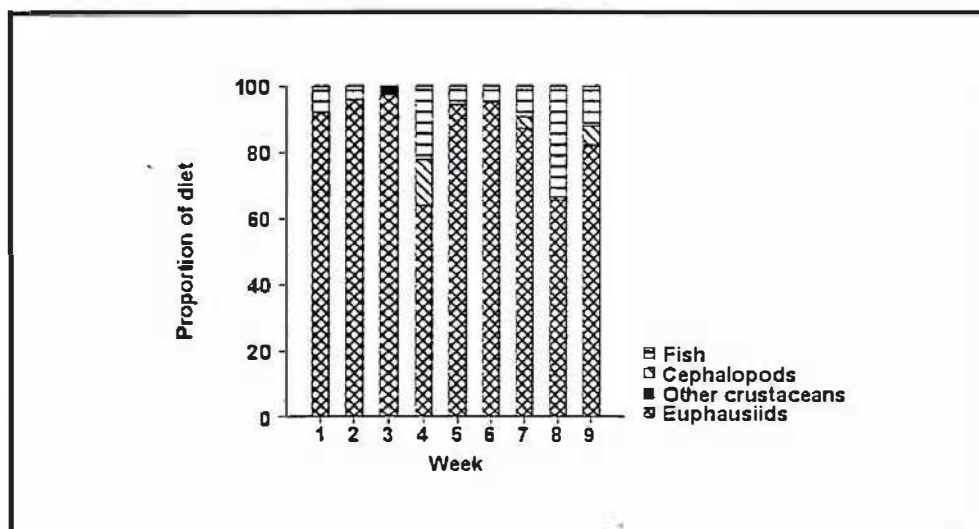
1995/6



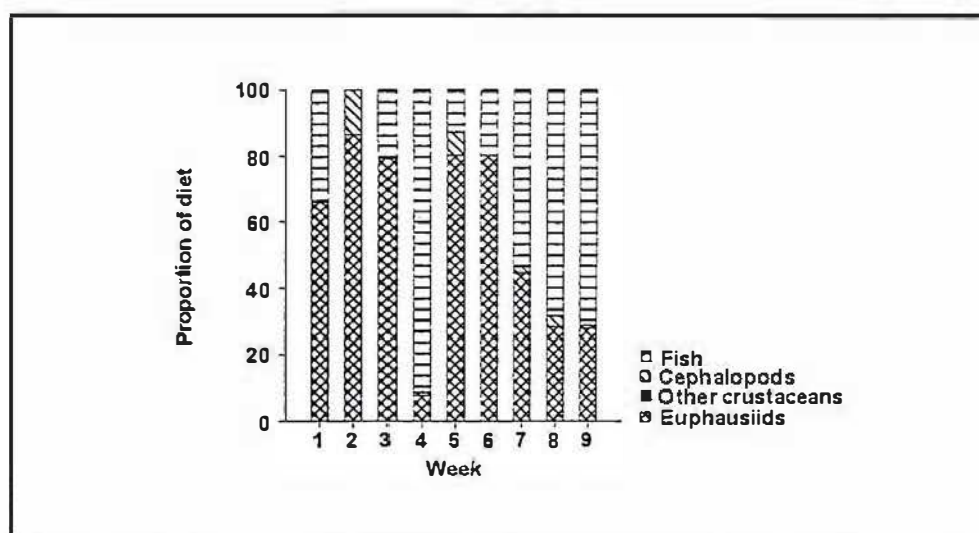
**Fig. 8.2** The proportion of major prey groups consumed by Rockhopper Penguins across the breeding season



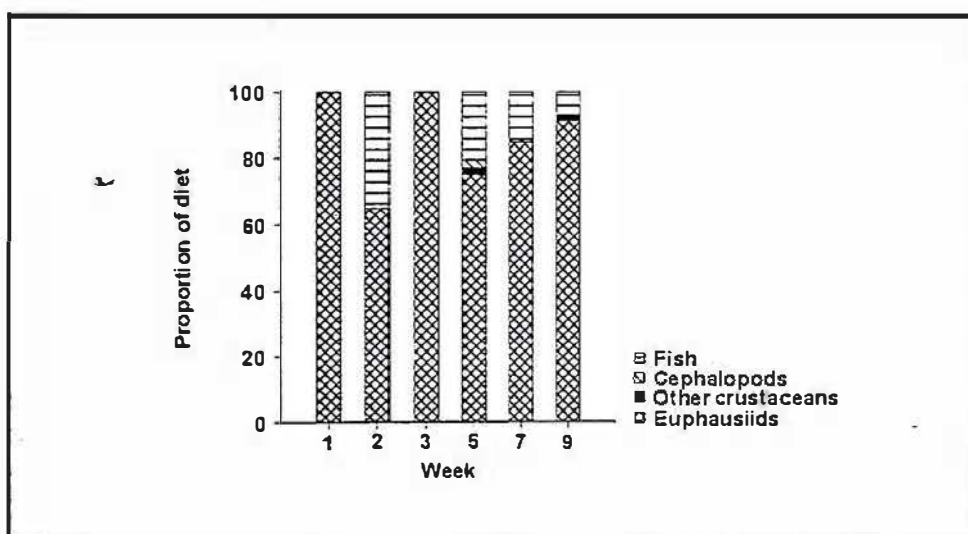
1993/4



1994/5



1995/6



**Table 8.3** Summary of the contribution of major prey groups to diet of Royal and Rockhopper Penguins (mean  $\pm$  standard deviation), listed by frequency of occurrence, percentage by mass and percentage by number. Only squid beaks from erosion classes one and two were used for estimates of percentage by mass and percentage by number

<i>Prey groups and dominant species</i>	<i>Royal Penguins</i>			<i>Rockhopper Penguins</i>		
	<i>Frequency of occurrence</i>	<i>% by mass</i>	<i>% by number</i>	<i>Frequency of occurrence</i>	<i>% by mass</i>	<i>% by number</i>
<u>Euphausiids</u>	75.2	26.7 $\pm$ 36.6	49.6 $\pm$ 40.6	86.1	59.8 $\pm$ 42.5	71.9 $\pm$ 39.4
<i>Euphausia vallentini</i>	65.0	20.3 $\pm$ 32.4	45.0 $\pm$ 40.6	79.3	56.7 $\pm$ 43.3	69.0 $\pm$ 40.9
<u>Other crustaceans</u>	21.0	1.4 $\pm$ 11.5	1.6 $\pm$ 11.6	19.5	1.0 $\pm$ 6.9	0.7 $\pm$ 6.7
<i>Themisto gaudichaudii</i>	1.3	4.4 $\pm$ 18.9	1.2 $\pm$ 10.1	0.2	3.0 $\pm$ 15.9	0.2 $\pm$ 1.7
<u>Cephalopods</u>	67.4	3.4 $\pm$ 12.1	0.5 $\pm$ 6.0	48.3	2.2 $\pm$ 10.5	0.8 $\pm$ 8.1
<u>Fish</u>	77.3	51.7 $\pm$ 42.6	29.9 $\pm$ 6.0	69.9	24.7 $\pm$ 36.3	15.3 $\pm$ 29.0
<i>Krefftichthys anderssoni</i>	67.8	43.9 $\pm$ 40.7	26.5 $\pm$ 32.3	51.3	18.5 $\pm$ 32.6	11.6 $\pm$ 26.6
<i>Electrona carlsbergi</i>	18.1	4.1 $\pm$ 13.4	1.3 $\pm$ 7.8	5.9	2.2 $\pm$ 11.5	0.3 $\pm$ 1.6
<i>E. subaspera</i>	10.5	2.0 $\pm$ 9.1	0.2 $\pm$ 2.4	1.3	1.0 $\pm$ 9.1	0.1 $\pm$ 1.0

Of the three taxa of euphausiids found in the diet, *Euphausia vallentini* was the most common (Table 8.3, Appendices 8.1 and 8.2). Only 331 of the 477,847 specimens of Euphausiids could be measured due to their degree of digestion (Table 8.4). There was an indication of two size classes in the euphausiids consumed, but there were insufficient undigested samples to test this statistically.

**Table 8.4** The standard length of euphausiids in diet samples. Mean  $\pm$  SD (range) are given

<i>Species</i>	<i>n</i>	<i>Standard length (mm)</i>
<i>Euphausia vallentini</i>	287	25.0 $\pm$ 0.3 (8.0 - 30.0)
<i>Thysanoessa gregaria</i>	44	18.0 $\pm$ 2.0 (14.0 - 23.0)

Of the seven taxa of crustaceans other than euphausiids, *Themisto gaudichaudii* was the most common (Table 8.3, Appendices 8.1 and 8.2). Due to the degree of digestion, none could be measured for length or mass, so these variables were extrapolated from other studies (G. Hosie, Australian Antarctic Division, unpubl. data). The degree of digestion also prevented measurements of eyes of crustaceans to which regressions of standard length could have been applied. The extrapolations from other studies may have resulted in less precise estimates of the percentage by mass contribution to the diet, as these penguins may not have been consuming crustaceans of various size classes in the same proportions as present in the Southern Ocean (as found in Krill *Euphausia superba* consumed by Macaroni Penguins, Hill *et al.* 1996). However, the resultant

error was unavoidable and was most likely small due to the minor dietary component this prey group constituted.

A total of 2021 squid of 16 taxa were recorded (Table 8.3, Appendices 8.1 and 8.2), with 1757 of these (86.9%) accumulated beaks. The proportion of accumulated to fresh beaks was higher during weeks one to three (prior to the hatching of chicks) than weeks 4 - 9 (Table 8.5).

**Table 8.5** The number and percentage of accumulated beaks in the samples before (weeks 1 - 3) and after (weeks 4 - 9) chicks hatched (all significantly different,  $P < 0.0001$ )

Season and week	Royal Penguins	$\chi^2_1$	Rockhopper Penguins	$\chi^2_1$
1993/4 weeks 1 - 3	238 (99.6)	121.7	72 (100)	37.0
weeks 4 - 9	27 (36.5)		12 (38.7)	
1994/5 weeks 1 - 3	630 (93.1)	262.0	164 (98.8)	76.2
weeks 4 - 9	20 (20.8)		25 (49)	
1995/6 weeks 1 - 3	314 (100)	166.4	242 (100)	121.7
weeks 4 - 9	9 (18.8)		4 (36.4)	

A number of the estimated lengths and masses of squid from regressions of LRL were improbable (Table 8.6), and reflect the fact that the regressions used were obtained from larger squid, which do not provide accurate estimates of small squid, and regressions for small squid are not currently available (P. Rodhouse pers. comm.). The estimates of contribution to the diet by squid were, therefore, imprecise. A further complication

is that mantle lengths of *Moroteuthis ingens* are sexually dimorphic, which is not reflected in the LRL, resulting in the need for sex-specific regressions (Jackson 1995). It was not possible to determine the sex of squid in this study, hence extrapolated mantle lengths of *M. ingens* from other *Moroteuthis* sp. were probably, at times, inaccurate. Again, some errors have probably occurred when estimating the percentage by mass contribution to the diet, but as cephalopods constituted a small part of the diet the resultant errors were probably minor.

Twelve taxa of fish were found in the diet of these species of penguin. The most important were myctophids, in particular *Krefftichthys anderssoni*. Whilst no *Protomyctophum* spp. were found in this study, it is possible that a small percentage of the most heavily eroded *K. anderssoni* otoliths were from this genus. As the proportion of this species and genus is unknown *K. anderssoni* is used, but is taken to include the *K. anderssoni*/*Protomyctophum* spp. complex.

Standard lengths could only be obtained for 937 (1.3%) of the 73,005 fish specimens due to digestion of whole bodies, or wear of otoliths. The otoliths of the three dominant species had two size classes (Fig. 8.3, Table 8.7). Although a precise measurement could not be taken on the majority of otoliths, it was possible to categorise them as "large" and "small" (*K. anderssoni* large: 1.1 - 1.95 mm small: 0.0 - 1.0 mm, *Electrona carlsbergi* large: 3.2 - 4.5 mm small: 1.8 - 3.2 mm, *E. subaspera* large: 3.0 - 4.5 mm small: 2.2 - 2.9 mm).



**Table 8.6** Estimated mantle lengths and masses of squid from Lower Rostral Lengths (LRL) of beaks (erosion category 1 and 2). Mean  $\pm$  SD (range) are given

Species	LRL (mm)	Mantle length (mm)	Mass (g)	Source of regression
<i>Moroteuthis knipovitchi</i> (n = 973)	1.7 $\pm$ 0.7 (0.3 - 5.8)	-194.3 $\pm$ 72.2 (-342.1 - 237.1)	11.3 $\pm$ 31.1 (0.01 - 425.9)	Rodhouse <i>et al.</i> (1990)
other <i>Moroteuthis</i> sp. (n = 93)	1.4 $\pm$ 0.5 (0.7 - 4.0)	4.7 $\pm$ 0.00 (4.70 - 4.73)	5.4 $\pm$ 13.7 (0.2 - 119.6)	Clarke (1986)
<i>Kondakovia longimana</i> (n = 45)	1.8 $\pm$ 0.7 (0.8 - 4.2)	13.2 $\pm$ 30.5 (-32.3 - 120.3)	0.4 $\pm$ 1.2 (0.001 - 6.4)	Clarke (1986)
<i>Histioteuthis</i> sp. (n = 6)	1.8 $\pm$ 0.9 (0.7 - 3.1)	26.4 $\pm$ 20.6 (1.9 - 55.3)	23.6 $\pm$ 22.2 (2.9 - 57.6)	Clarke (1986)
<i>Lampadioteuthis</i> sp. (n = 9)	1.6 $\pm$ 0.6 (0.6 - 2.4)	none available	none available	-
<i>Martialia hyadesi</i> (n = 84)	2.0 $\pm$ 1.2 (0.2 - 6.2)	160.5 $\pm$ 36.8 (107.9 - 284.7)	61.0 $\pm$ 77.0 (0.4 - 431.5)	Rodhouse <i>et al.</i> (1990)
<i>Todarodes</i> sp. (n = 19)	1.3 $\pm$ 0.4 (0.6 - 2.3)	68.7 $\pm$ 15.4 (42.9 - 104.6)	7.9 $\pm$ 6.5 (1.0 - 27.3)	Clarke (1986) based on <i>T. pacificus</i>
<i>Brachioteuthis</i> sp. (n = 1)	0.3	22.4	0.8	Clarke (1986) based on <i>P. boschmai</i>
<i>Pholidoteuthis</i> sp. (n = 6)	1.8 $\pm$ 0.5 (1.0 - 2.4)	85.6 $\pm$ 19.5 (52.4 - 109.9)	16.2 $\pm$ 9.8 (2.6 - 31.6)	Clarke (1986)
<i>Onychoteuthis</i> sp. (n = 10)	2.4 $\pm$ 0.2 (2.2 - 2.7)	118.4 $\pm$ 9.9 (102.3 - 135.8)	47.6 $\pm$ 11.8 (30.3 - 70.5)	Clarke (1986) based on <i>O. banksi</i>
<i>Gonatus</i> sp. (n = 4)	0.9 $\pm$ 0.1 (0.9 - 1.0)	-3.2 $\pm$ 2.7 (-6.9 - -0.5)	0.4 $\pm$ 0.1 (0.3 - 0.5)	Clarke (1986)
Cranchid sp. (n = 1)	3.2	107.4	12.0	Clarke (1986)



There were significant differences in the size class of *K. anderssoni* consumed by Royal and Rockhopper Penguins each year (1993/4  $\chi^2_1 = 8424.4$ ,  $P < 0.0001$ ; 1994/5  $\chi^2_1 = 1169.1$ ,  $P < 0.0001$ ; 1995/6  $\chi^2_1 = 6730.7$ ,  $P < 0.0001$ ), with Rockhopper Penguins taking more small fish.

Within each species there were significant inter-annual differences in the size of fish consumed (Royal Penguins  $\chi^2_2 = 124.5$ ,  $P < 0.0001$ ; Rockhopper Penguins 4870.2,  $P < 0.0001$ ). During 1994/5 Royal Penguins consumed more small fish than during the other years, whilst Rockhopper Penguins consumed more large fish during 1994/5 compared to the other years.

A similar pattern was observed in *Electrona* spp., with significantly different sizes taken by the penguins (*E. carlsbergi* 1993/4  $\chi^2_1 = 10.1$ ,  $P < 0.002$ ; 1994/5  $\chi^2_1 = 13.8$ ,  $P < 0.0001$ ; 1995/6  $\chi^2_1 = 6.3$ ,  $P < 0.01$ ; *E. subaspera* 1993/4  $\chi^2_1 = 10.6$ ,  $P < 0.001$ ; 1994/5  $\chi^2_1 = 180.0$ ,  $P < 0.0001$ ; 1995/6 Rockhopper Penguins did not take any of this species). Royal Penguins took smaller *E. carlsbergi* than did Rockhopper Penguins in each year, but larger *E. subaspera* during all years except 1993/4.

Significant inter-annual differences in the size of *Electrona* species were also found (*E. carlsbergi* Royal Penguins  $\chi^2_2 = 136.2$ ,  $P < 0.0001$ ; Rockhopper Penguins  $\chi^2_2 = 80.6$ ,  $P < 0.0001$ ; *E. subaspera* Royal Penguins  $\chi^2_2 = 22.9$ ,  $P < 0.0001$ ; Rockhopper Penguins  $\chi^2_2 = 120.0$ ,  $P < 0.0001$ ). Both species took more small *E. carlsbergi* during 1994/5, and Royal penguins took smaller *E. subaspera* during 1993/4, but the opposite was true

of Rockhopper Penguins. Differences in size classes could not be assessed by stage in the breeding season due to insufficient data.

**Table 8.7** Standard lengths and masses of fish in each size class, derived from whole undigested fish and estimated from otoliths. Mean  $\pm$  SD (range) are given

<i>Fish species</i>	<i>Size class</i>	<i>n</i>	<i>Standard Length (mm)</i>	<i>Mass (g)</i>
<i>Krefftichthys anderssoni</i>	1	83	13.2 $\pm$ 4.8 (4.6 - 25.3)	0.02 $\pm$ 0.03 (0.001 - 0.13)
	2	695	46.8 $\pm$ 5.4 (29.4 - 60.3)	1.08 $\pm$ 0.4 (0.2 - 2.3)
<i>Electrona carlsbergi</i>	1	97	57.4 $\pm$ 6.4 (44.8 - 75.1)	3.6 $\pm$ 1.1 (1.8 - 7.2)
	2	30	91.7 $\pm$ 7.6 (76.3 - 103.0)	12.7 $\pm$ 2.7 (7.6 - 17.2)
<i>E. subaspera</i>	1	10	62.9 $\pm$ 4.8 (56.2 - 69.3)	4.4 $\pm$ 1.1 (3.0 - 5.9)
	2	19	100.2 $\pm$ 9.1 (80.9 - 114.2)	19.8 $\pm$ 5.5 (9.7 - 29.3)

**Fig. 8.3** The frequency of different otolith size classes (erosion categories 1 and 2) from samples (Royal and Rockhopper Penguins combined).

**A** *Krefflichthys anderssoni* ( $n = 781$ )

size class 1: 0.0 - 1.0 mm

size class 2: 1.01 - 1.95 mm

**B** *Electrona carlsbergi* ( $n = 127$ )

size class 1: 1.95 - 3.2 mm

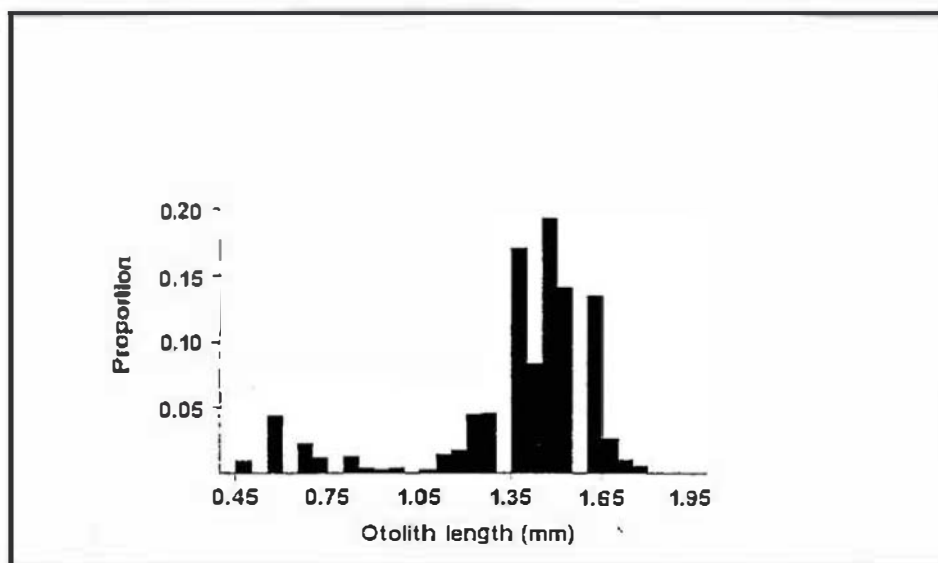
size class 2: 3.25 - 4.35 mm

**C** *E. subaspera* ( $n = 29$ )

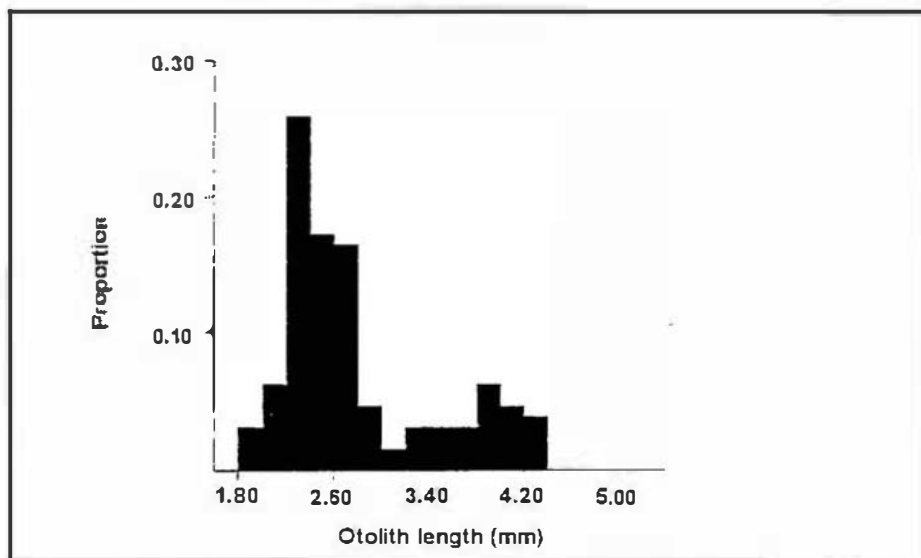
size class 1: 2.2 - 2.9 mm

size class 2: 3.0 - 4.5 mm

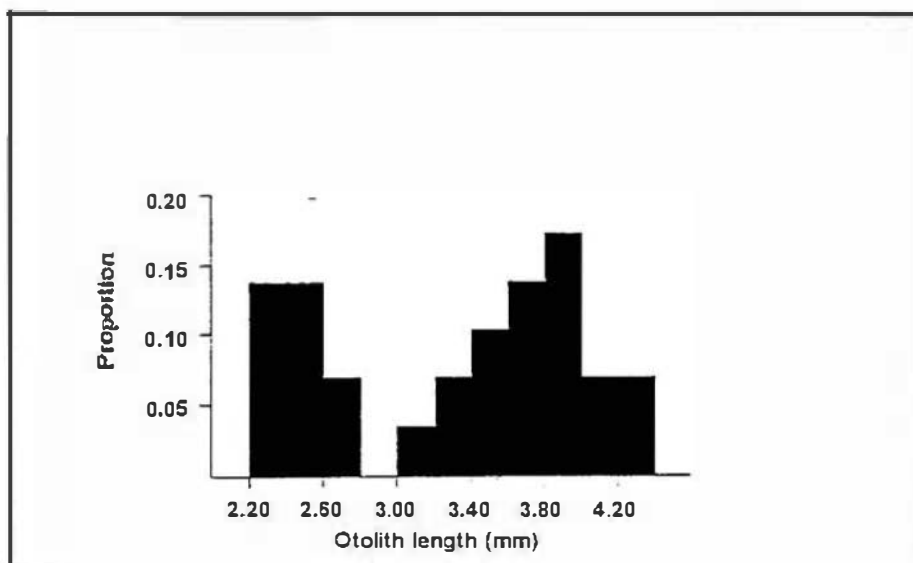
*Kreffichthys anderssoni*



*Electrona carlsbergi*



*E. subaspera*



*Degree of digestion*

Significant differences in the degree of digestion of euphausiids were found between the species during 1993/4 and 1995/6, with samples from Royal Penguins more digested. Significant differences were also found between the species in digestion of fish during 1994/5 and 1995/6, with Rockhopper Penguins bringing ashore fish that were more digested in 1994/5, but Royal Penguins bringing ashore more digested fish in 1995/6 (Table 8.8).

Significant inter-annual differences were found in the degree of digestion of euphausiids in both species, with those brought ashore during 1993/4 the least digested, and those during 1994/5, the most. The degree of digestion of fish showed no inter-annual variability in Royal Penguins, but did in Rockhopper Penguins, with greater digestion observed during 1994/5 (Table 8.9).

The degree of digestion of euphausiids did not vary across weeks in the 1993/4 or 1995/6 breeding seasons in either species, but did during 1994/5 (Table 8.10). There were no differences in degree of digestion of fish between stages in the 1993/4 or 1995/6 breeding seasons in either species, but there were in 1994/5 (Table 8.10). Both euphausiids brought ashore by Royal Penguins, and fish brought ashore by both species, were more digested in the later, compared to the earlier, part of the breeding season.

**Table 8.8** Allocation of euphausiids and fish to the three categories of degree of digestion during each year of the study. **Significant differences between species are shown in bold.**

Categories (see materials and methods):

1. Heavily digested
2. Moderately digested
3. Lightly digested

<i>Year</i>	<i>Penguin species</i>	<i>Euphausiids</i>				<i>Fish</i>			
		<i>1</i>	<i>2</i>	<i>3</i>	<i>Statistical comparisons</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>Statistical comparisons</i>
1993/4	Royal	33	36	10	$\chi^2_2 = 14.6, P < 0.001$	22	34	10	$\chi^2_2 = 4.3, P > 0.05$
	Rockhopper	10	51	11		18	20	16	
1994/5	Royal	45	32	0	$\chi^2_2 = 0.07, P > 0.05$	30	36	18	$\chi^2_2 = 6.9, P < 0.03$
	Rockhopper	36	28	0		37	17	11	
1995/6	Royal	11	17	0	$\chi^2_2 = 6.4, P < 0.04$	21	14	4	$\chi^2_2 = 8.7, P < 0.01$
	Rockhopper	3	23	1		4	11	7	



**Table 8.9** Allocation of euphausiids and fish to the three categories of degree of digestion derived from diet samples of Royal and Rockhopper Penguins. **Significant differences between years are shown in bold.**

Categories (see materials and methods):

1. Heavily digested
2. Moderately digested
3. Lightly digested

<i>Penguin species</i>	<i>Year</i>	<i>Euphausiids</i>				<i>Fish</i>			
		<i>1</i>	<i>2</i>	<i>3</i>	<i>Statistical comparisons</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>Statistical comparisons</i>
Royal	1993/4	33	36	10	$\chi^2_4 = 17.7$ <b>P &lt; 0.001</b>	22	34	10	$\chi^2_4 = 6.6$ , P > 0.05
	1994/5	45	32	0		30	36	18	
	1995/6	11	17	0		21	14	4	
Rockhopper	1993/4	10	51	11	$\chi^2_4 = 42.0$ , <b>P &lt; 0.0001</b>	18	20	16	$\chi^2_4 = 13.0$ , <b>P &lt; 0.011</b>
	1994/5	36	28	0		37	17	11	
	1995/6	3	23	1		4	11	7	

**Table 8.10** Comparisons of the degree of digestion of euphausiids and fish in the diet of Royal and Rockhopper Penguins across the breeding season. **Significant differences are shown in bold**

Year	Royal <i>Euphausiids</i>	Penguins <i>Fish</i>	Rockhopper <i>Euphausiids</i>	Penguins <i>Fish</i>
1993/4	$\chi^2_{10} = 12.7$ $P > 0.05$	$\chi^2_2 = 6.4$ $P > 0.05$	$\chi^2_{10} = 13.1$ $P > 0.05$	$\chi^2_2 = 6.4$ $P > 0.05$
1994/5	$\chi^2_1 = \mathbf{4.3}$ $P < \mathbf{0.04}$	$\chi^2_2 = \mathbf{25.9}$ $P < \mathbf{0.004}$	$\chi^2_1 = 2.5$ $P > 0.05$	$\chi^2_2 = \mathbf{22.6}$ $P < \mathbf{0.01}$
1995/6	$\chi^2_1 = 0.1$ $P > 0.05$	$\chi^2_2 = 2.2$ $P > 0.05$	$\chi^2_1 = 0.01$ $P > 0.05$	$\chi^2_2 = 4.5$ $P > 0.05$

#### *Dietary overlap*

##### Pre-hatching

There were significant differences in the diet of the 18 groups assessed by the analysis of similarity ( $S = 1.2$ ,  $P < 0.0001$ ). The cluster analysis derived two groups (Fig. 8.4) and the composition of these groups is listed in Table 8.11. The prey items responsible for these clusters were (correlation coefficients): *Euphausia vallentini* (0.84), *Thysanoessa gregaria* (0.58), unidentified euphausiids (0.55), *Themisto gaudichaudii* (0.71) and *K. anderssoni* (0.69) (Fig. 8.4).

##### Post-hatching

Significant differences were also found in 31 groups in the post-hatching diet ( $S = 1.4$ ,  $P < 0.0001$ ). The cluster analysis determined that there were four groups which differed in their dietary composition (Fig. 8.5). The penguins (species, years and weeks of the

breeding season) that constituted these groups are given in Table 8.12. The dietary items which significantly contributed to these groups (correlation coefficients) were *Euphausia vallentini* (0.97), *Thysanoessa gregaria* (0.66) and *K. anderssoni* (0.96) (Fig. 8.5).

**Table 8.11** Allocation (%) of Royal and Rockhopper Penguins to dietary groups (1 - 2) during each year and week of the breeding season, as derived from the cluster analysis. Pre-hatching diet. **Groups with the majority of cases in bold**

Year	Week	Royal Group 1	Penguins Group 2	Rockhopper Group 1	Penguins Group 2
1993/4	1	<b>76</b>	24	0	<b>100</b>
	2	38	<b>62</b>	0	<b>100</b>
	3	<b>80</b>	20	0	<b>100</b>
1994/5	1	<b>71</b>	29	20	<b>80</b>
	2	<b>62</b>	38	50	50
	3	0	<b>100</b>	<b>67</b>	33
1994/5	1	40	<b>60</b>	<b>60</b>	40
	2	20	<b>80</b>	23	<b>77</b>
	3	37	<b>63</b>	<b>67</b>	33

**Table 8.12** Allocation (%) of Royal and Rockhopper (RH) Penguins to dietary groups (1 - 4) during each year and week of the breeding season, as derived from the cluster analysis. Post-hatching diet. **Groups with the majority of cases in bold**

<i>Year</i>	<i>Week</i>	<i>Royal Penguin Groups</i>				<i>RH Penguin Groups</i>			
		<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>
1993/4	4	<b>60</b>	0	20	20	20	20	0	<b>60</b>
	5	20	13	27	<b>40</b>	0	0	10	<b>90</b>
	6	<b>50</b>	10	10	30	0	0	0	<b>100</b>
	7	<b>43</b>	19	9	29	7	7	0	86
	8	<b>90</b>	0	0	10	31	6	0	<b>63</b>
	9	<b>47</b>	32	0	21	0	15	0	<b>85</b>
1994/5	4	<b>100</b>	0	0	0	<b>80</b>	20	0	0
	5	<b>70</b>	0	12	18	0	15	0	<b>85</b>
	6	<b>88</b>	0	0	12	12	12	0	<b>76</b>
	7	<b>82</b>	18	0	0	<b>36</b>	27	0	<b>36</b>
	8	<b>90</b>	10	0	0	<b>55</b>	28	0	17
	9	<b>68</b>	32	0	0	<b>63</b>	12	0	25
1995/6	4	<b>100</b>	0	0	0	0	0	0	0
	6	10	20	0	<b>70</b>	11	0	0	<b>89</b>
	7	<b>80</b>	10	0	10	11	0	0	<b>89</b>
	9	<b>80</b>	20	0	0	0	0	0	<b>100</b>

**Fig. 8.4** Plot of the two dietary groups that were derived from the cluster analysis (A). Pre-hatching diet.

(See Table 8.12 for allocation of penguins to groups)

× Group 1

○ Group 2

(B) The contribution of the significant prey items to each group

E *Euphausia vallentini*

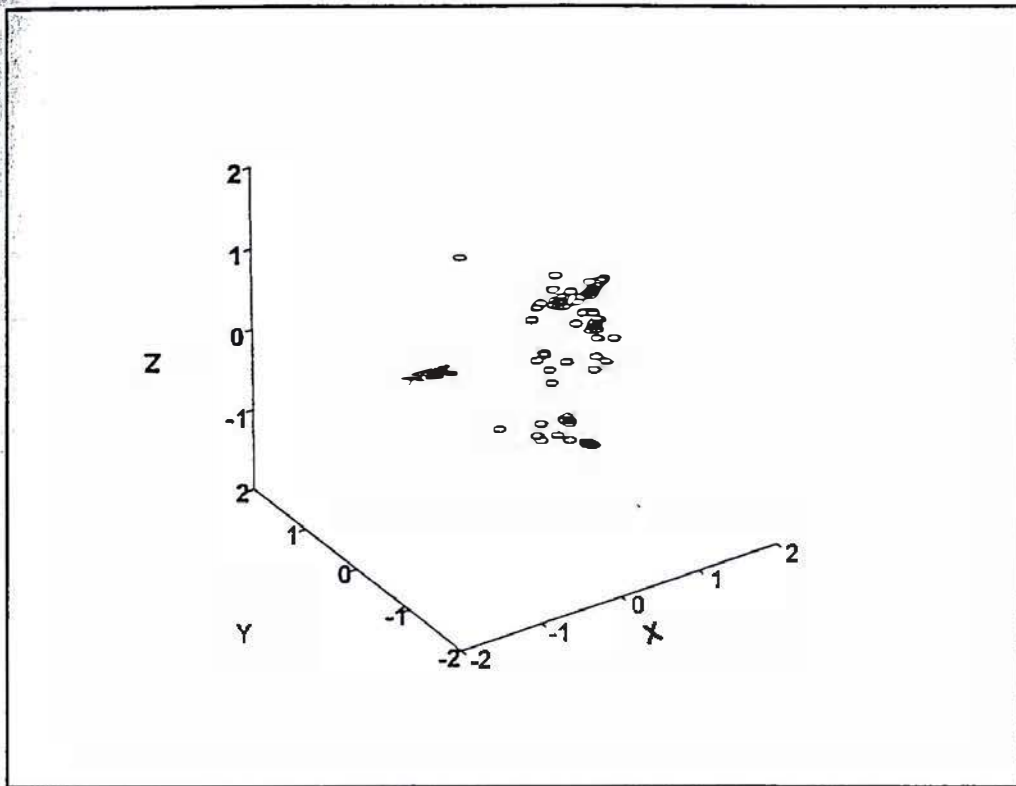
T *Thysanoessa gregaria*

U Unidentified euphausiids

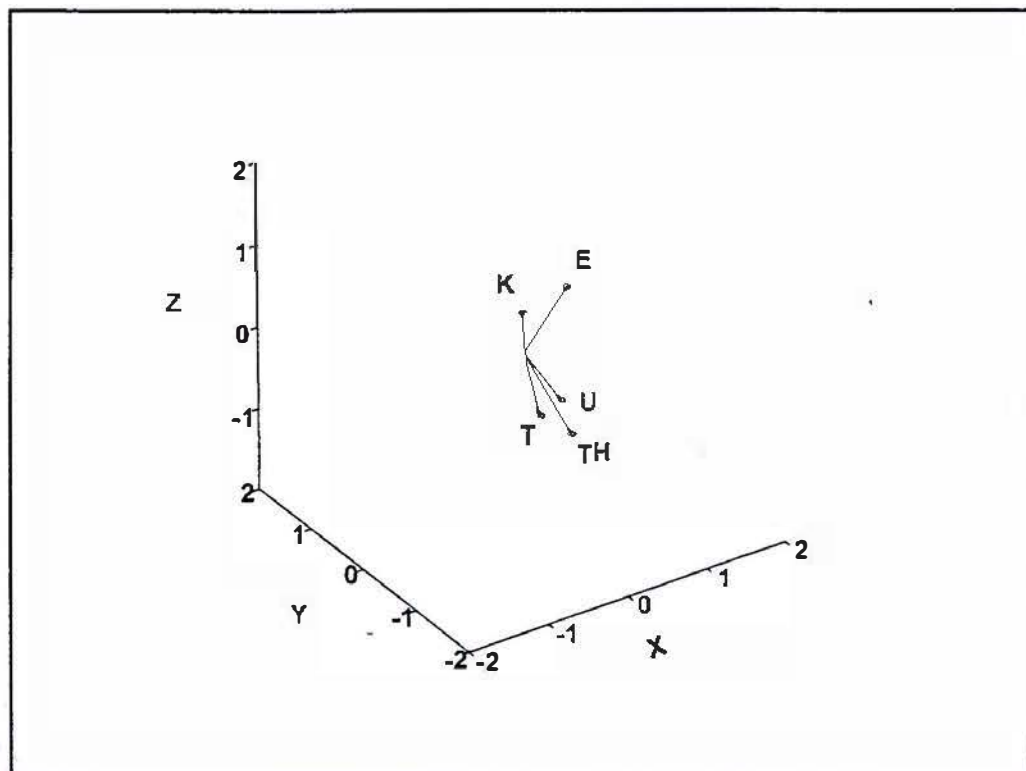
TH *Themisto gaudichaudii*

K *Krefftichthys anderssoni*

A



B





**Fig. 8.5** Plot of four dietary groups that were derived from the cluster analysis (A). Post-hatching diet.

(See Table 8.13 for allocation of penguins to groups)

- Group 1
- Group 2
- × Group 3
- ☆ Group 4

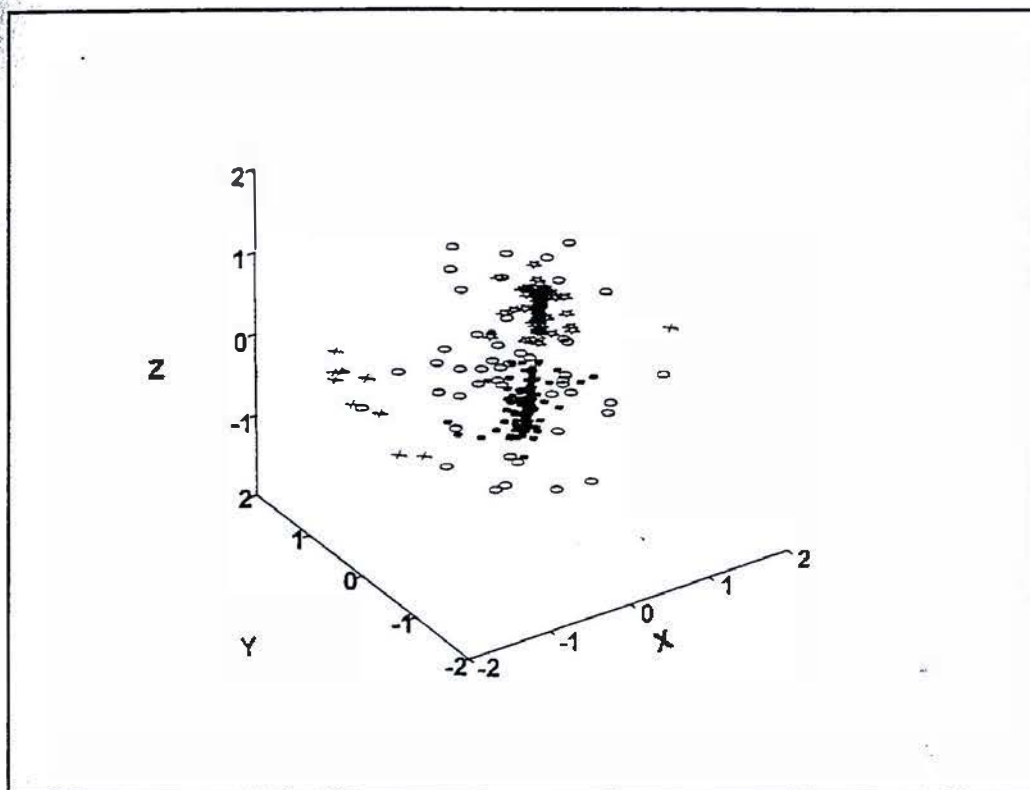
(B) The contribution of the significant prey items to each group

E *Euphausia vallentini*

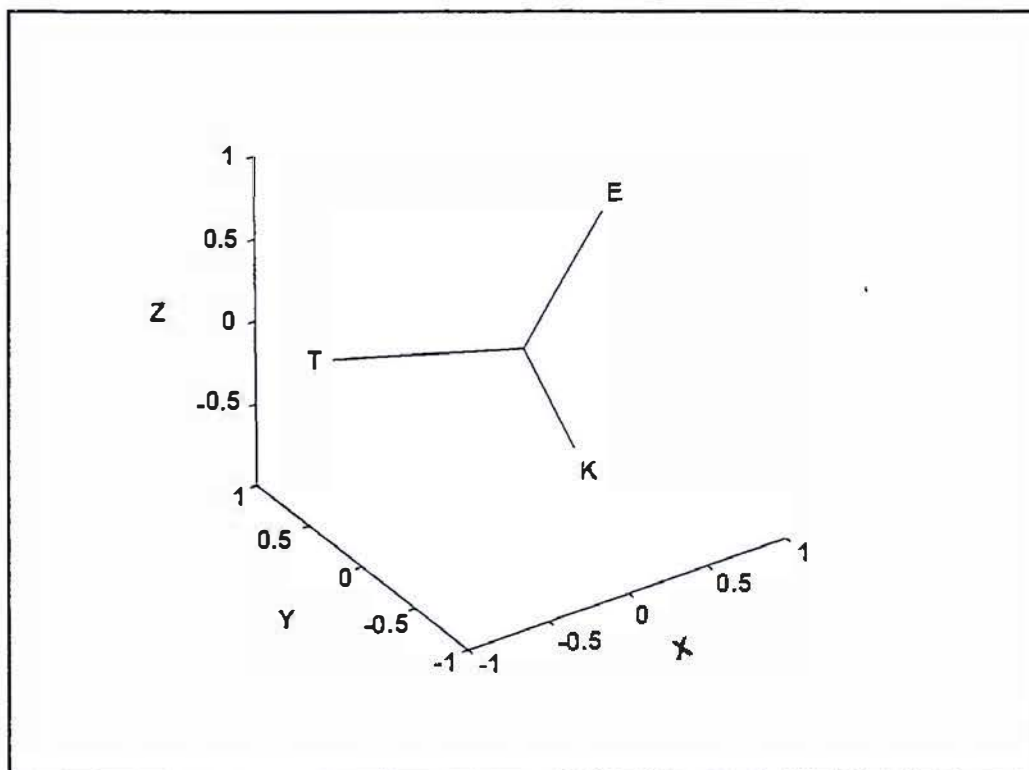
T *Thysanoessa gregaria*

K *Krefftichthys anderssoni*

A



B



## 8.4 Discussion

### *Effects of stomach flushing*

The advantages of the stomach flushing technique for obtaining diet samples from seabirds are considerable, with birds not being sacrificed, and the collection of entire stomach samples rather than only portions, as occurs with emetics (Duffy & Jackson 1986). Provided adults are only flushed once during the chick-rearing period, fledging rates, growth rates, mass gain of chicks, and overall breeding success is not affected (Clarke & Kerry 1993, Robertson *et al.* 1994b). Nor are there any immediate impacts to adults, with foraging trip durations of recently flushed birds being the same as controls (Robertson *et al.* 1994b). However there is some evidence in Yellow-eyed Penguins that adults flushed in one season had a reduced breeding success in the subsequent one (van Heezik *et al.* submitted).

The protocol of only flushing an individual once in any season was used during this study in an attempt to minimise any effects on adults or chicks. Although the reduction of the number of birds flushed during the final season of this study was adopted in order to minimise any possible impact, further work is required on the effects of flushing on breeding success to ascertain if there are any longer-term impacts (Clarke & Kerry 1993, Robertson *et al.* 1994b).

### *The diet of Royal and Rockhopper Penguins*

The prey taxa consumed by Royal and Rockhopper Penguins were very similar, and did not differ substantially between years or stages in the breeding season. The diet of both

species was dominated by small, gregarious, pelagic prey, with the most important prey items being euphausiids (particularly *Euphausia vallentini*) and myctophid fish (particularly *Krefftichthys anderssoni*).

The three different ways of describing diet (frequency of occurrence, percentage by number and percentage by mass) yielded slightly different results (Appendices 8.1 and 8.2). Obviously small, abundant prey were over-emphasised by measures of frequency of occurrence and percentage by number.

#### *Biology of the prey species and penguin foraging*

The species of prey taken were predominantly those found in the vicinity of the Polar Frontal Zone (PFZ), the foraging zones of both species during the breeding season (Chapters 5 and 6). It is in this zone that productivity is thought to be high due to the mixing of nutrients, with prey found either in higher concentrations or closer to the surface (Ainley & Jacobs 1981, Hulley 1981, Foster 1984, Abrams 1985, Lutjeharms *et al.* 1985, Gon & Heemstra 1990, Schneider 1990).

The euphausiids recorded have a circumpolar distribution and are associated with the PFZ, although predominantly in the northern regions (Mauchline & Fisher 1969). It is probable that the size class of euphausiids varied across the season, but this could not be elucidated due to the degree of digestion of samples. At the Crozet Islands recruitment of post-larval *E. vallentini* occurs in December to January (Ridoux 1988), and therefore the abundance of younger fish is greater at this time, which may also

occur at Macquarie Island.

The other crustaceans in the diet were also pelagic species, with the most frequently occurring, *Themisto gaudichaudii*, usually found in large swarms. It is the most common and abundant hyperiid amphipod in the Southern Ocean (Jazdzewski 1982). Whilst this species may have been a targeted prey item, it is possible that some of the other crustaceans consumed were incidental prey present in swarms of targeted species, or secondary prey items obtained from fish or squid.

The cephalopods were from eight families, with the most commonly occurring from the Onychoteuthidae (*Moroteuthis* spp., *Kondakovia longimana* and *Onychoteuthis* spp.). Almost all species recorded in this study are present in or around the PFZ (Rodhouse & Prince 1993, Rodhouse pers. comm. in Croxall & Prince 1994).

The most common squid consumed by both species of penguin was *Moroteuthis knipovitchi*. *Moroteuthis* spp. and *Kondakovia longimana* are relatively large and muscular, mid- to deep-water species associated with island and continental masses (Nesis 1987, Rodhouse *et al.* 1992), although the latter species is found in shallower water as summer progresses (Nemoto *et al.* 1985). Both the size and deep water habitat of these species of squid may make them largely inaccessible to these penguins. Royal and Rockhopper Penguins are capable of diving over 100 m, but rarely do so, concentrating diving activity below 60 m (Chapter 7). However, species of albatross, which are surface feeders, manage to exploit some deep water squid (Croxall & Prince

1994), hence the location of squid in the water column may not be as simple as that described above.

The size, and more particularly the colouring, of cephalopod beaks (Clarke 1986), indicated that most squid consumed were probably juveniles. Juvenile squid are more likely to be found in the upper layers of the water column (Nemoto *et al.* 1985, Rodhouse & Clarke 1988), making them more accessible to these species of penguin. The dietary emphasis on smaller squid by these penguins may have also been facilitated by them being easier to catch and consume, and/or present in a greater abundance than larger specimens.

A greater number of accumulated cephalopod beaks were found in the diet of both species of penguin prior to, compared to after, hatching of chicks. This may be of biological significance, with prey other than squid being consumed during the breeding season due to its low energy content (Croxall & Prince 1982). King Penguins *Aptenodytes patagonicus* consumed more squid outside the breeding season, which is thought to be linked with its lower nutritional value compared to oil-rich fish (Adams & Klages 1987, Cherel & Ridoux 1992), the latter being essential to the growth and development of chicks (Heath & Randall 1985, van Heezik & Davis 1990, Cherel & Ridoux 1992). However, this assumes that species can actively select prey that are nutritionally superior. Alternatively, the difference in the proportion of accumulated beaks before and after chicks hatched may represent a bias in the data induced by the adults regurgitating beaks to chicks during feeding



The fish consumed were primarily of the Myctophidae (*K. anderssoni*, *Electrona* spp., *Gymnoscopelus* spp.), which are pelagic, circumpolar in their distribution, and associated with the PFZ (Hulley 1981, Williams & McEldowney 1990). Small numbers of Paralepididae (*Magnisudis prionosa*), Congiopodidae (*Zanclorhynchus spinifer*) and Nototheniidae (*Notothenia neglecta*, *Pleurogramma* spp., *Paranotothenia magellanica*) were also consumed.

Myctophids represent the second most abundant group of organisms (after Krill *E. superba*) in Antarctic waters, and have been found to be important dietary components of other species of penguin (Adams & Klages 1987, Hindell 1988a, 1989). Of the myctophids, *K. anderssoni*, *E. carlsbergi*, *E. antarctica* and *Gymnoscopelus nicholsi* constitute more than 80% of the fish biomass in this region and are found in dense shoals (Sabourenkov 1991). *K. anderssoni* is commonly recorded in water less than 200m, although south of the PFZ they are found in waters 50 - 100 m in depth (Bekker 1983). *Electrona* spp. are predominantly north of the PFZ and in water 250 - 500 m, and *Gymnoscopelus* spp. in the top 200m (Hulley 1981, Williams & McEldowney 1990). The depths at which a number of these fish species are found are, therefore, outside the diving range of Royal and Rockhopper Penguins, particularly as many fish species undergo diel migrations to deeper water during the day, and these penguins are diving predominantly during the day (Sabourenkov 1991, Chapter 7). The consumption of these myctophids is probably possible because they are found closer to the surface in the region of the PFZ, and in spring and summer are found in the upper layers of the water column (Hulley 1981, Gon & Heemstra 1990, Sabourenkov 1991).

The two size classes found in the dominant myctophids indicate that different age classes were exploited. The smaller sized *K. anderssoni* and *E. carlsbergi* were probably juveniles, as this species is sexually mature at standard lengths of approximately 54 mm and 83 mm, respectively (Hulley 1981). Both species of penguin consumed smaller individuals in December, which correlates with the spawning of these species in late spring, early summer (Hulley 1981).

Of the other species of fish, *Magnisudis prionosa*, an oceanic species, and *Pleurogramma* spp., a neritic group, are pelagic, found in the mid-depths, and to 100m, respectively (Williams & McEldowney 1990). The remaining species consumed were benthic, inshore fish found in waters to 100m in depth, although *Paranotothenia magellanicus* is found from the sublittoral zone to 255 m (Fisher & Hureau 1985a, Williams 1988). The low frequency of occurrence of these species of fish in the diet confirms the offshore foraging habits of Royal and Rockhopper Penguins (Croxall & Lishman 1987, Chapters 5 and 6). Rockhopper Penguins took a greater proportion of these benthic species than Royal Penguins, indicating that they were foraging closer inshore.

The distribution in the water column of a number of the prey species did not correlate with the known diving behaviour of Royal and Rockhopper Penguins (Chapter 7). This is most likely related to the discrepancy between what marine predators consume and what is caught during net-hauls, which is because of the difficulty of catching these prey with nets in the same proportions as predators do (Croxall *et al.* 1985, Hill *et al.* 1996).

*Seasonal and inter-annual changes in diet*

There were fewer prey taxa consumed before chicks hatched compared to after hatching. This may have some biological significance, although it is difficult to infer much from this difference as dietary analysis conducted in this manner only represents food items consumed during the last stages of a foraging trip, and is not necessarily representative of the entire trip. The long foraging trips and the lack of provisioning food for chicks during the incubation period no doubt resulted in the bulk of digestion of prey occurring at sea, and hence that brought ashore was largely accumulated and well-digested items.

The prey consumed did not vary systematically over the breeding season in either species, although there was a trend for Royal Penguins to consume more fish as the season progressed (Fig. 8.1). This suggests that both species of penguin opportunistically consumed patches of prey encountered.

Changes in diet across the breeding season have been found in both these species previously (Hindell 1988a, b). While inter-locality differences have been found in the diet of Royal and Rockhopper Penguins on Macquarie Island (Horne 1985, Hindell 1988a, b), the most likely explanation for the lack of seasonal variation in diet in this study is inter-annual differences in prey distribution and abundance around the island. The east coast sites where previous studies were undertaken by Hindell (1988a, b) were within 10 km of the Sandy Bay site, which is well within the normal distances these species travel to forage (Chapters 5 and 6).

The degree of digestion of euphausiids and fish varied across the breeding season during some, but not all years, of the study. During 1994/5 both prey groups were more digested as the season progressed, suggesting that these prey were consumed further offshore than during the other seasons. This implies that the distribution of these prey was variable between years, or that the foraging zones used by the penguins are not consistent, or both. The sea surface temperatures of foraging zones of Royal and Rockhopper Penguins were found to be generally consistent between the years (Chapter 6) suggesting that the former explanation is more likely.

Inter-annual variation in the proportion of prey items consumed was apparent only in pre-hatching diets, with the allocation of Royal Penguins to group 2 (greater reliance on euphausiids) in 1995/6, and Rockhopper Penguins to group 2 in 1993/4, being greater than the other years. This, again, suggests a variability in the prey resources at sea at this time and the apparent opportunism of these penguins to exploit what is available.

Both the quantity of food brought ashore during the breeding season, and adult masses (Chapter 9) early in the breeding season varied inter-annually. Both species had lower masses during the 1993/4 season suggesting that food may have been more difficult to obtain during the winter, non-breeding period. The variability in quantity of food brought ashore during the breeding season were also variable, and differences found in the degree of digestion between years suggested that distance from shore where prey were obtained was not constant.

Whilst there are probably continual, minor fluctuations in the distributions and abundance of prey each year, and possibly across the breeding season, longer-term cycles probably also exist. These cycles are related to features such as the Antarctic Circumpolar Wave which bring warm water anomalies to the Southern Ocean with a periodicity of 4 - 5 years, affecting the distribution of prey stocks of marine predators (White & Peterson 1996). There was no suggestion of warm water anomalies during the years of this study and breeding success across the three years was consistent (Fig. 1 White & Peterson 1996, Chapter 9). Only longer-term dietary and breeding success studies will ascertain the impact of such events on these species of penguin.

### *Quantity of food*

The quantity of food brought ashore peaked in early to mid-creche and then decreased until chicks fledged. Royal Penguins brought ashore a maximum of 20% of their body mass in food and Rockhopper Penguins, 21%. This is similar to the maximum quantity of food brought ashore by other species of penguin (eg. King 15%, Emperor *A. forsteri* 7.5%, Adélie, Chinstrap *Pygoscelis antarctica*, Gentoo *P. papua* and Macaroni Penguins 20%, Croxall & Lishman 1987, Cherel & Ridoux 1992, Robertson *et al.* 1994a). On average Royal and Rockhopper Penguins brought ashore 5-10% of their body weight. Average loads for other species of penguin are described as half the maximum quantities listed above (see review by Croxall & Lishman 1987), suggesting that Royal and Rockhopper Penguins brought ashore a similar quantity of food in relation to their body mass as other species of penguin breeding in the Southern Ocean.



Quantity of food brought ashore, used as an indicator of parental effort, suggested that both sexes contributed a similar amount of effort during creche stage, although there was a trend for males to bring less food ashore. Warham (1975) stated that males brought less food ashore during early creche as they prioritised replenishing their own body stores after their extended fast.

The decrease in body mass of females of both species during guard stage (Chapter 9) (when only females are providing food for the chicks) suggests that this time may be the most physiological stressful, as is the case in Adélie Penguins (Culik 1994). As chicks are newly hatched at this time, food must be supplied at regular intervals as they have few fat reserves on which they can survive (Brown 1987). This limits the degree of foraging that females can devote to their own maintenance. Later in the season, when both parents are foraging, a greater proportion of time is probably available for obtaining food for both chicks and adult maintenance.

#### *Comparisons to previous studies*

The diet of Royal and Rockhopper Penguins were generally similar to previous studies, indicating with a reliance on crustaceans (particularly euphausiids) and fish (Table 8.13). All penguin species fed on a wide range of small to moderate, open water, shoaling or swarming prey that are typically found within 100 m of the surface (Croxall *et al.* 1985, Brown & Klages 1987, Ridoux 1994). The main species taken agrees with the known distribution of euphausiids in the Southern Ocean (Ridoux 1994). As found previously, the larger crested penguins generally consumed more fish (Cooper *et al.*



1990).

The relative proportions of prey items, however, varied between localities. For example, the *E. c. chrysocome* and *E. c. moseleyi* subspecies of Rockhopper Penguins consumed more cephalopods than did *E. c. filholi* (Table 8.13). Differences between the localities most likely reflects the local distribution and abundance of prey resources (Brown & Klages 1987). Species of crested penguin breeding in the Atlantic sector where Krill dominates, have diets composed predominantly by this species. However, at more northern localities where this species is absent and is not replaced another single euphausiid species, the diet is more catholic (Ridoux 1994). Differences in diet have also been found between different colonies on a single island (Croxall & Furse 1980, Horne 1985, Hindell 1988a). These differences are probably related to differences in oceanic circulation and possibly the differing weather conditions, which make different coasts generally more rough. It is speculated that higher concentrations of phytoplankton, favoured prey of euphausiids, are more abundant in sheltered areas (Hindell 1988a).

Seasonal differences were detected at some localities, with Rockhopper Penguins exhibiting a significant dietary shift over the breeding season (Brown & Klages 1987, Hindell 1988a, Tremblay *et al.* 1997). However, these differences were not found in this or some other previous studies (Croxall & Prince 1980b). Inter-annual differences were found in some studies (Brown & Klages 1987). The lack of consistency in seasonal and inter-annual variability in diet at the different localities suggests that the

penguins probably opportunistically respond to the specific prey resources at each site, which most likely differ according to the local oceanic conditions.

**Table 8.13** Comparison of the diets of Royal, Macaroni and Rockhopper Penguins (percentage by mass). (Only the studies where % mass data were available have been included)

<i>Species</i>	<i>Site</i>	<i>Important dietary components</i>	<i>Source</i>
Royal	Macquarie Island	50% euphausiids, 30% fish (myctophids)	This study
Royal	Macquarie Island	51% euphausiids, 24% <i>K. anderssoni</i>	Hindell 1988a
Royal	Macquarie Island	62% and 54% fish, 26% and 3% euphausiids	Horne 1985
Macaroni	Heard Island	41% fish, 22% euphausiids	Green 1993
Macaroni	Crozet Islands	59% crustaceans ( <i>E. vallentini</i> and <i>Themisto gaudichaudii</i> ), 28% fish	Ridoux 1994
Macaroni	Marion and Gough Is.	100% euphausiids ( <i>Thysanoessa</i> spp. and <i>Euphausia</i> spp.)	Williams & Laycock 1981
Macaroni	Marion Island	90% crustaceans ( <i>E. vallentini</i> and <i>Thysanoessa vicina</i> , 5% and 10% fish	Brown & Klages 1987
Macaroni	South Georgia	98% euphausiids, 2% fish	Croxall & Prince 1980a
Macaroni	South Shetland Is.	100% and 37% euphausiids, 0% and 63% fish	Croxall & Furse 1980
Macaroni	South Shetland Is.	96% crustaceans, 4% fish	Jabłoński 1985

<i>Species</i>	<i>Site</i>	<i>Important dietary components</i>	<i>Source</i>
Rockhopper ( <i>E. c. filholi</i> )	Macquarie Island	60% euphausiids, 25% fish (myctophids)	This study
Rockhopper ( <i>E. c. filholi</i> )	Macquarie Island	70% euphausiids, 17% fish	Horne 1985
Rockhopper ( <i>E. c. filholi</i> )	Macquarie Island	70% euphausiids ( <i>E. vallentini</i> ), 16% <i>K. anderssoni</i>	Hindell 1988b
Rockhopper ( <i>E. c. filholi</i> )	Heard Island	91% crustaceans, 8% fish	Klages <i>et al.</i> 1989
Rockhopper ( <i>E. c. filholi</i> )	Crozet Islands	71% crustaceans, 17% cephalopods, 11% fish	Ridoux 1994
Rockhopper ( <i>E. c. filholi</i> )	Marion Island	100% and 91% euphausiids, 0% and 6% fish	Brown & Klages 1987
Rockhopper ( <i>E. c. chrysocome</i> )	Falkland Islands	53% cephalopods, 45% crustaceans	Croxall <i>et al.</i> 1985
Rockhopper ( <i>E. c. chrysocome</i> )	Falkland Islands	50% cephalopods, 49% crustaceans	Thompson unpubl. data in Cooper <i>et al.</i> 1990
Rockhopper ( <i>E. c. moseleyi</i> )	Amsterdam Is.	50% cephalopods, 40% crustaceans	Duroselle & Tollu 1977
Rockhopper ( <i>E. c. moseleyi</i> )	Amsterdam Is.	44% and 15% cephalopods, 25% and 64% fish, 31% and 21% crustaceans	Tremblay <i>et al.</i> 1997
Rockhopper ( <i>E. c. moseleyi</i> )	Gough Island	92% crustaceans	Klages <i>et al.</i> 1988

*Overlap in diet*

Royal Penguins consumed a greater variety of prey taxa (35) than Rockhopper Penguins (25), with Royals taking a greater diversity of crustaceans, squid and fish. This finding concurs with the observation that of all sympatrically breeding crested penguins it was always the larger congener which consumed the greatest number of prey taxa (Klages *et al.* 1989, Cooper *et al.* 1990). Further, Rockhopper Penguins took more benthic, inshore fishes, suggesting a greater degree of foraging closer inshore, as found previously in these and other sympatrically breeding crested penguins (Klages *et al.* 1989, Hindell *et al.* 1995).

Substantial differences were found in the proportions of prey taxa taken by Royal and Rockhopper Penguins both before and after the hatching of chicks. Before chicks hatched Royal Penguins were predominantly allocated to group 1 which had less euphausiids, whilst Rockhopper Penguins were associated with group 2 (more euphausiids). This difference was more substantial after the hatching of chicks, with Royal Penguins being allocated to group 1 (*K. anderssoni*) compared to Rockhopper Penguins which were allocated mainly to group 4 (*Euphausia vallentini*).

The three week asynchrony in the breeding season of these two species (Chapter 9) would have little impact on the differences in diet found in this study. The lack of variability in diet across the breeding season in either species suggests that the dietary differences would remain relatively constant.

Rockhopper Penguins also consumed smaller *K. anderssoni* and *E. subaspera* than Royal Penguins. As differences in the size classes of prey are thought to be more related to the habitat in which seabirds forage than body size of the predator (Ainley *et al.* 1992) it is most likely that these differences represent separate foraging grounds of the penguin species. The two size classes recorded in *K. anderssoni* are thought to represent juveniles and sexually-mature adults (Hulley 1981). The distribution of age classes may differ, with juveniles staying close inshore (Hulley 1981). Differences between the species in the degree of digestion of both fish and euphausiids, and assuming that the species have similar digestive function and regulation of digestion, provides further evidence that prey were consumed from different zones.

Finally, Rockhopper Penguins remained at a lower mass throughout the 1993/4 season (Chapter 9), indicating contrasting foraging success between the species in this year, or a reliance on different prey species or food sources which had different nutritional value.

The differences in diet detected in this study support the contention that closely related species often only exhibit differences in the size of prey taken, whilst more taxonomically distant species feed on different prey taxa (Ashmole & Ashmole 1967). The degree of dietary differences between predators is dependent upon the diversity of prey in the local environment (Diamond 1983). For example, at the Galapagos Islands, the greater diversity of marine habitats compared to other oceanic sites may have resulted in a greater range of prey species and therefore more opportunity for the



segregation of food resources within the seabird community (Harris 1977). The degree of difference in the diet of penguin species at Macquarie Island will also presumably be determined to by the complexity and diversity of the marine environment. The limited shelf area around Macquarie Island tends to suggest that there may be less microhabitats than at some other subantarctic sites, such as the Crozet Islands (Ridoux 1994).

In comparison to other species of penguin breeding on Macquarie Island Royal and Rockhopper Penguins have very similar diets. However, when diet of these two species are examined at a finer scale they show a number of dissimilarities. They consumed prey in differing proportions, of different size classes, and the degree of digestion of prey suggested they most likely took prey from different stocks, suggesting that the overlap in resource use is not substantial. This is contrary to previous assessments of dietary overlap in these species at this site (Cooper *et al.* 1990, Hindell *et al.* 1995). The comparisons made by Cooper *et al.* (1990) were based on the presence or absence of prey taxa and did not take into account proportions nor different size classes, nor therefore, the different parts of the environment where prey were obtained. There may have also been dietary differences between the years in which this and previous studies (Cooper *et al.* 1990, Hindell *et al.* 1995) were undertaken, or that dietary segregation between these species is greater in colonies located in close proximity to each other.

### 8.5 Summary

A three year study of the diet of Royal and Rockhopper Penguins was carried out at two nearby colonies on Macquarie Island to determine the degree of overlap in resource use.

Diet in both species was dominated by euphausiids and myctophid fish, in particular *Euphausia vallentini* and *Krefftichthys anderssoni*. Prey items were those found in the region of the polar frontal zone, confirming the importance of this zone to these penguins. The pre-hatching diet of both species was variable between years, and the differences in the quantity of food brought ashore and degree of digestion of prey suggested inter-annual differences in the distribution of prey resources. No dietary differences were detected in either species across the season, which is a reflection of the variability in individual diets at all stages, suggesting that foraging by individuals may have been in separate areas. Significant differences were found in the diet of the species, with Royal Penguins consuming more myctophid fish and Rockhopper Penguins consuming more euphausiids. Differences were also found in the size class of prey items taken and the degree of digestion of food, suggesting that prey were consumed in different sectors of the ocean. It is concluded that the overlap in diet is not great in individuals from these two spatially close colonies, and contrary to previous studies, indicates a separation in the resources utilised by both species. The difference to previous studies is most likely a reflection of the different methods used to assess overlap and, to a lesser extent, the years and colonies in which the comparisons were made.

## 8.6 Acknowledgments

This work was carried out with field assistance from Jane Wilson, Mary-Anne Lea, Kirsten Le Mar and Paul Scofield, to whom I am grateful. I would also like to thank Malcolm Clarke, Graham Ross, Graham Hosie and Dick Williams who assisted with the

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**Appendix 8.1.** Number and (frequency of occurrence, %) of taxa in the diet of Royal and Rockhopper Penguins (accumulated and fresh cephalopod beaks included)

<i>Taxa</i>	<i>Royal Penguins</i>			<i>Rockhopper Penguins</i>			<i>All</i>
	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	
<b>Crustaceans - euphausiids</b>	152281 (81.6)	71068 (75.4)	31186 (64.2)	111057 (95.6)	77816 (82.4)	34439 (77.8)	477847 (80.0)
<i>Euphausia vallentini</i>	127548 (64.9)	62384 (68.0)	31106 (59.7)	109119 (86.8)	76133 (76.1)	34219 (72.2)	440509 (71.3)
<i>Thysanoessa gregaria</i>	24703 (11.4)	8684 (7.4)	80 (4.5)	1892 (7.7)	1683 (5.4)	220 (5.6)	37262 (7.4)
Unid. euphausiid	30 (5.3)	0	0	46 (1.1)	0	0	76 (1.3)
<b>Other crustaceans</b>	148 (26.3)	325 (17.9)	75 (17.9)	85 (20.9)	15 (8.8)	460 (35.2)	1108 (20.4)
<i>Themisto gaudichaudii</i>	106 (21.9)	321 (15.4)	59 (14.9)	80 (19.8)	14 (7.7)	446 (24.1)	1026 (17.0)
Gamarid amphipod	1 (0.9)	1 (0.8)	13 (1.5)	5 (2.2)	1 (1.1)	13 (11.1)	34 (2.2)
<i>Primno macropa</i>	34 (1.7)	0	0	0	0	0	34 (0.4)

<i>Taxa</i>	<i>Royal</i>		<i>Penguins</i>	<i>Rockhopper</i>		<i>Penguins</i>	<i>All</i>
	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	
<i>Hyperiella dilatata</i>	1 (0.9)	0	0	0	0	0	1 (0.2)
<i>Hyperiella</i> sp.	3 (2.6)	3 (1.6)	3 (3.0)	0	0	0	9 (1.3)
<i>Cyllopus lucasii</i>	2 (0.9)	0	0	0	0	0	5 (0.2)
Unid. crustaceans	1 (0.9)	0	0	0	0	1 (1.8)	5 (0.4)
<b>Cephalopods</b>	313 (59.6)	773 (67.5)	362 (80.6)	103 (37.4)	217 (52.7)	253 (59.3)	2021 (59.1)
<i>Moroteuthis knipovitchi</i>	252 (39.5)	633 (53.7)	320 (62.7)	67 (23.1)	181 (36.3)	187 (44.4)	1640 (42.8)
<i>Moroteuthis ingens</i>	0	1 (0.8)	3 (4.5)	0	10 (3.3)	49 (5.6)	63 (1.8)
<i>Kondakovia longimana</i>	1 (0.9)	60 (11.4)	8 (9.0)	1 (1.1)	2 (2.2)	7 (7.4)	79 (5.2)
<i>Onychoteuthis</i> sp.	0	20 (0.8)	0	0	0	0	20 (0.2)

<i>Taxa</i>	<i>Royal</i>		<i>Penguins</i>	<i>Rockhopper</i>		<i>Penguins</i>	<i>All</i>
	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	
<i>Histioteuthis eltaninae</i>	0	2 (0.8)	0	0	0	0	2 (0.2)
<i>Histioteuthis</i> sp.	0	0	1 (1.5)	1 (1.1)	1 (1.1)	0	3 (0.6)
<i>Alluroteuthis</i> sp.	0	1 (0.8)	0	0	0	0	1 (0.2)
<i>Lampadioteuthis</i> sp.	7 (2.6)	1 (0.8)	0	3 (1.1)	0	0	11 (0.9)
<i>Martialia hyadesi</i>	31 (13.2)	34 (15.4)	8 (7.5)	21 (6.6)	10 (8.8)	0	104 (9.8)
<i>Todarodes</i> sp.	5 (1.7)	3 (1.6)	10 (13.4)	2 (1.1)	0	3 (3.7)	23 (3.0)
<i>Brachioteuthis</i> sp.	1 (0.9)	0	0	0	0	0	1 (0.2)
<i>Pholidoteuthis</i> sp.	0	6 (3.3)	0	1 (1.1)	1 (1.1)	0	8 (1.1)
<i>Gonatus</i> sp.	0	3 (0.8)	0	0	0	0	3 (0.2)



<i>Taxa</i>	<i>Royal</i>		<i>Penguins</i>	<i>Rockhopper</i>		<i>Penguins</i>	<i>All</i>
	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	
<i>Galiteuthis</i> sp.	0	2 (0.8)	0	1 (1.1)	0	0	3 (0.4)
Cranchid sp.	0	0	0	0	1 (1.1)	0	1 (0.2)
Unid. cephalopods	15 (9.6)	6 (4.9)	11 (10.4)	6 (6.6)	11 (7.7)	7 (9.3)	56 (7.8)
<b>Fish</b>	13527 (59.6)	30001 (95.9)	12518 (73.1)	4011 (64.8)	11084 (82.4)	1864 (57.4)	73005 (74.1)
<i>Krefflichthys anderssoni</i>	12905 (57.0)	28575 (78.0)	12269 (67.2)	3853 (46.2)	9889 (59.3)	1586 (46.3)	69077 (60.6)
<i>Electrona carlsbergi</i>	561 (19.3)	1101 (20.3)	225 (11.9)	11 (3.3)	414 (11.0)	1 (1.9)	2313 (12.8)
<i>Electrona subaspera</i>	35 (7.9)	100 (14.6)	12 (7.5)	36 (2.2)	84 (1.1)	0	267 (6.5)
<i>Electrona</i> sp.	13 (4.4)	203 (5.7)	6 (3.0)	1 (1.1)	3 (2.2)	0	226 (3.1)
<i>Gymnoscopelus</i> spp.	2 (1.8)	0	1 (1.5)	0	0	0	3 (0.6)

<i>Taxa</i>	<i>Royal</i>		<i>Penguins</i>	<i>Rockhopper</i>		<i>Penguins</i>	<i>All</i>
	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	
<i>Nototheniid larvae</i>	5 (1.8)	0	0	88 (11.0)	643 (12.1)	270 (7.4)	1006 (5.0)
<i>Zanclorhynchus spinifer</i>	1 (0.1)	5 (1.6)	0	12 (6.6)	0	0	18 (1.7)
<i>Magnisudis prionosa</i>	1 (0.1)	2 (1.6)	1 (1.5)	0	3 (3.3)	1 (1.8)	8 (1.5)
<i>Notothenia neglecta</i>	0	7 (3.3)	2 (1.5)	3 (2.2)	38 (6.6)	0	50 (2.4)
<i>Paranotothenia magellanica</i>	0	1 (0.8)	0	0	0	0	1 (0.2)
<i>Pleurogramma antarctica</i>	0	2 (0.8)	0	0	0	0	2 (0.2)
Unid. fish	3 (2.6)	5 (1.6)	2 (1.5)	7 (3.3)	8 (7.7)	5 (9.3)	30 (3.9)



[illegible]

Taxa	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
<i>Lampadio-teuthis</i> sp.	0	0	0	0	0	0	0.01 0.7	0	0.006 0.3	0	0	0	0	0	0	0	0	0.01 2.4
<i>Martialia hyadesi</i>	0	0	0	0	0.008 3.8	0	0.007 3.2	0.006 0.6	0.006 1.9	0	0	0	0	0	0	0.007 2.1	0	0.003 1.9
<i>Todarodes</i> sp.	0	0	0	0	0	0	0.009 0.7	0	0.003 0.05	0	0	0	0	0	0	0	0.006 0.3	0
<i>Brachio-teuthis</i> sp.	0	0	0	0	0	0	0	0	0.003 0.006	0	0	0	0	0	0	0	0	0
<i>Pholido-teuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gonatus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cranchid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galiteuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.003 0.8
Unidentified cephalopods	0	0	0	0	0.008 -	0.004 -	0.01 -	0.03 -	0.03 -	0	0	0	0	0.008 -	0	0.003 -	0.006 -	0.003 -
<i>Krefftichthys anderssoni</i>	0.6 0.09	0	20.3 14.0	14.3 47.7	2.0 18.0	5.9 40.8	4.2 30.2	19.2 74.2	13.5 49.6	0.5 2.63	0.07 0.005	0	4.2 19.2	0.04 0.9	0.2 4.3	1.2 6.3	4.8 28.0	6.5 8.1

[illegible]



Taxa	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
<i>Pleurogramma antarctica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unid. fish	0.6 -	0	0	0.02 -	0	0	0	0	0.003 -	0	0	0	0	0.04 -	0.01 -	0.003 -	0	0



[illegible]

<i>Taxa</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>
<i>Martialia hyadesi</i>	0.1 0.8	0.2 7.7	0	0.04 3.4	0.03 1.8	0.003 0.5	0.01 1.1	0	0.1 5.7	0	0	0	0	0.01 6.2	0	0	0.02 2.6	0.001 0.8
<i>Todarodes</i> sp.	0	0	0	0	0.01 0.2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Brachio-teuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pholido-teuthis</i> sp.	0	0	0	0	0	0	0.003 0.3	0	0.02 0.4	0	0	0	0	0	0	0	0	0
<i>Gonatus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cranchid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galiteuthis</i> sp.	0	0	0	0	0	0	0	0	0.01 0.2	0	0	0	0	0	0	0	0	0
Unidentified cephalopods	0	0	0	0.04 -	0.007 -	0.007 -	0.003 -	0.01 -	0	0.7 -	1.1	0	0.3 -	0	0.01 -	0	0.009 -	0.01 -
<i>Krefftichthys anderssoni</i>	89.8 10.3	36.5 14.2	52.5 64.4	55.5 90.8	27.3 55.4	24.3 66.4	24.3 75.7	32.7 78.6	57.8 70.8	0.6 4.7	0	1.5 7.1	68.5 72.3	0.1 1.2	2.2 10.2	7.3 38.3	19.8 55.1	19.7 64.2
<i>Electrona carlsbergi</i>	0	0	0.04 4.4	0.5 1.8	0.1 0.9	0.1 1.3	0.8 6.3	2.2 8.5	5.7 13.4	0	0	0	0	0	0.007 0.4	0.6 9.3	1.1 13.4	0.3 2.1
<i>Electrona subaspera</i>	0.1 5.6	0	0	0	0.1 2.5	0.007 0.3	0.03 1.9	0.08 2.8	0.6 5.3	0	0	0	0	0	0	0.009 6.0	0	0.6 4.9

<i>Taxa</i>	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
<i>Electrona</i> sp.	0	46.1 7.5	0.1 11.6	0	0	0	0.003 0.1	0.01 0.1	0.02 0.1	0	0	0	0	0	0	0	0.009 0.06	0.007 0.1
<i>Gymnoscop-</i> <i>elus</i> sp.	0	0	0	0	0	0	0	0	0	0.7 7.6	0	0	0	0	0	0	0	0
Nototheniid larvae	0	0	0	0	0	0	0	0	0	0	0	0	8.5 19.1	1.1 8.9	0.5 8.9	0	0.004 0.003	0
<i>Zanclorhyn-</i> <i>chus spinifer</i>	0	0	0	0	0.04 1.8	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Magnisudis</i> <i>prionosa</i>	0	0	0.04 0.01	0	0	0	0.003 0.009	0	0	0	0	0	0	0	0	0	0.004 0.01	0.004 0.04
<i>Notothenia</i> <i>neglecta</i>	0	0	0	0	0.04 0.5	0.003 0.1	0	0	0.01 0.009	0	0	0	0	0.2 2.3	0.01 0.2	0	0	0
<i>Paranototh-</i> <i>enia</i> <i>magellanica</i>	0	0	0	0	0	0.003 0.1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pleurogram-</i> <i>ma antarctica</i>	0.2 5.9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified fish	0.4 -	0.2 -	0	0	0	0	0	0	0	0.7 -	0.8 -	0	0	0.005 -	0.007 -	0	0	0

**C. 1995/6**

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<i>Taxa</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>7</i>	<i>9</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>5</i>	<i>7</i>	<i>9</i>
Unidentified crustaceans	0	0	0	0	0	0	0	0	0	3.2	0	0	0
<i>Moroteuthis knipovitchi</i>	0	0	0	0.1 0.6	0.04 5.2	0.04 2.0	0.02 0.1	0	0	0	0.03 2.5	0	0
<i>Moroteuthis ingens</i>	0	0	0	0	0	0.009 0.2	0	0	0	0	0	0.008 0.5	0
<i>Kondakovia longimana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Onychoteuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Histioteuthis eltaninae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Histioteuthis</i> sp.	0	0	0	0.02 0.09	0	0	0	0	0	0	0	0	0
<i>Alluroteuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lampadioteuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Martialia hyadesi</i>	0	0	0	0	0	0	0.02 0.7	0	0	0	0	0	0

<i>Taxa</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>7</i>	<i>9</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>5</i>	<i>7</i>	<i>9</i>
<i>Todarodes</i> sp.	0	0	0	0.02 0.1	0.01 0.8	0	0	0	0	0	0	0	0
<i>Brachioteuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pholidoteuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gonatus</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Cranchid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Galiteuthis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified cephalopods	0	0	0	0.02 -	0	0.009 -	0.09 -	0	0	0	0	0.03 -	0.007 -
<i>Krefflichthys</i> <i>anderssoni</i>	15.2 13.6	75.2 29.8	15.3 13.6	65.8 95.4	1.4 15.9	19.8 67.9	93.9 89.6	0	0.4 19.34	0	5.3 15.5	1.7 13.3	6.9 7.1
<i>Electrona</i> <i>carlsbergi</i>	0	0	0	0	0.005 0.8	0.9 6.4	2.1 9.1	0	0.03 6.5	0	0	0	0
<i>Electrona</i> <i>subaspera</i>	0	0	0	0	0.04 5.7	0.04 1.4	0.02 0.2	0	0	0	0	0	0

<i>Taxa</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>4</i>	<i>5</i>	<i>7</i>	<i>9</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>5</i>	<i>7</i>	<i>9</i>
<i>Electrona</i> sp.	0	0.5 9.1	0	0	0	0.04 0.5	0	0	0	0	0	0	0
<i>Gymnoscopelus</i> sp.	0	0	0	0.02 0.08	0	0	0	0	0.03 1.3	0	0	0	0
Nototheneid larvae	0	0	0	0	0	0	0	0	0	0	2.7 3.8	0.8 1.3	0
<i>Zanclorhynchus</i> <i>spinifer</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Magnisudis</i> <i>prionosa</i>	0	0	0.3 0.2	0	0	0	0	0	0	0	0.02 1.3	0	0
<i>Notothenia</i> <i>neglecta</i>	0	0	0	0	0.01 0.1	0	0	0	0	0	0	0	0
<i>Paranotothenia</i> <i>magellanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pleurogramma</i> <i>antarctica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified fish	0	0	0	0	0.01 -	0	0	1.8 -	0.03 -	3.2 -	0.02 -	0	0.007 -

## Chapter 9

### Aspects of the breeding biology of Royal and Rockhopper Penguins: a comparative and inter-annual study

#### 9.1 Introduction

The ecology of marine predators such as seabirds is intimately linked with biotic and abiotic aspects of the oceanographic environment. Parameters such as growth rates of chicks and breeding success are known to vary inter-annually for a range of marine predators. This variability has been correlated with differences in diet, which in turn has been related to the abundance and accessibility of prey (Testa *et al.* 1991, Williams & Rodwell 1992, Boyd & Roberts 1993, Chastel *et al.* 1993, Thompson 1993, Guinet *et al.* 1994, Chastel *et al.* 1995a, b, Guinet *et al.* in press).

Prey in the marine environment are patchy and often unpredictable in distribution, characteristics which have been linked to abiotic factors such as fronts, eddies and the Antarctic Circumpolar Wave (ACW) (Ainley & Jacobs 1981, Ainley *et al.* 1983, Abrams 1985, Croxall *et al.* 1988, Hunt 1988, Schneider 1990, Boyd & Roberts 1993, Chastel *et al.* 1993, White & Peterson 1996). The ACW, for example, is a series of coupled, warm water anomalies affecting climate regulation and dynamics in the Southern Ocean (White & Peterson 1996). Warm water events may result in prey moving either into deeper water or beyond the foraging ranges of seabirds, thereby impacting on foraging success and consequently breeding parameters (Guinet *et al.* in

press).

Penguins are a highly specialised group of seabirds, whose breeding biology is closely linked to their patchy and unpredictable food source. Small clutches (1 - 2 eggs), for example, is thought to have evolved in response to patchy and unpredictable food resources and the constraints related to transporting food from feeding grounds to the nest site (Stonehouse 1967, Ashmole 1971, Ricklefs 1983). Penguin reproductive output may have evolved to a minimum level in order to cope with these difficulties (Ricklefs 1983). Breeding success in a number of species also shows large inter-annual and geographical differences which may be associated with prey distribution and/or environmental factors (Trivelpiece *et al.* 1983, Heath & Randall 1985, Brown & Klages 1987, Boersma *et al.* 1990, van Heezik 1990, van Heezik & Davis 1990, Williams & Croxall 1991, Thompson 1993, Watanuki *et al.* 1993, Crawford & Dyer 1995).

Four species of penguin breed on Macquarie Island. Two, Royal *Eudyptes schlegeli* and Rockhopper *E. chrysocome* Penguins, are closely related crested (eudyptid) penguins. Royal Penguins are endemic to the island and Rockhopper Penguins are a circumpolar species comprising three subspecies, of which the *E. c. filholi* subspecies breeds on Macquarie Island (Marchant & Higgins 1990). Although some aspects of their breeding biology have been studied at this site (Warham 1963, Smith 1970, Carrick 1972, Warham 1971, St Clair & St Clair 1996, St Clair *et al.* 1995, see Chapter 1), no multi-year comparisons have been made. Longer-term studies are required on both species in order to better understand inter-annual differences in their breeding

biology and possible links with aspects of the marine environment.

The purpose of this study was, therefore, to examine inter-annual variability in the breeding biology of Royal and Rockhopper Penguins, and to relate this to foraging ecology and environmental factors.

## 9.2 Materials and methods

The aspects of breeding biology assessed in both species were: adult masses throughout the breeding season; parental attendance patterns; breeding chronology; egg morphometrics; chick growth rates and fledging masses; and breeding success (measured as the number of chicks that survived until fledging).

The study was undertaken at two colonies during the 1993/4, 1994/5 and 1995/6 breeding seasons; the upper Royal Penguin colony at Sandy Bay and the Rockhopper Penguin colony at Brothers Point, southern end of Sandy Bay, both on the east coast of Macquarie Island (54° 33' 57" S, 158° 54' 57" E). The Royal Penguin colony consisted of approximately 5000 breeding pairs. It was 1.43 km inland, at an altitude of 108 - 123 m (Hull & Wilson 1996b), and had an area of approximately 1700 m<sup>2</sup> (Fig. 9.1). The vegetation was predominantly tussock grass *Poa foliosa*, although it was denuded in the colony. The penguins accessed the colony from Sandy Bay beach via Finch Creek.

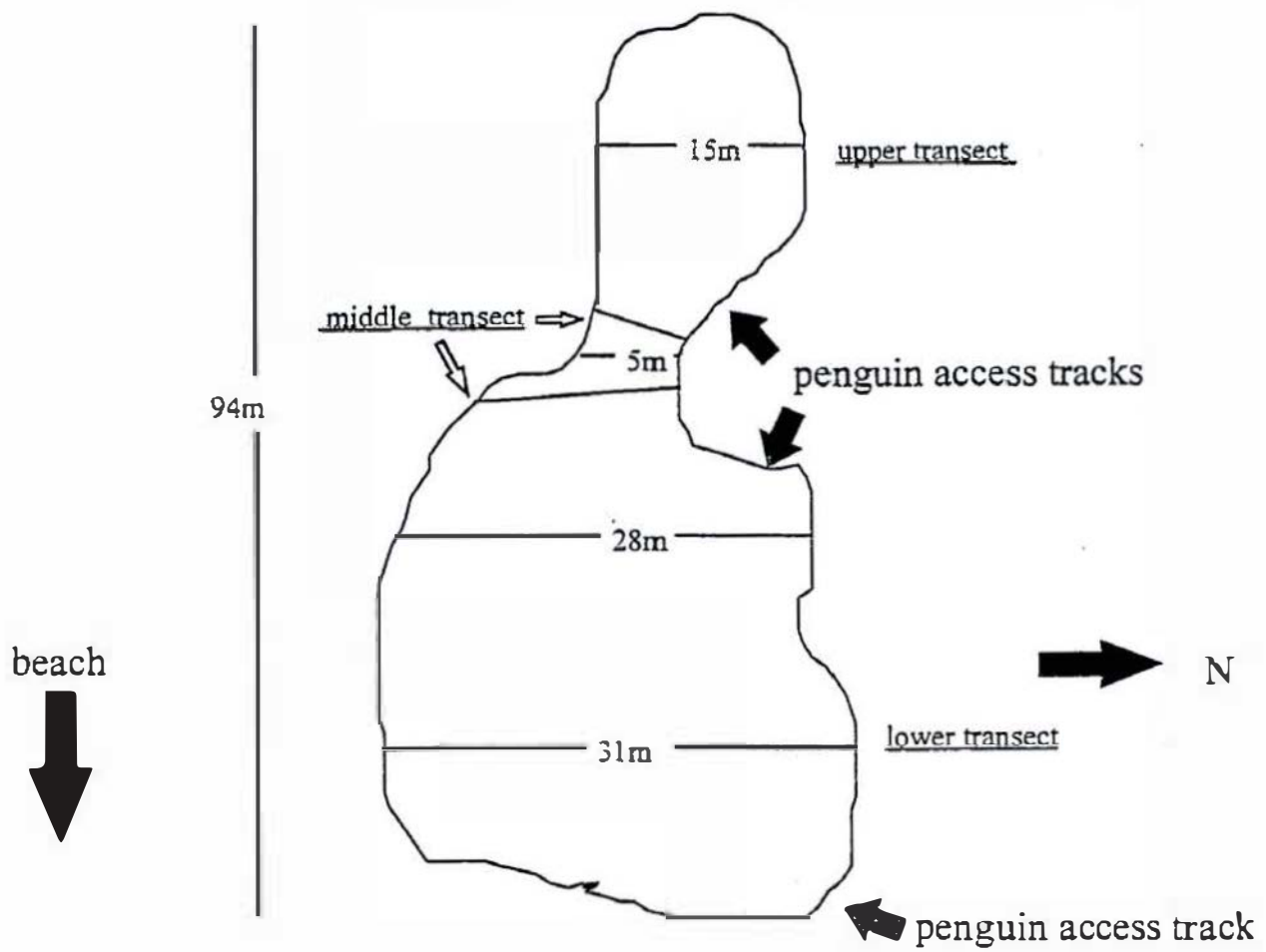
There were approximately 2000 breeding pairs in the Rockhopper Penguin colony. It



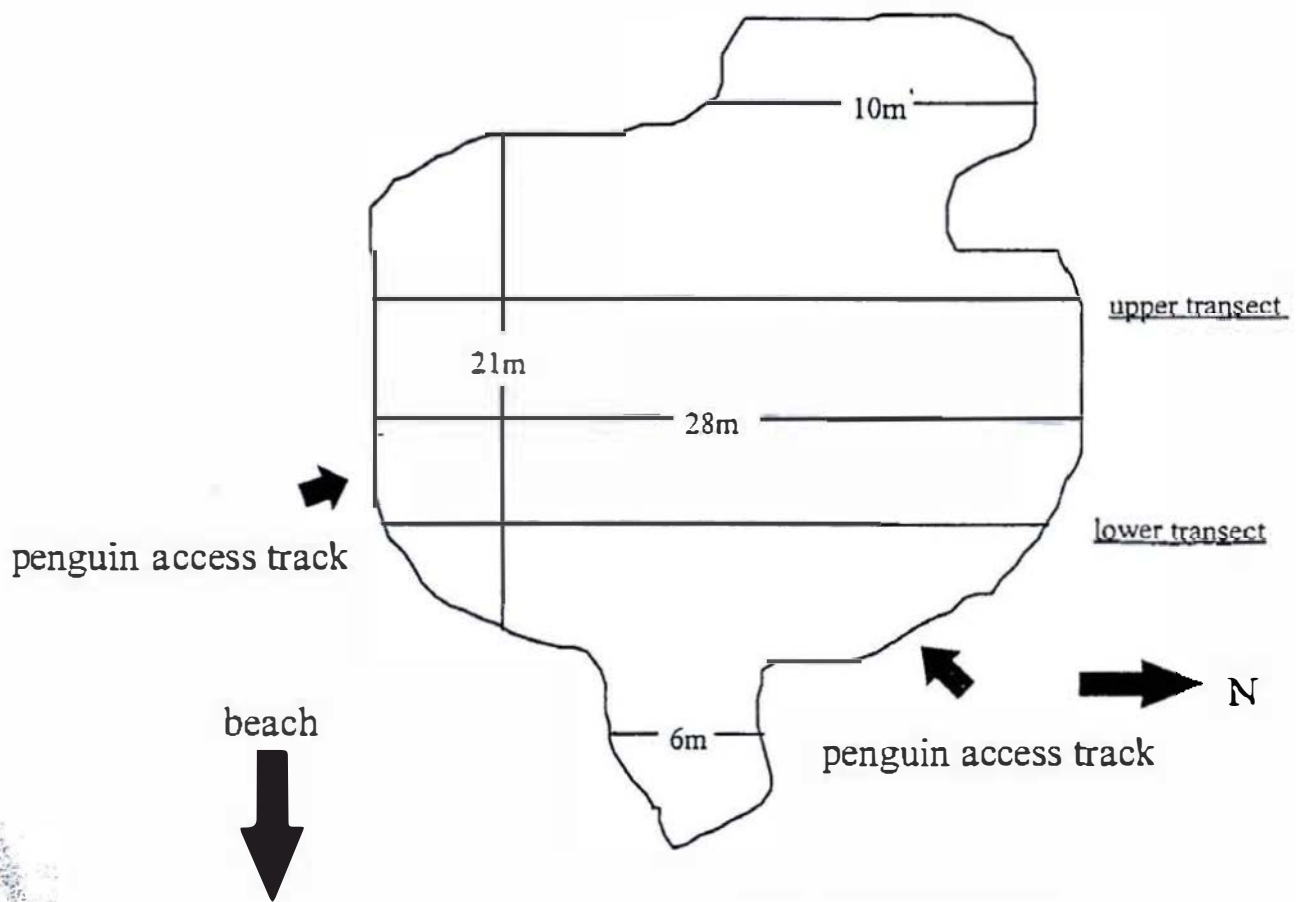
was located at the rear of a small cove on steeply sloping ground (Fig. 9.1), on terrain covered with loose boulders on a substrate of rock, with the areas around the colony also vegetated with tussock grass. The colony was approximately 777 m<sup>2</sup> in area, and at an altitude of 3 - 37 m. Penguins reached the colony via two tracks, one on each side.

**Fig. 9.1** The dimensions of the Royal (A) and Rockhopper (B) Penguin colonies at Sandy Bay (not to scale). The points where the penguins accessed the colonies are shown.

A



B



### 1. *Adult mass change*

For both species, breeding adults were weighed on the beaches below the colonies during the following times of each year ( $n$  refers to the number of penguins weighed each year):

1. Male return to the island following the winter period at sea ( $n \approx 100$ );
2. Female return to the island following the winter period (which is approximately ten days after the males) ( $n \approx 100$ );
3. Male departure following the four week fast during the incubation period ( $n = 15$ );
4. Female departure following the fast during incubation ( $n = 15$ );
5. Male return from long foraging trip during incubation ( $n = 15$ );
6. Female return from long foraging trip during incubation ( $n = 15$ );
7. Guard stage (only females forage during this stage) as they departed and returned from foraging ( $n = 15$  on departure, two sessions when returning from foraging  $n = 15$  per session);
8. Creche stage - weekly measurements of both sexes ( $n = 15$  during each of 12 sessions: six sessions as birds departed to forage and six when they returned). Only 10 sessions (5 departing and 5 returning from foraging) were undertaken on Rockhopper Penguins as their creche period was shorter than Royal Penguins.

Breeding adults (indicated by plumage characteristics [Warham 1975] and presence of a brood patch) were randomly selected, weighed and allocated to sex using bill depth and length (Hull in press, also Chapter 2). Individuals were marked with a small patch

of water-soluble paint to avoid re-weighing, and then released. Birds returning from a foraging trip were sampled as they left the water and moved up the beach to the colony. Those departing were sampled as they moved onto the beach from the colony access tracks.

Mass data were divided into pre- and post-hatching for analysis, as the mass of penguins pre-hatching constituted changes associated with adult maintenance and the energy requirements for laying and incubating eggs, whilst post-hatching changes were associated with adult maintenance and food for chicks. Mass was compared between years using Analysis of CoVariance (ANCOVAs).

Mass data were also compared when the quantity of food carried by individuals was removed (derived from penguins stomach flushed, Chapter 8). Mass change (minus food) was assessed over the breeding season, and between years using ANOVAs.

## *2. Parental attendance*

Nest attendance times were recorded remotely using an Advanced Telemetry Systems (ATS) DCC II data logger coupled with an R2100 receiver, and VHF transmitters attached to the penguins. The ATS system was powered by re-chargeable 12 V batteries, and used for two weeks in one colony and then re-located to the other colony for two weeks. The system was programmed to continuously scan the colony for each transmitter frequency for one minute, every 90 minutes.

The VHF transmitters were two-stage radio transmitters 47 x 25 x 11 mm, packaged in black, hydrodynamic waterproof housings (Faunatech, Eltham Victoria). Each weighed 9 g, was streamlined to reduce drag and had a 20 cm flexible antenna (see Hull 1997, also Chapter 4). Twelve transmitters were deployed at both colonies during the 1993/4 and 1995/6 seasons, and 16 during the 1994/5 season. Nests were randomly selected in each colony and a transmitter attached to the lower medial portion of the birds' back using a cyanoacrylate adhesive (Loctite 401). Transmitters were attached to both members of a breeding pair that had an egg. All attachments were made at the nest using the techniques described by Hull & Wilson (1996a, also Chapter 3). If a pair failed the breeding attempt, the transmitters were removed and, provided it was prior to creche stage, were deployed on another pair.

Foraging trip durations were determined from direct observations and from the ATS system. Observations were carried out on randomly selected breeding penguins (different individuals to those above) as they moved on to the beach. They were then captured, banded with a velcro flipper band and released (Table 9.1). The day and time of departure was noted. Observations for returning birds were carried out from a hide on the beach at the base of access tracks during daylight hours in each stage of the breeding season (5:00 - 18:00 hours during incubation, 3:00 - 20:00 hours around the solstice). Observations were continued for one week during each stage, around the time penguins were due to return to the colony. Velcro bands were removed when birds returned to the beach after foraging.



**Table 9.1** The numbers of Royal and Rockhopper Penguins marked for observations of foraging trip durations

<i>Stage of breeding season</i>	<i>Royal Penguins</i>	<i>Rockhopper Penguins</i>
Incubation - males	15	15
Incubation - females	10	30
Guard	10	20
Creche	10	30

*3. Nest monitoring: breeding chronology, egg morphometrics, chick growth and fledging mass, and breeding success*

Fifty nests of each species were monitored each year to record breeding chronology, egg morphometrics, chick growth rates, and breeding success. Nests were situated in three transects in the Royal Penguins colony, and on two in the Rockhopper Penguin colony (due to the smaller size of the latter colony) (Fig. 9.1).

During the 1993/4 season nests were marked in both colonies after pairs had been established. In the subsequent seasons, all nest marking was carried out prior to the return of the penguins to minimise disturbance in the colonies (see Hull & Wilson 1996a, also Chapter 3). Nests in the Royal Penguin colony were marked with metal stakes with the nest closest to each stake being monitored. In the Rockhopper Penguin colony aluminium tags (2 cm<sup>2</sup>) with embossed numbers were attached to rocks adjacent to nests, with the closest nests being monitored. Markers were left in place between seasons with the same nests being monitored unless a pair moved or a marker was lost.

All stakes and tags were removed at the end of the study.

Once pairs had formed, adults were banded with metal flipper bands and sex determined using bill depth and length (Hull in press, also Chapter 2). Breeding birds were weighed in bags with a Pesola balance, at the nest during the 1993/4 season, but not weighed in subsequent seasons due to the apparent disturbance this procedure caused (Hull & Wilson 1996a, also Chapter 3). Nests were monitored twice weekly prior to the hatching of chicks, and once weekly thereafter. During monitoring, the adults present were identified and details of the nest contents described.

For descriptions of breeding chronology, the median dates of events were used, except in the case of first return of males of both species to the island, where the first sightings at Sandy Bay were used.

### *Egg morphometrics*

As close to egg laying as possible, the maximum length and width of A (first laid) and B (second laid) eggs was measured with calipers, and each egg weighed in a small bag with Pesola balance. Eggs were obtained by gently raising the adult with a hand under the breast and removing the egg, and then replacing it in the same manner. Egg dimensions were compared between the years using one-way Analysis of Variance (ANOVAs).

The "investment" by females in both A and B eggs was compared between the species

(data arcsine transformed) by determining the percentage of the female mass just prior to laying (this could only be carried out during the 1993/4 season as mass of adults was not taken at the nest during the other seasons).

### *Chick growth*

The mass of chicks was recorded as close as possible to hatching (usually within two days) and then once weekly thereafter until the end of creche when chicks moved on to the beach to depart the colony. Brooded chicks were retrieved and returned in the same manner as eggs. Once chicks entered creches they were caught by hand.

At one week of age a uniquely-numbered aluminium fish fingerling tag (10 mm x 2 mm) was inserted into the webbing of the right foot to identify chicks. At three weeks of age a small, individually numbered velcro band was secured to the right flipper to assist with identification, as once chicks entered creche stage it was difficult to observe the fingerling tags in the mud of the colony. Each week during weighing the velcro band was loosened to allow for flipper growth. Just prior to fledging, the fingerling tags and velcro bands were removed and the chicks were banded with a permanent metal flipper band. Chick growth rates were compared between species and years using Gompertz equations which takes into account non-linear growth rates (Zullinger *et al.* 1984). These equations derived three variables: maximum mass; growth rate; and maximum growth rates (see Ricketts & Prince 1981). Comparisons between the species and years were made by comparing overlaps in the confidence limits of the variables.

Fledging masses were recorded by randomly selecting newly fledged chicks as they departed the island. Chicks were weighed and marked with a small patch of water-soluble paint to avoid re-weighing in the subsequent few days. However, chicks did not remain on the beach for more than two days before entering the water and did not return to the beach once they had departed, therefore duplicate measurements of the same individual was unlikely. Chicks from the current breeding season were distinguishable from first year birds by their smaller size, different call and different plumage. Fledging mass was compared between years using one-way ANOVAs.

### *Breeding success*

Breeding success was compared between years, species and transect lines using Chi-squared ( $\chi^2$ ) analyses. The date of the demise of eggs or chicks was recorded and the reasons compared using  $\chi^2$  analysis. The following categories were used to describe reasons for nest failures: deserted (where the adults and nest contents had disappeared); predation of egg (where the adults were present with no egg and it was not in the surrounding area); broken egg; rolled away (where the egg was at the side of the nest); never hatched (but remained in the nest); chick died (when the chick was observed dead in the nest); predation of chick (when the chick had disappeared and was not in the surrounding area, but adults were present); unknown (when the fate of the nest could not be categorised into the above groups).

There would have been some instances when eggs or chicks were taken by predators which prompted the abandonment of the nest. Hence, some of the desertions described

may represent cases of predation. Therefore, these categories can only be used as an approximate guide.

In addition, the relative breeding success of central and peripheral nests was compared using  $\chi^2$  analysis. Peripheral nests were defined as those that were the first from the edge of the colony on any transect line; and central nests were defined as those further in the centre of the colony (c.f. Ainley *et al.* 1983). Due to the apparent heterogeneity of nesting microhabitat in the Rockhopper Penguin colony, nests were categorised as either: exposed (no shelter from rocks or tussock); in a rock cavity; in the lee of rocks; or in tussock grass. Breeding success was also compared between nests in different microhabitats using  $\chi^2$  analysis.

### 9.3 Results

#### *Adult masses*

##### Pre-hatching

The masses of both species of penguin were greatest when birds returned to the island after wintering at sea, and lowest following the incubation fasting periods (Fig. 9.2). Male Royal Penguins exhibited an average loss of 25.8% body weight between these periods, and females 26.1%. Male Rockhopper Penguins lost on average 29.7% and females 38.3% of body mass between these two periods.

The pre-hatching mass change differed significantly between the species in each year of the study (1993/4  $F_{1, 583} = 12.0$ ,  $P < 0.001$ ; 1994/5  $F_{1, 487} = 7.1$ ,  $P < 0.008$ ; 1995/6  $F_{1, 487} = 12.0$ ,  $P < 0.001$ ).

$_{1565} = 43.9, P < 0.0001$ ). Rockhopper Penguins exhibited a greater loss in mass during weeks 3 and 4 compared to Royal Penguins (Fig. 9.2).

Significant differences were also found in mass change within each species across the years (Royal Penguins  $F_{2,969} = 21.1, P < 0.0001$ ; Rockhopper Penguins  $F_{2,588} = 28.7, P < 0.0001$ ). During the 1993/4 season Royal Penguins returned to the island with a lower mass, and did not exhibit the same degree of mass change as the other two seasons (Fig. 9.2). Rockhopper Penguins did not lose the same quantity of mass during weeks 3 and 6 of the 1994/5 season compared to the other two seasons (Fig. 9.2).

### Post-hatching

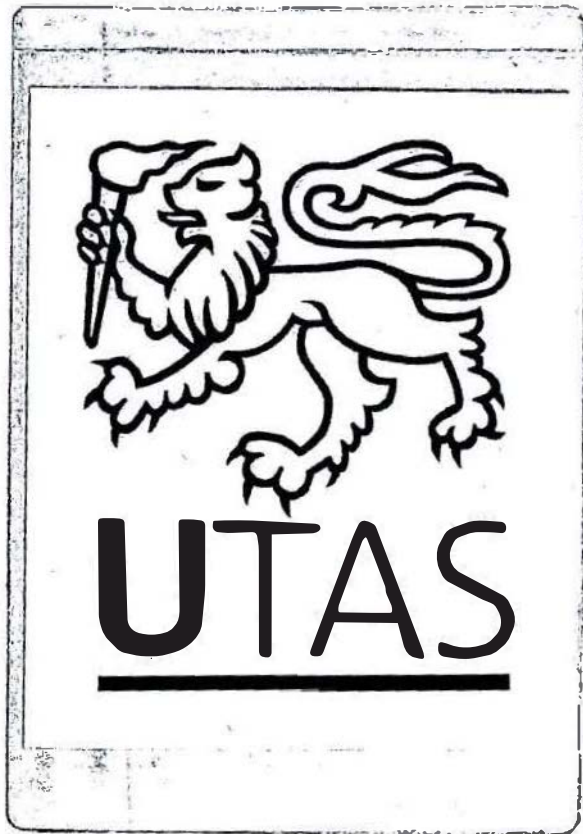
In contrast, the pattern of post-hatching mass change was not significantly different between the years in either species (Royal Penguins  $F_{2,685} = 1.8, P > 0.05$ , Rockhopper Penguins  $F_{2,565} = 0.3, P > 0.05$ ), nor was it between the species ( $F_{1,1258} = 0.4, P > 0.05$ ) (Fig 9.3). The mean decrease in mass while ashore for Royal Penguins was 17.9%, and 7% in Rockhopper Penguins.

There were significant differences in adult mass change between the sexes during creche stage in Royal Penguins ( $F_{1,506} = 6.0, P < 0.01$ , Fig. 9.4), but not in Rockhopper Penguins ( $F_{1,425} = 0.02, P > 0.05$ , Fig. 9.3). Male Royal Penguins entered creche stage at a lower mass than females, but gained more mass during the subsequent weeks.

The mass minus food data showed the same patterns as that above (Table 9.2). Royal



and Rockhopper Penguins had the lowest masses during late guard stage.



**Table 9.2** The mean mass  $\pm$  SD (kg) of Royal and Rockhopper Penguins during all stages and years of the study. **Significantly different**

Stage in breeding season	Royal Penguins Comparisons				Rockhopper Penguins Comparisons			
	1993/4	1994/5	1995/6	between years	1993/4	1994/5	1995/6	between years
Male return	5.4 $\pm$ 0.3	5.7 $\pm$ 0.4	6.1 $\pm$ 0.3	$F_{2,41} = 15.7$ $P < 0.001$	3.3 $\pm$ 0.1	3.6 $\pm$ 0.3	3.9 $\pm$ 0.2	$F_{2,10} = 7.7$ $P < 0.01$
Female return	5.1 $\pm$ 0.3	5.7 $\pm$ 0.3	5.5 $\pm$ 0.5	$F_{2,33} = 9.2$ $P < 0.001$	3.4 $\pm$ 0.2	3.8 $\pm$ 0.5	3.8 $\pm$ 0.3	$F_{2,35} = 5.0$ $P < 0.01$
Male incubation	4.6 $\pm$ 0.7	6.0 $\pm$ 0.3	5.8 $\pm$ 0.8	$F_{2,18} = 9.1$ $P < 0.002$	3.8 $\pm$ 0.2	4.2 $\pm$ 0.8	4.1 $\pm$ 0.5	$F_{2,12} = 0.4$ $P > 0.05$
Female incubation	5.0 $\pm$ 0.3	5.3 $\pm$ 0.6	5.3 $\pm$ 0.2	$F_{2,16} = 1.0$ $P > 0.05$	2.9 $\pm$ 0.2	3.3 $\pm$ 0.2	-	$t = 4.1$ $P < 0.003$
Early guard	4.4 $\pm$ 0.3	4.6 $\pm$ 0.3	4.3 $\pm$ 0.2	$F_{2,39} = 6.8$ $P < 0.003$	2.7 $\pm$ 0.2	2.9 $\pm$ 0.3	3.0 $\pm$ 0.3	$F_{2,29} = 4.9$ $P < 0.01$
Late guard	4.4 $\pm$ 0.3	4.6 $\pm$ 0.2	-	$t = 0.1$ , $P > 0.05$	2.3 $\pm$ 0.2	2.4 $\pm$ 0.2	-	$t = 0.9$ $P > 0.05$
Early creche	4.8 $\pm$ 0.6	5.0 $\pm$ 0.4	4.8 $\pm$ 0.3	$F_{2,45} = 0.7$ $P > 0.05$	2.3 $\pm$ 0.2	2.7 $\pm$ 0.5	2.8 $\pm$ 0.2	$F_{2,32} = 5.9$ $P < 0.007$
Mid creche	4.9 $\pm$ 0.3	5.0 $\pm$ 0.5	-	$t = 1.0$ $P > 0.05$	2.7 $\pm$ 0.4	3.0 $\pm$ 0.4	-	$t = 1.8$ $P > 0.05$
Late creche	4.9 $\pm$ 0.6	4.9 $\pm$ 0.4	5.0 $\pm$ 0.5	$F_{2,44} = 1.0$ $P > 0.05$	2.5 $\pm$ 0.3	2.9 $\pm$ 0.3	2.9 $\pm$ 0.3	$F_{2,42} = 14.6$ $P < 0.001$
Comparisons between stages	$F_{8,105} = 6.3$ $P < 0.001$	$F_{8,114} = 25.9$ $P < 0.001$	$F_{6,60} = 21.4$ $P < 0.001$		$F_{8,82} = 27.7$ $P < 0.001$	$F_{8,82} = 14.6$ $P < 0.001$	$F_{5,100} = 43.7$ $P < 0.001$	

**Fig. 9.2** Changes in mass of Royal ( $n = 975$ ) and Rockhopper ( $n = 594$ ) Penguins during the early part of the breeding season (prior to chicks hatching).

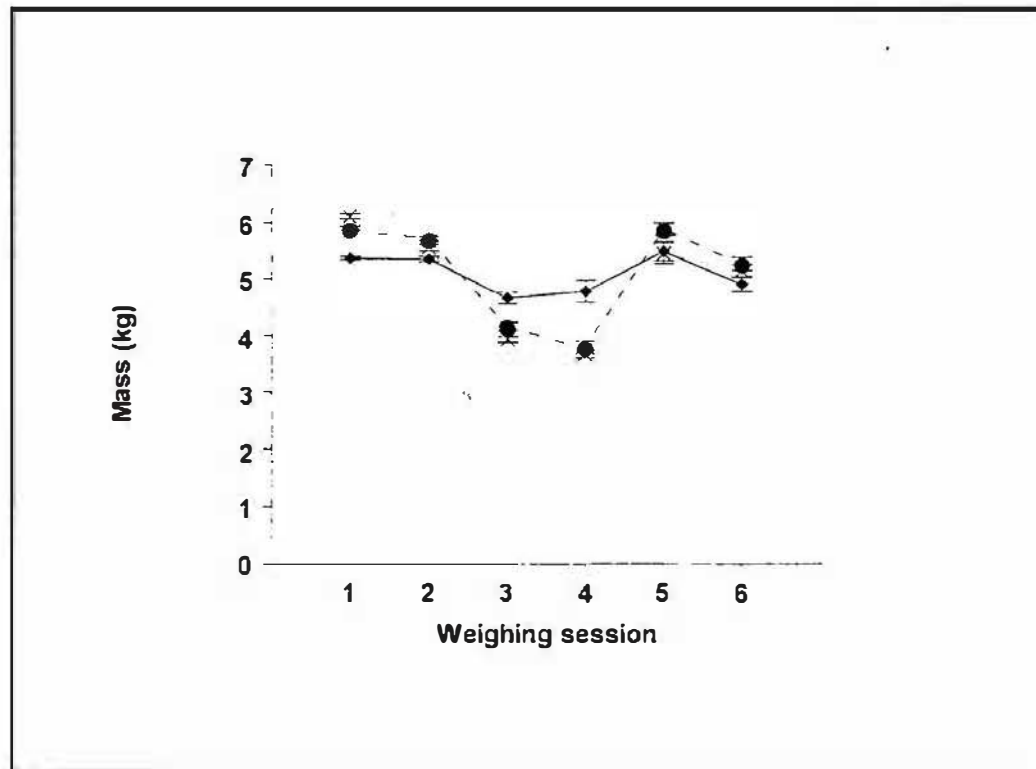
◆ — ◆ 1993/4

● - - ● 1994/5

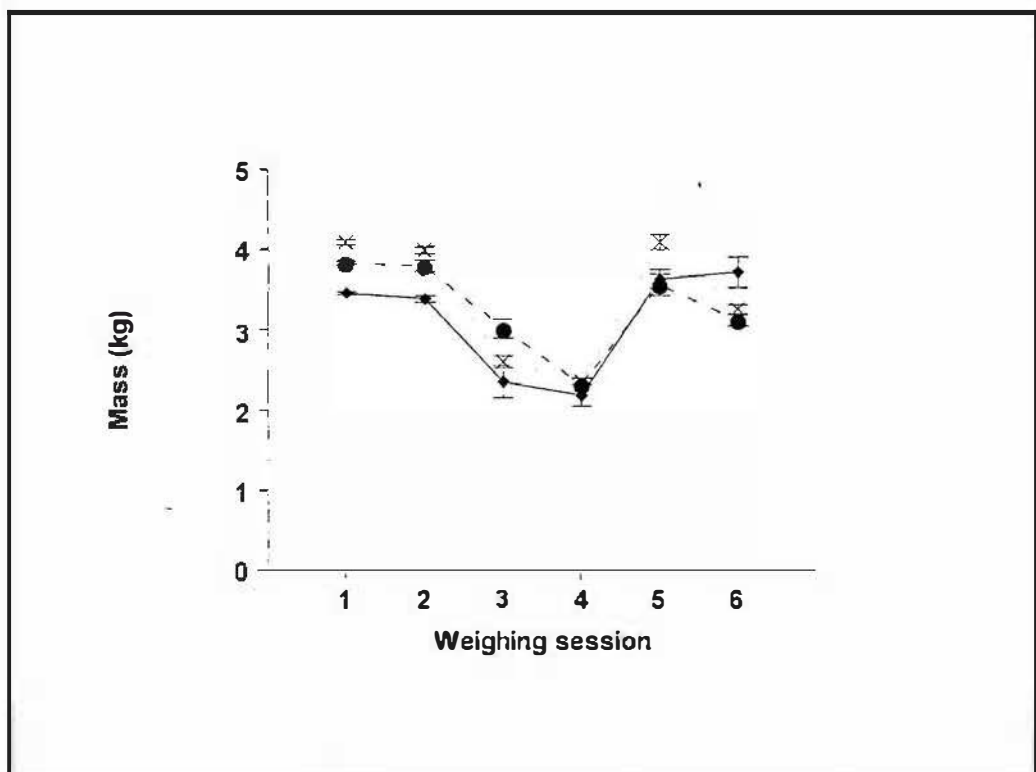
X ..... X 1995/6

1. Males return to the island
2. Females returning to the island
3. Males departing after long fast during incubation
4. Females departing after long fast during incubation
5. Males returning from long foraging trip during incubation
6. Females returning from long foraging trip during incubation

## Royal Penguins



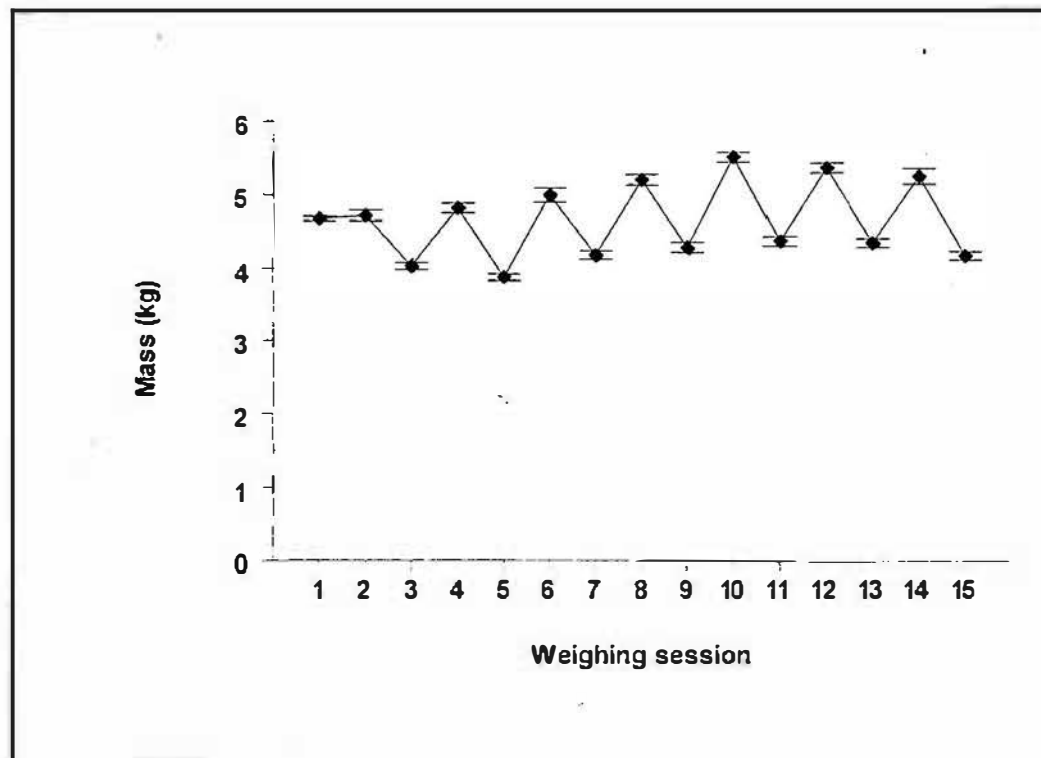
## Rockhopper Penguins



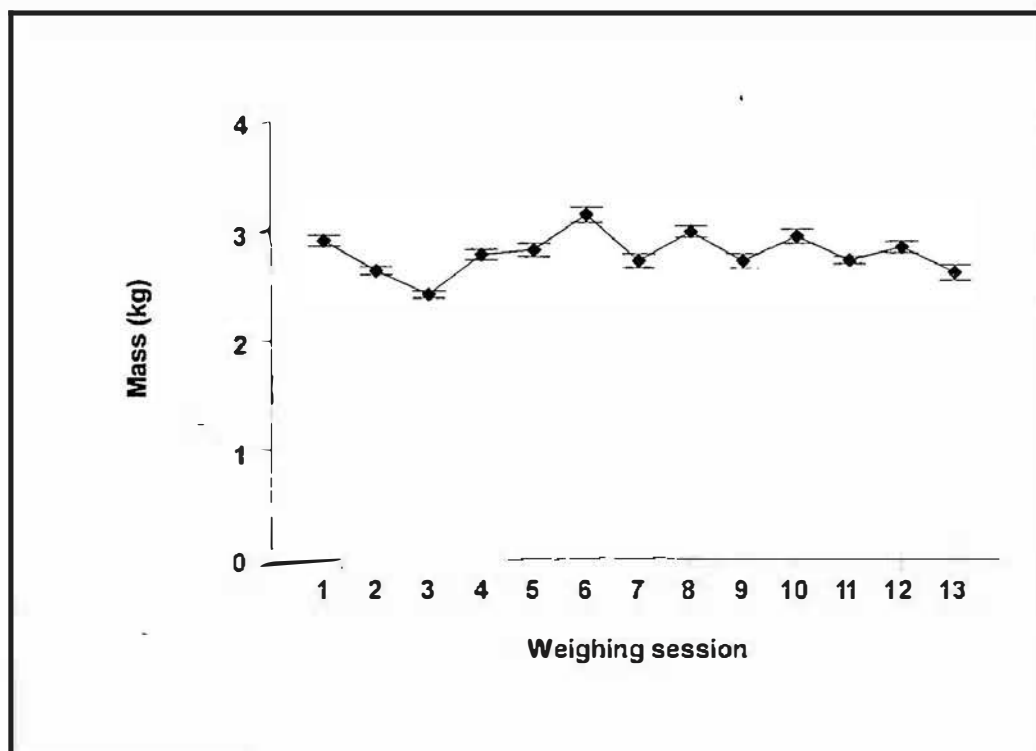
**Fig. 9.3** Changes in mass of Royal ( $n = 691$ ) and Rockhopper ( $n = 571$ ) Penguins following the hatching of chicks.

1. Guard stage females returning from foraging
2. Guard stage females returning from foraging
3. Guard stage females departing for foraging
4. Creche stage returning from foraging
5. Creche stage departing for foraging
6. Creche stage returning from foraging
7. Creche stage departing for foraging
8. Creche stage returning from foraging
9. Creche stage departing for foraging
10. Creche stage returning from foraging
11. Creche stage departing for foraging
12. Creche stage returning from foraging
13. Creche stage departing for foraging
14. Creche stage returning from foraging
15. Creche stage departing for foraging

## Royal Penguins



## Rockhopper Penguins





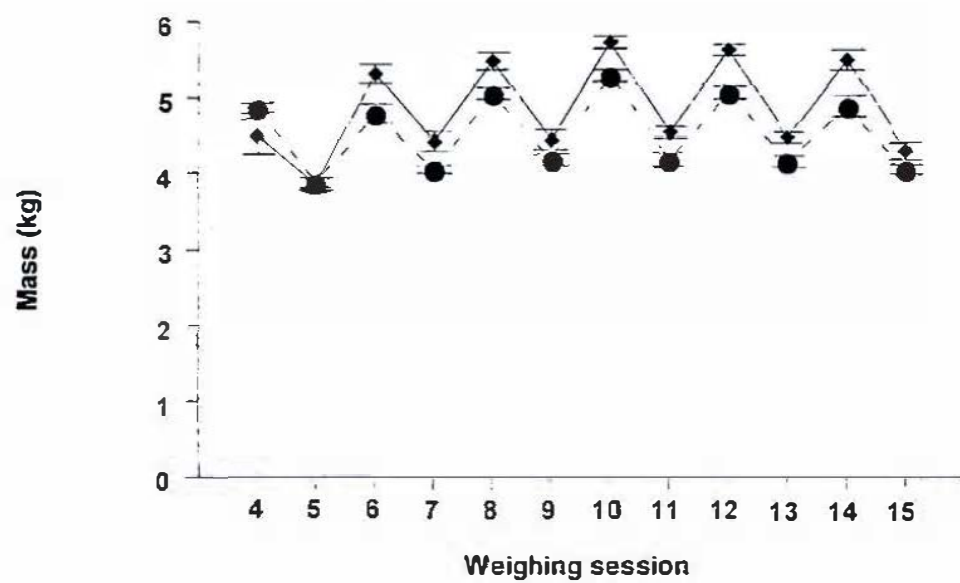
**Fig. 9.4** Comparison of mass changes in male ( $n = 194$ ) and female ( $n = 316$ )

Royal Penguins.

◆ — ◆ males

● - - ● females

4. Creche stage returning from foraging
5. Creche stage departing for foraging
6. Creche stage returning from foraging
7. Creche stage departing for foraging
8. Creche stage returning from foraging
9. Creche stage departing for foraging
10. Creche stage returning from foraging
11. Creche stage departing for foraging
12. Creche stage returning from foraging
13. Creche stage departing for foraging
14. Creche stage returning from foraging
15. Creche stage departing for foraging



*Parental attendance and foraging trip durations*

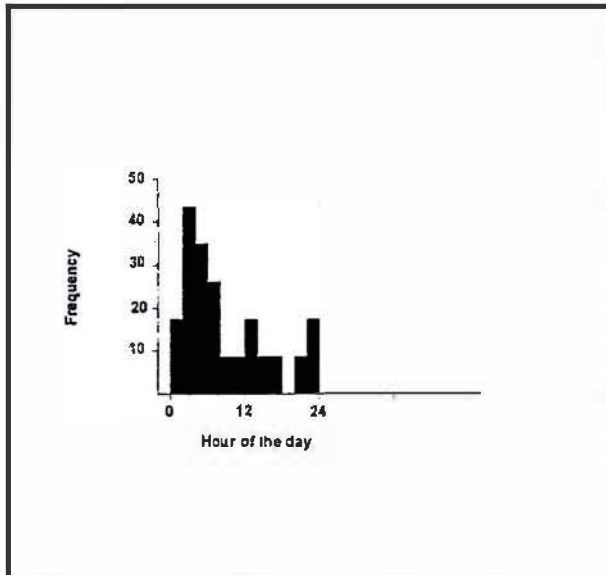
Foraging trip durations and parental attendance times are given in Table 9.3 and Fig. 9.5. Few data, and none of foraging trip durations, were available from the ATS system due to it being moved between colonies every two weeks. Foraging trips were longer during the incubation period in both species (Royal Penguins  $F_{2,47} = 171.6$ ,  $P < 0.001$ , Rockhopper Penguins  $F_{3,76} = 67.2$ ,  $P < 0.0001$ ). Other than females during incubation ( $t = 0.7$ ,  $P > 0.05$ ) Rockhopper Penguins undertook significantly shorter foraging trips throughout the breeding season than Royal Penguins (incubation - males  $t = 16.7$ ,  $P < 0.0001$ , guard  $t = 2.5$ ,  $P < 0.02$ , creche  $t = 8.4$ ,  $P < 0.0001$ ).

**Table 9.3** Foraging trip durations (days) and attendance times (hours) of Royal and Rockhopper Penguins. Mean  $\pm$  standard deviation are given for foraging trip durations, and mean (range) for attendance times

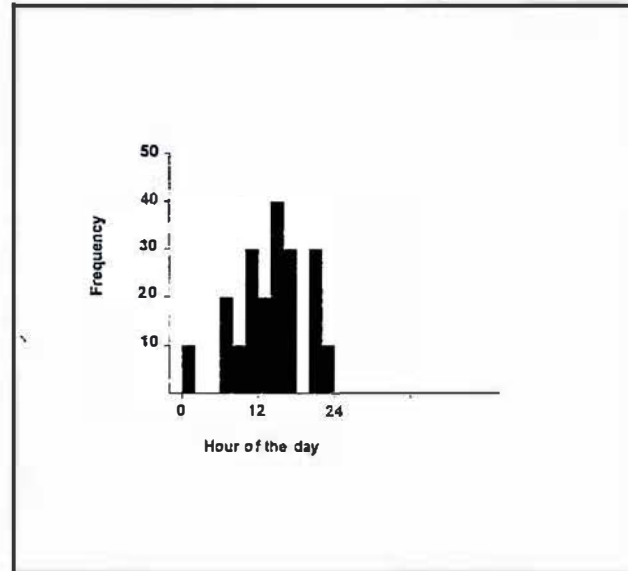
	<i>Royal Penguins</i>	<i>n</i>	<i>Rockhopper Penguins</i>	<i>n</i>
<u>Foraging trip durations</u>				
Incubation - males	22.9 ± 1.7	15	14.5 ± 0.9	12
Incubation - females	15.9 ± 2.6	9	10.4 ± 3.4	26
Guard	3.3 ± 1.5	4	5.8 ± 2.1	23
Creche	4.3 ± 2.9	6	3.7 ± 1.3	19
<u>Attendance times</u>				
Guard	10 (3 - 21)	11	7 (6 - 8)	2
Creche	10 (3 - 11)	8	112 (72 - 168)	3

**Fig. 9.5** Frequency distribution of the departure and return times of Royal and Rockhopper Penguins derived from the remote nest attendance recorder

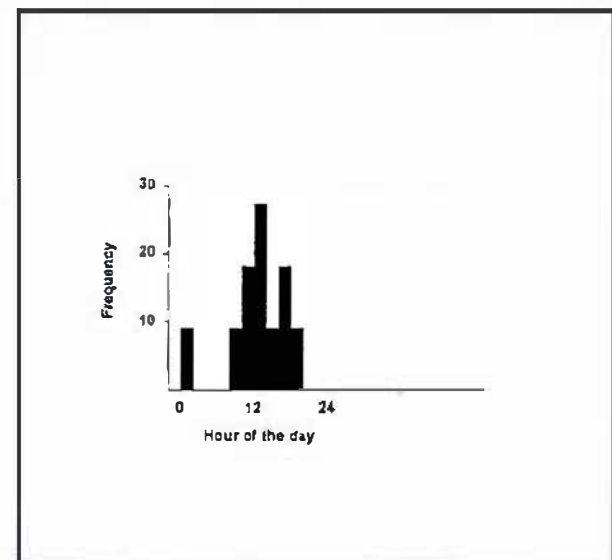
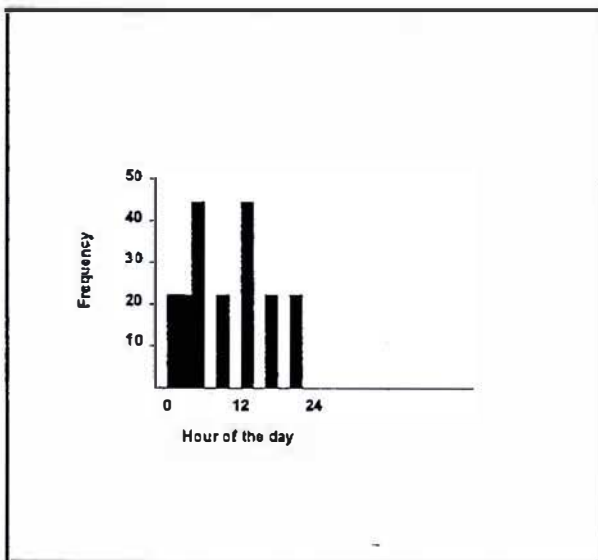
Departure times  
Royal Penguins



Return times



Rockhopper Penguins



*Breeding chronology*

Royal and Rockhopper Penguins showed considerable synchrony between individuals and years (Table 9.4). The duration of Rockhopper Penguin fasts was unlikely and suggests that some individuals departed the colony during the night.

**Table 9.4** Dates (median, except for first male return) of events in the breeding season of Royal and Rockhopper Penguins at Sandy Bay ( - not witnessed)

<i>Event</i>	<i>Royal Penguins</i>			<i>Rockhopper Penguins</i>		
	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>	<i>1993/4</i>	<i>1994/5</i>	<i>1995/6</i>
First males return	22/9	20/9	20/9	17/10	16/10	14/10
Females return	4/10	4/10	1/10	20/10	18/10	20/10
A eggs laid	19/10	18/10	18/10	14/11	13/11	14/11
B eggs laid	25/10	24/10	24/10	19/11	17/11	17/11
Males depart	26/10	27/10	26/10	29/11	27/11	27/11
Males return	11/11	12/11	12/11	6/12	5/12	6/12
Females depart	13/11	13/11	13/11	7/12	5/12	6/12
Females return	23/11	23/11	23/11	20/12	19/12	15/12
Chicks hatch	25/11	23/11	24/11	20/12	21/12	18/12
Chicks creching	20/12	20/12	22/12	14/1	15/1	13/1
Chicks fledge	1/2	30/1	31/1	24/2	21/2	22/2
Forage for moult	31/1	31/1	31/1	25/2	25/2	25/2
Return to moult	-	15/3	10/3	-	6/3	10/3
Depart the island	-	21/4	-	-	25/4	-
Duration of male fast (days)	34	37	36	43	43	41
Duration of female fast (days)	30	32	28	48	48	49
Duration of incubation (days)	31	30	30	31	32	29
Duration of chick rearing (days)	66	68	68	66	64	69



*Egg morphometrics*

There were no significant differences between the years in the dimensions of either A or B eggs in either species (Table 9.5).

**Table 9.5** Dimensions of A (first laid) and B (second laid) eggs of Royal and Rockhopper Penguins. Results of statistical comparisons between the three years are shown (all non-significant,  $P > 0.05$ ). \* per Warham (1975)

<i>Dimension</i>	<i>Royal Penguins</i>	<i>F value</i>	<i>n</i>	<i>Rockhopper Penguins</i>	<i>F value</i>	<i>n</i>
A length (cm)	$7.2 \pm 0.5$	$F_{2,96} = 1.5$	99	$6.5 \pm 0.4$	$F_{3,138} = 0.6$	141
A width (cm)	$5.3 \pm 0.5$	$F_{2,96} = 1.8$	99	$4.9 \pm 0.2$	$F_{3,136} = 1.9$	141
A mass (g)	$116.7 \pm 25.6$	$F_{2,96} = 1.8$	99	$88.2 \pm 13.8$	$F_{3,136} = 1.9$	139
B length (cm)	$7.8 \pm 0.4$	$F_{2,116} = 0.4$	119	$7.1 \pm 0.3$	$F_{3,127} = 0.5$	130
B width (cm)	$5.9 \pm 0.3$	$F_{2,116} = 0.3$	119	$5.3 \pm 0.3$	$F_{3,127} = 0.2$	130
B mass (g)	$150.4 \pm 21.2$	$F_{2,116} = 0.4$	119	$115.2 \pm 14.8$	$F_{3,126} = 0.1$	129
Mean egg dimorphism *	1.34	-	-	1.27	-	-
Clutch mass (% female, overall)	6.3	-	-	7.0	-	-

There were significant differences in the investment of A eggs between the species ( $t_2 = 4.5$ ,  $P < 0.05$ ), and in the investment of B eggs ( $t_{90} = 4.7$ ,  $P < 0.0001$ ). Rockhopper Penguin B eggs were 4.2% of female mass, compared to 3.6% in Royal Penguins, while A eggs were 2.5% and 3.1% of female Royal and Rockhopper Penguin mass, respectively. When egg masses were scaled for the different size of adults, the

investment in A eggs was not significantly different between the species ( $F_{1, 42} = 3.7$ ,  $P > 0.05$ ), but was in B eggs ( $F_{1, 90} = 20.8$ ,  $P < 0.0001$ ).

### *Chick growth*

Hatching masses of Royal Penguin B chicks and Rockhopper Penguin A and B chicks are given in Table 9.6.

**Table 9.6** Hatching masses (g) of Royal and Rockhopper Penguins. No Royal Penguin A eggs hatched during this study

<i>Penguin and chick</i>	<i>n</i>	<i>Mean <math>\pm</math> standard deviation (g)</i>
Royal B	11	103.4 $\pm$ 10.2
Rockhopper A	8	67.5 $\pm$ 8.4
Rockhopper B	25	82.6 $\pm$ 8.5

Both maximum masses and maximum growth rates of Royal and Rockhopper Penguin chicks did not differ between the species (Table 9.7). Chick growth rates were also the same during all years, except 1994/5. Rockhopper Penguins grew at a slower rate during this year (Fig. 9.6).

### *Fledging mass*

There were no significant differences in the masses at which chicks fledged between years in Royal Penguins ( $F_{2, 304} = 0.1$ ,  $P > 0.05$ ), but there were in Rockhopper Penguins

( $F_{2, 175} = 6.5$ ,  $P < 0.002$ ), with chicks from 1995/6 fledging at significantly higher masses than the other two years (Table 9.8).

**Table 9.7** The parameters derived from the Gompertz equations for Royal and Rockhopper Penguin chick growth rates in each year of the study

A = asymptote (maximum mass)

B = growth rate

C = maximum growth rate

<i>Parameter</i>	<i>Year</i>	<i>Royal</i>	<i>Penguins</i>	<i>Rockhopper</i>	<i>Penguins</i>
		<i>lower 95%</i>	<i>upper 95%</i>	<i>lower 95%</i>	<i>upper 95%</i>
A	1993/4	4.253	4.974	2.357	2.593
B		0.301	0.410	0.381	0.485
C		1.749	5.351	4.227	4.596
A	1994/5	4.045	4.557	1.918	2.510
B		0.427	0.578	0.252	0.408
C		4.659	5.048	3.959	5.011
A	1995/6	4.464	5.539	2.456	2.816
B		0.261	0.378	0.323	0.434
C		5.107	5.978	4.547	5.078

**Fig. 9.6** Growth rates of Royal and Rockhopper Penguin chicks from hatching to just prior to fledging.

Royal Penguins all years combined

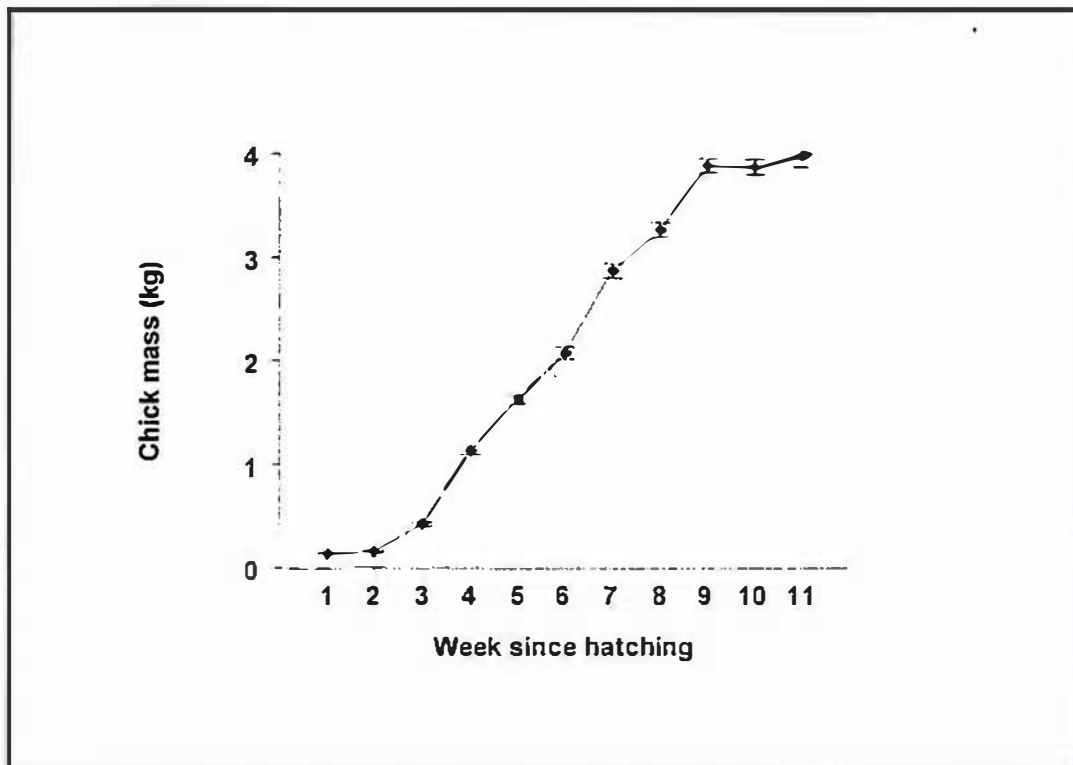
Rockhopper Penguins

◆-◆ 1993/4

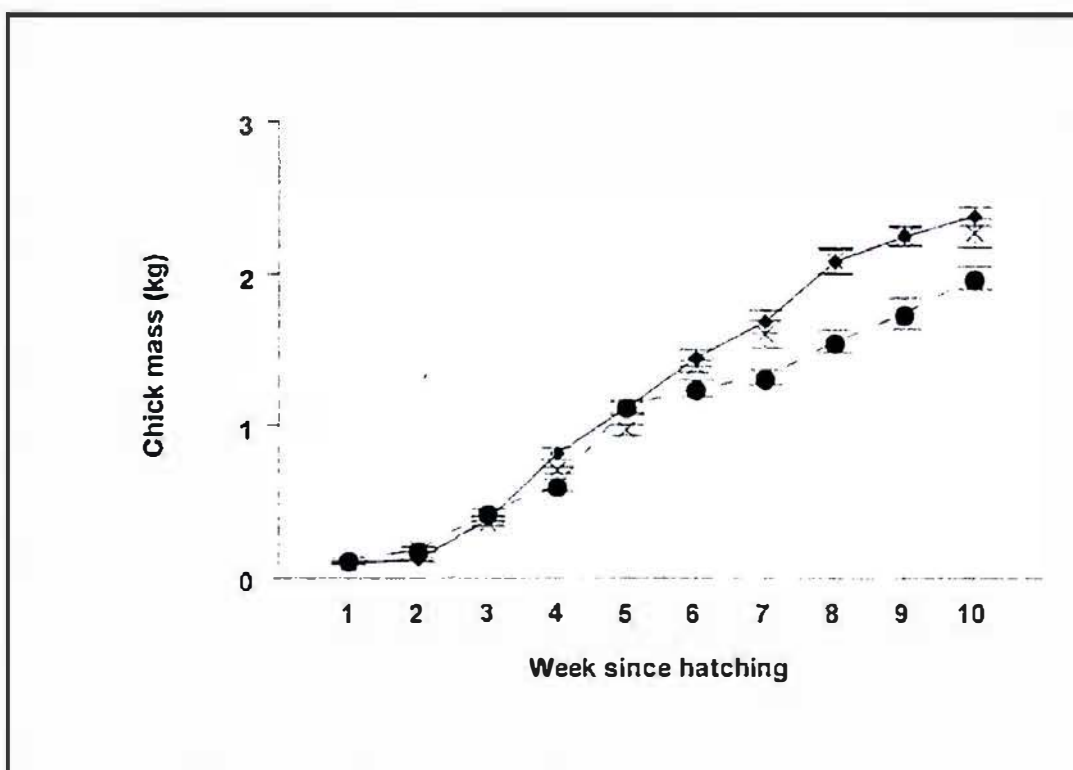
○-○ 1994/5

X...X 1995/6

## Royal Penguins



## Rockhopper Penguins





**Table 9.8** Fledging masses of Royal and Rockhopper Penguin chicks

<i>Penguins</i>	<i>n</i>	<i>Mean mass <math>\pm</math> standard deviation (kg)</i>
Royal all years	307	$3.6 \pm 0.3$
Rockhopper 1993/4	35	$2.2 \pm 0.2$
Rockhopper 1994/5	34	$2.3 \pm 0.4$
Rockhopper 1995/6	109	$2.4 \pm 0.2$

Royal Penguin chicks were 78.3% of the adult average mass at fledging, whilst Rockhopper Penguin chicks were 82.1% of the adult average mass.

#### *Breeding success*

No Royal Penguin A eggs hatched and were presumably ejected prior to the laying of the B eggs (St Clair & St Clair 1996). Further, no Rockhopper Penguins successfully raised chicks from A eggs during any year. The majority (Royal Penguins B eggs 94.3%, Rockhopper Penguin A eggs 98.0%, B eggs 79.7%) of nest failures occurred during the incubation period and the reasons for these failures are given in Table 9.9.

**Table 9.9** Observed causes of breeding failures in Royal and Rockhopper (RH) Penguins. As no Royal Penguin A eggs were incubated beyond the first 4 days, the data are only for B eggs

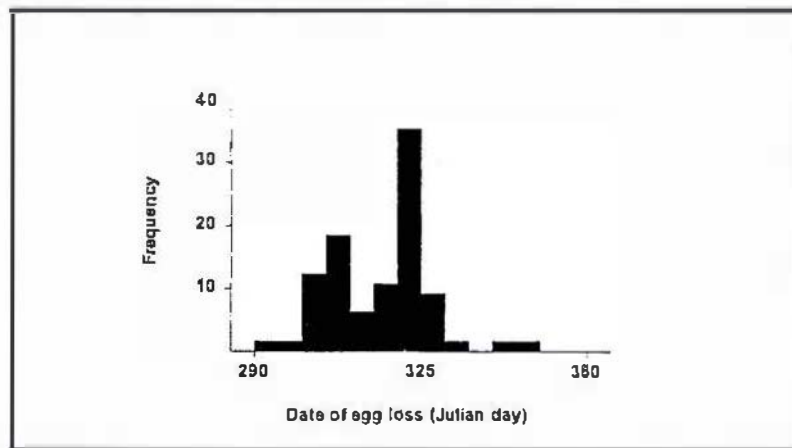
(Total laid)	Deserted	Predation of egg	Broken egg	Rolled away	Never hatched	Chick died	Predation of chick	unknown
Royal (70)	24	40	1	0	1	0	4	0
RH A (150)	2	107	1	8	2	2	1	27
RH B (79)	5	48	2	2	1	2	14	5

The dates of egg losses are given in Fig. 9.7. The peak in egg loss for Royal Penguins was Julian day 305 (November 1) and day 320 (November 16). Rockhopper A eggs were lost primarily around days 320, 340 and 350 (December 6 - 16), and B eggs from days 330 to 350 (November 26 - December 16).

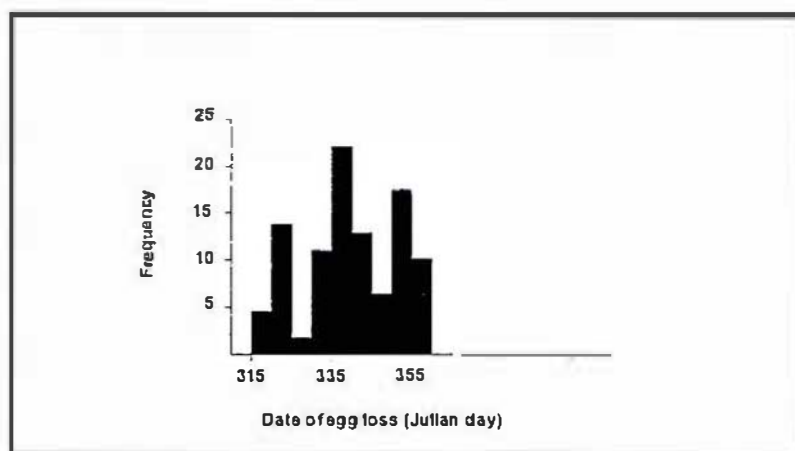
Breeding success (to fledging) was 53.3% in Royal Penguins and 47.3% in Rockhopper Penguins, and was constant between the years (Royal Penguins  $\chi^2_2 = 0.03$ ,  $P > 0.05$ ; Rockhopper Penguins  $\chi^2_2 = 1.5$ ,  $P > 0.05$ ). There were no significant differences in breeding success between the species ( $\chi^2_2 = 0.6$ ,  $P > 0.05$ ).

**Fig. 9.7** Frequency distribution of the dates when Royal Penguin B eggs, and Rockhopper Penguins A and B eggs were lost

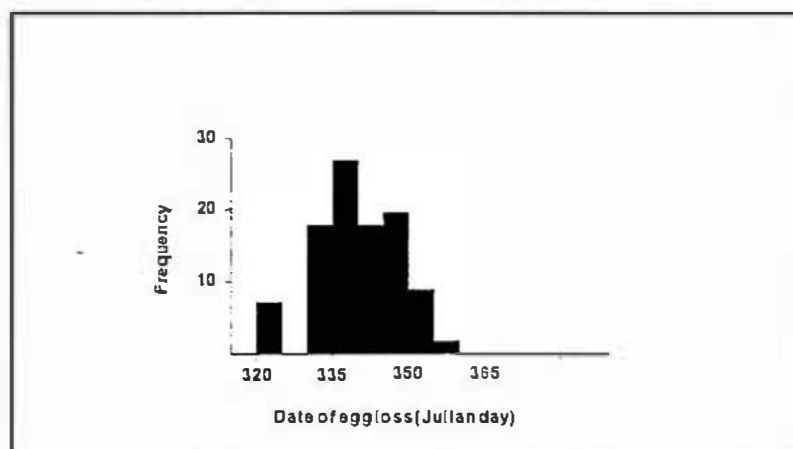
### Royal Penguin B eggs



### Rockhopper Penguin A eggs



### Rockhopper Penguin B eggs



There were no significant differences in breeding success across different transects in either species (Royal Penguins  $\chi^2_2 = 0.2$ ,  $P > 0.05$ ; Rockhopper Penguins  $\chi^2_1 = 0.2$ ,  $P > 0.05$ ), nor between Royal Penguin nests on the periphery of the colony and those centrally located ( $\chi^2_2 = 0.1$ ,  $P > 0.05$ ). However, Rockhopper Penguin breeding success differed between peripheral and central nests ( $\chi^2_1 = 4.2$ ,  $P < 0.05$ ), with those on the periphery less successful (22.0%) than those centrally located (55.3%). There were no significant differences in the breeding success of Rockhopper Penguin nests found in different microhabitats ( $\chi^2_3 = 2.5$ ,  $P > 0.05$ ).

There were no significant differences in breeding success of pairs that carried transmitters compared to unencumbered birds in either species (Royal Penguins  $\chi^2_2 = 0.8$ ,  $P > 0.05$ ; Rockhopper Penguins  $\chi^2_2 = 2.2$ ,  $P > 0.05$ ), indicating that the attachment of a transmitter to each individual of a pair did not have a deleterious effect on this parameter.

A summary of the differences between Royal and Rockhopper Penguin breeding variables assessed in this study is given in Table 9.8.

**Table 9.8** Summary of the breeding biology variables examined during the study, with significant differences between years of the study and species indicated by an asterix (\*)

<i>Variable</i>	<i>Inter-annual comparisons</i>		<i>Species comparisons</i>
	<i>Royal</i>	<i>Rockhopper</i>	
Mass	*	*	*
- pre-hatching	lowest 1993/4	highest 1994/5	RH greater loss after fasting
- post-hatching	-	-	-
Foraging trip durations	-	-	*
			Royals > RH
Breeding chronology	-	-	*
			RH fasted longer
Eggs	-	-	RH > investment B eggs
Chick growth patterns	-	-	Royals > RH
Fledging masses	-	* 1995/6 chicks heavier	RH > in relation to adults
Breeding success	-	-	-
egg losses	-	-	Royals: mate return RH: predation

#### 9.4 Discussion

Royal and Rockhopper Penguins, like other members of the crested penguins, exhibit a great deal of similarity in several aspects of their breeding biology. Minor exceptions to other species in this group are differences in the duration of foraging trips prior to



moulting (Williams & Croxall 1991). This genus differs to other groups of penguins in having a longer laying period and a second egg which hatches before the first (Williams 1981, Williams & Croxall 1991). Unlike other groups of penguins, females undertake the first incubation shift, and it is only the female that provisions chicks with food during guard stage (Warham 1975).

Some differences in aspects of breeding biology exist between Royal Penguins and the closely related Macaroni Penguin *E. chrysolophus*. Royal Penguins only undertake two incubation shifts, one by the female and one by the male, whilst Macaroni Penguins at South Georgia undertake three shifts with the first carried out by both sexes (Williams & Croxall 1991). This results in Royal Penguins undertaking longer foraging trips which would probably allow larger distances to be travelled during foraging. Further, the extended fasting periods during incubation probably have different physiological effects on the two species. Royal Penguins may have lost greater condition making them more vulnerable to the late return of mates than Macaroni Penguins are. This difference between these two closely related species may be a proximate response to the availability of prey resources surrounding the two localities, or may relate to the small size difference between the species.

#### *General breeding biology of Royal and Rockhopper Penguins*

The synchrony between individuals and years in the breeding chronology of Royal and Rockhopper Penguins has been described previously (Gwynn 1953, Warham 1971, 1972), and has been found in other subantarctic eudyptid penguins (Williams & Croxall

1991). It is no doubt linked to the restricted breeding window available to these species, due to climatic conditions (Croxall & Prince 1980a). This hypothesis is supported by correlations between the sea surface temperature at which the penguins breed and laying dates. Rockhopper Penguins breed 10 days later for every 1° C decline in sea surface temperature (Warham 1971, 1972). The Royal/Macaroni Penguin complex exhibits a similar trend, with the more southerly Macaroni Penguin breeding later than Royal Penguins (Croxall & Prince 1980a).

Like other species of penguins, the total investment in clutches by Royal and Rockhopper Penguins was low compared to other birds (Lack 1968, Williams 1990). This small investment in clutches may be due to the difficulties in obtaining sufficient food during the breeding season (Lack 1968), hence penguins have adjusted to a minimum reproductive output (Ricklefs 1983). Although Royal and Rockhopper Penguins laid two eggs, only one chick was ever raised to fledging, as has been found previously (Warham 1975). As these are fairly long-lived species (Marchant & Higgins 1990), this may be a low risk breeding strategy that is advantageous when faced with unpredictable food resources.

For both species, changes in mass throughout the breeding season followed a regular pattern with birds returning to the island with the greatest mass, and losing the largest quantity during fasts. Assessing mass minus food indicated that the lowest weights occurred during guard stage. This stage, therefore, appeared to be the most energetically taxing for both species, as has been found in other seabirds (Ricklefs

1983). Adélie Penguins *Pygoscelis adeliae* retain the minimum amount of food for themselves during this stage, and therefore, lose mass. Following creching, adult masses increase as more food is allocated to adult maintenance (Wilson *et al.* 1991b, Culik 1994). The foraging by only female Royal and Rockhopper Penguins during guard stage when chicks are small and require food on a regular basis, most likely allows little foraging time for adult maintenance.

Breeding success during the three years of this study was higher than in some previous studies of penguins (Carrick & Ingham 1970, Smith 1970, Williams & Stone 1981, Davis *et al.* 1989), suggesting the abundance and availability of prey was probably not a limiting factor. Only Royal Penguins at a small west coast colony on Macquarie Island, and Rockhopper Penguins at Tristan da Cunha have exhibited a higher breeding success (54% and 51%, respectively) (Williams & Stone 1981, Hindell *et al.* 1996).

Nest failures in Royal and Rockhopper Penguins at Macquarie Island occurred primarily during incubation. Royal Penguin A eggs were lost during the 4-day interval in egg laying, and were probably ejected by the female (St Clair *et al.* 1995). The majority of Royal Penguin B, and Rockhopper Penguin A and B egg losses were due to Great Skua *Catharacta skua* predation. Predation by Southern Giant Petrels *Macronectes giganteus* and destruction of nests by Southern Elephant Seals *Mfrounga leonina* were not important causes of death of pre-fledged chicks, although they have been found to be important in other studies (Warham 1971). There was an indication of a higher proportion of Rockhopper Penguin (71%) than Royal Penguin eggs (57%) lost to

predation by skuas.

The higher predation of Rockhopper Penguin eggs by skuas may be a function of: (1) the smaller eggs of Rockhopper Penguins which are presumably easier for predators to remove and depart the colony with, (2) the smaller size of Rockhopper Penguins thereby reducing their ability to defend their nest from predation as effectively as larger species, or (3) Rockhopper Penguins attempting to incubate two eggs, with the A egg incubated in a different position than the B egg, making it more prone to predation (Burger & Williams 1979). All these factors may have some importance but further investigation is required to determine the extent.

The differences in breeding success between Rockhopper Penguin peripheral and central nests may also reflect their greater vulnerability to predation pressure from Great Skuas. Predation pressure on the edge of colonies has been found to be an important variable in breeding success in other species of bird (Frere *et al.* 1992, Emslie *et al.* 1995). The resultant lower breeding success at peripheral nests makes them of poorer quality, with competition for central nests high. The ability to hold higher quality nests is thought to be positively related to age (Zack & Stutchbury 1992).

The lack of difference in breeding success between central and peripheral nests in Royal Penguins may have been due to less predation pressure at this colony compared to the Rockhopper Penguin colony.

Royal Penguin egg losses tended to occur when males returned late from the long foraging trip following fasting, resulting in females abandoning the breeding attempt. Late return of mates has also been attributed to breeding failures in other species of penguin (Davis, L.S. 1982, 1988, Ainley *et al.* 1983, Trivelpiece *et al.* 1983, Y. Le Maho unpubl. data), and is probably triggered by fasting birds reaching a threshold mass, which prompts re-feeding (Cairns 1992). In King Penguins *Aptenodytes patagonicus* there is a decrease in protein and adipose tissue during fasting until a critical level is reached (half the body protein). Unless relieved by mates, King Penguins will abandon nests at approximately 9 kg, thereby prioritising adult survival over that of the egg or chick (Y. Le Maho unpubl. data).

The arrival and departure times of both species confirmed that they were diurnal foragers (Chapter 7). The duration of foraging trips was longer during incubation, possible because the penguins did not have to return regularly to the colony to feed chicks. Rockhopper Penguins undertook longer foraging trips in this study compared to previous studies (Williams 1982). The possibility that some Rockhopper Penguins returned to the colony at night outside the hours of observation and hence were missed cannot be eliminated. Therefore, until a closer examination is made of trip durations either through 24 hour observation or using electronic surveillance, the trip durations of Rockhopper Penguins must be viewed with caution.

#### *Differences between the species*

Rockhopper Penguins lost more mass during incubation than did Royal Penguins, which



is most likely related to the former's smaller size. A mass-specific relationship has been found with metabolic rate, with penguins scaling at 0.74 to the power of body mass (Croxall 1982). This results in Rockhopper Penguins expending more energy than Royal Penguins during incubation. At Marion Island a 2.77 kg Rockhopper Penguin, for example, expended 7014 kJ/day, compared to 1031.8 kJ/day in a 4.84 kg Macaroni Penguin (Brown 1984). These latter estimates, however, are based on birds that were isolated from the colony, and hence do not include energy expenditure related to agonistic interactions with other individuals (Davis *et al.* 1989).

The larger mass of eggs as a proportion of female mass, and the fact that Rockhopper Penguin chicks fledged at a relatively larger size than did Royal Penguin chicks, suggests that the former species invested more energy in the breeding attempt. The quantity of food brought ashore for chicks (Chapter 8) was the same between the species except during 1993/4, implying that the greater investment in breeding by Rockhopper Penguins is only in the larger eggs and proportionately longer chick rearing period. The similarities in growth rates of chicks between the species tends to reinforce this contention, and is contrary to the suggestion that growth rates of birds are related to their size, with larger species having slower rates (Ricklefs 1973).

Royal Penguins undertook longer foraging trips in all stages except during incubation (females). This would facilitate foraging further offshore, as has been found in estimated foraging zones and dietary differences (Chapters 6 and 8). The larger size of Royal Penguins would enable a larger quantity of food (although not proportionately)



to be brought ashore than the smaller Rockhopper Penguin, hence chicks could be fed larger, less frequent meals, and adults could make less regular visits to the colony.

During 1994/5 Royal Penguin chicks grew at a faster rate than did Rockhopper Penguin chicks. This suggests differences in foraging success and the ability of adults to provision chicks with food, which could be related to either differential foraging zones and access to different prey stocks, or differential foraging abilities. Comparisons of foraging zones of the two species suggests the former is more likely.

#### *Inter-annual comparisons*

Little inter-annual variability was found in breeding parameters in this study. Differences were found in adult pre-hatching masses and fledging masses of Rockhopper Penguins. Differences in fledging masses in Rockhopper Penguins did not correlate with differences in the quantity of food brought ashore, but may have had some relationship with the degree of digestion of prey, which is an indication of how far afield birds had to forage for food (Chapter 8). However, these differences were not reflected in breeding success.

The inter-annual differences in adult arrival mass in both species suggest differential foraging success during the winter, non-breeding period. This difference in arrival rates was not reflected in other breeding parameters such as breeding success and indicates that arrival rates in these species are not a good predictor of breeding success, as they may be in other species (Williams & Stone 1981).

The value of adult arrival mass as a predictor of breeding success is most likely related to whether species are "capital" or "income" breeders (Drent & Daan 1980). Capital breeders, are those that build up substantial reserves which they rely on during breeding season. These species are more susceptible to breeding failure if food is in short supply during the early part of the breeding season. Capital breeders tend to be longer-lived species, such as petrels, and if sufficient body reserves are not acquired do not partake in a breeding attempt (Carrick 1972, Drent & Daan 1980, Chastel *et al.* 1995a). Conversely, income breeders are less reliant on reserves acquired prior to the breeding season, but continually replace lost body condition throughout the season. These species tend to be shorter-lived and the strategy necessitates foraging inshore (Drent & Daan 1980).

The more inshore foraging behaviour and less vulnerability to the late return of mates in Rockhopper Penguins may indicate that they may be less capital breeders than Royal Penguins. If this is the case, the breeding success of the two species will be affected slightly differently during years when the abundance and availability of prey is low.

Adélie and Chinstrap *P. antarctica* Penguins behaved as capital breeders with an apparent shortage in food supply early in the breeding season not allowing adults to recover from fasts in time to relieve mates. Conversely, Gentoo Penguins *P. papua* fed inshore and were not affected by shortages early in the breeding season, with the latter species and therefore have a different means of dealing with years of low food availability (Trivelpiece *et al.* 1983). Galapagos *Spheniscus mendiculus*, African *S.*

*demersus* and Humboldts *S. humboldti* Penguins behaved more like capital breeders, and did not breed if prey resources were scarce early in the season, but once they began breeding were committed to the attempt. Magellanic Penguins *S. magellanicus* on the other hand were more like income breeders and did not exhibit this same flexibility in deferring the breeding attempt, and were found to be much more variable in breeding success and chick growth rates (Boersma *et al.* 1990).

The lack of inter-annual differences in the majority of breeding parameters suggests that: (1) Royal and Rockhopper Penguins were less vulnerable than other species to changes in the biotic and abiotic aspects of the marine environment; or (2) that the three years of this study were relatively similar in conditions. The high breeding success experienced by these two species relative to previous studies indicates that these years may have been three "good" ones where food abundance and availability was relatively high. Therefore, the situation may be the same as it is for Yellow-eyed Penguins *Megadyptes anti podes*, where differences in growth rates and breeding success were not detected until it was a very "poor" season (van Heezik & Davis 1990).

Although differences were detected in sea surface temperatures around Macquarie Island during this study (Chapters 5 and 6), there were no large warm water anomalies (see Fig. 1 of White & Peterson 1996). As the ACW operates on a periodicity of 4 - 5 years, presumably warm water anomalies will be in the vicinity of Macquarie Island over the subsequent few seasons. The impact of these anomalies on prey stocks and Royal and Rockhopper Penguins can then be examined.

Assessment of the breeding parameters during "poor" years will be instructive in determining the relationship between aspects of the breeding biology of these species and the abiotic marine factors. Such investigations will also enable a closer examination of the hypothesis that Royal and Rockhopper Penguins differ in their degree of capital versus income breeders. It is possible, for example, that the two species may exhibit differential vulnerability to good and bad years, linked with biotic and abiotic aspects of the marine environment.

### 9.5 Summary

Aspects of the breeding biology (adult mass changes over the season, parental attendance and foraging trip durations, egg morphometrics, chick growth and breeding success) were compared between Royal and Rockhopper Penguins over three years. Both species exhibited very similar breeding biology to other species of eudyptid penguins, and a great deal of synchrony in breeding chronology between individuals and between years. Mass changes suggested that the most taxing time for both species was during guard stage, when only the female is foraging for food for chicks. Rockhopper Penguins lost a greater proportion of mass during incubation, had a greater investment in clutches and had shorter foraging trips than Royal Penguins. There was also an indication that breeding failures in Rockhopper Penguins were more related to skua predation, whilst in Royal Penguins the primary cause was late return of mates. Few inter-annual differences were found in either species, with only arrival masses varying and fledging masses in Rockhopper Penguins. It is concluded that these two species, whilst being very similar, may differ in the degree they are capital versus income

breeders, and that the three years of this study were probably "good" years. Further research conducted during "poor" years would be instructive in determining if there are differential impacts on Royal and Rockhopper Penguins.

## **9.6 Acknowledgments**

I would like to thank Mary-Anne Lea, Jane Wilson, Kirsten Le Mar and Paul Scofield for assistance in the field. Mark Hindell, Melissa Geise and Di Moyle all made valuable comments on drafts of the manuscript, for which I am grateful. Funding was provided by the Antarctic Scientific Advisory Committee, SeaWorld Research and Rescue Foundation and the Trans-Antarctic Association, to all of whom I would like to express my appreciation. Work was carried out under Macquarie Island special permits MII/34/94, MII/3/95 and MII/13/96.

## Chapter 10

### General Discussion

#### 10.1 Objectives of the study

Penguins (Sphenisciformes) are taxonomically and ecologically distinct from other seabirds, and are well adapted to, and reliant upon, the marine environment where they spend the bulk of their time (Stonehouse 1967). They constitute the majority of the avian biomass in the antarctic and subantarctic and are therefore important components of these ecosystems (Prevost 1981, Croxall 1984, Croxall & Lishman 1987). Describing the ecology of penguins is, therefore, fundamental to understanding and managing these environments. However, until the recent development of data logging and telemetric techniques, little was known about their foraging ecology and interactions with biotic and abiotic aspects of the marine environment.

The foraging ecology of penguins is influenced by a number of factors. Many species in the higher latitudes have a limited temporal window in which they can breed due to the harsh climate (Croxall & Prince 1980a, Furness & Birkhead 1984). For a number of species this results in highly synchronous breeding timetables both within individuals and between species. This presumably places a great deal of pressure on food resources in the vicinity of colonies (Ashmole 1971). Commitments at the nest and being flightless restricts the duration of foraging trips and the extent of foraging zones during



the breeding season. Food resources are potentially limiting around colonies, and demand for them is presumably further increased when two or more ecologically similar species breed sympatrically (Croxall & Prince 1980a, Cooper *et al.* 1990, Hindell *et al.* 1995). These demands for food resources have led to speculation that in order to co-exist species must minimise the degree of overlap in resource use by segregating aspects of their foraging ecology. The proximate factors that may differ between species are hypothesised to be: (1) Foraging zones (the three dimensional use of the ocean); (2) Diet; or (3) Breeding timetables (Croxall & Prince 1980a, Brown & Klages 1987, Cooper *et al.* 1990, Hindell *et al.* 1995).

These hypothesised factors were tested on two sympatrically breeding species of penguin, Royal *Eudyptes schlegeli* and Rockhopper *E. chrysocome* Penguins. These species are taxonomically and ecologically similar and breed sympatrically on subantarctic Macquarie Island. Little was known about the foraging ecology of Royal and Rockhopper Penguins, and this thesis had the dual aim of describing their foraging ecology and testing the above hypotheses. The following variables were examined: foraging zones, diving behaviour, diet and breeding biology (in particular the asynchrony in breeding timetables). These aspects were examined in a multi-year framework in order to assess inter-annual variability.

## 10.2 Results of the study

The thesis was divided into two sections, the first describing methodological aspects of the study, and the second, the foraging ecology of, and overlap in resource use between,

the species.

### Section A Methodological aspects

The use of morphometric indices to allocate individuals to sex was important in this study. Although some work had been carried out on their morphometrics, an analysis of the most reliable indices and development of discriminant function formulae to identify the sex of individuals in the field had not been undertaken. Both species were sexually dimorphic and could be allocated to sex with an accuracy of 97% and 93% in Royal and Rockhopper Penguins respectively (Chapter 2). An important finding of this study was that the morphometric data differed to those collected previously, although the same indices were used. This highlighted the need for care when morphometrics of species or populations are compared using data collected by different individuals. It is recommended in future comparative studies, or those involving a number of researchers, that this potential source of error be examined. Caution should be applied to studies where inter-population comparisons have been made and this potential source of error not tested.

Breeding success was a key variable in the study. However, the collection of these data was based on the premise that they were representative of birds under normal conditions and not influenced by the collection process. No differences in breeding success were detected and provided specific protocols were observed by investigators (moving slowly, crouching and not removing birds from nests), there was no short term impact on breeding success (Chapter 3). It was therefore assumed that the breeding success

rates obtained were representative of birds under natural conditions. Future studies need to both minimise the impact, and examine any effects of researchers collecting data on populations (see Giese 1995). This is important both for ethical reasons and to ascertain that data collected are representative of birds under natural conditions.

Central to examining aspects of foraging ecology in species of penguin is the deployment of external devices. However, recent studies have shown that the addition of such devices can significantly impact on foraging trip durations, swimming speed, food intake, movement and energetics of penguins (Wilson *et al.* 1986, Gales *et al.* 1990, Culik & Wilson 1991). The degree of impact is related to their position on the bird, device size (frontal cross-sectional area), and the degree of streamlining (Bannasch *et al.* 1994). Although the impact of devices has been studied in some penguin species with some device models, the issue had never been explored in Royal and Rockhopper Penguins, nor with the devices used for this project. These issues were examined in Chapter 4 in Royal Penguins using models of VHF transmitters and Time Depth Recorders (TDRs).

The attachment of the small, streamlined VHF transmitters had no measurable impact on Royal Penguins. However, there were substantial impacts from the larger, unstreamlined TDRs. The attachment of these devices resulted in a reduced likelihood that birds would continue the breeding attempt, increased foraging trip durations, increased water influx and decreased fat levels acquired during foraging. These effects were not constant between the sexes and across stages in the breeding season which

most likely related to the differing energetic demands of the sexes and stages in the breeding season. The impact of TDRs was most likely related to increased drag resulting from their lack of streamlining. Therefore, some of the data collected from these devices in subsequent parts of the thesis, particularly foraging trip durations, return rates and swimming speed, were regarded as conservative and not entirely representative of unencumbered birds. Devices used in future studies should be as small and streamlined as possible to minimise any impacts. Until it can be determined that impacts are minimal it cannot be assumed that the data collected are completely representative of birds under natural conditions, potentially leading to inaccurate conclusions about aspects of a species foraging ecology.

### Section B Foraging ecology

The foraging zones of both Royal and Rockhopper Penguins were offshore and far further from Macquarie Island (up to 600 km in Royal Penguins and 480 km in Rockhopper Penguins, Chapters 5 and 6) than had previously been estimated (Horne 1985, Scott 1994). Previous estimates were extrapolations from either the same species from different localities, or from Macaroni Penguins. This highlights the need to undertake foraging ecology studies at each locality rather than attempt to extrapolate from other localities. Differences in the biotic and abiotic aspects of the oceanic environments at each site are probably fundamental determinants of the foraging ecology of species breeding there.

Royal and Rockhopper Penguins foraged in deep water (greater than 2000 m,

predominantly 4000 - 5000 m in depth) in the vicinity of the Emerald Basin on the south-eastern side of Macquarie Island (158 - 160° E and 54 - 56° S). Although the techniques used to determine the foraging grounds of both species (geolocation, SST and foraging trip durations, Chapter 6) gave only approximations of the foraging zones, the data suggested that waters characterised by mean sea surface temperatures of 6.8 - 10.8°C were used, indicating the northern section of the Polar Frontal Zone (PFZ). The water masses in which both species travelled were constant between years except during 1995/6 when Rockhopper Penguins were in cooler water early in the breeding season. As the position of the PFZ moved over the breeding season (Chapters 5 and 6), the water temperatures in which both species travelled generally did not, suggesting a reliance on a specific part of the zone, and a non-random use of the environment (c.f. Baum 1987, Hunt *et al.* 1986).

The prey resources to the eastern side of Macquarie Island are completely unknown, but it is likely they were either in higher abundance or closer to the surface in the PFZ, as has been found in other parts of this zone (Hulley 1981, Gon & Heemstra 1990). However, they are likely to be patchy in distribution as found previously (Jouventin *et al.* 1994, Wilson *et al.* 1995). The variability in diet and diving behaviour between individual Royal and Rockhopper Penguins also suggests this. It appeared that individuals were accessing different prey stocks or exhibited different foraging abilities. Changes in the foraging zone coefficient across the breeding season (with large, circular tracks during incubation and more direct tracks during guard and creche stage) implied that the distribution, and possibly abundance of prey, was not constant across the



breeding season.

Although the sections of the PFZ in which both species foraged remained constant across the breeding season, the extent of foraging zones varied. The extent of foraging zones was most likely dictated by commitments at the nest. During the incubation period foraging trip durations were longer (Royal Penguins: incubation males 22.9 and females 15.9 days; Rockhopper Penguins: incubation males 14.5 and females 10.4 days). At this stage adults did not have to return to the colony in a limited amount of time to provide food for chicks. Adults could therefore spend time replenishing lost body condition resulting from the long fasts ashore (30 - 49 days). However, during chick provisioning young chicks required food on a regular basis necessitating that adults return to the nest at shorter intervals (3 - 4 days). Once chicks hatched adults had the dual role of foraging for their own maintenance, and provisioning chicks.

Both species of penguin were heaviest when they returned after winter foraging. Royal Penguins lost between 25.9% (males) and 26.1% (females) of their body mass, whilst Rockhopper Penguins lost between 29.7% (males) and 38.3% (females) of their body mass. Using mass as an indicator, guard stage was the most energetically taxing for these species. This was linked with the stage in the breeding season, with the female undertaking all foraging to provide food for the young chick, whilst the male remained at the nest. The lack of time for the female to forage for her own maintenance resulted in a depletion of mass (Chapter 8). Mass was not measured in males at this stage, but it may have also been an energetically taxing stage due to the fast being undertaken.



Foraging activity, indicated by diving and meandering behaviour from satellite tracking (Chapters 5 and 7), was primarily during daylight hours (between 4:00 - 21:00), with little or no diving below 6 m at night. Royal Penguins dived for 38.9% of a 24 hour period in Royal Penguins and Rockhopper Penguins 36.6% of a 24 hour period, with the degree of diving activity remaining constant over the breeding season. Although the length of daylight increased as the season progressed this did not correspond with an increase in the hours in which diving below 6m took place, suggesting that the penguins were either obtaining sufficient food during these hours, or that increased foraging activity was not profitable in terms of physiological constraints of increased diving. The emphasis on daylight foraging is probably linked with these penguins being predominantly visual predators, and therefore being able to forage more efficiently during daylight hours (Croxall *et al.* 1993, Wilson *et al.* 1993, Cannell 1994). Future studies examining the regions of the water column where food is obtained (such as with direct measurement using stomach temperature transmitters) will assist with clarifying this issue.

Although both species dived to, and were capable of diving over, 100 m they rarely did so, spending the majority of their time at depths less than 60 m, with dives by Royal Penguins being on average 1.7 minutes in duration and in Rockhopper Penguins 1.2 minutes. These relatively short and shallow dives were most likely related to maximising foraging efficiency, as less time is spent diving anaerobically. Anaerobic respiration results in byproducts which are energetically costly to remove (Chappell *et al.* 1993). Further, less time is spent in the ascent and descent phases of a dive, which

are probably less profitable in terms of foraging time (Boyd *et al.* 1995). This confirms the suggestion that diving behaviour is probably more linked with maximising foraging efficiency and the location of prey than it is to the physiological constraints of diving (Lishman & Croxall 1983).

The diet of both species was dominated by small, gregarious, pelagic prey (Chapter 8). Royal Penguins (average, by mass) consumed 49.6% euphausiids (in particular *Euphausia vallentini*), 1.6% other crustaceans, 0.5% cephalopods and 29.9% fish (predominantly *Krefftichthys anderssoni*). Rockhopper Penguins consumed (average, by mass) 71.9% euphausiids (in particular *Euphausia vallentini*), 0.7% other crustaceans, 0.08% cephalopods and 15.3% fish (predominantly *Krefftichthys anderssoni*). There were no seasonal changes in the proportions of prey items consumed across the breeding season in either species of penguin, although fewer prey taxa were found before, as opposed to after, the hatching of chicks. However, there were some differences observed in other dietary variables across the breeding season, in particular the size of myctophid fish, with smaller fish being consumed in December, which corresponds with the recent spawning of these species. Digestion rates of prey varied across the breeding season only during 1994/5, when prey were taken further offshore later in the season.

The diving behaviour and diet of these species of penguin did not always correspond well with the distribution of these prey in the water column as described from net hauls. This discrepancy probably reflects that marine predators are better indicators of the

distribution of prey resources than net hauls can describe (Croxall *et al.* 1985). However, it may also reflect that species of penguin selectively forage on specific age and/or sex classes of prey, and that the escape mechanisms of different cohorts of prey are not equally successful for avoiding predators and nets (Hill *et al.* 1996).

Royal and Rockhopper Penguins were similar in many aspects of their breeding biology. They were both highly synchronous in breeding timetables between individuals and years, regulated most likely by the climatic constraints of the latitude at which they breed (Croxall & Prince 1980a, Furness & Birkhead 1984). Like other species of penguins (Lack 1968, Williams 1990), the investment in clutches was low compared to other birds, constituting 6.3% of maternal mass in Royal Penguins and 7.0% in Rockhopper Penguins.

Breeding success in Royal Penguins was, on average, 53.3% and 47.3% in Rockhopper Penguins, and consistent between years in both species. Most breeding failures in both species occurred during incubation. Royal Penguins did not attempt to incubate A eggs and 94.3% of the breeding failures occurred during incubation. Rockhopper Penguins attempted to incubate both A and B eggs, with 98.0% of A egg failures and 79.7% of B egg failures occurring during incubation. Whilst predation was the most common form of failure of nests in both species, a higher proportion of Royal Penguin nests failed due to the late return of mates than due to predation, compared to Rockhopper Penguins. This longer duration of foraging trips and consequently longer fasting periods by mates on shore of Royal Penguins explains their vulnerability to the late

return of mates. The adult fasting on shore may approach the threshold mass that prompts abandonment (as found in King Penguins, Y. Le Maho unpubl. data), more so in Royal Penguins than Rockhopper Penguins. Conversely, the smaller size of Rockhopper Penguins probably makes them less able to withstand predation by skuas.

### 10.3 Inter-annual comparisons

A number of the foraging ecology variables that were examined during this study, in particular foraging zones and diving behaviour, showed little inter-annual variation. However, inter-annual dietary differences were detected, such as the proportions of prey consumed (pre-hatching diet), quantity of food brought ashore, degree of digestion of prey and adult masses. This indicates that whilst the penguins have maintained a consistent pattern in their foraging behaviour, prey resources encountered were not constant. Royal and Rockhopper Penguins therefore exhibited some degree of flexibility in the prey resources consumed, most likely regulated by what was encountered within preferred foraging sectors.

The inter-annual differences in diet were not reflected in the majority of breeding biology parameters, with the exception of Rockhopper Penguin fledging masses. Breeding success remained constant throughout the study, implying that these species can consume a variety of prey resources without deleteriously affecting reproductive success. However, there is most likely a finite dietary range these species can exploit, and large changes in diet may impact on breeding success. The population of Rockhopper Penguins at nearby Campbell Island has exhibited declines of up to 94%,

which has been linked to prey moving outside the foraging range of the penguins, resulting in a reduction in the quantity of food brought ashore and forcing them to switch to other prey species. These prey were thought to be less nutritionally valuable to Rockhopper Penguins and resulted in low breeding success (Cunningham & Moors 1994).

The consistent breeding success found during this study suggests that the three years may have been relatively "good" years with sufficient prey of adequate nutritional value being accessible. No warm water anomalies in the Antarctic circumpolar wave were apparent during these years (Fig. 1 in White & Peterson 1996), and hence prey stocks were presumably not affected.

Further research examining "poor" years is required to determine the impact of warm water events, or other environmental perturbations, on various breeding and foraging parameters in these species. If prey stocks moved further offshore and beyond the foraging zones of these penguins, such as might occur during a warm water anomaly, either switching of prey or a reduced foraging success may occur. The impact of such an environmental perturbation may not have a similar effect on both Royal and Rockhopper Penguins due to the differences in aspects of their foraging ecologies.

#### **10.4 Overlap in resource use by Royal and Rockhopper Penguins**

A number of similarities were found in the foraging ecology of Royal and Rockhopper Penguins, with a reliance on the same general sectors of the ocean, similar taxa of prey



consumed and comparable breeding biology. In this section I examine each of the three aspects of foraging ecology which are hypothesised to differ between sympatrically breeding species:

### *1. Foraging zones*

One of the mechanisms that would minimise the overlap in resource use between potentially competing species is differential foraging zones, either through the exploitation of different regions of the ocean, or different diving depths (Croxall & Prince 1980a, Hindell *et al.* 1995). Although overlaps were observed in the three dimensions of the ocean used by the penguins, Royal Penguins foraged further offshore and spent more time at greater depths than the latter. An assessment of the use of areas of the ocean on a contemporaneous basis indicated that overlaps were small, and hence differences in foraging zones did contribute to a separation in resource between these species.

### *2. Diet*

Dietary differences between the species could be in the species, proportions, or size of prey consumed (Ridoux 1994, Hindell *et al.* 1995). Royal Penguins consumed a greater diversity of prey taxa, more myctophid fish and generally larger size classes than Rockhopper Penguins. Dietary differences, along with dissimilar degrees of digestion of food, implied that prey were taken from different stocks, and reinforcing the contention that foraging was undertaken in different sectors of the ocean.



The limited separation in diet between similar species is no doubt related to the fact that they are similar taxonomically and hence can operate within specific morphological and behavioural limits, which determines the degree to which they can diverge (Ashmole & Ashmole 1967). Further, the degree of dietary difference would be dependent upon the diversity of prey in the local environment and the number of microhabitats in that environment (Diamond 1983, Ridoux 1994).

Therefore, differences in diet indicated that there was minimal overlap in resource use by these species.

### *3. Breeding timetables*

The third hypothesised ecological difference that may assist with a segregation of resource use is asynchrony in breeding seasons, resulting in peaks in food demands occurring at different times (Brown & Klages 1987). As the asynchrony in breeding in these species is only three weeks there is still some overlap in the times when both species are feeding large chicks, which is presumably when the demand for resources is highest. Therefore, the asynchrony alone does not assist with minimising competition for resources. However, in conjunction with the different foraging zones of the species (dictated predominantly by the extent of foraging zones during different stages in the breeding season), the overlap in resource use is further reduced. Differences in foraging zones have been thought to assist with differences in diet as birds foraging further offshore accessed different prey species (Adams & Brown 1989). The lack of seasonal differences in diet in both species indicates that the asynchrony in breeding

timetables would not result in a reliance on different prey species.

The greater reliance on offshore foraging by Royal Penguins compared to Rockhopper Penguins suggested that the two species may differ in their degree of capital versus income breeding. Royal Penguins may be more capital breeders meaning that they rely more on investing in larger reserves prior to the breeding season than Rockhopper Penguins, which gained energy throughout the season.

The results of this study suggest that a combination of variables (foraging zones, diet and asynchrony in breeding timetables) have contributed to a reduction in the overlap in resource use between Royal and Rockhopper Penguins. In these closely related penguins the differences are a small scale segregation, as found in other congeneric crested penguins (Ridoux 1994).

However, some of the differences found in the foraging ecology and breeding biology of these species, such as diving and quantity of food brought ashore, can be linked to the different size of the species. This suggests that autecological factors may be equally important in explaining differences observed, as are proximate factors resulting in ecological segregation. Factors such as predation, weather, and intra-specific competition (Sinclair & Norton-Griffiths 1982, Connell 1983, Suhonen 1993) may also be important in determining the ecology of these two species of penguin.

Finally, the ecological differences between these two species of penguin may not have

occurred due to the avoidance of competition for limited resources. The food resources around Macquarie Island may not be limited, or only be limited during "poor" years. An examination of the food resources in the marine environment around Macquarie Island will allow further speculation as to whether this cause may have resulted in inter-specific competition, necessitating resource partitioning.

In conclusion, this study has examined a number of aspects of the foraging ecology and breeding biology of Royal and Rockhopper Penguins on a contemporaneous basis. It has determined that differing foraging zones, diet and asynchrony in the breeding season all contribute to reducing the overlap in resource use between the species, and therefore presumably competition during a time when demands for resources were most likely at their greatest. The three year study found few inter-annual variations in parameters examined and it is speculated that the years in which the study was undertaken were all "good" years. Further research examining foraging ecology and breeding biology during years when warm water anomalies are present will be invaluable for understanding the effect on these species of penguin. A closer examination of the contention that these species differ in their degree of capital versus income breeding, and whether they are affected differently during "poor" years would also make for interesting further study.

## References

- Abrams R.W. 1985. Environmental determinants of pelagic seabird distribution in the African sector of the Southern Ocean. *J Biogeog* 12: 473-192.
- Abrams R.W. & D.G.M. Miller. 1986. The distribution of pelagic seabirds in relation to the oceanic environment of Gough Island. *S Afr J Mar Sci* 4: 125-137.
- Adams N.J. 1987 Foraging range of King Penguins *Aptenodytes patagonicus* during summer at Marion Island. *J Zool Lond* 212: 475-482.
- Adams N.J. & N.T. Klages 1987. Seasonal variation in the diet of the King Penguin *Aptenodytes patagonicus* at sub-antarctic Marion Island. *J Zool, Lond* 212: 475-482.
- Adams N.J. & C.R. Brown. 1989. Dietary differentiation and trophic relationships in the sub-Antarctic penguin community at Marion Island. *Mar Ecol Prog Ser* 57: 249-258.
- Adams N.J., C. Moloney & R. Navarro. 1993. Estimated food consumption by penguins at the Prince Edward Islands. *Ant Science* 5(3): 245-252.
- Agnew D.J. & K.R. Kerry. 1995. Sexual dimorphism in penguins. In: Dann, P., I. Norman & P. Reilly. (Eds). "The penguins. Ecology and Management". Surrey Beatty & Sons, Melbourne. Pp. 299-318.
- Ainley D.G. & S.S. Jacobs. 1981. Sea-bird affinities for ocean and ice boundaries in the Antarctic. *Deep Sea Res* 28: 1173-1185.
- Ainley D.G., R.E. LeResche & W.J.L. Sladen. 1983. Breeding biology of the Adélie

Penguin, University of California Press, Berkeley.

- Ainley D.G., C.A. Ribic & W.R. Fraser. 1992. Does prey preference affect habitat choice in Antarctic seabirds? *Mar Ecol Prog Ser* 90: 207-221.
- Amat J.A., J. Vinuela & M. Ferrer. 1993. Sexing Chinstrap Penguins (*Pygoscelis antarctica*) by morphological measurements. *Colonial Waterbirds* 16: 213-215.
- Ancel A., G.L. Kooyman, P.J. Ponganis, J.P. Gendner, J. Lignon, X. Mestre, N. Huin, P.H. Thomson, P. Robisson & Y. Le Maho. 1992. Foraging behaviour of Emperor Penguin as a resource detector in winter and summer. *Nature* 360: 336-339.
- Ashmole N.P. 1971. Sea bird ecology and the marine environment. In: Farner D.S. & J.R. King (Eds). "Avian Biology. Vol. 1". Academic Press, New York. Pp. 223-286.
- Ashmole N.P. & M.J. Ashmole 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. *Bull Peabody Mus Nat Hist* 24: 1-131.
- Axelrod J. & T.D. Reisine. 1984. Stress hormones: their interaction and regulation. *Science* 224: 452-459.
- Baldwin J., J-P Jardel, T. Montague & R. Tomkin. 1984. Energy metabolism in penguin swimming muscles. *Mol Physiol* 6: 33-42.
- Ball N.J. & C.J. Amlaner. 1980. Changing heart rates of herring gulls when approached by humans. In: Amlaner, C.J. & D.W. McDonald (Eds). "A handbook of biotelemetry and radio tracking". Pergamon Press, Oxford. Pp: 589-594.

- Bannasch R., R.P. Wilson & B. Culik. 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. Exp. Biol.* 194: 83-96.
- Barrett R. T., M. Peterz, R.W. Furness & J. Durinck. 1989. The variability of biometric measurements. *Ring. & Migr.* 10: 13-16.
- Baum W.M. 1987. Random and systematic foraging, experimental studies of depletion, and schedules of reinforcement. In: Kamil A.C., J.R. Krebs & H.R. Pulliam (Eds). "Foraging behaviour". Plenum Press, New York, Pp. 587-607.
- Bekker V.E. 1983. Myctophids of the world oceans. Academy of Sciences USSR, Moscow.
- Boersma P.D., D.L. Stokes & P.M. Yorio. 1990. Reproductive variability and historical change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. In: Davis L.S. & J.T. Darby (Eds). "Penguin biology". Academic Press, United Kingdom. Pp.15-43.
- Bost C.A., J.Y. Georges, C. Guinet, Y. Cherel, K. Pütz, J.B. Charrassin, Y. Handrich, T. Zorn, J. Lage & Y. Le Maho. 1997. Foraging habitat and food intake of satellite tracked King Penguins during the summer at Crozet Archipelago, Southern Indian Ocean. *Mar Ecol Prog Ser.* 150:21-33.
- Boyd I.L. 1993. Selecting sampling frequency for measuring diving behavior. *Mar Mammal Science* 9: 424-430.
- Boyd I.L. & J.P. Roberts. 1993. Tooth growth in male Antarctic fur seals (*Arctocephalus gazella*) from South Georgia: an indicator of long-term growth history. *J Zool, Lond* 229: 177-190.



- Boyd I.L., K. Reid & R.M. Bevan. 1995. Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Anim Behav* 50: 769-784.
- Brown C.R. 1984. Resting metabolic rate and energetic cost of incubation in Macaroni Penguins (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*). *Comp Biochem Physiol* 77A: 345-50.
- Brown C. R. 1987. Travelling speed and foraging range of Macaroni and Rockhopper Penguins at Marion Island. *J. Field Ornithol.* 58: 118-125.
- Brown C.R. & N.T. Klages. 1987. Seasonal and annual variation in diets of Macaroni (*Eudyptes chrysolophus chrysolophus*) and Southern Rockhopper (*E. chrysocome chrysocome*) Penguins at sub-Antarctic Marion Island. *J Zool Lond* 212: 7-28.
- Brown C.R., N.T. Klages & N.J. Adams. 1990. Short and medium-term variation in the diets of penguins at Marion Island. *S Afr J Antarct Res* 20: 13-20.
- Burger A.E. 1990. Maximum diving depths and underwater foraging in alcids and penguins. In: Montevecchi W.A. & A.J. Gaston (Eds). "Behavioural, ecological and oceanographic influences on the feeding ecology of marine birds. Canadian Wildlife Service Occasional Papers, Ottawa. Pp. 9-15.
- Burger A.E. & A.J. Williams. 1979. Egg temperatures of the rockhopper penguin and some other penguins. *Auk* 96: 100-105.
- Burling R.W. 1961. Hydrology of Circumpolar Waters south of New Zealand. New Zealand Oceanography Institute Memoir 10, Wellington.
- Cairns D.K. 1992. Bridging the gap between ornithology and fisheries science: use of

seabird data in stock assessment models. *Condor* 94: 811-824.

Cannell B. 1994. The feeding behaviour of Little Penguins, *Eudyptula minor* (Forster). PhD thesis, Department of Ecology and Evolutionary Biology, Monash University, Victoria Australia.

Carrick J. 1972. Population ecology of the Australian Black-backed Magpie, Royal Penguin, and Silver Gull. *Wildlife Research Report* 2: 41-99.

Carrick R. & S.E. Ingham 1970. Ecology and population dynamics of Antarctic sea birds. In: Holdgate M.W. (Ed). "Antarctic Ecology, Volume 1". Academic Press, London. Pp. 505-525.

Chappell M.A., V.H. Shoemaker, D.N. Janes, T.L. Bucher & S.K. Maloney. 1993. Diving behavior during foraging in breeding Adélie Penguins. *Ecology* 74: 1204-1215.

Chastel O., H. Weimerskirch & P. Jouventin. 1993. High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*. A 27 year study. *Oecologia* 94: 278-285.

Chastel O., H. Weimerskirch & P. Jouventin. 1995a. Body conditions and seabird reproductive performance: a study of three petrel species. *Ecology* 76(7): 2240-2246.

Chastel O., H. Weimerskirch & P. Jouventin. 1995b. Influence of body condition on reproductive decision and reproductive success in the Blue Petrel. *Auk* 112(4): 964-972.

Cherel Y & V. Ridoux. 1992. Prey species and nutritive value of food fed during

- summer to King Penguin *Aptenodytes patagonicus* chicks at Possession Island, Crozet Archipelago. *Ibis* 134: 118-127.
- Clark K.R. & R.H. Green. 1988. Statistical design and analysis for a "biological effects" study. *Mar Ecol Prog Ser* 46: 213-226.
- Clarke B.D. & W. Bemis. 1979. Kinematics of swimming of penguins at Detroit Zoo. *J Zool Lond* 188: 411-428.
- Clark M.R. & P.R. Dingwall. 1985. Conservation of Islands in the Southern Ocean. International Union for the Conservation of Nature and Natural Resources.
- Clarke J. & K. Kerry. 1993. The effects of monitoring procedures on Adélie Penguins. *CCAMLR Science* 1: 155-164.
- Clarke M.R. 1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford.
- Cooper J, C.R. Brown, R.P. Gales, M.A. Hindell, N.T.W. Klages, P.J. Moors, D. Pemberton, V. Ridoux, K.R. Thompson & Y.M. van Heezik. 1990. Diets and dietary segregation of crested penguins (*Eudyptes*). In: Davis L.S. & J.T. Darby (Eds). "Penguin Biology". Academic Press, California. Pp. 131-156.
- Cooper J., M.N. Bester, A.L. Plos & J.P. Bloomer. 1993. Demography and doubts: effects of human disturbance on Wandering Albatrosses and Giant Petrels at Marion Island. In: Fraser, W.R. & W.Z. Trivelpiece (Eds). "Workshop on researcher-seabird interactions". July 15-17, 1993. Monticello, Minnesota, USA. Pp:37.
- Connell J.H. 1983. On the prevalence and relative importance of interspecific

- competition: evidence from field experiments. *Am. Nat.* 122(5): 661-696.
- Copson G.R. & D.E. Rounsevell. 1987. The abundance of Royal Penguins (*Eudyptes schlegeli* Finsch) breeding at Macquarie Island. ANARE Res note 41.
- Crawford R.J.M. & B.M. Dyer. 1995. Responses by four seabird species to a fluctuating availability of Cape Anchovy *Engraulis capensis* off South Africa. *Ibis* 137: 329-339.
- Croll D.A., S.D. Osmeck & J.L. Bengtson. 1991. An effect of instrument attachment on foraging trip duration in Chinstrap Penguins. *Condor* 93: 777-779.
- Croll D.A., A.J. Gaston, A.E. Burger & D. Konnoff. 1992. Foraging behavior and physiological adaptation for diving in Thick-billed Murres. *Ecology* 73: 344-356.
- Croll D.A., J.K. Jansen, M.E. Goebel, P.L. Boveng & J.L. Bengtson. 1996. Foraging behavior and reproductive success in Chinstrap Penguins: the effects of transmitter attachment. *J. Field Ornithol* 67: 1-9.
- Croxall J.P. 1982. Energy costs of incubation and moult in petrels and penguins. *J Anim Ecol* 51: 177-194.
- Croxall J.P. 1984. Seabirds. In: Laws R.M. (Ed). "Antarctic ecology, Volume 2". Academic Press, London.
- Croxall J.P. & J.R. Furse. 1980. Food of chinstrap penguins *Pygoscelis antarctica* and macaroni penguins *Eudyptes chrysolophus* at Elephant Island group, South Shetland Islands. *Ibis* 122: 237-245.

- Croxall J.P. & P.A. Prince. 1980a. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol J Linn Soc* 4: 103-131.
- Croxall J.P. & P.A. Prince. 1980b. The food of Gentoo Penguins *Pygoscelis paua* and Macaroni Penguins *Eudyptes chrysolophus* at South Georgia. *Ibis* 122: 245-253.
- Croxall J.P. & P.A. Prince 1982. Calorific content of squid (Mollusca: Cephalopoda). *Br Antarct Surv Bull* 55: 27-31.
- Croxall J.P., P.A. Prince, A. Baird & P. Ward. 1985. The diet of the southern rockhopper penguin *Eudyptes chrysocome chrysocome* at Beauchene Island, Falkland Islands. *J. Zool. Lond* 206: 485-496.
- Croxall J.P. & G.S. Lishman. 1987. The food and feeding ecology of penguins. In: Croxall, J P. (Ed) "Seabirds feeding ecology and role in marine ecosystems". Cambridge University Press, Cambridge. Pp.101-131.
- Croxall J.P., T.S. McCann, P.A. Prince & P. Rothery. 1988. Reproductive performance of seals and seabirds at South Georgia and Signy Islands, South Orkney Islands, 1976-1987: implications for Southern Ocean monitoring studies. In: Sahrhage D. (Ed). "Antarctic ocean and resource variability". Springer-Verlag, Berlin. Pp. 261-285.
- Croxall J.P. & R.W. Davis. 1990. Metabolic rate and foraging behaviour of *Pygoscelis* and *Eudyptes* penguins at sea. In: Davis L.S. & J.T. Darby (Eds). "Penguin Biology". Academic Press, California.. Pp. 207-228.
- Croxall J.P., D.R. Briggs, A. Kato, Y. Naito, Y. Watanuki & T.D. Williams. 1993. Diving pattern and performance in the Macaroni Penguin *Eudyptes chrysolophus*. *J Zool Lond* 230: 31-47.



- Croxall J.P. & P.A. Prince. 1994. Dead or alive, night or day: how do albatrosses catch squid? *Ant Science* 6(2): 155-162.
- Culik B.M. 1994. Energy requirements of pygoscelid penguins: a synopsis. Reports on Polar Research. *Berichte zur Polarforschung* 150. 76 pages.
- Culik B., D. Adelung & A.J. Woakes. 1990. The effect of disturbance on the heart rate and behaviour of Adélie Penguins (*Pygoscelis adeliae*) during the breeding season. In: Kerry, K.L. & G. Hempel (Eds). "Antarctic Ecosystems. Ecological Change and Conservation". Springer-Verlag, Berlin. Pp.177-182.
- Culik B.M. & R.P. Wilson. 1991. Swimming energetics and performance of instrumented Adélie Penguins (*Pygoscelis adeliae*). *J. Exp. Biol.* 158: 355-368.
- Culik B.M. & R.P. Wilson. 1992. Field metabolic rates of instrumented penguins using doubly-labelled water. *J. Comp. Physiol.* 162B: 567-573.
- Culik B.M., R. Bannasch & R.P. Wilson. 1994. External devices on penguins: how important is shape? *Marine Biol.* 118: 353-357.
- Cumpston J.S. 1968. Macquarie Island. ANARE Scientific Reports, Series A (1). Australian Antarctic Division, Department of External Affairs.
- Cunningham D.M. & P.J. Moors. 1994. The decline of Rockhopper Penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* 94: 27-36.
- Davies D.H. 1956. The South African pilchard *Sardinops ocellata* and Maasbanker *Trachurus*: bird predators, 1954-1955. *Invest Rep Div Fish Un S Afr* 23: 1-40.



- Davis B.W. 1988. Heritage conservation in Antarctic and subantarctic jurisdictions: the case of Macquarie Island. *Royal Society of Tasmania* 122(1): 9-14.
- Davis L.S. 1988. Coordination of incubation routines and mate choice in Adélie Penguins (*Pygoscelis adeliae*). *Auk* 105: 428-432.
- Davis L.S. 1982. Timing of nest relief and its effect on breeding success in Adélie Penguins (*Pygoscelis adeliae*). *Condor* 84: 178-183.
- Davis L.S. & E.A.H. Spiers. 1990. Mate choice in penguins. In: Davis, L.S. & J.T. Darby (Eds). "Penguin biology". Academic Press, San Diego. Pp. 377-397.
- Davis L.S. & G.D. Miller. 1992. Satellite tracking of Adélie Penguins. *Polar Biol.* 12: 503-506.
- Davis L.S., P.D. Boersma & G.S. Court. 1996. Satellite telemetry of the winter migration of Adélie Penguins (*Pygoscelis adeliae*). *Polar Biol* 16: 221-225.
- Davis R.W., J.P. Croxall & M.J. O'Connell. 1989. The reproductive energetics of gentoo (*Pygoscelis papua*) and macaroni (*Eudyptes chrysolophus*) penguins at South Georgia. *J. Anim. Ecol* 58: 59-74.
- Deacon G.E.R. 1982. Physical and biological zonation in the Southern Ocean. *Deep-Sea Res* 29: 1-15.
- Diamond A.W. 1983. Feeding overlap in some tropical and temperate seabird communities. *Studies in Avian Biol* 8: 24-46.
- Drent R.H. & S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.

- Duffy D.C. & S. Jackson. 1986. Diet studies of seabirds: a review of methods. Colonial Waterbirds 9: 1-17.
- Duroselle T. & B. Tollu. 1977. The Rockhopper Penguin (*Eudyptes chrysocome moseleyi*) of Saint Paul and Amsterdam Islands. In: Llano G.A. (Ed). "Adaptations within Antarctic Ecosystems. Proceedings of the Thirds SCAR Symposium on Antarctic Biology". Smithsonian Institution, Washington. Pp. 579-604.
- Ealey E.M.H. 1954. Analysis of stomach contents of some Heard Island birds. Emu 54: 204-210.
- Edge K-A. 1996. Parental investment in penguins: a phylogenetic and experimental approach. PhD Thesis. Department of Zoology, University of Otago, New Zealand.
- Elton C.S. & R.S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. J Ecol 42: 460-496.
- Emslie S.D., N. Karnovsky & W. Trivelpiece. 1995. Avian predation at penguin colonies on King George Island, Antarctica. Wilson Bull 107(2): 317-327.
- Fischer W. & J.C. Hureau. 1985a. FAO species identification sheets for fishery purposes. Southern Ocean. Volume I. Food and Agriculture Organization of the United States and Commission for the Conservation of Antarctic Marine Living Resources.
- Fischer W. & J.C. Hureau. 1985b. FAO species identification sheets for fishery purposes. Southern Ocean. Volume II. Food and Agriculture Organization of

the United States and Commission for the Conservation of Antarctic Marine Living Resources.

Ford G. & D.W. Krumme. 1979. The analysis of space use patterns. *J Theor Biol* 76: 125-155.

Foster T.D. 1984. The marine environment. In: Laws R.M. (Ed). "Antarctic Ecology, Vol. 2". Academic Press, London. Pp. 345-371.

Fowler G.S. 1993. Field studies, tourism and stress responses in Magellanic Penguins. In: Fraser, W.R. & W.Z. Trivelpiece (Eds). "Workshop on researcher-seabird interactions". July 15-17, 1993. US National Science Foundation Office of Polar Programs. Monticello, Minnesota, USA. 44 pages.

Fraser W.R. & W.Z. Trivelpiece. 1993. Workshop on researcher-seabird interactions. US National Science Foundation Office of Polar Programs. Monticello, Minnesota.

Frere E., P. Gandini & P.D. Boersma. 1992. Effects of nest type and location on reproductive success of the Magellanic Penguin *Spheniscus magellanicus*. *Mar Ornithol* 20(1/2): 1-6.

Furness B.L., R.C. Laugksch & D.C. Duffy. 1984. Cephalopod beaks and studies of seabird diets. *Auk* 101: 619-620.

Furness R.W. & T.R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311: 655-656.

Gales R. 1988a. Sexing adult Blue penguins by external measurements. *Notornis* 35: 71-75.

- Gales R. 1988b. The use of otoliths as indicators of Little Penguin *Eudyptula minor* diet. *Ibis* 130: 418-426.
- Gales R.P. 1989. Validation of the use of tritiated water, doubly-labelled water and <sup>22</sup>-Sodium for estimating food, energy and water intake in Little Penguins, *Eudyptula minor*. *Physiol Zool* 62: 147-169.
- Gales R.P., C. Williams & D. Ritz. 1990. Foraging behaviour of the Little Penguin, *Eudyptula minor*: initial results and assessment of instrument effect. *J Zool* 220: 61-85.
- Gause G.F. 1934. The struggle for existence. Williams and Wilkins, Baltimore.
- Geise M.A. 1995. A quantitative analysis of the effects of human activity on the behaviour, physiology and breeding success of the Adélie Penguin (*Pygoscelis adeliae*). PhD thesis, LaTrobe University, Victoria Australia.
- Gon O. & P.C. Heemstra. 1990. Fishes of the Southern Ocean. JBL Smith Institute of Ichthyology, Grahamstown.
- Gordon A. L. 1972. On the interaction of the Antarctic Circumpolar Current and the Macquarie Ridge. In: Hayes D.E. (Ed). "Antarctic Oceanology II. The Australian - New Zealand sector". American Geophysical Union, National Academy of Sciences, New York. Pp 71-78.
- Green B. & R.P. Gales. 1990. Water, sodium, and energy turnover in free-living penguins. In: L.S. Davis & J.T. Darby (Eds) "Penguin Biology" Academic Press, San Diego. Pp. 245-268.
- Green K. 1993. The diet of Macaroni Penguins (*Eudyptes chrysolophus*), over

- breeding season 1992/1993 at Heard Island. In: Green K. (Ed). "Heard Island Report". Australian National Antarctic Research Expeditions 1992. Australian Antarctic Division, Tasmania. Pp. 117-119.
- Green K, R. Williams & M.G. Green. (submitted). Foraging ecology and diving behaviour of Macaroni Penguins *Eudyptes chrysolophus* at Heard Island.
- Groscolas R. 1990. Metabolic adaptations to fasting in Emperor and King Penguins. In: Davis, L.S. & J.T. Darby (Eds). "Penguin biology". Academic Press, San Diego. Pp. 269-296.
- Groscolas R., L. Schreiber & F. Morin. 1991. The use of tritiated water to determine protein and lipid utilization in fasting birds: a validation study in incubating Great-winged Petrels, *Pterodroma macroptera*. *Physiol Zool* 64: 1217-1233.
- Guinet C., P. Jouventin & J-Y Georges. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Ant Science* 6(4): 473-478.
- Guinet C., O. Chastel, M. Koudil & P. Jouventin (in press). Response by a seabird to an Antarctic Circumpolar Wave of climatic anomalies. *Proceed Royal Soc Lond*.
- Gwynn A.M. 1953. The egg-laying and incubation periods of Rockhopper, Macaroni and Gentoo Penguins. Australian National Antarctic Research Expeditions Reports Series B, Volume 1: 1-29.
- Haney J.C. 1986. Seabird affinities for Gulf Stream frontal eddies: responses of mobile marine consumers to episodic upwelling. *J Mar Res* 44: 361-384.

- Haney J.C. & P.A. McGillivray. 1985. Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance. *Biol Ocean* 3: 401-430.
- Harris M.P. 1977. Comparative ecology of seabirds in the Galapagos Archipelago. In: Stonehouse B & C.M. Perrins (Eds). "Evolutionary ecology". MacMillan Press, London.
- Hartley P.H.T. 1948. The assessment of the food of birds. *Ibis* 90(3): 361-381.
- Hayes D.E. & M. Talwani. 1972. Geophysical investigation of the Macquarie Ridge complex. In: Hayes D.E. (Ed). "Antarctic Oceanology II. The Australian-New Zealand Sector". Amer Geophys Union Antarc Res Series 19: 211-234
- Heath R.G.M. & R.M. Randall. 1985. Growth of Jackass penguin chicks (*Spheniscus demersus*) hand reared on different diets. *J Zool, Lond* 205: 91-105.
- Heath R.G.M. & R.M. Randall. 1989. Foraging ranges and movements of jackass penguins (*Spheniscus demersus*) established through radio telemetry. *J Zool Lond* 217: 367-379.
- Hill H.J., P.N. Trathan, J.P. Croxall & J.L. Watkins. 1996. Comparison of Antarctic Krill *Euphausia superba* caught by nets and taken by Macaroni Penguins *Eudyptes chrysolophus*: evidence for selection? *Mar Ecol Prog Ser* 140(1-3): 1-11.
- Hill R.D. 1994. Theory of geolocation by light levels. In: Le Boeuf B.J. & R.M. Laws (Eds). "Elephant seals: Population ecology, behavior, and physiology". University of California Press, Berkeley. Pp. 227-236.



- Hindell M.A. 1988a. The diet of the Royal Penguin *Eudyptes schlegeli* at Macquarie Island. *Emu* 88: 219-226.
- Hindell M.A. 1988b. The diet of the rockhopper penguin *Eudyptes chrysocome* at Macquarie Island. *Emu* 88: 227-233.
- Hindell M.A. 1989. The diet of the king penguin *Aptenodytes patagonicus* at Macquarie Island. *Ibis* 130: 193-203.
- Hindell M.A., G.G. Robertson & R. Williams. 1995. Resource partitioning in four species of sympatrically breeding penguins. In: P. Dann, I. Norman & P. Reilly (Eds). "The Penguins. Ecology and Management". Surrey Beatty and Sons, Melbourne. Pp. 196-215.
- Hindell M.A., M-A. Lea, & C.L. Hull. 1996. The effect of wearing flipper bands on adult survival and reproductive success in the Royal Penguin *Eudyptes schlegeli*. *Ibis* 138: 557-560.
- Horne R.S.C. 1985. Diet of Royal and Rockhopper Penguins at Macquarie Island. *Emu* 85: 150-156.
- Hull C. L. 1997. The effect of carrying devices on breeding Royal Penguins *Eudyptes schlegeli*. *Condor* 99: 530-534.
- Hull C.L. (in press). Morphometric indices for sexing adult Royal, *Eudyptes schlegeli*, and Rockhopper Penguins, *E. chrysocome*, at Macquarie Island. *Mar Ornithol* 24(1).
- Hull C.L. & J. Wilson. 1996a. The effect of investigators on the breeding success of Royal, *Eudyptes schlegeli*, and Rockhopper, *E. chrysocome*, Penguins at

- Macquarie Island. *Polar Biol* 16: 335-337.
- Hull C.L. & J. Wilson. 1996b. Location of colonies in Royal Penguins, *Eudyptes schlegeli*: Potential costs and consequences for breeding success. *Emu* 96: 135-138.
- Hull C.L, M. A. Hindell & K.J. Michael (in press). The foraging zones of Royal Penguins during the breeding season, and their association with oceanographic features. *Mar Ecol Prog Ser* 153: 217-228.
- Hulley P.A. 1981. Results of the research cruises of FRV 'Walter Herwig' to South America. LVIII. Family Myctomphidae (Osteichthys, Myctophimorphes). *Arch Fisch Wiss* 31(1): 1-300.
- Hunt G.L. 1988. The distribution of seabirds at sea: Physical and biological aspects of their marine environment. *Proc Int 100 DO-G Meeting. Current Topics in Avian Biol Bonn* 167-171.
- Hunt G.L. 1990. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Res* 8: 43-54.
- Hunt G.L., Z.A. Eppley & D.S. Schneider. 1986. Reproductive performance of seabirds: the importance of population and colony size. *Auk* 103: 306-317.
- Hunt G.L. & D.C. Schneider. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall J.P. (Ed). "Seabirds: Feeding ecology and role in marine ecosystems". Cambridge University Press. Pp. 7-41.
- Hutchinson G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposium on*

- Quantitative Biology. 22: 415-427.
- Hyslop E.J. 1980. Stomach contents analysis - a review of methods and their application. J Fish Biol 17: 411-429.
- IUCN/SSC. 1996. Penguin conservation assessment and management plan workshop workbook. A collaborative workshop. 8-9 September 1996, South Africa. British Antarctic Survey, SCAR subcommittee on bird biology, Percy Fitzpatrick Institute of Ornithology, IUCN/SSC Conservation Breeding Specialist Group.
- Jackson G.D. 1995. The use of beaks as tools for biomass estimation in the deep water squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. Polar Biol 14: 9-14.
- Jazdzewski K. 1982. Amphipod crustaceans in the diet of pygoscelid penguins of the King George Island, South Shetland Islands, Antarctica. Pol Polar Res 2: 133-144.
- Jones R.B., I.J.H. Duncan & B.O. Hughes. 1981. The assessment of fear in domestic hens exposed to a looming human stimulus. Behav Processes 6: 121-134.
- Jones R.B. & J.M. Faure. 1981. The effects of regular handling on fear responses in the domestic chicken. Behav Processes 6: 135-144.
- Jouventin P., D. Capdeville, F. Cuento-Chaillet & C. Boiteau. 1994. Exploitation of pelagic resources by a non-flying seabirds: satellite tracking of the King Penguin throughout the breeding cycle. Mar Ecol Prog Ser 106: 11-19.
- Kerry K.R., D.J. Agnew, J.R. Clarke & G.D. Else. 1992. Use of morphometric

- parameters for the determination of sex of Adélie Penguins. *Wildl. Res.* 19: 657-664.
- Kerry K.R., Clarke J.R. & G.D. Else. 1995. The foraging range of Adélie Penguins at Bechervaise Island, MacRobertson Land, Antarctic as determined by satellite telemetry. In: Dann P., T. Norman & P. Reilly (Eds). "The penguins. Ecology and Management". Surrey Beatty and Sons, Melbourne. Pp. 216-243.
- Kirkwood J.M. 1982. A guide to the Euphausiacea of the Southern Ocean. ANARE Research Notes 1: 1-45.
- Kirkwood R. & G. Robertson. 1997. The foraging ecology of female Emperor Penguins in winter. *Ecol Monogr* 67: 155-176.
- Klages N.T.W., R.P. Gales & D. Pemberton. 1989. Dietary segregation of Macaroni and Rockhopper Penguins at Heard Island. *Aust Wildl Res* 16: 599-604.
- Kooyman G.L. 1989. *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin.
- Kooyman G.L., Y. Cherel, Y. Le Maho, J.P. Croxall, P.H. Thorson, V. Ridoux & C.A. Kooyman. 1992. Diving behavior and energetics during foraging cycles in King Penguins. *Ecol Monogr* 62(1): 143-163.
- Kooyman G.L. & T.G. Kooyman. 1995. Diving behavior of Emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor* 97: 536-549.
- Lack D. 1968. *Ecological adaptations for breeding in birds*. Methuen and Co., London.
- Lishman G.S. & J.P. Croxall. 1983. Diving depths of the Chinstrap Penguin *Pygoscelis*

- antarctica*. Br Antarct Surv Bull 61: 21-25.
- Livezey B.C. 1989. Morphometric patterns in recent and fossil penguins (Aves, Sphenisciformes). J Zool, Lond 219: 269-307.
- Lorentsen S-H. & R. Røv. 1994. Sex determination of Antarctic Petrels *Thalassoica antarctica* by discriminant analysis of morphometric characters. Polar Biol 14: 143-145.
- Lutjeharms J.R.E. & D.J. Baker. 1980. A statistical analysis of the meso-scale dynamics of the Southern Ocean. Deep Sea Res 27A: 145-159.
- Lutjeharms J.R.E., N.M. Walters & B.R. Allanson. 1985. Oceanic frontal systems and biological enhancement. In: Siegfried W.R., P.R. Condy & R.M. Laws (Eds). "Antarctic nutrient cycles and food webs". Springer-Verlag, Berlin. Pp.11-21.
- McConnell B.J., C. Chambers & M.A. Fedak. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarctic Science 4: 393-398.
- Marchant S. & P.J. Higgins. 1990. Handbook of Australian, New Zealand and Antarctic Birds. Volume 1 Ratites to Ducks. Part A Ratites to Petrels. Oxford University Press, Melbourne.
- Mauchline J. & L.R. Fisher. 1969. The biology of euphausiids. Adv Mar Biol 7: 1-454.
- Murie J.O., L.S. Davis & I.G. McLean. 1991. Identifying the sex of Fiordland Crested Penguins by morphometric characters. Notornis 38: 233-238.

- Nagy K. A. 1980. CO<sub>2</sub> production in animals: analysis of potential errors in the doubly-labelled water method. *Am J Physiol* 238: R466-R473.
- Nagy K.A. 1983. The doubly-labelled water (<sup>3</sup>H<sup>18</sup>O) method: guide to its use. UCLA Laboratory of Biomedical and Environmental Sciences Publication No. 12-1417.
- Nagy K.A. & D.P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am J Physiol* 238: R454-R465.
- Nagy K.A. & B.S. Obst. 1992. Food and energy requirements of Adélie Penguins (*Pygoscelis adeliae*) on the Antarctic Peninsula. *Physiol Zool* 65: 1271-1284.
- Nagy K.A., W.R. Siegfried & R.P. Wilson. 1984. Energy utilization by free-ranging Jackass Penguins, *Spheniscus demersus*. *Ecology* 65: 1648-1655.
- Nemoto T., M. Okiyama & M. Takahashi. 1985. Aspects of the roles of squid in food chains of marine Antarctic ecosystems. In: Siegfried W.R., P.R. Condy & R.M. Laws (Eds). "Antarctic Nutrient cycles and food webs". Springer-Verlag, Berlin. Pp. 415-420.
- Nesis K.N. 1987. Cephalopods of the world: squids, cuttlefishes, octopuses and allies. THF Publications, Neptune City.
- Nimon A.J., R.C. Schroter & B. Stonehouse. 1995. Heart rate of disturbed penguins. *Nature* 374: 415.
- Obrecht H.H., C.J. Pennycuik & M.R. Fuller. 1988. Wind tunnel experiments to assess the effect of back-mounted transmitters on bird body drag. *J Exp Biol* 135: 265-273.



- Perissinotto R. & C.D. McQuaid. 1992. Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Mar Ecol Prog Ser* 80: 15-27.
- Perry G. 1973. Can the physiologist measure stress? *New Sci* 60: 175-177.
- Prevost J. 1981. Population, biomass and energy requirements of Antarctic birds. In: El-Sayed S.Z. (Ed). "Biomass, vol II". Scott Polar Research Institute, Cambridge. Pp. 125.
- Pütz K. 1994. Untersuchungen zur Ernährungsökologie von Kaiserpinguinen (*Aptenodytes forsteri*) und Königspinguinen (*Aptenodytes patagonicus*). PhD Thesis, University of Kiel, Germany.
- Pütz K. & C.A. Bost. 1994. Feeding behaviour of free-ranging King Penguins (*Aptenodytes patagonicus*). *Ecol* 75(2): 489-497.
- Radok R. 1966. Ocean surface waves and swell. In: "Symposium on Antarctic Oceanography". SCAR. Heffer and Sons, Cambridge. Pp. 30-33.
- Randall R.M., B.M. Randall & D. Baird. 1981. Speed and movement of Jackass Penguins and their possible use of ocean currents. *S Afr J Sci* 77: 420-421.
- Reid T.A., C.L. Hull & E.J. Woehler. (in press). Shipboard observations of penguins at sea, 1991 - 1995. Proceedings of the Third International Penguins Conference, Cape Town, South Africa. *Mar Ornithol*
- Ricketts C. & P.A. Prince. 1981. Comparison of growth of albatrosses. *Ornis Scand* 12: 120-124.

- Ricklefs R.E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115(2): 178-201.
- Ricklefs R.E. 1983. Some consideration on the reproductive energetics of pelagic seabirds. *Studies in Avian Biol* 8: 84-94.
- Ridoux V. 1988. Subantarctic krill, *Euphausia vallentini* Stebbing, preyed upon by penguins around Crozet islands (Southern Indian Ocean): population structure and annual cycle. *J Plankton res* 10(4): 675-690.
- Ridoux V. 1994. The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Marine Ornithol* 22(1): 1-192.
- Robertson G., B. Green & K. Newgrain. 1988. Estimated feeding rates and energy requirements of Gentoo Penguins, *Pygoscelis papua*, at Macquarie Island. *Polar Biol* 9: 89-93.
- Robertson G., R. Williams, K. Green & L. Robertson. 1994a. Diet composition of Emperor Penguin chicks *Aptenodytes forsteri* at two Mawson Coast colonies, Antarctica. *Ibis* 136: 19-31.
- Robertson G., S. Kent & J. Seddon. 1994b. Effects of the water-offloading technique on Adélie Penguins. *J Field Ornithol* 65(3): 376-380.
- Rodhouse P.G. & M.R. Clarke. 1988. Distribution of the early-life phase of the Antarctic squid *Galiteuthis glacialis* in relation to the hydrography of the Southern Ocean in the sector 15° to 30° E. *Mar Biol* 91: 353-357.
- Rodhouse P.G., P.A. Prince, M.R. Clarke & A.W.A. Murray. 1990. Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Mar Biol* 104: 353-362.

- Rodhouse P.G., T.R. Arnborn, M.A. Fedak, J. Yeatman & A.W.A. Murray. 1992. Cephalopod prey of the Southern Elephant Seal, *Mirounga leonina* L. Can J Zool 70: 1007-1015.
- Rodhouse P.G. & P.A. Prince. 1993. Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. Polar Biol 13: 373-376.
- Rounsevell D.E. & N.P. Brothers. 1984. The status and conservation of seabirds at Macquarie Island. ICBP Technical Publication 2: 587-592.
- Sabourenkov E.N. 1991. Mesopelagic fish of the Southern Ocean - summary results of recent Soviet studies. Selected Scientific Papers. Scientific Committee for the Conservation of Antarctic Marine Living Resources.
- St Clair C.C., J.R. Waas, R.C. St Clair & P.T. Boag. 1995. Unfit mothers? Maternal infanticide in royal penguins. Anim Behav 50: 1177-1185.
- St Clair C.C. & R.C. St Clair. 1996. Causes and consequences of egg loss in rockhopper penguins, *Eudyptes chrysocome*. Oikos 77(3): 459-466.
- Samour H.J. & D.M. Jones. 1983. Blood sampling technique in penguins (Sphenisciformes). Vet Record 113: 340.
- Schneider D.C. 1990. Seabirds and fronts: a brief overview. Polar Res 8: 17-21.
- Scolaro J.A. 1987. Sexing fledglings and yearlings of Magellanic Penguins by discriminant analysis of morphometric measurements. Colonial Waterbirds 10: 50-54.
- Scott J. 1994. Marine Conservation at Macquarie Island. A marine conservation

- strategy and an account of the marine environment. Tasmanian Parks and Wildlife Service and Ocean Rescue 2000.
- Selkirk P.M., R.D. Seppelt & D.R. Selkirk. 1990. Subantarctic Macquarie Island: Environment and Biology. Studies in Polar Research, Cambridge University Press, Cambridge.
- Sinclair A.R.E. & M. Norton-Griffiths. 1982. Does competition or facilitation regulate migrant ungulate populations in the Serengeti? A test of hypotheses. *Oecologia* 53: 364 - 369.
- Smith G.T. 1970. Studies of the behaviour and reproduction of the Royal Penguin *Eudyptes chrysolophus schlegeli*. PhD Thesis. Australian National University, Canberra, Australia.
- Stewart B.S., S. Leatherwood, P.K. Yochem & M-P. Heide-Jørgensen. 1989. Harbor seal tracking and telemetry by satellite. *Mar Mammal Science* 5: 361-375.
- Stewart B.S. & R.L. DeLong. 1995. Double migrations of the Northern Elephant Seal *Mirounga angustirostris*. *J Mammal* 76: 196-205.
- Stonehouse B. 1967. The general biology and thermal balances of penguins. *Adv Ecol Res* 4: 131-196.
- Suhonen J. 1993. Predation risk influences the use of foraging sites in tits. *Ecology* 74(4): 1197-1203.
- Tabachnik B.G. & L.S. Fidell. 1989. Using multivariate statistics. Harper Collins Publishers, New York.

- Tchernia P. 1980. Descriptive Regional Oceanography. Pergamon Press, Oxford.
- Testa J.W., G. Oehlert, D.G. Ainley, J.L. Bengtson, D.B. Siniff, R.M. Laws & D. Rounsevell. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the Phocid seals. *Can J Fish Aquat Sci* 48: 631-639.
- Thompson K.R. 1993. Variation in Magellanic Penguin *Spheniscus magellanicus* diet in the Falkland Islands. *Mar Ornithol* 21: 57-67.
- Tremblay Y., E. Guinard & Y. Cherel. 1997. Maximum diving depths of northern rockhopper penguins (*Eudyptes chrysocome moseleyi*) at Amsterdam Island. *Polar Biol* 17: 119-122.
- Trivelpiece W.Z., S.G. Trivelpiece, N.J. Volkman & S.H. Ware. 1983. Breeding and feeding ecologies of pygoscelid penguins. *Ant J US* 18: 209-210.
- Trivelpiece W.Z., J.L. Bengtson, S.G. Trivelpiece & N.J. Volkman. 1986. Foraging behaviour of Gentoo and Chinstrap Penguins as determined by new radiotelemetry techniques. *Auk* 103: 777-781.
- Trivelpiece W.Z., S.G. Trivelpiece & N.J. Volkman. 1987. Ecological segregation of Adélie, Gentoo, and Chinstrap Penguins at King George Island, Antarctica. *Ecol* 68(2): 351-361.
- van Heezik Y. & P. Seddon. 1989. Stomach sampling in the Yellow-eyed Penguin: erosion of otoliths and squid beaks. *J Field Ornithol* 60(4): 451-458.
- van Heezik Y. & L. Davis. 1990. Effects of food variability on growth rates, fledging sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes antipodes*. *Ibis* 132: 354-365.

- van Heezik Y.M., J.T. Darby & P.J. Seddon. (submitted). Penguin pumping problems? Proceedings of the Third International Penguin Conference, Cape Town. Mar Ornithol.
- Veit R.R., E.D. Silverman & I. Everson. 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. J Anim Ecol 62: 551-564.
- Walker K., G. Elliott, D. Nicholls, D. Murray & P. Dilks. 1995. Satellite tracking of Wandering Albatross (*Diomedea exulans*) from the Auckland Islands: Preliminary results. Notornis 42: 127-137.
- Warham J. 1963. The Rockhopper Penguin, *Eudyptes chrysocome*, at Macquarie Island. Auk 80: 229-256.
- Warham J. 1971. Aspects of breeding behaviour in the Royal Penguin *Eudyptes chrysolophus schlegeli*. Notornis 18: 91-115.
- Warham J. 1972. Breeding seasons and sexual dimorphism in Rockhopper Penguins. Auk 89: 86-105.
- Warham J. 1975. The crested penguins. In: Stonehouse B. (Ed.). "The biology of penguins". MacMillan Press, London. Pp. 189-269.
- Watanuki Y., A. Kato, Y. mori & Y. Naito. 1993. Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparisons between years. J Anim Ecol 62: 634-646.
- Weavers B.W. 1992. Seasonal foraging ranges and travels at sea of Little Penguins *Eudyptula minor*, determined by radiotracking. Emu 91: 302-317.



- White L.C. & R.A. Garrott. 1990. Analysis of wildlife radiotracking data. Academic Press, San Diego.
- White W.B. & R.G. Peterson. 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* 380: 699-702.
- Williams A.J. 1981. Why do penguins have long laying intervals? *Ibis* 123: 202-204.
- Williams A.J. 1982. Chick-feeding rates of Macaroni and Rockhopper Penguins at Marion Island. *Ostrich* 53(3): 129-134.
- Williams A.J. & W.R. Siegfried. 1980. Foraging ranges of krill-eating penguins. *Polar Rec* 125: 159-162.
- Williams A.J. & P.A. Laycock. 1981. Euphausiids in the diet of some sub-Antarctic *Eudyptes* penguins. *S Afr J Antarct Res* 10/11: 27-28.
- Williams A.J. & C. Stone. 1981. Rockhopper Penguins *Eudyptes chrysocome* at Tristan da Cunha. *Cormorant* 9: 59-66.
- Williams R. 1988. The nearshore fishes of Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania* 122: 233-245.
- Williams R. & A. McEldowney. 1990. A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Islands. *Australian National Antarctic Research Expeditions Notes* 75: 1-173.
- Williams T.D. 1990. Growth and survival in macaroni penguin, *Eudyptes chrysolophus*, A- and B-chicks: do females maximise investment in the large B-egg? *Oikos* 59: 349-354.

- Williams T.D. & J.P. Croxall. 1991. Annual variation in breeding biology of macaroni penguins *Eudyptes chrysolophus*, at Bird Island, South Georgia. *J Zool, Lond* 223: 189-202.
- Williams T.D. & S. Rodwell. 1992. Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni Penguins. *Condor* 94: 636-645.
- Williams T.D., D.R. Briggs, J.P. Croxall, Y. Naito & A. Kato. 1992. Diving pattern and performance in relation to foraging ecology in the gentoo penguin, *Pygoscelis papua*. *J Zool, Lond* 227: 211-230.
- Wilson G.J. 1983. Distribution and abundance of Antarctic and Subantarctic penguins: a synthesis of current knowledge. *Biomass Sci Ser* 4: 1-46.
- Wilson R.P. 1984. An improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55(1): 109-112.
- Wilson R.P. 1995. Foraging ecology. In: Williams T.D. (Ed). "The penguins". Oxford University Press, Oxford. Pp. 81-106.
- Wilson R.P., W.S. Grant & D.C. Duffy. 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology* 67: 1091-1093.
- Wilson R.P., K.A. Nagy & B.S. Obst. 1989a. Foraging ranges of penguins. *Polar Rec* 25: 303-307.
- Wilson R.P., N.R. Coria, H.J. Spairani, D. Adelung & B. Culik. 1989b. Human-induced behaviour in Adélie Penguins *Pygoscelis adeliae*. *Polar Biol* 40: 77-80.

- Wilson R.P. & B.M. Culik. 1991. The cost of a hot meal: facultative specific dynamic action may ensure temperature homeostasis in post-ingestive endotherms. *Comp Biochem Physiol* 100A(1): 151-154.
- Wilson R.P., B.M. Culik, D. Adelung, H.J. Spairani & N.R. Coria. 1991a. Depth utilisation by breeding Adélie Penguins, *Pygoscelis adeliae*, at Esperanza Bay, Antarctica. *Mar Biol* 109: 181-189.
- Wilson R.P., B. Culik, H.J. Spairani, N.R. Coria & D. Adelung. 1991b. Depth utilization by penguins and Gentoo Penguin dive patterns. *J Orn* 132: 47-60.
- Wilson R.P., W.B. Culik, R. Danfeld & D. Adelung. 1991c. People in Antarctica - how much to Adélie Penguins *Pygoscelis adeliae* care? *Polar Biol.* 11: 363-370.
- Wilson R.P., K. Pütz, C.A. Bost, B.M. Culik, R. Bannasch, T. Reins & D. Adelung. 1993. Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Mar Ecol Prog Ser* 94: 101-104.
- Wilson R.P. & M-P.T. Wilson. 1995. The foraging behaviour of the African Penguin *Spheniscus demersus*. In: Dann P., I. Norman & P. Reilly. (Eds). "The Penguins. Ecology and Management". Surrey Beatty & Sons, Melbourne. Pp. 244-265.
- Wilson R.P., J.A. Scolaro, G. Peters, S. Laurenti, M. Kierspel, H. Gallelli. & J. Upton. 1995. Foraging areas of Magellanic Penguins *Spheniscus magellanicus* breeding at San Lorenzo, Argentina, during the incubation period. *Mar Ecol Prog Ser* 129: 1-6.
- Wilson R.P., B.M. Culik, G. Peters & R. Bannasch. 1996. Diving behaviour of Gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. *Mar biol*

126: 153-162.

- Wilson, R.P., C.A. Bost, K. Pütz, J-B Charrassin, B.M. Culik & D. Adelung. 1997. Southern rockhopper penguin *Eudyptes chrysocome chrysocome* foraging at Possession Island. *Polar Biol.* 17:323-329.
- Wilson R.P. & G. Peters. (submitted). The foraging behaviour of the Chinstrap Penguin *Pygoscelis antarctica* at Ardley Island, Antarctica.
- Woehler E.J., C.L. Hodges & D.J. Watts. 1990. An atlas of the pelagic distribution of seabirds in the southern Indian Ocean, 1981 to 1990. ANARE Research Notes 77.
- Woehler E.J. 1992. Records of vagrant penguins from Tasmania. *Marine Ornithol* 20: 61-73.
- Woehler E.J. 1995. Bill morphology of Royal and Macaroni Penguins, and geographic variation within Eudyptid penguins. In: Dann, P., I. Norman, & P. Reilly (Eds). "The penguins. Ecology and Management". Surrey Beatty & Sons, Melbourne. Pp. 319-330.
- Woehler E.J., R.L. Penney, S.M. Creet & H.R. Burton. 1994. Impacts of human visitors on breeding success and long-term population trends in Adélie Penguins at Casey, Antarctica. *Polar Biol* 14: 269-274.
- Wray S., W.J. Cresswell, P.C.L. White & S. Harris. 1992. What, if anything, is a core area? An analysis of the problems of describing internal range configurations. In: Priede I.M. & S.M. Swift. (Eds). "Wildlife Telemetry. Remote monitoring and tracking of animals". Ellis Horwood, London. Pp. 256-271.

- Zack S. & B.J. Stutchbury. 1992. Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behav* 123 (3-4): 194-219.
- Zullinger E.M., R.E. Ricklefs, K.H. Redford & G.M. Mace. 1984. Fitting sigmoidal equations to mammalian growth curves. *J Mamm* 65(4): 607-636.