Short and medium-term variation in the diets of penguins at Marion Island

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Seasonal (within a breeding season) and year-to-year changes in the diets of the four species of penguins breeding at Marion Island are reviewed. King and gentoo penguins, which are resident at the island throughout the year, show seasonal changes in the relative proportions of different prey types (fish, cephalopods and crustaceans) consumed. However, the few available data suggest that prey species of king penguins vary little from year-to-year, whereas those of gentoo penguins show some variation. In contrast to king and gentoo penguins, macaroni and rockhopper penguins show marked seasonal and annual variation in both the relative proportions of prey type consumed and the species composition of their diets. Seasonal changes reflect changes in their foraging behaviour during chick-rearing, but year-to-year changes are probably related to hydrographic events, which are known to occur in the vicinity of the island and which alter prey species composition and availability.

Seisoenale veranderinge (binne 'n enkele broeiseisoen) en veranderinge van jaar tot jaar in die dieet van die vier pikkewynsoorte wat op Marion-eiland broei, word beskou. Koning- en gentoepikkewyne, wat dwarsdeur die jaar op die eiland bly, toon seisoenale veranderinge in die relatiewe proporsies van die verskillende prooispesies, maar min jaar-tot-jaar-veranderinge. Daar is min data oor koningpikkewyne beskikbaar, maar dit dui daarop dat die prooitipes wat in hulle dieet voorkom, van jaar tot jaar min verander. Die data suggereer egter dat daar wel veranderinge is in die prooitipes wat deur gentoepikkewyne geëet word. Daarteenoor toon macaroni- en geelkuifpikkewyne duidelike seisoenale en jaarlikse verandering in sowel die relatiewe proporsies van die prooitipe geëet, as die spesiesamestelling van hulle diëte. Seisoenale veranderinge reflekteer veranderinge in hulle kossoekgedrag wanneer kleintjies grootgemaak word, maar veranderinge van jaar tot jaar hou waarskynlik verband met hidrografiese gebeurtenisse wat wel in die omgewing van die eiland voorkom en wat die prooispesiesamestelling en -beskikbaarheid verander.

Introduction

Penguins are particularly abundant in the Antarctic and sub-Antarctic but, until recently, surprisingly little was known about their diets. However, recognition of their importance as predators of marine resources (e g Mougin and Prevost, 1980, Croxall and Prince, 1982) has stimulated numerous studies on their food and feeding ecologies (see review by Croxall and Lishman, 1987). Despite an increase in diet studies, there remain relatively few quantitative data spanning full breeding seasons and even less spanning more than one season. The few available data suggest generally little variation in the diets of penguins in Antarctica both during their respective breeding seasons (Croxal and Prince, 1980, Volkman *et al*, 1980, Lishman, 1985) and annually (Trivelpiece *et al*, 1983, Croxall and Lishman, 1987), although more recent evidence for Adélie penguins (*Pygoscelis adeliae*) suggests that such changes may occur at some localities (Green and Johnstone, 1988, Puddlecombe and Johnstone, 1988). Four species of penguins, king penguins (*Aptenodytes patagonicus*), gentoo penguins (*Pygoscelis papua*), macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*E. chrysocome*) breed at Marion Island in the sub-Antarctic (46°52 S,37°51 E). In contrast to the case at most Antarctic and sub-Antarctic localities, recent studies at Marion Island have demonstrated both seasonal and annual variation in diets of the breeding penguins. This paper reviews current information, both published and unpublished, on the diets of the four species of penguins at Marion Island with the objective of highlighting and attempting to explain these short-term (within a breeding season) and medium-term (year-to-year) variations.

Data base

Information on general composition of the diets (i e relative proportions of each prey type) and prey species con-

sumed by the four species of penguins at Marion Island were obtained from a recent series of quantitative diet studies. King and gentoo penguins are resident at the island and were sampled over a period of one year (Adams and Klages, 1987, 1989). This limited quantitative data base allows assessment of short-term changes, but year-to-year changes are restricted to comparisons with previous less detailed studies and opportunistic samples (La Cock *et al*, 1984, NJ Adams, unpublished data).

Macaroni and rockhopper penguins were sampled over two successive summer breeding periods (Brown and Klages, 1987) and additional information was obtained from less detailed studies (Williams and Laycock, 1981) and from opportunistic sampling (FitzPatrick Institute, unpublished data).

Results and discussion

Short-term changes

In general, king penguins fed on fish and cephalopods, whereas gentoo, macaroni and rockhopper penguins fed on crustaceans, fish and cephalopods, although in different proportions and frequently on different species (see below). During years in which intensive sampling took place, changes in prey composition were evident in all four species of penguins over the course of the respective sampling periods. For example, king penguins, which have an extended breeding season of 14 months, fed predominantly on pelagic squid in winter, but consumed almost exclusively fish in summer (Adams and Klages, 1987). This may indicate either a greater availability of cephalopods within reach of the penguins in winter (when the lower ambient light levels may trigger mesopelagic squid to rise in the water column), a decrease in the availability of fish at this time, or both.

In gentoo penguins, crustaceans tended to predominate in the diet early in the year, changing to more fish from about July, when this species begins breeding (Adams and Klages, 1989). Williams (1981) first described from changes in guano colour a seasonal change in the diet of gentoo penguins from crustaceans to fish and suggested that this was in response to the summer influx of large numbers of macaroni and rockhopper penguins which potentially competed for available resources, especially crustaceans. However, Adams and Klages (1989) have subsequently demonstrated that the change in diet occurs several months before the arrival of macaroni and rockhopper penguins. Seasonal changes in the diets of gentoo penguins are, as in king penguins, thus thought to reflect changes in prey availability rather than changes in prey selection. However, in contrast to king penguins, gentoo penguins restrict their foraging to within 40 km from shore (Adams and Wilson, 1987). At present, we are uncertain of the factors leading to changes in prey availability in this region because the biology of *Nauticaris marionis*, the predominant crustacean in the diets of gentoo penguins, and the marine fish fauna of the Prince Edward Islands remain largely unexplored (Gon and Klages, 1988) and the effect of hydrological events in the nearshore region on these is unknown.

Seasonal changes in prey availability undoubtedly also affect the composition of the diets of macaroni and rockhopper penguins, but changes in foraging patterns are also an important factor. Both species feed exclusively on crustaceans early in their respective chick-rearing periods, when they forage relatively close to their colonies. However, as the chicks grow the penguins forage farther afield and their diets include an increasing proportion of pelagic fish and cephalopods (Brown, 1987, Brown and Klages, 1987).

In contrast to the situation at the Prince Edward Islands, most penguins in the Antarctic and sub-Antarctic show little seasonal variation in diet. However, Puddlecombe and Johnstone (1988) and Green and Johnstone (1988) have demonstrated changes in diet in Adélie penguins before and after chick hatching at Magnetic Island, East Antarctica. More recently, Hindell (1989a) reported seasonal variations in the relative proportions of certain prey species of royal penguins at Macquarie Island (54° S), although rockhopper penguins at the same locality showed little variation (Hindell, 1989b).

Medium-term changes

General composition of the diets

Intensive sampling from king penguins has been carried out only over a single year (1984/85), but some quantitative information on relative numbers of fish and cephalopods is available from 40 samples covering six months between September 1981 and May 1982 (NJ Adams, unpublished data). During this period, fish comprised an average of 21% (range 3 — 49%) and cephalopods the balance. This is in marked contrast to later sampling when fish generally comprised between 80 and 95% by numbers of the diet (Adams and Klages, 1987). However, the absence of very small otoliths in the early samples and their presence in large numbers in 1984/85 suggest that early sorting techniques may have been inadequate to recover these, resulting in an underestimate of numbers of fish consumed. Confirmation of potential large variations in prey composition of king penguins must therefore await further intensive sampling.

Although there is relatively little information on gentoo penguins, samples collected over a full year, March to March inclusive, nevertheless still demonstrate differences in general composition of their diets. Thus, in March 1984, the overall diet comprised 82% crustaceans and the balance fish, whereas in March 1985 crustaceans were absent, the diet consisting of 85% fish and 15% cephalopods (Adams and Klages, 1989). Similarly, the diet of gentoo penguins in September 1982 differed markedly from that in the same month in 1984, consisting of 70% fish and 30% crustaceans and 44% fish and 56% crustaceans, respectively (La Cock *et al*, 1984, Adams and Klages, 1989).

Quantitative information on the relative proportions of different prey types in the diets of macaroni and rockhopper penguins is available for three breeding seasons between 1983/1984 and 1987/1988 (Table 1). In both species, crustaceans predominated in all years. Fish was not present in measurable quantities in either species of penguin in 1983/1984 and contributed only 4 — 5% of the

Table I

General composition (% by mass) of the diets of four species of penguins at Marion Island. Figures in parentheses are % composition based on mass reconstituted from fish otoliths and cephalopod beaks

Species	Year	Crustaceans	Fish	Cephalopods
King penguins	1984/85	—	87 (69)	14 (31)
Gentoo	1982	30	70	<1
penguins	1984/85	44	54	2
Macaroni	1983/84	98 (87)	— (5)	2 (8)
penguins	1984/85	88 (62)	10 (25)	2 (13)
	1987/88	83	16	1
Rockhopper	1984	100 (92)	— (4)	<1 (5)
penguins	1985	91 (81)	6 (14)	3 (5)
	1988	96	4	<1

Table 2

Prey species composition of the diet of king penguins at Marion Island. +++ major component, ++ minor component, + present, − absent. Data from Adams and Klages (1987) and NJ Adams (unpublished data)

Prey species	Sample years	
	1981/82	1984/85
Crustaceans		
Nauticaris marionis	−	+
Euphausia sp.	−	+
Fishes		
Krefftichthys anderssoni/ Protomyctophum tenisoni[a]	++	+++
Protomyctophum normani	−	+++
P. bolini	−	++
Electrona carlsbergi	+	+++
Gymnoscopelus spp.	+	++
Lepidonotothen squamifrons[b]	−	+
Paranotothenia magellanica[c]	−	+
Magnisudis prionosa[d]	+	++
Cephalopods		
Kondakovia longimana	+	+++
Moroteuthis knipovitchi	+	++
Histioteuthis eltaninae	+	++
Martiala hyadesi	+	+
Gonatus antarcticus	+	+
Galiteuthis glacialis	−	+
Brachioteuthis spp.	+	+
Alluroteuthis spp.	+	++
Unknown Oegopsid	+	++

[a] Regarded in king penguins as a species complex because of difficulties in separating the two species on the basis of their otoliths
[b] Formerly *Notothenia squamifrons*
[c] Formerly *Notothenia magellanica*
[d] Previously erroneously identified as *Paralepis coregonoides*

mass of the diets on the basis of recovered otoliths. The proportion of fish recovered from macaroni penguins has increased in subsequent years, amounting to 10% and 16% of the diet in 1984/1985 and 1987/1988, respectively, and up to 25% of the diet on the basis of reconstituted biomass. Fish has also increased in the diets of rockhopper penguins, comprising between 6 and 4% of the measurable material in 1985 and 1988, respectively, and 14% of the reconstituted biomass in 1985. Cephalopods generally comprise only a small proportion (< 5%) of identifiable material, although they may contribute more on the basis of reconstituted biomass estimated from "beaks" found in the samples.

Similar changes in relative proportions of prey have been observed in the diet of rockhopper penguins at Gough Island (40° S), where samples collected in three successive years between 1984 and 1986 had similar proportions of crustaceans, but demonstrated an increase in the proportion of fish and a decrease in the proportion of cephalopods (Klages *et al*, 1988).

Croxall and Lishman (1987) concluded that the relative proportions of prey taken by Antarctic penguins was remarkably constant from year to year. More recently, however, Green and Johnstone (1988) have reported changes in relative proportions of crustaceans and fish in the diets of Adélie penguins between the 1982/83 and 1983/84 breeding seasons. Furthermore, Croxall and Furse (1980) reported differences in the proportions of prey taken by macaroni penguins at two nearby islands in the South Shetland Island group (61° S) in the same season and Horne (1985) and Hindell (1989a) reported differences in the diets of royal penguins sampled on opposite sides of Macquarie Island (55° S). Such differences are generally assumed to reflect local availability of prey.

Variation in prey species

King penguins show little variation in prey species from one year to another, species found in samples in 1981/82 and 1984/85 overlapping almost completely (Table 2). The slightly greater species diversity in 1984/85 is probably due to the greater number of samples collected, the longer sampling period (12 vs 9 months) and improved sorting techniques.

As with king penguins, the greater species diversity, especially of fish, in the diets of gentoo penguins in 1984/85 compared with 1982 (Table 3) can probably be

Table 3

Prey species composition of gentoo penguins at Marion Island. Conventions and footnotes as for Table 2. Data from La Cock *et al* (1984) and Adams and Klages (1989)

Prey species	Sample years	
	1982	1984/85
Crustaceans		
Nauticaris marionis	+++	+++
Euphausia vallentini	–	+++
Themisto gaudichaudii	–	+
Nematocarcinus longirostris	–	+
Vibilia sp.	–	+
Primno sp.	–	+
Hyperiella sp.	–	+
Fishes		
Lepidonotothen squamifrons[b]	+++	+++
Paranotothenia magellanica[c]	+	–
Notothenia acuta	–	++
N. coriiceps	+	–
Channichthys rhinoceratus	–	++
Krefftichthys anderssoni	–	++
Protomyctophum normani	–	++
P. tenisoni	–	++
P. bolini	–	++
Protomyctophum sp.	+	
Electrona carlsbergi	+	+
Gymnoscopelus nicholsi	+	++
Dissostichus eleganoides	–	+
Muraenolepis sp.	–	+
Cephalopods		
Kondakovia longimana	+	+
Octopus sp.	+	+++

attributed to the more intensive sampling. Overall, the benthic shrimp, *Nauticaris marionis*, and the fish, *Lepidonotothen squamifrons*, were the most important prey species, but the cannichtyiid fish, *Channichthys rhinoceratus*, and the crustacean, *Euphausia vallentini*, also comprised a substantial proportion of the diet in 1984/85 (Adams and Klages, 1989). *C. rhinoceratus* is considered a demersal species endemic to the cooler waters around Kerguelen (49° S) and Heard (60° S) islands (Gon and Klages, 1989). Although too large to be consumed by macaroni and rockhopper penguins, *C. rhinoceratus* has not been found in the diets of king penguins, suggesting that its presence in the diet of gentoo penguins is an unusual event, possibly resulting from unusual hydrographic conditions (Adams and Klages, 1989). *Euphausia vallentini*, which comprised almost 100% of the diet of gentoo penguins in January and February 1985, was also preyed upon extensively by macaroni and rockhopper penguins at the same time and were probably available close inshore.

The most striking variability in year-to-year prey species composition is evident in macaroni and rockhopper penguins (Tables 4 and 5), for which most information is available. The earliest samples from 1973/74 identified *Thysanoessa macrura* as the predominant crustacean consumed by macaroni penguins and this species was the only crustacean identified from rockhopper penguins (Williams and Laycock, 1981). Despite intensive sampling it has not subsequently been recovered from either species of penguin, although it is frequently the most abundant euphausiid in net hauls in the region (Allanson *et al*, 1985, Boden and Parker, 1986). Similarly, *Euphausia lucens*, present in the diet of rockhopper penguins in 1983 and common in net hauls in the same year and the following year (Boden and Parker, 1986), has not subsequently been recovered from stomach samples.

Notable differences in crustacean composition were also evident in two years of intensive sampling. In particular, *Nauticaris marionis*, the most abundant crustacean in the diets of both macaroni and rockhopper penguins in 1983/84, was absent in the following year, being largely replaced by *Thysanoessa vicina* (Brown and

Table 4

Prey species composition of macaroni penguins at Marion Island. Conventions and footnotes as for Table 2. Data from Williams and Laycock (1981), Brown and Klages (1987), FitzPatrick Institute (unpublished data)

Prey species	Sample years			
	1973/74	1981/82	1983/84	1984/85
Crustaceans				
Nauticaris marionis	–	–	+++	–
Euphausia vallentini	+	+	++	+++
Thysanoessa macrura	++	–	–	–
T. vicina	–	+	++	+++
Themisto gaudichaudii	–	++	+++	++
Primno sp.	–	–	++	+
Cyllopus sp.	–	–	–	++
Hyperiella sp.	–	–	–	+
Nematocarcinus longirostris	–	–	++	+
Fishes				
Krefftichthys anderssoni	–	+++	++	+++
Protomyctophum tenisoni	–	+++	+++	+++
P. normani	–	+	++	+++
P. bolini	–	+	–	+
Electrona carlsbergi	–	++	+++	+
E. subaspera	–	–	–	+
Gymnoscopelus sp.	–	+	–	+
Lepidonotothen squamifrons[b]	–	–	–	+
Magnisudis prionosa[d]	–	–	–	+
Dissostichus eleganoides	–	–	–	+
Cephalopods				
Kondakovia longimana	–	++	+++	+++
Moroteuthis knipovitchi	–	+	+	–
Alluroteuthis antarcticus	–	+	–	+
Unknown Oegopsid	–	+	–	–
Octopus sp.	–	–	++	++

Table 5

Prey species composition of rockhopper penguins at Marion Island. Conventions and footnotes as for Table 2. Data from Williams and Laycock (1981), Brown and Klages (1987), FitzPatrick Institute (unpublished data)

Prey species	Sample years			
	1974	1983	1984	1985
Crustaceans				
Nauticaris marionis	–	–	+++	+
Euphausia vallentini	–	–	+++	+++
E. lucens	–	+	–	–
Thysanoessa macrura	+++	–	–	–
T. vicina	–	–	–	+++
Themisto gaudichaudii	–	+	–	+
Primno sp.	–	–	–	+
Vibilia sp.	–	–	–	+
Fishes				
Krefftichthys anderssoni	–	+	+++	+++
Protomyctophum tenisoni	–	+	+++	+++
P. normani	–	+	–	+++
P. bolini	–	+	–	–
Gymnoscopelus sp.	–	+	–	–
Paranotothenia magellanica	–	–	+	++
Cephalopods				
Kondakovia longimana	–	+	+++	++
Octopus sp.	–	+	+++	+++

Klages, 1987). Similar year-to-year differences were evident in the fish component of the diets of the two species of penguins. *Electrona carlsbergi*, important in the diet of macaroni penguins in 1983/84, was virtually absent the following year (Table 4). In addition, *Protomyctophum normani*, present only in small numbers in macaroni penguins and not at all in rockhoppers in 1983/84, was the third most abundant fish consumed by macaroni penguins and the second most abundant consumed by rockhopper penguins to following season (Tables 4 and 5).

In addition to Marion Island, there is evidence to suggest some year-to-year variation in the prey species composition of royal penguins at Macquarie Island. For example, Horne (1985) reported substantial numbers of the amphipods *Primno macropa* and *Themisto gaudichaudii* in their diets in 1982, whereas these species were absent in the more intensive sampling of Hindell in 1985 (Hindell, 1989a). Also, Horne reported squid to comprise 30 — 40% of the diet, but Hindell recorded <5%. The latter, however, may be an artifact of the differences in sampling period; Horne's samples were collected only over a period of two weeks and Hindell's over the entire season. Among Antarctic penguins, relative proportions of *Euphausia superba* and *E. chrystallorophias* in the diets of Adélie penguins in east Antarctica have been shown to change from year to year, as have the relative proportions of benthic (inshore) and pelagic (offshore) fish species (Green and Johnstone, 1988). These changes have been attributed to either a change in foraging area of the Adélie penguins in response to a decrease in inshore food supplies or a movement of *E. superba* to inshore waters, with the former being the favoured explanation.

Stomach contents and net hauls

Macaroni and rockhopper penguins, in particular, take a wide range of suitably sized crustacean and fish prey. Nevertheless, net hauls in the vicinity of the Prince Edward Islands frequently contain pelagic crustaceans seldom found in penguin stomach samples (e g *Euphausia similis*, *E. longirostris* and *Thysanoessa macrura;* see Table 6). However, net sampling is usually carried out in winter when macaroni and rockhopper penguins are away from the islands. The absence of potential prey species in the diets of the penguins in summer suggests some seasonal variation in zooplankton distribution and abundance. Futhermore, crustaceans present in the waters around the Prince Edward Islands, based on net hauls carried out between 1980 and 1985 (Miller, 1982, Allanson *et al*, 1985, Boden and Parker, 1986), show a wide species diversity with changes in the dominant forms. For example, zooplankton samples from two successive years, 1982 and 1983, showed the four dominant zooplankton components to differ markedly, leading Allanson *et al* (1985) to infer that separate communities had been sampled.

Whether sampled by nets or by using penguins as biological samplers, zooplankton from Marion Island

Table 6

Prey species (crustaceans) and potential prey species recovered from net hauls in the vicinity of the Prince Edward Islands. Data from Miller (1982), Allanson *et al* (1985), Boden and Parker (1986) and BP Boden (unpublished data)

Species	Sample years			
	1980	1982	1983	1985
Euphausia vallentini	+	+	−	+
E. lucens	−	+	+	−
E. similis	−	+	+	+
E. longirostris	+	+	−	+
Thysanoessa macrura	−	+	+	+
Themisto gaudichaudii	+	+	+	−
Primno macropa	−	+	+	−
Vibilia antarctica	−	+	+	−
V. armata	−	+	+	−

waters include species normally associated with subtropical and Antarctic waters as well as the expected sub-Antarctic forms (Tables 4-6). For example, *Thysanoessa macrura* is generally regarded as an Antarctic species with *T. vicina* its warm-water counterpart. In contrast, *Euphausia lucens* is considered to be a subtropical species and is a common crustacean in the diet of rockhopper penguins at Gough Island (40° S) (Klages *et al*, 1988). Its presence in the waters around the Prince Edward Island represents an extension beyond its normal southerly limits (Boden and Parker, 1986). The presence of the above and other species in the vicinity of the Prince Edward Islands is thought to occur through advection of foreign water masses past the islands. Grindley and Davis (1985) have suggested that upwelling of Antarctic water in the lee of Marion Island is responsible for variation in the species composition of zooplankton, but most recent authors suggest the major source to be a system of eddies which concentrate, contain and transport zooplankton in waters similar to their normal environment (Allanson *et al*, 1985, Boden and Parker, 1986). The advection of these eddies, with their own characteristic fauna, past the Prince Edward Islands thus alters the composition of the zooplankton community. A complex pattern of currents in the vicinity of the islands may result in a weakening of the Antarctic Polar Front in the region (Deacon, 1983), further facilitating the exchange of species across normal boundaries.

Less easily explained is the variation in abundance of inshore species, especially *Nauticaris marionis*. Their absence from the diets of macaroni and rockhopper penguins in 1985 and their scarcity in the diets of gentoo penguins in the same year is surprising, especially as Adams and Klages (1989) reported the presence of ovigerous females late in 1984. Clearly, further investigation of hydrological effects on species composition of penguin prey in the nearshore regions is warranted.

Whatever the mechanisms, hydrological events appear to play a major role in determining the availability of prey species suitable for penguin consumption, especially for macaroni and rockhopper penguins which forage at distances intermediate to gentoo and king penguins. Such hydrological events might account for the relatively opportunistic feeding habits of the penguins which are reflected in their high dietary diversity indices and low dietary overlap indices compared with those of penguins and other seabirds at some localities in the Southern Ocean (Adams and Brown, 1989).

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