Temporal variation in the diet of the Gentoo Penguin *Pygoscelis papua* at sub-Antarctic Marion Island

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Abstract.—The diet of the Gentoo Penguin *Pygoscelis papua* at sub-Antarctic Marion Island was sampled by stomach pumping at monthly intervals from March 1984 to March 1985. Overall, fish accounted for 53% of the diet by mass, crustaceans 44% and cephalopods 2%. Crustaceans predominated between March and June 1984; a marked increase in the proportion of fish in July coincided with the start of egg laying by Gentoo Penguins. Fish accounted for almost all of the diet in January and March 1985. Juvenile nototheniid fish, in particular *Notothenia squamifrons*, formed the bulk of the fish component; myctophids and *Channichthys rhinoceratus* were less common. The pelagic euphausiid *Euphausia vallentini* accounted for about 50% by mass of the overall crustacean component lumped over the entire study period. The decapod shrimp *Nauticaris marionis* was the most important crustacean species consumed during June to September 1984. Cephalopods, predominantly octopods, were taken mainly in February and March 1985. The hypothesis that seasonal changes in diet occur in direct response to the arrival of crested penguins (*Eudyptes* spp) early in summer is not supported by the data. Changes in diet appear to reflect local changes in the availability of prey species within the inshore waters exploited by Gentoo Penguins. *Received 10 March 1988, accepted 25 November 1988.*
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Studies of the diets of both migrant and resident penguins in the Southern Ocean region have concentrated on birds during the chick-rearing period, with little information for the non-breeding season (see Croxall and Lishman 1987). The Gentoo Penguin *Pygoscelis papua* is a year-round resident at sub-Antarctic Marion Island (van Zinderen Bakker 1971), and at some other breeding sites in the Southern Ocean (Watson 1975), affording opportunities for sampling its diet throughout the year.

Williams (1981) suggested that seasonal changes in the diet and earlier, winter breeding by Gentoo Penguins at Marion Island, compared to populations at higher latitudes, ensured a crustacean diet during incubation and early chick rearing. He suggested that a switch by Gentoo Penguins to a fish diet later in the season, deduced from a change in color of the excreta, was a response to the arrival of large numbers of two species of potentially competing, summer-resident crested penguins, the Macaroni *Eudyptes chrysolophus* and the Rockhopper *E. chrysocome*. However, food samples collected at Marion Island in September 1982 showed that fish are common in the diet of Gentoo Penguins before the arrival of the other penguin species (La Cock *et al.* 1984). We report here on a more comprehensive set of samples collected throughout a single year at Marion Island. Our principal objective was to investigate temporal changes in diet.

METHODS

A total of 144 stomach samples was collected from Gentoo Penguins at three colonies distributed along a nine kilometre stretch of the east coast of Marion Island (46° 53'S, 37°54'E) from March 1984 to March 1985 inclusive. Using the technique of Wilson (1984), we stomach pumped an average of 11 birds a month as they returned to their landing beaches in the evening. We did not attempt to distinguish the breeding status of the birds. Gentoo Penguins at Marion Island tend chicks from late July to December. Consequently, during this period, we probably sampled both breeding and non-breeding birds.

Immediately after collection, samples were drained through a 0.5 mm sieve. Subsequently, drained samples were weighed to the nearest gram and then stored at 4°C until sorting, generally completed within 24 h of collection. Soft identifiable material was sorted into fish, cephalopod and crustacean components (further separated into shrimps, euphausiids and amphipods) and weighed. Since fish muscle is digested more rapidly than squid, which is in turn digested more rapidly than crustacea muscle (Jackson *et al.* 1987), we may have overestimated, in particular, the mass of crustaceans in mixed samples. However, most stomach samples from Gentoo Penguins contained one prey type only (see below).

Most fish were recovered with heads separated from the remainder of the body. Consequently, analyses were based on identification and measure-

ment of otoliths (Adams and Klages, 1987). We estimated standard length (SL) and mass of fish from regressions relating otolith diameter to these parameters. Regressions not available in Adams and Klages (1987) and Brown and Klages (1987) are given in Duhamel (1981), Hecht and Cooper (1986), and Hecht (1987). Since otoliths were removed from intact fish crania, digestion and hence measurement error were minimal.

Crustacean species were identified with the aid of published keys (Bowman and Gruner, 1973; Kirkwood, 1982; 1984). Total length of intact individuals was measured from the anterior margin of an eye to the tip of the telson. Numbers of crustaceans in each sample were estimated by dividing total mass by the average mass of an individual crustacean of each respective species. Actual numbers and fresh mass of prey ingested will be underestimated in well-digested samples.

Most of the small cephalopods were recovered intact, and numbers were counted directly. The identification of squid beaks was facilitated by a reference collection at the Port Elizabeth Museum, and confirmed by comparison with the literature (Clarke, 1986). We estimated dorsal mantle length (DML) and mass of squid from regressions relating lower rostrum length (LRL) to these parameters (Adams and Klages, 1987). Juvenile octopods were not identified.

Table 1. Numbers and frequency of occurrence of prey items identified from Gentoo Penguin stomach samples at Marion Island.

Prey species	Total number	% numbers of prey class	% frequency of occurrence
FISH			
Notothiniidae			
Notothenia squamifrons	1231	58.6	50.7
Unident. juv. nototheniids	442	21.1	14.6
Notothenia acuta	27	1.3	11.1
Dissostichus eleginoides	11	0.5	6.3
Channichthyidae			
Channichthys rhinoceratus	132	6.3	12.5
Myctophidae			
Protomyctophum normani	122	5.8	4.2
Gymnoscopelus nicholsi	32	1.5	4.2
Protomyctophum tenisoni	30	1.4	4.9
Krefftichthys anderssoni	24	1.1	3.5
Protomyctophum bolini	21	1.0	4.2
unid. myctophids	15	0.7	4.9
Electrona carlsbergi	4	0.2	1.4
Gymnoscopelus sp.	1	<0.1	0.7
Muraenolepidae			
Muraenolepis sp.	4	0.2	0.7
Unident. fish	3	0.1	1.4
CRUSTACEANS			
Euphausiacea			
Euphausia vallentini	55 496	86.4	25.7
Hippolytidae			
Nauticaris marionis	8 685	13.5	33.3
Amphipoda			
Themisto gaudichaudii	77	0.1	4.9
Hyperiella sp.	13	<0.1	2.1
Unident. amphipods	12	<0.1	2.1
Vibilia sp.	2	<0.1	1.4
Primno sp.	2	<0.1	1.4
Nematocarcinidae			
Nematocarcinus longirostris	3	<0.1	1.4
CEPHALOPODS			
Octopoda			
Unident. juv. octopods	810	94.9	18.8
Decapoda			
Unident. juv. squid	25	2.9	9.0
Kondakovia longimana	9	1.1	3.5
Onychoteuthidae LRL >2mm	5	0.6	3.5
Onychoteuthidae LRL < 2mm	5	0.6	3.5
GASTROPODA			
Margarella expansa	4	100.0	2.1
ECHINODERMATA			
Ophiuroidea	1	100.0	0.7

RESULTS

Mean mass of food samples was 139.2 ± 130.5 g (range: 8 – 650 g, n = 144), similar to the 147 g recorded by La Cock *et al.* (1984). Mean monthly sample mass was highest in December at 332 g.

General Composition of the Diet

Thirty species or species groups were identified (Table 1), with fish comprising the largest single group (11 species). However, samples from individual penguins were largely homogeneous consisting of a single species of crustacean or fish (see also Jablonski 1985, Croxall *et al.* 1988). Fifty-eight percent of stomach samples contained only a single prey taxon, 26% contained two taxa and 10% contained three taxa (analysis based on taxa comprising at least 5% by mass of individual samples).

Fish and crustaceans accounted for 53.5 and 44.4% respectively of the total annual diet by mass (Table 2). However, considerable changes in proportions of fish, crustaceans and cephalopods occurred over the year (Table 3, Fig. 1). Crustaceans accounted for over 75% of the diet by mass from March to June 1984 but decreased to 0% by March 1985. Cephalopods accounted for more than 10% of the diet only in February and March 1985.

Fish

The fish component of the diet was dominated by the family Nototheniidae, particularly *Notothenia squamifrons*. It is likely that most of the unidentified juvenile nototheniids were also this species (Table 1). Nototheniids accounted for over 90% of the fish component during June to October 1984. Myctophids and the channichthyid *Channichthys rhinoceratus* appeared more commonly in the diet from October and accounted for most of the food items in March 1985 (Table 3).

Fish of 78.8 - 84.1 mm (5.9 - 7.3 g) were the most frequently taken size class. When plotted on a monthly basis, there was no evidence of any progressive change in size-class distribution throughout the year. However, during January and February smaller fish between 28.6 - 41.8 mm (0.2 - 0.7 g) accounted for the most frequently taken size class, whereas larger individuals (76.2 - 84.1 mm, 5.3 - 7.3 g) were more numerous during the remaining months. Standard parameters for all fish species are given in Table 4.

Crustaceans

Euphausia vallentini and *Nauticaris marionis* made up nearly all of the crustacean component. During winter (March to August 1984), *N. marionis* formed the largest part of the crustacean component, but *E. vallentini* subsequently increased to nearly 100% in January and February 1985 (Table 3). Mean length of *E. vallentini* was 22.5 mm ± 1.74 (n = 681), considerably smaller than that of *N. marionis* (35.1 mm ± 5.18, n = 1481).

Cephalopods

Cephalopods accounted for just over 10% of the diet during February and March 1985 but seldom occurred in the remaining months (Table 3). Most cephalopods were small octopods (DML < 15 mm). The only squid identified were juveniles of the species *Kondakovia longimana* of estimated dorsal mantle length and mass of 58.4 ± 11.4 mm and 9.6 ± 3.8 g (n = 4) respectively.

DISCUSSION

Fish (Ealey 1954, Volkman *et al.* 1980) and, in particular, nototheniids may form a substantial portion of the diet of the Gentoo Penguin throughout its range. The most important prey species by mass in the

Table 2. Aggregate per cent prey composition by wet mass consumed by Gentoo Penguins at Marion Island.

	Fish	Crustaceans	Cephalopods
Wet mass (%) Mean	53.5	44.4	2.1
SD	46.9	47.4	9.8
Range	(0-100)	(0-100)	(0-51.8)

Table 3. Percent composition by mass of main prey types consumed by Gentoo Penguins at Marion Island by month.

Species	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Crustaceans													
Euphausia va lentini	16.5	42.8	47.1	4.5	4.2	8.9	17.6	23.6	29.7	11.6	1.0	36.2	0
Nauticaris marionis	65.8	42.8	51.0	70.8	23.9	26.7	38.1	4.7	4.2	7.0	0	0	0
Themisto gaudichaudii	0	0	0	0	0	0	0	0	0	0	0	1.8	0
Fish													
Notothenidae	0	0	0	23.5	66.4	62.5	44.3	68.4	45.1	79.1	71.4	35.2	13.5
Myctophidae	0	14.4	0	0	0.5	1.9	0	1.6	20.8	1.9	4.8	10.0	48.2
Channichythidae	0	0	0	0	0	0	0	0	0	0	21.9	6.1	23.7
Muraenolpidae	0	0	0	0	4.3	0	0	0	0	0	0	0	0
Unidentified	16.8	0	1.4	0	0	0	0	0	0	0	0	0	0
Cephalopods	0	0	0.5	1.2	0.7	0	0	1.7	0.2	0.4	0.9	10.7	14.6

diet of Gentoo Penguins at Marion Island was *Notothenia squamifrons* (incorrectly identified as *Harpagifer georgianus* in La Cock *et al.* 1984, N. T. Klages pers. obs.) whereas *N. rossi* and *N. larseni* were consumed at southerly sites (Croxall and Prince 1980a, Jablonski 1985). *N. squamifrons* is widely distributed occurring around the islands of the southern Indian and, less commonly, the South Atlantic Oceans

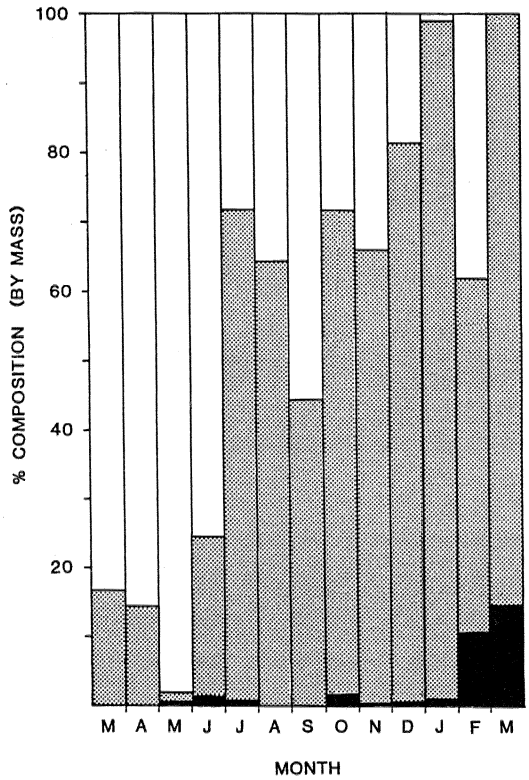

Figure 1. Variation in the diet of the Gentoo Penguin at Marion Island throughout a single year. Unshaded segment: crustaceans, stippled segment: fish, shaded segment: cephalopods.

(Duhamel *et al.* 1983). *N. squamifrons* taken by Gentoo Penguins at Marion Island, all in the range 28 - 134 mm, were larval or juvenile fish of 0 - 4 years (Duhamel and Ozouf-Costaz 1985). The occurrence of large numbers of unidentified juvenile nototheniids in the diet in November and December preceded an increase in the relative abundance of small-size class *N. squamifrons* in the diet in January and February 1985. This may reflect growth of these larval fish.

Juvenile *Channichthys rhinoceratus*, were the largest and second most abundant fish in the diet. Adults were presumably too large for consumption. The species had previously been considered a demersal species endemic to the colder waters around Kerguelen (48°27′–50°S, 60°27′–70°35′E) and Heard Islands (53°01′S, 73°23′E) (Kock *et al.* 1985). The presence of this species in the relatively warm waters around Marion Island was surprising. However, hydrographical evidence (Benon and Murail 1979) and sampling of zooplankton (Grindley and Lane 1979, Boden and Parker 1986) suggests that advection of foreign water masses past the island with associated fauna may occur (Boden & Parker 1986).

The appearance of myctophids in the diet of Gentoo Penguins coincided with the increase in relative abundance of these fish in the diet of King Penguins *Aptenodytes patagonicus* during summer, suggesting increased availability (Adams and Klages 1987). Small numbers of myctophids have previously been reported in the diet of Gentoo Penguins of unknown status at Marion Island (La Cock *et al.* 1984).

Table 4. Summary of otolith diameter (OD), estimated standard length (SL) and estimated mass of fish recovered from Gentoo Penguin stomach samples at Marion Island.

Species	N	OD (mm) Mean SD	Range	Estimated SL (mm) Mean SD	Range	Estimated mass (g) Mean SD	Range
Notothenidae							
Notothenia squamifrons	1109	2.43±0.87	(0.8-5.8)	71.1±18.7	(23.3–155.5)	5.6±4.1	(0.1-56.3)
Notothenia acuta	47	3.19±0.64	(1.38-4.7)	85.0±20.3	(38.6-126.4)	9.2±6.6	(0.6-28.3)
Dissostichus eleginoides	17	3.52±0.73	(2.19-5.27)	105.7±42.6	(42.4-215.1)	10.6±16.9	(0.3-65.0)
Channichthyidae							
Channichthys rhinoceratus	170	1.48±0.38	(0.97-2.45)	170.3±36.8	(127.0-238.3)	21.1±18.9	(6.8-61.9)
Myctophidae							
Protomyctophum normani	61	2.38±0.10	(2.19–2.6)	77.7± 3.7	(70.0-85.2)	6.4± 0.9	(4.7-8.3)
Protomyctophum tenisoni	57	1.63±0.13	(1.3-1.78)	49.2±4.9	(37.0-54.8)	1.8±0.5	(0.8-2.3)
Krefftichthys anderssoni	35	1.51±0.25	(0.97-1.87)	49.6±11.2	(25.2-66.0)	2.0±1.1	(0.2-4.3)
Gymnoscopelus nicholsi	12	6.20±0.19	(5.91-6.55)	156.2±5.7	(147.4-166.7)	44.3±4.8	(37.4-53.3)
Protomyctophum bolini	4	2.00±0.38	(1.7-2.35)	57.7±12.2	(46.1-67.3)	1.5±0.8	(0.8-2.2)
Muraenolepidae							
Muraenolepis sp.	7	2.7±0.58	(1.87-3.4)	141.1±46.6	(76.8-200.8)	24.9±20.8	(2.3-60.6)

Two species of crustacean *Euphausia vallentini* and *Nauticaris marionis*, were of almost equal importance by mass at Marion Island. This is in contrast to the situation at sites south of the Antarctic Polar Front, where the crustacean component of the diet of the Gentoo Penguin is dominated by a single species, *E. superba*. *E. vallentini* was the most important prey consumed by Macaroni and Rockhopper penguins during the 1984-1985 summer, and remained abundant in the diet of Rockhopper Penguins in March 1985 (Brown and Klages 1987) when it was absent from the diet of the Gentoo Penguin. Both species of crested penguins probably forage farther offshore during late chick-rearing than do Gentoo Penguins (Brown 1987, Adams and Wilson 1987). This may indicate a movement of euphausiids out of the immediate inshore waters during February and March 1985.

Due to its benthic nature, adult *N. marionis* may be available to Gentoo Penguins only within a few kilometers of the shore (Adams and Wilson 1987). The size (average length: 35.1 mm) of *N. marionis* taken by Gentoo Penguins at Marion Island in 1984-1985 is clearly greater than juveniles (maximum length: 23 mm) taken by crested penguins during December 1983 to February 1984 (Brown and Klages 1987) and by Gentoo Penguins in September 1982 (La Cock *et al.* 1984). The absence of juvenile *N. marionis* in the diet of Gentoo and crested penguins at Marion Island during January to March 1985 is difficult to explain, since at least some adult individuals recovered during April to September 1984 were ovigerous (N. J. Adams pers. obs.).

The occurrence of octopods in the diet of Gentoo Penguins is apparently unique to the Marion Island site. The appearance of juvenile octopods in the diet coincided with their occurrence in the diet of Rockhopper Penguins late in the chick-rearing period (Brown and Klages 1987). Adult octopods are generally benthic and solitary. The appearance of large numbers of juveniles in the diet suggests highly seasonal spawning, coupled with a tendency to form dense aggregations in shallower water. In contrast, the small number of juvenile squid in the diet of the inshore foraging Gentoo Penguin again emphasizes the generally pelagic nature of squid (Adams and Klages 1987).

Gentoo Penguins apparently switched from a largely crustacean diet during March to June 1984 to a largely fish diet during July 1984 to March 1985. This change coincided with peak egg laying and could not be considered as a direct response to the arrival, in October and November, of the largely, euphausiid consuming and hence potentially competing crested penguins (cf. Williams 1981). Moreover, the most important crustacean component by mass in the diet during March 1984 to September 1984 was adult *N. marionis* (not taken by Macaroni and Rockhopper penguins) and not krill (euphausiids) as intimated by Williams (1981). The large variation in abundance and prey-species composition of crustaceans in penguin diet from year-to-year, indicated by the differences in the diet of the Macaroni and Rockhopper Penguins in two years at Marion Island (Brown and Klages 1987) and Gentoo Penguins in March 1984 and March 1985 may reflect a greater degree of unpredictability in availability of crustacean prey than at higher latitudes. Switches in diet may merely reflect local changes in availability of particular prey within the inshore area exploited by Gentoo Penguins.

Average meal size of Gentoo Penguins at Marion Island is small (La Cock *et al.* 1984, this study) compared to those recovered from breeding penguins at higher latitudes (Croxall and Prince 1980a, Jablonski 1985, Volkman *et al.* 1980). Evaluation of the magnitude of this difference is complicated by the unknown ratio of breeders to non-breeders sampled at Marion Island. However, the difference appears real and may reflect reduced food availability compared to more southerly sites. This view is supported by the small total breeding population (Adams and Wilson 1987), low breeding success and long growth period (Williams 1980) of Gentoo Penguins at Marion Island and suggests that the population is food limited (La Cock *et al.* 1982). However, in contrast to the southern populations which breed in summer (Croxall and Prince 1980b), Gentoo Penguins at Marion Island begin breeding in the austral winter (Williams 1980). The infrequent feeding of King penguin chicks (Cherel *et al.* 1987, Pers. obs.) and dispersal of *Eudyptes* penguins away from the island during winter suggest food availability is low. Consequently, having excluded direct competition with crested penguins for crustacean prey (Williams 1981), the reason for winter breeding by Gentoo Penguins remains unclear.

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