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Spatial and temporal variation in the diet of the gentoo penguin (*Pygoscelis papua*) at Kerguelen Islands

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Abstract Benthic divers are dependent on local resources and may therefore adopt different foraging strategies to cope with their energetic requirements in varying situations. We investigated the diet of gentoo penguins (*Pygoscelis papua*) at Kerguelen Islands, comparing its spatial and temporal variations with the general prey distribution. The study was conducted at four sites over 2 years. In total, 212 stomach contents were collected over the entire breeding season. The diet was composed mainly of neritic fish and crustaceans, with important spatial and seasonal variations. Fish dominated the diet at localities facing the open sea (from 38.0% to 94.6% by mass), whereas crustaceans dominated at the more protected site (84.3% by mass). Fish were more abundant in the winter diet and *Euphausia vallentini*, the major crustacean species, was more abundant in the summer diet. No inter-year variations were detected. These results are consistent with local prey availability, and highlight the large plasticity of the gentoo penguin diet and foraging behaviour.

Introduction

Penguins are the main avian consumers in the Southern Ocean, representing up to 80% of the bird biomass in sub-Antarctic regions (Williams 1995). Sub-Antarctic penguins evolved different feeding strategies, ranging from pelagic feeders like king and macaroni penguins (*Aptenodytes patagonicus* and *Eudyptes chrysolophus*, e.g. Cherel and Ridoux 1992; Bost et al. 1997; Green et al. 1998) to inshore benthic feeders like gentoo, rockhopper and chinstrap penguins (*Pygoscelis papua*, *E. chrysocome* and *P. antarctica*, e.g. Williams et al. 1992; Wilson and Peters 1999; Tremblay and Cherel 2000). Together with imperial cormorants (*Phalacrocorax atriceps*), gentoo penguins are the main avian benthic consumers of the sub-Antarctic (e.g. Croxall and Prince 1980a; Ridoux 1994). As they forage near their breeding colonies, they are bound to be very dependent on local marine resources (Bost and Jouventin 1990; Bost et al. 1994). The diet of the gentoo penguin varies greatly with locality, consisting mainly of krill at Antarctic localities (Croxall and Prince 1980b; Volkman et al. 1980; Williams 1991), except for one study (Coria et al. 2000), whereas fish was more important at sub-Antarctic localities (Adams and Klages 1989; Ridoux 1994; Clausen and Pütz 2002) or dominant (Hindell 1989; Klages et al. 1990; Robinson and Hindell 1996).

While most studies have highlighted the temporal variations of the diet, none have investigated the spatial variations of the diet at the scale of the same island, except at Macquarie Island (Hindell 1989). With about 7,000 km^2 of land, the Kerguelen Archipelago is the most extensive island group of the Southern Ocean (Fig. 1) and has the largest ichthyofauna diversity of the southern Indian Ocean (Duhamel 1987). Almost 40,000 pairs of gentoo penguins, 12% of the world population, breed annually on this archipelago (Bost and Jouventin 1990). They breed in small colonies along the coast, experiencing a range of oceanographic conditions (Bost and Jouventin 1990). The large diversity of these conditions allowed us to study the gentoo feeding ecology. In this paper, our aims were: (1) to describe variations of the diet among selected sites at Kerguelen Islands between colonies facing the sea and a sheltered one, and (2) to compare seasonal diet variations with historical data on

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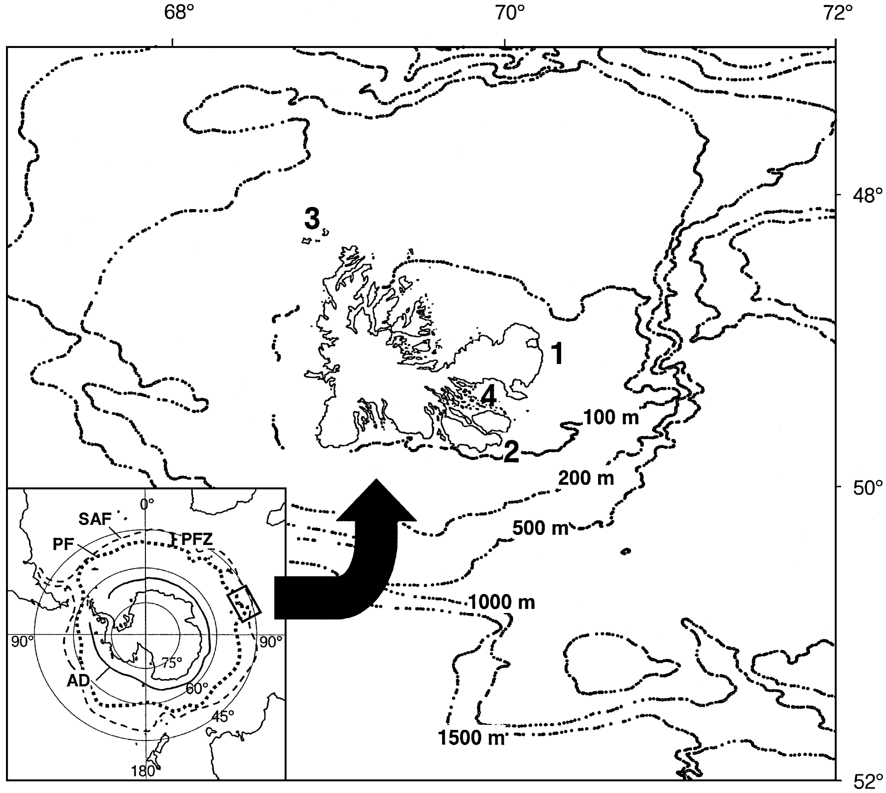

Fig. 1 Map and localization of Kerguelen Archipelago (48°45–50°00S, 68°45–70°58E) (*AD* Antarctic Divergence; *PF* Polar Front; *PFZ* Polar Frontal Zone; *SAF* Sub-Antarctic Front). Sites where stomach contents were collected are indicated by numbers (*1* Cape Ratmanoff; *2* Ronarc'h and Jeanne d'Arc Peninsula; *3* Nuageuses Islands; *4* Morbihan Gulf). Depths are indicated by isobaths 100, 200, 500, 1,000 and 1,500 m isobaths

availability of some key prey. This study was conducted over 2 years on several sites, from winter to summer each year, including two whole breeding seasons.

Materials and methods

Sites and collection of stomach samples

The Kerguelen plateau is the largest submarine plateau of the Southern Ocean and its coastal waters form suitable areas for the maintenance of a shallow-water ichthyofauna (Duhamel 1987). The numerous fjords and bays of the archipelago also provide fish with important spawning sites. Finally, the strong southwest to northeast currents and the location of the Polar Front just east of the archipelago (Park et al. 1993) make the Kerguelen plateau the most productive area (both primary and secondary productions) of the sub-Antarctic localities (Duhamel 1987; Blain et al. 2001).

Two main types of oceanographic conditions are found at Kerguelen Archipelago: sheltered bays with kelp belts, muddy sand and a low tidal amplitude, such as Morbihan Gulf, and sites exposed to the open sea (Fig. 1). The latter type includes the extensive flat peninsula surrounded by sandy beaches at the eastern part of the archipelago (Courbet Peninsula with Cape Ratmanoff) (Riaux-Gobin and Bourgoin 2002), isolated islets such as Nuageuses Islands surrounded by kelp belts, and steep cliffs broken by deep sandy valleys (Ronarc'h and Jeanne d'Arc Peninsula).

Stomach samples were collected from gentoo-penguin breeding colonies in four localities: Cape Ratmanoff (R), Ronarc'h and Jeanne d'Arc Peninsula (RJ), Nuageuses Islands (N) and Morbihan Gulf (G). R (northeast), RJ (southeast) and N (northwest), three "open-sea" localities, are located at about 30, 40 and 100 km from the 500-m isobath, respectively. R is the closest to the Polar Front. G (east) is a "closed-sea" locality, situated in a large gulf of about 700 km^2. This gulf is a partially enclosed area with a mean depth around 100 m (maximal depth about 200 m) connected with the open ocean via a sill at about 50 m depth located in its eastern part.

A total of 159 samples were collected in 1987 (65 at R, 58 at G, 24 at RJ and 12 at N) and 53 in 1989 (22 at R and 31 at G). The samples were randomly collected from breeding adults caught upon their return from foraging trips by the non-destructive method of water off-loading (Wilson 1984). Three successive flushes were performed. Maximal care was taken to handle the birds so as to minimize stress. After collection, the samples were drained on a sieve of 0.5-mm mesh size, weighed and preserved in 70% ethyl alcohol or frozen.

Identification of prey items

At the laboratory, the contents were sorted into different categories of prey: crustaceans, fishes, annelids, cephalopods, others. Identification of crustaceans relied on the examination of their exoskeleton. Total body length was measured in intact specimens from the eye to the telson or estimated from regressions on eye diameter (Bost et al. 1994). All the hard parts of fish recovered were used for identification, with special attention given to tail bones and otoliths. Standard lengths of fish were determined by measuring the length of whole undigested fish, or estimated from allometric relations based on the caudal length or the otoliths (Hecht 1987). Body weights were determined from undigested or reconstituted fish (Ridoux 1994). Annelids and squid were identified from whole bodies and lower beaks for squid (Clarke 1986; Ridoux 1994 and unpublished data). Accumulated beaks were not considered when calculating the proportion by number and mass of the species in the diet.

Diet composition

The diet composition was described in terms of frequency of occurrence, percentage by number and percentage by mass. We used the reconstituted biomass method to provide quantitative data on the mass of each prey taxon occurring in any individual bias sample (see Ridoux 1994 for details). For unidentified nototheniids at G, we considered the mean mass of *Nototheniops mizops*, the most common nototheniid for the present study. For a same species, the mean mass was adjusted by season when the sample size was sufficient. This was the case for the decapod *Euphausia vallentini*, the fishes *Gobionotothen acuta*, *Zanchlorhynchus spinifer*, *Harpagifer kerguelensis* and unidentified nototheniids at R, and the decapod *Euphausia vallentini*, the amphipod *Parathemisto gaudichaudii* and fish larvae at G.

Diet variations

Spatial and seasonal variations

For statistical comparison of the diet by mass between localities, stomach contents were randomly chosen from one open-sea locality (R, $n=45$) and one closed-sea locality (G, $n=45$), all seasons pooled. For the comparison of mean prey sizes, all data from R and G in 1987 were examined.

Seasonal variations of the main prey groups in the diet were studied over five periods of the 1987 breeding season at one open-sea locality (R: early winter, late winter, early spring, late spring, summer) and four periods at the closed-sea locality (G), same periods except one (early spring, Table 1). For mean prey sizes, the variations were studied when we obtained sufficient data for each season (i.e. for *Euphausia vallentini*, *Parathemisto gaudichaudii* and Nototheniidae), and all data from R and G in 1987 were considered.

Interannual variations

Comparison of the diets between 1987 and 1989 was made from R and G data, with the same sample size for each year at the same times (early winter and spring).

Statistics

Values are given as means ± SD unless stated otherwise. Effects of locality and period on the biomass of prey groups and key species were tested by the Scheirer-Ray-Hare two-way ANOVA of ranks (Sokal and Rohlf 1995). Differences between diet composition by mass were tested by the *G*-test. Differences between mean prey sizes were tested by the bilateral *t*-test or ANOVA, followed by the Tukey post-hoc test in the case of seasonal variations. In all tests, $P<0.05$ was accepted as indicating statistical significance.

Results

General diet composition at Kerguelen Archipelago

A total of 25 prey types was recovered in 1987 from the 159 stomach samples. Table 2 shows the frequency of occurrence of identified preys (all four localities pooled). Among these, 11 fish, 5 crustacean, 7 cephalopod and 2 annelid species (or taxa) were identified. In terms of frequency of occurrence, fish and crustaceans were the most common groups. Among fish, Nototheniidae were the most often represented, with five identified species. Channichthyidae were mostly represented by *Champsocephalus gunnari*. The congiopodid *Z. spinifer* was often found. Crustaceans were dominated by two species, *Euphausia vallentini* and *Parathemisto gaudichaudii*. Among cephalopods, Decapodiformes were found slightly more often than Octopodiformes. Finally, prey species diversity was always higher in open-sea localities than in the closed-sea one. Of the 25 species identified, 20 could be found at Cape Ratmanoff, 17 at Nuageuses Islands, Ronarc'h and Jeanne d'Arc Peninsula and 10 at Morbihan Gulf.

Diet composition by number

Crustaceans dominated the diet by number whatever the oceanic environment (Figs. 2a, 3a). For all localities, fish was the second prey group by number. Cephalopods were found in all open-sea localities but always represented less than 2%. The diet by number was thus almost entirely composed of crustaceans and fish in the closed-sea locality (Morbihan Gulf) while it tended to be much more diverse in the open-sea localities (Cape Ratmanoff, Ronarc'h and Jeanne d'Arc Peninsula, Nuageuses Islands).

Table 1 Sampling design and sample numbers used for the statistical comparisons. In the southem hemisphere, winter corresponds roughly to months from late June to late September and summer begins in December (*Total n* total number of stomach contents sampled; *n1* sample number randomly chosen for the spatial comparison; *n2* sample number randomly chosen for the seasonal comparison; *n3* sampIe number chosen for the interannual comparison)

Sampling site	Season	Year	Total *n*	*n*1	*n*2	*n*3
Morbihan Gulf	Early winter	1987	24	16	16	13
	Late winter	1987	16	16	16	-
	Early spring	1987	-	-	-	-
	Late spring	1987	10	8	8	10
	Summer	1987	8	5	5	-
	Early winter	1989	15	-	-	9
	Spring	1989	16	-	-	14
Cape Ratmanoff	Early winter	1987	16	16	16	8
	Late winter	1987	16	16	16	-
	Early spring	1987	20	-	20	14
	Late spring	1987	8	8	8	-
	Summer	1987	5	5	5	-
	Early winter	1989	8	-	-	8
	Spring	1989	14	-	-	14
Ronarc'h and Jeanne d' Arc Peninsula	Late spring	1987	13	-	-	-
	Summer	1987	11	-	-	-
Nuageuses Islands	Late spring	1987	12	-	-	-

Table 2 Prey species identified from the stomach contents of 159 gentoo penguins at Kerguelen archipelago (*n* number of items; *FO* frequency of occurrence; *%FO FO* as percentage of all samples)

Species	*n*	FO	%FO
Fish	4460	142	89.3
Larvae (unidentified species)	454	13	8.2
Nototheniidae			
Larvae	3013	47	29.6
Nototheniops mizops	85	23	14.5
Gobionotothen acuta	119	15	9.4
Lepidonotothen squamifrons	16	10	6.3
Paranotothenia magellanica	24	14	8.8
Dissostichus eleginoides	27	4	2.5
Unidentified nototheniids	102	33	20.8
Channichthyidae			
Champsocephalus gunnari	185	43	27.0
Channichthys rhinoceratus	3	3	1.9
Congiopodidae			
Zanchlorhynchus spinifer	171	36	22.6
Harpagiferidae			
Harpagifer kerguelensis	156	17	10.7
Myctophidae			
Krefftichthys anderssoni	8	4	2.5
Unidentified myctophids	2	2	1.3
Muraenolepididae	1	1	0.6
Unidentified fish	94	38	23.9
Crustaceans	115620	131	82.4
Euphausiacea			
Euphausia vallentini	95012	92	57.9
Thysanoessa sp.	30	1	0.6
Amphipoda			
Parathemisto gaudichaudii	19016	92	57.9
Gammarid amphipods	1543	22	13.8
Isopoda	19	12	7.6
Cephalopods	115	30	19.5
Decapodiformes	73	20	12.5
Onychoteuthidae			
Kondakovia longimana	13	5	3.1
Onychoteuthis sp.	8	5	3.1
Moroteuthis sp.	8	3	1.9
Gonatidae			
Gonatus antarcticus	29	6	3.8
Brachioteuthidae			
Brachioteuthis picta	3	2	1.3
Neoteuthidae			
Alluroteuthis sp.	1	1	0.6
Unidentified Decapodiformes	11	3	1.9
Octopodiformes	42	18	11.2
Octopodidae			
Octopus sp.	39	9	5.7
Unidentified Octopodiformes	3	3	1.9
Annelids	204	21	13.2
Platynereis magellanica	121	16	10.1
Unidentified annelids	83	8	5.0

Diet composition by reconstituted mass

There were highly significant differences by mass in diets between the closed-sea locality Morbihan Gulf and the open-sea locality Cape Ratmanoff (*G*-test: $G_3 = 97.681$, $P < 0.001$, 1987 data). In open-sea localities, fish dominated the diet (Fig. 2b). This dominance was strong at Cape Ratmanoff (with Nototheniidae and *C. gunnari* representing 37% and 12%, respectively) and Nuageuses Islands (with *C. gunnari* representing 80%) and less marked at Ronarc'h and Jeanne d'Arc Peninsula, where all prey groups were well represented (with *C. gunnari* and *Euphausia vallentini* representing 25% and 24%, respectively). Annelids were absent only from Nuageuses Islands samples. In the closed-sea locality, crustaceans constituted the bulk of the diet by mass (Fig. 3b), with *Euphausia vallentini* representing 74%.

Seasonal variations

Mass of prey groups

At both localities considered, the diet of gentoo penguins varied extensively over the study period. At the open-sea locality (Cape Ratmanoff), the diet composition by mass evolved from a quasi-exclusive fish diet in winter to a more diversified one in spring and summer (Fig. 4a). The proportion of crustaceans reached its maximum in early spring (20%). The importance of annelids increased substantially during summer (59%) when they formed the most important part of the diet. Finally, cephalopods appeared in late winter and reached their maximum in early spring (14%). In contrast, the mass composition of the diet in the closed-sea locality (Morbihan Gulf) was more diversified in winter, and almost exclusively composed of crustaceans in summer (Fig. 4b). Annelids were present only in early winter (4%) and early spring (13%).

These variations were statistically significant for fish, crustaceans and cephalopods between colonies ($P < 0.001$) and seasons ($P < 0.05$), with no effect (NS) of both factors combined. No significant effect was detected for the proportion of annelids because of the few stomachs containing them.

Mass of key species

There was a clear seasonal trend for changes in the mass of the prey groups. At both Cape Ratmanoff and Morbihan Gulf, the proportion by mass of fish caught by gentoo penguins decreased from late winter to summer, mainly because of the decrease of icefish (*C. gunnari*) in the diet at the open-sea locality and Nototheniidae in the diet at the closed-sea locality (Fig. 5). At the same time, the proportion by mass of crustaceans, mainly *Euphausia vallentini*, increased. This latter trend was particularly marked in the closed-sea locality, where a clear switch occurred in the diet composition as early as September. The proportions of Nototheniidae and *Parathemisto gaudichaudii* dropped then to low levels whereas *Euphausia vallentini* represented 61% of the diet and remained dominant until December.

Prey sizes

Mean sizes of prey species measured for the open-sea and closed-sea localities from August to December 1987 are reported in Table 3. When found in both localities,

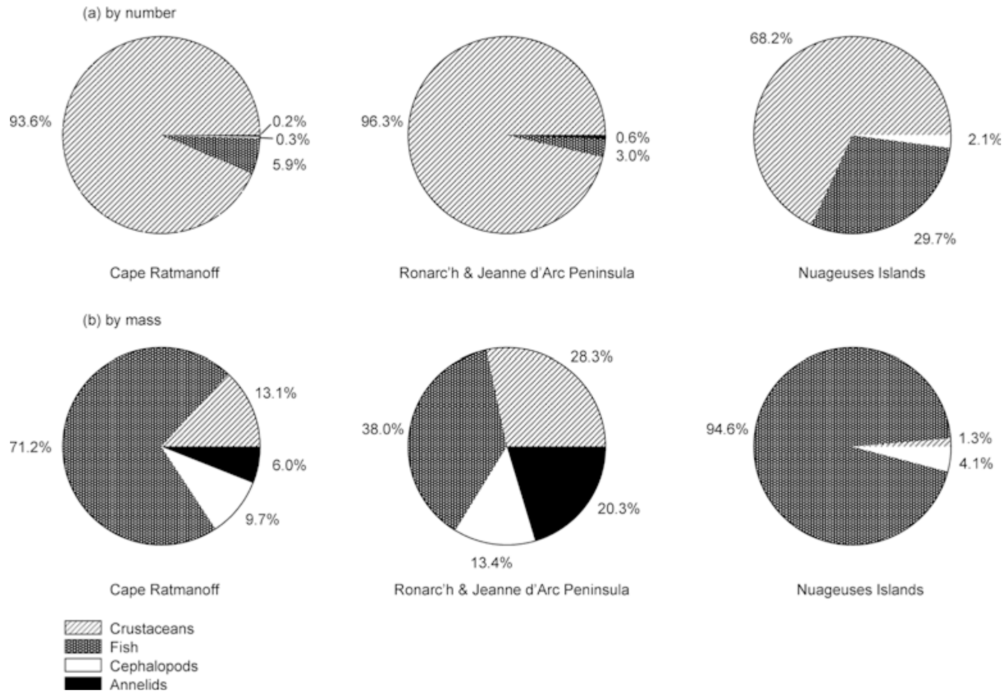

Fig. 2a,b Composition of the gentoo penguin diet at open-sea localities, Kerguelen Archipelago: **a** composition by number; **b** composition by mass. All data collected in 1987 were pooled. Number of stomach contents = 65, 24 and 12 for Cape Ratmanoff, Ronarc'h and Jeanne d'Arc Peninsula and Nuageuses Islands, respectively

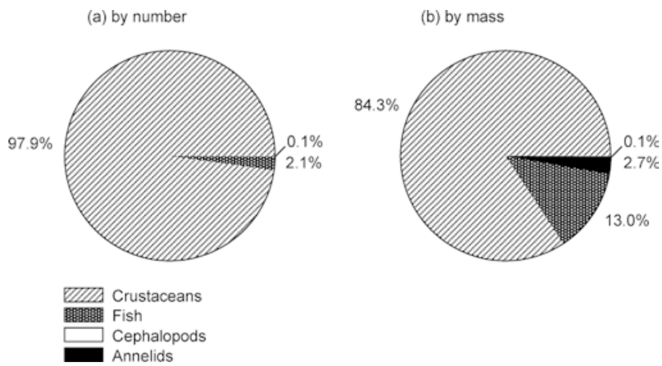

Fig. 3a,b Composition of the gentoo penguin diet at a closed-sea locality (Morbihan Gulf), Kerguelen Archipelago: **a** composition by number; **b** composition by mass. All data collected in 1987 were pooled. Number of stomach contents = 58

the standard length of fish caught by gentoo penguins in the same period was generally greater at the open-sea locality, except *H. kerguelensis*, which was of a similar size at both localities. *C. gunnari* was the largest fish caught in both localities. In contrast, the mean length of the commonest crustacean, *Euphausia vallentini*, was greater at the closed-sea locality compared to the open-sea one. Isopoda were similar in size at both localities.

Seasonal changes in prey size were examined for three key groups: *Euphausia vallentini*, *Parathemisto gaudichaudii* and Nototheniidae (Table 4). In both localities, the mean length of Nototheniidae did not vary significantly ($F = 1.111$ for Cape Ratmanoff, NS and $F = 1.540$ for Morbihan Gulf, NS) despite an apparent decrease from early (95.9 mm) to late (75.1 mm) spring. The mean length of *Euphausia vallentini* showed significant variations among the seasons in both localities, especially in the closed-sea locality ($F = 4.233$ for Cape Ratmanoff, $P < 0.01$ and $F = 10.995$ for Morbihan Gulf, $P < 0.001$, Table 4). In general, *Euphausia vallentini* exhibited smaller size classes in the open-sea locality than in the closed-sea one. At the latter situation, its mean length increased from early to late winter and decreased from late winter to late spring and summer. For *Parathemisto gaudichaudii*, data were available only for the closed-sea locality (Morbihan Gulf, Table 4). Mean length of *Parathemisto gaudichaudii* caught increased significantly ($F = 26.349$, $P < 0.001$) from early winter until summer.

Comparisons between years

In 1989, the general features of localities in terms of percentage by number were the same as in 1987 (Table 5). There was no change in diet between years for the main prey groups.

For each locality, there was no statistical difference between years for the main prey groups in terms of percentage by mass (Table 5, *G*-test: $G_3 = 5.879$ for Cape Ratmanoff, NS; $G_3 = 1.165$ for Morbihan Gulf, NS). There were, however, highly significant differences in the diet between both localities in 1989, as in 1987 (*G* test: $G_3 = 58.870$, $P < 0.001$).

Discussion

We showed that the gentoo penguin diet at Kerguelen Archipelago is extremely diverse, both spatially and

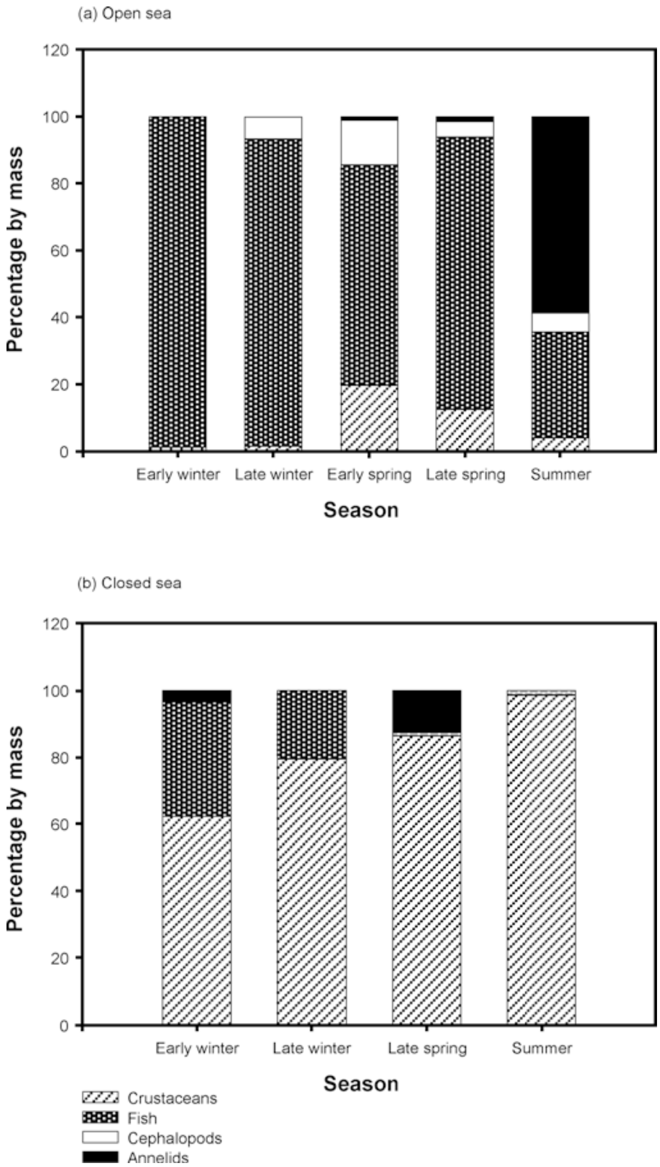

Fig. 4a,b Seasonal variations of the gentoo penguin diet at Kerguelen Archipelago. Data are for 1987. **a** Composition by mass at an open-sea locality (Cape Ratmanoff); **b** composition by mass at a closed-sea locality (Morbihan Gulf). Number of stomach contents for both localities = 16 for early winter, 16 for late winter, 20 for early spring (Cape Ratmanoff only), 8 for late spring and 5 for summer

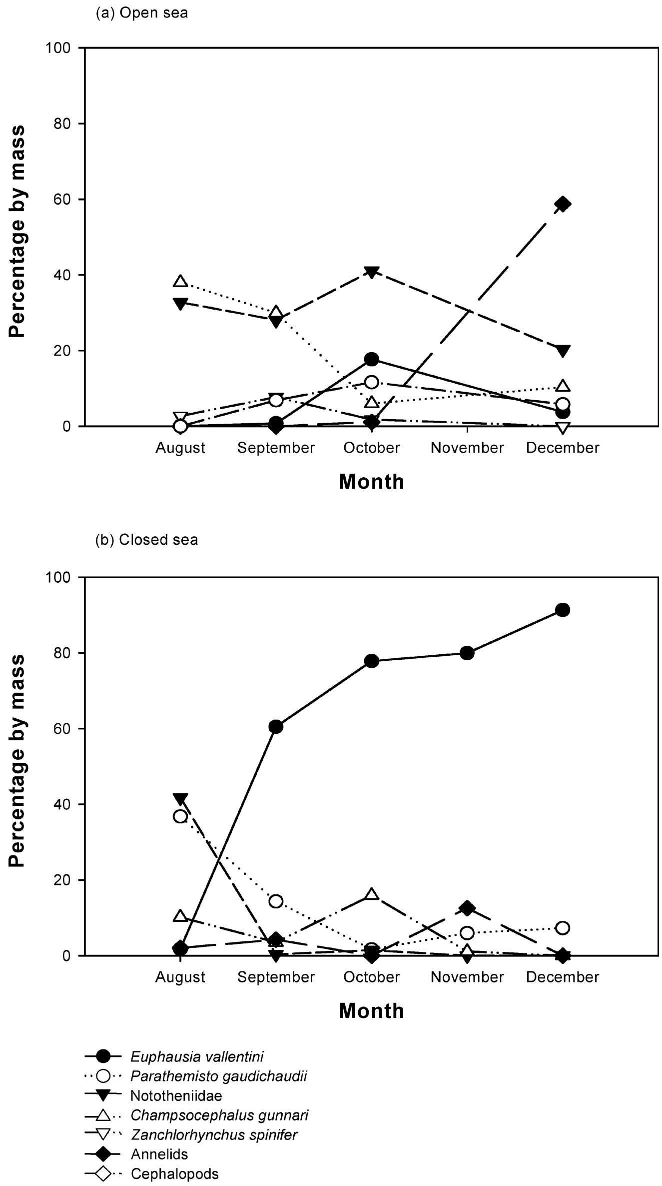

Fig. 5a,b Seasonal variations of key species by mass in the gentoo penguin diet at Kerguelen Archipelago. Data are for 1987. **a** Open-sea locality (Cape Ratmanoff); **b** Closed-sea locality (Morbihan Gulf)

seasonally. Such a diversity may be linked to the high diversity of the oceanographic conditions in the feeding areas of the penguins. Most of the fish species found in the diet were representative of the benthic ichthyofauna in Kerguelen neritic waters, such as the majority of nototheniid species and *Z. spinifer*, or semipelagic (*C. gunnari*) (Duhamel 1987). Gentoo penguins also preyed upon two of the most important macrozooplancton crustacean species in sub-Antarctic waters, *Euphausia vallentini* and *Parathemisto gaudichaudii* (Ridoux 1988; Bocher et al. 2001). Cephalopods were represented in the diet principally by onychoteuthid squids (*Kondakovia longimana*, an epipelagic to semipelagic species, Cherel et al. 2000), gonatid squids (*Gonatus antarcticus*) and octopods. The presence of *K. longimana* confirms the extent of its range in the Polar Frontal Zone (Cherel and Weimerskirch 2003).

Comparisons with other studies

The diet of gentoo penguins has previously been studied at seven localities. It emerges from all these studies that gentoo penguins are opportunistic feeders, preying upon either benthic or pelagic species as soon as they are available in the inshore waters. Going from north to

Table 3 Mean length ± SD of prey species found in stomach contents of gentoo penguins at Kerguelen Archipelago in open-sea (Cape Ratmanoft) and closed-sea (Morbihan Gulf) conditions. Data are for 1987. Number of items measured is indicated in *parentheses* (*t* Student *t*-value)

Prey species	Mean length (mm)		*t*-test	
	Open sea	Closed sea	*t*	*P*
Nototheniops mizops	91.7 ± 15.7 (13)	68.9 ± 21.4 (19)	−2.925	**
Gobionotothen acuta	77.3 ± 47.5 (42)	-		
Lepidonotothen squamifrons	144.7 ± 21.4 (3)	54.6 ± 10.9 (6)	−8.676	***
Paranotothenia magellanica	70.1 ± 446 (10)	-		
Unidentified nototheniids	91.1 ± 43.4 (42)	55.0 ± 14.2 (2)		
Champsocephalus gunnari	190.1 ± 60.8 (20)	121.0 ± 54.0 (17)	−3.624	***
Zanchlorhynchus spinifer	41.3 ± 10.1 (62)	-		
Harpagifer kerguelensis	32.7 ± 7.4 (53)	31.3 ± 10.6 (19)	−0.656	NS
Fish larvae	30.9 ± 5.1 (77)	28.1 ± 2.6 (85)		
Euphausia vallentini	22.9 ± 0.3 (315)	24.9 ± 2.9 (860)	10.559	***
Parathemisto gaudichaudii	-	13.8 ± 1.6 (841)		
Gammarid amphipods	16.9 ± 1.5 (41)	-		
Isopoda	27.1 ± 2.3 (8)	27.6 ± 5.4 (9)	0.250	NS
Octopus sp.	6.0 ± 1.4 (26)	-		
Platynereis magellanica	116.4 ± 20.3 (16)	-		

P probability associated with the *t*-test; ***$P < 0.00l$; **$P < 0.0l$; *NS* $P > 0.05$.

Table 4 Seasonal variations in prey size caught by gentoo penguin in open-sea (Cape Ratmanoff) and closed-sea (Morbihan Gulf) localities. Data are for 1987. Number of items measured is indicated in *parentheses*

Season	*E. vallentini*		*P. gaudichaudii*		Nototheniidae	
	Open sea	Closed sea	Open sea	Closed sea	Open sea	Closed sea
Early winter	-	25.0 ± 2.9 (255)	-	13.3 ± 1.2 (436)	85.9 ± 57.5 (7)	69.1 ± 21.6 (17)
Late winter	23.0 ± 2.5 (31)	25.9 ± 2.2 (180)	-	14.1 ± 1.2 (83)	87.8 ± 50.0 (19)	54.6 ± 14.7 (8)
Early spring	22.8 ± 3.1 (194)	-	-	-	95.9 ± 46.6 (38)	-
Late spring	23.8 ± 3.2 (59)	24.5 ± 3.2 (301)	-	13.9 ± 1.4 (140)	75.1 ± 39.5 (29)	-
Summer	21.5 ± 2.6 (31)	24.5 ± 3.1 (124)	-	14.4 ± 1.5 (100)	77.1 ± 27.2 (17)	67.5 ± 7.8 (2)

Table 5 Composition of the gentoo penguin diet by reconstituted mass (%) and by number (%, in *parentheses*) at an open-sea locality (Cape Ratmanoff) and a closed-sea locality (Morbihan Gulf), Kerguelen Archipelago. Data are for 1987 and 1989 (*n* 45 randomly chosen stomach contents for each year). For each prey group considered, the difference between the diets by mass at open-sea and closed-sea localities was highly significant ($P < 0.00l$), except where indicated by an *asterisk*

Prey groups	1987		1989	
	Cape Ratmanoff	Morbihan Gulf	Cape Ratmanoff	Morbiban Gulf
Fish	65.1 (5.0)	15.4 (2.5)	56.4 (13.9)	17.0 (1.3)
Crustaceans	18.6 (94.8)	77.7 (97.4)	30.9 (83.2)	80.7 (98.7)
CephaIopods	15.3 (0.2)	0.0 (0.0)	9.7 (2.9)	0.0 (0.0)
Annelids	1.1 (0.1)	6.8 (0.1)	3.0* (0.1)	2.3 (0.1)

south in its range, the diet seems to become less diverse and dominated by crustaceans instead of fish.

Overall, the diet of gentoo penguins at Kerguelen Islands is characterized by a moderate dominance of fish. In this respect, Kerguelen is distinguishable from Crozet-Marion Islands and the Falklands, where the diet is more balanced between fish and crustaceans, and from Macquarie and Heard Islands where the diet is strongly dominated by fish. Heard and Kerguelen Islands belong to the same submarine plateau, but fish caught by gentoo penguins at Heard Island are mainly myctophids, as at Macquarie Island. This fish group also forms a large part of the gentoo penguins' diet at Crozet and Marion Islands but is very scarce at Kerguelen and the Falkland Islands. Throughout the gentoo penguin range, the diet at Kerguelen Islands is characterized by a great diversity of fish species, covering six distinct taxonomic groups. However, Kerguelen is the locality where Nototheniidae are the most diverse in terms of species.

The strong dependence shown locally on two crustacean species (*Euphausia vallentini* and *Parathemisto gaudichaudii*) is similar to that observed close to the Antarctic Peninsula, at South Georgia Island and South Shetland Islands, where the gentoo penguins feed mostly on Antarctic krill (*Euphausia superba*).

The importance of cephalopods in the diet of gentoo penguins at Kerguelen is intermediate between that at Marion, Crozet and Heard Islands on the one hand, and that at Falkland and Macquarie on the other. Two of the most important species at Kerguelen (*K. longimana* and *Gonatus antarcticus*) are also reported in the diet of gentoo penguins at Crozet. *K. longimana* alone has been reported in the diet of gentoo penguins at Marion and Heard Islands, and *Gonatus antarcticus* at Falkland and Macquarie Islands.

Our study is the first to report the presence of annelids in the gentoo penguin diet. Indeed, annelids may locally and seasonally constitute an important part of the diet at Kerguelen Islands.

Intrasite variability at Kerguelen Archipelago

Interestingly, the diet of gentoo penguins varies as much across Kerguelen as it does over the entire range of the species. On Kerguelen, local physical and biotic features are essential for interpreting the two diet types observed in gentoo penguins: a diet dominated by crustaceans for individuals feeding at the closed-sea locality, and another dominated by fish and more diversified for those feeding at the open-sea localities.

Open sea

At the open-sea localities, gentoo penguins fed mainly on demersal and semipelagic fish species. This is probably related to the richness of the Kerguelen plateau ichthyofauna. However, the diets were different among the three open-sea localities located at three extremities of the archipelago. First, Ronarc'h and Jeanne d'Arc Peninsula (the southeastern locality) is located near the Polar Front, and the large number of seabird colonies on its coast (Weimerskirch et al. 1989) suggests that the southeast of the archipelago is a productive area. There, gentoo penguins had a mixed diet, with the most important items by mass being *C. gunnari*, *Euphausia vallentini*, annelids and cephalopods. Few data are available on the cephalopod distribution around Kerguelen. Our data suggest that the southeastern part of the archipelago may be a zone of abundance for this group, as shown from the black-browed albatross diet (Cherel et al. 2000). The southeast area of Kerguelen is not known to be particularly favourable for *C. gunnari* but 1987 was a year of high abundance for this species (Duhamel 1987, 1995). The high macroplanktonic biomass in the eastern part of Kerguelen (Koubbi 1993) may explain the contribution of *Euphausia vallentini* in the diet. Second, Cape Ratmanoff (the eastern locality) is the nearest of our localities to the Polar Front and therefore thought to be a particularly productive site (Blain et al. 2001). In this locality, the gentoo penguin diet was dominated by nototheniids, *Euphausia vallentini* and *C. gunnari*. *C. gunnari* and *Lepidonotothen squamifrons*, two abundant plankton-eating species, are preferentially located on the eastern part of the plateau (Duhamel 1993). They constitute, therefore, a predictable resource for gentoo penguins breeding at Cape Ratmanoff. Third, Nuageuses Islands (the northern locality) is the farthest locality from the Polar Front. There, the samples of gentoo-penguin diet were consistently dominated by *C. gunnari*. The north of the archipelago is an important spawning ground for *C. gunnari*, and the north/northeastern shelf contains the most important icefish biomass (Duhamel 1993). Additionally, the zooplanktonic biomass is weaker west of the archipelago (Koubbi 1993), as reflected in the diet.

Closed sea

At the closed-sea locality (Morbihan Gulf), gentoo penguins feed mainly on two species of swarming crustaceans (*Parathemisto gaudichaudii* and *Euphausia vallentini*) and complete their diet with fish larvae, *C. gunnari* and some Nototheniidae. The poor prey diversity at Morbihan Gulf can be related to its relatively simple but nonetheless productive ecosystem. The low tidal amplitude there allows an active and continuous sedimentation of detritic particles that supports a flourishing secondary production (Riaux-Gobin and Bourgoin 2002). Phytoplankton blooms in spring and late summer (Delille et al. 2000) induce a sharp rise in mesozooplankton biomass (Razouls et al. 1996, 1997). This biomass supports, in turn, important populations of omnivorous (*Euphausia vallentini*) and carnivorous (e.g. *Parathemisto gaudichaudii*) crustaceans. The species caught by the gentoo penguins are among the most abundant species of macrozooplankton in the gulf (Bocher et al. 2001). *Parathemisto gaudichaudii* occurs in high densities in Morbihan Gulf (Bocher et al. 2001), in all seasons (Bost et al. 1994) and thus forms an important part of the diet of many seabirds (Cherel et al. 2002a, 2002b). Its abundance seems to decrease from the western part of Morbihan Gulf to the open gulf and shelf (Bocher et al. 2001), which may explain its scarcity in the gentoo diet at the open-sea localities. *Euphausia vallentini* is also an important component of many sub-Antarctic seabird diets (Ridoux 1988). Few studies have dealt with the abundance and life-cycle of *Euphausia vallentini* in the vicinity of Kerguelen (Koubbi 1992; Bost et al. 1994). This euphausiid seems to be less abundant than *Parathemisto gaudichaudii* at G (Bost et al. 1994). However, *Euphausia vallentini* is difficult to sample due to the ability of individuals to group in numerous, very mobile and patchy swarms (Perissinotto 1989). Therefore, its density may have been underestimated. Also, the Morbihan Gulf ecosystem seems favourable for such an omnivorous species that occurs in coastal and neritic sub-Antarctic waters (Ridoux 1988; Pakhomov 1993). This idea is reinforced by the greater mean size of *Euphausia vallentini* in this locality compared to the open sea. At Morbihan Gulf, the fish diet is characterized by the slightly higher proportion of fish larvae and the smaller mean size of individuals compared to Cape Ratmanoff. This can be explained by the presence of a kelp belt, habitat for juvenile fish (Duhamel 1987). The larvae are probably Nototheniidae, since larvae of *Gobionotothen acuta* and *Notothenia cyanobrancha* are among the most abundant in the Morbihan Gulf ichthyoplankton (Koubbi et al. 2001). The portion of Nototheniidae juveniles or adults in the gentoo penguins' diet is explained by three species of this group (*Notothenia cyanobrancha*, *Notothenia rossii* and *Paranotothenia magellanica*) dominating the demersal ichthyofauna in the gulf. However, the presence of *C. gunnari* at Morbihan Gulf is very surprising because the gulf is connected to the open ocean via a sill at only 40–50 m depth, when the preferred bathymetric zone of this species is between 100 and 500–600 m (Duhamel 1987). However, adults migrate annually to the inner shelf (75–100 m depth) for spawning (Duhamel 1995) and may be followed by some juveniles or subadults in a more pelagic phase and, therefore, be able to enter the gulf (G. Duhamel, personal communication).

Seasonal variability

The proportion by mass of fish caught by gentoo penguins decreased from late winter until summer in both the open-sea locality (Cape Ratmanoff) and the closed-sea locality (Morbihan Gulf). At the open-sea locality, this was mainly the consequence of the icefish decrease in the diet. This species may become accessible in winter to inshore feeders, such as gentoo penguins, during their spawning migration. The increase of Nototheniidae in the diet at the end of winter may compensate for the reverse migration of *C. gunnari* to the outer shelf. The decrease of the mean size of Nototheniidae in summer may be linked to the arrival in the coastal zone of *Notothenia rossii* juveniles (Duhamel 1987) and *L. squamifrons* larvae (Koubbi et al. 2000, 2001). At the closed-sea locality, the decrease in the proportion of fish in the diet was probably the consequence of the decrease of the Nototheniidae. No extensive fishing data exist on Nototheniidae availability. Concerning crustaceans, *Parathemisto gaudichaudii* drastically decreased in the diet between August and September. Since the highest abundance of this species in Kerguelen waters occurs during summer months (Bost et al. 1994; Bocher et al. 2001), its decrease in the gentoo penguin diet is not explained by a decrease of its availability. The most probable hypothesis is an important change in the abundance or availability of *Euphausia vallentini*. At Morbihan Gulf, a phytoplanktonic bloom occurs from September to November (Razouls et al. 1997; Delille et al. 2000), leading to the increase of the zooplanktonic biomass (Razouls et al. 1997). The decrease of the *Euphausia vallentini* mean length size in the gentoo diet between winter and summer may indicate a recruitment phase. Indeed, the breeding period of *Euphausia vallentini* occurs from September to late November at Crozet Islands (Ridoux 1988). Therefore, the rapid decrease of *Parathemisto gaudichaudii* and Nototheniidae in the diet may be the consequence of the formation of *Euphausia vallentini* swarms in a period of growth and reproduction and to an increase in abundance due to the recruitment.

Conclusions

Our study has shown a large plasticity in the diet of gentoo penguins at Kerguelen Islands. This confirms that this species is opportunistic, with an ability to forage on benthic, semipelagic or mesopelagic resources in shallow waters. They are, indeed, able to feed on swarming crustaceans, solitary annelids, fast-moving cephalopods and motionless benthic fish, as well as on pelagic ones. Such a flexibility has only been reported in some coastal feeders like cormorants (Grémillet et al. 1998; Wanless et al. 1998; Kato et al. 1991, 2000). It would be interesting to carry out a detailed analysis of the diving behaviour and associated food intake in gentoo penguins.

We have observed radical switches of the gentoo penguin diet in the course of the seasons in both open-/closed-sea situations. Furthermore, the diet variation of gentoo penguins at Kerguelen, both spatially and seasonally, is consistent with available data on the life-cycle of the prey species and their local availability. These results confirm that studies of seabird diet can provide original information on the local availability and characteristics of marine prey populations (Ridoux 1988). More studies are necessary to investigate the modalities of such unexpected dietary switches. They will involve combining information on diet and at-sea foraging activities with synchronous estimates of prey-population abundance and distribution (Cairns 1992; Montevecchi 1993).

Finally, our study highlighted how limited the possibilities are to extrapolate information on the foraging habits of coastal seabirds gathered at a specific site, even to other sites on the same island.

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