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Gentoo penguin *Pygoscelis papua* diet as an indicator of planktonic availability in the Kerguelen Islands

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Abstract Since penguins rely on the main planktonic resources of the Southern Ocean, knowledge of their diet may be used for monitoring these resources. During winter and spring of 1987 and 1989, we investigated the composition of the diet of gentoo penguins, *Pygoscelis papua*, in relation to changes in the availability of two prey species, *Euphausia vallentini* and *Themisto gaudichaudii*, sampled during plankton surveys in the Kerguelen Islands. The comparison between plankton surveys and diet analysis was performed on samples taken 2–4 km from the studied colonies. Data on the abundance of zooplankton derived from penguins' diet matched closely those from net hauls during a year of high plankton availability (1987). On the other hand, a weaker correspondence was found during a year of restricted availability (1989). The mean sizes of amphipods caught by penguins and net hauls were very similar but the size distribution showed comparatively fewer small and large individuals in net-hauls than in penguin stomachs. Detailed studies on the feeding range and foraging effort of penguins are therefore needed in the near future to validate the potential of penguin diet as a measure of plankton abundance.

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Introduction

Penguins are major consumers of Southern Ocean marine resources, mainly feeding on planktonic crustaceans, small fishes and squids (Croxall and Lishman 1987). Highly specialized diving birds, penguins forage in three dimensions, tracking prey throughout their habitat range. Thus, knowledge of penguin diet may be used in monitoring plankton stocks of species such as krill (Everson 1977; CCAMLR 1987, 1990; Croxall et al. 1985, 1988).

However, the few studies that have attempted to compare the characteristics of penguin diet with data on marine resources obtained simultaneously by oceanographic or commercial fisheries vessels have been restricted to the Antarctic krill, *Euphausia superba* (Croxall and Lishman 1987; Croxall et al. 1988; Whitehead et al. 1990). Very little information has been collected in the sub-antarctic region (Brown et al. 1990). Logistical problems make it particularly difficult to get simultaneously reliable data on the prey taken by penguins and on oceanographic samples available in the same area.

In this study, we investigated changes in the composition of diet of gentoo penguin, *Pygoscelis papua*, with regard to local availability of two planktonic crustaceans, *Euphausia vallentini* and *Themisto gaudichaudii*, within the Kerguelen archipelago. These species are known to be important prey components of planktivorous penguins and other pelagic predators of the Southern Ocean (Ridoux 1988; Brown et al. 1990). The gentoo penguin is an inshore feeder with a restricted foraging area (Trivelpiece et al. 1986; Adams and Wilson 1987; Williams et al. 1992). Therefore, it is potentially very dependent upon local marine resources (Croxall et al. 1988; Bost and Jouventin 1990). We compared the relative abundance and size of crustaceans caught by gentoo penguins with data from plankton surveys obtained during the same period and in the same local area during two breeding seasons. Finally, we discuss the validity and possible bias of the information provided either by conventional sampling or by using penguins as biological samplers of planktonic resources.

This study was carried out at Morbihan Bay (49 30S, 70 15E), Kerguelen archipelago (48 27–50 00S, 68 27–70 35E), between August and November 1987 and September and November 1989. The Kerguelen archipelago oceanic zone is situated south of the polar front (Park et al. 1991). It consists of a main island surrounded by numerous islets with a total surface area of 7,200 km^2. The coastline is convoluted with numerous deep fjords and bays, the largest being Morbihan Bay (Fig. 1). About 2,300 pairs of gentoo penguins breed within this area, the total Kerguelen population being about 40,000 pairs (Bost and Jouventin 1990).

Materials and methods

Collection and analysis of stomach food samples

Gentoo penguin stomach contents were sampled from 3 breeding colonies containing between 70 and 330 pairs (Fig. 1). For this study, 56 samples were collected in 1987 (13 in August and 11 in September, i.e. during laying and incubation; 15 in October, i.e. during hatching; 17 in November, i.e. at the end of the chick rearing period) and 30 in 1989 (14 in September and 16 in November). The analysis of diet variation between 1987 and 1989 was performed from stomachs sampled in September and November (Table 1). The samples were collected from breeding adults by the non-destructive method of water off-loading (Wilson 1984). Three flushes were performed. After collection, the samples were drained and preserved in 70% ethyl alcohol or frozen. The contents were sorted into different prey types (crustaceans, fishes and others). Prey species were counted in total or estimated from randomly chosen subsamples of 20 g. When extensive digestion of crustaceans had occurred, pairs of eyes were enumerated as they stay intact longer than other parts of the body. Total body length (BL) was measured in intact specimens from the eye to the telson, or estimated from the following regressions on eye diameter (ED mm): BL = 1.74 ED + 0.07 for *Euphausia vallentini*, $r = 0.98$, $n = 151$; BL = 0.56 ED − 0.15 for *Themisto gaudichaudii*, $r = 0.96$, $n = 90$ (Ridoux and Bost unpublished data).

Plankton abundance

Since *E. vallentini* and *T. gaudichaudii* are the major prey species of gentoo penguins in Morbihan Bay (Bost 1991), we compared their abundance during the 1987 and 1989 breeding seasons. As part of a plankton sampling program focused on the study of ichtyoplankton, monthly surveys have been carried out throughout the year from December 1986 (Koubbi 1992). Seven localities were sampled in 1987 and eight to nine in 1989. Four oceanographic surveys were performed during simultaneous time-course sampling of crustaceans in gentoo penguin diets (August and October 1987; September and November 1989; Table 3). These surveys were carried out within 2–4 km of the studied colony (Fig. 2), at a depth of 20–50 m. Visual observations suggested that gentoo penguins breeding in Morbihan Bay usually foraged very close to their colony (less than 4 km away, Bost unpublished data). The time that elapsed between stomach sampling and plankton surveys differed by 3 and 6 days (Table 3). All samples were obtained using a conical bongo net with a 0.5 mm mesh, towed at speeds of 2–3 knots. The abundance of species was expressed as numbers per 10 m^3. The methodology used for the area is given by Koubbi et al. (1991). Only macroplanktonic species (length greater than 10 mm) and their early stages were counted for this study. In addition, we compared the length distribution of the amphipod *T. gaudichaudii* sampled by net-hauls with that caught by gentoo penguins.

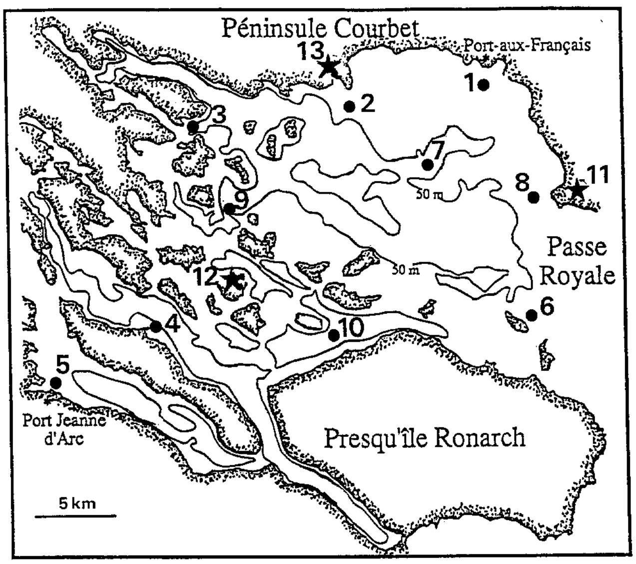

Fig. 1 Map of Morbihan Bay, Kerguelen archipelago (49 30S, 70 15E) with sampling sites. The numbers 1 to 10 refer to the location of planktonic stations (1, Port aux Français; 2, Molloy; 3, île Haute; 4, Port Bizet; 5, Port Jeanne d'Arc; 6, Antares; 7, Channer; 8, Pointe Guite; 9, Passe Vercors; 10, Fosse de l'Hydrographie). The breeding colonies of gentoo penguins sampled are indicated by the numbers 11 to 13 (11, Pointe Guite; 330 pairs; 12, Penn Island, 300 pairs; 13, Molloy, 70 pairs)

Results

General composition of the diet

The contributions of main prey species to the diet of gentoo penguins are shown in Table 1. The euphausiid *E. vallentini* and the amphipod *T. gaudichaudii* represented the bulk of the diet by number (and by mass) during the two breeding seasons, the remaining components representing only 1.3 (1989) to 4.05% (1987) by numbers. *E. vallentini* was always caught in greater numbers than *T. gaudichaudii* but accounted for a lesser proportion in 1989 (59.4 vs 81.8% in 1987, $t = 2.19$, $P < 0.05$; Table 1). The fish (mainly notothenid larvae, sub-adults of *Notothenia mizops*, adults of *Harpagifer kerguelensis*, sub-adults of *Champsocephalus gunnari*) represented only 13.9 (1987) to 15.78% (1989) by mass of the overall diet.

Table 1 Composition of gentoo penguin stomachs by numbers in 1987 and 1989 (September and November data pooled at Morbihan Bay, Kerguelen archipelago)

	No. of stomachs sampled	*Euphausia vallentini*	*Themisto gaudichaudii*	Fish	Others
1987	28	81.8 ± 24.8 (0 – 100%)[a]	14.1 ± 18.6 (0 – 99.8%)	3.8 ± 22.8 (0 – 96%)	0.25 ± 0.54 (0 – 4%)
1989	30	59.4 ± 42.5 (0 – 100%)	39.2 ± 37.8 (0 – 99.2%)	1.17 ± 23.5 (0 – 100%)	0.11 ± 0.92 (0 – 2.8%)

[a] Numbers in parentheses are range of percentage composition

Table 2 Mean abundance of *Themisto gaudichaudii* and *Euphausia vallentini* sampled over Morbihan Bay by net-hauls during the study period

	Sampling dates	Number of stations	*Themisto gaudichaudii* (No. $10\,m^{-3}$)	*Euphausia vallentini* (No. $10\,m^{-3}$)
1987	17/8	7	16.94430 ± 17.56796	2.86088 ± 1.193506
	29/9	7	21.66350 ± 35.28116	1.26668 ± 1.32570
1989	5/9	8	7.59863 ± 7.13179	0.97870 ± 1.2759
	21-25/11	9	11.6594 ± 10.4779	0

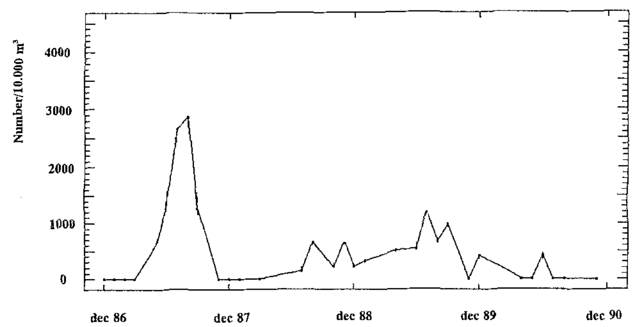

Fig. 3 Mean abundance of *Euphausia vallentini* (individuals $/10^4\,m^3$) sampled at Morbihan Bay, Kerguelen archipelago, from 1987 to 1990

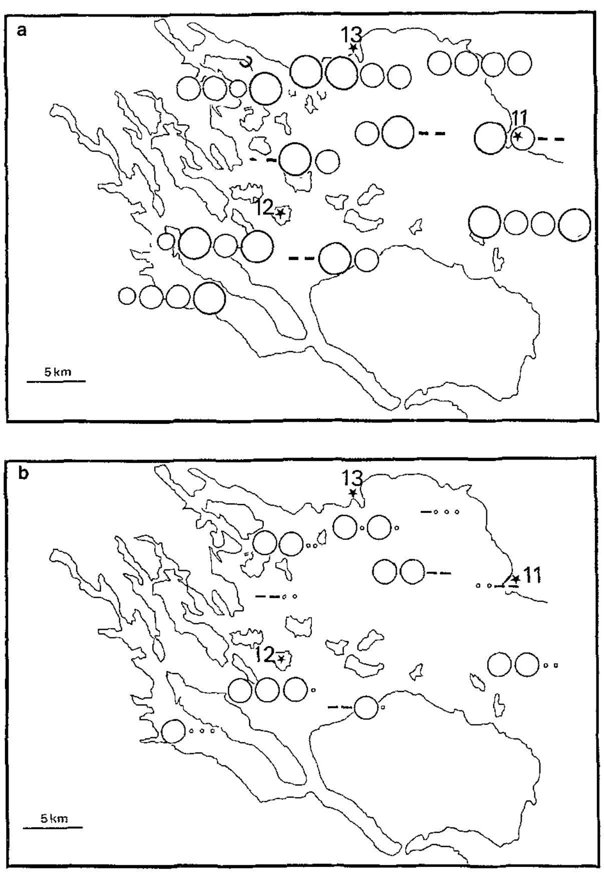

Fig. 2a, b Density of *Themisto gaudichaudii* (**a**) and *Euphausia vallentini* (**b**) (individuals/$10\,m^3$) in Morbihan Bay, Kerguelen archipelago from four series of net-hauls (August 1987, September 1987, September 1989, November 1989). Densities appear with respect to the sampling chronology. o, 0 indiv/$10\,m^3$; ○, d < 1 indiv $10\,m^3$; ○, 1–10 indiv/$10\,m^3$; ○, > 10 indiv/$10\,m^3$

Abundance of Crustaceans

Table 2 indicates the average densities of *E. vallentini* and *T. gaudichaudii* sampled by net-hauls in Morbihan Bay during the study periods. The density of *E. vallentini* varied between 0 and 3.6376/$10\,m^3$. Net-hauls indicated that this species occurred only in Morbihan Bay during the winter period (Fig. 2a and 3). The average density at the end of winter was, however, about three times lower in 1989 than in 1987 ($U = 6.8$, $P > 0.05$; Table 2). *T. gaudichaudii* was present in Morbihan Bay at any season (Fig. 2b). Its density varied between 0 and 50 individuals/$10\,m^3$ (Table 2).

During each sampling period, plankton surveys showed extensive differences between local abundance of *E. vallentini* and *T. gaudichaudii* and the mean abundance of the species inside Morbihan Bay (Fig. 2). Thus in August 1987, swarms of *E. vallentini* were not detected around the gentoo penguin colony which was simultaneously sampled (Pointe Guite; Fig. 2a) although their mean density in Morbihan Bay (2,8608 indiv/$10\,m^3$) was high in comparison with values recorded from 1986 to 1989 (Fig. 3).

Comparison of net-haul samples with penguins' diet composition

The relative proportions of crustaceans caught by penguins differed markedly over the four sampling periods (Table 3). The proportion of *E. vallentini* caught in August (winter) ranged from 0% in 1987 to 76% in

Table 3 Percentages of principal zooplankton species (*Euphausia vallentini* and *Themisto gaudichaudii*) caught by gentoo penguins and from net-hauls in the immediate vicinity of sampled colonies in 1987 and 1989

	Sampling dates	Sampling area	Gentoo penguin			Net-haul		
			Euphausia vallentini	*Themisto gaudichaudii*	Others	*Euphausia vallentini*	*Themisto gaudichaudii*	Others
1987	17-20/8 ($n = 13$)	Pointe Guite	0%	99.4%	0.63%	0%	100%	0%
	29/9-4/10 ($n = 15$)	Port Bizet	96%	4%	0%	95.5%	0.5%	0%
1989	30/8-5/9 ($n = 14$)	Molloy	75.9%	24%	0.1%	99.7%	0.3%	0%
	24/11-27/11 ($n = 16$)	Molloy	48%	51.9%	0.1%	0%	100%	0%

1989 (by numbers) and the proportion of *T. gaudichaudii* caught in August varied from 99% in 1987 to 24% in 1989. During winter and spring 1987, net-haul data recorded in the immediate vicinity of the colony showed trends very similar to those of penguin diet (Table 3). During winter 1989, the results of diet analysis matched those of net-haul but the relationship was less tight. By then, *E. vallentini* and *T. gaudichaudii* accounted respectively for 76 and 24% of the diet even though these species constituted 99 and 0.3% of net-haul catches during the same period. During spring 1989, *E. vallentini* accounted for 48% of prey caught by gentoo penguins although no swarms of euphausiids could be detected during plankton surveys. On the other hand, *T. gaudichaudii* accounted for 52% of the diet even though amphipods made up 100% of net-haul catches during the same period (Table 3).

Comparison of length of amphipods caught by penguins and in plankton surveys

Figure 4 shows the length frequency distribution of *T. gaudichaudii* in winter and spring from penguins and from the plankton surveys. The length-frequency distributions were very similar in August 1987 (Kolgomorov-Smirnov, $X_1^2 = 2.6$, $P > 0.05$; Fig. 4a). However, in September 1987 (Fig. 4b) and 1989 (Fig. 4c), net-haul samples contained comparatively fewer small (less than 12.6 mm) and large individuals (more than 16.3 mm) than the sampled stomachs (Kolgomorov-Smirnov, $X_1^2 = 13.36$ and 9.9 respectively, $P < 0.01$). These categories were virtually absent in net-haul catches, while they made up 7 and 16% respectively of the total amount of amphipods caught by gentoo penguins. The size range 10.7–20.4 mm consists for the most part of sub-adults (Kanne 1966). In August, the length frequency distribution of *T. gaudichaudii* caught by penguins and net-hauls showed a peak between 12 and 13 mm. In September, the peak lay between 14 and 15.5 mm. No significant difference was found in the mean length of amphipods measured for penguins and plankton surveys during two of three simultaneous sampling periods (September 1987 and 1989; Table 4). The size of *T. gaudichaudii* caught by penguins differed according to the year, with a larger size in 1989 ($t = 5.6$, $P > 0.001$; Table 4). The same trend was observed between samples from net-hauls in winter ($F = 2.95$, $P > 0.001$).

Discussion

Simultaneity in abundance between diet composition of penguins and plankton surveys

Although comparative data were collected during only four periods, our results are comprehensive enough to evaluate the information provided by these two sampling methods. The study showed firstly that data concerning the abundance of zooplankton derived from stomach contents may not always correspond with data obtained by ocenographic vessels even at a microgeographical scale. Other studies on the relationship between seabird diet and prey availability as determined by standard methods have also given contradictory results. Some studies showed a statistically significant relationship between abundance of a particular prey species in stomach contents and fish stocks (e.g. Anderson et al. 1982; Crawford et al. 1983; Hislop and Harris 1985; Montevecchi et al. 1988). In contrast, other studies found no correlation between relative abundance of shoaling fishes in fisheries catches and penguin diet (Duffy et al. 1987).

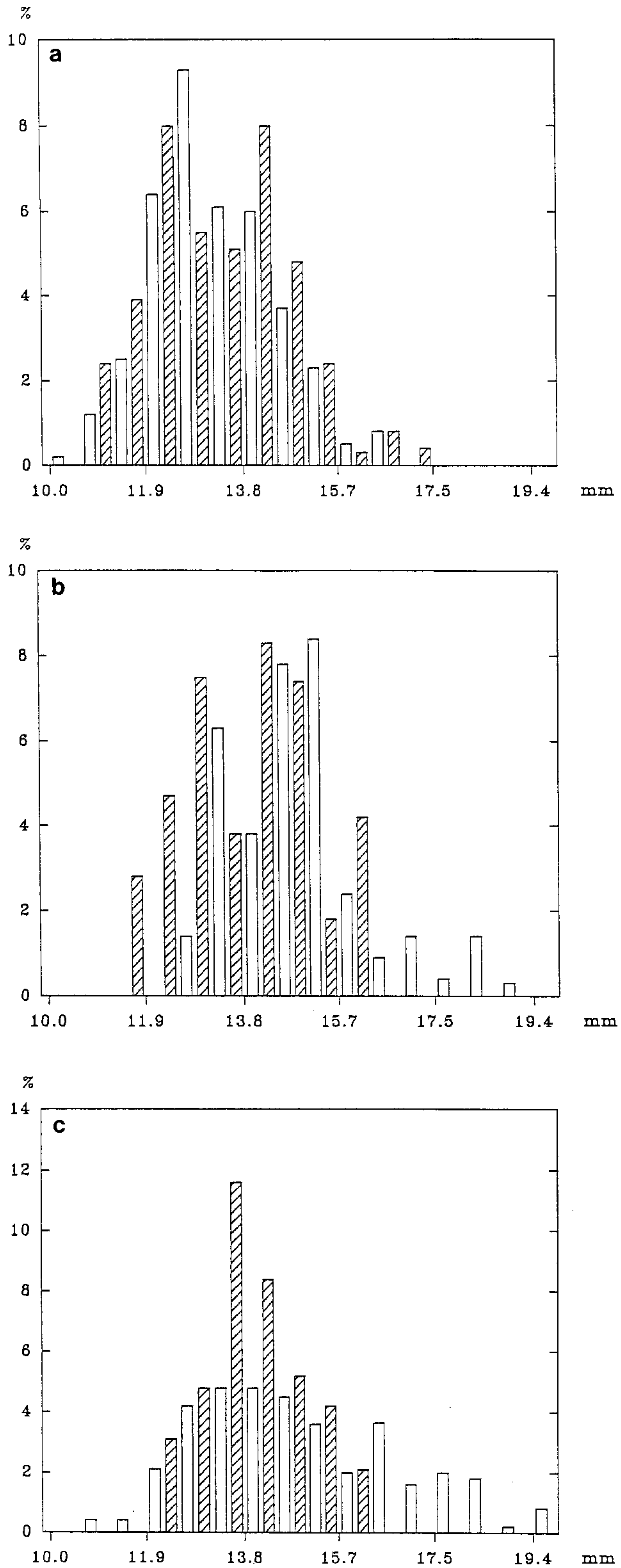

Fig. 4a–c Comparison of length frequency distribution of *Themisto gaudichaudii* caught by gentoo penguins (*open bars*) and net-nauls (*hatched bars*) at Morbihan Bay: **a** August 1987; **b** September 1987; **c** September 1989

Our results suggest that the simultaneity of data for stomach contents and net-hauls depends upon the magnitude of changes in absolute abundance of prey species. In Morbihan Bay, *E. vallentini* migrates into coastal zones during winter, because of mixing of water due to the high frequency of storms, and migrates offshore at the end of spring (Koubbi 1992). The simultaneity between penguin diets and net-hauls was highest in 1987. This year could be noted as one of high availability of euphausiid swarms in comparison with data from 1986 to 1989 (Koubbi 1992). In contrast, as determined by the same methodology, the year 1989 revealed a lower availability of euphausiids (and amphipods) during the end of winter and spring in Morbihan Bay. During the same year, the simultaneity in abundance between net-hauls and penguin stomachs was less tight, especially during spring. Although no swarms of *E. vallentini* were detected by sampling in Morbihan Bay during this period, this species represented about half of the diet of sampled gentoo penguins.

The lack of concurrence during these years may be explained by the sampling techniques of using net-hauls especially during periods of low plankton abundance. The plankton surveys were focused on fish larvae and the sampling technique may have been inadequate for euphausiid studies. Euphausiid swarms are patchy in distribution, very mobile (Mackintosh 1972; Siegel 1985; Perissinotto 1989) and it may be possible to miss them when stocks are low even at a microgeographical scale. In addition, euphausiids exhibit net avoidance, resulting in a much lower estimation of abundance by net-haul than that obtained by acoustic surveys (Hempel 1985; Everson 1988). Likewise, densities of *T. gaudichaudii* are hard to evaluate because this species is found in very dense swarms that move rapidly in the water column (Kanne 1966).

Gentoo penguins were able to catch about half of their food from euphausiid stocks during spring 1989, although no euphausiid swarms were detected during oceanographic surveys. However, it might be a mistake to believe that data derived from penguins' diet are more appropriate to monitor the absolute abundance of planktonic stocks without further information on the feeding behaviour of the sampled penguins. Firstly, as pointed out by Wilson (1992) and Montevecchi and Berruti (1990), percentage abundance of prey in seabird diets gives a relative measure of prey availability rather than a measure of absolute abundance. Thus, the decrease of euphausiids in penguins' diet during winter and spring 1989 (and the absence of detection of euphausiid swarms by oceanographic surveys in Morbihan Bay during the same sampling periods) may result from a migration of swarms into deeper strata (Perissinotto 1989). Nevertheless, this is not supported in our case due to the diving capabilities of gentoo

Table 4 Comparison of mean length (mm) of *Themisto gaudichaudii* caught by gentoo penguins and in net-hauls at Kerguelen Islands during three sampling periods

	Gentoo penguins	Net-hauls	*t*
August 1987	13.20 ± 0.5 (305)	13.60 ± 1.3 (109)	3.13 ($P < 0.01$)
September 1987	14.10 ± 0.5 (88)	13.90 ± 1.2 (85)	1.13 ($P > 0.05$)
September 1989	14.90 ± 1.8 (149)	14.60 ± 0.98 (78)	1.6 ($P > 0.05$)

penguin (Wilson et al. 1991; Williams et al. 1992); at Kerguelen Islands, the maximal diving depths reached more than 150 m (Bost, unpublished) are close to the maximum depth of Morbihan Bay. This suggest a real decrease in euphausiid abundance during 1989 in comparison with 1987.

Another bias may be that penguins do not forage randomly (Wilson 1992) and maximize their foraging efficiency (Wilson et al. 1992). Evidence from studies on other species suggests that seabirds aggregate in areas where prey is likely to be plentiful and concentrated (Hunt et al. 1990, Hunt and Harrison 1990). Gentoo penguins may thus concentrate at more productive areas. Finally, diet studies without ancillary data on foraging effort may be misleading when interpreting prey switching. Large changes in foraging effort may result in only small changes in the components of a seabird's diet (Burger and Piatt 1990; Cairns 1992; Wilson 1992). Indeed, gentoo penguins were able to catch enough euphausiids during November 1989 to provide around half of their diet although the availability of stocks was apparently low. Accordingly, during the same period (i.e. at the end of the breeding cycle), the foraging trips of the sampled birds were found to be 1.6 times longer with a meal size reduced by 60% in comparison with 1987, indicating a significant increase in their foraging effort (Bost 1991).

Comparison of length of prey caught by penguins and in plankton surveys

The analysis of size distribution of amphipods such as *T. gaudichaudii* caught by penguins may be an easy way to estimate their local growth and life history as hypothesized for *E. superba* and *E. vallentini* (Croxall and Pilcher 1984; Croxall et al. 1985; Ridoux 1988). The comparison with plankton survey catches showed a greater size variation in individuals taken by penguins. This may be explained by a greater homogeneity within rather than between swarms and by a difference in the locality of swarms sampled by penguins and net-hauls (Croxall et al. 1985). Increases in the length of amphipods caught by penguins between winter and spring is probably a consequence of a steady increase in immature size (Kanne 1966).

Conclusion

Studies of the diet of inshore foraging penguins in sub-antarctic areas has the potential to provide indirect evidence about the status and biology of planktonic populations not usually commercially exploited. Recent advances in remote-sensing technology allow diet studies to be coupled with accurate investigations on localisation of feeding areas, depth of feeding, and amount of food ingested by penguins (Wilson 1992). This approach will permit the documentation of the spatial distribution of prey caught by penguins (both vertically and horizontally) and will allow experimental and detailed simultaneous net-haul operations at the same scale. Such future work is greatly needed to validate the potential of penguin diets as biological samplers of abundance and distribution of prey stocks.

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