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Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–85

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Abstract: The total annual food consumption of the seabird and seal community breeding at Iles Kerguelen was estimated to be 1.8×10^6 t in 1985. This biomass included *c.* 0.99×10^6 t (55%) of crustaceans, 0.46×10^6 t (26%) of myctophid fish, 0.07×10^6 t (4%) of other fish species, and 0.26×10^6 t (15%) of squid. During the same year, the mass of prey consumed in Crozet waters was previouly estimated to be 3.1×10^6 t, the total food consumption in the Indian Ocean area including the two archipelagos thus totalling *c.* 5×10^6 t in 1985. Four species of top predators, the king penguin, macaroni penguin, elephant seal, and fur seal, consumed 59% and 56% of the amount of prey eaten in 1985 by the whole community at Kerguelen and Crozet islands, respectively. Between 1962 and 1985, population changes of these four species induced 18 and 41% increases in their food consumption at Kerguelen and Crozet islands. Population changes included a moderate increase in the number of macaroni penguins and a marked rise of king penguin populations. Assuming that the diet of king penguin was similar in 1962 and 1985, its population increase will have required a concomitant increase of 0.6×10^6 t in the consumption of myctophid fish in Crozet and Kerguelen waters.

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Introduction

Censuses of breeding populations of seabirds and seals have been conducted on Crozet and Kerguelen islands since the early 1960s. These long-term monitoring programmes allowed detection of major changes in population sizes of species playing a key role in the predation of marine resources in surrounding waters. Population changes previously described (Jouventin *et al.* 1984, Jouventin & Weimerskirch 1991, Guinet *et al.* 1992) are thought to result from multiple factors such as recovery from past exploitation (Jouventin & Weimerskirch 1990, 1991), a possible use of food resources made available from whale stock depletion (Croxall *et al.* 1984, Jouventin & Weimerskirch, 1990) and long-term fluctuations in the abundance and/or availability of the major prey species (Guinet *et al.* 1992).

Our knowledge of the food and feeding ecology of seabirds and pinnipeds breeding on the subantarctic islands has improved considerably over the last decade. This knowledge, combined with models of seabird and seal energy requirements, allows an estimation of the impact of these top predators on the surrounding marine resources. Calculations of the biomass consumed by birds and seals have been undertaken for most of the subantarctic islands. Pioneering works included those on pinnipeds at Marion Island (Condy 1981) and seabirds at South Georgia (Croxall *et al.* 1984). Croxall *et al.* (1984) proposed a model to estimate food consumption of the seabird and seal communities at South Georgia and in the Scotia Sea. This model, based on annual individual energetic needs of the different species, was later used to estimate the biomass consumed annually by the seabird community breeding at Iles Crozet (Ridoux 1989, 1992) and by seabirds and pinnipeds from Heard and McDonald islands (Woehlher & Green 1992).

Using the same model, the present study provides an estimate of the food consumed in 1985 by the seabird and pinniped community breeding at Iles Kerguelen where such evaluation was not previously available. Comparison is also made with the Crozet community for the same year and, due to important changes in some predator populations between the 1960s and 1980s, a comparison of the impact of seabirds and seals on marine resources in the vicinity of Crozet and Kerguelen islands was established between the reference years 1962 and 1985.

Methods

Modelling procedure

To estimate food consumption information requires knowledge on the population size, food composition and energy requirements of each species throughout the year. For this study, we followed the procedure outlined by Croxall *et al.* (1984) which has been used to estimate food consumption at Iles Crozet (Ridoux 1989), and at Heard and McDonald islands (Woehler & Green 1992). We also estimated food consumption in two different years (1962 and 1985), assuming that an increase in predator biomass required a concomitant rise in prey consumption and that no major changes have affected the composition of the diet between these years.

The main limits of the model are:

1) the level of winter impact is largely hypothetical because there is little data for most species in winter, and
2) only the breeding populations were considered (Croxall *et al.* 1984). Consequently, the estimated food consumption is underestimated and the precision of the model depends mainly on the accuracy of population censuses.

Population sizes in 1962 and 1985

The reference year for Kerguelen was 1985, because an inventory of its avifauna was completed at that time (Jouventin & Stonehouse 1985, Weimerskirch *et al.* 1989, Jouventin & Weimerskirch 1990, 1991). Population changes at Crozet and Kerguelen islands were calculated as the differences between surveys carried out in 1962 and 1985. During these two years several major breeding colonies of king and macaroni penguins were counted (Bauer 1967), as well as the elephant seal populations. Population trends were calculated only for species having good censuses during the two reference years. For example, due to a lack of census data in the 1960s, no population change data were available for burrowing petrels.

Iles Crozet. At Ile de la Possession, the population of king penguins grew at about 3% y^{-1} between 1961 and 1985 (Weimerskirch *et al.* 1992). From Bauer (1967) we estimated that 364 400 birds were breeding at Ile aux Cochons and at Ile de la Possession in 1962. Despin *et al.* (1972) estimated that about 80 000 King Penguins were breeding on Ile de l'Est in 1971. According to the annual growth rate of 3% y^{-1} found on Possession Island (Weimerskirch *et al.* 1992) we estimated that in 1962 the king population at East Island was about 59 300 pairs in 1962 which gave us an estimated total breeding population of about 424 000 pairs for the whole Crozet archipelago that year. In the mid 1980s, the census indicated 800 000 pairs of king penguins breeding in January (Guinet *et al.* 1995) which gave us an estimated total breeding population of 885 500 pairs (about 10.5% of the birds have not yet laid their egg in January (Weimerskirch *et al.* 1991)). The total number of macaroni penguins was estimated to increase by 20% between 1962 and 1985 (Jouventin & Weimerskirch 1991).

The two species of breeding fur seals have been monitored annually at Ile de la Possession. Populations grew at an annual rate of 19.2 and 17.4% for subantarctic and Antarctic fur seals, respectively (Guinet *et al.* 1994), two values close to the maximum growth rate observed for these species (Bester 1980, Hes & Roux 1983, Boyd *et al.* 1990). On the other hand, the elephant seal population of Possession decreased at an annual rate of -5.7% (Barrat & Mougin 1978, Guinet *et al.* 1992) over the period. This rate of decrease was extrapolated to the census available for Ile de l'Est (Despin *et al.* 1972) and Ile aux Cochons (unpublished data).

Iles Kerguelen. Population sizes and annual growth rates were available for king and macaroni penguins (Weimerskirch *et al.* 1989). Fur seals were censused at Iles Nuageuses in 1984 (Jouventin & Stonehouse 1985). No complete census of the elephant seal population was conducted on Kerguelen (Pascal 1981, Guinet *et al.* 1992), but, the bulk of the population is thought to breed on the Courbet Peninsula (Pascal 1981, Guinet *et al.* 1992), which is counted annually. Thus, while the elephant seal breeding population is underestimated, data on population trends are accurate assuming no change in colony site.

To compare the impact of marine birds and mammals on surrounding marine resources, the biomass consumed by king and macaroni penguins, and elephant and fur seals were calculated for both localities. Fur seals were taken into account as their numbers are increasing rapidly, and they are thus likely to play a key role in marine ecosystems in the coming years.

Dietary composition and energy content

The main source of information on the diet of seabirds was the extensive work conducted in the early 1980s at Iles Crozet (Ridoux 1994). Limited data on the food of Kerguelen species was also available, for prions (Bretagnolle *et al.* 1990) and the black-browed albatross (unpublished results). These data were used to estimate the relative proportion by mass of major prey items. When no data were available from Crozet or Kerguelen islands, it was assumed that the food was similar to that found at the closest breeding locality (Crozet, Marion or Heard islands).

The diet of Antarctic fur seals was assumed to be identical to that from Heard Island (Green *et al.* 1989, 1991). Since no dietary differences between the two species of fur seals were found at Marion Island (M. Bester, personal communication), it was assumed that both seals had the same diet at Crozet. Because dietary information by mass of prey items is very limited for elephant seals, we followed the general diet composition of 75% squid and 25% fish given by Laws (1984).

We used the calorific values of prey cited by Croxall *et al.* (1984) and used by Ridoux (1989) and Woehlher & Green (1992), i.e. squid: 3.47 kj g^{-1} fresh mass, crustaceans 4.35 kj g^{-1}, and fish (except myctophid fish) 3.97 kj g^{-1}. The low calorific value for myctophid fish of 3.97 kj g^{-1} used by Croxall *et al.* (1984), Ridoux (1989), and Woehlher & Green 1992) produced an over-estimate of the quantity of prey consumed. We used a calorific value of 7.00 kj g^{-1} measured from myctophid fish found in stomachs of king penguins (Cherel & Ridoux 1992). Carbon content of the prey was estimated to be 0.4 g C g^{-1} d.w. (Curl 1962). Wet mass was multiplied by 0.27 to convert to dry mass.

Energy requirements

Mean body masses of birds and seals (Table I) followed published data from Crozet and Kerguelen islands indicating that no intraspecies mass differences occurs between the two

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Table I. Breeding population estimates (minimum pairs) and estimated biomass (tonnes) for the 35 species of seabirds breeding on Iles Kerguelen.

Species		S1 Mass (g)	Minimum breeding population pairs	Total biomass (t)	Biomass (t) Crustaceans	Myctophids	Other fish	Cephalopods	Other	Total (t)
King penguin	*Aptenodytes patagonicus*	12 100	173 000	4 187	0	146 236	0	12 028	0	158 264
Macaroni penguin	*Eudyptes chrysolophus*	4 300	1 800 000	15 480	441 891	199 564	0	71 273	0	712 728
Rockhopper penguin	*Eudyptes chrysochome*	2 900	85 500	496	21 722	3 243	0	4 791	0	29 756
Gentoo penguin	*Pygoscelis papua*	7 200	35 000	5 040	12 935	6 926	5 903	446	26	26 237
Blue petrel	*Halobaena caerula*	210	200 000	84	11 339	1 943	0	5 118	280	18 680
Antarctic prion	*Pachyptila desolata*	140	3 000 000	840	233 313	61 647	0	0	0	294 960
Thin-billed prion	*Pachyptila belcheri*	145	850 000	123	52 015	20 454	0	7 431	0	79 900
White chinned petrel	*Procellaria aequinoctialis*	1 210	200 000	242	8 310	18 048	9 789	12 593	2 243	50 984
Black-bellied storm petrel	*Fregetta tropica*	50	7 500	1	79	0	43	12	80	214
Wilson's storm petrel	*Oceanites oceanicus*	30	350 000	11	4 340	0	581	0	0	4 921
Grey-backed storm petrel	*Garodia nereis*	40	4 000	0	128	0	0	0	0	128
Kerguelen diving petrel	*Pelecanoides urinatrix*	140	750 000	210	66 360	0	0	0	0	66 360
South Georgian diving petrel	*Pelecanoides georgicus*	120	1 500 000	360	125 970	0	0	0	0	125 970
Kerguelen petrel	*Pterodroma macroptera*	330	40 000	26	2 790	0	12	228	830	3 858
White headed petrel*	*Pterodroma lessoni*	700	35 000	25	3 115	0	0	3 115	0	6 230
Grey petrel	*Pterodroma cinerea*	1 070	7 500	16	10	0	707	1 790	36	2 542
Soft-plumaged petrel	*Pterodroma mollis*	300	5 000	3	426	0	0	86	35	547
Fairy prion	*Pterodroma turtur*	140	5 000	1	416	0	0	20	0	436
Cape pigeon	*Daption capense*	450	4 000	4	373	0	14	14	319	720
Wandering albatross	*Diomedea exulans*	9 580	1 095	21	0	0	65	334	37	436
Black-browed albatross	*Diomedea melanophris*	3 660	3 200	23	0	0	461	927	0	1 387
Grey-headed albatross	*Diomedea chrysostoma*	3 480	7 900	55	353	0	0	3 072	0	3 424
Yellow-nosed albatross	*Diomedea chororhynchos*	2 060	50	0	1	0	9	6	0	15
Sooty albatross	*Poebetria fusca*	2 600	4	0	0	0	0	1	1	1
Light-mantled sooty albatross	*Poebetria palpebrata*	3 150	4 000	25	344	0	218	1,126	333	2 021
Northern giant petrel	*Macronectes halli*	4 500	1 600	14	0	0	0	4	316	320
Southern giant petrel	*Macronectes giganteus*	4 500	4	0	0	0	0	0	1	1
Kerguelen cormorant	*Phalacrocorax verrucosus*	2 230	6 500	29	0	0	3 330	0	0	3 330
Total seabirds				27 316	986 229	458 062	21 130	124,414	4 536	1 594 371
Elephant seals	*Mirounga leonina*	Mass	Minimum number	Total biomass						
	cows	390 000	41 000	15 990	0	0	37 310	111 930	0	149 240
	bulls	2 300 000	2 660	6 118	0	0	7 407	22 222	0	29 630
Fur seals	*Arctocephalus gazella*									
	cows	40 000	10 000	400	0	4 055	4 055	0	0	8 110
	bulls	140 000	1 000	42	0	630	630	0	0	1 260
Total pinnipeds				22 550	0	4 685	49 402	134 152	0	188 240
Grand totals					986 229	462 747	70 533	258 566	4536	1 782 611

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localities (Jouventin *et al.* 1985, Weimerskirch *et al.* 1986, 1989). The energy requirement of seabird species was estimated from that proposed by Croxall *et al.* (1984) for South Georgia, but it was corrected by a factor to take into account the differences in bird weights and in the mean ambient temperature between localities. Following Ridoux (1992), we calculated the ratio of the Existence Energy Requirement (EER) for birds at Crozet and Kerguelen and at South Georgia using the equation (Kendeigh *et al.* 1977):

$$EER\ (kcal\ d^{-2}) = 4.142 x BM^{0.5444} - (T\ x\ 0.2761\ x\ BM^{0.2818})$$

BM = body mass (g); T = ambient temperature (°C) (5°C at Crozet and Kerguelen and 0°C at South Georgia);

Table II. Prey consumption trends in tonnes per year over the last three decades on Iles Crozet based on the population size change of five species of seabirds and seals (see text for further details).

		Predator numbers		Change	Crustaceans		Myctophids	
		1962	1985	%	1962	1985	1962	1985
Macaroni penguin	*Eudyptes chrysolophus*	5 000 000	6 000 000	20%	613 800	736 560	277 200	332 640
King penguin	*Aptenodytes patagonicus*	828 000	1 771 000	113%	0	0	356 337	744 683
Elephant seal	*Mirounga leonina*							
	female	11 155	3 395	-70%	0	0	0	0
	male	617	177	-70%	0	0	0	0
Antarctic fur seal	*Arctocephalus gazella*							
	female	0	30	-	0	0	0	12
	male	0	10	-	0	0	0	6
Subantarctic fur seal	*Arctocephalus gazella*							
	female	0	108	-	0	0	0	43
	male	0	48	-	0	0	0	29
Totals					613 800	736 560	633 537	1 077 413
Change %					20%		70%	

		Other fish		Cephalopods		Totals (t)	
		1962	1985	1962	1985	1962	1985
Macaroni penguin	*Eudyptes chrysolophus*	0	0	99 000	118 800	990 000	1 188 000
King penguin	*Aptenodytes patagonicus*	0	0	30 986	64 755	387 323	809 438
Elephant seal	*Mirounga leonina*						
	female	10 151	3 089	30 453	9 269	40 604	12 358
	male	1 289	493	3 866	1479	5 155	1 972
Antarctic fur seal	*Arctocephalus gazella*						
	female	0	12	0	0	0	24
	male	0	6	0	0	0	12
Subantarctic fur seal	*Arctocephalus gazella*						
	female	0	43	0	0	0	86
	male	0	29	0	0	0	58
Totals		11 440	3 672	164 305	194 303	1 423 082	2 011 948
Change %		-70%		18%		41%	

and we thus calculated the correcting factor

$$EER_{Crozet\text{-}Kerguelen}/EER_{Georgia}$$

According to Lavigne *et al.* (1986) and Innes *et al.* (1987), marine mammals have metabolic rates similar to those of terrestrial mammals of similar size and their energy ingestion (EI) is identical to that of other terrestrial carnivores. We therefore calculated the EI for seals using the equation: $EI = 9.80 \times BM^{0.63}$ (eq. 11 in Table II–Innes *et al.* 1987), using the body mass of pinnipeds following that cited in Woehler & Green (1992).

Results

Prey biomass consumed in 1985 in Kerguelen waters

In 1985, the total biomass of the breeding seabird community at Iles Kerguelen was estimated to be *c.* 27 500 t and that of breeding elephant seals and fur seals 22 600 t (Table I). During that year, the total food consumption amounted to 1.8×10^6 t of prey, 1.6×10^6 t (89.5%) being consumed by seabirds and 0.2×10^6 t (10.5%) by seals (Table I).

At Kerguelen, the seabird community was dominated by the four species of penguins which represented 92% of the seabird biomass, the remainder being mainly petrels. Macaroni penguin was by far the most abundant species, accounting for 57% of the total seabird biomass and the consumption was estimated to 0.71×10^6 t of marine prey per year. This amount was 46% of the total prey consumed by seabirds and 42% of that consumed by both seabirds and pinnipeds. Overall, the four penguin species consumed 0.93×10^6 t of marine organisms per year (58% of the total seabird consumption), and the petrel group 0.66×10^6 t (41%). The annual prey consumption by seabirds was 62% crustaceans, 30% myctophids <1% other fish and 8% squid (Table I).

The pinniped community at Kerguelen was largely dominated by southern elephant seals which accounted for 98% of the seal biomass and consumed 95% of the total amount of seal prey. Antarctic fur seals accounted for the remaining 2% of biomass and 5% of consumption. Of the 0.19×10^6 t of prey consumed by seals was estimated to be fish other than myctophids, 0.01×10^6 t (3%) were myctophids, and 71% were cephalopods.

Table III. Prey consumption changes in tonnes per year over the last three decades on Iles Kerguelen based on the population size change of long term monitored species, (see text for further details).

		Predator numbers 1962	Predator numbers 1985	Change %	Crustaceans 1962	Crustaceans 1985	Myctophids 1962	Myctophids 1985
Macaroni penguin	*Eudyptes chrysolophus*	3 000 000	3 600 000	20%	360 780	441 891	166 320	199 584
King penguin	*Aptenodytes patagonicus*	78 400	346 000	341%	0	0	32 963	145 472
Elephant seal	*Mirounga leonina*							
	female	60 000	41 000	-32%	0	0	0	0
	male	3 900	2 660	-32%	0	0	0	0
Antarctic fur seal	*Arctocephalus gazella*							
	female	300	10 000	233%	0	0	92	3 041
	male	30	1 000	233%	0	0	14	473
Totals					360 780	441 891	199 389	348 570
Change %					20%		74%	

		Other fish 1962	Other fish 1985	Cephalopods 1962	Cephalopods 1985	Totals (t) 1962	Totals (t) 1985
Macaroni penguin	*Eudyptes chrysolophus*	0	0	59 400	71 280	586 500	712 755
King penguin	*Aptenodytes patagonicus*	0	0	2 867	12 650	35 830	158 122
Elephant seal	*Mirounga leonina*						
	female	54 600	37 310	163 800	111 929	218 400	149 239
	male	10 861	7 404	43 442	22 220	54 303	29 624
Antarctic fur seal	*Arctocephalus gazella*						
	female	92	3 041	0	0	184	6 082
	male	14	473	0	0	29	946
Totals		65 567	48 228	269 509	218 079	895 246	1 056 768
Change %		-26%		-19%		18%	

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Changes in prey consumption between 1962 and 1985 at Kerguelen and Crozet islands

Changes in prey consumption of king and macaroni penguins, and of elephant and fur seals were estimated according to population changes. In 1985, these four species consumed 56% of the total amount of food eaten by the seabird and seal community at Crozet (Ridoux 1992), and 59% at Kerguelen (this study). However, despite a similar overall predation impact, these four species had a different relative importance in the two localities.

At Crozet, the estimated quantity of food eaten by the four species of predators increased from 1.42×10^6 t in 1962 to 2.01×10^6 t in 1985, a 41% increase in 23 years (Table II). At Kerguelen, this quantity also rose, from 0.90×10^6 t in 1962 to 1.06×10^6 t in 1985, an 18% increase during the study period (Table III).

Predation on myctophid fish, crustaceans and cephalopods in Crozet waters increased respectively by 66% (from 0.63–1.08×10^6 t), 20% (from 0.61–0.74×10^6 t), and 18% (from 0.16–0.19×10^6 t) between 1962 and 1985. Similar trends were found for the Kerguelen community, i.e. a 70% increase in myctophid fish (from 0.20–0.35×10^6 t) a 15% increase for crustaceans (from 0.36–0.44×10^6 t), but a 19% decrease for squid during that period.

Annual carbon flux

The annual prey consumption of seabirds and seals provide an estimate of the annual C flux of 192 500 t C y^{-1} in 1985 for Kerguelen and 292 000 t C y^{-1} in 1985 for Crozet.

Discussion

The accuracy of our calculations is determined by the precision of the population estimates, the model itself, and the errors arising from its use for localities other than South Georgia. For example, the size of the breeding populations of burrowing petrels are not well known (accuracy 25%). We are, however, confident in population changes of the four main species for which prey consumption trends were calculated, i.e. the king penguin, macaroni penguin, elephant seal, (despite uncertainty in total number of elephant seals at Kerguelen) and fur seal. These data were obtained on several large breeding colonies representing a large proportion of the total number of the breeding population for each of these species. The main objective of the results is to highlight changes over time rather than the absolute amount of food consumed.

Table IV. Estimates of the annual food consumption (in millions of tonnes) made by seabirds and pinnipeds for the major subantarctic breeding localities.

	South Georgia	Crozet Is.	Kerguelen Is.	Heard Is.	Total
Seabirds	7.8	3.1	1.6	0.4	12.9
Pinnipeds	1.7	< 0.1	0.2	0.1	2
Totals	9.5	3.1	1.8	0.5	14.9

In 1985, the consumption of marine resources by seabirds and seals on was estimated as 3.1×10^6 and 1.8×10^6 t at Crozet and Kerguelen islands, respectively giving a total for area of *c.* 5×10^6 t in 1985. The higher impact on marine resources at Crozet Iles resulted mainly from the larger king and macaroni penguin populations in this area, while petrels had a higher relative impact at Kerguelen.

The small difference in prey consumption by king and macaroni penguins in Crozet waters found in this study compared to Ridoux (1989) (2.0 versus 2.1×10^6 t) resulted from two errors with opposite effects. First, the difference in the energy content of myctophids (7.00 kj g^{-1} in this study versus 3.95 kj g^{-1} used by Ridoux) induced a 77% over-estimation of the quantity of myctophid fish consumed by king penguins, and, second, the population size of this species used by Ridoux was underestimated by 94% according to the new data available for Crozet archipelago (Guinet *et al.* 1995). Macaroni penguins preyed mainly on crustaceans and thus the change in energy content used for myctophids had a limited effect on the estimate of prey consumed (1.2×10^6 t in the present study compared to 1.4×10^6t obtained by Ridoux in 1989).

Croxall *et al.* (1984) estimated that the seabirds at South Georgia consumed annually about 7.8×10^6 t of marine organisms. The populations of elephant seals (with an estimated pup production of 102 000 in 1985, Rothery & McCann 1987) and fur seals (*c.* 1 500 000 individuals, Lunn *et al.* 1993), we calculated consumed *c.* 1.7×10^6 t y^{-1} at South Georgia. Thus, total annual consumtion of seafood each year in South Georgian waters is 9.5×10^6 t (Table IV). At Heard and McDonald islands breeding seabirds and seals were estimated to consume 0.5×10^6 t y^{-1} (Woehler & Green 1992).

At Crozet and Kerguelen, the increase in food consumption between 1962 and 1985 is mainly related to the increase in the king penguin population. At Kerguelen a decrease in the number of elephant seals paralleled the rise in king penguin population limited the increase in consumption to 18%. Note that, due to their small number, elephant seals were already a predator of limited importance in terms of biomass consumption at Crozet in 1962, and, despite their rapid increase in numbers, fur seals remained predators of minor importance at both localities.

King penguins are specialist myctophid consumers, preying mainly upon *Krefftichthys anderssoni, Electrona carlsbergi* and *Protomyctophum tenisoni* (Cherel & Ridoux 1992, Cherel *et al.* 1993). Since it is unlikely that king penguins have changed their diet over the study period, their increase in number indicated a drastic rise in the consumption of myctophids between 1962 and 1985. Macaroni penguins also eat myctophids, but the bulk of their diet consists of crustaceans, mainly euphausiids.

The increase in the quantity of prey consumed by king and macaroni penguins paralleled a drastic removal of baleen whales from the Crozet and the Kerguelen area, and thus a drop in the impact of whales on trophic resources. A minimum of

40 388 whales—pygmy blue whales (*Balaenoptera musculus*), fin whales (*B. physalus*) and sei whales (*B. borealis*) and sperm whale (*Physeter catodon*)—were declared to be caught between 1960 and 1975 by the Russian and Japanese fleets (IWC 1994). This number included 17 624 individuals officially removed from the Kerguelen area. These catches are likely to be underestimates since Russians fished, on a world basis, 48% more whales than they reported (IWC 1994). The impact of the removal of large whales on marine resources was therefore likely to be more important than indicated here. Since baleen whales feed mainly on crustaceans, a major effect of whale removal could be an increase in the population of crustacean-eating seabirds through an increase in the availability of their main prey. *Euphausia vallentini* and copepods was the main food of pygmy blue whales, fin whales (*B. physalus*) and sei whales (*B. borealis*) hunted in waters off Crozet (Pervushin 1968). We estimated that the killing of whales in Crozet and Kerguelen waters between 1960 and the end of the whaling period reduced annual whale prey consumption by 2.3×10^6 t.

On Crozet, Ridoux (1992) indicated that macaroni penguin is the major crustacean consumer (*Euphausia vallentini* being the main prey), and that three species of petrels, Salvin's prion (*Pachyptila salvini*), South Georgia diving petrel (*Pelecanoïdes georgicus*) and common diving petrel (*P. urinator*), also account for a substantial part of the crustaceans eaten. Among these species, macaroni penguins have the closest similarity to whales in their feeding habits, and are thus potentially the species which should have benefited the most directly from the decrease in whale numbers. Interestingly, the population of macaroni penguins shows only a limited increase over the period 1962–1985.

The paradox observed at both Crozet and Kerguelen islands is that the depletion of baleen whales stocks should have directly benefitted species of predators preying upon crustaceans, but the highest growth rates were observed in king penguin and fur seal populations which are major consumers of myctophid fish. Fur seals are still recovering from sealing, but the king penguin population is thought to exceed historic levels at Iles Crozet. This suggests either that myctophid availability has increased over the last decades or that myctophid stocks off Crozet and Kerguelen were able to sustain a greater predation pressure.

Subantarctic and Antarctic myctophid fish eat mainly pelagic crustaceans (Hulley 1990, Perissinotto & McQuaid, 1992). Ridoux (1994) indicated that myctophid fish recovered from macaroni and king penguins were found to contain planktonic crustaceans, particularly *Euphausia vallentini* and *Themisto gaudichaudii*. *Electrona carlsbergi* and *Gymnoscopelus andersoni* are major predators of copepods and the dominant euphausid prey in the Polar Frontal Zone was *Euphausia vallentini* (Kozlov & Tarverdiyeva 1989, Oven *et al.* 1990, Gerasimova 1990). Kozlov (in press) described the myctophid community of the mesopelagic zone in the Southern Ocean as a major consumer of abundant copepod, amphipod and euphausid species. This author indicated that observed differences in the diets of myctophids from various areas are mainly determined by regional and seasonal variability in zooplankton composition. It is therefore tempting to hypothesize that myctophid stocks may have been enhanced by the biomass of crustaceans freed by the removal of baleen whales.

King penguin is the species presenting the greatest change in population size between 1962 and 1985. The differences observed in the rate of increase of macaroni and king penguin populations suggest that king penguins are more efficient in exploiting myctophid fish than macaroni penguins. King penguins possess greater diving abilities than macaronis (Kooyman *et al.* 1992, Croxall *et al.* 1993). During the chick-rearing period, king penguins forage further away than other subantarctic penguin species, and it has been suggested that the zonation of foraging areas accounts for most of the difference between the penguin diets (Adams & Brown 1989). For example, king penguins are the only penguin species from Crozet that is able to forage during the summer part of its breeding period at the Antarctic Polar Front 500 km south of Crozet where myctophid fish occur in large concentrations (Pakhomov *et al.* 1994) and is even able to reach the pack ice limits –3000 km away– in winter (Jouventin *et al.* 1994). Macaroni penguins as well as fur seals have a theoretical foraging range of 150 km during the breeding season but in winter the extent of their movements remains unknown.

Due to a lack of data on the foraging use of the waters off Crozet and Kerguelen islands by the seabirds and seals as well as a lack of knowledge of the ecosystem primary and secondary production, it is difficult today to put the consumption of seabirds and pinnipeds into a production context. Future studies providing estimates of such productivity together with long-term changes in the biomass consumed by the major predators will contribute to our understanding of the trophodynamic of the Southern Ocean in relation both to present human activities and to the recovery of marine mammal and seabird populations which have been heavily disturbed by humans in the past.

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