

The diet of the Antarctic fur seal *Arctocephalus gazella* at the South Orkney Islands in ten consecutive years

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Abstract To improve the knowledge on the Antarctic fur seal foraging behavior, evaluate whether changes in its diet are associated with changes in prey availability, and evaluate whether fisheries had negative impacts on Antarctic fur seal populations, a total of 1359 scats of non-breeding males were collected in ten consecutive sampling periods between 1994 and 2003 at Laurie Island, South Orkney Islands. Antarctic krill was the most numerous prey throughout the sampling period followed in importance by fish prey. Antarctic krill also predominated by reconstructed mass, except during 1994 and 1998 when penguins were the most important prey, and during 1995 when fish dominated. Among fish, demersal-benthic species (mainly *Gobionotothen gibberifrons*, *Chaenocephalus aceratus* and *Chionodraco rastrospinosus*) dominated the diet except in 1997, 1998, 1999 and 2002 when myctophids (mainly *Gymnoscopelus nicholsi* and *Electrona antarctica*) were the most important fish prey. In seasons when fish dominated the diet, the diet was primarily comprised of demersal species. Although our results are in overall agreement with previous studies, the contribution to the diet of the main preys changed throughout the sampling period, probably in parallel with changes in prey abundance. According to historical results on fish consumption, the

fisheries carried out in the past have had negative impacts on seal populations from the South Orkney Islands.

Keywords Antarctic fur seal · Diet composition · South Orkney Islands · Antarctica

Introduction

The study of top predator diets is of particular importance in understanding their role in marine ecosystems. Long-term studies reveal how top predator populations are affected by anthropogenic and environmental changes, may reveal information on the occurrence of prey species and, under certain conditions, have the potential to monitor trends in prey populations (Casaux 2003; Casaux et al. 2003). Despite their importance, few long-term studies (Ciaputa and Jacek 2006; Davis et al. 2006) have focused on the diet of one of the main Antarctic top predators, the Antarctic fur seal (*Arctocephalus gazella*), and none of them have been carried out in the South Orkney Islands (SOI), one of the main fishing grounds of the Southern Ocean (Fig. 1).

Commercial fishing in the SOI region (FAO Statistical Subarea 48.2) started in the 1977/1978 season. A total of 250,263 t of finfish was caught until the closure of the fisheries in the area in the 1990/1991 season, but the bulk of the catches were fished during the first 3 years of exploitation (Kock 1992). As reported for Kerguelen Island (Duhamel 1990) and the South Shetland Islands (SSI) (Barrera-Oro and Marschoff 1991), fisheries are expected to change the structure of the fish community around the SOI. There is insufficient information available to corroborate this hypothesis, evaluate trends in fish populations,

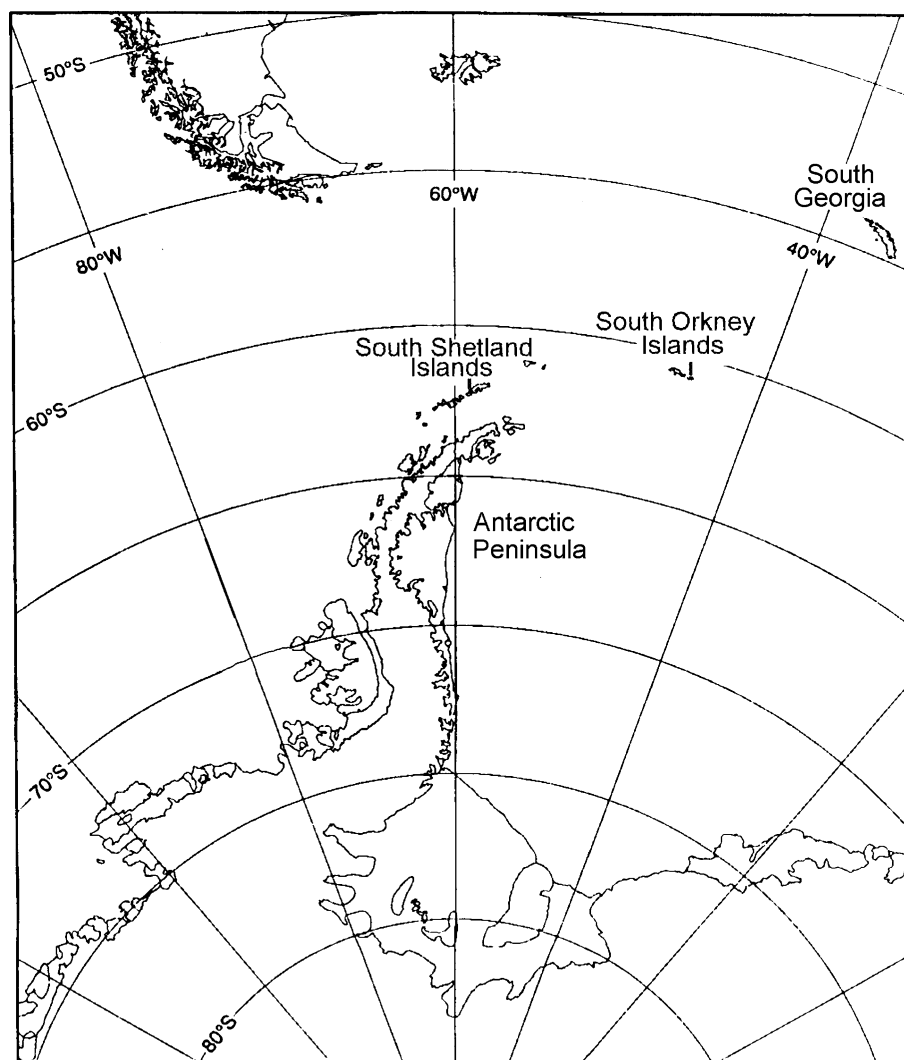
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Fig. 1 Map showing the location of the South Orkney Islands



and therefore to understand the impact of the fisheries on top predator populations.

The Antarctic fur seal is an opportunistic feeder (Casaux et al. 2004) and its diet likely reflects prey availability at the foraging grounds (Casaux et al. 2003). Traditionally, the seals' diet has been studied by analyses of stomach contents. Such samples usually contain a mixture of hard parts and partially digested soft tissues. The hard remains serve to identify specimens of prey and to estimate their original size and mass. However, some biases are inherent in the estimation of the number of ingested organisms; e.g., cephalopod beaks are resistant to the digestive juice (Clarke and MacLeod 1982) and may remain in the stomachs for several days, whereas otoliths from some fish species pass through rapidly (Miller 1978, quoted by Clarke 1980; North et al. 1983; Prime and Hammond 1987), which implies that their relative importance is over- and underestimated, respectively. Additionally, the size and mass of the fish ingested could be underestimated

since, for some species, the otoliths are considerably eroded 3 h after feeding even to the extent of being completely eroded (da Silva and Neilson 1985; Green and Burton 1987; Murie 1987). Partially digested soft tissues, on the other hand, do not provide reliable identification or estimation of the relative importance of species of prey (Prime and Hammond 1987). The most important problem of stomach content analyses method is that in order to obtain a representative sample, several seals need to be killed or, if stomach lavaging is used, too much time is required in the field with additional biases associated. Although the analysis of feces avoids these two last kinds of problems, the underestimation of the number and mass of the prey ingested, mainly fish, is higher.

The objective of this study was to examine the diet of the Antarctic fur seal by analyzing scats collected during ten consecutive years at Laurie Island, SOI. Diet data were used to improve the knowledge on its foraging behavior, evaluate whether changes in its diet are associated with

changes in prey availability, evaluate whether the fisheries negatively interacted with this seal and analyze whether prey availability determines the number of individuals that haul out at the SOI.

Materials and methods

A total of 1359 Antarctic fur seal scats were collected during every 2 weeks census carried out from the 1994/1995 (hereafter 1994) to the 2003/2004 (2003) at beaches on Laurie Island (60°44'S–44°44'W), SOI (Table 1). For each sampling season, census and sample collection began when seals arrived at the study area and finished when they left. For consistency, the samples were grouped seasonally (see details in Table 1). Only non-breeding males haul out at the sampling area (Carlini et al. 2006). Given that the number of seals ashore (Table 1) and peak haul-out dates varied considerably between seasons (see Carlini et al. 2006), the number of samples and the sampling periods also differed between seasons.

As commented above, the estimates of the number and mass of prey species represented in scats of seals usually give biased results. However, given that the same sampling and analysis protocols were applied throughout the study, the biases do not invalidate the analysis of the seasonal changes in the diet.

Samples were individually washed through sieves (mesh 0.54 mm) with water, and prey remains were sorted to the lowest taxonomic level possible using reference collections and identification keys. The contribution of prey to the diet of seals is expressed as frequency of occurrence percentage (the percentage of the number of samples in which a prey is represented), importance by number percentage (the percentage of the number of specimens in which a determined prey species occurred in relation to the total number of prey

represented in the samples) and importance by mass percentage (the percentage mass of a determined prey species in relation to the total mass of prey represented in the samples). In order to estimate the approximate number of individuals of the Antarctic krill (*Euphausia superba*) present in each sample, we considered the number of eyes and telsons or the dry weight of the total of carapaces present in the sample according to the technique described by Casaux et al. (1998a). The highest of these three estimates was considered as the minimum number of krill specimens present per sample. The mass of the individuals was estimated by considering the mass of entire specimens. Amphipods, mysids and pyggononids were represented by exoskeleton remains, and their masses were estimated by considering the mass of entire specimens.

Cephalopods were represented in the samples by beaks or eye lenses and were identified using the illustrations and descriptions in Clarke (1980), Lipinski and Woyciechowski (1981), Okutani and Clarke (1985) and Fischer and Hureau (1988). The number of individuals represented in the samples was estimated by the number of upper and lower beaks or eye lenses. The lower hood length of octopod beaks (identified as *Pareledone* sp.) was measured to the nearest 0.01 mm with vernier callipers and the mass of the individuals estimated using the relationship developed by Rodhouse et al. (1992). The squids were tentatively identified as *Psychroteuthis glacialis*, and the mass of the individuals was estimated considering the rostral length of the lower beak and applying the relationship described in Gröger et al. (2000). The number of gastropods and bivalves represented in the scats was estimated considering the number of shells present in the samples, and the mass was estimated by considering entire specimens.

Bones, otoliths and eye lenses indicated the presence of fish in the scat samples. The sagittal otoliths present in the samples were identified to species level, when possible,

Table 1 Detail of the sampling periods, abundance of Antarctic fur seals (taken from Carlini et al. 2006), number of scats collected and containing food remains, and number of prey and mass (in tons) represented in the samples collected at the South Orkney Islands

| | Sampling period | Number of seals | Scats collected | Scats with remains | No. of preys | Mass |
|-----------|------------------|-----------------|-----------------|--------------------|--------------|-------|
| 1995 | January–May | | 220 | 204 | 19,327 | 43.7 |
| 1996 | January–June | 8626 | 147 | 144 | 32,243 | 66.3 |
| 1997 | January–April | 17,516 | 231 | 209 | 781 | 42.6 |
| 1998 | January–April | 4911 | 85 | 80 | 46,336 | 42.7 |
| 1999 | January–July | 13,339 | 189 | 120 | 38,459 | 63.3 |
| 1900 | January–April | 14,770 | 93 | 63 | 42,932 | 47.2 |
| 2001 | January–March | 5352 | 50 | 50 | 41,134 | 49.8 |
| 2001/2002 | October–February | 15,648 | 193 | 185 | 187,760 | 290.7 |
| 2003 | March–April | 6774 | 67 | 60 | 48,745 | 61.2 |
| 2003/2004 | October–February | 11,297 | 84 | 80 | 71,346 | 59.1 |

using our own reference collection (R. Casaux) and illustrations and descriptions in Hecht (1987), Williams and McEldowney (1990) and Reid (1996). The otoliths belonging to specimens of each species were sorted into right and left; the higher count of right and left otoliths was considered as the number of fish of the corresponding species present in each scat sample. The otoliths length were measured to the nearest 0.01 mm, and the fish body length and mass was estimated using the equations in Hecht (1987), Williams and McEldowney (1990) and Casaux et al. (1998a) (see details in Table 3).

Given that penguins were represented almost exclusively by feathers, we could not accurately estimate the number of individuals represented in the samples. Casaux et al. (2004) reported for the SSI that a fur seal was seen killing and eating penguins on three consecutive occasions. We arbitrarily considered one individual taken per scat sample although it is likely to be an underestimate of penguins consumed. Casaux et al. (2004) observed that most of the penguins preyed on by seals were fledging chicks and that only viscera and muscle tissues were ingested. Thus, the weight of penguins consumed per scat sample was assumed to be the mean mass reported for *Pygoscelis antarctica* fledging chicks (2910 g, Moreno et al. 1998) minus the mean mass of carcasses of penguins killed by seals (mean = 956.25 g, SD = 233.01, range 550–1400, $n = 16$; Casaux et al. 2004) found along the shore of Harmony Point, SSI (see Casaux et al. 2004).

In order to evaluate whether the number of seals ashore at Laurie Island is determined by prey availability, the abundances of seals reported by Carlini et al. (2006) for that island were correlated with the overall contribution (in number or mass) of the main prey to the diet of seals in the corresponding seasons.

Results

Except for the 1995 season, when fish were the most common prey, Antarctic krill had the highest frequency of occurrence, followed by fish and occasionally by penguins (during the 2002 season only) (Table 2). Antarctic krill was the most numerous prey throughout the sampling period followed in importance by fish. This crustacean also dominated by reconstructed mass, except during 1994 and 1998 when penguins had the greatest mass, and during 1995 when fish did. The remaining prey items represented in the samples scarcely contributed to the diet of seals, and some of them might be secondary prey items (i.e., they came from the stomachs of the prey directly ingested by seals).

Twenty-nine fish species belonging to six families were represented in the scat samples (Table 3). Demersal-

benthic fish (mainly the nototheniid *Gobionotothen gibberifrons* and the channichthyids *Chaenocephalus aceratus* and *Chionodraco rastrospinosus*) dominated in the diet in all years except 1997, 1998, 1999 and 2002, when myctophids (mainly *Gymnoscopelus nicholsi* and *Electrona antarctica*) were the most important fish prey. Overall, *G. nicholsi*, followed by *G. gibberifrons*, were the species that contributed most to the fish component of the seal diets. The size of the fish ingested ranged between 2.4 (*E. antarctica*) and 60.3 (*C. aceratus*) cm (Online Resource 1) and varied according to the seasons (ANOVA, $p < 0.00001$). Significantly larger fish were ingested in 2003 (Newman–Keuls, $p < 0.0001$ compared to the rest of the seasons), and fish prey was significantly smaller in 1995 ($p < 0.01$). Interestingly, the contribution of *G. gibberifrons* to the diet is correlated to the size of the specimens of this species ingested (Spearman test, $r = 0.87$, $p < 0.01$, Fig. 2).

In seasons when fish strongly contributed to the diet, fish prey was predominately demersal species (Tables 2, 3; Fig. 3). The presence of demersal fish in the diet was negatively, but not significantly, related to the ingestion of pelagic fish (Spearman test, $r = -0.37$, ns), penguins ($r = -0.55$, ns) and krill ($r = -0.38$, ns) (Fig. 3). Similarly, the consumption of krill and penguins was negatively correlated ($r = -0.49$, ns).

The abundance of seals reported by Carlini et al. (2006) for Laurie Island fluctuated widely throughout the study period (Table 1) and is not correlated (Spearman test, ns) with the overall contribution (either in number or in mass) of the main prey to the diet of seals in the corresponding seasons.

Discussion

In agreement with previous results reported for breeding and non-breeding Antarctic fur seal individuals from other localities in the Southern Ocean (Reid 1995; Cherel et al. 1997; Kirkman et al. 2000; Makhado et al. 2008) and also from the study area (Daneri and Coria 1992; Daneri 1996; Daneri and Carlini 1999; Casaux et al. 2003), our analysis shows that the importance of krill, fish or penguins varies seasonally in the diets of non-breeding male Antarctic fur seals. Although krill dominated the diet throughout most of the study period, its contribution to the diet strongly fluctuated among seasons. Unfortunately, there is no concurrent information on trends in krill availability for the area to compare with the pattern of krill consumption observed in seals. However, the consumption of krill by penguins was so little from the 1996/1997 to the 1999/2000 summer seasons that Lynnes et al. (2004) postulated little or no recruitment of krill at the SOI during that time. This pattern

Table 2 The composition of the diet of Antarctic fur seals at Laurie Island, South Orkney Islands, as reflected by the analysis of scats collected during the summers 1994/1995–2003/2004

| | 1994/1995 | | | 1995/1996 | | | 1996/1997 | | | 1997/1998 | | | 1998/1999 | | |
|-------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|
| | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % |
| Penguins | 6.6 | 0.1 | 53.7 | 4.6 | 0.0 | 17.7 | 13.4 | 0.0 | 33.6 | 6.3 | 0.0 | 22.5 | 13.3 | 0.0 | 48.4 |
| Fish | 45.6 | 1.2 | 8.8 | 74.4 | 3.0 | 40.9 | 50.7 | 0.8 | 26.2 | 20.0 | 0.4 | 6.4 | 33.3 | 0.9 | 11.0 |
| Ascidians | – | – | – | 0.8 | 0.0 | 0.0 | – | – | – | – | – | – | – | – | – |
| Mollusks | | | | | | | | | | | | | | | |
| Squids | 7.1 | 0.1 | 9.2 | 9.3 | 0.1 | 10.9 | 3.8 | 0.0 | 2.3 | 3.8 | 0.0 | 2.0 | 4.2 | 0.0 | 2.2 |
| Octopods | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Bivalves | 0.6 | 0.0 | 0.0 | 3.1 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | – | – | – | – | – | – |
| Limpets | 0.6 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | 1.4 | 0.0 | 0.0 | – | – | – | 0.8 | 0.0 | 0.0 |
| Snails | 1.1 | 0.0 | 0.0 | 3.9 | 0.0 | 0.0 | 2.9 | 0.0 | 0.0 | – | – | – | – | – | – |
| Crustaceans | | | | | | | | | | | | | | | |
| Amphipods | 0.6 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | – | – | – | – | – | – | 0.8 | 0.0 | 0.0 |
| Krill | 69.2 | 98.7 | 28.4 | 54.3 | 96.8 | 30.6 | 70.8 | 99.1 | 37.9 | 83.8 | 99.6 | 69.1 | 76.7 | 99.1 | 38.4 |
| Mysids | – | – | – | 0.8 | 0.0 | 0.0 | – | – | – | – | – | – | – | – | – |
| Pyggononids | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Algae | 2.8 | – | – | 2.3 | – | – | 1.4 | – | – | 1.3 | – | – | 1.7 | – | – |
| | 1999/2000 | | | 2000/2001 | | | 2001/2002 | | | 2002/2003 | | | 2003/2004 | | |
| | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % | <i>F</i> % | <i>N</i> % | <i>M</i> % |
| Penguins | 9.5 | 0.0 | 24.8 | 10.0 | 0.0 | 19.6 | 14.1 | 0.0 | 17.5 | 23.3 | 0.0 | 44.7 | 1.3 | 0.0 | 3.3 |
| Fish | 41.3 | 0.8 | 15.3 | 50.0 | 0.3 | 26.2 | 57.8 | 0.4 | 35.8 | 13.3 | 0.1 | 2.5 | 25.0 | 0.1 | 14.1 |
| Ascidians | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Mollusks | | | | | | | | | | | | | | | |
| Squids | 3.2 | 0.0 | 1.2 | 4.0 | 0.0 | 0.6 | 8.7 | 0.0 | 4.9 | 5.0 | 0.0 | 1.2 | 5.0 | 0.0 | 3.2 |
| Octopods | – | – | – | – | – | – | 0.5 | 0.0 | 0.0 | – | – | – | 2.5 | 0.0 | 0.8 |
| Bivalves | – | – | – | – | – | – | 2.2 | 0.0 | 0.0 | 3.3 | 0.0 | 0.0 | 3.8 | 0.0 | 0.1 |
| Limpets | – | – | – | – | – | – | 0.5 | 0.0 | 0.0 | – | – | – | 1.3 | 0.0 | 0.0 |
| Snails | 1.6 | 0.0 | 0.0 | – | – | – | – | – | – | 1.7 | 0.0 | 0.0 | 1.3 | 0.0 | 0.0 |
| Crustaceans | | | | | | | | | | | | | | | |
| Amphipods | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Krill | 85.7 | 99.2 | 58.6 | 94.0 | 99.6 | 53.5 | 92.4 | 99.6 | 41.8 | 88.3 | 99.8 | 51.7 | 96.3 | 99.9 | 78.4 |
| Mysids | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Pyggononids | 1.6 | 0.0 | 0.0 | – | – | – | – | – | – | – | – | – | – | – | – |
| Algae | 1.6 | – | – | – | – | – | 1.6 | – | – | 8.3 | – | – | 2.5 | – | – |

Percentage frequencies of occurrence (*F* %), number (*N* %) and mass (*M* %)

was not observed for seals. The recruitment of a single krill cohort entering the population in 1995/1996 in the region (see Loeb et al. 2001; Fraser and Hofmann 2003; Osman et al. 2004) was predicted to cause an increase in the abundance of krill between 1996/1997 and 1997/1998 followed by a decrease in the subsequent seasons, especially in 1998/1999 and 1999/2000. The predicted trend in krill biomass (Lynnes et al. 2004) was reflected in fur seal diets, except during the 1999/2000 season when krill consumption by seals was expected to be low.

In seasons when krill consumption decreased, the diet was augmented with penguins and fish. The importance of penguins as prey of the Antarctic fur seal at the SOI and the SSI was previously reported by Daneri and Coria (1992) and Casaux et al. (1998b, 2003). Our results confirm the suggestions by Casaux et al. (2004) indicating that penguins may occasionally constitute the main prey of Antarctic fur seals. The consumption of krill and penguins were negatively correlated which suggests that penguins were not heavily preyed upon at the krill swarms. Except

Table 3 Fish represented by the otoliths found in scats of Antarctic fur seals collected at Laurie Island, South Orkney Islands, during the summers 1994/1995–2003/2004

| | 1994/1995 | | | 1995/1996 | | | 1996/1997 | | | 1997/1998 | | | 1998/1999 | | |
|---|-----------|------|------|-----------|------|------|-----------|------|------|-----------|------|------|-----------|------|------|
| | F % | N % | M % | F % | N % | M % | F % | N % | M % | F % | N % | M % | F % | N % | M % |
| Bathydraconidae | | | | | | | | | | | | | | | |
| <i>Gerlachea australis</i> ^a | – | – | – | – | – | – | 0.5 | 0.1 | 0.3 | – | – | – | – | – | – |
| <i>Gymnodraco acuticeps</i> ^b | – | – | – | – | – | – | 0.5 | 0.1 | 0.1 | – | – | – | – | – | – |
| <i>Parachaenichthys charcoti</i> ^a | – | – | – | 1.6 | 0.3 | 0.3 | 0.5 | 0.1 | 1.1 | – | – | – | – | – | – |
| Channichthyidae | | | | | | | | | | | | | | | |
| <i>Chaenichthys rhinoceratus</i> ^a | – | – | – | – | – | – | 1.0 | 0.3 | 0.3 | – | – | – | – | – | – |
| <i>Chaenocephalus aceratus</i> ^a | 1.1 | 0.9 | 12.6 | 3.9 | 0.8 | 19.6 | 1.0 | 0.5 | 4.3 | – | – | – | 0.8 | 0.3 | 3.0 |
| <i>Chaenodraco wilsoni</i> ^b | – | – | – | – | – | – | 0.5 | 0.6 | 2.6 | – | – | – | – | – | – |
| <i>Champscephalus gunnari</i> ^a | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| <i>Chionodraco rastrospinosus</i> ^a | 0.6 | 0.9 | 16.8 | 7.8 | 2.4 | 12.7 | 3.8 | 3.5 | 9.9 | – | – | – | 0.8 | 2.1 | 10.6 |
| <i>Cryodraco antarcticus</i> ^b | – | – | – | 4.7 | 0.7 | 6.7 | 3.4 | 1.5 | 3.8 | – | – | – | – | – | – |
| <i>Pseudochaenichthys georgianus</i> ^a | – | – | – | 2.3 | 1.1 | 4.5 | 1.9 | 0.5 | 1.2 | – | – | – | – | – | – |
| Nototheniidae | | | | | | | | | | | | | | | |
| <i>Gobionotothen gibberifrons</i> ^c | 1.1 | 2.3 | 12.1 | 12.4 | 3.3 | 23.6 | 11.5 | 13.1 | 55.7 | 1.3 | 0.5 | 1.4 | 1.7 | 0.9 | 13.3 |
| <i>Notothenia coriiceps</i> ^c | 0.6 | 0.4 | 2.2 | 0.8 | 0.1 | 0.2 | – | – | – | – | – | – | – | – | – |
| <i>Nototheniops larseni</i> ^a | 2.2 | 1.8 | 2.5 | 14.1 | 14.1 | 14.4 | 9.6 | 5.5 | 3.5 | 1.3 | 4.8 | 9.9 | – | – | – |
| <i>Nototheniops nudifrons</i> ^c | 0.6 | 0.4 | 0.4 | 3.9 | 5.1 | 3.8 | 1.4 | 0.9 | 0.3 | 1.3 | 2.7 | 4.7 | – | – | – |
| <i>Pagothenia bernacchii</i> ^c | – | – | – | – | – | – | – | – | – | – | – | – | 0.8 | 0.3 | 2.4 |
| <i>Pleuragramma antarcticum</i> ^a | – | – | – | 0.8 | 0.1 | 0.1 | 0.5 | 0.1 | 0.1 | – | – | – | – | – | – |
| <i>Trematomus newnesi</i> ^c | 1.7 | 1.3 | 1.6 | 2.3 | 0.3 | 0.1 | – | – | – | – | – | – | – | – | – |
| Harpagiferidae | | | | | | | | | | | | | | | |
| <i>Harpagifer antarcticus</i> ^c | – | – | – | 0.8 | 0.2 | 0.1 | – | – | – | – | – | – | – | – | – |
| Myctophidae | | | | | | | | | | | | | | | |
| <i>Electrona carlsbergi</i> ^b | – | – | – | – | – | – | 2.9 | 1.4 | 0.3 | – | – | – | – | – | – |
| <i>Electrona antarctica</i> ^a | 13.2 | 26.8 | 3.9 | 25.6 | 43.8 | 4.1 | 10.1 | 24.5 | 1.3 | 8.8 | 34.8 | 8.1 | 10.0 | 24.6 | 4.0 |
| <i>Gymnoscopelus braueri</i> ^a | – | – | – | 0.8 | 0.2 | 0.1 | 1.0 | 0.4 | 0.0 | – | – | – | – | – | – |
| <i>Gymnoscopelus nicholsi</i> ^a | 12.6 | 40.5 | 43.9 | 13.2 | 10.6 | 8.1 | 14.4 | 39.7 | 14.9 | 10.0 | 46.0 | 74.6 | 21.7 | 64.1 | 66.5 |
| <i>Gymnoscopelus opisthopterus</i> ^a | – | – | – | 1.6 | 0.4 | 0.4 | – | – | – | – | – | – | – | – | – |
| <i>Krefflichthys anderssoni</i> ^a | 0.6 | 0.4 | 0.1 | 1.6 | 0.5 | 0.2 | – | – | – | – | – | – | – | – | – |
| <i>Lampanychthus achirus</i> ^a | 0.6 | 0.4 | 0.3 | – | – | – | – | – | – | – | – | – | – | – | – |
| <i>Protomyctophum choriodon</i> ^a | – | – | – | 0.8 | 0.1 | 0.0 | 0.5 | 0.1 | 0.0 | – | – | – | – | – | – |
| <i>Protomyctophum normani</i> ^a | 0.6 | 0.4 | 0.2 | 3.1 | 1.2 | 0.1 | 3.4 | 1.5 | 0.1 | – | – | – | 1.7 | 1.2 | 0.2 |
| <i>Protomyctophum tenisoni</i> ^a | – | – | – | – | – | – | 1.0 | 0.3 | 0.0 | – | – | – | – | – | – |
| Paralepididae | | | | | | | | | | | | | | | |
| <i>Notolepis coatsi</i> ^a | 1.1 | 2.2 | 3.4 | 2.3 | 1.5 | 1.1 | 1.0 | 0.8 | 0.3 | 1.3 | 1.1 | 1.4 | – | – | – |
| Unidentified | | | | | | | | | | | | | | | |
| | 10.4 | 21.3 | – | 27.1 | 13.2 | – | 7.2 | 4.5 | – | 6.3 | 10.2 | – | 5.0 | 6.4 | – |
| | 1999/2000 | | | 2000/2001 | | | 2001/2002 | | | 2001/2003 | | | 2001/2004 | | |
| | F % | N % | M % | F % | N % | M % | F % | N % | M % | F % | N % | M % | F % | N % | M % |
| Bathydraconidae | | | | | | | | | | | | | | | |
| <i>Gerlachea australis</i> ^a | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| <i>Gymnodraco acuticeps</i> ^b | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| <i>Parachaenichthys charcoti</i> ^a | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Channichthyidae | | | | | | | | | | | | | | | |
| <i>Chaenichthys rhinoceratus</i> ^a | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| <i>Chaenocephalus aceratus</i> ^a | 1.6 | 0.3 | 3.9 | 20.2 | 21.4 | 61.2 | 14.1 | 9.0 | 13.4 | – | – | – | – | – | – |

Table 3 continued

| | 1999/2000 | | | 2000/2001 | | | 2001/2002 | | | 2001/2003 | | | 2001/2004 | | |
|---|-----------|------|------|-----------|------|------|-----------|------|------|-----------|------|------|-----------|------|------|
| | F % | N % | M % | F % | N % | M % | F % | N % | M % | F % | N % | M % | F % | N % | M % |
| <i>Chaenodraco wilsoni</i> ^b | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Champsocephalus gunnari</i> ^a | — | — | — | — | — | — | 0.5 | 0.3 | 0.3 | — | — | — | — | — | — |
| <i>Chionodraco rastroripinosus</i> ^a | — | — | — | 6.0 | 8.6 | 14.5 | 6.5 | 4.6 | 5.0 | 5.0 | 6.4 | 28.2 | 3.8 | 40.0 | 24.4 |
| <i>Cryodraco antarcticus</i> ^b | 1.6 | 0.6 | 3.1 | — | — | — | — | — | — | — | — | — | 3.8 | 6.7 | 8.3 |
| <i>Pseudochaenichthys georgianus</i> ^a | — | — | — | 2.0 | 1.4 | 1.0 | — | — | — | — | — | — | — | — | — |
| Nototheniidae | | | | | | | | | | | | | | | |
| <i>Gobionotothen gibberifrons</i> ^c | — | — | — | 12.0 | 15.7 | 14.9 | 30.8 | 48.9 | 77.0 | 1.7 | 2.1 | 4.6 | 6.3 | 37.8 | 66.4 |
| <i>Notothenia corticeps</i> ^c | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Nototheniops larseni</i> ^a | 4.8 | 1.5 | 2.0 | 8.0 | 10.7 | 3.6 | 6.5 | 4.9 | 0.9 | — | — | — | — | — | — |
| <i>Nototheniops nudifrons</i> ^c | — | — | — | 6.0 | 7.9 | 1.5 | 0.5 | 0.3 | 0.1 | — | — | — | 1.3 | 2.2 | 0.1 |
| <i>Pagothenia bernacchi</i> ^c | — | — | — | — | — | — | — | — | — | — | — | — | 1.3 | 2.2 | 0.4 |
| <i>Pleuragramma antarcticum</i> ^a | 1.6 | 0.3 | 0.7 | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Trematomus newnesi</i> ^c | — | — | — | — | — | — | 0.5 | 0.3 | 0.1 | — | — | — | — | — | — |
| Harpagiferidae | | | | | | | | | | | | | | | |
| <i>Harpagifer antarcticus</i> ^c | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Myctophidae | | | | | | | | | | | | | | | |
| <i>Electrona carlsbergi</i> ^b | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Electrona antarctica</i> ^a | 15.9 | 10.6 | 1.6 | 12.0 | 15.7 | 0.5 | 4.9 | 4.6 | 0.1 | 1.7 | 8.5 | 0.9 | 3.8 | 6.7 | 0.1 |
| <i>Gymnoscopelus braueri</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Gymnoscopelus nicholsi</i> ^a | 36.5 | 82.6 | 88.8 | 14.0 | 10.7 | 2.9 | 7.0 | 22.8 | 3.2 | 5.0 | 83.0 | 66.3 | 1.3 | 2.2 | 0.3 |
| <i>Gymnoscopelus opisthopterus</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Kreftichthys anderssoni</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Lampanychthus achirus</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Protomyctophum choriodon</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Protomyctophum normani</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Protomyctophum tenisoni</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Paralepididae | | | | | | | | | | | | | | | |
| <i>Notolepis coatsi</i> ^a | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Unidentified | 11.1 | 4.1 | — | 6.0 | 7.9 | — | 7.0 | 4.3 | — | — | — | — | 1.3 | 2.2 | — |

Percentage frequencies of occurrence (F %), number (N %) and mass (M %)

^a Equations taken from Hecht (1987)

^b Equations taken from Williams and McEldowney (1990)

^c Equations taken from Casaux et al. (1998a)

for pelagic fish and penguins, the contributions to the diet of the remaining main prey were inversely correlated among them. This pattern might reflect that seals foraged opportunistically on the resources available each season and that the abundance of resources strongly fluctuated among seasons. Lynnes et al. (2004) observed that Adélie (*Pygoscelis adeliae*) and Chinstrap (*P. antarctica*) penguins at the SOI relatively low breeding outputs (also for Chinstrap penguins during the 1997/1998 summer season) and success with low numbers of adults returning to breed during the 1999/2000 summer season. The reduced availability of penguins was reflected in fur seal diets and is in

line with the seals' opportunistic foraging behavior proposed above.

Most of the studies on Antarctic fur seal diets report that pelagic fish species are the most important fish prey (Green et al. 1991; Klages and Bester 1998; Daneri and Carlini 1999; Kirkman et al. 2000; Guinet et al. 2001; among others). At the SOI pelagic fish dominated from 1997 to 1999 and in 2002, while demersal fish species dominated in years (1995, 2000 and 2001) when fish made up the most important component of fur seal diets. The composition of samples suggested that seals foraged predominantly on pelagic or on demersal-benthic resources, probably

Fig. 2 Seasonal changes in the contribution (in terms of biomass) of *Gobionotothen gibberifrons* to the diet of Antarctic fur seals at Laurie Island, South Orkney Islands, and size of the specimens represented in the samples

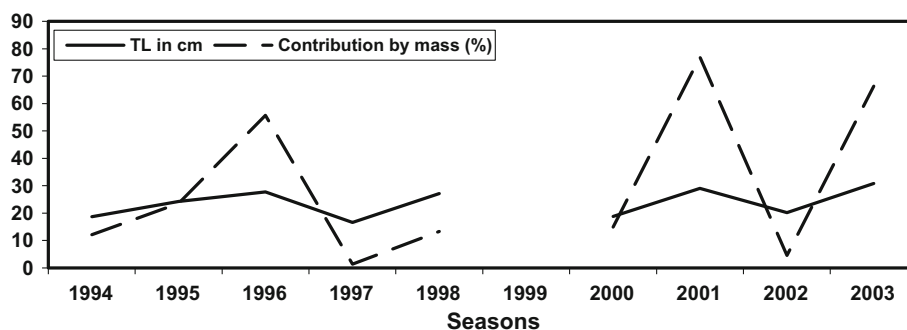
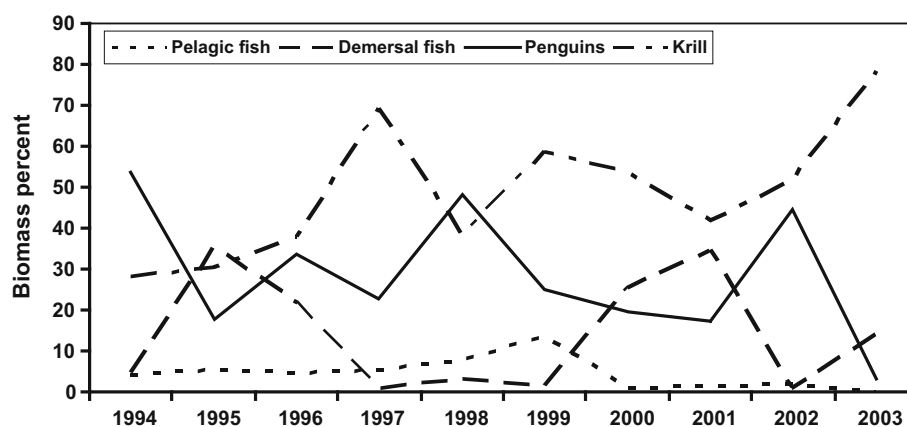


Fig. 3 Seasonal changes in the contribution to the diet by mass of the main preys of the Antarctic fur seal at Laurie Island, South Orkney Islands



according to their availability. Although demersal-benthic resources might present a fairly constant abundance in waters around the SOI, it is probable that when pelagic preys are present and abundant in the foraging area seals forage intensively on them rather than on more predictable resources such as demersal-benthic nototheniids and channichthyids, probably due to a relatively higher energy return. Likewise, Plötz et al. (1991) observed at the Weddell Sea that in years with high pelagic fish biomass *Pleuragramma antarcticum* constituted the bulk of the diet of Weddell seals, whereas in years of low biomass this species was absent in the diet and was replaced by benthopelagic fish species which showed a constant biomass throughout their studies. Among demersal-benthic fish, *G. gibberifrons*, followed by *C. aceratus* and *C. rastrispinosus*, was the species that most contributed to the diet of seals at the SOI. The contribution of *G. gibberifrons* to the diet fluctuates in parallel with the size of the specimens ingested (Fig. 2), and this might be reflecting the pass of strong year classes through the system as well as larger prey size preferences by seals.

As observed at Kerguelen Island (Duhamel 1990) and at the SSI (Barrera-Oro and Marschoff 1991), it is probable that the commercial fisheries carried out in the past negatively affected the offshore reproductive stocks of *G. gibberifrons* at the SOI, which might have resulted in a

diminution of their inshore stocks. After the closure of the fisheries, the continuous and/or incipient recovery of the inshore stocks of this species is being observed at those archipelagos (Duhamel 1990; Barrera-Oro et al. 2000). Information on the diet of the South Georgia shag *Phalacrocorax georgianus* supports the suggestion that the fisheries negatively affected the stocks of *G. gibberifrons* at the SOI as well as suggests the recovery of this fish in inshore waters of this archipelago (Casaux and Ramón 2002). Daneri and Coria (1993) observed that during the 1987/1988 summer season, when the bulk of the catches were already fished and the fisheries were considered not remunerative (see Kock 1992, for review), myctophids were largely the main fish prey of Antarctic fur seals at the SOI and that *G. gibberifrons* was almost absent from the samples. Based on that information, they concluded that there was no competition for fish between fur seals and fisheries. In the present study, *G. gibberifrons* significantly contributed to the diet of Antarctic fur seals at the SOI, apparently mainly in years of scarce pelagic prey availability, which contradicts the speculations of Daneri and Coria (1993) and suggests that the fisheries negatively impacted the seals. Besides, the comparison of our information with that provided by Daneri and Coria (1993) seems to support the suggestions by Casaux and Ramón (2002) regarding the negative impact of the fisheries on the

stocks of *G. gibberifrons* as well as the incipient recovery of this fish in inshore waters of the SOI.

The number of Antarctic fur seals that haul out on beaches of the SOI seems to be increasing (Carlini et al. 2006), probably due to immigration (Kightley and Caldwell 1982) from the increasing and expanding South Georgia population (Payne 1977; Boyd 1993). Despite this overall increase, Carlini et al. (2006) reported that during a long-term study total numbers of animals ashore at Laurie Island at peak haul-out varied enormously among years, with lowest numbers in 2001 (2531 animals) and a maximum in 2005 (16,610 animals). These authors tested whether such variation in seals' numbers could be related to ocean-wide events such as El Niño–Southern Oscillation (ENSO) which has a profound effect on weather and oceanic conditions, thus probably determining the number of animals observed. However, Carlini et al. (2006) did not find a clear connection between the number of seals at peak haul-out and ENSO, and El Niño (1997/1998 and 2002/2003) and La Niña (1998/1999 and 2000/2001) events involved seasons with similar numbers of seals at Laurie Island at peak haul-out. Thus, they concluded that the big inter-annual differences in numbers together with the observed variations in the peak dates support the idea that local conditions, with their potential effects on food availability in the area, could have an effect on the numbers of animals hauled out in a given year. In this sense, we tested the relationship between seal numbers and diet composition (a gross indicator of food availability). Seal abundances reported by Carlini et al. (2006) are not correlated with the overall contribution (either in number or in mass) of the main preys to the diet of seals in the corresponding seasons. If food availability certainly determines the number of seals that haul out each season, the absence of correlation between seal abundances and diet composition suggests that seals respond to regional, instead of local, or to a finer timescale conditions of food availability.

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