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L. P. Osman · R. Hucke-Gaete · C. A. Moreno
D. Torres

Feeding ecology of Antarctic fur seals at Cape Shirreff, South Shetlands, Antarctica

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Abstract This study examined the diet of Antarctic fur seals, *Arctocephalus gazella*, from an active breeding colony at Cape Shirreff (62°28′S, 60°48′W), Livingston Island, South Shetland Archipelago, Antarctica. It analysed faecal samples from five consecutive years (1997–2001) and length distribution of krill taken by trawl nets in the vicinity of Livingston Island. Antarctic krill, *Euphausia superba*, was the most frequent prey item, followed by several myctophid species (*Gymnoscopelus nicholsi*, *Electrona antarctica* and *Electrona carlsbergi*), squid and penguin remains. From 1998 to 2001, a modal progression in krill size was evident, suggesting that *A. gazella* was depending on a strong krill cohort, at least over the study period. Analysis of size distribution and size selectivity of krill preyed upon by fur seals suggests a preference for larger krill (> 34 mm), despite the broader size range of preys items available.

Introduction

Antarctic marine communities have shorter food webs relative to other marine systems (Knox 1970), an attribute that permits more detailed studies of processes that affect trophic interactions. One approach to understanding these interactions is the study of higher order predators, which elucidates both their function in the trophic chain, and factors underlying more or less diversified diets.

L. P. Osman (✉) · R. Hucke-Gaete · C. A. Moreno
Instituto de Ecología y Evolución,
Universidad Austral de Chile, Casilla 567,
Valdivia, Chile
E-mail: laylaosman@uach.cl

D. Torres
Instituto Antártico Chileno,
Luis Thayer Ojeda 814, Santiago, Chile

In the pelagic food web, the Antarctic krill (*Euphausia superba* Dana) is of central importance in the Southern Ocean since it provides a major trophic link between primary producers and higher trophic levels (Loeb et al. 1997). It forms characteristic concentrations consisting of many swarms, which are the target of krill fisheries and krill-eating predators such as whales, seals and penguins (Ichii et al. 1998). Of these predators, the Antarctic fur seal (*Arctocephalus gazella* Peters) has received considerable attention because it was subjected to a catastrophic exploitation during the nineteenth century (Bonner 1968), and it is considered to be an indicator of the state of the marine environment (Agnew 1997). The study of the trophic ecology of *A. gazella* is fundamental to assess its role as predator in the food web and provide information about potential competition for food resources with other predators and commercial fisheries. Its diet has been examined in various locations throughout its distributional range: e.g. South Georgia (Bonner 1968; Reid 1995; Reid and Arnould 1996); South Orkneys (Daneri and Coria 1992, 1993); South Shetlands Islands (Daneri 1996; Casaux et al. 1998; Daneri and Carlini 1999); Antarctic Peninsula (Casaux et al. 2003); Scotia Arc (Daneri et al. 1999); Ile de Croy (Cherel et al. 1997); and Heard (Green et al. 1989, 1991); Marion (Klages and Bester 1998); Bouvet (Kirkman et al. 2000) and Macquarie Islands (Green et al. 1991). Main findings from these studies indicate that krill and/or various fish species seem to constitute the bulk of the diet, but the relative proportions of the different prey species may vary between the sexes, geographic locations and years (Daneri and Carlini 1999).

In the Antarctic Peninsula sector, the waters lying north of the South Shetland Islands are one of the most important krill-fishing regions in the Southern Ocean (Ichii et al. 1998) and, in contrast to other areas, information on the diet of *A. gazella* has been based on non-reproductive colonies comprising mostly adult and subadult males (Daneri 1996; Casaux et al. 1998; Daneri and Carlini 1999). Here we document the diet of *A. azella* at Cape Shirreff, which with an estimated population of ca. 20,000 animals (Hucke-Gaete 1999) is the most important breeding site within the South Shetlands (Bengtson et al. 1990; Hucke-Gaete 1999). The aims of this study were to characterize the prey composition and diet selectivity of *A. gazella* and thus gain a measure of the degree of overlap between the size selectivity of fur seals and krill fisheries.

Materials and methods

Study area

Cape Shirreff (Fig. 1) is a low elevation, ice-free peninsula located towards the western end of the north coast of Livingston Island, South Shetland Islands, Antarctica, situated at 62°28′S, 60°48′W, between Barclay Bay and Hero Bay (Anonymous 1994). The Chilean government, through the Instituto Antártico Chileno, has been developing a long-term monitoring program on *A. gazella* at this area since 1991 (Torres 1995). The main objectives of this program are the study of its reproductive performance in relation to availability of prey resources, environmental variability and human-induced impacts, such as fisheries and marine debris.

Scat collection and diet analysis

The diet of *A. gazella* was studied through the analysis of faecal samples (n = 69, 73, 21, 33, 38) collected opportunistically from November to February of austral summer seasons 1996/1997 to 2000/2001 (hereafter referred to as the year in which summer seasons ended; e.g. 1996/1997 = 1997).

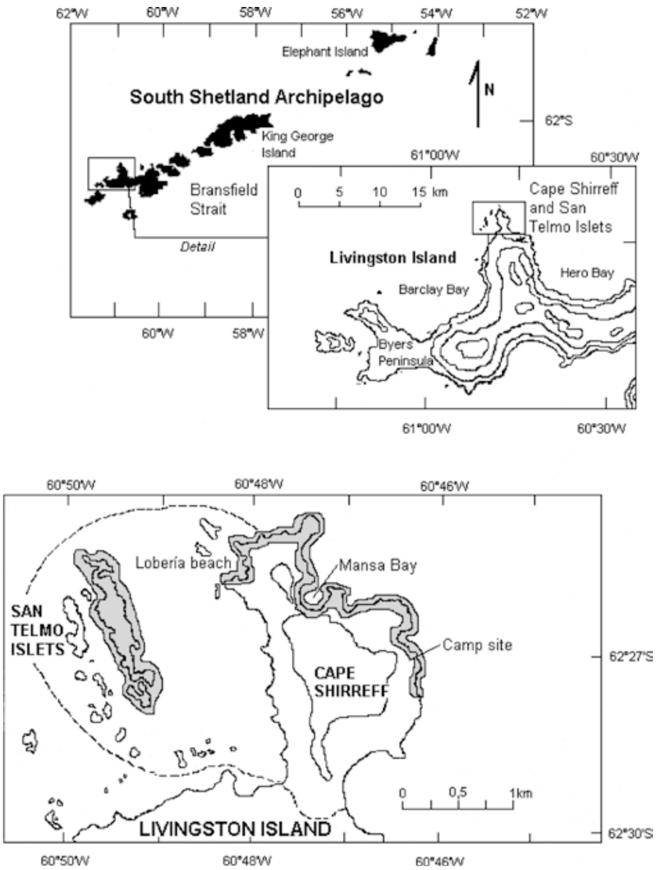

Fig. 1 Map of Cape Shirreff (62°28′S; 60°48′W), Livingston Island, South Shetland Islands, Antarctica. *Shaded areas* show the distribution of furseal colonies

Scat collection was concentrated in areas used predominantly by lactating females and those occupied by subadult males and juveniles. Care was taken to collect only whole fresh scats; these were preserved in 70% ethanol and returned to the laboratory for further analysis. Faecal samples were passed through consecutive sieves of 2 mm, 1 mm and 0.5 mm mesh size under fresh running water. All hard prey remains such as krill carapaces, fish otoliths and cephalopod mandibles were removed for identification and measurement. Frequency of occurrence of the main prey items was calculated as the number of scats containing a prey taxon (e.g. krill, fish, squid or penguin) divided by the total number of scats containing identifiable prey remains, and expressed as percent frequency of occurrence (%F). Frequency of items was ascertained but only the identification and measurements of krill and fish otoliths are considered here. Composition of fish remains were expressed as number of otoliths, percentage of the total number (N%), frequency of occurrence and percent frequency of occurrence (%F).

From each scat containing krill, random samples of 30 carapaces with no signs of erosion were measured (mm) for removed carapace length (RCL) and width (RCW). Carapaces smaller than 13 RCL were classified as coming from juveniles (sensu Staniland 2002), and total krill lengths (AT) were estimated using the formula given by Staniland (2002) in which AT = 2.52 + 3.31 RCL. Following Reid and Measures (1998), a discriminant function (D = −1.04−0.146 RCL + 0.256 RCW) was applied to the caparace lengths and widths to distinguish between the sexes for those carapaces larger than 13 RCL. Males were classified as those individuals with a negative discriminant function score and females as those with a positive score. Total krill length was then calculated using separate regression equations for males (AT = 13.9 + 2.29RCL) and females (AT = 15.3 + 2.09RCL) (Reid and Measures 1998). Mean total length (TL) of krill preyed upon by *A. gazella* each year was constrasted against a von Bertalanffy growth model for Antarctic krill provided by Siegel (1987) and described below:

$$L_t = L_\infty\left[1 - \exp\left(-k(t - t_0) + \frac{ck \bullet sen[2\pi(t - t_s)]}{2\pi}\right)\right]$$

where L_t is the krill length at time t and L_∞ is the maximum size of krill. Equation constants are t_s = −0.0272; t_0 = 0.1418; c = 0.9598; L_∞ = 61 mm and k = 0.4728 (Siegel 1987).

Prey size selectivity was examined by comparing the sizes of krill contained in scats with krill length frequency data coming from annual net trawl samples obtained in the waters lying in the vicinity of Livingston Island (kindly provided by Dr. Valerie Loeb from the US-AMLR Program). Both data sets were grouped into 2 mm classes and the total number and percentage of individuals in each class was obtained. A logistic selection pattern was fitted to each cumulative frequency distribution by least square regression using 100 iterations.

When possible, fish otoliths were identified to species level using keys provided by Hecht (1987), Williams and McEldowney (1990) and Reid (1996). Otoliths showing little or no signs of erosion were measured to estimate the standard length (SL). Standard lengths of the myctophids *Gymnoscopelus nicholsi* (Gilbert), *Electrona antarctica* (Gunther) and *Electrona carlsbergi* (Tåning) were estimated from otolith size using regression formulae of Williams and McEldowney (1990) and Reid (1996). As for krill, fish size selectivity was assessed by calculating the cumulative frequency distribution of the predominant fish found in the diet (in 10 mm classes) and fitting a logistic selection pattern using least squares.

Results

Krill was the most commonly encountered prey item, with a yearly percent frequency of occurrence between

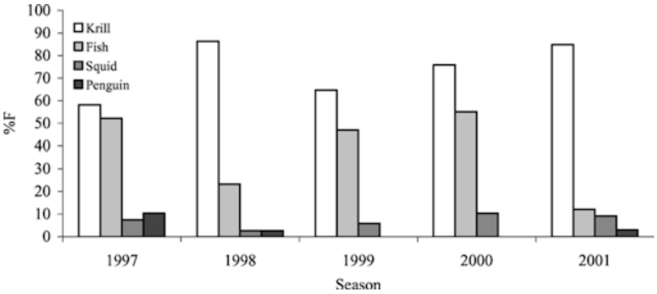

Fig. 2 Percent frequency of occurrence (*%F*) of the different food items recovered from *A. gazella* scat samples at Cape Shirreff during five consecutive seasons

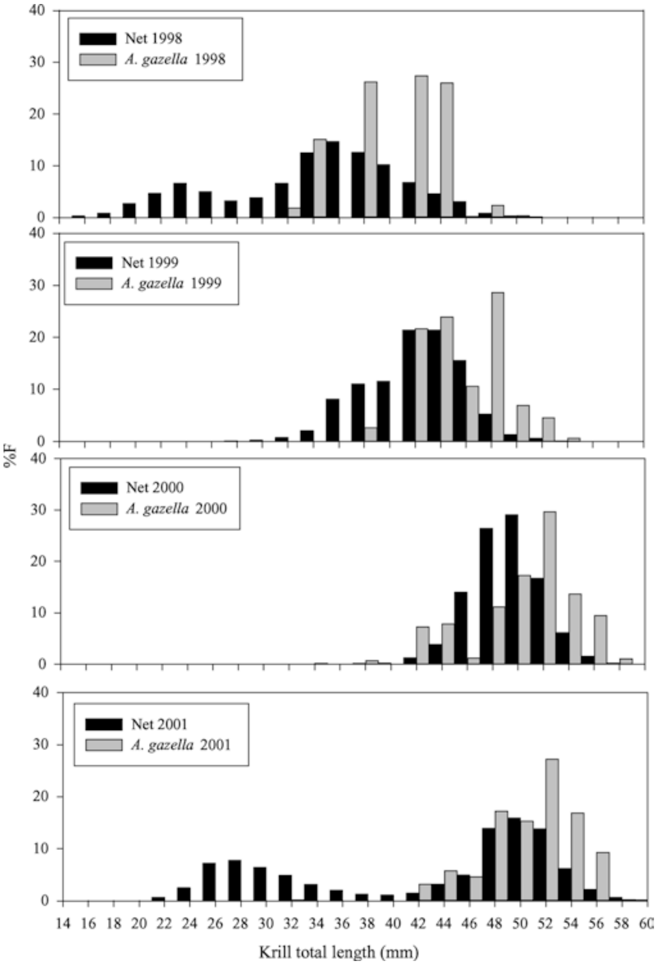

Fig. 3 Krill (*Euphausia superba*) length-frequency distributions represented in Antarctic furseal diets (1998–2001) (*grey bars*) and scientific trawl nets (*black bars*) (1998–2001)

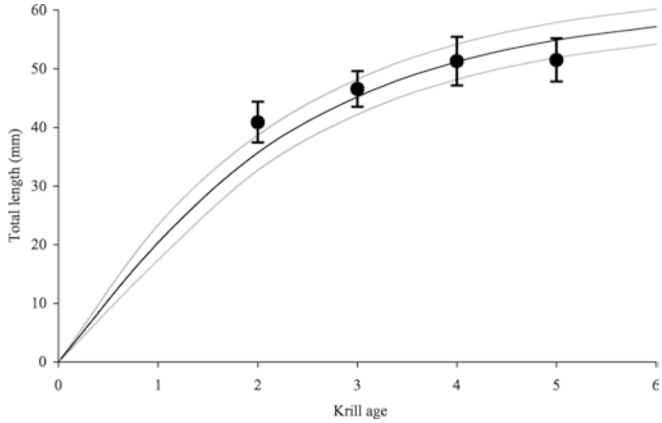

Fig. 4 Krill (*Euphausia superba*) theoretical growth curve (*black line*) (Siegel 1987), with standard deviation (SD) for the model (*grey lines*) and the means and SD of the sizes of krill eaten by Antarctic fur seals (*filled circles*) at Cape Shirreff

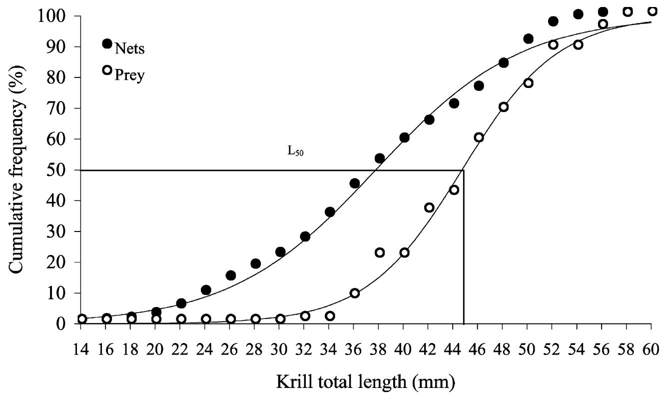

Fig. 5 Cumulative percent curves of krill sizes sampled by nets (*filled circles*) and preyed by Antarctic fur seals (*unfilled circles*). L_{50} indicates 50%

58% and 86% of scats containing identifiable remains ($n=67$, 73, 17, 29, 33). Fish occurred between 12% and 55%, squid between 2% and 10% and penguins between 0% and 10% (Fig. 2). A significant between-year difference was found in the occurrence of krill, fish, squid and penguin ($X^2_{12}=29.9$, $P<0.005$).

A total of 1680, 300, 630 and 840 krill carapaces were measured for each year from 1998 to 2001. Mean sizes (TL), respectively, were 40.9 mm ± 0.2 (95% CI), 46.6 mm ± 0.3 (95% CI), 51.3 mm ± 0.3 (95% CI) and 51.5 mm ± 0.2 (95% CI), showing a modal progression across the study period (Fig. 3). The means of back-calculated krill lengths compared to the Antarctic Peninsula krill-growth model of Siegel (1987) (Fig. 4) are within the expected variation for the model. The modal progression found in krill eaten by *A. gazella* is also clearly represented in net samples across the study period and reflects lengths found in the environment (i.e. prey; Fig. 3). The length-frequency distributions of net-sampled krill ranged from ca. 15 mm to 60 mm TL with 50% selectivity (L_{50}) = 37 mm TL (Fig. 5). In contrast, krill preyed by *A. gazella* < 34 mm TL were not represented and the L_{50} was 45 mm TL (Fig. 5). The proportions of juvenile, male and female krill in the scats were significantly different across the study period ($X^2_6=2381$, $P<0.001$), with an increasing proportion of females and a reduction in juvenile stages from 1998 to 2001 (Fig. 6).

A total of 3743 otoliths representing 13 fish species were recovered from the faecal samples. *Gymnoscopelus*

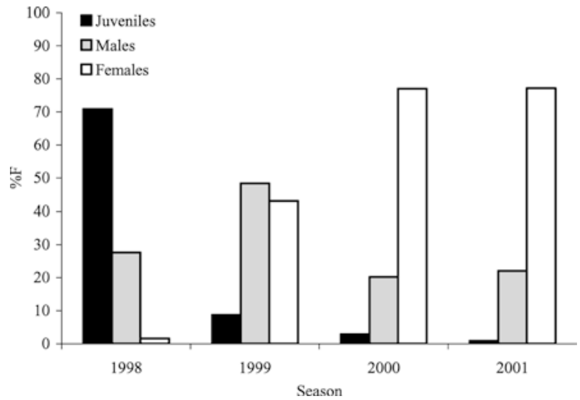

Fig. 6 Proportion of juvenile, male and female krill from *A. gazella* scat samples at Cape Shirreff from 1998 to 2001

nicholsi, *Electrona antarctica* and *Electrona carlsbergi* constituted the main species (Table 1), both in numbers of otoliths recovered and percent frequency of occurrence, across the study period (Table 1). Otoliths of *G. nicholsi* and *E. antarctica* were present all years; however, *E. carlsbergi* were found only in 1997, 1998 and 1999. When present, *E. carlsbergi* constituted one of the primary fish prey items. Since *G. nicholsi*, *E. antarctica* and *E. carlsbergi* were the most frequent fish prey, only these were considered in terms of their contribution in mass, resulting in *G. nicholsi* as the main contributor (Table 2). Estimated length-frequency distributions of these three species (Fig. 7) indicate similar selection size for *E. antarctica* and *E. carlsbergi*, with L_{50} reaching 58 mm SL and 56 mm SL, respectively. The selection value for *G. nicholsi* was larger with an L_{50} of 116 mm SL.

Discussion

Main prey items

During the five breeding seasons included in this study at Cape Shirreff, krill composed the main prey item in

Table 1 Species composition obtained from fish remains recovered from scats of Antarctic fur seals at Cape Shirreff, expressed as percent frequency of occurrence (*F%*) and percent of the total number of otoliths recovered (*N%*)

	1997		1998		1999		2000		2001	
	F%	*N%*	*F%*	*N%*	*F%*	*N%*	*F%*	*N%*	*F%*	*N%*
F. Myctophidae										
Electrona antarctica	36.4	24.8	41.7	2.3	75.0	11.4	75.0	36.3	50.0	1.2
Gymnoscopelus nicholsi	81.8	38.0	58.3	4.0	87.5	8.2	81.3	49.3	100.0	86.3
G. bolini	3.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
G. braueri	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.2	0.0	0.0
G. fraseri	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.1	0.0	0.0
Electrona carlsbergi	6.1	1.9	50.0	75.2	37.5	45.5	0.0	0.0	0.0	0.0
Krefftichthys anderssoni	6.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Protomyctophum bolini	3.0	0.1	0.0	0.0	0.0	0.0	6.3	0.1	0.0	0.0
P. choriodon	0.0	0.0	8.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Lampanyctus achirus	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.2	0.0	0.0
Gymnoscopelus sp.	18.2	8.2	8.3	0.5	0.0	0.0	37.5	4.3	50.0	12.1
Electrona sp.	0.0	0.0	16.7	0.3	12.5	23.6	0.0	0.0	0.0	0.0
Myctophidae spp.	57.6	20.7	50.0	12.5	50.0	9.0	31.3	4.2	25.0	0.4
F.Notothenidae										
Lepidonotothen larseni	3.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pleuragrama antarcticum	3.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Notothenidae spp.	0.0	0.0	0.0	0.0	12.5	0.1	12.5	0.2	0.0	0.0
F. Channichthyidae										
Champsocephalus gunnari	3.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Channichthuidae spp.	0.0	0.0	8.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0
F. Scorpelarchidae										
Scorpelarchidae spp.	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.4	0.0	0.0
Undetermined	27.3	5.7	33.3	4.4	37.5	2.1	31.3	4.6	0.0	0.0

Table 2 Fish prey mass mean (g) and percent frequency of mass (*M%*) of the main prey items obtained from scat samples of *A. gazella* collected at Cape Shirreff

	1997		1998		1999		2000		2001	
	Mean	*M%*	Mean	*M%*	Mean	*M%*	Mean	*M%*	Mean	*M%*
Electrona antarctica	3.87	12.08	5.49	16.49	5.35	15.15	4.73	16.58	3.99	14.23
Electrona carlsbergi	4.36	13.60	4.48	13.44	4.12	11.67	0.00	0.00	0.00	0.00
Gymnoscopelus nicholsi	23.84	74.33	23.33	70.07	25.86	73.18	23.80	83.42	24.07	85.77

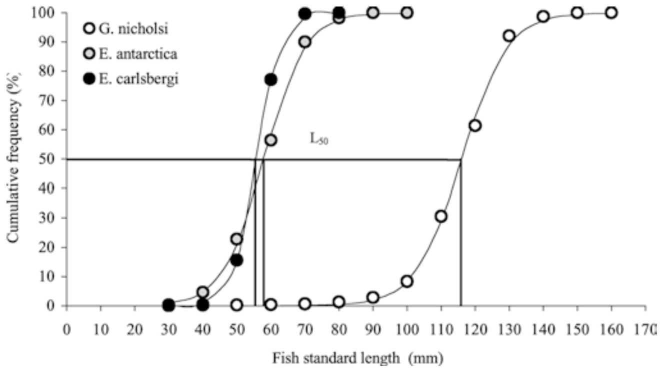

Fig. 7 Selectivity curves of fish size preyed by *A. gazella*. L_{50} shows where 50% is selected

terms of percent frequency of occurrence. Of the four fish families consumed by *A. gazella*, myctophids were the most important, with *G. nicholsi*, *E. antarctica* and *E. carlsbergi* the primary prey species. The very low occurrence of squid and penguin remains (feathers) indicated that these are not fundamental prey of *A. gazella* at Cape Shirreff.

Prey composition found in this study is similar to that reported for other islands of the South Shetland archipelago (Daneri 1996; Casaux et al. 1998; Daneri and Carlini 1999). *E. carlsbergi* was one of the main prey species found in this study; however it was not represented in the diet from 2000 to 2001. This occurrence could be related to a sampling artifact due to the small number of samples obtained during those years or to changes in availability of this species in the South Shetlands, since *E. carlsbergi* has been found in the diet of *A. gazella* at Nelson Island (Casaux et al. 1998) but not at King George Island (Daneri 1996; Daneri and Carlini 1999).

Prey dynamics and size selectivity

Krill size distributions showed a sequential modal progression across the study period (Fig. 3). From 1998 to 2001, the progression in size of preyed and net-sampled krill is evident (Fig. 3), suggesting that *A. gazella* was depending on a single large krill cohort that was recruited in 1995 (Loeb et al. 1997; Siegel et al. 1998), assuming a life-span of approximately 6 years (Siegel 1987). This is supported by applying the growth model of *E. superba* proposed by Siegel (1987) to preyed krill size (Fig. 4). Length-frequency distribution of preyed and net-sampled krill in the vicinity of Livingston Island generally overlapped on mid-sizes. However, krill represented in the diet of *A. gazella* tended towards larger sizes (Fig. 3). This difference suggests that *A. gazella* selectively preys upon larger krill despite a wider size range available. This is further supported by observations made during 1998 and 2001 when two krill size modes were available in the environment (both large and small individuals) but only larger krill (>34 mm TL) were represented in the scats (Fig. 3). It is important to note that the net-sampled krill was obtained from a wider area than those preyed upon by *A. gazella* in preferred foraging grounds, but both demonstrate the same modal progression, confirming that trawls and predators were taking krill from the same population. In this regard, Siegel (1988, 2000) describes how different developmental stages of krill have a characteristic spatial separation. Juveniles inhabit coastal waters of the Antarctic Peninsula shelf, Bransfield Strait and a narrow band extending across the northern shelves of the South Shetland Islands associated with a countercurrent flowing from east to west in nearshore waters. In contrast, adult spawning stages primarily occur over the continental slope and in oceanic regions. Although the juvenile stages are closer to the Cape Shirreff breeding colonies, and in spite of being readily available, they are not preyed upon. Selection of larger krill sizes suggests offshore, possibly extensive, feeding trips by the fur seals and could be related to the fact that larger mature krill have a higher energy content than smaller sizes, especially so if they include gravid females, which have a higher energy content than males (Clarke 1980). In the Antarctic Peninsula area, Siegel and Loeb (1994) reported that female krill (L_{50}) reach maturity at 34.6 and 35.9 mm TL and that males (L_{50}) reach maturity at 43.4 and 43.7 mm TL. Given that the minimum threshold krill size found in this study was 34 mm TL and that 50% (L_{50}) of the preyed krill were >45 mm TL (Fig. 5), *A. gazella* was selectively preying upon larger mature individuals. In relation to this, the proportion of juvenile, male and female krill found in the scats showed different proportions across the study period ($X^2_6=2381$, $P<0.001$), with an increasing amount of females from 1999 to 2001 (Fig. 6).

Among the three dominant myctophid species, sexual maturity is attained at 160–180 mm for *G. nicholsi*, ca. 83 mm for *E. carlsbergi* and 74 mm for *E. antarctica* (Hulley 1990). Estimated sizes of these fishes in scat samples suggest that *A. gazella* preys upon immature stages of *G. nicholsi* and *E. carlsbergi* and both immature and mature *E. antarctica*. The size range and fish diversity found in the present study have also been described for *A. gazella* on other islands of the South Shetlands (Daneri 1996; Casaux et al. 1998; Daneri and Carlini 1999), and because studies in other areas (e.g. South Georgia and Heard Island) have identified different and larger fish prey species (Green et al. 1989; Reid 1995; Reid and Arnould 1996), it is likely that fur seals are feeding on locally available fish.

Our results indicate that the population of *A. gazella* at Cape Shirreff depends mostly on krill and myctophid fish. The size of the krill preyed indicates a selective size-dependent feeding behaviour, which is biased towards larger components of the krill population, and suggests a strong relation to an energetic benefit. In relation to this, the way in which a predator captures its prey depends on morphological and physiological adaptations, which should balance the time required for searching and catching prey in order to fulfill its energetic demands. In this sense *Euphausia superba*, throughout much of its life, occurs within 100 m from the surface. They aggregate in discrete schools, variable in size and shape, with individuals grouped by size and maturity stage (Hamner and Hamner 2000). Although fur seals can dive >100 m to feed, they probably only efficiently exploit krill in the upper 30 m and at intervals of a relatively few minutes (Boyd 1996). These diving bouts should allow them to catch an adequate quantity of krill during every dive in order to supply their energetic demands. If the schools of larger krill and smaller krill have, on average, the same number of individuals, then the schools of smallest krill will be more reduced in size than those of larger sizes, given that the latter will occupy a larger volume in the water column. It is also possible that larger krill individuals are easier to find by the action of larger photophores. This could have implications for the searching and visualization of krill schools by fur seals. Besides the difficulty of finding the school because it becomes too small a target, fur seals might not be able to prey on smaller-sized krill individuals due to a buccal morphological restriction. In this way, the selective size-dependent feeding behaviour of *A. gazella* could be linked to an energetic benefit and influenced by the searching and visualization of schools and/or to a possible morphological impediment. Our results suggest that the availability of prey and the effects of prey size and energy content could affect the feeding behaviour of *A. gazella*, and that these factors might condition a more or less diversified diet.

Implications for fisheries management and effects of environmental variability

Antarctic krill is considered a keystone species in the Southern Ocean because of the link it provides between primary productivity and a diverse array of predators (Loeb et al. 1997). It has been suggested that krill reproduction and survival are significantly affected by the extent and duration of ice cover (Loeb et al. 1997), and that there may have been an overall decrease in krill biomass, at least in the South Atlantic Sector, over the last decade (Siegel and Loeb 1995), due to long-term changes in the physical environment in the Antarctic Peninsula region (King 1994; Murphy et al. 1995). Changes in krill availability have been shown to have adverse effects on krill-dependent predators at South Georgia (Croxall et al. 1988, 1999; Reid and Croxall 2001). Since the most frequent prey item was krill in the diet of *A. gazella* at Cape Shirreff, it is expected that the population should be sensible of changes in krill availability. Moreover, considering its size-dependent feeding behaviour, the population should also be sensible of a predominance of small-sized krill.

The waters north of the South Shetlands correspond to one of the most important krill-fishing regions in the Antarctic (Ichii et al. 1998). Here, the krill stock shows a changing distribution pattern as summer progresses (Siegel 1988). These changes are reflected in Japanese fishing operations, which tend to concentrate over the slope and inshore waters during mid-summer (January-February) (Ichii et al. 1998), overlapping with the foraging areas of *A. gazella* at Cape Shirreff (Goebel et al. 2001). If the *A. gazella* population breeding at Cape Shirreff depends strongly on the abundance of larger krill, a strong potential competitor (such as *Homo sapiens*) could have detrimental effects in years of low krill availability since fishing fleets and fur seals are exploiting krill in the same spectrum sizes, in the same area and at the same time.

This highlights the importance of continuing the long-term fur-seal monitoring programme at Cape Shirreff in order to investigate the biological dynamics of Antarctic marine ecosystems, in relation to physical phenomena and the ecological impacts and processes that influence and determine the population dynamics of *A. gazella*.

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