

Diet of grey-headed albatrosses at the Diego Ramírez Islands, Chile: ecological implications

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Abstract: The diet of grey-headed albatrosses at Diego Ramírez was analysed and compared to that of the sympatric black-browed albatross. Diet composition was inferred from an analysis of prey hard parts present in 103 chick regurgitates obtained during breeding seasons 2000, 2001 and 2002. The squid *Martialia hyadesi* predominated in the diet samples in 2001 and 2002 (89% and 81% of reconstituted mass), but was absent from the 2000 samples. Reconstituted mean mass per sample in 2000 was significantly lower than in 2001 and 2002. Chick growth rate during 2000 was also the lowest recorded. This suggests that *M. hyadesi* plays an important role in the breeding performance of grey-headed albatrosses at Diego Ramírez. Low presence of *M. hyadesi* in grey-headed albatrosses' diet at South Georgia in 2000, a year with significant low breeding success, suggests ocean-wide processes affecting the availability of this prey to both populations simultaneously. Overlap in diet composition, and inferred feeding areas, between the sympatric albatross species at Diego Ramírez was minimal. Grey-headed albatrosses fed mainly on species associated with the Antarctic Polar Front, whereas black-browed albatrosses consumed benthopelagic species frequently caught in fishing operations in southern Chile.

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Introduction

Grey-headed albatrosses (*Thalassarche chrysostoma* [Foster, 1785]) forage over vast areas of ocean even during breeding seasons, when time away from colonies and distance travelled are constrained by the need to feed their young regularly. For example, at Campbell Island (52°33'S, 169°09'E) and Marion Island (46°54'S, 37°45'E), grey-headed albatrosses foraged more than 1000 km from their colonies during breeding (Waugh *et al.* 1999, Nel *et al.* 2000). This capacity for long oceanic flight allows this albatross species to have access to a range of marine habitats, including oceanic frontal zones (such as the Antarctic Polar Frontal Zone) and waters associated with seamounts, continental shelves and slopes surrounding them. In all colonies studied, grey-headed albatrosses exploit both 'natural' food sources and food made available by commercial fisheries (e.g. Rodhouse *et al.* 1996, Waugh *et al.* 1999, Nel *et al.* 2000, Cherel *et al.* 2002).

The Diego Ramírez Islands (56°31'S, 68°44'W) are one of eight known breeding sites for grey-headed albatrosses in the world and constitutes the second largest breeding population of the species (Gales 1998). It is the southernmost breeding site for the species, situated in the Drake Passage, 60 nautical miles (n.m.) south-west of the Cape Horn (Chile) and 430 n.m. north-west from the Antarctic Peninsula, in close proximity to the Antarctic

Polar Front (Fig. 1). The particular location of the Diego Ramírez Islands offers grey-headed albatrosses the potential to exploit cephalopods and fish in sub-Antarctic and Antarctic waters (Waugh *et al.* 1999, Nel *et al.* 2001, Cherel

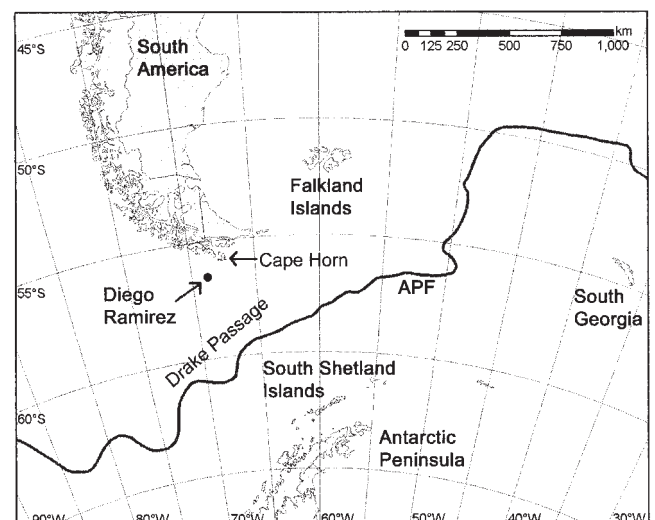


Fig. 1. Location of Diego Ramírez Islands (56°31'S, 68°44'W), showing their proximity to the South American continent, the Antarctic Peninsula and the approximate location of the Antarctic Polar Front (APF).

Table 1. Diet composition by frequency of occurrence (FO), number (N) and mass (M, reconstituted mass) of grey-headed albatrosses during January–February at Gonzalo Island, Diego Ramirez. Values are presented in percentage and between parenthesis are the number of samples with that specific prey (f(n)), number of individuals (n) or grams (g).

Species	Year 2000			Year 2001			Year 2002		
	%FO (f(n))	%N (n)	%M (g)	%FO (f(n))	%N (n)	%M (g)	%FO (f(n))	%N (n)	%M (g)
Fish	5.6 (1)	0.2 (1)	-	9.5 (4)	1.3 (15)	0.2 (79)	55.8 (24)	42.1 (206)	5.2 (1914)
Family Bathylagidae									
<i>Bathylagus</i> sp. Günther, 1878	-	-	-	-	-	-	7.0 (3)	0.6 (3)	0.5 (195)
Family Myctophidae									
<i>Electrona antarctica</i> Günther, 1878	-	-	-	4.8 (2)	0.8 (9)	0.1 (45)	39.5 (17)	29.4 (144)	2.8 (1022)
<i>Electrona carlsbergi</i> Taning, 1932	-	-	-	2.4 (1)	0.1 (1)	0.0 (9)	2.3 (1)	0.2 (1)	0.0 (9)
<i>Gymnoscopelus fraseri</i> Paxton, 1979	-	-	-	2.4 (1)	0.1 (1)	0.1 (25)	4.7 (2)	0.8 (4)	0.2 (77)
<i>Gymnoscopelus hintonoides</i> Hulley, 1981	-	-	-	-	-	-	11.6 (5)	2.0 (10)	0.3 (113)
<i>Gymnoscopelus nicholsi</i> Gilbert, 1911	-	-	-	-	-	-	16.3 (7)	2.5 (12)	1.3 (482)
<i>Gymnoscopelus</i> sp.	5.6 (1)	0.2 (1)	-	2.4 (1)	0.1 (1)	-	20.9 (9)	2.0 (10)	-
<i>Krefflichthys andersoni</i> Lönnberg, 1905	-	-	-	-	-	-	7.0 (3)	1.8 (9)	0.0 (15)
Myctophidae indet.	-	-	-	4.8 (2)	0.2 (2)	-	7.0 (3)	0.6 (3)	-
Family Macrouridae									
Macrouridae sp.	-	-	-	2.4 (1)	0.1 (1)	-	2.3 (1)	0.2 (1)	-
Family Melanonidae									
<i>Melanonus gracilis</i> Günther, 1878	-	-	-	-	-	-	11.6 (5)	1.0 (5)	-
Unidentified fish	-	-	-	-	-	-	9.3 (4)	0.8 (4)	-
Cephalopod	22.2 (4)	0.9 (6)	32.4 (956)	81.0 (34)	16.2 (184)	94.5 (31920)	65.1 (28)	27.4 (134)	91.8 (33999)
Family Gonatidae									
<i>Gonatus antarcticus</i> Lönnberg, 1905	11.1 (2)	0.3 (2)	23.3 (688)	7.1 (3)	0.4 (4)	3.4 (1157)	2.3 (1)	0.2 (1)	0.7 (251)
Family Onychoteuthidae									
<i>Kondakovia longimana</i> Filippova, 1971	-	-	-	2.4 (1)	0.1 (1)	0.6 (212)	2.3 (1)	0.4 (2)	7.7 (2865)
Family Batoteuthidae									
<i>Batoteuthis skolops</i> Young & Rosser, 1968	5.6 (1)	0.3 (2)	2.6 (78)	7.1 (3)	0.4 (5)	0.7 (241)	-	-	-
Family Histoteuthidae									
<i>Histoteuthis</i> sp. B	11.1 (2)	0.3 (2)	6.4 (190)	2.4 (1)	0.1 (1)	0.2 (58)	9.3 (4)	0.8 (4)	0.9 (326)
Family Neoteuthidae									
<i>Alluroteuthis antarcticus</i> Odhner, 1923	-	-	-	-	-	-	2.3 (1)	0.2 (1)	1.2 (440)
Family Omastrephidae									
<i>Maritulia hyadesi</i> Rochebrune & Mabile, 1889	-	-	-	81.0 (34)	14.9 (170)	88.8 (29971)	62.8 (27)	25.2 (123)	80.6 (29827)
Family Mastigoteuthidae									
<i>Mastigoteuthis psychrophila</i> (Nesis, 1977)	-	-	-	-	-	-	2.3 (1)	0.2 (1)	0.1 (21)
Family Cranchiidae									
<i>Galiteuthis glacialis</i> Chun, 1906	-	-	-	7.1 (3)	0.3 (3)	0.8 (282)	2.3 (1)	0.2 (1)	0.3 (103)
<i>Taonius</i> sp. (cf pavo)	-	-	-	-	-	-	2.3 (1)	0.2 (1)	0.4 (166)

Species	Year 2000			Year 2001			Year 2002		
	%FO (f(n))	%N (n)	%M (g)	%FO (f(m))	%N (n)	%M (g)	%FO (f(m))	%N (n)	%M (g)
Crustacean	100 (18)	98.9 (646)	40.7 (1202)	78.6 (33)	82.5 (939)	4.3 (1452)	90.7 (39)	30.5 (149)	2.6 (957)
Amphipoda									
Gammaridea sp.	38.9 (7)	1.4 (9)	8.9 (263)	14.3 (6)	0.6 (7)	0.6 (204)	34.9 (15)	3.1 (15)	1.2 (438)
Hyperiidae									
<i>Themisto gaudichaudii</i> Guerin, 1825	61.1 (11)	20.8 (136)	0.5 (14)	4.8 (2)	1.8 (21)	0.0 (2)	18.6 (8)	7.8 (38)	0.0 (4)
Isopoda									
<i>Anuropus antarcticus</i> Hale, 1952	5.6 (1)	0.2 (1)	0.1 (4)	2.4 (1)	0.1 (1)	0.0 (4)	2.3 (1)	0.2 (1)	0.0 (4)
Valvifera sp.	-	-	-	-	-	-	2.3 (1)	0.2 (1)	-
Isopoda sp.	5.6 (1)	0.2 (1)	-	-	-	-	-	-	-
Decapoda									
Acantheplhyridae									
<i>Acantheplhyra pelagica</i> Risso, 1816	5.6 (1)	0.2 (1)	0.4 (12)	-	-	-	-	-	-
<i>Acantheplhyra</i> sp.	-	-	-	-	-	-	4.7 (2)	0.4 (2)	0.1 (24)
Paguridae									
<i>Pagurus</i> sp.	-	-	-	-	-	-	2.3 (1)	0.2 (1)	-
Pasiphaeidae									
<i>Pasiphaea longispina</i> Rathbun, 1902	61.1 (11)	6.3 (41)	8.1 (238)	26.2 (11)	1.8 (20)	0.3 (116)	30.2 (13)	7.2 (35)	0.5 (203)
Pasiphaeidae sp.	16.7 (3)	0.6 (4)	0.8 (23)	14.3 (6)	1.0 (11)	0.2 (64)	14.0 (6)	1.8 (9)	0.1 (52)
Decapoda sp. 1	5.6 (1)	0.2 (1)	-	-	-	-	-	-	-
Decapoda sp.	-	-	-	7.1 (3)	0.3 (3)	-	-	-	-
Euphausiacea									
<i>Euphausia superba</i> Dana, 1852	27.8 (5)	53.3 (348)	11.8 (348)	9.5 (4)	70.3 (800)	2.4 (800)	2.3 (1)	0.2 (1)	0.0 (1)
Mysidacea									
Gnathophausiidae sp. 1	16.7 (3)	0.8 (5)	2.1 (63)	9.5 (4)	0.4 (4)	0.1 (50)	11.6 (5)	1.0 (5)	0.2 (63)
Gnathophausiidae sp. 2	22.2 (4)	0.8 (5)	2.1 (63)	14.3 (6)	0.7 (8)	0.3 (101)	4.7 (2)	0.4 (2)	0.1 (25)
Gnathophausiidae sp. 3	-	-	-	2.4 (1)	0.1 (1)	0.0 (13)	-	-	-
Gnathophausiidae sp.	16.7 (3)	0.6 (4)	1.7 (50)	4.8 (2)	0.2 (2)	0.1 (25)	18.6 (8)	1.6 (8)	0.3 (101)
Mysidacea sp.	16.7 (3)	0.5 (3)	1.3 (38)	2.4 (1)	0.1 (1)	0.0 (13)	2.3 (1)	0.2 (1)	0.0 (13)
Unidentified crustacean	44.4 (8)	13.3 (87)	2.9 (87)	21.4 (9)	5.3 (60)	0.2 (60)	30.2 (13)	6.1 (30)	0.1 (30)
Other	11.1 (2)	-	26.9 (794)	4.8 (2)	-	0.9 (314)	14.0 (6)	-	0.4 (154)
Penguin	11.1 (2)	-	26.9 (794)	4.8 (2)	-	0.9 (314)	7.0 (3)	-	0.2 (75)
Unidentified bones	-	-	-	-	-	-	7.0 (3)	-	0.2 (79)
Total	18	653	2953	42	1138	33765	43	489	37024

et al. 2002, Xavier *et al.* 2003a), as well neritic fish over the continental shelf off South America (see Cherel *et al.* 1999). However, the diet of Diego Ramírez grey-headed albatrosses had not been assessed prior to this study. The sympatric black-browed albatross (*T. melanophrys* [Temminck, 1839]) population from Diego Ramírez have a high degree of dependence on local fisheries as a food source (Arata & Xavier 2003), which in turn impacts negatively on the adult survival (Arata & Moreno 2002). As the Chilean Patagonian toothfish fishery operates in the continental slope surrounding the Diego Ramírez Islands (Moreno *et al.* 2003), some degree of interaction of grey-headed albatrosses with this fishery can also be expected, as it was described for the South Georgia population (Ashford *et al.* 1995).

Here we provide the first description of the diet of the grey-headed albatross chicks at the Diego Ramírez Islands. We use this information to estimate feeding habitat preferences during breeding, niche partitioning with the sympatric black-browed albatross population at Diego Ramírez, and to explain interannual differences on chick growth rate. Finally, we discuss some preliminary hypotheses on the factors affecting the availability of main prey of grey-headed albatrosses, and consequently their breeding performance, during chick-rearing.

Materials and methods

Study site and logistics

The Diego Ramírez archipelago comprises three main islands: Norte Island and surrounding islets (24 ha), Bartolomé Island (93 ha, 190 m height) and Gonzalo Island (38 ha, 140 m height) (Schlatter & Riveros 1997). The islands are inhabited by black-browed and grey-headed albatrosses breeding in mud flat and tussock grass habitats. The Chilean navy operates a lighthouse and look-out station at Gonzalo Island, which they resupply three times a year. Navy visits to the island provided the opportunity to conduct the current research but limited the time available to November–February of each year.

Diet analysis

A total of 103 food samples from grey-headed albatross chicks were collected at Gonzalo Island during January and February of 2000 ($n = 18$), 2001 ($n = 42$) and 2002 ($n = 43$). These were taken in two sampling events, one at the beginning of the post-brooding stage, end of January, and the other 2–3 weeks later, during February. Samples were obtained from chicks immediately after they had been fed by a parent, by inverting the chick over a plastic bag and gently squeezing its stomach and massaging its throat. This procedure induced the chick to vomit into the bag. Chicks were made to vomit only once during the season. Stomach emptiness of each sampled chick was verified by palpation

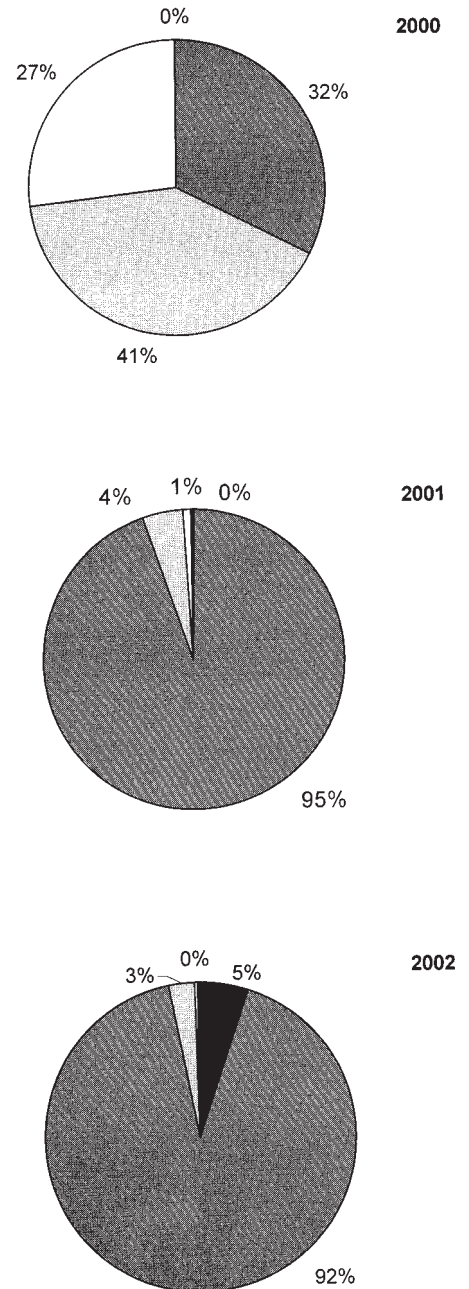


Fig. 2. Contribution of each prey item to the total diet by reconstituted mass (fish = black, cephalopod = dark grey, crustacean = light grey, carrion = white).

of its abdominal wall.

Samples were weighed whole (total mass), drained through a 1 mm mesh sieve and weighed again (solid mass) using an electronic balance (± 1 g). Solid fractions were then preserved in 95% ethanol in individual bags and sent to the laboratory.

Fish prey were identified and quantified from the otoliths found in the samples using the keys of Hecht (1987), Williams & McEldowney (1990), Smale *et al.* (1995) and Reid (1996). Otolith length and width was measured to

± 0.01 mm using a reticule ocular in a binocular microscope, if not disabled by erosion. Fish length and mass were estimated from the otolith dimensions using the formulas in Williams & McEldowney (1990) and Reid (1996), after being corrected for erosion as described by Reid & Arnould (1996). Length and mass equations for *Gymnoscopelus hintonoides* were estimated from raw data presented in Williams & McEldowney (1990) and they are: $SL = 19.152e^{0.655OW}$ ($r^2 = 0.76$), $Mass = 0.0533e^{2.179OW}$ ($r^2 = 0.84$), $n = 6$, fish range = 33–137 mm, where SL equals standard fish length (mm) and OW equals otolith width (mm).

The number of fish present in each sample was estimated from the number of otoliths pairs (left/right) of similar sizes and unpaired otoliths. Total mass composition of each fish species was estimated from the otolith numbers and the mean reconstituted individual prey masses estimated from measurable otoliths.

The cephalopod beaks were identified according to Clarke (1986), Rodhouse *et al.* (1992) and a beak reference collection held at the British Antarctic Survey, UK. The lower rostral length (LRL) of the cephalopod beaks was measured to ± 0.01 mm with vernier callipers. Allometric equations predicting mantle length and mass from LRL were taken from Clarke (1986) and Rodhouse *et al.* (1990) and used to estimate total mass composition for each cephalopod species.

Crustaceans were identified using the keys of Retamal (1981), Kirkwood (1982, 1983), Barnard (1991), Murano (1999) and Vinogradov (1999). The number of individuals present was estimated using eye pairs or head numbers. The mass of crustacean species was determined using wet mass estimations from samples where crustaceans were only lightly digested and only one crustacean species was present; for a few species it was not possible to estimate individual mass (see Table I). To account for mass loss due to digestion, a further correction factor was applied at the end of the study: arbitrary factors of 1.2 and 1.5 were applied depending upon whether digestion was considered to be light or medium, respectively. For *Themisto gaudichaudii* an arbitrary wet mass of 0.1 g per individual was used.

Diet composition was assessed using frequency of

occurrence, numerical abundance and percentage by mass (reconstituted mass from hard part remains) following Duffy & Jackson (1986) to enable comparison with other dietary studies and to allow for biases peculiar to each method of analysis. The number and mass frequency of each prey type was estimated in relation to the number and mass of all prey found during the same year. For cephalopods, mass contribution was estimated only from beaks considered to be fresh (i.e. with buccal muscles still attached to it). This distinction was drawn because of the long persistence of cephalopods beaks in seabird stomachs (Furness *et al.* 1984).

Chick's growth rate

Chick's growth rate was estimated each season to assess potential effects of interannual changes of diet mass and/or composition on breeding performance. Thirty chicks were weighed twice per week from hatching to end of February and their growth rate was estimated during their linear growth phase, i.e. between 15 and 60 days old (Tickell & Pinder 1975). Interannual comparison of the linear models was made using dummy variables (Zar 1999, p. 436).

Diet comparison with black-browed albatrosses at Diego Ramírez

Diet overlap between grey-headed and black-browed albatrosses (Arata & Xavier 2003) at Diego Ramírez was assessed using the dietary overlap index described by Croxall *et al.* (1997). Two indexes were estimated, the first using only mass contribution of each main prey item (fish, cephalopod, crustacean, other) and the second, using all prey items found in the diet of both albatrosses species.

Results

Diet composition

We obtained 103 samples of chick regurgitates during early chick rearing (January–February) of the grey-headed albatross during 2000, 2001 and 2002. The mean mass of samples was similar between 2001 and 2002 but it was significantly lower during 2000 respect 2002 ($t = -2.044$,

Table II. Solid and liquid constituents of the diet of grey-headed albatrosses at Gonzalo Island, Diego Ramírez

Parameter	Year 2000*		Year 2001		Year 2002	
	Mean (1 SD)	Range	Mean (1 SD)	Range	Mean (1 SD)	Range
Total mass by sample (g)	1044 (296)*	530–1600	1121 (358)	333–1960	1248 (468)	607–2152
Solid mass (g)	432 (200)*	175–670	432 (207)	62–998	364 (225)	49–1044
Liquid mass (g)**	656 (161)*	440–910	689 (246)	200–1360	884 (314)	356–1509
% solid	38.4 (14.0)*	22.6–56.0	37.9 (12.7)	12.1–74.8	28.1 (11.3)	6.1–55.3
% liquid	61.6 (14.0)*	44.0–77.4	62.1 (12.7)	25.2–87.9	71.9 (11.3)	44.7–93.9
N	6*		42		43	

*only includes samples taken in February by problems in the filtering process during January 2000

**estimated from difference between total and solid mass

$P = 0.046$) (Table II). The liquid component of the samples was only partially filtered during January 2000 due to saturation of the sieve used, caused by solidification of the oil fraction of the sample; this problem was subsequently rectified. However, the solid mass could not be estimated for those samples. To compare sample solid mass between years, we used only the mean solid mass for February each year. These were 432 g, 503 g and 502 g in 2000, 2001 and 2002 respectively, differences were not significant ($F_{(2,44)} = 0.299, P = 0.743$).

During 2000 crustaceans were the main prey taken (41% by reconstituted mass) while cephalopods were of secondary importance, contributing 32% to the total mass.

On the contrary, cephalopods dominated the diet in 2001 and 2002, with 95% and 92% of total estimated mass, respectively (Fig. 2).

Fresh cephalopods were represented by nine taxa belonging to eight squid families. Cephalopods were present in 22%, 81% and 65% of all samples in 2000, 2001 and 2002, respectively, and accounted for 32%, 95% and 92% of the total reconstituted mass in the same years (Table I). In 2000, when the squid contribution was low, the main species taken was *Gonatus antarcticus*, with 23% by mass, followed by *Histioteuthis* sp. B (6% by mass). During 2001 and 2002, *Martialia hyadesi* was the predominant species, accounting for 89% and 81% of the total mass and

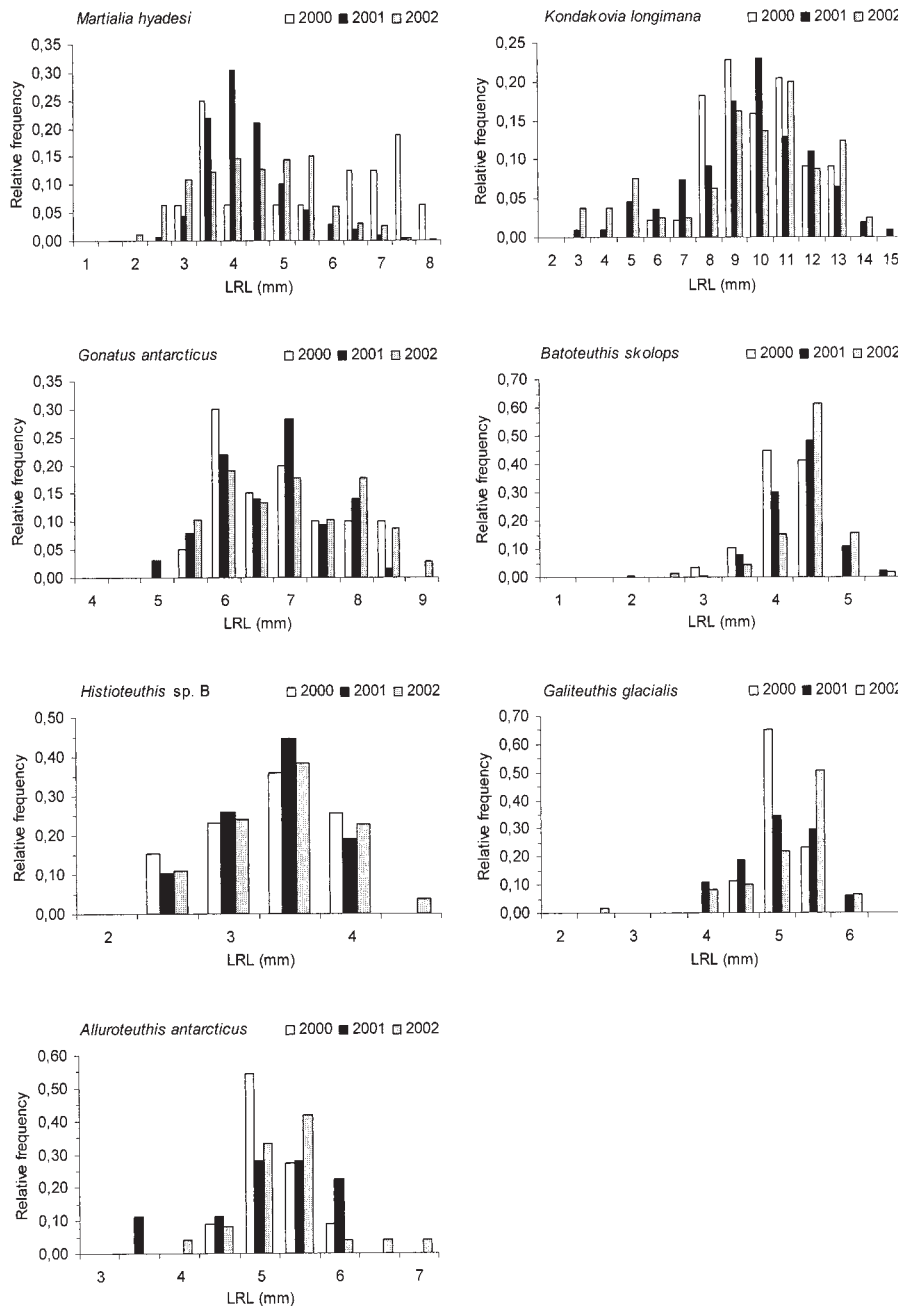


Fig. 3. Lower Rostral Length (LRL) accumulative frequency of cephalopod beaks found in grey-headed albatross stomachs.

being present in 81% and 63% of the samples of both years, respectively. *Kondakovia longimana* was the only other species of importance by mass (8%) in 2002.

Considering all the beaks found in the samples, cephalopods were represented by 18 squid taxa and one Octopodidae (Appendix I). *Martialia hyadesi* was the dominant species by number (75% and 42%) and reconstituted mass (74% and 40%) during 2001 and 2002. By contrast, this species represented only 8.0% by number and 9.7% by mass during 2000. Other species important by number were *G. antarcticus*, *Batoteuthis skolops*, *Histioteuthis* sp. B and *Galiteuthis glacialis* (in 2000); *K. longimana* was significant by mass in all years. Length frequency distribution of the beaks' lower rostral length (LRL), of the more abundant species in the diet, shows a similar frequency distribution between years (Fig. 3). Only *M. hyadesi* presented a different pattern, with a bimodal distribution in the beak LRL frequency during 2000 that corresponds to mantle length sizes of 193 ± 11 mm and 297 ± 13 mm. During 2001 and 2002, the mantle length frequency of this species was unimodal, with means of 212 ± 24 mm and 217 ± 35 mm, respectively.

Thirteen crustacean taxa were found in the diet of grey-headed albatrosses during the three years sampled. They were present in 100%, 79% and 91% of all samples, and accounted for 99%, 83% and 31% of the total number of individuals recorded, during years 2000, 2001 and 2002, respectively (Table I). Crustaceans were the main prey item during 2000 with 41% of the total mass estimated. During 2001 and 2002, they contributed less than 5% to the total reconstituted mass despite their high contribution by number, given their low individual weight. The most important crustacean was *Euphausia superba*, which represented 11.8%, 2.4% and 0.0% of the total mass during 2000, 2001 and 2002, respectively. In 2000, Gammarideans (8.9%), Pasiphaeidae (8.9%) and Gnathophausiidae species (5.9%) were the only other crustacean important by mass (Table I).

Fish were represented by nine taxa, six of them being myctophids. Fish prey accounted by less than 6% by mass in all years. During 2002, when fish had the higher representation, myctophids were present in 56% of samples, accounted for 42% of individual prey and 5% by mass of the reconstituted diet (Table I). The species more represented were *Electrona antarctica* and *Gymnoscopelus* sp. (including *G. nicholsi*). The size of the myctophids consumed were in the following ranges: *E. antarctica*, 61–99 mm; *G. nicholsi*, 140–157 mm; *G. hintonoides*, 79–90 and 97–110 mm; *Krefflichthys andersoni*, 47–58 mm.

Other items found in the samples were penguin remains and unidentified bones (Table I, 'others'). During 2000, penguin remains represented 27% of the total reconstituted mass, mainly accounted by a penguin leg (eroded) found in one sample. In 2001 only penguin feathers (314 g) were

found, while a single piece of penguin skin (75 g) was found in 2002. Unidentified bones and flesh were also recorded during 2002.

Another item found in the diet samples was plastic litter with two bottle tops in both 2000 and 2002.

Overall, mean reconstituted mass per sample during the two sampling times each year was lower in 2000, with 84 g and 191 g sample⁻¹ in January and February, respectively. In both 2001 and 2002, mean reconstituted masses per sample were >500 g in January and >1000 g in February (Fig. 4).

Chick's growth rate

Chick's growth rates estimated were lower in 2000 and

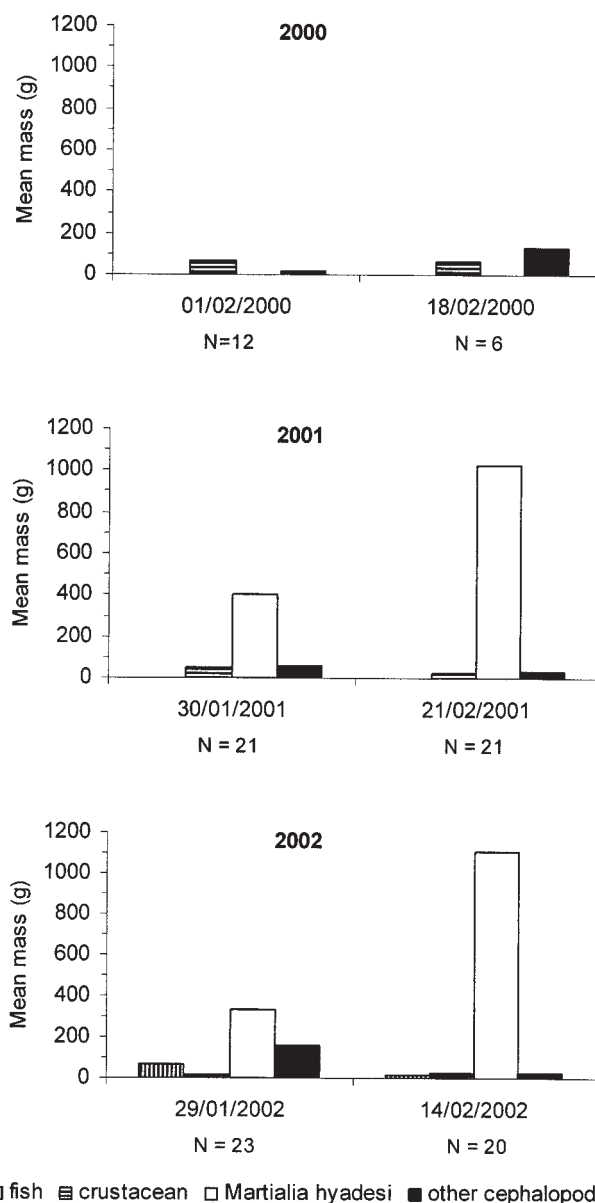


Fig. 4. Reconstituted mean mass per sample of the main prey items in the grey-headed albatross diet for each sampling date.

Table III. Adjusted model for the linear growth phase (15–60 days old) of grey-headed albatross chicks during 2000, 2001 and 2002 seasons at Gonzalo Island, Diego Ramírez.

Season	Growth rate (g·d ⁻¹) mean ± SD	P	Intercept (g) mean ± SD	P	Chicks sampled*	r ²
2000	45.2 ± 2.9	0.0000	292.3 ± 103.8	0.0059	25	0.7284
2001	65.9 ± 2.2	0.0000	-233.6 ± 79.4	0.0035	27	0.7344
2002	77.4 ± 2.0	0.0000	-490.4 ± 80.5	0.0000	21	0.8409

*chicks alive at the moment of the last sampling event each season

higher in 2002 (Table III). Interannual differences were all significant, as it is revealed by the dummy variable estimates of the slopes (AGE*YEAR: 2000 vs 2001 = 0.0207, $P = 0.000$; 2000 vs 2002 = 0.0322, $P = 0.000$; 2001 vs 2002 = 0.0115, $P = 0.000$).

Diet comparison with black-browed albatrosses at Diego Ramírez

The dietary overlap index with black-browed albatrosses at Gonzalo Island between main prey items (fish, cephalopod, crustacean, other) was 0.079, 0.310, and 0.204 during breeding seasons 2000, 2001 and 2002, respectively. Between all prey species it was 0.004, 0.286, and 0.107, during the same seasons.

Discussion

Diet composition

Squid were the main prey of grey-headed albatrosses at the Diego Ramírez Islands during early chick rearing in 2001 and 2002, with crustacean or fish as secondary prey items. However in 2000, crustacean, squid and carrion contributed similarly by reconstituted mass to the diet, whereas fish otoliths were not found. Despite the former, fish remains were found in 13 of the 18 samples taken in 2000. Mean solid mass per sample was lower in 2000 (February), although differences were not statistically significant, whereas mean reconstituted mass per sample was significantly lower in that year. It is possible, therefore, that fish were under-represented in the diet sampling analysis in 2000.

In terms of specific prey, the diet of grey-headed albatrosses was dominated by the squid *Martialia hyadesi*, a species known to live along the Antarctic Polar Front (Rodhouse *et al.* 1996). Secondary species, including myctophids (*E. antarctica* and *G. nicholsi*) and other cephalopods (mainly *G. antarcticus* and *K. longimana*), are also found at the Antarctic Polar Front (Williams & McEldowney 1990, Xavier *et al.* 1999). During 2000, when a shortage of *M. hyadesi* occurred, main prey found in samples were carrion, the squid *G. antarcticus*, krill and other crustaceans, most of them also known to inhabit

Antarctic/sub-Antarctic waters. The presence of one species of the family Macrouridae, a deep-water fish family that is a common bycatch in the Patagonian toothfish fishery (Arata, personal observation), in one sample both in 2001 and 2002 is the single evidence that suggests some interaction with fishing activities. These results indicate that grey-headed albatrosses feeding young chicks at Diego Ramírez Islands exploit mostly Antarctic/sub-Antarctic waters during January–February, with minimal association with commercial fishing operations over the continental shelf of southern Chile.

Dependence on Martialia hyadesi

Martialia hyadesi plays a key role during the breeding period of grey-headed albatrosses at Diego Ramírez. The absence of this prey species in 2000 caused the mean reconstituted mass per sample to be significantly lower during this season (Fig. 4). This lower food amount given to the chicks would in turn explain the significant low chick growth rate estimated during 2000. Similar results were recorded for the grey-headed albatross population at South Georgia (Xavier *et al.* 2003a), where a shortage of *M. hyadesi* was also found in 2000, causing breeding success to decline. This is the first record in literature that the breeding output of two different albatross populations has been affected by the availability of a single prey species simultaneously. Giving that dietary differences between these populations suggest different foraging areas (see below), this finding implies a large scale process affecting the availability of *M. hyadesi* in the south-west Atlantic Ocean and Drake Passage regions.

There is interest in the development of a commercial fishery for this squid in the South-west Atlantic Ocean (González & Rodhouse 1998). This fishery may have serious implications for the conservation of grey-headed albatrosses, considering that about 70% of the world breeding pairs are nesting on South Georgia and Diego Ramírez Islands (Gales 1998). Therefore, it should be a priority task to understand the factors affecting the inter-annual variability in *M. hyadesi* abundance, and applying this knowledge to the management of any future fishery.

Martialia hyadesi availability to albatrosses

The processes affecting the distribution and abundance of *M. hyadesi* are poorly understood. Considering the life history traits of squids, with high fecundity, high mortality during early life stages and lower mortality as adults, abundance of *M. hyadesi* could be determined mainly by processes affecting eggs and newly hatched individuals, as has been described for the squid *Illex argentinus* (Waluda *et al.* 1999).

Size of the squids found in the stomach samples indicates that grey-headed albatrosses consume juveniles hatched

during the previous spawning season (autumn–winter, González *et al.* 1997). As *M. hyadesi* is semelparous, probably spawning at two years old (González & Rodhouse 1998), abundance of *M. hyadesi* juveniles could depend on the direct effect of environmental variables during the previous spawning event or past environmental anomalies that affected the spawning stock, two years previously. Note, however, that the absence of *M. hyadesi* from grey-headed albatross diet samples does not mean the total failure of the *M. hyadesi* cohort. As flying predators, albatrosses can only dive to a few metres beneath the surface and thus, when squid abundance is under a given threshold, albatrosses could not be able to detect them.

We tested the effect of environmental anomalies on the *M. hyadesi* recruitment using information of *M. hyadesi* presence in grey-headed albatross diet samples taken at South Georgia and compared it with the occurrence of ENSO events and sea surface temperature anomalies, such as the Antarctic Circumpolar Wave (ACW) (see Appendix II). Both environmental factors have been previously associated with *M. hyadesi* abundance (Xavier *et al.* 2003a, González *et al.* 1997). The contingency analysis showed no correlation between *M. hyadesi* availability to albatrosses and the ACW anomaly (ACW at South Georgia: $P = 0.476$; ACW at Drake Passage: $P = 0.238$). By contrast, ENSO events are weakly correlated with the occurrence of *M. hyadesi* in the grey-headed albatross diet at South Georgia ($P = 0.091$). However, this was mostly due to *M. hyadesi* being available in years that did not follow ENSO events ($n = 8$). Two of the four cases when the availability of *M. hyadesi* to albatrosses was low, matched with the occurrence of ENSO events. The other two cases of low presence of *M. hyadesi* in grey-headed albatross diet samples happened two years after the last ENSO event and could be explained by a reduced spawning stock hatched under ENSO conditions. This circumstantial evidence suggests that ENSO events could affect the recruitment of *M. hyadesi* and, subsequently, the breeding performance of grey-headed albatrosses.

Comparison with other diet studies

The importance of *M. hyadesi* in the diet of Diego Ramírez grey-headed albatrosses is similar to that at other breeding islands: South Georgia (56°30'S, 38°40'W; Xavier *et al.* 2003a), Marion (Nel *et al.* 2000) and Campbell Island (Waugh 1998), perhaps reflecting the exploitation of the same habitat (Antarctic Polar Front) throughout their breeding range. Although at the other breeding islands *M. hyadesi* is also important in grey-headed albatross diet, it represents less than 55% by mass, in comparison with the 81–89% by mass found in this study in 2001 and 2002. This difference could be explained by an interaction of the following causes: a greater relative abundance of *M. hyadesi* in Drake's Passage in comparison to other

regions, low competition for this prey in this area, and/or a greater abundance of alternative prey in other regions. *M. hyadesi* is abundant in the epipelagic ecosystem of the Antarctic Polar Front in the South-west Atlantic Ocean (Rodhouse & White 1995) and thus, it is likely to have great abundance in the Drake's Passage as well. Moreover, strong competition for *M. hyadesi* within the foraging range of grey-headed albatrosses nesting at Diego Ramírez during the breeding season, when most predators are central place foragers, seems unlikely. At South Georgia, where *M. hyadesi* is important in the diet as well but represents a lower fraction of it (Xavier *et al.* 2003a), the grey-headed albatross breeding size is five times larger than at Diego Ramírez (Gales 1998), leading to a higher intra-specific competition for this prey. Diet at South Georgia seems to be compensated with Antarctic krill, which is abundant in close proximity to the islands. This prey is further away from Diego Ramírez Islands and thus, its presence in our diet samples was low. Then, although the distribution and abundance of potential albatross' prey in the Drake Passage are poorly known, it seems that the great abundance of *M. hyadesi* and relative low abundance of alternative prey, combined with a relative lower inter and intra-specific competition for it, may explain the highest presence of *M. hyadesi* in the diet of grey-headed albatrosses found in this study.

Fish and crustacean prey had a low representation in our diet samples. Myctophid fish and Antarctic krill, main secondary prey at Diego Ramírez, are distributed in Antarctic waters, roughly over 500 km away. These species are common prey at Marion, South Georgia and Kerguelen islands, which are located in or south of the Antarctic Polar Frontal Zone (Nel *et al.* 2000, Chérel *et al.* 2002, Xavier *et al.* 2003a). Antarctic krill is also a common prey at South Georgia (Xavier *et al.* 2003a). The Diego Ramírez Islands are located north of the Antarctic Polar Front, which could explain the low contribution of these Antarctic prey. Similar result was found at Campbell Island, located in the sub-Antarctic Zone, where the fish southern blue whiting (*Micromesistius australis*) taken over the Campbell shelf is a frequent prey (Waugh *et al.* 1999). Thus, distance from breeding islands to the Antarctic Polar Front seems to determine the main dietary differences between populations. The biogeographical area where Diego Ramírez is located determine a different prey availability compared to other breeding sites and could reinforce the importance of *M. hyadesi*. The importance of other fish species living over the South American continental shelf could diminish as a consequence of strong competition with the sympatric black-browed albatross (see below).

Grey-headed albatrosses at South Georgia, the closest breeding population of this species to Diego Ramírez, also prey mostly on *M. hyadesi* during chick rearing in 'normal' years (Xavier *et al.* 2003a). Niche theory predicts mechanisms reducing intra-specific competition, with

spatial segregation of feeding areas between populations being the main mechanism for niche partitioning proposed for albatrosses (Cherel *et al.* 2002). The evidence suggests that this mechanism also operates in this case. Secondary prey items of South Georgia and Diego Ramírez grey-headed albatross populations differed. South Georgia albatrosses consume significant amounts of Antarctic krill and the lamprey *Geotria australis* (Croxall *et al.* 1997, Xavier *et al.* 2003a), whereas at Diego Ramírez Antarctic krill was poorly represented and *G. australis* was totally absent from the samples. These results support the hypothesis for niche segregation and suggest that albatrosses at both localities do not overlap in their foraging areas during the chick rearing season. During 2000, when *M. hyadesi* was almost absent in diet samples at both localities, grey-headed albatrosses at South Georgia fed mainly on Antarctic krill (61% by mass), with other prey species representing less than 10% (Xavier *et al.* 2003a). At Diego Ramírez, penguin remains (27% by mass), the squid *Gonatus antarcticus* (23% by mass) and Antarctic krill (12% by mass) were the main prey taken by grey-headed albatrosses. That year grey-headed albatrosses at South Georgia foraged near the South Shetland Islands shelf (Xavier *et al.* 2003b, using satellite tracking), an area within the foraging range of albatrosses from Diego Ramírez. This suggests that in years of low *M. hyadesi* availability, the foraging distribution of both populations may overlap, leading to potential intraspecific competition between these two populations.

Comparison with black-browed albatross diet at Diego Ramírez

The diets of grey-headed and black-browed albatrosses nesting at Diego Ramírez were highly segregated. The diet of black-browed albatrosses was dominated by hoki (66–89%), *Macruronus magellanicus*, a benthopelagic species that commonly occurs as bycatch in fisheries at Southern Chile (Arata & Xavier 2003). As fisheries in Southern Chile are concentrated over the continental shelf, black-browed albatrosses during breeding seasons must feed mainly over shelf waters. In contrast, grey-headed albatrosses fed mostly on *M. hyadesi*, which is most prevalent in Antarctic/sub-Antarctic waters. This pattern is consistent with the at-sea distribution described for these two albatross species elsewhere (Prince *et al.* 1998, Waugh *et al.* 1999, Cherel *et al.* 2000), and gives further support to the hypothesis that spatial segregation is the main mechanism of niche partitioning between these two albatross species (Cherel *et al.* 2002).

The trophic niche segregation of these two albatross species at Diego Ramírez is the highest recorded. Diet overlap reported for other colonies (considering all prey taxa and using the same index) are 0.64 and 0.67–0.98 at South Georgia (Croxall *et al.* 1997, Xavier *et al.* 2003a) and

0.84 at Kerguelen (estimated from Cherel *et al.* 2002). The difference with the values estimated in this study (< 0.29) is remarkable. This difference possibly reflects the location of the Diego Ramírez Islands near both the vast South American continental shelf and the Antarctic Polar Front, whereas other breeding islands are more oceanic, having a smaller continental shelf that leads to a higher overlapping in their foraging areas. The congregation of black-browed albatrosses along fishing boats seems to accentuate the foraging difference between both species found elsewhere. Information about at-sea distribution of both species nesting at Diego Ramírez is needed to confirm the presumed segregation in their foraging areas during the breeding season and, potential intraspecific competition with the closest population at South Georgia, particularly during years of poor availability of their main prey.

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Appendix I. The cephalopod component of the diet of the grey-headed albatross (frequency of occurrence [FO], number [N] and mass [M, reconstituted mass]) during January – February at Gonzalo Island, Diego Ramirez, derived from all beaks (including fresh and eroded ones) found in stomach samples. Values are presented in percentage and between parenthesis the number of samples with that specific prey (f(n)), number of individuals (n) or grams (g).

Species	Year 2000			Year 2001			Year 2002		
	%FO (f(n))	%N (n)	%M (g)	%FO (f(n))	%N (n)	%M (g)	%FO (f(n))	%N (n)	%M (g)
Teuthoidea									
Family Gonatidae									
<i>Gonatus antarcticus</i> Lönberg, 1905	72.2 (13)	10.05 (20)	10.1 (5992)	64.3 (27)	2.57 (64)	4.0 (18033)	73.8 (31)	7.35 (68)	11.2 (22772)
Family Onychoteuthidae									
<i>Kondakovia longimana</i> Filippova, 1971	72.2 (13)	22.11 (44)	46.4 (27466)	73.8 (31)	4.38 (109)	15.2 (69198)	71.4 (30)	8.65 (80)	28.2 (57610)
<i>Moroteuthis ingens</i> (Smith, 1881)	5.6 (1)	0.50 (1)	6.5 (3868)	-	-	-	-	-	-
<i>Moroteuthis knipovitchi</i> Filippova, 1971	11.1 (2)	1.01 (2)	4.4 (2587)	2.4 (1)	0.04 (1)	0.1 (554)	7.1 (3)	0.32 (3)	1.5 (3153)
Family Batotheutidae									
<i>Batoteuthis skolops</i> Young & Rosser, 1968	61.1 (11)	14.57 (29)	1.6 (938)	78.6 (33)	9.61 (239)	1.9 (8812)	73.8 (31)	17.08 (158)	3.1 (6276)
Family Brachioteuthidae									
<i>Brachioteuthis</i> "B"	-	-	-	-	-	-	7.1 (3)	0.32 (3)	0.0 (43)
<i>Brachioteuthis ? picta</i> Chun, 1910	-	-	-	9.5 (4)	0.16 (4)	0.0 (31)	9.5 (4)	0.54 (5)	0.0 (42)
Family Histoteuthidae									
<i>Histoteuthis</i> sp. B	77.8 (14)	19.60 (39)	4.8 (2852)	64.3 (27)	2.33 (58)	0.9 (4150)	73.8 (31)	8.97 (83)	3.1 (6409)
Family Psychroteuthidae									
<i>Psychroteuthis glacialis</i> Thiele, 1920	11.1 (2)	1.51 (3)	4.1 (2440)	9.5 (4)	0.20 (5)	0.7 (3084)	26.2 (11)	1.41 (13)	4.3 (8720)
Family Neoteuthidae									
<i>Alluroteuthis antarcticus</i> Ohdner, 1923	44.4 (8)	5.53 (11)	7.4 (4353)	31.0 (13)	0.72 (18)	1.6 (7401)	40.5 (17)	2.59 (24)	5.0 (10218)
Family Ommastrephidae									
<i>Martalia hyadesi</i> Rochebrune & Mabile, 1889	44.4 (8)	8.04 (16)	9.7 (5743)	100 (42)	75.96 (1890)	73.9 (337349)	92.9 (39)	42.49 (393)	39.6 (80796)
Family Chiroteuthidae									
<i>Chiroteuthis veranyi</i> Ferussac, 1835	16.7 (3)	1.51 (3)	0.4 (234)	19.0 (8)	0.40 (10)	0.2 (794)	21.4 (9)	1.08 (10)	0.4 (746)
Family Mastigoteuthidae									
<i>Mastigoteuthis psychrophila</i> (Nesis, 1977)	5.6 (1)	0.50 (1)	0.1 (70)	11.9 (5)	0.24 (6)	0.1 (323)	21.4 (9)	0.97 (9)	0.2 (392)
Family Cranchiidae									
<i>Mesonychoteuthis hamiltoni</i> Robson, 1925	-	-	-	2.4 (1)	0.04 (1)	0.0 (62)	4.8 (2)	0.22 (2)	0.1 (250)
<i>Galiteuthis glacialis</i> Chun, 1906	38.9 (7)	13.07 (26)	3.7 (2176)	50.0 (21)	2.57 (64)	1.2 (5357)	59.5 (25)	6.38 (59)	2.6 (5265)
<i>Taonius</i> sp. (cf pavo) Steenstrup, 1861	11.1 (2)	1.51 (3)	0.8 (468)	16.7 (7)	0.28 (7)	0.3 (1351)	16.7 (7)	0.86 (8)	0.6 (1161)
<i>Nototeuthis dimegacoryle</i> Nesis & Nikitina, 1986	-	-	-	-	-	-	11.9 (5)	0.54 (5)	0.1 (191)
Family Loliginidae									
<i>Loligo gahi</i> Orbigny, 1835	-	-	-	-	-	-	2.4 (1)	0.11 (1)	0.0 (36)
Octopoda									
Family Octopodidae									
Octopodidae indet.	-	-	-	-	-	-	2.4 (1)	0.11 (1)	-
Unknown	5.6 (1)	0.50 (1)	-	14.3 (6)	0.48 (12)	-	-	-	-
Total	18	199	59187	42	2488	456498	42	925	204080

Appendix II. *Martialia hyadesi* availability to albatrosses (as found in grey-headed albatross diet samples) was examined in relation to the occurrence of ENSO events and sea-surface temperature anomalies in the Antarctic Circumpolar Wave (ACW) in the Drake Passage (D.P.) and South Georgia (S.G.) areas. ENSO events and ACW anomalies during the second semester of each year, when squid recruits, were correlated with squid availability during the following summer (when samples were taken) because these events could affect the early stages of development of *M. hyadesi*. *M. hyadesi* presence in grey-headed albatross diet is from Prince (1980), Clarke & Prince (1981), Rodhouse *et al.* (1990), Reid *et al.* (1996), Xavier *et al.* (2003a) and this study.

ENSO occurrence and ACW anomalies were obtained from the internet: <http://acw.ucsd.edu/ACW/index_evolution.html> and <<http://ingrid.ideo.columbia.edu/SOURCES/Indices/ensomonitor.html>>. *M. hyadesi* availability and ENSO or ACW anomalies were correlated through contingency tables and the significance of correlations were assessed statistically using the Fisher's exact test. Data used in the analyses are presented below.

Year	<i>M. hyadesi</i> availability	ENSO 2nd semester on	ACW on 2nd semester at S.G.	D.P.
1975		No		
1976	High	No		
1977	High	Yes		
1981		No		
1982		Yes	warm	cold
1983		Yes	cold	normal
1984	Low	No	normal	warm
1985		No	warm	warm
1986	High	Yes	warm	cold
1991		Yes	cold	cold
1992		No	cold	cold
1993		No	warm	warm
1994	Low	No	normal	normal
1995		No	normal	cold
1996	High	No	warm	cold
1997	High	Yes	cold	warm
1998	Low	No	cold	warm
1999	High	No	warm	warm
2000	Low	No	warm	normal
2001	High	No	normal	cold
2002	High	yes		