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## Dietary evidence for spatial foraging segregation in sympatric albatrosses (*Diomedea* spp.) rearing chicks at Iles Nuageuses, Kerguelen

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**Abstract** The food of three closely related and sympatric species of mollymawks (*Diomedea* spp.), the black-browed (BBA, *D. melanophrys*), grey-headed (GHA, *D. chrysostoma*) and yellow-nosed (YNA, *D. chlororhynchos*) albatrosses, was compared at Iles Nuageuses, Kerguelen, during the chick-rearing period. BBA preyed almost equally upon cephalopods (39% by fresh mass), fish (31%) and penguins (31%), while GHA fed more on squids (52%, 16% and 28%, respectively) and YNA fed more on fish and not on penguins (13%, 84% and 0%, respectively). Crustaceans were always a minor component of the diet (< 3%). Patagonian toothfish was the main fish prey, and *Todarodes* sp. the main cephalopod prey for the community. Accumulated beaks emphasise the importance of juvenile ommastrephid squids in the diet of mollymawks, accounting for 81%, 71% and 55% of the total number of beaks in BBA, GHA and YNA samples, respectively. BBA preyed also upon a significant number of the octopod *Benthoctopus thielei* (12%) and of the cranchiid squid *Galiteuthis glacialis* (4%), while GHA fed more on *G. glacialis* (18%) and on the onychoteuthid *Kondakovia longimana* (8%). When feeding on the same prey, prey size was similar for the albatross species. Comparison of overall prey biogeography together with the presence/absence of prey species indicators of water masses indicates segregation through different foraging areas among the three mollymawks. BBA forage almost exclusively over the shelf and upper slope waters surrounding the Kerguelen Archipelago. By contrast, GHA and YNA feed mainly in oceanic waters, YNA favouring the warm subtropical waters, and GHA the cold Antarctic waters. It is thus remarkable that birds from the

same breeding grounds forage over such a wide latitudinal range, from about 35–40°S to 60–65°S, encompassing the Subtropical Zone for YNA, the Antarctic Zone for GHA and the Antarctic Polar Frontal Zone (where Kerguelen is located) for the three species.

### Introduction

Most albatross species live in the Southern Ocean where they breed on scattered islands located mainly in the subantarctic zone (Tickell 2000). Mollymawks (*Diomedea* spp.) dominate the community of southern, large procellariiforms both by their diversity and number of individuals. They are medium-sized albatrosses with wing spans of just over 2 m, all have a black and white plumage, and they share common habits and features that distinguish them from other species (Tickell 2000). Generally more than one mollymawk species inhabits a given island, with the largest diversity found in the southern Indian Ocean, at Crozet and Kerguelen archipelagos, where four and three species breed, respectively (Weimerskirch et al. 1986, 1989). The two archipelagos are the only places where the black-browed *D. melanophrys* (BBA), grey-headed *D. chrysostoma* (GHA) and yellow-nosed albatrosses *D. chlororhynchos* (YNA) occur sympatrically, thus providing a unique opportunity to investigate the ecological relationships among a set of potentially competing, large, marine apex predators (Weimerskirch et al. 1986).

At Kerguelen, GHA outnumbered BBA (7,900 versus 3,200 breeding pairs), while the population of YNA is very small (50 pairs). BBA breeds both on the mainland and north of the archipelago, where the three species breed on the remote Ile de Croy (Iles Nuageuses). Reproductive cycles of BBA, GHA and YNA overlap greatly in time (Weimerskirch et al. 1986, 1989), thus raising the question of niche partitioning in taxonomically closely related species. Evolutionary biology predicts that, if trophic resources are limited, potential

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competitors that coexist in a community should, at the very least, exhibit niche differentiation (Begon et al. 1990). This may result from dissimilar diet and differential use of the marine habitat. Accordingly, closely related and sympatric species of seabirds have been found to feed on different prey (e.g. skuas: Pietz 1987; kittiwakes: Lance and Roby 1998; diving petrels: Bocher et al. 2000), or to feed on the same items, but with different proportions (sooty albatrosses: Ridoux 1994; crested penguins: Hull 1999) and different sizes (pygoscelid penguins: Lishman 1985; prions and blue petrels: Bocher et al. 2001). Alternatively, the lack of dietary segregation is interpreted as being a consequence of a superabundance of food during the study period (e.g. murres: Barrett et al. 1997; Bryant and Jones 1999).

No previous detailed study compared the food and feeding ecology of BBA, GHA and YNA at the same site, but preliminary food analysis and visual observations at sea suggested that, at Crozet, BBA feed on fish in shelf waters, GHA on squids in cold oceanic waters, and YNA on a mixture of squid and fish in warm northern oceanic waters (Weimerskirch et al. 1986; Ridoux 1994). The main objectives of the present study were threefold: (1) to provide the first detailed description of the food of mollymawks during the chick-rearing period at Iles Nuageuses, (2) to compare the prey caught by BBA at Ile Nuageuses with that taken at the same time in an adjacent colony located on the Kerguelen mainland (Cherel et al. 2000), and (3) to use the known biogeography of the prey to test the hypothesis that differences in the foraging zones are most important in reducing interspecific trophic competition between albatrosses (Weimerskirch et al. 1986, 1988). Finally, food analysis allowed us to look at potential interactions between mollymawks and Kerguelen fisheries, since birds are attracted by longliners and trawlers targeting the Patagonian toothfish *Dissostichus eleginoides*, and are thus at risk of drowning on hooks or being killed by the netsonde cable (Cherel et al. 1996; Weimerskirch et al. 2000).

## Materials and methods

### Study site, birds and field collection of samples

The study was carried out on Ile de Croy (Iles Nuageuses) located north of the Kerguelen Archipelago (48°38'S; 68°38'E). Due to the remoteness of the island and the difficulty of landing and staying there, field work was completed during 3 days only: 5, 6 and 7 March 1994. A total of 81 dietary samples were collected from albatross chicks, including 35 BBA samples, 38 GHA samples and 8 YNA samples. Only 11 YNA chicks were found amongst numerous BBA and GHA chicks; three of them did not regurgitate, two regurgitated accumulated items only and the six remaining chicks had also fresh items in their stomachs. BBA and GHA samples generally contained both fresh and accumulated items. Some of them were taken after a returning parent had completed feeding chicks (BBA,  $n=3$ ; GHA,  $n=18$ ; YNA,  $n=0$ ), and the others were collected from chicks that, by appearance, had a full belly. Stomach contents were obtained by up-ending chicks over a plastic bucket and massaging the stomach and throat. All samples were returned deep frozen ( $-20^{\circ}\text{C}$ ) to the laboratory in France for analysis.

### Food analysis

Food analysis followed Cherel et al. (2000). Each sample was thawed, drained and accumulated cephalopod beaks subsequently sorted. Accumulated beaks (beaks without flesh attached) were analysed separately from fresh items, and they were not considered when calculating the reconstituted proportion by mass in the diet of the different prey species. Fresh remains were divided into broad prey classes (fish, cephalopods, crustaceans, penguins and others), which were weighed to calculate their proportion by fresh mass in the diet.

Identification of prey relied almost totally on the examination of otoliths and bones for fish, chitinous beaks for cephalopods and exoskeletons for crustaceans. Items were identified by comparison with material held in our own collection and by reference to the available literature, including Andersen (1984), Iwami (1985) and Williams and McEldowney (1990) for fish; Clarke (1986) for cephalopods; and Clarke and Holmes (1987), Baker et al. (1990), Vinogradov et al. (1996) and Murano (1999) for crustaceans. Length of uneroded or slightly eroded otoliths and dentary bones of fish, lower rostral length (LRL) of squid beaks, lower hood length (LHL) of octopus beaks, and eye diameter or total length (TL) of crustaceans were measured with a vernier caliper or using an ocular scale in a binocular microscope. Fish standard length (SL), cephalopod dorsal mantle length (DML), crustacean total length and prey body masses (M) were calculated using regression equations (Clarke 1986; Hecht and Cooper 1986; Adams and Klages 1987; Rodhouse and Yeatman 1990; Rodhouse et al. 1990; Williams and McEldowney 1990; Ridoux 1994; Jackson 1995; Gröger et al. 2000; authors' unpublished data). For the few species for which no relationships were available, length and M were estimated using equations for closely related species or for species with a similar morphology.

Data were statistically analysed using SYSTAT 9 for WINDOWS (Wilkinson 1999). Values are means  $\pm$  SD.

## Results

The mean total mass of dietary samples was not significantly different among albatross species (*Diomedea melanophrys*, *D. chrysostoma*, *D. chlororhynchos*), neither was the mass of the liquid fraction (Table 1). Masses of the solid fraction and of fresh items were, however, much lower in YNA samples than in BBA and particularly GHA samples. The difference can be partly explained by the fact that a greater proportion of stomach contents was collected immediately after a returning parent had completed feeding chicks for GHA than for BBA and YNA. The average fish fresh mass (45–72 g) was identical for the three albatross species, but GHA fed more on cephalopods (149 g) than BBA (78 g) and YNA (11 g), and GHA more on crustaceans (4.6 g) than YNA (2.4 g) and BBA (<0.1 g). Noticeable was the lack of penguin remains (but see below) and of other organisms in YNA samples when compared to both BBA and GHA stomach contents (Table 1).

### Black-browed albatross

Overall (i.e. all the 35 samples pooled), chick food of BBA at Iles Nuageuses in early March 1994 was almost equally dominated by cephalopods (39% by fresh mass), fish (31%) and penguins (31%), while crustaceans and other various organisms were negligible (<1%) (Table 1). Estimation of the reconstituted mass of the diet increased

**Table 1** *Diomedea melanophrys*, *D. chrysostoma*, *D. chlororhynchus*. Mass and composition of the food in stomach contents of albatross chicks at Iles Nuageuses, Kerguelen

	Black-browed albatrosses (n = 35)	Grey-headed albatrosses (n = 38)	Yellow-nosed albatrosses (n = 6)	Kruskal–Wallis statistics	P
Mass (g)	769 ± 331	835 ± 340	585 ± 309	3.14	0.208
Liquid fraction (g)	563 ± 278	546 ± 267	500 ± 323	0.30	0.861
Solid fraction (g)	206 ± 128	289 ± 164	85 ± 86	14.20	0.001
Fresh items (g)	202.0 ± 126.7	283.4 ± 163.4	84.8 ± 85.5	13.92	0.001
Fish (g)	61.9 ± 86.9	44.7 ± 111.7	71.6 ± 93.1	3.35	0.187
Cephalopods (g)	77.8 ± 102.1	148.5 ± 172.2	10.8 ± 17.1	6.00	0.050
Crustaceans (g)	0.01 ± 0.04	4.6 ± 25.1	2.4 ± 4.4	16.61	< 0.0001
Penguins (g)	61.8 ± 116.9	80.1 ± 149.7	0	2.83	0.243
Others (g)	0.5 ± 2.4	5.4 ± 31.6	0	0.35	0.841
Accumulated beaks (n)	33.9 ± 26.4	85.7 ± 76.9	10.7 ± 9.0	13.98	0.001
Parasitic nematodes (n)	3.1 ± 4.7	0.9 ± 1.4	3.8 ± 6.1	4.70	0.095
Stones (n)	2.7 ± 3.9	1.1 ± 2.4	0.3 ± 0.5	5.93	0.052
Overall composition:					
Fish (%)	30.7	15.8	84.5		
Cephalopods (%)	38.5	52.4	12.8		
Crustaceans (%)	< 0.1	1.6	2.8		
Penguins (%)	30.6	28.3	0		
Others (%)	0.2	1.9	0		

the importance of fish (48%), did not change the proportion of cephalopods (37%) and lowered the amount of penguins (15%) (Table 2). In terms of individual food samples, cephalopods prevailed by fresh mass in 37% (n = 13) of the stomachs, and fish and penguin flesh each in 31% (n = 11) of the remaining samples.

A total of 113 fresh prey items was recovered from the 35 dietary samples, including 43 cephalopods (belonging to three distinct species) and 33 fishes (eight species). Three different taxa accounted for most of the prey by number and by reconstituted mass. They were the ommastrephid squid *Todarodes* sp. (33% by reconstituted mass), the nototheniid *Dissostichus eleginoides* (32%) and unidentified penguins (15%). Other significant prey items (> 1% by number and by reconstituted mass) were the channichthyid *Channichthys rhinoceratus*, unidentified ommastrephid squids (probably *Todarodes* sp.), unidentified nototheniids and the muraenolepidid *Muraenolepis marmoratus/orangiensis* (Table 2). Crustaceans, together with bivalves and annelids, were apparently fish prey secondarily ingested by albatrosses.

#### Grey-headed albatross

Cephalopods ranked first in the diet of GHA (52% and 55% by fresh and reconstituted masses, respectively). Penguin flesh (28% and 13% by fresh and reconstituted masses) and fish (16% and 29%) were also important prey classes, while crustaceans and other organisms were minor but significant food items (2% by fresh mass) (Tables 1, 2). Cephalopods prevailed by fresh mass in 55% (n = 21) of the stomachs, penguin flesh in 24% (n = 9), fish in 16% (n = 6), and crustaceans (the Antarctic krill *Euphausia superba*) and carrion of undetermined origin each in 3% (n = 1) of the remaining samples.

A total of 731 fresh prey items were recovered from the 38 dietary samples, including 608 crustaceans (belonging to 10 distinct species), 72 cephalopods (2 species) and 39 fishes (13 species). The two most common prey were the Antarctic krill *Euphausia superba* (n = 377) and the hyperiid amphipod *Themisto gaudichaudii* (n = 194), each having been found in 34% (n = 13) of the samples. Noticeable was also the occurrence of large crustacean species, including the mysid *Neognathophausia gigas*, the gammarid *Eurythenes* sp. and the carid shrimp *Pasiphaea scotiae*, in the stomach contents (Table 2). Owing to their relatively small size, in comparison to that of cephalopods and fish, crustaceans, however, accounted for a negligible percentage by reconstituted mass of the diet, except *E. superba* (1%). GHA fed on two size classes of Antarctic krill, with modes at 35–40 mm and at 50–55 mm (Fig. 1), which correspond to large juvenile and adult individuals, respectively (Mauchline and Fisher 1969).

Two different taxa accounted for a large proportion by reconstituted mass of the diet. They were the ommastrephid squid *Todarodes* sp. (47% by reconstituted mass) and unidentified penguins (13%). Other significant prey items (> 1% by reconstituted mass) included mainly fishes (*Dissostichus eleginoides*, *Channichthys rhinoceratus*, the macrourids *Macrourus carinatus/holotrachys* and *?Coryphaenoides lecointei*, the icefish *Champscephalus gunnari* and the paralepidid *Magnisudis prionosa*) together with unidentified ommastrephids and squids (Table 2).

#### Yellow-nosed albatross

The food of YNA chicks was dominated by fish, which alone accounted for 84% of diet by fresh mass. Other significant food sources were cephalopods (13% by fresh mass) and, to a lesser extent, crustaceans (3%) (Table 1).

**Table 2** *Diomedea melanophrys*, *D. chrysostoma*. Food items found in stomach contents of black-browed ( $n = 35$ ) and grey-headed ( $n = 38$ ) albatrosses at Iles Nuageuses, Kerguelen. Numbers in *parentheses* are percentage contribution

	Black-browed albatross			Grey-headed albatross		
	Occurrence <i>n</i> (%)	Number <i>n</i> (%)	Reconstituted mass g (%)	Occurrence <i>n</i> (%)	Number <i>n</i> (%)	Reconstituted mass g (%)
<b>CARRION</b>	<b>14 (40.0)</b>	<b>14 (12.4)</b>	<b>4,302.4 (15.0)</b>	<b>12 (31.6)</b>	<b>12 (1.6)</b>	<b>4,318.0 (13.9)</b>
Aves						
Unidentified	13 (37.1)	13 (11.5)	4,288.3 (15.0)	10 (26.3)	10 (1.4)	4,111.0 (13.2)
Spheniscidae						
Unidentified carrion	1 (2.9)	1 (0.9)	14.1 (<0.1)	2 (5.3)	2 (0.3)	207.0 (0.7)
<b>OSTEICHTHYES</b>	<b>24 (68.6)</b>	<b>33 (29.2)</b>	<b>13,630.0 (47.6)</b>	<b>20 (52.6)</b>	<b>39 (5.3)</b>	<b>9,146.4 (29.4)</b>
Paralepididae						
<i>Magnisudis prionosa</i>				3 (7.9)	3 (0.4)	509.9 (1.6)
Myctophidae						
<i>Gymnoscopelus fraseri</i>				1 (2.6)	2 (0.3)	11.4 (<0.1)
<i>Metelectrona ventralis</i>				1 (2.6)	1 (0.1)	3.5 (<0.1)
Muraenolepididae						
<i>Muraenolepis marmoratus/orangiensis</i>	2 (5.7)	2 (1.8)	328.1 (1.1)	1 (2.6)	1 (0.1)	164.0 (0.5)
Moridae						
<i>Antimora rostrata</i>				1 (2.6)	1 (0.1)	284.1 (0.9)
Macrouridae						
? <i>Coryphaenoides lecointei</i>				1 (2.6)	1 (0.1)	472.2 (1.5)
<i>Macrourus carinatus/holotrachys</i>				2 (5.3)	3 (0.4)	1,416.6 (4.5)
Melamphidae						
Melamphidae sp. A				1 (2.6)	1 (0.1)	31.3 (0.1)
Congiopodidae						
<i>Zanclorhynchus spinifer</i>	3 (8.6)	3 (2.7)	239.5 (0.8)	2 (5.3)	2 (0.3)	92.5 (0.3)
Nototheniidae						
<i>Dissostichus eleginoides</i>	15 (42.9)	18 (15.9)	9,064.1 (31.6)	8 (21.1)	8 (1.1)	2,865.1 (9.2)
<i>Lepidonotothen squamifrons</i>	1 (2.9)	1 (0.9)	407.8 (1.4)			
<i>Notothenia rossii</i>	1 (2.9)	1 (0.9)	919.4 (3.2)			
<i>Paranotothenia magellanica</i>	1 (2.9)	1 (0.9)	59.9 (0.2)	1 (2.6)	1 (0.1)	59.9 (0.2)
Unidentified	2 (5.7)	2 (1.8)	782.9 (2.7)			
Channichthyidae						
<i>Champscephalus gunnari</i>	1 (2.9)	1 (0.9)	92.6 (0.3)	3 (7.9)	8 (1.1)	999.5 (3.2)
<i>Channichthys rhinoceratus</i>	4 (11.4)	4 (3.5)	1,735.7 (6.1)	4 (10.5)	5 (0.7)	2,233.8 (7.2)
Unidentified fish				2 (5.3)	2 (0.3)	2.5 (<0.1)
<b>CEPHALOPODA</b>	<b>21 (60.0)</b>	<b>43 (38.1)</b>	<b>10,725.6 (37.4)</b>	<b>29 (76.3)</b>	<b>72 (9.8)</b>	<b>17,252.7 (55.4)</b>
Ommastrephidae						
<i>Todarodes</i> sp.	18 (51.4)	37 (32.7)	9,407.9 (32.8)	24 (63.2)	61 (8.3)	14,699.7 (47.2)
<i>Martialia hyadesi</i>	1 (2.9)	1 (0.9)	261.2 (0.9)			
Unidentified	2 (5.7)	3 (2.7)	762.8 (2.7)	5 (13.2)	7 (1.0)	1,686.9 (5.4)
Onychoteuthidae						
<i>Moroteuthis ingens</i>				1 (2.6)	1 (0.1)	143.2 (0.5)
Unidentified squids	1 (2.9)	1 (0.9)	254.3 (0.9)	3 (7.9)	3 (0.4)	722.9 (2.3)
Octopodidae						
<i>Benthoctopus thielei</i>	1 (2.9)	1 (0.9)	39.5 (0.1)			
<b>BIVALVIA</b>						
<i>Gaimardia trapesina</i>	1 (2.9)	11 (9.7)	2.3 (<0.1)			
<b>CRUSTACEA</b>	<b>5 (14.3)</b>	<b>10 (8.8)</b>	<b>1.7 (&lt;0.1)</b>	<b>22 (57.9)</b>	<b>608 (83.2)</b>	<b>437.4 (1.4)</b>
Mysidaceans						
<i>Neognathophausia gigas</i>				4 (10.5)	4 (0.5)	30.0 (0.1)
Isopoda						
Isopoda sp.	1 (2.9)	1 (0.9)	0.5 (<0.1)			
Amphipoda						
<i>Themisto gaudichaudii</i>	3 (8.6)	6 (5.3)	0.4 (<0.1)	13 (34.2)	194 (26.5)	17.4 (<0.1)
<i>Cylopus magellanicus</i>				2 (5.3)	9 (1.2)	0.5 (<0.1)
<i>Vibilia antarctica</i>				1 (2.6)	1 (0.1)	<0.1 (<0.1)
<i>Hyperia gaudichaudii</i>				1 (2.6)	1 (0.1)	0.5 (<0.1)
<i>Eurythenes</i> sp.				1 (2.6)	1 (0.1)	0.5 (<0.1)

Table 2 (Contd.)

	Black-browed albatross			Grey-headed albatross		
	Occurrence <i>n</i> (%)	Number <i>n</i> (%)	Reconstituted mass g (%)	Occurrence <i>n</i> (%)	Number <i>n</i> (%)	Reconstituted mass g (%)
Unidentified Gammaridea	1 (2.9)	2 (1.8)	0.3 (<0.1)			
Euphausiacea						
<i>Euphausia superba</i>				13 (34.2)	377 (51.6)	321.2 (1.0)
Caridea						
<i>Pasiphaea scotiae</i>				6 (15.8)	10 (1.4)	52.3 (0.2)
<i>Pasiphaea</i> sp.				1 (2.6)	1 (0.1)	5.3 (<0.1)
Copepoda						
Unidentified Pennellidae/ Sphyriidae				1 (2.6)	1 (0.1)	0.7 (<0.1)
Thoracica						
<i>Lepas australis</i>	1 (2.9)	1 (0.9)	0.5 (<0.1)	1 (2.6)	9 (1.2)	9.0 (<0.1)
<b>POLYCHAETA</b>						
<i>Platynereis australis</i>	1 (2.9)	2 (1.8)	2.0 (<0.1)			
<b>TOTAL</b>		<b>113 (100.0)</b>	<b>28,664.0 (100.0)</b>		<b>731 (100.0)</b>	<b>31,154.4 (100.0)</b>

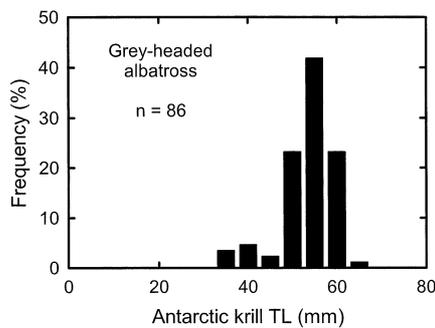


Fig. 1 *Diomedea chrysostoma*. Length-frequency distribution of Antarctic krill (*Euphausia superba*) consumed by grey-headed albatrosses at Iles Nuageuses, Kerguelen

No fresh penguin remains were found in the samples, but a few accumulated penguin feathers occurred in two of the eight stomach contents. Among the six samples containing fresh items, fish prevailed by mass in three of them, cephalopods in two, and crustaceans in the last one.

Three species of fish were identified: one specimen of the scopelarchid *Benthallbella macropinna*, four individuals of *Scomberesox saurus*, which occurred in two samples, and remains of *Dissostichus eleginoides* (including one tail), which were also found in two samples. Only two fresh cephalopods were identified: one *Todarodes* sp. and one unidentified ommastrephid. Finally, three large crustaceans were found in three different samples; they included two mysids (*Neognathophausia gigas* and one unidentified *Neognathophausia*) and one carid shrimp (*Notostomus auriculatus*; see Holthuis and Sivertsen 1967; Iwasaki and Nemoto 1987).

#### Accumulated cephalopod beaks

The mean number of accumulated cephalopod beaks per sample was much higher in GHA stomach contents than

in BBA and YNA samples ( $n=86$ , 34 and 11, respectively; Table 1). Accordingly, we identified 1,181 beaks (both lower and upper beaks, see Cherel et al. 2000) from the 35 BBA samples, 3,184 beaks from the 38 GHA samples and 67 beaks from the 8 YNA samples (Table 3). The cephalopod diet was more diverse in GHA (20 taxa) than in BBA and YNA (12 taxa each).

Accumulated beaks indicate the predominance of ommastrephid squids in the cephalopod diet of the three albatross species. Overall ommastrephids accounted for 81%, 71% and 55% of the total number of identified cephalopod beaks in BBA, GHA and YNA samples, respectively. Both BBA and GHA caught two different ommastrephid species, *Martialia hyadesi* and *Todarodes* sp. (probably *T. angolensis*, or a species closely related to *T. angolensis*; see Cherel and Weimerskirch 1995). BBA preyed also upon a significant number of the octopod *Benthoctopus thielei* (12%) and of the cranchiid squid *Galiteuthis glacialis* (4%), while GHA fed more on *G. glacialis* (18%) and on the onychoteuthid *Kondakovia longimana* (8%). Table 3 shows that some cephalopod species were found in the diet of one albatross species only, such as *B. thielei* for BBA, *Psychroteuthis glacialis*, *Alluroteuthis antarcticus* and *Mastigoteuthis psychrophila* for GHA, and some rarely encountered species (*Moroteuthis robsoni*, *Ancistrocheirus lesueurii* and *Cycloteuthis akimushkini*) for YNA.

Depending on the cephalopod species, albatrosses fed on juveniles, subadults and/or adult squids (Table 4). The three albatross species caught almost exclusively juvenile ommastrephids, adult squids being rare in the diet of BBA and GHA, and no adult beaks having been identified from YNA samples. The sizes of juvenile *Todarodes* sp. (two-sample *t*-test,  $t=1.02$ ,  $P=0.309$ ) (Fig. 2) and *Martialia hyadesi* ( $t=1.29$ ,  $P=0.210$ ) eaten by BBA and GHA were identical, as was the size of adult *Galiteuthis glacialis* ( $t=0.05$ ,  $P=0.957$ ) (Table 4). Using allometric equations, DML (and M) of juvenile

**Table 3** *Diomedea melanophrys*, *D. chrysostoma*, *D. chlororhynchos*. Comparison of the cephalopod diet of black-browed ( $n = 35$ ), grey-headed ( $n = 38$ ) and yellow-nosed ( $n = 8$ ) albatrosses at Iles Nuageuses, Kerguelen. Values are number and the percentage contribution by number (in parentheses) of accumulated lower and upper beaks

	Lower beaks			Upper beaks		
	Black-browed <i>n</i> (%)	Grey-headed <i>n</i> (%)	Yellow-nosed <i>n</i> (%)	Black-browed <i>n</i> (%)	Grey-headed <i>n</i> (%)	Yellow-nosed <i>n</i> (%)
<b>TEUTHOIDEA</b>						
Architeuthidae						
<i>Architeuthis dux</i>		3 (0.2)			2 (0.1)	1 (2.7)
Ommastrephidae						
<i>Todarodes</i> sp.	71 (13.9)	184 (13.5)		4 (0.6) <sup>a</sup>	1 (0.1) <sup>a</sup>	
<i>Martialia hyadesi</i>	11 (2.2)	21 (1.5)		0 <sup>a</sup>	1 (0.1) <sup>a</sup>	
Ommastrephidae sp.	305 (59.8) <sup>b</sup>	736 (54.2) <sup>b</sup>	18 (60.0) <sup>b</sup>	566 (84.4) <sup>c</sup>	1,312 (71.9) <sup>c</sup>	19 (50.0) <sup>c</sup>
Onychoteuthidae						
<i>Moroteuthis ingens</i>	8 (1.6)	5 (0.4)		2 (0.3)	4 (0.2)	
<i>Moroteuthis robsoni</i>			1 (3.3)			0
<i>Moroteuthis</i> sp. B (Imber)	0			1 (0.1)		
<i>Kondakovia longimana</i>	4 (0.8)	123 (9.1)		3 (0.4)	133 (7.3)	
Psychroteuthidae						
<i>Psychroteuthis glacialis</i>		11 (0.8)			9 (0.5)	
Brachioteuthidae						
<i>Brachioteuthis ?riisei</i>	0			1 (0.1)		
Gonatidae						
<i>Gonatus antarcticus</i>		7 (0.5)	3 (10.0)		6 (0.3)	4 (10.5)
Enoploteuthidae						
<i>Ancistrocheirus lesueuri</i>			1 (3.3)			0
Octopoteuthidae						
<i>Octopoteuthis</i> sp.		1 (0.1)	2 (6.7)		1 (0.1)	3 (7.9)
<i>Taningia danae</i>			1 (3.3)			0
Histiototeuthidae						
<i>Histiototeuthis eltaninae</i>	1 (0.2)	2 (0.1)		1 (0.1)	2 (0.1)	
<i>Histiototeuthis atlantica</i>		1 (0.1)	2 (6.7)		8 (0.4)	2 (5.3)
<i>Histiototeuthis</i> sp.		2 (0.1)			0	
Neoteuthidae						
<i>Alluroteuthis antarcticus</i>		5 (0.4)			2 (0.1)	
<i>Nototeuthis dimegacotyle</i>		1 (0.1)			1 (0.1)	
Cycloteuthidae						
<i>Cycloteuthis akimushkini</i>			1 (3.3)			0
Mastigoteuthidae						
<i>Mastigoteuthis psychrophila</i>		4 (0.3)			0	
<i>Mastigoteuthis</i> sp. ? <i>Mastigoteuthis</i> A (Clarke)	1 (0.2)	1 (0.1)		0	0	
Chiroteuthidae						
<i>Chiroteuthis veranyi</i>	4 (0.8)	1 (0.1)	0	3 (0.4)	1 (0.1)	2 (5.3)
Batoteuthidae						
<i>Batoteuthis skolops</i>		6 (0.4)	0		11 (0.6)	4 (10.5)
Cranchiidae						
<i>Taonius</i> sp. B (Voss)		1 (0.1)			2 (0.1)	
<i>Galiteuthis glacialis</i>	27 (5.3)	243 (17.9)	1 (3.3)	23 (3.4)	330 (18.1)	2 (5.3)

Table 3 (Contd.)

	Lower beaks			Upper beaks		
	Black-browed n (%)	Grey-headed n (%)	Yellow-nosed n (%)	Black-browed n (%)	Grey-headed n (%)	Yellow-nosed n (%)
<b>OCTOPODA</b>						
Octopodidae						
<i>Benthoctopus thielei</i> <sup>d</sup>	78 (15.3)			67 (10.0)		
<b>TOTAL</b>	<b>510</b>	<b>1,358</b>	<b>30</b>	<b>671</b>	<b>1,826</b>	<b>37</b>
Unidentifiable beaks (eroded)	0	7	5	4	67	13

<sup>a</sup>Upper beaks of adults from *Todarodes* sp. and *Martialia hyadesi*

<sup>b</sup>Eroded lower beaks of juveniles from *Todarodes* sp. and *M. hyadesi*

<sup>c</sup>Eroded and intact upper beaks of juveniles from *Todarodes* sp. and *M. hyadesi*

<sup>d</sup>Possibly including some *Graneledone* sp. (see Cherel et al. 2000)

*Todarodes* sp. and *M. hyadesi*, and adult *G. glacialis* averaged  $204 \pm 15$  and  $202 \pm 17$  mm ( $236 \pm 46$  and  $230 \pm 49$  g),  $239 \pm 7$  and  $247 \pm 15$  mm ( $244 \pm 26$  and  $276 \pm 53$  g), and  $227 \pm 17$  and  $227 \pm 12$  mm ( $102 \pm 18$  and  $102 \pm 13$  g) for BBA and GHA, respectively. BBA fed on octopods (*Benthoctopus thielei*) with a large size range ( $70 \pm 11$  mm and  $133 \pm 52$  g), including different age classes. Individuals of *Kondakovia longimana* eaten by GHA also showed a large range in size, ML and M averaging  $393 \pm 93$  mm and  $1647 \pm 1020$  g, respectively. These values were not, however, representative of the mean size eaten, because first the eroded state of lower beaks precluded any measurements on the majority of beaks from juvenile squids, as previously noted in penguin diet (Cherel and Weimerskirch 1999), and, second, GHA fed more on juvenile *K. longimana* (76%) than upon adults (24%). The largest cephalopods caught by albatrosses were all adult onychoteuthid squids that belong to three different species: *Moroteuthis ingens* (LRL: 10.1 mm; DML: 385 mm; M: 1,851 g) for BBA, *K. longimana* (LRL: 15.7 mm; DML: 563 mm; M: 4,177 g) for GHA, and *Moroteuthis robsoni* (LRL: 9.5 mm; DML: 633 mm; M: 2,478 g) for YNA.

## Discussion

Dietary segregation was found at Iles Nuageuses between the three sympatric and closely related species of mollymawks (*Diomedea melanophrys*, *D. chrysostoma*, *D. chlororhynchos*). During chick-rearing, BBA prey almost equally upon cephalopods, fish and penguins, while GHA feed more on squids and YNA feed more on fish. Prey species composition indicates different foraging zones on the basis of known prey biogeography. BBA forage almost exclusively over the shelf and upper slope waters surrounding the Kerguelen Archipelago. By contrast, GHA and YNA feed mainly in oceanic waters, YNA favouring the warm subtropical waters, and GHA the cold Antarctic waters. It is thus remarkable that birds from the same breeding grounds forage over such a wide latitudinal range, from about 35–40°S to 60–65°S, encompassing the Subtropical Zone for YNA, the

Antarctic Zone for GHA and the Antarctic Polar Frontal Zone where Kerguelen is located (Park and Gambèroni 1997) for the three species. Partitioning of foraging areas occurred both short- and long-term, as indicated respectively by fresh items collected over three consecutive days and by accumulated cephalopod beaks that persist in seabird stomachs for months.

### Black-browed albatrosses: foraging in Kerguelen waters

At Iles Nuageuses, BBA preyed almost equally upon cephalopods, fish and penguins. At the same time, birds from the Kerguelen mainland (Canyon des Sourcils Noirs) fed much more on fish (69% versus 31% by fresh mass), but less on cephalopods (11% versus 39%) and penguins (17% versus 31%), crustaceans being negligible at both colonies (Cherel et al. 2000, unpublished data). Fish prey species were almost identical (except the lack of skate remains at Iles Nuageuses) with *Dissostichus eleginoides* ranking first at both localities in summer 1994; however, birds fed less on the nototheniid *Lepidonotothen squamifrons* and on the channichthyid *Channichthys rhinoceratus* at Iles Nuageuses. Perhaps, the most noticeable prey difference between colonies concerns the squid prey. In summer 1994, *Todarodes* sp. was the main item at Iles Nuageuses, but not on the mainland (33% versus 3% by reconstituted mass), thus explaining by itself the predominance of cephalopods in the diet of BBA at the former locality. A more cephalopod diet at Iles Nuageuses was also supported by the analysis of accumulated items. On average, chicks from this locality contained twice the amount of accumulated beaks found in samples from Canyon des Sourcils Noirs (34 versus 17 beaks per sample). They fed less on the cranchiid *Galiteuthis glacialis* (5% versus 26% of all beaks, lower and upper beaks pooled together), but much more on ommastrephids (76% versus 47%). Note also that the main ommastrephid prey at Canyon des Sourcils Noirs was *Martialia hyadesi*, not *Todarodes* sp., while the reverse is true at Iles Nuageuses, thus suggesting that most of the ommastrephid beaks too eroded to be identified to the species level were

**Table 4** *Diomedea melanophrys*, *D. chrysostoma*, *D. chlororhynchus*. Measured squid lower rostral length (LRL) and octopod lower hood length (LHL) of fresh and accumulated beaks identified from stomach contents of albatrosses at Iles Nuageuses, Kerguelen.

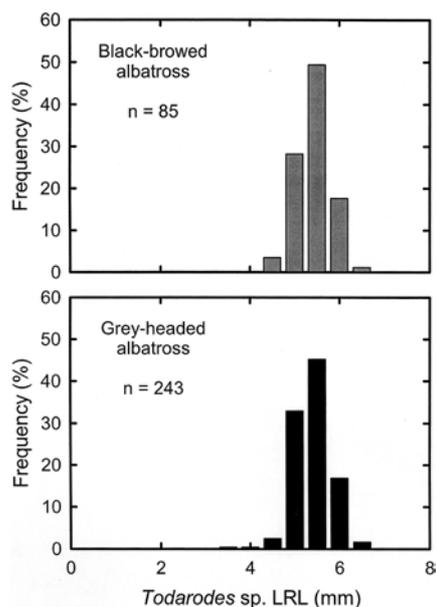
Beaks with undarkened, darkening and darkened wings were considered as belonging to juveniles, subadults and adults, respectively. Values are means  $\pm$  SD with ranges in parentheses

	Biogeography in the Southern Ocean (mainly from Nesis 1987)	Age	Black-browed		Grey-headed		Yellow-nosed	
			<i>n</i>	LRL/LHL	<i>n</i>	LRL	<i>n</i>	LRL
<i>Todarodes</i> sp. (cf. <i>angolensis</i> )	Kerguelen waters	Juveniles	85	5.2 $\pm$ 0.4 (4.4–6.1)	243	5.2 $\pm$ 0.4 (3.3–6.5)	1	5.1
<i>Martialia hyadesi</i>	Subantarctic	Juveniles	6	4.6 $\pm$ 0.2 (4.3–4.9)	21	4.9 $\pm$ 0.5 (3.5–5.9)		
<i>Moroteuthis ingens</i>	Subantarctic (antarctic)	Juveniles	1	3.6	3	3.6 $\pm$ 0.1 (3.5–3.8)		
<i>Moroteuthis robsoni</i>	Subtropical and subantarctic	Adults	2	8.7–10.1			1	9.5
<i>Kondakovia longimana</i>	Antarctic	Juveniles			15	8.3 $\pm$ 1.5 (5.1–9.8)		
		Adults	1	10.4	30	12.6 $\pm$ 1.4 (10.7–15.7)		
<i>Psychroteuthis glacialis</i>	Antarctic	Adults			9	7.0 $\pm$ 0.3 (6.4–7.3)		
<i>Gonatus antarcticus</i>	Subantarctic (antarctic)	Subadults/adults			7	6.0 $\pm$ 0.9 (5.2–7.4)	2	7.3–7.7
<i>Ancistrocheirus lesueuri</i>	Tropical to subtropical (subantarctic)	Adult					1	7.9
<i>Octopoteuthis</i> sp.		Subadult					1	10.8
<i>Histioteuthis eltaninae</i>	Subantarctic (antarctic)	Adults	1	3.6	2	3.4–3.5		
<i>Histioteuthis atlantica</i>	Subtropical and subantarctic	Subadults/adults			1	3.9	2	4.8–5.7
<i>Histioteuthis</i> sp.					2	2.9–4.5		
<i>Alluroteuthis antarcticus</i>	Antarctic	Subadults/adults			3	4.9 $\pm$ 0.5 (4.4–5.4)		
<i>Nototeuthis dimegacotyle</i>	Subantarctic	Subadult/adult			1	3.7		
<i>Cycloteuthis akimushkini</i>	Tropical and subtropical	Adult					1	14.6
<i>Mastigoteuthis psychrophila</i>	Subantarctic and antarctic	Adults			3	3.7 $\pm$ 0.1 (3.6–3.9)		
? <i>Mastigoteuthis</i> (Clarke)	Subtropical and subantarctic (antarctic)	Adult			1	6.8		
<i>Chiroteuthis veranyi</i>	Subtropical and subantarctic	Adults	3	6.3 $\pm$ 0.3 (6.0–6.6)	1	6.5		
<i>Batoteuthis skolops</i>	Subantarctic (antarctic)	Adults			5	4.2 $\pm$ 0.1 (4.0–4.3)		
<i>Taonius</i> sp. B (Voss)	Subantarctic	Subadult			1	7.7		
<i>Galiteuthis glacialis</i>	Antarctic (subantarctic)	Adults	7	5.3 $\pm$ 0.4 (4.7–5.7)	217	5.3 $\pm$ 0.3 (3.6–6.0)		
<i>Benthoctopus thielei</i>	Kerguelen plateau	Various	44	5.0 $\pm$ 0.9 (2.5–6.4)				

actually *Todarodes* beaks at the latter locality. Such large differences in the relative proportion of squid prey were also found at the Falklands, in the only other study investigating inter-locality variations (but not in the same year) in the feeding habits of BBA within a given archipelago (Thompson 1992).

Both satellite tracking and prey biogeography indicated that BBA from the mainland foraged almost exclusively in specific sectors over the outer shelf and inner shelf-break of the Kerguelen archipelago (Cherel et al. 2000). Birds from Iles Nuageuses were not tracked, but

since they caught the same items as BBA from Canyon des Sourcils Noirs, prey biogeography (details in Cherel et al. 2000) also indicates feeding in Kerguelen waters. The idea is supported by observations at sea of colour-marked individuals from both colonies showing that BBA forage in neritic and slope waters and over adjacent banks (Weimerskirch et al. 1988). Interestingly, breeding birds from different colonies seemed to have mostly separate foraging zones (Weimerskirch et al. 1988), which is the likely explanation for the inter-colony dietary differences noted here. While there is an



**Fig. 2** *Diomedea melanophrys*, *D. chrysostoma*. Length-frequency distribution of lower beaks of *Todarodes* sp. consumed by black-browed and grey-headed albatrosses at Iles Nuageuses, Kerguelen (LRL lower rostral length)

overlap in the northern and southern waters of the archipelago, birds from Iles Nuageuses and Canyon des Sourcils Noirs probably favour the eastern and western shelf to forage, respectively, thus minimising potential competition for resources (Weimerskirch et al. 1988; Cherel et al. 2000).

Foraging in neritic waters is in agreement with the feeding ecology of BBA at other localities. South Georgia breeding birds forage mainly at the edge of the peri-insular shelf and shelf slope of South Georgia and the South Orkney Islands (Wood et al. 2000), where they feed on fish, cephalopods and on the Antarctic krill *Euphausia superba* (Prince 1980; review in Cherel and Klages 1998). At the Falkland Islands, BBA are resident all year long on the Patagonian shelf (Grémillet et al. 2000), and they prey upon fish, cephalopods and the lobster krill *Munida gregaria* (Thompson 1992). The picture is, however, complicated by the presence of many fisheries in Falkland waters, thus precluding easy separation of natural prey from discards and offal (Thompson 1992; but see also Cherel et al. 1999). When comparing other breeding grounds, it is distinct that birds from Kerguelen, including GHA, feed much more on penguins (probably mainly macaroni penguins, *Eudyptes chrysolophus*; discussion in Cherel et al. 2000) than birds from elsewhere (review in Cherel and Klages 1998).

Grey-headed albatrosses: foraging from Kerguelen to southern Antarctic waters

At Iles Nuageuses, GHA is mainly a squid-eater, which is in agreement with data obtained at other localities, i.e.

Crozet Islands (Ridoux 1994), South Georgia (Prince 1980) and Campbell Island (Waugh et al. 1999), but birds from Marion Island feed more on fish than on squid (Hunter and Klages 1989; Nel et al. 2001). The main prey are juvenile ommastrephids; *Martialia hyadesi* dominate the cephalopod diet at most localities (Rodhouse et al. 1990; Waugh et al. 1999; Nel et al. 2001), but not at Kerguelen where it is a minor item, being replaced by *Todarodes* sp. Other important squid prey at Iles Nuageuses were *Galiteuthis glacialis* and the larger onychoteuthid *Kondakovia longimana*, which is, again, in general agreement with data gathered elsewhere (Rodhouse et al. 1990; Imber 1991; Ridoux 1994; Nel et al. 2001). All these squid species have essentially an oceanic distribution, being also present in slope waters (Nesis 1987; Rodhouse 1997; Nesis et al. 1998; Cherel and Weimerskirch 1999). The main fish prey of GHA at Iles Nuageuses is a mixture of shelf (*Zanclorhynchus spinifer*, channichthyids), slope (*Antimora rostrata*, macrourids, *Dissostichus eleginoides*) and oceanic species (*Magnisudis prionosa*, myctophids, melamphaid) (Gon and Heemstra 1990). *Magnisudis prionosa* and myctophids were previously found in the food of GHA at Marion Island, Campbell Island and South Georgia, where the species also feeds on slope and neritic fish species (Reid et al. 1996; Waugh et al. 1999; Nel et al. 2001). Taken together, the biogeography of squid and fish prey, therefore, suggest that GHA forage mainly in slope and oceanic waters, but also over the shelf.

At Iles Nuageuses, crustaceans were minor components of the diet by both fresh and reconstituted mass; they included species with a broad latitudinal distribution (e.g. *Themisto gaudichaudii*, Vinogradov et al. 1996), the oceanic *Pasiphae scotiae* (Clarke and Holmes 1987) and, interestingly, a significant amount of Antarctic krill (*Euphausia superba*). The latter species does not occur in Kerguelen waters (Pakhomov 1993), and its northern limit south of the archipelago is 59°S, with the highest densities always recorded further south (Hosie et al. 1988; Miquel 1991; Pakhomov 2000). Since Iles Nuageuses are located at 49°S, the presence of *E. superba* in its diet indicate that GHA foraged regularly in southern Antarctic waters located at >1,000 km from its breeding ground. Other truly Antarctic prey include *Psychroteuthis glacialis*, *Alluroteuthis antarcticus* and *Galiteuthis glacialis*, all being squids of the high latitudes of the Southern Ocean (Filippova and Yuhkov 1982; Lu and Williams 1994; Nesis et al. 1998; Gröger et al. 2000). Foraging in oceanic Antarctic waters was previously noted from the few observations at sea of colour-marked GHA from Iles Nuageuses (Weimerskirch et al. 1988), and from satellite-tracked birds from Marion (Nel et al. 2001), an island lying at 47°S. There, GHA show a strong association with eddies, and an individual that fed at the edges of a southern cold-core eddy returned with specimens of *E. superba* (Nel et al. 2001). Birds from South Georgia also forage in oceanic waters, feeding on *M. hyadesi* at the Antarctic Polar Front and catching *E. superba* in Antarctic waters, both in the

oceanic zone and in the vicinity of their colony, where Antarctic krill is a main component of the micronekton community (Rodhouse et al. 1996; Croxall et al. 1997; Wood et al. 2000).

#### Yellow-nosed albatrosses: foraging from Kerguelen to subtropical waters

Almost no information is available on the dietary habits of YNA (Cherel and Klages 1998). In the southern Indian Ocean, it is a fish-eater both at Crozet and Kerguelen, complementing its diet mainly with squids (Ridoux 1994; present study). At Iles Nuageuses, the few fresh items that were identified to the species level included *Dissostichus eleginoides* and *Todarodes* sp., which commonly occur in Kerguelen waters (Duhamel 1992; Cherel and Weimerskirch 1995). Other items were oceanic species. The large mysid *Neognathophausia gigas* and the shrimp *Notostomus auriculatus* have a wide distribution; *N. gigas* is, however, not abundant in Antarctic waters (Pequegnat 1965) and *N. auriculatus* was not recorded south of 45°S (Iwasaki and Nemoto 1987). Both species were found in the food of YNA at Tristan da Cunha Archipelago (Holthuis and Sivertsen 1967), which is located in the subtropics. The two remaining prey species, the scopelarchid *Benthalbella macropinna* and the scomberesocid *Scomberesox saurus*, had never been found previously in the food of any seabird at Kerguelen (present study; authors' unpublished data). *B. macropinna* is circumglobal in the Southern Hemisphere, including both warm and cold waters (Gon and Heemstra 1990), while *S. saurus* is a common epipelagic species in subtropical waters only, not occurring south of the Subtropical Front (Hubbs and Wisner 1980). Importantly, *S. saurus* is one of the most common fish prey of YNA at the subtropical Amsterdam Island (authors' unpublished data), located north of the Kerguelen archipelago. Taken together, these data strongly suggest that YNA from Iles Nuageuses forage both in Kerguelen waters and in the northern and warmer oceanic waters of the subtropics.

Generalization from only a few chicks sampled in a short period can be misleading, but the consistency of results across prey biogeography allows some confidence that the principal conclusions concerning foraging areas are valid. Furthermore, accumulated beaks confirm that YNA feed, at least in part, in northern waters, because *Architeuthis dux*, *Moroteuthis robsoni*, *Ancistrocheirus lesueuri*, *Octopoteuthis* sp., *Taningia danae*, *Histioteuthis atlantica* and *Cycloteuthis akimushkini* are known to occur in subtropic and northern subantarctic regions (Clarke 1986; Nesis 1987). Finally, distribution at sea confirms that YNA do not occur south of Kerguelen nor in Antarctic waters, while the species is common to the north of the archipelago and in subtropical waters (Weimerskirch et al. 1986), where the few Kerguelen birds probably mixed with those breeding in large numbers at Amsterdam Island.

#### Trophic segregation among albatrosses

Comparison of the dietary habits of the three sympatric species of mollymawks from Iles Nuageuses shows segregation through different foraging areas during the chick-rearing period. For example, the noticeable presence/absence of prey species indicators of water masses show that BBA forage over the shelf (the octopod *Benthoctopus thielei*; Nesis 1987), GHA in oceanic southern Antarctic waters (the squid *Psychroteuthis glacialis* and *Euphausia superba*), and YNA in subtropical waters (the fish *Scomberesox saurus*). Using satellite tracking, previous comparison of the feeding ecology of sympatric GHA and BBA at South Georgia and Campbell Island are in agreement, with BBA favouring neritic waters and GHA the oceanic zone (Prince et al. 1998; Waugh et al. 1999; Wood et al. 2000). A recent study on North Pacific albatrosses also shows largely non-overlapping foraging zones for the sympatric Laysan *Diomedea immutabilis* and black-footed *D. nigripes* albatrosses from the Hawaiian Islands (Fernandez et al. 2001). All together these findings support the view that minimising the overlap in foraging zones is the most important factor in reducing interspecific competition in albatrosses (Weimerskirch et al. 1986, 1988).

Theoretically, mollymawks could also segregate by additional mechanisms, but all the available evidence to date indicate that they are quite similar in their behaviour at sea. The overall activity budget of BBA, GHA and YNA is not fundamentally different (Weimerskirch and Guionnet 2002), their main feeding method is surface-seizing (Warham 1990), and BBA and GHA possess identical diving capabilities (Prince et al. 1994), which is in agreement with the similarity of their vision both in air and under water (Martin 1998). In that context, differences in prey species probably result more from distinct foraging areas than from prey selection. Accordingly, when feeding on the same item, BBA and GHA catch individuals of the same size (for example *Todarodes* sp., *Martialia hyadesi*, *Galiteuthis glacialis*).

The three species of mollymawks differ in size: BBA is the largest species (about 3.7 kg), GHA ranks second (3.4 kg) and YNA is by far the smallest (2.5 kg) (Weimerskirch et al. 1989). When competing for natural food at sea, larger albatross species tend to exclude smaller ones (Weimerskirch et al. 1986), suggesting a hierarchy at sea in the decreasing order BBA, GHA and YNA. This is likely to be an operating mechanism by which BBA exclude successfully smaller mollymawks from shelf waters. Accordingly, observations at sea off the Crozet Islands indicate low densities of YNA over the shelf, where BBA, and to a lesser extent GHA, is more abundant (Stahl et al. 2002). A significant number of neritic prey were, however, taken by GHA and YNA from Iles Nuageuses. Three different non-exclusive explanations may account for this: (1) neritic prey were taken opportunistically during the outward and inward travelling times from oceanic feeding areas, (2) they performed some specific foraging trips nearby the colony

and/or (3) birds foraged behind fishing vessels to feed on offal and discards in Kerguelen waters.

Several procellariiforms, including mollymawks, use a twofold foraging strategy during the chick-rearing period, adults alternating between short (ST) and long trips (LT) during which they feed in nearby and distant foraging areas, respectively (Weimerskirch et al. 1994). The neritic Kerguelen BBA do not use this strategy (Weimerskirch et al. 1994), but the oceanic GHA from Marion Island (Nel et al. 2000) and YNA from Amsterdam Island (Weimerskirch et al. 1994) perform both kinds of trips. It is therefore likely that GHA and YNA from Iles Nuageuses forage in Kerguelen waters during ST and alternate with LT in southern Antarctic and subtropical waters, respectively, therefore explaining the presence of prey with different latitudinal distribution in the food samples. YNA is thus probably the first known species from Kerguelen to perform LT in subtropical waters only, while GHA belongs to a group of procellariiforms, including smaller species, which travel to southern Antarctic waters during LT (Weimerskirch et al. 1994, 1999; Catard et al. 2000; Cherel et al. 2002a,b).

At Kerguelen, two fisheries, both targeting *Dissostichus eleginoides*, operated during summer 1994 within the foraging ranges of mollymawks from Iles Nuageuses: three Ukrainian longliners on the western slope and one French trawler at the northern edge of the shelf. The two fisheries produced offal, but few fish and squid occurred as bycatch (Cherel et al. 2000). We found no bait remains in dietary samples from BBA, GHA and YNA, but *D. eleginoides* was the main fish prey of BBA and GHA, and we identified it in two YNA stomach contents. Patagonian toothfish was also the main item of BBA from the mainland (Cherel et al. 2000). As previously detailed (Cherel et al. 2000), most *D. eleginoides* were probably natural prey, as found for the wandering albatross *Diomedea exulans* at Crozet (Weimerskirch et al. 1997b). However, the presence of skeletal remains of very large individuals and of tails (thrown overboard with head and gut from the trawler) in samples suggested that BBA, GHA and YNA interact with the fisheries. Accordingly, mollymawks, especially GHA and BBA, attend in large numbers both longliners and trawlers in Kerguelen waters (Cherel et al. 1996; Weimerskirch et al. 2000). Therefore, the three mollymawk species from Kerguelen are at risk of being killed by the hooks of longliners operating in slope waters during the breeding season. Furthermore, YNA will potentially encounter pelagic longliners targeting tunas in subtropical waters, also a major threat to Kerguelen wandering albatrosses, as has been demonstrated for individuals breeding at Crozet and elsewhere (Weimerskirch et al. 1997a).

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## References

- Adams NJ, Klages NT (1987) Seasonal variation in the diet of the king penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. *J Zool Lond* 212:303–324
- Andersen NC (1984) Genera and subfamilies of the family Nototheniidae (Pisces, Perciformes) from the Antarctic and Subantarctic. *Steenstrupia* 10:1–34
- Baker A de C, Boden BP, Brinton E (1990) A practical guide to the euphausiids of the world. Natural History Museum Publications, London
- Barrett RT, Asheim M, Bakken V (1997) Ecological relationships between two sympatric congeneric species, common murres and thick-billed murres, *Uria aalge* and *U. lomvia*, breeding in the Barents Sea. *Can J Zool* 75:618–631
- Begon M, Harper JL, Townsend CR (1990) Ecology: individuals, populations and communities, 2nd edn. Blackwell, Cambridge
- Bocher P, Cherel Y, Hobson KA (2000) Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. *Mar Ecol Prog Ser* 208:249–264
- Bocher P, Cherel Y, Labat JP, Mayzaud P, Razouls S, Jouventin P (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. *Mar Ecol Prog Ser* 223:261–276
- Bryant R, Jones IL (1999) Food resources use and diet overlap of common and thick-billed murres at the Gannet Islands, Labrador. *Waterbirds* 22:392–400
- Catard A, Weimerskirch H, Cherel Y (2000) Exploitation of distant Antarctic waters and close shelf-break waters by white-chinned petrels rearing chicks. *Mar Ecol Prog Ser* 194:249–261
- Cherel Y, Klages N (1998) A review of the food of albatrosses. In: Robertson G, Gales R (eds) Albatross biology and conservation. Surrey Beatty, Chipping Norton, pp 113–136
- Cherel Y, Weimerskirch H (1995) Seabirds as indicators of marine resources: black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters. *Mar Ecol Prog Ser* 129:295–300
- Cherel Y, Weimerskirch H (1999) Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new information from seabird predators. *Mar Ecol Prog Ser* 188:93–104
- Cherel Y, Weimerskirch H, Duhamel G (1996) Interactions between longline vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality. *Biol Conserv* 75:63–70
- Cherel Y, Waugh S, Hanchet S (1999) Albatross predation of juvenile southern blue whiting (*Micromesistius australis*) on the Campbell Plateau. *NZ J Mar Freshw Res* 33:437–441
- Cherel Y, Weimerskirch H, Trouvé C (2000) Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Mar Ecol Prog Ser* 207:183–199
- Cherel Y, Bocher P, de Broyer C, Hobson KA (2002a) Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen, Southern Indian Ocean. *Mar Ecol Prog Ser* 228:263–281
- Cherel Y, Bocher P, Trouvé C, Weimerskirch H (2002b) Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Mar Ecol Prog Ser* 228:283–299
- Clarke A, Holmes LJ (1987) Notes on the biology and distribution of *Pasiphaea* species from the Southern Ocean. *Br Antarct Surv Bull* 74:17–30
- Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon, Oxford
- Croxall JP, Prince PA, Reid K (1997) Dietary segregation of krill-eating South Georgia seabirds. *J Zool Lond* 242:531–556
- Duhamel G (1992) Biologie et exploitation de *Dissostichus eleginoides* autour des Iles Kerguelen. *Sel Sci Pap Sci Comm Conserv Antarct Mar Living Resour* 1991:85–106
- Fernandez P, Anderson DJ, Sievert PR, Huyvaert KP (2001) Foraging distributions of three low-latitudes albatross (*Phoebastria*) species. *J Zool Lond* 254:391–404

- Filippova JA, Yukhov VL (1982) New data on the genus *Alluroteuthis* Odhner, 1923 (Cephalopoda: Oegopsida) (in Russian). *Antarktika* 21:157–168
- Gon O, Heemstra PC (1990) Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown
- Grémillet D, Wilson RP, Wanless S, Chater T (2000) Black-browed albatrosses, international fisheries and the Patagonian Shelf. *Mar Ecol Prog Ser* 195:269–280
- Gröger J, Piatkowski U, Heinemann H (2000) Beak length analysis of the Southern Ocean squid *Psychroteuthis glacialis* (Cephalopoda: Psychroteuthidae) and its use for size and biomass estimation. *Polar Biol* 23:70–74
- Hecht T, Cooper J (1986) Length/mass relationships, energetic content and the otoliths of Antarctic cod *Paranotothenia magellanica* (Nototheniidae: Pisces) at sub-Antarctic Marion Island. *S Afr J Zool* 21:294–296
- Holthuis LB, Sivertsen E (1967) The Crustacea Decapoda, Mysidacea and Cirripedia of the Tristan da Cunha Archipelago, with a revision of the “frontalis” subgroup of the genus *Jasus*. *Res Norw Sci Exp Tristan da Cunha* 1937–1938 52:1–55
- Hosie GW, Ikeda T, Stolp M (1988) Distribution, abundance and population structure of the Antarctic krill (*Euphausia superba* Dana) in the Prydz Bay Region, Antarctica. *Polar Biol* 8:213–224
- Hubbs CL, Wisner RL (1980) Revision of the sauries (Pisces, Scomberesocidae) with descriptions of two new genera and one new species. *Fish Bull* (Wash DC) 77:521–566
- Hull CL (1999) Comparison of the diets of breeding royal (*Eudyptes schlegeli*) and rockhopper (*Eudyptes chrysolome*) penguins on Macquarie Island over three years. *J Zool Lond* 247:507–529
- Hunter S, Klages NTW (1989) The diet of grey-headed albatrosses *Diomedea chrysostoma* at the Prince Edward Islands. *S Afr J Antarc Res* 19:31–33
- Imber MJ (1991) Feeding ecology of Antarctic and sub-Antarctic Procellariiformes. In: *Acta XX Congressus Internationalis Ornithologici*. New Zealand Ornithological Congress Trust Board, Wellington, pp 1402–1412
- Iwami T (1985) Osteology and relationships of the family Channichthyidae. *Mem Natl Inst Polar Res Ser E* 36:1–69
- Iwasaki N, Nemoto T (1987) Pelagic shrimps (Crustacea: Decapoda) from the Southern Ocean between 150°E and 115°E. *Mem Natl Inst Polar Res Ser E* 38:1–40
- Jackson GD (1995) The use of beaks as tools for biomass estimation in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biol* 15:9–14
- Lance BK, Roby DD (1998) Diet and postnatal growth in red-legged and black-legged kittiwakes: an interspecies comparison. *Colon Waterbirds* 21:375–387
- Lishman GS (1985) The food and feeding ecology of Adélie penguins (*Pygoscelis adeliae*) and chinstrap penguins (*P. antarctica*) at Signy Island, South Orkney Islands. *J Zool Lond* 205:245–263
- Lu CC, Williams R (1994) Contribution to the biology of squid in the Prydz Bay region, Antarctica. *Antarc Sci* 6:223–229
- Martin GR (1998) Eye structure and amphibious foraging in albatrosses. *Proc R Soc Lond B Biol Sci* 265:665–671
- Mauchline J, Fisher LR (1969) The biology of euphausiids. *Adv Mar Biol* 7:1–454
- Miquel JC (1991) Distribution and abundance of post-larval krill (*Euphausia superba* Dana) near Prydz Bay in summer with reference to environmental conditions. *Antarc Sci* 3:279–292
- Murano M (1999) Mysidacea. In: Boltovskoy D (ed) *South Atlantic zooplankton*. Backhuys, Leiden, pp 1099–1140
- Nel DC, Nel JL, Ryan PG, Klages NTW, Wilson RP, Robertson G (2000) Foraging ecology of grey-headed mollymawks at Marion Island, southern Indian Ocean, in relation to longline fishing activity. *Biol Conserv* 96:219–231
- Nel DC, Lutjeharms JRE, Pakhomov EA, Ansoorge IJ, Ryan PG, Klages NTW (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Mar Ecol Prog Ser* 217:15–26
- Nesis KN (1987) *Cephalopods of the world*. Squids, cuttlefishes, octopuses and allies. TFH Publications, Neptune City, N.J.
- Nesis KN, Nigmatullin CM, Nikitina IV (1998) Spent females of deepwater squid *Galiteuthis glacialis* under the ice at the surface of the Weddell Sea (Antarctic). *J Zool Lond* 244:185–200
- Pakhomov EA (1993) Macroplankton of the waters contiguous to the Kerguelen Archipelago. In: Duhamel G (ed) *Campagnes SKALP 1987 et 1988 aux îles Kerguelen à bord des navires “SKIF” et “KALPER”*. Inst Fr Rech Technol Polair Rapp Camp Mer 93–01:104–112
- Pakhomov EA (2000) Demography and life cycle of Antarctic krill, *Euphausia superba*, in the Indian sector of the Southern Ocean: long-term comparison between coastal and open-ocean regions. *Can J Fish Aquat Sci* 57[Suppl 3]:68–90
- Park YH, Gambérone L (1997) Cross-frontal exchange of Antarctic intermediate water and Antarctic bottom water in the Crozet Basin. *Deep-Sea Res II* 44:963–986
- Pequegnat LH (1965) The bathypelagic mysid *Gnathophausia* (Crustacea) and its distribution in the eastern Pacific Ocean. *Pacif Sci* 19:399–421
- Pietz PJ (1987) Feeding and nesting ecology of sympatric south polar and brown skuas. *Auk* 104:617–627
- Prince PA (1980) The food and feeding ecology of grey-headed albatross *Diomedea chrysostoma* and black-browed albatross *D. melanophris*. *Ibis* 122:476–488
- Prince PA, Huin N, Weimerskirch H (1994) Diving depths of albatrosses. *Antarc Sci* 6:353–354
- Prince PA, Croxall JP, Trathan PN, Wood AG (1998) The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. In: Robertson G, Gales R (eds) *Albatross biology and conservation*. Surrey Beatty, Chipping Norton, pp 137–167
- Reid K, Croxall JP, Prince PA (1996) The fish diet of black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at South Georgia. *Polar Biol* 16:469–477
- Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Mar Ornithol* 22:1–192
- Rodhouse PG (1997) Large and meso-scale distribution of the ommastrephid squid *Martialia hyadesi* in the Southern Ocean: a synthesis of information relevant to fishery forecasting and management. *Korean J Polar Res* 8:145–154
- Rodhouse PG, Yeatman J (1990) Redescription of *Martialia hyadesi* Rochebrune and Mabile, 1889 (Mollusca: Cephalopoda) from the Southern Ocean. *Bull Br Mus (Nat Hist) Zool* 56:135–143
- Rodhouse PG, Prince PA, Clarke MR, Murray AWA (1990) Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Mar Biol* 104:353–362
- Rodhouse PG, Prince PA, Trathan PN, Hatfield EMC, Watkins JL, Bone DG, Murphy EJ, White MG (1996) Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions. *Mar Ecol Prog Ser* 136:37–50
- Stahl JC, Bartle JA, Jouventin P, Roux JP, Weimerskirch H (2002) Atlas of seabird distribution in the south-west Indian Ocean. *Mar Ornithol* (in press)
- Thompson KR (1992) Quantitative analysis of the use of discards from squid trawlers by black-browed albatrosses *Diomedea melanophris* in the vicinity of the Falkland Islands. *Ibis* 134:11–21
- Tickell WLN (2000) *Albatrosses*. Pica, Sussex
- Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid amphipods (Amphipoda, Hyperiidea) of the world oceans. Science Publishers, Lebanon
- Warham J (1990) *The petrels, their ecology and breeding systems*. Academic, London
- Waugh SM, Weimerskirch H, Chérel Y, Shankar U, Prince PA, Sagar PM (1999) Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Mar Ecol Prog Ser* 177:243–254
- Weimerskirch H, Guionnet T (2002) Comparative activity pattern during foraging of four albatross species. *Ibis* 144:40–50

- Weimerskirch H, Jouventin P, Stahl JC (1986) Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* 128:195–213
- Weimerskirch H, Bartle JA, Jouventin P, Stahl JC (1988) Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor* 90:214–219
- Weimerskirch H, Zotier R, Jouventin P (1989) The avifauna of the Kerguelen Islands. *Emu* 89:15–29
- Weimerskirch H, Chastel O, Ackermann L, Chaurand T, Cuénot-Chaillet F, Hindermeyer X, Judas J (1994) Alternate long and short foraging trips in pelagic seabird parents. *Anim Behav* 47:472–476
- Weimerskirch H, Brothers N, Jouventin P (1997a) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biol Conserv* 79:257–270
- Weimerskirch H, Cherel Y, Cuénot-Chaillet F, Ridoux V (1997b) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* 78:2051–2063
- Weimerskirch H, Fradet G, Cherel Y (1999) Natural and experimental changes in chick provisioning in a long-lived seabird, the Antarctic prion. *J Avian Biol* 30:165–174
- Weimerskirch H, Capdeville D, Duhamel G (2000) Factors affecting the number and mortality of seabirds attending trawlers and long-liners in the Kerguelen area. *Polar Biol* 23:236–249
- Wilkinson L (1999) SYSTAT 9 for Windows. SPSS, Chicago
- Williams R, McEldowney A (1990) A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Islands. ANARE (Aust Natl Antarct Res Exped) Res Notes 75:1–173
- Wood AG, Naef-Daenzer B, Prince PA, Croxall JP (2000) Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *J Avian Biol* 31:278–286