



Feeding ecology, isotopic niche, and ingestion of fishery-related items of the wandering albatross *Diomedea exulans* at Kerguelen and Crozet Islands

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ABSTRACT: Feeding ecology and isotopic niche of the wandering albatross *Diomedea exulans* were investigated in the poorly studied population on the Kerguelen Islands and compared to that on the Crozet Islands. Fish (48% by mass) and cephalopods (46%) were similarly important in chick food at Kerguelen, while cephalopods (87%) dominated the diet at Crozet. Fish prey included mainly deep-sea species, with the Patagonian toothfish *Dissostichus eleginoides* being the main item. Cephalopod beaks were identified, most of which were from adult oceanic squids. Albatrosses preyed upon the same taxa at both localities, but in different proportions. *Histioteuthis atlantica* (30% by number), *Galiteuthis glacialis* (13%), and *Kondakovia longimana* (10%) were the main squid prey at Kerguelen, while *K. longimana* (35%) and *H. eltaninae* (23%) dominated at Crozet. Chick feather $\delta^{15}\text{N}$ values were higher in wandering albatrosses than in other oceanic seabirds of the 2 communities, indicating that the wandering albatross is an apex consumer together with the sperm whale and sleeper shark that have similar $\delta^{15}\text{N}$ values. Satellite-tracked wandering albatrosses foraged in local subantarctic waters and farther north, with some Crozet birds overlapping with those from the Kerguelen population in western Kerguelen waters. Anthropogenic items (e.g. plastic fragments, hooks) were found in half the food samples. All fishery-related items were from the local toothfish fishery. The high number of hooks from Crozet indicated the presence of a fairly large number of illegal longliners in the area during the Austral winter 1998. A review of the feeding habits of *Diomedea* spp. highlights the need for more dietary investigations to achieve effective conservation and management of this endangered group of charismatic seabirds.

KEY WORDS: Cephalopod · Diet · Hook · Satellite tracking · Seabird · Southern Ocean · Stable isotopes

INTRODUCTION

Albatrosses of the genus *Diomedea* are the largest of all living flying birds (wingspan up to 3.5 m). The genus comprises 7 species and subspecies including some of the most endangered seabirds, the Amsterdam *D. amsterdamensis* and Tristan *D. dabbenena* albatrosses (Agreement on the Conservation of Albatrosses and Petrels: www.acap.aq/). *Diomedea* alba-

trosses breed on scattered islands and archipelagoes of the Southern Ocean and fringing subtropical waters. Only 1 species has a circumpolar distribution: the wandering albatross *D. exulans*, which breeds in the Indian, Pacific, and Atlantic Oceans (Weimerskirch et al. 2015; www.acap.aq/). Its large size and tameness make the wandering albatross an ideal model animal for long-term demographic and biological investigations. The species is one of the best

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known seabirds, with most tracking studies having been conducted at 3 locations, namely the Crozet Islands (Jouventin & Weimerskirch 1990), Marion Island (Nel et al. 2002), and South Georgia (Prince et al. 1992). Its basic biology has been poorly investigated elsewhere, especially at the Kerguelen Islands that host ~15% of the population worldwide (~8000 pairs worldwide; www.acap.aq/).

Wandering albatrosses forage primarily in oceanic waters of the Antarctic, Subantarctic, and Subtropical Zones (Weimerskirch 1998, Xavier et al. 2004), where they feed primarily on fish and on a large diversity of cephalopods (Cherel & Klages 1998). Albatrosses are strongly attracted to and interact with fishing vessels and, consequently, fishery-related mortality is responsible for alarming declines in their populations (Weimerskirch et al. 1997a, Barbraud et al. 2012). Birds are attracted by offal, bycatch, and the targeted fish, with the primary source of incidental mortality being hooks and the associated baits from longlines (www.acap.aq/). In the 1990s, a demersal longline fishery developed in the southern Atlantic and spread rapidly to other regions of the Southern Ocean (Nel et al. 2002). The fishery targets the Patagonian toothfish *Dissostichus eleginoides*, a natural prey of wandering albatrosses over their traditional foraging grounds, namely in slope waters surrounding subantarctic islands where the birds nest (Weimerskirch et al. 1997b, Weimerskirch 1998, Lord et al. 2006). Albatrosses congregate in significant numbers in the vicinity of longliners, increasing their risk of being injured or killed during fishing operations (Cherel et al. 1996, Weimerskirch et al. 2000).

The main aim of the present study was to document the diet, foraging ecology, and relationships with fisheries of the wandering albatross population from the Kerguelen Islands. A combination of methods (satellite tracking, stomach content analysis, and stable isotopes) was used to make direct comparisons with the better known Crozet Island population, which was sampled in the same years using the same methods as the Kerguelen population. Foraging areas of breeding birds were investigated by performing the first satellite-tracking of wandering albatrosses at the Kerguelen Islands. Stomach contents were collected in the same year (1998) that corresponded to the peak in the Patagonian toothfish fishery in Kerguelen waters, with illegal longlining representing ~70% of the catch (Lord et al. 2006). Consequently, relationships with fisheries were investigated through careful examination of anthropogenic items in food samples. Stomach content analy-

sis of large chicks allowed identification and quantification of prey species and prey size, and potential seasonal dietary changes were investigated during the long chick-rearing period of the species (from March to December; www.acap.aq/). The feeding habits of albatrosses in the genus *Diomedea* were then reviewed from the literature to highlight the key prey groups and prey species, but also the lack of dietary information on this endangered seabird taxon. Finally, stable isotopes were used as a complementary indirect method to delineate the foraging habitats ($\delta^{13}\text{C}$ value as a proxy) and trophic levels ($\delta^{15}\text{N}$ value as a proxy) of the wandering albatross. We focused on the trophic position of the species relative to other Procellariiformes and to other consumers to study the trophic structure of the seabird community and of the whole ecosystem, respectively. Recent investigations showed that wandering albatrosses are apex consumers of the subantarctic seabird assemblages (Jaeger et al. 2013), but, to our knowledge, no information is available at the ecosystem level. Wandering albatrosses forage on the same prey as some marine mammals and predatory fish, suggesting a closely related trophic level with the larger sleeper sharks and sperm whales (Cherel & Duhamel 2004).

MATERIALS AND METHODS

Study site, birds, and dietary sampling and analysis

Dietary studies were conducted in the same year (1998) at the Kerguelen (49°S, 70°E) and Crozet (46°S, 51°E; Possession Island) archipelagoes in the southern Indian Ocean. Stomach contents from large chicks were collected at Kerguelen (n = 30) and Crozet Islands (n = 33). Due to the long chick-rearing period of the wandering albatross, ~10 large chicks were sampled when they were ~3, 5, and 7 mo old (June, August, and October) to assess time-related dietary changes. Food samples were taken from randomly selected chicks either after a returning parent had completed feeding them, or after successive daily weighing indicated that they had been fed recently. Samples were obtained by up-ending chicks over a plastic bucket and massaging the stomach and throat. If needed, chicks were flushed once using the offloading technique (Wilson 1984). Collection of a single meal has no detrimental effects in terms of survival and development of large albatross chicks (Phillips 2006). Food samples were all returned deep-frozen (-20°C) to the laboratory in France for analysis.

Each sample was thawed, drained, and weighed (solid fraction; Cherel et al. 2000). Accumulated items, mostly cephalopod beaks and spermatozoa, were subsequently sorted and weighed. Beaks can persist in predator stomachs for weeks and even months, thus overemphasizing their importance in seabird diets (Xavier et al. 2005). Following Cherel & Klages (1998), accumulated beaks (without flesh attached) were consequently analyzed separately from fresh items. Fresh items (solid fraction minus accumulated items) were divided into broad prey classes (fish, cephalopods, crustaceans, carrion, and others), which were weighed to calculate their proportion by mass in the diet. Species identification of prey relied almost entirely on the examination of otoliths and bones for fish, chitinized beaks for cephalopods, and exoskeletons for crustaceans. Special care was taken to use all fish hard parts recovered in stomach contents (bones, cartilaginous elements, otoliths, scales, thorns, teeth), with an emphasis on some distinctive bones (premaxilla, maxilla, dentary, articular, parasphenoid, opercle, vertebrae, and caudal skeleton) to identify items to the lowest possible taxon. In the same way, the morphology of both lower and upper beaks, instead of that of lower beaks only, was used to determine cephalopod prey (Cherel et al. 2000, Xavier et al. 2011). It was not possible to differentiate upper beaks of the common *Histioteuthis atlantica* from those of the rarer *H. bonnellii corpuscula*.

Items were identified by comparison with material held in our own collection and by reference to the available literature, including Andersen (1984), Williams & McEldowney (1990), and Duhamel et al. (2005) for fish, Murano (1999) for crustaceans, and Clarke (1986) and Xavier & Cherel (2009) for cephalopods. Species names of cephalopods followed either recent and ongoing taxonomic revisions (Young et al. 2016) or well-known beaks with still no species correspondence (Clarke 1986, Imber 1992, Cherel et al. 2004). Length of uneroded or slightly eroded otoliths (OL) and of dentary bones (ML for mandible length) of fish, lower rostral length (LRL) of squid beaks, and lower hood length (LHL) of octopus beaks were measured with a Vernier caliper. Fish standard or total length (SL or TL), cephalopod dorsal mantle length (DML), and prey mass were calculated using regression equations (Clarke 1986, Williams & McEldowney 1990, Smale et al. 1995, Lu & Ickeringill 2002, Xavier & Cherel 2009). For the few species where no relationships were available, lengths were estimated using equations for closely related species or for species with a similar morphology.

Satellite tracking

Nine and 45 breeding albatrosses were satellite-tracked in 1998 during the brooding period (April) and during the incubation and brooding periods (January to April) at Kerguelen and Crozet Islands, respectively. The remoteness of albatross nests at Kerguelen made the field work more difficult compared to the more accessible, and thus more investigated, birds from Crozet (Weimerskirch et al. 1993). The difficulty of recovering satellite tags during the chick-rearing period, when birds stay briefly near their nest, precluded working in June to October. Hence, there was a temporal mismatch between the tracking period (late incubation and brooding) and the period of dietary sampling (mid- to late-chick rearing). The 2 periods are marked by different feeding behaviors, with wandering albatrosses increasing their foraging range in winter (Weimerskirch et al. 1993). Wandering albatrosses were fitted with satellite transmitters (Microwave 100 and T2038 Toyocom) weighing between 55 and 80 g, i.e. below the 3% body mass limit recommended for flying birds (Phillips et al. 2003). The transmitters were fitted on back feathers with adhesive tape and glue. They were left on the birds for 1 to 3 successive foraging trips. Satellite fixes were obtained through the Argos system. All locations (classes A, B, 0, and 1 to 3) were used, but unrealistic positions were filtered out by removing those with an estimated speed above 90 km h⁻¹ (McConnell et al. 1992; details in Weimerskirch et al. 1993).

Kernel analysis was used to map the density distribution of the 2 populations. Serial independence of the locations is not required with this method (de Solla et al. 1999), but homogeneous sampling frequency is needed (Wood et al. 2000). Thus, satellite fixes on a regular 2 daily fixes basis were re-sampled to deal with irregular Argos transmissions. Kernels were calculated using the kernelUD function in the 'adehabitatHR' R package (Calenge 2006), with a smoothing parameter value of 0.5 to account for satellite transmitter error. Ninety-five percent density contours are considered to represent the home range (Gallerani Lawson & Rodgers 1997, Brothers et al. 1998), and 75 and 50% density contours to indicate outer and inner core areas, respectively. Maps were generated using the 'maps' R package. Overlaid bathymetry was downloaded from the NOAA Coast Watch website (<http://coastwatch.pfeg.noaa.gov/erddap/index.html>). Position of the Polar (PF) and Subtropical Fronts (STF) was estimated from Aviso products (Altimetric Sea Level Anomaly;

<http://ctoh.legos.obs-mip.fr/applications/mesoscale/southern-ocean-fronts>; Sallee et al. 2008) and from data in Belkin & Gordon (1996), respectively.

Stable isotope analysis

Chick $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are good proxies to compare habitats and trophic positions within seabird communities, because they integrate the isotopic values of assimilated food caught in the vicinity of the colonies by parent birds during the breeding season. Body feathers were collected from large Procellariiformes, including albatrosses and giant petrels, which breed at Kerguelen and Crozet Islands. For each study species, 4 dorsal body feathers were sampled from randomly chosen chicks at the end of the chick-rearing period. To avoid potential inter-annual variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values linked to a shift in baseline values (Jaeger & Cherel 2011), all feathers were sampled in the same year (2005), which was different from the year of tracking and stomach sampling (1998). In Procellariiformes, body feathers of chicks grow almost synchronously in the mid- to the second half of the chick-rearing period and thus present low intra-individual isotopic variation (Phillips & Hamer 2000, Carravieri et al. 2014). Hence, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured for a single feather per individual. Prior to isotopic analysis, feathers were cleaned of surface lipids and contaminants by immersion in a solution of 2:1 chloroform:methanol for 2 min in a beaker, followed by 2 successive methanol rinses. Each whole body feather was air dried, calamus was removed, and the feather was cut into small pieces with scissors. Tissue $\delta^{15}\text{N}$ values were also compared between the wandering albatross and other non-avian predators from the Kerguelen Islands, namely female elephant seals *Mirounga leonina* (n = 32, whole blood, Cherel et al. 2008), female Antarctic fur seals *Arctocephalus gazella* (n = 10, whole blood, Cherel et al. 2008), Patagonian toothfish (n = 36, muscle), porbeagle sharks *Lamna nasus* (n = 7, muscle), sleeper sharks *Somniosus antarcticus* (n = 20, muscle), and sperm whales *Physeter macrocephalus* (n = 3, skin). Muscle and skin samples were freeze-dried and ground in a mortar, and lipids were subsequently extracted using cyclohexane. Tissue sub-samples were then weighed (~0.4 mg) with a microbalance, packed in tin containers, and nitrogen and carbon isotope ratios were determined by a continuous flow mass spectrometer (Micromass Isoprime) coupled to an elemental analyzer (Euro Vector EA 3024). Results are presented in

the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors <0.15 and <0.20‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

The isotopic method was validated in the southern Indian Ocean. $\delta^{13}\text{C}$ values of consumers reflect the latitudinal $\delta^{13}\text{C}$ gradient at the base of the food web and thus indicate their latitudinal foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010), while $\delta^{15}\text{N}$ values change according to their trophic position in the increasing order planktivorous species < piscivorous species < fish and squid eaters (Cherel et al. 2010). To help interpret $\delta^{15}\text{N}$ values of Procellariiformes, they were compared to values of body feathers from a consumer known to feed on mesopelagic fish, namely chicks of the myctophid-eating king penguin *Aptenodytes patagonicus* (Cherel et al. 2010). Since isotopic discrimination factors are tissue specific, isotopic comparisons amongst tissues require correcting raw isotopic values. $\delta^{15}\text{N}$ values from Kerguelen consumers were measured on various tissues, including whole blood, muscle, skin, and feathers, which, indeed, present different $\delta^{15}\text{N}$ discrimination factors (Vanderklift & Ponsard 2003). However, an analysis using corrected (estimated) $\delta^{15}\text{N}$ values did not fundamentally alter the main isotopic finding of the study (the 2 clusters of species, see below); hence, statistical analysis was performed on the raw (measured) $\delta^{15}\text{N}$ values. All data were statistically analyzed using SYSTAT 13. Values are presented as means \pm SD.

RESULTS

Diet

Kerguelen

The fresh component of the stomach contents of large wandering albatross chicks was composed almost equally of fish (48% by mass, 35% by number, all 30 samples pooled) and cephalopods (46 and 30%, respectively; Tables 1 & 2). Other food sources were negligible by mass, but crustaceans and gelatinous plankton accounted for a significant number of prey (13 and 15%, respectively).

We identified 112 fresh prey items (Table 2). The main fish was the Patagonian toothfish *Dissostichus eleginoides* (19% by number), with other species including skates and the morid *Antimora rostrata*. All

Table 1. Mass and composition of stomach contents of wandering albatross *Diomedea exulans* chicks at Kerguelen and Crozet Islands in 1998. Values are means \pm SD. A few stomach samples contained no or very few accumulated items, thus explaining the lower number of samples that were used to calculate the mean number of accumulated beaks per sample. Mann-Whitney *U*-tests were performed to compare the 2 localities, and Kruskal-Wallis *H*-tests compared seasons within each locality. Significant differences ($p < 0.05$) are highlighted in **bold**; na: not applicable

	Total	Statistics Kerguelen vs. Crozet		June 1998	August 1998	October 1998	Statistics Temporal changes	
		<i>U</i>	<i>p</i>				<i>H</i>	<i>p</i>
Kerguelen								
Stomach samples (n)	30			10	10	10		
Solid fraction (g)	388 \pm 185			353 \pm 182	461 \pm 205	350 \pm 162	1.9	0.391
Accumulated items (g)	54 \pm 29			35 \pm 25	51 \pm 16	76 \pm 30	9.2	0.010
Fresh items (g)	334 \pm 181			318 \pm 175	409 \pm 200	275 \pm 157	2.2	0.326
Fish (g)	161 \pm 203			175 \pm 217	181 \pm 242	128 \pm 159	0.3	0.865
Cephalopods (g)	152 \pm 158			126 \pm 144	192 \pm 171	140 \pm 165	0.8	0.676
Crustaceans (g)	0.4 \pm 1.0			0.7 \pm 1.6	0.2 \pm 0.4	0.3 \pm 0.6	0.3	0.853
Carrion (g)	9.2 \pm 27.8			16.5 \pm 40.9	9.7 \pm 26.3	1.4 \pm 3.0	0.1	0.966
Others (g)	10.7 \pm 33.4			0.2 \pm 0.7	26.9 \pm 53.7	5.0 \pm 15.9	5.9	0.051
Overall composition:								
Fish (%)	48.3			55.0	44.1	46.7	na	na
Cephalopods (%)	45.6			39.5	46.9	50.8	na	na
Crustaceans (%)	0.1			0.2	<0.1	0.1	na	na
Carrion (%)	2.8			5.2	2.4	0.5	na	na
Others (%)	3.2			<0.1	6.6	1.8	na	na
Accumulated beaks (g)	26.9 \pm 22.0			8.3 \pm 6.6	24.0 \pm 14.9	48.4 \pm 19.6	15.9	<0.0001
Accumulated beaks (n)	(27) 192 \pm 108			(8) 101 \pm 35	(10) 158 \pm 41	(9) 311 \pm 96	19.5	<0.0001
Crozet								
Stomach samples (n)	33			10	12	11		
Solid fraction (g)	673 \pm 322	758	<0.0001	836 \pm 297	766 \pm 281	424 \pm 245	9.5	0.009
Accumulated items (g)	104 \pm 59	771	<0.0001	62 \pm 27	115 \pm 49	130 \pm 72	9.1	0.011
Fresh items (g)	569 \pm 325	720	0.002	774 \pm 285	651 \pm 275	294 \pm 222	12.0	0.003
Fish (g)	68 \pm 184	309	0.009	84 \pm 185	105 \pm 254	13 \pm 26	3.5	0.174
Cephalopods (g)	497 \pm 286	851	<0.0001	689 \pm 265	536 \pm 228	280 \pm 226	10.2	0.006
Crustaceans (g)	0.4 \pm 1.4	428	0.202	0.7 \pm 2.0	0.3 \pm 0.7	0.5 \pm 1.5	0.4	0.805
Carrion (g)	3.4 \pm 16.0	428	0.111	0.0	9.4 \pm 26.2	0.0	na	na
Others (g)	0.2 \pm 0.7	404	0.039	0.0	0.0	0.5 \pm 1.2	na	na
Overall composition:								
Fish (%)	11.9	na	na	10.9	16.1	4.3	na	na
Cephalopods (%)	87.4	na	na	89.0	82.4	95.4	na	na
Crustaceans (%)	<0.1	na	na	<0.1	<0.1	0.2	na	na
Carrion (%)	0.6	na	na	0.0	1.4	0.0	na	na
Others (%)	<0.1	na	na	0.0	0.0	0.2	na	na
Accumulated beaks (g)	48.1 \pm 37.6	677	0.012	18.1 \pm 7.2	51.3 \pm 35.0	71.9 \pm 39.8	13.6	0.001
Accumulated beaks (n)	(30) 248 \pm 133	518	0.071	(10) 136 \pm 56	(10) 266 \pm 76	(10) 343 \pm 154	14.7	0.001

cephalopods were oceanic squids, with the main item being the onychoteuthid *Kondakovia longimana* (10%). Other squids included the histioteuthid *Histioteuthis atlantica* and the cranchiid *Taonius* sp. B (Voss). A significant number of the pelagic tunicate *Pyrosoma atlantica* was found in 3 food samples. Crustacean prey included large deep-sea mysids and females of large copepods that parasitize fish. Seasonal changes were observed neither in the mass of the solid and fresh fractions of food samples nor in the mass of the main prey groups, but sample sizes were relatively low (Table 1).

Crozet

The food of albatrosses from Crozet Islands was overall dominated by cephalopods (87% by fresh mass, 58% by number), with fish ranking second (12 and 29%, respectively; Tables 1 & 2). Fresh remains of cephalopods were found in all 33 samples. Other prey groups were negligible. We identified 119 fresh prey items (Table 2). All cephalopods were oceanic squids, with the main item being *K. longimana* (35% by number). Other squids included the ommastrephid *Martialia hyadesi*, the onychoteuthid *Onykia in-*

Table 2. Frequency of occurrence and numbers of fresh prey items identified from stomach contents of wandering albatross *Diomedea exulans* chicks at Kerguelen and Crozet Islands in 1998

Species	Kerguelen (n = 28)				Crozet (n = 33)			
	Occurrence		Number		Occurrence		Number	
	n	%	n	%	n	%	n	%
Carrion	7	25.0	7	6.3	2	6.1	2	1.7
Unidentified carrion	7	25.0	7	6.3	2	6.1	2	1.7
Fish	25	89.3	39	34.8	19	57.6	34	28.6
Rajidae								
<i>Bathyrja</i> sp.	4	14.3	4	3.6				
Paralepididae								
<i>Magnisudis prionosa</i>	1	3.6	1	0.9	1	3.0	1	0.8
Myctophidae								
<i>Lampadena notialis</i>	1	3.6	1	0.9				
Muraenolepididae								
<i>Muraenolepis marmoratus</i>	1	3.6	1	0.9	2	6.1	2	1.7
Macrouridae								
<i>Macrourus carinatus/holotrachys</i>	1	3.6	1	0.9	2	6.1	3	2.5
Moridae								
<i>Antimora rostrata</i>	2	7.1	2	1.8	2	6.1	2	1.7
<i>Halargyreus johnsonii</i>					1	3.0	1	0.8
Oreosomatidae								
Unidentified Oreosomatidae					2	6.1	2	1.7
Nototheniidae								
<i>Dissostichus eleginoides</i>	19	67.9	21	18.8	16	48.5	18	15.1
Channichthyidae								
<i>Champscephalus gunnari</i>	1	3.6	1	0.9				
Unidentified fish	5	17.9	7	6.3	5	15.2	5	4.2
Cephalopods	23	82.1	34	30.4	33	100.0	69	58.0
Ommastrephidae								
<i>Martialia hyadesi</i>	2	7.1	2	1.8	6	18.2	6	5.0
Onychoteuthidae								
<i>Kondakovia longimana</i>	6	21.4	11	9.8	20	60.6	42	35.3
<i>Onykia ingens</i>					3	9.1	3	2.5
Gonatidae								
<i>Gonatus antarcticus</i>					1	3.0	1	0.8
Histioteuthidae								
<i>Histioteuthis atlantica</i>	3	10.7	4	3.6				
<i>Histioteuthis eltaninae</i>					2	6.1	2	1.7
<i>Histioteuthis miranda</i>					1	3.0	1	0.8
Batoteuthidae								
<i>Batoteuthis skolops</i>					2	6.1	3	2.5
Cranchiidae								
<i>Taonius</i> sp. B (Voss)	2	7.1	5	4.5	1	3.0	1	0.8
Unidentified squid	12	42.9	12	10.7	10	30.3	10	8.4
Crustaceans	9	32.1	15	13.4	5	15.2	7	5.9
Mysida								
<i>Neognathophausia ingens</i>	3	10.7	3	2.7	2	6.1	2	1.7
<i>Neognathophausia gigas</i>					1	3.0	1	0.8
Unidentified <i>Neognathophausia</i>	5	17.9	5	4.5				
Amphipoda								
<i>Themisto gaudichaudii</i>					1	3.0	1	0.8
Copepoda								
Unidentified <i>Lophoura</i>	1	3.6	1	0.9	2	6.1	2	1.7
Unidentified <i>Sphyrion</i>	2	7.1	6	5.4				
Unidentified crustacean					1	3.0	1	0.8
Others	4	14.3	17	15.2	2	6.1	7	5.9
Pyrosomida								
<i>Pyrosoma atlantica</i>	3	10.7	16	14.3	2	6.1	7	5.9
Unidentified gelatinous plankton	1	3.6	1	0.9				
Total			112	100.0			119	100.0

gens, and the batoteuthid *Batoteuthis skolops*. The only significant fish prey was the Patagonian toothfish (15%), with other species including the rattail *Macrourus carinatus/holotrachys*, morids, and oreosomatids. The tunicate *P. atlantica* was found in 2 food samples. Crustacean prey included large mysids and parasitic copepods.

Seasonal mass variations were observed in various components of the food samples. While mass of accumulated items increased with time, masses of the solid fraction and fresh items decreased from June to October (by 49 and 62%, respectively). The decreases resulted from a 59% drop in the mass of cephalopods in food samples over the chick-rearing period, with no concomitant mass changes in other prey groups (Table 1).

Comparison between sites

The mass of food samples (solid fraction) was overall 73% higher at Crozet than at Kerguelen (Table 1). The difference was driven by cephalopods rather than fish, with mass of fresh squids being 3.3 times higher in Crozet than Kerguelen food samples. Accordingly, masses of accumulated items and of accumulated beaks were higher in Crozet samples, as was the number of accumulated cephalopod beaks.

Plastic particles were found in 15 (50%) and fishery-related items (bait remains and hooks/snoods) were found in 18 (55%) stomach contents from Kerguelen and Crozet Islands. Only 1 Kerguelen sample contained 1 hook, thus contrasting with the higher hook prevalence in Crozet samples (17 hooks in 13 [39%] samples, up to 4 hooks in 1 sample, equality of proportion tests, $Z = 3.44$, $p = 0.001$). Notably, some hooks were intact, but most were partially corroded. Hooks were attached or not with their corresponding snoods (branch lines). In a few cases, the past presence of hooks

in food samples was indicated by the finding of knotted snoods without attached hooks, meaning that the hooks had been completely digested in the birds' stomach after ingestion.

Accumulated cephalopod beaks

The mass and number of accumulated beaks increased from June to October at both localities (Table 1). A total of 12 860 accumulated beaks were sorted and analyzed from the 63 food samples. The number included 5118 and 7422 identifiable beaks from Kerguelen and Crozet Islands, respectively. Fifty different cephalopod taxa were identified, with many more squids (Oegopsida, 47 taxa) than octopu-

ses (Octopoda, 3 taxa; Table 3). Almost all beaks were fully darkened, indicating that they belonged to adult individuals and not to juvenile and immature specimens.

Kerguelen

Forty-one cephalopod taxa were identified in Kerguelen food samples. Three main species (>10% by number) together accounted for 52.6% of the total number of accumulated beaks, by decreasing order: *H. atlantica* (29.7%), *Galiteuthis glacialis* (12.5%), and *K. longimana* (10.4%). Fourteen common species (>1%) together accounted for 39.2% by number, including *H. eltaninae* (7.2%), *Taonius* sp. B (Voss)

Table 3. Cephalopod diet of the wandering albatross *Diomedea exulans* at Kerguelen and Crozet Islands in 1998. Values are frequency of occurrence and numbers of accumulated upper and lower beaks that were sorted from stomach samples of large chicks. Equality of proportion tests (large-sample tests) were performed to compare relative beak numbers between the 2 localities. Significant differences ($p < 0.05$) are highlighted in **bold**; na: not applicable

Species	Kerguelen (n = 30)				Crozet (n = 33)				Statistics on numbers (%)	
	Occurrence		Number		Occurrence		Number		Z	p
	n	%	n	%	n	%	n	%		
Decapoda										
Architeuthidae										
<i>Architeuthis dux</i>	21	70.0	50	1.0	5	15.2	9	0.1	6.88	<0.0001
Ommastrephidae										
<i>Illex argentinus</i> (bait)					3	9.1	6	0.1	na	na
<i>Martialia hyadesi</i>	29	96.7	246	4.8	32	97.0	369	5.0	0.42	0.674
<i>Todarodes</i> sp.	16	53.3	65	1.3	3	9.1	9	0.1	8.26	<0.0001
Onychoteuthidae										
<i>Filippovia knipovitchi</i>	26	86.7	132	2.6	31	93.9	261	3.5	2.96	0.003
<i>Kondakovia longimana</i>	28	93.3	531	10.4	33	100.0	2594	35.0	31.27	<0.0001
<i>Moroteuthopsis</i> sp. B (Imber)	6	20.0	10	0.2					na	na
<i>Notonykia africanae</i>	1	3.3	2	<0.1	3	9.1	5	0.1	0.66	0.510
<i>Onychoteuthis banksii</i> complex	2	6.7	5	0.1	1	3.0	1	<0.1	2.12	0.034
<i>Onychoteuthis</i> sp. 2 (Imber)	1	3.3	1	<0.1	1	3.0	1	<0.1	0.26	0.792
<i>Onychoteuthis</i> sp. C (Imber)	12	40.0	20	0.4	2	6.1	3	<0.1	4.51	<0.0001
<i>Onykia ingens</i>	8	26.7	16	0.3	33	100.0	332	4.5	13.94	<0.0001
<i>Onykia robsoni</i>	16	53.3	47	0.9	3	9.1	5	0.1	7.29	<0.0001
Pholidoteuthidae										
<i>Pholidoteuthis massyae</i>					1	3.0	2	<0.1	na	na
Psychroteuthidae										
<i>Psychroteuthis glacialis</i>	3	10.0	7	0.1					na	na
Brachioteuthidae										
<i>Slosarczykovia circumantarctica</i>					4	12.1	4	0.1	na	na
Gonatidae										
<i>Gonatus antarcticus</i>	22	73.3	84	1.6	22	66.7	108	1.5	0.83	0.404
Ancistrocheiridae										
<i>Ancistrocheirus lesueurii</i>	13	43.3	34	0.7	8	24.2	14	0.2	4.24	<0.0001
Lycoteuthidae										
<i>Lycoteuthis lorigera</i>					2	6.1	2	<0.1	na	na
Octopoteuthidae										
<i>Octopoteuthis</i> sp.	9	30.0	47	0.9	2	6.1	3	<0.1	7.67	<0.0001
<i>Taningia danae</i>	16	53.3	80	1.6	6	18.2	8	0.1	9.60	<0.0001
Lepidoteuthidae										
<i>Lepidoteuthis grimaldii</i>	2	6.7	3	0.1	6	18.2	13	0.2	1.80	0.072

(continued on next page)

Table 3 (continued)

Species	Kerguelen (n = 30)				Crozet (n = 33)				Statistics on numbers (%)	
	Occurrence		Number		Occurrence		Number		Z	p
	n	%	n	%	n	%	n	%		
Histioteuthidae										
<i>Histioteuthis atlantica</i> (lower beaks)	29	96.7	799	15.6	28	84.8	142	1.9	28.62	<0.0001
<i>Histioteuthis bonnellii corpuscula</i> (lower beaks)	16	53.3	21	0.4	20	60.6	45	0.6	1.49	0.136
<i>Histioteuthis b. corpuscula/atlantica</i> (upper beaks)	28	93.3	720	14.1	23	69.7	165	2.2	25.45	<0.0001
<i>Histioteuthis eltaninae</i>	27	90.0	371	7.2	33	100.0	1721	23.2	23.53	<0.0001
<i>Histioteuthis macrohista</i>	17	56.7	40	0.8	5	15.2	6	0.1	6.38	<0.0001
<i>Histioteuthis miranda</i>	20	66.7	61	1.2	17	51.5	49	0.7	3.14	0.002
<i>Histioteuthis</i> sp.	2	6.7	2	<0.1	3	9.1	4	0.1	0.37	0.709
<i>Stigmatoteuthis hoylei</i>	3	10.0	7	0.1	2	6.1	4	0.1	1.54	0.123
Neoteuthidae										
<i>Alluroteuthis antarcticus</i>	28	93.3	170	3.3	30	90.9	187	2.5	2.65	0.008
<i>Nototeuthis dimegacotyle</i>	13	43.3	37	0.7	8	24.2	13	0.2	4.78	<0.0001
Cycloteuthidae										
<i>Cycloteuthis sirventi</i>	27	90.0	166	3.2	20	60.6	69	0.9	9.39	<0.0001
<i>Discoteuthis laciniosa</i>					2	6.1	4	0.1	na	na
Mastigoteuthidae										
<i>Mastigoteuthis psychrophila</i>	14	46.7	30	0.6	11	33.3	18	0.2	3.06	0.002
<i>Mastigoteuthis</i> sp. A (Imber)	3	10.0	7	0.1					na	na
Chiroteuthidae										
<i>Asperoteuthis lui</i>	8	26.7	22	0.4	20	60.6	64	0.9	2.88	0.004
<i>Chiroteuthis veranyi</i>	12	40.0	32	0.6	16	48.5	39	0.5	0.73	0.464
<i>Chiroteuthis</i> sp. F (Imber)					4	12.1	6	0.1		na
Batoteuthidae										
<i>Batoteuthis skolops</i>	22	73.3	68	1.3	30	90.9	249	3.4	7.10	<0.0001
Cranchiidae										
<i>Galiteuthis glacialis</i>	30	100.0	640	12.5	33	100.0	660	8.9	6.52	<0.0001
<i>Galiteuthis</i> sp. 3 (Imber)	5	16.7	7	0.1	2	6.1	4	0.1	1.54	0.123
<i>Galiteuthis</i> stC sp. (Imber)	3	10.0	6	0.1					na	na
<i>Mesonychoteuthis hamiltoni</i>	3	10.0	4	0.1	4	12.1	9	0.1	0.74	0.461
<i>Taonius</i> sp. B (Voss)	18	60.0	361	7.1	19	57.6	125	1.7	15.31	<0.0001
<i>Taonius</i> sp. (Clarke)	20	66.7	101	2.0	17	51.5	73	1.0	4.66	<0.0001
<i>Teuthowenia pellucida</i>	22	73.3	52	1.0	4	12.1	5	0.1	7.76	<0.0001
Oegopsida sp. A (Cherel)					2	6.1	3	<0.1	na	na
Octopoda										
Octopodidae										
Undetermined Octopodidae	7	23.3	10	0.2	2	6.1	4	0.1	2.33	0.020
Stauroteuthidae										
<i>Stauroteuthis gilchristi</i>					1	3.0	2	<0.1	na	na
Cirrata sp. A (Cherel)					1	3.0	2	<0.1	na	na
Unknown uneroded beaks	4	13.3	4	0.1	1	3.0	1	<0.1	1.78	0.075
Total			5118	100.0			7422	100.0		
Unidentifiable beaks (eroded)	19	63.3	115		23	69.7	205			

(7.1%), and some very large species like *Taningia danae* and juveniles of the giant squid *Architeuthis dux* (Table 3). Comparisons highlighted seasonal variations in squid eaten by wandering albatrosses. The proportions of *K. longimana* and *H. atlantica* increased progressively from June to October (from 5.1 to 13.0% and from 12.2 to 18.1%; equality of proportion tests [large-sample tests], $Z = 6.28$ and 3.92 , respectively, both $p < 0.0001$), while that of *G. glacialis* decreased (from 19.6 to 7.1%, $Z = 10.42$, $p < 0.0001$). Two taxa were either absent (*Octopoteuthis* sp.) or rare (*Taonius* sp. B [Voss]) in June and August

samples but became common (1.7%) and main (12.7%) items, respectively, in October samples.

Crozet

Forty-six cephalopod taxa were identified in Crozet food samples. Two main species (>10%) together accounted for 58.1% of the total number of beaks, namely *K. longimana* (35.0%) and *H. eltaninae* (23.2%). Nine common species (>1%) together accounted for 36.0% by number, including *G. glacialis*

lis (8.9%) and *M. hyadesi* (5.0%) (Table 3). Marked seasonal variations in the proportions of beaks included a progressive increase in *K. longimana* from June to October (from 12.4 to 48.5%, $Z = 23.02$, $p < 0.0001$), while *H. eltaninae* and *G. glacialis* decreased (from 30.7 to 17.6% and from 18.3 to 4.4%, $Z = 9.96$ and 15.61 , respectively, both $p < 0.0001$). *Taonius* sp. B (Voss) was a rare item in June (0.4%) and August (0.6%), but it became a common squid prey in October (3.1%). Three samples (1 in June and 2 in August) contained beaks of the ommastrephid *Illex argentinus*, which is one of the most common bait species used by toothfish longliners.

Comparison between sites

Wandering albatrosses preyed overall upon the same cephalopod taxa at both localities, but in different proportions. Four oegopsid families accounted for 83.4 and 88.9% of the total number of cephalopod prey at Kerguelen and Crozet, respectively. Birds from Kerguelen fed more on histioteuthids (39.5 versus 28.8%, $Z = 12.52$, $p < 0.0001$), cranchiids (22.9 versus 11.8%, $Z = 16.50$, $p < 0.0001$), and ommastrephids (6.1 versus 5.2%, $Z = 2.17$, $p = 0.030$), but much less on onychoteuthids (14.9 versus 43.1%, $Z = 33.39$, $p < 0.0001$) than Crozet albatrosses. At the species level, Kerguelen samples included more beaks of *H. atlantica* and *G. glacialis*, and fewer beaks of *K. longimana* and *H. eltaninae* than Crozet samples (Table 3).

Prey size

The range of smallest and largest cephalopods caught by wandering albatrosses were specimens of *H. macrohista* (estimated DML: 5.1 cm, Crozet) and from *A. dux* (125 cm, Kerguelen), respectively. The lightest and heaviest squid were individuals from *Slosarczykovia circumantarctica* (estimated body mass: 0.006 kg, Crozet) and again from *A. dux* (body mass: 45.5 kg, Kerguelen), respectively. Measured LRL from beaks of the same squid species were not statistically different between the 2 localities in 11 species and they were significantly different in 14 species, with cephalopods from Kerguelen being larger in 9 species (Table 4). LRL from the main 4 cephalopods (*K. longimana*, *H. atlantica*, *H. eltaninae*, *G. glacialis*) varied significantly among localities, but the differences were small and their length-frequency distributions demonstrate that wandering

albatrosses from Kerguelen and Crozet overall preyed upon the same size classes (Figs. 1 & 2). Those 4 squid species differed greatly in their estimated body masses in the following increasing order: *H. eltaninae* (0.07 ± 0.02 kg, Crozet) < *G. glacialis* (0.11 ± 0.01 kg, Kerguelen) < *H. atlantica* (0.37 ± 0.10 kg, Kerguelen) << *K. longimana* (2.17 ± 0.80 and 2.69 ± 1.03 kg at Crozet and Kerguelen Islands, respectively).

In contrast to cephalopods, only a few dietary remains allowed estimation of fish size. Fish length and body mass averaged 43 ± 15 cm and 1.37 ± 1.68 kg ($n = 10$), respectively, with the smallest and largest specimens being 1 icefish *Champscephalus gunnari* (26 cm SL, 131 g) and 1 Patagonian toothfish (67 cm SL, 4.55 kg), respectively.

Satellite tracking

Breeding wandering albatrosses were tracked during 17 (9 birds) and 46 (45 birds) foraging trips at Kerguelen and Crozet Islands, respectively. Trip duration (4.0 ± 2.9 and 5.6 ± 3.8 d, respectively), maximum range from the colony (569 ± 423 and 624 ± 358 km) and the total distance covered during a single trip (1984 ± 1392 and 2522 ± 1904 km) were not significantly different between Kerguelen and Crozet birds (Mann-Whitney $U = 477$, 462, and 440, $p = 0.185$, 0.272, and 0.453, respectively). Breeding wandering albatrosses from both localities remained essentially at latitudes 42 to 52° S that correspond to the Subantarctic Zone sensu lato, between the STF in the north and the PF in the south (Park & Gamberoni 1997). A few birds crossed the STF and foraged in warmer waters of the Subtropical Zone (Fig. 3). Albatrosses from the 2 localities segregated longitudinally. The smaller number of Kerguelen birds foraged mainly in the vicinity of the archipelago (62–80° E), while the higher number of Crozet birds showed a wider longitudinal range (40–68° E), with some individuals foraging in western Kerguelen waters. Consequently, kernel analysis indicated a larger overlap of Crozet birds over the foraging grounds of Kerguelen albatrosses (0, 19, and 37% for 50, 75, and 95% location densities, respectively) than the reverse (0, 11, and 18%; Fig. 3).

Stable isotopes

Feather isotopic values of wandering albatross chicks were either not significantly different ($\delta^{13}\text{C}$:

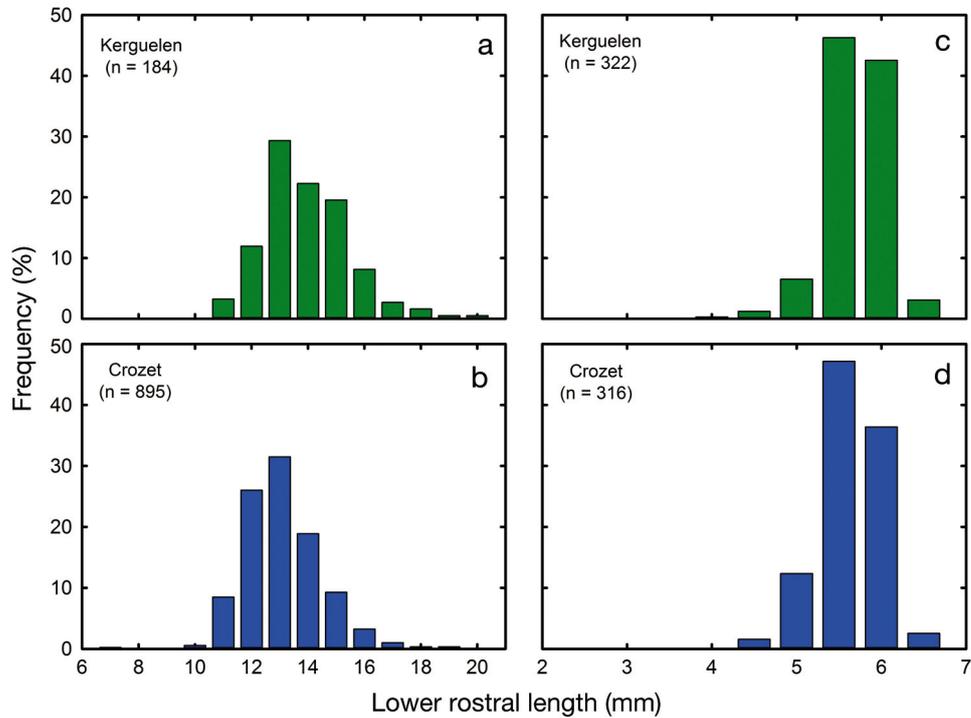


Fig. 1. Length-frequency distribution of lower rostral length of (a,b) the onychoteuthid squid *Kondakovia longimana* and (c,d) the cranchiid squid *Galiteuthis glacialis* in the diet of wandering albatross *Diomedea exulans* chicks from (a,c) Kerguelen and (b,d) Crozet Islands

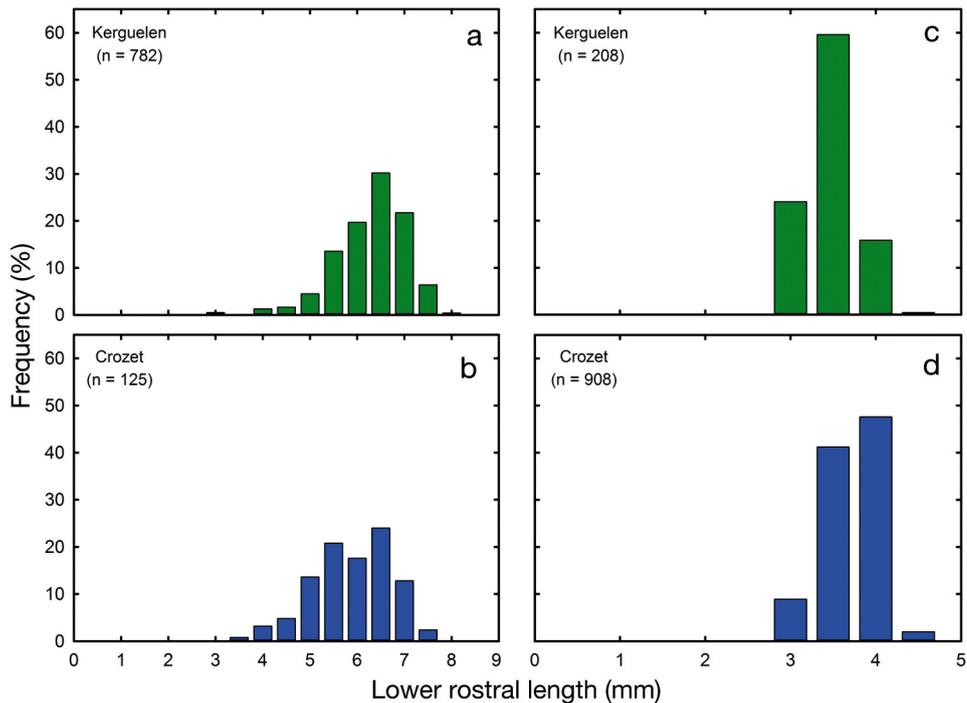


Fig. 2. Length-frequency distribution of lower rostral length of the histioteuthid squids (a,b) *Histioteuthis atlantica* and (c,d) *H. eltaninae* in the diet of wandering albatross *Diomedea exulans* chicks from (a,c) Kerguelen and (b,d) Crozet Islands

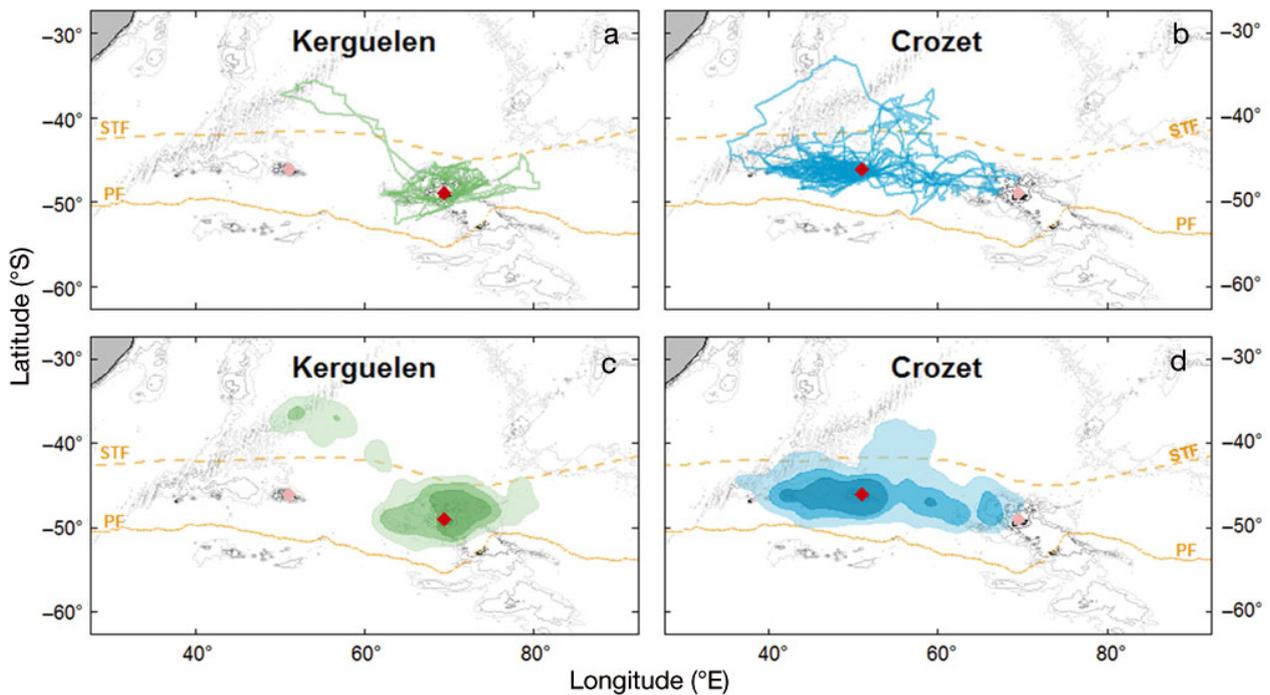
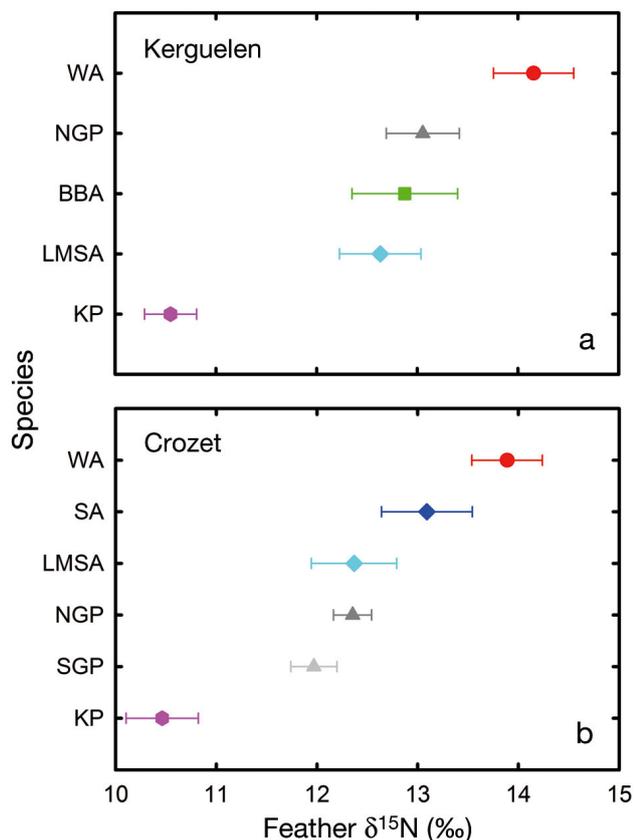


Fig. 3. (a,b) Satellite tracks and (c,d) the corresponding density contours resulting from kernel analysis (decreasing darker tone: 50, 75, and 95 % location densities of the core foraging area) of breeding wandering albatrosses *Diomedea exulans* from (a,c) Kerguelen and (b,d) Crozet Islands in 1998. PF: Polar Front; STF: Subtropical Front



$n = 15$ and 21 , -19.3 ± 0.4 and -19.4 ± 0.4 ‰ at Kerguelen and Crozet Islands, respectively, 2-sample t -test, $t = 1.12$, $p = 0.272$) or marginally significantly different ($\delta^{15}\text{N}$: 14.2 ± 0.4 and 13.9 ± 0.3 ‰, respectively, $t = 2.13$, $p = 0.041$) between the 2 localities.

Feather isotopic values of albatrosses, giant petrels, and king penguins segregated in both their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (ANOVA, Kerguelen: $F_{4,67} = 53.68$ and 88.48 , Crozet: $F_{5,68} = 72.84$ and 161.65 , respectively, all $p < 0.0001$; Fig. 4). When compared to other large sympatric Procellariiformes and to king penguins, wandering albatross chicks presented higher dorsal body feather $\delta^{15}\text{N}$ values at both Kerguelen (post hoc Tukey's honestly significant difference tests, all $p \leq 0.003$) and Crozet Islands (all $p < 0.0001$).

Fig. 4. Feather $\delta^{15}\text{N}$ values of large Procellariiformes and king penguins *Aptenodytes patagonicus* (KP) at (a) Kerguelen and (b) Crozet Islands. Species were deliberately placed in a trophic sequence of increasing $\delta^{15}\text{N}$ values. Values are means \pm SD. BBA: black-browed albatross *Thalassarche melanophris*; LMSA: light-mantled sooty albatross *Phoebastria palpebrata*; NGP: northern giant petrel *Macronectes halli*; SA: sooty albatross *P. fusca*; SGP: southern giant petrel *M. giganteus*; WA: wandering albatross *Diomedea exulans*

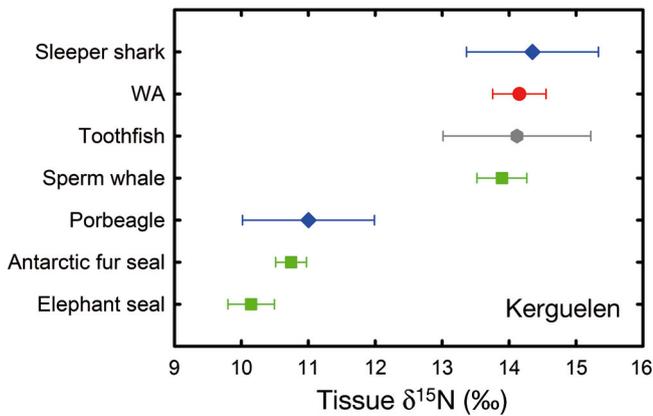


Fig. 5. Tissue $\delta^{15}\text{N}$ values of predators from Kerguelen Islands. Species were deliberately placed in a trophic sequence of increasing $\delta^{15}\text{N}$ values. Values are means \pm SD. WA: wandering albatross *Diomedea exulans*

Tissue $\delta^{15}\text{N}$ values of wandering albatross and of non-avian predators from the Kerguelen Islands segregated in their $\delta^{15}\text{N}$ values (Kruskal-Wallis: $H = 90.17$, $p < 0.0001$) (Fig. 5). Conover-Inman tests for all pairwise comparisons indicated that the mean $\delta^{15}\text{N}$ value of wandering albatrosses was higher than $\delta^{15}\text{N}$ values of elephant seals, Antarctic fur seals, and porbeagle sharks (all $p < 0.0001$), but it was not significantly different from the values of sperm whales, Patagonian toothfish, and sleeper sharks ($p = 0.566$, 0.757 , and 0.441 , respectively).

DISCUSSION

Diet

Food of wandering albatross chicks includes primarily fish and cephalopods, with carrion ranking third (reviewed in Table 5). Fish and cephalopods were equally important at the Kerguelen Islands, in agreement with studies conducted at 2 other major breeding sites, South Georgia and Marion Island. In contrast, food composition at the Crozet Archipelago is unique, being consistently dominated by cephalopods in multiple studies over different years. Among other *Diomedea* albatrosses, a predominance of cephalopods was also found in the 2 species of the neritic southern *D. epomophora* and northern *D. sanfordi* royal albatrosses in the Pacific Ocean. Food mass and composition of wandering albatrosses at the Kerguelen Islands did not present seasonal variations, while significant changes were found at the Crozet Islands. There, the fresh mass of food samples decreased considerably during the late chick-rearing period, with the cephalopod component of the diet dropping by 59%. This, together with a lower feeding rate and declining adult body mass (Weimerskirch & Lys 2000), suggests either a lowering of feeding conditions at sea from August onwards or that chick provisioning behavior changes as chicks approach fledging mass and adults prepare for flight feather molt.

Table 5. Review of the available information on mass and composition of fresh food from stomach contents of *Diomedea* albatrosses; nd: no data

Locality	Sampling year	Stomach samples (n)	Solid mass mean \pm SD (g)	Fresh mass mean \pm SD (g)	Fish (%)	Cephalopods (%)	Others (%)	Reference
Wandering albatross <i>D. exulans</i>								
South Georgia	1983 & 1984	79	nd	nd	41.5	39.5	20.0	Prince & Morgan (1987)
	1999	18	426	nd	53.1	42.1	4.8	Xavier et al. (2004)
	2000 (Mar–Apr)	9	nd	nd	45.6	32.0	22.3	Xavier et al. (2003b)
	2000 (May–Aug)	20	630	nd	84.3	11.3	4.4	Xavier et al. (2004)
	2009	35	nd	nd	59.4	38.4	2.2	Ceia et al. (2012)
Marion	1988–1989	50	523 \pm 425	nd	36.5	58.6	4.9	Cooper et al. (1992)
Crozet	1982	37	nd	297 \pm 339	14.9	76.7	8.4	Ridoux (1994)
	1992	24	511 \pm 243	427 \pm 216	24.3	72.4	3.3	Weimerskirch et al. (1997b)
	1994	10	nd	623 \pm 336	10.7	75.9	13.4	Cherel & Weimerskirch (1999, unpubl. data)
Kerguelen	1998	33	673 \pm 322	569 \pm 325	11.9	87.4	0.7	This study
	1998	30	388 \pm 185	334 \pm 181	48.3	45.6	6.1	This study
Northern royal albatross <i>D. sanfordi</i>								
Chatham	nd	nd	nd	nd	14	85	1	Marchant & Higgins (1990)
New Zealand	nd	nd	nd	nd	15	80	5	Marchant & Higgins (1990)
Southern royal albatross <i>D. epomophora</i>								
Campbell	nd	nd	nd	nd	21	75	4	Marchant & Higgins (1990)

Fish prey of wandering albatrosses is difficult to identify due to their low number and digestion state. However, 2 consistent features are notable: (1) individual fishes are of medium to large size (>10 cm), and (2) most of them belong to deep-water benthopelagic species (Croxall et al. 1988, Cooper et al. 1992, Xavier et al. 2003b, 2004, Ceia et al. 2012, this study). The prevalence of deep-sea fish is also indicated by the occurrence of their associated large female parasitic copepods in food samples (Ridoux 1994, this study). How albatrosses catch deep-sea fish remains unclear (Croxall et al. 1988, Cherel et al. 2000). Some are undoubtedly eaten in association with fishing vessels (Nel et al. 2002), but they were already natural prey of albatrosses before development of fisheries in the Southern Ocean (Ridoux 1994, Weimerskirch et al. 1997b). Wandering albatrosses are surface-feeders and scavengers (Prince & Morgan 1987, Cherel & Klages 1998). They thus probably feed on dead, dying, or incapacitated fish that rise to the surface, which is the most likely explanation for the abundance of deep-sea squids in their diet (Nesis et al. 1998, Cherel & Weimerskirch 1999, Xavier & Croxall 2007).

Diomedea albatrosses are the seabirds that prey upon the largest diversity of cephalopods (Imber 1992, Croxall & Prince 1996). Accumulated beaks from food samples of wandering albatross from Kerguelen Islands confirm this typical feature. Overall, wandering albatrosses from different localities fed on the same cephalopod species, but in different proportions. A dietary review highlights 6 main characteristics of cephalopods eaten by *Diomedea* albatrosses (Table 6). First,

Table 6. Review of the available information on the main cephalopod prey (>10% by number in at least 1 study) of *Diomedea* albatrosses. Studies that included <10 samples (stomach contents and/or boluses) and/or <500 accumulated beaks were excluded. Only lower beaks were numbered and identified. Beaks from *Histioteuthis* type B (Clarke) refer to the sum of those from *H. atlantica* and *H. eltaninae*. Percentages >10% are indicated in **bold**

Species & locality	Years of sampling	Number of samples (lower beaks)	<i>Illex argentinus</i>	<i>Filipovia knipovitchi</i>	<i>Kondakovia longimana</i>	<i>Onychia ingens</i>	<i>H. atlantica</i>	<i>H. eltaninae</i>	<i>Histioteuthis</i> type B (Clarke)	<i>Galioteuthis glacialis</i>	<i>Taonius</i> sp. B (Voss)	Benthic octopods	Reference
Wandering albatross <i>D. exulans</i>													
South Georgia	1975–1978	22 (1491)	0.3	1.8	29.3	0.1	8.0	7.9	n/a	4.9	15.1	0.1	Imber (1992)
	1983–1984	79 (3707)	22.8	1.3	12.4	0.7	4.4	14.1	n/a	17.7	2.0	0.2	Imber (1992)
	1989–1999	269 (15355)	2.3	3.2	21.5	0.1	na	na	19.5	4.5	20.4	0.1	Xavier et al. (2003a)
Marion	1988–1989	50 (773)	na	14.4	16.2	3.1	3.9	18.1	n/a	14.0	2.2	0.0	Cooper et al. (1992)
Crozet	1982	37 (1238)	na	3.5	52.5	4.8	na	na	15.1	4.9	1.2	0.0	Ridoux (1994)
	1992	32 (1057)	na	2.8	9.9	38.7	6.4	12.8	n/a	9.8	0.2	0.0	Unpubl. data
	1994	32 (723)	na	2.2	50.4	5.0	3.9	6.0	n/a	10.3	0.1	0.0	Unpubl. data
	1998	33 (3867)	na	3.4	34.0	4.1	3.3	25.6	n/a	8.9	1.7	0.1	This study
Kerguelen	1998	30 (2657)	na	2.5	10.1	0.3	30.1	8.0	n/a	12.3	6.8	0.2	This study
Tristan albatross <i>D. dabbenena</i>													
Gough	1979	14 (559)	0.0	1.8	0.2	2.0	54.0	0.0	n/a	1.1	7.3	0.0	Imber (1992)
Antipodean albatross <i>D. antipodensis antipodensis</i>													
Antipodes	1978 (1985)	26 (3011)	na	7.8	2.6	1.7	20.3	16.3	n/a	13.4	10.2	0.0	Imber (1992)
	2001	25 (2374)	na	9.4	1.7	1.3	22.9	13.1	n/a	13.3	8.6	0.1	Xavier et al. (2014)
Gibson's albatross <i>D. antipodensis gibsoni</i>													
Auckland	2001	23 (1882)	na	0.9	0.3	4.4	30.2	1.6	n/a	8.7	7.7	0.0	Xavier et al. (2014)
Northern royal albatross <i>D. sanfordi</i>													
Chatham	1973–1983	34 (987)	na	0.0	0.0	31.8	45.1	0.1	n/a	0.0	0.5	0.2	Imber (1999)
New Zealand	1981–1996	151 (2134)	na	0.1	0.1	14.8	34.4	0.5	n/a	5.8	5.6	23.4	Imber (1999)
Southern royal albatross <i>D. epomophora</i>													
Campbell	1974–1997	79 (1394)	na	0.7	3.9	18.9	25.5	2.1	n/a	5.2	23.1	2.9	Imber (1999)

birds feed almost exclusively on adult squids, as indicated by both the wholly darkened beaks and the corresponding estimated body sizes of cephalopods (Cherel & Weimerskirch 1999, Xavier et al. 2003a). Second, albatrosses target oceanic squids (Cherel & Klages 1998), with the exception of the northern royal albatrosses that prey significantly on benthic octopodids over the New Zealand shelf (Imber 1999). Third, 3 families dominated the squid diet, namely Onychoteuthidae, Histioteuthidae, and Cranchiidae. The same 3 families constitute a significant part of the food of cetaceans, including the sperm whale *Physeter macrocephalus*, in the Southern Ocean (Clarke 1980, 1996). Fourth, *Diomedea* species forage on several species of histioteuthids, with *Histioteuthis eltaninae* being generally the main species in southern waters and *H. atlantica* farther north. The only latitudinal exception is the predominance of *H. atlantica* at Kerguelen Islands (this study). Fifth, while Tristan, Antipodean *D. antipodensis antipodensis*, and Gibson's *D. a. gibsoni* albatrosses do not prey significantly on onychoteuthids, wandering and royal albatrosses target primarily *Kondakovia longimana* and *Onychia ingens*, respectively, which, owing to their large size, form a major part of the birds' diet by mass (Cooper et al. 1992, Imber 1999, Xavier et al. 2003a). Sixth, the southernmost *Diomedea* species prey upon large numbers of *Galiteuthis glacialis* and/or *Taonius* sp. B (Voss), while Tristan and northern royal albatrosses do not feed significantly on cranchiids (Table 6).

Seasonal dietary changes of wandering albatrosses included consistent variations in the proportions of some squid beaks in both Kerguelen and Crozet food samples. Three species illustrate well those temporal variations and the usefulness of cephalopod consumers as biological samplers of poorly known oceanic squids (Cherel & Weimerskirch 1999). The proportion of beaks of *G. glacialis* decreased over time, those of *K. longimana* increased, while beaks of *Taonius* sp. B (Voss) occurred in significant numbers in October samples only. Beaks were from adult squids, and post-spawning moribund or dead cranchiids and onychoteuthids are known to rise to and float at the sea surface where they become available for the birds (Nesis et al. 1998, Lynnes & Rodhouse 2002). Our study confirms that *K. longimana* reproduces during the winter months not only in Crozet (Cherel & Weimerskirch 1999) but also in Kerguelen waters. Our results also indicate that *G. glacialis* spawns in fall and early winter, and *Taonius* sp. B (Voss) in late winter in the southern Indian Ocean.

Foraging zones and habitat

Biogeography of fresh prey indicates that adults fed their chicks with cephalopods and fishes caught in slope and oceanic waters surrounding the Kerguelen and Crozet Islands (Cherel et al. 2004, 2011, Duhamel et al. 2005). Feeding primarily in subantarctic waters is also supported by feather isotopic values, with all chick $\delta^{13}\text{C}$ values clustering from -20.3 to -18.5% , i.e. between the estimated isotopic positions of the PF and STF (Jaeger et al. 2010). Indeed, satellite-tracked birds in late incubation and during the brooding period in 1998 foraged mainly in a radius of ~ 600 km around the archipelagoes. Wandering albatrosses from Kerguelen segregated at sea from Crozet birds by favoring eastern Kerguelen waters, while Crozet albatrosses primarily foraged in western Crozet waters (Fig. 4). Some Crozet birds foraged off western Kerguelen, thus inducing an overlap between the foraging grounds of wandering albatrosses from the 2 archipelagoes (Weimerskirch 1998, Weimerskirch et al. 2015, this study).

A close examination of accumulated beaks highlights 2 relevant features about the latitudinal feeding zones of wandering albatrosses during the winter months. (1) The near lack of beaks from the endemic Antarctic species *Psychroteuthis glacialis* (Collins & Rodhouse 2006) precludes birds feeding significantly at high latitudes in winter. This is in agreement with satellite tracking and isotopic investigations during incubation at the Crozet Islands showing that only old males forage in Antarctica, while younger males and females favor subantarctic and subtropical waters, respectively (Lecomte et al. 2010, Jaeger et al. 2014, Weimerskirch et al. 2014). (2) Some cephalopods were temperate and warm-water species (*Ancistrocheirus lesueurii*, *H. bonnellii corpuscula*, *H. miranda*; Voss et al. 1998, Young et al. 2016), thus indicating foraging north of the STF. There is thus a mismatch between fresh items that were caught locally and some accumulated items that were taken farther away in warmer waters. The mismatch is easily explained by breeding wandering albatrosses performing long looping trips during which they first feed for themselves, with the resulting accumulated beaks being regurgitated to the chicks together with fresh prey that are caught either on the way back to the colonies or during shorter commuting trips to nearby waters (Weimerskirch et al. 1997b, Weimerskirch 1998). A main and expected conclusion of satellite tracking, prey biogeography, and stable isotopes is that wandering albatrosses from Kerguelen behave at sea

essentially as those from Crozet and Marion Islands during the chick-rearing period, with dietary differences being likely related to the local environments, such as the predominance of *H. atlantica* over *H. eltaninae* in Kerguelen waters and the reverse in Crozet waters (Table 3; Cherel et al. 2004).

Wandering albatross as an apex predator/scavenger

At both Kerguelen and Crozet Islands, wandering albatrosses had higher dorsal body feather $\delta^{15}\text{N}$ values than smaller albatrosses and giant petrels, the major Southern Ocean seabird scavengers. Identical isotopic results were found in South Georgia, where the wandering albatross dominates over the northern and southern giant petrels and over the black-browed, grey-headed, and light-mantled sooty albatrosses (Y. Cherel & R. A. Phillips unpubl. data). Hence, whatever the breeding locality, the wandering albatross is the species with the highest trophic position within the communities of oceanic seabirds, which also include many species of meso-predators, such as penguins and smaller Procellariiformes (Blévin et al. 2013).

Tissue $\delta^{15}\text{N}$ comparison amongst various predators from the Kerguelen Islands highlighted the high trophic position of the wandering albatross. The species showed higher $\delta^{15}\text{N}$ values than the king penguin, other myctophid eaters (elephant seal and Antarctic fur seal), and the porbeagle shark that feeds on both micronektonic fish and juvenile squids (Lea et al. 2002, Cherel & Duhamel 2004, Cherel et al. 2008). In contrast, the high $\delta^{15}\text{N}$ value of wandering albatross clustered with those from 3 large to very large predators, the Patagonian toothfish, sleeper shark, and sperm whale. Wandering albatross, toothfish, and sleeper shark are opportunistic predators and scavengers (Cherel & Duhamel 2004, Cherel et al. 2004), while sperm whales target primarily adult squids (Mikhalev et al. 1981). Together with the colossal squid *Mesonychoteuthis hamiltoni* (Cherel et al. 2008), the 4 species thus constitute the apex consumers of the pelagic ecosystem in Kerguelen waters.

Relationships with fisheries

Anthropogenic items were found in half of the food samples collected in 1998. They included plastic fragments, bait remains, and hooks/snoods. Plastic

pieces are common in stomach contents of seabirds (Wilcox et al. 2015), and they are more frequent in *Diomedea* species than in smaller albatrosses (Jiménez et al. 2015). Wandering albatross chicks from Kerguelen and Crozet Islands contained low plastic loads in their stomach, which contrasts with the higher loads of albatross chicks from the North Pacific (Auman et al. 1998, Young et al. 2009) and minimizes potential deleterious mechanical and physiological effects from plastic consumption.

Bait used on toothfish longlines includes fish and squids that do not occur naturally in the southern Indian Ocean. Accordingly, sardine *Sardinops* sp. and *Illex argentinus* have been identified in the diet of the commonest seabird attracted by fishing vessels, the white-chinned petrel *Procellaria aequinoctialis*, from Crozet and Kerguelen Islands (Catard et al. 2000, Delord et al. 2010). The presence of beaks of *I. argentinus* in the present work adds the wandering albatross to the list of seabirds that consume baits and are thus at risk of being directly killed by hooks during longline operations. Another, more indirect risk for wandering albatross is related to the presence of severely or completely corroded hooks in their stomachs (Nel & Nel 1999, Phillips et al. 2010, this study). Their vulture-like hyperacidic gastric fluids (Grémillet et al. 2012) digest hooks that could lead to the absorption of harmful heavy metals whose effects on the birds remain to be determined.

The amount of fishing gear found in association with the wandering albatross is an order of magnitude greater than in other Procellariiformes (Phillips et al. 2010). The strong relationship between fisheries and the species is exemplified by the presence of a large number of hooks and snoods in Crozet food samples. As reported elsewhere (Nel & Nel 1999, Phillips et al. 2010), all hooks and snoods were from the local Patagonian toothfish fishery that uses an automatic baited system, and not from tuna industry located farther north that uses larger hooks. Its wide gape allows the wandering albatross to swallow large prey (Phillips et al. 2010). Hence, the species scavenges on sizeable discarded non-target fish and toothfish heads that are rejected during processing and dumped without the hooks being removed, a procedure that is forbidden by Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) fishery regulations (Nel & Nel 1999, Phillips et al. 2010). Only 1 legal longliner (Crozet), and 2 legal trawlers plus a single longliner (Kerguelen) operated in the area during the Austral winter 1998. At that time, 5 illegal longliners were arrested in Kerguelen waters by

the French Navy, which did not patrol Crozet waters. Moreover, landing of Patagonian toothfish indicated that at least 8 illegal longliners fished around Kerguelen and 3, possibly as many as 15, operated in Crozet waters in winter 1998 (G. Duhamel pers. comm.). Stomach hooks from Crozet birds indirectly confirm the presence of a fairly large number of illegal vessels in the area during the study period. This timing agrees with the beginning of considerable poaching in 1996 that increased quickly to unsustainably high levels during the subsequent years in both the westernmost Marion Island and easternmost Kerguelen Archipelago (Nel & Nel 1999, Lord et al. 2006). Remarkably, the composition of wandering albatross food remained apparently unaffected by the presence of fishing vessels, with squid consistently dominating the chick diet at the Crozet Islands (Ridoux 1994, Cherel & Weimerskirch 1999, this study).

Perspectives

Since *Diomedea* albatrosses are threatened by interactions with commercial fisheries and environmental changes (Barbraud et al. 2012), understanding their prey requirements and dietary flexibility is important for their effective conservation and management. A review of *Diomedea* feeding habits pinpoints the need for more direct dietary investigations on this endangered group of apex marine predators. Four features are notable: (1) only anecdotal information is available during the most inaccessible phases of albatross life, in early years at sea and during the inter-breeding period; (2) most stomach sample studies focused on chick diet, because birds carry no food in their stomach when they land during other breeding stages; (3) composition of the chick food is well-described only for the wandering albatross (Table 5); (4) owing to the large number of accumulated beaks, cephalopod prey is detailed in all but 1 taxa (Table 6); (5) nothing is known about the feeding habits of the Amsterdam albatross, the rarest and most localized *Diomedea* species. As a starting point, we consequently recommend: (1) to collect food samples from recently fed large chicks to determine fresh prey composition, species, and size; (2) to validate on chicks the promising and non-invasive DNA-based dietary analysis of feces (Bowser et al. 2013); and (3) to generalize the latter approach on adults during different breeding stages, and on non-breeding adults and immature albatrosses when present on land.

Acknowledgements. We thank S. Caille, T. Guionnet, and D. Secondi, who helped during the field work; G. Guillou (LIENSs, La Rochelle) for stable isotope analysis; and G. Duhamel (MNHN, Paris) for providing information about the legal and illegal fisheries in Kerguelen and Crozet waters during the study period. This work was supported financially and logistically by the Institut Polaire Français Paul Emile Victor (Programme No. 109, H.W.) and the Terres Australes et Antarctiques Françaises.

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