Polar Biol (1992) 12:477-484

Polar Biology

The diet of the Wandering Albatross *Diomedea exulans* at Subantarctic Marion Island

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Received 22 August 1991; accepted 19 January 1992

Summary. The diet of the Wandering Albatross at Subantarctic Marion Island was studied by inducing recently fed chicks to regurgitate and by stomach flushing adults about to feed chicks. Liquid comprised 70.2% of stomach content mass recovered from chicks. Solid material comprised cephalopods (58.6% by mass), fish (36.5%) and crustacean, cetacean and seabird material as minor items. Twenty-three taxa of cephalopods were identified, the onychoteuthid squid *Kondakovia longimana* being the most important. Estimated average mass of squid was 694 g with a maximum of over 8 kg. Diet of the Wandering Albatross at Marion Island was broadly similar to that at other studied localities. The high proportion of cephalopods known to float after death in the diet, and the deep-water habits of the few fish identified, suggest that scavenging plays an important role in foraging behaviour.

Introduction

It is only in recent years that quantified studies have been undertaken which allow temporal, geographical and interspecific comparisons of seabird diets in the Southern Ocean (e.g. Croxall and Lishman 1987; Prince and Morgan 1987; Cooper et al. 1990). Because of the generally confiding nature of southern seabirds, and, for the larger species at least, their habit of breeding in easily accessible colonies at a few localities, it is possible to obtain adequate numbers of diet samples for such comparisons. The recent abilities to sample diets (Prince 1980; Wilson 1984) and to identify remains of prey species of southern seabirds by their hard parts, converting measurements taken from these to estimated lengths and masses using identification guides and allometric equations (e.g. Kirkwood 1984; Clarke 1986; Hecht 1987), allow analysis of a species' diet in terms of its original constitution, including mass. However, unequal digestion rates and retention of indegestible material introduce some biases to such an approach (e.g. Furness et al. 1984; Wilson et al. 1985; Jackson 1990).

The Wandering Albatross *Diomedea exulans* is a large seabird which breeds at a number of southern temperate and Subantarctic oceanic islands (Watson 1975). It feeds its chicks large meals by regurgitation at intervals over a long growth period, which encompasses the winter months (Tickell 1968). Chicks readily regurgitate their stomach contents on handling after having been fed, thus allowing analyses of their diet without recourse to stomach flushing (Wilson 1984) or the need to kill and dissect birds.

Here we describe the diet of the Wandering Albatross at Marion Island, Prince Edward Islands, southern Indian Ocean. We discuss the population's diet in terms of a previous study at Marion Island of the cephalopod component of the diet (Imber and Berruti 1981), in relation to studies done elsewhere (e.g. Prince and Morgan 1987; Ridoux, in press) and in terms of the foraging methods adopted by the species.

Methods

The stomach contents of 50 Wandering Albatross chicks were collected from Marion Island (46°54'S, 37°45'E) from September to December 1988 (35 samples) and from June to August 1989 (15 samples). Occupied nests were kept under observation in areas of large concentrations of nesting birds (East Cape-Skua Ridge; Long Ridge-Storm Petrel Bay; and Kaalkoppie-Le Grange Kop). After a returning parent had completed feeding its chick and had moved away from the nest, samples were collected by inverting the chick over a large bucket and gently squeezing the stomach and massaging the throat. When no more food was forthcoming the chick was replaced on its nest. No chick was sampled more than once.

Samples were weighed to the nearest 10 g with a Pesola spring balance. The samples were then reweighed after the liquid portion had been drained through a 1-mm mesh sieve. For 11 samples, only drained mass was recorded. Samples were then preserved by adding 96% ethanol and deep-freezing. At the laboratory in South Africa samples were defrosted and the preservative drained off prior to sorting . Each prey item was weighed to the nearest gram after sorting.

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An additional five samples were obtained from adults by multiple stomach-flushing (Wilson 1984; Ryan and Jackson 1986; Gales 1987) breeding birds on arrival at their nests and before they had fed their chicks at Nellie Humps, Marion Island during April 1991. Approximately 5-7 l of lukewarm water was used for each of up to three flushes until only clear water emerged. Samples were drained and then treated in the same manner as were samples obtained from chicks. Sampled birds were released unharmed at their nest sites.

Cephalopod mandibles ("beaks") were collected loose from the samples or removed from buccal masses when cephalopods were only partially digested. The number of cephalopods ingested was calculated from a count of lower beaks. Beaks were identified to the lowest possible taxon by comparison with material held in the reference collections of the Port Elizabeth Museum, by the use of Clarke (1986) and on the advice of PG Rodhouse of the British Antarctic Survey.

Lower rostral lengths (LRL) (Clarke 1962) of the beaks were measured to the nearest 0.1 mm using Vernier calipers. Regressions (Clarke 1986; Rodhouse et al. 1990, Port Elizabeth Museum, unpublished data) were used to estimate dorsal mantle length (DML) and mass of the cephalopods from LRL.

Fish were invariably found in an advanced stage of digestion and otoliths were therefore used for identification purposes, using material held in the Port Elizabeth Museum reference collection and illustrations in the literature (Schwarzhans 1981; Nolf 1985; Härkönen 1986; Hecht 1987). In most cases identification to family level only was possible. The identity of cetacean remains was confirmed by comparison with material supplied by VG Cockcroft, marine mammalogist of the Port Elizabeth Museum. Crustaceans were identified using the key in Kirkwood (1984).

The composition of the diet is expressed in terms of mass, numbers and frequency of occurrence.

Results

Solid and liquid constituents

The mean mass of 39 stomach samples obtained from chicks was 1,630 g, comprising 523 g of solid and 1,131 g of liquid fractions (Table 1). Loose cephalopod beaks formed 0.6% of the total mass and 1.8% of the solid fraction. These beaks are thought to be derived from previous meals and to have accumulated in the chicks' stomachs (e.g. Furness et al. 1984). The mean drained mass without accumulated beaks was 514 g. Liquid formed 70.2% of total mass for 39 samples, and had a large range (Table 1). There was no significant correlation between the individual mass of a regurgitation and its liquid proportion ($r=-0.0715$; $P<0.1>0.5$). The mean number of prey items (not including isolated beaks) from chick samples was 15.7±29.2 (range 1–125).

Table 1. Solid and liquid constituents of the diet of the Wandering Albatross at Marion Island, 1988–1989

Parameter	Mean	Standard deviation	Range	Sample size
Total mass (g)	1 630	1 054	190–4 180	39
Drained mass (g)	523	425	20–1 900	50
Liquid mass (g)	1 131	724	40–3 420	39
% liquid	70.2	–	21.1–97.9	39
% solids	28.8	–	2.1–78.9	39

Five regurgitations obtained from adults had a mean drained mass of 486±234 g (range 77–747 g), not significantly different ($t=-0.191$; $P>0.9$) from mean drained mass of samples obtained from chicks.

Prey class constituents

Cephalopod flesh occurred in 48 chick samples and contributed 58.6% to drained food mass less the mass of isolated beaks (Table 2). Isolated beaks were found in the two remaining samples, bringing the frequency of occurrence of cephalopods in the diet to 100%. Fish remains contributed 36.5% to drained mass and occurred in 30 samples. Cetacean, crustacean and seabird material occurred relatively rarely and contributed only 4.9% to drained mass (Table 2).

The five samples from adults were made up of single prey items (four of fish, one of squid), except that two samples containing fish also contained isolated squid beaks.

Cephalopods

A total of 773 cephalopod lower beaks was recovered from stomach contents of chicks and 23 taxa were identified. All taxa were squid (Teuthoidea). The onychoteuthid squid *Kondakovia longimana* occurred most frequently, in 52% of samples (Table 3). Most squid taxa were identified from isolated beaks only, but 29 were found with flesh attached, of which 20 (69%) were *K. longimana.*

Information on the relative abundance and contributions by estimated mass of squid taxa is given in Table 3, along with mean LRLs and estimated mean dorsal mantle lengths (DMLs) and masses. Squids of the families Onychoteuthidae, Histioteuthidae and Cranchiidae formed 79.8% of all specimens by numbers and 87.8% by estimated mass. *Histioteuthis eltaninae*, *K. longimana*, *Moroteuthis robsoni* and *Galiteuthis glacialis* were the most abundantly recorded taxa, forming together 62.7% of all beaks identified. Their size-frequency distributions are given in Fig. 1, showing single peaks for all taxa.

Table 2. Occurrence of broad prey classes in the diet of wandering albatross chicks at Marion Island, 1988–1989

	Frequency of occurrence		Relative proportion of drained mass (%)[a]
	No.	%	
Cephalopods	48[b]	96.0	58.6
Fish	30	60.0	36.5
Crustaceans	2	4.0	0.1
Cetaceans	8	16.0	4.7
Seabirds	2	4.0	0.1
Jellyfish	1	2.0	<0.1

[a] Less mass of isolated beaks, thought to have accumulated from previous meals

[b] Isolated squid beaks were found in the remaining two samples, bringing the frequency of occurrence to 100%.

Table 3. Relative abundance, frequency of occurrence, estimated sizes and relative contribution by mass of squid identified from stomach contents of wandering albatross chicks at Marion Island, 1988–1989

Taxa	Relative abundance		Frequency of occurrence		Lower rostral length (mm)			Dorsal mantle length (mm)			Mass (g)			% relative mass
	No.	%	No.	%	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	
Gonatidae														
Gonatus antarcticus	25	3.2	10	20.0	6.4	1.1	4.6–9.3	39	47.1	241–442	287	173.1	84–872	1.4
Enoploteuthidae														
Ancistrocheirus lesueuri	5	0.6	3	6.0	8.1	0.7	6.9–8.8	290	29.9	240–317	1 489	428.4	798–1 897	1.5
Octopoteuthidae														
Octopoteuthis rugosa	2	0.3	1	2.0	8.3	1.1	7.2–9.4	143	–	124–163	161	–	113–209	0.1
Taningia danae	3	0.4	3	6.0	13.1	1.5	10.9–14.3	426	115.6	263–519	2 891	1 007.6	1 474–3 730	1.7
Onychoteuthidae														
Kondakovia longimana	125	16.2	26	52.0	12.4	1.4	5.9–16.2	439	51.5	199–582	2 051	712.0	192–4 629	50.1
Moroteuthis knipovitchi	111	14.4	11	22.0	6.4	0.7	4.6–10.8	290	60.8	149–758	672	410.6	195–4 431	14.6
M. ingens	24	3.1	12	24.0	9.6	1.0	7.7–12.9	635	103.7	432–979	3 113	1 286.5	1 356–8 253	14.6
M. robsoni	11	1.4	6	12.0	7.3	0.9	6.2–9.4	394	97.1	274–611	1 227	573.5	635–2 726	2.6
Pholidoteuthidae														
Pholidoteuthis boschmaii	3	0.4	2	4.0	7.2	0.1	7.1–7.3	307	3.4	303–311	708	22.7	681–736	0.4
Histioteuthidae														
Histioteuthis eltaninae	140	18.1	13	26.0	3.5	0.4	2.5–4.7	63	9.0	42–91	89	24.2	41–176	2.4
H. atlantica	30	3.9	12	24.0	5.0	1.1	3.2–8.1	98	25.1	57–166	220	116.1	72–618	1.3
H. miranda	35	4.5	15	30.0	5.8	0.9	3.6–7.2	114	19.8	66–146	292	97.7	95–471	2.0
Histioteuthis sp.	6	0.8	3	6.0	4.3	0.8	3.1–5.2	82	17.3	55–102	149	58.9	67–222	0.2
Neoteuthidae														
Alluroteuthis antarcticus	51	6.6	11	22.0	5.1	0.4	4.2–5.9	156	11.3	129–181	422	88.9	232–642	4.1
Chiroteuthidae														
Chiroteuthis sp.	40	5.2	13	26.0	6.0	1.0	2.6–7.5	158	24.7	75–195	104	39.7	10–181	0.8
Lepidoteuthidae														
Lepidoteuthis grimaldi[a]	1	0.1	1	2.0	11.4	–	–	?	–	–	?	–	–	–
Mastigoteuthidae														
Mastigoteuthis sp.	8	1.0	7	14.0	6.5	1.3	3.5–7.7	187	37.5	100–221	288	120.6	44–430	0.5
Cycloteuthidae														
Cycloteuthis akimushini	8	1.0	4	8.0	13.1	1.2	11.4–14.6	406	38.3	353–451	1 009	182.5	762–1 234	1.6
Discoteuthis laciniosa	11	1.4	6	12.0	6.5	1.8	3.4–8.7	155	33.8	96–197	221	103.9	52–374	0.5
Cranchiidae														
Galiteuthis glacialis	108	14.0	13	26.0	5.3	0.5	2.9–7.6	228	22.3	130–322	104	24.8	25–238	2.2
Mesonychoteuthis hamiltoni[b]	3	0.4	3	6.0	10.2	0.8	9.1–11.1	?	?	?	1 942	427.9	1 371–2 401	1.1
Taonius pavo	17	2.2	12	14.0	8.7	1.8	4.4–10.7	524	109.7	258–645	266	95.6	56–394	0.9
Teuthowenia pellucida	6	0.8	1	2.0	5.6	0.3	5.1–6.1	241	12.3	220–261	118	14.8	94–143	0.1

[a] Regressions for LRL/DML and LRL/mass not available

[b] LRL/DML regression not available

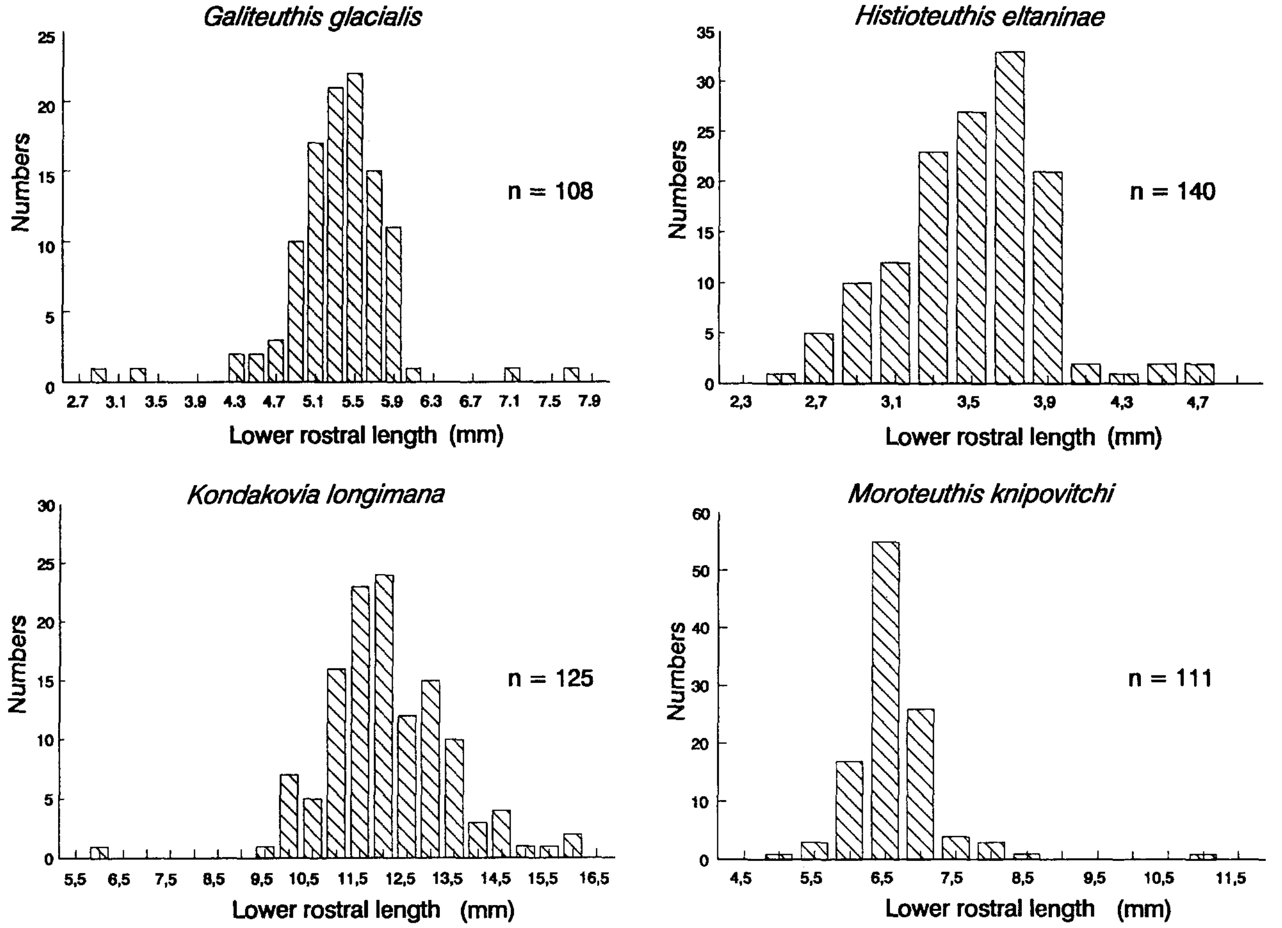

Fig. 1. Size distribution of four species of squid taken abundantly by Wandering Albatrosses at Marion Island

Estimated sizes ranged from a *H. eltaninae* with a DML of 42 mm to a *M. ingens* with a DML of 980 mm. The largest intact squid mantle measured was 350 mm in length, although crowns of arms containing beaks were found that must have come from squids of a greater DML than 350 mm. Estimated individual masses ranged from a *Chiroteuthis* sp. of 10 g, to a *M. ingens* of 8,253 g. The mean mass of 772 squid was 694 g, with taxa ranging from means of 89 g (*H. eltaninae*) to 3,113 g (*M. ingens*). The four most abundant taxa contributed 66.1% of the total reconstituted mass; the large *K. longimana* contributing 47.8% alone (Table 3).

The isolated beaks from adult samples represented four individuals of the species *Gonatus antarcticus*, *H. miranda* (2) and *Teuthowenia pellucida*. Their sizes were similar to the means of each species obtained from chicks (Table 3).

Fish

Only 10 pairs of otoliths were recovered, nine from chick regurgitations. One pair of otoliths matched specimens of the Slender Frostfish *Benthodesmus elongatus*, Trichiuridae, in the reference collection. Another pair from an adult sample matched those of a cuskeel *Spectrunculus grandis*, Ophidiidae. Three pairs were tentatively identified as belonging to the family Macrouridae (grenadiers), one to the Oreosomatidae (oreos) and one to the Ophidiidae (cuskeels). The remainder could not be identified. Lengths and masses of these fish could not be estimated because appropriate regressions are unavailable.

Other material

The bulk of the remainder of the stomach contents from chicks consisted of pieces of unidentified cetacean blubber with skin attached, totalling 1,177 g, almost certainly originating from dolphins or small whales, based on the texture and thickness of the skin. Cetacean remains were found in eight samples, and weighed on average 160 ± 17 g with a range from 31 to 343 g.

One unidentified femur of a bird accompanied by feathers, and the tip of the bill of a Whitechinned Petrel *Procellaria aequinoctialis*, also accompanied with feathers, were present in two samples. Bird remains totalled only 14 g.

A single natant decapod crustacean *Nematocarcinus longirostris* and part of a reptant crab *Lithodes* sp. were the only crustacean remains found. Jellyfish (Cnidaria) remains were found in one sample and weighed 6 g.

Seven samples from chicks contained a total of 822 g of plant material, weighing usually less than 20 g (two samples < 1 g), although one contained 689 g. Identified plant material was of the fern *Blechnum penna-marina*, the forb *Azorella selago* and grasses, all used as nesting material by Wandering Albatrosses at Marion Island (personal observation). Five regurgitations contained a total of 15 g of plastic material. Plant and plastic material have not been included in the calculations of contributions to drained mass (Table 2).

Discussion

Meal sizes and solid and liquid constituents

Samples obtained from Wandering Albatross chicks ($n = 37$) on Ile de la Possession, Iles Crozet contained, on average, 482 g of liquid and 297 g of solid material (Ridoux, in press), less than in the current study. Tickell (1968) estimated that meals fed to Wandering Albatross chicks ranged from 113–2,112 g ($n = 53$), based on reweighings immediately before and after an individual meal. These figures are not strictly comparable with those of the present study, which in some cases at least, will represent more than a single meal.

Liquid formed 61.9% of the Wandering Albatross chick diet in the Iles Crozets study (Ridoux, in press). The liquid component of the diets of three species of adult albatrosses ranged from 47.7% to 55.4% (Prince 1980; Thomas 1982; Hunter and Klages 1989). The larger average figure obtained in this and the Iles Crozet study (and the large range) is presumably due to liquid accumulating in chick stomachs from previous meals. Thomas (1982) noted that Light-mantled Sooty Albatross *Phoebetria palpebrata* chicks regurgitated very variable amounts of liquid.

Prey class constituents

Quantitative studies of the diet of the Wandering Albatross have been undertaken at Bird Island, South Georgia in 1983–1984 (Prince and Morgan 1987; Croxall et al. 1989; Rodhouse et al. 1988; Rodhouse 1989) and Ile de la Possession, Iles Crozet in 1982 (Ridoux, in press). Earlier studies have been based on small samples and sometimes only on the collection and analysis of cephalopod beaks (e.g. Voisin 1969; Mougin 1970; Imber and Russ 1975; Clarke et al. 1981; Imber and Berruti 1981; Williams and Imber 1982). Based on these studies, the diet of the Wandering Albatross consists primarily of cephalopods and fish, with carrion (seabirds, cetaceans, etc.) forming a minor part (Table 4). Crustaceans are rarely taken. Cephalopods predominated at Iles Crozet (Table 4). Fish at Marion Island formed 35.4% of the diet by mass, 41.5% (or 45%) at South Georgia but only 14.9% at Iles Crozet (Table 4). Carrion (18.8%) was more prevalent in terms of mass in the South Georgian diet than at Marion Island, but cephalopods less so. On a frequency of occurrence basis fish occurred more commonly at South Georgia than at Marion Island but less so at Iles Crozet (Table 4).

The crustacean and carrion portions of the South Georgian diet have not been detailed (Prince and Morgan

Table 4. Geographical variation of broad prey classes in the diet of the wandering albatross

Locality/parameter	Cephalopods	Fish	Crustaceans	Other	No. samples	Source
Marion Island, Prince Edward Islands						
Frequency of occurrence (%)	96.0	60.0	4.0	22.0	50	This study
Relative mass (%)	58.6	36.5	0.1	4.9	50	This study
Bird Island, South Georgia						
Relative mass (%)	80	10	present	present	?	Croxall and Prince (1980)
Relative mass (%)	39.5	41.5	0.2	18.8	79	Prince and Morgan (1987)
Frequency of occurrence (%)	–	93	–	–	80	Croxall et al. (1988)
Relative mass (%)	–	45	–	–	80	Croxall et al. (1988)
Estimated mass (%) 1983	39.5	–	–	–	79	Rodhouse et al. (1987)
1984	29.7	–	–	–	79	Rodhouse et al. (1987)
Ile de la Possession, Iles Crozet						
Frequency of occurrence (%)	66.7	42.9	0.0	0.0	21	Mougin (1970)
Frequency of occurrence (%)	72.7	18.2	0.0	9.2	11	Voisin (1969)
Frequency of occurrence (%)	71.0	35.5	0	3.2	31	Weimerskirch and Jouventin (1986)[a]
Frequency of occurrence (%)	91.7	27.7	2.8	25.0	37	Ridoux (in press)
Relative mass (%)	76.7	14.9	0.1	8.4	37	Ridoux (in press)
Adams Island, Auckland Islands						
Frequency of occurrence (%)	100	57	0	0	7	Imber and Russ (1975)[b]

[a] Stated to be from Voisin (1969) and Mougin (1970), but combining these two data sets give frequency of occurrences of squid 68.8%, fish 34.4%, crustaceans 0.0% and other 3.1%, with an n of 32

[b] Includes two samples collected from off mainland New Zealand

1987). The parasitic copepod *Sphyrion lumpi* was recorded as a minor item in the Iles Crozet diet, thought to have been ingested with fish (Ridoux, in press). Penguin feathers and presumed whale blubber were the only carrion reported from Iles Crozet (Ridoux, in press). Voisin (1969) reported penguin feathers in one sample and also reported vegetation and soil in regurgitations. Ryan (1987) recorded plastic particles in seven of 156 samples (mainly regurgitations) of the Wandering Albatross from the Prince Edward and Gough Islands, with a maximum number of 33 particles in one sample and a mean mass per sample of 3.1 g (maximum 184 g).

The only previous study of the diet of the Wandering Albatross at Marion Island was an analysis of 515 cephalopod beaks from five regurgitation casts and the contents of one chick collected from April to November 1974 (Imber and Berruti 1981). Thirty-four taxa were identified, including one octopod *Alloposus mollis*, represented by a single specimen. All other beaks were of teuthioid squid (Table 5). The 1974 and 1988–1989 samples are broadly similar (Table 5), with the same four species being the most abundant. Differences may be ascribed both or either to temporal trends and to the fact that whole stomach samples tend to contain a greater proportion of smaller beaks, which are thought to be less resistant to erosion in the stomach and therefore less likely to accumulate in regurgitation casts (Imber 1973; Imber and Berruti 1981; Hunter and Klages 1989). For example, the small squids *Histioteuthis eltaninae* and *Galiteuthis glacialis* (estimated mean masses 89 g and 104 g, respectively, in the 1988–1989 samples) formed 6.7% and 9.7% of the 1974 collection, mainly from casts, but 18.1% and 14.0%, respectively, of the whole-stomach collections (Table 5). In contrast, the larger squid *Moroteuthis knipovitchi* (mean mass in 1988–1989 samples 672 g) formed 35.9% of the 1974 collection, but only 14.4% of the 1988–1989 collection, suggesting that it is relatively resistant to erosion in the stomach. Real differences in abundance between sampling periods can, however, not be discounted. This pattern did not occur in the case of the very large *Kondakovia longimana* (Table 5). In support of this bias, Hunter and Klages (1989) found that both the large *M. knipovitchi* and *K. longimana* were relatively over-represented and the small *H. eltaninae* was relatively

Table 5. Relative abundance of squid beaks obtained by collecting regurgitation casts and by analysing stomach contents of wandering albatrosses at Marion Island

Taxa	Regurgitation casts ($n=6$)		Stomach contents of chicks ($n=50$)	
	No.	%	No.	%
Gonatidae		(2.5)		(3.2)
Gonatus antarcticus	13	2.5	25	3.2
Enoploteuthidae		(0.7)		(0.6)
Ancistrocheireus lesueuri	4	0.7	5	0.6
Octopoteuthidae		(1.3)		(0.7)
Octopoteuthis rugosa	0	–	2	0.3
Octopoteuthis sp.	4	0.7	0	–
Taningia danae	3	0.6	3	0.4
Onychoteuthidae		(52.8)		(35.1)
Kondakovia longimana	73	14.1	125	16.2
Moroteuthis knipovitchi	185	35.9	111	14.4
M. ingens	10	1.9	24	3.1
M. robsoni	4	0.7	11	1.4
Undescribed gen. & sp.	1	0.2	0	–
Pholidoteuthidae		(0.0)		(0.4)
Pholidoteuthis boschmai	0	–	3	0.4
Histioteuthidae		(15.3)		(27.3)
Histioteuthis eltaninae	35	6.7	140	18.1
H. atlantica	10	1.9	30	3.9
H. miranda	4	0.7	35	4.5
H. dofleini	1	0.2	0	–
H. macrohista	3	0.6	0	–
H. meleagroteuthis	26	5.0	0	–
H. ?bruuni	1	0.2	0	–
Histioteuthis sp.	0	–	6	0.8
Psychroteuthidae		(0.7)		(0.0)
Psychroteuthis glacialis	4	0.7	0	–
Neoteuthidae		(5.0)		(6.6)
Alluroteuthis antarcticus[b]	26	5.0	51	6.6
Architeuthidae		(0.4)		(0.0)
Architeuthis sp.	2	0.4	0	–
Ommastrephidae		(0.2)		(0.0)
Martialia hyadesi	1	0.2	0	–
Chiroteuthidae		(4.4)		(5.2)
Chiroteuthis picteti	2	0.4	0	–
C. macrosoma	3	0.6	0	–
Chiroteuthis sp. E	18	3.4	0	–
Chiroteuthis sp.	0	–	40	5.2
Lepidoteuthidae		(0.0)		(0.1)
Lepidoteuthis grimaldii	0	–	1	0.1
Mastigoteuthidae		(0.2)		(1.0)
Mastigoteuthis sp. A	1	0.2	0	–
Mastigoteuthis sp.	0	–	8	1.0
Cycloteuthidae		(1.5)		(2.4)
Cycloteuthis sirventi	7	1.3	0	–
C. akimushkini	0	–	8	1.0
Discoteuthis discus	1	0.2	0	–
D. laciniosa	0	–	11	1.4
Cranchiidae		(13.7)		(17.0)
Galiteuthis glacialis[c]	50	9.7	108	14.0
G. armata	4	0.7	0	–
Megalocranchia maxima	1	0.2	0	–
Mesonychoteuthis hamiltoni	1	0.2	0	–
Taonius pavo	3	0.4	17	2.2
T. belone	1	0.2	0	–
T. cympoctypus	12	2.3	0	–
Teuthowenia pellucida	0	–	6	0.8
Alloposidae		(0.2)		(0.0)
Alloposus mollis	1	0.2	0	–
Total no. taxa	34		23	
Total no. specimens	515		773	

[a] Includes the stomach contents of a chick (Imber and Berruti 1981)

[b] Misidentified as *Galiteuthis glacialis* by Imber and Berruti (1981)

[c] Misidentified as *Teuthowenia antarctica* by Imber and Berruti (1981)

under-represented in regurgitation casts of Grey-headed Albatrosses at Marion Island obtained by Brooke and Klages (1986), in comparison to their numbers in whole-stomach regurgitations.

Because of the above bias, comparisons between localities of the cephalopod component of the diet of Wandering Albatrosses should only be made where the methods of sample collection and analysis are similar. The South Georgia and Iles Crozet samples (Rodhouse et al. 1987; Ridoux, in press) allow such a comparison. At South Georgia, 3,421 beaks representing 46 taxa were identified. The greater number of taxa recorded may reflect the larger number (80) of samples analysed. The most abundant species included *K. longimana*, *H. eltaninae* and *Galiteuthis glacialis* (totalling 42.4% by numbers), species also abundant at Marion Island (48.3%). However, *M. knipovitchi* was less abundant at South Georgia (1.9% as compared with 14.4% at Marion Island). The most abundant species at South Georgia was *Illex* sp. (23.8% by numbers), a taxon not recorded at Marion Island. *Illex* squid are warm-water species and Rodhouse (1989) suggests that their preponderance in the South Georgia diet in 1984 was due to Wandering Albatrosses exploiting a warmer water community in that year, probably as a result of the 1984 collapse of the Antarctic Krill *Euphausia superba* community adversely affecting the food web in the vicinity of South Georgia. The four most abundant squid taken by Wandering Albatrosses at Marion Island (*K. longimana*, *M. knipovitchi*, *H. eltaninae* and *G. glacialis*) were of similar sizes to those taken at South Georgia (Rodhouse et al. 1987).

Thirty-four squid taxa ($n = 1317$ lower beaks) were identified in the Iles Crozet study. The most abundant species were *K. longimana* and *H. eltaninae*, of similar sizes to those taken at Marion Island.

Because the hard parts of fish do not last as long in the stomachs of seabirds as do those of cephalopods (Furness et al. 1984) and perhaps because fish flesh is digested faster than that of cephalopods (Wilson et al. 1985; Jackson 1990), fish may be under-represented in dietary analyses of the Wandering Albatross. This also presumably accounts for the relatively few specific identifications made, even though fish can form an important part of the diet (Table 4). The fish diets of the Wandering Albatross at the Auckland Islands and at South Georgia (Imber and Russ 1975; Croxall et al. 1988) show little overlap with that for Marion Island. Unidentified fish of the grenadier family Macrouridae were taken at both Marion Island and South Georgia. No fish were specifically identified in the Iles Crozet study (Ridoux 1992).

Foraging by the Wandering Albatross: predation or scavenging?

Uncertainty exists in the literature as to the way in which some Southern Ocean seabirds, including the Wandering Albatross, obtain their cephalopod prey. Imber and Russ (1975) considered that bioluminescent squid that practise diel vertical movements predominated in the diet of Wandering Albatrosses, because they were relatively easily captured at night. However, Clarke et al. (1981) and Rodhouse et al. (1987) noted that many squid taken by Wandering Albatrosses at South Georgia were not bioluminescent and, furthermore, that bioluminescent squid have downwardly directed photophores shaded from above. They suggested that albatrosses mainly scavenge squid, perhaps including those regurgitated by Sperm Whales *Physeter catodon* based on the size of some specimens taken, or found at the sea surface as a result of post-breeding mass mortality. The mesopelagic habits and large size of some of the squid taken by Wandering Albatrosses suggest that they are unavailable while alive. Weimerskirch and Jouventin (1986) thought it unlikely that surface-seizing (Harper et al. 1985; Harper 1987) albatrosses could catch fast-moving prey such as squid, and postulated that they scavenged dead animals found floating on the sea surface. In opposition to this, Harper (1987), based on direct observations made at sea, considered that Wandering Albatrosses actively hunt for large alive squid at the sea surface and are able to subdue them. Harper (1987) reported that 93% ($n = 119$) of his observations of Wandering Albatrosses feeding on "natural food" were made at night. Prince and Morgan (1987) showed that Wandering Albatrosses feeding chicks at South Georgia spent more hours at night on the sea surface while foraging than during the day, lending support to the importance of nocturnal foraging. However, during incubation, when daylight hours were longer, the situation was reversed. Wilson et al. (1992) have shown, with the aid of ingested temperature-sensitive devices, that Wandering Albatrosses can capture prey both during the day and night.

Lipinski and Jackson (1989) have shown that most cephalopod species can be assigned to two classes: those that sink after death and those that float. They analysed the ratios of "floater" and "sinker" cephalopods in the diets of several species of southern procellariiform seabirds and found that "floaters" predominated, strongly suggesting that scavenging on dead and moribund cephalopods takes place at the sea surface. To test the validity of this hypothesis for Wandering Albatrosses at Marion Island, the combined collections for 1974 and 1988–1989 (Table 5) were classified into "floater" and "sinker" taxa. Of a total of 1,288 specimens, only five (0.4%), of the two taxa *Psychroteuthis glacialis* and *Alloposus mollis*, were deemed to be "sinkers" (Lipinski and Jackson 1989). "Floater" cephalopods also greatly predominated when data from other studies (Imber and Russ 1975; Clarke et al. 1981; Rodhouse et al. 1987, Ridoux 1992) are combined with those from Marion Island (95.7% by numbers, $n = 6\,834$). These findings lend credence to the hypothesis that Wandering Albatrosses take at least a significant proportion of their cephalopod diet by scavenging, helping to explain how they are able to obtain both deep-living and large species.

The four fish families recorded from Marion Island Wandering Albatrosses are all of deep-water benthopelagic or bathypelagic habits (Smith and Heemstra 1986; Gon and Heemstra 1990). Fish taken by Wandering Albatrosses in the New Zealand region were also deep-water species (Imber and Russ 1975). Croxall et al. (1989), in their analysis of the fish diet of the Wandering Albatross at South Georgia, point out that several benthic species, such as the eelcod *Muraenolepis microps*, Muraenolepididae, which are not available as discards from commercial trawlers, are found in the diet. They tentatively suggest that post-spawning mortality may make such species available at the surface, in a way suggested for cephalopods (Clarke et al. 1981; Lipinski and Jackson 1989). Post-spawning mortality may also have made the fish recorded from Marion Island available to Wandering Albatrosses.

The fact that Wandering Albatrosses are well known to scavenge for discarded wastes in the wakes of ships, and the presence of cetacean carrion in their diet at Marion Island, also supports the importance of scavenging as a foraging method for this species.

Acknowledgements. Avian research at Marion Island forms part of the South African National Antarctic Research Programme, and receives financial and logistic support from the South African Department of Environment Affairs. We thank P.G. Rodhouse for help with the identification of squid beaks, M.R. Lipinski for information on "floater" and "sinker" squid and N.J. Adams and three anonymous referees for their comments on draft manuscripts.

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