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CEPHALOPOD REMAINS IN REGURGITATIONS OF THE WANDERING ALBATROSS *Diomedea exulans* L. AT SOUTH GEORGIA

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Abstract. Regurgitations of the chicks of wandering albatrosses near their nests included 762 upper beaks (mandibles) and 532 lower beaks of cephalopods. Ten complete samples and eight further samples were collected. Lower beaks were identified, their lower rostral lengths measured and the wet weight of squids represented by beaks was estimated. Twenty-five species of cephalopod are present in the diet. Analysis of the complete samples shows the three most important species in the diet to be *Kondakovia longimana* (40.0% by number), *Taonius pavo* (16.9%) and *Histioteuthis (?) eltaninae* (8.7%). While the large *Taningia danae* only comprises 1.3% by number, it may contribute over 5% by weight.

The species and size ranges of beaks are compared with those occurring in the stomachs of sperm whales killed by whalers in the Southern Hemisphere (Clarke, 1980). The ten complete samples contain an average of 44 beaks which probably represents about 200 days' accumulation. Both Antarctic and warm-water cephalopods are present in the diet. These albatrosses possibly scavenge some of their food from the vomit of sperm whales.

Detailed identification of the cephalopods in the diet of wandering albatrosses *Diomedea exulans* L. has only been attempted once and that from regurgitations and stomach contents of seven birds from New Zealand (Imber and Russ, 1975). The present work is based upon 18 samples of cephalopod beaks and a few flesh remains found by the nests of wandering albatrosses at South Georgia.

Material and Methods

On Bird Island, South Georgia, Croxall and Prince collected squid beaks regurgitated by the chicks of wandering albatrosses beside their nests. All but one sample (December 1975) were collected between early November 1976 and mid-January 1977. Ten samples (* on Table I) were essentially intact as regurgitated, but small beaks were probably overlooked in other samples which were either dispersed on the ground or had been deposited in tall grass.

The squid lower beaks were identified by comparison with beaks removed from specimens and described elsewhere (Clarke, 1962*a*, *b*, 1980; Clarke and MacLeod, 1974, 1976; Clarke and Stevens, 1974; Clarke and others, 1976). The present analysis depends upon techniques developed from an early search for criteria (Clarke, 1962*b*) to a point where many species can be readily identified from lower beaks (Mangold and Fioroni, 1966; Iverson and Pinkas, 1971; cited papers by Clarke and others).

Experience of cephalopod beak identification has been gained by the first author from studies of stomach contents of birds (Ashmole and Ashmole, 1967; Harris, 1973), sperm whales, other cetaceans, seals and fish (Clarke, 1977).

Lower rostral length (LRL) and, in *Alloposus*, lower hood length (LHL) were measured with vernier calipers to an accuracy of 0.005 cm. LRL distribution of the more numerous species (Figs 1 and 2) and the size at which the lower wings become dark are employed in comparisons with previously described collections. Unless otherwise stated, comparisons are with data given by Clarke (1980). LRL to wet weight of squid relationships are used to calculate percentage weights of the various species of cephalopod in the diet (Clarke, 1962*b*, 1980).

Results

Family Cranchiidae

This family contributes the secondmost lower beaks to the diet (25.1%; Table II) but, because they belong to three small species and one large species only represented by a single young squid, the family only comprises 4.3% of the weight of cephalopods represented in the diet.

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TABLE I. CEPHALOPOD BEAKS FROM THE NESTS OF WANDERING ALBATROSSES AT SOUTH GEORGIA. DISTRIBUTION IN TEN COMPLETE (*) AND EIGHT PART SAMPLES

Cephalopods represented by beaks	1*	2*	3*	4*	5*	6*	7*	8*	9*	10*	11	12	13	14	15	16	17	18	Total Birds	Total Beaks
Mesonychoteuthis sp. A		8	6		1			4		2									5	21
Taonius pavo	2	5	13	1	13	1	11	12	3	6	2		20						12	89
(?) Crystalloteuthis	2	1	3		5	1	6	1	1	1									9	21
Mesonychoteuthis hamiltoni							1												1	1
Kondakovia longimana	2	12	23	43	9	10	5	12	29	12	5	5	28	2	2	1	9	2	18	211
Moroteuthis robsoni				2			1		4	2						1			4	10
Moroteuthis knipovitchi		1						1					1						3	3
Onychoteuthis banksi										1									1	1
Histioteuthis sp. A. *H. (?) meleagroteuthis*					1														1	1
H. bonnellii	1																		1	1
H. dofleini		1																	1	1
Histioteuthis sp. B. *H. (?) eltaninae*	2	14	8		2		5	6	3	4	2								9	46
H. (?) atlantica		6	6		8		6			4			1						6	31
Gonatus antarcticus	2	5	1		1		4	1	3		1		1						9	19
Gonatus sp. A		1			1		2	3	2	2									6	11
Octopoteuthis sp. A		1	1	1	1		2	1					1						7	8
Taningia danae				1	2			1	2	1									5	7
Mastigoteuthis sp. A		1					2	2	3	1				2		4			7	15
Ancistrocheirus lesueuri		1		1		1	1	3	1										6	8
Lepidoteuthis grimaldii					4														2	5
Todarodes (?) sagittatus		1				1										1			2	2
Chiroteuthis veranyi			2							1									2	3
Chiroteuthis sp.										2									1	2
Pholidoteuthis boschmai (A)	1																		1	1
Alloposus mollis			1	1	2			1					1	3		(2†)			6	9
Unidentified intact beaks								1		3										4
TOTAL LOWER BEAKS	12	58	64	50	50	14	46	49	51	42	10	5	53	7	2	7	9	2		532
TOTAL SPECIES	7	14	10	7	13	5	12	13	10	14	4	1	7	3	1	4	1	4	25	

† Upper beaks only.
* Complete samples.

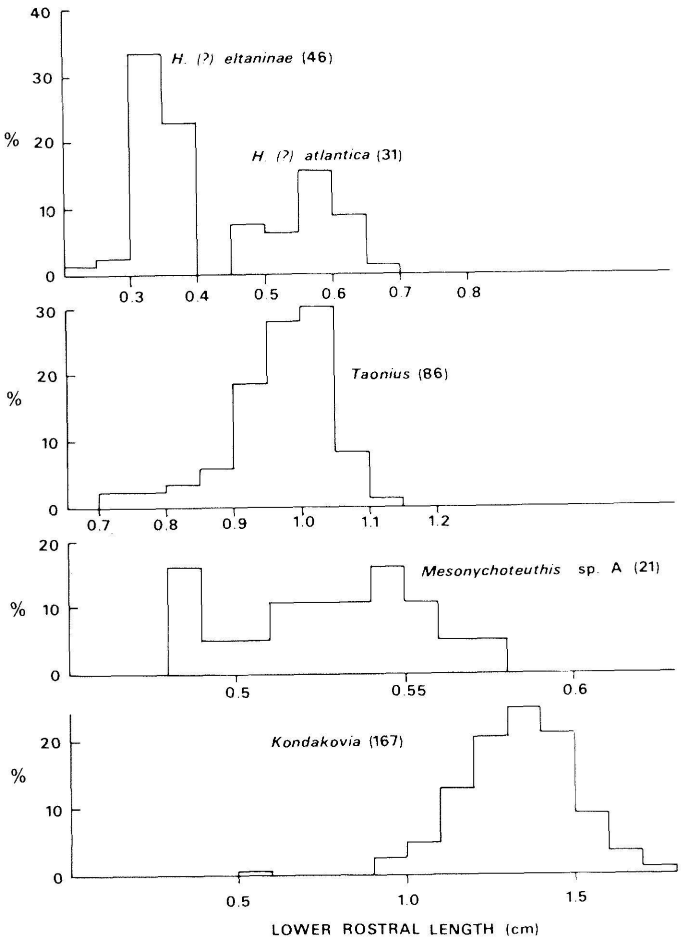

Fig. 1. Lower rostral length frequencies of beaks of several species of cephalopod collected near the nests of wandering albatrosses at South Georgia.

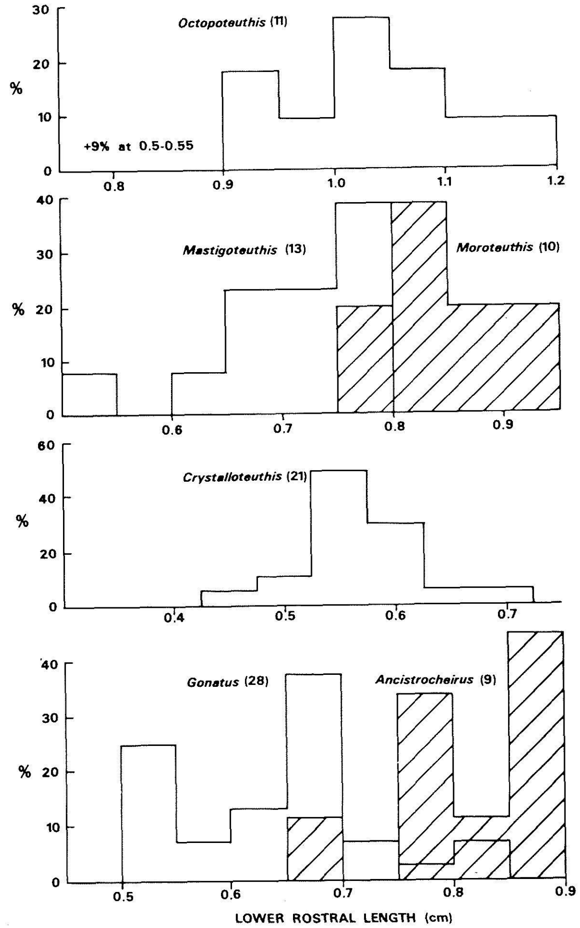

Fig. 2. Lower rostral length frequencies of beaks of several species of cephalopod collected near the nests of wandering albatrosses at South Georgia.

TABLE II. CEPHALOPOD BEAKS FROM THE NESTS OF WANDERING ALBATROSSES AT SOUTH GEORGIA. THE IMPORTANCE BY NUMBER AND WEIGHT OF CEPHALOPODS REPRESENTED BY BEAKS

Family	*Species*	*Number*	*%*	*Estimated weights* *Mean* (kg)	*Total* (kg)	*Total* (%)	*Family contribution* % *by number*	% *by weight*
CRANCHIIDAE	*Mesonychoteuthis* sp. A	21	4.0	0.086	1.8	0.2	25.1	4.3
	† *Taonius pavo*	89	16.8	0.319	28.4	3.4		
	* *(?) Crystalloteuthis*	21	4.0	0.278	5.8	0.7		
	* *Mesonychoteuthis hamiltoni*	1	0.2	0.378	0.4	—		
ONYCHOTEUTHIDAE	* *Kondakovia longimana*	211	40.0	3.165	667.8	81.1	42.7	83.2
	x *Moroteuthis robsoni*	10	1.9	1.644	16.4	2.0		
	* *Moroteuthis knipovitchi*	3	0.6	0.371	1.1	0.1		
	† *Onychoteuthis banksi*	1	0.2	0.162	0.2	—		
HISTIOTEUTHIDAE	† *Histioteuthis* (A) *H. (?) meleagroteuthis*	1	0.2	0.106	0.1	—	15.2	1.1
	† *H. bonnellii*	1	0.2	0.182	0.2	—		
	† *H. dofleini*	1	0.2	0.176	0.2	—		
	* *Histioteuthis* (B) *H. (?) eltaninae*	46	8.7	0.072	3.3	0.4		
	† *H. (?) atlantica*	31	5.9	0.192	6.0	0.7		
GONATIDAE	* *Gonatus antarcticus*	19	3.6	0.350	6.7	0.8	5.7	1.0
	Gonatus sp. A	11	2.1	0.161	1.8	0.2		
OCTOPOTEUTHIDAE	† *Octopoteuthis* sp. A	8	1.5	0.318	2.5	0.3	2.8	5.8
	x *Taningia danae*	7	1.3	6.521	45.7	5.5		
MASTIGOTEUTHIDAE	* *Mastigoteuthis* sp. A	15	2.8	0.381	5.7	0.7	2.8	0.7
ENOPLOTEUTHIDAE	† *Ancistrocheirus lesueuri*	8	1.5	1.476	11.8	1.4	1.5	1.4
LEPIDOTEUTHIDAE	† *Lepidoteuthis grimaldii*	5	0.9	1.331	6.7	0.8	0.9	0.8
OMMASTREPHIDAE	x *Todarodes (?) sagittatus*	2	0.4	0.478	1.0	0.1	0.4	0.1
CHIROTEUTHIDAE	† *Chiroteuthis veranyi*	3	0.6	0.088	0.3	—	1.0	—
	Chiroteuthis sp.	2	0.4	0.039	0.1	—		
PHOLIDOTEUTHIDAE	† *Pholidoteuthis boschmai* (A)	1	0.2	0.834	0.8	0.1	0.2	0.1
ALLOPOSIDAE	† *Alloposus mollis*	9	1.7	0.914	8.2	1.0	1.7	1.0
	TOTAL IDENTIFIED	527	100.0	1.457	823.6	99.5	100.0	99.5

* Known from Antarctic.
x Known from South Georgia and warmer waters.
† Typical of warmer waters.

Mesonychoteuthis sp. A

Lower beaks identified as this genus (Fig. 3c and d) are very close to those referred elsewhere to *Galiteuthis armata* Joubin, 1898 (Fig. 3a and b), but they are not identical with them. They differ in having wings which slope more forward from the jaw angle (a, Fig. 3c) so that the wing forms a smaller angle with the jaw edge (b, Fig. 3c). In addition, the wings are broader opposite the jaw angle (c, Fig. 3c) than in *G. armata,* in which they narrow between the hood and the free extension of the wing. Indentification of these as a new species of *Mesonychoteuthis has only* recently become possible since the beaks have been found with arms in good condition attached. The arm suckers and hooks conclusively show these beaks belong to a species of this genus. The size of these beaks is too small, relative to the state of darkening, for them to belong to the only named member of the genus *M. hamiltoni* (see Clarke, 1980). However, McSweeney (1970) described small *Mesonychoteuthis* which he considered *M. hamiltoni* but whose beaks show a stage of darkening far in advance of *M. hamiltoni* at that size. It seems probable his description is of the same species as the beaks described here. These beaks have an LRL distribution with a *range of 0.48-0.58 cm* (Fig. 1). Beaks identified as *Galiteuthis armata* from sperm whales caught

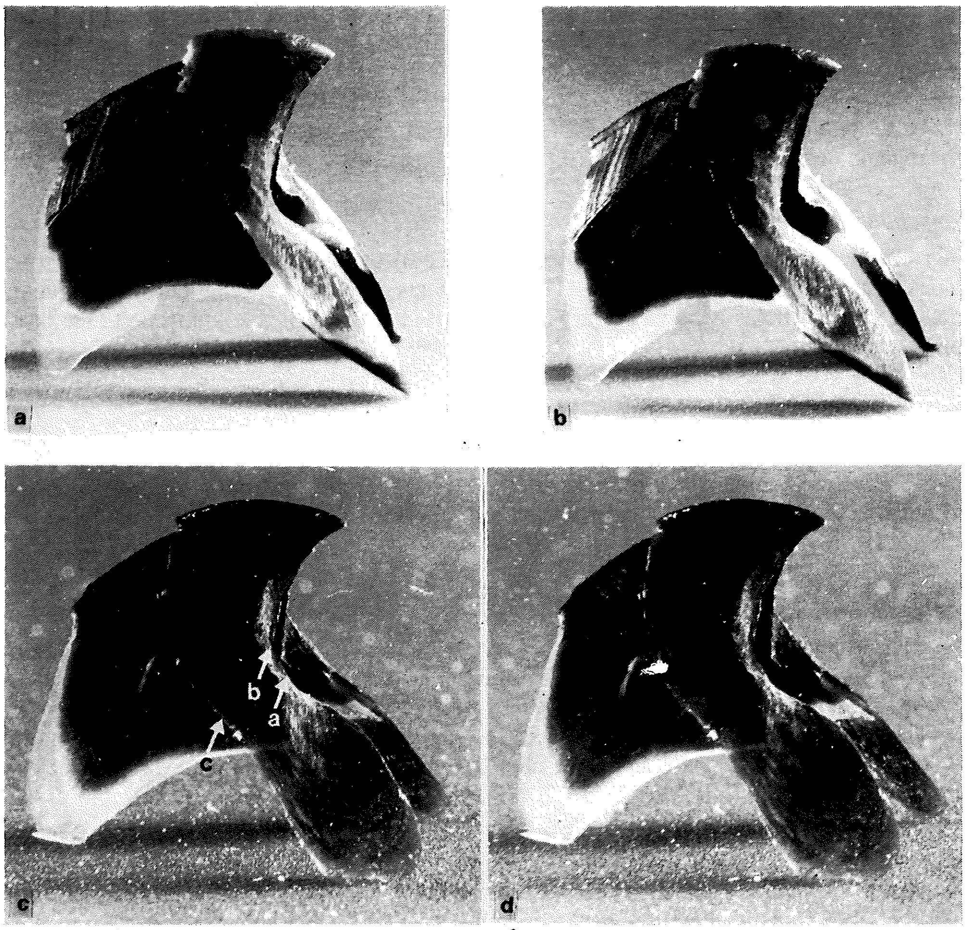

Fig. 3. *Mesonychoteuthis.* Stereo pair of a lower beak of species A (c and d) to show the three features which distinguish it from beaks of a species thought to be *Galiteuthis armata* from sperm whale stomachs (a and b). The *Mesonychoteuthis* sp. A beak is from a younger specimen but the features indicated are retained in older specimens.

off South Africa have a main peak at 0.56–0.62 cm. In these whales there is also the suggestion of a secondary peak near 0.5 cm in several months. Beaks of this secondary peak resemble these from albatrosses and should probably be re-named as *Mesonychoteuthis* sp. A.

The species comprises 4.0% of the lower beaks and 0.2% of the weight of cephalopods in the diet.

Taonius pavo (Lesueur, 1821)

Lower beaks identified as this species or a very close relative comprise about 16.9% of the total number of lower beaks but only 3.4% of the weight of cephalopods represented by beaks. The species occurs in all the complete samples. They have an LRL distribution with a peak at 1.0–1.05 cm (Fig. 1). This peak is very close to the peak of this species found in sperm whales at South Africa and Albany (Western Australia) which has peaks at 0.91–0.97 cm and 1.06–1.08 cm, respectively.

(?) Crystalloteuthis (placed in synonymy with *Galiteuthis* by Voss, 1980)

4% of the lower beaks are the same as beaks from sperm whales caught off Durban having a similar LRL distribution which were identified tentatively as members of this genus. Voss (1980) has recently placed this genus in synonymy with *Galiteuthis* but these beaks differ from those referred to the latter genus elsewhere (Clarke, 1980). It occurs in 90% of the complete samples. The LRL distribution has a peak at 0.525–0.575 cm (Fig. 2). The species contributes 0.7% to the weight of cephalopods in the diet.

Mesonychoteuthis hamiltoni Robson, 1924

Only one beak of a small member (LRL = 1.05 cm) of this Antarctic species was collected. The species grows to a considerable size (LRL = 4.8 cm; Clarke, 1980) and forms a large part of the diet of sperm whales around South Georgia and in the rest of the Antarctic (23% and 14% by number, respectively).

Family Onychoteuthidae

This family, including representatives of the two Antarctic and one warmer-water species, contributes 42.7% of the lower beaks and comprises 83% of the weight of cephalopods in the diet (Table II).

Kondakovia longimana Filippova, 1972

The great majority of the Onychoteuthidae, contributing 40% of all lower beaks, belong to this species and it occurs in all the complete samples. Because this is a large species with an estimated mean weight of over 3 kg, it comprises 81.1% of the weight of cephalopods in the diet.

The LRL distribution has a distinct peak at 1.3–1.4 cm with a range for all but one of the beaks at 0.9–1.8 cm (Fig. 1). This agrees closely with the distribution of the same species from sperm whales caught off South Georgia.

Moroteuthis knipovitchi Filippova, 1972

This smaller Antarctic species is only represented by three lower beaks and was in 20% of the complete samples. Two of the three beaks had an LRL of 0.59 cm which lies near the peak of the LRL distribution for the species from sperm whales caught in the Antarctic. The third is rather smaller (0.45 cm) than those found in sperm whales. The species represents about 0.1% of the weight of cephalopods in the diet.

Moroteuthis robsoni Adam, 1962

A species which is probably near its southern limit at South Georgia, this contributes only 1.9% of the lower beaks and represents 2% of the weight of cephalopods in the diet (Table II). It was present in 40% of the samples. The LRLs have a range of 0.75–0.95 cm (Fig. 2) which includes most of the range of the species in sperm whales from South Georgia (approx. 0.7–0.9 cm).

Onychoteuthis banksi (Leech, 1817)

One lower beak with an LRL of 0.45 cm was indistinguishable from a beak removed from a specimen of this very widespread species which was caught in the Atlantic. The squid from which it came has an estimated weight of 162 g and the species comprises less than 0.1% of the total weight.

Family Histioteuthidae

This family, which forms a large part of the diet of sperm whales in warmer more northerly waters (e.g. about 46% off Durban, South Africa) contributes 15.2% of the lower beaks and only represents 1.1% of the weight of cephalopods in the diet.

Identification of these species, partly based upon size and the stage of darkening of the wing, is only sure for *Histioteuthis bonnellii* and *H. dofleini* of which sperm whales provided much material including beaks and complete specimens.

Histioteuthis (?) meleagroteuthis (Chun, 1910)

One beak with an LRL of 0.42 cm is closely similar to beaks tentatively identified as this species from sperm whales.

Histioteuthis bonnellii Férussac, 1835

One beak belonging to this species with an LRL of 0.55 cm fell within the LRL of beaks from sperm whales caught off South Africa (about 0.42–0.6 cm). The species was not found in samples from Antarctic sperm whales.

Histioteuthis dofleini (Pfeffer, 1912)

One beak with an LRL of 0.54 cm lies below the peak of beaks of this species from South Africa.

Histioteuthis (?) eltaninae (Voss, 1969)

This is the most numerous histioteuthid in the collection, comprising 8.7% of all beaks but, because of its small size, it contributes only 0.4% to the weight of cephalopods in the diet. It was present in 80% of the complete samples. The LRL distribution lies mainly between 0.3 and 0.4 cm (Fig. 1) which corresponds to the upper half of the range of beaks tentatively identified as this species from sperm whales.

Histioteuthis (?) atlantica (Hoyle, 1885)

Contributing 5.9% of the number of beaks, this group comprises 0.7% of the weight of cephalopods represented. The size distribution, having a peak at 0.55–0.60 cm and a range of 0.45–0.70 cm, occupies the higher half of the range of *Histioteuthis atlantica* from sperm whales caught off South Africa and Albany. As the beaks came from six samples and they closely resemble *H. atlantica*, this difference in LRL distribution is surprising, particularly since the South African samples covered 9 months, and it does not seem possible that the difference is due to a seasonal bias in sampling. It is possible, therefore, that this is not *H. atlantica* but an Antarctic species of *Histioteuthis*, not represented in sperm whale stomach contents.

Family Gonatidae

This high latitude family comprises 5.7% of the beaks and 1.0% of the weight of cephalopods in the diet. All the beaks are very closely similar to those of *Gonatus antarcticus* but they fall into two size groups which are separable on the extent of their darkening as well as by size alone (Fig. 2). The larger beaks agree in size with *G. antarcticus* collected from sperm whales in the Antarctic and are named accordingly.

Gonatus antarcticus (Lönnberg, 1898)

This species contributes 3.6% of the lower beaks and 0.8% of the weight of cephalopods represented by beaks. It occurs in 70% of the complete samples. The LRL range is roughly 0.61–0.82 cm with a peak at 0.68–0.7 cm which is close to the distribution of beaks from sperm whales caught off the South Orkney Islands. The few beaks with an LRL above 0.75 cm might be representatives of a larger group present in whales caught near the South Shetland Islands. It is not known whether this indicates a seasonal (growth), distributional or a specific difference.

Gonatus sp. A

A group of smaller beaks with a range of 0.50–0.61 cm probably represents another, as yet undescribed, species. This contributes 2.1% to the lower beaks and 0.2% of the weight of cephalopods in the diet. It occurs in 60% of the complete samples. It was possibly represented by very few beaks in the sperm whale samples from the Antarctic and was not separated from *G. antarcticus*. It cannot be distinguished from the larger beaks on the basis of form and is distinct from the beaks described by Imber (1978) as *G. berryi* and *G. phoebetriae*.

Family Octopoteuthidae

Two species of this family contribute 2.8% of lower beaks and 5.8% of the weight of cephalopods in the diet.

Octopoteuthis rugosa Clarke, 1980

Seven lower beaks belong to this species which contributes 1.5% of the lower beaks and 0.3% to the weight of cephalopods in the diet (Table I). It occurs in 60% of the complete samples. The LRL distribution has a main peak at 1.0–1.05 cm (Fig. 2) which is at the same length as the main peak of the species in South Africa (1.0–1.1 cm). The species does not live in Antarctic waters.

Taningia danae Joubin, 1931

Seven beaks representing 1.3% of lower beaks belong to this large squid which comprises 5.5% of the weight of cephalopods in the diet. It was present in 50% of the complete samples. The LRL range of 0.78-1.76 cm spans the main part of the range for the species from South African sperm whales. Flesh of the species was collected from sperm whales caught off South Georgia but this is probably near the southern limit if its distribution.

Family Mastigoteuthidae

(?) Mastigoteuthis sp. A

Fifteen lower beaks belong to a species which was described but not named from two specimens collected from sperm whale stomachs at Leith in South Georgia. The latter were tentatively placed in the genus *Mastigoteuthis*, although they also have affinities with *Chiroteuthis* (Clarke, 1980).

This species contributes 2.8% of the lower beaks and 0.7% of the weight of cephalopods in the diet. It occurs in 50% of the complete samples. The LRL distribution has a peak at 0.75–0.80 cm (Fig. 2). The peak for the beaks probably of this species in Antarctic sperm whales lies at 0.64–0.66 cm but the present beaks lie within the LRL range of the latter.

Family Enoploteuthidae

Ancistrocheirus lesueuri (d'Orbigny, 1839)

This species contributes 1.5% of the beaks and just 1.4% of the weight of cephalopods in the diet. The LRL distribution has a peak near 0.75–0.90 cm (Fig. 2) which spans the peak of the species from South Africa in sperm whales. It does not live in Antarctic waters, south of South Georgia.

Family Lepidoteuthidae

Lepidoteuthis grimaldii Joubin, 1895

This species contributes 0.9% of the beaks and 0.8% of the weight of cephalopods in the diet. The LRLs have a range of 0.78–1.52 cm which falls within the range of those from South Africa in sperm whales. The species probably does not live in Antarctic waters.

Family Ommastrephidae

Todarodes (?) sagittatus (Lamarck, 1799)

This species contributes 0.4% of the beaks and 0.1% of the weight of cephalopods in the diet (Table I). Their LRL range is 0.63–0.69 cm which is smaller than the range of the species in sperm whales but is near the top of the range of the species (0.23–0.61 cm) in *Diomedea chrysostoma* and *D. melanophris*, the grey-headed and black-browed albatrosses, respectively (Clarke and Prince, 1981).

Family Chiroteuthidae

Chiroteuthis veranyi (Férussac, 1835)

Three beaks are indistinguishable from *Chiroteuthis veranyi* removed from specimens caught in nets.

The species represents 0.6% of the beaks. The beaks have darkened wings at LRLs of 0.52, 0.55 and 0.64 cm. Two additional beaks with LRLs of 0.42 and 0.43 cm are probably *Chiroteuthis* but the species cannot be determined.

Family Pholidoteuthidae

Pholidoteuthis boschmai Adam, 1950

One beak belongs to this species, specimens of which were collected from stomachs of sperm whales caught off South Africa and Albany. The beak has an LRL of 0.75 cm representing a squid of about 0.8 kg.

OCTOPODA

Family Alloposidae

Alloposus mollis Verrill, 1880

This species contributes 1.7% of the beaks and about 1.0% of the weight of cephalopods in the diet. It was present in 40% of the complete samples. The hood lengths have a range of 1.39–2.31 cm which were probably from octopods weighing about 0.55–1.16 kg.

Unidentified

Seventy-one tips and four small intact lower beaks cannot be identified.

Conclusions and Discussion

Twenty-five species are present in the samples and, of these, 16 species are positively identified and named, while a further nine species belong to species recovered from sperm whales but not definitely identified to species.

The ten complete samples contain all species (Table I). The samples of squid beaks regurgitated by chicks are the product of digestion of many meals and the approximate duration of accumulation can be estimated. Given a chick requirement of about 300 g squid per day (Tickell, 1968), the overall consumption during the 277-day fledgling period will be about 83 kg. The mean squid weight from the samples is 1.56 kg and thus the chick would expect to receive about 53 squid during its development. The ten complete samples contain an average of 44 beaks which would thus represent about 230 days' accumulation.

Cephalopod distribution

Some species (* in Table II) certainly live in the Antarctic but not in warmer waters, while three species (X in Table II) which live off South Georgia, are not known from higher latitudes but are common in warmer water. Twelve species († in Table II) live in warmer waters and most of these also occur off South Africa. We have no information on *Gonatus* sp. A and *Mesonychoteuthis* sp. A. Breeding wandering albatrosses at South Georgia are concentrated to the north-west end of the island, on Bird Island, with smaller colonies in the Bay of Isles (north coast) and off the south coast at Annenkov Island (Croxall, 1979). Bird Island wandering albatrosses, which have been marked with colours, are sighted principally to the north of South Georgia (Tickell 1968; unpublished B.A.S. data). On the basis of capture–recapture information, Tickell (1968) calculated the minimum known distance a bird could travel as 200 nautical miles (371 km) per day. As each adult only feeds its chick approximately every 6 days, this would give a minimum range of about 1 000 km. This accords well with recent sightings of marked breeding albatrosses at distances up to approximately 1 500 km from the breeding colony at a time when they would be feeding young chicks. With this potential foraging range, it is not surprising to find a significant proportion of squid, typical of the warmer waters north of the Antarctic Convergence, in the wandering albatross samples, even though the species that makes up the bulk of the diet (*Kondakovia longimana*) is from colder waters.

Comparison with other samples from wandering albatross

The 18 samples contained 532 beaks with a mean of 29.6 per sample; the ten complete samples provided a mean of 44 beaks per sample. This is similar to the average of 40 beaks per sample for the seven whole-stomach samples from Auckland birds studied by Imber and Russ (1975). However, five of their samples from adults provided only 32 beaks, the remaining 249 coming from the two chicks collected. This is a high number of beaks per sample but not only will the complete stomach contents contain many beaks that would not necessarily have been regurgitated, but the average weight of the New Zealand squid (0.41 kg) is only 26% that of the South Georgia squid (1.56 kg).

In other respects the New Zealand and South Georgia sets of samples are not dissimilar with totals of 31 and 25 species recorded, respectively, of which about 45% are common to both collections. In the South Georgia material, Onychoteuthidae are much more (42.7% compared with 7%), and Histioteuthidae much less (15.2% compared with 53% by numbers) important by numbers and weight, Chiroteuthidae (10% by number in New Zealand) are hardly represented (1.0%) and, although there are many more cranchiid beaks, the family is much less important by weight. The differences between the two regions may be a reflection of the latitude at which the albatrosses are sampling since the onychoteuthids involved are mainly from cold Antarctic water while the histioteuthids involved are from warmer water.

Comparison with samples from sperm whales

Twenty-two species in these albatross samples are almost certainly the same as species found in sperm whales previously examined in the Antarctic and around South Africa (Clarke, 1980). Only three species, *Mesonychoteuthis* sp. A, *Gonatus* sp. A and *Chiroteuthis* sp. were not recorded from sperm whales by Clarke (1980) but they may all have been present in very small numbers. There are, however, some notable differences between the two diets. First, there are differences in size of the cephalopods sampled in a few instances. While they overlap in size, *Histioteuthis (?) eltaninae, H. (?) atlantica* and *Mastigoteuthis* sp. A have larger beaks and *Todarodes* has smaller beaks in the albatross samples than in the sperm whale samples. Secondly, the different species are present in very different proportions in samples from the two predators. Fig. 4 shows the percentages of all the commoner (>1%) cephalopod species from the albatrosses (in descending order) compared with the percentages for these species in sperm whales caught off South Georgia (see Clarke and MacLeod, 1976). Species from sperm whales comprising more than 1% and not included in Fig. 4 only total about 15%.

Wandering albatross feeding methods

Apart from daytime observations of the wandering albatross scavenging for offal from ships,

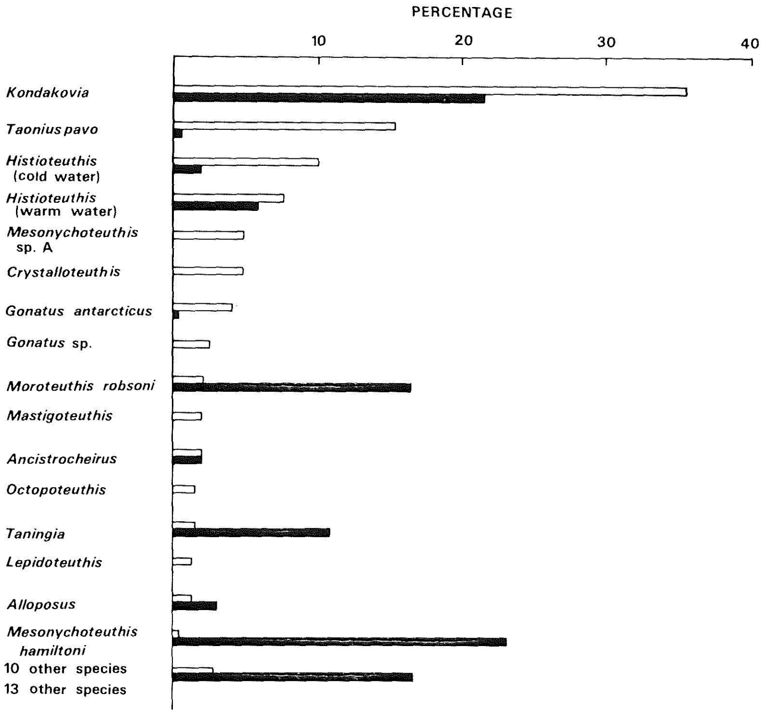

Fig. 4. The frequency % of beaks of species of cephalopods in regurgitations from near nests of wandering albatrosses at South Georgia (white) compared with the frequency % of the beaks of the same species in sperm whales caught in the Antarctic (black; see Clarke, 1980).

there is virtually no information on its feeding behaviour and techniques. This is of importance when considering the source of some of the large squid in its diet.

Prince (1980) has indicated that, judging from the condition of their squid prey, general data and feeding ecology, it is very likely that grey-headed and black-browed albatrosses capture living squid on the sea surface, probably at night. The principal squid prey of these species is *Todarodes (?) sagittatus* up to 410 g in weight (11% body weight of the albatross). By analogy, one would expect the wandering albatross to be able to deal with squid up to about 900 g in weight. This would cover most of the species in Table I, with the notable exception of *Taningia* (mean weight 6.5 kg but only 5% of the diet by weight) and *Kondakovia* (mean weight 3.2 kg but 83% of the diet by weight). It is hardly conceivable that *Taningia* could be captured alive and such large *Kondakovia* would certainly be extremely active well-armed prey, even for the razor-sharp powerful bill of a wandering albatross. Unpublished data on light-mantled sooty albatrosses (*Phoebetria palpebrata*) indicate that about half its diet by weight is made up of squids with a mean weight of about 700 g (25% albatross body weight) and if this species takes live material then one might expect wandering albatrosses to manage squid up to about 2.5 kg. However, without observations of the albatrosses' actual feeding technique it must remain uncertain as to whether they could capture living specimens of squid of such size.

Another remarkable feature of the diet is the nature of some of the cephalopods consumed. Several of the families represented are believed, on the basis of worldwide capture by nets (e.g. Clarke, 1966; Clarke and Lu, 1974, 1975; Lu and Clarke, 1975*a, b*; Roper and Young, 1975), to be deep living particularly in their later life. Thus, individuals as large as those represented in the albatross by beaks belonging to the families Octopoteuthidae, Chiroteuthidae, Mastigoteuthidae, Lepidoteuthidae and Enoploteuthidae are not known ever to approach the sea surface.

Sperm whales, which feed on the squid in these families and take substantial quantities of large *Kondakovia* (and also *Taningia*) regularly vomit their stomach contents not only during the approach, chase and capture by Man but also periodically to empty their stomachs of cephalopod beaks which do not pass further down the gut (Clarke, 1980). Thus it is not rare for whalers or marine biologists to observe freshly vomited cephalopods floating on the sea surface even without a sperm whale being actually chased. Clarke has collected rarely seen squids from such vomit on at least three occasions. When such an occasion arises, sea birds are rapidly attracted and Clarke once filmed a wandering albatross picking up a rare squid (probably a *Chiroteuthis*) from the sea in daylight just after a sperm whale had vomited at capture. Incidentally, at the same time cape pigeons (*Daption capensis*) were busily tearing apart a large *Taningia*.

Is it possible that vomit from sperm whales (and perhaps other odontocetes also) could provide sufficient squid for wandering albatrosses to fulfil their dietary requirements by scavenging?

We have noted earlier that wandering albatrosses are unlikely to be able to travel further than 1500 km from South Georgia while rearing chicks. This would barely permit them to reach lat. 45°S and, as few female sperm whales venture south of this parallel, access to vomit would be restricted to that provided by males. Furthermore, wandering albatrosses rear their chicks through the austral winter at a time when it is uncertain how many male sperm whales are within foraging range of South Georgia.

It appears then that the source of many of the squid in wandering albatross diet and the ability of the albatross to capture large squid (if they are not scavenging buccal masses and attached flesh from whale vomit) must still be regarded as an unresolved problem.

Imber and Russ (1975) believed that wandering albatrosses feed chiefly at night, detecting squid prey mainly through their bioluminescence, based on 82% by numbers (but only 49% by weight) of their squid being bioluminescent species. However, only 52% by numbers and 17% by weight of the squids found in our samples are bioluminescent (after Herring, 1977), which provides little support for Imber and Russ' hypothesis. In addition, all 16 luminescent species except for the two octopoteuthids use their luminescence to break up or hide their silhouettes from below against the down-welling light and it is improbable that the light emitted can be observed from above because the light organs are specially screened to avoid this (Young, 1977). Thus, the large proportion of squid with light organs is more likely to be a reflection of the undoubted high proportion of oceanic squid possessing photophores than to be due to a greater ability of the albatrosses to catch luminous squids.

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Note added in proof

A recent opportunity to examine the beaks described by McSweeney (1970) and other material kindly made available by Dr Nancy Voss showed that the beaks described here as *Mesonychoteuthis* sp. A should most probably be referred to *Galiteuthis glacialis* rather than to a small *Mesonychoteuthis* species.