DIETARY STUDIES OF LIGHT-MANTLED SOOTY ALBATROSSES *PHOEBETRIA PALPEBRATA* FROM MACQUARIE AND HEARD ISLANDS

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SUMMARY

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Collections of dietary material from Light-mantled Sooty Albatrosses *Phoebetria palpebrata* were made at Macquarie Island in 1970 and 1993, and at Heard Island in 1992. Comparisons between regurgitated stomach contents and casts confirmed earlier speculation that the size distributions of squid beaks differed between the two, probably due to the loss of smaller beaks by digestion. The diets of Light-mantled Sooty Albatrosses at Macquarie Island had greater similarities to those at Marion Island than to those at Iles Crozet and South Georgia, due to the greater importance of fish and the lower importance of crustaceans in the diet at Macquarie Island. Squid species taken by Light-mantled Sooty Albatrosses were similar at Macquarie Island and Heard Island, with a greater proportion of *Histioteuthis eltaninae* and *Martialia hyadesi* at Macquarie Island compensated for by greater consumption of *Galiteuthis/Teuthowenia* spp. at Heard Island. Species composition based on casts at Macquarie Island differed less between 1970 and 1993 than between seasons, either due to a real stability in the diet or to chance sampling during years of similar diet, prey availability or abundance.

INTRODUCTION

The Light-mantled Sooty Albatross *Phoebetria palpebrata* has a circumpolar distribution, breeding on South Georgia, Marion Island, Prince Edward Island, Iles Crozet, Iles Kerguelen, Heard Island, Macquarie Island, Auckland Island, Campbell Island and Antipodes Island (Marchant & Higgins 1990), and is most commonly seen at sea between the Antarctic Polar Front and the Antarctic pack ice (Johnstone & Kerry 1976, Woehler *et al.* 1990). Light-mantled Sooty Albatrosses are biennial breeders (Kerry & Colback 1972) and return to breed at Macquarie Island on about 1 October, with egg-laying occurring between 20 October and 5 November. Incubation lasts 64–71 days until late December or early January, and fledglings leave between mid-May and mid-June (Kerry & Garland 1984). The breeding season at Heard Island follows a similar pattern (Downes *et al.* 1959).

The Light-mantled Sooty Albatross feeds by surface seizing, surface filtering and plunging (reviewed by Harper 1987). Birds are known to forage widely during the breeding season, with birds from Macquarie Island travelling on average 1500 km to their foraging grounds (Weimerskirch & Robertson 1994). Detailed dietary studies of Light-mantled Sooty Albatrosses have only been conducted at South Georgia (Thomas 1982), Marion Island (Berruti & Harcus 1978, Imber & Berruti 1981, Cooper & Klages 1995) and Iles Crozet (Weimerskirch *et al.* 1986, Ridoux 1994). The diet at these breeding localities is comprised mainly of cephalopods, fish, crustaceans and carrion; the same food groups were present in smaller samples collected at South Georgia (Murphy 1936), Iles Crozet (Mougin 1970), Iles Kerguelen (Falla 1937), Heard Island (Downes *et al.* 1959) and Campbell Island (Sorenson 1950).

There was a decrease in the reproductive success of Light-mantled Sooty Albatrosses at Macquarie Island between the breeding seasons of 1970/71 and 1980/81; postulated to be caused by a change in the availability of food (Kerry & Garland 1984). At Macquarie Island, the breeding population comprised an estimated 500–700 pairs during the early 1970s (Kerry & Colback 1972). In 1992/93 768 nests were counted, representing an estimated 1000 to 1200 pairs for the whole island for one year and therefore an estimated breeding population of about 2000 pairs (T. Disney unpubl. data). At Heard Island, the population was estimated at 500–700 pairs in 1957 (Downes *et al.* 1959) and at 100–300 pairs in 1987/88 (R. Kirkwood pers. comm.). Except for the count in 1992/93 on Macquarie Island, these estimates suffer from a lack of comprehensive coverage of the two islands and cannot be taken as evidence of population change in either direction. However, Brothers (1991) postulated a high level of mortality for the species, estimated at more than 4000 birds per year as a result of longline fishing, and it is possible that the Heard Island population may have decreased. The present study, therefore presents dietary information from immediately before the decrease in reproductive success at Macquarie Island, and throughout the period of tuna longline fishing which commenced in the 1950s in the Southern Ocean.

METHODS

Dietary material of Light-mantled Sooty Albatrosses was collected from Macquarie Island (54°30'S, 158°57'E) in 1970 by K.R. Kerry and G.W. Johnstone. The material consisted of regurgitations from adults and chicks induced by the presence of an intruding human, as well as material found regurgitated beside nests, and also casts of undigested remains. Casts were collected in 1992 and 1993 from around the nests of Light-mantled Sooty Albatrosses at Heard Island (53º05'S, 73º30'E) and Macquarie Island, respectively. In the 1970 collection at Macquarie Island, some material was identified at the nest and immediately discarded. Because of the uncertainty about the treatment of samples and the long period of storage, beaks were not separated into fresh and accumulated categories.

Fish remains were classified as benthic or pelagic based on characteristics of the vertebrae: the length-width ratio, the diameter of the lumen of the centrum, and the degree of ribbing of the bone (Green & Burton 1987). Squid beaks were identified by using Clarke (1986), and a reference collection of rostons compiled by M.R. Clarke mainly from whale stomachs, and another compiled by K. Green from seal stomachs and droppings. Beaks from the cranchiid genera *Galiteuthis* and *Teuthowenia* could not be separated and are referred to as *Galiteuthis/Teuthowenia*. Allometric equations relating lower rostral length of squid beaks to whole, wet body mass were obtained from Rodhouse (1990) and Clarke (1986), except for *Todarodes fillipovae* (ln mass = 2.309lnr + 2.388) from M. Dunning (pers. comm.) and *Alluroteuthis antarcticus* (ln mass = 3.60lnr + 0.37) from Green & Burton (1993).

Squid were divided into ‘Antarctic’ and ‘non-Antarctic’ forms according to their occurrence south or north of the Antarctic Polar Front, following the classification in Rodhouse *et al.* (1987) and Rodhouse (1988, 1989, 1990). However, it must be noted that the distribution of squid in the Southern Ocean is still poorly known (Rodhouse *et al.* 1987). Species representation by squid beaks in casts and regurgitations was compared using the Mantel Test (Patterson 1986); the same test was also used to compare the squid component between 1970 and 1993. For these comparisons, only samples containing more than 10 squid beaks were used and the squid species were confined to those eight that were represented in the complete data set by at least 20 beaks.

TABLE 1

Percentage frequency of occurance of prey in regurgitations of Light-mantled Sooty Albatrosses at Macquarie Island for 1970

Item	Feb	Mar	Apr	May
Fish	56.3	55.0	57.1	60.0
Squid	100.0	90.0	71.4	73.3
Octopus	0.0	5.0	0.0	0.0
Crustacean	37.5	50.0	46.4	46.7
Bird	18.8	40.0	32.1	10.0
No.	**16**	**20**	**28**	**30**

RESULTS

At Macquarie Island, 94 regurgitations and 23 casts were collected in the breeding season of 1969/70 and 27 samples (mainly casts) in the non-breeding season of 1970. Fifty casts were collected in 1993. Seven casts were collected on Heard Island.

Prey composition

The frequency of occurrence of fish in regurgitations at Macquarie Island was 55–60% in 1970. Squid occurred in approximately 70–100% of regurgitations on a monthly basis in 1970. Bird material in regurgitations was highest in March. Crustaceans occurred in between 45 and 50% of samples in all months at Macquarie Island except February (Table 1).

Flesh in regurgitations from Macquarie Island in 1970 came mainly from squid and fish, and included whole squid. Vertebrae in regurgitations were from both benthic and pelagic fish. The maximum length of benthic fish reconstructed from vertebrae exceeded 60 cm. Benthic fish remains were also found in casts at Heard Island. However, in the absence of otoliths specific identification of fish remains was not possible. Crustaceans were generally only represented by fragments or a few individuals. Crustacean species found in regurgitations from Macquarie Island were mainly unidentifiable decapods, however, the large deep water prawn *Pasiphaea rathbunae* was represented in one stomach by five heads and seven tails. Other identifiable crustaceans from samples collected at Macquarie Island were the amphipods *Vibilia* sp., *Hyperiella dilatata*, *Hyperiella* sp., *Cyllopus* sp. and *Themisto gaudichaudi*, and unidentified gammarids and hyperiids. In addition, there were salps and unidentified euphausiids. Bird remains in samples from both Macquarie and Heard Islands were mainly of penguin feathers, although petrel feathers were present in Macquarie Island samples.

Comparison between casts and regurgitations

There was no significant difference between the composition of the squid component in the diet between casts and regurgitations (Mantel test, $G = 5.179$ $P = 0.223$). There were, however, significant differences between the sizes of beaks of *Psychroteuthis glacialis* (t-test, $P < 0.001$), *Alluroteuthis antarcticus* (t-test, $P < 0.05$) and *Galiteuthis/Teuthowenia* (t-test, $P < 0.01$) obtained from the two sampling methods with all being larger in casts than in regurgitations (Table 2).

Inter-annual and geographical differences

There was no significant difference between the composition of the squid component in the diet between 1970 and 1993 (Mantel test, $G = 4.022$, $P = 0.096$). There was, however, a doubling of the proportion of beaks of *Kondakovia longimana* and *Histioteuthis eltaninae* by number which was mainly offset by the decreases in the proportion of *Galiteuthis/Teuthowenia*. In terms of the proportions by mass, there were few differences between 1970 and 1993. There was a 75% increase in the representation of *K. longimana*, but this was not balanced by any great change in other species. There were few data from Heard Island, but by comparison with Macquarie Island there were lower proportions of *Martialia hyadesi* and *H. eltaninae* which were compensated for by higher proportions of *Galiteuthis/Teuthowenia* and *K. longimana* (Table 4). By mass, however, there was a decrease in all species except for increases in *K. longimana* and *Moroteuthis ingens* (Table 5).

TABLE 2

Comparison of percent contribution by numbers for those samples containing at least 10 beaks for each type of sample for 1970, and between size of beaks of beaks from regurgitations and casts in 1970 for the eight squid most commonly taken by Light-mantled Sooty Albatrosses. Significance levels are for comparisons in size using the *t*-test

	Composition by numbers (%)		Average size of beaks (mm) (Mean±SD)		
Species	**Regurgitations**	**Casts**	**Regurgitations**	**Casts**	***P***
Gonatus antarcticus	3.2	1.8	6.0±0.2	6.0±0.7	NS
Kondakovia longimana	4.2	4.9	9.0±2.3	7.7±2.5	NS
Histioteuthis eltaninae	13.0	5.4	3.2±0.3	3.4±0.6	NS
Psychroteuthis glacialis	5.3	2.9	3.7±0.3	4.8±0.7	<0.001
Alluroteuthis antarcticus	4.2	7.8	4.6±0.4	5.3±0.8	<0.05
Martialia hyadesi	5.3	9.6	4.6±0.9	5.5±1.1	NS
Chiroteuthis joubini	11.6	13.3	6.6±0.4	6.5±0.9	NS
Galiteuthis/Teuthowenia	53.7	54.2	4.5±0.4	4.7±0.6	<0.01

Seasonal differences

The major differences between non-breeding and breeding season casts at Macquarie Island was the reduced proportion of *A. antarcticus*, which was compensated for in numbers by an increase in *Galiteuthis/Teuthowenia* and *M. hyadesi* (Table 4). By mass, however, there was a decrease in *K. longimana*, *M. ingens* and *A. antarcticus* compensated for by an increase in *M. hyadesi*, *Todarodes* sp. and *Galiteuthis/Teuthowenia* (Table 5).

DISCUSSION

General

Size calculations for some *K. longimana* preclude predation on them by Light-mantled Sooty Albatrosses. Ammonium contents of *K. longimana* fall within the range for squid with positive buoyancy (Lu & Williams 1994) and it is likely that many such squid were scavenged at the ocean surface. At Marion Island, 97.6% of squid taken by Light-mantled Sooty Albatrosses had positive buoyancy, and scavenging for dead squid is probably an important foraging technique (Cooper & Klages 1995). The scavenging of large squid at the sea surface may result in no beaks being ingested, thus leading to an under-representation of large squid in any form of diet analysis, whether it be by regurgitation or cast (Imber & Berruti 1981).

The crustacean component of the diet was mainly Antarctic Krill *Euphausia superba* at Iles Crozet (Weimerskirch *et al.* 1986, Ridoux 1994), and comprised 90% of crustaceans at South Georgia and 40% by mass of the diet overall (Thomas 1982), and was the only prey recorded in the Ross Sea (Ainley *et al.* 1984). Although unidentified euphausiids occurred in the present study, no krill was identified despite the high probability of birds foraging in Antarctic waters near the northern edge of the pack-ice (Weimerskirch & Robertson 1994). Others crustacean remains found by Thomas (1982) in samples at South Georgia included decapods and the amphipods *Cyllopus* and *Themisto gaudichaudi* (both found in the present study). The amphipods were regarded as too small to have been taken deliberately and Thomas (1982) suggested that they may have been taken as secondary prey. In the present study, the deep-water prawn *Pasiphaea rathbunae*, also found from Light-mantled Sooty Albatrosses from Iles Crozet by Ridoux (1994), was probably taken as a result of scavenging.

Sources of bias

Stomach samples or regurgitations of whole meals are thought to contain greater amounts of smaller beaks than regurgitated casts due to
1) some digestion of smaller beaks by the time the cast is ejected (Imber 1973, Imber & Berruti 1981, Hunter & Klages 1989, Cooper *et al.* 1992, Cooper & Klages 1995); and
2) collection of beaks from around nests (where small beaks may be hard to see) might reinforce this bias towards larger beaks (Clarke *et al.* 1981). However, there have been few data presented to confirm this: Hunter & Klages (1989) found fewer and smaller *K. longimana,* fewer *Moroteuthis* and more *H. eltaninae* from stomach samples of Grey-headed Albatrosses *Thalassarche chrysostoma* than in an earlier collection of casts by Brooke & Klages (1986); Cooper *et al.* (1992) found a similar result for Wandering Albatrosses *Diomedea exulans*. Both studies admitted the possibility of inter-annual

TABLE 3

Monthly percent contribution by numbers to all regurgitations for the eight squid most commonly taken by Light-mantled Sooty Albatrosses at Macquarie Island

Species	Feb	Mar	Apr	May
Gonatus antarcticus	3.2	4.8	2.5	5.7
Kondakovia longimana	9.5	0.0	2.5	2.9
Histioteuthis eltaninae	19.0	4.8	2.5	5.7
Psychroteuthis glacialis	9.5	4.8	10.0	0.0
Alluroteuthis antarcticus	1.6	0.0	10.0	28.6
Martialia hyadesi	7.9	4.8	10.0	22.9
cf *Chiroteuthis joubini*	3.2	14.3	20.0	8.6
Galiteuthis/Teuthowenia	46.0	66.7	42.5	25.7
No.	**63**	**21**	**80**	**35**

TABLE 4

Proportions (%) of squid by numbers identified from beaks in regurgitations and casts of Light-mantled Sooty Albatrosses at Macquarie Island 1970 (breeding and non-breeding) and 1993, and for Heard Island 1992

	Macquarie				Heard
	1970	**1970**	**1970**	**1993**	**1992**
	Casts	**Regurgitations**	**Casts**	**Casts**	**Casts**
Family and species	**Non-breeding**	**Breeding**	**Breeding**		
Gonatidae					
***Gonatus antarcticus*	2.5	3.3	1.6	1.3	2.1
Onychoteuthidae					
***Kondakovia longimana*	5.9	4.3	4.7	10.7	14.9
**Moroteuthis knipovitchi*	0.4	0.9	0.4	0.1	0.0
**Moroteuthis ingens*	0.4	0.5	0.3	0.5	2.1
Histioteuthidae					
Histioteuthis sp. A	0.0	0.5	0.4	0.0	0.0
Histioteuthis eltaninae	7.5	8.1	5.1	10.6	2.1
Histioteuthis sp.	0.0	0.5	0.0	0.0	0.0
Psychroteuthidae					
***Psychroteuthis glacialis*	2.9	7.1	3.4	1.4	0.0
Brachioteuthidae					
**Brachioteuthis* sp.	0.0	0.9	0.1	0.0	0.0
Neoteuthidae					
**Alluroteuthis antarcticus*	13.4	9.0	6.9	4.3	2.1
Ommastrephidae					
***Martialia hyadesi*	2.5	10.4	8.8	10.0	2.1
Todarodes sp.	0.4	0.0	3.1	0.0	0.0
Chiroteuthidae					
*cf *Chiroteuthis joubini*	14.6	11.3	12.4	15.0	14.9
Joubiniteuthidae					
Joubiniteuthis portieri	0.8	0.5	0.0	0.0	0.0
Cranchiidae					
***Galiteuthis/Teuthowenia*	46.4	40.8	52.0	42.8	59.6
**Mesonychoteuthis hamiltoni*	0.4	0.5	0.0	0.0	0.0
**Taonius pavo* (large type)	0.0	0.0	0.1	0.0	0.0
Unidentified squid	1.7	1.4	0.5	3.2	4.2
Number of beaks	**258**	**211**	**739**	**1685**	**47**

*Antarctic species (see Methods).
**North and South of the Antarctic Polar Front.

differences as a possible explanation for the observed differences in diet compositions. The smaller size range of fresh beaks compared to accumulated beaks from the same regurgitations from Light-mantled Sooty Albatrosses was commented on by Ridoux (1994). It is surprising, considering the ease of collection of casts, that no previous quantitative comparison has been made between the two methods.

The present collection of dietary material using two different methods in 1970 presented the opportunity for such a comparison and confirmed the existence of differences in beak size between casts and regurgitations but not both in species composition. The collection of regurgitations and casts in the same breeding season allowed a great degree of confidence in these comparisons. *Galiteuthis/Teuthowenia*, *A. antarcticus* and *P. glacialis* were all significantly larger in casts than in regurgitations in the present study, and *M. hyadesi* (t-test, $P = 0.054$) was almost so. Care must be taken in the case of *Galiteuthis/Teuthowenia* because differences between the two sources of material may have been due either to a different species mix or size-specific retention of beaks in the stomach of birds. Unlike the finding of Hunter & Klages (1989) and the assumption of Cooper & Klages (1995), however, there was no significant difference in the sizes of *K. longimana* beaks which, in the present study, were in fact slightly larger in regurgitations than in casts. The difference could be due to a lack of predation on *K. longimana* and a greater reliance on scavenging of larger specimens of this species. This would mean that there would be fewer smaller beaks in the original meals and therefore any loss due to digestion would not have

TABLE 5

Proportions (%) of squid by mass, identified from beaks in regurgitations and casts of Light-mantled Sooty Albatrosses at Macquarie Island 1970 (breeding and non-breeding season) and 1993, and for Heard Island 1992

	Macquarie				Heard
	1970	1970	1970	1993	1992
	Casts	Regurgitations	Casts	Casts	Casts
Family and species	Non-breeding	Breeding	Breeding		
Gonatidae					
***Gonatus antarcticus*	1.5	3.2	2.0	1.6	0.7
Onychoteuthidae					
***Kondakovia longimana*	33.2	5.6	20.6	36.1	67.2
**Moroteuthis knipovitchi*	0.7	3.3	1.2	0.4	0.0
**Moroteuthis ingens*	10.8	0.2	5.7	1.7	5.5
Histioteuthidae					
Histioteuthis sp. A	0.0	0.3	0.3	0.0	0.0
Histioteuthis eltaninae	2.6	3.7	2.4	4.8	0.5
Histioteuthis sp.	0.0	0.6	0.0	0.0	0.0
Psychroteuthidae					
***Psychroteuthis glacialis*	3.9	15.5	2.5	0.5	0.0
Brachioteuthidae					
**Brachioteuthis* sp.	0.0	0.1	0.0	0.0	0.0
Neoteuthidae					
**Alluroteuthis antarcticus*	18.1	20.0	13.4	9.0	1.3
Ommastrephidae					
***Martialia hyadesi*	4.0	21.8	13.4	15.1	3.7
Todarodes sp.	0.4	0.0	5.8	0.0	0.0
Chiroteuthidae					
*cf *Chiroteuthis joubini*	7.8	7.6	10.2	11.4	5.8
Joubiniteuthidae					
Joubiniteuthis portieri	0.0	0.0	0.0	0.0	0.0
Cranchiidae					
***Galiteuthis/Teuthowenia*	16.2	17.2	22.3	19.4	15.3
**Mesonychoteuthis hamiltoni*	0.7	0.9	0.0	0.0	0.0
**Taonius pavo* (large type)	0.0	0.0	0.2	0.0	0.0

*Antarctic species (see Methods).
**North and South of the Antarctic Polar Front.

a significant impact upon overall size distribution. The present study therefore highlights the difficulties in comparing diets based on different collection methods, and it may be virtually impossible to separate real differences in diet from differences due to the method of collection. However, the cephalopod component should be comparable where the sampling methods are similar (Cooper *et al.* 1992) and therefore comparisons across years in the present study (1970 to 1993) should be valid when based on beaks from casts only.

Comparison between localities

Thomas (1982) regarded krill and squid as important in the diet of Light-mantled Sooty Albatrosses at South Georgia, but regarded squid and perhaps fish more important at Marion Island, a finding confirmed by Cooper & Klages (1995). At Iles Crozet, squid predominated overall with the amounts of fish and crustaceans being somewhat similar (Ridoux 1994). The results of the present study are similar to those at Marion Island, and regurgitations at Macquarie Island were generally dominated by the flesh of fish and squid. Krill was not found in the diet despite birds foraging in Antarctic waters. The occurrence of crustaceans, though relatively high, was of only a few individuals per sample and no crustacean ever predominated. This differs from Iles Crozet where Weimerskirch *et al.* (1986) recorded crustaceans predominating in 17.8% of samples. At Iles Crozet, Weimerskirch *et al.* (1986) recorded frequencies of occurrence for squid of 95.6% (c.f. 80.9% at Macquarie Island), 31.1% for fish (57.4%), 42.2% for crustaceans (45.7%) and carrion (mainly penguins) of 40.0% (24.5%). Frequencies of occurrence, however, are difficult to compare, and at South Georgia, Thomas (1982) recorded fish occurring in over 50% of samples but making up only 11% by mass of samples. Similarly in the present study, crustaceans appeared in 45.7% of samples but generally consisted of small amounts, often just eyes. Components were not weighed at

Macquarie Island in 1970, however, examination of field data indicates that the mass of fish remains would be closer to that of squid rather than crustaceans. On the balance of evidence, as with Marion Island, fish seemed more important at Macquarie Island than at Iles Crozet, although more samples in similar years may be necessary to confirm such a preliminary comparison. No dates were given for collection at Iles Crozet by Weimerskirch *et al.* (1986) so the differences in the bird component may be due to the timing of sampling. The differences in diets between islands relate, no doubt, to the foraging areas and the high krill availability in waters south of South Georgia, compared to Antarctic waters in sectors south of Marion, and Macquarie Islands. The higher occurrence of krill in samples collected at Iles Crozet and Marion Island however, is possibly due more to long-distance foraging by Light-mantled Sooty Albatrosses due to interspecific competition with the Sooty Albatross *Phoebetria fusca* and resultant dietary segregation (but see Berruti & Harcus 1978). All of these inter-island diet comparisons are made with the recognition that inter-annual differences have generally not been determined.

The squid component of the diet in the present study has similarities with Light-mantled Sooty Albatrosses at Marion Island. There, *Galiteuthis*, *Teuthowenia*, *K. longimana*, and *H. eltaninae* dominated in casts, contributing 64.3% by number of beaks (Berruti & Harcus 1978, Imber & Berruti 1981) compared to 61.8% in 1970 and 64.1% in 1993 at Macquarie Island. In regurgitations, the figure was 56.0% for Marion Island (Cooper & Klages 1995) and 53.2% for Macquarie Island. The combined figure for casts and regurgitations at Iles Crozet was 67.3% (Ridoux 1994). The major differences between samples were the complete absence of *Teuthowenia* from samples at Iles Crozet, the general lack of *M. hyadesi* in samples from Marion Island (three beaks in the two studies) and the greater representation of *H. eltaninae* and *Moroteuthis knipovitchi* at Marion Island (24.2% and 6.1%) from casts (Berruti & Harcus 1978, Imber & Berruti 1981) and regurgitations (25.6% and 4.7%) (Cooper & Klages 1995) compared to Macquarie Island in casts in 1970 (5.1% and 0.4%) and 1993 (10.6% and 0.1%) and regurgitations (8.1% and 0.9%). Heard Island paralleled the situation at Marion Island somewhat, with fewer *M. hyadesi* than at Macquarie Island, but also fewer *H. eltaninae*. This may be due to its location south of the Antarctic Polar Front which was also reflected in the increased amounts of *K. longimana* and *M. ingens*. However, diets at South Georgia (Thomas 1982) differed markedly from those at all of the above islands with *Mesonychoteuthis* and ?*Discoteuthis* constituting 78.7% by numbers of all squid beaks, with *Galiteuthis* and *Teuthowenia* being totally absent, and *K. longimana* represented by only one beak.

Seasonal differences

One major difference in the diet of Light-mantled Sooty Albatrosses throughout the breeding season at Macquarie Island was in the frequency of bird remains, which was highest in March. This suggests that the amount of bird material taken may have been influenced by the local availability of dead penguins through the penguin breeding season. Despite being from a similar period, bird remains (mainly penguin feathers) were found in only 22% of samples from South Georgia between January and April (Thomas 1982). This contrasts with a range of 23.5–52.4% in the present study and may, again, reflect the higher abundance of krill south of South Georgia either in the initial choice of prey by Light-mantled Sooty Albatrosses or in the availability of penguin carcasses. At Marion Island, Imber & Berruti (1981) found dramatic changes in the monthly samples between January and May. Seasonal changes in the present study were both contrary to and in accord with trends at Marion Island where the amount of *H. eltaninae* in samples increased as the breeding season progressed whereas at Macquarie Island it started high then decreased. The decrease of *Galiteuthis/Teuthowenia* from a maximum in February, March and April was reflected at Marion Island, as was the increase in *A. antarcticus* over the season (n.b. *A. antarcticus* was misidentified as *G. glacialis* by Imber & Berruti (1981): see Cooper & Klages (1995)). Imber & Berruti (1981) were unable to assign seasonal dietary changes to changes in the absolute number or relative availability of food at the ocean surface. However, seasonal changes in the diet of Light-mantled Sooty Albatrosses were mirrored in the diet of the Sooty Albatross. Imber & Berruti (1981) suggested changes in the feeding behaviour of albatrosses at different times of the breeding season that would explain differences in diet, in particular, a reduction in foraging range after eggs hatched and chicks had to be fed. However, in the present study the increase in frequency of *A. antarcticus* and the decrease in *H. eltaninae* actually suggest greater foraging into Antarctic seas, rather than birds remaining north of the Antarctic Polar Front.

Inter-annual differences

The squid component of the diet of Light-mantled Sooty Albatrosses at Macquarie Island in the present study was similar in 1970 and 1993, with *Galiteuthis*, *Teuthowenia*, ?*Chiroteuthis joubini*, and *M. hyadesi* contributing 73.2% by number of beaks in 1970 and 67.8% in 1993. However, between 1970 and 1993, there were increases in the proportion of beaks of *K. longimana* and *H. eltaninae*, offset mainly by decreases in the number of *Galiteuthis/Teuthowenia*. By mass, however, the main difference was an increased proportion of *K. longimana* in 1993 relative to 1970. There was, however, no significant difference in the squid component of the diet.

Implications for environmental monitoring

Longevity of Light-mantled Sooty Albatrosses has been adversely affected by longline fishing since the first samples were collected in this study (Brothers 1991). The minimal differences in the diet across this interval of 25 years with changing demographic parameters is significant. Birds appeared to be foraging in similar zones in the 1970s, 1980s and 1990s (Johnstone & Kerry 1976, Woehler *et al.* 1990, Weimerskirch & Robertson 1994, E.J. Woehler pers. comm.). This lack of change is important in cross-referencing studies where, for example, the Macquarie Island population of the Southern Elephant Seal *Mirounga leonina* has decreased by about 40–50% (Hindell & Burton 1987). The decrease is thought to be food-related (H.R. Burton pers. comm.). Cephalopods with potential commercial value are *M. hyadesi*, *M. knipovitchi*, *M. ingens*, *M. robsoni*, *K. longimana* and *G. antarcticus* (Rodhouse 1990). Species of *Moroteuthis* seem unimportant in the diet of Light-mantled Sooty Albatrosses at Macquarie Island as does *G. antarcticus*, and *M. robsoni* did not appear at all. *Martialia hyadesi* and *K. longimana*, however, were important, constituting 27% by mass of the squid component of the diet in 1970 from regurgitations and 34% from casts increasing to 51% in 1993, suggesting that there has been no decrease in these species. This increase may not necessarily reflect increased availability of live prey, however, as many of the *K. longimana* would have been scavenged. Comparison of diets of different predators may be useful in elucidating causal mechanisms in decreased population estimates (Green *et al.* 1992). However, although Southern Elephant Seals and Light-mantled Sooty Albatrosses forage in similar areas (Green & Burton 1993, Weimerskirch & Robertson 1994) their diets are quite different: Southern Elephant Seals concentrating more in numbers on *H. eltaninae* which generally constituted more than 50% of beaks, and in mass on large-bodied squid such as *Moroteuthis*, *Kondakovia*, *Todarodes* and some *Alluroteuthis.* The slight changes in diet of Light-mantled Sooty Albatrosses over 25 years during the same period in which the population of the Southern Elephant Seal has collapsed (Hindell & Burton 1987) suggests that changes in squid availability may not have occurred in shared foraging areas, and the cause of decreases may have to be looked for elsewhere.

The similarity in the diet of Light-mantled Sooty Albatrosses at Macquarie Island over 25 years (there is less difference than the seasonal change reported by Imber & Berruti (1981) or in the present study) may indicate an inter-annual stability in prey resources or the chance sampling of two similar years. The difficulty in comparing between years without more extensive sampling has been commented on by Hunter & Klages (1989). The present study further indicates that to make any use of data on inter-annual differences requires continual monitoring over a number of consecutive years to examine levels of inter-annual fluctuations before comparing widely separate years.

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