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Cephalopod prey of the sooty albatrosses *Phoebetria fusca* and *P. palpebrata* at Marion Island

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The sooty albatross *Phoebetria fusca* and light-mantled sooty albatross *P. palpebrata* are largely allopatric in their breeding and pelagic ranges, but breed sympatrically at Marion Island. Regurgitated casts of food remains (mainly cephalopod beaks) were analysed to assess differences in the foods of these two species at Marion Island. Lower beaks of cephalopods were identified to species, and the masses of whole animals were estimated. Thirty-seven cephalopod species were identified from 3 295 beaks derived from both albatrosses. The mean estimated cephalopod prey mass (219 g and 295 g for *P. fusca* and *P. palpebrata* respectively) was high, as digestion tends to eliminate smaller, less resistant beaks. Kondakovia

longimana was the most important species by mass, and the Onychoteuthidae, Cranchiidae and Histioteuthidae the most important families in the food of both species. Most cephalopod prey species were bioluminescent, but non-bioluminescent cephalopods constituted a higher proportion by mass. Remains of fish, birds and crustaceans were present in small amounts. Differences in species composition and mass of cephalopod prey between the two albatrosses were small, and partitioning of food resources by spatial separation of feeding areas is apparently more significant in the segregation of *P. fusca* and *P. palpebrata* at Marion Island.

Table 1

Cephalopoda, identified from beaks found in regurgitated casts of *Phoebetria fusca* at Marion Island, March-May 1975. Beak measurements and mass estimation follow Clarke (1962). Importance of family is found by summing the products of the numbers multiplied by mean mass of all species within each family, and expressed as a percentage of the total sum.

Order Family Species	Beak measurement (mm)				Estimated mass (g)		Importance of family (%)
	No.	Mean	Range	<i>n</i>	Mean	Range	
Octopoda							
Alloposidae	2						1
<i>Alloposus mollis</i>	2	—	—	—	—	—	
Teuthoidea							
Ommastrephidae	4						1
<i>Nototodarus</i> sp.	4	5,8	5,1- 6,3	4	354	240- 440	
Onychoteuthidae	414						70
<i>Moroteuthis ingens</i>	9	9,8	8,9-10,0	9	1603	1250-1750	
<i>Moroteuthis knipovitchi</i>	239	6,6	4,4- 8,1	75	488	160- 940	
<i>Moroteuthis robsoni</i>	6	7,3	6,3- 8,1	6	707	440- 940	
Undescribed genus and species	4	—	—	—	—	—	
<i>Kondakovia longimana</i>	156	10,5	4,3-14,6	96	1850	140- 5400	
Gonatidae	39						1
<i>Gonatus antarcticus</i>	37	5,5	4,6- 6,0	29	97	71- 120	
<i>Gonatus phoebetriae</i>	2	—	—	—	—	—	
Psychroteuthidae	11						1
<i>Psychroteuthis glacialis</i>	9	5,6	3,6- 7,0	15	300	175- 650	
<i>Psychroteuthis</i> sp. B	2	3,2	3,2	1	63	63	
Enoploteuthidae	2						1
<i>Ancistrocheirus lesueurii</i>	2	7,1	6,0- 8,2	2	65	115- 215	
Octopoteuthidae	4						1
<i>Octopoteuthis</i> sp.	4	9,5	8,2-11,2	4	278	195- 400	
Histioteuthidae	809						8
<i>Histioteuthis atlantica</i>	5	3,8	3,2- 5,3	5	107	62- 175	
<i>Histioteuthis dofleini</i>	1	—	—	—	—	—	
<i>Histioteuthis eltaninae</i>	715	2,8	1,9- 3,5	90	48	21- 73	
<i>Histioteuthis macrohista</i>	9	4,4	3,3- 5,4	5	124	66- 185	
<i>Histioteuthis meleagroteuthis</i>	69	4,7	2,9- 6,9	25	146	50- 290	
<i>Histioteuthis miranda</i>	9	—	—	—	—	—	
<i>Histioteuthis</i> sp.	1	2,8	2,8	1	46	46	
Chiroteuthidae	95						2
<i>Chiroteuthis macrosoma</i>	21	6,2	5,4- 6,9	16	244	165- 330	
<i>Chiroteuthis picteti</i>	23	4,2	2,0- 6,0	15	90	10- 220	
<i>Chiroteuthis</i> sp. E	49	4,3	3,8- 5,1	44	89	62- 145	
<i>Chiroteuthis veranyi</i>	2	4,5	4,5- 4,6	2	102	100- 105	
Mastigoteuthidae	1						1
<i>Mastigoteuthis</i> sp. C	1	—	—	—	—	—	
Cycloteuthidae	2						1
<i>Cycloteuthis serventi</i>	1	10,4	10,4	1	430	430	
<i>Discoteuthis</i> sp.	1	11,0	11,0	1	520	520	
Cranchiidae	1401						19
<i>Taonius belone</i>	1	6,0	6,0	1	170	170	
<i>Taonius cymoctypus</i>	21	8,1	6,3- 9,3	21	351	190- 460	
<i>Taonius pavo</i>	31	5,2	4,3- 5,8	30	125	80- 160	
<i>Teuthowenia megalops impennis</i>	1	4,7	4,7	1	96	96	
<i>Teuthowenia antarctica</i>	1184	4,2	3,5- 6,0	90	74	50- 170	
<i>Galiteuthis armata</i>	1	2,8	2,8	1	30	30	
<i>Galiteuthis glacialis</i>	157	4,8	3,7- 7,1	71	99	56- 290	
<i>Mesonychoteuthis hamiltoni</i>	4	9,4	8,0-10,8	2	485	330- 640	
<i>Bathothauma lyromma</i>	1	5,2	5,2	1	123	123	
Neoteuthidae	1						1
<i>Alluroteuthis antarcticus</i>	1	—	—	—	—	—	
Unidentified	4						1

Table 2

Cephalopoda, identified from beaks found in regurgitated casts of *Phoebetria palpebrata* at Marion Island March-May 1975. Beak measurements and mass estimation follow Clarke (1962). Importance of family is found by summing the products of the numbers multiplied by mean mass of all species within each family, and expressed as a percentage of the total sum.

Order Family Species	Beak measurement (mm)				Estimated mass (g)		Importance of family (%)
	No.	Mean	Range	<i>n</i>	Mean	Range	
Teuthoidea							
Onychoteuthidae	78						73
<i>Moroteuthis knipovitchi</i>	26	5,8	4,8- 7,3	18	410	215- 670	
<i>Kondakovia longimana</i>	52	9,4	6,1-13,2	33	1490	390-3800	
Gonatidae	8						1
<i>Gonatus antarcticus</i>	8	5,8	5,0- 6,7	7	115	84- 150	
Psychroteuthidae	18						6
<i>Psychroteuthis glacialis</i>	17	6,0	3,6- 7,6	14	400	175- 180	
<i>Psychroteuthis</i> sp. B	1	—	—	—	—	—	
Octopoteuthidae	1						1
<i>Taningia danae</i>	1	4,0	4,0	1	320	320	
Histioteuthidae	104						4
<i>Histioteuthis eltaninae</i>	102	2,7	2,1- 3,5	95	47	26- 73	
<i>Histioteuthis meleagroteuthis</i>	1	3,0	3,0	1	54	54	
<i>Histioteuthis miranda</i>	1	4,8	4,8	1	145	145	
Chiroteuthidae	13						1
<i>Chiroteuthis macrosoma</i>	7	5,7	5,5- 6,5	3	201	175- 272	
<i>Chiroteuthis picteti</i>	6	2,7	1,2- 4,1	5	34	10- 74	
Mastigoteuthidae	1						1
<i>Mastigoteuthis</i> sp. C	1	3,5	3,5	1	170	170	
Cranchiidae	187						16
<i>Taonius cymoctypus</i>	2	7,2	6,8- 7,6	2	260	220- 330	
<i>Taonius pavo</i>	2	4,9	4,8- 5,0	2	110	105- 115	
<i>Teuthowenia antarctica</i>	105	4,2	3,1- 5,0	84	76	36- 115	
<i>Galiteuthis glacialis</i>	76	5,1	3,8- 5,7	65	116	60- 140	
<i>Mesonychoteuthis hamiltoni</i>	2	—	—	—	—	—	
Neoteuthidae	1						1
<i>Alluroteuthis antarcticus</i>	1	3,0	3,0	1	60	60	

Introduction

The sooty albatross, *Phoebetria fusca*, and the light-mantled sooty albatross, *P. palpebrata*, are similar in size (Berruti, in press) and coloration (Cox, 1976). *Phoebetria fusca* has a pelagic range between 50°S and 30°S in the Atlantic and Indian Oceans, and breeds on islands between 37°S and 47°S. *Phoebetria palpebrata* has a circumpolar pelagic range between 40°S and 60°S, and breeds on islands between 46°S and 54°S in the Atlantic and Indian Oceans, and in the Australasian region (Watson, 1975). The two species are largely allopatric in distribution, but breed sympatrically at the Prince Edward and Crozet islands (Watson, 1975) and probably also at Kerguelen Island (Pascal, 1978). The food of the two species was investigated as part of a general study of their co-existence at Marion Island (Berruti, 1977).

Methods

The investigation depended on the analysis of regurgitated casts of food remains. Fresh regurgitated casts were collected monthly at nest sites of *P. fusca* and *P. palpebrata* on Marion Island (46°54'S, 37°45'E) from October 1974 to May 1975. The casts consisted largely, or entirely, of the beaks and spermatophores of cephalopods. Only the cephalopod remains were analysed in detail, and the results reported here are based on samples obtained from March to May 1975.

The lower beaks of cephalopods were sorted into types, subsequently identified by Dr M. J. Imber (Wildlife Services,

Department of Internal Affairs, New Zealand). The rostral length of the lower beak was measured to an accuracy of 0,3 mm, using dividers and a steel rule. Thirty randomly chosen beaks of each species were measured in each monthly sample containing more than 30 beaks of that species. Badly broken beaks were not measured. Particular difficulty was experienced in dealing with beaks of *Kondakovia longimana*, in which the 'shoulder' and 'wing' of small beaks were often broken above the jaw angle. For this species, lower rostral lengths were estimated from a representative sample of small, broken beaks.

Cephalopod mass was estimated from regressions of lower rostral length against mass, as developed for separate cephalopod families by Clarke (1962), except for members of the Psychroteuthidae, Cycloteuthidae, Neoteuthidae and Mastigoteuthidae, whose mass was estimated from the regression of lower rostral length against mass for all oegopsid families (Clarke, 1962), since separate regressions were not available for these families.

Results

Totals of 2 789 and 411 lower beaks of cephalopods, of 37 species, were identified in the casts of *P. fusca* and *P. palpebrata* respectively (Tables 1 and 2). Thirty-seven and 18 species were identified for *P. fusca* and *P. palpebrata* respectively. All species except one (*Alloposus mollis*: Octopoda) belong to the Oegopsida, the pelagic squids. Only ten species contri-

buted to more than 1% of the beaks obtained from either *P. fusca* or *P. palpebrata* (Table 3). *Kondakovia longimana* contributed 48% and 64% of the cephalopod prey mass taken by *P. fusca* and *P. palpebrata* respectively. This was calculated by multiplying the estimated mean mass of each cephalopod species by the total number of beaks of that species and dividing by the estimated total mass of cephalopods eaten, and then expressed as a percentage. The most important families by mass, and in decreasing order of importance for both sooty albatrosses, were the Onychoteuthidae and Cranchiidae. The mean mass per individual cephalopod prey was estimated at 219 g and 295 g for *P. fusca* and *P. palpebrata*, respectively. The largest cephalopods taken by both kinds of birds were *K. longimana* of 5 400 g and 3 800 g. The mean masses of *P. fusca* and *P. palpebrata* respectively are 2 512 g and 2 823 g (Berruti, in press). Sooty albatrosses presumably ingest only portions of very large cephalopods which are probably taken when moribund or dead, as suggested for other seabirds which fed on squid (Ashmole & Ashmole, 1967; Imber, 1973).

At least 80% and 71% of the cephalopods taken respectively by *P. fusca* and *P. palpebrata* are bioluminescent (Filippova, 1972; Imber, 1976; Roeleveld, pers. comm.). However, nonbioluminescent cephalopods contributed at least 68% and 79% of the total cephalopod mass taken by *P. fusca* and *P. palpebrata* respectively, as the relatively large-bodied *K. longimana* and *Moroteuthis knipovitchi* are non-bioluminescent.

Both sooty albatrosses at Marion Island also fed on fish, birds and crustaceans in small amounts.

Discussion

The process of digestion in the stomachs of seabirds tends to eliminate relatively less resistant small and immature cephalopod beaks. For instance, Imber (1973) found that *Spirula spirula* (estimated mean mass = 10 g) constituted 25% of the stomach contents of great-winged petrels *Pterodroma macrop-tera*, but only 0.3% of the beaks found in regurgitated casts. Imber suggested that cast formation begins when a single large pair of beaks, too large to pass through the bird's

gizzard, is ingested. Both factors should result in an over-estimation of the importance of the larger cephalopods in the diets of seabirds. Further, Clarke (1962) warned that the mass versus rostral length regressions for each cephalopod family may be markedly different for different species within each family. The estimates of mean mass per individual cephalopod prey (219 g for *P. fusca* and 295 g for *P. palpebrata*) are probably on the high side. If either *P. fusca* or *P. palpebrata* takes proportionately more small squid, differential digestion would mask this difference. The greater number of species apparently taken by *P. fusca* might be explained entirely by the relatively large sample of beaks available for this species.

Evidence for scavenging is provided by the occurrence of feathers of rockhopper penguins *Eudyptes chrysolome* in the food remains of *P. fusca* and *P. palpebrata*, and feathers of macaroni penguins *E. chrysolophus* in the food remains of *P. fusca* (Berruti, 1977). It is unlikely that sooty albatrosses kill live, healthy penguins.

Cephalopods were the most frequently found items in the stomach contents of *P. fusca* and *P. palpebrata* at the Crozet islands (Mougin, 1970) and constitute the most important food of four other species of albatross: *Diomedea chrysostoma* (Tickell, 1964), *D. melanophris* (Tickell, 1964), *D. irrorata* (Harris, 1973) and *D. exulans* (Imber & Russ, 1975). It appears that there is a considerable overlap in the species composition and size of the cephalopod diets of *P. fusca* and *P. palpebrata* at Marion Island. Methods of prey capture and detection are not known. Both *P. fusca* and *P. palpebrata* probably obtain most of their food at night, when cephalopods migrate vertically to the surface of the sea (Imber, 1973). Ashmole (1968) suggested that surface-feeding seabirds will catch any suitably-sized prey on the sea surface, and are essentially non-selective with respect to the taxonomic affinities of their prey. Thus, the differences in species composition and size of cephalopods taken by the two sooty albatrosses may merely reflect relative availability of cephalopods in different feeding zones.

Phoebetria fusca and *P. palpebrata* breed at approximately the same time of year (Berruti, in press). Competition between these two species for nest sites at Marion Island does not appear to be significant, and breeding adults of the two populations have spatially separated feeding areas with *P. fusca* feeding primarily to the north of the Antarctic Convergence, and *P. palpebrata* to the south (Berruti, in press). This ecological difference does not necessarily indicate that there was, or is, competitive exclusion between the two species, but it may now be of importance in allowing the two populations to co-exist at Marion Island.

Table 3

Abundance and estimated mean mass of cephalopod species, contributing at least one per cent of all cephalopod beaks in the regurgitated casts, of *Phoebetria fusca* or *P. palpebrata* at Marion Island, March-May 1975.

Species	<i>P. fusca</i>		<i>P. palpebrata</i>	
	No. of beaks (%)	Mass (g)	No. of beaks (%)	Mass (g)
<i>Moroteuthis knipovitchi</i>	9	488	6	410
<i>Kondakovia longimana</i>	6	1 850	13	1 490
<i>Gonatus antarcticus</i>	1	97	2	115
<i>Psychroteuthis glacialis</i>	1	300	4	400
<i>Histioteuthis eltaninae</i>	26	48	25	47
<i>Histioteuthis meleagroteuthis</i>	2	146	1	54
<i>Chiroteuthis macrosoma</i>	1	244	2	201
<i>Chiroteuthis picteti</i>	1	90	1	34
<i>Chiroteuthis sp. E</i>	2	89	0	—
<i>Taonius pavo</i>	1	125	1	110
<i>Teuthowenia antarctica</i>	42	74	26	76
<i>Galiteuthis glacialis</i>	6	99	18	116

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Standing crop and production estimates of selected Marion Island plant communities

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Standing crop and above-ground standing biomass increases during the growth season are provided for three plant communities on Marion Island (sub-Antarctic). The values support previous observations that low-altitude sub-Antarctic vegetations accumulate large quantities of aboveground plant matter and that they are more productive than most northern hemisphere tundra vegetations.

Introduction

Despite recent efforts inspired by the International Biological Programme, little is known regarding the primary production and standing crops of sub-Antarctic vegetation. Available data to date are confined to Macquarie Island (Jenkin, 1975) and South Georgia Island (Smith & Walton, 1975). Huntley (1972) and Smith (1976, 1977) provide standing crop values of several lowland plant communities on Marion Island. Additional information for three of these communities (fernbrake, *Acaena magellanica* drainage-line and tussock grassland) on the island's eastern coastal plain is presented in this account, and preliminary estimates of their annual production are provided. Comprehensive descriptions of the communities are provided in Smith (1976).

Methods

The standing crop values shown in Table 1 are those at the approximate time of maximum above-ground biomass in the growing season and were derived from the harvested quadrat method described in Smith (1976). Primary production was estimated in two ways: (a) as the difference between peak biomass (living material) and that at the start of the growing season, and (b) the difference between the corresponding standing crop (living and dead material) values.

Results and discussion

Biomass and standing crops

Standing crop and production estimates for the three communities are presented in Table 1; some values for similar communities on other sub-Antarctic islands are also provided. Only general conclusions can be drawn from comparisons between the islands since different methods have been used and these give values which are known to vary, even within the same site (Walton, Greene & Callaghan, 1975). In addition, biomass varies seasonally. As Holdgate (1977) points out, there are two statistical problems in comparing available standing crop and productivity estimates from sub-Antarctic regions, namely the reliability and inter-comparability of the methods, and the relationship of the sample sites to the localities in which they occur. None of these localities has been studied sufficiently well to provide data on the variability in biomass and production within them, and many of the estimates are derived from small atypical areas of sheltered or highly productive vegetation.

Most of the available data, however, indicate that large above-ground biomass values occur in sub-Antarctic vegetation, in contrast to tundra areas of the northern hemisphere with their bitterly cold, continental winters. Large amounts of dead material, predominantly in the form of standing dead, accumulate in sub-Antarctic vegetation and this is reflected in the high standing crop figures in Table 1.

Above-ground biomass and standing crop estimates for 1972 and 1974 from the same communities on Marion Island are very similar but the below-ground values differ between the two dates. This is probably in error, since the 1972 below-ground estimates were based on only 4 samples each.

The 1969 value for the above-ground biomass of fernbrake