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Cephalopods as prey. I. Seabirds

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SUMMARY

We review quantitative studies of the cephalopod diet of seabirds, with details of all species forming more than 5% by numbers or mass of seabird diets. Although squid are widespread as food for marine birds, only for some albatross and petrel species are they consistently as important as fish or crustaceans. Nevertheless, several penguins, auks and terns take significant quantities of squid at some sites and seasons. Although most of the detailed studies have been on temperate and polar seabirds in the southern hemisphere, squid may play a key role in the diet of many tropical seabirds. Generally, squid may be more important to many marine birds outside the breeding season than hitherto documented. Many species and families of squid are eaten by seabirds but Ommastrephidae, Onychoteuthidae, Histioteuthidae and Gonatidae probably make the greatest contributions. Evidence for size and species selectivity, except as constrained by the size and habits of seabirds, is weak. How seabirds catch squid is reviewed, covering the topics of scavenging and live capture and association with cetaceans. In general, seabirds have much smaller known and potential impact on squid stocks than do marine mammals. However, seabirds are probably the best samplers of squid populations currently available and can provide valuable data for the identification of potential, and management of existing, commercial fisheries. Future research needs, especially for studying the dynamics of squid–seabird interactions, are reviewed.

1. INTRODUCTION

The last decade has seen a revolution in our knowledge of seabird–cephalopod interactions, based largely on the use of Clarke (1986), which made widely available methods for determining the size and identity of cephalopods using beaks retrieved from predator stomach samples. This paper reviews the results of the main quantitative studies of the cephalopod diet of seabirds. On this basis various aspects of the role of squid as prey for seabirds are discussed and the potential importance of seabirds as predators on squid is assessed.

2. SQUID AS PREY OF SEABIRDS

(*a*) *Background*

There have been quantitative studies of the diet of many species in most groups within the main orders of seabirds. Thus at least some data are available for penguins, procellariforms (albatrosses, petrels, storm petrels), pelecaniforms (gannets, boobies, frigatebirds, shags, tropicbirds) and auks/alcids, studies of the more pelagic species in these groups being especially relevant. For some groups of seabirds, either species are chiefly coastal (most gulls, many cormorants and sea ducks) or they have been inadequately studied at places or times when interactions with squid are likely (e.g. pelagic terns and gulls and numerous species in winter) or studies indicate that squid are rare or absent in their diet (e.g. diving petrels (Pelecanoididae), most auklets, kittiwakes (*Rissa*)). The main quantitative studies of the squid prey of seabirds are summarized in tables 1–5. Before reviewing these it is important to recognize some of the shortcomings of and biases inherent in these data.

First, the selection of species investigated is substantially biased towards polar and subpolar regions of the southern hemisphere. Tropical species are relatively poorly represented as, more surprisingly, are species of the temperate and polar northern hemisphere, particularly in the Atlantic Ocean. Procellariform and penguin species have been more investigated than other groups but, at least for the former, this reflects the importance of squid in their diet.

Second, most species studied have only been investigated at one site (and enough data exist to indicate that quite substantial site-specific differences may occur) and usually only during their chick-rearing period. Except for albatrosses, this covers only about 20% of the year; a particular deficiency is the lack of data outside the breeding season.

Third, the contribution of cephalopods to predator diets has been assessed in different ways (by number, frequency of occurrence (FOO), volume and mass, each with different biases) and using different methods (e.g. wet mass of flesh, estimates using regressions of beak lower rostral length (LRL) against mantle length (ML) and/or body mass). Many authors have noted the biases involved in the quantification of dietary composition of predators. Particular difficulties with squid are that it is digested more slowly than fish and its beaks are more resistant to digestion than otoliths

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Table 1. *Composition (proportion (%) by frequency of occurrence (FOO), number (no.) and mass) and size (mean mass (g) estimated from beak LRL) of cephalopods taken by emperor penguin* (Aptenodytes forsteri) *at various sites around the Antarctic continent*

			Squid[c]			*Gonatus*				*Kondakovia*				*Psychroteuthis*				*Alluroteuthis*				
site	date	N[b]	FOO	no.	mass	FOO	no.	mass	size	FOO	no.	mass	size	FOO	no.	mass	size	FOO	no.	mass	size	reference
Weddell Sea	Nov 1986	30	80	3	10									91				9			*ca.* 10	Klages 1989
Weddell Sea	Mar 1986 Jul–Aug 1988	26	100	74	89	54	2	5		31	2	32		81	28	48						Ainley *et al.* 1992[d]
Weddell Sea	Feb 1990	29	90	?	?	7	1	< 1 }	*ca.* 11	28	20	50	272	86	37	13	*ca.* 10	76	36	37		Piatkowski & Putz 1994
Weddell Sea	Feb 1992	29	97	?	?	7	10	< 1		31	25	48	115	93	45	23 }		79	20	29	*ca.* 20	Piatkowski & Putz 1994
Terre Adelie	Sept 1982	12	—	—	—	42	8	18		25	2	14		100	88	68 }	*ca.* 20					Offredo *et al.* 1985
Terre Adelie	Oct–Nov 1982	29	93	1	3		3	27			1	21			95	51	3; 430					Offredo & Ridoux 1986
AAT[a] (Amanda Bay)	Aug–Oct 1982	44	36	4	3		1	23	181						99	77	3; 430					Gales *et al.* 1990
AAT[a] (Auster)	Jul–Oct 1988	115	58	48	45	4	< 1	2		6	2	3		31	77	29 }	*ca.* 20	28	12	44 }	*ca.* 2	Robertson *et al.* 1994
AAT[a] (Taylor)	Nov 1988	38	55	73	69					3	1	1		34	84	32 }		29	11	63 }		Robertson *et al.* 1994

[a] AAT = Australian Antarctic Territory.
[b] N = sample size.
[c] Squid as proportion (%) of overall diet.
[d] Diet composition based exclusively on reconstitution from squid beaks/fish otoliths. (This study also recorded *Galiteuthis* to comprise 42% by number and 14% by mass of cephalopods.)

and therefore accumulate more effectively (Jackson & Ryan 1986, Furness *et al.* 1984, Van Heezik & Seddon 1989, Wilson *et al.* 1985); this tends to lead to overestimation of the squid contribution to the overall diet. Various studies have allowed for some or all of these biases (e.g. by using beaks only with flesh attached and/or by classifying other beaks into different erosion categories (Jackson & Ryan 1986, Hindell 1988*a*, Van Heezik & Seddon 1989). Piatkowski & Putz (1994) illustrate well the consequences of some of these differences in terms of length–frequency analysis of squid. Furthermore, the equations used to estimate squid mass (for many purposes the most appropriate index of predator diet composition) are often based on few specimens covering a restricted size range; in addition Jackson (1995) has noted that in highly sexually dimorphic squid (e.g. *Moroteuthis ingens*) beaks are essentially monomorphic, thereby introducing further discrepancies.

All these difficulties need further critical attention. Nevertheless for present purposes it is unlikely that, beyond overestimating the squid element of seabird diets (particularly in studies relying on beak material), the data in tables 1–5 are seriously misleading in terms of a general overview of the importance of squid to different groups and species of seabirds.

(*b*) ***Penguins*** (***Spheniscidae***)

These seabirds, pre-eminently adapted among birds for life underwater, with the capacity for long, frequent and deep bouts of wing-propelled diving in pursuit of prey (reviewed in Croxall *et al.* 1993) are relatively well studied, particularly in the Southern Ocean south of the Antarctic Polar Front. The diet of emperor penguins has been investigated at more sites and seasons than most penguins. As a species restricted to the circum-Antarctic pack-ice it offers a unique insight into the squid fauna of this region (table 1). Although squid only predominated in its diet in the Mawson region of Australian Antarctic Territory, some combination of four squid species were typical of its diet throughout its range. *Psychroteuthis* was usually numerically predominant (though sometimes the larger *Kondakovia* may dominate by mass) and several authors noted the bimodality in size of this species. Viewing the length–frequency data in temporal sequence (figure 1) suggests that larger immature squid (2–4 mm LRL) are taken abundantly in spring and early summer (September–December), with adults eaten in relatively small numbers in late summer and winter (February–August) and apparently absent in midsummer (November–December). This pattern is not easy to reconcile with linear growth during a one-year life cycle (Offredo *et al.* 1985). It may partly reflect seasonal and/or geographical changes in availability of different size classes within the pack-ice but could also indicate that high latitude squid may have lifespans longer than one year.

For the remaining Antarctic and sub-Antarctic penguin species, squid rarely comprise more than 10% of the breeding season diet (table 2). However, the

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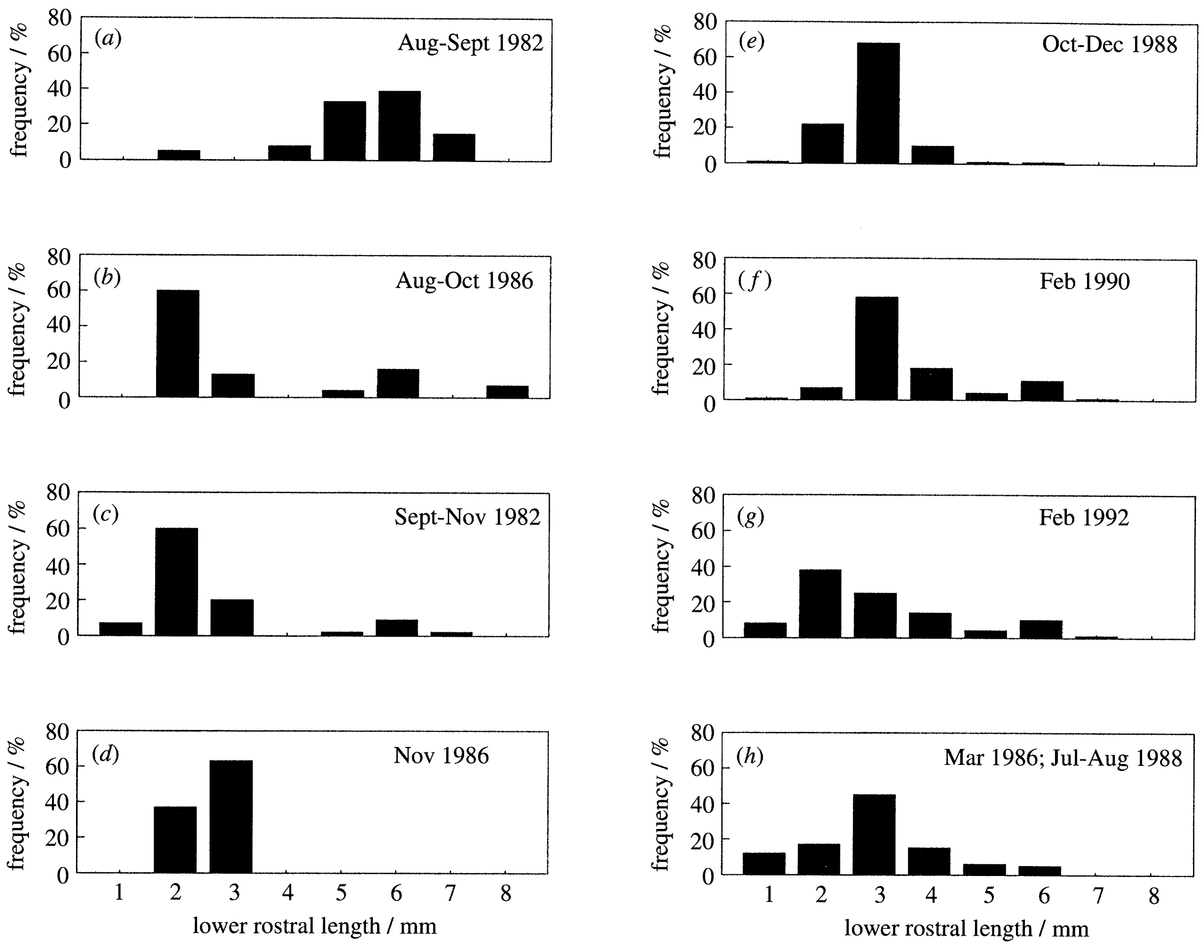

Figure 1. Frequency distributions of lower rostral lengths of beaks of *Psychroteuthis glacialis* consumed by emperor penguins. Data arranged in approximate temporal sequence through the year. Sources: (*a*) Offredo *et al.* 1985; (*b*) Gales *et al.* 1990; (*c*) Offredo *et al.* 1985, Offredo & Ridoux 1986; (*d*) Klages 1989; (*e*) Robertson *et al.* 1994; (*f*) and (*g*) Piatkowski & Putz 1994; (*h*) Ainley *et al.* 1992.

large king penguins (which like emperors feed mainly on small fish) consistently took small quantities of *Kondakovia* and/or *Moroteuthis* spp. at all sites studied. Moreover these squid were particularly important in the winter diet, at least at Indian Ocean sites (Cherel *et al.* 1996) and the availability of onychoteuthids at this time may be an important influence on the ability of king penguins to remain in association with their breeding sites (where they will often have over-wintering chicks) all year round. Furthermore, data for Adelie penguins in winter (Ainley *et al.* 1992) suggested that squid may be more important in their diet at this time; this might well be true for other penguins in the region.

Whereas *Kondakovia* is nearly ubiquitous in the squid diets of high latitude penguins, at the northern margins of the Southern Ocean *Gonatus* and *Galiteuthis* become more important in penguin diets; *Gonatus* was the commonest species taken by all three penguin species which breed abundantly in the Falkland Islands (Thompson 1994; see also table 7). Ommastrephids *Nototodarus* spp. were similarly dominant in the squid diet of several penguin species in the Australasian region. Squid were rarely a major element in the diet of more temperate penguins and although the more northerly species are poorly studied this is true of the African penguin and probably also of its less well-known congeners in South America. One exception may be the little penguin for which *Nototodarus gouldi* was consistently the most important squid prey (and sometimes the second commonest species in the overall diet), usually associated with *Argonauta* and *Loliolus* at several sites in southern Australia (Cullen *et al.* 1992). The typical sizes of these squid, 60 mm and 40 mm ML for *Nototodarus* and *Loliolus* respectively, equate to specimens of about 6 g wet mass. Over 26 months there were considerable fluctuations in squid abundance but no clear seasonal pattern. Broadly similar results came from studies in the colder waters off Tasmania (Gales & Pemberton 1990); in warmer waters near the northern limit of the little penguin's range, the only cephalopod species found was *Idiosepium notoides* (Klomp & Wooller 1988).

(*c*) *Albatrosses* (*Diomedeidae*)

Cephalopods are a major component of the diet of many species in this group of large-sized, wide-ranging seabirds which typically feed by seizing prey while on the surface of the water (never taking prey while in flight). However, they are now known to have greater

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Table 2. *Composition (by frequency of occurrence (FOO), number (no.) and mass) and size of the main (> 5 % by numbers or mass) cephalopod prey of penguins*

			proportion (%) of squid in diet			main cephalopod prey				
							proportion (%)[a]			
species	site	No.	FOO	no.	mass (g)	species	mass	no.	mass (g)[b]	reference
king	Marion	12	90	24	14–31[c]	*Kondakovia longimana*	99	98	34 (5–481)	Adams & Klages 1987
Aptenodytes patagonicus	Macquarie	144	40	1	2	*Moroteuthis* sp.	99	97	32 (1–579)	Hindell 1988*a*
	Heard	24	*ca.* 10	3	2	*Kondakovia longimana*	57	33	16	Klages *et al.* 1990
	Crozet[d]	15	100	25	57	*Moroteuthis ingens*	43	66	6	Cherel *et al.* 1993
	Crozet	36	86	2	8	*Kondakovia longimana*	23	25	151 (3–904)[e]	Ridoux 1994
						Moroteuthis knipovitchi	43	36	118 (1–480)[e]	
						Onychoteuthis sp.	20	39	270 (100–467)	
Adelie	Adelie Land	105	18		3	*Psychroteuthis glacialis*	100	100	14	Ridoux & Offredo 1989
Pygoscelis adeliae										Offredo *et al.* 1985
	Weddell Sea[f]	40	2	< 1	54	*Psychroteuthis glacialis*	19			Ainley *et al.* 1992
						Kondakovia longimana	81			
gentoo	Macquarie	64	*ca.* 50	1	19	*Moroteuthis* sp.	46	87	28 (1–103)	Hindell 1989
P. papua						*Martialia hyadesi*	54	13	229 (2–474)	
	Heard	55	50	< 1	1	*Kondakovia longimana*	100	100		Klages *et al.* 1990
	Crozet	116	34	< 1	2	*Kondakovia longimana*[g]	22	21[f]	*ca.* 50 (1–10)	Ridoux 1994
									77 (1–195)[e]	
						Onychoteuthis sp.	67	1	*ca.* 250	
									454 (401–507)[e]	
	Marion	144	*ca.* 30	< 1	2	*Kondakovia longimana*[g]	?	20	10	Adams & Klages 1989
	Falklands	43	95	35	25	*Gonatus antarcticus*	22	90	2	Thompson 1989, 1994
	(New Is)					Sepiolid sp.				
						Loligo (gahi)				
macaroni	Crozet	30	80	1	10	*Gonatus* sp.	17	82	< 1	Ridoux 1994
Eudyptes chrysolophus						*Kondakovia longimana*	72	4	16 (1–100)	
						Brachioteuthis sp.	1	11	< 1	
	Marion	75	71	< 1	12	*Kondakovia longimana*		99	58 (12–112)	Brown & Klages 1987
	Heard	66	8	< 1	< 1	*Kondakovia longimana*				Klages *et al.* 1989
						Moroteuthis sp.				
royal	Macquarie	182	12	< 1	2	*Moroteuthis* sp.	79	88	30 (1–260)	Hindell 1988*b*
E. schlegeli						*Martialia hyadesi*	92	17	52 (1–318)	
rockhopper	Macquarie	77	6	< 1	2	*Moroteuthis* sp.	8	83	16 (1–824)	Hindell 1988*c*
E. chrysocome						*Martialia hyadesi*	92	17	61 (3–440)	Cooper *et al.* 1990
	Heard	58	15	< 1	1	?*Kondakovia*		33		Klages *et al.* 1989
	Marion	84	46	< 1	5	*Kondakovia longimana*		100	61 (45–75)	Brown & Klages 1987
	Crozet	17	76	1	17	*Gonatus* sp.	23	84	< 1	Ridoux 1994
						Kondakovia longimana	53	9	*ca.* 5	
						Galiteuthis sp.	6	< 1	12	
						Pholidoteuthis sp.	8	1	9	
						Argonauta argo	6	1	3	

	Falklands	29		21	53	*Gonatus antarcticus*	100	100	< 1	Croxall *et al.* 1985
	(breeding)	63	95		43	*Gonatus antarcticus*		*ca.* 70	< 1	Thompson 1989
	(moult)	13	100		39	*Gonatus antarcticus*		86	1	Thompson 1989
						Loligo gahi		11	12	
	Gough	91	26		2	? *Todarodes*	100	100	49	Klages *et al.* 1988
Fiordland *E. pachyrhynchus*	S. New Zealand	48			85	*Nototodarus* (*sloani*)	?	61	*ca.* 5	van Heezik 1989
						Moroteuthis ingens	75	39	*ca.* 10	
						Octopus maorum	15	?	?	
	Stewart Island (N.Z)	21	80	1	16	*Nototodarus sloani*	650	19		van Heezik 1990*a*
						Octopus maorum	50	81		
yellow-eyed *Megadyptes antipodes*	S. New Zealand	512	47	3	9	*Nototodarus* (*sloani*)	*ca.* 95	*ca.* 95		van Heezik 1990*b*
	Stewart Island (N.Z.)	22	36	1	12	*Nototodarus sloani*	*ca.* 95	57		van Heezik 1990*a*
						Octopus maorum	*ca.* 4	30		
						Ocythoe tuberculata	*ca.* 1	10		
African (jackass) *Spheniscus demersus*	S. Africa	247		11	5	*Loligo reynaudi*		96	116	Rand 1960; Randall *et al.* 1981
magellanic *S. magellanicus*	Falklands (New Is)	40	*ca.* 100	32	*ca.* 50	*Gonatus antarcticus*		94	1	Thompson 1993
	Falklands (Volunteer)	24	*ca.* 100	78		*Gonatus antarcticus*	77	77	1	Thompson 1993
						Loligo gahi	13	13	*ca.* 10	
	Stewart Island (NZ)	28	*ca.* 60	3	61	*Nototodarus sloani*	*ca.* 45	*ca.* 45	44	van Heezik 1990*a*
						Moroteuthis ingens	*ca.* 45	*ca.* 45	41	
						Octopus maorum	*ca.* 10	*ca.* 15	15	
little *Eudyptula minor*	Maria Bay (Tas)	399	80	14	20	*Nototodarus gouldi*	*ca.* 90	90	92	Gales & Pemberton 1990
						Octopus	*ca.* 70	70	8	
	Fort Direction (Tas)	125	14	< 1	< 1	*Nototodarus gouldi*	*ca.* 90	90	92	Gales & Pemberton 1990
						Octopus	*ca.* 70	70	8	
	Albatross Is (Tas)	153	96	16	26	*Nototodarus gouldi*	*ca.* 90	90	92	Gales & Pemberton 1990
						Octopus	*ca.* 70	70	8	
	Philip Is (Vic) (1979–1983)	770	34			*Nototodarus gouldi*			67	Montague & Cullen 1988
						Argonauta nodosa			20	
						Loliolus noctiluca			7	
	Philip Is (Vic) (1985–1988)	705	69		22	*Nototodarus gouldi*	70	70	6	Cullen *et al.* 1992
						Argonauta nodosa	24	24		
	Port Campbell (Vic)	413	69		23	*Nototodarus gouldi*			68	Cullen *et al.* 1992
						Argonauta nodosa			21	
	Rabbit Island (Vic)	457	23		4	*Loliolus noctiluca*			16	Cullen *et al.* 1992
	Penguin Is (WA)	236	2	< 1	< 1	*Idiosepium notoides*			2	Klomp & Wooller 1988

[a] Of cephalopods.
[b] Mean with range in parenthesis.
[c] Range over study period.
[d] June–July samples only.
[e] Accumulated (as opposed to fresh) beaks.
[f] Diet composition by reconstitution from otoliths/beaks.
[g] Most other cephalopods unidentified.

Table 3. *Composition by mass (%), number (%) and size (mean mass (g) of individuals calculated from LRL) of main cephalopod diet of subantarctic albatrosses*

(Data confined to species forming > 5 % by numbers or mass of the diet of any albatross. Identifications in source papers corrected following Imber 1992 (table 2).)

species	wandering albatross *Diomedea exulans*									grey-headed albatross *D. chrysostoma*								
site proportion (%) squid in diet	South Georgia 40			Marion Island 59			Crozet Islands 77			South Georgia 49			Prince Edward Island 34			Crozet Islands 89		
	mass	no.	size	mass	no.	size	mass	no.	size	mass	no.	size	mass	no.	size	mass	no.	size
Gonatus antarcticus	1	1	250	1	3	290	< 1	4	200	3	2	200	1	1	150[b]	< 1	1	148
Kondakovia longimana	58	10	3400	50	16	2000	57	23	3700	11	2	860	51	46	190	70	12	1900
Moroteuthis knipovitchii	2	4	720	15	14	670	3	7	900	1	< 1	1000	17	2	980	3	1	800
M. ingens	4	1	3250	15	3	3100	13	7	2500				6	1	100			
M. robsoni	1	1	1400	3	1	1200	< 1	< 1	1850									
Histioteuthis eltaninae	2	21	70	2	18	90	1	16	90	1	1	80	18	37	80	1	3	70
H. sp. A	1	2	120				1	14	250									
Psychroteuthis glacialis[c]	1	2	190				< 1	< 1	200	5	1	630						
Alluroteuthis antarcticus	8	10	390	4	7	420	< 1	4	170	< 1	1	370				< 1	1	130
Martialia hyadesi[a]	2	3	350							70	80	140				12	30	120
Illex illecebrosus	12	24	320															
Chiroteuthis sp.	1	1	75	1	5	100	< 1	1	*ca.* 100	< 1	< 1	50	1	2	75	< 1	1	80
Galiteuthis glacialis	3	19	85	2	14	100	1	8	100	7	14	70	3	6	90	11	38	90
Batoteuthis sp.	3	1	30													3	12	70
Onychoteuthis sp.																		
reference	Rodhouse *et al.* 1987			Cooper *et al.* 1992			Ridoux 1994			Rodhouse *et al.* 1990			Hunter & Klages 1989			Ridoux 1994		

[a] Includes also *Todarodes filippovae* at Crozet Islands.
[b] Single specimen.
[c] Present (6% by mass) in samples from light-mantled sooty albatross at Marion reported in Berruti & Harcus (1978).

species	black-browed albatross *D. melanophris*						sooty albatross *Pheobetria fusca*						light-mantled sooty albatross *P. palpebrata*								
site	South Georgia			Crozet Islands			Marion Island			Crozet Islands			South Georgia			Marion Island			Crozet Islands		
proportion (%) squid in diet	21			*ca.* 10			42			41			47			34			56		
	mass	no.	size	mass	no.	size	mass	no.	size	mass	no.	size	mass	no.	size	mass	no.	size	mass	no.	size
Gonatus antarcticus	4	2	260[b]				1	19	200	10	31		5	7	300	1	1	200	7	27	
Kondakovia longimana							35	20	1800	33	4		13	2	1000[b]	34	8	1450	69	16	
Moroteuthis knipovitchii							19	9	800[b]	22	7		3	1	1000	14	5	1000			
M. ingens							7	10	2900												
M. robsoni							24	3	1150							17	5	1200			
Histioteuthis eltaninae							5	8	75				< 1	1	70[c]	6	26	85	2	13	
H. sp. A										6	23										
Psychroteuthis glacialis[c]				(5)	11					11	15		48	20	570				5	18	
Alluroteuthis antarcticus							7	35	500				6	2	400	16	11	480			
Martialia hyadesi[a]	74	60	170	90	78	130	< 1	5	320				< 1	6	180	1	1	400			
Illex argentinus																					
Chiroteuthis sp.	1	2	65[b]	5	11	48[b]	16	48	40				< 1	< 1		2	14	35			
Galiteuthis glacialis	18	32	75				16	25	85				21	59	80	6	23	90			
Batoteuthis sp.										3	10								3	14	
Onychoteuthis sp.										4	6										
reference	Rodhouse & Prince 1993			Ridoux 1994			Cooper & Klages 1995			Ridoux 1994			Thomas 1982; Prince & Morgan 1987			Cooper & Klages 1995			Ridoux 1994		

Table 4. *Composition (by frequency of occurrence (FOO), number (no.) and mass) and size of the main (> 5% by numbers or mass) cephalopod prey of petrels*

			proportion (%) of squid in diet			main cephalopod prey[c]	proportion (%) by			
species	site[a]	N[b]	FOO	no.	mass (g)	species	mass	no.	mass (g)	reference
northern giant petrel *Macronectes halli*	Crozet	30		3	1	*Kondakovia longimana*	88	60	2264 (21–5988)	Ridoux 1994
						Moroteuthis knipovitchii	4	20	186 (110–293)	
						M. ingens	8	3	3371	
Antarctic petrel *Thalassoica antarctica*	AAT	39	8		*ca.* 75	*Psychroteuthis glacialis*	100	100		Norman & Ward 1992
	Weddell Sea	117	6–10	1	22	*Psychroteuthis glacialis*	*ca.* 5			Ainley *et al.* 1992
						Gonatus antarcticus	*c.* 95			
Antarctic fulmar *Fulmarus glacialoides*	AAT		3			*Gonatus antarcticus*	100	100		Norman & Ward 1992
	Ross Sea	13	100		94	*Gonatus antarcticus*	30	*ca.* 10		Ainley *et al.* 1984
	Weddell Sea	68	10–20	3	53	*Psychroteuthis glacialis*	51	*ca.* 60		Ainley *et al.* 1992
						Galiteuthis glacialis	19	*ca.* 30		
Cape petrel *Dapton capense*	Ross Sea	4	75		97					Ainley *et al.* 1984
	Weddell Sea	48	3–5	1	19	*Gonatus antarcticus*	47			Ainley *et al.* 1992
						Psychroteuthis glacialis	11			
						Galiteuthis glacialis	42			
snow petrel *Pagodroma nivea*	Weddell Sea	181	2–3	< 1	< 1	*Galiteuthis glacialis*	*ca.* 50	*ca.* 50		Ainley *et al.* 1992
						Psychroteuthis glacialis	*ca.* 50	*ca.* 50		
white-chinned petrel *Procellaria aequinoctialis*	Benguela	106	10	25	11[d]	*Taonius* sp.	36	43	48 (46–297)	Jackson 1988
						Gonatus sp.	17	9	118 (53–646)	Lipinski & Jackson 1989
						Histioteuthis sp.	27	14	108 (62–253)	
						Lycoteuthis diadema[e]	8	10	(50)[e]	
						Sepia sp.	6	19	(7–50)	
	South Georgia	91	35	1	19	*Martialia hyadesi*	52	57	92 (7–297)	Croxall *et al.* 1995
						Gonatus antarcticus	42	14	294 (161–418)	
						Galiteuthis glacialis	2	14	11 (10–13)	
	Marion (1978)	18				*Gonatus* sp.	65	58	214 (110–407)	Lipinski & Jackson 1989
						Taonius sp.	16	33	95	
						Histioteuthis sp.	14	25	105 (89–203)	
	Marion (1991)	34	18	< 1	17	*Martialia hyadesi*	78	33	288	Cooper *et al.* 1992*b*
						Histioteuthis sp.	22	67	41 (22–60)	
	Crozet	30	52	3	25	*Gonatus antarcticus*	62	31	332 (238–465)	Ridoux 1994
						Kondakovia longimana	2	16	21 (19–25)	
						Histioteuthis sp. A	6	19	54 (26–83)	
						Todarodes/Martialia	?	13		
						Moroteuthis knipovitchi	6	6	167 (76–258)	
						Galiteuthis glacialis	10	3	586	

	Weddell Sea	12	*ca.* 35	4	61	*Gonatus antarcticus*	3	*ca.* 25		Ainley *et al.* 1992
						Kondakovia longimana	67	*ca.* 25		
						Psychroteuthis glacialis	3	*ca.* 25		
						Galiteuthis glacialis	26	*ca.* 25		
Westland petrel *P. westlandica*	Westland, New Zealand	12	100			*Histioteuthis* spp.		45	100	Imber 1976
						Enoploteuthis sp.		15	65	
						Chiroteuthis sp.		12	100	
						Nototodarus sloani		9	75	
						Teuthowenia pellucida		8	50	
Parkinson's petrel *P. parkinsoni*	Gt Barrier, New Zealand	68	96			*Ommastrephes bartrami*	31	6	400 (22–3000)	Imber 1976
						Symplectoteuthis sp.	4	6	45 (8–200)	
						S. ?luminosa	3	6	35 (15–75)	
						Brachioteuthis spp.	3	7	27 (5–50)	
						Abralia ?astrolineata	8	12	50 (40–64)	
						Lycoteuthis diadema	15	21	54 (3–215)	
						Histioteuthis spp.	3	8	127 (23–175)	
						Taonius sp.	4	6	44 (12–150)	
						Teuthowenia pellucida	5	2	165 (60–210)	
						Octopoteuthis sp.	7	2	225 (150–300)	
						Discoteuthis sp.				
grey petrel *P. cinerea*	Crozet	30	87	62	70	*Gonatus antarcticus*	21	20	214	Ridoux 1994
						Moroteuthis ingens	60	20	603	
						Histioteuthis eltaninae	8	40	42 (37–47)	
						Chiroteuthis sp.	11	20	104	
Kerguelen petrel *Lugensa brevirostris*	Crozet	30	17	5	6	*Kondakovia longimana*	79	18	994 (281–1707)	Ridoux 1994
						Bathyteuthis abyssicola	1	12	12 (10–14)	
						Batoteuthis sp.	9	18	78 (67–88)	
						Taonius sp.	?	12	?	
						Galiteuthis glacialis	7	24	47 (36–53)	
	Marion	22	95		70	*Psychroteuthis* sp.	25	9	203	Schramm 1986
						Gonatus antarcticus	44	18	179	
						Histioteuthis sp.	6	18	24	
						Chiroteuthis sp.	3	9	23	
						Taonius sp.	17	36	35	
						Galiteuthis glacialis	5	9	37	
	Weddell Sea	29	14	2	24	*Galiteuthis glacialis*	100	100		Ainley *et al.* 1992

Table 4. (*cont.*)

			proportion (%) of squid in diet			main cephalopod prey[c]	proportion (%) by			
species	site[a]	N[b]	FOO	no.	mass (g)	species	mass	no.	mass (g)	reference
great-winged petrel *Pterodroma macroptera*	Marion	21	100		90	*Psychroteuthis* sp.	18	8	331 (36–979)	Schramm 1986
						Gonatus antarcticus	23	17	200 (67–507)	
						Moroteuthis robsoni	6	11	39 (34–40)	
						Histioteuthis eltaninae	2	5	73 (37–133)	
						H. atlantica	9	2	561 (471–639)	
						H. miranda	4	11	64 (25–118)	
						Chiroteuthis sp.	8	12	120 (54–220)	
						Taonius sp.	6	1	1131	
	Crozet	27	52	27	64	*Gonatus antarcticus*	26	16	218 (122–496)	Ridoux 1994
						Lycoteuthis sp.	2	6	36 (27–48)	
						Histioteuthis sp. A	15	17	127 (26–392)	
						Histioteuthis sp. B	3	5	85 (29–236)	
						Megalocranchia sp.	5	5	151 (58–200)	
						Taonius sp.	29	24	168 (51–287)	
	Northern New Zealand	145	94	72	58	*Argonauta nodosa*	9	10	85 (< 10–350)	Imber 1973
						Spirula spirula	5	25	10	
						Sepioteuthis bilineata	7	3	220 (< 10–900)	
						Gonatus antarcticus	7	4	170 (85–250)	
						Octopoteuthis sp.	6	3	220 (25–650)	
						Histioteuthis spp.	29	30	90 (11–210)	
						Taonius sp.	18	13	140 (80–350)	
						Teuthowenia pellucida	8	13	60 (3–120)	

soft-plumaged petrel	Crozet	12	8	4	16	*Lycoteuthis* sp.	21	25	31	Ridoux 1994
P. mollis						*Histioteuthis eltaninae*	33	25	48	
						Bathyteuthis abyssicola	12	25	17	
						Taonius pavo	34	25	50	
	Marion	9	100		89	*Psychroteuthis* sp.	23	9	183	Schramm 1986
						Gonatus antarcticus	36	9	293	
						Chiroteuthis sp.	22	45	35 (21–61)	
						Batoteuthis sp.	6	9	48	
						Galiteuthis glacialis	13	27	40 (23–54)	
dark-rumped petrel	Galapagos	83	86		46	*Octopoteuthis nielseni*	5	4	52	Imber *et al.* 1992
P. phaeopygia						*Onychoteuthis banksi*	17	16	44	
						Gonatus antarcticus	6	1	291	
						Pholidoteuthis boschmai	8	9	35	
						Histioteuthis heteropsis	11	4	109	
						Sthenoteuthis oualaniensis	9	28	13	
						Chiroteuthis veranyi	2	5	17	
						Mastigoteuthis dentata	11	10	44	
						Galiteuthis pacifica	7	5	56	
blue petrel	Marion	49	35	2	16	*Bathyteuthis abyssicola*				Steele & Klages 1986
Halobaena caerulea	Crozet	33	70	< 1	27	*Gonatus* sp.			< 1	Ridoux 1994
sooty shearwater	California	213	90	4	5	*Loligo opalescens*	95+	20		Chu 1984
Puffinus griseus	Benguela	42	4	1	< 1	*Loligo* (*reynaudi*?)				Jackson 1988
short-tailed shearwater	Tasmania	396	28			*Gonatus antarcticus*	18	11		Skira 1986
P. tenuirostris						*Histioteuthis atlantica*	19	12		
						Nototodarus gouldi	38	44		
	Victoria	307	13			*Nototodarus gouldi*		59		Montague *et al.* 1980
	Bering Sea				14	*Berryteuthis anonychus*			1–57	Ogi *et al.* 1980
						Gonatus spp.				
Wilson's storm-petrel	Ross Sea	28	54	30	45	*Psychroteuthis*		100	1–10	Ainley *et al.* 1984
Oceanites oceanicus	South Georgia	51	2	1	2					Croxall *et al.* 1988

[a] AAT = Australian Antarctic Territory.
[b] Number of samples.
[c] Of beaks identified to genus.
[d] Percent dry mass.
[e] Assuming mean mass = 50 g (cf. Imber 1976).

diving abilities (capable of plunge-diving to depths of 5 m in the smaller albatrosses (mollymawks)) than hitherto appreciated (Prince *et al.* 1994). Albatross diets have been most widely and extensively studied in a range of sub-Antarctic species (table 3). Although the squid prey include species from a considerable range of families, relatively few comprise the main diet of any albatross at any one site; nevertheless some clear patterns emerge. Thus *Gonatus*, *Moroteuthis*, *Histioteuthis* (two species), *Alluroteuthis* and *Galiteuthis* were common to the diet of most species studied in the South Atlantic and Indian Oceans and all were of remarkably similar size across sites and species. *Kondakovia* often appeared to be the most important species, because of its large size (but at least for wandering and sooty albatrosses this may be misleading because of the potential likelihood of it being scavenged; see below); nevertheless the size taken is larger in wandering than in sooty albatrosses and smaller still in grey-headed and black-browed albatrosses. The ommastrephid *Martialia* (subadults) was the most important species in the diet of albatrosses foraging over oceanic shelf areas (black-browed albatross) or near the Antarctic Polar Frontal Zone (grey-headed albatross); it was less common but larger (adult) in diets of wandering and sooty albatrosses. *Chiroteuthis* was particularly variable in size but both the largest (from wandering albatrosses) and smallest (from sooty albatrosses) came from the same site (Marion Island). Thus the cephalopod diet of sub-Antarctic albatrosses is basically of relatively large (but subadult) onychoteuthids and smaller (including adult and subadult) ommastrephids; the former more important to wandering and sooty albatrosses, the latter to mollymawks. However, yellow-nosed albatrosses *Diomedea chlororhynchos* in the Indian Ocean seemed to take onychoteuthids (*Kondakovia*, *Moroteuthis knipovitchi*) at Prince Edward Island (Brooke & Klages 1986) but ommastrephids (*Todarodes filippovae*) at the Crozet Islands (Ridoux 1994). This difference is similar to that in grey-headed albatrosses at the same sites and would merit research into the foraging areas of these albatrosses.

The few data from other southern albatrosses suggest that *Nototodarus and Histioteuthis* spp. were the main prey of Buller's albatross *D. bulleri* in New Zealand (West & Imber 1986), whereas *Loligo* dominated the diet of black-browed albatrosses foraging over the Patagonian Shelf from the Falkland Islands (Thompson 1992). Both *Nototodarus* and *Loligo* are subject to substantial local squid fisheries which may influence the diet of the albatross. Northern populations of wandering albatrosses (e.g. at Gough Island) ate more *Histioteuthis* than southern populations (Imber 1992).

Mainly qualitative data for tropical albatrosses indicate that squid and flying fish dominate the diet. Few squid have been identified in diet studies but ommastrephids (especially *Symplectoteuthis*) predominated in the diet of black-footed and Laysan albatrosses at Hawaii (Harrison *et al.* 1983; see also table 5); *Histioteuthis* and *Octopoteuthis* (with five other families) were reported from waved albatrosses *D. irrorata* at Galapagos (Harris 1973).

(*d*) *Petrels and storm petrels* (*Procellaridae and Hydrobatidae*)

These are geographically the most widespread members of the order Procellariformes and include numerous species (particularly in the genus *Pterodroma* and its relatives) that are among the most pelagic of all seabirds in temperate and tropical latitudes. Species in some genera (especially *Procellaria*, *Puffinus*, *Calonectris*) are accomplished wing-propelled divers (reaching depths of 10–20 m; see brief review in Huin 1994); otherwise all species principally take prey by seizing at the sea surface, doing this in flight being characteristic of *Pterodroma* species. Storm petrels rarely dive and feed mainly by dipping while pattering across the sea. The prions *Pachyptila* tend to have specialized foraging techniques predisposed towards crustaceans, but at least Antarctic prion *P. desolata* took a considerable variety of cephalopods in winter in the Benguela region (Lipinski & Jackson 1989). Fulmarine petrels (the genera *Macronectes*, *Fulmarus*, *Thalassoica*, *Daption*, *Pagodroma*) have particularly catholic diets and *Macronectes* species are primarily scavenging omnivores. A comprehensive review of feeding methods and of diet in the Procellariformes up to 1985 appears in Prince & Morgan (1987). Only the main, and more recent, quantitative studies are summarized in table 4.

For most species of southern high latitudes (i.e. south of the Antarctic Polar Front) squid are no more than locally important in the breeding season diet, but there are suggestions that squid (and fish) may be of greater significance in winter (Ridoux & Offredo 1989; Ainley *et al.* 1992). *Psychroteuthis*, *Gonatus* and *Galiteuthis* are the main genera consistently taken. Sub-Antarctic petrels at and north of the Antarctic Polar Front tend to take more squid in their diet and of a greater diversity of species, with ommastrephids (mainly *Martialia*/*Todarodes* in the Atlantic and Indian Oceans and *Nototodarus* in Australasian waters), *Gonatus* and histioteuthids, together with onychcoteuthid squid in some species (especially in the Indian Ocean), of particular importance. In more temperate southern waters there is a still greater diversity of squid prey with histioteuthids dominating (and enoploteuthids sometimes common). Some species, like the black petrel, breeding in northern New Zealand, range far enough also to feed on tropical ommastrephids (*Ommastrephes*, *Symplectoteuthis*) and lycoteuthids.

The only truly tropical *Pterodroma* recently studied (dark-rumped petrel at the Galapagos; Imber *et al.* 1992) showed great diversity of prey with representatives of eight families making significant contributions by number or mass, presumably reflecting the variety of prey available over the very large oceanic range of this species. This study indicates the potential for repeating earlier diet studies of tropical seabirds (Ashmole & Ashmole 1967; Harrison *et al.* 1983; see also table 5) now that more squid taxa can be reliably identified to species. In north temperate waters many fewer procellariform species occur, though those that do can be very abundant, either as breeding species (e.g. northern fulmar *Fulmarus glacialis*) or winter visitors (e.g. short-tailed shearwater, sooty shearwater, great shearwater *Puffinus gravis*). Very few have had their diet critically or quantitatively studied but squid are undoubtedly important in the diet of some species. Thus of resident species, juvenile squid (species unknown) formed 95% of the diet of the northern fulmar in the Gulf of Alaska (Sanger 1987), though squid were much less common (and mainly ommastrephids) in their diet in the North Atlantic (Furness 1994). Squid (mainly ommastrephids) were present in 40–83% of samples from Manx shearwaters *Puffinus puffinus* in the North Atlantic (Thompson 1987; Furness 1994) and formed 26–36% of the diet of Cory's shearwater *Calonectris diomedea* in the Azores (Furness 1994). Of visitors from the southern hemisphere, 20% by mass of the diet of short-tailed shearwaters in the North Pacific was squid (mainly larval gonatids) (Ogi *et al.* 1980), though squid were less common in their diet in the Gulf of Alaska (Sanger 1987). Squid (mainly *Loligo opalescens* but gonatids were also common) formed 5–6% by volume of the diet of sooty shearwaters off California (Chu 1984) and rather more (species unknown) in Alaska (Sanger 1987). In the western North Atlantic 33% by mass of the diet of great shearwater (but only 1% of the diet of sooty shearwaters) comprised *Illex illecebrosus* (up to a maximum mass of 175 g) (Brown *et al.* 1981). Finally, although few quantitative diet studies of storm petrels have been undertaken and even fewer squid identified, FOO information suggests that squid are not uncommonly taken by temperate and polar species (Sanger 1987; Croxall *et al.* 1988; Furness 1994) and are perhaps common in the diet of tropical species (Harrison *et al.* 1983).

(*e*) *Auks/alcids, etc.* (*Alcidae*)

The northern hemisphere ecological equivalents of penguins are the alcids. The larger species show wing-propelled diving performance (reviewed in Burger 1991) not greatly inferior to small penguins but, being flighted, have much larger potential foraging ranges. However cephalopods seem to be much less important in their diet, most species favouring fish and zooplanktonic crustaceans (Vermeer *et al.* 1987). Only in the larger species (puffins (*Fratercula*) and guillemots (*Uria*)) are squid of any real importance. Thus Wehle (1983) found that although squid (gonatids) typically comprised less than 5% by volume of prey of tufted puffins *F. cirrhata*, at some sites in some years they formed 15–30% of the diet. Similarly, sympatric horned puffins *F. corniculata* occasionally took over 10% by volume of gonatids. Atlantic puffins *F. arctica* offshore in winter in the Norwegian Sea took 43% by number (86% FOO) of *Gonatus fabricii* but less than 1% (14% FOO) inshore around the Faroes in winter (Falk *et al.* 1992). Guillemots took mainly fish in the breeding season but in one of the few studies outside this time Ogi *et al.* (1980) showed that squid made up 73% by mass overall of the diet of Brünnichs guillemot *U. lomvia* in the western North Pacific. All squid taken were juvenile, the main species being *Gonatopsis borealis* (60–100 mm ML), *Berryteuthis magister* (40–100 mm ML) and *B. anonychus* (80–100 mm ML); squid larvae were also important at times. Squid dominated the diet of Brünnichs guillemot in spring in several oceanic domains (including the west sub-Antarctic Gyre, the sub-Arctic Current, the Westwind Drift, the northern subtropics, the East Kamchatka Current and the Sea of Okhotsk) but were absent in samples from the Gulf of Anadyr (Ogi & Hamanaka 1982). However the winter diet of the same species around Greenland was dominated by crustaceans and capelin with *Gonatus fabricii* only 1% by mass (6% FOO) of the diet (Falk & Durinck 1993). There are no comparable data for other alcids and auklets but, although they are probably too small in size even to take juvenile squid in winter, they are certainly potential predators on larval squid at this time.

(*f*) *Pelecaniformes*

The seagoing shags and cormorants (Phalacrocoracidae) are coastal, mainly benthic-foraging piscivores, some species of these foot-propelled divers having submersion capacities exceeding all but the largest penguins (Croxall *et al.* 1991). A few species also take octopus, e.g. 31% FOO of small individuals and 8% FOO of larger *Pareledone* in the diet of South Georgia shags *Phalacrocorax georgianus* (Wanless *et al.* 1992) and this may not be atypical of other members of the genus in similar habitats (e.g. Ridoux 1994).

Of the Sulidae most species specialize in catching prey by plunge diving (to 3–5 m depth; Adams & Walter 1993) on shoaling fish prey. Gannets (*Morus*) are chiefly piscivorous. Thus the Australasian gannet *M. serrator* took less than 1% by mass of squid (and a monthly maximum of only 6%); all material identified was *Nototodarus* and this only occurred in the diet between September and January (Wingham 1985). The best studied species, Cape gannet *M. capensis* had a 12-year average of 0.6% (range 0.1–9.7%) by number, 3% (1–16%) FOO and 1.6% (0.2–13.6%) by mass of squid, almost all *Loligo reynaudi* with traces of *Ommastrephes bartrami* (Klages *et al.* 1992). In northern gannets *M. bassanus* there are major differences between populations. In the northwest Atlantic they took up to 10% by mass of *Illex illecebrosus* (Montevecchi *et al.* 1988) but squid was unreported in their diet in Britain (Nelson 1978) and Norway (Montevecchi & Barrett 1987). Of the tropical boobies (*Sula*) only the red-footed *S. sula* takes substantial amounts of squid: 25% by volume (species unknown) at Christmas Island, Indian Ocean (Schreiber & Hensley 1976); 27% by volume (ommastrephids of five species) at the Hawaiian Islands (Harrison *et al.* 1983; see also table 5). Other species take much smaller quantities of squid which, when identified, have usually been ommastrephids (Dorward 1962, Harrison *et al.* 1983, 1984).

Frigatebirds (*Fregatidae*) never alight on the water and feed by plucking items from the surface in flight and by kleptoparasitizing other seabirds, mainly boobies (Furness 1987). They are chiefly piscivorous but the great frigatebird *Fregata minor* studied at Aldabra and Christmas Islands (at opposite sides of the Indian Ocean) and Hawaii took 14–30% of squid by

Table 5. *Composition of cephalopod diet of seabirds at the Hawaiian Islands*

(From Harrison *et al.* 1983.)

species	N[a]	squid in diet (% by vol.)	squid % identified[b]	Ommastrephidae[d] %[c]	A	B	C	D	E	size (mm)[e]	other families/ species
black-footed albatross *Diomedea nigripes*	172	32	6	96			2		2	74 ± 3 (42–120)	Cranchiidae, Octopoteuthidae
Laysan albatross *D. immutabilis*	183	65	2	96		2	1			71 ± 2 (28–144)	Lepidoteuthidae, Mastigoteuthidae (*Mastigoteuthis* sp), Enoploteuthidae (*Thelidoteuthis alessandrini*), Onychoteuthidae, Histioteuthidae
Bonin petrel *Pterodroma hypoleuca*	144	21	10	85						46 ± 7 (20–72)	Enoploteuthidae (*Pterygoteuthis microlampas*), Histioteuthidae
Bulwer's petrel *Bulweria bulweri*	100	21	6	100							
wedge-tailed shearwater *Puffinus pacificus*	233	29	37	100		12	5		1	63 ± 3 (29–115)	Octopoda
Christmas shearwater *P. nativitatis*	182	48	84	99		13	2		4	62 ± 2 (25–107)	Onychoteuthidae
sooty storm-petrel *Oceanodroma tristrami*	10	29	0								
great frigatebird *Fregata minor*	284	14	76	100		6	2	1		78 ± 2 (42–118)	
masked booby *Sula dactylatra*	305	3	85	100		9	6		3	90 ± 3 (46–1280)	
red-footed booby *S. sula*	360	27	83	100	1	6	9	2	2	78 ± 1 (40–208)	
brown booby *S. leucogaster*	244	5	66	100	4	3	1	1		81 ± 4 (41–129)	
red-tailed tropic-bird *Phaethon rubricauda*	270	18	34	98	1	11	9		1	82 ± 3 (23–128)	Onychoteuthidae (*Onychoteuthis* sp.)
sooty tern *Sterna fuscata*	356	53	78	100		20	5		2	51 ± 2 (18–104)	
grey-backed tern *S. lunata*	272	4	37	100		4					
brown noddy *Anous stolidus*	354	33	83	100	1	17	2	1		53 ± 2 (19–96)	Onychteuthidae (*Onychoteuthis* sp.)
black noddy *A. minutus*	494	7	61	98		10	1			32 ± 1 (11–67)	Onychoteuthidae (*Onykia* sp)
blue-grey noddy *Procelsterna cerulea*	111	1	3	100							
white tern *Gygis alba*	241	12	83	100		12	2		5	50 ± 6 (14–99)	

[a] Number of samples.
[b] To level of family.
[c] Of squid identified to family.
[d] A: *Ommastrephes* sp.; B: *Symplectoteuthis* sp.; C: *S. uvalaniensis*; D: *S. luminosa*; E: *Hyaloteuthis pelagicus*.
[e] Mean ± standard error (range in parentheses) mantle length.

mass (all ommastrephids at Hawaii) (Harrison *et al.* 1983 (and see table 5); Diamond 1975; Schreiber & Hensley 1976). At Aldabra the sympatric lesser frigatebird *F. ariel* took similar quantities of squid to *F. minor* but 89% of them during the wet season, unlike its congener whose squid diet was evenly distributed across wet and dry seasons (Diamond 1975).

The only tropicbird (Phaethontidae) whose squid diet (17% by volume) has been studied is the red-tailed *P. rubricauda* at Hawaii where ommastrephids predominated in the diet (Harrison *et al.* 1983; see also table 5).

(*g*) *General*

There are numerous anecdotal and qualitative records of cephalopods as prey of seabirds, including in groups not treated above (e.g. gulls, sea ducks), many referenced in Croxall (1987). Although further work, perhaps especially outside the breeding season, may reveal squid/octopus to be important in their diet, such work is unlikely greatly to change the broad conclusions based on the foregoing review. Thus in the most general terms penguins are rarely dependent on cephalopods, though at certain times and places particular squid species may be among their commonest prey. Similar conclusions apply to shearwaters and auks, which also mainly catch prey by wing-propelled pursuit while diving. For all three groups, however, there are suggestions that squid may be much more important outside the breeding season when predators and prey may both be more dispersed and potentially less reliant on shoaling fish and/or crustaceans.

In contrast, for many albatross and petrel species squid are undoubtedly as important in their diet as fish and crustaceans. The limited studies of tropical species indicate that this is just as true in these regions as in higher latitudes. For some shags and cormorants, octopus may be taken frequently, but in general among the pelecaniforms studied quantitatively only red-footed booby and frigatebirds seem to take substantial amounts of squid. Some tropical terns, however, may depend extensively on squid (see table 5).

3. SQUID–SEABIRD INTERACTIONS

There is relatively little evidence of selectivity among squid species by seabird predators. Thus although ommastrephids, onychoteuthids and histioteuthids feature widely in seabird diets this probably reflects features of their size and distribution rather than any other selectivity on the part of the predator. The relative absence of cranchiids from seabird diets is, however, more puzzling (Imber 1992).

There are some indications, however, that different groups/species of seabirds exploit squid prey of different sizes. Thus all penguins, even emperors and kings with their large size and exceptional deep diving and foraging abilities (Kooyman *et al.* 1992, Putz & Bost 1994, Kooyman & Kooyman 1995), take squid that are mainly juvenile and small (10–100 g) both in absolute terms and compared with those taken by seals and albatrosses/petrels. This may reflect the propensity for penguins to target shoaling prey of sizes facilitating multiple captures at speed during single dives. In addition there is some evidence that sympatric penguins of different sizes exploit squid prey of different sizes (figure 2) although these differences are small and unlikely to be revealed in most other existing studies of seabird diets.

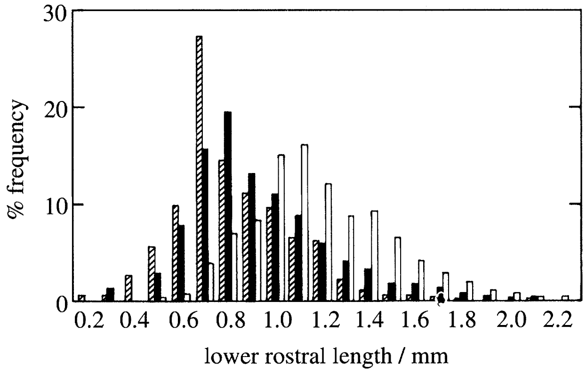

Figure 2. Frequency distributions of lower rostral lengths of beaks of *Gonatus antarcticus* taken by gentoo (solid areas, $n = 596$), magellanic (open areas, $n = 925$) and rockhopper penguins (hatched areas, $n = 118$)in the Falkland Islands in December 1986 (from Thompson 1994).

Albatrosses and the larger petrels all commonly take prey in the 50–300 g range (and frequently much larger individuals, but these may well be scavenged; see below). However, except for *Kondakovia* and *Martialia* (see above) there is little evidence of different sizes of squid being taken by related and/or sympatric species of seabirds of different sizes.

Among a range of tropical seabirds at a single site, where ommastrephids form the bulk of the identified squid (table 5), the largest prey (70–90 mm) are taken by albatrosses, frigatebirds and boobies, with smaller squid (60 mm) taken by shearwaters, still smaller squid (46–53 mm) by petrels and larger terns and the smallest squid (32 mm) by the smallest tern. While some of these differences undoubtedly reflect the structural size of the predators, others may also relate to interspecies differences in foraging areas and methods.

Overall, therefore, many of the differences in the species and size of squid taken are as likely to reflect the availability of squid within the foraging range of largely opportunistically foraging seabirds rather than strong selectivity for squid of particular sizes or species.

However, the size, nature and characteristics of some squid taken by predators have led to active debate over the extent to which flying seabirds can catch large squid unaided, or depend on the activities of other predators (fish, cetaceans), or scavenge squid that have died post-spawning or been regurgitated by other predators (especially cetaceans) (Clarke *et al.* 1981; Lipinski & Jackson 1989; Imber 1992; Croxall & Prince 1994).

Unaided live capture of squid requires seabirds being able to catch them at or near the surface by seizing or diving. The tendency of many squid to perform diel vertical migrations may significantly assist in this, particularly for seabirds able to feed at night. Two potential widespread sources of scavenged squid have been suggested: vomit from cetaceans (Clarke *et al.* 1981; Clarke & Goodall 1994) and post-spawning mortality (Rodhouse *et al.* 1987). Furthermore, Lipinski & Jackson (1989) suggested, based on observations of cephalopods taken by seabirds in the Benguela region and assessment of their likelihood to float (because of gas-filled endoskeleton or high concentrations of ammonium chloride) or sink after death, that most seabirds scavenged dead squid and that this may be generally true for other species and systems.

It is not disputed that most seabirds are likely to scavenge food whenever available. Also, given that flying seabirds cannot transport more than 20–30 % of their body weight (Croxall *et al.* 1984), squid estimated to be larger than this (e.g. > 150 g for many *Pterodroma* petrels and > 1000 g for mollymawks) are very likely to have been scavenged. This can sometimes be a significant proportion of the diet of some species. In a comprehensive review of the size, nature and ecology of squid taken by the four albatross species breeding at South Georgia, Croxall & Prince (1994) concluded that wandering and light-mantled sooty albatrosses probably did depend significantly on scavenged squid but that black-browed and grey-headed albatrosses were unlikely to do so. Particular evidence in favour of live capture in these latter two species were observations of intact, subadult (i.e. pre-spawning) squid of a sinking species (*Martialia*) being delivered to chicks for several months of the year. Given the lengthy chick-rearing period of many albatross and petrel species, it is unlikely that they can rely on the often highly seasonal post-spawning mortalities of squid. Furthermore, although wandering albatross diet does show strong similarities with that of some sympatric smaller cetaceans (Clarke & Goodall 1994), this is less so for many petrels and it is difficult to believe that small squid (< 100 g) are made available through cetacean vomit sufficiently frequently to sustain them. However, the frequent observations of associations between seabirds and cetaceans in tropical and temperate waters (Enticott 1986; Pierotti 1988; Pitman & Ballance 1992) certainly indicates considerable scope for scavenging and also for seabirds profiting from the activities of cetaceans (and larger predatory fish) in driving squid prey towards the surface. In these situations Pitman & Ballance (1992) distinguish between the mobile seabirds exploiting live prey (boobies by plunge-diving; terns, frigatebirds and *Pterodroma* petrels and shearwaters seizing prey aerially) and *Procellaria parkinsoni* diving to scavenge parts of large squid dropped by the cetaceans.

Thus a propensity to subsist largely on scavenged squid may be confined to certain species and groups of seabirds and intimately linked to association with cetaceans. Similarly the successful capture of live squid by a variety of other species and groups of seabirds may be greatly facilitated by the predatory activities of tuna and small cetaceans. These interactions clearly deserve much further study.

Another topic under re-evaluation is the extent to which seabirds with limited diving abilities rely on feeding at night to catch squid and the role of squid bioluminescence in assisting them. Recent work with albatrosses suggests that the wandering albatross feeds mainly in daytime (Weimerskirch & Wilson 1992; Cooper *et al.* 1993) and that mollymawks are more diurnal than previously thought but may show peaks of activity around dawn and dusk (Prince *et al.* unpublished). With Pitman & Ballance's (1992) observation of extensive diurnal feeding (albeit scavenging) in *Procellaria* petrels (formerly believed to be extensively nocturnal) this is also a timely topic for further research, as is the role of bioluminescence now that there is good evidence that the diet of some albatrosses and petrels is predominantly of non-bioluminescent species (Croxall & Prince 1994; Croxall *et al.* 1995). However it is still true that most albatrosses and petrels predominantly take cephalopods which are near-surface dwellers (e.g. *Argonauta*, *Ocythoe*) or make diel vertical migrations (Imber 1992).

4. ROLE OF SEABIRDS AS SQUID PREDATORS

(*a*) *Impact of predators on squid stocks*

Although cephalopods are an important food of a wide variety of pelagic seabirds, especially procellariforms, the impact of seabirds on squid populations is probably much less important. Estimates of annual squid consumption by seabirds in various parts of the world (table 6) indicate that consumption nowhere exceeds 0.5 million tonnes (mt) and in most cases is 100000 t or less. Only in Hawaii and California do squid make up more than 20% of the overall food intake by seabirds – re-emphasising the potential importance of squid for seabirds in particular and trophic interactions in general in tropical and low latitude marine communities.

Overall, therefore, it appears that seabirds are considerably less important consumers of squid than are marine mammals (Clarke 1983; Rodhouse *et al.* 1993; Klages 1996). Furthermore, because seabirds mainly eat juvenile squid they may have somewhat less impact on squid populations than if they ate adults – but to the extent that many squid are semelparous and live for only one year, this distinction may be less important than with prey taxa of longer lives.

It is, of course, quite possible that seabirds may exert significant local effects on specific squid populations but, despite the huge numbers of larval/juvenile squid that can be consumed by penguins (Thompson 1994) and guillemots (Ogi *et al.* 1980) it is unlikely that this will have any real impact on recruitment to the adult spawning population. Nevertheless, a consumption of 3 billion individual *Gonatus* around one breeding colony of rockhopper penguins in the Falkland Islands (Thompson 1994; table 7) testifies both to the importance of squid for seabirds and to the immense fecundity and potential abundance of squid.

If the squid consumption per unit area by seabirds (from table 6) is regarded as an index of squid abundance/availability, then there is a clear distinction between the eastern Atlantic, Mediterranean and Heard Island areas (all 1000–10000 g/km^2) and the Bering Sea, Newfoundland, California, Hawaii and the other two sub-Antarctic areas (all 400000–500000 g/km^2, except for Prince Edward Islands (833000 g/km^2)). Refinement (with more accurate delimitation of the seabird foraging areas) and extension (to other areas where seabirds are known to eat squid) of this approach might yield interesting insights into broad-scale squid distribution and abundance, complementary to those derived from other methods.

(*b*) *Seabirds as samplers/monitors of squid*

One of the most useful roles of seabirds as squid predators is as a sampling tool. As Clarke (1977) emphasized, predators are able to provide much information on squid which is difficult or impossible to

Table 6. *Estimates of annual consumption (tonnes) of squid by seabirds in various areas*

locality	area (km²)	consumption by seabirds: squid	consumption by seabirds: all prey	squid as % of food intake	reference
NE Atlantic	15000000	40000	4500000	< 1	Furness 1994
Mediterranean	2000000	3000	100000	3	Furness 1994
Iberian Atlantic	9000000	63000	400000	16	Furness 1994
SE Bering Sea	132700	60000	400000	15	Schneider *et al.* 1986, 1987
Georges Bank, Newfoundland	52500	21000	105000	20	Schneider *et al.* 1987
Gulf of St Lawrence	214000	300	93752	< 1	Cairns *et al.* 1991
California Coast	215000	100000	193000	52	Briggs & Chu 1987
Hawaiian Islands	*ca.* 500000	223000	410000	54	Harrison & Seki 1987
Prince Edward Islands, S. Indian Ocean	125000	100000	586000	17	Brown 1989 Adams *et al.* 1993
Heard/McDonald Islands, S. Indian Ocean	*ca.* 125000	1200	421330	< 1	Woehler & Green 1992
South Georgia	1000000	466000	7820000	6	Croxall & Prince 1987

Table 7. *Consumption of* Gonatus antarcticus *by penguins breeding at New Island and Steeple Jason Island, Falkland Islands*

(Data from Thompson 1994.)

species	samples	sites/ years	proportion (%) squid by mass[a]	proportion (%) *Gonatus* by no.[a]	Mean size (ML in mm) *Gonatus*[a]	consumption: tonnes	consumption: no. (millions)
gentoo	103	7	24 (3–68)	55 (0–98)	*ca.* 35 (17–66)	80	36
magellanic	142	9	54 (1–93)	78 (0–99)	*ca.* 33 (18–62)	247	132
rockhopper	88	4	36 (10–50)	46 (2–89)	*ca.* 31 (17–60)	4475	3094

[a] Range in parenthesis.

acquire using conventional sampling gear. In particular they catch larger specimens and a greater diversity of species than nets (Rodhouse 1990). In addition to providing information on distribution and sometimes abundance of species throughout the world's oceans, the relative ease of sampling seabirds should enable them to provide data of relevance to understanding squid demography and population fluctuations; the data on squid length–frequency distributions in figures 1 and 2 indicate how much valuable information can readily be acquired in this way.

Moreover, as Montevecchi *et al.* (1988) and Montevecchi & Myers (1995) have shown, the catch of squid by seabirds can correlate well with data from fisheries surveys and catches and can provide important indices of squid abundance/availability at various temporal and spatial scales. Thus harvests of *Illex illecebrosus* by gannets and inshore fisherman in Newfoundland waters were significantly associated over a 15-year period and major reductions in squid availability to gannets preceded failures in the local pelagic fishery. The proportion of squid in gannet diets also correlated with fishery-independent research surveys of squid abundance at scales of thousands of kilometres (figure 3).

There would seem to be substantial potential for using data on squid eaten by predators to illuminate a variety of topics concerning squid abundance and distribution and its potential availability to commercial fisheries. Furthermore, squid dietary data from predators can also provide unique information of the status and distribution of squid resources that cannot easily be surveyed and/or have not been subject to commercial fishing. Thus the scope for commercial exploitation of *Martialia hyadesi* in areas adjacent to the Antarctic Polar Front in the South Atlantic has almost exclusively been inferred using data from predators (Rodhouse *et al.* 1993).

The potential for more precise localization of squid resources is becoming greatly enhanced with the use of satellites to track the locations and behaviour of seabird (and seal) predators (Ancel *et al.* 1992; Prince *et al.* 1992, 1996; Jouventin *et al.* 1994; Weimerskirch *et al.* 1994; Cherel & Weimerskirch 1995; Rodhouse *et al.* 1996). When combined with diet sampling of returning birds this is a powerful tool for research on squid resources as well as on squid–predator interactions.

(*c*) *Seabird-fishery interactions*

The local consumption of commercially exploited squid species by seabirds is currently not perceived as a problem in terms of seabird impact on the fishery (e.g. Lipinski 1992). In the only critical study to date, Thompson (1992) calculated that black-browed albatrosses in the Falklands at the commencement of the commercial fishery for *Loligo* in 1987 consumed 9500 t, or 9% of the estimated stock. In contrast the commercial fishery caught some 46% of the stock in

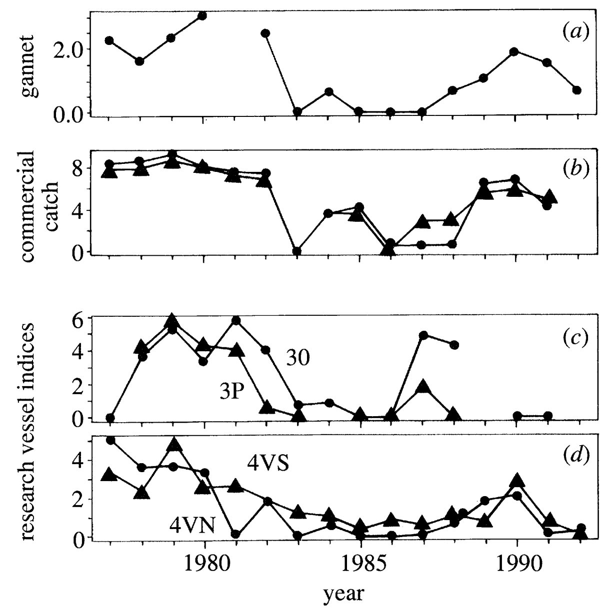

Figure 3. (*a*) Consumption of *Illex illecebrosus* by northern gannets (% mass of diet) on Funk Island, Newfoundland; (*b*) in relation to catches by inshore fisheries in the same area; (*c*) and (*d*) in relation to research vessel trawl survey indices in adjacent NAFO statistical divisions. All data, transformed by log (catch + 1), from Montevecchi & Myers (1995).

1987. The albatrosses have subsequently benefited from the fishery to the extent that they now eat one-half of the waste, totalling 5% of the catch, jettisoned by the trawlers, thereby meeting some 10–15% of their energy demands. Nevertheless, on balance the fishery is clearly liable to pose a greater threat than benefit to the albatrosses.

5. THE FUTURE

The ability to determine both the size and identity of squid taken by seabirds and the locations of their foraging activity should mean that we are on the threshold of being able to investigate the dynamics of squid–seabird interactions rather than reconstructing them retrospectively through diet studies. However to take best advantage of opportunities to study squid–seabird interactions in the field and to use seabirds to provide information on the distribution and abundance of squid, as well as being potential aids in the rational management of squid stocks, requires further development of some of the tools for this task. Thus we need:

(*i*) More, and more critical, studies of diet (especially in tropical and north temperate regions) and of the squid component, with correction for known biases;

(*ii*) More comprehensive guides to beak identification (especially of tropical species) using modern visual imaging techniques;

(*iii*) Improved equations relating beak dimensions to mantle length and mass;

(*iv*) More widespread use by seabird biologists of mantle length data and the relation of this to equivalent information on live squid in order to investigate demographic implications;

(*v*) Studies of the interactions between marine mammals and seabirds with accompanying investigation of the scavengeability of different groups of squid;

(*vi*) Research into relationships between the location and timing of seabird foraging events involving squid and topographic (e.g. shelf slope) and oceanographic (e.g. fronts, gyres) features.

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