

Dead or alive, night or day: how do albatrosses catch squid?

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Abstract: For many albatross species squid are important prey. Whether albatrosses depend on scavenging (e.g. of vomit from cetaceans, post-spawning die-offs or fishery waste) or on live-capture of squid (e.g. via diel vertical migrations in association with aggregations of squid prey) is controversial. This review of the nature of interactions between squid and the four species of albatross breeding at South Georgia uses data on the foraging range, methods and timing of feeding of the albatrosses in relation to the size, distribution, buoyancy characteristics (floaters or sinkers), bioluminescence and prey of the squid and access to fishery waste. We conclude that most evidence for scavenging needs critical re-evaluation; nevertheless, whereas wandering albatrosses and possibly light-mantled sooty albatrosses probably depend significantly on scavenged squid, black-browed and especially grey-headed albatrosses are unlikely to do so.

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Introduction

For several species of albatross, squid are the single most important class of prey in their diet. The ability of such albatrosses consistently to locate and catch squid must therefore be an important feature of their feeding ecology. However, how albatrosses actually catch squid has long been a puzzle. As a predator, albatrosses are supremely adapted for economic long-distance flight; their long wings and light bodies suggest that they are likely to be restricted to seizing prey at the sea surface, using their sharp and powerful beaks. Most pelagic squid are themselves active predators with highly developed sensory systems and rapid reflexes; furthermore, net captures suggest that such squid may inhabit mainly mid- and deep-water levels.

With this background, it is not surprising that albatrosses were regarded as at least partial scavengers of squid, depending variously on regurgitations from squid-eating cetaceans (Clarke *et al.* 1981), post-spawning die-off (Lipinski & Jackson 1989) and access to waste from fishery operations (Thompson 1992). However, the fact that at least some albatross species feed their chicks with whole squid over periods of several months (Prince 1980, Rodhouse *et al.* 1993) suggests that they may also have the ability to catch live squid. This was believed to occur through squid reaching the ocean surface when tracking the vertical migration of their fish and zooplankton prey (Roper & Young 1975) and possibly further facilitated by many squid being bioluminescent (Imber & Russ 1975). To the extent that albatrosses took live prey, they were believed to feed predominantly during nighttime, taking advantage of vertical migrations (Imber & Russ 1975, Prince & Morgan 1987). Recently, however, direct evidence on timing of ingestions by wandering albatrosses at sea (Weimerskirch & Wilson 1992) suggests that daytime feeding may be the predominant mode, at least for this species.

In this paper, we review the various lines of evidence, mainly

circumstantial, which provide insights into how and when albatrosses catch cephalopod prey.

Background

Scope

For most purposes, we confine discussion to the four species of albatross breeding at South Georgia. This has the advantage of eliminating differences due to location and methods of study. Despite this geographical and taxonomic restriction, the albatross species at South Georgia cover most of the range of life histories and adaptations shown by the family (Prince *et al.* 1994). South Georgia albatrosses belong to both genera of the family, both sub-genera of *Diomedea* (great albatrosses and mollymawks), include annual and biennial breeders, large and small species, and summer and winter breeders. They are therefore likely to be a reasonably typical cross-section of at least the Southern Ocean element of the family.

Squid diet of South Georgia albatrosses

General information on the importance of squid to the four albatross species, the duration and timing of the chick-rearing period (when the diet samples were obtained) and on foraging range are summarized in Table I. Full data on the squid diet of these albatrosses at South Georgia can be found in Clarke *et al.* 1981, Clarke & Prince 1981, Thomas 1982, Prince & Morgan 1987, Rodhouse *et al.* 1987, Rodhouse *et al.* 1990, Imber 1992, and Rodhouse & Prince 1993. Data from the main studies are summarized in Table II (which is restricted to squid species which contribute at least 5% by either numbers or mass to at least one albatross species) and Fig. 1 (where the combined contribution of species not listed in Table II is indicated).

Table I. Aspects of breeding biology and squid consumption of South Georgia albatrosses. For sources of data see text and Fig. 2.

Species	Squid in diet (%)*	Annual consumption (tonnes)	Chick-rearing period (months)	Foraging	
				radius (km)**	range (°S)
Wandering albatross	40	1200	April–Nov	2500	24–67
Grey-headed albatross	49	20600	Jan–May	700	47–63
Black-browed albatross	21	4600	Jan–April	500	49–64
Light-mantled sooty albatross	47	2300	Jan–May	1000	50–67

* Proportion by wet mass
 ** While rearing chicks

These data indicate that wandering albatrosses (*Diomedea exulans*) take by far the greatest diversity of squid, but that no one species is numerically dominant in their diet. However, *Histioteuthis*, *Illex* (in some years only), *Galiteuthis* and *Kondakovia* all make significant contributions by number. By mass, however, *Kondakovia* contributes on average one-half of the diet, with only *Illex* (and that not in every year) adding more than 10%. This is a very different pattern than observed for the other three species of albatross. In black-browed and grey-headed albatrosses (*Diomedea melanophris*) and (*D. chrysostoma*), *Martialia* dominates the diet by both numbers and mass. In light-mantled sooty albatrosses (*Phoebastria palpebrata*), *Galiteuthis* and *Psychroteuthis* together contribute 80% of the numbers (60% *Galiteuthis*) and 70% of the mass (48% *Psychroteuthis*).

Sources of evidence on albatross-squid interactions

There are very few direct observations of albatrosses eating squid and most are under circumstances that may be atypical of natural feeding methods (e.g. at illuminated ships or active fishing vessels, etc). However, there are a variety of sources of circumstantial, indirect evidence, especially with respect to whether albatrosses take live or dead squid, which are summarized in Table III.

Table II. Composition by mass and numbers of squid diet of albatrosses at South Georgia.

Species	Wandering albatross		Grey-headed albatross		Black-browed albatross		Light-mantled sooty albatross	
	Mass	Number	Mass	Number	Mass	Number	Mass	Number
<i>Gonatus antarcticus</i>	+	+	+	+	+	+	5	
<i>Kondakovia longimana</i>	58	10	11	+			13	+
<i>Histioteuthis eltaninae</i>	+	21	+	+	+	+	+	+
<i>Psychroteuthis glacialis</i>	+	+	5	+			48	20
<i>Alluroteuthis antarcticus</i>	5	+	+	+			6	
<i>Martialia hyadesi</i>	+	+	71	80	74	60	+	6
<i>Illex argentinus</i>	12	24						
<i>Galiteuthis glacialis</i>	+	19	7	14	18	32	22	60

Legend: + indicates less than 5% contribution; bold indicates main prey item.

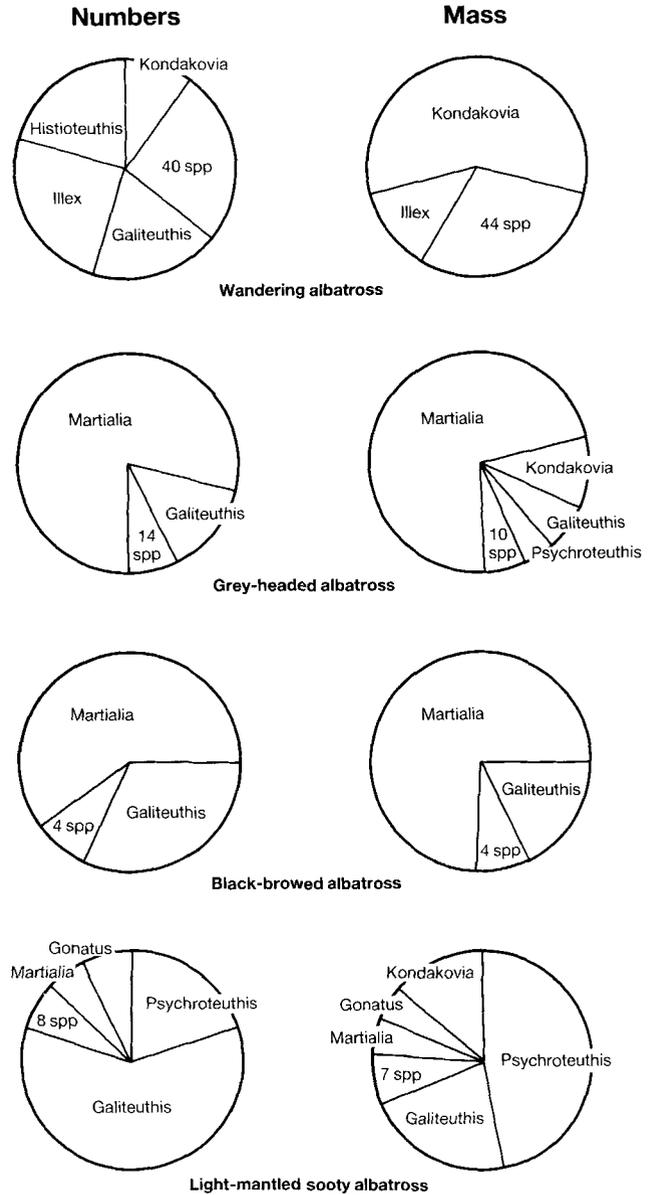


Fig. 1. Composition, by numbers and wet mass, of squid diet of albatrosses at South Georgia. See text for sources of data.

Table III. Sources of indirect evidence for nature of squid prey of albatrosses, together with an indication of those characteristics most likely to be associated with capture of live or dead prey.

Characteristic	Live	Dead
Squid		
Size	Small	Large
Nature	Epipelagic	Midwater
	Sinks	Floats
Albatross		
Feeding method	Surface plunge Shallow and deep plunge Pursuit dive	Surface seize
Feeding time	Ship avoider	Ship follower
Foraging area	Night	Day
	Restricted	Extensive

Evidence from albatrosses

Foraging range

Ranges of South Georgia albatrosses during the chick-rearing period are shown in Fig. 2. This indicates the very large range of wandering albatrosses (though female and male birds have, respectively, more northerly and southerly distributions within this overall range), very different from the other species. The two mollymawks have rather similar distributions, though black-browed albatrosses are more associated with shelf areas (at South Georgia and the South Orkney Islands) than grey-headed albatrosses, which tend to be more pelagic and predominantly forage at and south of the Antarctic Polar Front. Light-mantled sooty albatrosses show a distinctly more southerly and easterly distribution than any of the other three species; this is consistent with data on their pelagic range in other sectors, and especially their affinity for ice-edge habitats (Weimerskirch & Robertson 1994).

Feeding methods

Most actual observations of feeding albatrosses (summarized in Harper *et al.* 1985, Harper 1987) report that they principally use surface-seizing methods. There are quite a few observations of shallow plunges and surface dives, particularly, but by no means exclusively, for birds seen in association with fishing trawlers discarding offal (Milledge 1977, Sinclair 1978, Oatley 1979, Prince 1980, Voisin 1981, Harper 1987, Harrison *et al.* 1991, Thompson 1992). There are also three records of pursuit diving, two for black-browed albatrosses, to depths in excess of 2 m (Nicholls 1979) and durations of up to 20s (Harper 1987) and one for a wandering albatross (Voisin 1981). Indirect evidence of feeding methods comes from recent data from dive-depth recorders attached to albatrosses (P.A. Prince, N. Huin & H. Weimerskirch, unpublished data). Both black-browed and grey-headed albatrosses can dive to 6 m depth and attain a mean maximum depth of 2–3 m. Similarly, light-mantled sooty albatrosses were recorded diving to a maximum depth of 12 m

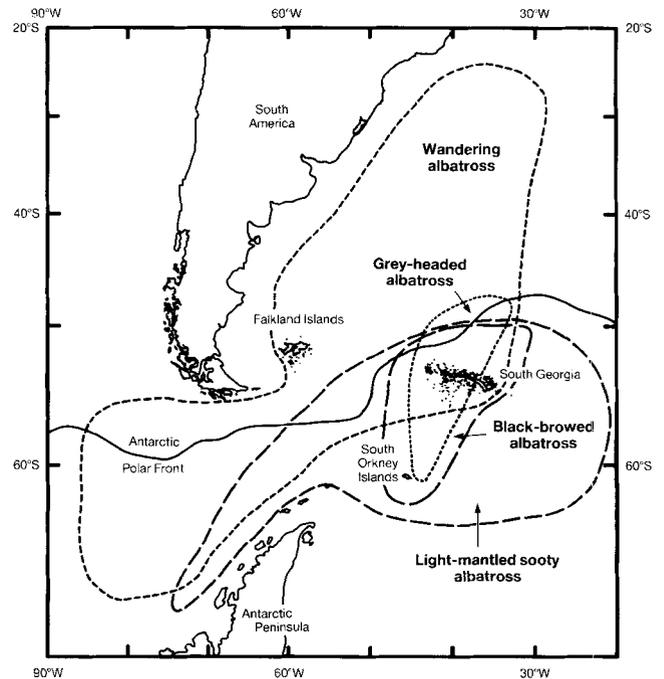


Fig. 2. Distribution at sea of albatrosses breeding at Bird Island, South Georgia while foraging during the chick-rearing period. Based on data from satellite-tracked birds (Prince *et al.* (1992) and P.A. Prince, A.G. Wood unpublished data), except for light-mantled sooty albatross, for which at-sea sightings have been used (see Thomas 1982).

and a mean maximum of 5 m. No diving was recorded for wandering albatrosses. These data indicate that the diving ability of at least some albatross species may have been significantly underestimated.

In addition, the relationship between albatrosses and ships may influence the nature of prey encountered and eaten. Wandering and black-browed albatrosses are well known as ship-following and ship-associated species; by contrast grey-headed and light-mantled sooty albatrosses are much less often associated with ships.

Time of feeding

The time of day when albatrosses feed may influence the kind of squid they encounter. Thus night-time foraging might be biased towards live squid migrating vertically towards the surface, whereas day-time foraging might involve exploitation of dead squid. Data on activity budgets (Prince & Francis 1984, Prince & Morgan 1987) indicated that albatrosses spent significant time on the water during the day and especially at night. Even wandering albatrosses, which spent most time on water during the day, still spent a disproportionate amount of time on the water at night, once day length was taken into consideration. However, time spent on the water does not necessarily reflect time feeding because other activities, such as resting, preening etc. may complicate the picture. Nevertheless,

Table IV. Mean mass (g) of squid prey taken by albatrosses at South Georgia.

Species	Wandering albatross	Grey-headed albatross	Black-browed albatross	Light-mantled sooty albatross
<i>Gonatus antarcticus</i>	250	200	260*	300
<i>Kondakovia longimana</i>	3400	860	–	1000*
<i>Histioteuthis eltaninae</i>	70 (180**)	80	160*	70*
<i>Psychroteuthis glacialis</i>	190	630	–	570
<i>Alluroteuthis antarcticus</i>	390	370	–	400
<i>Martialia hyadesi</i>	350	140	170	180
<i>Illex argentinus</i>	322	–	–	–
<i>Galiteuthis glacialis</i>	85	70	75	80

* One specimen only

** *Histioteuthis atlantica*

because albatrosses cannot exploit prey without being in contact with the water, such data may still indicate absolute (and interspecies differences in) potential opportunities for feeding. Recently, however, devices to record the timing of influx of cold material (ingestions of prey and/or water) by albatrosses at sea have become available (Wilson *et al.* 1992). The results of deployment of these devices in wandering albatrosses (Weimerskirch & Wilson 1992, Cooper *et al.* 1993) suggest that, although ingestion takes place during both day and night, most of the largest ingestions occur during the day. The only other albatross for which similar data are currently available is the black-browed albatross, where ingestion events are also widely distributed throughout day and night (P.A. Prince, R. Bevan, P. Butler, A.J. Woakes unpublished data). However, ingestions during the day need not solely reflect scavenging; equally, ingestions at night need not reflect capture of live prey, though Cooper *et al.* (1993) believed this to be the case.

Nevertheless, these new data suggest that daytime feeding may be more important than hitherto recognized; however, significant species-specific differences may exist. Data for albatross species less likely to associate with fishing vessels are particularly needed.

Evidence from squid

Size

The size of squid prey may indicate the likelihood of albatrosses being able to catch them alive, as opposed to exploiting them only when moribund or dead. Data on the average size of squid prey (Table IV) show that a considerable range in size is taken. For several species (*Gonatus*, *Histioteuthis*, *Alluroteuthis*, *Galiteuthis*) there is strong similarity in the average size of prey taken by each of the four albatross species. Significant differences, however, occur in *Kondakovia* and *Martialia*, where wandering albatrosses take much larger prey. These differences are

Table V. Proportions (%) by number and mass of squid eaten by albatrosses at South Georgia which are potentially scavenged, using different criteria for upper size (mass) limit of live capture.

Criterion	Wandering albatross	Grey-headed albatross	Black-browed albatross	Light-mantled sooty albatross
> 500g				
Number	14	3	0	23
Mass	67	17	0	69
> 350g				
Number	19	4	0	24
Mass	71	18	0	71
> 200g				
Number	55	4	2	33
Mass	91	21	4	76

interesting, because if all albatrosses were scavengers on dead squid one would expect them, to the extent that their ranges overlap, to take prey of similar sizes. The interspecies differences in average size of *Psychroteuthis* taken probably simply reflect differences in the proportion of large and small forms of this taxon.

The upper size, above which albatrosses cannot readily capture live squid, is unknown. Harper's (1987) observations of squid of 30–40 cm being disabled by wandering albatrosses would suggest that squid up to 400–500 g (if *Martialia*) would be manageable. Intact squid up to this size are regularly delivered to mollymawk chicks at South Georgia (Prince 1980). If we assume (conservatively) that squid heavier than 500 g cannot usually be captured alive we can assess the contribution of scavenged squid to albatross diets (Table V). Use of this criterion suggests that by mass, though not by number, most squid prey of wandering and light-mantled sooty albatrosses are scavengeable, whereas the opposite is true for grey-headed and black-browed albatrosses. Reducing the upper limit for mass of scavengeable prey does not materially change the situation, except that higher proportions of the squid diet by numbers would be scavenged. If our initial assumptions are correct, the conclusions about the very different contribution of scavenged prey to the diet of different albatross species are very robust to changes in threshold values for size of squid.

Other characteristics

Aspects of the biology of squid may be revealing in assessing their likely interactions with albatrosses. Foremost among these are: whether squid float or sink when dead; their distribution (especially vertical); whether they are bioluminescent or not; what they eat; whether they are targets for commercial fisheries. Some of these characteristics are summarized in Table VI. Distributional data come from sources summarized in Rodhouse *et al.* (1992a), buoyancy data from Lipinski & Jackson (1989) and P.G. Rodhouse (unpublished data), bioluminescence information chiefly from Nesis (1987).

Table VI. Characteristics of distribution, buoyancy and luminescence of the main squid prey of albatrosses at South Georgia. See text for sources of data.

	Distribution			
	Geographical	Vertical	Buoyancy	Bioluminescence
<i>Gonatus antarcticus</i>	SA, A	Epi-(MW)	?Float	-
<i>Kondakovia longimana</i>	SA, (A)	(Epi)-MW-Deep	?Float	-
<i>Histioteuthis eltaninae</i>	CT, SA	(Epi)-MW-(Deep)	Float	+
<i>Psychroteuthis glacialis</i>	(SA), A	MW?	?Sink	-
<i>Alluroteuthis antarcticus</i>	(SA), A	(Epi)-MW-(Deep)	Float	-
<i>Martialia hyadesi</i>	CT, SA	Epi-(MW)	Sink	-
<i>Illex argentinus</i>	CT	Epi-(MW)	Sink	-
<i>Galiteuthis glacialis</i>	SA, A	(Epi)-MW-Deep	Float	+

A: occurs south to Antarctic Continental Shelf

SA: occurs south of Antarctic Polar Front

CT: occurs north of Antarctic Polar Front

Epi: epipelagic, mainly 0-250m

MW: midwater, mainly 250-700m

Deep: deepwater, mainly >1000m

Parentheses indicate less common occurrence.

Buoyancy

That most squid species taken by Procellariiformes are believed to float when dead (Lipinski & Jackson 1989) has been taken as the strongest evidence that albatrosses predominantly feed on scavenged squid (Weimerskirch *et al.* 1986, Lipinski & Jackson 1989, Cooper *et al.* 1993). However, classification into floaters and sinkers is based on very few empirical data (five species in three genera in Lipinski & Jackson (1989) plus a more detailed study on the sinker *Martialia* by P.G. Rodhouse (unpublished)) and relies mainly on the presence or absence of buoyancy mechanisms (i.e. those species with gas-filled endoskeletons or high concentrations of ammonium chloride are believed to be floaters), also definitively known for relatively few species. In addition, there are anecdotal data of various squid being observed floating; however these observations are not necessarily evidence that these species always float when moribund or dead and such records are inevitably biased, because, by definition, there can be no equivalent records of sinkers. Despite these drawbacks, if we accept the assumptions of Lipinski & Jackson (1989) that all Alluroteuthidae, Cranchidae, Gonatidae and Histioteuthidae float and that most Ommastrephidae (and certainly *Martialia* and *Illex*) sink, then the only remaining problems are the assignment of Onychoteuthidae and Psychroteuthidae. Of onychoteuthids, Lipinski & Jackson (1989) classified *Moroteuthis* as a sinker (though noting that adults might float); Cooper *et al.* (1993), despite following Lipinski & Jackson (1989), classified it as a floater and Clarke (1966) and Imber (1992) have reported floating specimens. *Kondakovia* has been classified as a sinker (Lipinski & Turoboyski 1983) but there are reports of floating specimens after mass mortalities (Clarke 1966). *Psychroteuthis* has been observed to float (Clarke 1966) but M. Lipinski & P.G. Rodhouse (personal communication 1993) believe it more likely to be a sinker.

Against this background, we have assessed in Table VII the proportion of squid eaten by South Georgia albatrosses that are potentially scavengeable (taking into account the uncertainties over the classification of *Kondakovia* and *Psychroteuthis*). This analysis, which is conservative in favour of scavenging, suggest

that up to 80% by mass (but only 60% by numbers) of wandering albatross and 45-90% of light-mantled sooty albatross squid prey might be scavengeable. In contrast, not more than 25-30% by mass of black-browed and grey-headed albatross squid prey is likely to have been scavenged.

Vertical distribution

Information on vertical distribution (mainly from net hauls) indicate that squid such as *Gonatus*, *Martialia* and *Illex* are not infrequently in surface waters, whereas *Kondakovia*, *Histioteuthis*, *Alluroteuthis*, *Galiteuthis* and probably *Psychroteuthis* are likely to be more typical of midwater zones (Rodhouse *et al.* 1992a). However such classification is complicated by vertical migration, which may be of a diel or ontogenetic nature (Roper & Young 1975). For wandering albatrosses, Imber (1992) calculated that for the 86% of cephalopods for which data are available, 79% could be taken live at the surface, 95% of them only, or mainly, at night.

Table VII. Proportions (%) by number and mass of squid, eaten by albatrosses at South Georgia, which are potentially scavenged, based on buoyancy characteristics (assuming floaters can be scavenged, sinkers cannot).

	Wandering albatross	Grey-headed albatross	Black-browed albatross	Light-mantled sooty albatross
<i>If Kondakovia and Psychroteuthis float</i>				
Number	65	21	40	92
Mass	80	28	26	92
<i>If Kondakovia floats and Psychroteuthis sinks</i>				
Number	63	20	40	73
Mass	78	23	26	45
<i>If Kondakovia and Psychroteuthis sink</i>				
Number	53	18	40	71
Mass	20	12	26	31

Clarke *et al.* (1981) and Rodhouse *et al.* (1987) considered the suggestion by Imber & Russ (1975) that bioluminescence in squid would assist detection by albatrosses to be unlikely because many squid commonly taken by albatrosses are not bioluminescent and, of those that are, the photophores are usually directed downwards. Imber (1992), in restating his hypothesis, has noted that all *Histioteuthis* have dorsal photophores and several other species taken by albatrosses have them on the tentacle tips. However, at least at South Georgia, of all those squid species of any significance in the diet of albatrosses (Table II), only *Histioteuthis* and *Galiteuthis* are bioluminescent (and *Galiteuthis* has only a single tiny photophore on the eye). It seems unlikely to us, therefore, that bioluminescence plays any significant role in the interactions between squid and albatrosses.

Diet

Most data on the diet of Southern Ocean squid indicate that macrozooplankton (especially Antarctic krill *Euphausia superba*) and micronekton are the main prey (Nemoto *et al.* 1985). However, Rodhouse *et al.* (1992b) noted that most diet studies had been performed on squid caught in association with krill fishing. They found that the main prey of *Martialia hyadesi* were myctophid fish (which mainly eat copepods), although *E. superba* was also often taken. Nevertheless both myctophids and krill are known to make extensive diel vertical migrations, bringing them towards the surface, especially at night, so the association of squid with their prey may help to make them available to albatrosses. The availability of squid to albatrosses may be further enhanced by the activities of diving predators, causing squid, and their prey, to move towards the surface (Fraser *et al.* 1989, Harrison *et al.* 1991).

Fisheries

Around the Falkland Islands, *Illex argentinus* and *Loligo gahi* are the main targets of major commercial fisheries, which occasionally catch significant quantities of *Martialia hyadesi*. There are, at present, no commercial squid fisheries south of the Antarctic Polar Front. Of South Georgia albatrosses, only the wandering albatross, therefore, is venturing into areas where squid waste associated with fishing operations could be available. Even for the Falkland fisheries, the availability of squid discards and offal is seasonally restricted and may be of relatively limited overall significance to albatrosses. Thus Thompson (1992) calculated that although black-browed albatrosses (the main albatross in the area) scavenged some 50% of the squid waste generated by the *Loligo* fishery (amounting to 5% of the reported catch), this represented only 10–15% of the total food required by the breeding population of albatrosses during the fishing season.

Conclusions

The argument favouring scavenging of certain squid is their size, and some characteristics (especially buoyancy), plus evidence that at least some albatrosses ingest prey mainly by day when live squid are unlikely to be near the surface. In addition, albatrosses are virtually restricted to surface-seizing and are readily associated with ships, particularly those engaged in fishing which, together with natural regurgitations by other squid predators, can provide significant amounts of prey.

General evidence against scavenging is that many squid are small enough to be taken alive, several squid very significant in albatross diets are certainly sinkers, albatrosses have a greater range of foraging behaviours, including diving, than hitherto suspected, several species seldom follow ships and, while breeding, do not occur in areas where squid are fished.

Our analysis has indicated that while scavenging for squid is potentially an important part of the foraging ecology of some albatrosses, it cannot be assumed that all albatrosses basically depend on scavenged squid (Weimerskirch *et al.* 1986, Weimerskirch & Wilson 1992, Cooper *et al.* 1993). The likelihood of scavenging contributing a significant proportion of the diet is greatest for wandering albatross, fairly high for light-mantled sooty albatross and rather low for grey-headed and black-browed albatrosses.

Fundamental unresolved questions relating to scavenging of squid concern their origins and availability to albatrosses throughout the year. Three sources of scavenged squid have been suggested: vomit from sperm whales (Clarke *et al.* 1981), post-spawning mortality of squid (Rodhouse *et al.* 1987) and, as floaters from some combination of these and other sources (Lipinski & Jackson 1989).

Clarke *et al.* (1981) noted similarities in the species of squid taken by sperm whales *Physeter macrocephalus* and wandering albatrosses and speculated whether the periodic regurgitation of accumulated squid material by these whales could provide adequate food for the albatrosses. Clarke *et al.* (1981) noted, however, that only male sperm whales are within the normal foraging range of albatrosses during their chick rearing period. Furthermore, as Imber (1992) observed, the beaks obtained from sperm whales and wandering albatrosses have only limited overlap in size. Clarke & Goodall (1994), however, noted that there is significant overlap in composition and size of squid in the diet of wandering albatrosses and some smaller Antarctic cetacea, such as long-finned pilot whales *Globicephala melas* and southern bottlenose whales *Hyperoodon planifrons*, so it is possible that regurgitation by these species may contribute to wandering albatross diet.

As squid are semelparous and live for no more than 1–2 years, we can anticipate substantial and regular post-spawning mortality. If this contributes significantly to the diet of albatrosses, then we should expect them to acquire squid that are adult, of a restricted range of size and only at certain times of year (because spawning of Southern Ocean squid is relatively synchronous and temporally restricted (Rodhouse 1991)). This

is certainly not the case for black-browed and grey-headed albatrosses, whose main prey from January–April, *Martialia hyadesi*, is exclusively intact subadults. Interestingly, adult *Martialia* are taken by southern elephant seals *Mirounga leonina*, sampled from November–January (Rodhouse *et al.* 1992a) and by wandering albatrosses sampled from May–September. *Martialia* is therefore available to squid predators at South Georgia almost year-round (Rodhouse *et al.* 1993). Both light-mantled sooty and wandering albatrosses take a wide size range of their main squid prey species, but a much greater proportion is adult. However, a time series of samples from wandering albatross chicks (Rodhouse *et al.* 1987) indicates that several squid species are taken from May–September.

Obviously albatrosses are well-placed to exploit squid, irrespective of whether they are regurgitated fragments or intact moribund post-spawners, providing that such squid float. There is need for much more work on this topic. Additionally Imber (1992) raises the interesting question of why albatrosses do not take many other species of squid belonging to floating families (e.g. cranchids), which are of similar ecology and abundance to related species which they do eat.

None of the foregoing denies that albatrosses readily scavenge squid or that this behaviour may not predominate in the feeding ecology of wandering and perhaps also light-mantled sooty albatrosses. However, it does suggest that scavenging is unlikely to be the primary feeding behaviour of black-browed albatrosses and especially of grey-headed albatrosses at South Georgia. Further work is required to explain many of the features hitherto uncritically used as evidence of scavenging in albatrosses generally. The limited data on squid diet for albatrosses at other Southern Ocean breeding sites is very similar for wandering albatross (Cooper *et al.* 1992, Imber 1992, Ridoux *in press*) and light-mantled sooty albatross (Cooper & Klages unpublished) and only dissimilar for black-browed and grey-headed albatrosses in their lesser dependence on *Martialia* (Hunter & Klages 1989, Ridoux *in press*). We believe, therefore, that the relative importance of scavenging and interspecies differences in albatross feeding ecology and behaviour identified at South Georgia may hold for other areas of the Southern Ocean. For albatrosses from other regions, more detailed studies of diet and feeding ecology are required before any reliable inferences can be drawn.

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