

Cephalopod predation by the king penguin *Aptenodytes patagonicus* from South Georgia

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ABSTRACT: The king penguin *Aptenodytes patagonicus* is a sub-Antarctic species that feeds primarily on mesopelagic fish and cephalopods in the vicinity of the Antarctic Polar Front (APF). We examined the cephalopod prey of adult penguins at a breeding colony on South Georgia during 4 austral summers, 1990 to 1994. The most important prey (~97% by mass) of the king penguins was found, in a related study, to be mesopelagic fish, mainly myctophids. The penguins' cephalopod prey, which constituted the remaining 3%, was shown in this study to be dominated by the ommastrephid squid *Martialia hyadesi*, both in terms of numbers and biomass. Other squid species were typical of the South Georgia/Antarctic Polar Front (APF) area but only relatively small specimens were present and, apart from *Gonatus antarcticus*, the presence of flesh indicated that they were probably mostly caught close to the island. *M. hyadesi* generally fell in the same size range as *M. hyadesi* exploited by commercial fisheries in the South Atlantic. In the 1992/93 summer, when krill was abundant at South Georgia, the amount of squid consumed, especially *M. hyadesi*, was substantially less than in the other years. This coincided with a reduction in the amount of the myctophid *Krefflichthys anderssoni*, which is the major prey of *M. hyadesi*, in the penguin diet. The total consumption of cephalopods by the king penguin at South Georgia is estimated to be about 75 000 t yr⁻¹. Of this, some 3600 to 6000 t yr⁻¹ is estimated to be *M. hyadesi*. This might underestimate consumption if the penguins consume a greater proportion of squid in the winter, as they do in other sectors of the Southern Ocean.

KEY WORDS: Cephalopods · King penguins · Oceanography · South Georgia

INTRODUCTION

King penguins *Aptenodytes patagonicus* are distributed throughout the sub-Antarctic and they breed on most of the peri-Antarctic islands. King penguins feed almost exclusively on mesopelagic fish and pelagic cephalopods. The importance of cephalopods in the diet changes seasonally. Recent data from samples taken at South Georgia, using the water off-loading technique, have shown that cephalopods contribute about 3% of the total mass of food consumed in summer and, at this time of year, the diet is dominated by myctophids (Olsson & North 1997). Elsewhere, at the peri-Antarctic islands of Possession (Crozet Archipelago) and Marion, research has shown that myctophids

are the major prey but, during winter, the importance of cephalopods as prey increases and they may contribute up to 64% of the total wet mass of food consumed (Adams & Klages 1987, Cherel et al. 1996). The trophodynamics of king penguins are of particular interest as their populations have been increasing steadily at almost all sites over at least the last 30 yr. At South Georgia the population has increased from about 2000 pairs in 1914 to 100 000 pairs in 1986 (Croxall et al. 1988) to about 400 000 pairs today (comprising some 25% of the world population) (P. A. Prince pers. comm.).

Whilst breeding, king penguins may forage over distances of up to 1200 km from the colony. From Possession Island in the Indian Ocean sector, they frequently forage in the direction of the Antarctic Polar Front (APF) (ca 300 km), to the south of the island, where it is assumed there is a predictable food resource (Jou-

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ventin et al. 1994). King penguins are effective divers. During the day they forage at depths of 100 to 300 m and at night they feed near the surface (<30 m) (Kooyman et al. 1992). This is consistent with their preying on the mesopelagic nekton community which, in the sub-Antarctic, largely migrates from circumpolar deep water (>200 to 300 m), where it remains during daylight, to Antarctic surface water at night (Piatkowski et al. 1994).

Until recently the biology of the Antarctic Polar Frontal Zone (APFZ) has received little attention, and this very large, remote region has generally been assumed to be relatively unproductive (Hempel 1985). Recent research has shown, however, that an important ecosystem exists in the Atlantic sector of the APFZ (Piatkowski et al. 1994, Rodhouse et al. 1994a, Pagès 1996). Squid are the top pelagic predators, replacing epipelagic fish, which are absent in these waters. The squid feed mainly on mesopelagic fish, which in turn feed on copepods and other small crustaceans (Rodhouse et al. 1992b). Satellite tracking has shown that squid predators breeding at South Georgia, notably grey-headed albatrosses (Rodhouse et al. 1996, Prince et al. 1997) and southern elephant seals (McConnell & Fedak 1996), regularly forage in the APFZ.

The most abundant squid in the Atlantic sector of the APFZ is the ommastrephid *Martialia hyadesi* (Rodhouse & White 1995). The *M. hyadesi* stock in the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) area appears to be large enough to support a fishery, provided adequate precautionary measures are taken (Rodhouse 1997). It is likely that a new fishery will develop in the future and so information about interactions of *M. hyadesi* with other dependent predator species, including king penguins, is of special interest.

In this paper we present data on the cephalopod prey of king penguins sampled at South Georgia over 4 summer seasons between 1990 and 1994, with special emphasis on interannual variability. This is particularly relevant because the period in question was marked by substantial fluctuations in the size of the Antarctic krill *Euphausia superba* stock in the area, which had important effects on the ecology of the krill-dependent higher predators breeding at South Georgia (Croxall et al. 1997, Reid et al. 1997). In 1993/94, 4 king penguins were satellite tracked, and we discuss the known distribution of the cephalopod prey in relation to the foraging areas of these penguins.

METHODS

Food samples were collected from the colony of about 4000 pairs of king penguins at Fortuna Bay,

South Georgia, over 4 summer seasons between 1990 and 1994. In 1990/91, 18 penguins were sampled once in January, whereas during the following 3 years samples were taken throughout the summer (Olsson & North 1997). Stomach contents from a total of 139 different penguins returning from the sea to feed the chick(s) were taken using procedures described by Wilson (1984), Hindell (1988) and Olsson & North (1997). Measurements of the relative proportions of fish and squid in the diet were based on the flesh mass of the 2 categories of food, assuming equal digestion rates.

Cephalopod beaks were removed from the samples and lower beaks identified by comparison with beaks from squid caught by nets and jigs in the Scotia Sea and by reference to Clarke (1986). Lower rostral lengths (LRL) of beaks were measured to 0.1 mm with Vernier calipers. Allometric equations given by Clarke (1986) and Rodhouse et al. (1990) were used to estimate mantle length (ML) and wet body mass (BM) from LRL. Beaks were also assigned to 1 of 4 categories: (1) with flesh still attached, identifiable and measurable, (2) without flesh, identifiable and measurable, (3) without flesh, identifiable but unmeasurable, (4) unidentifiable and unmeasurable. The presence of flesh was not recorded in the first year of the study.

In 1993/94, 4 penguins were fitted with Toycom 2038 microwave platform terminal transmitters (PTTs) weighing between 65 and 75 g. These were attached using the method described by Prince et al. (1992). PTT data from the tagged penguins were relayed to Toulouse (France) via the Argos satellite system and sent daily to BAS headquarters in Cambridge (UK). The PTT positional information was loaded into PC Arc/Info (ESRI), a geographical information system (GIS). Plots of individual foraging trips, and a compilation of all trips, were generated with the GIS.

RESULTS

Cephalopod species

Cephalopod species identified from beaks in the regurgitations of king penguins are listed for each year of the study in Table 1. Numbers are for all samples from all penguins combined for each year. All the cephalopods in the diet were squid; there were no octopodids. A total of 2706 beaks was counted; 2021 beaks were identified and 1451 beaks were measured. Measured beaks represented an estimated total of 250 kg of squid wet mass. A relatively large proportion of the beaks collected (25%) were unidentifiable because they were too damaged or degraded. Further-

Table 1 *Aptenodytes patagonicus*. Cephalopod beaks found in the stomach contents of 134 king penguins sampled at South Georgia during 4 austral summers (cephalopod species ranked in order of importance in terms of mass for all years combined; values in parentheses are percentages; n: number of king penguins sampled)

Cephalopod species	1990/91	n = 18	1991/92	n = 67	1992/93	n = 20	1993/94	n = 34
	No.	No. measurable	No.	No. measurable	No.	No. measurable	No.	No. measurable
<i>Martialia hyadesi</i>	394 (45)	154 (56)	401 (52)	187 (42)	22 (18)	18 (18)	255 (26)	218 (35)
<i>Moroteuthis knipovitchi</i>	18 (2)	17 (6)	63 (8)	63 (14)	16 (13)	16 (16)	155 (16)	88 (14)
<i>Kondakovia longimana</i>	71 (9)	66 (24)	65 (8)	65 (15)	33 (27)	33 (34)	209 (22)	209 (33)
<i>Psychroteuthis glacialis</i>	31 (4)	29 (11)	107 (14)	107 (24)	26 (21)	26 (26)	58 (6)	58 (9)
<i>Alluroteuthis antarcticus</i>	1 (<1)	1 (<1)	5 (<1)	5 (1)	1 (<1)	1 (1)	21 (2)	21 (3)
<i>Gonatus antarcticus</i>	0	0	5 (<1)	5 (1)	2 (2)	2 (2)	6 (<1)	6 (<1)
<i>Brachioteuthis ?picta</i>	5 (<1)	5 (2)	12 (2)	12 (3)	3 (2)	3 (3)	34 (4)	34 (5)
<i>Histioteuthis</i> sp. B	2 (<1)	2 (<1)	0	0	0	0	0	0
Unidentifiable	315 (39)	0	115 (15)	0	20 (16)	0	235 (24)	0
Total	837	274	773	444	123	99	973	634

Table 2. *Aptenodytes patagonicus*. Percent occurrence of cephalopod species and estimated wet mass (g) of cephalopods represented by identifiable beaks in the stomach contents of 134 king penguins at South Georgia during 4 austral summers (cephalopod species ranked in order of importance in terms of mass for all years combined; n: number of king penguins sampled; values in parentheses are percentages)

Cephalopod species	1990/91	n = 18	1991/92	n = 67	1992/93	n = 20	1993/94	n = 34
	% occurrence	Mass	% occurrence	Mass	% occurrence	Mass	% occurrence	Mass
<i>Martialia hyadesi</i>	95	28 574 (80)	27	84 309 (74)	15	6 780 (48)	56	48 875 (57)
<i>Moroteuthis knipovitchi</i>	61	4 290 (12)	36	13 248 (12)	35	3 236 (23)	68	14 405 (17)
<i>Kondakovia longimana</i>	78	826 (2)	39	5 008 (4)	40	2 322 (16)	74	11 956 (14)
<i>Psychroteuthis glacialis</i>	61	747 (2)	58	8 724 (8)	50	1 695 (12)	56	6 633 (8)
<i>Alluroteuthis antarcticus</i>	6	1 027 (3)	8	2 081 (2)	5	140 (1)	32	3 193 (4)
<i>Gonatus antarcticus</i>	0	0	6	613 (1)	10	83 (1)	12	417 (<1)
<i>Brachioteuthis ?picta</i>	22	29 (<1)	15	48 (<1)	10	9 (<1)	32	147 (<1)
<i>Histioteuthis</i> sp. B	6	90 (<1)	0	0	0	0	0	0
Total		35 582		114 030		14 263		85 627

more, of those that were identified a relatively large proportion (28%) were unmeasurable because of damage. No measurable beaks were unidentifiable, the only reason beaks could not be identified was because of their condition, not because they were from species that could not be recognised.

Overall, the commonest species of squid in the diet was *Martialia hyadesi*. In 1992/93, however, *Kondakovia longimana* and *Psychroteuthis glacialis* were more abundant. Of the squid taken by the penguins, 3 species, *M. hyadesi*, *Gonatus antarcticus* and *Histioteuthis* sp. B (probably *H. eltaninae*), have known distributions that extend as far north as the Subtropical Convergence; the other 5 species all have Antarctic or sub-Antarctic distributions (see Rodhouse et al. 1992a). All species are muscular and by inference strong swimmers. Of the 8 species of squid identified, only *Brachioteuthis ?picta* and *Histioteuthis* sp. B have photophores.

Cephalopod mass

Percent occurrence and wet mass data for squid in the diet of king penguins, for each year of the study, are shown in Table 2. Four species, *Martialia hyadesi*, *Moroteuthis knipovitchi*, *Kondakovia longimana* and *Psychroteuthis glacialis*, dominated the diet, contributing over 90% of the total mass in each year. These are all muscular species that grow to a relatively large size. By far the most important squid, in terms of wet mass, was *M. hyadesi*, although the proportion of penguins in which it was present varied between 95 and 15% over the 4 years of the study.

Presence of attached flesh

The percentage of beaks, of each cephalopod species, with flesh attached is shown in Table 3. The pres-

Table 5. *Aptenodytes patagonicus*. Annual variation in the estimated cephalopod mass (g) per penguin represented by beaks in the stomach contents (the % column represents the percentage of total cephalopod mass represented by the 5 species in the table)

Year	<i>Martialia hyadesi</i>	<i>Moroteuthis knipovitchi</i>	<i>Kondakovia longimana</i>	<i>Psychroteuthis glacialis</i>	<i>Alluroteuthis antarcticus</i>	Total	%
1990/91	1587	238	45	420	57	1977	>99
1991/92	1258	198	75	130	31	1702	>99
1992/93	339	161	116	85	7	713	>99
1993/94	1438	423	351	195	94	2518	>99

Total cephalopod mass represented by beaks varied by a factor of about 3.5 over the 4 years of the study and this was largely accounted for by variation in the amount of *Martialia hyadesi* consumed. The lowest quantities were present in the 1992/93 season. This coincided with the year when the proportion by occurrence and mass of the myctophid *Krefflichthys anderssoni* in the diet of the penguins fell to the lowest levels observed in the study. It was replaced by *Protomyctophum choriodon*, especially at the end of the season (Olsson & North 1997).

King penguin foraging range in 1993/94

The foraging ranges of the 4 satellite tracked penguins in 1993/94 are illustrated by the range polygons in Fig. 1. All 4 penguins foraged to the north of South Georgia up to a maximum distance of about 500 km from the breeding colony. The physical oceanography of the APFZ was well characterised in 1993/94 by a shipboard oceanographic survey and remote sensed imagery, coincident with the penguin satellite tracking programme (Trathan et al. 1997), and so it is possible to relate the foraging range of the penguins to the major contemporary oceanographic features.

The APF was found to run to the south of the Maurice Ewing Bank and then curved northwards to the east of the Bank. The area to the east of the Bank was characterised by mesoscale features (meanders in the APF or warm core rings 80 to 140 km across) with anti-cyclonic rotation that were associated with the bathymetry of the Falkland Ridge. One of these features, centred at about 50° 00' S 37° 30' W, was an area where satellite-tracked grey-headed albatrosses were preying on *M. hyadesi* (Rodhouse et al. 1996). The range polygons in Fig. 1 show that 2 of the penguins were foraging in this area of mesoscale activity; 1 of these 2 crossed to the north side of the APF whilst the other 3 ranged over a shorter distance and foraged over deep water between South Georgia and the APF. This is a highly variable oceanographic area where the

Weddell Scotia confluence passes to the north of South Georgia from the east. In 1994 the area was characterised by the presence of cold, relatively low salinity water.

Total cephalopod consumption by king penguins

Total food consumption by a single king penguin has been estimated to be ca 316 kg yr⁻¹ (Croxall et al. 1990). If the current estimate for the proportion of cephalopods in the diet during the breeding season (ca 3%) applies throughout the year, total cephalopod consumption of cephalopods per bird would be some 9.4 kg yr⁻¹. During the present study the proportion of *Martialia hyadesi* in the diet fell in the range 48 to 80% (Table 2), so we can calculate that consumption of *M. hyadesi* was some 4.5 to 7.6 kg yr⁻¹ per bird and between 3600 and 6080 t yr⁻¹ for the South Georgia population of 400 000 pairs during the present study.

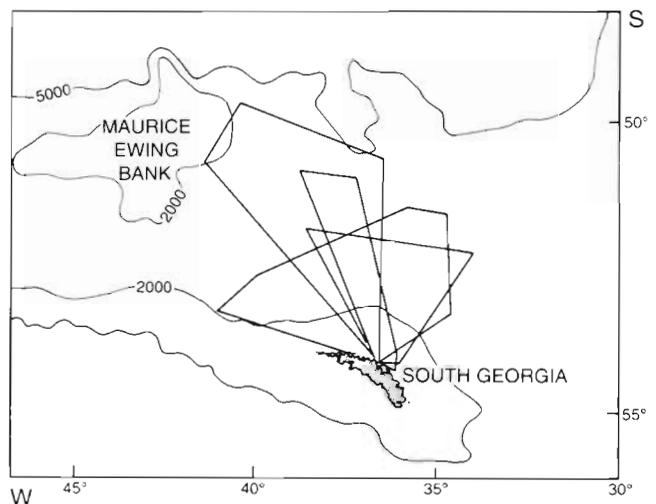


Fig. 1. *Aptenodytes patagonicus*. Antarctic Polar Frontal Zone to the north of South Georgia showing range polygons of 4 satellite tracked king penguins during the 1993/94 summer (maps based on British Admiralty Chart number 4024)

DISCUSSION

This paper deals exclusively with the cephalopod prey of king penguins, which contributed about 3% of the total diet at South Georgia during the study period. The cephalopods were dominated by the ommastrephid squid *Martialia hyadesi* from the same size range as *M. hyadesi* caught by the commercial fishery in the South Atlantic (Rodhouse 1991). The distribution of this squid is primarily associated with the APFZ (Rodhouse in press), but it is known to occur closer to South Georgia during the austral winter (Gonzalez & Rodhouse 1998). The other squid species are all known from the South Georgia area. They have been caught with scientific and commercial gear (Rodhouse 1990), and they occur in the diet of several higher predators breeding on the island (Rodhouse et al. 1987, 1990, 1992a, 1993, Croxall et al. 1995). Most have typically pelagic distributions although larger specimens of *Moroteuthis ingens* and *Psychroteuthis glacialis* than those found in the penguin stomach contents have been caught in bottom trawls (Rodhouse 1989). The presence of flesh on beaks of all species except those of *M. hyadesi* and *Gonatus antarcticus* suggests that the relatively small numbers of these species are caught close to the breeding colony. The absence of flesh from virtually all *M. hyadesi* suggests that this species does not occur close to South Georgia during the austral summer and is probably caught by the penguins while they are foraging close to the APFZ.

In 1992/93 squid were less important in the diet than in other years due to a substantial decrease in the amount of *Martialia hyadesi*. This coincided with a change in the dominant fish in the diet from *Krefflichthys anderssoni* to *Protomyctophum choriodon*. An analysis of the diet of *M. hyadesi* in 1989 at the APFZ showed that *K. anderssoni* was the most important prey, and so the reduction in both of these species in 1992/93 may well have been linked. Given the relatively minor importance of cephalopods in the diet of king penguins during the summer at South Georgia, we conclude that the penguins are primarily targeting myctophids and that squid are incidental in the diet.

The 1992/93 season, when less squid were consumed, corresponded with a period of relatively high krill abundance at South Georgia (Croxall et al. 1997, Reid et al. 1997). Although king penguins are not krill predators, changes in the relative abundance of krill may indicate other changes in the ecosystem that the penguins respond to. In 1993/94 krill was particularly scarce (Brierley & Watkins 1996) and in that year the mean duration of penguin foraging trips was significantly increased and, in common with other predators, breeding success was much reduced (Boyd et al. 1995, Olsson 1997, Olsson & Brodin 1997).

The estimate of total annual cephalopod consumption by king penguins from the South Georgia colony might be low if they consume a higher proportion of squid out of the breeding season, as has been shown for king penguins in the Indian Ocean sector (Adams & Klages 1987, Cherel et al. 1996).

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