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The diet of white-chinned petrels *Procellaria aequinoctialis*, Linnaeus 1758, in years of contrasting prey availability at South Georgia

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Abstract: The diet of breeding white-chinned petrels was studied during the summers of 1996 and 1998 at South Georgia. Krill abundance/availability was high throughout 1996 but apparently low at the beginning of the 1998 breeding season. The diet of white-chinned petrels was similar between years and consistent with previous studies. Krill *Euphausia superba* (41–42% by weight) was the single most important prey item followed by fish (39–29%) and squid (19–25%). Meal mass was consistent (110 g in 1996, 119 g in 1998) between years but a significant decrease (46%) in feeding frequency in 1998 (0.54 meals day^{-1} compared to 0.75 meals day^{-1} in 1996) resulted in 19% less food delivered to chicks in 1998 than in 1996. Breeding success, however, was consistent between years at 44% and similar to that recorded previously at Bird Island. This is in contrast to black-browed and grey-headed albatrosses, both of which experienced almost total breeding failure in 1998. It is suggested that their varied and versatile feeding methods, together with their greater diving ability, capacity to feed at night and extensive foraging range, help white-chinned petrels minimise the effects of krill shortage.

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Key words: diet, feeding frequency, inter-annual variation, krill, meal size, white-chinned petrel

Introduction

An estimated 70 million seabirds breed at South Georgia and consume around 7.8 million tonnes of food annually of which 73% is Antarctic krill *Euphausia superba* Dana 1852 (Croxall & Prince 1987). The dependence of so many seabirds on a single prey item has led to speculation as to how this resource is partitioned between species. Croxall *et al.* (1997) suggested that a combination of differences in diet, feeding methods, foraging behaviour and foraging range of seabirds breeding at South Georgia operate to promote a degree of ecological segregation. The abundance of krill at South Georgia and its availability to marine predators exhibits strong seasonal and inter-annual variation (Priddle *et al.* 1988, Boyd *et al.* 1994, Croxall *et al.* 1999). In most years there may be enough food available to generate only low levels of interspecies competition; however, competition may be intense in years when this food resource is scarce (Croxall *et al.* 1997, 1999).

The white-chinned petrel *Procellaria aequinoctialis* Linnaeus 1758, with a breeding population of *c.* 2 million birds (Croxall *et al.* 1984), is the third most important avian consumer of krill at South Georgia and the most important avian consumer of fish and squid (Croxall *et al.* 1995). Despite this role its diet has only been studied in detail during a single season and in a year (1986) of high krill availability (Croxall *et al.* 1995, 1997, 1999). Species with an apparently similar diet, such as the grey-headed albatross *Diomedea chrysostoma* Forster 1785 and Antarctic prion *Pachyptila desolata* Gmelin 1789, exhibit significant inter-annual variation in the proportion of krill and other prey species in their diet (Prince 1980, Liddle 1994, Reid *et al.* 1997). However, the mixed diet of these species seems to act to reduce inter-annual variability in breeding success, in comparison with species more dependent on krill (Liddle 1994, Croxall *et al.* 1998, 1999). Here we present data on the diet, meal size and feeding frequency of white-chinned petrels during two summers of contrasting krill availability in order to evaluate the response of white-chinned petrels to variations in food supply.

Methods

Collection of food samples

Food samples were collected from 8 February–25 March 1996 and between 10 January–25 February 1998 on Bird Island, South Georgia (54°01'S, 38°03'W). Adults were captured at dusk as they landed near their breeding burrow, held over a large funnel (200 mm diameter) which drained into a plastic bag and induced to regurgitate. Occasionally adults had to be gently massaged around their stomach to encourage vomiting, but often they regurgitated on handling, sometimes before they could be positioned over the funnel; in these instances the liquid fraction of the food sample was lost. Chicks that had been fed during the night, as determined from twice daily weighings, were food sampled the following morning. Chicks were removed from their nest through a removable cover over the nest chamber or by reaching into the nest from the tunnel entrance. Samples were collected from

20 adults and 20 chicks in 1996 and 10 adults and 30 chicks in 1998.

Analysis of food samples

Food samples were analysed according to Croxall *et al.* (1995). For samples where the entire food sample was collected, the liquid fraction was drained off before sorting and the proportion by weight of this fraction calculated. The resultant food mass was sorted into three components: squid, fish and crustaceans (euphausiids, amphipods and decapods) and each component weighed. Any remaining unidentifiable material was weighed and assumed to occur in the same proportion as identifiable remains and was added pro-rata to their total mass.

Cephalopod beaks were removed and stored in alcohol for later analysis. Fish otoliths were removed, counted and identified using Williams & McEldowney (1990), Hecht (1987) and Reid (1996). Left and right otoliths were matched if their length was within one graticule unit (0.15 mm, inserted in a binocular microscope at x6.5 magnification) and the minimum number of fish in the sample calculated. Fish length was calculated using the regressions in Croxall *et al.* (1995) and Reid (1996), using the otolith erosion categories described in Reid & Arnould (1996). For *Patagonotothen guntheri* Norman 1937 the relationship between fish length (TL) and mass (TW) was described by the equation

$$TW = 0.396\ TL - 32.7\ (n = 50,\ r^2 = 0.95)$$

(M. White unpublished data). No regression equation was available for the Macrouridae recovered in 1998. The number of squid in food samples was calculated from the number of upper or lower beaks (whichever was greater) and crustaceans from pairs of eyes. Intact krill carapaces were removed, stored in alcohol and measured under a binocular microscope; the generalized regression in Hill (1990) was used to estimate total body length.

Provisioning rate and meal size

Provisioning rate was determined in both years over a ten day period between 4–14 February, just after the chick brooding period finished and at the start of their period of rapid linear growth (Hall 1987). Chicks were weighed within one hour of dusk and up to one hour after dawn using Pesola® spring balances. Following Croxall *et al.* (1995), a feed was recorded when there was a mass increase over the previous weighing in excess of 1% of the balance capacity. For consistency with Croxall *et al.* (1995), meals in excess of 300 g were assumed to result from two feeds between weighings and were excluded from meal size analyses but were recorded as two feeds for provisioning rate analyses. This occurred on four occasions in 1996 (360–540 g) and once (450 g) in 1998. Meal size data obtained from adults was corrected for 15% residual stomach contents after Croxall *et al.* (1995).

Results

Meal size and provisioning rate

The size of meal recovered from both adult birds and chicks in 1996 and 1998 is shown in Table I. There was no difference in meal size from chicks and adults in 1996 (Mann-Whitney test, $U = 407$, NS) but in 1998 meal sizes from chicks were significantly larger than those obtained from adults ($U = 107$, $P<0.05$). Although not significantly smaller ($U = 334.5$, NS), adult samples from 1998 weighed only 79 g compared with 109 g in 1996. When meal sizes in each year were combined they averaged 110 g in 1996 and 119 g in 1998 and were not significantly different ($U = 1518$, NS). These estimates of meal size were 14–22 g (11–16%) less than that recorded in 1986 by Croxall *et al.* (1995) (Table I). Mean meal sizes as determined from twice daily chick weighings were greater by 18–27% than meals from adults, although this was not significantly different in either year (two-sample *t*-test, 1996:

Table I. Mean meal size (range, sample size in parentheses) from food samples and 12 hourly chick weighings and mean feeding frequency of white-chinned petrels at Bird Island, South Georgia (1986 data from Croxall *et al.* 1995).

		1986	1996	1998
Meal size (g)	Adult[1]	147.7 ± 61.7 (49–300, *n* = 74)	109.5 ± 46.3 (43–222, *n* = 20)	79.0 ± 33.8 (40–136, *n* = 10)
	Chick	–	111.1 ± 54.2 (27–221, *n* = 20)	131.4 ± 61.7 (33–249, *n* = 30)
	All diet samples	131.9 ± 65.4 (26–300, *n* = 91)	110.3 ± 49.4 (27–222, *n* = 40)	118.6 ± 60.2 (33–249, *n* = 40)
	12 hr weighings	167.1 ± 74.3 (37–477, *n* = 477)	130.4 ± 64.8 (30–290, *n* = 77)	146.3 ± 70.5 (30–300, *n* = 53)
Feeding frequency (meals day^{-1})	Mean ± s d	0.69 (0.30–0.98, *n* = 212)	0.75 (0.50–1.0, *n* = 81)	0.54 (0.30–0.80, *n* = 55)
	% feeds in day	–	30.9	50.1
	% feeds at night	–	69.1	49.9

[1] corrected for 15% residual stomach contents (Croxall *et al.* 1995)

t_{85} = 1.66, NS, 1998: t_{83} = 1.97, NS).

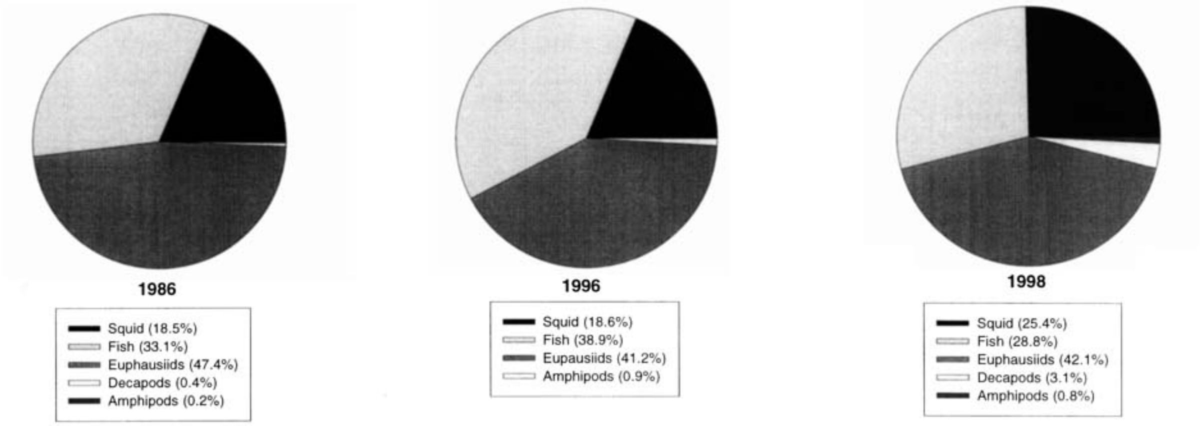
Chicks selected for monitoring had a mean (± s d) body mass of 541 ± 31 g (range: 315–640, n = 11) in 1996 and 496 ± 38 g (range: 320–680, n = 11) in 1998 (t_{20} = 3.04, P <0.01). Feeding frequency over the 10 day weighing period varied from 0.50–1.0 meals per day per chick in 1996 and 0.30–0.80 in 1998 (Table I). Chicks were fed every 1.3 days in 1996, significantly more often than the 1.9 days in 1998 (Mann-Whitney test, U = 83, P <0.01). A feeding frequency of 0.69 meals day^{-1} was reported by Croxall *et al.* (1995) from 1986; this is intermediate between our values for 1996 (0.75) and 1998 (0.54) (Table I). However using 300 g as a threshold above which mass increases represent two feeds will underestimate true feeding frequency. If a threshold of 200 g is used (i.e. slightly less than twice the average meal size in 1996 and 1998) then estimates of feeding frequency increase to 0.84 in 1996 and 0.63 in 1998 (one meal every 1.2 days in 1996 and 1.6 days in 1998). However, chicks were still fed 25% more often in 1996 compared to 1998. The total food fed to each chick over the 10 day period was, on average, 34% greater in 1996 (1027 g, range: 680–1320 g) than in 1998 (764 g, range: 470–1180 g). Mean provisioning rate (g day^{-1}), using all diet samples as a measure of meal size, was 82.7 g in 1996 and 64.0 g in 1998, 91% and 70% of the value of 91.0 g day^{-1} reported from 1986. Mean total food intake can be calculated from mean feeding frequency x mean meal size x fledging period for a fledging period of 98 days (Hall 1987). Chicks were estimated to receive 11.30 kg in 1986, 9.58 kg in 1996 and 7.74 kg in 1998.

As chicks were weighed at dawn and dusk we could determine whether chicks were fed during the night or during daylight. In 1996 around two-thirds of meals (69%) were delivered during the night, compared with only one half during 1998 (Table I).

Composition of food samples

The mean liquid content (± s d) of twenty five food samples obtained from the 1998 chick regurgitates was 36.8 ± 12.7% (range: 16.5–62.2%). Only one intact sample was obtained from adult birds during 1998 (with a liquid fraction of 40.9%) and four during 1996 (mean 21.3 ± 2.9%, range: 15.2–27.5%). Euphausiids accounted for the largest proportion by mass and frequency of occurrence in all years, followed by fish and squid (Fig. 1). There were small differences in the relative

a. Proportion of weight (%)



b. Frequency of occurrence (%)

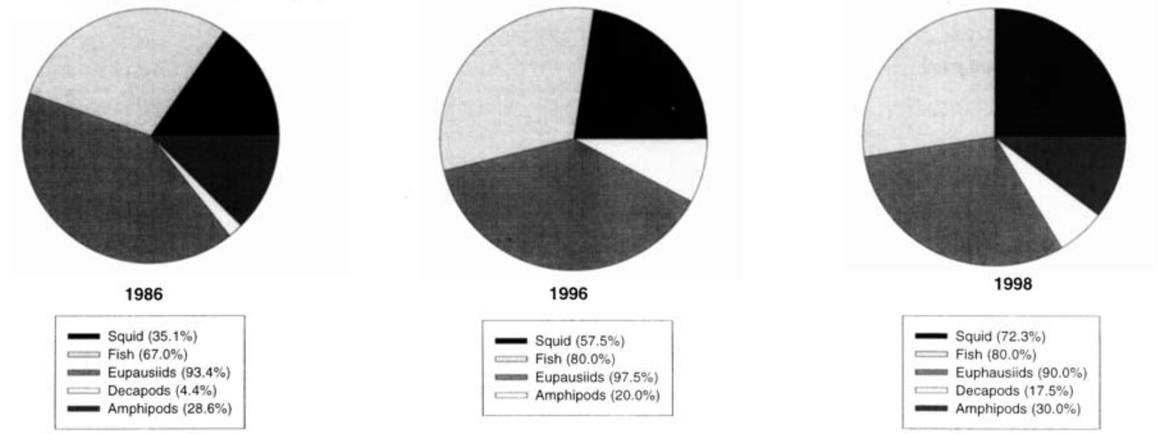


Fig. 1. Composition of the diet of white-chinned petrels during three summers at Bird Island, South Georgia **a.** as a proportion of total weight and **b.** frequency of occurence.

proportions of each major food type between the three years studied but these were not significant ($\chi^2_4 = 0.49$, NS). In 1996 and 1998 the proportion of euphausiids by mass was constant at 41–42% but squid occupied a greater proportion of the diet of white-chinned petrels in 1998 (25.4%) compared to 1986 and 1996 (18.6%) and also occurred in more samples in 1998 (72.3%). The proportion of fish decreased from 38.9% in1996 to 28.8% in 1998.

Crustaceans

All identifiable remains of crustaceans were krill, the amphipod *Themisto gaudichaudii* Guérin, 1825 and the decapod *Notocrangon antarcticus* Pfeffer 1887. Krill occurred in 39 of the 40 samples in 1996 and 36 of the 40 samples obtained in 1998. If the total number of all individuals is calculated, euphausiids accounted for 87.2% of prey items in 1996 (*n* = 1308) and 86.7% (*n* = 1237) in 1998. The length-frequency distributions of krill (estimated from intact carapaces) are shown in Fig. 2. The mean length (± s e) was 47.2 ± 1.0 mm (range: 35.4–60.0) in 1996 and 46.1 ± 0.9 mm (range: 33.1–60.7) in 1998. The modal length was smaller in 1996 (39–41 mm) compared to 1998 (42 mm) but there was no significant difference in krill length-frequency distributions (Kolmogorov-Smirnov one tailed test, $D = 0.20$, NS). Comparing the length-frequency distribution of krill recovered from white-chinned petrels to those of krill caught in scientific trawl nets (RMT) (Fig. 2) off the western end of South Georgia research cruises (JR11 and JR28) shows that white-chinned petrels fed on the larger krill in the area (Kolmogorov-Smirnov one tailed test, 1996: $D = 0.25$, $P < 0.01$, 1998: $D = 0.21$, $P < 0.01$). White-chinned petrels consumed more

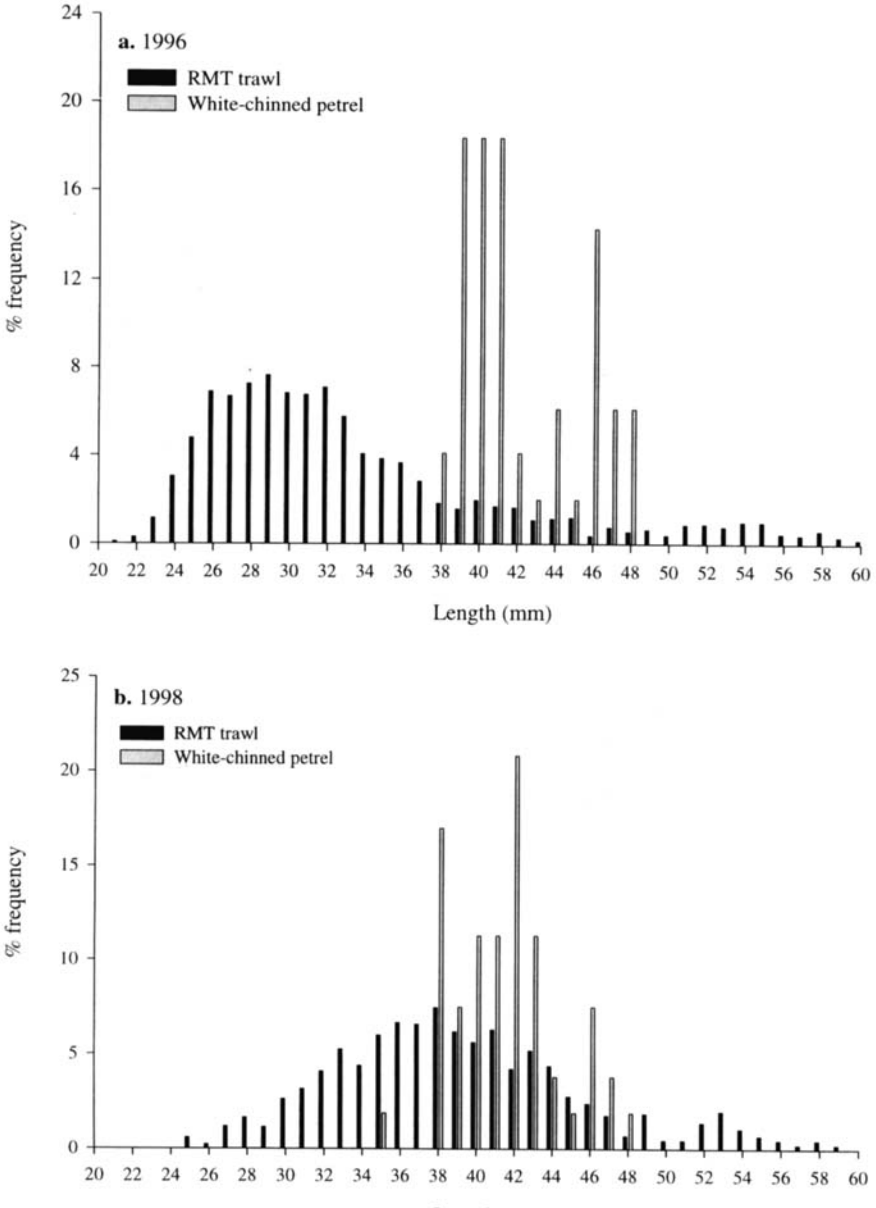


Fig 2. Length–frequency distribution of Antarctic krill from white-chinned petrel food samples in the summer and from trawl catches around South Georgia. **a.** 1996 (*n* = 49) and **b.** 1998 (*n* = 53).

decapods in 1998 (3.1%), compared to <1% in 1986 and 1996; the proportion of amphipods was <1% in all years studied.

Squid

In 1996, only six beaks (two of which were unidentifiable) were recovered from white-chinned petrel food samples despite squid flesh occurring in 23 of the 40 samples (57.5%). Each of the four beaks belonged to a different species (Table II): *Illex argentinus* (Castellanos 1960), *Mastigoteuthis psychrophila* (Nesis 1977), *Psychroteuthis glacialis* Thiele 1921 and *Histioteuthis* B (probably *Histioteuthis eltaninae* Voss 1969). In 1998, when squid occurred in 16 of the 40 samples (40%), 43 beaks were recovered representing 3.5% of all identifiable prey items (n = 1237). *Brachioteuthis? picta* Chun 1910 (identified from Rodhouse *et al.* 1991) was the most frequently recorded squid species, occurring in one third of the samples with identifiable squid but, due to its small size, accounted for only 3% of the total mass (Table II). Although a single specimen of *Kondakovia longimana* Filippova 1971 accounted for nearly 30% of the total mass of squid recovered in 1998, *Galiteuthis glacialis* Chun 1906 was the most important squid species, occurring in 25% of samples and accounting for 21% of the total mass.

Fish

The frequency of occurrence of fish species in food samples from 1996 and 1998 is shown in Table III. In both years lantern fish (Myctophidae) accounted for most of the otoliths recovered followed by notothenids. Myctophids alone were found in 67% of samples from adults with otoliths in 1996 (n = 9) and 20% in 1998 (n = 5). Notothenids were found exclusively in 22% of samples in 1996 and 40% in 1998, with both myctophids and notothenids in only one adult sample in each year.

Eleven species of fish were identified from the 146 otoliths recovered in 1996 with the notothenid *Lepidonotothen larseni* Loennberg 1905 being the most numerous, accounting for 31%. The two myctophid species *Electrona antarctica* Günther 1878 and *Gymnoscopelus nicholsi* Gilbert 1911 occurred in more food samples but in smaller numbers. Although only about one half the number of otoliths were found in 1998 as in 1996, twelve fish species were identified. *Electrona antarctica* Günther 1878 and *E. carlsbergi* Taning 1932 were the most abundant myctophid species and *Patagonotothen guntheri* and *Lepidonotothen larseni* the most abundant notothenids (Table III). Species from the genus *Gymnoscopelus* were frequent in both years but especially in 1996. In 1996 one sample was dominated by *Muraenolepis australis* Norman 1937; individuals of the family Macrouridae were identified in a single sample from 1998.

Discussion

Diet

The diet and feeding ecology of white-chinned petrels at South Georgia was first described by Croxall *et al.* (1995). They showed that although krill was the most important prey type, squid and fish were also frequently consumed, contributing about 51.6% of the overall diet even in 1986 a year of high local krill abundance. When compared to the diet of white-chinned petrels at breeding sites in the Indian and Pacific Oceans (Jackson 1988, Cooper *et al.* 1992), birds at South Georgia differed in that squid was the least and crustaceans the most important constituent of the diet. From a single year study, Croxall *et al.* (1995) were uncertain whether the predominance of krill in white-chinned petrel diet at South Georgia reflected the greater abundance and availability of krill (relative to fish and squid) around South Georgia than in the Indian Ocean or whether the year studied (1986) was a year when krill was in greater abundance/

Table II. Composition of the squid component of the diet of white-chinned petrel on Bird Island, South Georgia during the 1996 and 1998 summers.

	Species	Frequency of occurrence[1] (%)	Beaks		Beak length (mm)		Estimated Mantle length (mm)		Estimated Mass (g)			
			No	%	Mode	Range	Mean ± s e	Range	Mean ± s e	Range	Total	%
1995–96	*Illex argentinus*	25.0	1	17	3.3	–	209.8	–	104.9	–	104.9	30.1
	Mastigoteuthis psychrophila	25.0	1	17	4.5	–	132.1	–	90.3	–	90.3	25.9
	Psychroteuthis glacialis	25.0	1	17	4.2	–	153.4	–	78.2	–	78.2	22.4
	Histioteuthis B	25.0	1	17	3.3	–	58.8	–	75.5	–	75.5	21.6
	Unidentifiable	–	2	33	–	–	–	–	–	–	–	–
1997–98	*Brachioteuthis ? picta*	33.3	8	18	3.0	2.7–3.4	78.5±1.6	70.6–83.5	8.5±0.3	7.55–9.85	67.8	3.0
	Galiteuthis glacialis	25.0	6	13	4.4	4.30–5.4	176.0±29.4	187.6–233.6	79.6±7.2	67.1–108.5	477.8	21.2
	Illex argentinus	16.6	4	9	2.8	2.31–3.3	202.0±2.9	193.1–208.9	74.4±10.4	43.9–101.1	297.5	13.2
	Histioteuthis B	12.5	3	7	3.8	3.02–3.9	67.2±5.8	53.1–75.6	96.5±136	63.3–113.5	289.6	12.8
	Gonatus antarcticus	8.3	2	4	5.6–6.2	5.60–6.2	210.4	196.7–224.1	196.1	161.1–231.0	392.1	17.4
	Kondakovia longimana	4.2	1	2	10.2	–	386.6	–	671.5	–	671.5	29.7
	Chiroteuthis sp.	4.2	1	2	5.0	–	134.7	–	61.9	–	61.9	2.7
	Unidentifiable	–	18	40	–	–	–	–	–	–	–	–

[1] of the food samples with identifiable squid, 1996 = 4, 1998 = 16.

Table III. Frequency of occurrence of fish and their length (mm) and mass (g) estimated from otolith dimensions in white-chinned petrel food samples from Bird Island, South Georgia during the 1996 and 1998 summers.

	Species	1995–96					1997–98				
		freq (%)	No. of otoliths (%)	Estimated Mean (range) fish length (mm)	Estimated fish mass (g) Mean (range)	Total (%)	freq (%)	No. of otoliths (%)	Estimated Mean (range) fish length (mm)	Estimated fish mass (g) Mean	Total (%)
Notothenidae	*Patagonotothen guntheri*	10.0	2 (1.4)	169 (166–171)	34 (33–35)	103 (4.1)	31.8	6 (9.5)	191 (156–226)	43 (29–56)	230 (16.5)
	Gobionotothen gibberfrons	3.3	1 (0.7)	115	9	9 (0.4)	9.1	2 (3.2)	180 (178–182)	43 (41–45)	86 (6.2)
	Lepidonothen larseni	26.7	44 (30.6)	124 (40–148)	18 (1–29)	804 (32.3)	27.3	6 (9.5)	155 (99–201)	41 (9–75)	243 (17.5)
	Gobionotothen marionensis	–	–	–	–	–	4.5	3 (4.8)	173 (138–194)	47 (22–63)	141 (10.1)
	Paranotothenia magellanica	–	–	–	–	–	4.5	1 (1.6)	111	30	30 (2.1)
	Unidentified Notothenidae	10.0	3 (2.1)	–	–	–	–	–	–	–	
Myctophidae	*Electrona antarctica*	30.0	19 (13.2)	72 (42–156)	8 (1–53)	154 (6.2)	27.3	6 (9.5)	69 (62–112)	6 (1–19)	38 (2.7)
	Electrona carlsbergi	16.7	11 (7.6)	82 (53–102)	5 (1–8)	50 (2.0)	31.8	17 (27.0)	92 (61–130)	7 (1–17)	120 (8.6)
	Protomyctophum choriodon	6.7	7 (4.9)	64 (44–102)	2 (1–7) (0.6)	16	–	–	–	–	–
	Gymnoscopelus nicholsi	33.3	15 (10.4)	195 (94–367)	72 (6–281)	1078 (43.3)	4.5	5 (7.9)	151 (108–180)	24 (8–36)	119 (8.6)
	Gymnoscopelus braueri	6.7	10 (6.9)	58 (42–69)	3 (1–4)	27 (1.1)	4.5	1 (1.6)	116	17	17 (1.2)
	Gymnoscopelus fraseri	3.3	1 (0.7)	51	35	35 (1.4)	13.6	3 (4.8)	132 (100–178)	16 (6–35)	64 (4.6)
	Gymnoscopelus bolini	–	–	–	–	–	4.5	3 (4.8)	198 (192–206)	?	?
	Gymnoscopelus sp.	10.0	8 (5.6)	–	–	–	–	–	–	–	–
	Unidentified Myctophidae	3.3	1 (0.7)	–	–	–	–	–	–	–	–
Gadoidae	*Micromesistius australis*	3.3	17 (11.8)	168 (134–198)	?	?	–	–	–	–	–
Channichtyidae	*Champsocephalus gunnari*	6.7	2 (1.4)	257 (246–267)	107 (92–121)	213 (8.6)	4.5	1 (1.6)	351	302	302 (21.7)
Macrouridae	Unidentified Macrouridae	–	–	–	–	–	4.5	3 (4.8)	?	?	?
	Unidentified otoliths	13.3	4 (2.8)	–	–	–	4.5	2 (3.2)	–	–	–

availability and the diet of white-chinned petrels simply reflected this. The proportion of krill in white-chinned petrel diet in 1996 (41%) and 1998 (42%) was very similar and not greatly different from 1986 (47%). However, the size was much smaller in 1996 (modal length 39–41 mm) and 1998 (mode 42 mm) compared to that reported by Croxall *et al.* (1995) for 1986 (mode 55 mm). Brierley *et al.* (in press) reported a mean krill length of 52.5 mm during February, 1986, 15 mm greater than the mean (37.8 mm, range 32.0–43.1) for the following seven years for which data is available. Clearly white-chinned petrels fed on exceptionally large krill in 1986 but generally appear to feed preferentially on the larger krill available, presumably to increase the unit return per prey capture. The 1996 and 1998 data suggest that krill is indeed the single most important prey item to white-chinned petrels at South Georgia but that they are a versatile species, well adapted to a broad-spectrum diet. They seem to be as adept in taking krill as fish and squid, and presumably favour krill whenever its abundance is sufficient to warrant the lower return per unit capture.

Although the diet was generally consistent between years, a few important differences in species composition are apparent. Myctophids dominated the fish diet in all years but the notothenid *Patagonotothen guntheri* was less abundant in 1996 and 1998 than in 1986. Croxall *et al.* (1995) thought it probable that white-chinned petrels obtained this species in 1986 mainly through associating with commercial fisheries in the Shag Rocks area (250 km east of Bird Island) to which *Patagonotothen guntheri* is restricted in the South Georgia region (Everson *et al.* 1992). *Patagonotothen guntheri* was fished there through the 1980s, with a reported catch of 16 000 tonnes in 1986 (Everson & Mitchell 1991) but there has been no directed fishery for this species since 1990. The most important notothenid in the diet in both 1996 and 1998 was *Lepidonotothen larseni.* This species frequently has been found in the diet of marine predators at South Georgia in recent years (Reid & Arnould 1996, Berrow *et al.* in press) suggesting that it may have increased in abundance. Overall, the main fish prey of white-chinned petrels are species primarily dependent on krill e.g. *Lepidonotothen larseni, Gymnoscopelus nicholsi, Electrona antarctica,* rather than those mainly taking copepods and amphipods. *Electrona carlsbergi*, a predator of copepods and hyperiids, was more evident in the diet in 1998.

The squid *Martialia hyadesi* was the most commonly taken cephalopod species in 1986, accounting for one half of the mass of squid consumed (Croxall *et al.* 1995) but was not recorded in the present study. *Illex argentinus* occurred in the diet in both 1996 and 1998 but was not recorded by Croxall *et al.* (1995). Around the Falkland Islands on the Patagonian shelf there is a substantial fishery for *Illex argentinus* in which *Martialia hyadesi* occurs as a minor catch (González *et al.* 1997). Stocks of *Illex argentinus* are caught in large numbers each year but catches of *Martialia hyadesi* have fluctuated considerably since 1985 with the largest catch (*c.* 26 000 tonnes) reported in 1986, the year this species was reported in the diet of white-chinned petrels (González *et al.* 1997).

Provisioning rate and meal size

The feeding frequency and meal size, as determined by daily weighing of chicks, varied between years. Chicks received on average around 130 g every 1.3 days in 1996 but 146 g every 1.9 days in 1998. The two years outside of this study for which provisioning rate data are available are intermediate: *c.* 150 g was delivered every 1.8 days in 1979 (Croxall & Prince 1980) and 167g every 1.5 days in 1986 (Croxall *et al.* 1995). Actual feeding frequency will be influenced by how we determined double feeds to the chick on the same day, but as the method is consistent it is the relative frequencies that are important. Overall, mean meal size was consistent but feeding frequency varied; we presume this reflects that, like most Procellariiformes, white-chinned petrels only return to the nest to provision the chick when the adult has a full meal to deliver (Berruti *et al.* 1985, Hamer & Hill 1993). In years when food is scarce, it presumably takes the adult bird longer to collect a full meal and thus feeding frequency to the chick declines, resulting in 19% less food being delivered to the chick during the fledging period in 1998 compared to 1996 and 46% less than in 1986. Although daily chick weighings were carried out over the same dates in 1996 and 1998, chicks had significantly lower body mass in 1998. This could be due to chicks being older and thus heavier in 1996 or evidence of reduced growth rates in 1998 during early chick-rearing. The age of each chick weighed was not known but there is some evidence that adults laid later in 1998 compared to 1997 (S. Berrow unpublished data), which could be attributed to reduced food supply during the pre-egg period (Warham 1990). White-chinned petrels, due to their extended fledging period, cannot delay laying for too long if they are to complete chick-rearing before the start of the winter. Thus reduced provisioning rates in 1998 may reflect both the younger age of the chick as well as increased foraging effort (longer trips) by adults.

Most petrels return to their burrow to feed their chicks at night (Warham 1996). We found that the proportion of nocturnal and diurnal feeds varied between years with half the feeds delivered during the day in 1998. If adults are experiencing difficulties in obtaining food (as suggested by the reduced feeding frequency) then it may be necessary for them to return immediately to the burrow on obtaining a full meal for the chick without waiting for darkness, as this could extend the interval between meals up to 8–10 hours. However, this may increase the risk of predation or kleptoparasitism by brown skuas *Catharacta loennbergi* Mathews 1912. The exact time of feeding and the cost and benefit of day and night provisioning needs further study.

Comparison with other seabirds at South Georgia

Prior to the current study it was thought that white-chinned petrels and grey-headed albatrosses might have rather similar overall diet composition, lacking obvious specialization for any one particular class of prey and, within prey class, having some similarities in prey species composition. The new data for white-chinned petrels indicate that while overall diet composition and prey species may be rather similar, the squid *Martialia hyadesi* is not a consistent feature of white-chinned petrel diet. This is rather different from the grey-headed albatross, where *M. hyadesi* has accounted for over 70%, by mass, of the squid component in the diet in four of the five years of sampling (Prince 1980, J. Xavier personal communication 1998). In 1998, however, *M. hyadesi* accounted for only 18% by mass of grey-headed albatross diet, being replaced by *Galiteuthis glacialis* (J. Xavier personal communication 1998), the squid which was also one of the most important in the white-chinned petrel diet in 1998.

Response of white-chinned petrels to changes in krill availability

The abundance and size of krill during the breeding season around South Georgia varies annually (Brierley *et al.* 1997, Reid *et al.* 1999). In years when krill abundance is low, widespread reproductive failure of krill-dependent predators at Bird Island has been reported (Croxall *et al.* 1988, Boyd

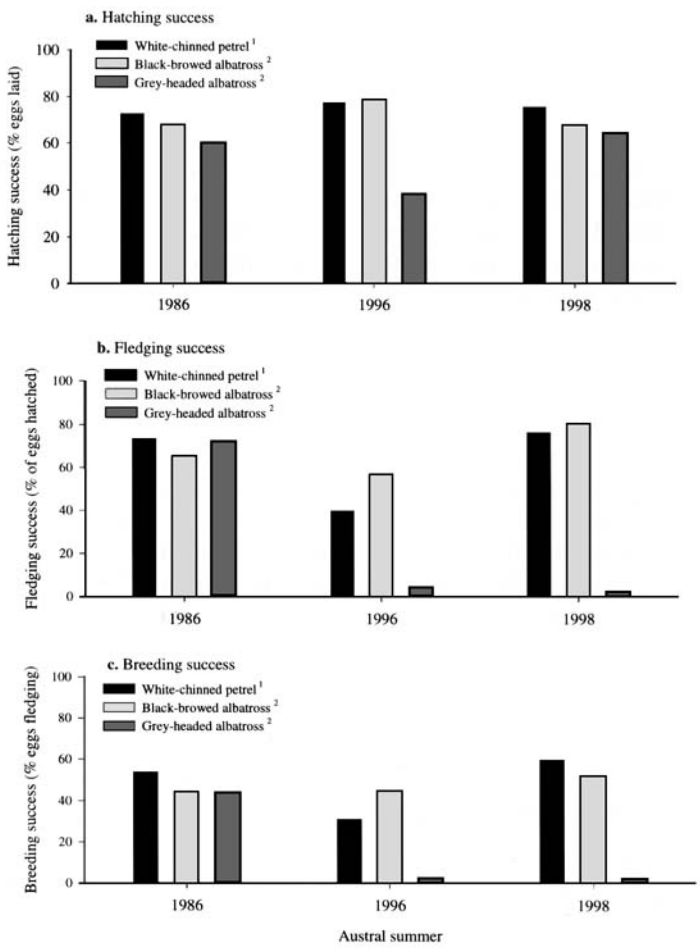


Fig 3. Breeding success of white-chinned petrels and black-browed and grey-headed albatrosses at Bird Island, South Georgia during the 1986, 1996 and 1998 summers. ([1]Hall 1987 and S. Berrow unpublished data, [2]Prince *et al.* 1994 and British Antarctic Survey unpublished data)

et al. 1994, Croxall *et al.* 1999). In January 1996, krill occurred at densities of 26.7 gm^{-2} off the north-west coast of South Georgia, which is similar to 29.7 gm^{-2} reported in February 1986 (Brierley *et al.* in press). In the 1997/1998 summer, in the same area, krill densities were 5 gm^{-2} in October/November 1997 and 21.4 gm^{-2} in January 1998.

The summer of 1996 was characterized by high breeding success of gentoo penguins *Pygoscelis papua* Forster 1781 (1.7 chicks fledged per pair), macaroni penguins *Eudyptes chrysolophus* Brandt 1837 (45% successful nests) and black-browed albatrosses (41%, Fig. 3) and low mortality (19.5%) of Antarctic fur seals *Arctocephalus gazella* Peters 1875 pups, indicating that krill was abundant throughout the breeding season. In 1998 the very low availability of krill in October/November had clear effects on the breeding performance of many predators (Fig. 3, British Antarctic Survey unpublished data). Over 95% of gentoo penguins, which lay in October, failed during incubation. Breeding success of black-browed albatrosses, which also lay in October and whose success is closely linked to the availability of krill (Prince *et al.* 1994) was 1.6% in 1998 (Fig. 3) compared with a 17 year mean of 28.6% (range: 0.0–63.6%) (Prince *et al.* 1994); 62% of the 1998 failures occurred during incubation. Peak parturition of Antarctic fur seals occurs in mid-December; mortality of pups in 1998 was 39% compared with a 13 year mean of 20.2% (range: 2.6–46.9%). Foraging trips by breeding female fur seals were long (mean 6.5 days compared with 4.8 days for the period 1989–1994), which is indicative of increased foraging effort, typical of years with low krill availability (Boyd *et al.* 1994). Although krill abundance and length–frequency data (Reid *et al.* in press) indicate that South Georgia experienced an influx of large krill towards the latter half of the season, many of the earlier-breeding predators had already failed in their breeding attempt.

The proportion of krill in white-chinned petrel diet was similar between years. There was also no difference in meal mass but the foraging trip duration (longer by 46%) resulted in 19% less food delivered compared to 1996. This did not result in breeding success being very different between years and hatching and fledging success were also similar (Fig. 3), suggesting that adult birds were finding sufficient food during both the incubation and chick-rearing periods. Reduced provisioning rate may result in chicks fledging at lower body mass with subsequent reduction in survival (Sagar & Horning, 1998) but this was not measured in the present study. Of possibly equal interest is the fact that white-chinned petrels

Table IV. Aspects of the feeding ecology and behaviour of white-chinned petrel and grey-headed and black-browed albatrosses breeding at Bird Island, South Georgia. Good year and bad year refer to years of relatively high local krill abundance and when krill was locally scarce, respectively.

Species	Krill in diet[1] (%)		Breeding success[1] (% of eggs fledging)		Time of feeding[2]	Max diving depth[3] (m)	Foraging range[4] (km^2)
	Good year	Bad year	Good year	Bad year			
White-chinned petrel	48	42	54	44	Day and night	12.8	124 000
Grey-headed albatross	16	2	60	27	Day	6.0	119 700
Black-browed albatross	39	5	31	3	Day	4.5	81 500

[1] Croxall *et al.* 1995, 1999, Berrow & Croxall (this paper)
[2] Huin & Prince 1997, Ashford *et al.* 1995, Barnes *et al.* 1997
[3] Huin 1994, Prince *et al.* 1994
[4] Wood *et al.* in press, Berrow *et al.* in press

fared much better than grey-headed albatrosses in 1998 (Fig. 3), the latter suffering their worst year for breeding success since records started in 1976 (Prince *et al.* 1994, Croxall *et al.* 1998).

The reason why white-chinned petrels are less influenced by the effects of krill shortage than some other South Georgia species is likely to reflect some combination of their diet (particularly scope for switching to prey other than krill), foraging methods and foraging range. We compare some of these attributes with two other South Georgia Procellariiformes in Table IV. This suggests that white-chinned petrels are considerably more versatile than albatrosses, particularly black-browed albatross, in when and where they can forage. Thus white-chinned petrels operate during both day and night, to greater depths and over larger areas. In years of krill scarcity they are able to switch to a range of other prey, including several taxa that are unlikely themselves to be extensively dependent on krill. (This probably differs from grey-headed albatross which relies mainly on fish and especially squid species that typically take much krill (e.g. *Martialia hyadesi*, *Champsocephalus gunnari*)). This switch may not be wholly cost-free as provisioning rate was somewhat reduced in 1998 and although fledging success seemed unaffected it is possible that chicks grew less well (and thereby fledged with smaller reserves). This would be similar to the response of macaroni penguin, which maintains breeding productivity in years of krill scarcity by switching to a diet of amphipods, albeit at the cost of fledglings being significantly lighter than in years of normal krill availability (Croxall *et al.* 1999).

In comparison with grey-headed albatross, our results suggest that some combination of the longer time available for foraging by white-chinned petrels, their larger foraging range, greater diving skills and ability to target squid species other than *Martialia hyadesi* in years when the latter is scarce may explain why white-chinned petrels fared better than grey-headed albatrosses in 1998.

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