

Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean

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ABSTRACT: The marine habitat exploited by black-browed *Diomedea melanophrys* and grey-headed albatrosses *D. chrysostoma* breeding at Campbell Island, New Zealand, was studied using satellite telemetry. Data were analysed in relation to the bathymetry and sea-surface temperature of the foraging zones. Black-browed albatrosses spent 55 % of their time on the Campbell Plateau but also carried out long foraging trips to the Polar Front and Antarctic Zone at a distance of over 2000 km. They relied heavily on juvenile *Micromesistius australis*, a schooling fish, during foraging trips to the shelf but over oceanic waters the squid *Martialis hyadesi* was the main prey taken. Grey-headed albatrosses spent 71 % of their time foraging over the deep waters of the Polar Frontal Zone where *M. hyadesi* comprised over 90 % of the mass of prey taken. No satellite-tracked birds fed over the shelf, but data from the duration of foraging trips and dietary analysis suggests that shelf-feeding is important for this species. Significant inter-species differences in the time spent in neritic and oceanic zones show that black-browed albatrosses are reliant primarily on shelf resources while grey-headed albatrosses are primarily oceanic feeders. In addition, the 2 species overlapped little in the zones used over oceanic waters, with black-browed albatrosses feeding in more southerly waters than grey-headed albatrosses. However, both species feed on *M. hyadesi* when foraging in association with the Polar Front.

KEY WORDS: Marine environmental · Albatross · Satellite tracking

INTRODUCTION

Productivity varies non-randomly in large marine ecosystems, typically being concentrated over shelves, shelf slopes and at frontal zones (Ashmole 1971, Hunt 1990, 1991, Schneider 1990). This productivity is usually closely associated with concentrations of biomass at all trophic levels (Abrams 1985, Lutjeharms et al. 1985). This is particularly so for top-level predators where advection and/or upwelling processes also contribute to increased prey densities (Genin et al. 1988, Murphy 1995). However, conventional techniques relating the density of wide-ranging top predators (e.g. seabirds, marine mammals) to marine-environmental

features have often failed to reveal strong relationships (Schneider 1990, Hunt 1991, Veit & Hunt 1991, Pakhomov & McQuaid 1996). This is partly due to the difficulties of observing individual predators while foraging (Brown 1980) and the fact that top predators can move considerable distances between feeding events and thus may often be seen in non-productive areas. There are also problems of measuring simultaneously hydrographic structure and process, as well as the distributions of predators and their prey (Hunt 1990, Murphy 1995).

Recently, satellite-tracking studies of large seabirds have enabled the development of new approaches for understanding predator-environment (Jouventin & Weimerskirch 1990, Weimerskirch et al. 1994b, 1997c) and predator-prey relationships (Rodhouse et al. 1996, Veit & Prince 1997). The spatial and temporal distrib-

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uation of birds of known status can be studied in relation to variables in their environment (Wilson et al. 1994). For example, foraging of both penguins and albatrosses has been found to be concentrated at the Polar Front (PF) (Rodhouse et al. 1996, Guinet et al. 1997, Hull et al. 1997, Prince et al. 1998). Wandering albatrosses *Diomedea exulans* rely heavily on resources at shelf-breaks during brooding and some parts of the chick-rearing period, as do black-browed albatrosses *D. melanophrys* from Kerguelen Island, Indian Ocean (Weimerskirch et al. 1997a, c). Several species of seabird exploit prey patches which are unrelated to physical oceanographic features (Veit & Prince 1997, Prince et al. 1998, Weimerskirch 1998a). Further to examining the location of foraging areas by diet-sampling satellite-tracked individuals, the distribution of prey species can be examined (Cherel & Weimerskirch 1995).

The influence of the marine physical environment on seabird ecology and resource usage can be examined by comparing the foraging strategies of species studied across several sites. Satellite-tracking studies of seabirds have so far been concentrated in the Atlantic and Indian Oceans (Weimerskirch et al. 1993, 1997a, b, c, Bost et al. 1997, Prince et al. 1998, Weimerskirch 1998a). Relatively little research has been focused on the Subantarctic Zone (SAZ) of the Pacific Ocean (Weimerskirch & Robertson 1994, Sagar & Weimerskirch 1996, Hull et al. 1997), although this region supports major commercial fisheries (Annala & Sullivan 1997) and a high diversity of petrels and albatrosses (Ainley et al. 1984, Warham 1996). This richness of top predators has been linked to the productivity of the waters south of the New Zealand mainland (Robertson & Bell 1984). The hydrography of the Southern Pacific Ocean is compli-

cated by the large area of the Campbell Plateau (Heath 1981). However, the constraints imposed on currents by this large sub-marine feature mean that there is little temporal variation in the 3 major oceanic fronts that subdivide this area (Heath 1981): (1) the Subtropical Front, (2) the Subantarctic Front and (3) the Polar Front (Fig. 1). The large shelf area of the Campbell Plateau and the long distance to the PF contrast with the foraging environment around the Crozet and Kerguelen Islands (Weimerskirch et al. 1993, 1994b, 1997c, Bost et al. 1997, Guinet et al. 1997) and South Georgia (Rodhouse et al. 1996, Prince et al. 1998) which have more limited shelf areas and are closer to the PF.

Our aims were to examine how 2 closely related and sympatric seabirds, black-browed *Diomedea melanophrys* and grey-headed albatrosses *D. chrysostoma* from the Pacific Southern Ocean, exploit and partition marine resources. To do this we conducted a simultaneous study of both species using satellite tracking to characterise their use of the marine ecosystem with reference to bathymetry and sea-surface temperature (SST), taking into account the time spent by individuals in different zones during their foraging trips. Diet samples taken from satellite-tracked birds were used to examine feeding associations in different foraging zones.

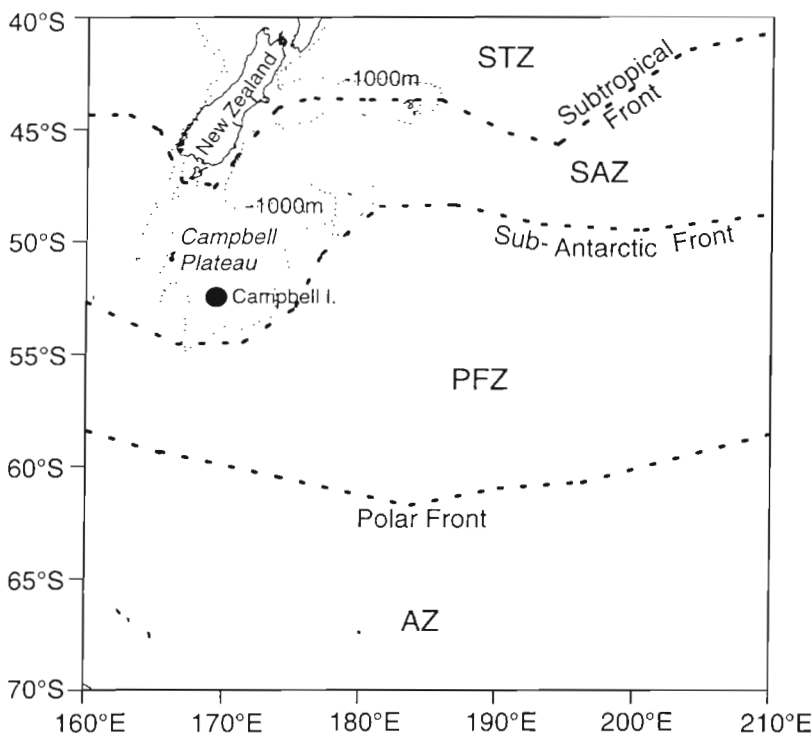


Fig. 1. Bathymetric and ocean-front features and water masses within the foraging zones of black-browed and grey-headed albatrosses *Diomedea melanophrys* and *D. chrysostoma* from Campbell Island. Oceanographic zones are defined primarily following Rintoul et al. (1997). The Antarctic Zone (AZ) lies south of the Polar Front (PF), which is defined as the northernmost extent of the 2°C isotherm near 200 m depth (Park et al. 1991), and characterised by the 3 to 5°C surface isotherms (Machida 1976). The Polar Frontal Zone (PFZ) lies to the north of this front and has its northernmost boundary at the Subantarctic Front, characterised by the 8 to 9°C surface isotherms (Belkin & Gordon 1996, Rintoul et al. 1997). The Subantarctic Zone (SAZ) covers the region of the Campbell Plateau and eastwards, until the Subtropical Front, here shown following the description of Heath (1981). The Subtropical Front has been described as a broad feature, extending across surface isotherms of 10 to 17°C (Belkin & Gordon 1996). Here we define it at 15°C (Burling 1961), and term the region to the north, the Subtropical Zone (STZ)

METHODS

Field study. Breeding albatrosses from Campbell Island (52°33' S, 169°09' E) were satellite tracked using the ARGOS satellite telemetry system, and with Toyocom T2038 (55 g) and Microwave M100 (20 to 30 g) Platform Terminal Transmitters (PTTs). Methods of deployment are described in Weimerskirch et al. (1997b). During February 1997, 11 foraging trips from 7 black-browed albatrosses *Diomedea melanophrys* and 5 foraging trips from 4 grey-headed albatrosses *D. chrysostoma* rearing chicks were obtained. Two successive trips were recorded for 4 black-browed albatrosses and 1 grey-headed albatross. One transmitter deployed on a grey-headed albatross did not function, however the trip duration was recorded, and a diet sample was taken from this bird.

Analysis. Satellite data contained 7 classes of location of varying accuracy (ARGOS 1996). Data from all classes were analysed and filtered to exclude locations if the average flight speed exceeded 75 km h⁻¹ (see Bevan et al. 1995). These data were analysed using GIS ARC-INFO (ESRI 1992) to integrate environmental databases and ARGOS satellite telemetry data. The bathymetry was interpolated from 500 m depth grids that were generated by ARC-INFO from a contour map sourced from The General Bathymetric Chart of the Oceans (GEBCO) (British Oceanographic Data Centre 1994). Integrated Global Ocean Services System (IGOSS) weekly sea-surface temperature (SST) data (Reynolds & Smith 1992) were interpolated with the satellite locations.

As the number of satellite locations received for each species was related to the number of satellite transmitters deployed and the time spent foraging by each individual bird, comparisons of habitat use cannot rely on the number of locations. Additionally, the number of locations recorded per hour of the day by the ARGOS tracking system is non-uniform and linked to the number of satellites passing overhead at any one time (Georges et al. 1997, Hull et al. 1997). Similarly, in this study, we found that the number of locations showed a bimodal distribution when plotted by hour, with few locations recorded between 10 and 12 h and 22 and 24 h local time.

For these reasons data were analysed to indicate the time spent rather than the number of locations recorded. Using MATLAB (MathWorks 1996), we generated density plots for each track, which gave the number of bird-hours spent in each 'square' of 0.5° (Fig. 2). It was assumed that between successive uplinks, birds travelled at constant speed and in a straight line. The number of bird-hours spent was analysed in relation to the environmental variables by assigning each square a mean SST (21 classes from -1.5 to 18.5°C, 1°C intervals) and bathymetric value

(12 classes from 250 to 5750 m, 500 m intervals). Using these values for each square where a bird passed time, we calculated the sum of hours spent in each variable class per individual. Groups of birds were compared using Mann-Whitney *U*-tests to examine differences in the mean proportion of time spent in 3 depth classes, corresponding to the continental shelf and the upper shelf break (less than 1000 m depth), lower shelf break (1000 to 3000 m depth) and oceanic waters (greater than 3000 m depth) and 5 temperature classes (less than 3°C, AZ; 3–5°C, PF; 5–9°C, PFZ; 9–15°C, SAZ; 15–19°C STZ). Statistics used follow Zar (1984), with $p < 0.05$ as the level of significance, and analysis was carried out using SYSTAT 6.0 (Wilkinson 1996). Values are given as mean \pm 1 standard deviation.

To test the effect of handling and fitting transmitters to breeding birds, foraging trip durations of transmitted birds were compared with a sample of 24 black-browed *Diomedea melanophrys* and 15 grey-headed albatross *D. chrysostoma* pairs feeding chicks (973 and 381 trips respectively), observed in the colony over the 14 d period during which the transmitters were deployed (Waugh et al. unpubl. data). For both species, the average durations of satellite-tracked trips were longer than those of observed birds (2-sample *t*-tests, separate variance: black-browed albatross, $t_{10} = -3.54$, $p < 0.005$, grey-headed albatross, $t_4 = -3.24$, $p < 0.05$). We can suppose that transmitted birds are more inclined to carry out relatively long foraging trips after handling than would occur by chance, but there is no evidence to show that these trips were not representative of long trips carried out by other birds in the colony. Indeed, for black-browed albatrosses, transmitted birds used the same zone as dyed breeding black-browed albatrosses from the same colony, 1 yr earlier (Waugh in press).

Dietary analysis. Diet samples were taken after foraging trips by 4 black-browed albatrosses *Diomedea melanophrys* and 5 grey-headed albatrosses *D. chrysostoma* fitted with satellite transmitters. Most samples were taken from adults directly, but 3 were taken from chicks just fed. For both groups of animals the same sampling procedure was used. The bird was inverted over a bucket or funnel for up to 2 min, and the stomach palpated gently. An additional diet sample was obtained from a bird returning after an 11 d trip carrying a temperature logger (Wilson et al. 1995), which gave information on the SST zone where it foraged (Weimerskirch et al. 1995). In addition, 10 diet samples were taken from each species from randomly selected chicks that had just been fed.

Material was preserved in isopropyl alcohol (Propan-2-ol) until sorted to differentiate fresh and accumulated remains. Fresh material only was used in our analysis. This was sorted into fish, cephalopod, and

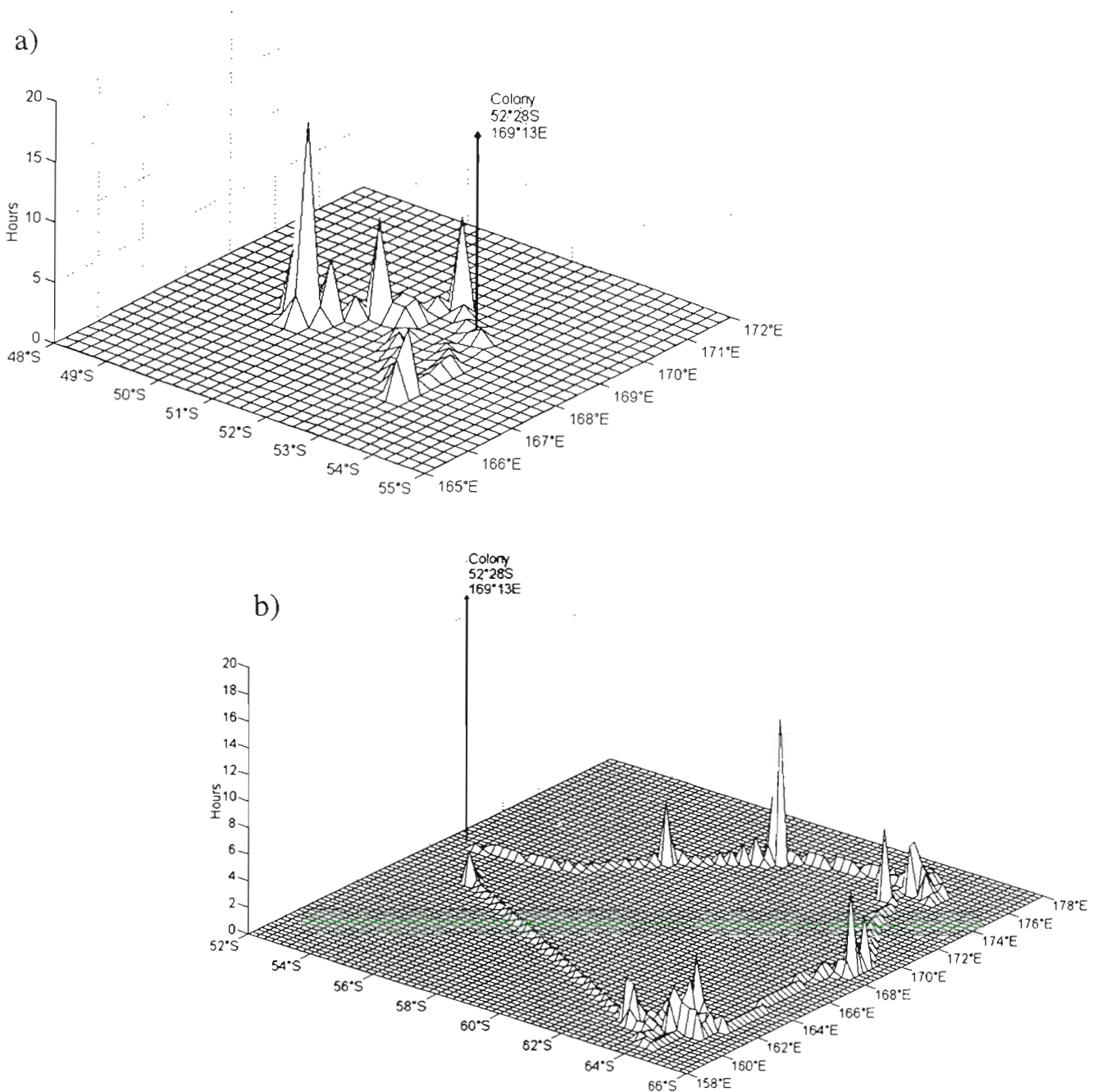


Fig. 2. *Diomedea melanophrys*. Allocation of time by a black-browed albatross during 2 foraging trips (a) over shelf waters of the Campbell Plateau and (b) over oceanic waters to the PF. Vertical line shows position of breeding site, peaks in the z-axis indicate areas where the bird moved slowly, presumably during intensive foraging bouts

'other' (predominantly carrion, crustacean, salp) groups. Carrion was defined as vertebrate flesh not from fish, and often was associated with feathers or fur in the diet samples. Identification of dietary material follows Cherel & Weimerskirch (1995). Allometric

equations given by Rodhouse & Yeatman (1990) were used to estimate the dorsal mantle length of *Martialia hyadesi*, and unpublished data (Y. Cherel, S. Hanchet) for the standard length of *Micromesistius australis*.

RESULTS

Black-browed albatross

Two distinct feeding zones were used during the 11 foraging trips followed—birds used neritic waters (less than 1100 m depth) close to Campbell Island during trips of short duration (less than 4 d, $n = 5$ trips, Fig. 3A), or they foraged over oceanic waters (over 3000 m deep) during longer trips (7.5 to 21 d duration, $n = 6$ trips, Fig. 3B). Four birds for which 2 successive tracks were recorded carried out a mixture of these 2 strategies: 3 undertook a neritic trip each before departing for longer oceanic foraging bouts; 1 bird carried out 2 successive neritic trips. The remaining 3 birds did 1 oceanic trip each. The birds using neritic waters travelled significantly fewer kilometres per day than those foraging over deep waters (neritic trips, mean distance = 386 ± 84 km d⁻¹, $n = 5$; oceanic trips, mean distance = 491 ± 108 km d⁻¹, $n = 6$, $F_{1,9} = 13.7$, $p < 0.01$).

Black-browed albatrosses *Diomedea melanophrys* used a large geographic zone, although half of the trips were restricted to the Campbell Plateau (Table 1). The maximum ranges during trips were 150 to 640 km for birds over neritic areas, and between 1550 and 2300 km during trips over oceanic waters. Data from individual trips were grouped according to the type of trip carried out, being either over shelf waters (less than 1100 m) or oceanic waters. For each group, the distribution of birds' time with respect to temperature and depth zones is shown in Table 2. A wide range of temperature zones was used (range -0.3 to 18.4°C), with birds ranging from the AZ to the STZ (Fig. 4A). The distribution of bird-hours with respect to temperature shows a major peak of activity in the SAZ (Fig. 4A), corresponding to the shelf waters around the breeding site, but an important second concentration of activity was evident at the PF (Table 2). Similarly, the distribution of time over depth zones (Fig. 4B) shows peaks of activity over the shelf and

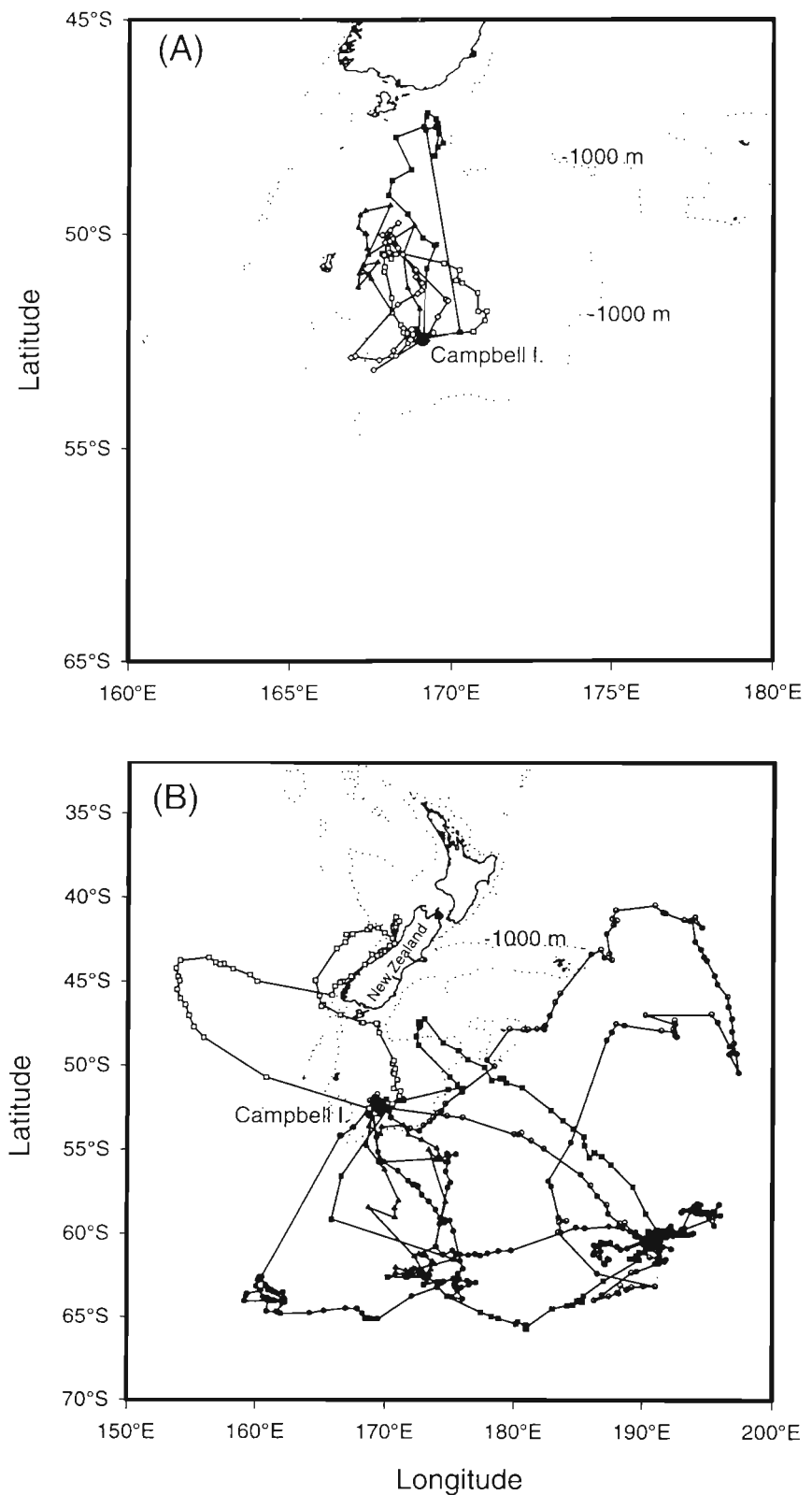


Fig. 3. *Diomedea melanophrys*. Foraging trips from black-browed albatrosses to neritic waters (A) over the Campbell Plateau and (B) over oceanic zones. Three birds had successive trips to neritic followed by oceanic waters

Table 1. *Diomedea melanophrys* and *D. chrysostoma*. Characteristics of individual foraging trips for black-browed albatrosses *D. melanophrys* (BBA) and grey-headed albatrosses *D. chrysostoma* (GHA). Bird no. indicates individual birds; a, b: successive trips by the same bird. Water depths of less than 1100 m are associated with trips over the Campbell Plateau. Dates given as d/mo/yr

Species	Bird no. /trip	First day of trip	Trip dur. (d)	Total dist. (km)	Distance d ⁻¹ (km) (SD)	n	Max. range (km)	Speed (km h ⁻¹) (SD)	n	Max. depth (m)	SST (°C) (range)	No. of locations
GHA	1	10/2/97	3.1	1839	601.9 (133.9)	2	807	30.9 (21.7)	2	6335	7.2–8.6	32
	2	4/2/97	12.0	8107	701.8 (242.1)	11	1609	31.6 (19.4)	11	5993	4.1–9.7	68
	3a	4/2/97	5.8	3234	554.6 (151.3)	5	985	28.2 (20.6)	5	6145	6.7–9.7	48
	3b	10/2/97	6.5	4231	624.7 (190.4)	5	1722	27.7 (19.7)	5	6104	3.4–8.6	62
	4	4/2/97	12.8	9422	743.5 (189.9)	11	2714	31.6 (19.2)	11	6123	4.1–12.5	90
BBA	1	4/2/97	13.8	10206	762.8 (328.9)	13	2221	31.1 (22.0)	13	5879	0.9–12.0	126
	2	4/2/97	21.0	7763	508.4 (256.2)	15	2265	22.3 (20.3)	15	5104	3.6–9.4	155
	3a	4/2/97	3.7	1338	331.3 (33.4)	3	344	19.9 (16.8)	3	1058	9.7–10.4	31
	3b	8/2/97	9.1	5943	597.6 (221.1)	8	1946	29.9 (21.5)	8	5908	–0.3–9.7	112
	4a	4/2/97	3.6	1645	470.5 (282.0)	3	638	51.4 (99.1)	3	986	9.7–12.6	32
	4b	7/2/97	16.0	11652	710.0 (204.0)	15	2310	22.6 (18.9)	15	6366	2.1–18.1	162
	5	4/2/97	9.9	5373	490.8 (252.2)	9	1550	24.9 (19.4)	9	5150	9.7–18.4	82
	6a	4/2/97	2.6	1317	484.5 (16.3)	2	398	22.9 (16.2)	2	514	9.7–12.0	20
	6b	7/2/97	7.5	4751	573.7 (336.3)	6	1559	30.3 (16.2)	6	5932	3.4–8.7	55
	7a	4/2/97	2.9	989	304.1 (56.6)	2	282	16.6 (11.9)	2	563	9.7–10.4	26
	7b	7/2/97	2.0	685	479.0 (–)	1	154	16.5 (12.9)	1	931	9.7–10.0	19

Table 2. *Diomedea melanophrys* and *D. chrysostoma*. Mean \pm SD proportion of time spent in depth and temperature zones by birds of 3 groups: (1) black-browed albatrosses *D. melanophrys* (BBA all), (2) black-browed albatrosses undertaking oceanic trips (BBA oceanic), and (3) grey-headed albatrosses *D. chrysostoma* (GHA all). ns: not significant

Group	Depth (m)			Temperature (°C)				
	<1000 Shelf	1–3000 Slope	>3000 Oceanic	0–3 AZ	3–5 PF	5–9 PFZ	9–15 SAZ	15–19 STZ
BBA all	0.55 \pm 0.45	0.07 \pm 0.12	0.38 \pm 0.39	0.09 \pm 0.20	0.17 \pm 0.26	0.10 \pm 0.13	0.58 \pm 0.43	0.06 \pm 0.15
BBA oceanic	0.18 \pm 0.19	0.12 \pm 0.14	0.70 \pm 0.20	0.16 \pm 0.26	0.31 \pm 0.28	0.19 \pm 0.12	0.23 \pm 0.21	0.10 \pm 0.19
GHA all	0.05 \pm 0.06	0.04 \pm 0.03	0.90 \pm 0.10	0.00 \pm 0.00	0.17 \pm 0.19	0.71 \pm 0.21	0.12 \pm 0.14	0.00 \pm 0.00
Test results								
BBA all vs GHA all	$U = 49.0$ $p < 0.01$	ns	$U = 3.0$ $p < 0.01$	ns	ns	$U = 0.00$ $p < 0.001$	$U = 44.5$ $p < 0.05$	ns
BBA oceanic vs GHA all	ns	ns	$U = 3.0$ $p < 0.05$	$U = 25.0$ $p < 0.05$	ns	$U = 0.0$ $p < 0.01$	ns	ns

oceanic waters but relatively little activity at the lower shelf break (Table 2).

The diet samples taken from birds fitted with devices showed that 2 prey types from 2 environments were exploited: the 2 birds which foraged over oceanic waters and at the PF delivered samples dominated by squid (99.4 and 100% by mass of fresh material). From these, 5 juvenile *Martialia hyadesi* (mantle length, ML: 225 to 262 mm) and 1 adult *Galiteuthis glacialis* were identified. The 3 birds which fed over the Campbell Plateau and the shelf of the New Zealand mainland delivered meals dominated by fish (91.0 to 96.5% by mass of fresh material). From these, 69 juvenile *Micromesistius australis* (standard length, SL: 88 to 106 mm) and 1 squid *Nototodarus sloanii* were identified. In addition, samples from 10 randomly selected chicks

were analysed to examine the major prey classes and species present. The mass of fresh remains in these was dominated by *M. australis* in 80% of cases, and this prey species was present in 100% of samples. Other fish species dominated in 20% of samples. Four individual *M. hyadesi* were found in 1 of these random samples, but this species was absent from the remainder, and cephalopods did not dominate in any samples.

Grey-headed albatross

The 5 grey-headed albatrosses *Diomedea chrysostoma* foraged over oceanic waters (depths greater than 6000 m), with trips of 3.1 to 12.8 d duration (Fig. 5). Birds travelled on average 645 ± 76 km d⁻¹ (n = 5). The

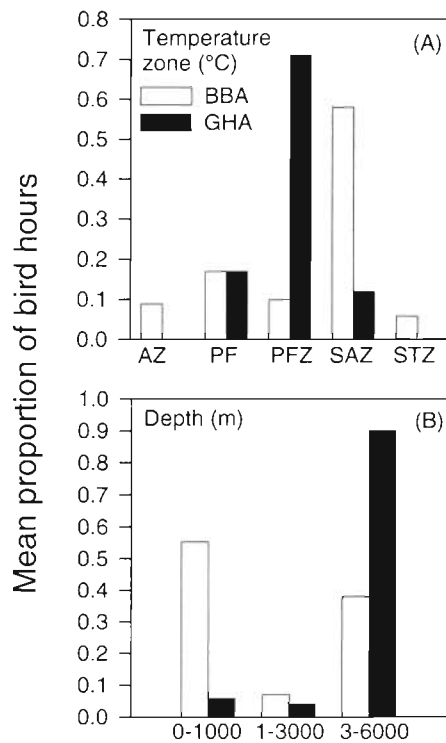


Fig. 4. *Diomedea melanophrys* and *D. chrysostoma*. Proportion of bird-hours spent in zones of different (A) temperature or (B) depth from the colony for black-browed and grey-headed albatrosses satellite-tracked from Campbell Island

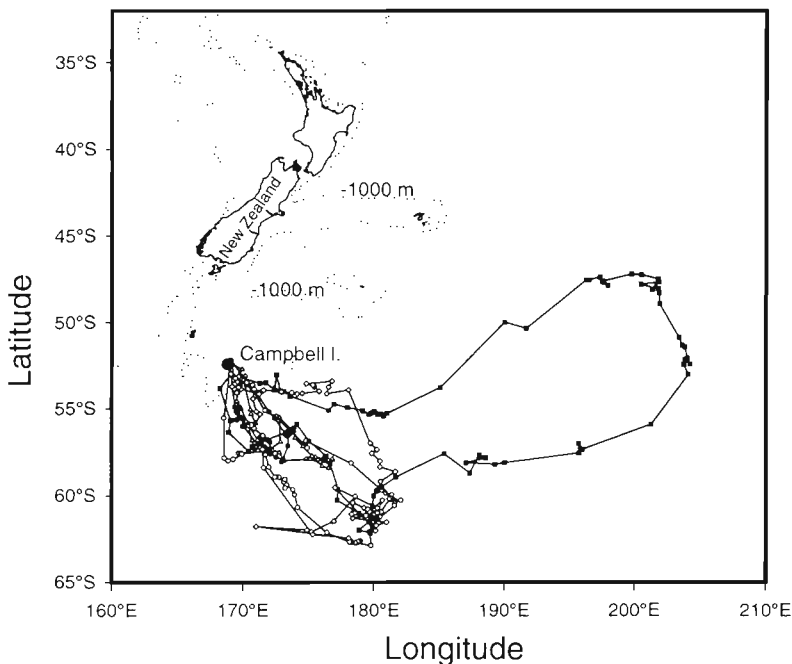


Fig. 5. *Diomedea chrysostoma*. Five grey-headed albatross foraging trips. Both birds foraged in Subantarctic Waters between Campbell Island and as far south as the PF, but spent relatively little time over the Campbell Plateau

grey-headed albatross travelled relatively long distances from the breeding site (maximum ranges 800 to 2700 km) and as far east as 204°E (Table 1). Grey-headed albatrosses used predominantly the PFZ but also the PF and SAZ (Fig. 4A), with the most southerly activity at the PF, but not over it into the AZ. Birds frequented oceanic waters almost exclusively (Table 2).

All diet samples from satellite-tracked grey-headed albatrosses *Diomedea chrysostoma* contained over 97.8% squid by mass of fresh material ($n = 5$). Twelve juvenile *Martialia hyadesi* (ML: 245 to 279 mm) and 1 *Galiteuthis glacialis* were identified. The mass of fish material was negligible in comparison to that of squid, although neritic gadiform fish from 5 different species were identified. In the diet of the 10 randomly sampled grey-headed albatross chicks, *M. hyadesi* was present in 80% of samples and dominated by mass of fresh material in 60%. The shoaling fish *Micromesistius australis* was present in 80% of samples, and dominated by mass in 20%, and other fish species dominated in the remaining 20% of samples.

Comparison between the species

Significant differences were found in the number of hours spent by birds of each species in depth and temperature zones (Table 2), with black-browed albatrosses *Diomedea melanophrys* spending more time over shelf areas and grey-headed albatrosses *D. chrysostoma* more over oceanic waters. Neither species used the lower shelf break to any great extent (Fig. 4B). The range of temperature zones used differed, with grey-headed albatross restricted to only 3 of the 5 zones used by black-browed albatrosses. In the 3 zones used by both species, grey-headed albatrosses spent significantly more time in the PFZ and significantly less time in the SAZ than black-browed albatrosses, with no differences found in the amount of time spent at the PF (Table 2).

Further comparison was made between grey-headed albatrosses *Diomedea chrysostoma* and those black-browed albatrosses *D. melanophrys* using the same environment, i.e. undertaking trips over deep waters to the south and east of the Campbell Plateau. These 2 groups of birds did not show significant differences in the daily distances travelled ($F_{1,8} = 0.4$, ns).

The hours spent by the 2 species differed in relation to depth and temperature zones (Table 2). Black-browed albatrosses spent less time over oceanic waters than grey-headed albatrosses. They showed higher usage of the SAZ and AZ than grey-headed albatrosses, which concentrated their time in the PFZ. At the PF, the proportion of bird-hours was equal between the 2 groups.

DISCUSSION

Black-browed albatross

Breeding black-browed albatrosses *Diomedea melanophrys* satellite-tracked from Campbell Island exploited a wide variety of marine environments, from the STZ to AZ. However, 2 marine environments were favoured. Firstly, birds performing trips of short duration fed on the continental shelf around Campbell Island. Secondly, they visited the PF during longer trips. The same individuals foraged during successive trips in the 2 environments, i.e. in 3 cases after a neritic trip, individuals undertook an oceanic trip. This 2-fold strategy appears to be crucial for chick provisioning at Campbell Island—provisioning rates of a larger sample of birds were studied contemporaneously to the satellite tracking, and showed that birds spent 40% of their time in long foraging trips (greater than 5 d duration), and delivered 15% of meals after such trips (Waugh et al. unpubl. data). This characteristic appears to be unique to the Campbell Island population, as at other sites conspecifics forage in relatively short trips. At the Kerguelen Islands, black-browed albatrosses use only the shelf waters during trips of 2 d on average (Weimerskirch et al. 1997b, H. Weimerskirch unpubl. data). In the Atlantic Ocean, they divide their time between 2 shelf areas at South Georgia and the South Orkney Islands, in addition to foraging at the PF (Prince et al. 1998), with an average trip duration of 2.1 d (P. Prince unpubl. data).

The exploitation of 2 marine environments through a 2-fold strategy of short and long trips has been observed in several species of albatross and petrel from other sites (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994a, 1995, 1997c, Weimerskirch 1998b). This strategy allows the exploitation of distant food resources, while allowing adults to increase the provisioning rate of the chick with shorter trips.

Exploitation of 2 distinct prey resources is apparent through the use of either neritic or oceanic waters by black-browed albatrosses *Diomedea melanophrys* from Campbell Island. Diet samples show that while foraging in short trips over the Campbell Plateau fish was

taken. Juveniles of *Micromesistius australis* were the main resource exploited. Cephalopod prey, in particular *Martialia hyadesi*, was taken when birds foraged at the PF and over oceanic waters.

The exploitation of locally rich zones is a common strategy throughout the range of the black-browed albatross, with birds from the Kerguelen Islands relying on fish stocks over shelf areas and squids, including *Martialia hyadesi* (Cherel & Weimerskirch 1995). At South Georgia, the diet shows high inter-annual variability depending on the availability of Antarctic krill *Euphausia superba* (Prince 1980, Rodhouse & Prince 1993, Croxall et al. 1997). When krill is abundant, black-browed albatrosses *Diomedea melanophrys* rely heavily on this patchy, but energy-rich, resource (Prince 1980, Veit & Prince 1997), although *M. hyadesi* is also an important component of the diet (Rodhouse & Prince 1993).

At all sites where black-browed albatross *Diomedea melanophrys* foraging strategies have been studied, feeding activity has been linked to the PF. At South Georgia, birds travel 200 km to the PF to the north of breeding sites to feed (Prince et al. 1998), while at Kerguelen Island, feeding over the shelf area coincides geographically with the PF (Weimerskirch et al. 1997b). Thus the use of the PF by birds from Campbell Island is not unusual, except that it is 2000 km from the breeding site and therefore birds must travel long distances to exploit resources there. The occurrence of *Martialia hyadesi* in the diets of black-browed albatrosses at these 3 sites may explain the strong association with the PF. This squid species is found in 'cool temperate waters of the Southern Ocean southwards to the Antarctic Polar Frontal Zone and possibly extending south of the Front' (Rodhouse & Yeatman 1990).

Grey-headed albatross

The 5 grey-headed albatrosses *Diomedea chrysostoma* tracked at Campbell Island foraged mainly in the SAZ and PFZ over oceanic waters. Studies of wandering albatrosses *Diomedea exulans* from the Crozet Islands show that they use long, looping foraging strategies over oceanic waters to maximise prey yield, which by covering long distances becomes dependable in quantity, though not in location (Weimerskirch et al. 1994b, 1997c). The grey-headed albatross from Campbell Island may exploit oceanic resources in a similar fashion, with a dependable but low-energy foraging strategy, with the main prey being cephalopod material, in particular *Martialia hyadesi*. The shoaling distribution of this species in association with the PF (Rodhouse in press) may allow some concentration of foraging activity. Squid

prey is less energy rich than fish (Clarke & Prince 1980), and grey-headed albatrosses from Campbell Island may supplement their diet by taking fish opportunistically. The occurrence of small amounts of neritic fish remains in the diet samples of satellite-tracked birds suggests that birds may use neritic resources when moving between the continental plateau and oceanic waters. However, shelf-only foraging trips may also occur, although none of the satellite-tracked birds foraged exclusively over the shelf. Feeding-frequency data from Campbell Island showed that over 95% of grey-headed albatrosses undertook trips of less than 2 d duration during the same period as the satellite tracking study and the proportion of individual birds' time spent in such short trips was substantial (0.56, $n = 28$; Waugh et al. unpubl. data). With average daily flight distances of 644 km (this study) this suggests that birds undertaking 2 d trips would spend more than half their time over shelf waters, as the shelf edge is approximately 250 km from Campbell Island at its closest. Furthermore, the shoaling fish *Micromesistius australis* was delivered to chicks by grey-headed albatrosses in 80% of cases from random diet samples, and dominated the fresh mass of 20%. The occurrence of this prey species, which is thought to be restricted to shelf areas (Hanchet 1997), suggests that grey-headed albatrosses from Campbell Island are commonly feeding on shelf resources when returning from long trips, and that birds are concentrating some foraging trips entirely over the shelf. Thus local food resources may be important for chick provisioning in addition to squid prey from the PFZ. Shelf feeding for grey-headed albatrosses from South Georgia is very limited, and these birds more commonly concentrate activity at the PF and over oceanic waters (Prince et al. 1998). At-sea studies have concluded that grey-headed albatrosses rarely use shelf areas (Ainley et al. 1984, Stahl et al. 1985, Weimerskirch et al. 1986). Either the birds from Campbell Island are more heavily reliant on shelf resources than conspecifics from other sites, or previous studies have failed to notice this less frequently employed foraging strategy, as none has combined satellite-tracking, provisioning and diet-sampling studies during the same study period.

Dietary studies of grey-headed albatrosses *Diomedea chrysostoma* show consistency across study sites, with cephalopod prey predominating. At South Georgia, squid made up 37 to 71% of the diet by mass (Croxall et al. 1997). As is the case for the satellite-tracked birds from Campbell Island, *Martialis hyadesi* dominated the squid diet of birds at South Georgia, comprising up to 79% of the biomass of squid (Clarke & Prince 1981, Rodhouse et al. 1990). At the Prince

Edward Islands, cephalopod prey dominated (Hunter & Klages 1989). *M. hyadesi* was rarely found by these authors; however, in more recent sampling it has been recognised that this species is indeed an important prey item at the Prince Edward Islands (N. Klages pers. comm.). Black-browed albatrosses *D. melanophrys* and grey-headed albatrosses returning with *M. hyadesi* prey foraged in different zones. Although this was a common prey species for both albatrosses, these differences in zone suggest that it is a widespread resource. *M. hyadesi* is important for albatrosses and larger petrels throughout the Southern Ocean (Clarke et al. 1981, Rodhouse 1989, Croxall et al. 1997, Cherel & Klages 1998).

Comparison between species

Inter-specific differences were clear in 2 aspects of the foraging behavior of black-browed albatrosses *Diomedea melanophrys* and grey-headed albatrosses *D. chrysostoma* satellite-tracked from Campbell Island. Firstly, the utilisation of resources over shelf areas and oceanic waters differed in extent between the 2 species. Thus, traditional perspectives of black-browed and grey-headed albatrosses as mainly neritic and oceanic feeders, respectively (Ainley et al. 1984, Weimerskirch et al. 1986, Prince et al. 1994), hold for the Campbell Island birds. However, at this site each species appeared to use a combined strategy exploiting both the neritic and oceanic environments to a greater extent than previous studies have indicated. Secondly, the oceanic zones exploited by the 2 species differed, suggesting an effective ecological separation, as found through at-sea observations in the Ross Sea and northwards (Ainley et al. 1984). Black-browed albatrosses had a distribution that was widespread across many temperature zones compared to grey-headed albatrosses. Black-browed albatrosses used waters to the south of the breeding site at the PF and in the AZ, while grey-headed albatrosses concentrated their activities at the PF and in the PFZ. Black-browed albatrosses also used the SAZ to a greater extent than grey-headed albatrosses. Use of the lower shelf break appeared to be limited to commuting for both species, despite the location of the Subantarctic Front close to this feature (Heath 1981). At Kerguelen Island, black-browed albatrosses feed commonly in association with the lower shelf break (Cherel & Weimerskirch 1995). This suggests that the foraging environments differ between the sites in this zone, inducing different foraging strategies for the 2 populations.

The foraging zones of several other seabird species have been studied in the New Zealand region, yet there appears to be little overlap between the ranges

described for these and the birds from Campbell Island. Wandering albatrosses *Diomedea exulans* tracked from the Auckland Islands (Walker et al. 1995) and southern Buller's albatross *D. bulleri bulleri* from the Snares (Sagar & Weimerskirch 1996) mostly exploited waters around the continental shelf of New Zealand or foraged in the mid-Tasman Sea. These zones were used, though infrequently, by the satellite-tracked black-browed albatrosses *D. melanophrys* from Campbell Island. More oceanic feeding species such as the light-mantled sooty albatrosses *Phoebastria palpebrata* (Weimerskirch & Robertson 1994) and royal penguin *Eudyptes schlegeli* (Hull et al. 1997) from Macquarie Island foraged in the area south of the Subantarctic Front. Royal penguins used waters to the northwest and south of Campbell Island; only the latter area was used by the albatrosses from Campbell Island on their return to the island, suggesting that they were exploiting this relatively rich area when travelling between the PF and the breeding site. Light-mantled sooty albatrosses travelled to the west from Macquarie Island and showed no overlap with the foraging ranges of the birds tracked from Campbell Island.

Conclusions

Black-browed albatrosses *Diomedea melanophrys* at Campbell Island showed similar foraging characteristics to conspecifics at other sites in exploiting relatively productive areas over shelves and at the PF. For this species, however, the long distance between the breeding site and the PF meant that a 2-fold strategy of oceanic and neritic trips was employed by individuals to use the resources at long distance. Grey-headed albatrosses *D. chrysostoma* foraged mainly over the PFZ, where they relied heavily on squid, and it is possible that shelf-feeding also occurred. Although only a limited number of individuals were studied, there is evidence for spatial ecological segregation between black-browed and grey-headed albatrosses, and of differential use within and between neritic and oceanic zones. Both species relied on 1 main squid prey species, *Martialia hyadesi*, although it was taken from different regions of the PFZ.

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