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Foraging behaviour in two Antarctic fur seal colonies with differing population recoveries

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ABSTRACT: We compared Antarctic fur seals *Arctocephalus gazella* breeding at 2 contrasting sites on South Georgia: one high density colony at Bird Island and one lower density colony at Cooper Bay. The population at Cooper Bay was considerably smaller than that at Bird Island despite ample suitable breeding area being available. At Cooper Bay, female seals were longer but weighed less than those breeding at Bird Island and, whilst both maintained the same rate of female pup growth, male pups grew faster at Cooper Bay. Although Bird Island seals dived deeper, they dived less often than Cooper Bay seals so that both populations spent comparable amounts of time in the bottom phase of dives actively foraging. Longer distance oceanic foraging trips that were observed at Bird Island were almost entirely absent from Cooper Bay. Both populations fed on Antarctic krill, but there was an absence of myctophid prey in the diet of seals at Cooper Bay. Evidence suggests that the favoured myctophid prey of fur seals at South Georgia, *Protomyctophum choriodon*, are absent from the colder waters around the south-east of the island. We propose that, if these energy-rich prey are unavailable in this region then seals at Cooper Bay may find it hard to offset the increased costs of foraging trips with longer duration and distance. This potentially reduced niche width means that the Cooper Bay population may be less buffered against environmental variability. Although food resources appeared to be sufficient during the period of our study, the south-eastern region of South Georgia has increased variability in food resources that, coupled with a smaller area in which to forage, might explain the reduced population size compared to the north-eastern end of the island.

KEY WORDS: Antarctic fur seal · *Arctocephalus gazella* · Foraging · GAMM · South Georgia · Niche width · Myctophid · Krill · *Euphausia superba* · Intraspecific competition

INTRODUCTION

Individual organisms must cope with environmental variability by either avoidance or behaviour adjustment, but the extent to which individuals can adapt differs amongst species. Understanding this flexibility is important for interpreting species-specific responses to changing environments. How well a population is buffered against perturbations can, in part, be determined by the size of niche it exploits. For example, populations tend to stabilize where competition between conspecifics is reduced by resource partitioning (Tschumy 1982) and the overall niche width of a species can be effectively increased if there are differences in resource use by different phenotypes (Bolnick et al. 2003). This partitioning can take the form of different diets, habitat use, or foraging behaviour (Schoener 1986).

In colonial animals foraging from a central place, intraspecific competition is likely to be higher closer to the colony, which can lead to localised depletion of resources (Ashmole 1963, Lewis et al. 2001). In the face of reduced food resources many animals are known to adapt their time activity budgets (Hixon et al. 1983, Furness & Birkhead 1984, Wanless et al. 1992, Boyd 1999, Davoren & Montevecchi 2003, Harding et al. 2007). This type of behavioural plasticity is a useful trait for marine predators living in a variable environment characterised by patchy and ephemeral food resources.

The waters around South Georgia are highly productive in Antarctic krill *Euphausia superba*, the principal

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prey of large numbers of land-based predators (Atkinson et al. 2001), including the Antarctic fur seal *Arctocephalus gazella* (Reid & Arnould 1996). Fur seal breeding success is closely correlated to krill abundance, with pup production and survival being negatively impacted during periods of low abundance (Forcada et al. 2005). During these 'bad' years, lactating females often struggle to find enough food to maintain their own condition and provision their pups (McCafferty et al. 1998). Female fur seals act as central place foragers, interspersing foraging periods at sea with time ashore suckling their pups. In the face of food stress they attempt to maintain provisioning by increasing the time they spend at sea and spend more time diving and dive deeper (Boyd et al. 1991, McCafferty et al. 1998). As such, time spent at sea foraging is used as a monitoring index, with an increase used to indicate poor local krill abundance (CCAMLR 1995).

The different hydrographic regimes around South Georgia exhibit contrasting nutrient and temperature characteristics, with waters to the east holding higher nutrient concentrations and having lower water temperatures compared with those in the north-west (Whitehouse et al. 1999, Atkinson et al. 2001). Primary productivity is much higher in this north-western region (Korb & Whitehouse 2004) and mezoplankton abundance is also similarly increased at the western, compared to the eastern, end (Shreeve et al. 2002). The krill found in the eastern end of the island tend to be small whereas larger krill, i.e. those favoured by seals (Reid et al. 1999), are found at the western end (Watkins et al. 1999).

Antarctic fur seals in South Georgia were hunted to near extinction during the first half of the nineteenth century (Bonner 1968). By the 1930s the first post-sealing pups were recorded at Bird Island, and the population subsequently expanded rapidly to a level with an estimated pup production of 269000 in 1990–1991 (Boyd 1993) that is now believed to be in excess of 4 million individuals (British Antarctic Survey [BAS] unpubl. data). However, this recovery is mostly confined to the beaches at the north-western end of South Georgia. Fur seals were first reported at the south-eastern end of the island, possibly as early as 1915 and definitely by 1946 (Bonner 1968). The first published report of breeding on the south-east of the island was in 1971, with 6 to 10 pups sighted in Cooper Bay (Payne 1977). However, whilst the north-western population has increased in density and rapidly expanded, spreading out from Bird Island mostly along the northern coast, the population around Cooper Bay has remained low (4518 adult females; Boyd 1993) and has not spread substantially beyond the immediate proximity of the bay.

We compared the ecology of lactating Antarctic fur seals at 2 contrasting breeding sites on South Georgia: one high density colony at Bird Island and one lower density colony at Cooper Bay. We concurrently measured the at-sea behaviour, diet, and pup growth at both Bird Island and Cooper Bay in order to:

(1) Assess the plasticity of their behaviour within environmental and physiological constraints and assess the populations' responses to differing environmental regimes.

(2) Investigate potential causes of the differences in the speed and size of the respective population recoveries.

MATERIALS AND METHODS

We tracked lactating female Antarctic fur seals *Arctocephalus gazella* on foraging trips to sea from 2 breeding beaches around South Georgia — Bird Island (Freshwater Inlet, 38.02° W 54.00° S) and Cooper Bay (35.49° W 54.47° S) — between December 2005 and March 2006. Females were caught using a noose pole and then held in a restraint board for a total handling time of <20 min (Gentry & Holt 1982). Standard length (with seal in ventral recumbency), girth (cm), and mass (kg) were measured, and instruments were glued onto the dorsal fur along the line of the spine using quickset 2-part epoxy resin. Seals were fitted with platform transmitter terminals (PTTs, Sirtrack; Kiwisat 101; 245 g, 13 × 6.5 × 1.9 cm) and time depth recorders (TDRs) with external temperature sensors (Wildlife Computers, MK7 and MK9; 50 g, 9.5 × 2.5 × 2.5 cm). Upon their return, seals were recaptured using the same method, and all instruments were recovered.

Biometrics. A linear model (LM) was used to compare the sizes of the seals at the 2 breeding beaches (Cran R, package stats). To remove potential biases associated with measuring mass at different stages of lactation we used data from 39 seals (25 from Bird Island and 14 from Cooper Bay) that were all caught within the perinatal period 1 to 2 d after giving birth. Mass was used as the response variable, with length, girth, location, and their interactions tested as the predictors. Models were compared using Akaike's Information Criterion (AIC). Effects were dropped if the simplified model had a lower AIC value (~ δAIC = 2), and residual plots were examined to assess model fits.

A group of 14 pups (11 male, 3 female) at Cooper Bay and 29 pups (17 male, 12 female) at Bird Island were caught within a day of their birth, assessed by the presence of a fresh umbilicus, and given individual marks with peroxide hair dye. These seals were then weighed on an opportunistic basis (maximum of once daily for up to 56 d) whenever the mother was at sea. Pup growth rates were compared using linear mixed effects models (Cran R, package nlme), with sex and breeding beach as explanatory variables and individual used as a random effect. Models were compared using AIC and a likelihood ratio test, and the model fit was assessed by examination of the residual plots and partial residual plots.

Location data. Foraging locations were estimated from satellite uplinks after filtering to remove potentially unreliable records. A 3-stage filtering algorithm was employed based on Austin et al. (2003), with only high accuracy (<3 km, Vincent et al. 2002) uplinks of class 1, 2, and 3 (Service Argos 2008) using the package diveMove in R (Luque 2007, R Development Core Team 2009). First, locations were rejected if the straight-line speeds required to travel to the 4 neighbouring locations (2 before and 2 after chronologically) were all >3 m s^{-1}. The second stage used an iterative forward/backwards averaging algorithm developed by McConnell et al. (1992), using a maximum mean velocity of 3 m s^{-1}. Third, locations where the distance from the previous location exceeded 60 km (the 99th percentile of distances between locations) were rejected.

Diving data. TDRs were programmed to record depth to a resolution of 1 m every 2 s. Each record was corrected for drift in the zero depth reading using dedicated software (Instrument Helper, Wildlife computers). To avoid inaccuracies in determining when seals were at the surface, only excursions to greater than 4 m were considered dives (Staniland et al. 2010). The TDR record was combined with the relevant filtered satellite position fixes to give an approximate location for each dive. When the timing of a dive fell between the times of 2 position fixes, the location was interpolated relative to the fixes assuming that the seal swam at a constant speed between them (Boyd et al. 1998). The depth of water at the interpolated location of each dive was estimated by selecting the nearest known depth value from a bathymetric dataset (Fretwell et al. 2009). The dive rate was defined as the mean vertical distance travelled per hour of the trip. Bottom time was defined as the time between the end of the descent and the beginning of the ascent. These points were taken to be when, within 35% of the maximum depth, the instantaneous rate of vertical movement decreased below the mean rate, which was measured between the surface and the maximum depth (Boyd et al. 1995).

Analysis. The seals' behaviours were analysed at the foraging trip and individual dive level. Where data deviated significantly from normal, appropriate transformations were used. Trip durations (square root transformed), mean depth of water in which diving took place and maximum distance reached from the breeding beach (log transformed) were compared between the 2 breeding beaches using data from the wet dry records of the TDRs and the at-sea location data. We used linear mixed effects models (lme package, R Development Core Team 2009) with breeding beach as a fixed effect and seal as a random effect, to take into account multiple trips from some seals. We also tested deployment date as a fixed effect in the models, as there was some temporal separation between the deployments at the 2 breeding beaches.

Mean values of each dive variable and the summed number of dives were calculated for each hour of each trip. Generalized additive mixed effects models (GAMM) were fitted to these mean values using individual seal (tag) as a random effect, and smooth terms were fitted using thin plate penalised regression splines (Wood 2006). Parameters used as the response variable were depth (m), total bottom time (s), and number of dives. Explanatory variables tested in the models were proportion of the time into the trip (trip time), distance from the breeding beach (km), seal mass (kg), solar elevation (degree), water depth as a factor (shelf < 1000 m < oceanic), and breeding beach. Solar elevations were calculated using the Maptools package in R (R Development Core Team 2009). The timing of sunrise and sunset differed between the 2 colonies because of the disparity in latitude. Therefore, we used solar elevation to compare changes in behaviour throughout the day and night.We also looked at the interaction between water depth and breeding beach. The intercept of these models was allowed to vary randomly with seal. We tested differences between the 2 regions by fitting models with separate smooth terms for the 2 breeding beaches. We accounted for autocorrelation using a structure of order 1 within individual seals (corAR1(form=~1|tag)) and using a power variance function to allow for within group heteroscedasticity (weights=varPower()). For number of dives and bottom time we used a negative binomial family distribution ($\theta = 0.501$ no dives, $\theta = 0.33$ bottom time) and for depth of dives we log-transformed the data and used a Gaussian family with an identity link function. Analyses were performed in R using the gamm function of the mgcv package (Wood 2006). Best model fits were assessed based on the lowest AIC of the fixed-effects component of the model and the approximate significance of smooth terms assessed by *F*-tests and the confidence intervals of the random-effects components of the model. Residual plots and partial residual plots were examined to assess model fits.

Environment. To investigate the overall conditions the seals were foraging in, we took the mean temperature, measured by the calibrated TDR external temperature sensor, at 35 m depth on each trip. The primary productivity at the 2 locations was assessed using the average chlorophyll *a* concentration between December 2005 and March 2006. Values were calculated from SeaWiFS (accessed via Environmental Data Connector, NOAA-PFEL) standard mapped images using rectangular areas defined by the seals' foraging ranges (Cooper Bay 54° S, 34° W to 55.2° S, 36° W; Bird Island 52.8° S, 38° W to 54.2° S, 40.5° W).

Diet. We collected 10 fresh whole scats on a weekly basis at each breeding beach between 21 December 2005 and 25 January 2006. Scats were processed according to the methods described in Reid (1995). Scats were broken up in water by gentle agitation so that prey remains were separated out. Material that was in suspension, e.g. krill carapaces, was poured into a sorting tray (35 × 45 cm) and examined. Ten carapaces were randomly sampled from each scat, where possible, to make a maximum weekly total of 100. Removed carapace lengths were measured under a binocular microscope with an eye piece graticule. The dense residue remaining after separation was examined under a binocular microscope and prey remains, such as fish otoliths and eye lenses, were picked out. Recovered otoliths were identified to species where possible using reference material and published guides (Reid 1996). Because of difficulties in identifying some eroded Nototheniid otoliths, those identified as *Lepidonotothen larseni* may include a few closely related species and were therefore described as an aggregation.

At Cooper Bay, the weekly samples were supplemented with enemas taken from satellite tracked seals (Staniland et al. 2003). These enemas were processed using the same the methods for scats. Krill sizes consumed at the 2 locations were compared using linear mixed effects models (Cran R, package nlme). Krill length was used as the response variable, and date and breeding beach were used as fixed effects. Date was also tested as a random effect. All models were fitted using maximum likelihood so that they were comparable. Best models were assessed based on the lowest AIC and residual plots were examined to assess model fits.

The fish component of the diet was compared between Bird Island and Cooper Bay using all scats and enemas collected within the sampling period. The data were expressed as the incidence of fish, calculated as the number of samples containing fish remains divided by the total number of samples, and compared between islands using a *G*-test of independence. The number of fish consumed at Bird Island was regressed against the week of sampling to check if diet was changing as the season progressed, and residuals were used to confirm if a linear model was the most appropriate.

Cooper Bay pup production. Pup production was estimated at Cooper Bay by direct counts immediately after the estimated peak of pupping (14 December 2005). Two researchers independently counted the number of pups within small sections of beach, until consensus, along the entire accessible coastline of Cooper Bay (~3.5 km). The total number of pups counted over 2 d was corrected using the percentage of pups born after the count days. This was calculated using repeated daily counts of a small section of beach (~200 m) that produced a total of 215 pups. Published data were used for Bird Island estimates (Forcada et al. 2005).

RESULTS

Location and environment

Seals at both locations foraged mostly over the shelf and shelf break areas although a number of females from Bird Island foraged in deeper water (Fig. 1a). The waters where the seals from Bird Island (BI) were foraging were significantly more productive than those around Cooper Bay (CB) (*t*-test; BI_{mean} = 1.14 mg chl m^{-3}, CB_{mean} = 0.36 mg chl m^{-3}, $t_{573} = 22.7$, $p < 0.01$: Fig. 1b). Seals at Cooper Bay foraged in significantly colder water shown by the mean temperature at 35 m in both locations (*t*-test; BI_{mean} = 3.2°C, CB_{mean} = 2.0°C, $t_{22.2} = -6.90$, $p < 0.01$). This was also reflected in the temperature ranges experienced at this depth (BI = 1.15 to 4.6°C, CB = 0.5 to 3.45°C; Fig 2).

Diving

Trip durations were significantly shorter at Cooper Bay compared to Bird Island (lme, $F_{2,52} = 764$, $p < 0.0001$, Table 1). The maximum distance reached from the breeding beach was also shorter for females at Cooper Bay (lme, $F_{2,48} = 23903$, $p < 0.0001$, Table 1) and these seals, on average, foraged in shallower water than those at Bird Island (lme, $F_{2,48} = 133$, $p < 0.0001$, Table 1). Date of deployment was not a significant factor in any of the models tested (trip duration, $AIC_{with\ date} = 259$, $AIC_{without\ date} = 229$; max. distance, $AIC_{with\ date} = 97$, $AIC_{without\ date} = 63$; water depth, $AIC_{with\ date} = 922$, $AIC_{without\ date} = 903$).

The model explaining mean maximum dive depth per hour showed that the solar elevation, distance from the breeding beach, and breeding beach were all significant covariates (Table 2). The smooth of solar elevation was different between the 2 breeding beaches with a more pronounced increase in depth around dusk and dawn for seals at Bird Island (Fig. 3a). Distance from the breeding beach showed a curvilinear pattern that was the same for both locations (Fig. 3b).

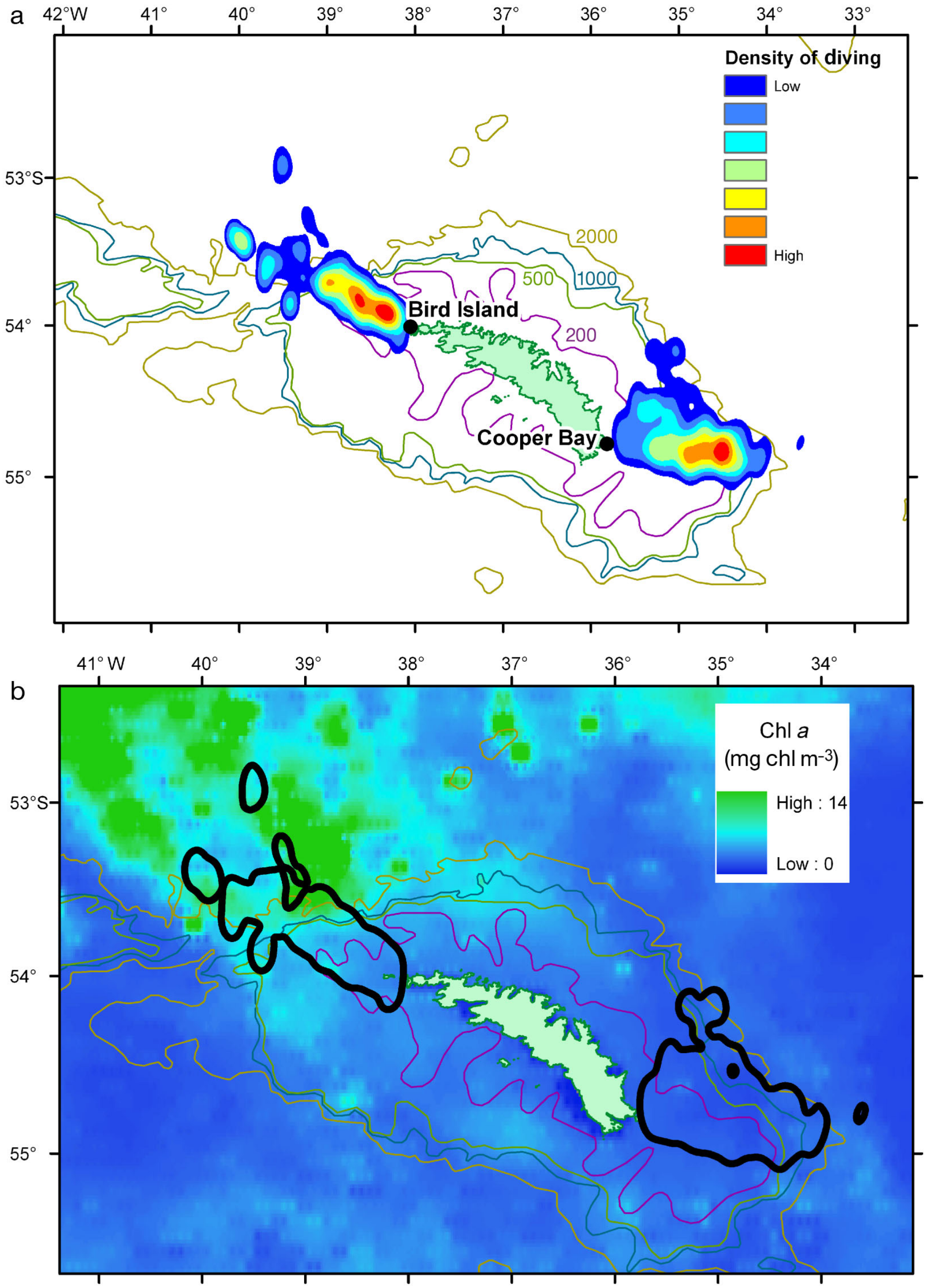

Fig. 1. *Arctocephalus gazella*. (a) Foraging density plots from 2 breeding beaches on South Georgia showing areas of high (red) and low (dark blue) numbers of dives. Contour lines are shown in m. (b) Foraging areas of the study seals (solid black lines) overlaying mean chlorophyll *a* concentrations for the period from December 2005 to March 2006

Dive depths were shallower close to the breeding beaches and increased to a peak at around 80 km from shore (Fig. 3b). Overall the dive depths at Cooper Bay were shallower than those at Bird Island (Fig. 3c).

Solar elevation, distance from the breeding beach, breeding beach, and the depth of water were significant explanatory variables for the number of dives per hour (Table 2). Seals at both breeding locations dived mostly at night, with a slight increase in activity at the highest solar elevations (Fig. 4a). The distance from the breeding beach had no effect on the activity of seals at Bird Island, whereas for seals at Cooper Bay, the frequency of diving was lower close to the breeding beach (Fig. 4b). Both populations dived more frequently when in shallower shelf waters, but Cooper Bay seals dived less per hour overall than seals foraging from Bird Island (Fig. 4c).

The increased frequency of diving in shelf waters was not reflected in the time spent in the bottom phase of dives, as neither island nor water depth were significant terms in the best model fit (Table 2). Solar elevation showed that the most active foraging time was at night (Fig. 5a) and peaked around a distance of 70 km from both breeding beaches (Fig. 5b).

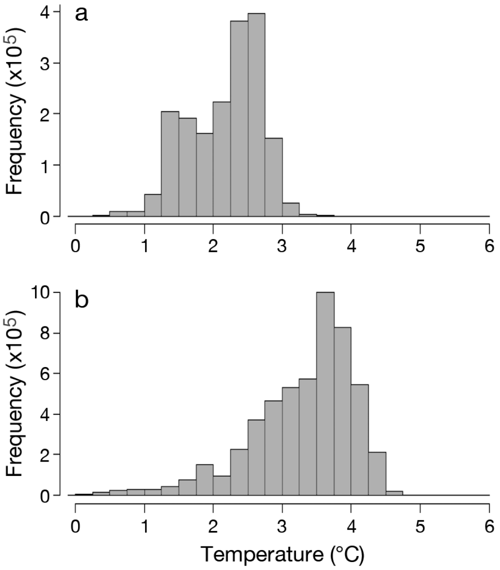

Fig. 2. *Arctocephalus gazella*. Histograms of temperature recorded at 35 m for each dive of female fur seals foraging at (a) Cooper Bay and (b) Bird Island

Biometrics

The best model explaining seal mass included length, girth, and breeding beach as significant terms (Table 3). Seals at Cooper Bay were on average almost 8 kg lighter than females at Bird Island of the same length. This was mostly because the seals at Cooper Bay were longer (mean length; CB = 132 cm, BI = 124 cm) and thinner (mean girth; CB = 83 cm, BI = 87 cm).

Over the period of study, pup growth approximated to a linear function. The best model fit used pup age, sex, breeding beach, and the interaction between them as explanatory variables (Table 4). Males were heavier on average than females, and pups at Cooper Bay were heavier than those at Bird Island. The growth rates of males were slightly higher than females and the males at Cooper Bay grew faster than those at Bird Island. There was no significant difference in the growth rates of females between the 2 areas; however, the sample size of female pups at Cooper Bay was low so the comparison had little power to detect differences.

Diet

The best model to describe krill lengths consumed by the seals showed that breeding beach was an important factor (Cooper Bay, coefficient = 2.33, SE = 0.40, df = 955, $t = 5.76$, $p < 0.001$), whilst date was a significant random effect ($\text{AIC}_{\text{with date}} = 6006.94$, $\text{AIC}_{\text{without date}} = 6141$). Krill were significantly larger at Cooper Bay (mean ± SE = 48.09 ± 0.24 mm) than at Bird Island (mean = 46.83 ± 0.28 mm).

There was no difference in the incidence of fish remains in scats between the 2 breeding beaches (Cooper Bay = 11/66, Bird Island = 8/50, $G = 0.009$, $p = 0.92$). All of the species identified from otoliths at Cooper Bay were nototheniids: 30 *Lepidonotothen larseni* agg., 2 *Champsocephalus gunnari*, and 2 *Trematomus hansoni.* At Bird Island, myctophid otoliths dominated, but they were all taken from 1 scat sample; the other scats contained nototheniid remains: 20 *Electrona carlsbergi*, 7 *Lepidonotothen larseni* agg., 2 *Champsocephalus gunnari*, and 1 *Gobionotothen gibberifrons*. There was also no evidence of a change in the amount of fish consumed at Bird Island between December 2005 and the end of March 2006 (linear regression: $F_{1,11} = 3.27$, $\text{coefficient}_{\text{week of sampling}} = 1.28$, $p = 0.098$).

Cooper Bay pup production

A total of 2394 pups were counted on the available breeding habitat at Cooper Bay. Repeated counts on a subsample of beach revealed that 83% of the total pups had been born by the date of the census; therefore, the corrected estimate of pup production was 2789. In the 1990–1991 breeding season, pup production on Bird Island was estimated at 45 826. Pup production on 2 neighbouring mainland areas (Undine: 54.04° S, 37.97° W and Elsehul: 54.03° S, 37.96° W), within 7 km of our Bird Island study site, was 79 083 (Boyd 1993).

DISCUSSION

The present study shows foraging differences between 2 breeding locations on South Georgia: Bird Island and Cooper Bay. The most obvious difference was in the lack of diving in deeper water by seals at Cooper Bay. Seals in this south-easterly region mostly confined their foraging to shallow shelf waters, close to the breeding beach, and this was reflected in their trip durations, which were much shorter.

Females at Cooper Bay were longer but thinner than those at Bird Island. Both populations maintained a steady pup growth, and male pups at Cooper Bay actually had a higher growth rate. The diet at both locations was dominated by Antarctic krill and the incidence of fish in the diet was comparable. However, despite sampling more scats at Cooper Bay, there were no myctophid fish found in the diet, and the seals here were foraging in colder waters.

The differences in the lengths of seals could be due to a number of factors. It is difficult to accurately measure the length of conscious seals, and a degree of caution must be taken when comparing these data. How-

Table 1. *Arctocephalus gazella*. Summary of deployment details of platform transmitter terminals, biometrics of seals, and associated trip/diving statistics from Cooper Bay and Bird Island. –: no data (seal not measured)

ID	Trip number	Deployment date	Length (cm)	Girth (cm)	Mass (kg)	Trip duration (h)	No. dives	Max. distance reached (km)	Water depth (m)
Cooper Bay									
sat1_1_9_jan	1	01-Jan-06	148	87	37	100	1125	175	360
sat1_15_18_jan	1	15-Jan-06	137	76	33	68	1079	160	198
sat1_16_26_dec	1	16-Dec-05	144	93	44	47	358	120	1526
sat1_16_26_dec	2					55	583	147	572
sat1_18_22_jan	1	18-Jan-06	130	79	30	88	1762	83	538
sat1_27_1_jan	1	27-Dec-05	145	86	41	81	881	149	370
sat1_9_14_jan	1	09-Jan-06	126	77	29	75	1096	180	339
sat2_1_6_jan	1	01-Jan-06	131	82	32	103	1074	207	807
sat2_15_20_jan	1	15-Jan-06	138	77	31	86	1138	120	240
sat2_16_26_dec	1	16-Dec-05	135	91	42	54	376	148	280
sat2_16_26_dec	2					53	553	126	194
sat2_16_26_dec	3					59	684	118	818
sat2_20_23_jan	1	20-Jan-06	127	80	32	38	788	102	143
sat2_27_31_dec	1	27-Dec-05	144	88	40	73	976	167	215
sat2_6_14_jan	1	06-Jan-06	122	73	24	174	2878	461	2597
sat3_10_14_jan	1	10-Jan-06	129	84	31	70	1056	187	487
sat3_15_19_jan	1	15-Jan-06	131	85	36	89	1427	159	298
sat3_16_25_dec	1	16-Dec-05	140	84	44	67	747	183	211
sat3_19_26_jan	1	19-Jan-06	129	84	39	111	1739	190	306
sat3_26_31_dec	1	26-Dec-05	143	79	34	62	858	169	483
sat3_31_5_jan	1	31-Dec-05	140	90	36	73	737	159	785
sat3_5_9_jan	1	05-Jan-06	127	74	25	88	1136	215	867
sat4_15_19_jan	1	15-Jan-06	136	90	38	79	1147	154	643
sat4_16_30_dec	1	16-Dec-05	126	82	30	128	987	260	2626
sat4_20_23_jan	1	20-Jan-06	123	74	27	36	673	77	193
sat4_3_6_jan	1	03-Jan-06	144	89	40	62	1095	170	539
sat4_30_2_jan	1	30-Dec-05	144	81	42	61	814	132	403
sat4_6_14_jan	1	06-Jan-06	134	88	33	27	378	88	184
sat4_6_14_jan	2					100	1229	205	532
sat5_1_7_jan	1	01-Jan-06	144	88	40	100	1524	211	610
sat5_12_18_jan	1	12-Jan-06	133	76	30	44	873	77	212
sat5_12_18_jan	2					30	616	89	154
sat5_16_23_dec	1	17-Dec-05	129	83	32	81	1391	149	142
sat5_18_24_jan	1	18-Jan-06	138	82	39	87	1377	150	211
sat5_23_1_jan	1	23-Dec-05	135	78	30	91	1113	159	543
sat5_23_1_jan	2					85	1322	194	391
sat5_7_11_jan	1	07-Jan-06	126	77	27	87	955	189	402
sat6_16_20_jan	1	16-Jan-06	134	79	31	78	1248	167	209
sat6_17_28_dec	1	17-Dec-05	142	86	39	32	309	123	553
sat6_17_28_dec	2					49	451	127	331
sat6_20_28_jan	1	20-Jan-06	144	86	42	129	1729	169	359
sat6_28_2_jan	1	28-Dec-05	139	84	34	78	879	98	1308
sat6_3_7_jan	1	03-Jan-06	143	101	43	66	1177	165	775
sat6_8_16_jan	1	08-Jan-06	138	82	33	105	1556	93	950
Mean			**136**	**83**	**35**	**76**	**1043**	**158**	**566**
Bird Island									
W7163/63	1	22-Feb-06	121	84	35	132	1566	300	2834
W7163/64	2					78	1406	139	221
W7302/02	1	04-Jan-06	121	89	43	59	470	131	204
w7303/03	1	09-Jan-06	124	71	34	82	951	149	959
W7304/04	1	17-Jan-06	129	81	38	65	847	107	178
W7306/06	1	22-Jan-06	108	74	27	69	1021	108	186
W7307/07	1	28-Jan-06	115	73	30	129	1468	236	898
W7309/09	1	02-Feb-06	125	85	36	140	1883	261	2157
W7310/10	1	08-Feb-06	115	69	27	178	864	331	2769
W7311/11	1	06-Feb-06	–	80	38	86	1127	152	273
W7313/13	1	15-Feb-06	131	78	37	118	1274	225	1181
W7314/14	1	21-Feb-06	129	80	35	73	319	58	135
W7316/16	1	03-Mar-06	129	80	40	144	1352	202	2597
W7344/44	1	21-Mar-06	117	71	23	73	668	130	1034
Mean			**122**	**78**	**34**	**102**	**1087**	**181**	**1116**

Table 2. *Arctocephalus gazella*. GAMMs used to explain variability in mean dive variables per hour. Estimates and significance terms are shown for the best model fit; factors in brackets are the colony (BI or CB) or water depth (shelf or oceanic) for which the estimate is derived. Degrees of freedom and rank of smooth terms are estimated. *Best competing models are shown with their Akaike's Information Criterion (AIC). BI: Bird Island; CB: Cooper Bay

Dive statistic (mean of hour)	Model term	AIC	— Parametric coefficients —			Approximate significance of smooth terms		
			Estimate	SE	*t*	df	*F*	p
Max. depth	Intercept	6873	3.13	0.07	43.23			<0.0001
	Breeding beach (BI)		−0.37	0.08	−4.45			<0.0001
	Solar elevation (BI)					6.38	16.25	<0.0001
	Solar elevation (CB)					2.65	27.79	<0.0001
	Distance from beach					5.99	18.30	<0.0001
*Max. depth = Solar elevation (by breeding beach) + Distance from beach (by breeding beach) + Breeding beach; AIC = 6877								
No. of dives	Intercept	15238	2.65	0.14	18.39			<0.0001
	Breeding beach (BI)		−0.66	0.19	−3.54			0.0003
	Water depth (shelf)		0.15	0.07	2.10			0.035
	Solar elevation					6.49	81.60	<0.0001
	Distance from beach (CB)					4.10	22.82	<0.0001
*No. of dives = Solar elevation + Distance from beach (CB) + Breeding beach × Water depth; AIC = 15241								
Bottom time	Intercept	17407	5.71	0.07	80.3			<0.0001
	Solar elevation					6.35	27.03	<0.0001
	Distance from beach					5.49	33.09	<0.0001
*Bottom time = Solar Elevation + Distance from beach + Proportion of time into trip; AIC = 17409								

ever, there were consistent differences between the 2 locations that would suggest there were real differences. It could be that seals at Cooper Bay were able to invest more into growth than those at Bird Island; if this were the case we might also expect them to have the same mass/length ratio, but they were actually significantly lighter and thinner. The seals at Cooper Bay may represent larger, older seals which, in turn, would suggest that younger, smaller seals are in some way selected against. Data from Bird Island suggest that younger seals are more susceptible to years of low food availability and suffer proportionally higher mortality than older seals (BAS unpubl. data). However, without appropriate age data, it is impossible to investigate this further.

The population at Cooper Bay was considerably smaller than that at Bird Island, despite the availability of ample suitable breeding areas. Within Cooper Bay, large stretches of sheltered beach and rock platforms adjacent to breeding areas were unused by seals, and other seemingly ideal bays close by were empty. At the north end of South Georgia, almost all flat accessible areas along the shore are used for breeding, and the density of individuals in the breeding colonies is much higher. The last published census of South Georgia took place in 1990–1991, a year of low pup production, and so the pup production estimate of 45 826 for Bird Island taken from this count is likely to be an underestimate (Boyd 1993). The published combined count from Cooper Bay, Larsen Harbour, and Cooper Island in the same census was 4518 breeding females, which would equate to 3207 pups (given a pregnancy rate of

Table 3. *Arctocephalus gazella*. Best fit linear model used to explain variability in mass between Cooper Bay and Bird Island (Akaike's Information Criterion, AIC = 202)

Model term	Value	SE	*t*	p
Intercept	−38.93	10.82	−3.60	<0.01
Length	0.35	0.10	3.56	<0.01
Girth	0.42	0.09	4.80	<0.001
Location (Cooper Bay)	−8.36	1.46	−5.72	<0.001

Table 4. *Arctocephalus gazella*. Best fit of generalized model of pup growth using a linear mixed effects with individual pup as a random effect

Model term	Value	SE	*t*	df	p
Intercept	7.02	0.222	31.7	625	<0.001
Sex	1.28	0.271	4.7	40	<0.001
Age (days after birth)	0.07	0.004	19.2	625	<0.001
Location (Cooper Bay)	0.76	0.276	2.8	40	0.053
Sex (male) × Age	0.02	0.005	4.3	625	<0.001
Sex (female) × Age × Location (Cooper Bay)	−0.01	0.012	−0.9	625	0.371
Sex (male) × Age × Location (Cooper Bay)	−0.03	0.005	5.8	625	<0.001

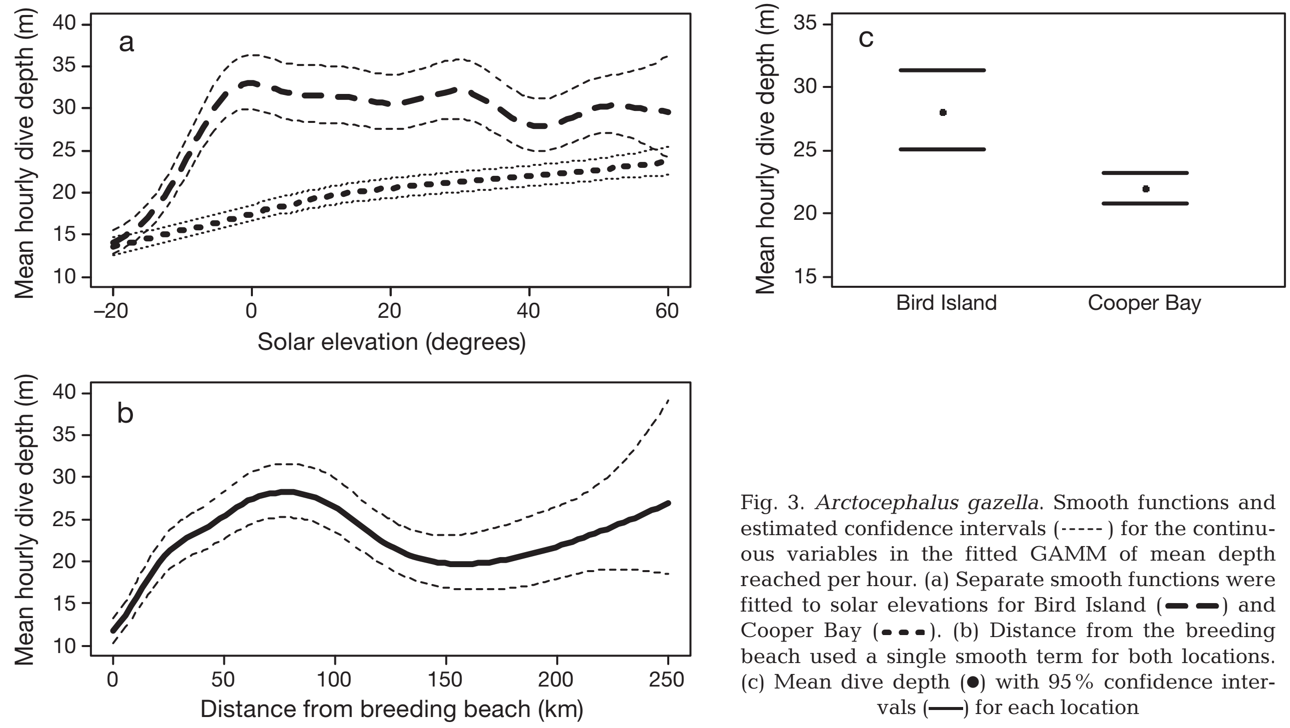

Fig. 3. *Arctocephalus gazella*. Smooth functions and estimated confidence intervals (-----) for the continuous variables in the fitted GAMM of mean depth reached per hour. (a) Separate smooth functions were fitted to solar elevations for Bird Island (▬ ▬) and Cooper Bay (• • •). (b) Distance from the breeding beach used a single smooth term for both locations. (c) Mean dive depth (●) with 95% confidence intervals (——) for each location

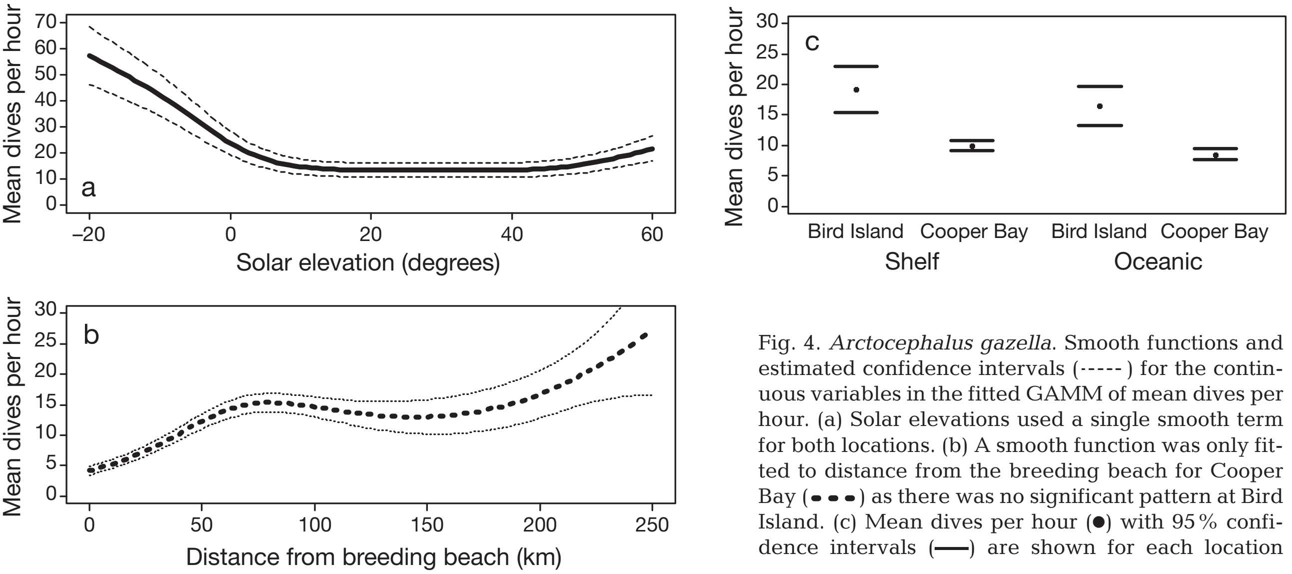

Fig. 4. *Arctocephalus gazella*. Smooth functions and estimated confidence intervals (-----) for the continuous variables in the fitted GAMM of mean dives per hour. (a) Solar elevations used a single smooth term for both locations. (b) A smooth function was only fitted to distance from the breeding beach for Cooper Bay (• • •) as there was no significant pattern at Bird Island. (c) Mean dives per hour (●) with 95% confidence intervals (——) are shown for each location

71%, Boyd 1993). Therefore, it appears that the Cooper Bay population estimated in the present study as 2789 pups has not grown significantly and has remained at a similar size over the 15 years between the studies. Recent aerial photography has confirmed this and shown no horizontal spreading of this south-eastern population (BAS unpubl. data).

If there were a consistent supply of plentiful food then we would expect the population at Cooper Bay to have expanded to take advantage of it. Other factors that can limit population size do not appear to be relevant in this case. Predation of adult seals is not thought to be a significant factor at South Georgia, and juvenile predation by leopard seals is confined to winter months (Forcada et al. 2009). Post weaning and adult winter survival are unlikely to differ significantly between the 2 colonies given their proximity in relation to the extensive movements of non-breeding seals

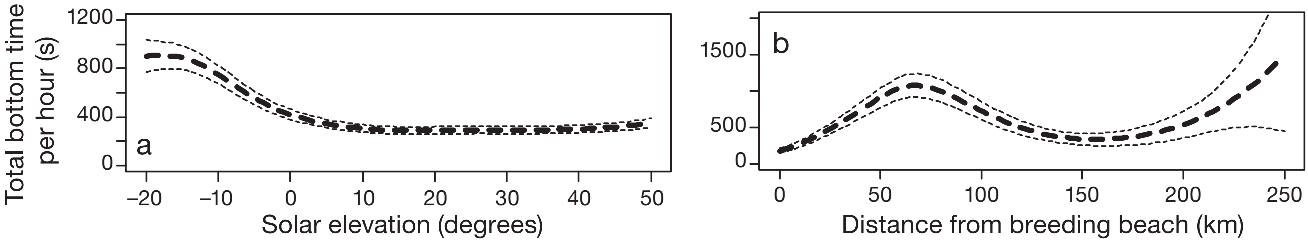

Fig. 5. *Arctocephalus gazella*. Smooth functions (▬ ▬) and estimated confidence intervals (-----) for the continuous variables. (a) Solar elevations and (b) distance from the breeding beach in the fitted GAMM for time spent in the bottom phase of dives per hour

and weaned juveniles (Boyd et al. 1998, 2002, Warren et al. 2006). Also, seals are known to recruit to Cooper Bay from the north of the Island, e.g. during the course of the study, an adult female tagged at Bird Island as a pup was observed raising her own pup at Cooper Bay. Given the available areas for breeding at Cooper Bay and the potential for recruitment, it seems highly likely that differences within the seals' summer foraging ranges are responsible for the smaller, less dense breeding population observed ashore.

The overall pattern of diving activity, measured by time spent in the bottom phase of dives, was the same at both locations. Time spent in the bottom phase of dives has been used as an indication of patch quality, with longer durations correlated with a higher net rate of energy intake (Thompson & Fedak 2001, Mori & Boyd 2004). Seals showed increased activity around 70 to 80 km from the 2 breeding beaches, which equates to the shelf break region. The shelf break region has a major influence on water mass distribution to the north of South Georgia, with a frontal zone near the 500 m isobath between more productive, warmer, less stratified shelf water and colder more saline water off shelf (Brandon et al. 1999). This front is an area characterised by higher krill densities (Trathan et al. 2003). The effect of travelling dives can be seen at both locations, with a higher frequency of shallower dives in shallow water, and at Cooper Bay close to the breeding beach. Although, overall, Cooper Bay seals undertook more frequent shallower dives than seals at Bird Island, both populations showed a pattern consistent with feeding on diurnally vertically migrating prey. Their diving was concentrated in the night, with deeper dives at dawn and dusk and fewer, deeper daytime dives. These patterns fit with other studies of this species when feeding predominately on krill (Croxall et al. 1985, Biuw et al. 2009) and fish (Lea et al. 2008, Staniland et al. 2010) and in the preference for the shelf break and the shelf areas at other breeding sites (Guinet et al. 2001, Lea et al. 2008).

Date of deployment was not a significant factor in the seals' trip characteristics so that any temporal mismatch in the deployment times is unlikely to be important in explaining differences between the 2 breeding beaches. The behaviour of seals at Bird Island has been well studied and long-duration, off-shelf foraging trips have been observed in December and throughout January (Staniland & Boyd 2003, Staniland & Robinson 2008, Staniland et al. 2010).

The waters in which the seals from Cooper Bay foraged were less productive than those around Bird Island at the north-western end of South Georgia, which is in line with previous studies (Whitehouse et al. 1999, Korb & Whitehouse 2004). Therefore, we might expect seals at Cooper Bay to adjust their foraging behaviour in the same way as the seals at Bird Island during years of low food availability. During these years, seals at Bird Island tend to alter their behaviour by extending trip durations and increasing the depth and frequency of diving (Boyd 1999) in order to find enough food to provision their pups. However, whilst Cooper Bay seals did increase their frequency of diving, their trip durations were significantly shorter and their diving was shallower than for seals at Bird Island.

Despite the large differences in primary productivity, surveys around South Georgia have, in general, shown a greater abundance of krill at the eastern end of the island compared to the western (Brierley et al. 1999b). The reduced instantaneous krill density in the west may be due to the greater levels of predator-induced mortality there (Brierley et al. 1999b). Given the concentration of Antarctic fur seals and larger numbers of krill-consuming macaroni penguins at the north-western end of the island, predator-induced mortality will be orders of magnitude higher in this region compared to the south-eastern end (Trathan et al. 2006).

Female pup growth was comparable for the 2 locations, and male pups actually had higher growth rates than at Bird Island. Evidence suggests that in Antarctic fur seals male pups grow faster when foraging conditions are favourable (Lea et al. 2006, Vargas et al. 2009). This would suggest that, despite the lower productivity, krill abundance is unlikely to be the sole factor limiting population size at Cooper Bay, at least in the year of our study.

Interestingly, the krill taken at Cooper Bay were larger than at Bird Island, which contradicts previous trawling surveys that found an absence of larger krill at the south-eastern end of the island (Watkins et al. 1999, Brierley et al. 2002). The main difference between our study and that of Watkins et al. (1999) was the presence of all size classes in the diet at the eastern end, whereas the larger 3+ stages were absent in trawl samples. However, fur seals are known to target larger female krill whereas trawl surveys can under-sample larger krill due to net avoidance (Reid et al. 1996). Whilst larger-sized krill were clearly available in the waters around both Cooper Bay and Bird Island, the relative abundance at the 2 locations was unclear, with no trawl data from the period of our study. Even if there were relatively fewer large krill at the south-eastern end of South Georgia, the fewer seals and lower intraspecific competition at Cooper Bay may mean that large krill are sufficiently abundant for seals to preferentially consume them in this region.

A strong positive correlation between trip durations and distance travelled has been recorded at Bird Island (Boyd et al. 1991, Staniland & Boyd 2003), and the shorter mean duration and distance trips at Cooper Bay fit with this pattern. The main cause of the smaller mean of trip durations at Cooper Bay was the absence of longer trips to deep water off-shelf that are common at Bird Island. It appears that the off-shelf niche is not exploited by the majority of seals at Cooper Bay, with only 2 seals out of 37 venturing beyond the shelf beak and almost all diving being concentrated over the South Georgia continental shelf east of the breeding beach.

A possible explanation as to why we observed a near absence of foraging in oceanic waters is that seals at Cooper Bay do not travel to deeper water off-shelf because there is plenty of food on-shelf for them. However, at Bird Island females forage both on- and off-shelf throughout the whole summer, and some seals apparently ignore food resources on-shelf closer to the island to travel to more distant oceanic waters (Staniland & Boyd 2003). Indeed, there appears to be a strong individual component influencing where females forage (Staniland et al. 2004). Similar specialization is also found in Antarctic fur seals breeding on Heard Island, where individuals show differences in their foraging distribution, with some seals foraging close to the island whilst others simultaneously foraged over a much wider area (Casper et al. 2010). Such specialization likely means that individuals will vary in their ability to forage in different environments and may struggle to adapt their behaviour when food availability in their preferred foraging locations is poor (Bolnick et al. 2003, Casper et al. 2010). Niche variation within a population, such as that observed at Bird Island, may help to buffer against loss of particular habitats or resources (Durell 2000)

The Ashmole halo theory predicts that larger colonies would have increased trip durations because intraspecific competition depletes resources close to the colony forcing individuals to forage further afield (Ashmole 1963). However, this was suggested for tropical ecosystems and, whilst it has been shown in temperate regions (Lewis et al. 2001), it is unlikely to be a major influence under normal conditions at South Georgia. The abundant krill population around South Georgia is maintained by currents (Antarctic Circumpolar Current, ACC) that are thought to advect krill swarms from further south (Everson 1976, Hofmann et al. 1998). Evidence suggests that macaroni penguins breeding on South Georgia swim across the continental shelf perpendicular to the main flow of the ACC to exploit krill patches flowing past (Trathan et al. 2006). Therefore, any localised depletion is likely to be replenished, at least within a year of typical krill recruitment within the ACC.

In a central place forager, increased travel distance has costs in both terms of extra energy expenditure and increased trip durations, which in turn lead to reduced provisioning opportunities (Orians & Pearson 1979). Indeed, lactating females foraging from Bird Island have been shown to have higher metabolic rates on longer duration trips, and this is thought to be caused by the higher cost of swimming further (Arnould et al. 1996). Staniland et al. (2007) suggested that seals at Bird Island foraging in more distant oceanic waters offset the increased time and energy costs by feeding on a greater number of energy-dense prey, i.e. myctophids (mean energy content: 6 kJ $g^{-1}{}_{\text{wet mass}}$) and icefish (5.4 kJ $g^{-1}{}_{\text{wet mass}}$) (Lea et al. 2002). Interestingly, no myctophid prey were found in any of the scats or enemas collected at Cooper Bay during the course of the study, despite more being sampled than at Bird Island. As myctophid fish tend to occur in oceanic water (Hulley 1998), it is unclear as to whether their absence from the diet is a cause or effect of the seals not exploiting this environment. The myctophid species *Protomyctophum choriodon* dominates the diet of seals at Bird Island, representing 37 % of the fish consumed (Reid & Arnould 1996, Reid et al. 2006, Staniland et al. 2007), probably as a result of its occurrence in surface waters (<200 m) exploited by Antarctic fur seals (Collins et al. 2008). The abundance of *P. choriodon* in the diet at Bird Island is closely linked with periods of warmer sea surface temperature values (>3°C) (Reid et al. 2006); this species is known to prefer waters of 5 to 15°C temperature (Hulley 1981). As Bird Island represents the southerly extreme of *P. choriodon* distribution it seems likely that the waters around Cooper Bay are too cold (<4°C) and the species is absent at the southern end of the island. Therefore, if there is a lack of energy-rich myctophid prey available, i.e within the vertical constraint of diving, to the seals offshore at Cooper Bay, this might explain the near absence of foraging in more distant oceanic waters. The capacity to offset increased foraging effort (longer transit times, deeper diving, and longer trip durations) by the consumption of more energy-rich prey has also been postulated as an explanation for colony differences in foraging for Antarctic fur seals breeding on the Kerguelen Islands (Lea et al. 2008) and individual differences at Heard Island (Casper et al. 2010). At Cooper Bay, the apparent reduction in niche width, i.e. only on-shelf foraging, will increase local intraspecifc competition and reduce the population's buffering against changes in the local environment, which may explain the slower recovery and smaller size of this population. Fluctuations in the recovery rate of other seal populations have been linked to environmental factors and in particular El Niño events (Gerber & Hilborn 2001). For example, Galapagos sea lions were severely affected by the 1982–83 El Niño event that caused increased mortality, local redistribution, and a slow recovery (Trillmich & Dellinger 1991).

The krill population at South Georgia is prone to large inter-annual fluctuations as it is reliant on recruitment from the Antarctic Peninsula in the ACC (Murphy et al. 1998, Brierley et al. 1999a). This environmental variability is correlated with the breeding success of a variety of marine predators at South Georgia (Croxall et al. 1999). At Bird Island, low krill abundance has been linked to low reproductive output and decreased adult female survival (Forcada et al. 2005). If food resources are a limiting factor in the size of the Cooper Bay population, then it is likely that it will be during these years of low resource availability that the effects are most apparent. The variability of krill abundance is much higher at the south-eastern end of the island (1.9 to 151 g m^{-2}) compared to the north-western end (7.4 to 45 g m^{-2}) (Brierley et al. 1999b). During the 2 'poor' krill years for which data are available, the south-eastern end of South Georgia had significantly lower densities of krill compared to the north-west, especially in on-shelf waters (Brierley et al. 1999b, Trathan et al. 2003). Given that female fur seals rely on predictable resources close to the breeding beach and that seals breeding at Cooper Bay may already have a restricted area of suitable foraging, it is possible that this increased environmental variability will have a negative impact on the population. With potentially reduced flexibility in terms of foraging, and if the food resources in the shelf waters around the Cooper Bay are significantly reduced, then females might be less able to cope, leading to increased pup mortality, lower mass at weaning, and reduced adult survival.

CONCLUSIONS

Seals at both locations foraged most intensively around the shelf break, with diving patterns consistent with the exploitation of prey migrating into surface waters at night. Although Bird Island seals dived deeper and less frequently, both populations spent the same amount of time in the bottom phase of dives actively foraging.

At Cooper Bay, seals were longer but thinner than those breeding at Bird Island. However, indications were that, at the time of our study, there were sufficient food resources at Cooper Bay as seals at both locations maintained at least the same pup growth for female pups, and male pups grew at a faster rate at Cooper Bay.

There were differences in the seals' behaviours between the 2 locations, with the seals at Cooper Bay concentrating their foraging in the shallow shelf and shelf break waters closer to the breeding beach; the longer distance oceanic foraging trips observed for seals at Bird Island were almost entirely absent from those at Cooper Bay. Whilst both populations fed on Antarctic krill and the incidence of fish in the diet was similar, there was a difference in the composition of fish species, with an absence of myctophids at Cooper Bay. Evidence suggests that the favoured myctophid prey of fur seals at South Georgia are absent from the colder waters around Cooper Bay. If these energy-rich prey are unavailable in the more distant oceanic environment, then seals at Cooper Bay may find it hard to offset the increased costs of foraging trips with longer duration and distance. This potentially reduced niche width would mean the Cooper Bay population may be less buffered against environmental variability. Although food resources appeared to be sufficient during the period of study, the south-eastern region of South Georgia has increased variability in food resources that, coupled with a potentially smaller area in which to forage, might explain the reduced population size compared to the north-eastern end of the island

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