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Fine-scale linkages between the diving behaviour of Antarctic fur seals and oceanographic features in the southern Indian Ocean

Mary-Anne Lea and Laurent Dubroca

Diving activity, foraging locations and pup provisioning behaviour of 10 female Antarctic fur seals (*Arctocephalus gazella*) were examined with respect to a range of oceanographic parameters (sea surface temperature, chlorophyll distribution and bathymetry) at the Kerguelen Archipelago in the southern Indian Ocean in February 2000. A multivariate analysis of the environmental parameters at each of the nightly foraging locations indicated the existence of two ecoregions within the foraging range of the seals. Five seals actively foraged in oceanic waters (1870 m) with relatively warm surface water (5.4°C) to the north and east of the colony (ecoregion 1), while four others travelled to the southeast (ecoregion 2) to waters typical of the surface expression of the Polar Front (3.7°C) located over the continental shelf break (597 m). Only one seal foraged in both regions. Diving behaviour, parameterised on a nightly basis using seven variables, clearly differed between regions, with the diving activity in the warmer ecoregion 1 being characterised by deep dives (55 m), and relatively little time spent diving (47%). Conversely, dives within ecoregion 2 were, on average, to shallower depths (34.5 m), and proportionately more time was spent diving (54%). Despite differences in environmental conditions encountered and associated differences in diving activity, the foraging success of mothers, in terms of daily pup mass gain per foraging cycle, was similar in both ecoregions. The study highlights the use of multivariate analysis in categorising the foraging zones and behaviour of Antarctic fur seals.

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Introduction

The distribution of resources in oceanic environments is often patchy, with many scale-dependent processes determining the distribution of nutrients and subsequent productivity. In the Southern Ocean (SO), phytoplankton blooms are often associated with coastal/shelf waters, sea-ice retreat and the position of major oceanic fronts (Moore and Abbott, 2000). In the Antarctic Polar Frontal Zone (PFZ), and the SO generally, waters are high in nutrients and low in chlorophyll (Abbott *et al.*, 2000), with spring blooms of phytoplankton initially being limited by light levels and late-spring mixing of the water column (Abbott *et al.*, 2000). Sea surface temperatures (SST) are an important component in models estimating local maximum rates of primary production (Behrenfeld and Falkowski, 1997; Moore and Abbott, 2000). As the austral summer progresses and the water column stratifies, grazing by zooplankton, iron availability (de Baar *et al.*, 1995; Trull *et al.*, 2001) and silica availability (Prego *et al.*, 1999) controls the maximum chlorophyll concentration (Abbott *et al.*, 2000). Variability in primary productivity is passed down the food chain to higher trophic levels: zooplankton (krill *Euphausia superba*), its consumers (mesopelagic fish and squid) and top-predators.

Krill and other crustaceans form the dietary basis of many seabirds and penguins (Hull, 1999; Bocher *et al.*, 2000; Bocher *et al.*, 2001) and their abundance at the meso-scale is generally related to hydrographic features such as fronts and eddies (Pakhomov and McQuaid, 1996; Ansorge *et al.*, 1999; Pakhomov and Froneman, 2000). The distribution of pelagic fish and squid (Duhamel *et al.*, 2000), which are preyed upon by top predators, is determined by the concentrations and migrations of macro-zooplankton in the water column (Froneman *et al.*, 2000; Reid and Hindell, 2000). Thus the influence of hydrographic features on the foraging distribution of higher order predators may be considerable. Black-browed albatross (*Diomedea melanophris*) breeding on the Kerguelen Archipelago are found in high concentrations over the continental shelf break, a region of increased productivity (Cherel *et al.*, 2000). Nel *et al.* (2001) have recently linked the foraging behaviour of grey-headed albatross (*Thalassarche chrysostoma*) to the occurrence of sea surface height anomalies representing eddies, in the vicinity of the Prince Edward Islands, while King penguins (*Aptenodytes patagonicus*) at the Crozet Archipelago are known to forage at the Polar Front (PF) in summer (Guinet *et al.*, 1997; Koudil *et al.*, 2000) and in Antarctic waters in autumn and winter (Charrassin and Bost, 2001).

Foraging success, and subsequent breeding success, of seabirds and seals are ultimately determined by the spatial and temporal occurrence of regions of oceanic productivity (Schneider, 1990; Hunt, 1991; Guinet *et al.*, 2001) and the ability of predators to locate and effectively exploit these patchily distributed resources. Relationships between prey concentration and predator distribution are often scale-dependent. At large scales, aggregations of seabirds may be indicative of high prey biomass (Mehlum *et al.*, 1996; Swartzman and Hunt, 2000), while at small scales (tens of kilometres) seabirds may appear to select frontal zones (Hunt, 1991; Mehlum *et al.*, 1998), which are often thought to represent regions of enhanced biological activity (Lutjeharms *et al.*, 1985). A recent study comparing aggregations of murres (*Uria* spp.) to capelin (*Mallotus villosus*) abundance at different spatial scales showed that correlations between the two species increased with increasing capelin density and patchiness at a scale of 200–300 km (Fauchald and Erikstad, 2002). At smaller scales (∼70 km), concordance increased only with increasing capelin patchiness. Thus the scale at which relationships between predators and prey are studied may affect the outcome (Wiens, 1989).

Finding a relationship between the spatial distribution of marine mammals, their prey and oceanographic features has proven to be even more challenging than for seabirds, largely because of the reduced chance of sighting sub-surface predators. Associations between the distribution of whales and oceanographic features (Tynan, 1997) and chlorophyll concentrations (Jaquet and Whitehead, 1996; Jaquet *et al.*, 1996) have been reported on relatively large

scales using whaling data. Other studies have identified relationships between the distribution of seals and frontal water masses using data-loggers (Hindell *et al.*, 1991; Boyd *et al.*, 2001; Field *et al.*, 2001; Bradshaw *et al.*, 2002). Few studies, however, have identified predator–prey relationships of marine mammals on smaller scales ($<1.0°$).

One species for which relationships between distribution, foraging activity and marine productivity at relatively small scales have been observed is the Antarctic fur seal (*Arctocephalus gazella*). This species exhibits flexible foraging behaviour, exploiting a mixture of krill, mesopelagic fish and squid on their feeding trips from their various breeding sites (Reid and Arnould, 1996; Cherel *et al.*, 1997; Goldsworthy *et al.*, 1997; Green *et al.*, 1997; Klages and Bester, 1998). Females are constrained by their brief lactation period (Boyd and McCann, 1989) and must locate reliable prey resources from December to April each year in the vicinity of their colony. As central-place foragers (Orians and Pearson, 1979) and because of the restricted fasting capabilities and high growth requirements of their pups (Guinet *et al.*, 2001), fur seals have a limited scope for exploring the marine environment in search of prey. Long-term research at South Georgia has indicated that in years when prey availability is diminished around the island, reproductive success is reduced and catastrophic breeding failures may occur (Boyd *et al.*, 1995).

The Kerguelen Archipelago, a summer breeding site for Antarctic fur seals, is located in a region of hydrographic complexity (Belkin and Gordon, 1996), bounded to the south by the PF (Figure 1a). Myctophid fish, their preferred, energy-rich prey in this region (Cherel *et al.*, 1997; Lea *et al.*, 2002a; Lea *et al.*, 2003), occur in high densities within the PFZ to the north and east of the Archipelago (Duhamel *et al.*, 2000). Fur seals typically prey on nocturnal surface migrating myctophids, spending up to 70% of their time at night diving (Lea *et al.*, 2002b). However, both the diving behaviour (Lea *et al.*, 2002b) and the direction of travel from the colony (Bonadonna *et al.*, 2001) of individual seals from the same colony vary. Guinet *et al.* (2001) observed that time spent diving was significantly related to oceanographic conditions (bathymetry and cholorophyll concentrations), forage fish distribution and distance from the colony at varying spatial scales (0.1–3.0°). For the majority of these parameters, the strength of the correlation decreased with increasing scale suggesting that fur seals were responding to small-scale changes in these features. The one exception to this was the association between diving activity and near-surface chlorophyll concentration, which was negative at the 0.1° scale and positive at the 1.0° scale (Guinet *et al.*, 2001).

Here we investigate whether female Antarctic fur seals change their diving activity on a nightly basis in relation to the environmental characteristics (Chl. *a* concentration, SST and bathymetry) encountered within their foraging areas. We examine fine-scale relationships (0.1–1.0°) between diving activity, as measured by seven diving parameters and environmental conditions. Because differences
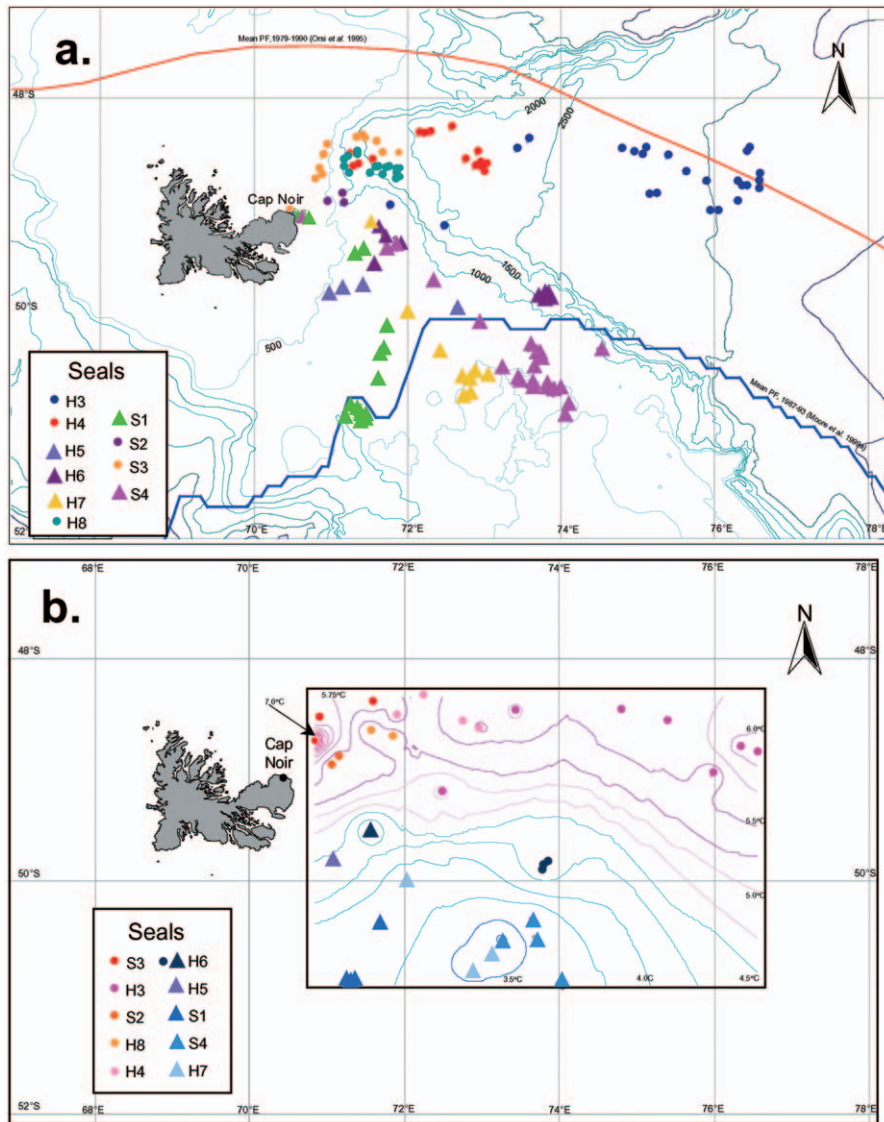
Figure 1. At-sea locations of 10 foraging female Antarctic fur seals in February 2000 from the breeding colony Cap Noir (Îles Kerguelen) and (a) local bathymetry (red and blue lines depict mean position of the Antarctic PF averaged over different time periods in the Kerguelen region), and (b) SST_{sat} contours (0.25°C; nocturnal locations only, n = 35; circles, ecoregion 1; triangles, ecoregion 2; see text).

in energy transfer from mother to pup may be anticipated under variable environmental conditions, a secondary aim is to investigate potential effects on the provisioning of the pups.

Study site

In the Kerguelen region, the PF is defined as the northern terminus of the 2.5°C isotherm in the 100–300 m layer of the water column (Belkin and Gordon, 1996). The PF generally passes south of the Kerguelen Archipelago (Park

et al., 1991; Sparrow and Heywood, 1996) but occasionally moves north of the islands (Moore *et al.*, 1999a; Figure 1a). Bottom topography of the Kerguelen Plateau exerts strong control (Gambéroni *et al.*, 1982; Sparrow and Heywood, 1996), forcing branches of the Antarctic Circumpolar Current (ACC; Orsi *et al.*, 1995) to within 2–3° latitude to the north of the Archipelago (Park *et al.*, 1991). The ACC comprises three fronts at this location (47–49°S, 65–75°E): the Sub-Tropical Front (STF), the Sub-Antarctic Front (SAF) and the PF. The STF to the north and the PF to the south bound the PFZ (Klyausov, 1990; Belkin and Gordon, 1996), which encompasses the Kerguelen

Archipelago. The PFZ to the east and downstream of the archipelago is an area of elevated nutrients (Prego *et al.*, 1999; Bucciarelli *et al.*, 2001), high primary productivity (Moore *et al.*, 1999b; Moore and Abbott, 2000; Blain *et al.*, 2001), abundant zooplankton (Pakhomov, 1997) and fish (Duhamel *et al.*, 2000).

Antarctic fur seals breed at several sites along the north and east coasts of the archipelago. Seals were studied at a breeding colony at Cap Noir (49°07′S, 70°45′E) on the northeast coast of the Courbet Peninsula where approximately 750 females breed annually. Seals arrive at the colony in November and December each year and give birth to a single pup, which they then suckle intermittently for approximately 4 months. Mothers forage at sea for between 2.7 and 17.9 days (Guinet *et al.*, 2001; Lea *et al.*, 2002b), returning to suckle their pups for approximately 2 days between trips (Lea, 2002).

Materials and methods

At-sea distribution of seals

In February 2000, 10 female seals were equipped with ARGOS satellite platform transmitter terminals (PTTs, ST-10 electronics, Telonics, AZ, USA potted by Sirtrack, New Zealand, $110 \times 42 \times 14$ mm). Seals were caught in the colony using a hoop net, and were held for up to 20 min on a restraint board while devices mounted on nylon webbing with cable ties were attached dorsally between the scapulae with two-part epoxy adhesive (AW2101; Ciba Specialty Chemicals Holding Inc., Switzerland). Locations of seals at sea were obtained via the ARGOS satellite system (Taillade, 1993). An Mk7 Time–Depth Recorder (TDRs, Wildlife Computers, Redmond, $100 \times 20 \times 10$ mm, 30 g) was attached dorsally to each PTT to enable diving behaviour to be associated with the seal's position at sea. The combined PTT/TDR packages ($110 \times 42 \times 25$ mm, 150 g, Bonadonna *et al.*, 2001) were hydro-dynamically shaped with nautical putty to reduce drag.

Seals and their pups were weighed, measured and given a unique identifying mark on the rump with Clairol hair dye (Born Blonde 3[TM], Bristol Myers Squibb, New South Wales, Australia). Pups were also weighed daily during their mother's absence with a Salter *Weightronix* spring balance (25 ± 0.02 kg) to obtain an estimate of pup mass gain (PMG) once the mother had returned. PMG is expressed in absolute terms as the quantity of mass gained while the mother was ashore (absolute PMG) and as daily PMG per foraging cycle (FC; sum of shore attendance and foraging periods in days; Guinet *et al.*, 1999, 2000; Guinet and Georges, 2000), which can be used as a comparative measure of foraging efficiency.

Only ARGOS class 3, 2, 1 and 0 locations were used in analyses (Boyd *et al.*, 1998). Data were filtered such that locations requiring a transit speed greater than 3 m s^{-1} were discarded. This speed had previously been de-termined for fur seals from Cap Noir carrying velocity TDRs (Wildlife Computers) as the highest speed generally attained (Bonadonna *et al.*, 2001). Because most (87%) of female foraging activity occurs at night (Lea *et al.*, 2002b), only nocturnal locations were regarded as identifying foraging zones. A mean nightly position was calculated if more than one location was recorded. Positional data were available for a total of 35 foraging nights, after removing incomplete nights owing to time spent by seals in transit to foraging areas. Distances from the colony (km) were calculated for each nocturnal foraging location using the great circle distance formula (Donnay, 1997).

Diving behaviour

Dive data were extracted using Wildlife Computers software. Offset and drift of pressure transducers were corrected using customised software (Dive ©, Stewart Greenhill, Murdoch University, Australia; see Lea *et al.*, 2002b). All TDRs were programmed to record depth (± 1 m) and temperature (± 0.1°C) every 5 s, and were calibrated in a thermostatically controlled bath after the study. Because all of them reliably recorded temperatures of 0–10°C to within 0.1°C, we subsequently used the calibrations supplied by the manufacturer. SST data (depth <4 m) were extracted from TDR records between 23:00 and 01:00 h (Georges *et al.*, 2000) to examine temporal changes in SST throughout the duration of a foraging trip. By sampling only at night, potential increases in temperature associated with solar radiation are avoided. However, some degree of thermal lag is anticipated owing to temperature changes associated with changes in depth (Charrassin and Bost, 2001; Field *et al.*, 2001). McCafferty *et al.* (1999) noted a lag of <10 s for dives of <60 m (mean = 3.9 s) during TDR deployments on Antarctic fur seals at South Georgia, while values exceeded 20 s for dives >60 m. Thus a slight lag in the response time during deeper dives may be anticipated also at Kerguelen.

Lea *et al.* (2002b) examined the diving behaviour of fur seals over 3 years using 12 dive parameters per foraging trip. We selected only those applicable to an individual foraging night, rather than to an entire trip. The duration of night periods (estimated range during the experimental period: 9.0–10.6 h) was calculated using sunrise and sunset times at Cap Noir estimated by AUSLIG software (Department of Industry Science and Resources, Canberra, Australia). The diving parameters were: (1) dive frequency (number of dives per hour of night); (2) mean dive depth (m); (3) mean dive duration (s); (4) vertical depth dived per hour (km h^{-1}; cumulative dive depth $\times 2$ per night divided by night period); (5) mean number of dives per bout; (6) proportion of all dives in bouts (%) and (7) time spent diving per night (%). Minimum criteria for bout inclusion were three dives greater than 6 m within a 20-min period (see Lea *et al.*, 2002b for a detailed definition of bout detection).

Environmental data

Bathymetric data at each foraging location were extracted from the *ETOPO5* database at 5′ lat. × 5′ long. resolution (NOAA, 1988). Multi-channel SST (SST_{sat}) data for February 2000 were obtained from the Physical Oceanography Distributed Active Archive Center by file transfer protocol.[1] Weekly average data for the descending path were used on an equal-angle grid of 2048 pixels longitude by 1024 pixels latitude (nominally referred to as the 18 km resolution). Surface Chl. *a* concentrations (mg m^{-3}) were obtained from global and regional ocean colour data obtained by the Sea-viewing Wide field-of-view Sensor (SeaWIFS). We used the SeaWIFS Level 3 monthly product containing monthly data that have been "binned" and spatially/temporally averaged into 9 km grid cells encompassing the globe. Because of the high level of cloud coverage in the Kerguelen region, the 8-day data were insufficient and we had to use the monthly record for February 2002.

To link diving behaviour and environmental parameters, we extracted the latter for the area corresponding to the dive locations. To evaluate effects of spatial range in our analysis, we calculated the mean for weekly SST_{sat} data within the area directly under the nocturnal diving location ($0.1° × 0.1°$) and in areas corresponding to circles with radii of 0.5 and $1.0°$ surrounding this location.

Software and analysis

Raw data were extracted using SeaDas software (SeaWIFs Data Analysis System).[2] All data extraction under and around the area of diving activity was done using ArcView GIS and Spatial Analyst Extension (ESRI).

Clustering and multi-dimensional scaling (MDS) of the environmental data at 35 nocturnal foraging locations were conducted at each of the three spatial scales (0.1, 0.5 and $1.0°$) to identify possible environmental groupings (ecoregions; Hargrove and Hoffman, 1999). This objective method of classification was chosen particularly because of the uneven number of foraging nights per seal (1–7) available. Although this creates dependency in the data, interpretation of the links between fine-scale foraging activity and environmental variables will be discussed on a per seal basis. The Unweighted Pair Group arithMetic Averaging (UPGMA; Belbin *et al.*, 1992) clustering algorithm and non-hierarchical agglomerative fusion strategy (Lea *et al.*, 2002b) were used to produce a dendrogram at each spatial scale. The number of potential ecoregions was selected by forcing the data into 2, 3, 4, 5 and 6 ecoregions. Subsequently, the physical characteristics were ordinated in three-dimensions by MDS, which attempts to reduce the distance between samples in space. The success of this procedure is determined by the stress level (measure

of lack of fit). A stress value of <0.1 corresponds to good ordination and indicates little chance of misinterpretation (Clarke, 1993). Foraging nights were assigned to an ecoregion at each of the three spatial scales based on the cluster analysis.

The seven dive parameters for each of the 35 foraging locations were then included in a backwards stepwise discriminant function analysis (DFA) to ascertain first, how many ecoregions could be reliably distinguished by the diving activity of seals and secondly, at which spatial scale the relationship was most accurate. Those diving parameters most influential in distinguishing between ecoregions were also identified by backwards DFA. Any univariate statistics such as regression analyses were conducted using only mean values per seal, which are reported ± standard error of the mean.

Results

At-sea distribution of seals

Of the 35 foraging nights for which at-sea locations of the 10 seals were recorded, only four occurred over the Kerguelen Plateau (<500 m), 13 over the continental shelf break (500–1000 m) and 18 over deeper water (>1000 m). Foraging locations were widely dispersed in an arc from the northeast through to the southeast of the colony (Figure 1a). Generally, seals travelled in two main directions (ENE/E and SE), but stayed within 450 km of the colony during foraging trips lasting at most 12.3 days (Table 1).

At the foraging locations, SST ranged from 3.0 to $6.2°C$ (Figure 1b), while Chl. *a* concentration was generally high and relatively stable over the area (0.29–0.39 mg m^{-3}). MDS and cluster analysis of the environmental variables at the three spatial scales (Figure 2) were obtained with lowest stress levels for two environmental groupings (ecoregions). Stress was lowest at the $1.0°$ spatial scale (0.028), but was also <0.05 at the other scales for the other two. Ecoregion 1 (warm and deep) was characterised by higher mean SST_{sat} and deeper water than ecoregion 2 (cool and shallow), although observed ranges showed a fair overlap (Table 2).

Diving activity within ecoregions

A total of 8386 dives were recorded (mean $240 ± 18$ dives per night). The proportion of time spent diving by a seal on a particular night was highly variable (10–72%) as were mean dive depths (11–99 m). Those diving parameters among the seven that were investigated were identified as being most influential in confirming ecoregion groupings by stepwise backwards DFA at each spatial scale and were compared with Jackknife classification matrices (Table 3). The highest level of correct assignment to an ecoregion was achieved for two groupings at the $0.5°$ spatial scale (89%; Wilks' $\lambda = 0.38$, approximate $F_{2,32} = 21.8$, $P < 0.0001$), using only two diving parameters: hourly vertical depth and the proportion of time spent diving (Table 3).

Higher vertical depths were achieved in ecoregion 1 while spending 7% less time diving during foraging nights than in ecoregion 2. Seals in ecoregion 1 also dived to greater mean depths, had fewer dives per bout and a lower proportion of overall dives in bouts (Table 4). Ecoregion 2 was characterised by a higher dive frequency.

Temporal variation in SST

Logged SST estimates at the foraging locations, as recorded by TDR (SST_{TDR}) and weekly averaged satellite passes (SST_{Sat}) were significantly correlated at the 0.1° scale ($r^2 = 0.72$, $P < 0.001$). However, the relationship appears to be curvilinear (Figure 3). The correlation between the two SST estimates at the other spatial scales (0.5 and 1°) while also significant, were more variable ($r^2 = 0.61$ and 0.48, respectively).

SST_{TDR} for all nights during all foraging trips (n = 75) were also extracted from dive records (Figure 4). Two seals foraging in ecoregion 1 (H3 and H4) spent most of their time in waters >~5°C), although H3 did visit a colder area on day 10. The other seals foraging only in ecoregion 1 (H8, S2 and S3), while making shorter trips, spent most of their time in slightly colder waters (4.5–5.0°C). Those seals assigned to ecoregion 2 foraged mostly in waters in the range of 3.5–4.0°C. Slightly higher values were recorded during the first or last night, in closer proximity of the colony. H6 was the only seal foraging in both ecoregions (Figure 4). She spent only 50% of the time diving during three nights in ecoregion 1 compared with 65% during her first night in ecoregion 2, while vertical depth attained also differed considerably (1.9 and 3.2 km h^{-1}, respectively). As SST encountered by H6 in the two ecoregions was quite similar, bathymetry and diving behaviour must have accounted for its assignment to either one. Thus it would appear that diving activity of a particular individual may change in response to changing environmental conditions even within a foraging trip.

Temperature profiles

The temperature–depth profiles during dives indicate that temperatures recorded in the upper 100 m were more variable for ecoregion 1, where deep dives were made more frequently (Figure 5). Although dives of up to 180 m depth were recorded, the number deeper than 100 m constituted only 2.8 and 1.3% of all dives in ecoregions 1 and 2, respectively. Below 80 m, temperatures dropped rapidly in both regions.

Foraging success and pup provisioning

Energy transfer to the pup was compared by ecoregion on a per foraging trip basis. Absolute PMG, daily PMG per FC and percentage mass gain of pups during the mother's shore attendance relative to mass upon her arrival were not significantly different for seals foraging in the two
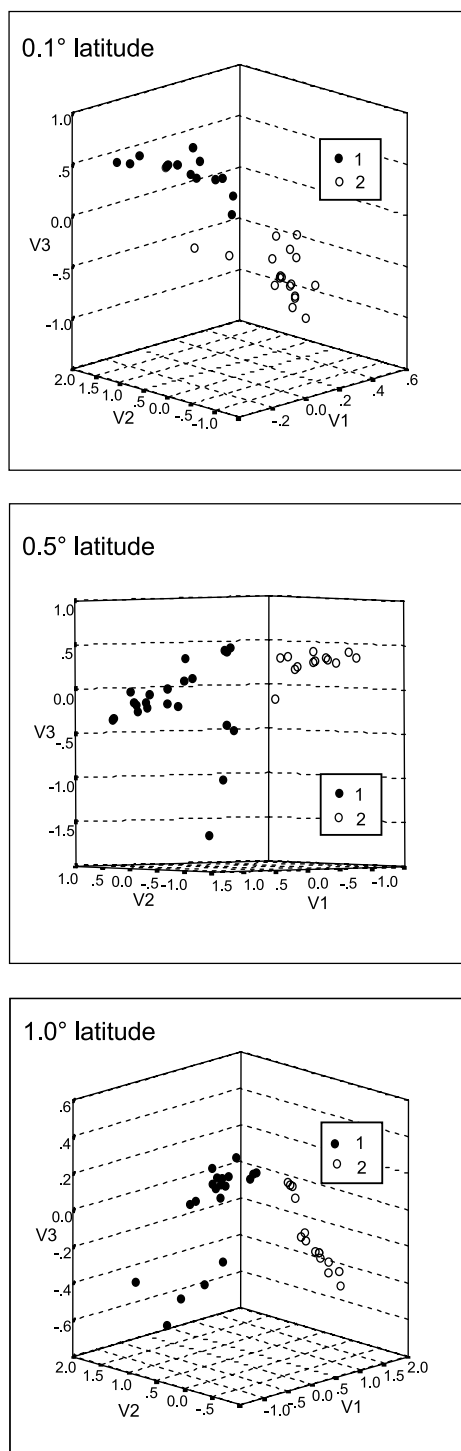

Figure 2. MDS plots for the two ecoregions (1 and 2) at three spatial scales (0.1, 0.5 and 1.0°) indicating the relationship between environmental parameters during 35 foraging nights (axes represent vectors that merely enable the plotting of the minimum dissimilarity distance between points).

Table 1. Deployment history (dd, departure date; T, trip length; n, number of nights; D_{max}, maximum distance travelled from the colony; MM, mean maternal mass and PMG, pup mass gain) for *Arctocephalus gazella* females in February 2000.

Seal	dd	T (days)	n	D_{max} (km)	Direction	MM (kg)	Pup sex	PMG (kg)	Daily PMG[a] (kg day^{-1})
H3	29.1.00	12.3	7	448	NE	34.8	F	3.84	0.242
H4	30.1.00	8.9	5	193	NE	29.4	M	2.47	0.225
H5	30.1.00	6.2	1	186	SE	29.7	F	2.01	0.255
H6	31.1.00	9.3	4	259	SE	33.9	M	2.94	0.241
H7	29.1.00	8.8	3	251	SE	28.3	F	2.62	0.237
H8	31.1.00	5.2	2	114	NE	31.5	M	2.06	0.294
S1	12.2.00	9.1	4	215	SE	33.6	M	—	—
S2	17.2.00	4.0	2	—	NE	31.7	F	0.65	0.109
S3	18.2.00	6.0	3	81	NE	31.1	F	1.38	0.175
S4	24.2.00	10.4	4	328	SE	33.1	F	3.78	0.298
Mean		8.0 ± 0.8	3.5	231 ± 37		31.7 ± 0.7		2.41 ± 0.35	0.231 ± 0.019

[a]Per foraging cycle (FT + SB; Guinet *et al.*, 1999; Guinet and Georges, 2000).

Table 2. Values of physical parameters encountered by seals at nocturnal foraging sites.

	Ecoregion 1 (n = 22)		Ecoregion 2 (n = 13)	
	Mean ± s.e.	Range	Mean ± s.e.	Range
Chl. *a* (mg m^{-3})	0.30 ± 0.01	0.29–0.39	0.30 ± 0.01	0.29–0.39
Depth (m)	1872 ± 192	161–3129	597 ± 26	466–757
SST_{sat} (°C)				
0.1° Lat.	5.38 ± 0.15	3.75–6.15	3.61 ± 0.12	3.00–4.65
0.5° Lat.	5.44 ± 0.14	4.28–7.35	3.71 ± 0.10	3.18–4.50
1.0° Lat.	5.60 ± 0.19	4.27–7.35	3.89 ± 0.17	3.2–5.64

Table 3. Jackknife classification assignment (jca), P-values and discriminatory dive parameters (ddp) of ecoregions identified by backwards DFA at three spatial scales.

Spatial scale (deg)	n	jca	P	ddp[a]
0.1	2	74	0.001	2,7
	3	57	0.001	2,3
	4	57	<0.0001	2,3,7
	5	51	<0.0001	2,3,7
	6	49	<0.0001	2,3,7
0.5	2	89[b]	<0.0001	4,7
	3	77	<0.0001	3,4,7
	4	57	<0.0001	3,4,7
	5	37	<0.0001	3,4,7
	6	49	<0.0001	3,4,7
1.0	2	80	<0.0001	2,7
	3	77	<0.0001	2,3,7
	4	69	<0.0001	3,4,7
	5	54	<0.0001	3,4,7
	6	46	<0.0001	3,4,7

[a]For codes see Table 4.
[b]Best assignment to ecoregion.

Table 4. Measures of nightly diving activity of seals foraging in the two ecoregions.

| Code	Dive parameters	Ecoregion 1 (warm and deep, n = 22)		Ecoregion 2 (cool and shallow, n = 13)	
		Mean ± s.e.	Range	Mean ± s.e.	Range
1	Dive frequency (h^{-1})	22.3 ± 2.3	6.4–41.7	30.0 ± 2.6	13.5–42.5
2	Mean dive depth (m)	55.6 ± 4.8	11.4–99.1	34.5 ± 3.3	19.6–56.7
3	Mean dive duration (min)	1.4 ± 0.1	0.4–2.4	1.2 ± 0.1	0.7–1.8
4	Vertical depth (km h^{-1})[a]	2.2 ± 0.2	0.4–3.3	2.0 ± 0.2	0.8–3.1
5	Dives per bout	8.8 ± 0.7	4.8–19.6	9.8 ± 0.6	6.4–14.6
6	Proportion dives in bouts	0.91 ± 0.03	0.45–1.0	0.95 ± 0.02	0.86–1.0
7	Proportion TSD[a]	0.47 ± 0.04	0.10–0.66	0.54 ± 0.03	0.34–0.72

[a]Parameters identified by DFA.
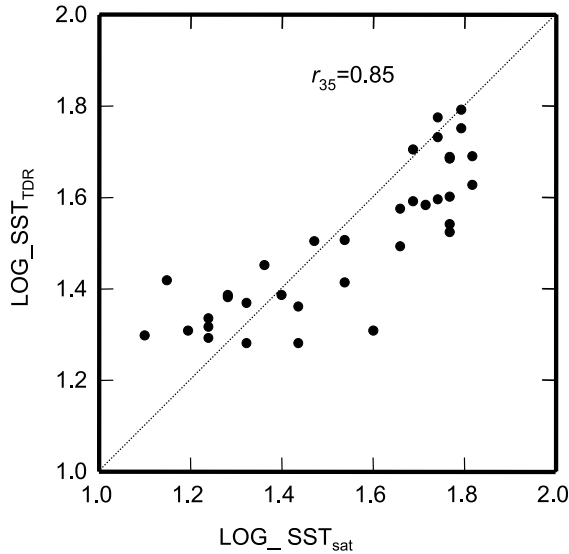
Figure 3. Relationship between log transformed SST as recorded by TDRs on seals at 35 nocturnal foraging locations (SST_{TDR}) and by satellite (SST_{sat}) at the 0.1° scale.
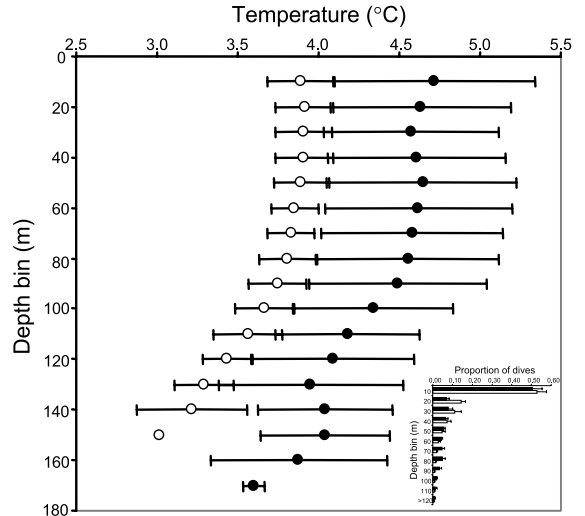

Figure 5. Mean temperature–depth profiles (with s.d.) during nightly diving episodes in ecoregion 1 (closed) and 2 (open). Insert: proportion of dives assigned to 10 m depth bins by ecoregion (filled, 1; unfilled, 2).

ecoregions (Table 5) despite the differences in environmental parameters and diving activity, although daily PMG tended to be less variable for pups whose mothers foraged in the cooler ecoregion 2 (Figure 6a). Also, none of the regressions of foraging success against SST_{sat} and SST_{TDR} were significant. However, all measures of foraging success were significantly correlated with mean depth attained by females during a foraging trip (Table 5 and Figure 6b). Mean dive depth, in turn, was negatively related to the duration of the foraging trip (Figure 6c; $F_{1,7} = 11.3$, $r^2 = 0.56$, $P < 0.05$).

Daily PMG per FC was not significantly correlated to mean values of nightly water depth ($r_9 = 0.19$, $P = 0.64$), while the relationship between daily PMG, mean depth and

Table 5. Different measures of foraging success, results of a paired t-test for differences between ecoregions and r^2 values for their correlation with mean dive depth.

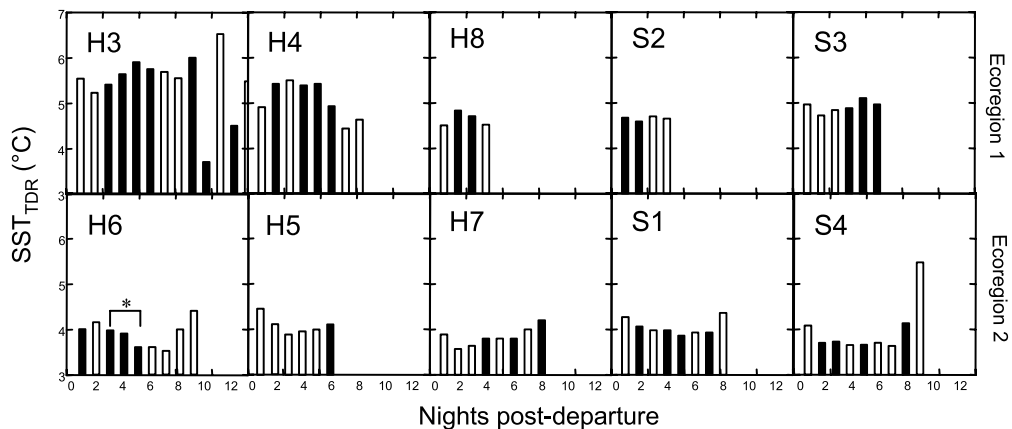|	Paired ecoregion comparison			Mean dive depth	
	Mean ± s.e.	t (df)	P	r^2	P
Absolute PMG (kg)	2.42 ± 0.35	−0.77 (7)	>0.05	0.76	<0.01
PMG_FC (kg day^{-1})	0.23 ± 0.02	−1.21 (7)	>0.05	0.54	<0.05
Proportional PMG	0.30 ± 0.06	−0.86 (7)	>0.05	0.72	<0.01

Figure 4. Nightly SST_{TDR} by ecoregion throughout each foraging trip (black bars, foraging nights; *, foraging nights of H6 assigned to ecoregion 1 by DFA).
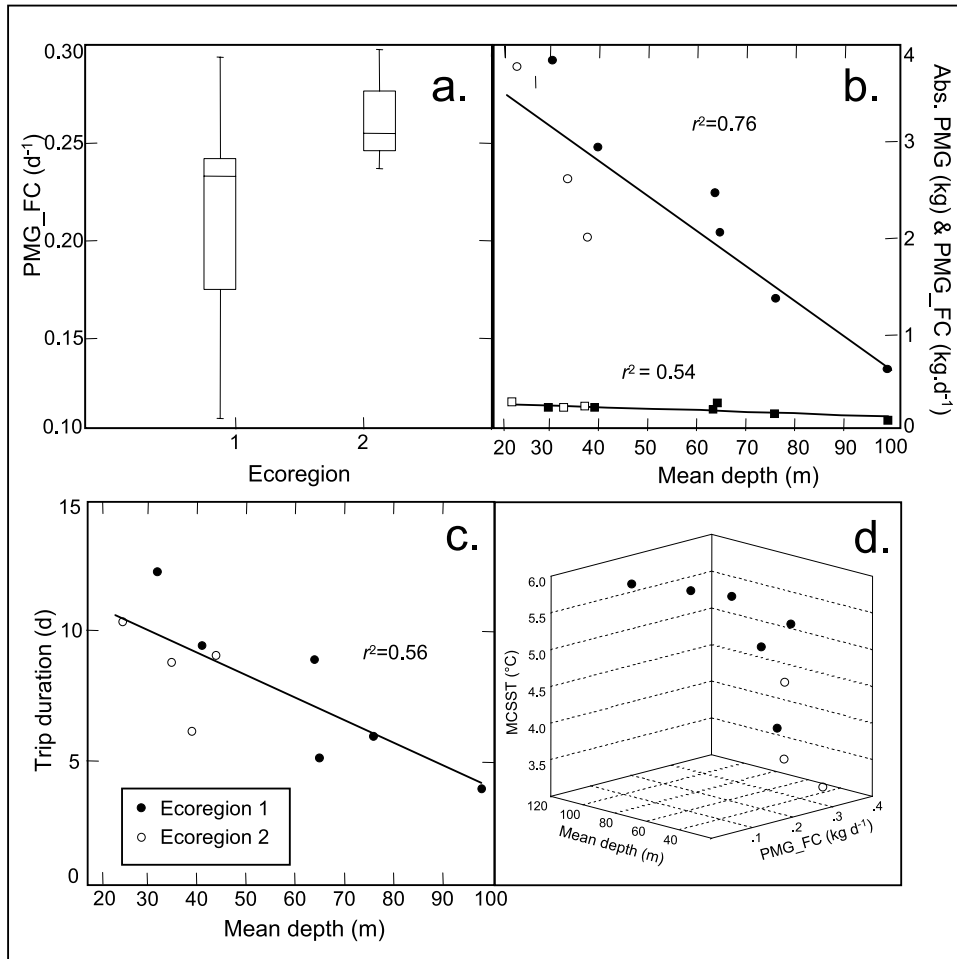
Figure 6. (a) Relationship by ecoregion for daily mass gain of pups (PMG_FC) (mean, confidence limits and range); (b) absolute PMG (circles) and PMG per foraging cycle (squares); (c) trip duration as a function of mean female diving depth and (d) three-dimensional relationship between mean depth, SST and daily mass gain.

SST_{sat} is more clearly illustrated in three-dimensions (Figure 6d). A continuum appears to exist, irrespective of ecoregion, with higher daily PMG being associated with shallow dive depths and lower SST.

Discussion

The multivariate and multi-scale approach to the categorisation of both environmental characteristics and diving behaviour adopted was successful in enabling the identification of a clear relationship between fine-scale characteristics of the marine environment and the foraging behaviour of Antarctic fur seals. At-sea distribution of female seals in February 2000 was divided into those foraging to the northeast and east of the colony and those which headed in a southeasterly direction (Bonadonna *et al.*, 2000, 2001). Seals foraged mostly over oceanic and shelf break waters and

spent little time diving over the continental shelf ($<500\,m$), in accordance with earlier investigations in the same area (Guinet *et al.*, 2001) and studies on the same species carried out at South Georgia (Boyd *et al.*, 1998; McCafferty *et al.*, 1998, 1999); Macquarie Island (Robinson, 2002) and at the Antarctic Peninsula (Goebel *et al.*, 2000). The Kerguelen Plateau extends from the archipelago in a southeasterly direction for several hundred nautical miles. Hence, nights of foraging activity in ecoregion 2, southeast of Cap Noir, are associated with low SST ($3.7°C$) over the continental shelf edge of the Plateau ($\sim600\,m$). This region is also regularly used by female Antarctic fur seals breeding at Heard Island (Green, 1997). The temperatures in this area were consistent with the surface expression of waters of the PF (Koudil *et al.*, 2000), although sub-surface and surface expressions of the PF are regularly separated by up to $8°$ latitude (Sparrow and Heywood, 1996). Generally, the range of SST above the PF

are in the vicinity of 1.6–2.5°C (austral spring) and 4.8–5.2°C (summer) (Belkin and Gordon, 1996). However, foraging activity in ecoregion 1, on average, tended to be associated with deeper (1870 m) and warmer (5.4°C) waters. The static variable depth and SST on a weekly temporal scale accounted for the differences in diving behaviour and together defined two main ecoregions encountered at the three spatial scales investigated. We were unable to detect any differences in Chl. *a* concentration between ecoregions at the temporal (monthly) and spatial scales used. Owing to persistent cloud cover in these latitudes, the resolution of the data (monthly) averages over a region of 81 km^2 may have been insufficient to detect small-scale variability in phytoplankton abundance. However, it is also possible that marine productivity has been generally high across the study area. Blain *et al.* (2001) have shown that iron input from the plateau, and favourable light conditions and mixing regime in summer induce high chlorophyll plumes downstream of the Kerguelen Plateau. Furthermore, our results concur with those of Guinet *et al.* (2001) that fur seal females tend to forage within areas characterised by high primary production and high SST and bathymetric gradients.

One of the most compelling findings was the difference in nightly diving activity in the two different ecoregions, particularly at the 0.5° scale for SST$_{sat}$. To date, few studies have attempted to correlate the diving behaviour of marine predators at a particular location with concurrent environmental parameters, although many have examined such relationships over the duration of a foraging trip (McCafferty *et al.*, 1999; Charrassin and Bost, 2001, 2002; Field *et al.*, 2001; Guinet *et al.*, 2001). Foraging to the northeast and east of the archipelago, in waters that were mostly warmer than in ecoregion 2, seals in ecoregion 1 dived to greater average depths and covered larger vertical distances per hour. Yet in cooler and shallower waters to the southeast, diving frequency was higher and more time was spent diving. The temperature profiles obtained during dives over oceanic waters to the northeast appear to represent waters of the PFZ (Field *et al.*, 2001). Temperatures remained relatively stable and high (4.5–5.0°C) to approximately 80 m, descending to <4°C at 150 m depth. The relative homogeneity of the upper water column may be indicative of some mixing of water masses. In the vicinity of the islands the mixed layer depth (MLD) ranges from 50 to 200 m, depending upon season (Bucciarelli *et al.*, 2001), and in some years may be around 60 m in January to the south of Kerguelen (50°40′S, 68°25′E; Park *et al.*, 1998). Biological productivity is greatest within the surface mixed layer (McCafferty *et al.*, 1999) and it has been suggested that prey may be concentrated at the thermocline (Charrassin and Bost, 2001), or at other discontinuities between water masses (Boyd and Arnbom, 1991). Our data however, do not seem to support the notion that the diving behaviour of seals in either ecoregion is related to the MLD, as the greatest proportion of dives occurred to depths of less than 60 m (Figure 5).

After an initial decrease in SST on departing the colony, nightly SST as measured by TDR tended to remain relatively stable within an ecoregion, although one seal foraging in ecoregion 1 visited a colder area on one night. Of the 10 individuals studied, only one seal appeared to switch between the two ecoregions during the same foraging trip, but in this case the temperature remained approximately similar and was more typical of ecoregion 2. Even seals conducting long, looping and possibly exploratory foraging trips (Bonadonna *et al.*, 2000) stayed mostly within the one ecoregion. Temporal variability in SST during foraging trips of Antarctic fur seals at South Georgia has also indicated that seals spending longer time at sea were often travelling further to warmer waters of the PF up to 350 km north of the island (McCafferty *et al.*, 1999).

The observed differences in foraging behaviour suggest that prey distribution also differed. Mesopelagic myctophid fish, which accounted for 96% by number of all fish and cephalopod prey in 2000 (Lea *et al.*, 2002a), are highly abundant in the PFZ (Duhamel *et al.*, 2000) and concentrated at the PF (Sabourenkov, 1991), which reaches its northernmost position here at 46–47°S (Belkin and Gordon, 1996). The nocturnal diving behaviour of the seals (Lea *et al.*, 2002b) reflects the diel migration of myctophids (Duhamel *et al.*, 2000; Bost *et al.*, 2002) and that of their zooplankton prey (Kozlov, 1995). Thus, differences may be expected in prey species consumed by seals foraging at different depths within each ecoregion, as species distribution differs markedly with depth in proximity to Cap Noir (Duhamel *et al.*, 2000). The higher incidence of dives in bouts (95 vs. 91%) suggests that the cooler waters of ecoregion 2 may exhibit greater prey availability. Foraging seals must locate their migrating prey in three-dimensions and little is currently known about the behaviour of myctophid schools on a small scale. However, behaviour and distribution of prey appear to be sufficiently influenced by differences in depth, associated SST and perhaps levels of upwelling in the two ecoregions to affect seal diving behaviour. To assess dietary preferences by ecoregion, data on fatty acid composition of milk samples (Lea *et al.*, 2002a) were available for six seals. Although sample size is limited, individual differences in fatty acid composition were larger than those between ecoregions. High monounsaturated fatty acid levels (MUFAs), indicative of myctophids (Saito and Murata, 1998; Lea *et al.*, 2002c), were common in both ecoregions (53–64%).

Interestingly, observed variation in diving activity between ecoregions, in terms of depth and intensity, was not reflected in the rate of energy transfer to the pup. This may of course be an artefact of the relatively small numbers of females studied, as a continuum appears to exist with seals foraging in regions typified by warm surface waters to depths greater than 50 m enabling lower rates of daily PMG per FC than seals diving more shallowly in cooler waters (Figure 6). However, the similarity in provisioning rates may also reflect an ability of seals to balance differences in prey

distribution and abundance within the water column through prey selectivity. Compositional analyses of fur seal milk samples during late lactation (February/March) indicated significantly higher milk lipid values in 2000 (53%) than in 1999 (43%), which is thought to be related to the increased occurrence of energy-rich *Gymnoscoplus* spp. in the diet in 2000 (Lea *et al.*, 2002a). Whether seals choose to forage in either ecoregion consistently during consecutive trips, based on experience gained and/or in an effort to reduce intra-specific competition, remains to be determined.

Conclusions

Our results build on those of Guinet *et al.* (2001), showing that strong relationships at smaller spatial scales (particularly 0.5°) exist between environmental parameters, most noticeably SST and bathymetry, and the diving activity of female fur seals on a nightly basis. That these females exhibited similar rates of foraging success regardless of the at-sea conditions encountered, and associated changes in diving behaviour, confirms the flexibility in foraging strategies previously identified for this species (Bonadonna *et al.*, 2000; Lea *et al.*, 2002b). We addressed the linkages between environmental conditions, diving behaviour and pup provisioning on a nightly and single foraging trip scale, and the costs and benefits associated with the use of either foraging behaviour may be cumulative, accruing over the duration of many sequential foraging trips. However, under the variable conditions encountered in February 2000 at Îles Kerguelen, it appears that, at least in the short-term, seals were capable of adjusting their at-sea behaviour to account for this variability and provision their pups effectively.

Acknowledgements

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