

Bathymetry and frontal system interactions influence seasonal foraging movements of lactating subantarctic fur seals from Marion Island

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ABSTRACT: Sixteen lactating subantarctic fur seals *Arctocephalus tropicalis* were satellite-tracked during the winter of 2006 (n = 6), summer of 2006/07 (n = 6) and autumn/winter (n = 4) of 2007, from Marion Island, Southern Ocean. Despite varied individual movement patterns, a favoured foraging area lay to the northeast of the island. In contrast to findings for populations at similar latitudes, seals from Marion Island did not undertake short overnight foraging trips, but trips consistently went beyond 300 km from the island. This aligns with the at-sea duration of lactating seals' foraging trips from temperate Amsterdam Island, but differs from subantarctic Crozet and Macquarie islands. Time spent at sea, maximum distances travelled and movement variation of tracks from the island varied seasonally. Faecal analysis suggests the diet comprised primarily myctophid fish with limited seasonal variation. Well-defined areas of restricted movement coincided with significant bathymetric features to the west/northwest of the Crozet Plateau, with the Del Caño Rise clearly being important. Positive and negative sea-surface height anomalies (compared to the mean) appeared to be preferred by most seals across seasons. Higher summer sea-surface temperatures correlated with the movements of some seals. Higher chlorophyll *a* concentrations dictated transit and foraging areas during summer. Bathymetrically influenced oceanographic variables likely explain these preferred long-distance eastward movements. The Îles Crozet and Marion Island subantarctic fur seals differ in their foraging ecology despite being neighbours. Conversely, the subantarctic fur seal populations from the distant Amsterdam and Marion islands appear to be similarly influenced by such environmental factors.

KEY WORDS: Otariid · *Arctocephalus tropicalis* · Foraging ecology · Satellite telemetry · Oceanography · Area-restricted movement · Diet · Del Caño Rise

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INTRODUCTION

Marine apex predators have been the focus over the past decade for their role as oceanographic indicators (Fedak 2004, Block 2005, Biuw et al. 2007). However, the complex interplay between frontal systems, bathymetry and other oceanographic variables at a meso-scale and sub-mesoscale are central to the prey habitat preference (Constable et al. 2003) that drives the population dynamics of top predators. Numerous island populations of such predators within the Southern Ocean enabled research pertaining to the ecology and

ocean habitats that are utilised by these predators. Otariids (fur seals and sea lions) have been subject to a number of foraging ecology studies and have been successfully used as oceanographic indicators (e.g. Lea & Dubroca 2003, Ciannelli et al. 2004). Their alternating central place foraging strategies (Orlans & Pearson 1979) during periods of maternal care, and more extensive foraging movements during the non-lactation period (Cherel et al. 2007), make them ideal study templates to address questions of predator foraging ecology and influences of oceanographic variability. However, for a holistic understanding of how environ-

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mental changes dictate the ecology of such predators, studies aimed at identifying foraging areas of several populations of these predators and the prevailing environmental conditions are required. The physical limitations to the extent of any one population's movements necessitate studies on numerous species (and populations) over large temporal and spatial scales.

Subantarctic fur seals *Arctocephalus tropicalis* have been intensively studied at a few localities in the Southern Ocean. Some studies have focused on comparative foraging ecology of subantarctic and Antarctic fur seals *A. gazella* at 2 of the 3 island groups where they breed sympatrically, namely Îles Crozet (Bailleul et al. 2005, Luque et al. 2007) and Macquarie Island (Robinson et al. 2002). Both these island systems are situated within the Polar Frontal Zone (PFZ), a diverse and heterogeneous oceanscape in the path of the Antarctic Circumpolar Current (ACC) bounded to the north by the Subantarctic Front (SAF) and to the south by the Antarctic Polar Front (APF) (Lutjeharms & Valentine 1984). At both these localities, overnight foraging trips comprise a large proportion (~40 to 50%) of the total number of trips during summer, with the longer trips rarely exceeding 10 d or 100 km from the particular island (Robinson et al. 2002, Bailleul et al. 2005, Luque et al. 2007). The position of Îles Crozet and Macquarie Island within the productive PFZ is hypothesised as one explanation for the predominance of short overnight foraging trips by those seals. Conversely, subantarctic fur seals at the more temperate Amsterdam Island, far north of the PFZ, have traditionally been portrayed as the 'marathon' seals of the species and research on their long-distance foraging migrations and lengthy at-sea time during attendance cycles have been emphasised (Georges et al. 2000, Beauplet et al. 2004). It is hypothesised that the latitudinal position of Amsterdam Island, far west/northwest of the putative feeding grounds (mostly along the Subtropical Front) necessitates lactating fur seals from there to undertake long, southeast and eastward trips (Beauplet et al. 2004). Clearly, studies of several populations of a species are required to address general questions pertaining to the biology of the species and the extensive ocean habitat that they utilise.

In this respect, foraging studies are lacking for several other localities where subantarctic fur seals occur. The Prince Edward Islands (comprised of Marion Island and the smaller Prince Edward Island) support a large, increasing population of subantarctic fur seals (Bester et al. 2003, Hofmeyr et al. 2006). Aspects of subantarctic fur seal population growth (Hofmeyr et al. 2006, 2007), attendance behaviour (Bester & Bartlett 1990, Kirkman et al. 2002) and species biology (Kerley 1983, 1985, Bester & Van Jaarsveld 1994) have been investigated at Marion Island. However, long-range

dispersal by subantarctic fur seals based on flipper-tagged individuals (Bester 1989), and a preliminary technical report on 4 lactating females tracked from the east coast of Marion Island (Osbourne et al. 2002) are the only previous movement studies for the area. These islands support the only other breeding population of the species (aside from Îles Crozet and Macquarie Island) located within the PFZ. Moreover, the Prince Edward Islands are situated along the SW Indian Ridge, a series of undersea mountain ranges and fracture zones or canyons that stretches from the mid-Atlantic Ridge in the west to the central Indian Ridge in the east. These bathymetric features interact with the ACC to form eddies, which enhance the mesoscale variability in this region of the PFZ (Lutjeharms & Valentine 1988).

Despite the seemingly abundant resources for fur seals in close proximity around the Prince Edward Islands, Kirkman et al. (2002) showed (using attendance patterns data) lengthy at-sea durations for lactating subantarctic fur seals from Marion Island. These at-sea trip durations correspond more closely with those from Amsterdam Island (Beauplet et al. 2004), than with those from the neighbouring Îles Crozet (Bailleul et al. 2005, Luque et al. 2007) or the more distant, but also within the PFZ, Macquarie Island (Robinson et al. 2002). This apparently inconsistent association between the latitudinal position of Marion Island and the duration of time spent at sea forms a central issue in the present study. Furthermore, based on the identification of highly productive foraging areas utilised by other Marion Island predators (Jonker & Bester 1998, Nel et al. 2001), it is hypothesised that fur seals may forage in similar locations to the west of the island. Several related ecologically important questions arise as a result. (1) Do the subantarctic fur seals from Marion Island feed close to the island owing to the island's location within the PFZ, (2) or do they feed in the same distant area (westwards of the island) as other Marion Island top predators, (3) or eastward, in areas utilised by the neighbouring Îles Crozet, or distant Amsterdam Island, fur seals? (4) Why do they have long winter foraging trips (Kirkman et al. 2002) as do Amsterdam Island fur seals (regardless of their foraging areas)? (5) How does the foraging ecology of the Marion Island fur seal population compare with that at other islands, within the PFZ (Îles Crozet), and away from the PFZ (Amsterdam Island)? (6) Can knowledge of their foraging ecology illuminate potential demographic changes underpinning the recently slowed population growth rate (Hofmeyr et al. 2006) at the Prince Edward Islands?

Foraging studies of lactating females in conjunction with data on prey availability gained from the rate of pup provisioning and growth rate can provide insights

into the aforementioned demographic changes. For instance, poor foraging conditions often result in longer foraging trips by fur seal mothers and slower pup growth (Boyd et al. 1997, McCafferty et al. 1998, Kirkman et al. 2003, Lea et al. 2006), affecting pup body mass at weaning, which is important for future survival (Beauplet et al. 2005). Therefore, the seasonal at-sea movements of lactating subantarctic fur seal females from Marion Island, incorporating related investigations of diet over concurrent time frames, are employed to address these questions.

MATERIALS AND METHODS

Study site. Marion Island ($46^{\circ} 54' S$, $37^{\circ} 45' E$) is situated in the southern Indian Ocean and has a coastline of approximately 107 km, with the nearest landmass being Îles Crozet (~950 km to the east; Fig. 1). Although subantarctic fur seals *Arctocephalus tropicalis* haul out around the entire coast of Marion Island (Hofmeyr et al. 2006), certain focal rookeries are studied here. Breeding adult female fur seals at Van den Boogaard (VdB) and Rockhopper Bay (RhB) colonies on the northeast coast (<0.1 km apart; Fig. 1) were selected to study at-sea movements. Due to the small number of seals available at these colonies (VdB and RhB), prey (scats) data was collected from the larger

Cape Davis breeding colony on the north coast (only ~15 km distant on a similar aspect of Marion Island; Fig. 1). Logistic limitations precluded use of the Cape Davis site for satellite-device deployments. Despite Lea et al. (2008) finding that spatially segregated colonies (~160 km apart) of Antarctic fur seals at Îles Kerguelen foraged in different areas, their diet was superficially similar. The proximity of the different study colonies in the present study thus offers the likelihood that individuals are feeding in similar areas with similar prey. To avoid erroneous conclusions if differences were to exist in foraging areas between colonies, these scat data were used to assess broad-scale similarity in prey preferences with other island populations.

Device deployments. At-sea movements were measured during a single foraging trip for each of 16 lactating females during 2006 and 2007, divided between winter, 1 May to 30 September 2006 ($n = 6$, 2006W); summer, 1 January to 28 February 2007 ($n = 6$, 2007S); and autumn/winter, 1 March to 30 August 2007 ($n = 4$, 2007W). Lactating females were selected at random at the VdB or RhB colonies and captured with a hoop net. A platform transmitter terminal (PTT; Kiwisat 101, Sir-track, 120 g, $110 \times 42 \times 14$ mm, 5.7cm^2 cross sectional area) linked to the ARGOS Collection and Location System was attached to the fur on the dorsal midline of the seal immediately posterior to the scapulae, using a

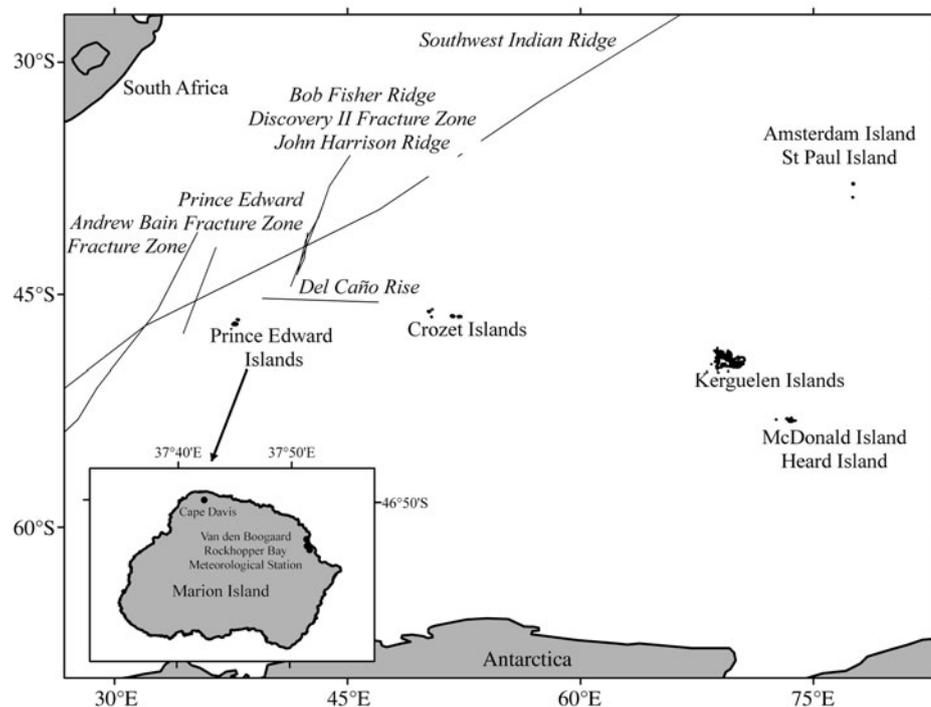


Fig. 1. Location of the Prince Edward Islands in the southern Indian Ocean. Major bathymetric features are presented with names in italics. Insert: Marion Island, depicting the 3 subantarctic fur seal *Arctocephalus tropicalis* study colonies, namely Van den Boogaard and Rockhopper Bay beaches, where lactating females carried satellite devices, and Cape Davis beach, where scat sampling was done

double-component, quick-setting epoxy resin (Araldite AW2101, CIBA-GEIGY Ltd.). Upon return from the foraging trip, the seals were recaptured and the devices were removed by careful clipping of the fur underneath. At each of the deployments and retrievals, the restrained seals were released within 30 min of capture. Study females and their pups were marked upon initial capture with uniquely numbered and colour-coded tags (Dalton Jumbo Rototags) at the trailing edge of each fore-flipper, to confirm the successful rearing of pups subsequent to removal of the mother's device and the return of a mother in the unlikely event of the loss of her tracking device.

Data analysis of at-sea movements. ARGOS locations were filtered to exclude those locations that required swimming speeds of $>3 \text{ m s}^{-1}$ (Bonadonna et al. 2000), irrespective of the location accuracy value assigned by ARGOS, to avoid excessive data loss (White & Sjöberg 2002). The filter resulted in the retention of 96% of the ARGOS locations. Regular trajectories were created by calculating average daily locations (Tosh et al. 2009). Locations were analyzed at a coarser temporal resolution in order to align auxiliary satellite data with our telemetry findings. Maximum distance from the colony and duration of the trips were calculated for each animal. Kernel density probabilities (Silverman 1986) were calculated for each track using least squares cross validation (Seaman & Powell 1996). Areas of restricted movement (ARM) were identified using a non-parametric kernel density estimator that identified areas of 50 and 95% probability of occurrence. These core areas of density (50%) are formed by animals remaining in one place for an extended time relative to the rest of the track. This approach is reliable in this case because the tracks are all regular over time, meaning equal sampling intervals have been created. The remainder of the locations all fell outside of the 50% probability kernel and were classified as transit locations. The spatial analysis was performed using the Spatial Analyst and Animal Movement Analyst (Hoodge & Eichenlaub 1997) extensions for ArcView 3.3 (ESRI 1998).

Bathymetric data (IOC IHO, BODC 2003), monthly sea-surface temperature (SST) (MODIS; Feldman & McClain 2008a), seasonal chlorophyll *a* (SeaWiFS; Feldman & McClain 2008b) and daily sea-surface height anomaly (SSHA)/altimetry data (produced by SSALTO/DUACS and distributed by AVISO with support from the Centre National d'Etudes Spatiales) were interpolated using bilinear interpolation to a 1° grid corresponding to the time period during which the track was recorded. For each altimetry data set, a median date value was selected for interpolation.

All the locations were pooled according to season and classified according to transit type and direction trav-

elled. Kruskal-Wallis analysis of variance (ANOVA) was used to test for intra- and inter-seasonal differences in mean values of SST, chlorophyll *a* concentration, bathymetry and sea-surface height values interpolated to the location data based on transit type and direction travelled. Inter-seasonal variation in SST, chlorophyll *a* concentration, bathymetry and sea-surface height values was evaluated using Kruskal-Wallis ANOVA.

Diet. Scats were collected from the subantarctic fur seal breeding colony at Cape Davis every month from May to August 2006 and from January to August 2007. Sample sizes were variable due to temporal variation in the numbers of animals ashore. While the breeding colonies are not exclusively used by lactating females, the collection site at Cape Davis consistently included $>90\%$ lactating females and their pups. Only fresh scats were collected (see Klages & Bester 1998, for procedure details) and individually processed (see Makhado et al. 2008). Species (identified using sagittal otoliths)-specific regressions were used to estimate prey size and mass, and, for species without published regressions, those of closely related species were used (for details see Makhado et al. 2008). The negative bias in cephalopod beak collection from scats (Ferreira & Bester 1998, de Bruyn et al. 2003) and the importance of fish in subantarctic fur seal diet at this locality (Klages & Bester 1998) preclude our use of species-specific cephalopod data in the present study. Cephalopod beaks were pooled as 'unidentified' in analyses. For fish, percentage frequency of occurrence was expressed as the number of times each species appeared within all scats containing otoliths, while percentage numerical abundance was the number of otoliths of each species present in all scats. Percentage contribution by mass and number for each species was calculated relative to the mass and number, respectively, of all species found in the scats over time and divided into set time frames (2006W, 2007S, 2007W).

RESULTS

All 16 fur seals *Arctocephalus tropicalis* provided tracks of at-sea movements. Duration of tracks (mean \pm SD) varied considerably (38 ± 21 d, range: 14 to 75 d; Table 1). When the incomplete tracks ($n = 3$) were excluded from the analysis, the mean maximum distance attained from the colony was 651 ± 123 km.

Winter 2006 at-sea movements

Four seals (S1, S4, S5 and S6) showed similar movements to the northeast of Marion Island (Fig. 2). However, S1 did not return to the island and was thus

Table 1. *Arctocephalus tropicalis*. Summary statistics for the at-sea movements of 16 subantarctic fur seals from Marion Island during 2006 and 2007. ARM: area of restricted movement

Seal ID	Seal mass (kg)	Deployment period	Track duration (d)	Season	Maximum distance travelled (km)	Daily distance travelled (km) (mean \pm SD)	Time spent in ARM (%)
S1	30	12–26 May 2006	14 ^a	Winter	521	12.5 \pm 8.3	36
S2	34	1 May–4 Jun 2006	34	Winter	813	33.0 \pm 60.7	–
S4	36	4 May–18 Jun 2006	45	Winter	515	15.0 \pm 28.8	20
S5	29	10 May–7 Jun 2006	28	Winter	649	23.6 \pm 39.7	57
S3	40	12 Jun–26 Aug 2006	75 ^a	Winter	1066	32.8 \pm 82.2	44
S6	37	15 Jun–14 Jul 2006	29	Winter	628	24.7 \pm 22.2	62
S7	20	22 Jan–10 Feb 2007	19	Summer	437	21.7 \pm 14.6	21
S10	26	23 Jan–16 Feb 2007	24	Summer	610	17.0 \pm 15.0	21
S13	26	2 Feb–3 Mar 2007	29	Summer	506	37.0 \pm 68.0	41
S15	36	7 Feb–23 Feb 2007	16	Summer	558	30.5 \pm 27.1	50
S8	26	14 Feb–2 Mar 2007	19	Summer	377	23.4 \pm 22.0	50
S11	26	18 Feb–7 Mar 2007	17	Summer	428	22.0 \pm 15.9	41
S14	34	4–21 Mar 2007	17	Autumn	318	12.0 \pm 8.4	–
S16	28	4–23 Mar 2007	19	Autumn	617	31.1 \pm 39.1	26
S9	33	14 Apr–23 Aug 2007	121 ^a	Winter	1252	26.4 \pm 32.0	36
S12	30	31 May–23 Jun 2007	23	Winter	395	24.6 \pm 23.8	43

^aIncomplete track (excluded from further statistical analysis)

excluded from further analyses. The 3 remaining seals all moved through cooler waters (Transit SST = $6.4 \pm 1.3^\circ\text{C}$) and displayed localized movements in areas of warmer water (ARM SST = $8.3 \pm 2.4^\circ\text{C}$). These animals remained within the ACC and did not cross over the SAF (Fig. 2A). The seals showed concentrated foraging movements across the Del Caño Rise and turned around just short of a clustered group of bathymetric features (Figs. 2B & 3A). These seals also frequented areas of higher ocean altimetry (sea-surface height — ARM = 6.3 ± 2.5 cm; Transit = 5.0 ± 3.2 cm; Fig. 2C). Seal S2 travelled to the west of the island directly over the intersection of the SW Indian Ridge and the Andrew Bain Fracture Zone. This seal did not display a specific ARM. Along its path it encountered colder water (SST = $5.9 \pm 1.2^\circ\text{C}$) and lower, more variable altimetry (sea-surface height = -1.9 ± 8.1 cm) than seals that travelled northeast. Seal S3 displayed a meandering track that closely followed an area of higher chlorophyll concentration associated with the subtropical Front (STF), but never returned to Marion Island, and was thus excluded from further analyses.

Summer 2006/2007 at-sea movements

All 6 seals tracked during the summer in early 2007 returned to the island. The mean duration of trips was 20 ± 5 d (range: 16 to 29 d), and the maximum distance attained from the colony was 486 ± 88 km (range: 377 to 610 km; Table 1).

Three seals (S8, S10 and S11) were tracked in a northeasterly direction (Fig. 2). In contrast to the

2006W movements, these seals travelled north of the SAF towards the STF, encountering higher SSTs, especially in ARMs (Transit SST = $8.5 \pm 1.5^\circ\text{C}$; ARM SST = $10.4 \pm 1.0^\circ\text{C}$; Fig. 2A). These seals travelled over the Del Caño Rise (Fig. 2B) and moved in the same area of bathymetric features as the fur seals tracked in the winter period of 2006 (Figs. 2B & 3C). These areas of warmer waters also coincided with regions of higher altimetry (sea-surface height — Transit = 0.7 ± 6.4 cm; ARM = 7.4 ± 3.7 cm). The remaining 3 summer tracks displayed varied patterns. Seal S13 travelled due west, crossing over the SW Indian Ridge and the Prince Edward Fracture Zone. A visual assessment shows that this seal travelled to an area of higher sea-surface height (Fig. 2C) and correspondingly higher chlorophyll *a* concentrations (Fig. 2D). Seal S15 travelled exclusively along the SAF, seemingly following a path characterized by homogenous SSTs (Transit SST = $7.9 \pm 0.5^\circ\text{C}$; ARM SST = $8.1 \pm 0.7^\circ\text{C}$) (Fig. 2A), heterogeneous sea-surface heights (Fig. 2C) and slightly higher chlorophyll *a* concentrations (Fig. 2D). Seal S7 travelled in a southerly direction to substantially colder waters (Transit SST = $5.7 \pm 0.9^\circ\text{C}$; ARM SST = $3.9 \pm 0.06^\circ\text{C}$).

Autumn/winter 2007 at-sea movements

During the autumn/winter period of 2007, 3 of the 4 seals tracked (S12, S14 and S16) returned to the island (Fig. 2). The mean trip duration for these 3 animals was 19.7 d (range: 17 to 23 d). They reached a mean maximum trip distance of 443 km from the island (range:

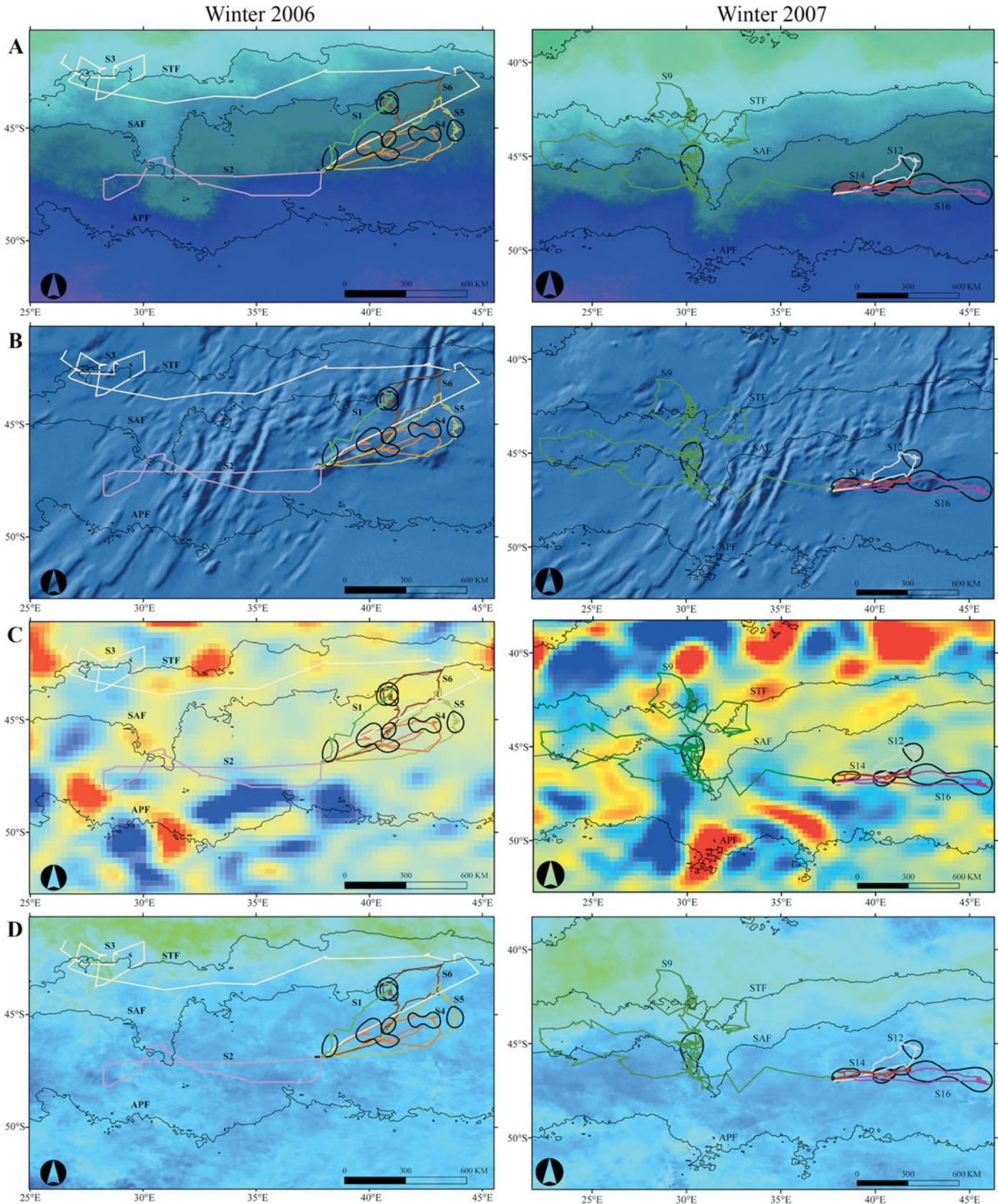


Fig. 2. *Arctocephalus tropicalis*. At-sea movement of lactating subantarctic fur seals in relation to Marion Island during winter 2006, winter 2007 and summer 2007. Areas of restricted movement are indicated by ellipsoids with: (A) sea-surface temperature overlay, (B) bathymetry overlay, (C) sea-surface height overlay and (D) chlorophyll a overlay. STF: Subtropical Front; SAF: Subantarctic Front; APF: Antarctic Polar Front; seal identification numbers, see Table 1

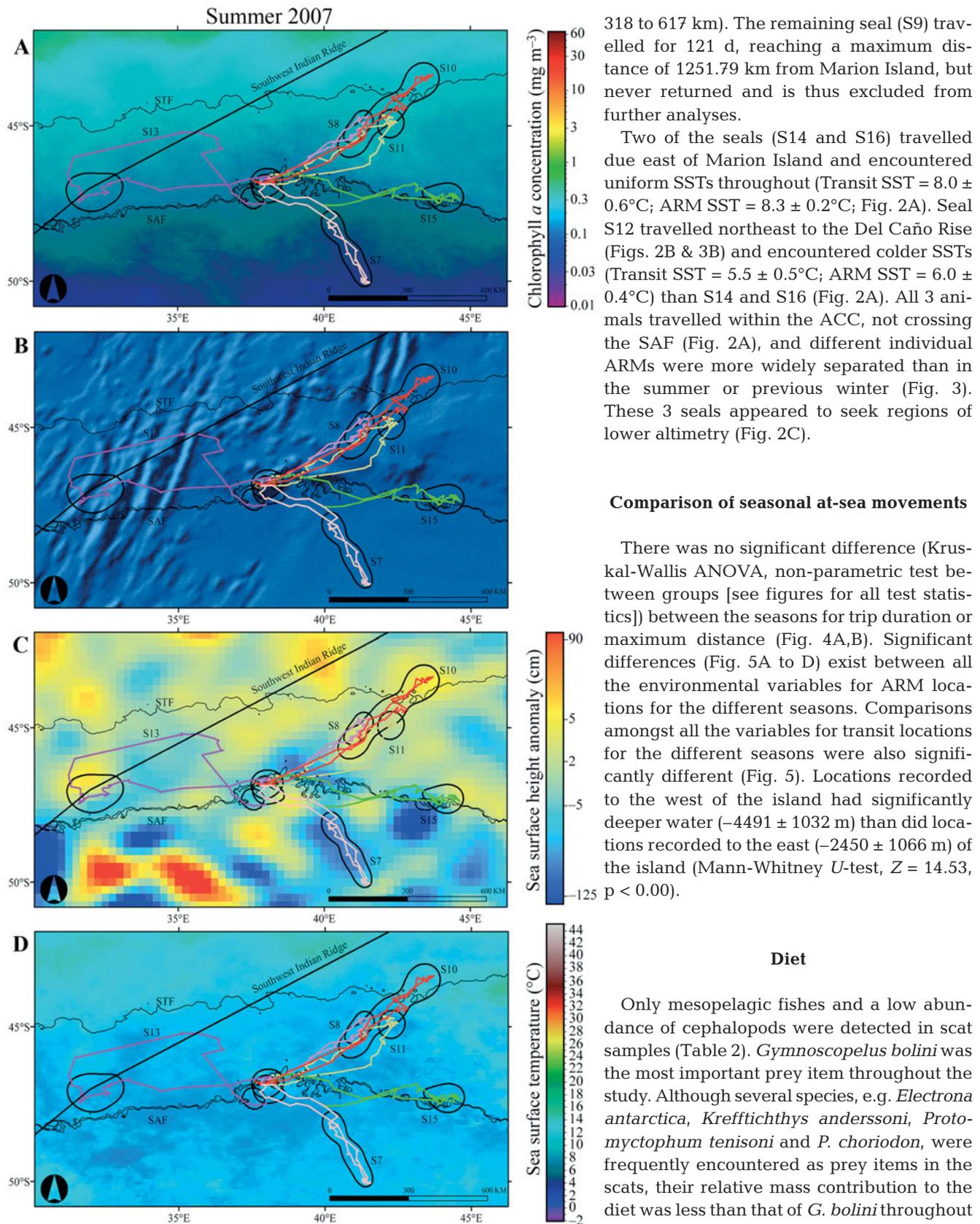


Fig. 2 (continued)

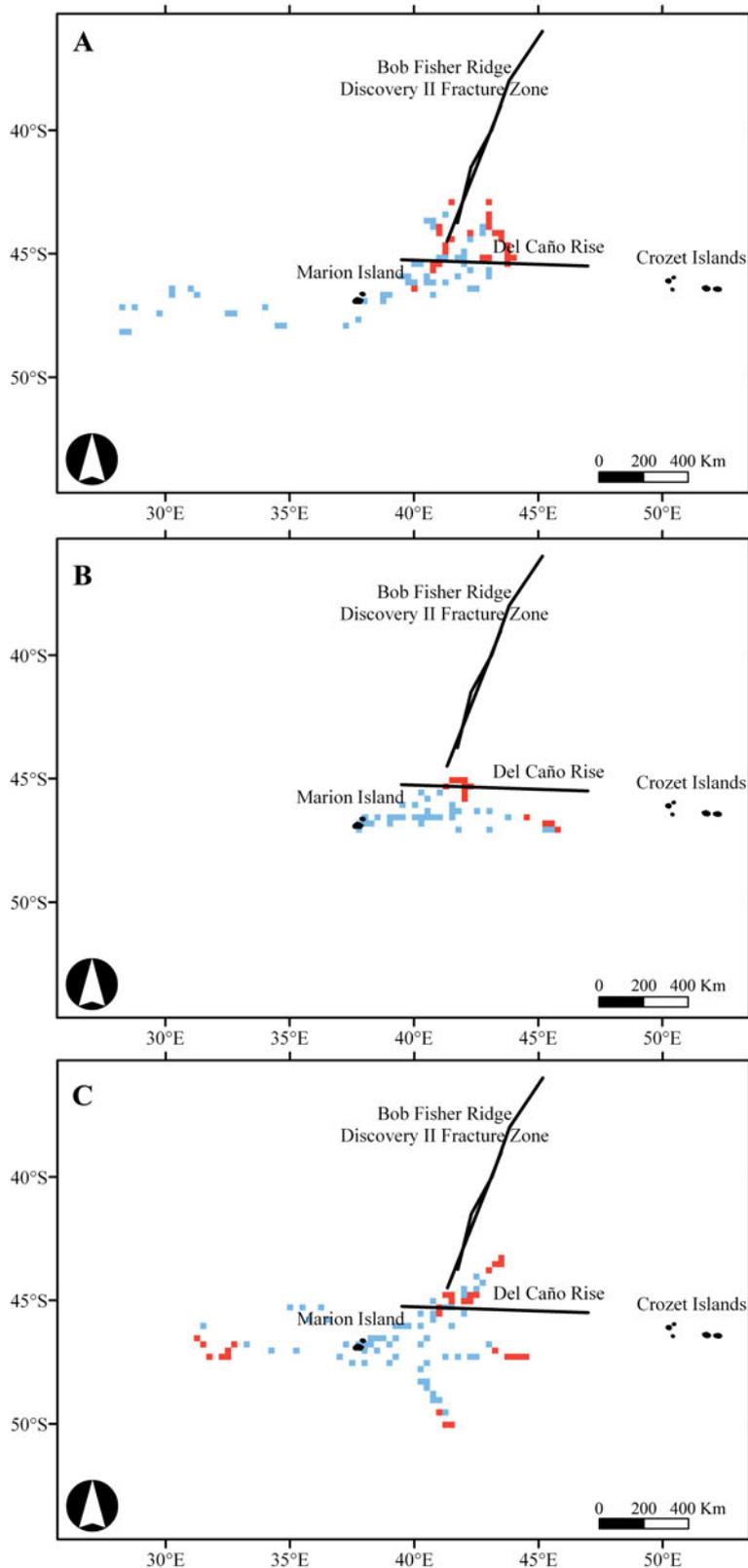


Fig. 3. *Arctocephalus tropicalis*. Relative position of locations within areas of restricted movement (ARMs; red) to transit locations (blue) for: (A) winter 2006, (B) winter 2007 and (C) summer 2007

prey mass other than *G. bolini* overall. Restricted sample sizes precluded comparison amongst the seasons of the present study, although some differences were evident (Table 2). Females appeared to utilise more (by mass) *G. piabilis* during later stages of lactation (autumn/winter 2007) as compared with early lactation (summer 2006/2007). Similarly, albeit at levels of comparatively less importance, the mass contribution of *Metelectrona ventralis* was higher during summer than during both winter periods.

DISCUSSION

The preferred long-distance eastwardly movement of lactating subantarctic fur seals *Arctocephalus tropicalis* from Marion Island stands in contrast to the expected behaviour. First, other top predators from Marion Island moved predominantly westward (e.g. Jonker & Bester 1998, Nel et al. 2001). Secondly, while subantarctic fur seals at the 2 other localities in the PFZ (Îles Crozet and Macquarie Island) feed within close proximity of these islands (<100 km), the seals from Marion Island feed at a great distance from their island rookeries (>400 km).

Inter-specific Marion Island comparisons

Oceanic areas of high productivity preferred by certain top predator species may be preferable for other species even if their foraging ecologies differ (Bost et al. 2009). Southern elephant seals *Mirounga leonina* consistently travel to the west and southwest of Marion Island (Jonker & Bester 1998), and recent data (M. N. Bester unpubl. data) correlate many of these westward movements with the Andrew Bain Fracture Zone. Similarly, grey-headed albatross *Thalassarche chrysotoma* concentrate their foraging in the same area (Nel et al. 2001). Notwithstanding the diverse foraging ecologies of these predators, the overlapping foraging area around the Andrew Bain Fracture Zone provides evidence for an area of productivity that could be attractive to other top predators. However, the evidence in the present study suggests otherwise for sub-

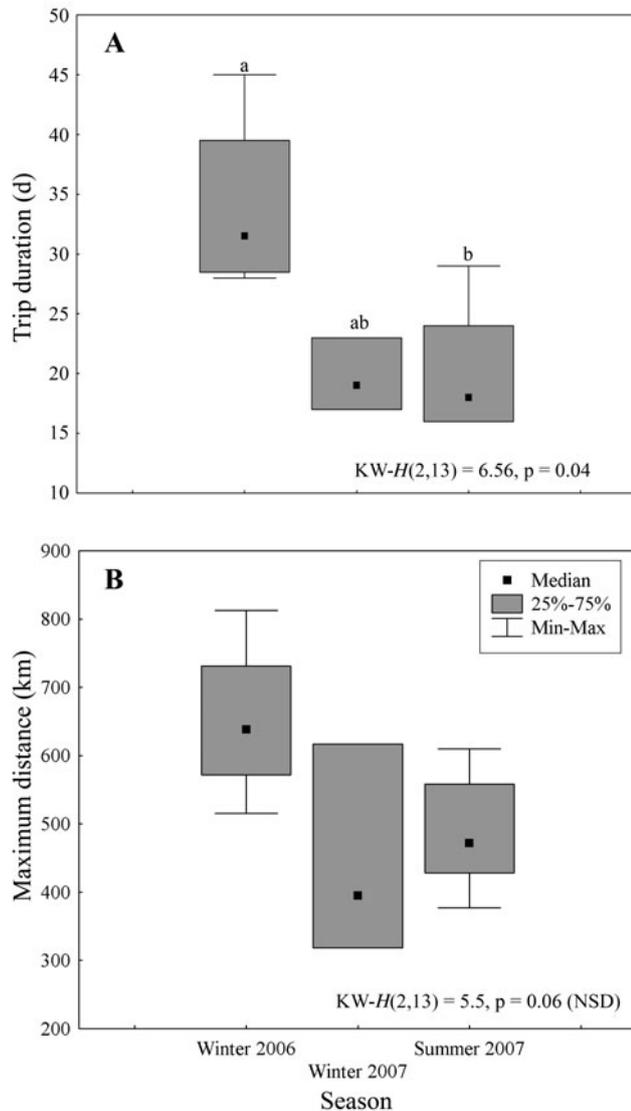


Fig. 4. *Arctocephalus tropicalis*. (A) Trip duration and (B) maximum distance from Marion Island reached for the 13 lactating fur seals that completed trips, instrumented at Marion Island over the 3 different deployment periods. The Kruskal-Wallis H -value is indicated in the figure, and significant differences are indicated by different letters. Significance is at $p < 0.05$

antarctic fur seals. Subantarctic fur seals are capable of long-distance movements (Table 1, Fig. 2) during foraging trips, and thus the distance to the Andrew Bain Fracture Zone from the island (direct route = 430 km) cannot be a limitation, and swimming upstream directly after a period of onshore fasting (but resting), is an unlikely hindrance. Alternatively, fur seals that foraged to the west of the island travelled through significantly deeper water (~4500 m mean depth) than those travelling to the east (~2500 m mean depth). Although fur seals rarely dive deeper than 200 m (Georges et al. 2000), the shallower benthos to the east

of Marion Island (Fisher & Goodwillie 1997) results in flow dynamics of differing bodies of water that are conducive to generating a shallow mixed layer; therefore, conditions more suitable to phytoplankton growth near the surface (Perissinotto & McQuaid 1992, Read et al. 2007) than over the deeper benthos to the west (Ansorge & Lutjeharms 2005). The potential for intermittent foraging during the transit phases to/from clearly defined ARMs could also explain the predominantly eastward, rather than westward, movement of the subantarctic fur seal females from the island. But why do these seals forage so far from Marion Island despite the island's location within the seemingly productive PFZ (Froneman et al. 1999, Bernard et al. 2007)? Indeed, this finding is contrary to the foraging ecology of subantarctic fur seals at both Îles Crozet and Macquarie Island.

Diet and between-island intra-species comparisons

Kirkman et al. (2002) found lengthy absences at sea for lactating subantarctic fur seals, between pup attendance sessions, but could not elaborate on the reasons for such long absences without concurrent at-sea movement data. The present study confirms that subantarctic fur seal females at Marion Island undertake equally lengthy foraging trips, as has been shown for Amsterdam Island fur seals (Beauplet et al. 2004). The Marion Island fur seals do not feed inshore and do not make overnight foraging trips, in contrast to fur seal behaviour during summer at the neighbouring Îles Crozet (Bailleul et al. 2005, Luque et al. 2007) and at Macquarie Island, which is located at a comparable latitude (Robinson et al. 2002).

The weaning masses of male and female pups from several Marion Island colonies were similar during 2006 and 2007 (M. N. Bester unpubl. data) and were comparable with previous years (Kirkman et al. 2002), indicating that foraging success rates (associated with at-sea movements) during these years were not anomalous. All pups of tracked mothers that returned, weaned successfully. Scat analyses in the present study indicated no distinct changes in the species composition of the predominantly myctophid fish diet, over the present study period or that of a previous study (Klages & Bester 1998). However, the relative contributions of the most important species in the diet, *Gymnoscopelus bolini*, *G. piabilis* and *G. nicholsi*, were markedly different to those in the latter study. The temporally restricted sampling in the present study (~1 yr) compared with that in the previous study (5 yr pooled) precludes adequate explanation of this result. Limited seasonal variation in the relative importance in species consumption is evident here. The period of

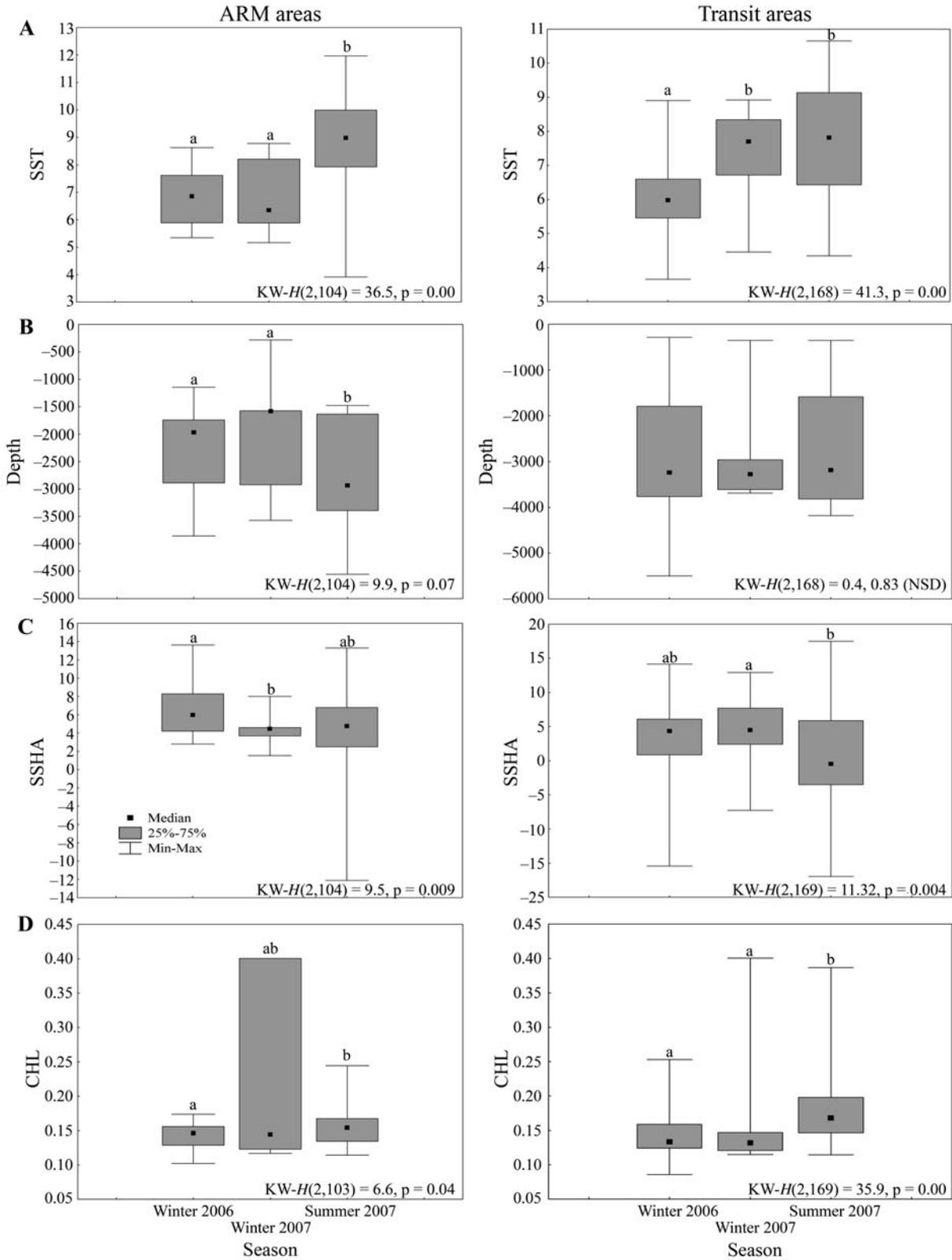


Fig. 5. Environmental characteristics: (A) sea-surface temperature (SST; °C), (B) bathymetry (m), (C) sea-surface height anomaly (SSHA; cm) and (D) chlorophyll a concentration (chl a, mg m⁻³) encountered for the areas of restricted movement (ARMs) and transit locations during each season. The Kruskal-Wallis *H*-value is indicated in the figure, and significant differences are indicated by different letters. Significance is at *p* < 0.05

Table 2. *Arctocephalus tropicalis*. Percentage frequency of occurrence (FO%), percentage numerical abundance (NA%) and percentage mass (Mass%) contribution of prey (Myctophidae) identified in scats (n = 192) collected from *A. tropicalis* at Marion Island, divided into 3 seasons (see 'Materials and methods')

Species of prey	Winter 2006 (n = 24)			Summer 2007 (n = 49)			Winter 2007 (n = 119)		
	FO%	NA%	Mass%	FO%	NA%	Mass%	FO%	NA%	Mass%
<i>Electrona antarctica</i>	4.17	0.23	0.01	13.04	0.65	0.04	3.88	0.55	0.03
<i>Electrona carlsbergi</i>	8.33	1.61	0.22	24.44	2.97	0.54	25.24	3.21	0.69
<i>Electrona subaspera</i>	41.67	28.97	7.23	31.11	3.36	1.72	47.57	6.08	2.23
<i>Gymnoscopelus bolini</i>	70.83	41.15	73.19	86.67	24.76	76.74	65.05	18.48	45.28
<i>Gymnoscopelus braueri</i>	4.17	0.92	1.82	4.44	0.13	0.38	3.88	0.20	3.20
<i>Gymnoscopelus fraseri</i>	20.83	4.60	0.97	53.33	5.30	1.22	50.49	33.13	7.43
<i>Gymnoscopelus nicholsi</i>	50.00	7.82	8.26	73.33	10.73	13.81	64.08	11.41	13.25
<i>Gymnoscopelus piabilis</i>	16.67	2.30	5.73	4.44	0.32	0.79	36.89	7.92	22.53
<i>Krefflichthys anderssoni</i>	8.33	0.69	0.01	80.00	11.51	0.21	47.57	9.94	1.96
<i>Lampichthys procerus</i>	0.00	0.00	0.00	8.89	0.32	0.12	2.91	0.38	0.82
<i>Metelectrona ventralis</i>	29.17	8.74	2.49	46.67	10.92	3.56	41.75	5.81	1.75
<i>Protomyctophum bolini</i>	0.00	0.00	0.00	6.67	0.19	0.01	3.88	0.14	0.01
<i>Protomyctophum choriodon</i>	0.00	0.00	0.00	20.00	1.42	0.20	4.85	0.27	0.06
<i>Protomyctophum tenisoni</i>	12.50	2.99	0.06	46.67	27.41	0.68	17.48	2.49	0.74
Unidentified squid	0.16	6.67	–	40.81	4.20	–	0.14	1.20	–

later lactation during 2007 (autumn/winter—coincident with predominantly due east foraging distribution from the island, rather than northeast as in 2006W; Figs. 2 & 3), as compared to earlier (2007S) lactation, showed markedly increased consumption of *G. piabilis* and *G. nicholsi* in relation to *G. bolini*, although the latter remained a dominant component. The high energy content and size of *G. piabilis* may result in this species being preferred by seals when available (e.g. during late gestation) (Lea et al. 2002). Despite the species composition of the diet identified here being superficially similar to that identified at Îles Crozet, the relative contribution of *G. piabilis* (and particularly *G. fraseri*) there dwarfs that of *G. bolini* and *G. nicholsi* during the summer (Luque et al. 2007). At Macquarie Island, the predominant prey component is *Electrona subaspera* (Robinson et al. 2002), which is unimportant in terms of mass contribution at Marion Island, albeit frequently encountered in scats. The fish species consumed at Marion Island (and by the fur seals from the other islands within the PFZ) differ from those preyed upon at Amsterdam Island, although the most important prey at all sites are mesopelagic fish from the family Myctophidae (Robinson et al. 2002, Beuplet et al. 2004, Luque et al. 2007). Clearly, based on satellite-tracking and dietary data, lactating fur seals from Amsterdam, Macquarie and Marion islands do not feed in overlapping areas (due to the vast distances between these islands). However, at all sites, the fur seals appear to seek similar oceanographic anomalies, presumed to be the ideal habitat for the seals' preferred prey, myctophids. Even the fur seals from Marion Island and the neighbouring Îles Crozet (the diets of which are more similar in species composition), which

are more likely to utilise similar foraging areas, are spatially separated (Bailleul et al. 2005, Luque et al. 2007). However, the Îles Crozet animals were only tracked in summer, when they remain within the limits of the Crozet archipelago. Complex interactions between frontal systems, bathymetry and biological oceanographic features may explain why the Îles Crozet fur seals feed close to their island rookeries and Marion Island seals do not.

Environmental linkages and long-distance movements

Downstream (to the east) of Marion Island substantial mixing of warmer SAF and colder APF water takes place (Perissinotto & McQuaid 1992, Ansorge et al. 1999). Together with some Marion Island nutrient runoff (Perissinotto et al. 2000), this creates an area conducive to phytoplankton growth and zooplankton assemblages from cooler and warmer waters (Perissinotto & McQuaid 1992). The fur seals that headed to the east and northeast of Marion Island appeared to focus their foraging phases (ARMs) in areas corresponding to several clustered bathymetric features, including the Bob Fisher Ridge, John Harrison Ridge, Discovery II Fracture Zone and, especially, the Del Caño Rise (Fig. 3). The Del Caño Rise is associated with the development of eddies, forming due to the interaction of large-scale circulation with sub-meso-scale structure, with annual phytoplankton blooms occurring in this vicinity as a result (Pollard et al. 2007, Read et al. 2007, Venables et al. 2007). A meander in a filament of the SAF between the Del Caño Rise to the

west and the Crozet Plateau to the east, resulting in the formation of eddies, is responsible for the entrainment of nutrient-rich water from the SAF into the associated bloom area (Read et al. 2007). The Del Caño Rise and Crozet Plateau form obstacles in the path of the SAF, causing weak circulation in the PFZ between the SAF and Îles Crozet and allowing dissolved iron and sediments from the Crozet Plateau and Islands to build up during winter. This situation (Pollard et al. 2007), augmented by the complex shape of these islands (Pollard et al. 2007, Read et al. 2007, Venables et al. 2007), gives rise to the characteristic annual phytoplankton blooms. These productive blooms probably explain why sympatric Antarctic and subantarctic fur seals from the Crozet Archipelago feed in the vicinity of their breeding colony beaches (50 to 100 km) and undertake overnight foraging trips (Bailleul et al. 2005, Luque et al. 2007), in contrast to the Marion Island subantarctic fur seals that range far and wide (present study). This difference could be due to the proximity of the SAF and APF to Marion Island, which cause fast flow of the water masses past the island, hindering the build-up of chlorophyll in entrained water near the island (Hunt et al. 2001). The absence of large bathymetric features immediately to the west of the island (disregarding the more distant Andrew Bain Fracture Zone) and the islands' simple (approximately oval) shape facilitate this fast flow. Thus, despite similar latitudinal location to Îles Crozet, which suggests that Marion Island seals should also make short foraging trips owing to their location within the productive PFZ, regional bathymetric features may explain why seals from Marion Island travel further from their breeding colonies (as with the Amsterdam Island fur seals).

Subantarctic fur seals at Amsterdam Island undertake extremely long winter foraging trips (>1000 km; ~30 d) to the east or south-east, which appears partially linked to the migration of the STF (Georges et al. 2000, Beauflet et al. 2004). At Marion Island they seem to be more dependent on the SAF, which migrates north in winter and south in summer, also resulting in longer winter foraging trips for the Marion Island fur seals (>800 km; ~30 d). However, our sample size is small, and individual variation may have an influence on results. It is perhaps significant that the only southerly foraging trip from Marion Island occurred during summer, which would coincide with a more southerly migration of the SAF. Biotic changes since 1976 suggest that the SAF, known to have a high degree of variability, may have moved southwards towards Marion Island (Pakhomov et al. 2000). Both the SAF and the APF have steep physical gradients (Lutjeharms 1985), which represent vital biogeographic limits (Pakhomov et al. 1994, Tarling et al. 1995), and are zones of enhanced biological activity (Lutjeharms 1985, Hunt et

al. 2001). Such variations in SSTs shape the distribution and abundance of zooplankton (Pakhomov et al. 1994), fish, squid and ultimately top marine predators (Beauflet et al. 2004). Therefore, southward movement of the SAF is likely to be responsible for the reduction in mesozooplankton biomass in waters adjacent to Marion Island, producing a bottom-up effect on top-predator populations (Hunt et al. 2001). A local depletion of mesozooplankton biomass around Marion Island could further contribute to the long-distance foraging trips undertaken by lactating fur seals to the bathymetrically influenced oceanographic environments around the Del Caño Rise.

Ecological implications

The present study illustrates that, despite the supposedly preferable location of Marion Island on the productive PFZ, the regional bathymetric influences on large-scale frontal systems appear to be of greater importance to local top predators than the mere proximity of such frontal systems to the island. Perhaps, then, the Marion Island fur seals do not have an easier time of finding prey than their Amsterdam Island long-distance travelling counterparts, with implications for similar bottom-up control of these populations. However, the local roles of competition with sympatric Antarctic fur seals and large penguin populations (Crawford et al. 2003) and of predation pressure by locally abundant killer whales at Marion Island (Tosh et al. 2008) remains to be explored. Killer whales at Marion Island are known to predate on seals and penguins (Condy et al. 1978) and are possibly an important determinant of inshore movements of seals. The foraging overlap by the 2 sympatric fur seal species at Îles Crozet does not appear to be functionally competitive (Bailleul et al. 2005, Luque et al. 2007), although the much larger populations of these 2 species at Marion Island (Hofmeyr et al. 2006) may result in some competition. Therefore, while the foraging ecology of Marion Island subantarctic fur seals appears to be chiefly dictated by the spatial availability of the preferred prey (myctophids) within the region, the roles of interspecific competition and/or killer whale predation pressure needs investigation to further understand the foraging choices that these fur seals make.

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