

Colony-specific foraging areas of lactating New Zealand fur seals

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ABSTRACT: During 2005 and 2006, 21 lactating New Zealand fur seals *Arctocephalus forsteri* were tracked from 4 breeding colonies in southern Australia. The distance between colonies ranged between 46 and 207 km. In total, 101 foraging trips were recorded (2 to 19 trips ind.⁻¹). Seals initiated foraging trips on a colony-specific bearing (Cape Gantheaume 141 ± 34°, Cape du Couedic 188 ± 12°, North Neptune Island 204 ± 12° and Liguanea Island 235 ± 19°). During autumn, seals from Cape du Couedic, North Neptune Island and Liguanea Island predominantly targeted distant oceanic waters associated with the subtropical front (STF), while seals from Cape Gantheaume targeted shelf waters associated with a seasonal coastal upwelling, the Bonney upwelling. The distance of each colony from the STF (based on the preferred colony bearing) or the Bonney upwelling in the case of Cape Gantheaume was correlated with the maximum straight-line distances travelled (Cape Gantheaume 119 ± 57 km, Cape du Couedic 433 ± 99 km, North Neptune Island 564 ± 97 km and Liguanea Island 792 ± 82 km). The organisation of colony-specific foraging grounds appears to be influenced by the proximity of colonies to predictable local upwelling features, as well as distant oceanic frontal zones. Knowledge of whether New Zealand fur seals utilise colony-specific foraging grounds may be important in predicting and identifying critical habitats and understanding whether management requirements are likely to vary between different colonies.

KEY WORDS: Colony separation · Subtropical front · Foraging ecology · New Zealand fur seal · Meta-population

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INTRODUCTION

Central place foraging theory predicts that animals either forage within close proximity to the central place provided that sufficient energy can be obtained, or they forage further from the central place if they can more than offset the increased travel costs through greater rates of energy uptake (Orians & Pearson 1979). As a result, the spatial distribution of foraging effort by a central place forager is likely to be influenced by a combination of previous experience and foraging success, local environmental cues and the needs of nutritionally dependant offspring (Bonadonna et al. 2001, Staniland & Boyd 2003). The way in which

central place foragers distribute their effort to optimise foraging success may also be regulated by the spatial partitioning of foraging areas (Sutherland 1983, Matthiopoulos et al. 2005). For instance, in a meta-population scenario, where groups of spatially separated populations have the ability to overlap foraging areas, competition from conspecifics may influence the distribution of foraging effort and give rise to colony-specific foraging areas.

Among marine central place foragers, colony-specific foraging areas have been documented for Antarctic fur seals *Arctocephalus gazella* (Boyd et al. 2002, Lea et al. 2002), northern fur seals *Callorhinus ursinus* (Robson et al. 2004), blue-eyed shags *Phalacro-*

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corax articeps (Wanless & Harris 1993), shy albatross *Diomedea cauta* (Brothers et al. 1998), Adelie penguins *Pygoscelis adeliae* (Ainley et al. 2004) and cape gannets *Morus capensis* (Gremillet et al. 2004). These studies suggest that the development of colony-specific foraging areas may be important in the partitioning of marine resources where multiple colonies occur in close proximity. In such cases, colony-specific foraging areas may reduce localised resource depletion, either during the early stages of the breeding cycle, when offspring are young, which may necessitate short foraging trips within close proximity to the colony, or in later stages of the breeding cycle, when individuals may travel further to forage (e.g. Harcourt et al. 2002, Thompson et al. 2003, Page et al. 2006).

Colony-specific foraging areas require that individuals travel in colony-specific directions when commencing a foraging trip, indicating highly integrated individual behaviour at the colony level (Bernstein et al. 1991, Robson et al. 2004). Site fidelity to foraging areas is an important factor in reinforcing colony-specific foraging areas and is likely to be influenced by the

availability of resources encountered during the previous foraging trip (Bonadonna et al. 2001, Robson et al. 2004, Matthiopoulos et al. 2005). Consequently, it is expected that the function of colony-specific foraging areas is dependent on some degree of habitat predictability in terms of the location, accessibility and quality of resources and the associated predictability in reproductive outcome (Switzer 1993, Irons 1998).

The New Zealand fur seal *Arctocephalus forsteri* is the most abundant fur seal species in the Australian–New Zealand region (Goldsworthy et al. 2003). In the state of South Australia, New Zealand fur seals breed at 36 locations, which represent ~85% of the Australian population (Shaughnessy 2005). However, of the 36 breeding colonies, 5 colonies within a 200 km radius account for ~82% of the Australian population and produce 17 600 pups each year (Shaughnessy 2005). These primary colonies are Cape Gantheuame and Cape du Couedic on Kangaroo Island, North and South Neptune Islands and Liguanea Island, and they form a region of critical habitat for this species (Fig. 1). Accordingly, New Zealand fur seals within South Australia provide a tractable species to assess whether

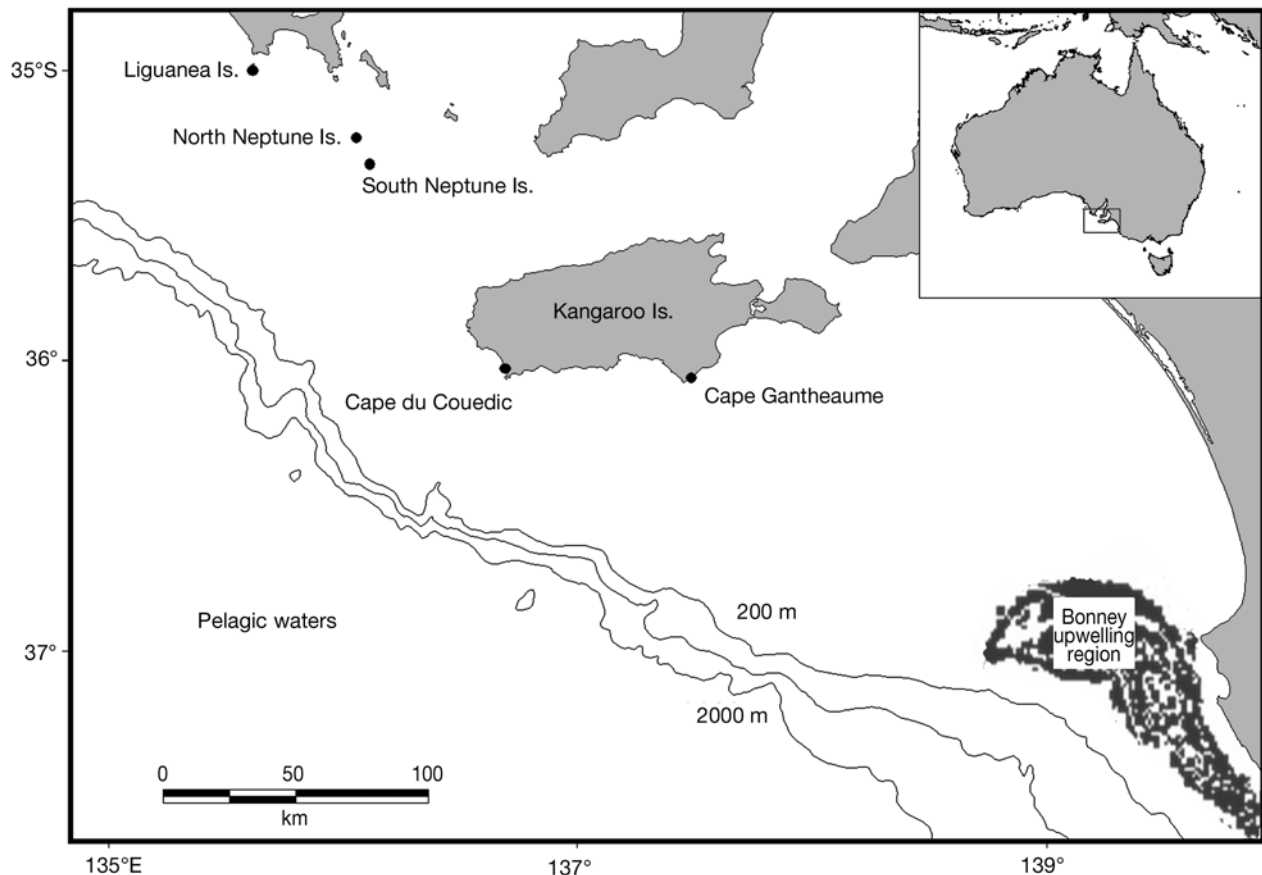


Fig. 1. The study area, showing the 4 study sites: Cape Gantheuame, Cape du Couedic, North Neptune Island and Liguanea Island. Also shown are South Neptune Island, and an example of a cold-water plume that is indicative of the Bonney upwelling during austral summer months

colonies in close proximity utilise colony-specific foraging areas.

As a result of their abundance and size, New Zealand fur seals are believed to consume the greatest biomass of pelagic resources within the Great Australian Bight of all marine mammal and seabird species (Goldsworthy et al. 2003). Nevertheless, despite the importance of New Zealand fur seals as top predators, their increasing abundance and the potential for fisheries interactions, our understanding of their foraging behaviour and the distribution of their foraging efforts is currently restricted to one colony, Cape Gantheaume on Kangaroo Island (see Page et al. 2006). The Cape Gantheaume colony is unique because it is within close proximity to the largest seasonal coastal upwelling in southern Australia, the Bonney upwelling (Lewis 1981, Butler et al. 2002). The Bonney upwelling is driven by alongshore winds. Between November and late April upwelled cold-water plumes are regularly observed at the sea surface and are associated with elevated nutrient concentrations that support enhanced levels of primary productivity (Butler et al. 2002). Lactating fur seals from Cape Gantheaume are known to target the Bonney upwelling (Page et al. 2006) and the subtropical front (STF) (Baylis et al. unpubl. data). The STF is a major ocean boundary that separates warm, saline, nutrient-poor subtropical waters to the north of the STF from relatively cool, less-saline, nutrient-rich subantarctic waters to the south (Bradford-Grieve et al. 1999). This front is a continuous oceanographic feature south of Australia, but is reported to end at the continental shelf of western Bass Strait near 40° S (Tomczak et al. 2004).

Given the close proximity of the largest New Zealand fur seal colonies to each other within southern Australia, knowledge of how colony-specific foraging grounds influence the spatial distribution of foraging effort may be important in predicting and identifying critical habitats. Furthermore, understanding the distribution of foraging effort across major breeding colonies is important in assessing the potential for fisheries interactions. This study aims to provide this knowledge by (1) comparing the habitat utilisation of New Zealand fur seals across 4 breeding colonies in south eastern South Australia, and (2) investigating whether the proximity of key oceanographic features influences colony-specific foraging grounds.

MATERIALS AND METHODS

Study site. This study was conducted at 4 sites: Cape Gantheaume (36° 04' S, 137° 27' E) and Cape du Couedic (36° 03' S, 136° 42' E) on Kangaroo Island, North Neptune Island (35° 13' S, 136° 03' E) and Li-

guanea Island (34° 59' S, 135° 37' E) (Fig. 1). Pup production in southern Australia indicates that New Zealand fur seal *Arctocephalus forsteri* populations are still recovering following the cessation of 19th and 20th century harvesting (Shaughnessy 2005). The estimated number of pups born during the 2005/2006 breeding season was 3120 at Cape Gantheaume, 2488 at Cape du Couedic, 4391 at North Neptune Island and 2072 at Liguanea Island (P. Shaughnessy & S. Goldsworthy unpubl. data). While Cape Gantheaume is within close proximity to the Bonney upwelling region, Cape du Couedic is the closest colony to the continental slope and the STF, the latter of which lies between 39 and 40° S (James et al. 2002, Kostianoy et al. 2004). North Neptune Island and Liguanea Island are the furthest colonies from the continental slope and the STF (Fig. 1).

Animal capture and handling. The foraging locations and directional movement of females were monitored using Kiwisat 101 satellite transmitters (Sirtrack) during 2005 and 2006. All units were deployed in April (post-moult), with multiple foraging trips recorded from the same individual to assess foraging site fidelity.

Lactating adult females were captured using a hoop net and manually restrained. Upon capture, anaesthesia was induced and maintained using Isoflurane (Veterinary Companies of Australia), administered via a portable gas anaesthetic machine (Komesaroff Small Animal Anaesthetic Machine, Medical Developments Australia). Standard total length (nose to tail) and axillary girth were measured to the nearest centimetre. Satellite transmitters were attached to guard hairs on the mid-dorsal line using a flexible araldite epoxy (Araldite 2017, Vantico). Devices were removed by cutting guard hairs attached to the unit using a scalpel blade. For certain re-captures, females were first immobilised with Zoletil (dose 2 mg kg⁻¹; Virbac), administered using 0.5 cc barb-less darts (Darts: Pneu-Dart), fired from a CO₂-powered tranquilliser gun (Taipan 2000, Tranquil Arms Company). The lightly anaesthetised females were then captured using a hoop net and manually restrained.

Satellite transmitter data treatment. The duration of a foraging trip was defined as the period of time between a seal's departure from the breeding site and its return to land (Page et al. 2006). Satellite location data were obtained through CLS ARGOS (Toulouse, France). The Location-Class B and Z positions were omitted due to the magnitude of their error (Robson et al. 2004). To further improve the accuracy of satellite tracks, the R statistical software (Version 2.0.1, R Development Core Team, R Foundation for Statistical Computing) and timeTrack package (Version 1.0–9, M. D. Sumner, University of Tasmania) were used to

apply the filter described by McConnell et al. (1992), based on a maximum horizontal speed of 2 m s^{-1} (Page et al. 2006). We assumed a constant horizontal speed between the filtered locations and interpolated a new position for each hour of time along the satellite track (Page et al. 2006).

Several parameters were calculated to summarise the spatial distribution of foraging effort. These parameters were extracted at 60 min time intervals along each interpolated satellite track (except for parameters that described minima, maxima, or totals). Behavioural parameters were calculated to describe (1) cumulative total distance travelled (sum of distances between locations), (2) maximum straight-line distance from the colony to the distal point reached, (3) linearity index (LI) values for outbound and inbound portions of each foraging trip (maximum straight-line distance/total distance) (Robson et al. 2004), (4) bearing from colony to each interpolated position, (5) average bearing and (6) horizontal travel speed (the distance between consecutive locations, divided by duration [60 min]).

Colony differences in foraging direction. To compare differences between colonies in the direction of movement during foraging trips, we first calculated the grand mean bearing for each individual (Zar 1996, Hamer et al. 2001). Individuals were then pooled according to colony to compute a mean colony bearing (Zar 1996). We examined each colony to establish whether bearings were uniformly distributed, or whether a preferred direction of travel was evident. This was done by calculating the statistic r , a measure of angular dispersion ranging from 0 (no mean angle) to 1 (data concentrated in the same direction) (Zar 1996). We used the Rayleigh test or, if the data were bimodal, the Rao's spacing test. Finally, to test whether mean colony bearings differed, we used the Watson-Williams F -test.

Meta home range. Austral autumn (April and May) was the only period during which all colonies were represented by tracking data. Therefore, in order to compare meta home ranges among colonies (see Robson et al. 2004), the first foraging trip for each seal during this period was selected for analysis. In addition, Cape du Couedic and Liguanea Island females were also tracked into austral winter months (June and July). Consequently, we selected the first June foraging trip for each of these individuals. For each individual's foraging trip, we randomly sampled 100 interval locations (recorded every 60 min) and pooled them according to colony. Meta home ranges were then estimated using 95% fixed kernel home ranges calculated through the Animal Movement extension (Hooge & Eichenlaub 1997) within ArcView GIS 3.2a. Meta home ranges were plotted using VerticalMapper (Version 2.5) (MapInfo Corporation) and MapInfo (Version 8.0).

Oceanographic parameters. Sea surface temperature (SST) and surface chl a concentration were calculated for each seal at 15 min intervals along each interpolated satellite track. SST data were obtained from the AVHRR sensor — part of the multi-channel sea surface temperature dataset, compiled by the U.S. Naval Oceanographic Office and distributed by the Global Ocean Data Assimilation Experiment. The surface chlorophyll a data were derived from the moderate resolution imaging spectroradiometer (MODIS) weekly average database, which has a 4 km^2 spatial resolution. If daily chlorophyll data were not available, the monthly average was used. The STF was mapped using mean monthly SST temperatures. In April, the STF was identified as the location of a 14°C isotherm at the sea surface (James et al. 2002, Tomczak et al. 2004). In June, the STF was defined as the location of the 12°C sea surface isotherm. The STF usually lies between 39 and 42°S (James et al. 2002).

Site fidelity. Directional persistence between consecutive foraging trips was used as a measure of site fidelity. Site fidelity was analysed by calculating a mean destination bearing from interpolated positions for each foraging trip for each individual. Bonadonna et al. (2001) defined a fidelity index to account for the influence of preferred colony direction on an individual's foraging trip. This study assumed that a preferred direction is a product of fidelity to specific foraging grounds. The V -test was used to determine whether the bearing of an individual's consecutive foraging trips differed significantly (Zar 1996).

All tests were conducted using SPSS Ver. 14.0 and the circular statistics package Oriana (V d.02c, Kovach Computing Service). All values are given as means (\pm SD) and are considered significant at the $p < 0.05$ level. Transformations to meet assumptions of normality and homogeneity of variances were performed as necessary. If normality could not be achieved, than equivalent non-parametric tests were used.

RESULTS

A total of 22 lactating females of *Arctocephalus forsteri* were satellite tracked from 4 breeding colonies. In April 2005, satellite transmitters were deployed on 7 seals: 5 at Cape Gantheaume and 2 at Cape du Couedic, Kangaroo Island. In April 2006, a total of 15 satellite transmitters were deployed: 5 each at Liguanea Island, North Neptune Island and Cape du Couedic. One satellite transmitter deployed at North Neptune Island stopped transmitting 4 d into deployment and was excluded from analysis. Individuals were tracked for an average of 5 foraging trips (range: 2 to 19 foraging trips) (Table 1). In total 1707 unfiltered

locations (Classes A, 0, 1, 2, 3) were recorded from the first foraging trip. Filtering removed 278 locations. After filtering, the average number of locations per day at sea was 5.2 ± 3.9 (Cape Gantheaume 4.4 ± 1.1 , Cape du Couedic 2.1 ± 0.8 , North Neptune Island 3.0 ± 2.0 and Liguanea Island 2.9 ± 1.0). The maximum straight-line distance from a colony during a foraging trip was 887 km, while the longest duration of a foraging trip was 32.4 d, both recorded by lactating females from Liguanea Island. There were no significant inter-colony differences in the girth (Kruskal-Wallis H -test: $p = 0.42$) or length (1-way ANOVA: $F_{3,20} = 1.43$, $p = 0.26$) of females selected for deployment.

Colony differences in foraging direction and meta home range

Seals tracked from Cape du Couedic during 2005 and 2006 were pooled due to limited sample size in 2005. A preferred direction of travel was evident for seals foraging from Cape Gantheaume ($r = 0.841$, Rayleigh test: $p = 0.020$), Cape du Couedic ($r = 0.977$,

Rayleigh test: $p < 0.001$) and Liguanea Island ($r = 0.945$, Rayleigh test: $p = 0.004$) (Fig. 2). With the exception of one seal, which foraged on the continental shelf, the other 3 seals from North Neptune Island also exhibited a preferred direction of travel (average bearing = $204 \pm 13^\circ$; $r = 0.976$, Rayleigh test: $p = 0.042$). The mean direction of travel differed significantly among breeding sites, with breeding site predicting the bearing of travel (Table 2, Fig. 2). Seals from Cape Gantheaume typically foraged southeast of the colony ($141 \pm 34^\circ$), while seals from Cape du Couedic foraged south of the colony ($188 \pm 12^\circ$). Seals from North Neptune Island and Liguanea Island typically foraged south-southwest of their colonies ($204 \pm 12^\circ$ and 235 ± 19 , respectively) (Table 2, Fig. 2). Pair-wise comparisons indicated that the difference in mean direction of travel approached significance between Cape du Couedic and North Neptune Island and between North Neptune and Liguanea Island (Table 2).

Differences in 95% kernel meta home range reflected maximum distances travelled to preferred foraging grounds. Early autumn meta home range size ranged from 13 280 km² for Cape Gantheaume,

Table 1. *Arctocephalus forsteri*. Summary data for New Zealand fur seal females on their first foraging trip in autumn, sampled from Cape Gantheaume (CG), Cape du Couedic (DC), North Neptune Island (NN) and Liguanea Island (LIG). Mean values (\pm SD). TL: total length

Colony Deployment date	ID	TL (cm)	Girth (cm)	Foraging location	Trip duration (d)	Max. distance (km)	Cumulative total distance (km)	Total deployment period (d)	Total trip no.	Mean bearing ($^\circ$)
CG										
4 Apr 2005	52469	138	68	Shelf	4.5	51	168	28.9	4	206 \pm 26
30 Mar 2005	52470	130	71	Shelf	3.3	126	374	29.6	5	125 \pm 2
10 Apr 2005	52471	137	76	Shelf	12	190	526	20.7	2	121 \pm 2
6 Apr 2005	52473	137	75	Shelf	7.4	107	296	20.4	2	117 \pm 7
5 Apr 2005	52472	134	76	Oceanic	17.2	448	1144	55.2	3	150 \pm 8
	Mean	135 \pm 3	73 \pm 4		8.9 \pm 5.7	184 \pm 155	502 \pm 382			
	Mean shelf	136 \pm 4	73 \pm 4		6.8 \pm 4	119 \pm 57	341 \pm 150			
DC										
16 Apr 2006	52469	131	65	Oceanic	14.8	366	877	72.1	4	197 \pm 10
21 Apr 2006	52470	122	68	Oceanic	24.8	467	1187	57.1	4	199 \pm 10
19 Apr 2006	52474	126	65	Oceanic	13.5	379	869	65.2	5	180 \pm 7
13 Apr 2005	52475	137	74	Oceanic	7.6	350	830	58.8	8	192 \pm 6
14 Apr 2005	52476	123	73	Oceanic	15.3	450	1004	41.5	3	186 \pm 1
18 Apr 2006	52477	–	–	Oceanic	10.8	383	1394	41.6	9	190 \pm 20
18 Apr 2006	55936	136	63	Oceanic	16.5	636	1456	58.7	5	161 \pm 9
	Mean	129 \pm 6	68 \pm 5		14.8 \pm 5.4	433 \pm 99	1088 \pm 260			
NN										
12 Apr 2006	52473	128	70	Oceanic	20.2	639	1542	51.4	2	216 \pm 5
12 Apr 2006	52475	137	72	Oceanic	13.9	455	1208	38.6	2	182 \pm 6
12 Apr 2006	55953	136	69	Oceanic	15.7	599	1229	59.4	3	208 \pm 2
13 Apr 2006	52476	140	68	Shelf	1.5	36	46	27.9	19	26 \pm 15
	Mean	135 \pm 5	70 \pm 2		12.8 \pm 8.0	432 \pm 275	1007 \pm 658			
	Mean oceanic	134 \pm 5	70 \pm 2		16.6 \pm 3	564 \pm 97	1327 \pm 187			
LIG										
6 Apr 2006	52468	126	74	Oceanic	32.4	811	2047	79.3	3	239 \pm 7
4 Apr 2006	52472	136	73	Oceanic	17.2	661	1492	70.7	4	232 \pm 14
4 Apr 2006	55956	129	76	Oceanic	23.7	798	2042	70.5	3	211 \pm 17
5 Apr 2006	55960	135	79	Oceanic	26.4	802	2114	78.9	7	269 \pm 30
6 Apr 2006	55961	131	76	Oceanic	24.6	887	1990	108.5	4	222 \pm 17
	Mean	131 \pm 4	76 \pm 2		24.9 \pm 5.5	792 \pm 82	1937 \pm 253			

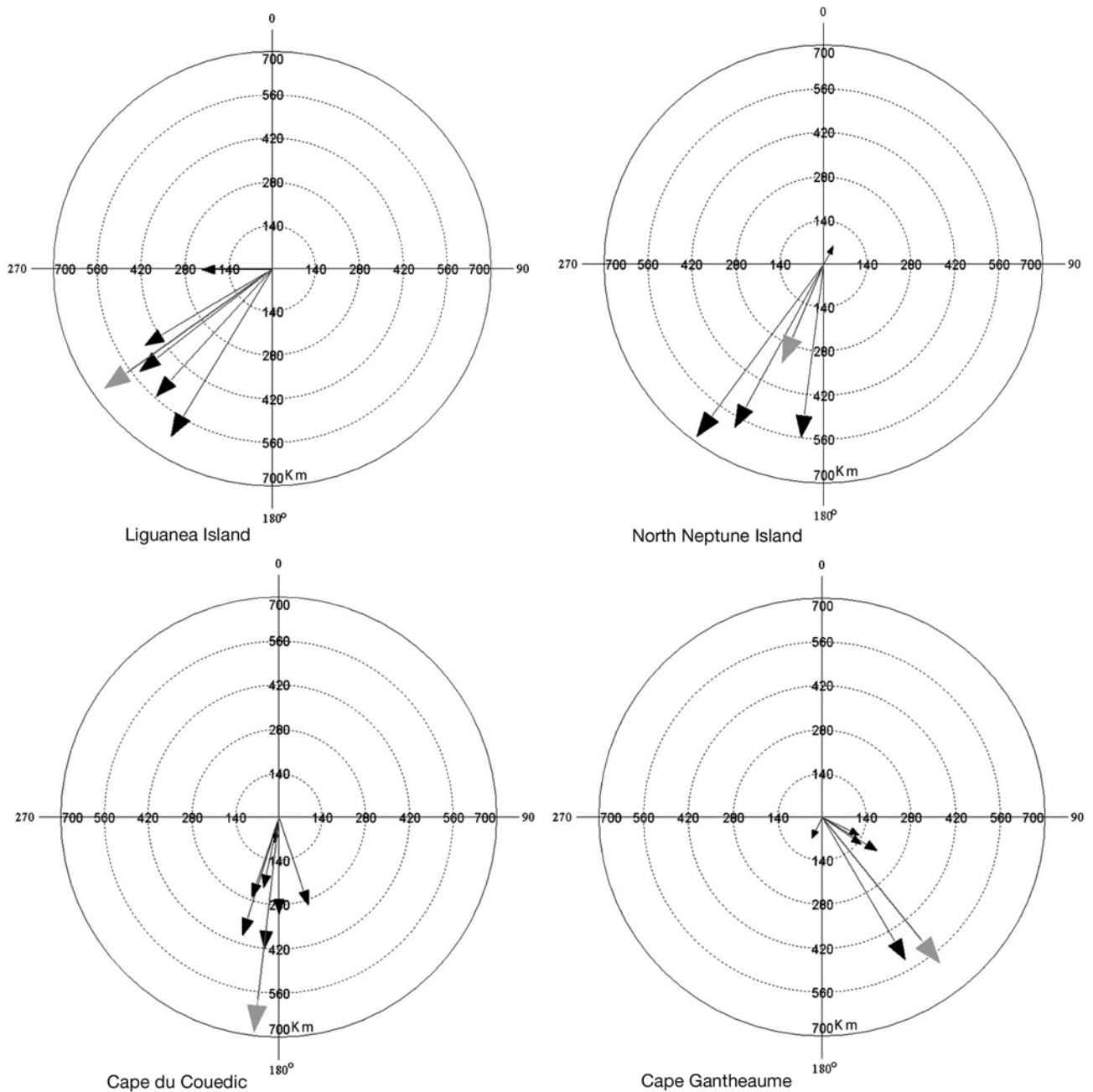


Fig. 2. *Arctocephalus forsteri*. Mean bearing and mean maximum distance calculated for each individual female New Zealand fur seal sampled from Cape Gantheaume ($n = 5$), Cape du Couedic ($n = 7$), North Neptune Island ($n = 4$) and Liguanea Island ($n = 5$). Presented in order of colony location from west to east. Grey vector denotes mean direction of colony and r-statistic

54 610 km² for Cape du Couedic, 74 180 km² for North Neptune Island to 172 400 km² for Liguanea Island (Fig. 3). Seals foraging from North Neptune Island overlapped with the meta home range of animals foraging from Liguanea Island and Cape du Couedic. This overlap accounted for 36% of the meta home range of North Neptune Island (23% overlap with Liguanea Island and 13% overlap with Cape du Couedic).

The winter meta home range for Liguanea Island and Cape du Couedic reflected seasonal differences in distances travelled during foraging trips. The meta home range of seals from Liguanea Island was greater in autumn (172 400 km²) compared to winter (33 160 km²). Seasonal decline in meta home range size was less pronounced at Cape du Couedic, with autumn and winter meta home area varying from 54 610 to 31 390 km², respectively (Fig. 4).

Table 2. *Arctocephalus forsteri*. Average colony bearings and associated statistical differences between colonies (Watson-Williams *F*-test), and average linearity indices calculated for 21 lactating New Zealand fur seals from Cape Gantheaume (CG), Cape du Couedic (DC), North Neptune Island (NN) and Liguanea Island (LIG). LI: linearity index. Mean values (\pm SD)

Colony	n	Mean bearing ($^{\circ}$)	DC	NN	LIG	LI	
						Outbound	Inbound
CG	5	141.6 \pm 34	0.012	0.030	0.001	0.84 \pm 0.11	0.78 \pm 0.16
DC	7	188 \pm 12		0.095	<0.001	0.85 \pm 0.04	0.83 \pm 0.03
NN	3	204 \pm 12			0.081	0.89 \pm 0.03	0.84 \pm 0.04
LIG	5	235 \pm 19				0.86 \pm 0.07	0.82 \pm 0.09

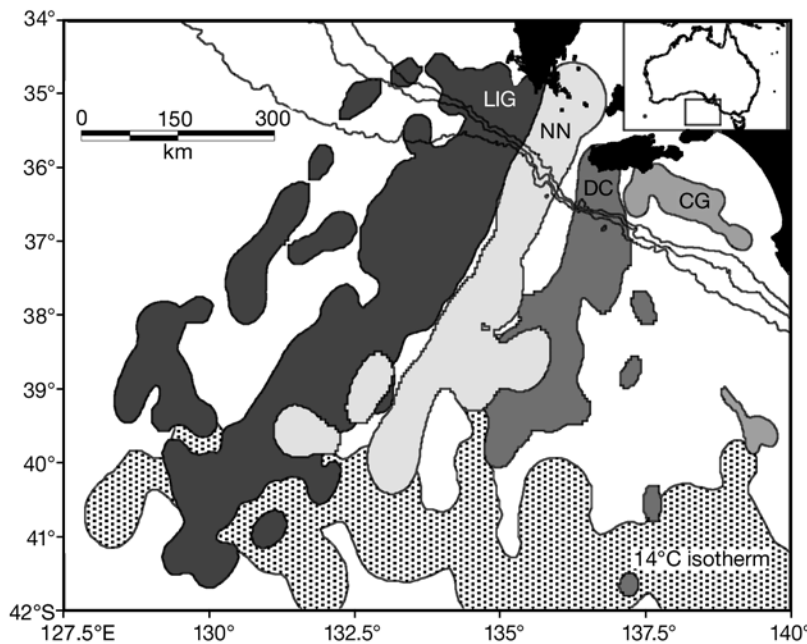


Fig. 3. *Arctocephalus forsteri*. Autumn meta home range of female New Zealand fur seals from 4 breeding colonies in South Australia: Cape Gantheaume (CG), Cape du Couedic (DC), North Neptune Island (NN) and Liguanea Island (LIG), and aggregated locations of the 14°C isotherm for April

Colony differences in oceanography

In April, females tracked from Cape Gantheaume foraged predominantly on the continental shelf, SE of Cape Gantheaume, in the region associated with the Bonney upwelling. In contrast, females from Cape du Couedic, North Neptune Island and Liguanea Island foraged predominantly off the continental shelf, in the region associated with the STF (39 to 42° S). As such, average SST recorded during foraging trips and experienced by females foraging at the STF (15.5 \pm 0.31°C) were lower than those encountered by females foraging on the continental shelf SE of Cape Gantheaume (17.64 \pm 0.92°C). Seals foraging off the continental shelf spent, on average, 7.6% (\pm 5.1) of their time in regions of <14°C SST, 27.0% (\pm 2.7) of their time in

regions of 14°C SST and 30.2% (\pm 2.7) of their time in regions of 15°C SST (Fig. 5). This finding suggests that seals spent more time at the northern boundary of the STF. During April and May, the average location of the STF (relative to the average colony bearing) was 700 km from Liguanea Island (39.75° S, 130.45° E), 520 km from North Neptune Island (39.51° S, 133.56° E), 400 km from Cape du Couedic (39.54° S, 135.89° E) and 460 km away from Cape Gantheaume (39.57° S, 140.34° E). Average surface chlorophyll *a* values recorded during foraging trips indicated the Bonney upwelling region was significantly higher in surface chlorophyll *a* values when compared to the STF (0.45 \pm 0.10 compared to 0.19 \pm 0.001 mg m⁻³, respectively) (1-way ANOVA: $F_{1,20} = 26.4$, $p < 0.001$).

Distance and duration of foraging trips

Colonies differed significantly in the maximum straight-line distance travelled (1-way ANOVA: $F_{3,20} = 12.9$, $p < 0.001$) and the cumulative total distance travelled (1-way ANOVA: $F_{3,20} = 11.8$, $p < 0.001$). Seals tracked from Cape Gantheaume foraged closer to the colony (184 \pm 155 or 119 \pm 57 km, excluding the one female foraging at the STF), when compared to seals from Cape du Couedic (433 \pm 99 km), North Neptune Island (564 \pm 97 km excluding the one female that foraged on the continental shelf) and Liguanea Island (792 \pm 82 km). In addition, females tracked from Liguanea Island travelled significantly greater cumulative total distances when compared with those for Cape Gantheaume, Cape du Couedic and females from North Neptune Island foraging at the STF (1-way ANOVA: $F_{3,19} = 21.4$, $p < 0.001$; Tukey HSD-test: $p < 0.05$ in all cases). These differences were correlated with the distance of colonies from the STF, or, in the case of on-shelf foragers at Cape Gantheaume, the Bonney upwelling.

The durations of foraging trips were positively correlated with maximum distance travelled (regression: $F_{1,20} = 63$, $p < 0.001$, $r = 0.76$). Females from Liguanea Island recorded significantly longer foraging trip durations than those from all other colonies (24.9 \pm 5.0 d) ($F_{3,20} = 12.9$, $p < 0.001$; Tukey HSD: $p < 0.05$ all compar-

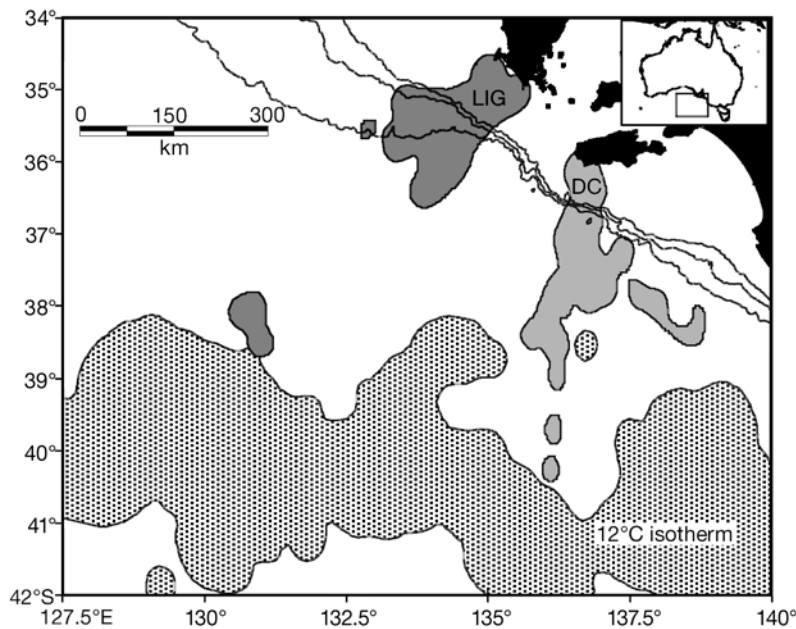


Fig. 4. *Arctocephalus forsteri*. Winter meta home range of female New Zealand fur seals from Cape du Couedic (DC) and Liguanea Island (LIG), and the aggregated locations of the 12°C isotherm in June

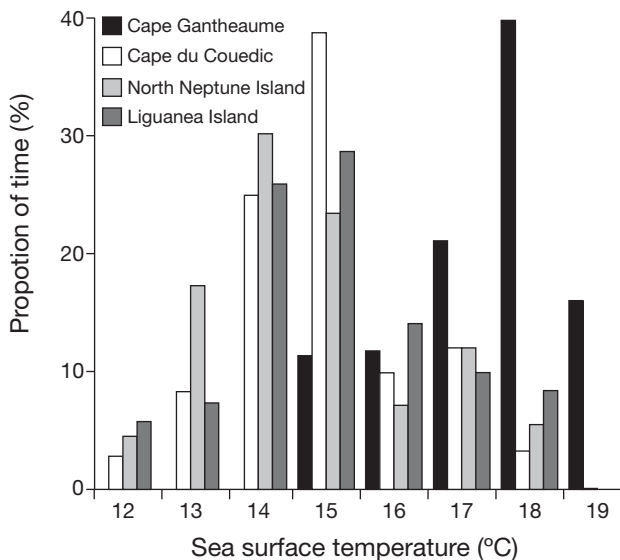


Fig. 5. *Arctocephalus forsteri*. Proportion of trip time and corresponding sea surface temperatures recorded by satellite-tracked New Zealand fur seal females from Cape Gantheaume, Cape du Couedic, North Neptune Island and Liguanea Island colonies

isons). Foraging trip duration did not differ significantly between Cape Gantheaume (8.9 ± 5.7 d), Cape du Couedic (14.8 ± 5.4 d) and North Neptune Island (16.6 ± 3.0 d) ($p > 0.05$). Similarly, the average travel speed of females did not differ significantly between colonies (1-way ANOVA: $F_{3,20} = 1.26$, $p = 0.32$).

Along with Cape Gantheaume females, some seals from Cape du Couedic, Liguanea Island and North Neptune Island were also recorded to forage on the continental shelf. The female from North Neptune Island travelled north of the colony, to utilise the lower Spencer Gulf region (Fig. 3, Table 1). During winter, a single female from Cape du Couedic and one from Liguanea Island deviated from oceanic foraging trips in early autumn to forage on the continental shelf. The Cape du Couedic seal tracked on the continental shelf foraged south-south-west of the colony (maximum distance: 40 km, duration 1.5 d). Similarly, the Liguanea Island female utilised the shelf region SW of Liguanea Island during winter (maximum distance: 60 km, duration: 5.9 d). At Cape du Couedic, the maximum distance and duration of foraging trips to oceanic waters did not differ significantly

between autumn and winter ($p > 0.05$ in all cases). Conversely, females from Liguanea Island foraged significantly closer to the colony during winter compared to autumn (267 ± 206 km and 792 ± 82 km, respectively; repeated measures ANOVA: $F_{2,4} = 41.5$, $p = 0.003$), although foraging trip durations were not significantly shorter (repeated measures ANOVA: $F_{2,4} = 4.6$, $p = 0.097$) (Table 3).

Individual movement and site fidelity

Typically, females travelled directly to and from foraging grounds. On average, the LI for the outbound portion of foraging trips was 0.85 ± 0.07 (range: 0.69 to 0.99) and for the return portion of the foraging trip was 0.82 ± 0.09 (range: 0.49 to 0.94). The LI for each colony is presented in Table 2. The outbound and inbound portions of foraging trips were also characterised by relatively high swimming speeds (3.2 ± 0.9 and 3.4 ± 0.8 km h⁻¹, respectively). Once at a foraging site, the direction of movement was variable (average LI = 0.31 ± 0.07 , range: 0.16 to 0.44), with lower horizontal travel speeds (1.31 ± 0.6 km h⁻¹), presumably associated with searching for prey (Weimerskirch 2007). The average difference between the directions of consecutive foraging trips for all females was $10.8 \pm 7.9^\circ$ (range: 1.3 to 30.4°) (Table 1). There was no significant difference in the average bearing of individual's consecutive foraging trips, despite trips being 12 to 108 d apart (V -test: $p \leq 0.001$ in all cases).

Table 3. *Arctocephalus forsteri*. Summary data for New Zealand fur seal females on their first foraging trip in winter, sampled from Cape du Couedic (DC) and Liguanea Island (LIG). Mean values (\pm SD)

Colony	ID	Foraging location	Trip duration (d)	Max. distance (km)	Cumulative total distance (km)
DC	52469	Oceanic	21.42	491	1026
	52470	Oceanic	16.29	219	726
	52474	Oceanic	13.58	217	508
	52475	Oceanic	6.00	172	453
	52476	Oceanic	16.42	459	1194
	55936	Oceanic	12.08	323	748
	52477	Shelf	1.54	40	93
	Mean		12.5 \pm 6.7	274 \pm 160	678 \pm 369
Mean oceanic		14.3 \pm 5.2	313 \pm 135	776 \pm 289	
LIG	52468	Oceanic	5.96	136	344
	52472	Oceanic	8.38	227	567
	55956	Oceanic	21.50	320	1333
	55961	Oceanic	25.63	591	1482
	55960	Shelf	5.92	60	149
	Mean		13.5 \pm 9.4	267 \pm 206	775 \pm 598
	Mean oceanic		15.4 \pm 9.7	319 \pm 197	931 \pm 560

DISCUSSION

Both colony location and proximity to key oceanographic features influenced the spatial distribution of foraging effort of female New Zealand fur seals *Arctocephalus forsteri*. Based on maximum foraging distances, individuals from different colonies had the potential to overlap considerably in their foraging locations. However, our data showed that overlap between meta home ranges was limited, and there was a clear separation of foraging areas between colonies. While it cannot be discounted that the observed separation of foraging areas may be an effect of small sample size, data collected from multiple foraging trips provide a compelling case, our results suggesting that lactating New Zealand fur seals commenced foraging trips on a pre-determined bearing. The findings of our study are consistent with studies on Antarctic and northern fur seals, and colonial breeding sea birds (Boyd et al. 2002, Gremillet et al. 2004, Robson et al. 2004). These studies suggest that colony-based separation of foraging habitat is a common strategy utilised in colonial breeding seabirds and seals to reduce competition for resources among meta-populations.

Oceanographic features

During autumn, lactating New Zealand fur seals from Cape du Couedic, North Neptune Island and Liguanea Island predominantly utilised distant oceanic waters associated with the STF. The correlation between oceanic fronts and the distribution of foraging

effort in seabirds and marine mammals is well established (e.g. Georges et al. 2000, Charrassin & Bost 2001, Spear et al. 2001). Frontal zones are generally accompanied by sharp salinity and temperature gradients that influence the exchange and mixing of marine resources and are characterised as regions of enhanced biological activity, where prey species may be concentrated (Spear et al. 2001). Although the STF is relatively weak compared with other frontal systems, it is a distinctive feature in any meridional crossing south of Australia and has been described as a region of high productivity (James et al. 2002, Tomczak et al. 2004).

In contrast to other colonies, females from Cape Gantheaume predominantly foraged on the continental shelf in autumn, in a region associated with the Bonney upwelling. The differences observed in the distribution of foraging effort between seals from Cape Gantheaume and all other colonies reflect the proximity of this colony to a seasonally predictable and productive coastal upwelling feature. Coastal upwellings in close proximity to Cape du Couedic, North Neptune Island and Liguanea Island colonies are also known to enhance productivity during summer and autumn months through the upwelling of the Flinders current (Kampf et al. 2004). These upwellings are a regional extension of the Bonney upwelling, but are less prominent and predictable when compared to the area where the seals from Cape Gantheaume foraged (Butler et al. 2002, Kampf et al. 2004). Consequently, the extended distances travelled by seals from Cape du Couedic, North Neptune Island and Liguanea Island colonies suggests the STF is likely to be less variable and more predictable than neritic or shelf-slope habitats near these colonies.

Trip duration and individual movement

The duration of foraging trips and distances travelled by New Zealand fur seals are among the longest documented for lactating fur seals. However, foraging trips longer than 20 d, which exceed distances of 500 km, are not unusual for temperate fur seals that have protracted lactation periods. Similar distances and durations have also been recorded in lactating Guadalupe *Arctocephalus townsendi* and Juan Fernandez *A. philippii* fur seals (Francis et al. 1998). In lactating sub-Antarctic fur seals *A. tropicalis*, the duration of foraging

ing trips have been recorded to be as long as 54 d, with maximum distances from the breeding colony greater than 1600 km (Beauplet et al. 2004). The extended foraging trips of these temperate and sub-Antarctic species are thought to reflect a degree of flexibility in their provisioning strategy, which is necessary for long lactation periods that encompass seasonal changes and variability in ocean productivity (Beauplet et al. 2004).

Extended foraging trips are performed to enable exploitation of distant and productive regions. Whilst these trips incur greater travel costs, they are likely to be profitable as they target regions such as frontal zones where there is a high chance of encountering suitable prey over an extended period (Weimerskirch et al. 2005). The predictability of fur seal foraging habitats is evident in the fact that fur seals tend to target the same oceanographic features between years (Bonadonna et al. 2001, Boyd et al. 2002, Robson et al. 2004). Predictability in the location of resources allows individuals to travel directly to known regions and thereby maximise foraging efficiency (Bonadonna et al. 2001). In our study, females travelled directly to foraging areas (i.e. 'commuted'). This behaviour has been reported for a number of other fur seal species targeting productive ocean features. For example, lactating sub-Antarctic fur seals from Amsterdam Island travelled directly to the STF region to forage (Georges et al. 2000) and Antarctic and northern fur seals commuted rapidly to shelf-break regions around the Kerguelen and Pribilof Islands, respectively (Bonadonna et al. 2001, Robson et al. 2004).

The current study found that upon reaching a foraging site, New Zealand fur seals reduced their horizontal travel speed and increased their turning rate. This behaviour is consistent with area-restricted search, where individuals increase their search effort in areas where prey are more likely to be encountered (Weimerskirch 2007). This pattern of habitat utilisation reflects a hierarchical patch system, which describes high-density, small-scale patches that are nested within low-density, large-scale patches (Fauchald et al. 2000). In the case of fur seals, individuals tend to target seasonally predictable large-scale oceanographic features (frontal zones, coastal upwellings, shelf-break regions) within which they search for patchily distributed prey (Bonadonna et al. 2001).

Colony separation and site fidelity

The distribution of predator populations is often found to be proportional to the distribution of resources (Fretwell & Lucas 1970). Thus, it is reasonable to assume the distribution and spatial density of New

Zealand fur seal populations in southern Australia reflects the accessibility and predictability of prey resources and proximity to suitable breeding habitat. With this in mind, density-dependent foraging habitat selection and predictions of the ideal free distribution (IFD) (Fretwell & Lucas 1970, Sutherland 1983) may provide a framework to explain the evolution and maintenance of colony-specific foraging areas in colonial breeding seals and seabirds. According to the IFD, individuals distribute foraging effort between habitat patches according to the density of conspecifics and associated density-dependent regulatory effects on resources (Maguire et al. 2006). When the IFD is reached (equilibrium), animals can no longer increase their resource intake rate by moving between patches such as the average gain is predicted to be equal for all individuals regardless of the patch they occupy (Moody & Houston 1995). The predictable nature of the STF and its occurrence as a continuous feature south of Australia may provide equal access to relatively predictable resources for New Zealand fur seals from all colonies. If we assume each colony's foraging area (or patch) is more or less equal in quality, then under the IFD there is no benefit for individuals to forage in different colony-specific foraging grounds (or patches), where increased interference from competition with conspecifics may reduce foraging success. Thus, the probability of animals moving between colony-specific foraging grounds should depend on fitness costs (Nichols & Kendall 1995).

The question of how fur seals are able to persistently initiate a foraging trip on a similar bearing and exhibit such strong fidelity to foraging grounds is less intuitive. Little is known about how an individual's decisions influence the collective spatial distribution of colony foraging effort, or if colony-preferred bearings are related to cultural foraging patterns governed by philopatry as has been speculated for Cape gannets *Morus capensis* (Gremillet et al. 2004). In the case of New Zealand fur seals, proximal cues such as bathymetric features and colony orientation do not adequately explain colony-specific bearings, as found by Boyd et al. (2002) for Antarctic fur seals at South Georgia. Seasonal differences in foraging location indicate that, even when trip distance and duration differed, New Zealand fur seals foraged along the same colony-specific bearing. These results are similar to those of Bonadonna et al. (2001) and Robson et al. (2004), who noted interannual persistence of colony-specific bearings, and suggest that seals learn the direction of travel to a predictable foraging region (i.e. STF and Bonney upwelling region), and initiate a foraging trip on that bearing. This type of memory-based knowledge is effective from an optimal foraging perspective, be-

cause it allows direct travel to known foraging regions. However, actual foraging routes are likely to be influenced by a number of factors, including previous foraging trip experience, local environmental cues and the distribution of preferred prey patches (Bonadonna et al. 2001, Boyd et al. 2002, Robson et al. 2004). Finally, in the case of central place foragers, philopatry to breeding site is likely to be important in disseminating and reinforcing colony-specific foraging routes (Robson et al. 2004). For long-lived species, fidelity to foraging site may be advantageous because familiarity with a particular area may enhance foraging success and maximise energy gain over the lifetime of an animal (Gentry 1998, Robson et al. 2004, Bradshaw et al. 2004).

Considerations for management

Based on the colony-specific foraging areas of lactating New Zealand fur seals described in the present study, there are likely to be spatial variations in the effect of operational and trophic interactions associated with commercial fishing activity. Management of these interactions will be specific for each fishery and will primarily be based on the degree of spatial overlap between seals and fishing activity. The majority of fishing operations in South Australia take advantage of the prevalence of commercial quantities of important fish species over the continental shelf and shelf-break regions (Caton & McLoughlin 2005, Linnane et al. 2006, Rogers & Ward 2006). As such, the likelihood of interaction will be greater between December and February, when pups are young and lactating seals are likely to be limited to foraging over the continental shelf, close to their colonies (Harcourt et al. 2002, Page et al. 2006). Furthermore, there is an increased likelihood of interaction during late winter, when seals may forage closer to the continental shelf, as observed in the present study.

In general, on-shelf foragers that spend time within marine fishery areas with low commercial fishing effort (such as those from Liguanea Island and Cape du Couedic) are less likely to interact with fisheries. On the other hand, on-shelf foragers that spend proportionally more time foraging within areas of high fishing effort (such as those from Cape Gantheaume and North Neptune Island) are more likely to interact with commercial fisheries (Caton & McLoughlin 2005, Linnane et al. 2006, Rogers & Ward 2006). Therefore, consideration for future fisheries management may be necessary for regions where fur seal foraging effort overlaps with significant commercial fishing effort, whereas a similar focus may be unnecessary at sites where the likelihood of interactions is relatively low.

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