

Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*)

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Abstract: This study examines whether lactating northern fur seals (*Callorhinus ursinus*) from different breeding sites on the Pribilof Islands in the eastern Bering Sea forage in separate areas. Satellite transmitters were attached to 97 northern fur seal females from nine breeding areas for 119 complete foraging trips during the 1995 and 1996 breeding seasons. Females from St. Paul and St. George islands tended to travel in different directions relative to their breeding site in both years of the study. St. Paul Island females dispersed in all directions except to the southeast, where St. George Island females foraged. Habitat separation was also observed among breeding areas on northeastern and southwestern St. Paul Island and to a lesser degree on northern and southern St. George Island. Although foraging direction led to geographical separation among sites, the maximum distance traveled and the duration of foraging trips did not differ significantly among islands in either year. The results of this study document that lactating fur seals from the same site share a common foraging area and that females from different breeding sites tend to forage in separate areas and hydrographic domains.

Résumé : Notre étude vérifie si les otaries à fourrure nordiques (*Callorhinus ursinus*) nourricières habitant les différentes aires de reproduction des îles Pribilof dans l'est de la mer de Béring recherchent leur nourriture dans des sites différents. Des émetteurs satellites ont été fixés à 97 otaries à fourrure provenant de neuf aires de reproduction, fournissant ainsi des données sur 119 excursions complètes de recherche de nourriture durant les saisons de reproduction 1995 et 1996. Les femelles des îles St-Paul et St-Georges avaient tendance à se déplacer dans des directions différentes de leur aire de reproduction durant les deux années de l'étude. Les femelles de l'île St-Paul se dispersaient dans toutes les directions, excepté vers le sud-est, où les femelles de l'île St-Georges recherchaient leur nourriture. Des séparations d'habitat s'observent aussi entre les aires de reproduction au nord-est et au sud-ouest de l'île St-Paul et, dans une moindre mesure, entre les aires au nord et au sud de l'île St-Georges. Bien que la direction des déplacements durant la recherche de nourriture ait entraîné une séparation des sites, la distance maximale des déplacements et la durée des sorties à la recherche de nourriture n'ont pas varié significativement d'une île à l'autre durant les deux années. Ces résultats montrent que des otaries à fourrure nourricières provenant d'une même aire de reproduction ont tendance à partager un même site de recherche de nourriture et que des femelles provenant d'aires de reproduction différentes tendent à rechercher leur nourriture dans des régions et des domaines hydrographiques séparés.

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Introduction

In colonial breeding species, foragers with dependent offspring are often concentrated around a central location, leading to possible local depletion of prey (Chapman 1961; Ashmole 1963; Lewis et al. 2001). Animals that disperse farther from the colony to feed should be compensated for

their increased travel costs if they encounter less depleted prey resources at greater distances (Hamilton et al. 1967). However, this hypothesis can be true only if groups of animals forage in discrete areas (Schoener 1971). Cairns (1989) hypothesized that breeding pelagic seabirds from neighboring colonies should feed in waters closer to their own colony than to any other, forming nonoverlapping zones bounded

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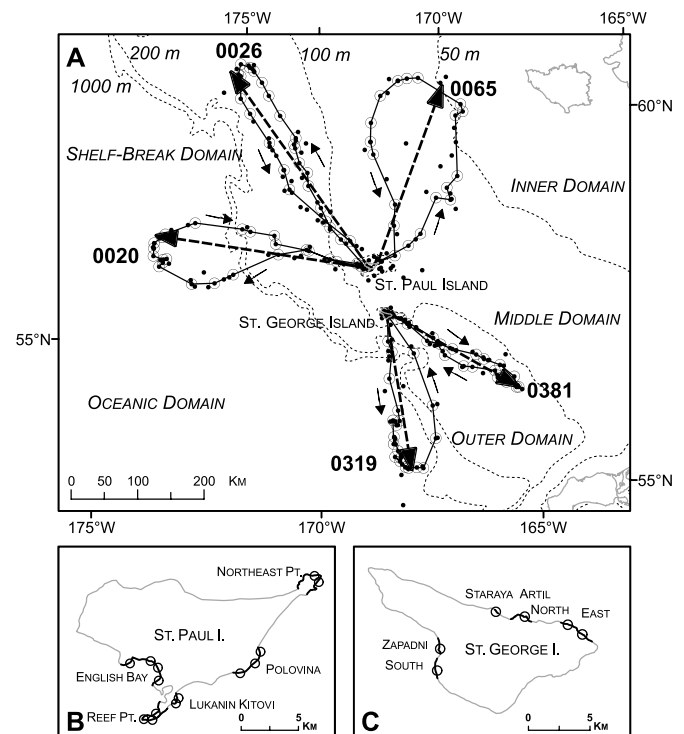
by the line of equidistance between sites (also see Furness and Birkhead 1984). Individual fidelity to foraging areas may be the proximate cause of separation of foraging areas among breeding sites if consistent features of local foraging areas allow animals to locate productive foraging grounds on successive trips (Charnov et al. 1976; Davies and Houston 1978; Andersson 1981). Recent telemetry studies tracking the movements of several marine central-place foragers (Orians and Pearson 1979) have demonstrated such fidelity to foraging areas among individuals from the same site (e.g., Boyd et al. 1998; Irons 1998; Bonadonna et al. 2001; Hamer et al. 2001; Hedd et al. 2001). Colony-specific foraging areas have also been documented for Antarctic fur seals (*Arctocephalus gazella*) (Boyd et al. 2002) and shy albatross (*Thalassarche cauta*) (Brothers et al. 1998), although these studies only compared foraging areas used by animals from two distinct breeding sites. In this study, we examine whether the foraging routes of lactating northern fur seals (*Callorhinus ursinus*) from eight breeding sites on the Pribilof Islands (57°N, 170°W) lead to separation of foraging areas among neighboring colonies.

Northern fur seals are well suited for the study of foraging behavior of colonial marine predators. They breed in dense colonies on a small number of islands located along the North Pacific Rim, where females give birth to a single pup during June–August (Gentry et al. 1986). The largest concentration, approximately 1 million fur seals or 74% of the worldwide population (based on 1994 estimates; Gentry 1998), occurs on the Pribilof Islands in the southeastern Bering Sea (Fig. 1A). Natal site fidelity among fur seals is strong and increases with age (Baker et al. 1995; Gentry 1998). Alternating periods of nursing and feeding constrain mothers to exhibit central-place foraging behavior (Orians and Pearson 1979; Gentry 1998), commuting to marine foraging areas where they consume pelagic fish and squid (Sinclair et al. 1994; Antonelis et al. 1997) in feeding bouts (Gentry et al. 1986) interspersed along their travel path (Loughlin et al. 1987; Goebel et al. 1991).

In the southeastern Bering Sea, the bathymetry associated with the margin of the continental shelf provides the underlying structure of fur seal foraging habitat. Predictable temperature, salinity, and current gradients form oceanographic fronts that separate discrete hydrographic domains or habitats that persist from year to year (National Research Council 1996; Stabeno et al. 1999). Marine predators such as fur seals are known to forage in association with physical oceanographic and bathymetric features in the marine environment that concentrate prey in space and time (e.g., Hunt 1990; Boyd et al. 1994; Sinclair et al. 1994; Hull et al. 1997; Polovina et al. 2000; Swartzman and Hunt 2000). In addition to aggregating prey, oceanographic features may provide a means of navigation for animals foraging and traveling within the three-dimensional marine environment (e.g., McConnell et al. 1992; Loughlin et al. 1999). Prey selection and diving behavior of northern fur seals have been shown to vary with foraging habitat (Kajimura 1984; Goebel et al. 1991; Sinclair et al. 1994; Antonelis et al. 1997).

Although variability in the foraging behavior of individual fur seals has been associated with their foraging habitat, utilization of specific foraging areas by different colonies has not been documented among northern fur seals. We used sat-

Fig. 1. (A) Argos locations and directional vectors for typical foraging trips by five female northern fur seals (*Callorhinus ursinus*) from breeding sites on the Pribilof Islands. The length of the vector is equal to the maximum distance from the breeding site. Satellite telemetry locations are shown as dots (all at-sea locations received from the Argos system) and circles (locations used to calculate the foraging-trip vector). Arrows beside trips indicate the direction of travel. The linearity indices (LI) for the outbound (LIO) and return (LIR) travel paths of each seal were as follows: female 0020, LIO = 0.83 and LIR = 0.93; female 0026, LIO = 0.98 and LIR = 0.94; female 0065, LIO = 0.72 and LIR = 0.83; female 0381, LIO = 0.95 and LIR = 0.96; female 0319, LIO = 0.73 and LIR = 0.94. Also shown are the traditional northern fur seal natal areas (lines) and rookeries (circles) on St. Paul (B) and St. George (C) islands.



ellite telemetry to determine whether the foraging direction of lactating northern fur seals from different breeding sites suggests habitat separation among breeding colonies. The study was conducted on St. Paul and St. George islands in the southeastern Bering Sea during the 1995 and 1996 breeding seasons.

Materials and methods

Study site, captures, and instrumentation

Northern fur seals breed at 14 traditional sites on St. Paul Island and 6 sites on St. George Island. In this study, “natal areas” consisting of adjacent breeding sites on St. Paul Island ($n = 5$) and St. George Island ($n = 4$), described by Baker et al. (1995), were used to define appropriate breeding sites for comparison of foraging patterns (Figs. 1B and 1C). Seals were instrumented at study sites at the four largest natal areas on St. Paul Island in 1995 and at two of the same areas (Reef and Vostochni rookeries) in 1996. Females were

instrumented at all natal areas on St. George Island in both years. Most females were instrumented for a single foraging trip; however, satellite transmitters were deployed on a subsample of females for two feeding trips (on St. Paul Island in 1995 and on St. George Island in 1996) to examine seasonal variation within individuals.

Lactating females with pups judged to be at least 5 years of age (Vladimirov and Nikulin 1993) were physically restrained (Gentry and Holt 1982) during attachment of satellite transmitters, time–depth recorders, and VHF radio transmitters. Larger females, ranging in size from 35 to 45 kg, were chosen to reduce the effects of instrumentation by lowering the instrument to body size ratio (White and Garrott 1990). Instruments were attached with marine epoxy glue to the dorsal pelage of each animal (Fedak et al. 1983). The attachment of telemetry devices may reduce swimming speed and increase foraging trip duration in pinnipeds (Walker and Boveng 1995; Boyd et al. 1997). While instrumentation may extend foraging trip duration, we assume that there is no effect on foraging direction or location (Boyd et al. 2002); however, we cannot confirm this assumption. Satellite transmitters were 0.5-W Telonics ST-6 and ST-10 units programmed with either a 4- or an 8-h transmission protocol (2 h on and 2 h off or 4 h on and 4 h off, respectively). The transmission period was calibrated with periods of optimal satellite coverage. To obtain a representative sample of each animal's movements in space and time, the transmission cycle was used as the basis of a sampling period from which the most accurate location was selected based on the quality code, or location class (LC), assigned by the Argos satellite data collection system.

The accuracy of locations for each LC is estimated by Service Argos as follows: LC 3 is accurate to 150 m, LC 2 is accurate to 350 m, LC 1 is accurate to 1000 m, and LC 0 is accurate to >1000 m. No accuracy estimates are given by Service Argos for LC A and LC B (Service Argos 1996). Prior to the deployment of instruments in each year of this study, ST-6 transmitters were allowed to transmit at a known location for approximately 24 h and the distance between the reference location and the location estimated by Service Argos was calculated for each LC following Boyd et al. (1998). The mean distance from the actual location was within 1–2 km for LC 1, LC 2, and LC 3, although in each case, it exceeded the error estimated by Service Argos (Table 1). Mean errors for LC 0 and LC A were, on average, within approximately 4–5 km of the actual location; however, LC B had a mean distance of 9.1 km away from the reference site. Several recent studies have also concluded that the relative accuracy of LC A and LC 0 is similar, whereas, on average, LC B locations are the least accurate (Vincent et al. 2002; White and Sjöberg 2002; Austin et al. 2003; but see Hays et al. 2001). Because of the extent of the mean error and potential maximum error of LC B fixes, we excluded them from the analysis. In addition to the LC filter, locations for each foraging trip were filtered to remove locations that indicated swim speeds exceeding 3 m/s.

Directional analysis

We compared the spatial distribution of foraging females from different breeding sites by considering discrete natal areas as sample populations (Figs. 1B and 1C); a directional

Table 1. Mean error (\pm SD) of positions calculated by the Argos system for ST-6 satellite transmitters tested on St. Paul and St. George islands during 1995–1996.

Location class	Mean distance (m)	Maximum distance (m)	Minimum distance (m)	<i>n</i>
3	278 \pm 262	1 857	22	91
2	903 \pm 663	3 679	65	78
1	1 496 \pm 1100	6 328	233	56
0	4 483 \pm 3572	17 868	344	40
A	4 131 \pm 4596	12 238	89	9
B	9 057 \pm 13 948	39 956	467	9

Note: Measurements were made from a fixed location recorded by GPS (57.127°N, 170.275°W).

vector was calculated to characterize the foraging area of each individual female using the mean bearing and maximum distance from the breeding site to locations at sea (Fig. 1). The mean bearing and maximum distance from the breeding site were converted to rectangular Cartesian coordinates X_i and Y_i by

$$[1] \quad X_i = d_i \sin(q_i)$$

$$[2] \quad Y_i = d_i \cos(q_i)$$

where q_i and d_i denote polar coordinates of the direction in radians and the maximum distance in kilometres for the i th of N foraging trips, respectively (Mielke 1986). The Cartesian coordinates for each trip were then used as multiple dependent variables in distribution free permutation tests (multiresponse permutation procedure; Mielke et al. 2001) to evaluate the probability that the observed distribution of vectors would occur under the null hypothesis of no difference in the direction and distance of foraging trips between breeding sites. For females sampled on two trips ($n = 22$), locations were pooled to calculate mean values for direction and distance parameters. In separate comparisons of foraging distance, however, one trip was randomly selected.

The use of the mean bearing assumes that the direction of a foraging trip is nonrandom and is accurately summarized as a linear path represented by a mean directional vector. This assumption was evaluated by calculating a linearity index (LI), the ratio of the distance between travel path endpoints and the total distance traveled (for a linear path, LI = 1), as a comparative measure of directed movement (Spencer et al. 1990). To remove the effect of nearshore locations on foraging vectors, evidence of diving bouts (determined from time–depth records when data were available) was used as an indication of when foraging activity commenced and ended during a foraging trip (Gentry et al. 1986; Goebel et al. 1991). Locations prior to the first and after the last diving bout of a foraging trip were excluded from the directional analysis. The duration of a foraging trip was defined as the period of time between a seal's departure from the breeding site and the time that it returned to land at the same location (Gentry et al. 1986; Goebel et al. 1991).

Meta-home range

A home range model was used to calculate a meta-home range area as a spatial measure of habitat use among seals from each breeding area. The term “meta-home range” in-

fers a network of home ranges for individual animals in which there is more interchange among members of each meta-home range than among members of different meta-home ranges. In this context, the meta-home range concept assumes that a rookery or breeding area constitutes an effective subpopulation with long-term stability and that the seals included in our tracking study are representative of the study population (Harris et al. 1990). This assumption is reasonable given the polygynous breeding structure and high degree of philopatry observed among otariids such as northern fur seals.

Meta-home ranges were estimated as the 95% fixed kernel home range (Worton 1989) from the pooled locations for females from each area. Compared with minimum convex polygon estimates, kernel home ranges are less biased by autocorrelation, less subject to the influence of outlying locations, and robust to changes in the spatial resolution of data (Hansteen et al. 1997; Swihart and Slade 1997). To reduce autocorrelation among sequential locations, the most accurate location was selected for each day of every foraging trip. A location was interpolated on days when no location was received from the Argos system. One foraging trip was randomly selected for females tracked for multiple trips, and then locations for one feeding trip made by each female were pooled based on the breeding area groupings identified in the vector analysis. All 95% fixed kernel polygons were calculated using the Animal Movement analysis extension (Hooe and Eichenlaub 2000) in ArcView 3.2 (Environmental Systems Research Institute, Inc. 1996).

Results

Between July and October 1995 and 1996, satellite transmitters were attached to 97 lactating females from breeding sites on St. Paul and St. George islands in the Pribilof Islands Archipelago and 119 complete tracks of foraging trips were recorded. Of 6134 locations recorded by the Argos system, 2304 locations were selected from representative sampling periods for detailed analysis. Fifty-five percent of the locations used in the analysis were Argos classes 1–3; however, of these, only 13.3% of the locations received from ST-10 transmitters were quality 1–3 compared with 67.4% of the locations received from ST-6 transmitters. The discrepancy in location quality between instrument types was probably because of the shorter (2 h) transmission period of the ST-10 transmitters, which decreased the likelihood of a satellite receiving multiple transmissions during a single satellite overpass. No systematic bias was introduced as a result of the use of different sampling intervals: the average number of locations per day for ST-6 transmitters (2.3 ± 0.4 SD, $n = 88$) was comparable with that of ST-10 transmitters (2.1 ± 0.5 SD, $n = 30$) and the mean time between consecutive locations differed little between instrument types ($10.4 \text{ h} \pm 3.1$ SD and $11.4 \text{ h} \pm 2.7$ SD, respectively).

Individual movements

Paths of individual females to and from foraging areas tended to be direct. For all females, the LI averaged 0.82 (± 0.01 SE, range 0.43–0.98) for the outbound portion of all foraging trips and 0.86 (± 0.01 SE, range 0.36–0.99) on the return, indicating strong directionality in the travel path (typ-

ical examples in Fig. 1). Some females who traveled directly to foraging areas on a straight path had relatively low LI values because of meandering movements within their foraging area (e.g., female 0065 in Fig. 1). High LI values for females at all areas indicate that the mean directional vector is an acceptable measure of the direction of a foraging trip. The circular variance associated with the mean bearing averaged 14.6° (range 1.6° – 46.6°). Large variance around the mean vector for a feeding trip was often due to a wide range of bearings during a feeding trip rather than undirected, meandering travel from point to point. The bearing to the first location after females began to forage was correlated with the mean bearing to all subsequent locations in the outbound portion of the trip ($P < 0.01$ in both years; Spearman rank correlation for circular data (Zar 1996)), indicating that females usually maintained their initial direction of travel.

Movement patterns by breeding site

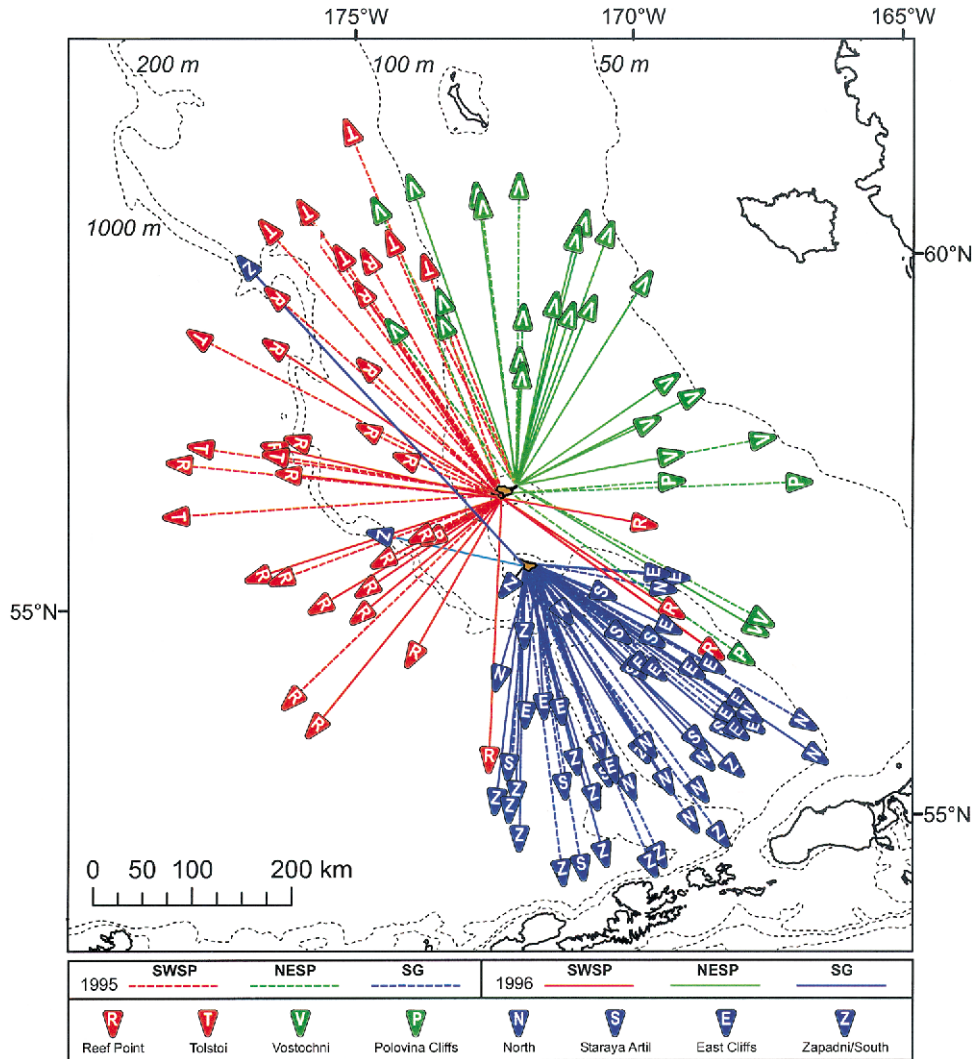
We found that breeding site predicted foraging area with very little overlap (Fig. 2). Foraging vectors differed between islands in both 1995 ($\delta = -16.68$, $P < 0.001$) and 1996 ($\delta = -13.21$, $P < 0.001$). At St. Paul Island, females from different breeding sites foraged in discrete areas in both years. The four largest breeding sites were sampled in 1995; females from Reef Point ($n = 7$) and English Bay ($n = 5$) on the southwestern side of the island traveled southwest to northwest of the island, whereas females from Northeast Point ($n = 6$) and Polovina ($n = 3$) on the northeastern side of the island traveled in directions northwest to southeast of the island (Fig. 2). The distribution of vectors differed among sites ($\delta = -4.90$, $P < 0.001$), and multiple comparisons indicated consistent differences among southwestern and northeastern breeding sites (all $P < 0.01$). In 1996, sampling was concentrated at Reef Point ($n = 16$) and Northeast Point ($n = 15$) and the distribution of vectors again differed among those breeding sites ($\delta = -12.59$, $P < 0.001$).

In contrast with St. Paul Island, nearly all females from St. George Island foraged in a smaller geographic area to the south and east of the island (Fig. 2). Only one St. George female traveled north of St. Paul Island, despite the fact that three sampled rookeries were located on the northern coast of St. George Island. She traveled farther (453.2 km) from the island than all other St. George Island females. Within the St. George Island foraging area, the distribution of vectors differed among breeding sites in 1995 ($\delta = -3.48$, $P = 0.004$, $n = 20$) but was less distinct in 1996 ($\delta = -1.51$, $P = 0.079$, $n = 25$). Multiple comparisons showed significant differences during 1995 between Staraya Artil and East Cliffs ($\delta = -2.4$, $P = 0.03$), between North and Zapadni/South rookeries ($\delta = -3.28$, $P = 0.008$), and between East Cliffs and Zapadni/South rookeries ($\delta = -4.85$, $P = 0.002$). In general, females from two northern rookeries, North and East Cliffs, traveled east and southeast of the island, while females from Zapadni/South rookeries on the south side traveled to the south and southeast. The directional vectors of females from Staraya Artil rookery, the westernmost breeding site on the north side of St. George Island, were intermediate to those of the other areas.

Foraging distance and trip duration

Although foraging direction evidenced geographical separ-

Fig. 2. Vectors showing the direction and maximum distance from the breeding site for lactating northern fur seals (*C. ursinus*) tracked by satellite during 1995 and 1996 from southwestern St. Paul (Reef rookery at Reef Point and Tolstoi rookery at English Bay), north-eastern St. Paul (Vostochni rookery at Northeast Point and Polovina Cliffs rookery at Polovina), and St. George islands (North, Staraya, and East Cliffs rookeries on northern St. George Island and Zapadni/South rookeries on southern St. George Island).



ration among sites, the maximum distance traveled did not differ among islands in either year (Table 2A). On both islands, females traveled slightly farther, on average, during 1995, but the difference was not significant when the islands were considered separately (Table 2B). If data for both islands were pooled, the average maximum distance in 1995 (260.8 ± 76.3 km) was significantly greater than that in 1996 (229.0 ± 64.6 km) ($t = 2.16$, $df = 77$, $P < 0.05$). Foraging trip duration was positively correlated with the distance traveled during a foraging trip (linear regression, $r^2 = 0.49$, $F = 89.55$, $P < 0.001$, $n = 97$). Foraging trips were briefer, on average, in 1996 (Table 1B), but the difference was significant only when the trips for both islands were pooled ($t = 2.45$, $df = 81$, $P < 0.05$).

Seasonal differences in foraging trips

Female northern fur seals instrumented for two foraging trips ($n = 22$) tended to forage in the same general direction

on both trips. The average difference between foraging directions for females tracked for two trips was 28.3° (SE 5.1° , range 0.8° – 102.8° , $n = 22$) and foraging direction did not differ significantly between trips made 4.9–8.7 weeks apart (Moore test for paired second-order mean angles, $R' = 0.539$, $P > 0.50$) (Zar 1996).

Meta-home range areas

Separate meta-home ranges were calculated for the north-eastern St. Paul Island and southwestern St. Paul Island breeding areas because of consistent differences in each year (Fig. 3). St. George Island areas were combined into one meta-home range based on the higher degree of overlap among sites. Meta-home ranges for the three areas showed little overlap relative to the size of the area within which females traveled. The meta-home ranges were larger than the combined area of overlap for each combination of sites (Table 3). Meta-home range estimates varied from 81 065 km²

Table 2. Duration and maximum distance of foraging trips made by female northern fur seals (*Callorhinus ursinus*) from breeding sites on St. Paul and St. George islands.

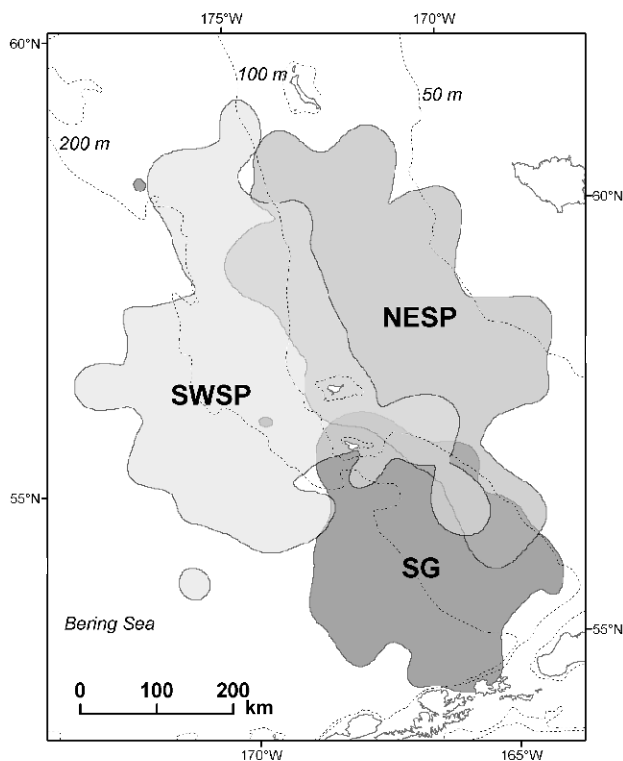
(A) Comparison between islands.*						
	1995			1996		
	<i>n</i>	Duration (days)	Maximum distance (km)	<i>n</i>	Duration (days)	Maximum distance (km)
St. Paul Island	21	8.8±2.0	263.2±82.5	31	8.0±2.0	231.5±54.9
St. George Island	20	8.6±2.2	258.2±71.3	25	7.5±1.9	225.9±76.1
<i>t</i>		0.38	0.21		1.01	0.31
df		38	39		52	42
<i>P</i>		0.70	0.84		0.32	0.76

(B) Comparison between years.*						
	St. Paul Island			St. George Island		
	<i>n</i>	Duration (days)	Maximum distance (km)	<i>n</i>	Duration (days)	Maximum distance (km)
1995	21	8.8±2.0	263.2±82.5	20	8.6±2.2	258.2±71.3
1996	31	8.0±2.0	231.5±54.9	25	7.5±1.9	225.9±76.1
<i>t</i>		1.41	1.54		1.70	1.47
df		42	32		37	42
<i>P</i>		0.17	0.13		0.10	0.15

Note: The results of Student's *t* tests assuming unequal variance are shown to compare mean values between groups for island of origin (A) and year in which satellite transmitters were deployed on individual seals (B).

*For females instrumented during both the early and late seasons, one foraging trip was randomly selected.

Fig. 3. Meta-home ranges for lactating northern fur seals (*C. ursinus*) from southwestern St. Paul (SWSP), northeastern St. Paul (NESP), and St. George islands (SG) and the zone of overlap between combinations of sites.



for St. George Island females to 140 077 km² for southwest St. Paul Island, whereas the overlapping portion of the meta-home range area ranged from 7.3% to 16.5% of the combined home range (Table 3). The spatial extent of overlap among foraging areas was greater between breeding areas on St. Paul Island than between either of the St. Paul Island areas and St. George Island.

Discussion

Separation of foraging areas by breeding site

Lactating females from St. Paul and St. George islands traveled in different directions to forage during both 1995 and 1996, resulting in colony-specific foraging areas among breeding sites. Females from nearby breeding sites exhibited relatively little variability in foraging direction, although the maximum foraging range (40–450 km) was several times the distance between breeding sites (2.6–25.8 km within islands, 70–92 km between islands). In particular, females from breeding sites on the north side of St. George Island consistently traveled southeast of the island despite the marginal increase in effort required to travel to areas utilized by St. Paul Island females. Our observations of a marine central-place forager suggest that although females from both islands traveled similar distances in both years, the greater distance between islands relative to the distance between breeding sites on each island results in more overlap among feeding areas within islands and greater separation of foraging habitat between the two islands.

Similarity in the early- and late-season foraging routes of females tracked for two trips indicates that fidelity to foraging areas exists among lactating northern fur seals. Foraging site fidelity has been reported for other marine central-place foragers including Steller sea lions (*Eumetopias jubatus*)

Table 3. Results of the meta-home range analysis for the St. George (SG), southwestern St. Paul (SWSP), and northeastern St. Paul (NESP) islands northern fur seal (*C. ursinus*) breeding areas.

Home range size		Home range overlap		
Breeding area	Home range (km ²)	Breeding areas	Overlap (km ²)	% overlap
SG	81 065	SG, NESP	14 919	7.8
SWSP	140 077	SWSP, SG	15 008	7.3
NESP	125 573	NESP, SWSP	37 676	16.5

Note: Values are given for the size of 95% fixed kernel meta-home ranges, the area of overlap, and the percent overlap between home range areas.

(Merrick and Loughlin 1997), northern elephant seals (*Mirounga angustirostris*) (Stewart and DeLong 1995), black-legged kittiwakes (*Rissa tridactyla*) (Irons 1998), Antarctic fur seals (Boyd et al. 1998; Bonadonna et al. 2001), and gray seals (*Halichoerus grypus*) (Sjöberg and Ball 2000). Two of these species, Antarctic fur seals (Boyd et al. 2002) and northern elephant seals (LeBoeuf et al. 2000), exhibit habitat separation by either sex or breeding site. Female fur seals likely remember the orientation of previous foraging trips and travel in a similar direction on subsequent trips. The correlation between the bearing to the location nearest the first diving bout and the average bearing for the trip in our study suggests that females begin a trip in a known direction and travel along a relatively linear path with foraging bouts interspersed along the way.

A simple explanation for the directional persistence observed within breeding sites is that seals repeatedly initiate a foraging trip on a bearing consistent with the general orientation of the site. Boyd et al. (2002) found that Antarctic fur seals at the island of South Georgia tended to forage along a bearing that was approximately perpendicular to the coastline and the margin of the continental shelf, resulting in colony-specific foraging areas determined by the local bathymetry gradient. A similar pattern was observed among Antarctic fur seals from a single colony in the Kerguelen Archipelago by Bonadonna et al. (2001), who proposed a colony-level memory of site-specific foraging zones integrated with individual memory of profitable prey patches exploited during successive trips. Our observations of site-specific foraging patterns indicate that foraging routes of individuals are likely influenced by a combination of local habitat structure (e.g., bathymetry or oceanographic fronts) and previous foraging experience. Lactating northern fur seals from St. Paul Island tended to forage in a direction within a 180° arc centered on a bearing perpendicular to the coastline, consistent with the predictions of Boyd et al. (2002). However, females from the breeding sites on the north side of St. George Island traveled primarily east and south of the island on a path parallel to the bathymetric gradient (Fig. 2), some on a bearing nearly opposite to the orientation of the rookery. The tendency for a group of animals to repeatedly travel in a direction unrelated to the general orientation of the coastline suggests that although rookery orientation may be involved in the initial departure direction, the most parsimonious explanation for the site-specific foraging patterns observed in this study entails route choice tactics related to colony-specific foraging areas.

Philopatry among northern fur seal females (Baker et al. 1995) may facilitate a tendency toward separate foraging

areas, leading to the persistence of these patterns across generations. Fidelity to a traditional breeding site among pinnipeds has a selective advantage in reuniting the sexes at a time and place where conditions are favorable for successfully rearing offspring (Stirling 1983; Baker et al. 1995). In an evolutionary context, the persistent use of a foraging area is likely to be coincident with fidelity to a breeding site. The repetition of a successful foraging pattern would be advantageous to seals from a particular breeding site if it provided a seasonally predictable food source across generations. Unfortunately, historical evidence to support the hypothesis of colony-specific foraging areas is limited. Prior telemetry data are restricted to radio-tracking studies conducted during the 1980s. These studies show at-sea locations of lactating fur seals from southwest St. Paul Island that are consistent with the patterns observed in our study (Loughlin et al. 1987; Goebel et al. 1991); however, the spatial coverage of the 1980s study is insufficient to evaluate colony-specific patterns.

To attempt to further evaluate the consistency of the observed foraging patterns across generations, we used the National Marine Mammal Laboratory's pelagic fur seal database that contains information on the location of northern fur seals killed at sea for research purposes from 1958 to 1974. Thirty-eight postpartum females ranging in age from 5 to 17 years old that were flipper tagged as pups at rookeries on the Pribilof Islands were collected in the Bering Sea from July through September 1960–1974. Of these, three were born at an area not included in this study. Of the 35 remaining females, 11 (31%) were collected at locations outside the meta-home range calculated in this study for the breeding area at which they were born. The remaining 69% were within the meta-home range area associated with their natal rookery in this study. A portion of the tagged females would be expected to have given birth somewhere other than their natal sites, as Baker et al. (1995) found that 71%–97% of females age 5 and older returned to their natal area. Although these data represent a small sample of seals, they indicate a tendency among lactating females to use the colony-specific foraging area of their natal site.

Implications for community structure

The foraging areas utilized by females from different breeding sites are characterized by unique marine habitats. The majority of the locations for females from St. George Island (84%) and southwestern St. Paul Island (72%) were recorded in the deeper waters of the Aleutian Basin, shelf break, and outer shelf domains where the marine community is dominated by a pelagic food web (Figs. 2 and 3) (National

Research Council 1996). In contrast, females from the north-eastern side of St. Paul Island tended to forage (83% of locations) in the stratified middle shelf domain where biomass is concentrated in the demersal and benthic communities (National Research Council 1996). Relatively few (<12%) of the locations for each foraging area were recorded in the inner domain around each island, indicating that seals transited quickly through this area at the beginning and end of foraging trips. Consistent oceanographic features that separate marine habitats, such as the middle shelf front, which occurs along the 100-m isobath, or the strong tidal currents between the islands resulting from the constricted northward flow of water in the outer shelf domain (National Research Council 1996; Stabeno et al. 1999), coincide with boundaries between meta-home range areas (Fig. 3). Hydrographic features such as these aggregate prey (Sinclair et al. 1994) and, along with the bathymetric gradient, may influence the foraging direction of seals as they navigate at sea. In a concurrent study of fatty acid signatures in the milk of females in this study, Goebel (2002) found that the diet and diving behavior of each foraging area reflected the habitat differences observed in the satellite telemetry data.

Fretwell (1972) theorized that individual foraging decisions result in the distribution of a predator population at equilibrium that is proportional to the distribution of resources in the environment. In the eastern Bering Sea, the divergent physical characteristics and community structure between shelf domains result in markedly different marine habitats that may be reflected at higher trophic levels (Cooney 1981). The oceanic, shelf break, and outer domains together contribute approximately 74% of new and total production annually, with the remaining 26% coming from the inner and middle shelf domains (National Research Council 1996; Springer and McRoy 1996). Relative values of secondary production are similar; however, the higher transfer efficiency of the pelagic habitat results in about 80% of total secondary production in the oceanic, shelf break, and outer domains and 20% in the inner and middle shelf domains. Based on the number of pups born at each rookery in 1994 (Antonelis et al. 1996), habitat separation among breeding sites suggests that the relative proportion of lactating females from northeastern St. Paul Island that likely forage in the middle and inner domains (27%) and from southwestern St. Paul and St. George islands that likely forage in the outer, shelf break, and oceanic domains (73%) may reflect the proportion of both primary and secondary production in their respective regions of the eastern Bering Sea. This suggests that the behavioral patterns that determine the distribution of an apex predator such as the northern fur seal may reflect the underlying physical and trophic structure of the marine ecosystem.

Based on the colony-specific foraging patterns observed in this study, environmental changes that influence the distribution and abundance of prey or shifts in the location of commercial fisheries may differentially impact the foraging habitat of fur seals from different breeding sites. The St. George Island population may be more vulnerable to such changes given the greater overlap among foraging females within a smaller geographic area. Alternatively, changes in the distribution of prey due to fisheries management actions

or environmental changes may alter the foraging patterns of Pribilof Island foragers.

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