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Oceanographic features related to northern fur seal migratory movements

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Abstract

Northern fur seals breeding on the Pribilof Islands are characterized by pelagic migrations that begin each fall and last approximately eight months. Previous studies have examined the early phases of the migration with respect to timing, location, and effects of ocean surface currents on movement. We used satellite telemetry and remotely sensed satellite data to examine relationships between oceanographic features and the movements of adult female fur seals in the Bering Sea and North Pacific Ocean during early, middle and late portions of their winter migration. Physical locations of 13 female fur seals were monitored during 2002–2003, and diving data were collected on a subset of the animals. Remotely sensed data were obtained to assess sea-surface temperatures, chlorophyll *a* concentrations, and sea-surface height anomalies encountered by the fur seals. Data from historical pelagic collection of fur seals also were summarized to describe winter diet and the distribution of different age and sex classes of the general migration of fur seals to the eastern North Pacific. Seals departed from the Pribilof Islands in November and moved in a southeasterly direction over the continental shelf as they left the Bering Sea. Their travel routes did not follow coastal or bathymetric features as they crossed the North Pacific Ocean, but instead corresponded to complementary water movement of the Alaska Gyre and the North Pacific Current. Winter foraging areas varied geographically and were associated with eddies, the subarctic–subtropical transition region, and areas that undergo coastal mixing due to the California Current. The results indicate that fur seals may cue on a variety of oceanographic features that aid in reducing energetic expenditures and optimize foraging opportunities.
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1. Introduction

The northern fur seal (*Callorhinus ursinus*) has a pelagic distribution that ranges across the North Pacific (Kenyon and Wilke, 1953; Gentry, 1998). The largest abundance of breeding fur seals is found on the Pribilof Islands (St. Paul and St. George Islands) in the Bering Sea where 982,000 northern fur seals (72% of the total) have been estimated to congregate during the summer months (Loughlin et al., 1994). During late fall, females and juveniles of both sexes migrate from

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the Pribilof Islands into the North Pacific Ocean, where they remain pelagic for approximately eight months until the following breeding season. Adult males remain close to the breeding colonies, likely wintering in Alaskan and Russian waters of the North Pacific Ocean and the Bering Sea (Kajimura, 1984; Bigg, 1990; Loughlin et al., 1999).

Oceanographic features undoubtedly influence northern fur seal migratory movements, but identification of the types, and the extent of these influences, is limited. Loughlin et al. (1999) examined the correlation between ocean surface currents and animal movement during the early portion of adult male migration. Male fur seal movements typically coincided with, but were not dependent on, ocean surface currents. Fur seals likely used these currents to facilitate the location of prey, as well as to aid in migration (Loughlin et al., 1999). Studies of loggerhead turtles (*Caretta caretta*), blue whales (*Balaenoptera musculus*), and Steller sea lions (*Eumetopias jubatus*) have explored the relationships of oceanographic features to the movements and seasonal distribution of these animals (Polovina et al., 2000; Moore et al., 2002; Fadely et al., 2003). Using features such as sea-surface height, temperature, and chlorophyll *a* concentration, Polovina et al. (2000) identified convergent fronts that were associated with loggerhead turtles traveling across the central North Pacific. Moore et al. (2002) showed that blue whale distributions were associated with cold water and sea-surface temperature fronts, while Fadely et al. (2003) found that habitat use, seasonal movements, and changes in immature Steller sea lion diving behavior coincided with changes in sea-surface temperature and chlorophyll *a* concentration.

The migratory pathways and winter foraging grounds of the northern fur seal have been described from extensive pelagic collections along the continental margins of the North Pacific Ocean (Kenyon and Wilke, 1953; Lander and Kajimura, 1982; Bigg, 1990). However, because these descriptions are the result of concentrated sampling near the coast, they do not encompass the entire range of spatial and temporal locations of fur seals during the migration period. Although the actual travel routes and movement patterns of individual fur seals have not been thoroughly explored, previous satellite and radio-telemetry tracking studies of free-ranging pups, females, and adult males have examined the timing and location of the early phases of the migration (Kiyota et al., 1992; Ragen et al., 1995; Loughlin et al., 1999; Baba et al., 2000). Northern fur seals were tracked as they migrated out of the Bering Sea, and as they began to travel into the North Pacific Ocean. However, all of the studies ended before or during February (~3 months into migration) and were unable to document the majority of the migration, including identification of a regional destination or winter foraging grounds.

The availability and species composition of prey consumed by northern fur seals are associated with the habitat used by seals during foraging. Antonelis et al. (1997) found that the summer diet of female fur seals varied among islands in the Bering Sea, and suggested that the differences were related to the bathymetric environment surrounding each island. Fur seal diet throughout the year has been examined from extensive historical pelagic collection of northern fur seals in the North Pacific Ocean, and revealed substantial variability in diet among regions and months during previous decades (Lander and Kajimura, 1982; Kajimura, 1984; Perez and Bigg, 1986). Northern fur seals foraging in the Bering Sea also exhibit a number of behavioral patterns that are associated with the bathymetric domain of the marine environment that they encounter (Goebel et al., 1991). While foraging over deep water fur seals tend to exhibit shallow night-time diving, following the movement of the deep scattering layer in the upper 40 m of the water column. In contrast, while foraging over the continental shelf, fur seals tend to dive during the day and the night with many of their dives reaching the ocean floor. Northern fur seals are opportunistic predators and likely adapt to forage on prey assemblages that occupy ocean depths within the reach of their diving capabilities.

We used satellite telemetry to examine the physical location and movements of 13 adult female northern fur seals from the Pribilof Islands during their winter migration. Using the location data we are able to describe for the first time the

early, middle and late phases of migration of individual fur seals. We also address diving and temperature data collected by the satellite transmitters on a subset of the animals. Through the use of established sea-surface current patterns and remotely sensed satellite data (sea-surface temperature, sea-surface chlorophyll *a* density, and sea-surface height anomalies), we assess relationships between fur seal movements and the corresponding oceanographic features of the surrounding habitat. Finally, while we did not collect data regarding food habits of fur seals or age composition of migrating fur seals in different regions, we summarize historical information from animals taken in pelagic collections from 1958 to 1974 to describe winter feeding habits and the distribution of different age and sex classes.

2. Methods

During 19–25 November 2002, 13 adult female fur seals were captured at Polovina Cliffs rookery on St. Paul Island, AK (Table 1). Satellite transmitters were attached to their pelage with 10-min epoxy. The satellite transmitters deployed, KiwiSat 101 PTT (Sirtrack Limited, Havelock North, New Zealand) and ST-16 SDR (Wildlife Computers, Redmond, WA, USA), were programmed to transmit every 45 s. To conserve battery life the transmitters were cycled to be on for four hours and off eight hours and had a saltwater switch that prevented transmission when underwater. Additionally, the satellite tags stopped transmitting when the fur seals were hauled out of the water for longer than four hours and would not re-initiate transmissions until the animal entered the water again. The 0.5 W KiwiSat 101 PTTs ($n = 10$) recorded ambient temperature and the 0.25 W ST-16 SDRs ($n = 3$) provided histogram distributions of maximum dive depths, durations, and time-at-depth summarized in four six-hour sampling bins. A full description of the SDR programming is contained in Loughlin et al. (2003). Bottom depth readings of the marine environment used by the fur seals were derived from ETOPO 2 gridded elevation data.

Table 1
Summary of satellite tracking dates, duration, distance and destination regions, listed by animal ID number for 13 adult female northern fur seals captured on St. Paul Island, AK during November 2002

ID	St. Paul departure (date)	Unimak Pass (date)	Destination region	Destination arrival (date)	Last transmission (date)	Tracking duration (days)	Tracking distance (km)
57	11/23/02	12/04/02	Coastal (WA, OR, BC)	3/10/03	[a]09/10/03	244	9272
58	11/23/02	12/01/02	Transition region	[b]3/20/03	05/14/03	172	5936
59	11/20/02	12/01/02			02/09/03	81	4402
60	11/24/02	12/23/02	Coastal (CA)	2/3/03	06/13/03	201	8078
61	11/22/02	12/02/02	Coastal (OR)	2/2/03	05/02/03	161	6126
62	11/24/02	01/01/03			01/10/03	47	2368
63	11/23/02	12/06/02	Transition region	[b]3/25/03	05/02/03	160	4948
64	11/26/02	12/18/02	Transition region	1/14/03	[a]09/04/03	233	9732
65	11/28/02	12/07/02	Coastal (WA, BC)	3/19/03	06/17/03	200	6487
66	11/26/02	11/29/02	Coastal (CA)	1/26/03	02/05/03	71	4541
67	11/26/02	12/04/02			02/01/03	67	2322
68	11/29/02	12/08/02	Coastal (CA)	1/31/03	02/24/03	87	4970
69	11/28/02	12/06/02	Coastal (WA, BC)	3/10/03	06/11/03	194	6369

[a]Satellite transmissions continued after females 57 and 64 had completed their migrations by returning to St. Paul Island on 7/25/03 and 7/18/03, respectively. Tracking duration and distance measurements do not include travel subsequent to the completion of the migration.

[b]Travel to the transition region was not direct for females 58 and 63, who initially went into the Gulf of Alaska prior to traveling in a southwesterly and southerly direction to the transition region, respectively.

Animal locations were calculated by Service Argos Inc. and were filtered iteratively based on time sampling/transmission intervals and maximum swim speed. Similar to the methods used by Robson et al. (2004), we selected the best location per animal per day based on Argos location quality rankings and calculated swim speed between sequential locations. When the swim speed between two locations exceeded 3 m/s, one of the two locations was arbitrarily removed and the calculation of swim speed was repeated. Of the 8927 locations estimated by Service Argos Inc., 1780 at-sea locations were used for our analysis. The proportion of days for which usable locations were received ranged from 0.75 to 1.0 among individual fur seals, and averaged 0.93 ($n = 13$; SE = 0.02).

Remotely sensed satellite imagery data were obtained from different sources. The sea-surface temperature (SST) and surface chlorophyll *a* (chl *a*) concentration data were acquired as part of NASA's Earth Science Enterprise. Each measurement was obtained as a monthly mean with a spatial resolution of 39 km^2, using algorithms developed by the MODIS Science Teams. The data were processed by the MODIS Adaptive Processing System (MODAPS) and the Goddard Distributed Active Archive Center (DAAC), and are archived and distributed by the Goddard DAAC (Greenbelt, MD). Sea-surface height (SSH) anomalies and the resulting geostrophic current bearings and velocities were obtained from the Colorado Center for Astrodynamics Research at the University of Colorado, Boulder. The temporal resolution of SSH anomalies allowed for data collection once during a 10-day satellite sampling cycle, and the spatial resolution was 0.25° latitude and longitude. Methodologies of altimetry processing and resampling can be found in Leben et al. (2002). Integration of fur seal locations and remotely sensed satellite data were linked via scripts using ArcMap™ 8.2 (ESRI, CA) so that each fur seal location was temporally and spatially linked to a SST, SSH, chl *a* concentration, geostrophic current and bearing, and bottom depth for analysis.

Data from the pelagic collection of northern fur seals between 1958 and 1974 were summarized to characterize the general migration of fur seals to the eastern North Pacific. We explored age, sex and diet of fur seals during the months of February–May in four different latitudinal regions: the Gulf of Alaska, British Columbia, Washington/Oregon, and California. Detailed analyses of these data have been previously conducted on various spatial and temporal scales and, for the diet data, using additional or different measures of prey relevance (Lander and Kajimura, 1982; Kajimura, 1984; Perez and Bigg, 1986; Bigg, 1990). For diet information, we calculated percent occurrence (PO) of the top five prey species found in each region. The PO of a given prey species pertains to the number of stomach samples containing that particular species out of all samples containing prey. Differing from the prior diet reports, we calculated the PO for each sex, and for both sexes combined in each region. To describe the sex-specific diet, data were combined for all four months in each region to avoid small sample sizes. Finally, we summarized the findings of Walker and Jones (1993), who analyzed the stomach contents of 21 northern fur seals taken from the North Pacific Transition Zone in the Japanese high seas squid driftnet fishery in 1990.

3. Results

3.1. Satellite tracking duration

Eight of the 13 female fur seals instrumented were tracked for at least 160 days, to the southern extent of their migrations (Table 1). The transmitters on the eight animals functioned long enough that we were able to detect northward movement before they stopped transmitting. Two of the animals were tracked for the complete migration back to St. Paul Island (Fig. 1; females 57 and 64). The total duration and distance traveled for these two females during their migration was 244 days/9272 km (female 57) and 233 days/9732 km (female 64). Of the remaining five fur seals, the transmitters on two animals stopped transmitting in February after the animals had traveled to the coastal waters off California. Transmissions from

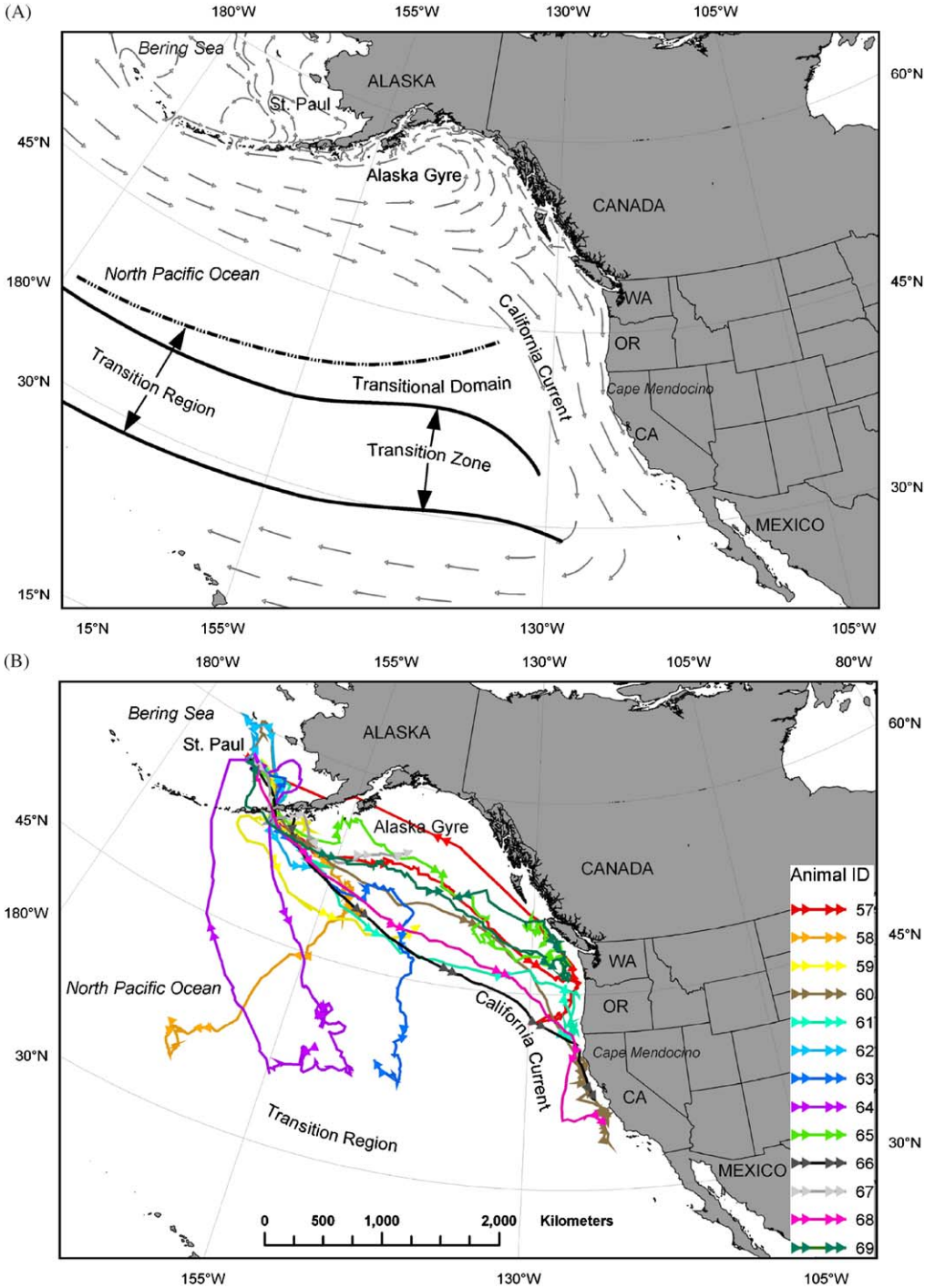

Fig. 1. Map of study area showing (A) major oceanographic and geographic features, and (B) the migratory routes of 13 female northern fur seals during the winter migration. Numbers identify individual fur seals.

the remaining three ended while the animals were migrating south in January and early February.

3.2. Fur seal locations and movement during migration

All female fur seals departed from St. Paul Island by 29 November, within five days of their capture and release (Table 1). The fur seals traveled over the continental shelf after leaving St. Paul, with most of them moving towards the Aleutian Islands and the North Pacific Ocean in a southeasterly direction (Figs. 1 and 2). However, three fur seals first traveled to the northwest or to the east of St. Paul Island prior to leaving the Bering Sea (females 60, 62 and 64). The duration of time spent in the Bering Sea after departure from St. Paul Island was greater for these fur seals (mean = 29.4 days; SE = 4.8 days) than for the 10 other fur seals (mean = 8.9 days; SE = 0.9 days). All fur seals entered the North Pacific Ocean at or near Unimak Pass, between 29 November 2002 and 1 January 2003 (median date = 6 December 2002; Table 1). The average swim speed (average of individual means, which were calculated from daily positions) of fur seals in the Bering Sea was 61.2 cm/s ($n = 13$; SD = 18.6 cm/s), or ~2.2 km/h.

The fur seals moved south to areas over deep water soon after entering the North Pacific Ocean. Though most individuals continued to travel to the east or southeast, further over deep water, there were some short-term exceptions. For instance, females 66 and 67 first traveled east–northeast towards Sanak Island and the Shumagin Islands, respectively, before returning to the deeper water to the southeast and continuing their southern

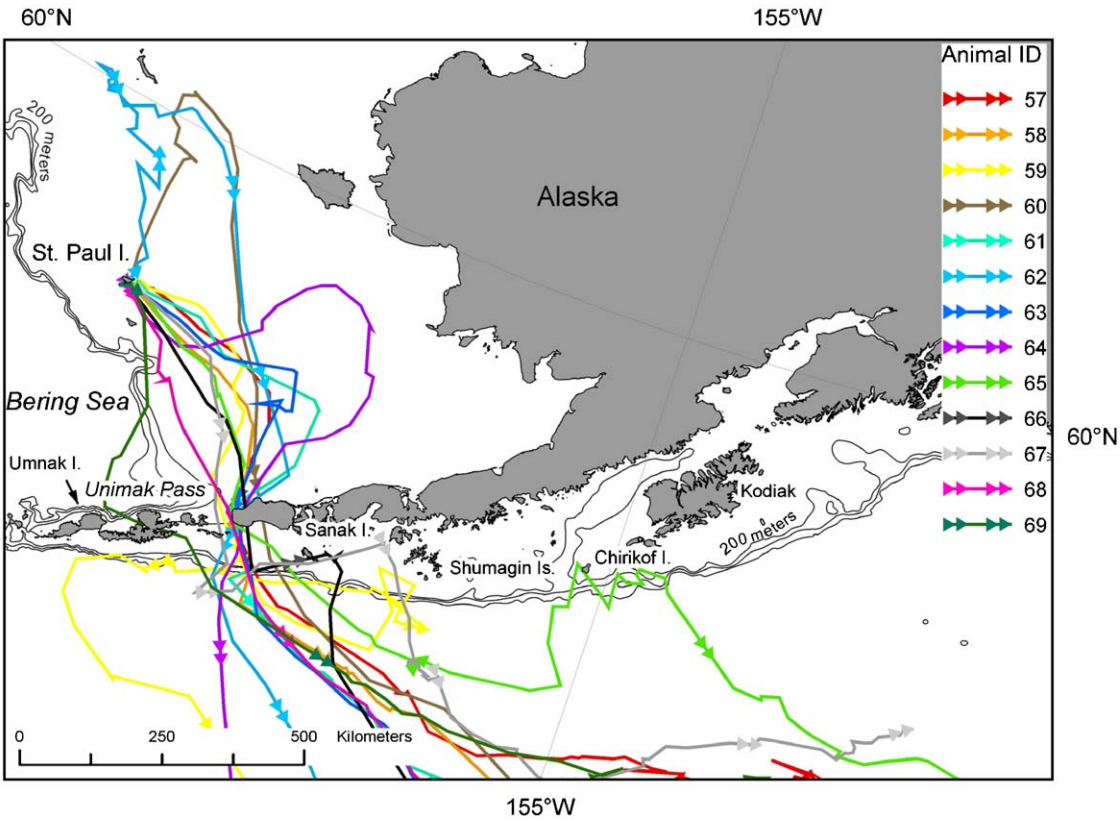

Fig. 2. Migratory movements of female fur seals during the early part of the winter migration. After exiting the Bering Sea over the continental shelf, fur seals moved through both coastal and pelagic waters of the North Pacific Ocean, as indicated by the 200, 500 and 1000 m bathymetric contours.

migrations (Fig. 2). Showing dramatic directional changes, female 59 first traveled northeasterly towards the Shumagin Islands, then turned to the southwest and moved to a point near Umnak Island before finally traveling to the southeast into the deeper water of the North Pacific. Lastly, female 65 traveled east, and then abruptly turned north towards Chirikof and Kodiak Islands after encountering a large anticyclonic eddy. After departing the area occupied by this oceanographic feature, female 65 continued to the east.

Transmitters on three of the females stopped transmitting when the animals were traveling in the Gulf of Alaska, during the early part of the migration (females 59, 62 and 67). These animals had not progressed enough to determine their winter foraging grounds or destination areas. Of the remaining animals, three were tracked into various areas of the transition region in the central North Pacific, and seven reached the coastal areas of the eastern North Pacific Ocean (Fig. 1). The latter included three females that first arrived near the continental shelf off Cape Mendocino, CA, and then continued south in the California Current along the coast of California. Four other females arrived near the coast of Washington and Oregon and spent approximately four months in those areas and off the coast of British Columbia, Canada.

Fur seal travel across the North Pacific followed water movements associated with the Alaska Gyre and the North Pacific Current. The amount of time spent in transit, however, varied greatly among females. Individuals arriving in the coastal areas off California or Oregon spent two months or less in transit from Unimak Pass, and arrived at these destination areas in late January or early February (Table 1). Female 60 spent only 42 days in transit, swimming 3413 km from Unimak Pass to the Cape Mendocino area. The three fur seals that arrived in the coastal areas off Washington spent more than three months in transit and arrived in March. Travel time to the transition region was more difficult to determine, particularly for two females who did not travel a direct route and reached this area in late March. Female 64, however, moved directly to the transition region and reached this area less than a month after departing from the Unimak Pass area.

While transit and arrival time are partially dependent upon the distance traveled, they are also affected by the swim speed of the animal. Average daily swim speed during transit was 59.4 cm/s ($n = 10$; SD = 19.8 cm/s) for all animals that reached destination areas, and ranged from 35.3 to 92.7 cm/s. The average swim speed during transit for fur seals that arrived off the coast of California was 79.3 cm/s ($n = 3$; SD = 11.7 cm/s), and only 43.6 cm/s ($n = 3$; SD = 1.0 cm/s) for those that arrived off the coast of Washington. In the winter foraging areas (after transit) the average speed was lower for most individuals, and ranged from 24.8 to 63.2 cm/s (Fig. 3). Although females 57 and 64 were tracked during the return trip to St. Paul Island, we only received enough locations to calculate a reliable estimate of swim speed for female 64. The average swim speed of female 64 during the return trip and while traveling to the transition region was similar (Fig. 3). Overall, the average speed of all fur seals for the entire duration of tracking was 48 cm/s ($n = 13$; SD = 12.4 cm/s), regardless of when satellite transmissions ended.

3.3. Fur seal dive data

Three northern fur seals were instrumented with ST-16 SDRs that, in addition to the location data, provided information on diving. Due to satellite coverage and a low transmission rate, only one-third of the total dive histograms were received for all time periods combined. Period 1, corresponding to the mid-morning, was underrepresented with regards to the percentage of transmissions received, while histograms in the other periods were received in similar proportions (Table 2). The average dive rate, however, was greater during periods representing nighttime hours than daytime hours; dives per hour were 2–8 times greater during Periods 0 and 3 than during Periods 1 and 2.

Fur seals were predominantly located over deep-water habitat during the migration. Ocean bottom depths less than 500 m were associated with only 14.8% of the fur seal locations (all individuals),

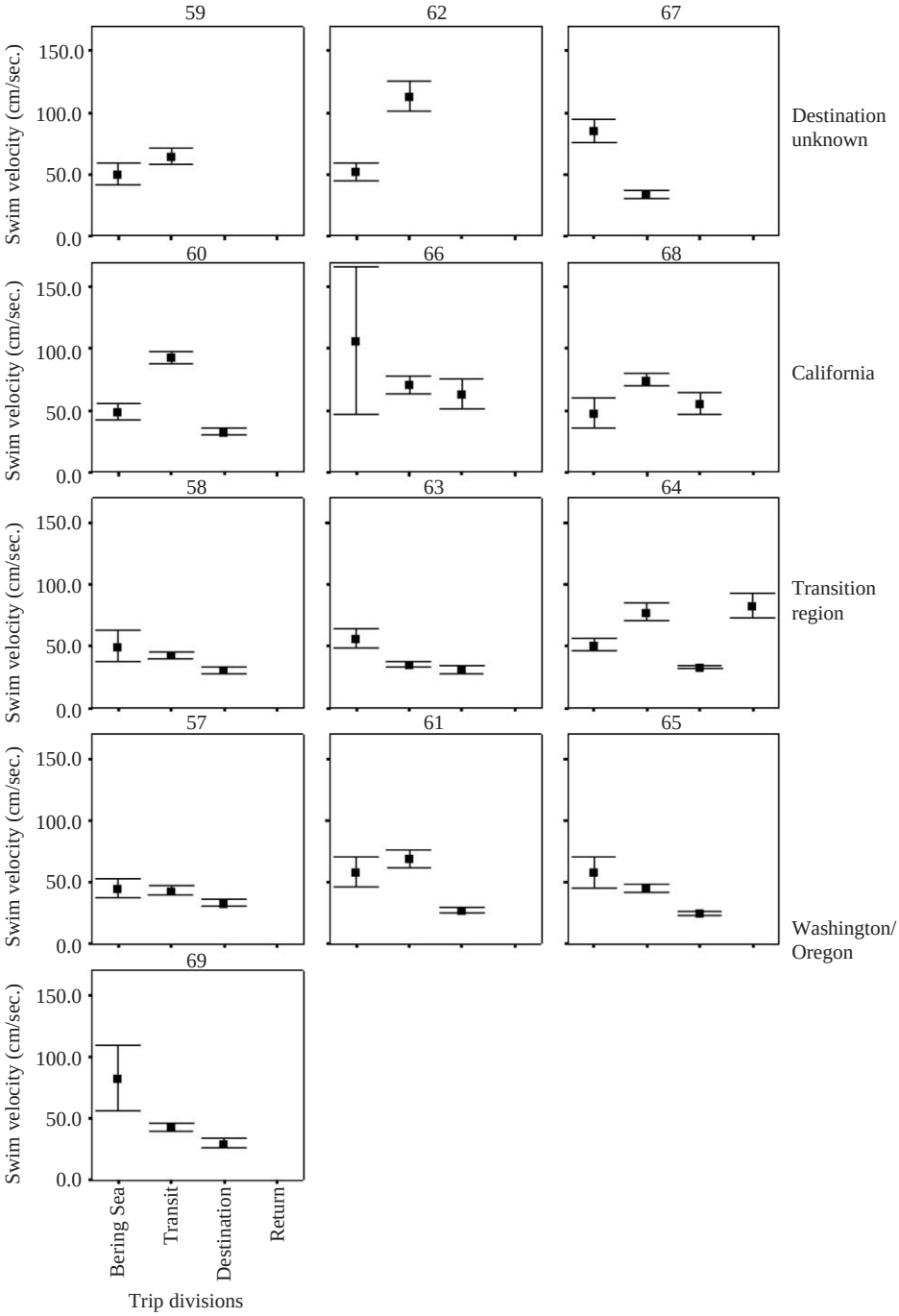

Fig. 3. Average swim speed (cm/s) of each fur seal during different segments of their migration, grouped by destination region. Shown at each segment is the mean ± the standard error.

Table 2
Percentage of total dive histograms received for each 6-hour period, and the respective dive rate (dives/h), for fur seals with ST-16 SDRs

	Period 0		Period 1		Period 2		Period 3	
	11:00–16:59 GMT		17:00–22:59 GMT		23:00–04:59 GMT		05:00–10:59 GMT	
ID	Received (%)	Rate	Received (%)	Rate	Received (%)	Rate	Received (%)	Rate
67	55	10	18	1	42	4	39	12
68	33	9	20	3	32	6	37	10
69	38	11	7	2	36	5	43	19
Average	42	10	15	2	37	5	40	16

Periods 0 and 3 represent nighttime hours, while Periods 1 and 2 represent daytime hours. Dive rate includes dives greater than 4 m in depth.

and 72.3% of these positions (10.7% of the total) were related to bottom depths of less than 100 m on the Bering Sea shelf (data not shown). For the three fur seals instrumented with SDRs, mean dive depth (dives greater than 4 m) and dive rate varied among individuals as they traveled in different geographic areas. Mean dive depth of individuals tended to be shallow (<25 m) when the animals reached their destination areas along the coast of the Eastern North Pacific, but did not show obvious or consistent trends from area to area (Fig. 4A). Average dive effort (rate) was lowest for individuals while in the Bering Sea; after leaving the Bering Sea, individual dive rates increased and were similar between the transit and the destination areas (Fig. 4B). Because dive depth is positively related to dive duration, it is likely that the observed dive rates were influenced by the depths of the dives. Lastly, the mean nighttime diving depth was greater (30–90 m) during the full moon than during the new moon (6–30 m; Fig. 5). This apparent relationship was most evident in the months before the animals reached the destination areas, after which diving was shallower in general.

3.4. Remotely sensed data

Sea-surface temperatures (SST) corresponding to the fur seal locations varied according to the geographic region occupied by the fur seals (Fig. 6). While in the Bering Sea and during their transit across the North Pacific, females that

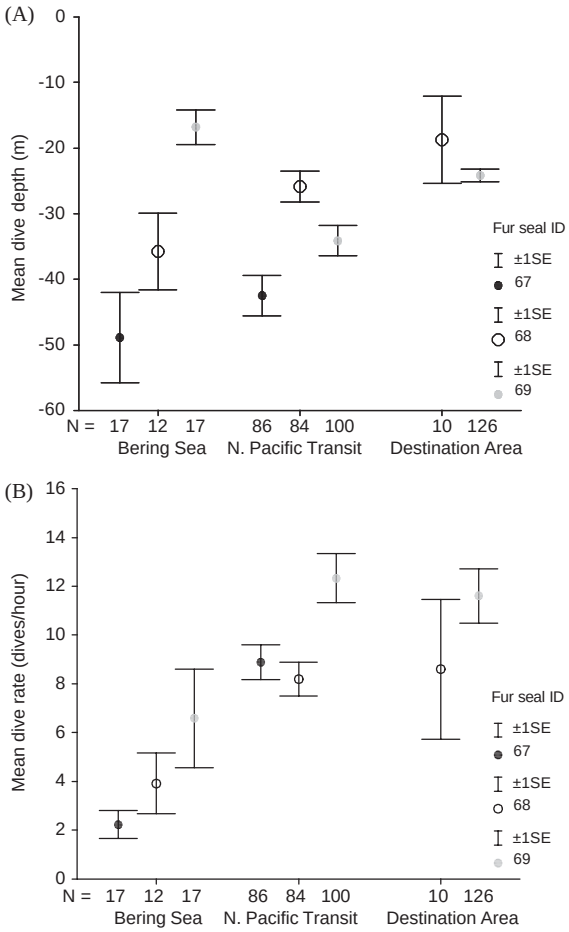

Fig. 4. Dive parameters, including (A) mean dive depth and (B) mean dive rate, of three female northern fur seals in different regions during the winter migration.

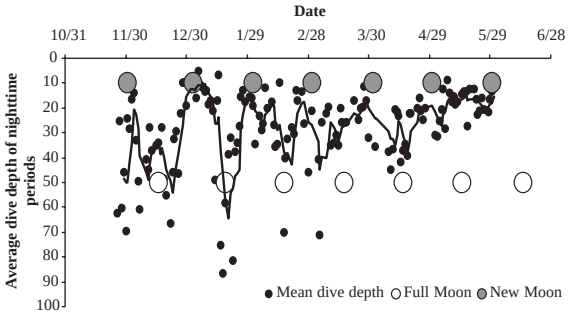

Fig. 5. Relationship between mean dive depths and the lunar cycle for nighttime dive periods. The trend line is a four-point moving average.

eventually reached destination areas experienced monthly average SST that ranged from 4.7 to 7.6 °C, among individuals. Upon arrival in the coastal areas off California, females encountered average SST of ~13 °C (mean = 13.4 °C; $n = 3$; SD = 0.1 °C), while those arriving off Washington and Oregon encountered average SST of ~10 °C (mean = 10.4 °C; $n = 4$; SD = 0.6 °C). The monthly average SST experienced by fur seals in the transition region were quite variable, ranging from 8.7 to 14.8 °C among individuals over the study period. Within individuals this variability was probably due to rapidly changing temperature regimes at this convergence of water masses, while among individuals it may have been affected by the timing of female arrival and the distant proximity between animals in this large geographic region. SST increased into the spring and eventually all fur seals in the transition region experienced mean monthly SST of over 13 °C.

Ambient temperature sensed by the Kiwisat 101 PTTs showed patterns of change similar to the remotely sensed SST while the fur seals traveled in different regions. However, the temperatures recorded by the PTTs tended to be about 2 °C higher than the remotely sensed data (data not shown). This discrepancy was likely due to heat conduction from the fur seals to the instruments, but could also be due to air temperatures being recorded when the fur seals were at the surface.

Surface chlorophyll *a* concentrations (chl *a*) associated with the fur seal locations also varied by geographic region (Figs. 7 and 8). Levels of chl *a* in the Bering Sea were not determined due to limited data while the animals were present. During transit across the North Pacific, monthly average chl *a* concentrations ranged from 0.08 to over 0.30 mg/m^3 among individuals. Monthly average chl *a* concentrations were highest in coastal areas (chl $a > 0.40$ mg/m^3 for all individuals and months of tenure) and increased while the fur seals remained in these areas (Fig. 8). Animals traveling to the transition region experienced the most consistent levels of chl *a*, with monthly averages at just over 0.2 mg/m^3.

Examination of sea-surface height (SSH) anomalies revealed three cyclonic and anticyclonic eddy features that were encountered by fur seals during their migration (Fig. 9). Fur seal movements at these eddies corresponded to the bearings of the geostrophic currents determined from the SSH anomalies. The majority of fur seal swim bearings calculated from daily positions at the eddies deviated by less than 45° from the geostrophic current bearings (Fig. 10A). Excluding the positions at eddy features, fur seal swim bearings in the North Pacific calculated daily over the duration of the satellite transmissions revealed only a slightly higher frequency of movements in a similar direction as the geostrophic currents (bearing deviation $< 90°$; Fig. 10B).

3.5. Data from pelagic collection of fur seals: sex, age and prey distribution

Data from historical pelagic collections indicate that fur seals were stratified by age and sex (Lander and Kajimura, 1982; Kajimura, 1984; Bigg, 1990). Female northern fur seals far outnumbered males in the scientific pelagic collections during February to May of 1958–1974, in all four geographic regions (Fig. 11). Females collected in the Gulf of Alaska tended to be older, while the youngest age classes were found in British Columbia and Washington/Oregon. Male fur seals in the collections followed a latitudinal trend with regards to distribution and age; more males and males of older age classes were represented in the Gulf of Alaska, while fewer and younger males were represented in the southern geographic regions.

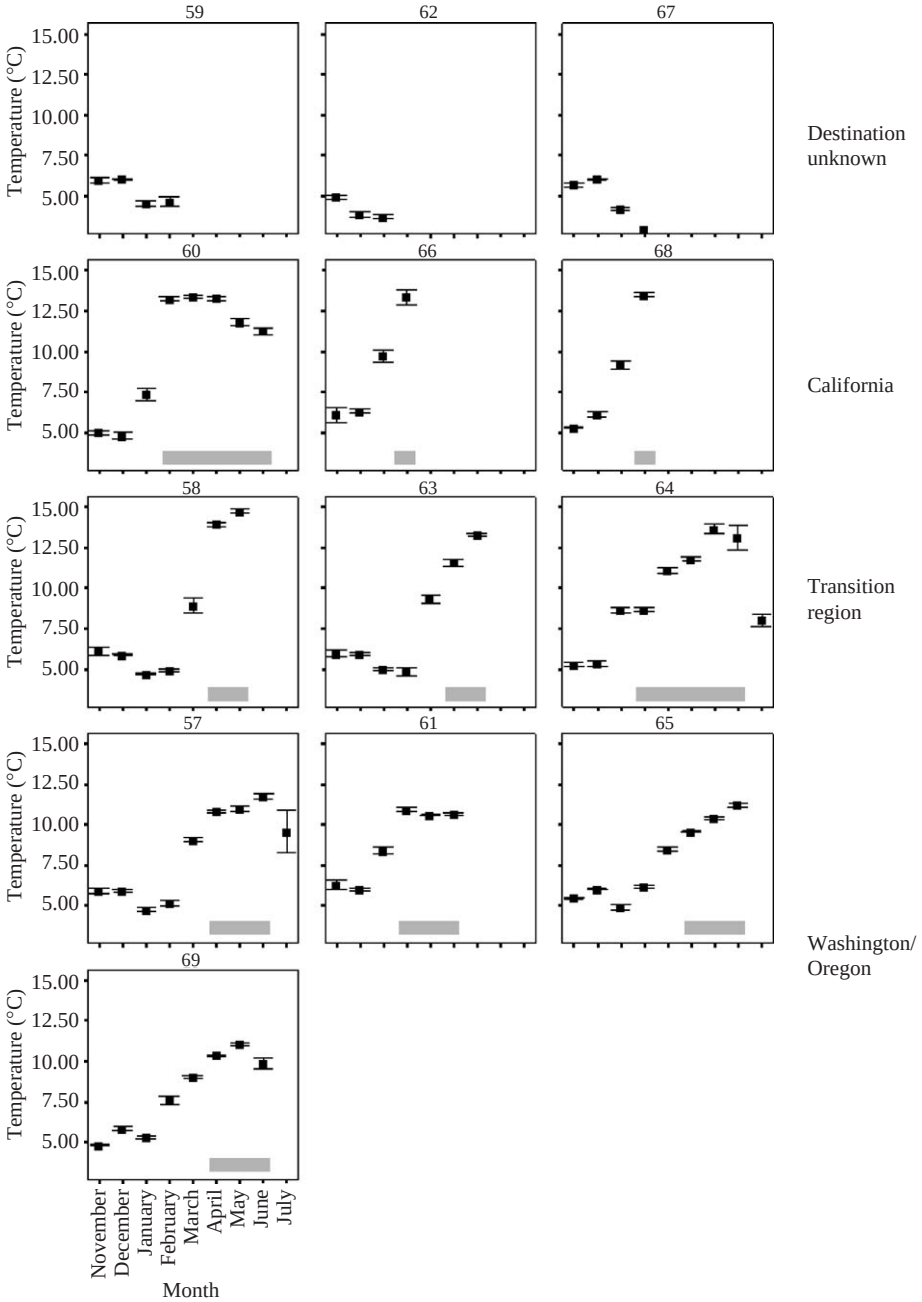

Fig. 6. Mean monthly sea-surface temperature (°C) encountered by each fur seal, grouped by destination region. Shown at each month is the mean ± the standard error. The gray bar indicates the months of tenure at the destination region.

Primary prey found in stomach samples from the pelagic collections varied among regions and among months within regions (Fig. 12). In the Gulf of Alaska and British Columbia regions a few primary prey species occurred in very high frequencies, while in the Oregon/Washington and California regions the primary prey were more evenly distributed. Pacific herring dominated

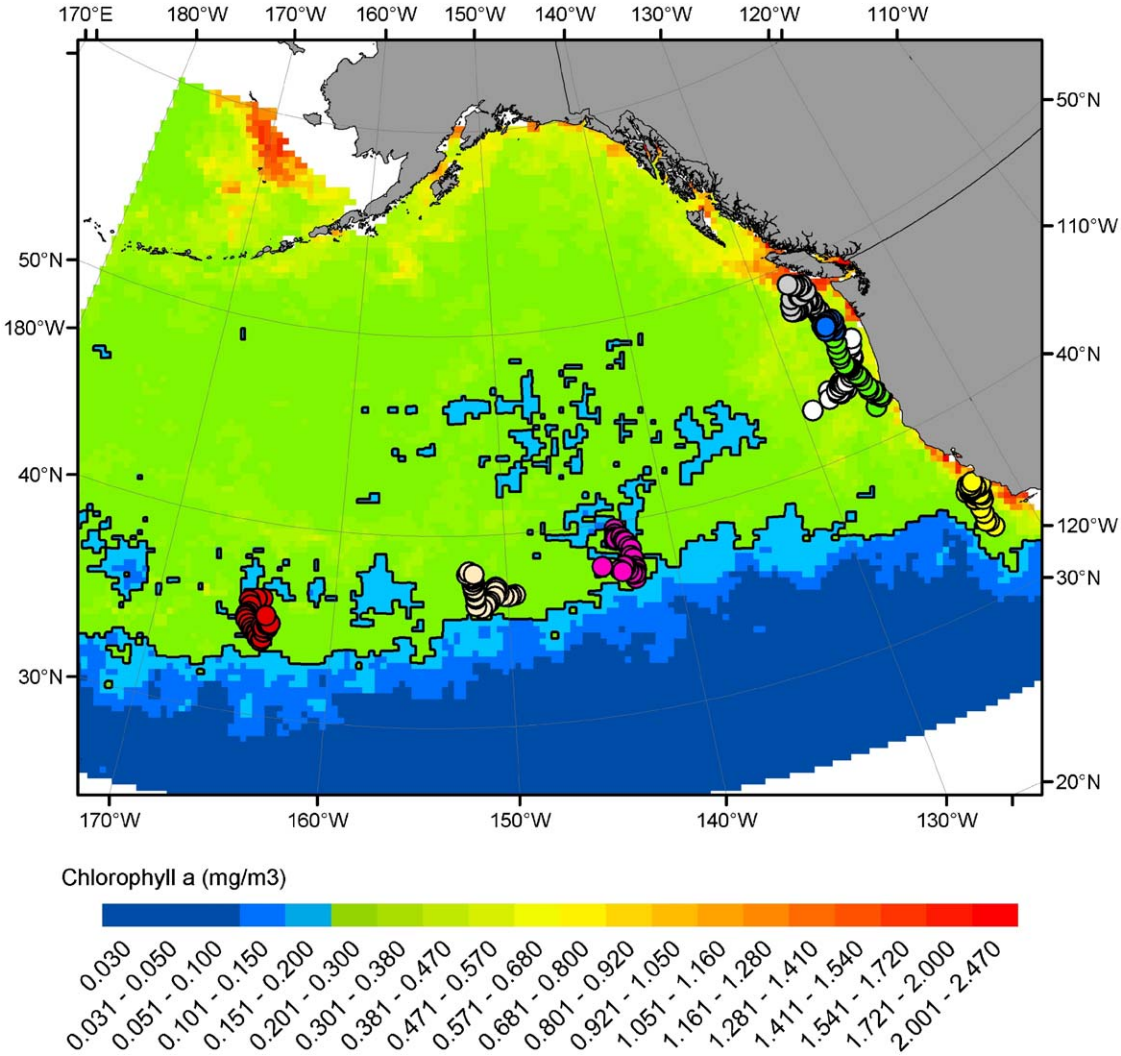

Fig. 7. Chlorophyll *a* concentration and daily satellite locations of eight northern fur seals (filled circles) in the North Pacific Ocean during April 2003. The black contour line indicates chl *a* density of 0.2 mg/m^3.

much of the diet in the Gulf of Alaska and British Columbia and was a primary prey in Oregon/Washington, as well. Gonatid squids and walleye pollock were also primary prey in these three regions, though they occurred at a much lower frequency. Northern anchovy and market squid were primary prey found only in Oregon/Washington and California. In the transition zone, myctophids, squids and Pacific saury were primary prey of northern fur seals.

Percent occurrence of primary prey species also varied between male and female fur seals, particularly in the Gulf of Alaska and in California (Fig. 13). In the Gulf of Alaska, gonatid squids and walleye pollock occurred at a higher frequency in the males' stomachs, while Pacific herring, capelin and, especially Pacific sand lance occurred at a higher frequency in the females' stomachs. In California, market squid occurred at a higher frequency in the males' stomachs, while Pacific

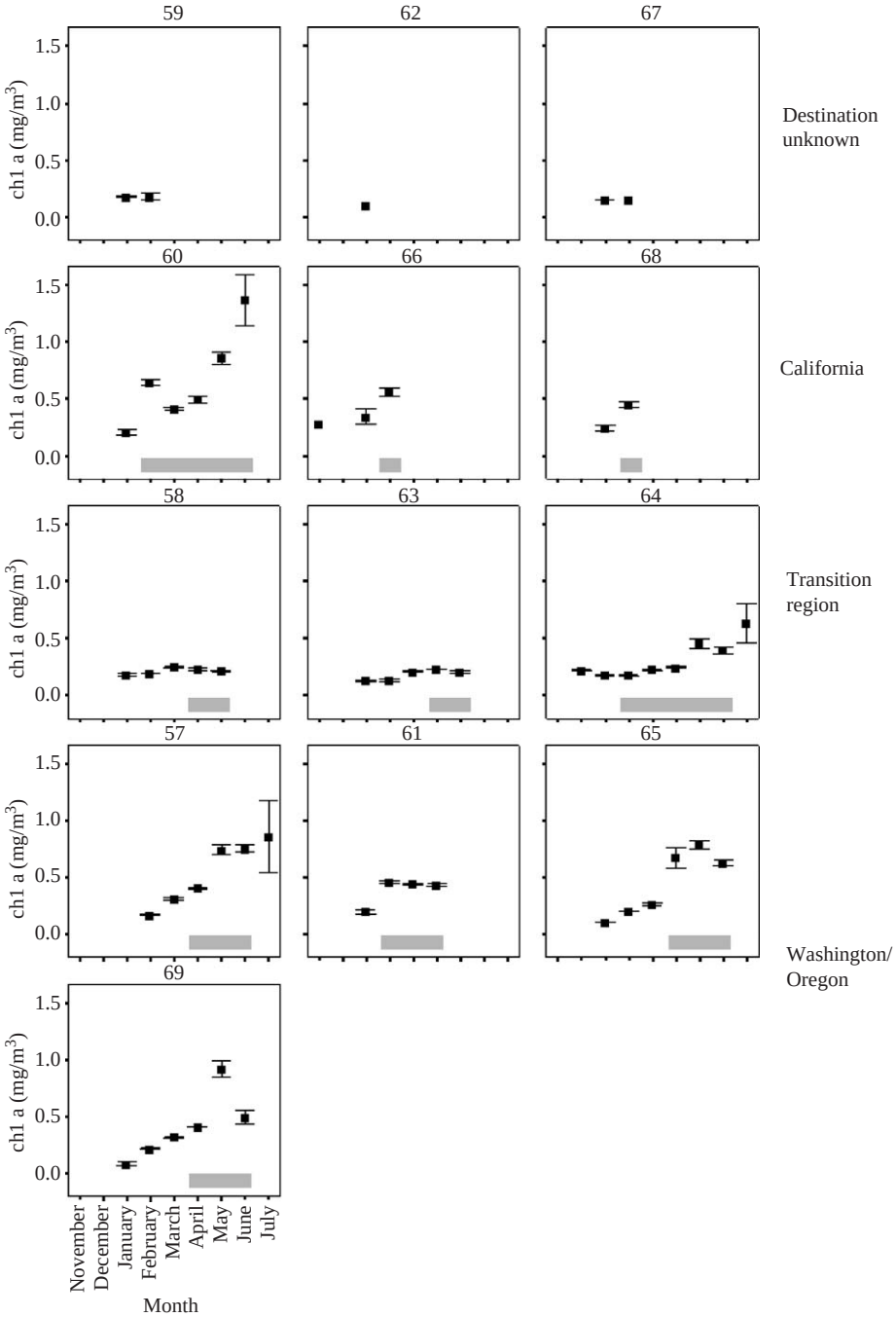

Fig. 8. Mean monthly sea-surface chlorophyll *a* concentration (mg/m^3) encountered by each fur seal, grouped by destination region. Shown at each month is the mean $\pm$ the standard error. The gray bar indicates the months of tenure at the destination region.

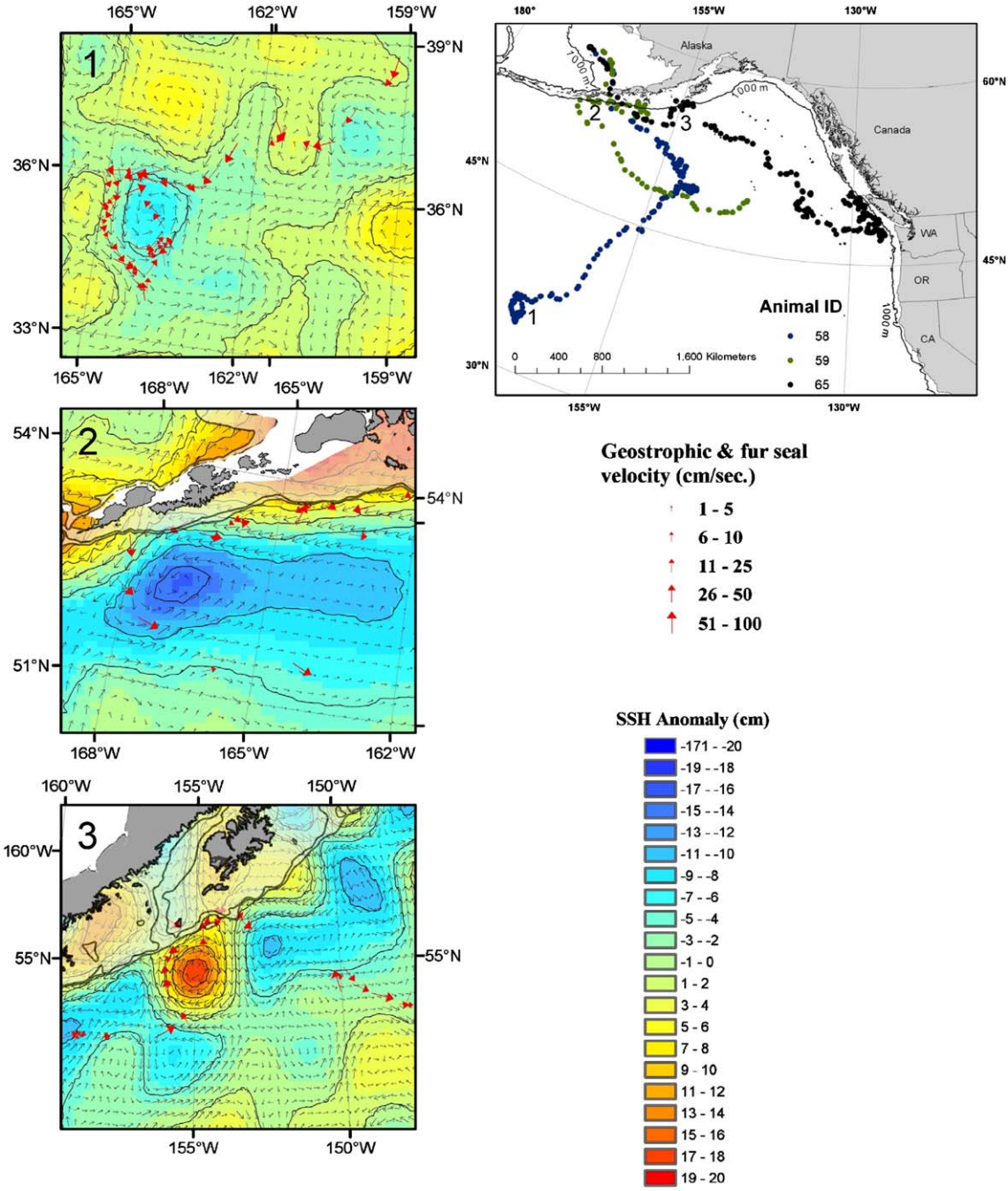

Fig. 9. Eddy features revealed by sea-surface height anomalies encountered by three fur seals during their migration, and the location of these eddies relative to the migration track of each fur seal. Geostrophic current (black arrows) and fur seal (red arrows) bearing and velocity are indicated by the direction and size of the arrows.

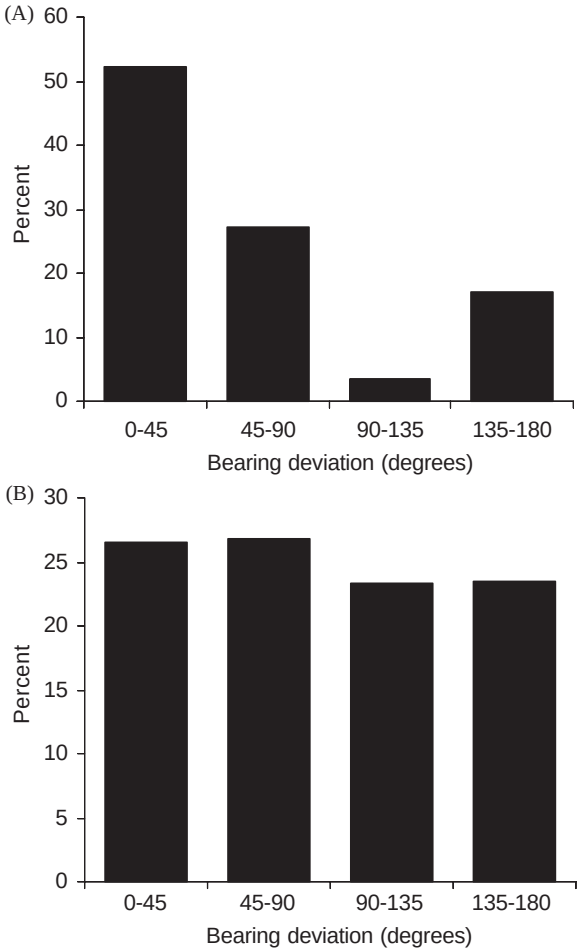

Fig. 10. Relationship between fur seal swim bearings and geostrophic current bearings. Bearing deviations (absolute value of the difference between fur seal and current bearing) were binned to show (A) distribution of deviations for three fur seals at eddy features, and (B) distribution of deviations for all fur seals while in the North Pacific (excluding positions near eddies).

saury, northern anchovy, and clubhook squids occurred at a higher frequency in the females' stomachs.

4. Discussion

Using satellite telemetry, we tracked the travel routes and movement patterns of individual female northern fur seals from St. Paul Island, AK, during the early, middle, and late phases of their migration that occurs between November and May each year. Eight females were tracked into or past May, representing a minimum of 160 days at sea. Two of these females were tracked for the entire duration of the migration. We believe that the tracking duration was extended by selecting post-molt individuals and by attaching the relatively small KiwiSat PTTs with a light application of epoxy (to minimize potential overheating of the hair follicles). Fur seal migrations have been explored previously using satellite and radio telemetry, but only during the early phases of the migration; all studies ended in or before February (Kiyota et al., 1992; Ragen et al., 1995; Loughlin et al., 1999; Baba et al., 2000). Using radio telemetry, Ragen et al. (1995) examined pup migration from the Pribilof Islands until shortly after they exited the Bering Sea through the Aleutian Islands. Kiyota et al. (1992) and Baba et al. (2000) tracked female fur seals with satellite transmitters after they left the Pribilof Islands and the Commander Islands (Russia), respectfully. Most of these females were tracked for 2–3 months, during which time some individuals moved well into the North Pacific Ocean. Finally, Loughlin et al. (1999) attached satellite transmitters to eight adult male fur seals in the fall, and tracked some of the animals until February. Four of these males migrated into the Gulf of Alaska, while three moved west towards the Kuril Islands and Japan. One male remained in the Bering Sea for the duration of the study.

The adult female fur seals in this study departed from St. Paul Island by 29 November 2002, and most moved in a southeasterly direction towards the North Pacific Ocean. Three of the 13 fur seals departing from St. Paul Island first traveled to the northwest or to the east prior to leaving the Bering Sea. The initial travel routes used by these animals were typical of summertime foraging trips, based on the direction and distance of travel from St. Paul Island (Loughlin et al., 1987; Robson et al., 2004). However, these females did not return to St. Paul Island and traveled east of the island as they moved towards the North Pacific Ocean. It is likely that the females made a final concentrated foraging effort prior to beginning their migration.

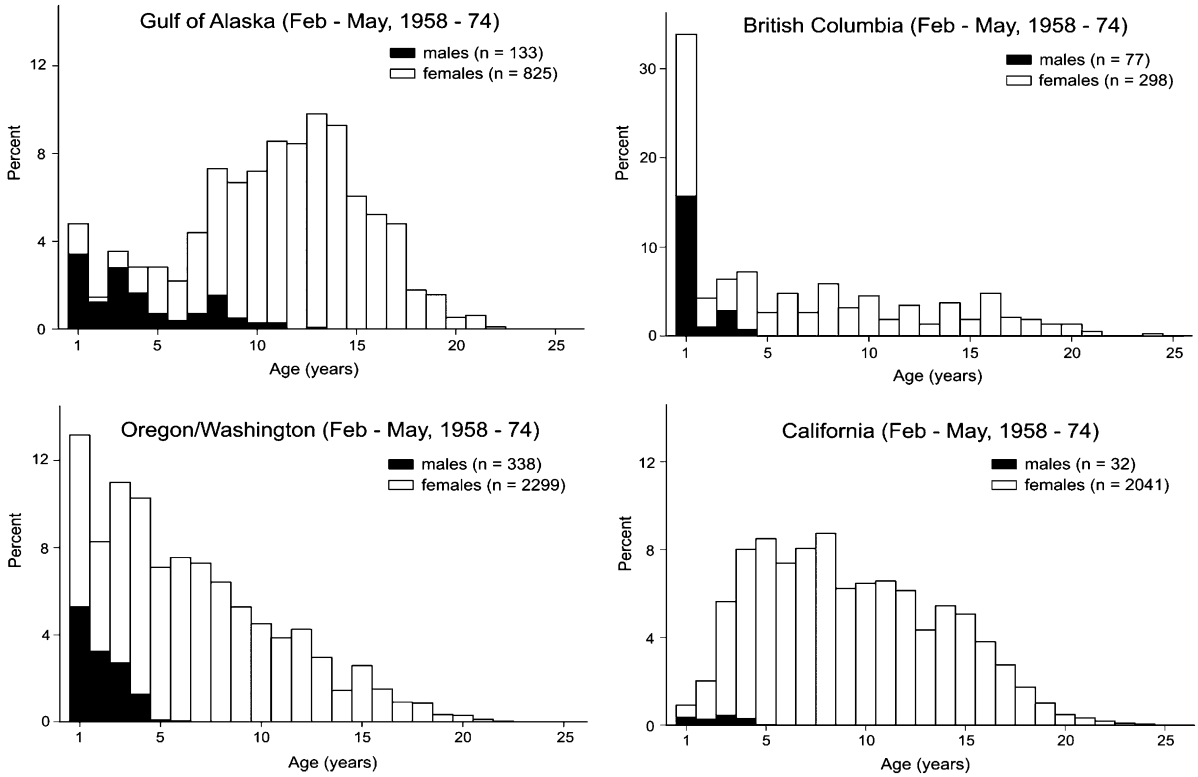

Fig. 11. Age and sex distribution of fur seals from pelagic collections (February–May, 1958–1974), by geographic region.

Dive records provide evidence for this behavior in adult male northern fur seals; Loughlin et al. (1999) found that males displayed diving bouts typical of foraging before exiting the Bering Sea in November and December.

The fur seals in our study traveled over the continental shelf while in the Bering Sea. A weak eastward current may have aided movement further onto the shelf (Stabeno et al., 1999). This route of travel positioned the animals away from the relatively strong northward Bering Slope Current (BSC), which forms the eastern boundary of the Bering Sea gyre (Schumacher and Reed, 1992). The BSC is thought to intensify during the fall–winter (Overland et al., 1994), which corresponds to the timing of migration of fur seals out of the Bering Sea. While the fur seals most likely swam against currents over the shelf, the weak nature of the flow of water in this area would reduce the energetic expenditures by the seals and may be preferable to fighting stronger currents.

By 1 January 2003 all of the fur seals had entered the North Pacific Ocean at or near Unimak Pass. While the females eventually traveled over deep water during transit in the North Pacific, some initially returned from deeper waters onto the shelf in areas along the Alaska Peninsula or the Aleutian Islands. It is not clear what the purpose of these movements were, as they did not correspond to the eventual direction of travel. While these indirect routes may have served to orient the animals, it is more likely that they provided foraging opportunities for the fur seals. One female moved into waters over the shelf only after she encountered and traveled along the outer edge of a large anticylonic eddy.

Fur seal transit across the North Pacific Ocean to winter foraging grounds followed the general patterns of water flow of the North Pacific Current

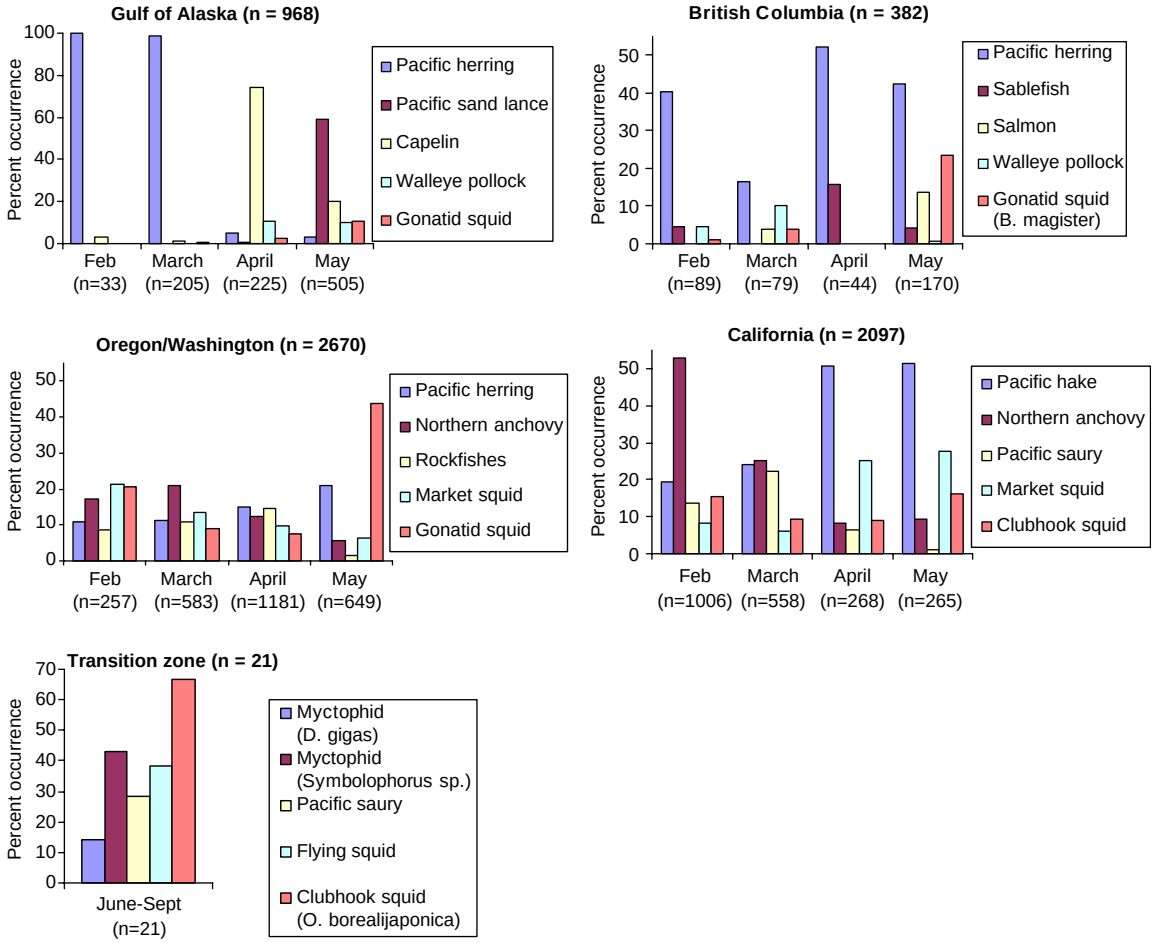

Fig. 12. Percent occurrence of primary prey species (top five species) in stomachs of northern fur seals collected at sea. Prey are listed by month and region of collections.

and the southern boundary current of the Alaska Gyre. The amount of time fur seals spent traveling across the North Pacific to the destination areas ranged from less than a month to $3\frac{1}{2}$ months and averaged 75 days. The transit durations, combined with the energetic requirements of swimming, indicate that foraging in this oceanic environment was necessary for most of these females prior to arriving in their winter foraging grounds. This notion is supported by dive behavior observed in a subset of the female fur seals. Fur seal dive rates were comparable among animals during transit and in the destination areas. Additionally, the dive depths were slightly greater for animals during transit, implying that the fur seals worked harder to meet their energetic demands. Daily location plots of individual fur seals revealed variability in the progress of migration; periods of slow movement may represent foraging bouts or, perhaps, rest periods.

Winter foraging areas were identified for 10 of the female fur seals tracked in this study. In broad terms, these areas were defined as the subarctic–subtropical transition region of the central North Pacific and the coastal areas of the eastern North Pacific. Within the coastal areas, the fur seals were segregated more specifically by the location of arrival and subsequent movements. Three animals

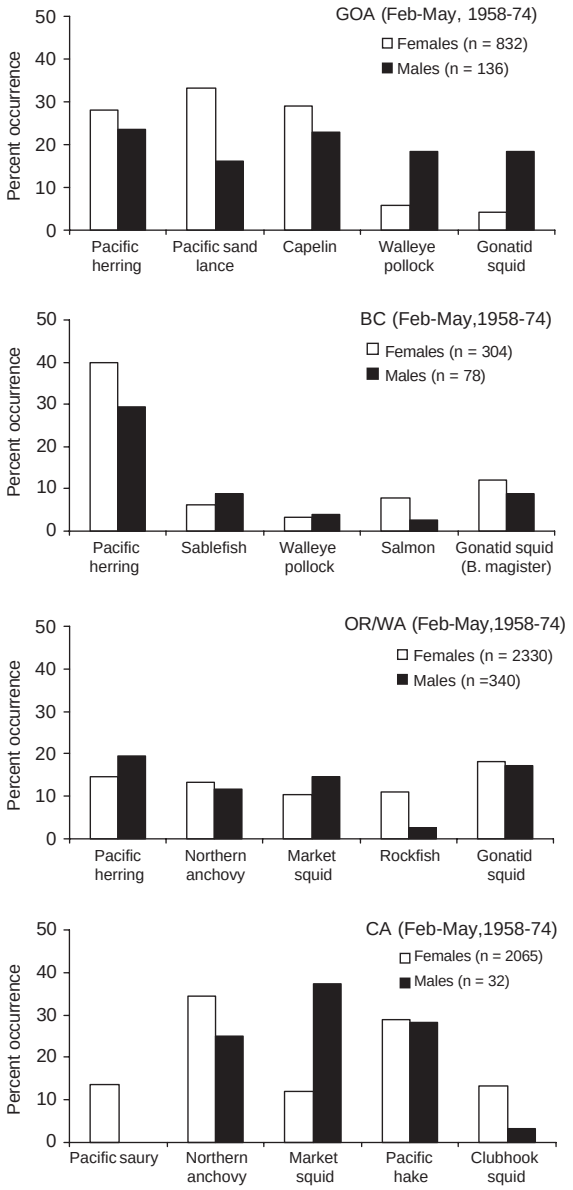

Fig. 13. Percent occurrence of primary prey in stomachs of male and female northern fur seals, by region (GOA = Gulf of Alaska; BC = British Columbia; OR/WA = Oregon and Washington; CA = California).

arrived off the coast of California near Cape Mendocino, and continued south in the California Current. Three fur seals arrived off the coast of Washington and one offshore of Oregon. These individuals spent the subsequent months in the waters off Washington, Oregon and British Columbia, Canada. Fur seal arrival times to these areas and the rates of transit across the North Pacific differed greatly among regions. Fur seals arrived off Washington no earlier than 10 March 2003 after traveling for an average of 97.3 days from Unimak Pass. During this time the average swim speed was 43.6 cm/s. By contrast, fur seals arrived off California no later than 3 February 2003, spent an average of 51 days in transit, and traveled at an average speed of 79.3 cm/s. Interestingly, the animals that wintered in Washington had the northernmost travel routes as they crossed the Gulf of Alaska. Thus, the slower transit time and speed may have resulted from less favorable currents in that part of the Alaska Gyre. Alternatively, these fur seals may have slowed their transit time due to foraging opportunities provided along this route.

The transition region has not been previously described as a component of the northern fur seal migratory pathway or winter foraging grounds. However, fur seals are known to occur in this oceanic area, often in association with the high-seas squid driftnet fishery (Walker and Jones, 1993; Mori et al., 2001). Of the 10 fur seals for which we determined winter foraging areas, three were tracked to the transition region. The physical and biological characteristics described for the subarctic-subtropical transition region (including the transitional domain and the transition zone) depict a complex area of convergent currents, fronts and eddies that concentrate plankton and nekton, which in turn attract higher trophic-level predators (Pearcy, 1991; Roden, 1991; Olson et al., 1994; Brodeur et al., 1999; Polovina et al., 2000, 2001).

Only Loughlin et al.'s (1999) study of adult males has examined the relationship between fur seal migration movements and oceanographic features (sea-surface currents). Our use of remotely sensed data to explore relationships between female fur seal migrations and sea-surface temperature, chlorophyll *a* concentrations, and height anomalies revealed several patterns. Female fur seals traveled out of the Bering Sea and across the North Pacific Ocean in SST of ~5–7 °C to reach warmer water in coastal areas of the eastern North

Pacific (~10–13 °C), and in the transition region of the central North Pacific (>13 °C). Similarly, the concentration of chl *a*, a measure of phytoplankton standing stocks, increased as the fur seals reached their destination areas. At the coastal foraging grounds, chl *a* concentrations continued to intensify as the season progressed, while the concentrations encountered by fur seals in the transition region remained relatively stable and consistently lower than in the other areas. The lower sea-surface chl *a* concentration in the transition region should not be taken as an indication that ocean productivity is minimal in this region, however. It is a dynamic environment with very high primary production likely below the surface or in patches, and with overall production at levels attractive to nekton moving north from extremely low levels in the transition zone and subtropical waters.

The approximate latitudinal boundaries of the transitional domain, the transition zone, and the transition region in general have been previously described (Pearcy, 1991; Roden, 1991). The fur seal locations received during their migration through this area clearly position the three individuals in the transition zone when applying these latitudinal boundaries. However, the physical and biological features that delineate these domains and zones shift in latitude both seasonally and annually (Polovina et al., 2000, 2001). This variability makes it difficult to position animals within the specific features at a given time using satellite locations alone. Linking the animal locations to remotely sensed oceanographic data, however, provides an alternate approach. The sea-surface temperatures and chlorophyll *a* concentrations associated with fur seal locations indicate that the three individuals in the central North Pacific were within the transitional domain (SST >13 °C) and may have crossed the subarctic boundary into the transition zone during their migration. The chlorophyll *a* concentrations encountered by the fur seals placed them in close vicinity to the Transition Zone Chlorophyll Front (TZCF; Fig. 7), defined by a chl *a* density of 0.2 mg/m^3 (Polovina et al., 2001).

Remotely sensed data of sea-surface height anomalies allowed for identification of three eddy features that were encountered by fur seals during migration (Fig. 9). One of these eddies occurred at the transition region, probably associated with fronts caused by the convergence of boundary currents of the Subarctic and Subtropical Gyres. Other eddies were observed south of the Alaska Peninsula and the Aleutian Islands, where the Alaska Stream moves along a complex bathymetric environment. The average velocity of the geostrophic currents experienced by fur seals at these eddies ranged from 8.5 to 16.1 cm/s, and fur seal movements around the eddies corresponded to the bearings of the geostrophic currents. Reduced energetic expenditures may be only one of many benefits that eddies present to fur seals. Eddy features are characterized by increased primary production and are known to transport and retain zooplankton from nearshore regions (Seki et al., 2001; Mackas and Galbraith, 2002; Mizobata et al., 2002). These traits of eddies, among others, likely help concentrate fur seal prey and increase foraging opportunities.

We could not collect fur seal diet information during migration, nor did we explore age or sex variation in migration patterns because we only tracked adult females. Data from the historical pelagic collection of northern fur seals indicated differences in the age and sex composition of migrating fur seals among winter foraging areas during previous decades (Lander and Kajimura, 1982; Kajimura, 1984; Bigg, 1990). Fur-seal diet also varied among the regions, and among months within the regions. Further, we found differences in diet between sexes, which may have resulted from their diving capability (and therefore depth of prey), or perhaps suggests selection of particular prey species due to different energetic requirements of male and female fur seals.

While the extensive pelagic collection of northern fur seals represents historical data, it provides valuable insight into the current use of open-ocean and coastal systems by the fur seal population during the annual migration. We believe that similar stratification of sex/age classes of fur seals should be expected among regions during present-day migrations. Fur seals are undoubtedly feeding while migrating across the open ocean, but appear to travel quickly to winter foraging destinations

that are characterized by high productivity. Considerable variability in diet is also probable among these regions, and among months, though the prey assemblages consumed by fur seals may have changed. Fur seals are opportunistic predators and likely meet their energetic demands by occupying habitat containing abundant prey species.

In summary, remotely sensed data used in conjunction with satellite telemetry can clearly enhance the understanding of at-sea animal movement. Using satellite telemetry, we described the timing and location of the winter migration of adult female fur seals from the Pribilof Islands, across the open ocean of the North Pacific, to coastal areas of the eastern North Pacific and to the transition region of the central North Pacific. We defined three winter foraging areas and found that fur seal travel routes, travel speed, and arrival time varied among the areas. Use of remotely sensed data allowed interpretation of the physical and biological characteristics of the environment encountered by the fur seals, and helped to explain small-scale movements by the fur seals. Female fur seals likely cued on a variety of oceanographic features during their winter migration. These features probably aid in reducing energetic expenditures during migration as well as optimize foraging opportunities.

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References

Antonelis, G.A., Sinclair, E.H., Ream, R.R., Robson, B.W., 1997. Inter-island variation in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. Journal of Zoology 242, 435–451.

Baba, N., Boltnev, A.I., Stus, A.I., 2000. Winter migration of female northern fur seals *Callorhinus ursinus* from the Commander Islands. Bulletin of the National Research Institute of Far Seas Fisheries 37, 39–44.

Bigg, M.A., 1990. Migration of northern fur seals (*Callorhinus ursinus*) off western North America. Canadian Technical Report of Fisheries and Aquatic Sciences 1764, 64pp.

Brodeur, R., McKinnell, S., Nagasawa, K., Pearcy, W., Radchenko, V., Takagi, S., 1999. Epipelagic nekton of the North Pacific Subarctic and Transition Zones. Progress in Oceanography 43 (2–4), 365–397.

Fadely, B.S., Robson, B.W., Sterling, J.T., Greig, A., Call, K.A., 2003. Defining marine habitat use of immature Steller sea lions through the use of satellite telemetry and GIS. Abstracts of the 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, NC, USA.

Gentry, R.L., 1998. Behavior and Ecology of the Northern Fur Seal. Princeton University Press, Princeton, NJ.

Goebel, M.E., Bengtson, J.L., Delong, R.L., Gentry, R.L., Loughlin, T.R., 1991. Diving patterns and foraging locations of female northern fur seals. Fishery Bulletin of US 89, pp. 171–179.

Kajimura, H., 1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. NOAA Technical Report NMFS SSRF-779, pp. 1–48.

Kenyon, K.W., Wilke, F., 1953. Migration of the northern fur seal, *Callorhinus ursinus*. Journal of Mammalogy 34, 86–98.

Kiyota, M., Baba, N., Loughlin, T.R., Antonelis, G.A., 1992. Characteristics of winter migration of female Pribilof fur seals. Abstracts of the 15th Symposium on Polar Biology, Tokyo, December 1992.

Lander, R.H., Kajimura, H., 1982. Status of the northern fur seal, Mammals of the Sea. FAO Fisheries Service No. 5., pp. 319–345.

Leben, R.R., Born, G.H., Engebre, B.R., 2002. Operational altimeter data processing for mesoscale ocean monitoring. Marine Geodesy 25, 1–22.

Loughlin, T.R., Bengtson, J.L., Merrick, R.L., 1987. Characteristics of feeding trips of female northern fur seals. Canadian Journal of Zoology-Revue Canadienne De Zoologie 65 (8), 2079–2084.

Loughlin, T.R., Antonelis, G.A., Baker, J.D., York, A.E., Fowler, C.W., Delong, R.L., Braham, H.W., 1994. Status of the northern fur seal population in the United States during 1992. In: Sinclair, E.H. (Ed.), Fur Seal Investigations, 1992. NOAA Technical Memorandum NMFS-AFSC-45, pp. 9–28.

Loughlin, T.R., Ingraham, W.J., Baba, N., Robson, B.W., 1999. Use of a surface-current model and satellite telemetry to assess marine mammal movements in the Bering Sea. In:

Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea: A Summary of Physical, Chemical, and Biological Characteristics, and A Synopsis of Research on the Bering Sea. University of Alaska Sea Grant, Fairbanks, Alaska, AK-SG-99-03, pp. 615–630.

Loughlin, T.R., Sterling, J.T., Merrick, R.L., Sease, J.L., York, A.E., 2003. Diving behavior of immature Steller sea lions (*Eumetopias jubatus*). Fishery Bulletin of US 101, 566–582.

Mackas, D.L., Galbraith, M.D., 2002. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: 1. Transport and loss of continental margin species. Journal of Oceanography 58 (5), 725–738.

Mizobata, K., Saitoh, S.I., Shiomoto, A., Miyamura, T., Shiga, N., Imai, K., Toratani, M., Kajiwara, Y., Sasaoka, K., 2002. Bering Sea cyclonic and anticyclonic eddies observed during summer 2000 and 2001. Progress in Oceanography 55 (1–2), 65–75.

Moore, S.E., Watkins, W.A., Daher, M.A., Davies, J.R., Dahlheim, M.E., 2002. Blue whale habitat associations in the Northwest Pacific: analysis of remotely-sensed data using a Geographic Information System. Oceanography 15 (3), 20–25.

Mori, J., Kubodera, T., Baba, N., 2001. Squid in the diet of northern fur seals, *Callorhinus ursinus*, caught in the western and central North Pacific Ocean. Fisheries Research 52, 91–97.

Olson, D.B., Hitchcock, G.L., Mariano, A.J., Ashjian, C.J., Peng, G., Nero, R.W., Podestá, G.P., 1994. Life on the edge: marine life and fronts. Oceanography 7 (2), 52–60.

Overland, J.E., Spillane, M.C., Hurlburt, H.E., Wallcraft, A.J., 1994. A numerical study of the circulation of the Bering Sea basin and exchange with the North Pacific Ocean. Journal of Physical Oceanography 24 (4), 736–758.

Pearcy, W.G., 1991. Biology of the transition region. In: Wetherall, J. (Ed.), Biology, Oceanography and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone. NOAA Technical Report NMFS 105, pp. 39–55.

Perez, M.A., Bigg, M.A., 1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fishery Bulletin of US 84, 957–971.

Polovina, J.J., Kobayashi, D.R., Parker, D.M., Seki, M.P., Balazs, G.H., 2000. Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. Fisheries Oceanography 9 (1), 71–82.

Polovina, J.J., Howell, E., Kobayashi, D.R., Seki, M.P., 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. Progress in Oceanography 49 (1–4), 469–483.

Ragen, T.J., Antonelis, G.A., Kiyota, M., 1995. Early migration of northern fur seal pups from St. Paul Island, Alaska. Journal of Mammalogy 76 (4), 1137–1148.

Robson, B.W., Goebel, M.E., Baker, J.D., Ream, R.R., Loughlin, T.R., Francis, R.C., Antonelis, G.A., Costa, D.P., 2004. Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). Canadian Journal of Zoology-Revue Canadienne De Zoologie 82 (1), 20–29.

Roden, G.I., 1991. Subarctic-subtropical transition zone of the North Pacific: large-scale aspects and mesoscale structure. In: Wetherall, J. (Ed.), Biology, Oceanography and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone. NOAA Technical Report NMFS 105, pp. 1–38.

Schumacher, J.D., Reed, R.K., 1992. Characteristics of currents over the continental slope of the eastern Bering Sea. Journal of Geophysical Research-Oceans 97 (C6), 9423–9433.

Seki, M.P., Polovina, J.J., Brainard, R.E., Bidigare, R.R., Leonard, C.L., Foley, D.G., 2001. Biological enhancement at cyclonic eddies tracked with GOES thermal imagery in Hawaiian waters. Geophysical Research Letters 28 (8), 1583–1586.

Stabeno, P.J., Schumacher, J.D., Ohtani, K., 1999. The physical oceanography of the Bering Sea. In: Loughlin, T.R., Ohtani, K. (Eds.), Dynamics of the Bering Sea: a summary of physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea. University of Alaska Sea Grant, Fairbanks, Alaska, AK-SG-99-03, pp. 1–28.

Walker, W.A., Jones, L.L., 1993. Food habits of northern right whale dolphin, Pacific white-sided dolphin, and northern fur seal caught in the high seas driftnet fisheries of the North Pacific Ocean, 1990. International North Pacific Fisheries Commission Bulletin 53 (II), 285–295.