

FORAGING ECOLOGY OF NORTHERN ELEPHANT SEALS

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Abstract. Sexual segregation in foraging is predicted from the great size disparity of male and female northern elephant seals, *Mirounga angustirostris*. Our aim was to test this prediction by measuring diving and foraging behavior, foraging locations, and distribution of the sexes during biannual migrations in the northeastern Pacific Ocean. Daily movements of 27 adult males and 20 adult females, during 56 migrations from Año Nuevo, California, USA, were determined by Argos satellite telemetry via head-mounted platform transmitter terminals. Diving records were obtained with archival time–depth–speed recorders attached to the backs of seals that were recovered when the seals returned to the rookery. Pronounced sex differences were found in foraging location and foraging pattern, as reflected by horizontal transit speed and diving behavior. Males moved directly north or northwest at a mean speed of 90 ± 27 km/d to focal foraging areas along the continental margin ranging from coastal Oregon (534 km away) to the western Aleutian Islands (4775 km away). Males remained in these areas (mean size = 7892 km²) for 21–84% of their 4-mo stays at sea. The predominance of flat-bottom dives in these areas suggests concentrated feeding on benthic prey. Migration distance and estimated mass gain were positively correlated with male size, and individual males returned to the same area to forage on subsequent migrations. In contrast, females ranged across a wider area of the northeastern Pacific, from 38° to 60° N and from the coast to 172.5° E. Focal foraging areas, indicated by a reduction in swim speed to <0.4 m/s, were distributed over deep water along the migratory path, with females remaining on them a mean of 3.5 d before moving to another one. Jagged-bottom dives that tracked the deep scattering layer prevailed in these areas, suggesting that females were feeding on pelagic prey in the water column. Females took roughly similar initial paths in subsequent migrations, but large deviations from the previous route were observed. We conclude that there is habitat segregation between the sexes. Females range widely over deep water, apparently foraging on patchily distributed, vertically migrating, pelagic prey, whereas males forage along the continental margin at the distal end of their migration in a manner consistent with feeding on benthic prey.

Key words: diving; foraging; habitat separation; migration; *Mirounga angustirostris*; northern elephant seals; resource partitioning; sex differences; sexual segregation.

INTRODUCTION

Sexual dimorphism in many mammals is associated with sexual segregation (e.g., Kenyon 1969, Bowers and Smith 1979, Gautier-Hion 1980, Clutton-Brock et al. 1987, Morris 1987, McCullough et al. 1989, Litvaitis 1990, Bleich et al. 1997). In the highly polygynous pinnipeds, where sexual size dimorphism evolved as a result of intrasexual competition among males (Stirling 1975, 1983, Alexander et al. 1979, Le Boeuf 1986), the larger size of males relative to females requires differential use of resources that can result in sexual segregation in foraging. Selection for great size in sexual competition affects performance in acquiring food (Le Boeuf et al. 1993) as males must acquire more resources to attain great size as well as to maintain it. For example, in pinnipeds that supplement their diets with warm-blooded prey such as birds or other seals, it is the males that exhibit this behavior (Riedman 1990).

The northern elephant seal, *Mirounga angustirostris*, is one of the most sexually dimorphic mammals, with adult males being 1.5–10 times larger than adult females (Deutsch et al. 1994). Based on this size difference, males are expected to consume about three times as much prey energy as females (Le Boeuf et al. 1993, Boyd et al. 1994). This may be achieved by more efficient prey capture, consumption of larger prey, or pursuit of different prey with a higher energy density than that taken by females. We expect that sex differences of this order will be obvious from a detailed study of behavior at sea, where all foraging occurs. That is, we expect that individual foraging success, strategy, and location will be reflected by mass gain, diving pattern, and movements during the period at sea (Le Boeuf et al. 1988, 1989, 1993).

Elephant seals alternate breeding on islands and peninsulas from central Baja California, Mexico to Oregon, USA with two extended foraging trips, or migrations, per year (Le Boeuf and Laws 1994). After weaning their pups in late winter, females forage at sea for about 70 d before returning to land to molt the pelage. Following one month ashore, the females return

to sea for eight months, a period coincident with gestation, before returning to the rookery to give birth. Males spend approximately four months at sea following the breeding season, returning to shore in summer to molt the pelage. After one month onshore, they return to sea for four months before returning to the rookery for the breeding season. Thus, although the energy requirements of adult males exceed those of adult females, they spend less time at sea foraging than females, eight months and ten months, respectively. Temporal segregation of the sexes during foraging at sea is minimal (Le Boeuf 1994).

The general movements of northern elephant seals during their biannual migrations are known from studies that estimate position from using light levels (day length) and sea surface temperature recorded on the animals with archival geographic location–time–depth recorders (GLTDRs; DeLong et al. 1992, Le Boeuf et al. 1993). The geolocation method may predict location to within $\pm 1^\circ$ of latitude or longitude (DeLong et al. 1992). Given this magnitude of error, it is not clear whether this technique can be used to couple location and apparent foraging area of seals with mesoscale data on bathymetry, oceanographic features, or fisheries data. It is not clear, for example, whether males are foraging near the continental shelf break (Le Boeuf et al. 1993) or far from the continental shelf over deep water (DeLong et al. 1992, Stewart and DeLong 1993). More accurate estimates of location are required to understand the animal's foraging ecology and the basis for the migratory routes. Satellite based telemetry can clarify important points such as these, by providing details at mesoscale resolution of meters to kilometers (Fancy et al. 1988). This has been demonstrated for the movements of gray seals, *Halichoerus grypus*; southern elephant seals, *Mirounga leonina*; walrus, *Odobenus rosmarus*; and narwhals, *Monodon monoceros* (McConnell et al. 1992b, Dietz and Heide-Jørgensen 1995, McConnell and Fedak 1996, Born and Knutsen 1997).

The general aim of the present study was to extend, amplify, and improve the measurement of transit and foraging behavior, foraging location, and distribution of the sexes of elephant seals during long feeding trips at sea. We aimed to better understand sexual segregation and the differences in foraging location previously observed in this species. Specifically, our aim was to: (1) determine the biannual migration paths, ultimate destinations, focal foraging areas, transit rate, and distance traveled of adult male and adult female northern elephant seals; (2) describe sex differences in foraging location, habitat utilization, and foraging behavior; (3) compare the migratory paths of individuals within the same year and in successive years; and (4) compare animal movements and ultimate destinations obtained from satellite telemetry with those obtained by the geolocation method in this study and in earlier studies.

METHODS

Subjects and field methods

The daily movements of 47 known-age northern elephant seals, individually tagged and dye-marked (Le Boeuf et al. 1988), were determined during 56 foraging trips that originated from Año Nuevo, California, USA, in 1995 (25 trips), 1996 (19 trips), and 1997 (12 trips). Twenty-seven adult males, 8–12 years of age, and 20 adult females, 6–8 years of age, were tracked at sea during the foraging trips following breeding (spring trip) or molting (fall trip). There were 29 deployments in the spring (16 males and 13 females) and 27 deployments in the fall (17 males and 10 females). Six males were tracked twice, five during foraging trips in the fall and subsequent spring, and one during the fall in successive years. Three females were tracked twice, two were tracked during both foraging trips in the same year, i.e., when not pregnant and when pregnant; the other was tracked in the spring in successive years.

Diving records were obtained from nine males (three in the spring and six in the fall) and 13 females (seven in the spring and six in the fall) using time–depth–swim speed recorders. Nine of the diving recorders were Mk3e GLTDRs (Wildlife Computers, Redmond, Washington, USA; Le Boeuf et al. 1996), 11 were Datagrabbers (S. B. Blackwell, Santa Cruz, California, USA; Fletcher et al. 1996), and two were Compact Acoustic Probes (CAPs; Burgess et al. 1998).

The seals were immobilized with a teletamine HCL/zolazepam HCL mixture (1 mg/kg for females; 0.4 mg/kg for males) administered intramuscularly. Subsequent intravenous injections of ketamine hydrochloride were administered when necessary to maintain immobilization (Briggs et al. 1975). Blubber thickness was determined with an ultrasound scanner (Scanprobe, Ithaca, New York, USA) and standard length and axillary girth were measured with a flexible tape (Gales and Burton 1987, Worthy et al. 1992, Webb et al. 1998). Lengths and girths were measured at six locations along the long axis of the seals to obtain morphometrics to determine body composition (Worthy et al. 1992). Half-watt satellite platform transmitter terminals or PTTs (Telonics, Mesa, Arizona, USA), Telonics ST-6, measuring $6.5 \times 13.7 \times 4.5$ cm and weighing 498 g were fastened with two cable ties and a stainless steel hose clamp to nylon seine net (0.48-cm mesh) attached to the top of the head (Fedak et al. 1983) with epoxy (Evercoat Ten-set, Fibre-Evercoat, Cincinnati, Ohio, USA). The antenna was angled forward 45° so that it was out of the water when the seal surfaced. Dive recorders were attached similarly to the pelage on the dorsal midline above the shoulders (Le Boeuf et al. 1988). After the epoxy mounts cured, the females were rolled into a nylon tarpaulin and weighed with a digital scale (capacity 1000 kg, accuracy ± 1 kg, Dyna-Link MSI-7200, Measurement Systems International, Se-

attle, Washington, USA) mounted to a tripod (Costa et al. 1986).

Males were not weighed. Mass was estimated for all males, however, at the time of instrument deployment and again for eight males when they returned from sea. A complete set of morphometric measurements was used and volumes were calculated according to the truncated cone method for determining body composition (Gales and Burton 1987), assuming a density of 0.94 g/mL for blubber and 1.1 g/mL for lean mass (Nordoy and Blix 1985, Haley et al. 1991, Worthy et al. 1992). This method, validated against platform scale mass measurements in 21 adult males, yields a mean error of <2% (D. Crocker, unpublished data).

When the seals returned to the rookery, the instruments were removed, leaving the epoxy mounts to fall off during the annual molt. All females were weighed again and standard measurements were taken.

Satellite tracking system

The Argos satellite system (Service Argos, Toulouse, France and Landover, Maryland, USA) was employed to determine location at sea. Transmitted signals were received by two National Oceanic and Atmospheric Administration (NOAA) near-polar orbiting satellites from Telonics ST-6 PTTs attached to the heads of migrating seals. Each PTT had a unique code number and transmitted a signal that was received by a satellite (uplinks) when it was above the horizon. PTT location was determined from the Doppler shift in frequency that occurred with satellite movement (Fancy et al. 1988, Priede and French 1991, French 1994) and was relayed to ground stations. Fourteen satellite orbits per day yielded global coverage. Locations were available by computer network ≤ 3 h of the last satellite overpass.

The PTTs were programmed to repeat the transmission signal every 34 s while the seal was at the surface. To achieve this transmission rate, Argos required that the PTT not transmit continuously for >2 h. This was insured by on board software that prevented transmission after a salt switch indicated that the unit was dry for >2 h, i.e., that the seal was out of the water. Elephant seals dive continuously while at sea, spending on average 2–3 min at the surface between dives lasting a mean of 20–22 min (Le Boeuf 1994).

Argos provides a Location Quality (LQ) for each location fix that depends primarily on the number of uplinks received. The accuracy of location fixes was obtained by comparing positions provided by the satellite system to the known location of all instrumented seals at Año Nuevo during the 1–2 d before they went to sea after instrument attachment (Table 1). The true location of the seals was assumed to be the epicenter of Año Nuevo Point at (37.110° N, 122.330° W), determined by Global Positioning System (GPS), accurate to 15 m, even though the seals may have been up to 500 m south, west, or north of this precise location.

TABLE 1. The accuracy of position fixes for different location qualities obtained by Argos satellite telemetry from all seals during 1–2 d at Año Nuevo Point, compared with the accuracy predicted by Argos (1997).

Argos Location Quality (LQ)	Argos accuracy predictions (km)	Transmitter fixes			
		Number	Mean accuracy (km)	SD (km)	Range (km)
3	<0.150	338	0.8	0.1	0.3–1.8
2	0.150–0.350	302	1.4	0.6	0.6–3.4
1	0.350–1.000	403	2.7	2.1	0.5–14.9
0	>1.000	323	9.3	15.5	0.6–78.4
A	...	164	28.3	50.7	0.5–123.1
B	...	78	48.4	70.4	0.7–237.6

Note: Argos does not estimate accuracy for a Location Quality of A or B.

We also used this method to compare the accuracy of each PTT.

Tracking with the geolocation method

We compared Argos satellite-determined tracks with independently obtained geolocation tracks of five seals that were carrying both types of instruments. The geolocation tracks were computed by one of us with no knowledge of the satellite tracks. The geolocation analysis software package from Wildlife Computers was used to estimate times of dawn and dusk on a daily basis, from which day length and the time of solar noon were calculated, yielding an estimate of latitude and longitude, respectively (De Long et al. 1992, Hill 1994). Longitudes used for the final tracks were always within the confidence range calculated by the software; in most cases they were the midpoint of the range. Ambiguities in latitude, particularly during the spring and fall equinoxes (Hill 1994), were resolved by matching daily mean sea surface temperature (SST) recorded by the TDR when close to the surface with weekly SST maps compiled from AVHRR data and available on the internet (NOAA/National Aeronautics and Space Administration Ocean Pathfinder SST data).¹ Daily adjustments to the latitude position using temperature were done in chronological order, since the animal's position on any one day is a function of its position the previous day (see Le Boeuf et al. 1996).

After adjusting times for local noon, we calculated the great circle distance between satellite and geolocation positions for each day, using spherical trigonometry (Congleton 1980). We also expressed this distance as a displacement vector (x , y) in a plane, which takes into account the direction (i.e., north, south) of the bias. When compared to the mean great circle distance (MGCD), the average displacement vector (ADV) can be used as a measure of directional bias in each record. For example, if $ADV/MGCD = 1$, daily geolocation positions always have the same directional

¹ URL = <http://podaac-www.jpl.nasa.gov/sst/>

TABLE 2. Mean number of locations per day, grouped by Argos location quality index for females and males.

Argos location quality index	Females		Males	
	Mean number of prefiltered locations per day	Mean number of postfiltered locations per day	Mean number of prefiltered locations per day	Mean number of postfiltered locations per day
3	0.01 (0.5)	0.01 (0.5)	0.01 (0.4)	0.01 (0.4)
2	0.03 (1.2)	0.03 (1.3)	0.01 (0.4)	0.01 (0.4)
1	0.09 (4.4)	0.09 (4.6)	0.03 (2.1)	0.03 (2.3)
0	0.46 (21.9)	0.46 (23.1)	0.31 (21.0)	0.31 (22.7)
A	0.49 (23.4)	0.47 (23.4)	0.28 (19.2)	0.26 (19.3)
B	1.02 (48.8)	0.94 (47.1)	0.81 (55.5)	0.74 (54.9)
All	2.10 (100.0)	2.00 (100.0)	1.45 (100.0)	1.36 (100.0)

Note: Numbers in parentheses show the percentage of the total.

bias relative to the satellite position. If AVD/MGCD = 0, the geolocation positions are scattered in all directions around the satellite position and there is no directional bias. The direction of the bias was expressed in degrees, where 0° = North, 90° = East, 180° = South, and 270° = West.

Data processing and definitions

Time series data for latitude and longitude coordinates were obtained daily from the Argos service while the seals were at sea. Locations obtained were filtered based on a maximum transit speed of 3.5 m/s (Table 1), the same criterion used by McConnell et al. (1992a).

Migratory travel time was defined as the time elapsed from a seal's departure to its return to land, as determined by Argos location coordinates, and presence at Año Nuevo indicated by visual scanning or a TDR record. Transit speed or horizontal swim speed for a given track segment was defined as the sum of distances traveled between points per unit time. This measure of travel speed is not to be confused with swimming speed through the water (Le Boeuf et al. 1992).

A daily transit speed was calculated using the highest quality location from each day, based on the great-circle distance between the daily locations and the time elapsed. When there was more than one location of equal quality, the location with the greatest time separation from the previous daily location was used. Daily transit speed was averaged over two-day intervals and plotted as a function of time at sea. Straight-line distance and straight-line speed refer to great-circle measurements made using only the first and last points in a given track portion. "Home" refers to Año Nuevo State Reserve, California (37.1° N, 122.3° W). The "farthest" point within a track is the location that represents the maximum displacement from home (great-circle distance) within that track. Spring migration refers to the first migration in the year, the period following breeding in winter. Fall migration refers to the second migration in the year, the period following a one-month residence on the rookery to molt (Worthy et al. 1992). We defined locations where a seal's calculated daily transit speed (the mean transit speed is

1.0 m/s or 3.6 km/h) dropped from 0.5–2.4 m/s to <0.4 m/s (1.44 km/h) over a two-day period or more as a focal foraging area (FFA). This is the transit speed that could result from the average error in a location (35.5 km), calculated from Table 1 and Table 2, divided by 24 h. Estimates of the size of foraging areas for males were calculated using the minimum convex polygon method and a 95% contour (Harris et al. 1990). This method yielded a better fit to the data than alternative methods.

We separated the final destinations and FFAs of males into five geographical categories along the coasts of the continental margin: Oregon, Washington, Canada, Alaska (54.5° N to 155° W), and the Aleutian Islands (west of 155° W; Figs. 1 and 2).

Diving behavior

Mean depth, duration, surface interval, and the percentage of time spent diving were calculated for each diving record. Dives were classified by three individuals according to their shapes (Le Boeuf et al. 1992, 1993). V-shaped dives with no distinct bottom time were classified as Type A dives and were assumed to represent transit or traveling dives. Dives with a distinct bottom time characterized by multiple vertical excursions were classified as Type D dives, or putative pelagic foraging dives. Dives with flat bottoms were classified as Type E dives, which may represent either bathymetrically constrained dives of seals traveling along the continental shelf or benthic foraging. Type C dives were distinguished by the second segment of the dive between descent and ascent, during which the seal stops swimming and drifts down or up, depending on its body composition. Oxygen saved from reduced locomotion during this dive may be used to process food (Crocker et al. 1997). The proportions of these dive types exhibited were calculated for the outward legs, foraging areas, and return legs of males (except C type dives) and for transit and FFAs of females.

In distributions of dive depth by time of day, we adjusted time of day to the local time zone based on the longitudinal position of the animal determined by satellite telemetry.

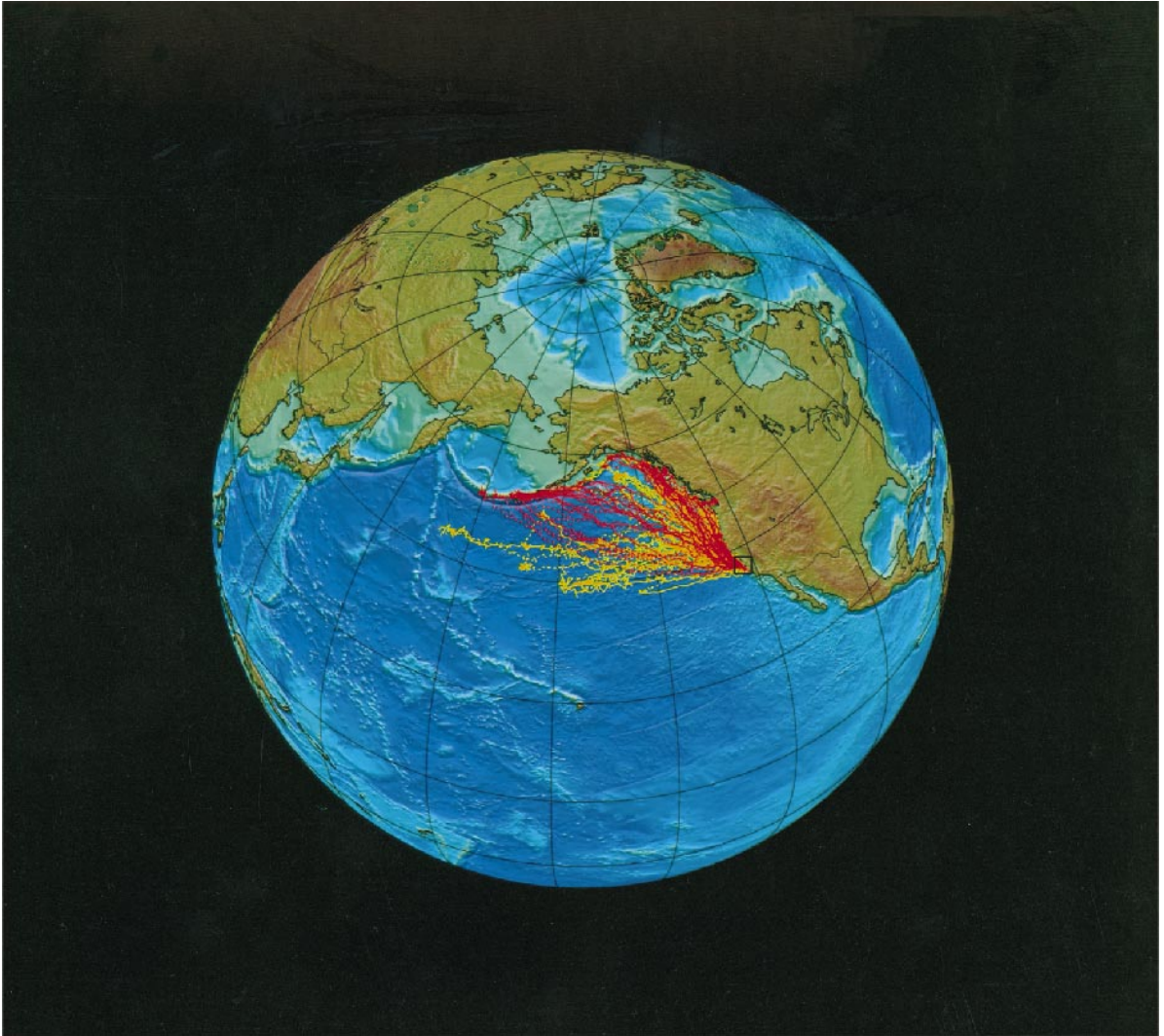


FIG. 1. Satellite tracks of 22 adult males (red) and 17 adult females (yellow) during spring and fall migrations from Año Nuevo, California (black square), during the years 1995, 1996, and 1997. Only those tracks that comprised 80–100% of the total time at sea are shown. Second trips of individuals in the same year or subsequent year are not shown.

RESULTS

Satellite performance

Accuracy of location fixes, when the seals were on or near the beach at Año Nuevo Point before departure, increased as a function of Argos LQ but were less accurate than predicted by Argos (Table 1). At best, the seals were fixed at a mean of 0.8 ± 0.2 km of the site (mean ± 1 SD; all values reported in this fashion throughout the paper are means ± 1 SD, unless otherwise noted). Low LQ values may have been due in part to the seals being temporarily in the water away from Año Nuevo at the time of the uplink. Moreover, since the precise location of the seals was not known, they may have been as much as 0.5 km from the assumed coordinates, accounting for part of the calculated error.

A total of 6787 location fixes were obtained after the seals left Año Nuevo and were at sea. The percentage distribution according to LQ was: LQ 3 = 0.5%, LQ 2 = 0.9%, LQ 1 = 3.6%, LQ 0 = 22.9%, LQ A = 21.7%, and LQ B = 50.3%. After filtering, there were 1.36 ± 0.36 locations per day for adult males and 2.00 ± 0.82 locations per day for adult females (Table 2). The mean was higher for females during the fall migration than the spring migration (2.1 ± 0.69 vs. 1.88 ± 0.90 locations per day, respectively).

In 39 deployments the seals were tracked the entire period at sea. This included 13 males and six females tracked in the fall and 11 males and nine females tracked in spring. Males were tracked 100% of the days at sea in spring and $89.9\% \pm 30\%$ of the days at sea in the fall. Females were tracked $91.2\% \pm 21\%$ of the days at sea in the spring and $76.8\% \pm 30.3\%$ of the

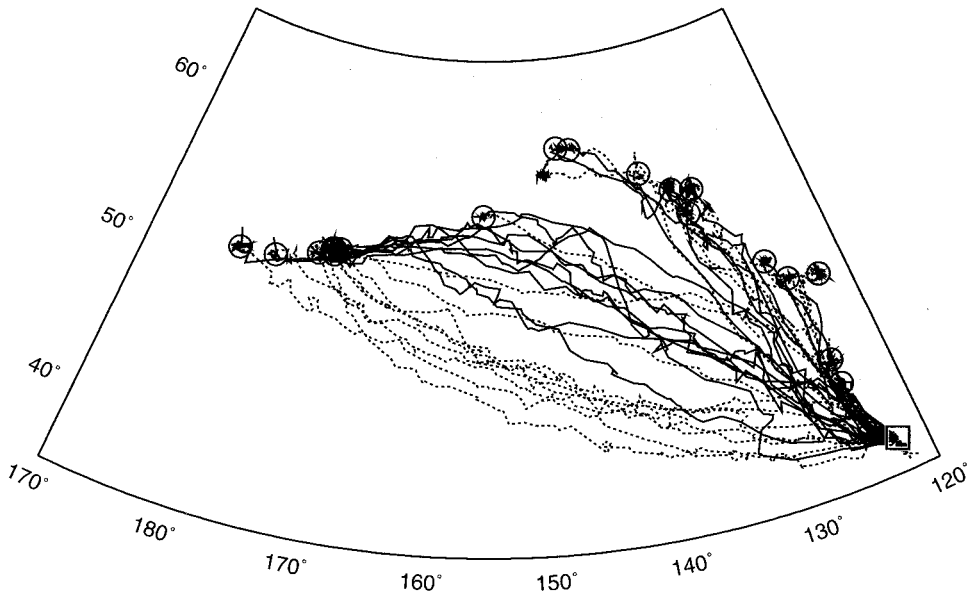


FIG. 2. Satellite tracks of 22 adult males showing the outgoing leg (solid line) and returning leg (dotted line) to the Año Nuevo rookery (open square). The final destinations or focal foraging areas (FFAs) are shown as open circles.

days at sea in the fall. Six satellite tags failed within one wk of deployment; six other tags functioned for 20–82 days before failing. Five tags failed due to dead batteries; one tag functioned intermittently from the start.

Mortality at sea

The satellite tags of eight seals, five males and three females, stopped transmitting while at sea and the seals did not return to the rookery. The nature and location of the last emissions raises the possibility that transmission stopped because the animals died en route. The last signals from three males (Reg, Ori, and Jer) were from the same place, the west coast of Baranov Island in southern Alaska, within a narrow time interval, 3–9 October 1995. All of them were headed north along the coast at the time of the last satellite uplink. The last signal from the two other males was in April 1997, west of north Vancouver Island, Canada (Hal), and near the coast in the northern Gulf of Alaska (Popi). Both males were still moving north. A female (Kia) was returning to the rookery when repeated satellite uplinks of high quality in the area between Queen Charlotte and Vancouver Islands suggested the PTT was on the deck of a ship for several days. In fall, the last signals from two females (Kar2, Her) were in the general area west of Vancouver Island on 17 August and 12 September 1995.

Movements and location at sea

The tracks of 23 males and 17 females, for which 80–100% of the foraging trip was tracked, are shown in Fig. 1. The routes and ultimate destinations of most

males and females were different. Therefore, we treat each sex separately.

Males.—

1. *General.*—From the Año Nuevo rookery in central California, all males moved directly north or northwest to destinations along the continental margin, diving continuously en route (Fig. 2). The ultimate destination of males ranged widely, from the coast of Oregon in the south to the western Aleutian Islands to the northwest. Males moved north, terminating their migrations at various points along the coast such as Oregon (2 seals), Washington (1 seal), Canada (4 seals), and Alaska (20 seals), a range extending from 42° to 58° N (Fig. 2 and Table 3). Nine males moved rather directly across the northeastern Pacific to the eastern Aleutian Islands in Alaska, then continued westward along the Aleutian chain to ultimate locations beyond 170° W, a mean distance of 4259 ± 251 km. Once males reached their destinations, they stopped traveling, and remained in the same general location for 1–3 mo before beginning the return trip to Año Nuevo.

2. *Transit.*—Males did not linger in the open ocean on the outward or return legs of their migrations, but moved steadily and rather directly to a FFA where they remained before starting the return trip to the rookery. The nine males that migrated to the western Aleutians took a more westerly return route than they did on the outgoing tracks (Fig. 2).

Transit duration to the FFA increased with distance between the rookery and the FFA (Fig. 3a and Table 3). Males reached Oregon and Washington in as little as 9 and 12 d, respectively, while other males took 38–50 d to reach the Aleutians. Consequently, the pro-

portion of the entire trip spent in transit was much higher for males with destinations in the Aleutians ($69.7\% \pm 5.88\%$) than males with destinations in Oregon, Washington, or Canada ($35.06\% \pm 11.6\%$). Males traveling to eastern Alaska were intermediate, spending a little more than 50% of the trip in transit ($54.1\% \pm 9.7\%$). Mean time spent returning to the rookery was marginally longer than the outgoing leg, 32.6 ± 11.3 d vs. 31.5 ± 11.4 d (Table 3).

Transit speed increased with the distance traveled on both the outgoing and returning legs (Fig. 4). Mean transit rates (Table 3) on the outgoing (89.8 ± 18.6 km/d) and return (85.6 ± 20.2 km/d) legs were not significantly different ($t = 1.39$, $df = 19$, $P > 0.05$).

3. *Focal foraging areas.*—FFAs are easily discerned from the tracks (Fig. 2), being locations where males stopped traveling and lingered for long periods at or near the final destination site furthest removed from the rookery. Males remained on FFAs for long periods, continuing to dive and apparently foraging intensively. These “by inspection” FFAs are identical to the quantitative definition of FFAs as a reduction in transit speed to <0.4 m/s over a two-day period. Fig. 5 shows the marked decrease in transit speed of males once males reached FFAs, the long uninterrupted time spent there, and the absence of rest periods to and from the FFAs.

All males exhibited a single FFA where they remained for 50.3 ± 19.1 d or a range of 26–89 days (Figs. 2, 5, 6, and Table 3). All FFAs were located near the continental shelf break. The FFAs of three males were clearly on the continental shelf, as indicated by satellite locations and depth of dives. The FFA of Pro was in Puget Sound, Washington, and consequently, he had a far lower mean diving depth than other males (84 ± 45 m vs. 341 ± 38 m for the rest of the males). The FFA of Ric was in the inland passage in southern Alaska and Pop never left the continental shelf in his short foraging trip to southern Oregon but no diving data were obtained for these two males because their diving instruments malfunctioned.

Shape, size, and location of FFAs are illustrated in Fig. 6. Mean size of FFAs was 7892 ± 4369 km² (Table 3). There was no relationship between FFA size and distance from Año Nuevo. The FFAs of seven of the nine males that migrated to the Aleutians were clustered around Amukta Pass; FFAs of the two other males were further west, one between Kanaga and Adak Islands and the other between Kiska and Amchitka Islands.

Time spent on the FFA decreased with its distance from Año Nuevo (Fig. 3b; $r = -0.63$, $df = 20$, $P < 0.05$). Indeed, males foraging off the coasts of Oregon, Washington, and Canada spent 83% more time in FFAs (68.3 ± 19.8 d) than males with FFAs in the Aleutians (37.4 ± 7.3 d).

4. *Mass and distance traveled and mass gain over the period at sea.*—Distance traveled to FFAs varied significantly with the mass of males at departure ($r =$

0.87 , $df = 19$, $P < 0.05$); the largest males undertook the longest migrations (Fig. 7a). For the eight males weighed before and after the migrations, mass gain per day on FFAs was also positively correlated ($r = 0.95$, $df = 6$, $P < 0.05$) with distance to FFAs (Table 3 and Fig. 7b), despite these males having to swim faster, taking more time to reach their destinations, and spending less time there (Figs. 3 and 4). If all mass was gained on FFAs and none in transit, the two males foraging in Canada gained a mean of 3.4 kg/d, the four males foraging in Alaska gained 6.6 kg/d, and the two males foraging in the Aleutians gained 12.8 kg/d. These differences in mass gain, however, are less discrepant when normalized to body mass. The mean percentage increase in mass at sea over departure weight (Table 3) was 22.1%, 27.5%, and 34.2% for these groups of males, respectively.

5. *Similarity of tracks and FFAs across seasons and years.*—Males, whose tracks were recorded twice, in the fall of one year and again in the spring of the following year, showed remarkably similar movement patterns and FFAs during both foraging trips (Fig. 8). Four of five males whose tracks led to the Aleutian Islands occupied virtually the same FFA in the fall and in the spring (Fig. 8a–d). A fifth male returned to his fall FFA in spring but continued to three degrees west of the original site (Fig. 8e). The male that remained on the continental shelf throughout transit and foraged off the coast of Oregon showed a similar pattern and direction the second year but extended his FFA to the coastal area off Cape Flattery, Washington (Fig. 8f).

Not only did some males return to specific sites, they also took nearly identical routes on both foraging trips (Fig. 8a–c). For example, the outgoing and returning routes for the male in Fig. 8a overlap along much of the route. Moreover, three males made landfalls on the outgoing trip in similar places in both years before continuing west to their respective FFAs (Fig. 8b–d). On each foraging trip, all males with FFAs in the Aleutian Islands took a more westerly return route than on the outgoing leg.

The similar location of FFAs in the Aleutian Islands from one year to the next is shown in more detail in Fig. 9. Note that FFAs were significantly smaller for all males during the second trip than during the first trip, a mean size difference of 4860 ± 1713 vs. $10\,559 \pm 3584$ km² ($t = 3.31$, $df = 5$, $P < 0.05$).

6. *Diving behavior.*—Diving behavior recorded for nine males revealed a mean dive depth of 312 ± 117 m and a mean maximum depth of 807 ± 228 m. No male had dives >1000 m. Mean dive duration was 22.3 ± 4.6 min and the mean maximum dive duration was 42.2 ± 8.1 min. Mean surface interval was 2.9 ± 2.7 min. Males dived at the rate of 2.79 ± 0.46 dives per hour and spent a mean of $11.7\% \pm 2.8\%$ of the time at sea at the surface. These statistics (mean dive depth, maximum dive depth, mean dive duration, mean surface interval, and percent time submerged) did not

TABLE 3. Movements and transit behavior of adult males migrating from Año Nuevo, California, during spring and fall in the years 1995, 1996, and 1997.

Male	Season year	Tracked length (days)	Mass		Mass gain				FFA location	Size of FFA (km ²)
			Depart (kg)	Return (kg)	(kg)	(kg/d)	(%)	(kg/d on FFA)		
Pop	F96	60							Oregon	2 190
Alt	F95	106	973						Oregon	8 501
Pro	F95	107	977						Washington	7 720
Hal†	S97	14	1 121						Canada	
Blu	S97	120							Canada	7 016
Dua	S97	109	996	1 173	177	1.62	17.8	2.60	Canada	2 670
Roc	S97	123	1 100	1 389	289	2.35	26.3	4.19	Canada	3 639
Ric	F97	109	1 068	1 345	277	2.54	25.9	6.02	Alaska	10 482
Ori†	F95	20	1 097						Alaska	
Jer†	F95	43	1 199						Alaska	
Rej†	F95	29	1 339						Alaska	
Popi†	S97	28							Alaska	
Cyo	S97	142	1 076						Alaska	13 938
Jed§	F95	97	1 156						Alaska	12 354
Pet	S97	120	1 145	1 558	413	3.44	36.1	8.08	Alaska	15 584
Bop	S97	99	1 081	1 273	192	1.94	17.8	5.48	Alaska	3 096
Ox‡	S97	107	1 105						Alaska	3 691
Moo	S97	114	1 274	1 654	380	3.33	29.8	6.91	Alaska	3 593
Lux	F96	116	1 345	1 801	456	3.93	33.9	14.71	Aleutians	7 770
Cap	F95	118	1 342						Aleutians	16 380
Max	F95	119	1 449						Aleutians	8 808
Pol	F95	120	1 489						Aleutians	12 342
Sam	F95	121	1 634						Aleutians	6 800
Joh	F95	125	1 208						Aleutians	4 289
Ari	F96	127	1 318						Aleutians	7 793
Jim	F95	132	1 311						Aleutians	11 563
Tra	S97	123	1 296	1 742	446	3.63	34.4	10.88	Aleutians	3 412
Mean		98.1	1 212	1 492	329	2.85	27.8	7.4		7 892
SD		38	170	230	111	0.85	7.2	3.9		4 369

Notes: The second tracks of six males that were deployed during two foraging trips are not included. FFA refers to focal foraging area.

† PTT quit, and seal did not return.

‡ PTT stopped working on return leg.

§ PTT turned on and off erratically.

change significantly as the seals moved from transit mode to foraging on their FFAs (*t* tests: paired two sample for means, *df* = 7, *P* < 0.05).

There were, however, pronounced differences in dive types exhibited in transit and in foraging areas (Table 4). Type A, or transit dives, predominated when males were traveling to their FFAs, making up 77% of the dives. This dive type was significantly more common during outgoing transit than in focal foraging areas (*t* test: paired two sample for means = 9.61, *df* = 4, *P* < 0.05). Relatively few Type D, pelagic foraging dives, and Type E, flat-bottom, benthic foraging dives, were observed during transit (18.7% of all dives). Indeed, most Type E dives in transit were recorded during departure from the rookery and return to it as the seals crossed the relatively shallow (<200 m) continental shelf. In contrast, the frequency of dive types was reversed on FFAs where flat-bottom, Type E dives made up >73% of the dives observed. Type E dives were statistically more common on foraging areas than in outgoing transit (*t* test: paired two sample for means = -12.8, *df* = 4, *P* < 0.05). The percentage of Type D dives was not significantly different in the two sit-

uations (*t* test: paired two sample for means = 1.54, *df* = 4, *P* > 0.05). We made no attempt to estimate the percentage of C type dives, because most male dives on FFAs appear to be bathymetrically constrained, making it difficult to distinguish these dives from flat-bottom dives. The sample size for return transit (three males) was too small to include in statistical tests, and was therefore omitted in Table 4. Nevertheless, the percentages of each dive type for these males on the return leg paralleled closely those on the outgoing leg.

Dive depth during transit (all dives) did not vary with time of day in three of six males (Fig. 10) and inspection reveals only a slight tendency for the dives of the other three males, Pol, Moo, and Bop, to be deeper at midday than at night. It is clear from inspection of Fig. 11 that dive depth did not vary with time of day once males were on the FFAs.

Females.—

1. *General.*—Movements of females were more variable and unpredictable than those of males. Females moved across a wider area of the northeastern Pacific than males, from 38° to 58° N and from near the coast

TABLE 3. Extended.

Año Nuevo to FFA (km)	Duration on FFA (days)	Time on FFA/trip duration (%)	Transit to FFA			Transit from FFA			Total transit time (%)
			Duration (days)	Speed (km/d)	Duration (%)	Duration (days)	Speed (km/d)	Duration (%)	
534	31	51.7	18	29.7	30	11	48.5	18.3	48.3
755	89	84	9	83.9	8.5	8	94.4	7.6	16
1 210	77	72	12	100.8	11.2	18	67.2	16.8	28
1 297	76	63.3	19	68.3	15.8	25	51.9	20.8	36.6
1 487	68	62.4	18	82.6	16.5	23	64.7	21.1	37.6
2 073	69	56.1	29	71.5	23.6	25	82.9	20.3	43.9
2 181	46	42.2	21	103.9	19.3	42	51.9	38.5	57.8
2 267	87	61.3	27	84.0	19	28	81.0	19.7	38.7
2 437	35		35	69.6					
2 964	51	42.5	31	95.6	25.8	38	78.0	31.7	57.5
2 497	35	35.4	32	78.0	32.3	30	83.2	30.3	64.6
3 025	51		34	89.0					
3 235	55	48.2	28	115.5	24.6	31	104.4	27.2	51.8
4 511	31	26.7	44	102.5	37.9	41	110.0	35.3	73.2
4 217	26	22	42	100.4	35.6	40	84.3	42.4	80
4 099	44	37	38	107.9	31.9	37	110.8	31.1	63
4 775	27	22.5	50	95.5	41.7	43	111.0	35.8	77.5
4 157	41	33.9	40	103.9	33.1	40	103.9	33.1	66.1
4 083	44	35.2	40	102.1	32	41	99.6	32.8	64.8
4 112	41	32.3	43	95.6	33.9	43	95.6	33.9	67.8
4 116	42	31.8	42	98.0	31.8	48	85.8	36.4	68.2
4 122	41	33.3	42	98.1	34.1	40	103.1	32.5	66.6
2 916	50.3	44.7	31.5	89.8	26.9	32.6	85.6	28.3	55.4
1 317	19.1	17.1	11.4	18.6	9.2	11.3	20.2	8.9	17.3

at 125° W to as far west as 172.5° E (Figs. 1 and 12). As a rule, females did not move directly to a site and remain there for long periods as males did and they did not favor the continental margin, but rather the open ocean over deep water. They appeared to forage at many sites en route.

2. *Transit and focal foraging areas.*—The direction taken from the rookery ranged from north to due west. The transit routes took a number of forms, of which these are examples: (1) Five females took the same

general return route as the outgoing route regardless of the outgoing direction (e.g., Fig. 13a). (2) Eight females took a looping path from the rookery, three with the return path to the rookery being east of the outgoing route and two the reverse, and two having a more northerly return to the rookery and one being the reverse. Spatially concentrated diving resembling male FFAs occurred in large areas at the distal end of the tracks of five females (e.g., Fig. 13b). (3) Three females showed large deviations along their routes (e.g., Fig.

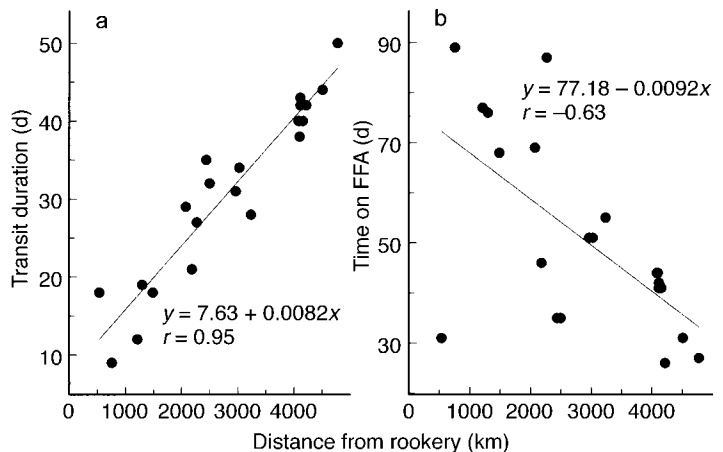


FIG. 3. (a) Transit duration to the focal foraging area (FFA) as a function of distance from the Año Nuevo rookery and (b) time on the FFA as a function of distance from the rookery.

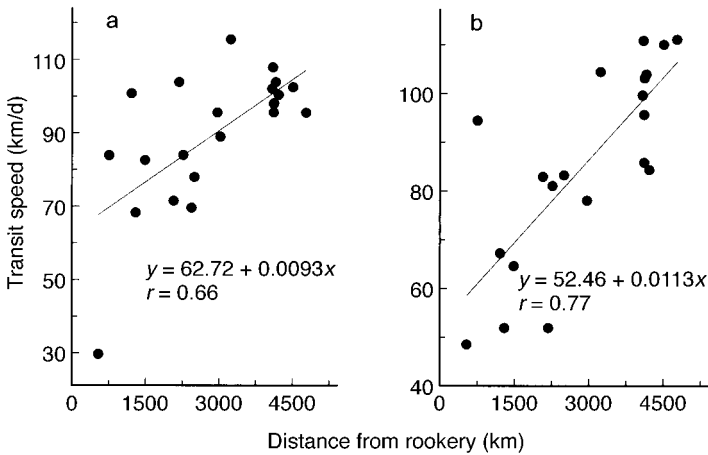


FIG. 4. Transit speed of males on the (a) outgoing and (b) returning legs as a function of distance between the focal foraging area (FFA) and the rookery.

13c). One moved due west after spending more than a month in a large area along the coast of Oregon. Another moved directly to a large area in the Gulf of Alaska where she remained for a month before moving to an area off the coast of Vancouver Island, only to return to the previous place before returning to the rookery. A third female meandered over large areas between the Queen Charlotte Islands off British Columbia and northern Washington.

For four spring and four fall females analyzed, transit speed was significantly faster during the first (64.6 ± 12.5 km/d) and last third (59.5 ± 12.2 km/d) of the foraging trip than the middle third (39.1 ± 16.7 km/d; $F = 14.6$, $df = 2, 10$, $P < 0.05$).

What appears to be FFAs in the tracks of some females (Figs. 12 and 13) are not strictly comparable to those of males. First of all, they were more than five times larger than those of males, having an area of $42,775 \pm 23,778$ km². By the definition of a FFA as "slow-or-no transit" of <0.4 m/s, females exhibited several FFAs within these large areas as well as outside of them (Fig. 14). That is, they moved long distances back and forth in these areas between periods of low transit rates.

Unlike the single FFAs of males (Figs. 2 and 5), each female had numerous FFAs of short duration spread out over much of the duration at sea and distributed over a wide geographical area (Figs. 14–16). Females spent $\sim 25\%$ of their time at sea on a FFA (Table 5), with no apparent difference between the spring and fall trips. Mean number of days on a FFA, before moving to another, was 3.6 ± 1.0 d in the spring and 3.1 ± 1.1 d in the fall.

Mass gain of females over the period at sea increased with the percentage of time at sea taken up by slow-or-no transit (Fig. 17a). Conversely, female mass gain over the period at sea decreased as the mean transit rate increased (Fig. 17b). Both trends are statistically significant (mass gain correlated with slow-or-no transit, $F = 5.56$, $df = 1, 14$, $P < 0.05$; mass gain inversely

correlated with mean transit rate, $F = 8.17$, $df = 1, 14$, $P < 0.05$). This inverse association between horizontal transit rate and mass gain suggests that successful foraging occurs during slow transit.

Mass at departure was positively correlated with mass gain at sea ($r = 0.86$, $df = 14$, $P < 0.05$) but not significantly correlated with the percentage increase in mass (spring trip, $r = -0.60$, $df = 7$, $P > 0.05$, fall trip, $r = 0.39$, $df = 5$, $P > 0.05$). Mass at departure and at-sea percentage mass gain over departure weight were not significantly correlated with distance traveled from the rookery ($r = -0.14$, $df = 21$, $P < 0.05$; spring trip, $r = -0.44$, $df = 7$, $P > 0.05$; fall trip, $r = 0.08$, $df = 5$, $P > 0.05$, respectively).

3. *Diving behavior in transit and on FFAs.*—As with males, there were no significant differences between summary statistics of diving behavior in normal transit speed vs. slow-or-no transit on a FFA. The frequency of dive types, however, changed as females decreased their transit speed (Table 4). At transit speeds >0.4 m/s, Type A transit dives were most frequent (48.3%) followed closely by Type D pelagic foraging dives (42.1%). Type C dives, which may reflect food processing and follow concentrated foraging (Crocker et al. 1997), made up 5% of the dive types. During slow transit speeds on FFAs, transit dives decreased significantly by 64.6% (t test: paired two sample for means = 11.0, $df = 9$, $P < 0.05$), pelagic foraging dives increased significantly by 71% (t test: paired two sample for means = -11.1, $df = 9$, $P < 0.05$), and putative food processing dives more than doubled in frequency to 10.6% (t test: paired two sample for means = -13.3, $df = 9$, $P < 0.05$). Type E dives were rare or nonexistent.

Dive depth varied with time of day both during transit and when females were on FFAs (Fig. 18). In both situations, dives were deeper during the day than at night.

4. *Location of FFAs.*—Generally, FFAs were distributed widely throughout most female tracks (Fig.

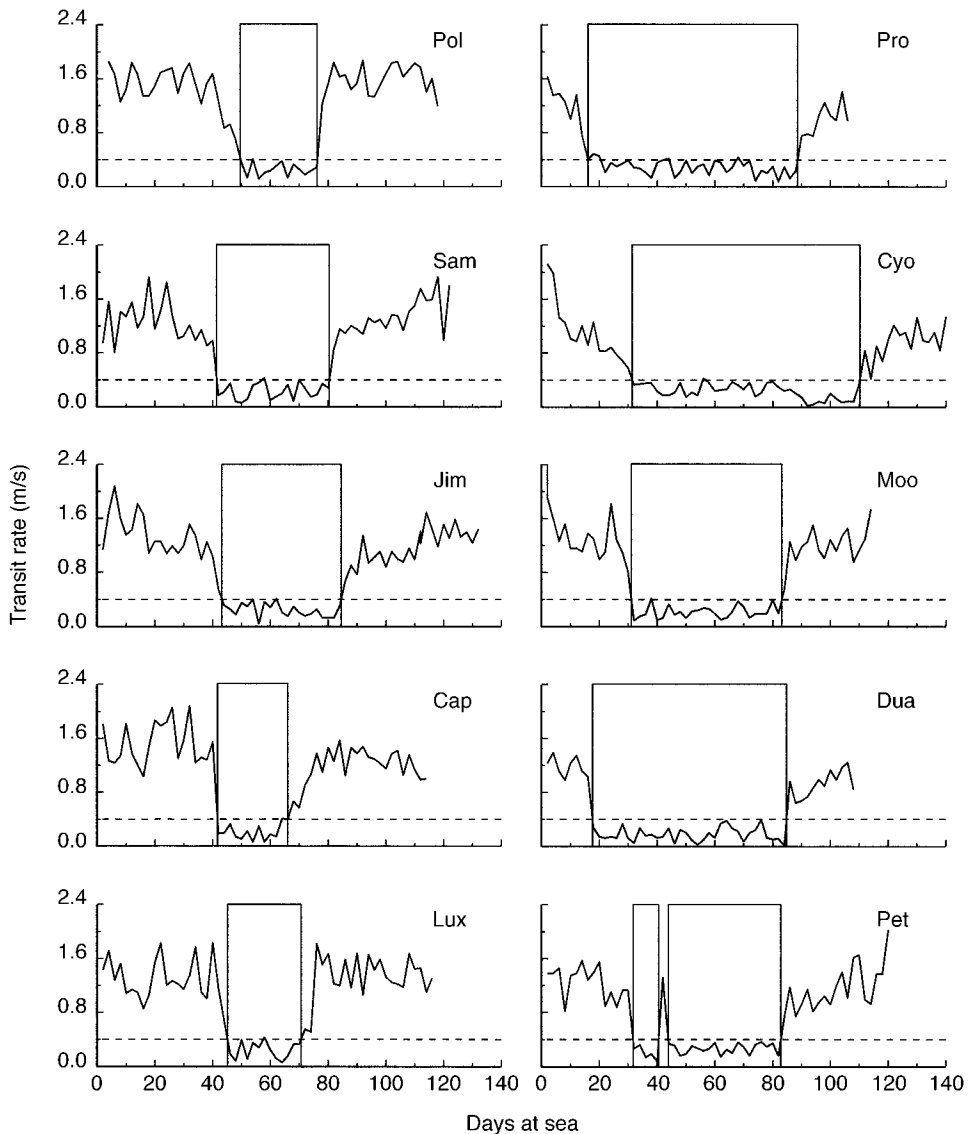


FIG. 5. Mean transit rates of 10 adult males averaged over two-day periods throughout the period at sea. Transit rates decreased to ≤ 0.4 m/s, shown as the shaded area below the dotted line, when the seals reached focal foraging areas (FFAs). FFAs for the five males on the left side of the figure were in the Aleutian Islands. FFAs for the other males were: Washington (Pro), Alaska (Cyo and Moo), and near Vancouver Island, Canada (Dua). Pet had two FFAs in the Gulf of Alaska.

14). In a few females, FFAs were concentrated in one or two general areas at the distal end of the trip. But even in these areas, females crisscrossed back and forth in transit from one FFA to the next. Moreover, no females restricted slow transit exclusively to these locations.

Four females spent considerable time near the continental margin, the location preferred by all males, one between Queen Charlotte and Vancouver Islands (Kia), one west of Baranov Island in Alaska (Ono), and two in the Gulf of Alaska (Mag and Deb). The pregnant female, Mag, increased her mass by 80.9%, a greater increase in mass than any other pregnant female and substantially greater than the mean increase for the

group, $56.7\% \pm 20.3\%$ (Table 5). The mass increase of two other females for which we measured mass gain (Ono and Deb) was similar to that of females that dived over the open ocean.

5. *Similarity of tracks and FFAs across seasons and years.*—Three females were tracked for two seasons, one in spring in 1995 and 1996, and two in spring and fall of 1995 (Table 5 and Fig. 19). The first female (Fig. 19a) took a similar route in both spring trips, with the outgoing leg lying west of the returning leg. The first trip was more distant than the second one. Only portions of the fall trip, which is usually about 2.5 times longer than the spring trip, were tracked for the other two females (62% and 19%, respectively). It is clear,

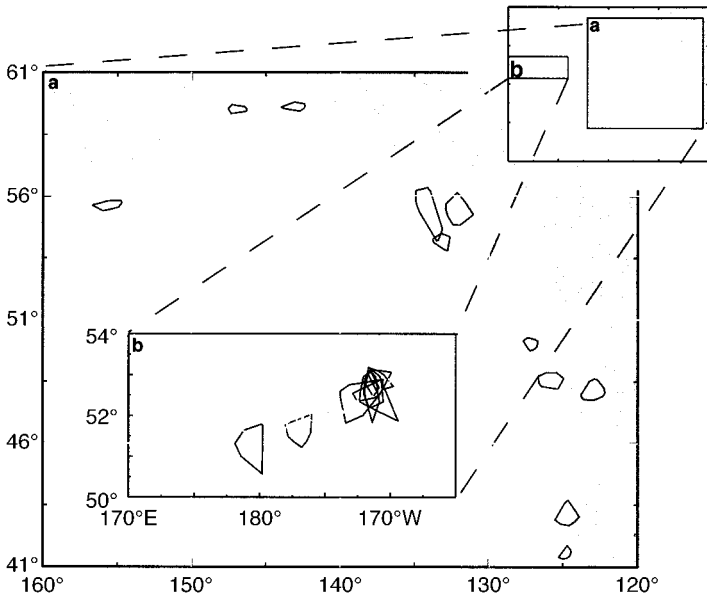


FIG. 6. Shape, size, and location of focal foraging areas (FFAs) of 23 male northern elephant seals, calculated as minimum convex polygons with a 95% contour. The inset depicts all FFAs in the Aleutian Island chain from 170° E to 165° W.

however, that both females moved in a similar direction on their fall trips as they did in spring, and both of them took a northward excursion from the previous path about half way through the outgoing leg (Fig. 19b, c).

Sex differences in diving behavior.—

1. *Summary dive statistics.*—The mean dive depth of females ($N = 13$) during the entire period at sea exceeded that of males ($N = 9$) by >144 m, 456 ± 52 m vs. 312 ± 117 m ($t = -4.6$, $df = 20$, $P < 0.05$). Similarly, the maximum depths of females exceeded those of males ($t = 2.5$, $df = 20$, $P < 0.05$); eight females dived over 1000 m (Table 5) whereas no male in the sample dived to this depth. The maximum dive durations of females also exceeded those of males, ($t = -2.48$, $df = 20$, $P < 0.05$), owing mainly to the

longer dives of gestating females during the fall trip (Table 5). Males, on the other hand, had significantly longer mean surface intervals between dives, 2.91 ± 0.54 min vs. 2.42 ± 0.32 min ($t = 2.7$, $df = 20$, $P < 0.05$). There were no sex differences in the dive rate or the percentage of time spent at the surface between dives.

Females exhibited a marked diel pattern in depth of dives during transit and on FFAs (Figs. 10 and 11), a pattern observed in only a few males during transit (Fig. 18).

2. *Dive types.*—There were marked sex differences in the frequency distribution of dive types during transit and during foraging, as defined by transit speed (Table 4). Females exhibited more Type D, pelagic foraging dives than males during transit ($t = -7.6$, $df = 13$, P

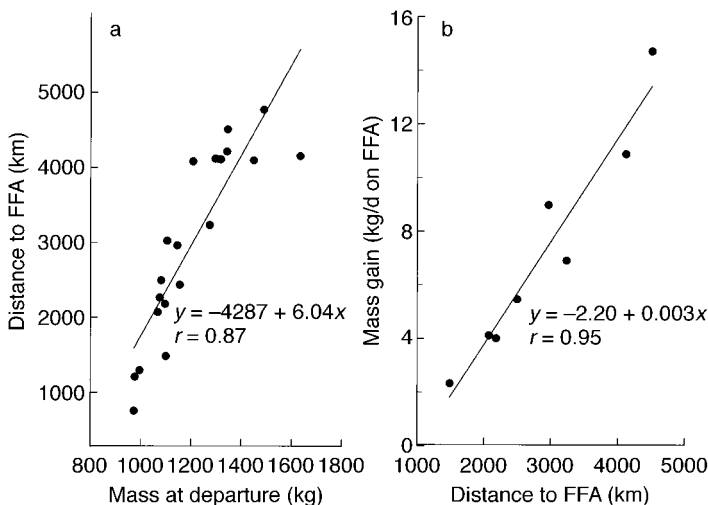


FIG. 7. (a) Distance traveled by males to focal foraging areas (FFAs) increased as a function of mass at departure from the rookery, and (b) mass gain per day spent on FFAs increased with the distance of the FFA from the rookery.

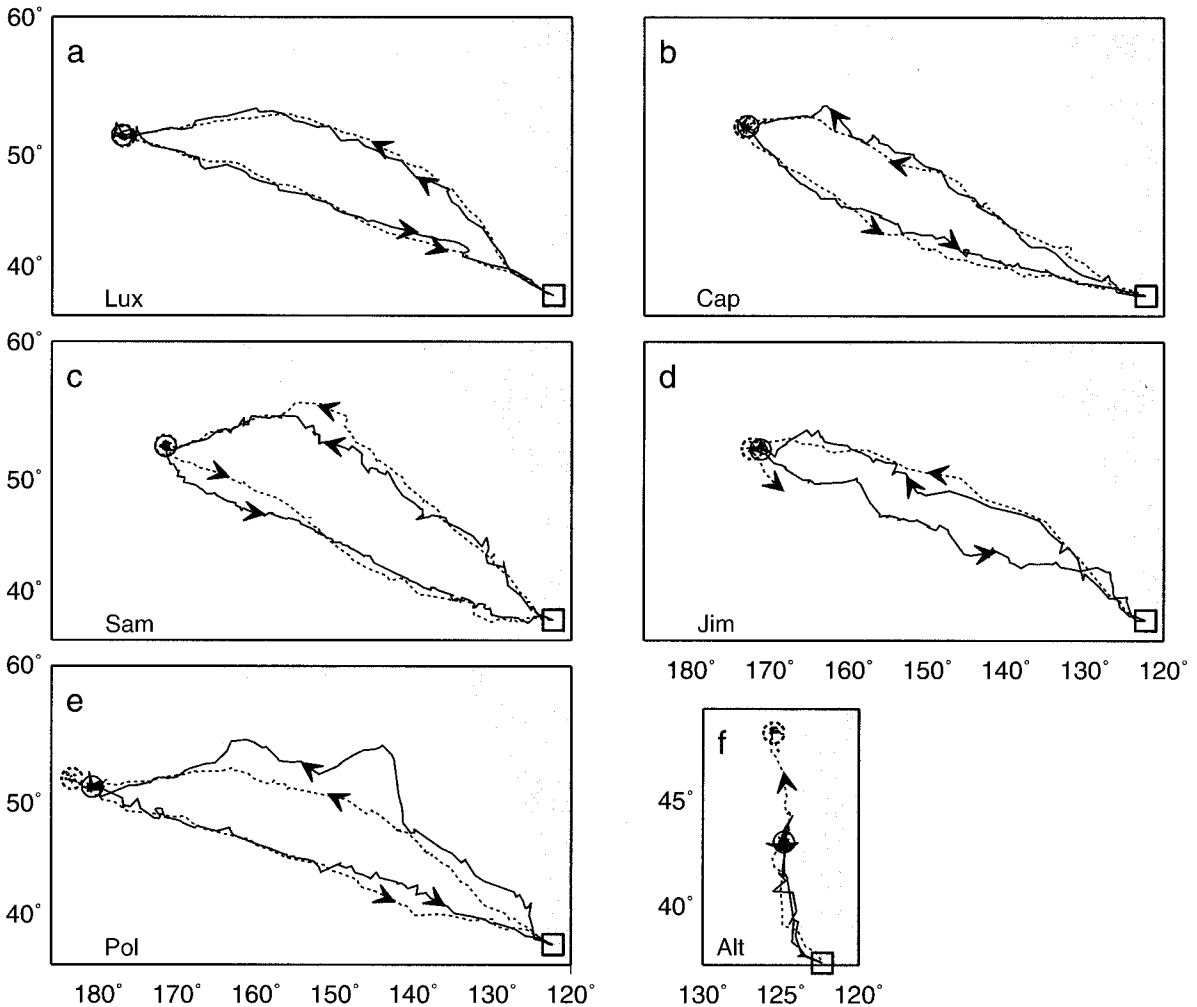


FIG. 8. Tracks and focal foraging areas (open circles) of the same six males recorded in the fall (solid lines) and the subsequent spring (dotted lines). The origin at the Año Nuevo rookery is indicated by an open square. Spring return tracks for two males (d and f) are incomplete; they stopped shortly after they began their return to the rookery.

< 0.05) and on FFAs ($t = -20.5$, $df = 13$, $P < 0.05$). The discrepancy was greatest on FFAs where these dives accounted for 72% of the dive types of females and only 2.8% of those of males. Flat-bottom, E type, benthic dives accounted for the greatest proportion of the dives of males on FFAs (73%). Females did not exhibit these dives except during the brief crossing of the continental shelf to and from the rookery. Males exhibited significantly more Type A transit dives during transit than females ($t = 5.3$, $df = 13$, $P < 0.05$); there were no sex differences in these dives on FFAs ($t = 0.94$, $df = 13$, $P > 0.05$).

Comparison of satellite and geolocation tracks

Fig. 20 shows that the tracks obtained from five seals with the Argos satellite system and the geolocation method are similar on a large scale. Both methods located the FFA of the male Sam2 in the Aleutian Island chain in the vicinity of Amukta Pass, with satellite

telemetry giving the most tightly focused position (Fig. 20a). The two methods also yielded generally similar tracks and final destinations for the four females, Pat (Fig. 20a), Mag and Jaz (Fig. 20b), and Yet2 (Fig. 20c), although the geolocation tracks occasionally deviate as much as 5° away from the satellite tracks.

Mean distances between geolocation and satellite positions (all animals combined) were 153.0 ± 12.0 km for class B hits ($n = 414$), 141.4 ± 9.6 km for class A hits ($n = 145$), 144.6 ± 8.7 km for class 0 hits ($n = 171$) and 139.6 ± 28.5 km for class 1 hits ($n = 25$, all values in this sentence are means ± 1 SE). These values were not statistically different from those obtained using only satellite hits occurring between 0900 and 1500 local time (i.e., within 3 h of solar noon, which corresponds to the "time" of the geolocation position). Geolocation and satellite positions were off by a mean of $0.99^\circ \pm 0.13^\circ$ of latitude and $0.96^\circ \pm 0.12^\circ$ of longitude ($n = 756$, ranges: 0.00° – 4.84° for

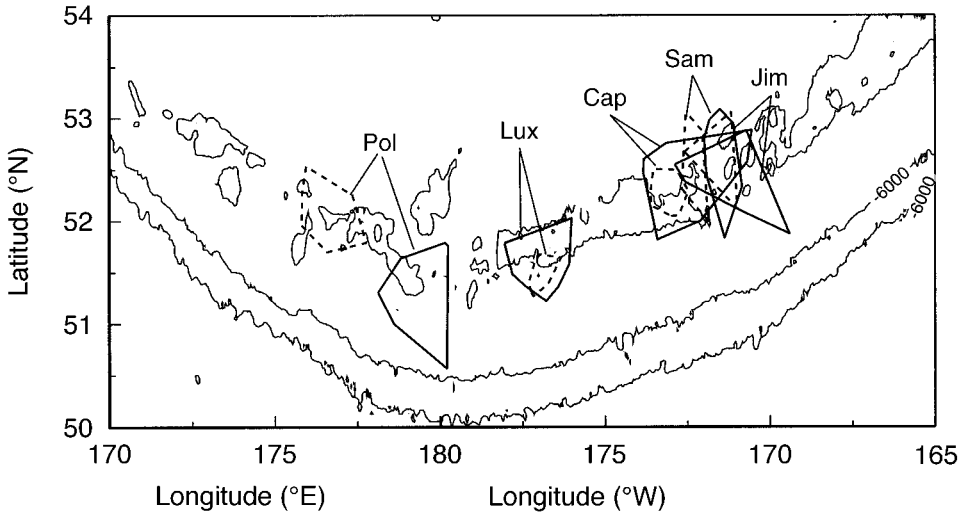


FIG. 9. Focal foraging areas (FFAs), calculated as minimum convex polygons, of the same five males foraging in the Aleutians Islands in fall (solid lines) and again in the following spring (dotted lines).

latitude, 0.00°–4.20° for longitude). Geolocation positions had a mean southern bias during fall migration (Sam2, Yet2, and Mag) and a mean northern bias during spring migration (Jaz) but Pat’s record showed the reverse trend. The mean ADV/MGCD ratio (average displacement vector/mean great circle distance) and the mean direction of the bias for each animal were as follows: 0.57 and 114° for Sam2, 0.76 and 350° for Pat, 0.22 and 193° for Mag, 0.43 and 359° for Jaz, and 0.22 and 155° for Yet2. For all animals combined, there was no evidence of a directional bias between geolocation and satellite positions by season.

DISCUSSION

Our results confirm that northern elephant seals segregate spatially by sex during both foraging trips per year and that adult males and females exhibit distinctive behaviors en route and during apparent foraging. These differences suggest that the sexes consume different prey. We summarize the data that support this hypothesis.

A case for sex differences in foraging.—Males moved

north to sites distributed along the continental margin of North America from Oregon to the Aleutian Islands in western Alaska. Seventy-four percent of the males in the sample ended up along the coast of Alaska. The end point of all male migrations was on or near the continental shelf break. Travel to these destinations was direct, rapid, and involved no stopping or backtracking. Diving behavior en route was continuous and dominated by transit dives that maximize horizontal distance covered (Le Boeuf et al. 1992), relatively few jagged-bottom pelagic foraging dives, and a dive pattern in which dive depth did not vary with time of day in most males and did so only slightly in a few males. This suggests that males set a high priority on reaching their destination quickly, they were not searching for prey in transit, and most of them did not vary the depth of their dives to track prey in the deep scattering layer that migrates closer to the surface at night and to deeper depths at midday. If they encountered prey in the water column, they did not remain long in the area to exploit it.

Once males reached their destinations, their behavior changed abruptly. They stopped moving, transit dive

TABLE 4. Mean percentage distribution of dive types (A, D, E, or C; see *Methods: Diving behavior*) of five adult males and 10 adult females in transit and on focal foraging areas.

Statistic	In transit (%)				On focal foraging area (%)			
	A	D	E	C	A	D	E	C
Males								
Mean	77.0	9.3	9.4	NA	20.8	2.8	73.2	NA
1 SD	±11.8	±8.1	±5.5	NA	±7.7	±2.2	±10.6	NA
Females								
Mean	48.3	42.1	2.7	5.0	17.1	71.9	0.1	10.6
1 SD	±9.0	±8.4	±1.3	±1.7	±6.9	±7.3	±0.1	±1.4

Notes: “In transit” was defined as a mean travel speed of >0.4 m/s for two or more days for females; in transit refers to the outgoing leg only for males. NA = not applicable.

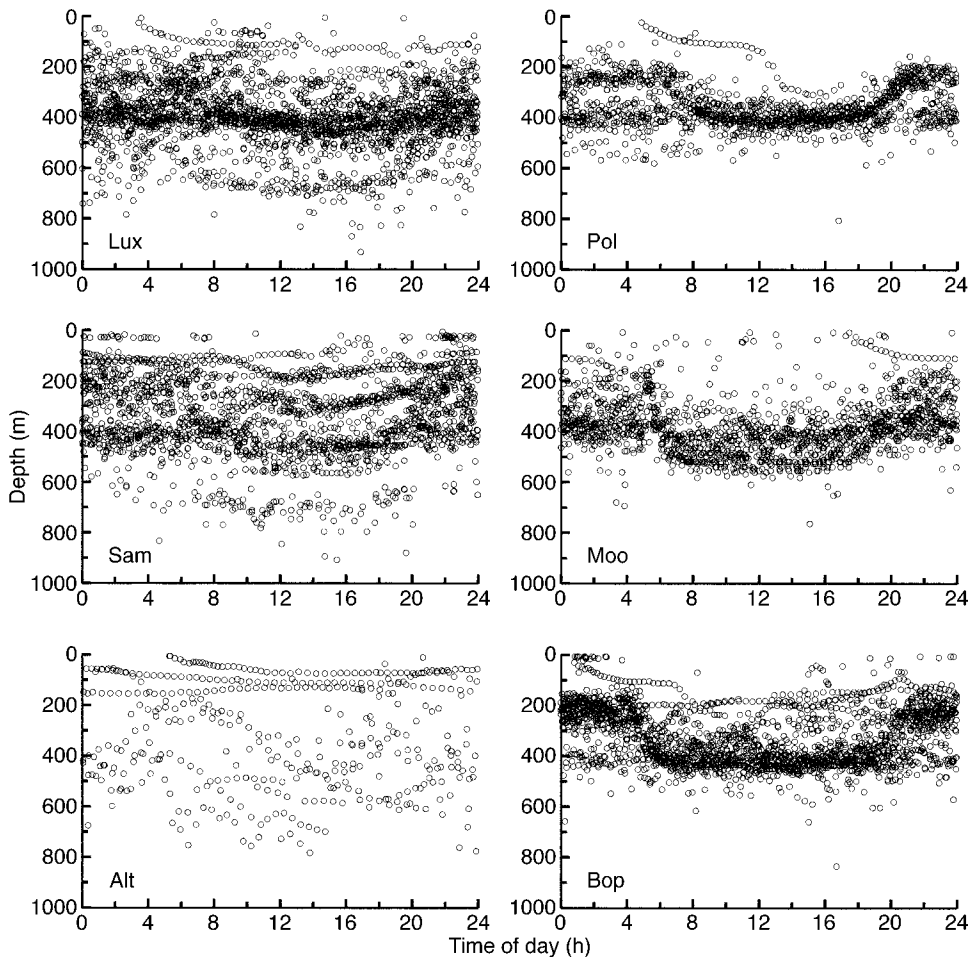


FIG. 10. Depth of all dives of six males during transit to and from their focal foraging areas (FFAs) as a function of time of day.

frequency decreased, and flat-bottomed benthic foraging dives became the most frequently displayed dive. Dive depth did not vary with time of day and the frequency of these dives with time of day was either constant or peaked at dawn and dusk (Le Boeuf et al. 1993), patterns consistent with feeding on benthic prey (Woodhead 1966). Males concentrated on average 45% of their time at sea at these relatively small, geographically fixed sites, and did not leave them until it was time to return to the rookery to breed or molt. This pattern suggests that male foraging is concentrated at these distal, coastal sites, which we termed focal foraging areas. The high frequency of flat-bottomed dives, combined with their uniform depth and crepuscular peak in frequency, suggests pursuit of benthic prey near the ocean bottom. In these dives, the seal descends rapidly to approximately the same depth where it remains for ~40% of the dive duration, before ending the dive with a rapid ascent to the surface. The dive shape and the uniform depth over successive dives suggest that the bottom of the dive is bathymetrically constrained. The male appears to be moving slowly over

the ocean bottom or along the continental slope in search of prey, or it appears to sit and wait for prey and then captures it (Le Boeuf et al. 1993). Diving records of males that include measurement of swim speed suggest that both of these strategies may be used, that is, males either move horizontally over the bottom of these dives, or come to a stop (D. Crocker, D. Costa, and B. Le Boeuf, *unpublished data*). Prey are evidently consumed at depth. These dives occur in long series often lasting several days and suggest long bouts of feeding (Le Boeuf et al. 1993).

The migratory and diving behavior of females is quite different from that of males. Females departing the rookeries on foraging migrations fanned out in various directions ranging from due west to due north. They did not proceed directly to a particular site and their paths were highly variable between individuals. Females traveled in the open ocean over deep water, often changing direction abruptly and unpredictably between bouts of slow-or-no transit lasting about three days. Females spent ~25% of their total time at sea at these stopping points, which were distributed through-

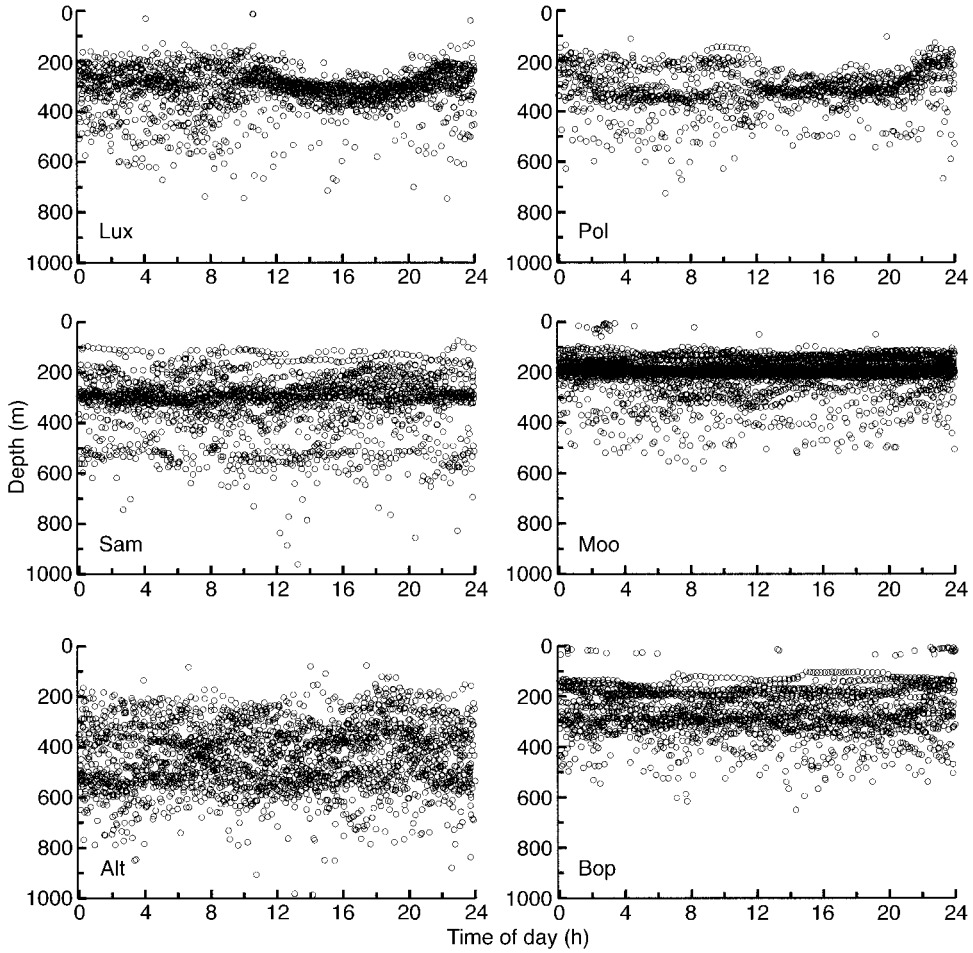


FIG. 11. Depth of all dives of six males on their focal foraging areas (FFAs) as a function of time of day.

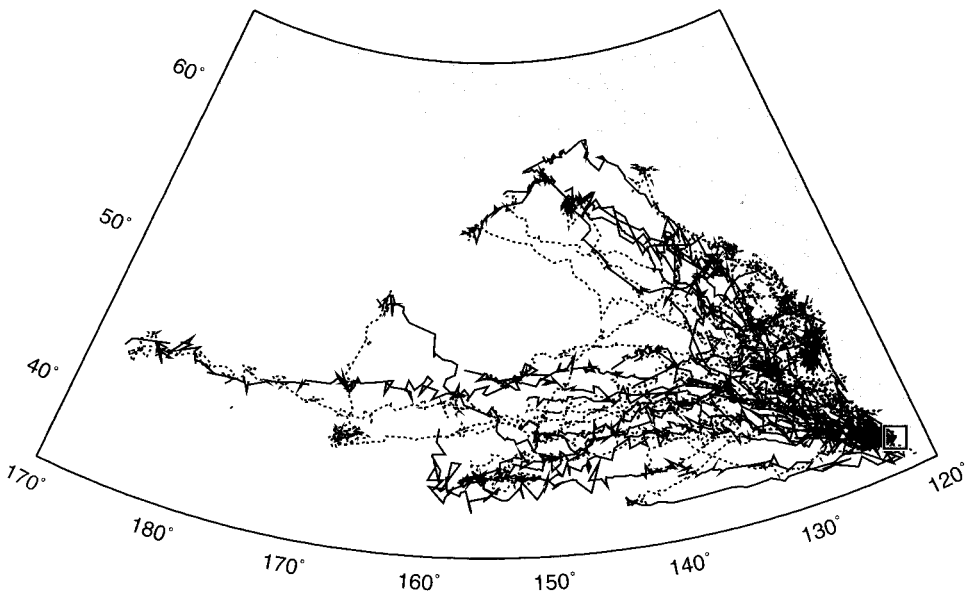


FIG. 12. Satellite tracks of 17 adult females showing the outgoing leg (solid line) and returning leg (dotted line) to the Año Nuevo rookery (open square).

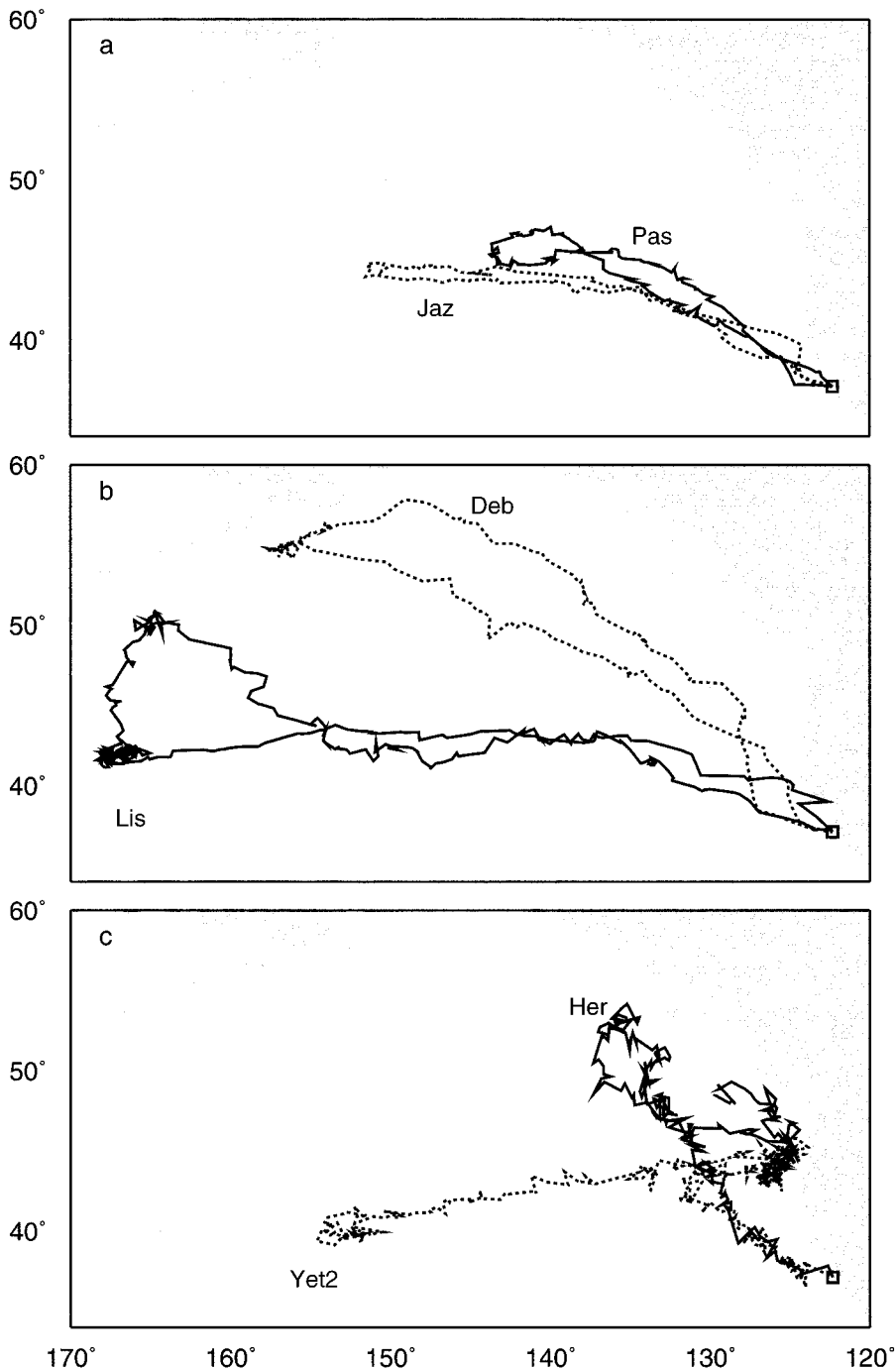


FIG. 13. Types of female tracks observed: (a) two females in spring make similar excursions to and from the rookery (open square); (b) two females in fall move to different places, and both spend considerable time foraging at the distal end of their tracks; and (c) these two females change their routes unpredictably: one forages off the coast of Oregon then moves directly west to forage at $\sim 153^\circ$ W before the record stops, and the other moves back and forth between the southern Gulf of Alaska and an area south of Queen Charlotte Island.

out the migratory paths of some females and concentrated in large areas at the distal ends of the migratory tracks of others. The location of these sites appeared to be spatially and temporally unpredictable. Females

often moved back and forth along their routes or within large favored areas.

As females moved to these stopping points, or between them, they exhibited predominantly transit type

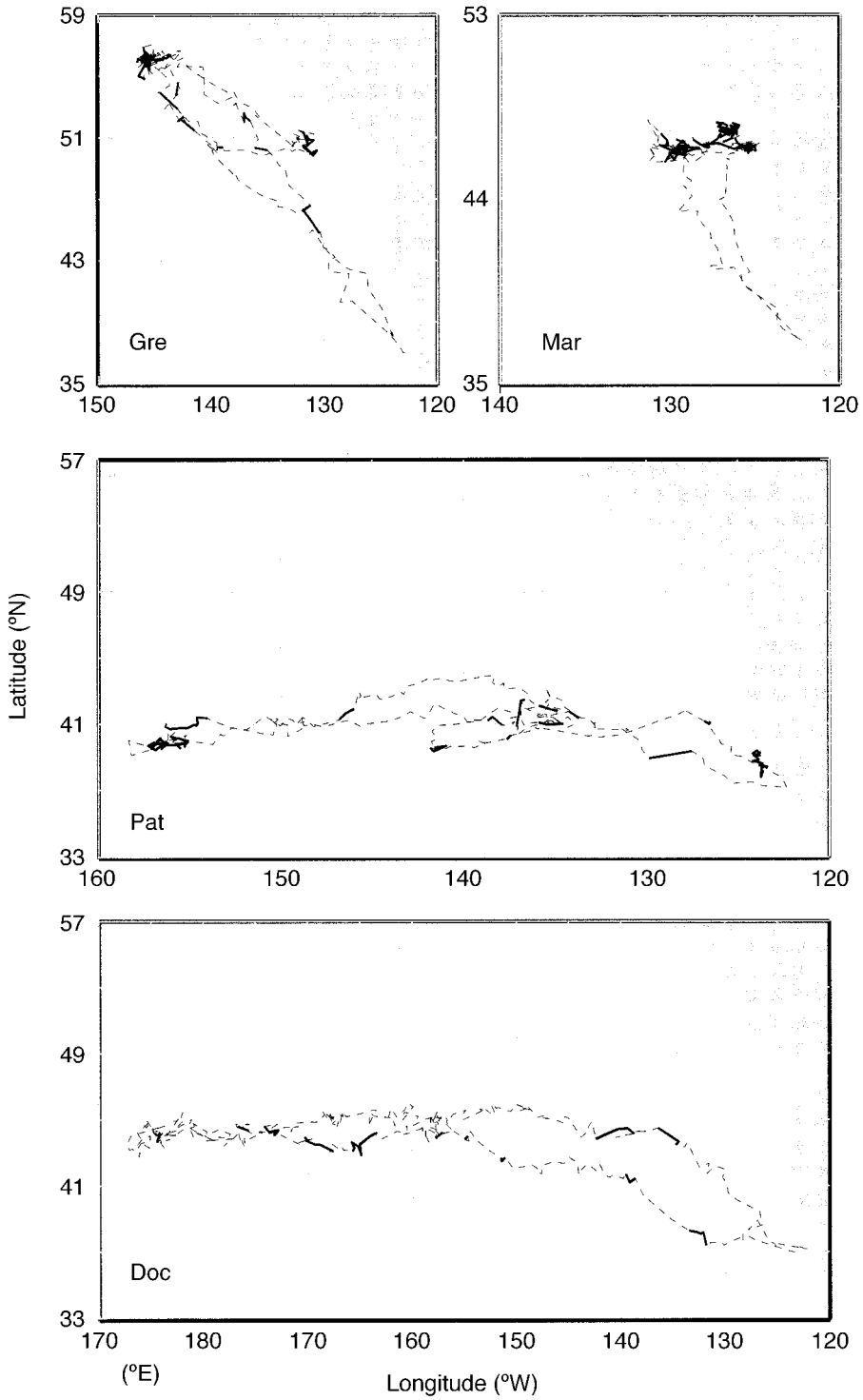


FIG. 14. Focal foraging areas (FFAs), measured as transit rates of ≤ 0.4 m/s, are shown on the tracks of four females as thickened lines.

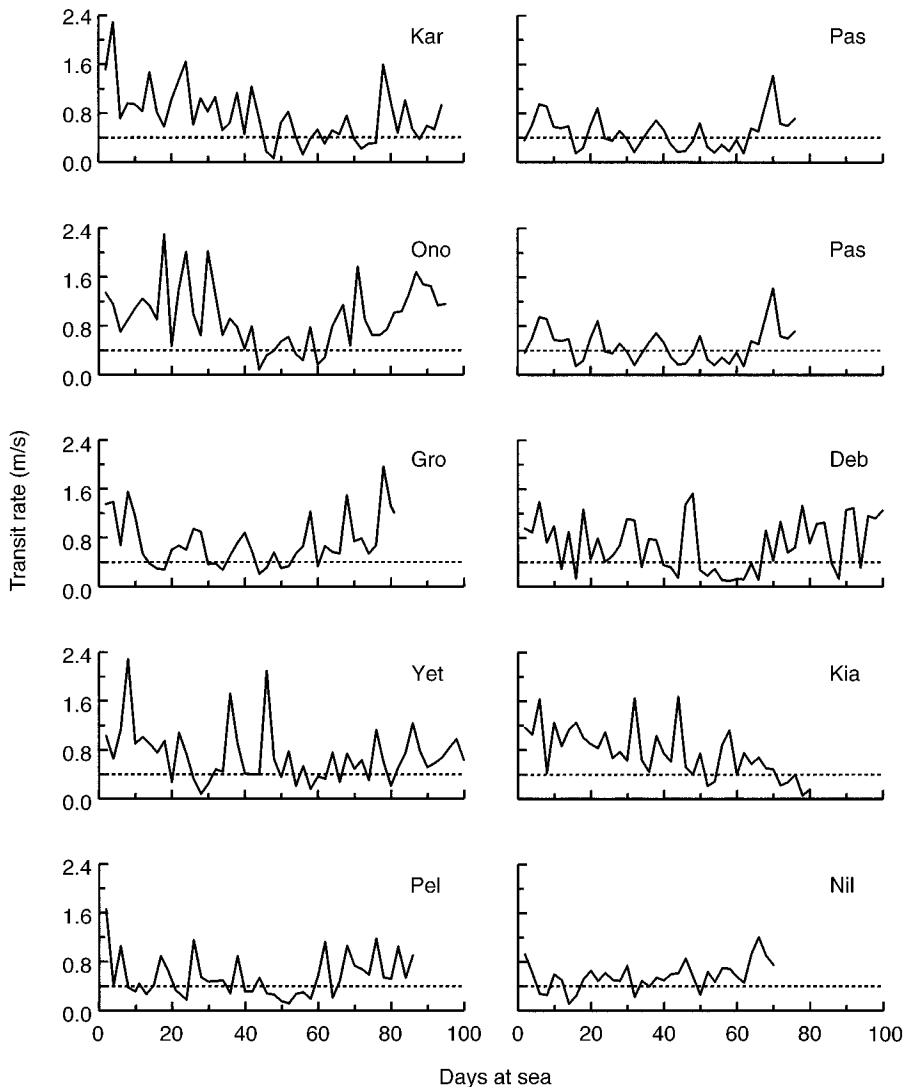


FIG. 15. Mean transit rates of adult females in spring, averaged over two-day periods, as a function of days at sea. Transit rates of ≤ 0.4 m/s, which define a focal foraging area, are shown below the dotted lines.

and pelagic foraging type dives in about equal frequency and to equal depths. Since these dives were deeper at midday than at night, females evidently synchronized their diving depth with that of prey in the deep scattering layer. This suggests that they were searching for prey while in transit and pursued prey when they encountered it. This hypothesis is supported by the presence of putative food processing dives in female diving records (Crocker et al. 1997).

When females stopped moving horizontally, their diving behavior changed. Transit dives dropped in frequency and pelagic foraging dives made up 72% of the dives displayed. Food processing dives doubled in frequency compared to when females were in transit. The diel pattern in diving depth changed with time of day. Evidently, foraging occurs predominantly at these stopping points which are indicated by the prev-

alence of pelagic foraging dives and a marked decrease in horizontal transit speed. Mass gain over the period at sea was highly and positively correlated with the percentage of time females spent in slow transit. During pelagic foraging dives, females dive at an abrupt angle of 55° from the surface at a swim speed of 0.84 ± 0.12 m/s. The bottom of the dive, which takes up $\sim 36\%$ of the entire dive duration, has a saw-tooth pattern owing to the seal making a mean of 2.4 ± 0.7 vertical excursions, each covering a mean vertical distance of 18.2 ± 12.7 m. These vertical excursions appear to represent pursuit and capture of prey. Ascent to the surface is equally abrupt and similar in duration to descent. These dives occur in long series lasting from several hours up to two days and they are observed daily in the records of most females (Le Boeuf et al. 1988, 1993).

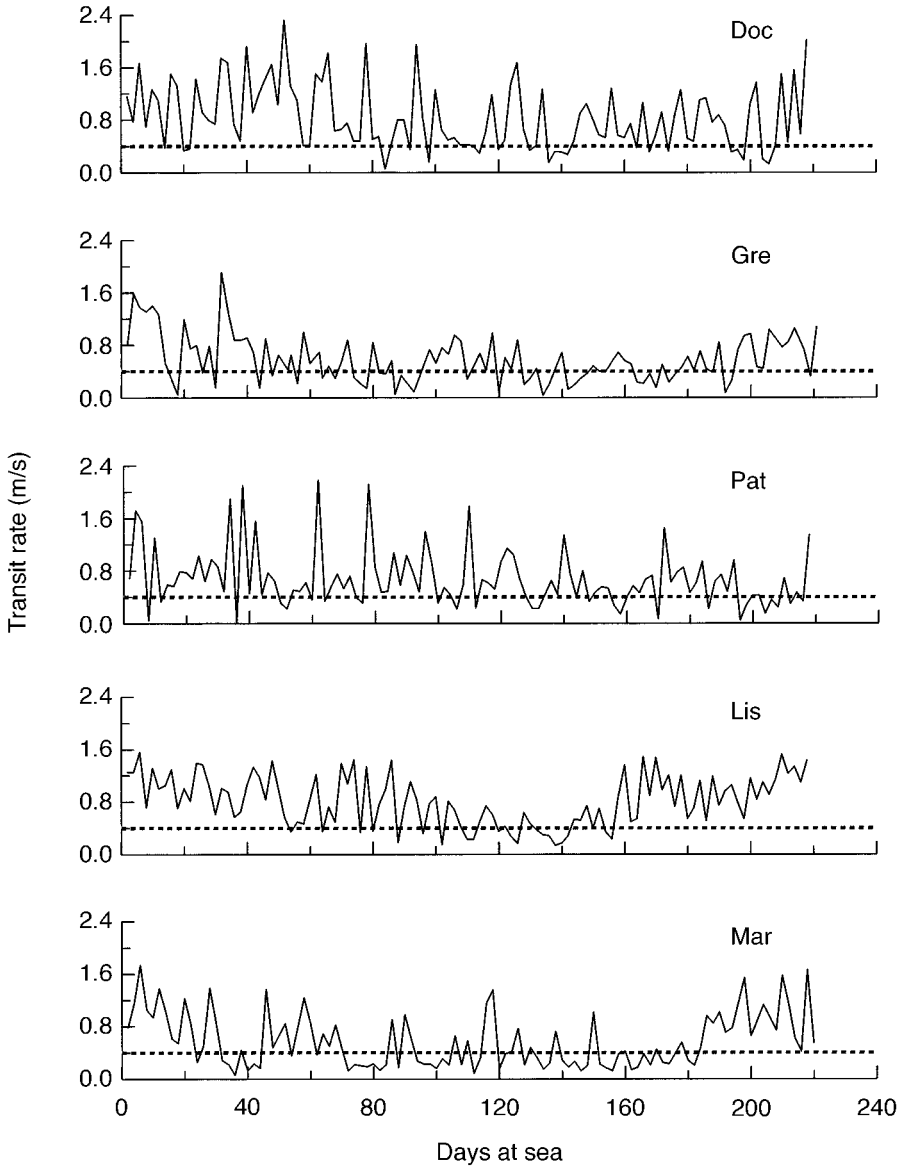


FIG. 16. Mean transit rates of adult females in fall, averaged over two-day periods, as a function of days at sea. Transit rates of ≤ 0.4 m/s, or time on focal foraging areas, are shown below the dotted lines.

The movements and diving pattern of females suggest that they feed predominantly on patchily distributed pelagic prey in the water column that migrate vertically with available light. The apparent foraging locations of females are not determined so much by geographical boundaries as by a cyclical pattern of vertical prey movement in the pelagic and mesopelagic environment.

Diet.—We do not know what elephant seals eat during most of the time that they are at sea and especially, what they eat while on focal foraging areas. Most of what is known about the diet of northern elephant seals comes from prey remains in dead animals and lavaged stomachs of animals returning to rookeries (Condit and

Le Boeuf 1984, Antonelis et al. 1987, 1994, DeLong and Stewart 1991). These methods, unfortunately, reflect only prey consumed during the last few days of transit (Helm 1984, Harvey et al. 1989). For wide-ranging species such as elephant seals, data collected at or near the coastal haul-out sites may not represent prey consumed offshore (Bowen et al. 1993). Nevertheless, prey remains from elephant seal stomachs show that they feed on a variety of epi- and mesopelagic, bioluminescent cephalopods, teleosts such as Pacific Hake, *Merluccius productus*, crustaceans, elasmobranchs, cyclostomes, and tunicates. These data reveal that males consume the same prey as females during part of the journey to and from focal foraging areas.

Males have also been observed eating benthic-dwelling elasmobranchs (Condit and Le Boeuf 1984) and are known to prey on cyclostomes, a behavior that is rare in females (Antonelis et al. 1994). Among juveniles, the prey of males is more diverse than the prey of females (Hacker 1986).

These limited observations, combined with the data presented in this study, suggest that females feed mainly on epi- and mesopelagic, bioluminescent cephalods, and Pacific Hake in the open ocean. Males may forage opportunistically on these prey while in transit but their principal prey appear to be benthic animals located along the continental margin, possibly elasmobranchs and cyclostomes. Once the specific prey consumed by elephant seals are identified, it will be possible to determine the relative energy density of the prey consumed by both sexes.

Quality of foraging areas.—The richest foraging areas for males were evidently those furthest from the rookery. But given the high correlation between mass at departure and distance traveled, only the largest males exploited these areas. Moreover, to reach these sites, males had to travel faster and take more time to reach their destination, which allowed them less time to spend there foraging. Nevertheless, most of the males in our sample traveled to the most distant site, the Aleutian Islands, and the extra effort was evidently worth it. The mean percentage mass increase over departure weight of males with foraging sites in the Aleutian Islands was 34%, compared to 27% for males in southern Alaska, and 22% for males in Canada. It is not clear whether the Aleutian site offers better forage absolutely or better forage only for large males. Perhaps only the largest males reach these distant sites because they have sufficiently large fat reserves needed for the 38–50 d migration following a 1–3 mo fast on land (Le Boeuf 1974). Moreover, large size increases the efficiency of long distance travel (Brodie 1975).

Males that traveled to the Aleutian Islands to forage showed a preference for one site near Amukta Pass. Amukta Pass and Amchitka Pass are the two deepest water passes through the Aleutian Islands that provide transport of water between the north Pacific Ocean and the Bering Sea (Reed and Stabeno 1997). The residual flow is northward, but this pass appears to be an important avenue for many migrating marine mammals, particularly fur seals, *Callorhinus ursinus*, and gray whales, *Eschrichtius robustus*, and it appears to be an area of high productivity, given the number of sea bird colonies and whales observed (L. Fritz, *personal communication*).

Among females, there was no relationship between distance traveled and percent increase in mass over departure weight during the spring or fall trip. Rather, success in foraging, as reflected by mass gain, was best predicted by total time spent in slow transit, that is, what appears to be the number of prey patches encountered and the amount of time spent exploiting

them. In the case of one pregnant female (Mag), the location of foraging near the continental margin area where males foraged, may have contributed to her success in gaining mass.

Reliability of routes in the individual.—The striking similarity of tracks and focal foraging areas of males recorded in both foraging trips in one year, and from year to year, implies a highly developed and reliable open water navigation ability as well as evidence for spatial memory and learning. Evidently, this enables males to utilize prey resources associated with permanent bathymetric features. Since most of our repeated samples were from males that migrated to the Aleutian Islands and only the largest males migrated this far, it is not clear when in development males might settle on a fixed foraging site. Studies of juveniles and subadult males suggest that this may not be until males reach their full adult size (Le Boeuf et al. 1993, 1996, Le Boeuf 1994). This also suggests that an individual male might return to a particular foraging area for several years, possibly for the rest of his life.

The few females in this study whose migrations were recorded twice showed a general tendency to take the same initial direction from the rookery, but they took excursions from the original route and were far less reliable than males. Two females began the same westward route on their second trip but deviated abruptly and returned eastward to linger near the coast for several weeks; one of them returned to the original route after a long delay. This variability in female foraging location is consistent with pursuing prey with a characteristic vertical distribution in the water column and a patchy spatial distribution that may be highly dependent on ephemeral oceanographic features such as discontinuities in water temperature (Boyd and Arnborn 1991, Hakoyama et al. 1994). Marine mammals may rely on oceanographic features such as frontal systems, thermocline depth, and bathymetry to concentrate or aggregate prey, which may facilitate effective foraging (Hui 1979, Winn et al. 1986, Reilly 1990, van Franeker 1992, Whitehead et al. 1992, Kenney et al. 1995). That is, oceanographic features may indirectly affect the distribution and ranging patterns of foraging females by physically concentrating their prey.

Sex differences in foraging strategies and repeatability of migratory paths lead one to expect sex differences in foraging success due to factors that affect the distribution and abundance of elephant seal prey, especially long-term cyclical variations such as those associated with El Niño Southern Oscillation (ENSO) events. It is not clear, however, which sex and their prey is most affected by these perturbations. During the severe 1982–1983 ENSO, compared to preceding and succeeding years, females spent more time at sea following reproduction; they began the breeding season later, fewer females returned to give birth, and females born in this year were primiparous later in life (Huber et al. 1991, Le Boeuf and Reiter 1991). Fewer males

TABLE 5. Mass change, movements, and diving behavior of adult females during the spring and fall migration.

Female	Track length		Depart mass (kg)	Return mass (kg)	Mass gain			Time on FFA			Mean transit rate (m/s)	Transit speed to distal point (km/d)	Distal point from rookery (km)	
	(d)	(%)§			(kg)	(kg/d)	(%)	Total (d)	(%)§	Mean (d)				SD (d)
Spring														
Kar	91	100	369	410	41	0.45	11.1	16	17.6	4	2.4	0.85	75.9	3035
Ono	93	100	360	397	37	0.40	10.3	14	15.1	2	0	0.94	53.5	2516
Gro	81	100	337	410	73	0.90	21.7	28	34.6	4.4	1.7	0.62	42.3	1439
Yet	105	100	279	328	49	0.47	17.6	30	28.6	3.1	1.8	0.71	56.2	2980
Ono2	64	71	425					8	12.5	2.7	1.2	0.83	59.6	2026
Pel	86	100	307	426	119	1.38	38.8	36	41.9	4.5	4	0.56	41.1	1849
Rus†	25	28	339					4	16	2	0	0.63	50.5	1516
Pas	79	100	327					36	45.6	6	3.6	0.49	54.6	2019
Jaz	69	100	390	415	25	0.36	6.4	18	26.1	2.3	0.8	0.74	73.4	2570
Deb	101	100	375	449	74	0.73	19.7	38	37.6	4.8	5.6	0.69	62.1	3290
Kia†	82	90	324					18	22	4.5	3.8	0.75	74.7	2614
Nil	90	100	340	405	65	0.72	19.1	14	15.6	2.8	1.7	0.57	62.3	1743
Mia	59	97	348	410	62	1.05	17.8	14	23.7	4	3.5	0.83	76.6	1916
Mean	79		348	406	60.6	0.72	18.1		25.9	3.6	2.3	0.7	60.2	2270
SD	21		37	33	28	0.3	9		11.0	1	2	0.1	12.2	603
Fall														
Bla‡	166	100	278	320	42	0.25	15.1	8	4.8	2	0	1.34	54.2	3254
Doc	219	100	284	461	177	0.81	62.3	50	22.8	3.3	2	0.84	57.7	5431
Gre	220	100	394	635	241	1.1	61.3	80	36.4	3.3	1.7	0.48	20.1	2828
Her†	74	35	257					14	18.9	2	0	0.67	64.1	2116
Kar2†	41	19	323					10	24.4	2	0	0.54	73.9	1627
Yet2	139	62	256					36	25.9	2.8	1.7	0.69	23.2	2815
Lis	231	100	308	485	177	0.77	57.5	42	18.2	3.3	2.9	0.84	24.6	3943
Mag	116	52	330	597	267	2.30	80.9	38	32.7	3.4	1.9	0.52	50.4	3125
Mar	221	100	301	501	200	0.90	66.4	96	43.4	5.6	3.7	0.57	38.8	3140
Pat	227	100	254	390	136	0.60	53.5	56	24.7	2.8	1.5	0.78	63.5	1398
Mean	165		299	484	177	0.96	56.7		25.2	3.1	1.5	0.7	47.1	2968
SD	70		43	110	73.7	0.65	20.3		10.7	1.1	1.2	0.3	19.2	1164

Notes: In spring, females were inseminated but not gestating. In fall, all females but one were gestating. Percentage of trip tracked, when less than 100%, was estimated as days tracked divided by mean trip duration, 90.6 ± 11 for spring females and 223 ± 5 for pregnant fall females. Time on FFA was measured as periods of two or more days when mean travel speed was <0.4 m/s.

† Lost at sea or did not return.

‡ Not pregnant.

§ Percentage of trip.

|| Includes pup for all fall females that gave birth.

returned to the rookery to breed during these El Niño years and those that returned were somewhat later than usual; the effect was most pronounced among young adults. In the strong 1997–1998 ENSO, adult females spent more time at sea than usual, less time foraging (in slow transit), more time traveling between prey patches, and gained less mass than usual (D. Crocker, D. Costa, and B. Le Boeuf, *unpublished data*).

Individual differences in foraging location.—Within each sex, there were great individual differences in the direction, route, and final destination of individuals. This is expected since individuals travel alone and great individual differences are consistent with observations of foraging habits and prey of many marine and terrestrial mammals (e.g., Lyons 1991). Whereas most males traveled over deep water to a coastal destination, a few males proceeded north over the continental shelf and never left it. The different location and dive shapes of these males suggest they may have been feeding, if

at all, on different prey en route than males that transited over deep water. This difference in behavior has also been observed in male southern elephant seals in Patagonia, Argentina (Campagna et al. 1998). Females were more variable than males and more unpredictable en route. Although most females foraged over deep water, a few of them spent some time foraging near the continental shelf, like males. The female that incurred the highest increase in mass over the period at sea (2.3 kg/d) employed this strategy. Her foraging success is not explained by superior size since her mass at departure was near the mode in the sample. Two other females that employed this strategy, however, did not gain significantly more mass than other females in the sample.

Sexual segregation and prey category.—In summary, location and behavior suggest that males on foraging areas are not diving for vertically migrating prey in the deep scattering layer as females appear to do but

TABLE 5. Extended.

Dives (no./h)	Time at surface (%)	Dive depth			Dive duration			Surface interval	
		Max. (m)	Mean (m)	SD (m)	Max. (min)	Mean (min)	SD (min)	Mean (min)	SD (min)
3.3	12.8	820	458	132	38	18	3.8	2.6	5.7
3.4	15.2	826	425	159	39	17.8	3.7	3.2	8.1
2.9	11.8	1 112	548	121	56.7	20.8	4.1	2.7	7.4
2.6	8.8	1 188	515	140	47	23.4	4.3	2.3	4.8
2.6	9.9	778	443	142	54	22.9	4.4	2.5	10
2.7	9.7	1 076	509	140	55.3	22.3	4.4	2.4	3.6
2.5	8.8	694	369	145	54.5	23.9	4.4	2.3	0.5
2.9	11.0	928	467	140	49.2	21.3	4.2	2.6	5.7
0.4	2.4	193	61	12	7.9	2.5	0.3	0.3	3.1
2.5	8.9	1 139	446	131	106	24.2	6.2	2.3	1.5
3.8	12.1	1 153	396	196	40.5	16	5.6	2.2	7.8
2.8	8.7	1 372	427	127	68	21.7	6.6	2.1	7.9
2.6	9.9	1 380	425	144	75.5	23.3	8.8	2.6	8.9
2.8	8.3	877	444	118	59.5	21.3	5.1	1.9	7.6
2.8	10.2	1 197	519	154	65.5	21.3	7	2.4	12
2.9	9.7	1 186	443	145	69.2	21.3	6.6	2.3	7.6
0.5	1.4	185.0	41	28	21.6	2.9	1.3	0.2	3.4

rather show a diving pattern consistent with pursuing benthic prey. This interpretation differs from that of DeLong and Stewart (1991, Stewart and DeLong 1994), who concluded from the offshore deep water locations estimated with early geographic location–time–depth recorders (GLTDRs) and a composite dive analysis

showing a diel pattern in depth of dives that both sexes originating on a southern California rookery fed throughout the period at sea on mesopelagic cephalopods in the deep scattering layer. Satellite data, however, puts males nearer to shore and their own data show clearly that their males did not show a diel pattern

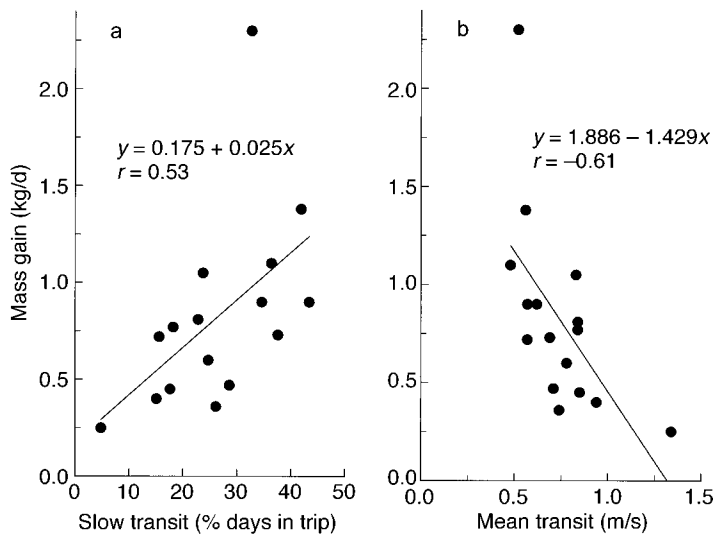


FIG. 17. Mass gain of females during the period at sea (a) as a function of the percentage of slow-or-no transit days and (b) as a function of mean transit rate.

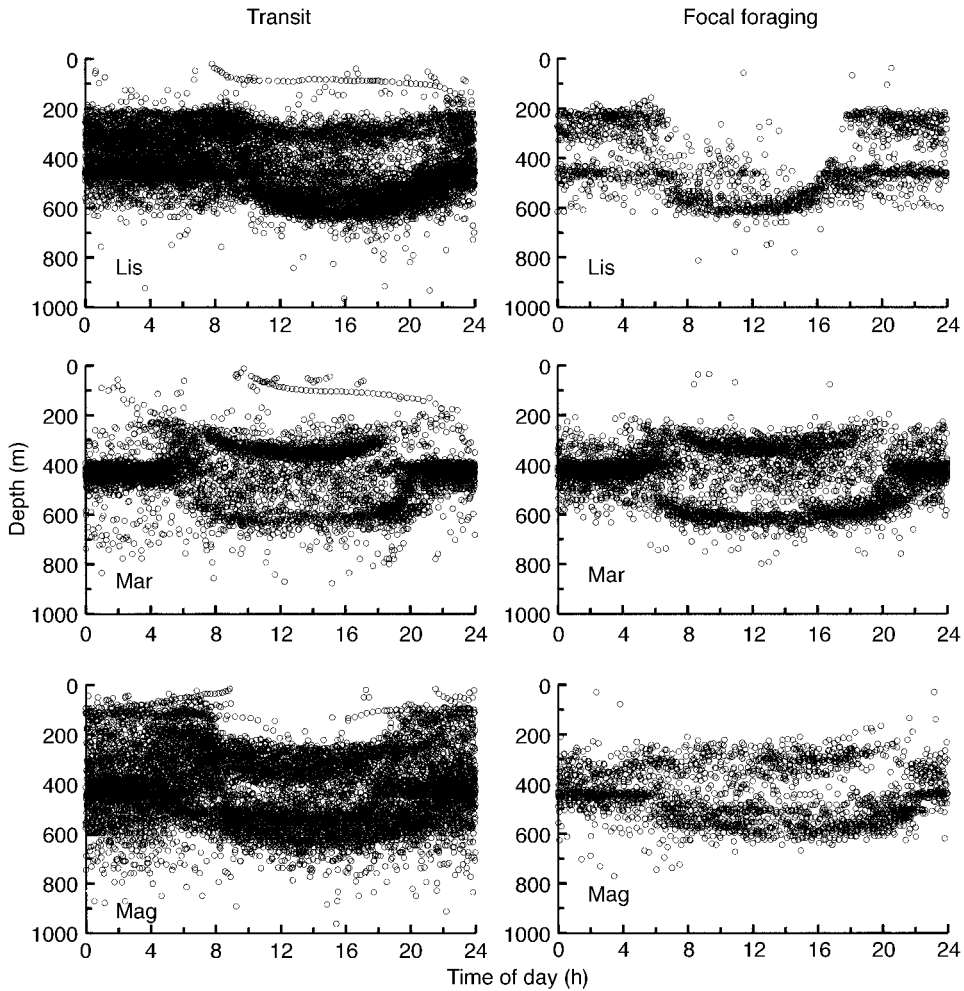


FIG. 18. Depth of all dives of three females during transit and on focal foraging areas as a function of time of day.

in diving depth in spring when they were on focal foraging areas.

Recent advances in techniques for identifying prey species of free-ranging marine mammals, like fatty acid analysis of milk or blubber (Iverson 1993, Iverson et al. 1997a, Smith et al. 1997) or isotope ratios of tooth annuli (Hobson and Sease 1998), may confirm these sex differences. Until then, we conclude from the data at hand that some males may forage opportunistically on similar pelagic prey as females while in transit, such as cephalopods and a few teleosts, but once males reach their focal foraging areas, which are located in a different habitat, they pursue different prey.

Methods of estimating animal location and foraging location: satellite tags vs. geolocation with light levels.—Our satellite records and the type of dives displayed suggest strongly that adult males concentrate their foraging efforts on or near the continental margin, not in the deep offshore waters estimated previously by archival GLTDRs. Early GLTDRs positioned the foraging areas of males migrating from San Miguel Island

in southern California 2–3° from land throughout their range (DeLong et al. 1992, Stewart and DeLong 1993, 1994, 1995, Stewart 1996). For example, track depictions of focal foraging areas of these males in the vicinity of the Aleutian Islands are located ~240–320 km south of land, well south of the Aleutian Trench, where water depths exceed several thousand meters (DeLong et al. 1992, Stewart and DeLong 1993, 1994, 1995). It is unlikely that males from southern California travel to open water destinations while males from central California travel to the continental margin. Indeed, three satellite tracked subadult males from southern California were recently reported as having focal foraging areas near the continental margin (Stewart 1997), just like central California males. We think the differences between telemetry estimates and early geolocation estimates in the literature are due to a systematic bias in the early instruments that caused them to position the seals further south and further off the coast than they really were. In fact, there were errors in measuring light levels in instruments fabricated before 1993, and the satellite sea

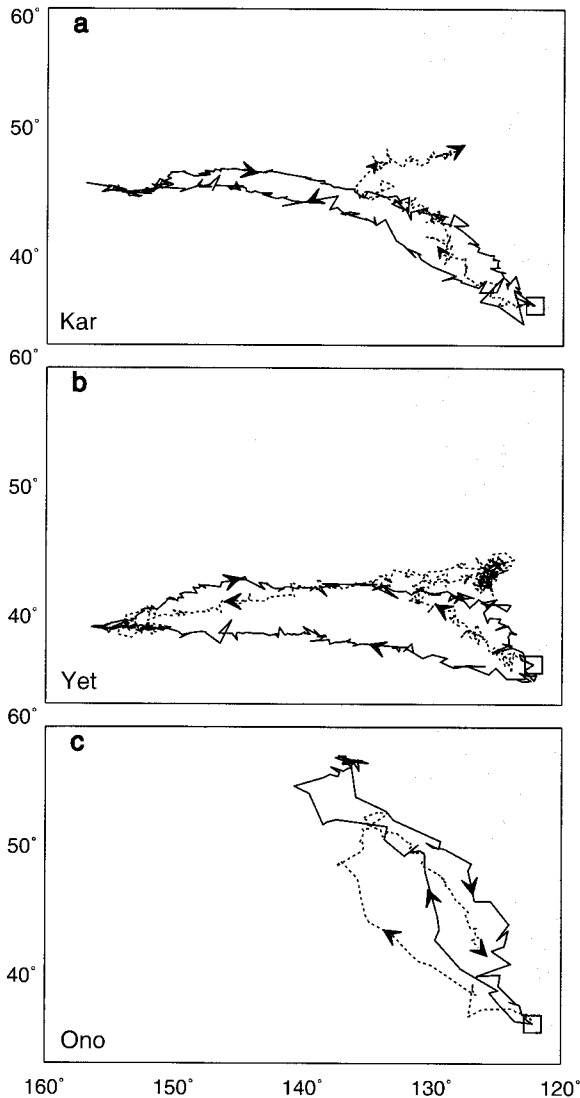


FIG. 19. Similarity of successive trips to sea by three females: (a) in spring Kar moved northwest to $\sim 158^\circ$ W before returning to the rookery (solid line); she began moving in the same northwest direction in the fall but took a 90° right turn toward Vancouver Island after which the PTT stopped transmitting; (b) in fall (dotted line), Yet begins in the same direction she took in the spring (solid line), but at $\sim 132^\circ$ W she returns to forage off the coast of Oregon for 30 d before returning to her former route and following it to its terminus; the PTT stopped signaling as she began her return to the rookery; (c) in spring 1995 (solid line), Ono moved north along the coast to Baranov Island before returning to the rookery; in spring 1996 (dotted line), she took a similar northerly route but did not go as far.

surface temperature data used to correct errors in latitude were available only twice per month. With the change from the Mk3+ to the Mk3e GLTDRs in 1993, the sensitivity of recording light levels was improved and the algorithm was changed, yielding positions closer to those obtained by satellite telemetry, as we show in this paper. In addition, precision in estimating latitude was

improved by the availability of satellite sea surface temperature data on a weekly basis.

Differences between the spatial distribution of adult females estimated by the two methods is more difficult to substantiate because of the inherent individual variation in the female pattern and possibly by the slightly different methods employed by two laboratories to estimate position from geolocation, which is a tedious and imprecise process that is subject to personal bias. Early GLTDR tracks of females from southern California in spring and fall were uniformly below 50° N (Stewart and DeLong 1993, 1994, 1995). In contrast, four of nine adult females and two of three juvenile females from central California tracked with GLTDRs moved north of this latitude (Le Boeuf et al. 1993). In the present study, 32% of the satellite-tracked, central California females moved north of 50° N. The magnitude of these differences suggests that the origin of females may limit their foraging location, especially to the north, or that bias was involved in the early estimates of position from geolocation. It is clear, however, from the data that we report here and from another study (Stewart and DeLong 1995) that measurements made with the newest GLTDRs, and associated software, and satellite telemetry can be quite similar, at least with respect to ultimate destinations.

Mortality at sea.—It is likely that eight seals died at sea in the same general area off the western coast of Canada and southern Alaska. They were located in this area when the last emissions from their satellite tags were received. If the tags had simply malfunctioned, we would have identified these animals when they returned to the rookery from individually numbered flipper tags. None of these animals were seen on the rookery again. Intense fishing in the area west of Baranov and Vancouver Islands in the fall and spring when the animals are migrating makes it likely that the seals were entrapped in nets or fishing gear. All four of the males involved were migrating north when their records ceased. Repeated uplinks of high quality from the tag of one female suggested the PTT was on the deck of a ship for several days.

Sexual segregation.—Sexual segregation during migration and foraging occurs in a variety of animals (Dingle 1996) and especially in the polygynous, sexually dimorphic ruminants and pinnipeds (Orr 1970, Riedman 1990, Main et al. 1996). Numerous hypotheses have been advanced to explain this phenomenon. One of these asserts that males compromise security for prey quality while females compromise prey quality for security (Geist 1981, Werner and Hall 1988, Abrahams and Dill 1989, Main and Coblenz 1990, Berger 1991, Bleich et al. 1997). For example, at certain times of the year, male mountain sheep graze in areas where predators are common (Bleich et al. 1997, Bleich 1999). Females and their offspring, in contrast, occupy areas with less nutritious forage than that of males but

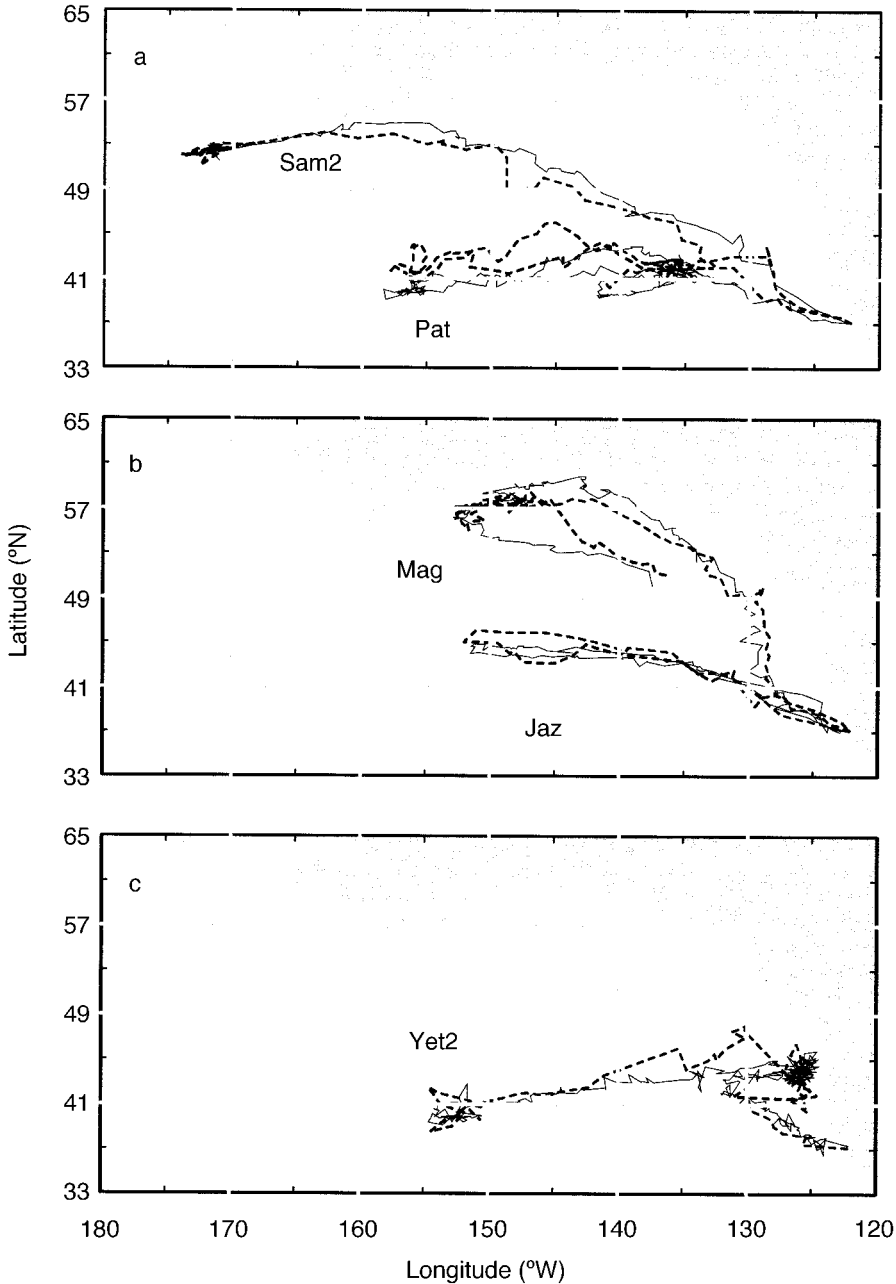


FIG. 20. Satellite tracks (solid lines) and geolocation tracks (dotted lines) obtained simultaneously from one male, Sam2 (a), and four females (a, b, c). Portions of the return tracks are omitted when locations were available for only one method.

having a lower density of predators and providing a better means of detecting and avoiding them. Male Asian elephants, *Elephas maximus*, move seasonally into areas where they feed on more nutritious food than females but in doing so, they incur higher mortality rates than females (Sukumar and Gadgill 1988). Adult male marine iguanas, *Amblyrhynchus cristatus*, which are three times heavier than females, get more resources by feeding on the same marine algae as females but in a different location (Trillmich and Trillmich 1986, Wi-

kelski and Trillmich 1997). Females and small males feed in the intertidal zone and hold on to rocks or scurry away when waves break over the area. This area is overgrazed. The largest males, those that can dive deeper and stay in the water longer without chilling (Bartholomew and Lasiewski 1965, Bartholomew 1966), feed on the relatively ungrazed and more abundant algae in the deeper subtidal zone. The risk, however, is that the larger males pursuing this strategy are more frequently swept out to other islands or out to sea where

they die. A similar explanation may explain, in part, sexual segregation in elephant seals.

Male elephant seals forage along the coast on possibly richer prey than females but at the risk of predation by killer whales, *Orcinus orca*, or white sharks, *Carcharodon carcharias*. The relative mass gain of males and females suggests that male prey are more nutritious or more abundant than female prey. For a given interval at sea, males gained 2.85 kg/d, much higher than the 0.72 kg/d gained by females in spring and the 0.96 kg/d gained by females in fall. Relative to body mass, however, females increased their departure mass as much or more (18.1% in spring and 56.7% in fall) than males (27.8%) over the total time spent at sea, or per day at sea (females 0.21%/d in spring and 0.30%/d in fall vs. males 0.24%/d). Although these data show that both sexes are equally efficient in their respective foraging patterns, males still must acquire an absolutely greater amount of prey. The greater food requirements of males require them to find prey patches that are denser, larger, or of higher quality prey. Indeed, effective foraging, especially during the growth spurt at puberty, determines eventual size attained, which is positively correlated with winning fights, social rank, and mating success (Le Boeuf 1974, Haley et al. 1994). In contrast, the lower absolute foraging requirements of females means that they are able to forage efficiently on smaller or more ephemeral food patches. Currently available data do not allow us to test or verify these potential differences in prey quality or abundance.

By foraging near the coast, male elephant seals risk greater exposure to their major predators than females feeding in the open ocean. The main predators on northern elephant seals are white sharks and killer whales (Ainley et al. 1981, 1985, Le Boeuf et al. 1982, Klimley 1985, Klimley et al. 1992, Le Boeuf and Crocker 1996). Both species are near surface predators that frequent coastal areas, not the open ocean (Klimley 1985, Dahlheim 1997). White sharks range along the coast from Mazatlán, Mexico to Queen Charlotte Island in western Canada (Klimley 1985). In central California, white sharks take elephant seals of all ages and sizes and there is no evidence that large males are less prone to predation than females (Le Boeuf et al. 1982). In a study at Año Nuevo, shark-bite wounds on males outnumbered those on females by a ratio of 5:1 even though females outnumbered males by a ratio of 2:1 or more (Le Boeuf and Crocker 1996). Killer whales have been observed along the entire northern elephant seal range, from central Baja California, Mexico, to western Alaska, USA. In the Aleutian Islands, where most of the male elephant seals in the present study foraged, killer whales are prevalent (Dahlheim 1997) and have caused a dramatic decline in the population of sea otters, *Enhydra lutris* (Estes et al. 1998). Unlike males, females appear to forage on less densely aggregated prey in the open ocean where predation is less likely. For example, Strasburg (1958) reports catching

6000 pelagic sharks belonging to 12 species throughout the northeastern Pacific where female elephant seals forage; no white sharks were caught or observed. Most females may be selected to avoid coastal areas because they do not get the proportional reproductive benefit from the coastal forage that males get, they cannot exploit the coastal prey as readily as males because of their smaller size, or the risk of getting these prey is too great. Males may also opt for this strategy, in part because the development of great size has made them less effective in capturing pelagic prey.

Purpose of migration: feeding or breeding and molting?—Are northern elephant seals migrating from terrestrial rookeries to obtain food at sea or are they migrating from foraging sites to breed and molt on land? Conventionally, one thinks of seals as being tied to land for breeding and occasionally going to sea to obtain nourishment (e.g., Bartholomew 1970). That is, being on land and in air is the normal state, and diving for food under oxygen constraint is the unusual state that has required numerous marine adaptations that characterize the pinnipeds. Viewed from this perspective, and using the terminology of Dingle (1996), males migrate undistractably, leaving their breeding habitat to journey to a specific foraging area without stopping along the way even if they encounter a rich prey patch. Females, in contrast, exhibit ranging behavior moving from one resource to another. They forage along a general path exploring en route and exploit prey when they find it. Large deviations from the general migratory path are common.

From the other perspective, one can make the case that being at sea is the normal state for elephant seals and that both sexes migrate from foraging habitats in order to breed. Northern elephant seals spend 67–83% of the year foraging at sea (Le Boeuf 1994). Approximately 90% of this time, or 7.2–9 months of the year, is spent underwater, which prompted descriptions of these seals as “surfacers” rather than as “divers” (Kramer 1988, Kooyman 1989). In terms of time, the terrestrial phase is the exceptional behavior in this species. From this perspective, both sexes interrupt foraging at sea to migrate to a traditional terrestrial rookery to breed and molt. We assume that significant hormonal changes accompany the migrations of both sexes, fitting Dingle’s definition of migration requiring that “migrating individuals are undistractable and special physiological mechanisms insure that the behavior takes place.” The fact remains that the sexes are sexually segregated while foraging before initiating the migration to the rookery.

In conclusion, although we cannot specify directly the species taken, the quantity consumed, and the manner in which northern elephant seals catch their prey, data from several sources provide a strong logic for inferring when and where foraging occurs and the general category of prey consumed. Males and females are clearly pursuing different foraging strategies. This in-

formation helps to elucidate the foraging ecology of this species.

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LITERATURE CITED

- Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risks of predation. *Ecology* **70**:999–1007.
- Ainley, D. G., R. R. Henderson, H. R. Huber, R. J. Boekelheide, S. G. Allen, and T. L. McElroy. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. *Southern California Academy of Sciences Memoirs* **9**:109–122.
- Ainley, D. G., C. S. Strong, H. R. Huber, T. J. Lewis, and S. H. Morrell. 1981. Predation by sharks on pinnipeds at the Farallon Islands. *United States National Marine Fisheries Fishery Bulletin* **78**:941–945.
- Alexander, R. D., J. L. Hoogland, R. D. Howard, K. M. Noonan, and P. W. Sherman. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. Pages 402–603 in N. A. Chagnon and W. Irons, editors. *Evolutionary biology and human social behavior: an anthropological perspective*. Wadsworth, Belmont, California, USA.
- Antonelis, G. A., M. S. Lowry, D. P. DeMaster, and C. H. Fiscus. 1987. Assessing northern elephant seal feeding habits by stomach lavage. *Marine Mammal Science* **3**:308–322.
- Antonelis, G. A., M. S. Lowry, C. H. Fiscus, B. S. Stewart, and R. L. DeLong. 1994. Diet of the northern elephant seal. Pages 211–223 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, California, USA.
- Bartholomew, G. A. 1966. A field study of temperature relations in the Galápagos marine iguana. *Copeia* **2**:241–250.
- Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* **24**:546–559.
- Bartholomew, G. A., and R. C. Lasiewski. 1965. Heating and cooling rates, heart rate, and simulated diving in the Galápagos marine iguana. *Comparative Biochemistry and Physiology* **16**:573–582.
- Berger, J. 1991. Pregnancy incentives, predation constraints, and habitat shifts—experimental and field evidence for Big-horn sheep. *Animal Behaviour* **41**:61–77.
- Bleich, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy* **80**:283–289.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* **134**:1–50.
- Born, E. W., and L. O. Knutsen. 1997. Haul-out and diving activity of male Atlantic walrus (*Odobenus rosmarus*) in northeast Greenland. *Journal of Zoology, London* **243**:381–396.
- Bowen, W. D., J. W. Lawson, and B. Beck. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scottish shelf. *Canadian Journal of Fisheries and Aquatic Science* **50**:1768–1778.
- Bowers, M. A., and H. D. Smith. 1979. Differential habitat utilization by sexes of the deer mouse, *Peromyscus maniculatus*. *Ecology* **50**:869–875.
- Boyd, I. L., and T. Arnbohm. 1991. Diving behavior in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biology* **11**:259–266.
- Boyd, I. L., T. A. Arnbohm, and M. A. Fedak. 1994. Biomass and energy consumption of the south Georgia stock of southern elephant seals. Pages 91–117 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, California, USA.
- Briggs, G. D., R. V. Hendrickson, and B. J. Le Boeuf. 1975. Ketamine immobilization of northern elephant seals. *Journal of the American Veterinary Medical Association* **167**:546–548.
- Brodie, P. F. 1975. Cetacean energetics, an overview of intraspecific size variation. *Ecology* **56**:152–161.
- Burgess, W. C., P. L. Tyack, B. J. Le Boeuf, and D. P. Costa. 1998. A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Topical Studies in Oceanography* **45**:1327–1351.
- Campagna, C., M. A. Fedak, and B. J. McConnell. 1999. Post-breeding distribution and diving behaviour of adult male southern elephant seals from Patagonia. *Journal of Mammalogy* **80**:1341–1352.
- Clutton-Brock, T. H., G. R. Iason, and F. E. Guinness. 1987. Sexual segregation and density-related changes in habitat use in male and female deer (*Cervus elaphus*). *Journal of Zoology, London* **211**:275–289.
- Condit, R., and B. J. Le Boeuf. 1984. Feeding habits and feeding grounds of the northern elephant seal. *Journal of Mammalogy* **65**:281–290.
- Congleton, C. A. 1980. *Navigational applications of plane and spherical trigonometry*. Cornell Maritime Press, Centerville, Maryland, USA.
- Costa, D. P., B. J. Le Boeuf, C. L. Ortiz, and A. C. Huntley. 1986. The energetics of lactation in the northern elephant seal. *Journal of Zoology, London* **209**:21–33.
- Crocker, D. E., B. J. Le Boeuf, and D. P. Costa. 1997. Drifting during diving in northern elephant seals: implications for food processing. *Canadian Journal of Zoology* **75**:27–39.
- Dahlheim, M. E. 1997. Photographic catalogue of killer whale, *Orcinus orca*, from the central Gulf of Alaska to the southeastern Bering Sea. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 131. Springfield, Virginia, USA.
- DeLong, R. L., and B. S. Stewart. 1991. Diving patterns of northern elephant seal bulls. *Marine Mammal Science* **7**:369–384.
- DeLong, R. L., B. S. Stewart, and R. D. Hill. 1992. Documenting migrations of northern elephant seals using day-length. *Marine Mammal Science* **8**:155–159.
- Deutsch, C., B. J. Le Boeuf, D. P. Costa, and B. J. Le Boeuf. 1994. Sex differences in reproductive effort in northern elephant seals. Pages 169–210 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, California, USA.
- Dietz, R., and M. P. Heide-Jørgensen. 1995. Movements and swimming speed of narwhals, *Monodon monoceros*, equipped with satellite transmitters in Melville Bay, northwest Greenland. *Canadian Journal of Zoology* **73**:2166–2109.
- Dingle, H. 1996. *Migration: the biology of life on the move*. Oxford University Press, Oxford, UK.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak.

1998. Killer whale predation on sea otters links oceanic and nearshore ecosystems. *Science* **282**:473–476.
- Fancy, S. G., L. F. Pank, D. C. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup, and W. L. Regelin. 1988. Satellite telemetry: a new tool for wildlife research and management. United States Fisheries Wildlife Resources Publication **172**.
- Fedak, M. A., S. S. Anderson, and M. G. Curry. 1983. Attachment of a radio tag to the fur of seals. *Journal of Zoology* **200**:298–300.
- Fletcher, S., B. J. Le Boeuf, D. P. Costa, P. L. Tyack, and S. B. Blackwell. 1996. Onboard acoustic recording from diving elephant seals. *Journal of the Acoustical Society of America* **100**:2531–2539.
- French, J. 1994. Wildlife telemetry by satellite. *Endeavor* **18**:32–37.
- Gales, N. J., and H. R. Burton. 1987. Ultrasonic measurement of blubber thickness of the southern elephant seal, *Mirounga leonina* (Linn.). *Australian Journal of Zoology* **35**:207–217.
- Gautier-Hion, A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology* **49**:237–269.
- Geist, V. 1981. On the reproductive strategies in ungulates and some problems of adaptation. Pages 111–132 in G. G. E. Scudder and J. L. Reveal, editors. *Evolution today*. Proceedings of the Second International Congress of Systematics and Evolutionary Biology, Carnegie Mellon University, Hunt Institute for Botanical Documentation, Pittsburgh, Pennsylvania, USA.
- Hacker, E. S. 1986. Stomach content analysis of short-finned pilot whales (*Globicephala macrorhynchus*) and northern elephant seals (*Mirounga angustirostris*) from the southern California Bight. United States National Marine Fisheries Fishery Bulletin, Southwest Fisheries Center Administrative Report **LJ-86-08C**.
- Hakoyama, H., B. J. Le Boeuf, Y. Naito, and W. Sakamoto. 1994. Diving behavior in relation to ambient water temperature in northern elephant seals. *Canadian Journal of Zoology* **72**:643–651.
- Haley, M. P., C. J. Deutsch, and B. J. Le Boeuf. 1991. A method for estimating mass of large pinnipeds. *Marine Mammal Science* **7**:157–164.
- Haley, M. P., C. J. Deutsch, and B. J. Le Boeuf. 1994. Size, dominance, and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Animal Behavior* **48**:1249–1260.
- Harris, S., W. J. Cresswell, P. G. Forder, W. J. Trewella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mammalian Review* **20**:97–123.
- Harvey, J. T., G. A. Antonelis, and C. J. Casson. 1989. Quantifying errors in pinniped food habit studies. Biennial Conference on Marine Mammals **8**:26.
- Helm, R. C. 1984. Rate of digestion in three species of pinnipeds. *Canadian Journal of Zoology* **62**:1751–1756.
- Hill, R. D. 1994. Theory of geolocation by light levels. Pages 227–236 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley, California, USA.
- Hobson, K. A., and J. L. Sease. 1998. Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Steller sea lions. *Marine Mammal Science* **14**:116–129.
- Huber, H. R., C. Beckham, and J. Nisbet. 1991. Effects of the 1982–83 El Niño on northern elephant seals on the South Farallon Islands, California. Pages 219–233 in F. Trillmich and K. A. Ono, editors. *Pinnipeds and El Niño: responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- Hui, C. A. 1979. Undersea topography and distributions of dolphins of the genus *Delphinus* in the southern California bight. *Journal of Mammalogy* **60**:521–527.
- Iverson, S. J. 1993. Milk secretion in marine mammals in relation to foraging: can milk fatty acids predict diet? Pages 263–291 in I. L. Boyd, editor. *Marine mammals: advances in behavioural and population biology*. Clarendon, Oxford, UK.
- Iverson, S. J., J. P. Y. Arnould, and I. L. Boyd. 1997a. Milk fatty acid signatures indicate both major and minor shifts in the diet of lactating Antarctic fur seals. *Canadian Journal of Zoology* **75**:188–197.
- Iverson, S. J., K. J. Frost, and L. F. Lowry. 1997b. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound. *Marine Ecology* **151**:255–271.
- Kenney, R. D., H. E. Winn, and M. C. Macaulay. 1995. Cetaceans in the Great South Channel, 1979–1989: right whale (*Eubalaena glacialis*). *Continental Shelf Research* **15**:385–414.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna 68. Bureau of Sport Fisheries and Wildlife, United States Government Printing Office, Washington, D.C., USA.
- Klimley, A. P. 1985. The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. *Southern California Academy of Sciences Memoirs* **9**:15–40.
- Klimley, A. P., S. D. Anderson, P. Pyle, and R. P. Henderson. 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia* **1992**:680–690.
- Kooyman, G. L. 1989. *Diverse divers: physiology and behavior*. Springer-Verlag, Berlin, Germany.
- Kramer, D. L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**:89–94.
- Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist* **14**:163–176.
- Le Boeuf, B. J. 1986. Sexual strategies of seals and walrus. *New Scientist* **1491**:36–39.
- Le Boeuf, B. J. 1994. Variation in the diving pattern of northern elephant seals with age, mass, sex, and reproductive condition. Pages 237–252 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley, California, USA.
- Le Boeuf, B. J., D. P. Costa, A. C. Huntley, and S. D. Feldkamp. 1988. Diving behavior of female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology* **66**:446–458.
- Le Boeuf, B. J., and D. E. Crocker. 1996. Diving behavior of elephant seals: implications for predator avoidance. Pages 193–206 in A. P. Klimley and D. G. Ainley, editors. *Great white sharks: the biology of *Carcharodon carcharias**. University of California Press, Berkeley, California, USA.
- Le Boeuf, B. J., D. E. Crocker, S. B. Blackwell, P. A. Morris, and P. H. Thorson. 1993. Sex differences in foraging in northern elephant seals. Pages 149–178 in I. L. Boyd, editor. *Marine mammals: advances in behavioral and population biology*. Oxford University Press, London, UK.
- Le Boeuf, B. J., and R. M. Laws, editors. 1994. *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley, California, USA.
- Le Boeuf, B. J., P. A. Morris, S. B. Blackwell, D. E. Crocker, and D. P. Costa. 1996. Diving behavior of juvenile northern elephant seals. *Canadian Journal of Zoology* **74**:1632–1644.
- Le Boeuf, B. J., Y. Naito, T. Asaga, D. Crocker, and D. P.

- Costa. 1992. Swim speed in a female northern elephant seal: metabolic and foraging implications. *Canadian Journal of Zoology* **70**:786–795.
- Le Boeuf, B. J., Y. Naito, A. C. Huntley, and T. Asaga. 1989. Prolonged, continuous, deep diving by northern elephant seals. *Canadian Journal of Zoology* **67**:2514–2519.
- Le Boeuf, B. J., and J. Reiter. 1991. Biological effects associated with El Niño Southern Oscillation, 1982–83, on northern elephant seals breeding at Año Nuevo, California. Pages 206–218 in F. Trillmich and K. A. Ono, editors. *Pinnipeds and El Niño: responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- Le Boeuf, B. J., M. Riedman, and R. S. Keyes. 1982. Shark predation on pinnipeds in California coastal waters. *United States National Marine Fisheries Fishery Bulletin* **80**:891–895.
- Litvaitis, J. A. 1990. Differential habitat use by sex of snowshoe hares (*Lepus americanus*). *Journal of Mammalogy* **71**: 520–523.
- Lyons, K. 1991. Variation in feeding behavior of female sea otters, *Enhydra lutris*, between individuals and with reproductive condition. Dissertation. University of California, Santa Cruz, California, USA.
- Main, M. B., and B. E. Coblenz. 1990. Sexual segregation among ungulates: a critique. *Wildlife Society Bulletin* **18**: 204–210.
- Main, M. B., F. W. Weckerly, and V. C. Bleich. 1996. Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* **77**:449–461.
- McConnell, B. J., C. Chambers, and M. A. Fedak. 1992a. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* **4**:393–398.
- McConnell, B. J., C. Chambers, K. S. Nicholas, and M. A. Fedak. 1992b. Satellite tracking of grey seals (*Halichoerus grypus*). *Journal of Zoology, London* **226**:271–282.
- McConnell, B. J., and M. A. Fedak. 1996. Movements of southern elephant seals. *Canadian Journal of Zoology* **74**: 1485–1496.
- McCullough, D. R., D. H. Hirth, and S. J. Newhouse. 1989. Resource partitioning between sexes in white-tailed deer. *Journal of Wildlife Management* **53**:277–283.
- Morris, D. W. 1987. Sexual differences in habitat use by small mammals: evolutionary strategy or reproductive constraint? *Oecologia (Berlin)* **65**:51–57.
- Nordoy, E. S., and A. S. Blix. 1985. Energy sources in fasting grey seal pups evaluated with computed tomography. *American Journal of Physiology* **24a**:R471–R476.
- Orr, R. T. 1970. *Animals in migration*. Macmillan, New York, New York USA.
- Priede, I. G., and J. French. 1991. Tracking of marine animals by satellite. *International Journal of Remote Sensing* **12**: 667–680.
- Reed, R. K., and P. J. Stabeno. 1997. Long-term measurements of flow near the Aleutian Islands. *Journal of Marine Research* **55**:565–575.
- Reilly, S. B. 1990. Seasonal changes in the distribution and habitat differences among dolphins in the eastern tropical Pacific. *Marine Ecology Progress Series* **66**:1–11.
- Riedman, M. 1990. *The pinnipeds: seals, sea lions, and walrus*. University of California Press, Berkeley, California, USA.
- Smith, S. J., S. J. Iverson, and W. D. Bowen. 1997. Fatty acid signatures and classification trees: new tools for investigating the foraging ecology of seals. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1377–1386.
- Stewart, B. S. 1996. Uncommon commuters. *Natural History* **2**:58–63.
- Stewart, B. S. 1997. Ontogeny of differential migration and sexual segregation in northern elephant seals. *Journal of Mammalogy* **78**:1101–1116.
- Stewart, B. S., and R. L. DeLong. 1993. Seasonal dispersion and habitat use of foraging northern elephant seals. *Symposia of the Zoological Society of London*, **66**:179–194.
- Stewart, B. S., and R. L. DeLong. 1994. Post-breeding foraging migrations of northern elephant seals. Pages 290–309 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley, California, USA.
- Stewart, B. S., and R. L. DeLong. 1995. Double migrations of the northern elephant seal, *Mirounga angustirostris*. *Journal of Mammalogy* **76**:196–205.
- Stirling, I. 1975. Factors affecting the evolution of social behaviour in the pinnipeds. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **169**:205–212.
- Stirling, I. 1983. The evolution of mating systems in pinnipeds. Pages 489–527 in J. F. Eisenberg and D. G. Kleiman, editors. *Advances in the study of mammalian behavior*. American Society of Mammalogists, Shippensburg, Pennsylvania, USA.
- Strasburg, D. W. 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. *United States National Marine Fisheries Fishery Bulletin* **58**:335–361.
- Sukumar, R., and M. Gadgil. 1988. Male–female differences in foraging on crops by Asian elephants. *Animal Behaviour* **36**:1233–1235.
- Trillmich, K. G. K., and F. Trillmich. 1986. Foraging strategies of the marine iguana, *Amblyrhynchus cristatus*. *Behavioral Ecology and Sociobiology* **18**:259–266.
- van Franeker, J. A. 1992. Top predators as indicators for ecosystem events in the confluence zone and the marginal ice zone of the Weddell and Scotia seas, Antarctica, November 1988 to January 1989. *Polar Biology* **12**:93–102.
- Webb, P. M., D. E. Crocker, S. B. Blackwell, D. P. Costa, and B. J. Le Boeuf. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology* **201**:2349–2358.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. *Ecology* **69**:1352–1366.
- Whitehead, H., S. Brennan, and D. Grover. 1992. Distribution and behavior of male sperm whales on the Scotian Shelf, Canada. *Canadian Journal of Zoology* **70**:912–918.
- Wikelski, M., and Trillmich, F. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* **52**:922–936.
- Winn, H. E., C. A. Price, and P. W. Sorenson. 1986. The distributional biology of the right whale (*Eubalaena glacialis*) in the western North Atlantic. Special issue 10. Report of the International Whaling Commission, Impington, Cambridge, UK.
- Woodhead, P. M. J. 1966. The behaviour of fish in relation to light in the sea. *Oceanography and Marine Biology* **4**: 337–403.
- Worthy, G. A. J., P. A. Morris, D. P. Costa, and B. J. Le Boeuf. 1992. Moulting energetics of the northern elephant seal. *Journal of Zoology, London* **227**:257–265.