

SPATIAL HABITAT USE PATTERNS OF SEA OTTERS IN COASTAL WASHINGTON

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Sea otter (*Enhydra lutris kenyoni*) movements, home range, and activity budgets were described from data collected during very-high-frequency radiotelemetry studies of 75 individuals on the outer coast of Washington State between 1992 and 1999. Sea otters were located at least once per week from 22 accessible sites along the coast. Over the 7-year study period, range expansion occurred from the core range north and east into the Strait of Juan de Fuca (SJF) as well as southward on the outer coast. Forty-three percent of the sea otters moved into the SJF at least once, most often in winter, using habitat that had not been occupied by sea otters since their extirpation 100 years ago. All sea otters spent portions of their time in the vicinity of Cape Alava, and many animals demonstrated consistent periodic seasonal shifts between specific portions of the coastline over several years. Ninety-five percent annual linear home ranges differed between sex and age classes. Adult males used the largest amount of coastline ($50 \text{ km} \pm 9 \text{ SD}$) and subadult females used the least ($24 \pm 9 \text{ km}$). Both adult males and females demonstrated high seasonal periodicity in range use in summer and winter. Twenty-four-hour time budgets in the core portion of the range revealed on average sea otters spent $41\% \pm 14\% \text{ SD}$ of the time foraging and $45\% \pm 13\%$ of the time resting (age and sex classes pooled). Adult and subadult female sea otters were most frequently found resting and foraging close to shore ($<1,000 \text{ m}$) and in shallow water (0–10 m), whereas adult and subadult males rested and foraged $>1,000 \text{ m}$ offshore and at depths between 10 and 30 m. Given current rates of population growth and observed mobility, sea otters in Washington have high potential for range expansion into unoccupied habitat such as Grays Harbor, Willapa Bay, the SJF, or along Vancouver Island.

Key words: dispersal, range expansion, sea otter, site fidelity, Washington

The sea otter (*Enhydra lutris kenyoni*, Wilson et al., 1991) population in Washington State was reintroduced to the outer coast in 1969–1970. By 2007 the population numbered at least 1,125 animals, having increased at an average rate of 8–10% per year since 1977 (Jameson 1998; Jameson et al. 1982,

1986). Sea otters in Washington are the result of a founding population of no more than 30 individuals (Jameson and Jeffries 1999; Lance et al. 2004). Currently, the core range of the Washington population spans approximately 120 km of coastline, a relatively small range compared to the several-hundred-kilometer ranges of populations in California and Alaska (Doroff et al. 2003; Jameson 1989; Ralls et al. 1995; Tinker 2004). Historically and pre-extirpation, this population was distributed along Vancouver Island, British Columbia, Canada, the entire Washington coast down to the mouth of the Columbia River, and south into Oregon.

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FIG. 1.—Map of listening sites where radiotagged sea otters (*Enhydra lutris*) were monitored from the Washington coast. Pooled resighting locations were grouped into regions according to different-colored stars. Figure includes the localities mentioned in the “Materials and Methods” and the approximate range of sea otters during the study. Shaded areas illustrate established population range (gray region) and new habitat initially used in 1995 (stippled region).

The current sea otter population in Washington is primarily distributed within rocky kelp forest habitat between Destruction Island and Makah Bay (~80 km between the 2 regions) on the outer coast (Fig. 1). In 1995, individuals moved to the north from Makah Bay and were initially sighted east of Cape Flattery in the Strait of Juan de Fuca (SJF) and by the late 1990s, sea otters were found in the SJF as far as Pillar Point (Fig. 1). This resulted in the population occupying habitat that had not been used by sea otters for almost a century since their extirpation, and this expansion nearly doubled the range of this population in <5 years. Since 2000, only a few sea otters have remained in the SJF east of Cape Flattery.

Annual aerial and ground-based population surveys along the outer coast and in the SJF combined with opportunistic sighting reports (Lance et al. 2004) have been the primary means of documenting the distribution of sea otters in Washington. Although these data have been useful for detecting general changes in distribution, no data have been presented quantifying individual movements, dispersal, and space-use patterns.

Factors surrounding the management of sea otters in Washington include fisheries conflicts, vulnerability to current (and developing) anthropogenic activities, and the potential for exchange between sea otters in British Columbia (Gerber et al. 2004; Lance et al. 2004). Here we quantify movements,

home range, spatial habitat-use patterns, and activity budgets of sea otters in Washington using very-high-frequency radiotelemetry data collected from individual animals between 1992 and 1999. These results are important for the management of the population because movement data from an increasing population provide a foundation for predicting rates of range expansion with respect to suitable unoccupied habitat (Tinker et al. 2008b).

MATERIALS AND METHODS

Study site.—The study was conducted on the coastline of Washington between Dungeness Spit along the northern coast (48°11.2'N, 123°5.8'W) out the SJF to Cape Flattery and south to the Washington–Oregon border (42°N, 124°13'W; Fig. 1). Coastal Washington has a typical eastern Pacific maritime climate, with average annual temperatures ranging from 2°C to 16°C, and average monthly precipitation ranging from 8 to 36 cm.

Telemetry data collection.—Sea otters were captured along the outer coast of Washington State using diver-operated Wilson traps (Ames et al. 1983). Captured otters were anesthetized, weighed, and measured following methods in Monson et al. (2001). Morphometric measurements and blood samples were collected, premolars were extracted for cemen-

tum aging, and unique very-high-frequency radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota) were implanted into the peritoneal cavity for tracking individuals. Sea otters were classified into age and sex classes: adult females (AF), adult males (AM), subadult females (SF), and subadult males (SM). Ages of sea otters were assigned in the field based on body mass, in the case of females on the presence of a pup, a nose scar or wound from mating, and tooth condition. The general age category was adjusted as necessary once the tooth cementum analysis was completed. Any sea otter <3 years old was classed as a subadult; those >3 years old were classed as adult. Individuals still with their mothers at capture were classed as pups. Animals were cared for according to the principles and guidelines of the Canadian Council on Animal Care, guidelines approved by the American Society of Mammalogists (Gannon et al. 2007), and Marine Mammal Protection Act research permit PRT-777239.

Following tagging and release, at least 1 technician was in the field monitoring sea otters on a year-round basis. During the summer months, 2 technicians were in the field and effort was divided so that more coastline could be covered. Technicians worked for 5 days per week except between mid-December and early January. Technicians were instructed to locate each tagged sea otter from land on a minimum weekly basis, although this frequency was not always possible due to weather conditions. Each accessible relocation site along the coast where sea otters were known to concentrate ($n = 22$; Fig. 1) was searched for 30–60 min before the technician moved on to the next site. Very-high-frequency signals of all tagged sea otters were searched for at each site. Access to most sites was only by fairly long hikes and separated by many miles, therefore only 1 or 2 search locations could be accessed each day.

Telemetry searches were conducted from sites using an Advanced Telemetry Systems receiver and a 4-element yagi antenna. When a signal was heard, a visual search for the sea otter was made with the aid of binoculars and a 50–80× Questar telescope (Questar Corporation, New Hope, Pennsylvania). Once the individual was sighted, the location was noted on large-scale detailed habitat maps (1:12,000). At the time of the visual observation, the activity state of each sea otter was recorded and placed into several activity categories, with primary categories being resting or foraging.

Visual sightings resulted in individual locations accurate to a few meters. When it was not possible to obtain a visual location cue, an effort was made to triangulate the position of the sea otter using very-high-frequency signals. Triangulation often was difficult to accomplish because of the distance between listening sites and logistical complexities of maneuvering along the coast by foot. Consequently, locations obtained via triangulation were sometimes based on the direction and quality of the signal. Individual sea otters were located no more than once each survey day; therefore, each location was treated as an independent sample. This sample of tagged sea otters was considered to be representative of the sea otter population in Washington.

Data analysis.—In order to make inferences on movement behaviors using robust sample sizes, the 22 resighting observation locations were grouped into 9 coastal regions (see Fig. 1) from the south proceeding north: 1) Destruction including Giants Graveyard, Perkins Reef, and Destruction Island; 2) Cedar including Cedar Creek, Saddle Rock, Bluff Point, and Chilean Memorial; 3) Yellow Banks; 4) Sand Point; 5) Alava including Cape Alava and South Ozette Island; 6) Arches including Point of Arches, Father and Son, and Duk Point; 7) Anderson Point; 8) Flattery including Cape Flattery and Tatoosh Island; and 9) SJF including Shipwreck Point, Bullman Beach, Waddah Island, Koitlah Point, and Midway Point. Analysis of seasonal dynamics was performed by allocating proportions of time spent by individual sea otters in different regions per month, $\hat{P}_{i,region,month}$. The proportions were estimated such that:

$$\hat{P}_{i,region,month} = \frac{n_{i,region,month}}{\sum_{region=1}^9 n_{i,region,month}}, \quad (1)$$

where n represents the number of resightings and i refers to the individual. Thus, an animal sighted 3 times in region A and once in region B was assumed to have split its time 75%:25% between the 2 regions. A monthly temporal period was chosen for the analysis so that multiple resightings could be included in each region (median number of sightings per individual per month was 2.67), while at the same time relatively detailed seasonal movements could be discerned without being overly biased by more frequent sightings at a single location.

Locations of sea otters were assigned to the closest point on the coast by perpendicularly projecting each location along the coastline. This reduced the dimension of the spatial data to a line and better approximated actual distances traveled, rather than linear displacements, many of which crossed land. The coastline delineation began at the southernmost extent of the range of tracked otters (at 47.5°N, 124.35°W near the Queets River, referred to as coastline kilometer = 0) and extended north and east to Clallam Bay (48.25°N, 124.3°W) in the SJF (coastline kilometer = 145). Cape Flattery was located at coastline kilometer 92. The coastal data were based on the CIA World Data Bank II (<http://www.evl.uic.edu/pape/data/WDB/>) accessed via the “maps” package in R (R Development Core Team 2006).

Kernel home ranges.—One-dimensional nonparametric distributions of coastal area use were obtained for each individual sea otter with >20 observations using Gaussian kernel estimates with a bandwidth of 3.75 coastal km (corresponding to a 95% coverage of 15 coastal km for each of the kernels). Observations were irregularly distributed in time, with intervals ranging from 4 days to >1 year; thus, each observation was weighted according to the density of neighboring points. For n observations X_i made at times T_i , weights were calculated according to:

$$W_1 = \max[2(T_2 - T_1), 30]/K \quad (2)$$

$$W_i = \max[(T_{i+1} - T_{i-1}), 30]/K, \quad (3)$$

TABLE 1.—Statistics on sample sizes of sea otters (*Enhydra lutris*) tracked and transmitter performance between 1992 and 1999 along the coast of Washington. Durations are recorded in days. AF = adult female, AM = adult male, SF = subadult female, and SM = subadult male.

Age–sex	No. individuals tracked	Average tracking duration (SD)	Maximum tracking duration	Minimum tracking duration	Average no. locations (SD)
AF	43	753 (579)	2,145	42	40 (31)
AM	14	729 (385)	1,483	125	36 (25)
SF	9	453 (354)	814	35	18 (19)
SM	9	453 (417)	1,382	7	21 (18)

where $2 \leq i \leq n - 1$;

$$W_n = \max[2(T_n - T_{n-1}), 30]/K, \quad (4)$$

where W_i is the weighting coefficient, and $K = \sum_i^n W_i$ is a normalizing factor. According to this weighting, 4 observations within a single month have one-fourth the weight of a single observation, but 1 observation over a 6-month period has no more weight than 1 observation in a single month. This weighting assured that neither overly sparse nor clustered observations had disproportionate weight in estimating the kernel distribution.

Kernel distributions also were calculated for 4 age and sex classes in 2 general periods: summer (May–October) and winter (November–April). A 95% coastal range–use estimate was obtained from each of these distributions (annual, summer, and winter). When an individual's range was highly multimodal or discontinuous along the coastline, the 95% range estimate excluded sections of the coast that were not visited.

Seasonal range overlap.—A seasonal distribution overlap index (SDOI) was calculated to quantify the bimodality in annual ranges for each individual. This was equal to the proportion of overlap between the 2 normalized distributions (summer and winter) for each animal. An SDOI = 0 indicated that the summer and winter distributions were nonintersecting and separate, whereas an SDOI = 1 indicated that there was no difference in the winter and summer coastal use. The effect of age and sex factors on the 95% home range and SDOI were tested using an analysis of variance (ANOVA) model with *P*-values derived from “type II” model comparisons to account for the unbalanced design. The R statistical package was used for all analyses (R Development Core Team 2006).

Activity budgets.—Activity budget data were collected from focal observations of a subset of animals in the core portion of the range observed over a continuous 24-h period. Otters were initially located by radiotelemetry and subsequently monitored by telescope as long as possible. Activity was determined by visual observation, or signal characteristics, and placed into 1 of 5 categories: resting, foraging, grooming, swimming, or active but not feeding. Observations of activity state were recorded at 10-min intervals and used to quantify individual activity budgets (see also Gelatt et al. 2002; Ralls and Siniff 1990). During hours of darkness, or when visual contact was lost, only resting, foraging, and active but not foraging categories were used.

Depth and distance from shore.—Geographic locations for sea otters were related to a depth value (m) based on a bathymetric grid in ArcINFO (www.esri.com; compiled from the National Oceanic and Atmospheric Administration bathymetric charts by the Strategic Environmental Assessments Division of the National Oceanic and Atmospheric Administration's Office of Ocean Resources, Conservation and Assessment). Data were used to determine depths and distance to the mainland coast for all resting and foraging locations. Locations were binned into 1 of 5 bathymetric depth categories (0- to 50-m depths in 10-m increments) and 1 of 6 offshore horizontal distance categories (between the coast and 4,000 m offshore in 500-m increments). Distribution of locations with sea otters resting and foraging was calculated across all depth or distance categories based on the total number of locations an individual spent in either activity state. The mean normalized proportion of time spent in each depth and distance bin was calculated for each age and sex class based on average values from individuals. Statistical models were developed to quantitatively describe sea otter activity states at each spatial location. The proportion of locations where otters were foraging or resting in each offshore depth or offshore distance bin was analyzed with the generalized linear model function, estimated using maximum likelihood based on a binary model (link = logit) structure. Individuals were used as the unit in all statistical analyses. Parameter estimates and standard errors were back-transformed.

RESULTS

Data were collected from 75 individual sea otters (52 females and 23 males) between 1992 and 1999. On average, individuals were tracked for 684 days \pm 515 SD (range 7 days to 5.9 years) with an average of 34 radio locations per individual \pm 29 SD (Table 1). The number of resightings per sea otter per month ranged from 1.6 (in December) to 5.8 (in August) with a mean of 2.9. In general, instrument longevity was better for adults, with average duration of radiotags of >2 years and maximum durations of >5 years. Instruments deployed on subadult animals lasted on average 1.3 years and maximum durations were shorter than 5 years (Table 1). Locations were obtained from animals throughout the range of the population, yet were clearly concentrated in focal areas on the outer coast such as Makah Bay, Cape Alava, Sand Point, and Yellow Banks.

Individual movements.—Tagged animals dispersed widely from their original tagging site and many traveled throughout

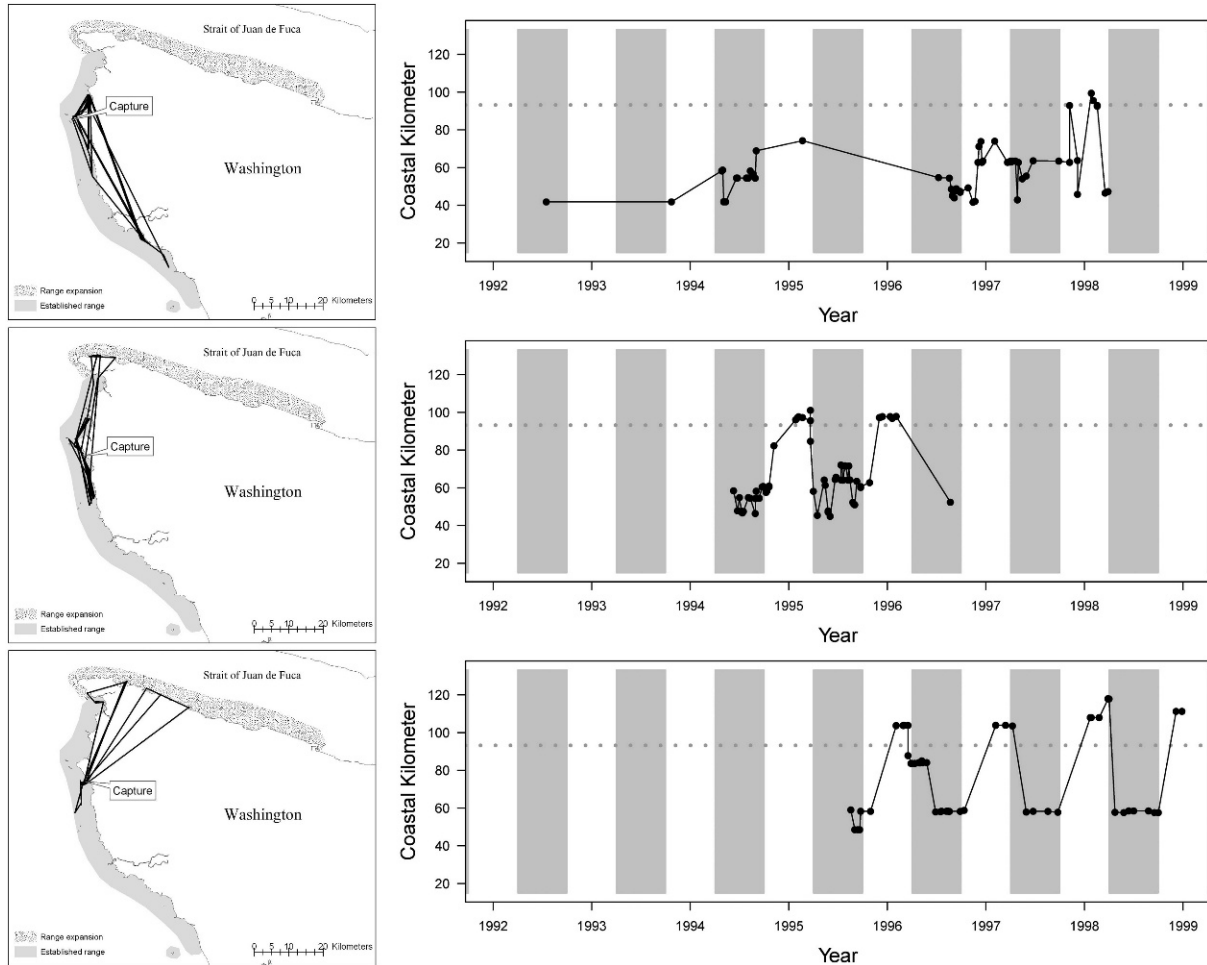


FIG. 2.—Movements of a) sea otter 09 (adult female), b) sea otter 02 (adult female), and c) sea otter 43 (adult male). Maps (left panels) show movement track lines along the coastline, whereas time series (right panels) show movement projected through time with respect to coastline kilometer. Note site fidelity to specific segments of the coastline in different seasons. Shaded bars represent winter (white) and summer (gray). Dashed line indicates the location of Cape Flattery.

the range of the population. All sea otters tracked in this study spent portions of the time on the outer coast, especially in the vicinity of Cape Alava; however, individuals showed high seasonal fidelity to specific portions of the coastline. Animals tracked for several years demonstrated consistent periodic shifts in summer and winter (Figs. 2a–c). The SJF or the southern portion of the outer coast were frequent wintering areas, whereas in summer, most individuals were located in the core range on the outer coast in the vicinity of Cape Alava and Sand Point. Shifts between sites sometimes covered distances of >45 km and often were made in <14 days. In some cases individuals displayed remarkable seasonal fidelity year after year (Figs. 2a and 2c), whereas in others there was no apparent pattern (Fig. 2b).

Seventy sea otters were monitored for >6 months, and of these, 43% moved north to Cape Flattery and east into the SJF during the study period ($n = 17$ females and 13 males). Movements into the SJF were strongly significantly biased toward adult animals, with 87% of adults entering these waters.

Kernel home ranges.—One-dimensional nonparametric distributions of coastal area use were obtained for each individual with >20 observations and used to estimate 95% annual kernel home ranges. Linear home ranges were highly variable between sex and age classes (Fig. 3; Table 2). On an average annual basis, adult males used the largest amount of coastline ($50 \text{ km} \pm 9 \text{ SD}$) and subadult females used the least ($24 \pm 9 \text{ km}$). Adult females had significantly smaller 95% home ranges than adult males ($38 \pm 10 \text{ km}$), yet had 95% ranges similar to those of subadult males. Age and sex were both significant factors for explaining differences in 95% home range (ANOVA, type II $P < 0.01$).

Ninety-five percent kernel home ranges also were calculated for each individual in summer and winter to determine seasonal periodicity. There was large variation in seasonal ranges and no clear patterns between age and sex classes were detected. In general, distributions for adult males were bimodal and clearly shifted from one section of the coast in summer to another in winter with little overlap (Fig. 4A). However, the sample size for adult males was small ($n = 7$)

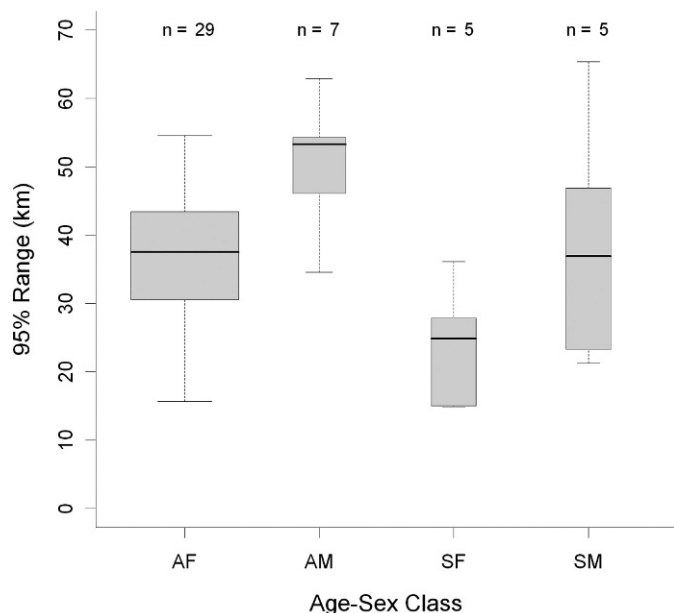


FIG. 3.—Box plot of mean 95% annual linear home ranges for each of 4 age–sex classes of sea otters (*Enhydra lutris*). Gray region is the 25th–75th percentile, the horizontal line is the median, and the dashed lines indicate 1.5 times the interquartile range. AF = adult female, SF = subadult female, AM = adult male, and SM = subadult male.

and in at least 2 of these cases there was significant overlap between the 2 seasons. Similar bimodal patterns were observed for several adult females; however, although some clearly shifted seasonally (Fig. 4B) others also remained in the same area year-round (Fig. 4C). Subadult females demonstrated the least seasonal periodicity in range use (Fig. 4D).

The SDOI, or proportion of summer and winter normalized distributions for each individual that overlapped, ranged from extremes of 0.1 (for a subadult male) to 0.97 (for a subadult female). Mean SDOIs for the 4 age–sex classes were 0.63 ± 0.2 SD for adult females, 0.5 ± 0.24 for adult males, 0.7 ± 0.26 for subadult females, and 0.46 ± 0.22 for subadult males. Overlap between summer and winter distribution was significantly lower for males (adult and subadults) than for females (ANOVA, type II $P = 0.03$). However, age was not significant (type II $P = 0.69$).

Population patterns.—Over the entire study period, the core area around Cape Alava remained important for females (both adults and subadults; Fig. 5). There was a small increase in use of Cape Flattery by females, together with exploration of

the southern extent of the range south of Destruction Island on the outer coast in 1995. The distribution of males was more dynamic, with individuals exploring both the northern and southern extent of the established range (Fig. 5). Between 1996 and 1998, there was a clear increase in the use of the SJF by males, both with respect to the amount of time animals spent in the area and the distance ventured east (Fig. 5).

Females were present at high frequency in the vicinity of Cape Alava throughout the year, with a slight decrease in January and February when females shifted north (Fig. 6). Males heavily used the SJF in winter months, especially between December and April (Fig. 6). However, between spring and fall, and especially in summer, males essentially used all portions of the coast equally. There was a small but consistent use of Destruction Island by females, and males only appeared in this area in winter. The distributions of time spent in different areas varied significantly between months for both sexes (chi-square contingency test, $P < 0.0001$).

Twenty-four-hour activity budgets.—Activity budget data were collected between August and November (1994–1997) within the core range on the outer coast, primarily between Point of Arches and Chilean Memorial, with the majority of observations collected in the vicinity of Cape Alava (Fig. 1). More than 762 h of activity data were collected from 25 sea otters observed at 10-min intervals for 24-h periods. Observations ranged from a minimum of 5 h 30 min to 24 h; however, 82% of the observation periods used in the analysis were a complete 24 h in duration. The focal animals included 16 adult females without pups, 5 adult females with pups, 1 adult male, 2 subadult males, and 1 subadult female. When ages and sexes were pooled, sea otters in Washington spent on average $41\% \pm 14\%$ SD of their time feeding and $45\% \pm 13\%$ of their time resting (Table 3). These values did not vary significantly when adult females with and without pups were examined. Comparative statistical analyses of adult males and subadults were confounded by low samples sizes of 1 or 2 animals in each category (Table 3).

Locations and habitat features.—Very-high-frequency telemetry locations collected from sea otters were mostly obtained during daylight hours; therefore, analyses of locations with respect to depth and distance were not confounded by diurnal patterns. In general, the proportion of locations obtained for resting sea otters declined with increasing offshore depth for all age–sex classes. Adult females spent the largest proportion of their total resting time ($76\% \pm 3\%$ SE) in the shallowest habitat (0–10 m). The 3

TABLE 2.—Statistics on 1-dimensional linear kernel home ranges for age and sex classes of sea otters (*Enhydra lutris*) tagged and monitored along the coast of Washington between 1992 and 1999, and fraction of seasonal overlap between summer and winter distributions. Animals used in the analysis had at least 20 telemetry locations each. AF = adult female, AM = adult male, SF = subadult female, and SM = subadult male.

Age–sex	No. individuals	Mean no. locations per individual (SD)	Mean 95% kernel range (SD)	Mean seasonal distribution overlap (SD)
AF	29	52 (26.2)	38 (10)	0.63 (0.2)
AM	7	54 (13.2)	50 (9)	0.50 (0.24)
SF	5	45 (24.4)	24 (9)	0.70 (0.26)
SM	5	40 (8.7)	39 (18)	0.46 (0.22)

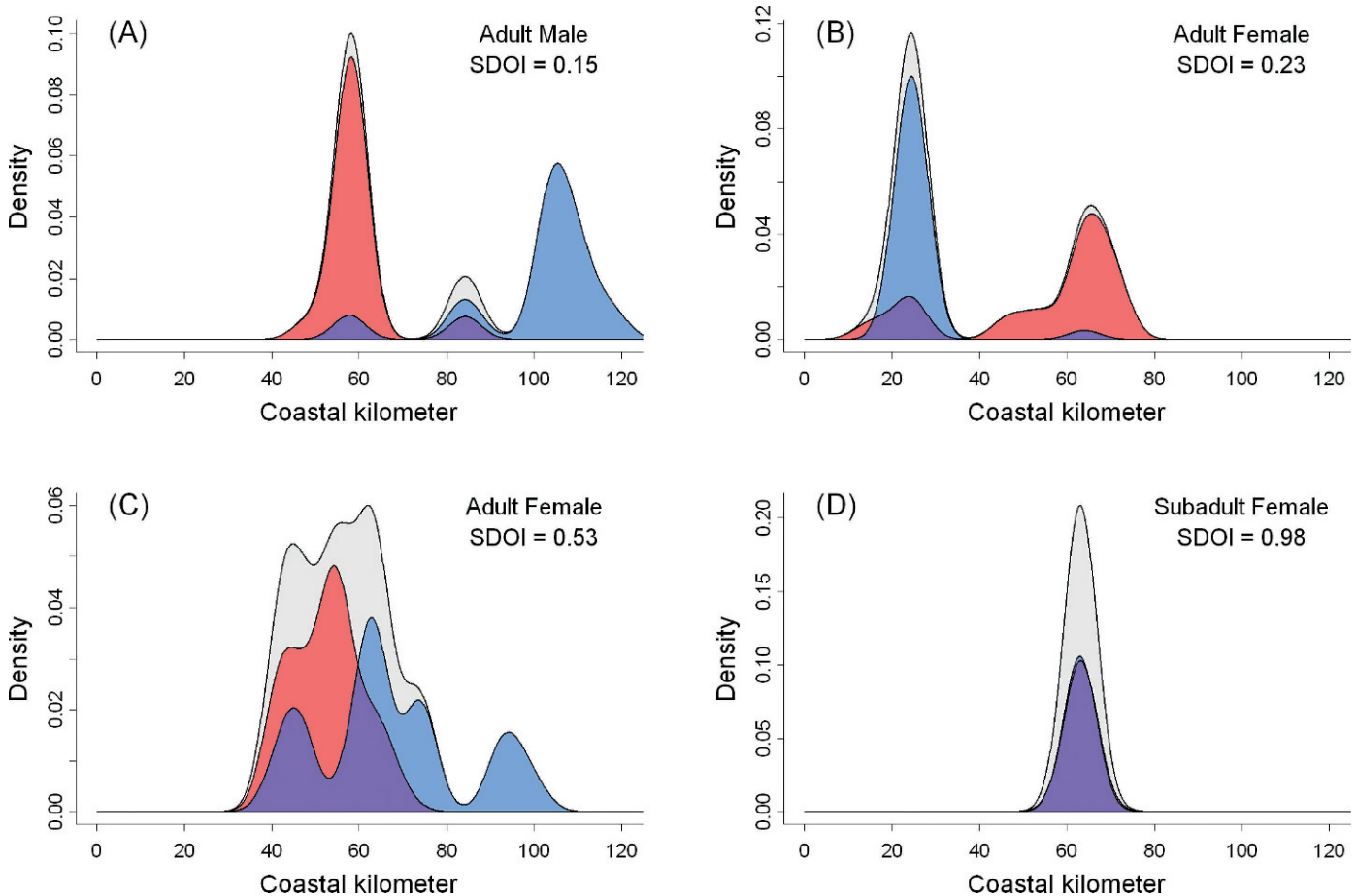


FIG. 4.—One-dimensional nonparametric kernel distributions of coastal area use shown for 4 selected individual sea otters (*Enhydra lutris*). The annual distribution for each individual is in gray, the summer distribution is in red, and the winter distribution is in blue. Seasonal distribution overlap index (SDOI), or proportion of overlap between summer and winter normalized distributions, is in purple. Distributions are shown for A) sea otter 43, B) sea otter 09, C) sea otter 02, and D) sea otter 22. See Fig. 2 for movements of 3 of these individuals.

other age–sex classes spent less time at 0–10 m (52%) and instead evenly distributed their time across the first 3 depth categories (to 35 m). Larger differences were detected in the proportion of foraging locations by offshore depth (Fig. 7). Adult female sea otter locations were generally close to shore (0–10 m; 60% \pm 5% SE of foraging time) and the proportion of foraging locations rapidly declined beyond 10 m to be negligible beyond 30 m. Adult males spent less time foraging in 0- to 10-m habitat (22% \pm 8%) and most of their time foraging between 10 and 30 m (32–34% \pm 8–9% of foraging time). Subadult male and female otters demonstrated patterns similar to their adult counterparts. Proportion of total foraging time for all age–sex classes (1–2%) was minimal beyond 40 m.

Female sea otters of both age classes tended to rest <1,000 m offshore (42–43% \pm 3–6% SE of resting time). Resting time for females declined by a factor of 2 at distances > 1,000 m from the coast and continued to decline, until negligible at 2,000 m. Adult males rested almost 1,000 m farther offshore than females, with a bimodal peak in resting time with 40% \pm 6% between 1,000 and 1,500 m and 11% \pm 3% between 2,000 and 2,500 m. Subadult males fell between the pattern detected for females (peaking between 500 and

1,000 m) and adult males (between 1,000 and 2,000 m). The greatest variability was detected when foraging time was distributed by distance from shore. Adult females spent the largest proportion of their foraging time <1,000 m from the coast (43% \pm 4%), with very similar patterns demonstrated by subadult females. However, adult and subadult males behaved differently. Foraging time of males was more evenly distributed across a wider range of offshore distances, and males spent far less time foraging close to shore, instead distributing their foraging time as far as 3,500 m offshore. Subadult males foraged between 2,000 and 2,500 m offshore. Variability was relatively high for parameter estimates in each age class and most confidence intervals were overlapping, suggesting that foraging time was highly variable with respect to offshore distance.

DISCUSSION

Population status and movements.—Recent surveys of sea otters in Washington demonstrate that the population has been growing rapidly, yet continues to occupy habitat primarily along the outer coast of the Olympic Peninsula between Destruction Island and Cape Flattery. In 2007, a minimum of

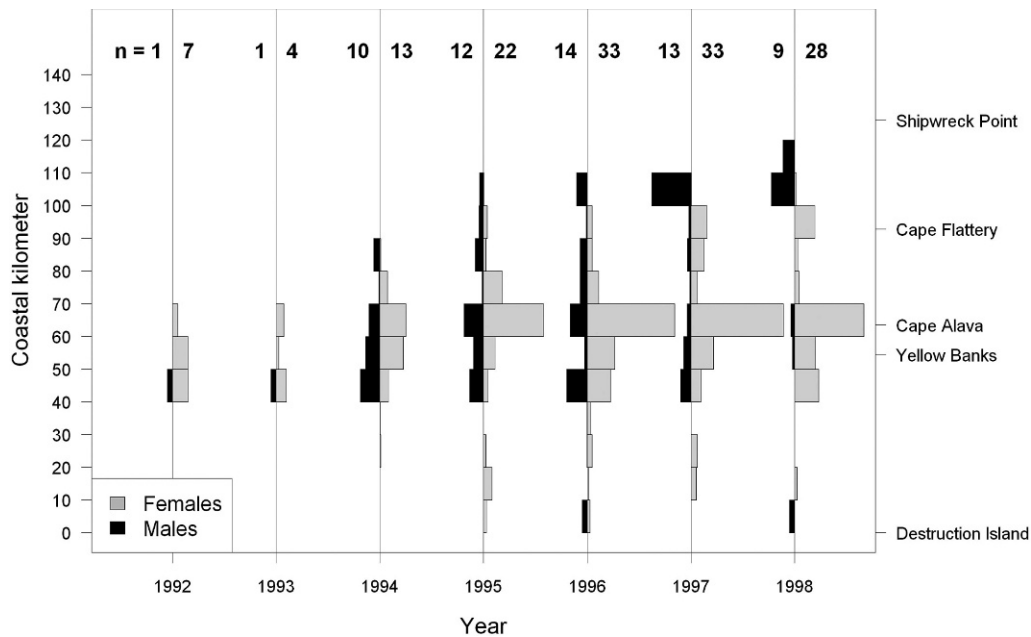


FIG. 5.—Vertical histograms and spatial distribution (in 10-km segments of the coast) by year for male and female sea otters (*Enhydra lutris*) on the outer coast of Washington (male = black, female = gray). Each individual is weighted equally in the analysis regardless of the number of resightings. The plot shows the increasing southward range expansion, primarily of males, since 1992.

1,125 otters occupied the core area with a rate of increase of 8.0% (95% confidence interval 7.1–8.9%) since 1989 based on an exponential growth model (Fig. 8). Nothing suggests that population growth is slowing down despite the relatively minimal range expansion. Nearly a decade after this study was completed few sea otters have been reported in the SJF east of Cape Flattery or in Neah Bay (Fig. 1).

Two primary observations were made based on the telemetry data collected between 1992 and 1999. First, the population range on the outer coast expanded both northward and southward over the study period, with the shift primarily driven by males. This observation also is confirmed by annual aerial surveys that documented increased sightings of sea otters in the southern portion of the range through 2007. Second, and concurrently, many individuals of both sexes displayed seasonal movements, primarily north and east, into the SJF. Almost one-half of the tagged sea otters moved into the SJF, or 33% of all females (primarily adult but also subadults) and 56% of males. Although examination of the data presented here supports the general hypothesis that males enter new areas 1st, range expansion in Washington is not limited to exploratory adult males (Kenyon 1969), but includes reproducing adult females. There are no indications that these large-scale movements are driven by seasonal or local changes in prey abundance. Movements into the SJF during winter may be related to refuge from the exposed outer coast; however, winter refuge does not appear to be critical because some individuals (including most of the females) remain on the outer coast year-round. Other individuals performed seasonal movements southward rather than northward.

Examination of foraging data indicates that sea otters exclusively targeted red urchins (*Strongylocentrotus francis-*

canus) when they moved into the SJF in 1995 (Laidre and Jameson 2006). However, during the 4 years that foraging patterns were monitored in the area, the proportion of red urchins in the diet declined rapidly and was replaced by bivalves or other prey (Laidre and Jameson 2006). This suggests that otters may have used the SJF for rich feeding opportunities, and moved back to the more optimal (and possibly more productive) habitat on the outer coast when those resources were exhausted. This also may explain why there have been few sea otter sightings in the SJF since 2000. It is possible that, had sea otters been monitored after 2000, the seasonal patterns would be far less marked.

Individual otters typically remain within an area known as a home range, which varies in size depending on season, reproductive status, sex, and age, and often comprises several heavily used areas interconnected by travel routes (Garshelis and Garshelis 1984; Jameson 1989; Ribic 1982). Individual sea otters tracked in this study had 95% home ranges that varied widely, with means for sex–age classes between 24 and 50 km (Table 2). Given that the total population range was at the time about 120 km, individual animals used a fairly substantial portion of their entire population range.

Sea otters on the mainland California coast have been reported to cover distances of >450 km of the coast annually (100% of the current range) and have covered hundreds of kilometers (>300 km) in several days (Jameson 1989; Tinker et al. 2006). In Prince William Sound, sea otters travel as much as 100 km over several days (Garshelis and Garshelis 1984). In Washington, shifts between sites sometimes covered distances of >45 km and often were made in <14 days.

We detected significant differences between sexes in the extent of coastal area used, with males generally having wider

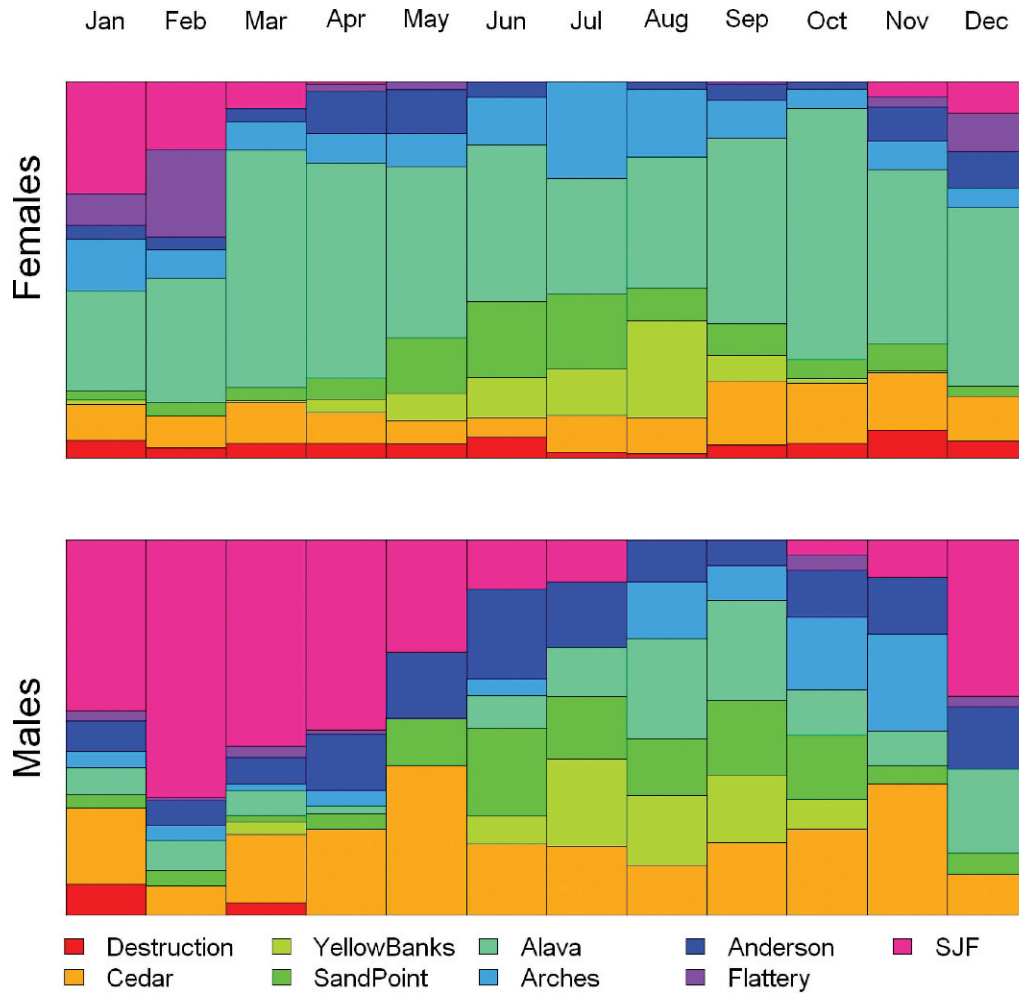


FIG. 6.—Monthly movements of sea otters (*Enhydra lutris*) shown using normalized estimated proportions of pooled resighting locations by month. Individuals were weighted equally in the analysis. Colored areas match geographic locations (stars) in Fig. 1. Sites in close proximity were pooled into the same regions shown in Fig. 1, from the south proceeding north: 1) Destruction including Giants Graveyard, Perkins Reef, and Destruction Island; 2) Cedar including Cedar Creek, Saddle Rock, Bluff Point, and Chilean Memorial; 3) Yellow Banks; 4) Sand Point; 5) Alava including Cape Alava and South Ozette Island; 6) Arches including Point of Arches, Father and Son, and Duk Point; 7) Anderson Point; 8) Flattery including Cape Flattery and Tatoosh Island; and 9) Strait of Juan de Fuca (SJF) including Shipwreck Point, Bullman Beach, Waddah Island, Koitlah Point, and Midway Point.

TABLE 3.—Twenty-four-hour activity budgets from 25 sea otters (*Enhydra lutris*) observed at 10-min intervals in coastal Washington. The mean percent of time in each category is shown together with the standard deviations (in parentheses). NA is noted if sample sizes were from a single animal. AFNP = adult female, no pup; AFP = adult female with pup; AM = adult male; SF = subadult female; and SM = subadult male.

Cohort	<i>n</i>	Time foraging (%)	Time resting (%)	Other (%)
AFNP	16	41 (14)	45 (13)	14 (6)
AFP	5	42 (16)	45 (13)	13 (6)
AM	1	26 (NA)	55 (NA)	19 (NA)
SF	1	32 (NA)	55 (NA)	13 (NA)
SM	2	59 (9)	31 (15)	10 (7)
Average	25	41 (14)	45 (13)	14 (6)

ranges. The significant difference detected between age classes, with adults using a greater amount of the coastline, may be due to behavior but the results are biased by the fact that the extent of time animals were observed as adults was greater than the time the animals were observed as subadults. Controlling for this bias unfortunately dilutes the power of the comparison given the small sample sizes. Males also exhibited more seasonal behavior than females, which were more likely to winter and summer in the same preferred habitat. However, there was very high individual variation within both sexes.

Availability of alternative habitat.—The current population range of sea otters in Washington varies markedly from the pre-exploitation range. Before extirpation, sea otters occupied habitat extending south to the Columbia River on the

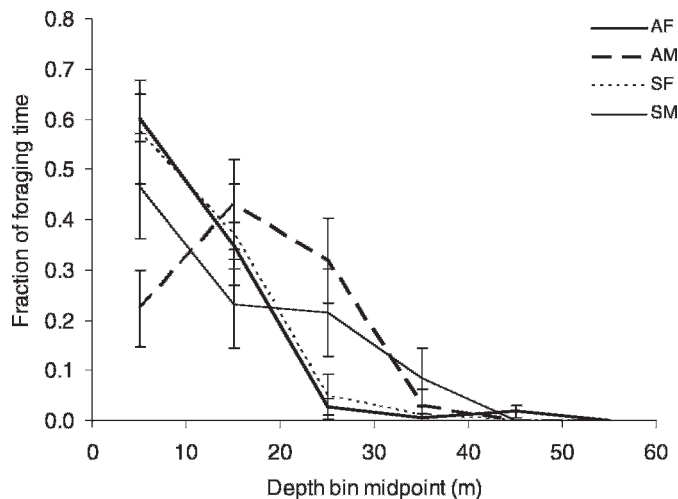


FIG. 7.—Distribution of total foraging time across depth bins (\pm SE) for each of 4 sex-age classes of sea otters (*Enhydra lutris*) in Washington. AF = adult female, AM = adult male, SF = subadult female, and SM = subadult male.

Washington–Oregon border (Scheffer 1940). Today, the population remains distributed from Destruction Island north to the entrance of the SJF. Exposed conditions and uncertain habitat quality have been suggested as potential barriers to southward expansion of the population (Laidre et al. 2002). Kelp is an important habitat variable because it provides resting refuge within preferred rocky habitat and almost no substantial kelp remains south of Destruction Island despite intensive surveys conducted down to the Columbia River.

Unoccupied sea otter habitat in the SJF is mixed habitat, falling somewhere between rocky substrate and sandy bottom (Laidre et al. 2002). Substantial unused *Macrocystis* and *Nereocystis* kelp canopy exists east to Dungeness Spit in the SJF extending offshore twice the distance used by sea otters on the outer coast (Berry et al. 2001; Shaffer 1998). However, this habitat is characterized by considerable anthropogenic

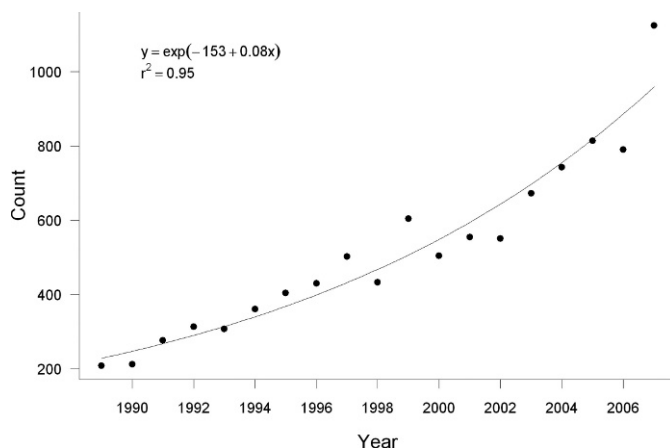


FIG. 8.—Exponential growth model fit to minimum population counts of sea otters (*Enhydra lutris*) in Washington based on surveys conducted between 1989 and 2007. The rate of increase is 8% (95% confidence interval 7.1–8.9%).

modification and it is unclear if a significant portion of the sea otter population will ever use it.

Outside of the state of Washington, abundant suitable sea otter habitat exists across the SJF along the coast of Vancouver Island and areas of the British Columbia coast (GREGG et al. 2008). Approximately 3,000 sea otters occupy the western and northern coasts of Vancouver Island, and another geographically separated population of 500 sea otters also inhabits the mainland coast of British Columbia near Bella Bella. Few data are available to assess habitat along the southern coast of Vancouver Island; however, ideal habitat and high food availability have facilitated an 18.6% per year growth rate for sea otters between 1977 and 1995 on northern Vancouver Island (Watson et al. 1997).

Isolated sea otter sightings have been documented in the eastern SJF, the San Juan Islands, and as far south as Olympia in Puget Sound, as well as south along the outer Washington coast to Grays Harbor; however, it is unknown to what extent sea otters will permanently colonize these areas of Washington (Lance et al. 2004). The sea otter population in Washington lacks continuous homogenous habitat throughout its range and the distribution of the population is consequently clumped around preferred habitat on the outer coast. Thus, large-scale and rapid long-distance movements between suitable habitat patches or preferred regions observed in this study are not surprising. Consequently, the major dynamics of movement for sea otters in Washington are currently best described as semiperiodic seasonal shifts within a core range, in contrast to linear dispersal models applied to otters in California (Krkošek et al. 2007; Tinker et al. 2008b).

Activity budgets.—Activity–time budgets for sea otters have been proposed to indicate population status with respect to density dependence (Eberhardt 1977; Estes et al. 1982, 1986). In general, populations thought to be close to equilibrium density spend more time foraging for resources because of limitations on prey availability. Sea otters in populations at low densities, or those still growing, spend less time foraging because of reduced pressure on prey availability (Estes et al. 1982, 1986; Gelatt et al. 2002). Sea otters in Washington spent on average 41% of their time foraging. This value is similar to that from other resource-limited sea otter populations (i.e., Alaska and California), which spent 40–50% of their time foraging (Gelatt et al. 2002; Tinker et al. 2008a). This suggests that sea otters in Washington, at least on the outer coast, may be close to resource limitation or equilibrium density (Laidre et al. 2002), which is somewhat puzzling given the continued exponential growth of the population (Fig. 8). Activity budgets in our study were collected in the core range on the outer coast and excluded the SJF or peripheral areas. Thus, these data may be biased toward higher portions of foraging time in sections of the range where resources were limiting, as found for sea otters in California where foraging time in the center of the range was twice that at the range periphery (Tinker et al. 2008a). Activity budgets were collected between late summer and early fall, thus no seasonal differences could be examined. Gelatt et al. (2002) also reported a wide range of

estimates of foraging time across cohorts (21–55%), similar to this study.

Because of similarities in foraging and resting time for age and sex classes, stratification of time by offshore depth and distance from the coast was comparable for different demographic units. In general, adult and subadult females behaved similarly in how total foraging and resting time was distributed by offshore depth and distance, suggesting minimal habitat partitioning between different ages. Adult and subadult males diverged from females and used deeper depths and farther offshore distances more frequently.

A large shallow shelf exists along the coast of Washington with depths of <40 m extending >10 km offshore. Sea otters may forage at relatively specific depths, yet because of the wide shelf are able to spread out in a larger area of habitat. This is reflected in the higher variability around parameter estimates with foraging time with respect to offshore distance. In general, depths or distances used for resting had less variability than those for foraging.

The results of this study suggest between 1992 and 1999 sea otters in Washington extended their range both northward and southward, with a clear shift in use of the SJF by individuals of all age and sex classes. Over this period, SJF prey resources were reduced and most sea otters left the SJF and moved back into their core range on the outer Washington coast. Seasonally, different regions of the range are important at different times, with Cape Alava remaining a high-use area by females. Alternative availability of sea otter habitat in Washington is variable, ranging from hundreds of kilometers of sandy habitat in the south, mixed kelp forests in the SJF, and ideal rocky coast across the SJF in Vancouver Island. These results overall indicate that sea otters have the potential for further population growth and expansion in Washington or beyond.

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