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Estimates of carrying capacity for sea otters in Washington state

Kristin L. Laidre, Ronald J. Jameson, Steven J. Jeffries, Roderick C. Hobbs, C. Edward Bowlby, and Glenn R. VanBlaricom

Abstract We obtained index estimates of carrying capacity (*K*) for the Washington sea otter (*Enhydra lutris kenyoni*) population as products of the density of sea otters at equilibrium within a portion of their existing range and the total amount of available habitat. We classified sea otter habitat as rocky, sandy, or mixed during aerial surveys along the Washington coast in March 2000. We characterized substrate type and kelp composition from the coast to the 40-m depth contour and computed area (km^2) and available coastline (km) within each habitat. We calculated maximum foraging depths and maximum distance from shore for 68 sea otters radiotagged between 1994 and 1998 and used the estimates to approximate the offshore extent of sea otter habitat. We used the most current population survey data (1996–1999) to obtain equilibrium densities of sea otters in rocky habitat in Washington. Because sea otters have only recently occupied sandy or mixed sites, the equilibrium densities for these habitats represent a proportional density based on current counts in the rocky equilibrium region in Washington and available data from the California sea otter population. Index estimates of *K* for the Washington sea otter population range from 1,372 (CV 0.13) to 2,734 (CV 0.13). These estimates are useful for sea otter management because they directly relate to the index counts used to monitor the population since 1977. Our results will facilitate decision-making by entrusted management agencies regarding stock assessment and population status under the United States Marine Mammal Protection Act.

Key words carrying capacity, *Enhydra lutris kenyoni*, sea otter, Washington

The original sea otter (*Enhydra lutris kenyoni*) population in Washington state was extirpated by fur-trade hunting in the early twentieth century (Wilson et al. 1991). The population was reestablished by translocations of 59 sea otters from Amchitka Island, Alaska, during the summers of 1969-1970 (Jameson et al. 1982). The translocated population began to grow exponentially in the late 1970s, a pattern thought to be typical of newly transplanted sea otter populations (Estes 1981, Jameson et al. 1982, Jameson et al. 1986, Bowlby et al. 1998, Bodkin et al. 1999). The reintroduced sea otter population has been growing at an average annual rate of about 10% since 1989 (Jameson 1998, Jameson and Jeffries 1999, R. Jameson, United States Geological Survey [USGS], unpublished data). During the summers of 2000 and 2001, the population index counts were 504 and 555 animals, respectively (R. Jameson, USGS, unpublished data).

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Washington's sea otters are protected under the United States Marine Mammal Protection Act (MMPA) of 1972 (Public Law 92-522) as amended. Under the MMPA, a population is no longer considered depleted when it reaches the lower limit of its optimum sustainable population (OSP) level. This limit, the maximum net productivity level (MNPL), is defined as a range of 50–70% of carrying capacity (K)—i.e., the maximum number of sea otters that can be supported by suitable habitat over an extended time period (Gerrodette and DeMaster 1990). Without complete information on density-dependent, age-specific birth and death rates, MNPL estimates can range from 50 to 80% of K (Taylor and DeMaster 1993). We defined MNPL as 60% of K, an operational definition that has evolved where the lower end of the OSP range is assumed to fall (DeMaster et al. 1996).

At least one attempt has been made to estimate K for sea otters along a portion of the Washington coastline, which was part of an assessment of potential release areas for translocation of southern sea otters (*E. l. nereis*; James Dobbin Associates, Inc., Washington D.C., unpublished report). Our study provides estimates of K for sea otters along the entire outer coast of Washington as the products of equilibrium densities of sea otters within specific habitats and the total amount of each habitat available.

A simple shore census combined with index counts from the air have generally been recognized by managers in Alaska, Washington, and California as the most accurate means of estimating sea otter abundance, comparing different population sizes, and monitoring trends through time (Estes et al. 1995, Bodkin and Ballachey 1996, Jameson and Jeffries 1999). This is because detection probabilities for sea otters vary widely with wind, sea state, group size, and activity, and are often relevant only to a specific section of surveyed coastline in a particular year (Geibel and Miller 1984, Estes and Jameson 1988, Udevitz et al. 1995, Bodkin and Ballachey 1996, Bodkin and Udevitz 1999). Our objective here was to use the combined annual index counts to estimate K for sea otters in Washington, which is the expected index count when the population is at carrying capacity.

Study area

The Washington state sea otter population is distributed along the outer Washington coast, northward from Split and Willoughby Rocks to Cape Flattery, and eastward to Pillar Point in the Strait of Juan de Fuca, with concentrations near Destruction Island, Cape Johnson, Sand Point, and Cape Alava (Figure 1). We conducted this study on the outer coastline of Washington between Dungeness Spit along the north coast of Washington (48°11.2′N, 123°5.8′W) and the Washington-Oregon border (42°N, 124°13′W). Coastal Washington has a typical eastern Pacific maritime climate, with average annual temperatures ranging from 2–16°C and average monthly precipitation ranging from 8–36 cm. We defined the study area between the coast and 40-m contour and included all major bays, harbors, and

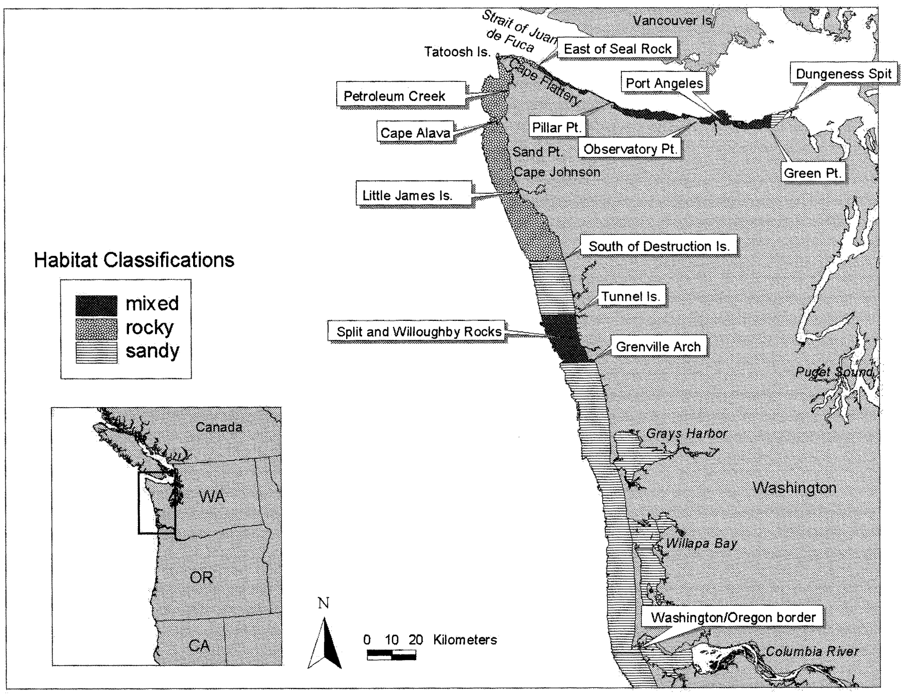

Figure 1. Map of habitat classifications (shown to the 40-m depth contour) along the Washington coast from Dungeness Spit to the Columbia River and locality names mentioned in the text. Habitats are classified as rocky, sandy, or mixed based on aerial surveys conducted in March 2000.

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river mouths. We divided the study area into 3 habitats following those used for the California coast in Laidre et al. (2001).

Methods

Habitat characterization

Rocky habitat had moderate (50%) to large (100%) amounts of kelp and moderate to large amounts of rocky coast and rocky subtidal substrate. Sandy habitat had exposed sandy beaches and was void of rocky coast, kelp, and rocky subtidal substrate. Mixed habitat had some (<50%) rocky coast, occasional headlands, and coves, but little or no kelp and minimal subtidal rocky substrate.

We recorded habitat classifications on 1:12,000 maps during an aerial survey based on visual observations of the amount of kelp and rocky substrate along the coast and corroborated the classifications with nautical charts (DeMaster et al. 1996, Laidre et al. 2001). We conducted the survey on 21 March 2000 in a fixed-wing aircraft (offshore extent determined by reefs and islands) at an altitude ranging from 150–450 m. Grays Harbor, Willapa Bay, and mouth of the Columbia River (to river mile 18) were included as potential sea otter habitat in Washington.

Offshore habitat delineation

We used radiotelemetry data collected from 68 sea otters (12 adult M, 36 adult F, 9 juvenile M, 9 juvenile F) captured, radiotagged, and located off the Washington coast from 1994 to 1998 to document offshore spatial habitat use. Telemetry data collection occurred biweekly throughout the year, with daily effort in spring and summer, primarily due to better weather conditions. We located each tagged sea otter from land and estimated its position using visual observation or triangulation on the radio signal based on direction and strength (White and Garrott 1990). We located individuals only once each survey day; therefore, each location was treated as an independent sample. We considered the tagged sea otters to be representative of the Washington sea otter population.

We imported location coordinates for each otter into the Geographic Information System (GIS) software packages ARC/INFO® and ArcView® (ESRI, Redlands, Calif.) to determine maximum depths and distances from shore for each sex and age class. We attached locations for all sex and age groups to a depth in a bathymetric grid to determine mean and maximum depths for resting and foraging otters, and mean and maximum distance from each location to the mainland coast (complied from the National Oceanic and Atmospheric Administration [NOAA] bathymetric charts by the Strategic Environmental Assessments Division of NOAA's Office of Ocean Resources, Conservation and Assessment). We also plotted locations of sea otters observed during aerial surveys to assess depths and distance from shore. We compared results with respect to activity state and sex and age class from this study to those reported for sea otters in California (Ralls et al. 1995).

Estimating habitat availability

Measures of sea otter habitat included linear (shoreline distance in each habitat in km) and sea surface area (km^2) between the coastline and the 20-, 30-, and 40-m depth contours. We converted coordinates obtained from NOAA nautical charts to decimal degrees for northern and southern boundaries of 6 regions along the Washington coast (Figure 1). The Columbia River mouth was cut at a line extending south from Grays Point, Washington to Tongue Point, Oregon. We created polygons in ARC/INFO® based on the intersections between the coastline, each depth contour, and the northern and southern boundaries for each habitat area. Three discrete regions were created within each habitat (0–20 m, 0–30 m, 0–40 m). We calculated linear distances between each northern and southern boundary along the Washington coastline and within each coastal estuary (Grays Harbor, Willapa Bay, and Columbia River) in ArcView®.

Density estimates

We used current survey data to obtain sea otter densities in rocky habitats along the outer coast of Washington. Densities in sandy and mixed habitats could not be calculated because sea otters have not been established in those habitats long enough for a reliable density estimate. Consequently, we calculated the equilibrium densities of sea otters in sandy and mixed habitats from sea otters in California (Laidre et al. 2001).

We used annual estimates of sea otter index abundance in Washington based on ground and aerial counts. We conducted two surveys daily for 3 days. Each survey was summed for the whole coast, and the index of abundance was the highest daily total (Jameson and Jeffries 1999). We chose the area between Petroleum Creek and Little James

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Island to represent equilibrium rocky habitat in Washington. Surface area for this region was calculated to each depth contour, and the linear distance of shoreline was measured between these 2 boundaries. We calculated annual density indices for 1996–99 and a 4-yr mean by dividing the number of sea otters within this region by the surface area (km^2) to each depth contour or by the length of coastline between the Petroleum Creek and Little James Island.

We calculated a ratio for sandy-rocky habitat densities and mixed-rocky habitat densities from California data (Laidre et al. 2001) and used it to assign potential sandy and mixed equilibrium densities (linear km and km^2) for Washington as a proportion of the average equilibrium density in rocky habitat in Washington. We used this ratio to calculate densities in sandy and mixed habitats from the coast to the 20-, 30-, and 40-m depth contours and linear habitat measures. We assumed that when sea otters reached carrying capacity in sandy and mixed habitats, they would utilize those habitats in a way similar to sea otters in California.

We estimated variability around the point estimate of the density index for rocky habitat by bootstrapping (Efron and Tibshirani 1993). Washington "as the otter swims" (WATOS) segments divided the coast into 0.5-km segments roughly along the 5-fathom contour. We binned sea otter counts into WATOS segments for each year. Bootstrapping was done using the individual WATOS segments within the equilibrium rocky region from 1996–1999. Counts for each segment were drawn at random with replacement from the 4-year pool and summed. We estimated density by dividing the sum of the counts by the total area of rocky habitat to each depth contour (20–40 m and linear). We repeated this process 10,000 times. We calculated a standard deviation (SD) and coefficient of variation (CV) for the pooled mean and determined a 95% confidence interval (CI) from the distribution of the bootstrap draws for rocky habitat in Washington. The variance estimated from this approach incorporated inter-annual and spatial variability in density.

We used the delta method to estimate variance around the sandy and mixed habitat density estimates in Washington (Seber 1973). The CV for sandy habitat in Washington was calculated as:

$$CV_{Wash\_sandy} = \sqrt{(CV_{Cal\_sandy})^2 + (CV_{Cal\_rocky})^2 + (CV_{Wash\_rocky})^2} \quad (1)$$

and the CV for mixed habitat in Washington was calculated as:

$$CV_{Wash\_mixed} = \sqrt{(CV_{Cal\_mixed})^2 + (CV_{Cal\_rocky})^2 + (CV_{Wash\_rocky})^2} . \quad (2)$$

There was no variability in the surface area calculations; therefore, CVs for the estimated number of sea otters in sandy and mixed habitats in Washington were the same as CVs for the density estimates.

Carrying capacity estimates

We calculated K as a product of the average equilibrium densities estimated for each habitat by contour boundary and total surface area for that habitat within each depth contour boundary. We calculated estimates of K for linear densities as a product of the equilibrium density of sea otters/km of coastline and the total km of coastline available for that habitat. Estimates of K were not nested, but were calculated from unique densities based on the same number of sea otters occupying a larger or smaller area. Density estimates were adjusted for each of the 3 coastal estuaries (i.e., Grays Harbor, Willapa Bay, and the Columbia River mouth) when the density in sandy habitat changed based on the varying offshore depth contour.

Results

Washington habitat

We classified one region as rocky habitat, 3 regions as sandy habitat, and 2 regions as mixed habitat during aerial surveys of the Washington coast (Figure 1). All 3 coastal estuaries were classified as sandy habitat. We estimated that 3,696 km^2 was available to sea otters in Washington to the 40-m contour (Dungeness Spit to the Washington–Oregon border), including all habitats and coastal estuaries. The areas of available rocky, sandy, and mixed habitat to the 40-m depth contour in Washington were estimated as 851, 2,409, and 436 km^2, respectively (Table 1). We estimated the linear distance from Dungeness Spit to the Washington–Oregon border, including coastal estuaries, to be 895 km. Linear distances along rocky, sandy, and mixed coastline off Washington were estimated as 145, 578, and 172 km, respectively.

Offshore sea otter habitat

All sea otters remained between Seal Rock and Destruction Island, within our rocky habitat. The

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Table 1. Dimensions of rocky, sandy, and mixed habitats (reported as sea surface area [km^2] from coastline to the 20-, 30-, or 40-m depth contour, and as linear shoreline distance [km]) for Washington sea otters.

Region[a]	Habitat[b]	20 m	30 m	40 m	Linear
DSEG	Sandy	23	26	29	15
EGSR	Mixed	118	158	191	139
SRDI	Rocky	210	464	851	145
DITI	Sandy	122	242	317	36
TIGA	Mixed	93	175	245	33
GAWO	Sandy	597	899	1,281	135
GH	Sandy	240	240	240	91
WB	Sandy	351	351	351	188
CR	Sandy	191	191	191	113

[a] Regions are listed beginning at the north coast of Washington and progressing south: Dungeness Spit to East Green Point (DSEG), East Green Point to east of Seal Rock (EGSR), East of Seal Rock to south of Destruction Island (SRDI), South of Destruction Island to Tunnel Island (DITI), Tunnel Island to Grenville Arch (TIGA), Grenville Arch to the Washington–Oregon border (GAWO), Grays Harbor (GH), Willapa Bay (WB), Columbia River mouth (CR).

[b] Habitat classifications based on aerial surveys flown in March 2000.

number of telemetry locations per individual varied. When individual locations (classified as either foraging or resting) were pooled regardless of age or sex, we obtained an average depth of 10 m (SE=0.1, maximum depth=54 m) and an average distance from shore of 812 m (SE=12.2, maximum distance=4,089 m). All average depth and distance from shore estimates were larger for the foraging activity state when examined with respect to sex and age class (Table 2). Telemetry locations were similar to the distribution of sea otter locations obtained during aerial surveys, supporting the use of those data to assess offshore limits of habitat use.

Student *t*-tests on data collected in this study and Ralls et al. (1995) resulted in several significant differences between average depth and average distance from shore for Washington (WA) and California (CA) sea otters. Juvenile males foraged (14-m depth WA vs. 30-m depth CA, $t_8=4.59, P \leq 0.001$) and rested (10-m depth WA vs. 28-m depth CA, $t_{10}=5.05$, $P \leq 0.001$) in deeper water in California. Juvenile females foraged and rested in deeper water in California (foraging: 12-m depth WA vs. 18-m depth CA, $t_{12}=2.79$, $0.001<P<0.002$; resting: 11-m depth WA vs. 23-m depth CA, $t_{12}=56.1$, $P<0.001$) and were located significantly farther offshore when foraging in Washington (945 m offshore WA vs. 471 m offshore CA, $t_{12}=4.55$, $P<0.001$). Adult female sea otters both foraged and rested in deeper water in California (foraging: 10-m depth WA vs. 22-m depth CA, $t_{38}=7.26, P<0.001$, resting: 9-m depth WA vs. 22-m depth CA, $t_{46}=14.66, P<0.001$). Adult female sea otters also foraged and rested farther offshore in Washington (foraging: 717 m offshore WA vs. 347 m offshore CA, $t_{38}=3.68$, $P<0.001$; resting: 670 m offshore WA vs. 376 m offshore CA, $t_{46}=3.42$, $0.001<P<0.002$). We excluded adult males from the analysis because of a sample size of $n=1$ in California; therefore, we made no comparisons for this group.

Density estimates

We calculated average equilibrium densities (otters/km^2) for Washington in 1996–1999 in rocky habitat as 4.55 (coast to 20 m), 2.38 (coast to 30 m), 0.97 (coast to 40 m), and 7.04 (linear coastline) (Table 3). The bootstrapped CV for pooled mean density estimate in rocky habitat was 0.17.

We used the average equilibrium densities calculated for California sea otters (Laidre et al. 2001) to obtain ratios for sandy-rocky and mixed-rocky habitats. Average equilibrium densities for sea otters in rocky habitat in California to the 40-m depth contour were 5.12 otters/km^2 (CV=0.05); sandy and mixed habitats were much lower at 1.07 otters/km^2 (CV=0.12), and 0.78 otters/km^2 (CV=0.25), respectively (Laidre et al. 2001). The ratio of sandy:rocky habitat

Table 2. Radiotelemetry statistics by sex, age, and behavior for average depth (m) and average distance from shore (m) collected from 68 radiotagged sea otters in Washington, 1994–1998.

	Foraging					Resting				
		Depth		Distance offshore			Depth		Distance offshore	
Sex–age class	n[a]	$\bar{x}$	SE	$\bar{x}$	SE	n[a]	$\bar{x}$	SE	$\bar{x}$	SE
Adult males	8	16	1.6	1,163	103.9	10	11	1.7	1,175	105.0
Adult females	28	10	0.8	717	57.1	36	9	0.3	670	46.7
Juvenile males	6	14	2.6	1,382	252.3	9	10	1.8	1,018	115.7
Juvenile females	5	12	2.0	945	129.2	7	11	0.9	676	94.6

[a] Sample sizes are reported for both behavior states because the number of individuals exhibiting the two behavior states varied.

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Table 3. Equilibrium densities (otters/km^2 or otters/km) for Washington sea otters with 25 years of constant occurrence in rocky habitat (i.e., from Petroleum Creek to Little James Island).

	1996	1997	1998	1999	All years		
Area of survey[a]	$n^b = 342$	$n^b = 357$	$n^b = 305$	$n^b = 335$	$\bar{x}$ [c]	SD[d]	95% CI[d]
20-m contour (73.5 km^2)	4.65	4.85	4.15	4.55	4.55	0.77	3.01–6.03
30-m contour (140.8 km^2)	2.43	2.53	2.17	2.38	2.38	0.40	1.57–3.15
40-m contour (346.8 km^2)	0.99	1.03	0.88	0.97	0.97	0.16	0.64–1.28
Linear distance (47.5 km)	7.19	7.51	6.41	7.04	7.04	1.19	4.66–9.32

[a] Sea surface area from coastline to the specified depth contour or linear shoreline distance.

[b] n = number of otters, estimated during spring survey counts in Washington, 1996–1999. Note, densities decrease as the same number of otters is distributed over a larger area.

[c] Coefficients of Variation for densities in rocky habitat calculated from the bootstrapping approach (constant regardless of depth contour) were 0.17.

[d] SD and 95% CI were obtained from the bootstrapping.

by area was 0.21, and the ratio for mixed:rocky habitat by area was 0.15. The ratio of sandy:rocky habitat and the ratio of mixed:rocky habitat for linear density were both 0.32. We used these ratios as multipliers to assign equilibrium densities of sea otters in sandy and mixed habitat in Washington, based on the known average equilibrium density observed in rocky habitat in California (Table 4).

Carrying capacity estimates

Estimated numbers of sea otters that could be supported by the Washington coastal environment to the 20-, 30-, and 40-m depth contours were 2,550 (95% CI = 1,869–3,233), 2,191 (95% CI = 1,643–2,737), and 1,372 (95% CI = 1,031–1,713), respectively (Table 5). The estimated number of sea otters that could be supported by the Washington coastal environment including coastal estuaries and bays based on the linear densities was 2,734 (95% CI = 2,082–3,452). Note that carrying capacity for the 20-m depth contour is much higher than that for the 40-m depth contour due to higher expected densities. The difference between the low (1,372 40-m contour) and high (2,734 linear) estimates of K was approximately 1,400 sea otters. This difference was primarily due to resulting low densities calculated for the deeper depth contours (40-m) lying 10–15 km offshore.

Table 4. Estimates of average equilibrium density for sea otters in sandy and mixed habitats in Washington, calculated from the average equilibrium density in rocky habitat in Washington from 1996–1999 (see Table 3) and the ratio of sandy–rocky and mixed–rocky habitat densities calculated for sea otters in California (Laidre et al. 2001).

	Sandy[a]	Mixed[b]
20 m[c]	0.95	0.69
30 m[c]	0.50	0.36
40 m[c]	0.20	0.15
Linear[d]	2.28	2.28

[a] Estimated Coefficient of variation for sandy habitat was 0.21.

[b] Estimated Coefficient of variation for mixed habitat was 0.31.

[c] Sea surface area from coastline to specified depth contour (otters/km^2).

[d] Linear shoreline distance (otters/km).

Discussion

Our radiotelemetry results for sea otters in Washington indicate that habitat use, relative to depths and distance from shore, differs from the California population (Table 2). Most age and sex classes of Washington sea otters appeared to be located farther offshore and in shallower water than California sea otters for both resting and foraging activity states. The shelf inside the 40-m isobath off the Washington coast (lying 8–14 km offshore) is much wider than the shelf off the California coast to the same depth (approximately 3 km offshore along the entire sea otter range in California). Therefore, sea otters in Washington must swim farther offshore to reach given water depths than those in California. Although sea otters in California reach the 40-m depth contour and appear to forage effectively (Ralls et al. 1988, Reidman and Estes 1988), it is possible that because of the travel distance involved, sea otters in Washington do not. If we based our limit of offshore habitat use on depth alone, it would support the selection of K to 10 or 20 m. However, our data indicated that in Washington, habitat use and availability were not only a function of mean foraging depth but also distance from shore. This has important implications for estimates of K for Washington because the limit of offshore habitat use affects the number of sea otters an area can support.

Sea otters studied by Ralls et al. (1995) were located using methods similar to those in our telemetry study. Daily position and activity state

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Table 5. Estimated carrying capacity (number of sea otters) in Washington (Dungeness Spit to Columbia River), assuming habitat included sea surface area contained within the 20-, 30-, or 40-m depth contour or was a linear function of coastline.

		Estimated carrying capacity (*K*) [a]			
Region[b]	Habitat	20 m	30 m	40 m	Linear
DSEG	Sandy	22	13	6	34
EGSR	Mixed	82	57	28	316
SRDI	Rocky	955	1,102	822	1,019
DITI	Sandy	116	120	64	82
TIGA	Mixed	64	63	36	75
GAWO	Sandy	568	447	258	309
GH	Sandy	229	119	48	208
WB	Sandy	333	174	71	431
CR	Sandy	182	95	39	259
Total without bays and estuaries [c]		1,807 (0.12)	1,802 (0.13)	1,214 (0.13)	1,836 (0.13)
Total with bays and estuaries [c]		2,550 (0.14)	2,191 (0.13)	1,372 (0.13)	2,734 (0.13)

[a] *K* was estimated as the product of area (Table 1) and density (Tables 3 and 4).

[b] Regions are listed beginning at the north coast of Washington and progressing south: Dungeness Spit to East Green Point (DSEG), East Green Point to east of Seal Rock (EGSR), East of Seal Rock to south of Destruction Island (SRDI), South of Destruction Island to Tunnel Island (DITI), Tunnel Island to Grenville Arch (TIGA), Grenville Arch to the Washington–Oregon border (GAWO), Grays Harbor (GH), Willapa Bay (WB), Columbia River mouth (CR).

[c] Coefficients of variation are in parentheses for each estimate of *K*.

were recorded in May 1985–April 1987 by triangulating on the radio signal (Ralls and Siniff 1990, Ralls et al. 1995). In both studies, sea otters were located once each day from land, during daylight hours. Biases toward resting otters or otters that were close to shore were inherent in both Ralls et al. (1995) and our study. Based on the results of this comparison, it appears to be inappropriate to use spatial patterns documented for California sea otters (Estes and Jameson 1988, Ralls et al. 1995, Ralls et al. 1996) to delineate offshore habitat use in Washington.

Equilibrium densities from our technique represented a proportional density based on current counts in the rocky equilibrium region. Densities reported here were representative of what could be supported in sandy and mixed habitats based on present population size in Washington. Although sea otters have occupied the area for 25 years, the rocky region between Petroleum Creek and Little James Island might not necessarily be at equilibrium. Trends in counts could be a result of immigration or shifts in distribution, rather than the classic equilibrium state where births are equal to deaths. This is particularly true for a population that is still growing and expanding in its range. Sea otters were first observed in the area chosen to represent equilibrium rocky habitat in Washington (Petroleum Creek to Little James Island) in 1977 (Jameson et al. 1982, 1986), and numbers increased steadily until approximately 1995 (Jameson and Jeffries 1999). Since then, numbers have remained relatively stable (Table 3). It has been suggested that sea otters have multiple equilibria, where a second, higher equilibrium density is reached following a diversification of diet (Estes 1990).

The increase in available habitat with increasing distance offshore was not linear in Washington, which made our results for the declining number of sea otters with increasing depth seem counterintuitive. This was most prevalent in the areas we classified as continuous sandy habitat. Sandy areas composed the largest fraction of the population estimated in this study (>60%). This introduced a large source of variability because potential densities in sandy habitat have been estimated based on the California population. It is not entirely clear how many sea otters could be supported by sandy habitat in the 2 regions.

The equilibrium density reported to the 40-m contour in Laidre et al. (2001) for rocky habitat in California (5.12 otters/km^2, CV=0.05) was over 5 times higher than the equilibrium density we report to the same contour for Washington (0.97otters/km^2, CV=0.17). Surface area estimates to 40 m for a given coastal distance in Washington are much greater than area estimates for a similar coastal distance in California. Therefore, the difference in density to the 40-m contour appears to be due to the difference in area contained from 40 m to the coast in California and Washington. High densities of sea otters using offshore habitat have been infrequent (Kenyon 1969), and current and historical evidence indicated this was relatively rare (Estes and Jameson 1988, Ralls et al. 1988, Riedman and Estes 1990).

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Assumptions that sea otters in Washington will reach similar densities to sea otters in California in similar habitats might not be valid. For example, sandy habitat in California is much more protected (e.g., Monterey and Estero Bays) than the sandy habitat in Washington (e.g., exposed sandy beaches from Point Grenville to the Washington-Oregon border). Washington's open sandy habitat might not be adequately sheltered for pupping and also might support a lower diversity and biomass of prey. Note, however, that Grays Harbor and Willapa Bay (sandy coastal estuaries) are comparable to intertidal and shallow subtidal sand and mud habitats found in Prince William Sound, Alaska, and have the potential to support large numbers of sea otters (Gerber and VanBlaricom 1999).

We chose the linear estimate (2,734 sea otters) as the best estimate for *K* in Washington because length of coastline appeared to be a better indicator of carrying capacity in this area. This was important if depth was not the limiting offshore factor. The linear equilibrium density we calculated for sea otters in rocky habitat in Washington (7.04 otters/km) was similar to that calculated for sea otters in rocky habitat in California (7.10 otters/km^2) (Laidre et al. 2001). Linear density, although independent of the location of offshore depth contours and shelf area, varies with coastline structure and complexity. Due to uncertainty, the linear estimate (also the highest estimate for *K*) is the most conservative in the interest of management decisions.

Previous estimates of *K* for sea otters in Washington (to 36-m depth) were 1,280 to 2,560 sea otters between Destruction Is-land and Observatory Point (west of Port Angeles) (James Dobbin Associates, Inc., Washington, D.C., unpublished report). A standard density of 3.1 otters/km^2 was used, based on average densities of sea otters within rocky and sandy-bottom habitats in California. We estimated this same area could support 856 sea otters (based on our sea otter densities calculated to the 30- and 40-m depth contours (i.e., those closest to 36 m).

If the densities reported in Laidre et al. (2001) to 40-m depths for the California sea otters population were used to estimate *K* for Washington, regardless of offshore area, *K* would be approximately 7,276 sea otters. This estimate is more than twice the other estimates reported here. If sea otter densities were dependent only on prey densities, and invertebrate biomass per unit area was independent of shelf width or distance from shore, it would be possible that the Washington coast could support this many sea otters. Habitat requirements for sea otters most likely include items beyond water depth and available prey. Along the open exposed coasts, kelp beds, protected coves, and reefs provide shelter for sea otters. Distance from shelter might be an important determinant in how far sea otters will forage offshore. Therefore, sea otter densities 3 km offshore at 40-m depth would most likely be higher than sea otter densities 10 km offshore at the 40-m depth. This might be particularly true for mature females with pups, where high energetic demands may make it a net loss to swim 10 km offshore to obtain food and return to shore for shelter.

The sea otter population in Washington is currently small and still growing. Based on our habitat classifications, sea otters are currently concentrated in rocky habitats with medium to high kelp concentrations (Figures 2, 3). This contrasts with the mid-nineteenth century when sea otters were abundant in sandy habitat from Grenville Arch to the Columbia River and were hunted in Gray's Harbor (Scammon 1874, Scheffer 1940). There are no available data on densities prior to local extinction. Although sea otters were released near Point Grenville (Figure 1), no groups have become established there. It appears sea otters in Washington have selected their preferred habitat (i.e., rocky)

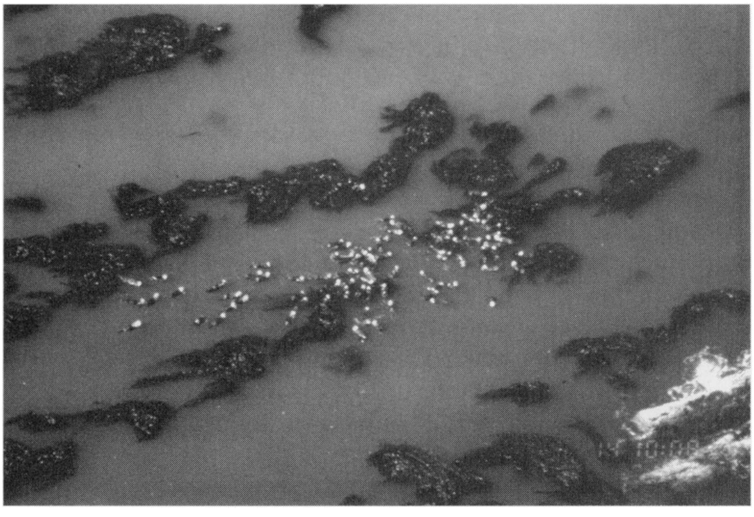

Figure 2. A large group of sea otters rests in typical rocky habitat near Destruction Island, Washington, July 2000. Photo by Steven J. Jeffries.

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Figure 3. Photograph taken near Teahwhit Head, looking north with LaPush, Washington in the background, shows "rocky" sea otter habitat between the Little James Island region and South of Destruction Island region in Figure 1. Photo courtesy of Olympic Coast National Marine Sanctuary (OCNMS).

and have been expanding their range and population size primarily in these regions. Recent observations suggest that increased use of sandy habitat south of Destruction Island may be occurring (R. J. Jameson, unpublished data).

Management implications

Understanding the limits in offshore habitat utilization by sea otters in Washington is important to accurately estimate *K*. Because estimates vary with equilibrium densities (dependent on available habitat within an equilibrium region) and the total amount of available habitat within the sea otter's range, it is important to delineate offshore habitat use accurately.

At this time it is not possible to predict the direction or extent of future expansion by the sea otter population in Washington or to determine whether sea otters will reach coastal estuaries and utilize them as sea otters do in California or Alaska. It also remains unclear whether Washington habitats will support the same density of sea otters as similar habitats in California. It is important to keep in mind that *K* may vary over time and is not a single value. Therefore, we conclude, given the current data as well as large sources of uncertainty in our model, that the best estimate of *K* for the Washington population is approximately 2,734 (95% CI = 2,082-3,452) sea otters. This results in an MNLP (60% of *K*) of 1,640 (95% CI = 1,249-2,071) sea otters. Grays Harbor, Willapa Bay, and the Columbia River have been extensively modified by humans, and it is unclear whether sea otters will reoccupy these coastal estuaries at the levels predicted here. Our linear estimate for *K*, excluding these areas, is 1,836 (95% CI = 1,386-2,286), which results in an MNLP of 1,101 (95% CI = 832-1,371).

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