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AN ESTIMATION OF CARRYING CAPACITY FOR SEA OTTERS ALONG THE CALIFORNIA COAST

KRISTIN L. LAIDRE
National Marine Mammal Laboratory,
Alaska Fisheries Science Center/NMFS/NOAA,
7600 Sand Point Way NE,
Seattle, Washington 98115, U.S.A.
E-mail: kristin.laidre@noaa.gov

RONALD J. JAMESON
United States Geological Survey,
Western Ecological Research Center,
200 SW 35th Street,
Corvallis, Oregon 97333, U.S.A.

DOUGLAS P. DEMASTER
National Marine Mammal Laboratory,
Alaska Fisheries Science Center/NMFS/NOAA,
7600 Sand Point Way NE,
Seattle, Washington 98115, U.S.A.

ABSTRACT

Carrying capacity (K) for the California sea otter (*Enhydra lutris nereis*) was estimated as a product of the density of sea otters at equilibrium within a portion of their existing range and the total area of available habitat. Equilibrium densities were determined using the number of sea otters observed during spring surveys in 1994, 1995, and 1996 in each of three habitat types where sea otters currently exist. Potential sea otter habitat was defined as from the California coastline to the 40-m isobath and classified as rocky, sandy, or mixed habitat according to the amount of kelp and rocky substrate in the area. The amount of habitat available to sea otters in California was estimated using a Geographic Information Systems (GIS) program. The estimated mean number of sea otters that could be supported by the marine environment to a depth of 40 m in California was 15,941 (95% CI 13,538–18,577). The GIS-based approach incorporated detailed bathymetric contours, produced repeatable and accurate estimates, and served as an innovative method of measuring sea otter habitat. We believe the approach described in this paper represents the best available information on how a sea otter population at equilibrium would be distributed along the California coast.

Key words: southern sea otter, *Enhydra lutris nereis*, carrying capacity, GIS, California.

In 1977 the southern or California sea otter (*Enhydra lutris nereis*) was listed as "threatened" under the U.S. Endangered Species Act (ESA) (42 FR 2965 January 14, 1977) due to small population size, human disturbance, competition with fisheries, and pollution, including the threat of a major oil spill. This listing, by default, gave the southern sea otter the status of "depleted" under the Marine Mammal Protection Act (MMPA) of 1972 (Public Law 92-522, 86 statute 1072). The U.S. Fish and Wildlife Service (USFWS) is mandated by both the ESA and the MMPA to manage the southern sea otter population until it recovers to a point where it is no longer considered threatened (U.S. Fish and Wildlife Service 2000) or depleted. This mandate requires the USFWS to develop recovery or delisting criteria for the population.

Under the MMPA, the southern sea otter population will no longer be considered depleted when it reaches the lower limit of its optimum sustainable population (OSP) level. This limit, the maximum net productivity level (MNPL), is generally defined as approximately 60% of the carrying capacity (K) (Gerrodette and DeMaster 1990). K is interpreted here to be the maximum number of sea otters that can be supported by the offshore California environment. Taylor and DeMaster (1993) report that MNPL can range from 50% to 80% of K, and without complete information on density-dependent age-specific birth and death rates, a single value cannot be adopted. For the purpose of this study, MNPL is defined as 50% of K.

Appropriate management of sea otters requires an understanding of the connections between sea otters and their environment. Sea otters occur in a wide variety of substrate types and community compositions, including rocky and soft bottom habitats. They are most common along rocky shores (Riedman and Estes 1990), which support diverse marine communities and include their preferred prey.

In rocky habitats prey refuges are size-selective and are generally available for smaller invertebrates in crevices, which physically prevent the entry of a sea otter (Kvitek and Oliver 1988). Otters first select the largest, calorically rich prey and later broaden their diets to alternate prey species when the availability of preferred species is reduced (Estes and Palmisano 1974, Kvitek *et al.* 1988). In contrast, soft-bottom habitat prey refuges are ill-defined and may not be size-selective. Soft-sediment burrowing prey have the advantage of a cryptic lifestyle and are often spread over a large geographical area (Morris *et al.* 1980). It is more efficient for sea otters to maximize the amount of prey biomass obtained per unit volume of sediment extracted rather than target large individual prey (Kvitek *et al.* 1988). For example, the effectiveness of sea otter foraging on bivalves is a function of the prey species and the nature of the substrate. In protected bays with deep-burrowing prey species, large individuals may be less vulnerable to sea otter predation (Kvitek *et al.* 1988). Smaller individuals are probably consumed more frequently than larger individuals because they live at shallower depths and are therefore more easily excavated. In contrast, along the exposed beaches of central California, large individuals of shallow-burrowing species (such as the Pismo clam, *Tivela stul-*

torum) are more vulnerable, because they are a more efficient prey item, and smaller individuals may have a refuge in size by being less advantageous, containing fewer calories for the effort (Miller *et al.* 1975).

The difference in substrate and prey refugia availability seems to affect sea otter densities, with greater densities of sea otters occurring in rocky-bottom habitats than soft-bottom habitats (Riedman and Estes 1990). At some point, given sufficient recovery, the number of sea otters in a particular habitat type theoretically could reach an equilibrium (*i.e.,* the average density, stable over time, that can be supported by a particular habitat type within the southern sea otter's range). If habitat-specific equilibrium densities are constant over time, then an objective measure of population status relative to carrying capacity can be estimated by comparing the current estimate of abundance with the estimate of K, which is derived by summing the product of habitat-specific equilibrium densities and habitat availability over all habitat types (see DeMaster *et al.* 1996). Such relationships can be analyzed with a Geographic Information System (GIS), a system of computer hardware and specialized software designed to analyze complex spatial data. GISs have been increasingly used in wildlife science because they provide a powerful tool to link and overlay multiple spatial factors (Buckland and Elston 1993).

Previous studies have estimated carrying capacity for the southern sea otter over a portion of its range using density estimates and habitat area, although none have employed a GIS. The California Department of Fish and Game (1976) estimated carrying capacity for the southern sea otter in California using the product of average density and available habitat out to 37 m. In 1984 equilibrium density was used to roughly estimate carrying capacity of four potential sea otter translocation zones in California, Oregon, and Washington (James Dobbin Associates, Inc. 1984). In both of these studies the area of suitable habitat for sea otters was estimated within the 20-fathom (36-m) contour using a polar planimeter and large-scale nautical charts. Although such data were considered reliable, a hand-calculated technique poses many limitations, which may be reduced through the use of a GIS. DeMaster *et al.* (1996) estimated carrying capacity for sea otters along the California coast to the 40-m isobath by stratifying the equilibrium density of sea otters in 1992 by habitat type using software developed by Forney (1988). Forney (1988) encountered irregularities in area calculations, inaccuracies in coastline data points, and distortion of contours using this non-GIS based method. These difficulties necessitated a more efficient and accurate method of calculating habitat areas.

The objectives of our study were to use a GIS to obtain a new estimate of K for the southern sea otter throughout its potential range in California and to evaluate the overall usefulness of a GIS package in estimating habitat area. This study, modeled after DeMaster *et al.* (1996), updates the present estimate for carrying capacity in the draft recovery plan for the southern sea otter (U.S. Fish and Wildlife Service 2000) and provides a comparison to the non-GIS-based habitat area calculation method (Forney 1988).

Methods

Habitat Characterization and GIS Techniques

Potential sea otter habitat was defined from the coastline to the 40-m bathymetric contour. Areas along the California coast ($n = 39$) were classified as one of three habitat types: rocky, sandy, or mixed. Rocky habitat was defined as moderate to large amounts of kelp and moderate to large amounts of rocky substrate; sandy habitat was defined as having no rocky coast and no kelp or rocky subtidal substrate; and mixed habitat was defined as habitat with some rocky coast, with occasional headlands and coves, but little or no kelp and minimal subtidal rocky substrate. Surface area included under each habitat is reported in Table 1, 2.

The GIS software packages ARC/INFO® and Arcview® (Environmental Systems Research Institute Inc., Redlands, CA) were used to estimate the amount of sea otter habitat along the California coast. The assessment of habitat quality in California waters was done by one of the authors (RJJ) based on aerial surveys of the coastline, experience with surface and subsurface characteristics of sea otter habitat, National Oceanic and Atmospheric Administration (NOAA) nautical charts, and previous habitat characterizations compiled by DeMaster *et al.* (1996), James Dobbin Associates, Inc. (1984), and California Department of Fish and Game (1976). The 40-m depth contour was created from data on the National Ocean Service (NOS) Hydrographic Survey CD-ROM (NOAA, National Ocean Service, 1305 East West Highway, Silver Spring, Maryland 20910). Raw data were extracted from the disk and used to create a file for ARC/INFO®.[1] The coastline file was compiled from NOAA bathymetric charts by the Strategic Environmental Assessments Division of NOAA's Office of Ocean Resources, Conservation and Assessment. The datum for both files was NAD83. Coordinates were obtained from NOAA nautical charts and converted to decimal degrees for the northern and southern boundaries of each of the 39 regions. All northern and southern boundaries were defined perpendicular to the coastline.[2] San Francisco Bay was defined east of a line drawn between Point Bonita and Mile Rocks, the northern and southern boundaries, respectively.

An ARC/INFO® programming script was built to create polygons between the coastline, the 40-m isobath, and the northern and southern boundaries for each habitat area. The ARC/INFO® script appended the intersections of these three elements and created discrete regions. The coverage was projected into the Albers Equal Area projection.

Due to the extreme detail of the coastline map contour, several river mouths were included, by default, in the calculated areas for each polygon. Because sea otters generally forage at sea and rarely swim upstream into rivers (Ried-

[1] Personal communication from R. Cosgrove, NMFS, Southwest Fisheries Science Center, P. O. Box 271, La Jolla, CA 92038-0271, March 1998.

[2] Personal communication from K. Forney, NMFS, Southwest Fisheries Science Center. P. O. Box 271, La Jolla, CA 92038-0271, March 1998.

Table 1. 1994–1996 equilibrium density estimates for sea otters in representative rocky, mixed, and sandy habitat types from California coast to 40-m isobath in sea otters/km². Estimates of SD, CV, and 95% CI are based on bootstrapping techniques.

Habitat type	$Area_{eq}$ (km²)	Number of sea otters* 1994	Number of sea otters* 1995	Number of sea otters* 1996	40 m depth 1994 Density (otters/km²)	40 m depth 1995 Density (otters/km²)	40 m depth 1996 Density (otters/km²)	SD	CV	95% CI
Rocky	329.2	1,694	1,694	1,662	5.15	5.15	5.05	0.25	0.05	4.65–5.62
Sandy	261.3	248	293	294	0.95	1.12	1.13	0.12	0.12	0.84–1.32
Mixed	60.7	45	42	56	0.74	0.69	0.92	0.19	0.25	0.44–1.16

* Numbers of sea otters counted in 1994–1996 spring sea otter surveys (USGS, unpublished data).

man and Estes 1990), the surface area of these features was subtracted from the larger polygons to reduce any overestimation of surface area. All river mouths which were not included in the area calculations are noted on the appropriate figure, so that results of this study may be accurately compared with other habitat estimates for California.

Density Estimates and K

Trends in the spring sea otter survey counts show sea otters increased steadily until the mid-1990s, peaking in 1996. Shortly thereafter, the number of animals counted in spring surveys progressively declined (U.S. Fish and Wildlife Service 2000, appendix D). Thus, the years 1994–1996 were selected as being representative high years and used for equilibrium density estimates. The "California As The Otter Swims" (CATOS) line, created by the California Department of Fish and Game, delineates the coast into 0.5-km intervals roughly along the 5-fathom contour. Spring sea otter survey records were binned into CATOS segments for each year.

Equilibrium densities were determined using the number of sea otters observed during spring surveys in each of the three habitat types where sea otters currently exist (USGS, unpublished data). Total surface area was calculated for each habitat type (*i.e.,* rocky, sandy, and mixed habitat). The area between the Monterey breakwater and Cayucos Point was chosen to represent rocky habitat; the combined area in Monterey, Estero, and Morro Bays was chosen to represent sandy habitat; and the area between Ano Nuevo Point and Sandhill Bluff was chosen to represent mixed habitat. Density estimates were calculated for each of the three years by dividing the number of sea otters within each region by the respective surface area.

After estimating the total available area for each of the three habitat types, the number of sea otters that could be supported was estimated as a product of the equilibrium density for each habitat type and the total surface area for the habitat type in square kilometers. The sum of these products provided an estimate of K for the entire coast of California. K was estimated independently for 1994, 1995, and 1996, with densities adjusted for each year. The estimated variance from these three estimates was assessed to represent variance produced by inter-annual differences in density. Habitat classifications are presented in Figures 1–3.

A bootstrapping approach was used to estimate the variability around the point estimate of K (Efron and Tibshirani 1986). CATOS segments were of uniform width and had approximately equal areas, therefore bootstrapping was done using the individual segment counts within equilibrium regions from 1994 to 1996 surveys. Counts for each segment were chosen at random (with replacement) from each habitat type and summed. Density was estimated by dividing the sum of the counts by the total area of the habitat type. This process was repeated 10,000 times. The values were used to calculate a SD and CV for the equilibrium densities and to determine 95% CI from the distribution of the bootstrap draws for each of the three habitat types. The

Table 2. Sea otter areas along California coast; calculated areas and calculated numbers of sea otters (rounded) that can be supported by each area included for regions from coast out to 40 m. Numbers of sea otters calculated from annual equilibrium density estimates for habitat type of area. Regions grouped by habitat type (rocky, sandy, or mixed) and within each group, by location from Oregon border to Mexican border along California coast.

Habitat type	Region	Area to 40 m (km^2)	40 m depth		
			Calculated # of sea otters (1994)	Calculated # of sea otters (1995)	Calculated # of sea otters (1996)
Rocky	Pt. St. George-Klamath River	181.5	935	935	916
	Patricks Pt.-Trinidad Head	35.0	180	180	177
	Cape Vizicanio-Fort Bragg	59.0	304	304	298
	Fort Bragg-Bodega Head	267.5	1,378	1,378	1,351
	Sandhill Bluff-Capitola Pier	84.0	433	433	424
	Monterey Breakwater-Cayucos Pt.	329.2	1,695	1,695	1,663
	Hazard Canyon-Pt. San Luis	41.8	215	215	211
	Pt. San Luis-Shell Beach	17.5	90	90	88
	Purissima Pt.-Santa Ynez River	37.7	194	194	191
	Pt. Mugu-Pt. Dume	44.9	231	231	227
	Corona Del Mar-Pt. La Jolla	300.4	1,547	1,547	1,517
	Pt. La Jolla-Bird Rock	13.0	67	67	66
	Channel Islands	646.8	3,331	3,331	3,266
Total rocky		2,058.3	K = 10,600	K = 10,600	K = 10,394
Sandy	Oregon Border-Pt. St. George	209.5	199	235	237
	Klamath River-Patricks Pt.	279.8	266	313	316
	Trinidad Head-Cape Mendocino	507.5	482	568	574
	Punta Gorda-Pt. Delgado	79.9	76	89	90
	Pt. Lobos-Pt. San Pedro	363.5	345	407	411

Table 2. Continued.

Habitat type	Region	Area to 40 m (km²)	40 m depth: Calculated # of sea otters (1994)	40 m depth: Calculated # of sea otters (1995)	40 m depth: Calculated # of sea otters (1996)
	Capitola Pier-Monterey Breakwater	182.5	173	204	206
	Cayucos Pt.-Hazard Canyon	78.8	75	88	89
	Shell Beach-Pt. Sal	199.9	190	224	226
	Lions Head-Purissima Pt.	80.9	77	91	91
	Ventura-Pt. Mugu	285.3	271	320	322
	Pt. Fermin-Corona Del Mar	353.6	336	396	400
	Bird Rock-Pt. Loma	47.7	45	53	54
	Pt. Loma-Mexican Border	156.7	149	176	177
	San Franscisco Bay	1029.1	978	1153	1163
Total Sandy		3,855.0	K = 3,662	K = 4,318	K = 4,356
Mixed	Cape Mendocino-Punta Gorda	63.1	47	44	58
	Pt. Delgado-Cape Vizićanio	128.9	95	89	119
	Bodega Head-Pt. Lobos	468.1	346	323	431
	Pt. San Pedro-Ano Nuevo Pt.	277.4	205	191	255
	Ano Nuevo Pt.-Sandhill Bluff	60.7	45	42	56
	Pt. Sal-Lions Head	26.1	19	18	24
	Santa Ynez R.-N. Pt. Pedernales	49.0	36	34	45
	N. Pt. Pedernales-Rocky Pt.	17.5	13	12	16
	Rocky Pt.-Pt. Conception	56.2	42	39	52
	Pt. Conception-Ventura	309.0	229	213	284
	Pt. Dume-Palos Verdes Pt.	180.0	133	124	166
	Palos Verdes Pt.-Pt. Fermin	19.9	15	14	18
Total Mixed		1,656.0	K = 1,225	K = 1,143	1,524
Grand Total		7,569.3	15,488	16,061	16,274

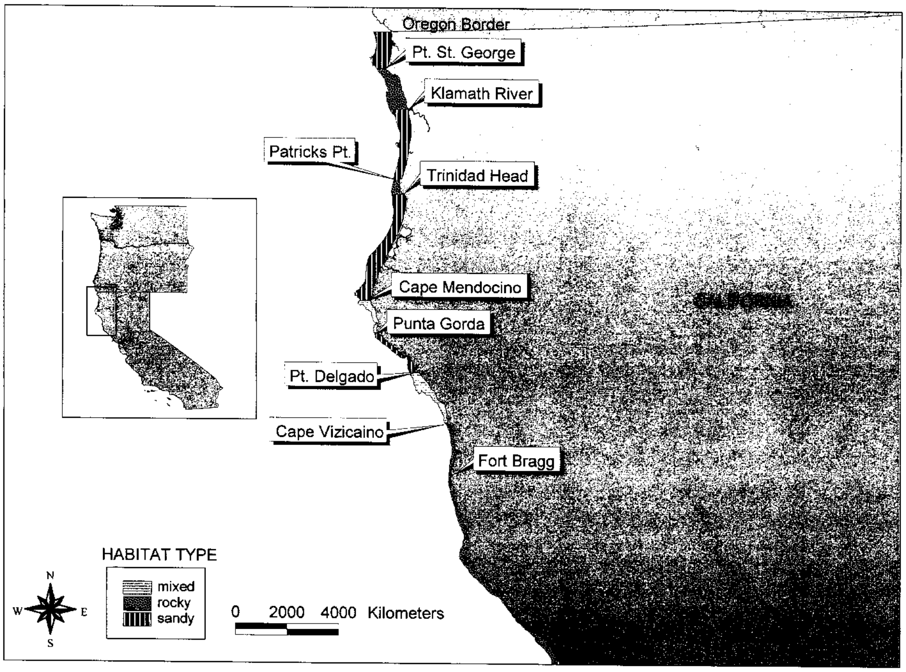

Figure 1. Sea otter habitat classifications from Oregon border to Fort Bragg. Western boundary of each area delineates sea otter habitat. Surface area estimates do not include Smith River, Klamath River, VanDuxen River, Albion River, Big River, and Garcia River mouths.

variance estimated from this approach incorporated variability in density caused by temporal and spatial factors.

Results and Discussion

Density Estimates

Habitat-specific equilibrium density estimates for 1994–1996 are reported in Table 1. For rocky habitat, equilibrium densities (otters/km^2) were calculated as 5.15, 5.15, and 5.05 for 1994, 1995, and 1996, respectively. The bootstrapped CV for the pooled mean was 0.05. For sandy habitat, equilibrium densities (otters/km^2) were calculated as 0.95, 1.12, and 1.13 for 1994, 1995, and 1996, respectively. The bootstrapped CV for the pooled mean was 0.12. For mixed habitat, equilibrium densities (otters/km^2) were calculated as 0.74, 0.69, and 0.92 for 1994, 1995, and 1996, respectively. The bootstrapped CV for the pooled mean was 0.25.

The variance of the three density estimates was also estimated using standard analytical techniques for comparison purposes. The standard deviation of the three annual equilibrium estimates for rocky, sandy, and mixed habitats was 0.06, 0.10, and 0.12, respectively. These values compare to the standard

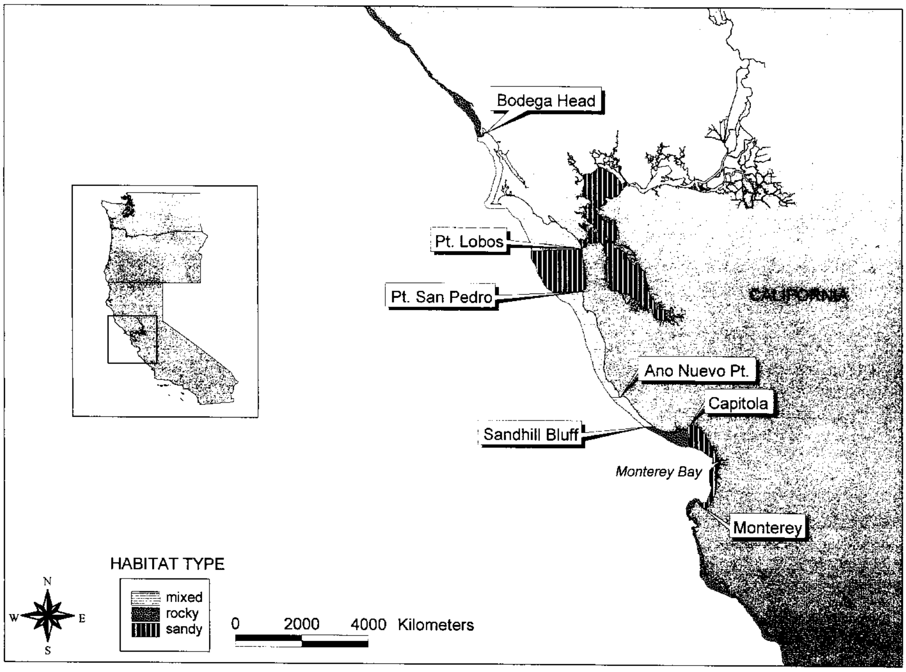

Figure 2. Sea otter habitat classifications from Bodega Head to Monterey. Western boundary of each area delineates sea otter habitat. Surface area estimates do not include Drakes Estero.

deviations obtained from the bootstrapping for rocky, sandy, and mixed habitats, 0.25, 0.12, and 0.19 (Table 1). The CVs estimated using standard analytical techniques for rocky, sandy, and mixed habitats, 0.01, 0.10, and 0.15, respectively, are smaller than the corresponding CVs obtained from the bootstrapping (0.05, 0.12, and 0.25) reported in Table 1. It is likely that the bootstrapped variability reported in Table 1 is a more accurate estimate of actual variability, as the bootstrap approach includes the interannual variability, as well as the variability caused by spatial differences in density.

K Estimates and MNPL

Considering the entire California coast as potential habitat for sea otters, we classified 13 regions as rocky habitat, 14 regions as sandy habitat, and 12 regions as mixed habitat. In rocky habitat the mean number of sea otters that could be supported to the 40-m depth contour was 10,532; in sandy habitat, 4,112; and in mixed habitat, 1,297. Because we assumed there was no variability in the way surface area was calculated, the CVs for the estimated number of sea otters in each habitat type are the same as the CVs calculated for the three equilibrium density estimates.

The estimated number of sea otters that could be supported by the California coastal environment out to a depth of 40 m was 15,488, 16,061, and

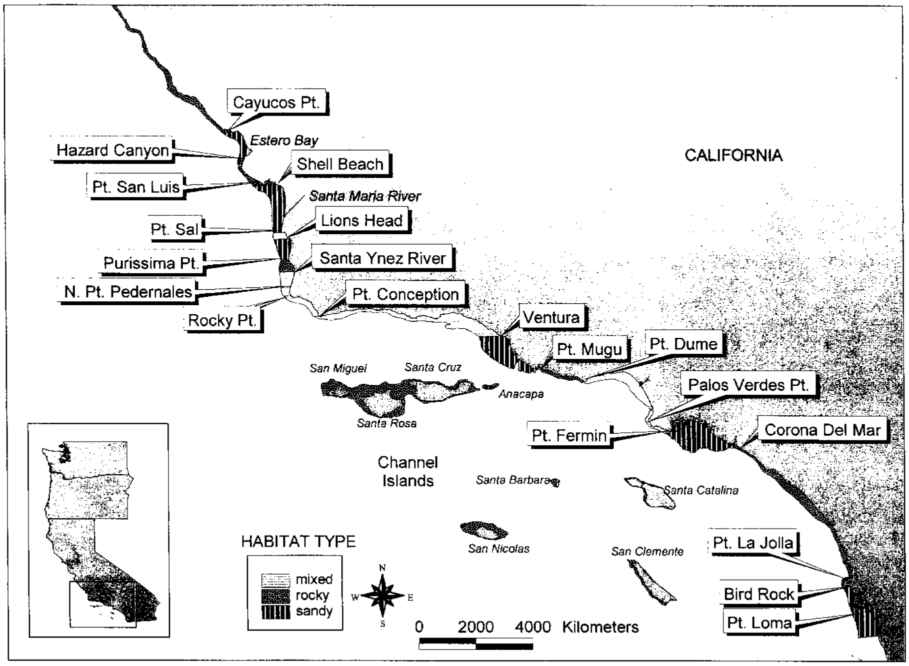

Figure 3. Sea otter habitat classifications from Cayucos Point to Mexican border. Western boundary of each area delineates sea otter habitat. Surface area estimates do not include Los Angeles Harbor, Newport Bay, and Mission Bay.

16,274 for each year 1994–1996, respectively (Table 2). The mean K calculated from these annual estimates was 15,941 (95% CI 13,538–18,577). Therefore, MNPL (50% of K) is 7,971 (95% CI 6,769–9,288) sea otters.

Our mean estimate for K (15,941 sea otters) is higher than the previous estimate (13,513) by DeMaster *et al.* (1996). Surface area calculations using a GIS-based approach produced smaller estimates in the equilibrium regions; this led to higher equilibrium density estimates for sea otters in the rocky and sandy habitat types than used by DeMaster *et al.* (1996). However, the equilibrium region used for mixed habitat in DeMaster *et al.* (1996) (Ano Nuevo to Santa Maria River) included large amounts of both optimal rocky and sandy habitat. In our study a more representative mixed equilibrium habitat region was selected (Ano Nuevo to Sandhill Bluff), which resulted in lower densities for mixed habitat.

Total area estimates for the three habitat classifications using a GIS-based approach were slightly less than the total habitat area estimates in DeMaster *et al.* (1996). Areas where sea otters would not normally be found (*e.g.*, river mouths) may have been included in their calculations, although this was not reported. Total sea otter habitat area along the California coast was estimated here as 7,569 km^2 using the GIS-based technique, where as DeMaster *et al.* (1996) estimated it to be 7,802 km^2. The GIS-based approach, compared to the approach used by DeMaster *et al.* (1996), calculated 329 km^2 *vs.* 401 km^2

for rocky habitat in equilibrium regions and 261 km^2 *vs.* 370 km^2 for sandy habitat equilibrium regions. A comparison of mixed habitat is not included here due to the new boundaries.

Taking into consideration the problems encountered estimating surface area using the non-GIS approach (Forney 1988), it is not surprising that the GIS-based method produced different area estimates. The current approach incorporates a high-quality, GIS-ready digital vector shoreline compiled from high scale (1:80,000–1:60,000) NOAA coast charts, as well as a detailed 40-m bathymetric curve contoured from a grid of NOS depth values along the California coast. The primary problems reported in Forney (1988) were related to inaccurate placement of the coastline due to lack of reference points beyond the zero depth contour and irregular distribution of depth values for contour creation. These problems introduced error due to manual digitizing and repeated scale and format conversions.

Published reports of equilibrium densities of sea otters in California include the California Department of Fish and Game (1976), who reported maximum densities of sea otters in rocky habitat (estimated from Monterey to Cayucos Pt., the same region used here for equilibrium rocky habitat) to be about 4.61 otters/km^2 (12 otters/mi^2). Their estimate of maximum densities in sandy habitat was about 0.38–0.77 otters/km^2 (1–2 otters/mi^2). Riedman and Estes (1988) reported average densities of 5 otters/km^2 in rocky habitat in California, and 0.8 otters/km^2 along clam beaches, or sandy habitat. Both of these sources estimated densities similar to our calculated equilibrium densities of 5.05–5.15 otters/km^2 in rocky habitat and 0.95–1.13 otters/km^2 in sandy habitat; however, neither reported equilibrium densities for mixed habitat. DeMaster *et al.* (1996) reported an equilibrium density of 3.85 otters/km^2 (13.21 otters/nmi^2) in rocky habitat, and 0.35 otters/km^2 (1.19 otters/nmi^2) in sandy habitat. Mixed equilibrium density was reported as 2.03 otters/km^2 (6.95 otters/nmi^2), however, this estimate is biased high because it includes a large area of rocky habitat.

Prior to commercial exploitation, there were an estimated 16,000–20,000 sea otters in California (California Department of Fish and Game 1976). There are few recent estimates for K for the southern sea otter in California. An estimate for K of 14,600 sea otters was calculated by California Department of Fish and Game (1976) based on densities of sea otters in 1974. This estimate was calculated from an average density of 3.84 otters/km^2 (10 otters/mi^2) for rocky habitat and 0.77 otters/km^2 (2 otters/mi^2) for sandy habitat. Because this figure was based on conservative population estimates and was noted to exclude habitat within bays, an overall estimate for K in California waters was given as 16,000 (California Department of Fish and Game 1976). Another estimate for K, 13,513 (from DeMaster *et al.* 1996), was used by the Southern Sea Otter Recovery Team in the draft southern sea otter recovery plan (U.S. Fish and Wildlife Service 2000). The present study provides a more accurate estimate for K (15,941), a value which concurs with the CDFG estimate and is essentially the same as the lower bound of the preexploitation abundance.

Sea otters may use coastal regions that were not included in our estimate.

Feinholz (1998) reported densities of 3–19 otters/km^2 in Elkhorn Slough (1.3 km^2), an estuarine area near Monterey Bay, California, in 1994 and 1995. This would amount to an additional 4–25 sea otters not in our estimate. This region, considered a seasonal estuary influenced by marine related cycles including tide, is currently the only estuarine area regularly used by sea otters throughout their entire range. These density estimates are higher than our estimates of equilibrium density for sandy habitat, possibly a function of the tendency of sea otters to congregate in large resting groups when in this estuarine area. Although this habitat is primarily soft bottom, the variation and fluctuation in sea otter density requires estuarine habitat to be considered separately from other soft-bottom habitats.

As an exercise, K was calculated out to the 50-m depth contour to address foraging tactics of juvenile sea otters. Sea otters cannot effectively forage in depths greater than 40 m (Riedman and Estes 1988); however, it has been reported that juveniles, particularly males, occasionally forage in deeper water than adults (Ralls *et al.* 1988). Recent evidence suggests sea otters reach waters deeper than 40 m in Monterey Bay, a sandy habitat (Forney *et al.,* in press) and may do so in rocky and mixed habitats as well. For example, between Pt. Sur and San Simeon, (a predominantly rocky habitat), juvenile male sea otters foraged at a mean depth of 30.1 m, while juvenile females and adult females foraged at 17.9 m and 22.0 m, respectively (adult males were not reported) (Ralls *et al.* 1995). The mean depth for juvenile males may be biased toward shallower depths due to a decline in reception of radio telemetry signals as sea otters moved farther offshore, presumably into deeper water.[3] Based on sea otter survey data from 1994–1996, the mean number of sea otters that could be supported by the California coastal environment out to a depth of 50 m was 16,758 (95% CI 14,306–19,474), where equilibrium density was adjusted appropriately for each isobath. When the 50-m contour was selected as the offshore boundary, the resulting equilibrium densities were lower than when the 40-m boundary was selected. However, the available habitat within the 50-m offshore boundary (9,325 km^2) was sufficiently increased over that within the 40-m offshore boundary (7,569 km^2) to offset the lower equilibrium densities. The proportion of the southern sea otter population that reaches the 50-m isobath and forages effectively is most likely small. The estimates of K to the 40-m isobath (15,941) and to the 50-m isobath (16,758) are within 10% of each other.

Our assumption that densities of sea otters are similar in areas with similar habitat types may not be true in all cases. For example, the soft-bottom habitat of Elkhorn Slough, mentioned earlier, is not equivalent to other soft-bottom habitats. Furthermore, all habitats with similar substrate may not support the same density of sea otters. Habitat variability occurs on annual, decadal, and multidecadal scales. Community and patch stability are subject to many types of disturbance events, which can change kelp forest structure and result in

[3] Personal communication from Katherine Ralls, Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008, March 2000.

between-area variation in recovery rates of kelp forests (Dayton *et al.* 1992). Disturbance events change community stability and result in considerable site-to-site variation, although in some areas it appears that some patch structure may persist (Dayton *et al.* 1992). Therefore, a rocky-bottom habitat at one site may not be equivalent in resources or stability to a rocky-bottom habitat at another site, although the structure of the sites may be similar. This may result in density estimate variability between sites with the same habitat. If a "preferred" rocky-bottom site was sampled when collecting data for estimating equilibrium density, estimates for K would be biased upward.

Our selection of equilibrium density areas was based on large regions of one homogeneous habitat type within the southern sea otter's existing range. For example, the area selected as equilibrium rocky habitat, Monterey to Cayucos Point, was an area once noted to contain some of the most productive rocky reefs and intertidal areas of the state (California Department of Fish and Game 1976).

We assumed that the habitat quality used to estimate equilibrium density was representative of the California coast. For this assumption to hold, habitat must be delineated consistently and accurately throughout the study area. Additional habitat surveys should be conducted along the California coast to determine any changes in habitat patches, specify site-to-site variability in more detail, and determine if recent disturbance events have altered habitats from the previous surveys. Furthermore, it would be useful to evaluate additional habitat variables (other than depth and substrate) that would limit sea otter growth. For example, the seaward limit of sea otter habitat may be a function of distance from shore or slope, in addition to depth. This may be particularly true where the 40-m isobath deviates far offshore. Further, harvest data from local shellfish fisheries could be an important covariate.

A population is thought to be at equilibrium with existing resources if the number of animals or the density is not increasing and if environmental disturbances are not limiting further growth (Estes 1990). This study assumed that observed densities were in equilibrium with the environment and that the densities were the maximal level that could be obtained. It is possible that the observed densities in the equilibrium regions actually were still increasing (or were measured at a time when the equilibrium densities had been exceeded), which would increase our estimated value for K.

In the spring of 2000 there were 1,371 sea otters counted in our rocky equilibrium region, 266 sea otters counted in our sandy equilibrium region, and 48 sea otters counted in our mixed equilibrium region. The resulting density estimates from the spring of 2000 did not result in any consistent change in equilibrium density estimates, as determined from data collected in 1994, 1995, and 1996. Clearly, environmental variability and subsequent population responses do not allow for exact measures of equilibrium densities or precise point estimates of K. The concept of a population moving toward a stable state eventually reaching K is confounded by ecological and behavioral processes which are not easily predicted using a standard population growth model.

In the future, the management of sea otters along the U.S. west coast will be contentious. However, management decisions will be aided considerably if they are based on the best available information on the maximum number of sea otters that could be sustained in a given area. We believe the approach described in this paper represents the best available information on how a sea otter population at equilibrium would be distributed along the California coast.

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