Management and Conservation Article

Estimating Carrying Capacity for Sea Otters in British Columbia

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ABSTRACT We estimated carrying capacity for sea otters (*Enhydra lutris*) in the coastal waters of British Columbia, Canada, by characterizing habitat according to the complexity of nearshore intertidal and sub-tidal contours. We modeled the total area of complex habitat on the west coast of Vancouver Island by first calculating the complexity of the Checleset Bay–Kyuquot Sound (CB–KS) region, where sea otters have been at equilibrium since the mid-1990s. We then identified similarly complex areas on the west coast of Vancouver Island (WCVI model), and adapted the model to identify areas of similar complexity along the entire British Columbia coast (BC model). Using survey data from the CB–KS region, we calculated otter densities for the habitat predicted by the 2 models. The density estimates for CB–KS were 3.93 otters/km^2 and 2.53 otters/km^2 for the WCVI and BC models, respectively, and the resulting 2 estimates of west coast of Vancouver Island complex habitat carrying capacity were not significantly different (WCVI model: 5,123, 95% CI = 3,337–7,104; BC model: 4,883, 95% CI = 3,223–6,832). The BC model identified the region presently occupied by otters on the central British Columbia coast, but the amount of coast-wide habitat it predicted (5,862 km^2) was relatively small, and the associated carrying capacity estimate (14,831, 95% CI = 9,790–20,751) was low compared to historical accounts. We suggest that our model captured a type of high-quality or optimum habitat prevalent on the west coast of Vancouver Island, typified by the CB–KS region, and that suitable sea otter habitat elsewhere on the coast must include other habitat characteristics. We therefore calculated a linear, coast-wide carrying capacity of 52,459 sea otters (95% CI = 34,264–73,489)—a more realistic upper limit to sea otters in British Columbia. Our carrying capacity estimates are helping set population recovery targets for sea otters in Canada, and our habitat predictions represent a first step in Critical Habitat identification. This habitat-based approach to estimating carrying capacity is likely suitable for other nonmigratory, density-dependent species. (JOURNAL OF WILDLIFE MANAGEMENT 72(2):382–388; 2008)

DOI: 10.2193/2006-518

KEY WORDS British Columbia, carrying capacity, endangered species, *Enhydra lutris*, habitat model, optimum habitat, recovery, sea otter, Species at Risk Act (SARA), species–habitat relationship.

Sea otters (*Enhydra lutris*) are currently listed as Threatened under the Canadian Species at Risk Act (SARA), though downlisting to Special Concern was recommended in April 2007 by the Committee on the Status of Endangered Wildlife in Canada (2007). The recovery planning process for species at risk under SARA requires recovery goals. Population recovery goals may be set relative to estimates of the regional carrying capacity (Laidre et al. 2001, 2002). We developed models to estimate habitat area and derived carrying capacity estimates to assist in formulating recovery goals for the British Columbia sea otter population.

Sea otters are a nonmigratory, nearshore species that feed primarily on benthic invertebrates in depths <40 m (Riedman and Estes 1990, Bodkin et al. 2004). Sea otter populations are density dependent with growth believed to be regulated by prey abundance. When sea otters expand into areas where prey are abundant, population growth is rapid until food becomes limiting and the population reaches equilibrium (i.e., births are offset by mortality and emigration; Estes 1990). This density dependence and nonmigratory behavior allows a habitat approach to be used for estimating carrying capacity (K).

Using a habitat approach, K is estimated by multiplying density of sea otters calculated for a portion of their range where they are at equilibrium by the total area defined as suitable habitat (DeMaster et al. 1996). This approach has been used in California (DeMaster et al. 1996, Laidre et al. 2001), Washington (Laidre et al. 2002), and Alaska, USA (Burn et al. 2003). The approach requires 1) sufficient survey data of representative areas where the population is at equilibrium and 2) spatial definitions of sea otter habitat. Calculation of available habitat requires a spatial model supported by physical data. In each of the above studies, the modeling approach was adapted to available physical data to characterize sea otter habitat. For instance, comprehensive substrate data available for coastal California and Washington allowed Laidre et al. (2001) to divide the Californian coast into 3 habitat classes: sandy, rocky, and mixed. Defining the seaward extent of the habitats as the 40-m isobath allowed Laidre et al. (2001) to calculate the area of each habitat class. Laidre et al. (2001) estimated maximum densities of otters (0.92–5.15 otters/km^2) for each habitat class based on survey data from representative sections of each habitat class where otters were believed to be at equilibrium. In Washington, where the 40-m isobath extends 10–15 km from shore, use of the 40-m isobath as a seaward habitat boundary was unreasonable, so a K based on coastline length was used because it was a better indicator of K in that area (Laidre et al. 2002). Burn et al. (2003) used a simpler habitat model for the Aleutian Islands, defining suitable otter habitat as the total area contained within 400 m from shore, the 40-m isobath, and bays and fjords <6 km across.

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With only bathymetric data available, we sought alternative physical descriptions of habitat. In British Columbia, we observed that sea otters occupy areas characterized by a complex coastline (e.g., reefs, small islets, embayments) and are found less frequently along stretches of straight coastline. We therefore hypothesized that complexity of the physical environment was related to sea otter habitat quality and, thus, defined sea otter habitat according to the complexity of the available bathymetric data. To obtain the most reasonable estimate of K for sea otters in British Columbia, we compared regional and coast-wide carrying capacities derived from the complex habitat analysis to estimates based on linear densities.

STUDY AREA

British Columbia includes all of Canada's Pacific coast, and is where the coast of North America changes from the relatively straight coastline found in Washington and further south, to an extremely crenulated coastline dominated by archipelagos and incised by long glacial fjords. Our analysis used survey data from a portion of the west coast of Vancouver Island, British Columbia to estimate K for all British Columbia coastal waters. Sea otters were extirpated from British Columbia by 1929 as a result of the maritime fur trade (Cowan and Guiguet 1960). The species was subsequently reestablished by the introduction of sea otters from Alaska into Checleset Bay, west coast Vancouver Island. Between 1969 and 1972, 89 otters were released in a series of 3 translocation efforts (Bigg and MacAskie 1978). The species was downlisted in Canada to Threatened in 1996, though the population was still considered to be relatively small (min. of 1,522 otters) and vulnerable to oil spills (Watson et al. 1997). Presently (2006) sea otters range along much of the west coast of Vancouver Island and in a small region of the central British Columbia coast (Fig. 1; Watson et al. 1997, Nichol et al. 2005). Recent counts (2001 to 2004) indicated a minimum population of 3,180 otters, of which 2,673 occurred on the west coast of Vancouver Island, with the remainder on the central British Columbia coast (Nichol et al. 2005).

METHODS

We began our analysis by characterizing habitat on the west coast of Vancouver Island according to currently occupied habitat in Checleset Bay–Kyuquot Sound (CB–KS) based on the following assumptions: 1) CB–KS was representative of high-quality habitat since it was selected as the site for reintroduction of the species (Kenyon 1969), 2) the habitat was representative of high-quality habitat elsewhere on Vancouver Island and the rest of the British Columbia coast, and 3) the number of sea otters occupying CB–KS reached equilibrium in the mid-1990s according to annual survey data collected since 1988 and, therefore, a carrying capacity density in this habitat (i.e., otters/km^2) could be calculated (Nichol et al. 2005).

We constructed the habitat model based on the assumption that coastline and bathymetric complexity served as a proxy for several habitat attributes. First, a complex coastline creates habitat that provides protection in the event of severe storms. Secondly, bottom complexity is often associated with reefs and appears to be a reasonable proxy for features that provide quality sea otter foraging habitat. Thus, we assumed that high-quality or optimum sea otter habitat on exposed regions of the coast could be characterized by the complexity of the nearshore intertidal and sub-tidal zones.

We applied our analysis to the west coast of Vancouver Island (WCVI model) to identify areas with a complexity similar to CB–KS (Fig. 1). We adapted this WCVI model (creating the BC model) to predict optimal habitat (i.e., similar to the CB–KS region) and optimal habitat K for the entire British Columbia coast. We also estimated coastline length for British Columbia and used this to estimate total (as opposed to optimal) coast-wide K based on a linear density (i.e., otters/km).

We used bathymetric data from the Canadian Hydrographic Service (CHS) in our analyses. The data are a composite of best available polygons from digital marine charts produced at various scales (I. Murfitt, Fisheries and Oceans Canada, unpublished data). We conducted the analysis using ArcView 3.2, ArcGIS 9, and SPlus 2000.

Optimum Habitat Definition

West coast Vancouver Island.—After investigating various combinations of contour lines, we settled on the 10–20-m depth contour to calculate relative complexity of nearshore areas for our WCVI model. We defined complexity as the relative nonlinearity in the contour lines (i.e., the less straight a line was, the higher the complexity it represented). To calculate this complexity, we placed a grid of 23.4-ha (0.23 km^2) hexagons over the 10–20-m depth contours and summed the line length within each hexagon to estimate its complexity. We chose hexagons because this shape reduced length bias due to orientation of the line segment. Potential bias is the ratio of the longest to the shortest distance through the shape. For a square, this ratio is 1.4, giving a potential error of 40%. Hexagons reduced this potential error to 15%.

We confirmed that contour length provided a reasonable measure of complexity by comparing the fractal dimension of the contours in each hexagonal cell to our summed contour lengths. The 2 approaches generated virtually identical results in terms of relative hexagon complexity.

We assigned the hexagon complexities to a 500×500-m (25-ha, 0.25-km^2) raster and smoothed the result using a circular moving average window with a radius of 3 km (ArcView neighborhood statistic). This reduced variation in the prediction and effectively consolidated areas containing a higher proportion of complex raster cells. We presumed that a radius of 3 km defined a reasonable area for an adult otter to explore in a day. We scaled the resulting surface onto the range [0, 1] to form the final complexity coverage.

We contoured the complexity at a threshold of 0.2 to define optimum habitat regions (a higher complexity threshold would select a smaller area). We retained only those areas >5 km^2 (after clipping against land) as part of

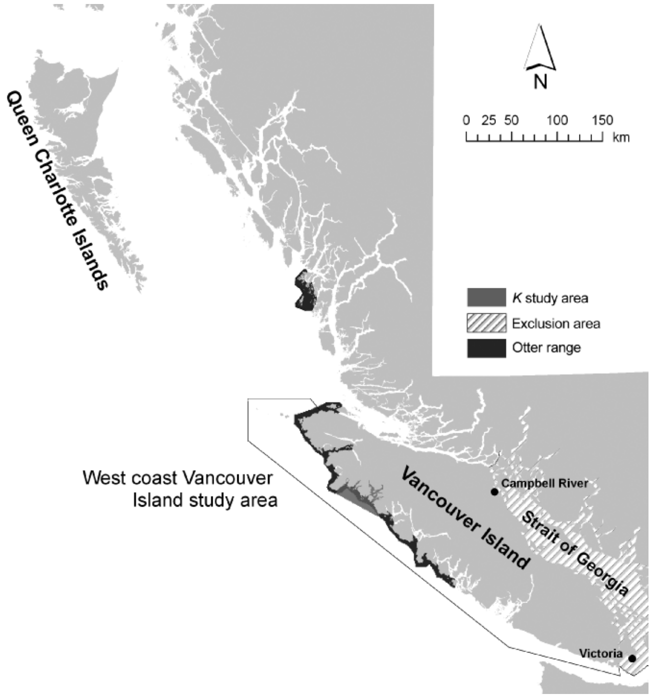

Figure 1. The coast of British Columbia, Canada, showing the west coast Vancouver Island study area, the carrying capacity (*K*) study area (Checleset Bay and Kyuquot Sound), the Strait of Georgia exclusion area, and the current (2006) range of sea otters in British Columbia.

optimal habitat. We selected this complexity threshold after an extensive exploratory analysis that compared model results with the known distribution of sea otters and the expected location of quality otter habitat, based on expert opinion derived from numerous small boat surveys. Thus, we chose a complexity threshold that best described known and potential distribution of sea otters along the west coast of Vancouver Island.

British Columbia Coast.—To calculate relative complexity of nearshore habitat for the British Columbia coast (BC model), we modified our definition of complexity to accommodate variability in resolution of the bathymetric data. We used this BC model to identify areas throughout the coast with similar complexity to the CB–KS region.

There were 2 aspects to this bathymetric variability. First, not all contours are equally represented on all charts (i.e., higher resolution charts include more contour lines). To minimize this regional bias, we pooled all representations of the 0–2-m depth and intertidal contours into one set of intertidal contours, resulting in a more consistent representation of the intertidal region across the entire coast. We excluded deeper contours (i.e., 10–20-m) from this analysis because representation of these depths was not consistent across all British Columbia waters. The second aspect of variable bathymetric resolution relates to the scale of the charts themselves. A feature on a low-resolution chart will appear less complex than the same feature on a higher resolution chart. We reduced this resolution bias by generalizing the coastline and the intertidal contours to a tolerance of 100 m. These 2 manipulations effectively removed resolution and representation biases between different regions of the coast and allowed us to apply the BC model to the entire coast.

We excluded the Strait of Georgia from the BC model, from Victoria to just north of Campbell River (Fig. 1). In addition to being considerably modified by urban development, there are no records of sea otters in this area at the time of European contact, and furthermore, sea otter remains have not been found in archaeological faunal assemblages in the region dating from 3,500 Before Present to European contact (Hanson and Kusmer 2001).

Estimating Otter Density in Optimum Habitat (CB–KS)

We used unadjusted counts of sea otters obtained by annual boat-based survey of CB–KS from 1995 to 2005 to estimate equilibrium population size and associated confidence intervals in this sub-region. Surveys followed established routes and we recorded number and location of sea otters whenever we encountered them along the survey route. Count locations therefore varied from year to year, depending on where we observed otters and, thus, may not be independent. We standardized sighting locations across years by defining focal sites to aggregate individual field observations. Our focal sites pooled individual field observations into spatial groups based on where animals were commonly seen. Focal sites served to concentrate count locations, increasing both independence of the counts and the site sample size.

Pooling counts by focal sites (a site central to a group of count locations) and assuming that each focal site was independent was the most ecologically reasonable approach to combining count data. We used pooled counts to calculate percentile-based confidence intervals, resampling 1,000 times from 30 bins (i.e., sites), each containing 11 counts. The percentile-based approach accounted for any nonnormal distribution in the data such as variability due to spatial and intra-annual temporal factors (Laidre et al. 2001).

Carrying Capacity Estimates

We calculated sea otter density in optimum habitat independently for the WCVI and BC models, based on the predicted area of the CB–KS region specific to each model. We then calculated estimates of optimum habitat *K* for the west coast of Vancouver Island and British Columbia by multiplying the model-specific densities by total predicted optimum habitat of each model.

We obtained the linear British Columbia *K* estimate by multiplying the linear sea otter density calculated for CB–KS (using survey data and coastline length in CB–KS) by the total British Columbia coastline length (excluding the Strait of Georgia; Fig. 1). We calculated coastline length using the CHS bathymetric data set. However, because coastline length depends on the scale of measurement (i.e., the resolution) and tide height (low tides expose more of the coast), we calculated coastline length after generalizing to 100-m tolerance, effectively removing any regional variation.

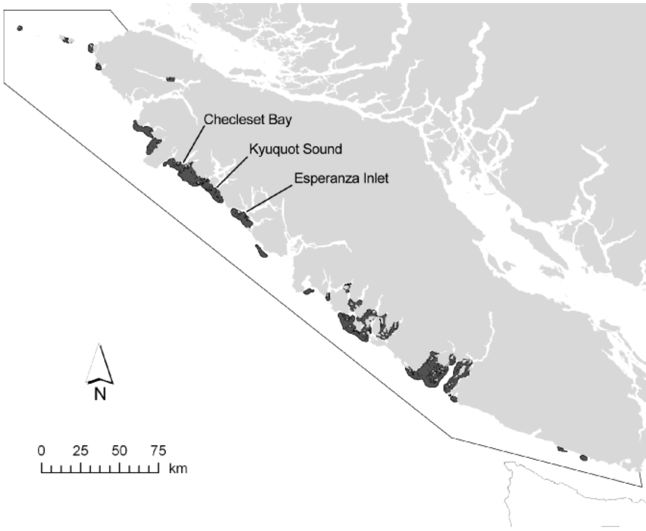

Figure 2. Predicted optimum sea otter habitat based on sub-tidal bathymetric complexity for the west coast Vancouver Island (WCVI; Canada) study area (outlined) from the WCVI habitat model.

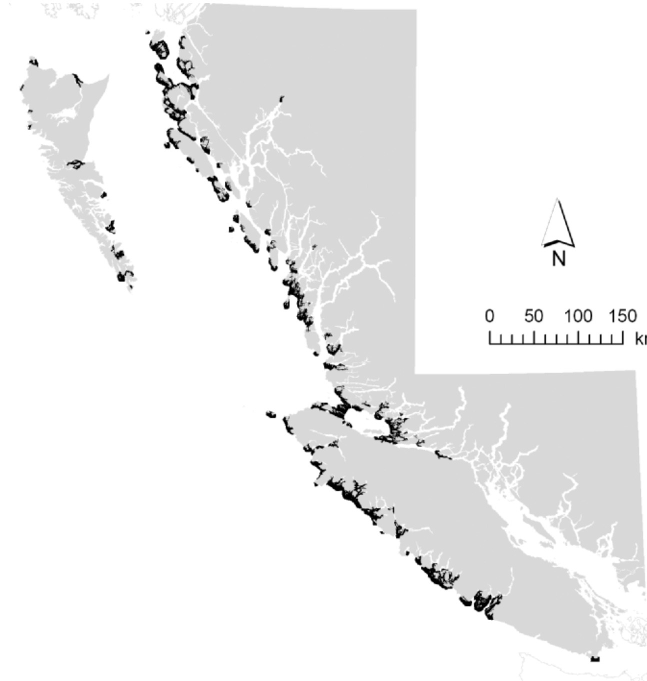

Figure 3. Predicted optimum sea otter habitat based on intertidal bathymetric complexity for all of British Columbia (BC; Canada) from the BC habitat model.

Habitat Model Validation

We validated the WCVI model by comparing predicted to observed values (survey data) in Esperanza Inlet, a location southeast of CB–KS where otters appear to be nearing equilibrium (L. M. Nichol, Fisheries and Oceans Canada, and J. C. Watson, Malaspina University-College, unpublished data), providing us an opportunity to evaluate the optimum habitat model in a region other than where it was developed. We calculated a population estimate for Esperanza Inlet from the survey data, and compared this estimate to a predicted *K* obtained by multiplying sea otter density (derived from the CB–KS region) by the size of predicted optimum habitat in Esperanza Inlet.

We validated the BC model by comparing its habitat area and population estimate for the west coast of Vancouver Island with those obtained from the WCVI model. If the west coast Vancouver Island results from the 2 models were similar, then the coast-wide optimum habitat identified by the BC model would likely be reasonably similar to the CB–KS region.

RESULTS

Habitat Predictions

The WCVI model identified 20 optimum habitat areas totaling 1,304 km^2 (Fig. 2). Areas ranged in size from 5.4 km^2 to almost 300 km^2 and were distributed throughout the study area. The estimated size of the CB–KS region was 267 km^2. The Esperanza Inlet optimum habitat area was predicted to be 73.8 km^2. On the province-wide scale, the BC model identified 5,862 km^2 of optimum habitat (Fig. 3), of which 1,930 km^2 was predicted on the west coast of Vancouver Island, with 423 km^2 in the CB–KS region (Table 1).

We calculated a length of 28,530 km for our generalized British Columbia coastline, which corresponds to other reported lengths (e.g., 27,200 km [Francis 2001]; 22,894 km [Natural Resources Canada 2006]). Of the 28,530 km of coastline in British Columbia, 4,900 km fell within our defined Strait of Georgia exclusion area (Fig. 1), leaving 23,630 km available as potential sea otter habitat (Table 1).

Carrying Capacity Estimates

We estimated a linear density of 2.22 animals/km and a predicted *K* of 52,459 (95% CI = 34,264–73,489) animals for British Columbia, 8,303 (95% CI = 5,423–11,631) for the west coast of Vancouver Island, and 1,057 (95% CI = 690–1,480) for CB–KS region. The BC model, with a density of 2.53 otters/km^2, predicted a coast-wide optimum habitat *K* estimate of 14,831 (95% CI = 9,790–20,751) animals, a west coast Vancouver Island estimate of 4,883 (95% CI = 3,223–6,832) animals, and 1,070 (95% CI = 706–1,497) for the CB–KS region. The WCVI model (3.93 otters/km^2) predicted optimum habitat *K* on the west coast of Vancouver Island to be 5,123 animals (95% CI = 3,337–7,104), with 1,050 (95% CI = 684–1,455) in the CB–KS region (Table 1).

Model Validation

We validated the WCVI model by comparing the predicted optimum habitat *K* in Esperanza Inlet to available count data. Counts of between 293 and 466 sea otters ($\bar{x} = 407$; 95% CI = 295–519) were obtained during 3 surveys of Esperanza Inlet made between 1997 and 2003 (L. M. Nichol and J. C. Watson, unpublished data). The 73.8 km^2 of predicted habitat in Esperanza Inlet gave an optimum *K* of 290 (95% CI = 189–402) animals. Thus, although there was considerable overlap in the confidence intervals, neither mean fell within the confidence interval of the other.

Table 1. Predicted regional habitat estimates and associated *K* estimates for Checleset Bay–Kyuquot Sound (CB–KS); west coast Vancouver Island (WCVI); mainland coast (MC); Queen Charlotte Islands (QCI); and all British Columbia (BC, with exclusion area removed), Canada, based on the WCVI and BC optimum habitat models and the BC linear model. We show predicted densities for each model and 95% confidence intervals for each *K* estimate.

	Model (density)											
	WCVI optimum (3.93 otters/km^2)				BC optimum (2.53 otters/km^2)				Linear (2.22 otters/km)			
Region	Habitat area (km^2)	*K* (otters)	95% CI (2.56–5.45)		Habitat area (km^2)	*K* (otters)	95% CI (1.67–3.54)		Habitat area (km)	*K* (otters)	95% CI (1.45–3.11)	
CB–KS	267	1,050	684	1,455	423	1,070	706	1,497	476	1,057	690	1,480
WCVI	1,304	5,123	3,337	7,104	1,930	4,883	3,223	6,832	3,740	8,303	5,423	11,631
MC					3,517	8,898	5,873	12,450	16,400	36,408	23,780	51,004
QCI					413	1,045	690	1,462	3,490	7,748	5,061	10,854
BC					5,862	14,831	9,790	20,751	23,630	52,459	34,264	73,489

Predictions from the BC model compared remarkably well to those of the WCVI model. In terms of west coast Vancouver Island optimal habitat, the BC model predicted 1,930 km^2, whereas the WCVI model predicted 1,304 km^2. The resulting optimum habitat population estimates were also very similar, with the BC model predicting 4,883 animals compared to the WCVI model's 5,123 animals. Both predictions fell within each other's confidence intervals (Table 1).

Spatial overlap between the BC and WCVI model habitat predictions was also high (Fig. 4), although WCVI model predictions were largely contained within predictions of the BC model. The BC model predicted more habitat in the sheltered waters away from the exposed coast.

DISCUSSION

Our complexity-based habitat models performed well for the west coast of Vancouver Island, identifying presently occupied habitat and unoccupied areas beyond the present range with similar complexity and generating a narrow range of reasonable *K* estimates. On the remainder of the coast, our model predicted a modest *K*, suggesting that complexity did not completely characterize sea otter habitat throughout coastal British Columbia. We believe the linear model therefore provides the best estimate of sea otter *K* for Canadian waters.

Otter Habitat

On the west coast of Vancouver Island, the high degree of spatial correspondence between the habitat predicted by the WCVI and BC models (Fig. 4) demonstrates that both models identified areas similar in complexity to CB–KS. This strongly supports the veracity of our coast-wide optimum habitat predictions from the BC model. However, this predicted optimal habitat makes up a small proportion of the central and northern mainland coast, which is dominated by inlets and long channels. Although such areas are not presently occupied by sea otters, there are historical observations of sea otters in inland waterways on the northern British Columbia coast (Lamb 1984). This suggests that other habitat types may become important as the population expands.

The Queen Charlotte Islands seem particularly under-represented, especially because historical accounts indicate the islands were an important trading destination during the fur trade, implying an abundance sea otters (Dixon 1789, Howay 1973, Lillard 1989, Dick 2006). Under-representation of habitat in this area could be due to uncorrected bias in the bathymetric data, but it is more likely that habitat characteristics in this region are not fully captured by the BC model. For example, bathymetric complexity in this region and on the central British Columbia coast is likely lower than on the exposed west coast because of the geological nature of the inland sea (Hecate Strait) these areas border.

Nevertheless, the ability of the complexity models to explain much of the observed sea otter distribution using a single variable (complexity) and 2 parameters (smoothing window size and threshold) implies that nearshore complexity does define a habitat type important to sea otters, particularly on the west coast of Vancouver Island. The density predicted by the WVCI model (95% CI = 2.56–5.45 otters/km^2) is similar to the highest habitat density calculated in California (95% CI = 4.65–5.62 otters/km^2; Laidre et al. 2001). Thus, the areas identified as optimum habitat by our models likely include some aspect of Critical Habitat as defined by both the SARA and the United States Endangered Species Act. However, any such definition would require a more detailed consideration of habitat including, for example, seasonal influences on habitat use. Thus, although our approach represents a first step towards identifying Critical Habitat for this species, we do not intend it to be definitive.

As the population of otters in British Columbia increases, continued surveys will refine the predictive model. The occupation of other habitat types will allow calculation of equilibrium densities by habitat type. Inclusion of additional habitat features will help refine the model but will likely require additional physical data (e.g., substrate types, exposure).

Model Calibration and Validation

Calibration of the complexity threshold proved surprisingly robust. There was a tight range of values that yielded reasonable predictions; higher thresholds omitted known high-use areas and lower values predicted habitat in regions

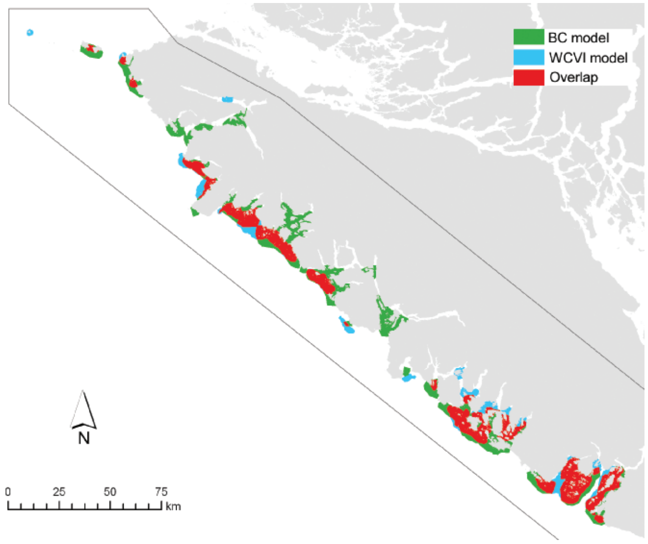

Figure 4. The spatial distribution of predicted optimum habitat based on bathymetric complexity for the northern portion of the west coast of Vancouver Island (WCVI), Canada, from both the British Columbia (green) and the WCVI (blue) models. Areas where the predictions overlap are shown in red.

observed to be poor for otters. This model behavior allowed us to quickly decide on the most appropriate threshold.

We explored several ways of grouping otter count data based on different independence assumptions regarding count locations. We concluded that grouping locations close together to represent a particular habitat patch (focal site) was the most appropriate ecological assumption, because a zero observation at an individual count location often meant that animals were making use of a different location within the focal site rather than abandoning the habitat area entirely. Our assumption about focal sites was supported by fairly consistent pooled counts at many focal sites between years, despite large fluctuations at individual count locations. By grouping count locations into larger, ecologically based groupings, we reduced the number of zero observations in the inter-annual data set and improved confidence intervals on population estimates, demonstrating how model performance can be improved by applying reasonable ecological assumptions.

Validation of the WCVI model by comparing the predicted *K* with the observed counts from Esperanza Inlet showed that our predicted *K* was lower. This may be due to sea otters in Esperanza Inlet occupying habitat types not identified by our model. Alternatively, our assumption of equal *K* among complex habitats may not always be true.

Carrying Capacity Estimates

We generated 3 estimates of *K* for the west coast of Vancouver Island, and 2 estimates for the British Columbia coast. All 3 models (WCVI, BC, and linear) resulted in near identical predictions for the CB–KS area. However, as the extents of the study were increased to Vancouver Island and the entire coast, the discrepancy between the BC optimum habitat and the linear model predictions increased (Table 1). At the coast-wide scale, the linear estimate of *K* was 4 times the BC model optimum habitat *K* prediction of 14,831 otters.

The coast-wide BC model optimum habitat *K* prediction is also low compared to historical accounts. Although there are no estimates of the pre–fur-trade sea otter population in British Columbia, annual harvests from 1799 to 1801 averaged 11,250 pelts, almost as high as the BC model optimum habitat *K* estimate. While it is difficult to determine the origin of these pelts, during these years most can likely be attributed to British Columbia and Southeast Alaska (Dmytryshyn and Crownhart-Vaughn 1976, Busch and Gough 1997). Sea otters continued to be sufficiently abundant to support an intense, unregulated fur trade for another $\geq$30 years, until depletion of the population in the 1830s (Busch and Gough 1997).

Our complexity-based estimates of *K* were, by definition, only for one (i.e., optimum) habitat type and must, therefore, be considered conservative. The linear coast-wide *K* estimate of 52,459 sea otters likely provides a more reasonable upper limit, despite the assumption that the entire coast would support the same density of otters as CB–KS. Based on the most recent (2001 to 2004) counts of 2,673 otters on the west coast of Vancouver Island, the current Vancouver Island population may be between 30% and 50% of *K* (based on point estimates for this area from the linear and optimum habitat models, respectively).

Just as sea otter diets diversify as preferred prey become increasingly scarce, sea otters likely occupy optimal habitat first and then suboptimal habitat, in accordance with the theory of an Ideal Free Distribution (Fretwell and Luca 1969). Different habitat types have been shown to support different densities of sea otters (Laidre et al. 2001, 2002). Sea otter *K* can also vary temporally, because otters modify their environment by removing herbivores, thereby altering their prey base (Estes 1990). Watt et al. (2000) further suggested that *K* may fluctuate on decadal scales in response to changes in oceanographic factors. Thus, although an equilibrium density can be inferred from population trends, *K* is best viewed as a dynamic population parameter.

MANAGEMENT IMPLICATIONS

Our *K* estimates provide useful measures against which management agencies may compare current population estimates to assess recovery for sea otters in Canada. Our habitat predictions likely represent an important aspect of sea otter Critical Habitat as defined by SARA, and thus represent a reasonable first step towards identifying Critical Habitat for the species. The density-based approach we applied to estimate *K* is robust, and may be applicable for other nonmigratory, density-dependent species.

ACKNOWLEDGMENTS

Field assistance was provided by L. Saville, G. Lemieux, A. McNaughton, A. Griffiths, M. Boogaards, S. Campania, S. Jepps, L. Gibson, D. Haggarty, P. Hughes, A. Keple, D. Lacroix, T. Pater, C. Vink, M. Theberge, and S. Wallace. Logistical support was provided by the Kyuquot and

Checleset First Nations and the Village of Kyuquot, particularly the Kayra, Osenenko, Norberg, and Chidley families. Modeling benefited from discussions with M. O regarding complexity, and with I. Murfitt regarding bathymetry. Funding was provided by the Species at Risk Act Program, Fisheries and Oceans Canada, Friends of the Ecological Reserves, and Malaspina University-College. Facet Decision Systems Inc., Vancouver, British Columbia provided in-kind contributions to the initial modeling. Two anonymous reviews and comments by the journal content editor contributed to clarity of the manuscript.

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Associate Editor: Green.