

Habitat associations of sea otters (*Enhydra lutris*) in a soft- and mixed-sediment benthos in Alaska

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We investigated the habitat associations of sea otters (*Enhydra lutris*) during resting and feeding in an area with a predominately soft- and mixed-sediment benthos supporting infaunal prey populations in a fjord in Alaska during the summer months of 2001–2003. Water depth and benthic sediments were sampled, analyzed, and mapped throughout the bay. Sea otter locations and behavior were determined during boat surveys, and water depth, benthic sediment type, and position in the bay (peripheral compared to central) were determined for each animal location. We used logistic regression analysis to determine whether the use of habitat by sea otters was nonrandom according to these variables. Water depth was the most significant habitat association for feeding behavior, with 39% of feeding dives occurring in water 0–10 m deep. Feeding behavior was not strongly associated with sediment type. Position in the bay was the most significant habitat association for resting behavior, with the majority (63%) of otters resting in the central areas of the bay. Overall, habitat associations were nonrandom, a possible reflection of selective pressure to maximize energy intake, minimize energy expenditure, and avoid terrestrial predators.

Key words: *Enhydra lutris*, feeding behavior, habitat associations, sea otter

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Historically, sea otters (*Enhydra lutris*) were abundant throughout the coastal regions of the North Pacific Ocean from northern Japan to Baja California, Mexico. Extensive commercial harvesting of sea otters for their fur began in the mid-1700s and continued until they were nearly extinct. In 1911 the International Fur Seal Treaty provided protection from further commercial harvest to the isolated, remnant populations of sea otters, which began to grow and reoccupy their former range, although fluctuations in regional populations remain dynamic (Doroff et al. 2003; Estes et al. 2005). Currently, the population of sea otters in Prince William Sound, located in south-central Alaska, is listed as stable or increasing under the Endangered Species Act (United States Fish and Wildlife Service 2005). Male sea otters began to reinhabit northeastern Prince William Sound in the late 1970s (Garshelis 1983; Rotterman and Simon-Jackson 1988). It remained an exclusively male area until the 1980s (Garshelis et al. 1984, 1986) but is now used by females with pups and territorial males (Gilkinson 2004; Pearson et al. 2006).

Many terrestrial and marine mammalian species are distributed in nonuniform patterns that can be attributed to habitat heterogeneity (Croll et al. 1998; Ingram and Rogan 2002; Naud et al. 2003). When a resource or habitat type is used

disproportionately to its availability, it is considered to be preferred or selected (Alldredge et al. 1998; Johnson 1980; Manly et al. 2002). Because it is assumed that animals will select habitat with the highest-quality resources or other favorable attributes, identifying these habitat features provides information on how animals meet their survival requirements and enables us to assess or predict habitat quality for different areas (Alldredge et al. 1998; Manly et al. 2002; McConnaughey and Smith 2000). Habitat characteristics that influence the distribution of marine mammals include water depth, depth gradient, sea surface temperature, and sediment type (Croll et al. 1998; Davis et al. 1998, 2002; Ingram and Rogan 2002).

Sea otters occupy dynamic coastal areas with both rocky and soft-sediment benthic habitats, are generally found close to shore (within approximately 1–2 km) within the 40-m isobathymetry contour, and prefer areas sheltered from wind and waves (Bodkin et al. 2004; Kenyon 1975; Riedman and Estes 1990; Rotterman and Simon-Jackson 1988). Throughout much of their range sea



otters are associated with large, floating canopies of kelp (e.g., *Macrocystis* and *Nereocystis*—Kenyon 1975; Miller 1974; Ribic 1982; Rotterman and Simon-Jackson 1988), although they also occur in areas without canopy-forming kelp. Sea otters use different areas while feeding and resting (Estes 1980; Estes et al. 1986; Garshelis 1983; Loughlin 1979; Ribic 1982), although little research has been conducted on the habitat characteristics associated with these areas. In this regard, habitat preference of sea otters remains poorly understood. In addition, most information comes from populations occupying rocky habitats, with less information on sea otters occupying soft-sediment habitats (Kvitek and Oliver 1988; Kvitek et al. 1993).

In this study, we examined habitat preference of sea otters in Simpson Bay, an area with a predominately soft- and mixed-sediment benthos in a fjord in northeastern Prince William Sound, Alaska. We collected data on both otter locations and available habitat to identify environmental variables influencing sea otter distribution. We hypothesized that sea otters would use available habitat nonrandomly (i.e., would exhibit identifiable habitat associations). To better determine the function of selected habitats, as suggested by North and Reynolds (1996), we examined habitat preference (bathymetry, sediment type, and position in the bay) of sea otters during 2 important activities, resting and feeding.

MATERIALS AND METHODS

Study area.—Simpson Bay (60.6°N, 145.9°W), located in northeastern Prince William Sound, Alaska (Fig. 1), was used as the study site because of the reliable presence of sea otters during the summer. It is approximately 21 km² in area, 7.5 km long in the northern and western bays, 5 km long in the eastern bay, and 2.5 km wide at the entrance of the bay. None of the large-bodied kelps (e.g., *Nereocystis*) that form canopies are present, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*), and sieve (*Agarum clathratum*) kelp cover the benthos in many areas of the bay from the subtidal to a depth of approximately 10 m (R. W. Davis, pers. obs.). The bay was recolonized by male sea otters in 1977, and females moved into the area between 1983 and 1985 (Garshelis 1983; Rotterman and Simon-Jackson 1988; Van-Blaricom 1988). Since 2002 the bay has been used during the summer (June–August) by an average ($\pm SD$) minimum of 119 \pm 9 sea otters, including adults and subadults (91 \pm 7) and pups (28 \pm 4), with an average minimum summer density of 5.7 otters/km² (R. W. Davis, pers. obs.). During the winter the number of otters in the bay decreases to about 50, although to where they disperse is poorly understood. This research was conducted under Letter of Confirmation MA-043219 from the United States Fish and Wildlife Service.

Otter surveys.—Sea otter surveys were conducted for approximately 641 h during 127 days from June to August over the 3-year period: 124 h during 24 days in 2001, 278 h during 54 days in 2002, and 239 h during 49 days in 2003. The study area was divided into 3 survey sections (North Bay, West Bay, and East Bay; Fig. 1) for logistical purposes.

A single survey comprised data collection in 1 of the 3 sections. The sections of the bay were surveyed in a systematic rotation, which allowed us to cover the entire bay every 1.5–2 days depending on weather. Dividing the study area into sections and surveying them in rotation also ensured a more uniform coverage of the entire area.

The research team, composed of a driver, recorder, and spotter, conducted surveys from a 5-m skiff between 0900 and 1700 h local time. To maximize otter encounters no systematic vessel track was followed. The boat opportunistically approached as many otters as possible but avoided approaching any individual more than once during a survey by not backtracking. Before an otter was disturbed we recorded the time, location, and behavior of the otter, and the presence of a pup. We then approached the otter to within 40 m and determined its location using a global positioning system (GPS 126; Garmin International, Inc., Olathe, Kansas). Only resting and feeding behavior (Packard and Ribic 1982; Shimek and Monk 1977), which together represent 41% of the daily activity budgets for males (Finerty et al. 2009) and 57% for females with pups (R. C. Wolt, Texas A&M University, pers. comm.) were analyzed for habitat associations. Sex was determined when possible by noting the presence of a penile ridge or testicular bulge for males or the presence of abdominal mammae or associated young pup for females (Estes 1980; Kenyon 1975; Riedman and Estes 1990; Rotterman and Simon-Jackson 1988). This study conformed to guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Habitat assessment.—Habitat characteristics were determined by sampling 198 stations spaced 400 m apart on a rectangular grid throughout the bay, although some stations were spaced more closely near the shoreline to provide better resolution. At each station, we measured water depth with a bathymeter (Garmin International, Inc.) and collected, where possible, 3 sediment samples with either an Eckman grab or a gravity corer.

Sediment sample analysis.—Grain size is a fundamental physical property of sediments, frequently used by both sedimentologists (Boggs 1995; Folk 1980) and biologists (Kvitek et al. 1989; McConnaughey and Smith 2000; Snelgrove and Butman 1994) to describe and classify benthic sediments. We determined the grain size distributions of each sediment sample using standard wet sieve and pipette analysis procedures (Boggs 1995; Folk 1980). Dispersant was mixed with a 15- to 20-g homogenized sample of wet sediment after large clasts were removed, and the sample was wet sieved through United States standard mesh sizes 5, 10, and 230 into a 1-liter graduated cylinder to separate the gravel and sand fractions. The graduated cylinder was filled to 1 liter with deionized water and homogenized. Two 20-ml samples were taken from specific depths within the cylinder at a measured time interval. Both the depth and timing varied with room temperature, according to standard protocols (Folk 1980), to determine the silt (4 Φ) and clay (8 Φ) fractions. All fractions were dried in an oven (80°C) and weighed on an electronic scale. Sediment type was then classified using a gravel–sand–mud ternary diagram modified from Shepard (1954). With the

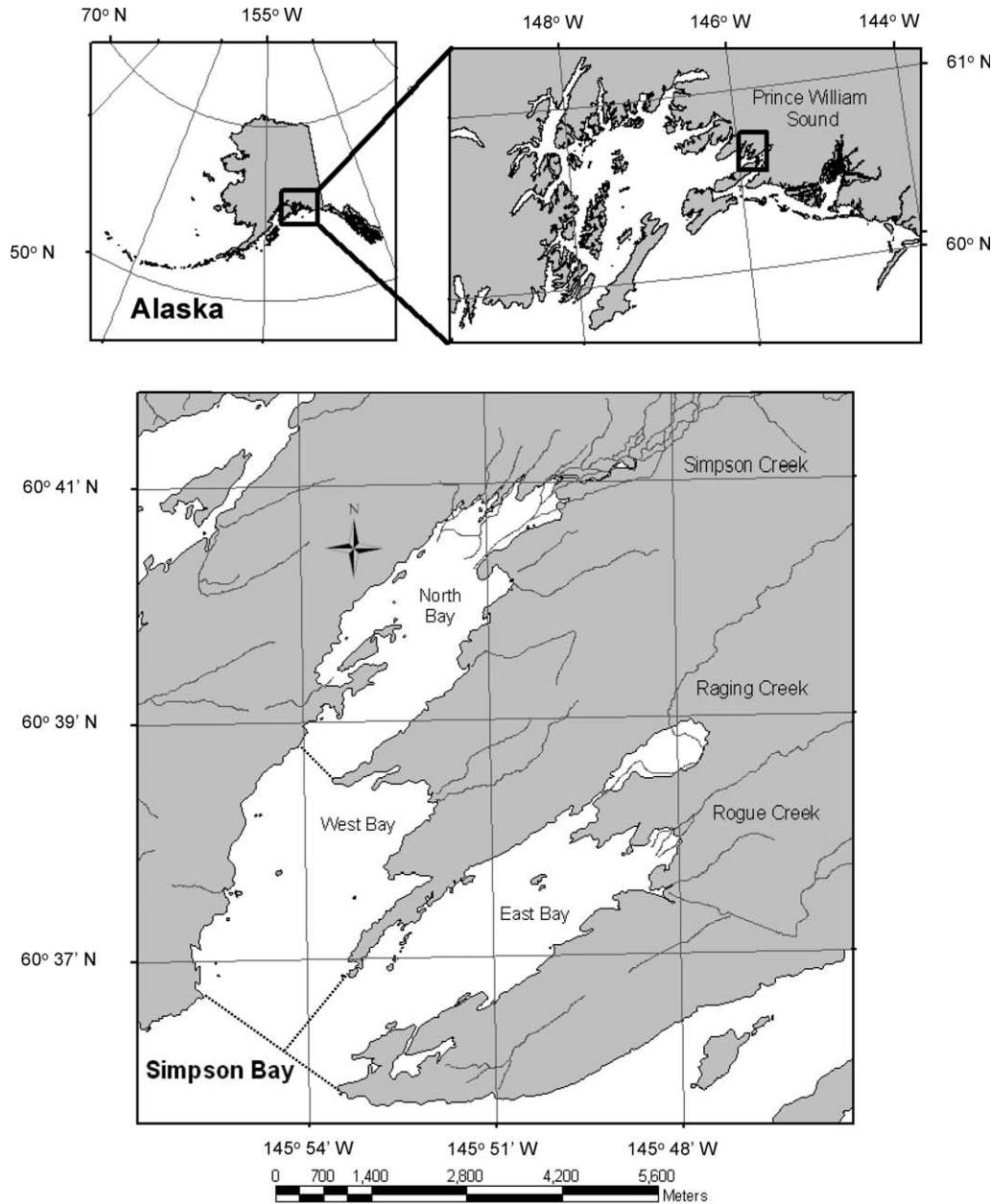


FIG. 1.—Location of Prince William Sound in Alaska (top left and right) and map of Simpson Bay within Prince William Sound (bottom). Maps after Noll et al. (2005).

Eckman grab, gravel sometimes prevented the jaws from closing completely, thereby allowing some of the finer sediments to escape and possibly biasing for a higher gravel proportion. This source of bias was reduced by averaging, where possible, triplicate samples at each station. An additional source of error might have resulted in areas with a benthos of closely spaced, large cobbles with some soft sediment. Although it was difficult to sample these areas, they might have supported infauna that was preyed upon by sea otters (R. W. Davis and F. Weltz, pers. obs.).

Habitat mapping.—Maps of bathymetry and sediment type were created for Simpson Bay using inverse distance-weighted interpolation in ArcGIS 8.1 (ESRI, Redlands, California). Prior to creating the maps, all depth measurements were

adjusted to the 0-tide level. Sediment category at each station was ranked from coarsest (gravel) to finest (mud) on a scale of 1–10 in the gravel–sand–mud system, and interpolation was based on these ranks. This approach would not reveal patchiness on a scale finer than 200 m. However, to check the accuracy of the sediment map it was compared with a high-resolution side-scan sonar mosaic of Simpson Bay created by Noll et al. (2005) during a study of the bay's sedimentary history. Overall, the sediment map matched the side-scan mosaic of the study area.

We overlaid otter feeding and resting locations on the bathymetry and sediment maps. A 40-m buffer was placed around each point to account for distance from the boat to the otter. Because the skiff location for otters near the shoreline

usually would be seaward from the animals, a small bias for slightly greater than actual depth might exist. We determined the following information for each location: depth, sediment type, distance from shore, and position within the bay. Depth was recorded in 10-m increments from 0 to 80 m, or >80 m. Gravel–sand–mud sediment types were (1–2) gravel and sandy gravel, (3) gravel–sand–mud, (4) muddy gravel, (5) gravelly sand, (6) sand, (7) muddy sand, (8) gravelly mud, (9) sandy mud, and (10) mud. Position within the bay was recorded as either central or peripheral, with central representing the middle one-third of the distance between the 2 shores. In all cases, the environmental variables represented the average for the buffer zone around each otter location.

To determine whether sea otters used habitat differently for feeding and resting we compared the locations for these 2 behaviors using logistic regression (Manly et al. 2002). To determine which environmental variables were associated with each behavior separately, resting and feeding locations were compared to unused, randomly selected locations using logistic regression. Regressions were run using SPSS version 11 (SPSS, Inc., Chicago, Illinois). Associations among habitat variables were determined by the *G*-test and binomial test (*Z*) and significantly associated variables that were not used in the same model. Final model selection was based on Hosmer–Lemeshow goodness-of-fit statistics and minimum Akaike information criterion (AIC) values. For the minimum AIC model we present the significance of the variable using the Wald statistic (Agresti 1996). We calculated AIC weights to assess the importance of the different models (Burnham and Anderson 2002).

RESULTS

We encountered otters during every survey, with a total of 2,013 encounters: 248 in 2001, 824 in 2002, and 941 in 2003. Of these, 303 otters were feeding and 653 were resting. The majority of animals were adults of undetermined sex (40%) and females with pups (43%). A greater number of otters were observed in West Bay than in either North Bay or East Bay during all 3 years.

Most (~71%) of the bay was <40 m in depth. The deepest areas were located at the entrance to the bay (maximum depth 125 m), the transition between North Bay and West Bay, and the center of East Bay. Benthic sediments were mostly mud (silt and clay), with some gravel and relatively little sand. Mud was the most frequent sediment type (39% of the benthos), followed by mixed mud (muddy gravel and muddy sand, 31%), and then mixed gravel (gravelly sand and gravelly mud, 19%). The benthos in North Bay was almost entirely fine sediment, and East Bay had a larger amount of coarse sediment. Sediment type was associated with water depth ($G_{15} = 311.36$, $P < 0.001$), with mud positively associated with water depths >40 m ($Z = 6.18$, $P < 0.05$) and mixed sediments (mixed mud and mixed gravel) positively associated with depths <20 m (mixed mud and 0–20 m: $Z = 5.91$, $P < 0.05$; mixed sand and 0–20 m: $Z = 4.50$, $P < 0.05$; mixed

gravel and 0–20 m: $Z = 3.98$, $P < 0.05$; gravel–sand–mud and 0–20: $Z = 3.56$, $P < 0.05$).

Water depth was associated with position in the bay ($G_3 = 540.73$, $P < 0.001$), with the 0- to 20-m zone ($Z = 13.53$, $P < 0.05$) and 20- to 40-m zone ($Z = 3.79$, $P < 0.050$) associated with the periphery and the 40- to 60-m zone ($Z = 14.63$, $P < 0.05$) and >60-m zone ($Z = 9.26$, $P < 0.05$) associated with the center area of the study area. Sediment type was associated with position in the bay ($G_5 = 174.79$, $P < 0.001$), with mud associated with center ($Z = 9.59$, $P < 0.05$) and mixed mud ($Z = 6.00$, $P < 0.05$), mixed sand ($Z = 2.47$, $P < 0.05$), mixed gravel ($Z = 3.55$, $P < 0.05$), and gravel–sand–mud ($Z = 3.40$, $P < 0.05$) associated with the periphery of the study area.

The majority (56%) of feeding dives occurred in shallow depths (0–20 m deep) near the shore, with a small, secondary peak (16%) at depths of 30–40 m (Figs. 2a and 3a). Resting behavior was most commonly (46%) observed over water that was 30–50 m deep (Figs. 2b and 3a). The majority (64%) of feeding behavior occurred in mud and mixed mud (gravelly mud and sandy mud) sediments (Figs. 3b and 4a). Resting behavior occurred most frequently (54%) over mud substrate (Figs. 3b and 4b). The majority (75%) of feeding dives took place in the peripheral portions of the bay, and resting behavior occurred most frequently (63%) in the central portion (Fig. 5).

Because of significant associations between the 3 habitat variables, the logistic regression analysis consisted entirely of single-variable models. All models for distance from shore had significantly poor Hosmer–Lemeshow goodness-of-fit test scores ($P < 0.01$) and thus were rejected. For feeding behavior the top AIC model was water depth (Wald test = 60.12, $d.f. = 8$, $P < 0.001$; Table 1). Specifically, feeding behavior occurred primarily (39%) in the depth range of 0–10 m (Fig. 3a). For resting behavior the top AIC model was position in the bay (Wald test = 215.92, $d.f. = 1$, $P < 0.001$; Table 1). Specifically, otters rested primarily (63%) in the central portion part of the bay (Fig. 5). For both feeding and resting the top AIC models more successfully predicted unused locations. The feeding model correctly predicted 56% of feeding locations and 72% of unused locations, and the resting model correctly predicted 63% of resting locations and 77% of unused locations. Water depth was the habitat variable that most strongly distinguished feeding and resting habitat (Wald test = 139.70, $d.f. = 8$, $P < 0.001$; Table 1). Specifically, feeding was more likely to occur (39%) in the 0- to 10-m depth class and resting (27%) in the 40- to 50-m depth class (Fig. 3a).

DISCUSSION

Sea otters in Simpson Bay did not use the area uniformly for either feeding or resting. If sea otters select foraging habitat according to optimal foraging theory, these areas should maximize energy intake relative to energy expenditure (Pyke et al. 1977; Quammen 1982). This assumption might be especially valid for sea otters because of their high, mass-specific resting metabolic rate. Without blubber for insulation sea otters rely on their dense fur and a metabolic rate that is

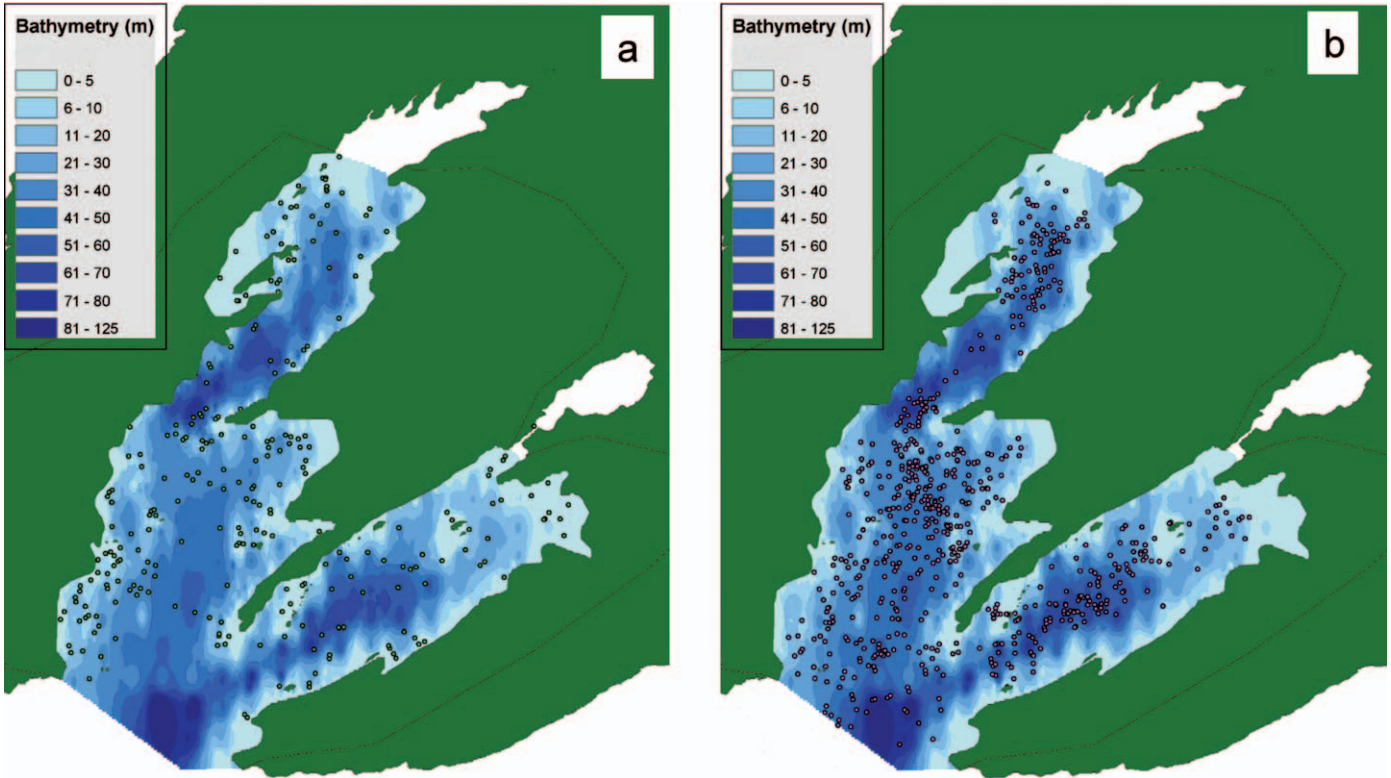


FIG. 2.—Bathymetry maps of Simpson Bay with sea otter a) feeding locations and b) resting locations indicated by colored circles. White areas in the upper North Bay and East Bay are tidal mud flats and tidal lagoon, respectively.

2–3 times higher than a terrestrial mammal of similar size to maintain core body temperature (Costa and Kooyman 1982; Davis et al. 1988; Kenyon 1981; Miller 1974; Riedman and Estes 1990). As a result, they consume ~25% of their body weight in food daily. Ostfeld (1982) noted that sea otters are good candidates for conforming to optimal foraging models,

not only because of their high metabolism and food consumption but also because they are asocial when feeding (habitat selection is independent of others) and energy-limited (no nutrient-based need for consuming more than 1 prey type).

Sea otters living in areas with a soft and mixed-sediment benthos, such as Simpson Bay, prey principally on benthic and

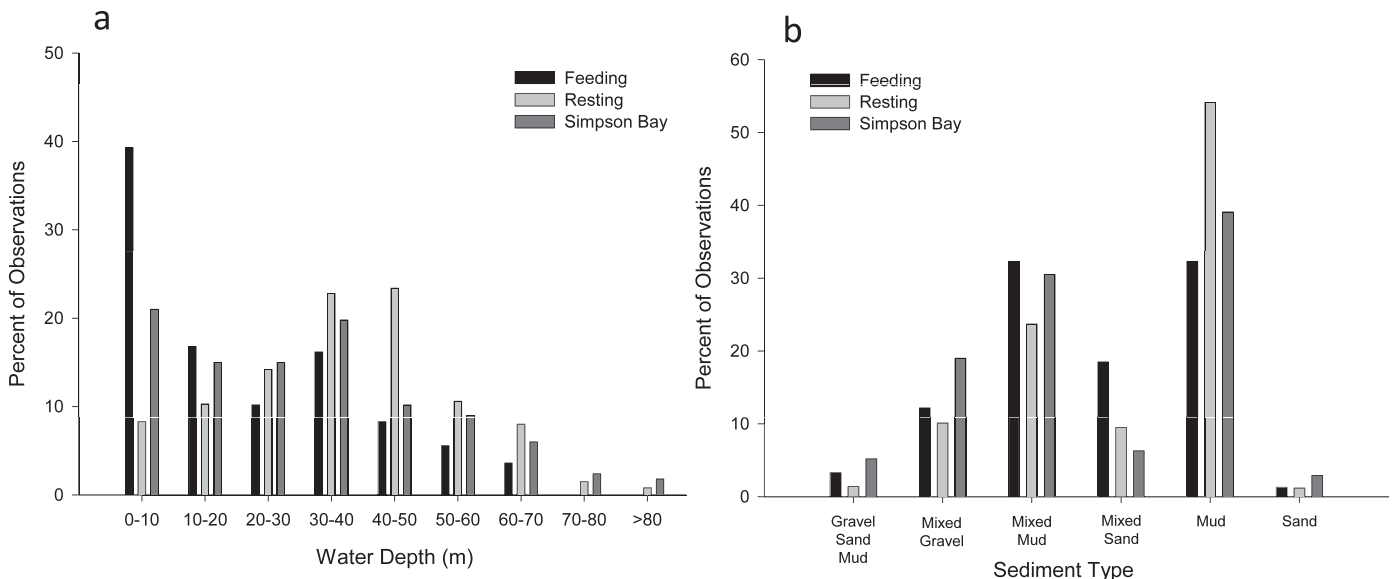


FIG. 3.—Percent of observations for sea otter feeding and resting locations in Simpson Bay and all of the Simpson Bay sampling stations for a) water depth and b) sediment type.

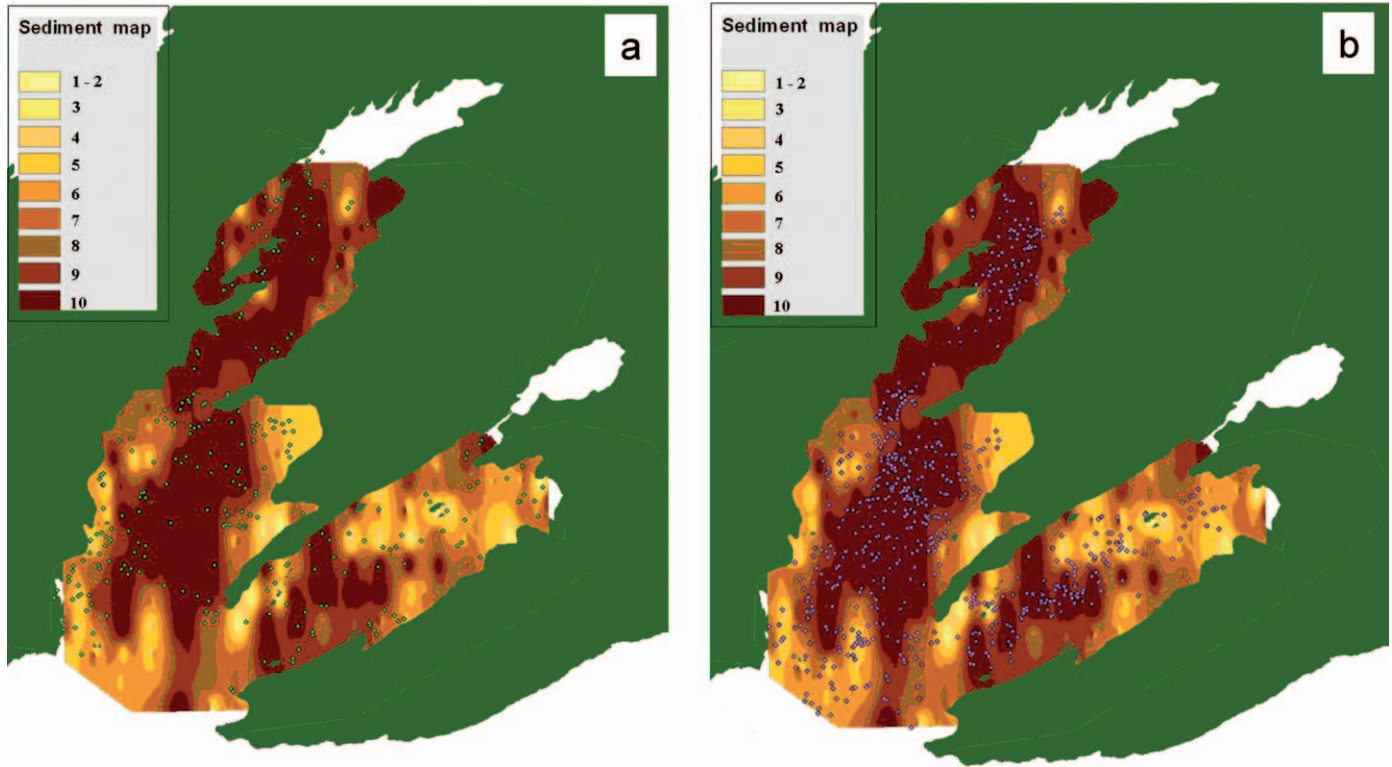


FIG. 4.—Sediment maps of Simpson Bay with sea otter a) feeding locations and b) resting locations indicated by colored circles. The sediment types are (1–2) gravel and sandy gravel, (3) gravel–sand–mud, (4) muddy gravel, (5) gravelly sand, (6) sand, (7) muddy sand, (8) gravelly mud, (9) sandy mud, and (10) mud.

epibenthic bivalves (Estes and Bodkin 2002; Kvitek et al. 1993). In Simpson Bay the majority (87%) of prey items were bivalves, including clams (e.g., butter clam [*Saxidomus giganteus*], Pacific little neck clam [*Protothaca staminea*], stained macoma [*Macoma inquinata*], bent-nose macoma [*Macoma nasuta*], truncate softshell clam [*Mya truncata*], Nuttall cockle [*Clinocardium nuttallii*], red scallop [e.g., *Clamys rubida*], and Pacific blue mussel [*Mytilus trossulus*]—R. C. Wolt, Texas A&M University, pers. comm.). Foraging

involves diving to the seafloor and locating epifauna such as scallops and mussels or excavating sediment to find infauna such as clams and cockles. The amount of sediment excavated can be considerable; sea otters make pits up to 1 m deep (Estes and Bodkin 2002), although most are <20 cm deep around Simpson Bay (R. W. Davis, pers. obs.). Thus, it was hypothesized that both water depth and sediment type influence the

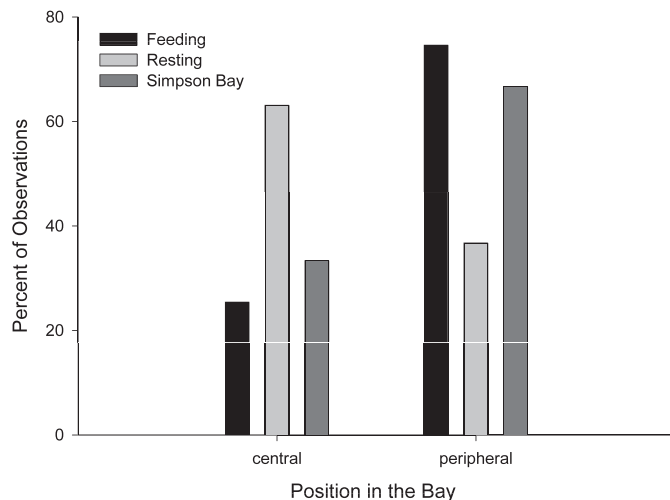


FIG. 5.—Percent of central and peripheral locations in Simpson Bay for sea otter feeding and resting behavior and the percent of these 2 areas for the entire bay.

TABLE 1.—Logistic regression models for feeding locations, resting locations, and feeding versus resting locations of sea otters in Simpson Bay, Alaska. AIC = Akaike information criterion.

Model	Residual deviance	AIC	ΔAIC	AIC weight
Feeding locations				
Water depth	781.96	1,584.28	0	1
Position in the bay	842.48	1,691.02	106.74	<0.001
Sediment type	856.77	1,727.73	143.45	<0.001
Null	867.18	1,738.38	154.10	<0.001
Resting locations				
Position in the bay	1,711.21	3,428.44	0	1
Water depth	1,793.12	3,606.39	177.95	<0.001
Sediment type	1,822.23	3,658.54	230.10	<0.001
Null	1,947.94	3,899.89	471.45	<0.001
Feeding versus resting locations				
Water depth	1,027.74	2,075.71	0	1
Position in the bay	1,071.45	2,148.93	73.23	<0.001
Sediment type	1,148.31	2,310.74	235.04	<0.001
Null	1,193.37	2,390.75	315.04	<0.001

amount of energy spent on foraging and are correlated with feeding locations of sea otters. Specific prey characteristics, such as the depth of soft-sediment benthic organisms, the difficulty of removing epibenthic species from rocks, and prey density also will affect energy expenditure.

Water depth could influence feeding locations because deeper dives require more energy due to the longer travel time to reach the seafloor. Boyd (1997) found that the most efficient reoxygenation rates for diving mammals are achieved when both dives and surface times are short. Therefore, if the availability and energy content of prey are similar in shallow and deep water, it is energetically more efficient for sea otters to forage in shallow water. Because foraging success rates in Simpson Bay were very high (~87%) at all depths (R. C. Wolt, Texas A&M University, pers. comm.), we assume this is the case. However, depth also might influence invertebrate distribution and nutritional quality in such a way that prey in shallower depths are a higher-energy food. Thouzeau et al. (1991) found that species diversity, density, and total biomass of benthic macroinvertebrates decreased with increasing depth. Our results indicate that depth was the primary habitat variable associated with feeding behavior, which is consistent with other studies (Bodkin et al. 2004; Garshelis 1983; Loughlin 1979; Shimek and Monk 1977). The tendency of otters to feed along the periphery of the bay, as opposed to the center, is probably due to the shallower water depths. However, additional information is needed on the distribution, abundance, and energy content of sea otter prey in Simpson Bay.

We hypothesized that the type of sediment would influence feeding locations because of its potential to influence prey diversity, distribution, and abundance (McConnaughey and Smith 2000; Quammen 1982; Thouzeau et al. 1991; Wong and Barbeau 2003). Kvitek et al. (1988) found that sediment type affected the burrow depth of sea otter prey. In addition, sediment type might influence the energetic cost of locating and excavating prey, because certain substrates are easier to displace than others, and certain grain sizes make prey more difficult to detect (Kotler et al. 2001). Our limited scuba observations indicate that infaunal prey are excavated from pockets among large boulders (R. W. Davis, pers. obs.). The ability of other benthic-invertebrate predators to detect prey is reduced in coarser-grained sediments (Lipcius and Hines 1986; Quammen 1982; Wong and Barbeau 2003) and higher heterogeneity (Sponaugle and Lawton 1990; Wong and Barbeau 2003). However, the results from our logistic regression analysis indicated that feeding behavior was not strongly related to sediment type in Simpson Bay. Although sea otters foraged in muddy substrates, most foraging occurred in areas with heterogeneous substrates. This is opposite of what was found for other predators of bivalves (crabs, sea stars, and birds). However, these species might not have the sea otters' ability to excavate sediment or tactilely distinguish prey. Gravel and small rocks might not hinder the ability of otters to locate food as they do with other predators, because sea otters have been observed moving even large rocks

(Kvitek et al. 1989; VanBlaricom 1988), and foraging success is uniformly high despite sediment type.

It is likely that the relatively higher number of feeding observations associated with the mixed sand substrate and slightly low number associated with mud (relative to the abundance of these sediment types) resulted from the association between depth and sediment type. Snelgrove and Butman (1994), in their review of invertebrate distribution, concluded that sediment grain size is not a strong determinant of invertebrate distribution. Even if different species of sea otter prey are associated with different sediment types (Ostfeld 1982), a strong association might not exist between feeding location and sediment type at the population level because sea otters show a great deal of individual variation in diet (Estes et al. 2003; Ralls et al. 1988; Riedman and Estes 1990). Thus, different individuals could have associations with specific sediment types when the population as a whole does not.

Results from our logistic regression analysis indicated that resting behavior was strongly related to the location in Simpson Bay, and it occurred primarily toward the central areas of the bay. The benefits that result from this behavior are not immediately apparent. The simplest explanation is that the otter avoids drifting onto shore while sleeping at the surface, possibly to avoid terrestrial predators. In discussing the evolution of rafting (floating in aggregations at the surface), Garshelis et al. (1984) provided evidence that a historic land predator, perhaps aboriginal humans, might have influenced the social behavior of sea otters. Water currents also can differ between the central and peripheral areas of the bay. However, a strong preference for certain habitat characteristics during resting was not apparent in other studies (Garshelis 1983; Garshelis and Garshelis 1984).

Resting and feeding behaviors occurred in areas with different water depth, sediment type, and position in the bay. Although the primary factor influencing location was different for each behavior, all aspects of the microhabitat differ because of associations between the habitat variables themselves. Water depth was the primary variable distinguishing feeding and resting habitats (Table 1) because of the strong correlation between depth and position in the bay, with shallow waters (primary feeding habitat) along the periphery and deeper waters (primary resting habitat) in the central areas of the bay. Other habitat variables might be associated with these 2 behaviors. That the models best predicted unused locations indicates that other variables not considered in this study likely influence the choice of areas used for feeding and resting. Understanding how invertebrate abundance and distribution are related to depth and sediment type is critical for a better understanding of the feeding distribution of sea otters. In addition, we need a better understanding of how hydrography, water currents, and prevailing wind conditions influence habitat associations. Females with pups in Simpson Bay tend to move to protected or sheltered waters (bays, inlets, or lees) during storm events or high winds (R. W. Davis, pers. obs.), but this behavior has not been examined in detail. In calm weather conditions, sea otters can be encountered farther

from shore (Kenyon 1975). Although we did not specifically examine the effect of wind speed and direction on the resting areas used by sea otters (Simpson Bay is a relatively low-energy environment compared to other sea otter habitats), we did observe that females with pups often were concentrated in protected areas (the upper part of North and East Bays or behind small islands) during strong winds.

Habitat use by animals occurs on different spatial and temporal scales, and the factors influencing an animal's location can be different at each scale (Allredge et al. 1998; Johnson 1980; Manly et al. 2002). We examined microhabitat (3rd-order) selection by examining variables associated with location in a bay. However, that otters are present in Simpson Bay is also the result of selection on a different scale. It is possible that the area as a whole is superior for either resting or feeding when compared to adjacent areas with lower densities of sea otters.

The habitat variables associated with feeding and resting behavior will differ throughout the sea otter's range, where areas such as southwestern Alaska and the Aleutian Islands also have rocky habitats with large-bodied kelps that form surface canopies and exposed, high-energy coastlines (Riedman and Estes 1990). Determining habitat preference by sea otters of different age and sex in these areas will require studies similar to this one and additional information on prey preference and the distribution and abundance of prey.

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