FORAGING DEPTHS OF SEA OTTERS AND IMPLICATIONS TO COASTAL MARINE COMMUNITIES

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ABSTRACT

We visually observed 1,251 dives, of 14 sea otters instrumented with TDRs in southeast Alaska, and used attribute values from observed dives to classify 180,848 recorded dives as foraging (0.64), or traveling (0.36). Foraging dives were significantly deeper, with longer durations, bottom times, and postdive surface intervals, and greater descent and ascent rates, compared to traveling dives. Most foraging occurred in depths between 2 and 30 m (0.84), although 0.16 of all foraging was between 30 and 100 m. Nine animals, including all five males, demonstrated bimodal patterns in foraging depths, with peaks between 5 and 15 m and 30 and 60 m, whereas five of nine females foraged at an average depth of 10 m. Mean shallow foraging depth was 8 m, and mean deep foraging depth was 44 m. Maximum foraging depths averaged 61 m (54 and 82 for females and males, respectively) and ranged from 35 to 100 m. Female sea otters dove to depths ≤20 m on 0.85 of their foraging dives while male sea otters dove to depths ≥45 m on 0.50 of their foraging dives. Less than 0.02 of all foraging dives were >55 m, suggesting that effects of sea otter foraging on nearshore marine communities should diminish at greater depths. However, recolonization of vacant habitat by high densities of adult male sea otters may result in initial reductions of some prey species at depths >55 m.

Key words: *Enhydra lutris*, sea otter, diving behavior, time-depth-recorders, TDR, foraging ecology, invertebrate fisheries, fisheries conflict.

During most of the early 20th century, sea otters were absent from large portions of their former habitat in the coastal North Pacific. During this absence, many sea otter prey populations responded to reduced predation by increasing in mean size, density, and biomass. Studies contrasting habitats with and without sea otters, or contrasting the same sites before and after sea otter recovery, provided evidence for their widely acknowledged role as predators in structuring nearshore marine

communities throughout much of the North Pacific Ocean (Estes and Duggins 1995). The top-down effects of otters have been documented in rocky coastal reef communities, as well as intertidal, and sedimentary habitat communities (Estes and Palmisano 1974, Kvitek and Oliver 1988, VanBlaricom 1988, Estes and Duggins 1995, Estes *et al.* 1998).

The effects of sea otters in the nearshore system can be illustrated by contrasting the rocky reef community with and without sea otters (Estes and Duggins 1995). When sea otters are present, they control the population densities and sizes of herbivorous sea urchins (*Strongylocentrotus* sp.) and attached macroalgae flourish due to minimal grazing pressure. In this "kelp-dominated" state, the nearshore ecosystem is characterized by relatively high diversity and biomass of red and brown algae (primarily "kelps" order Laminariales). These kelps are highly productive and provide food and habitat for invertebrates and fish that in turn support higher trophic levels, such as predatory fish, birds, and mammals (Simenstad *et al.* 1978, Irons *et al.* 1986, Bodkin 1988, Duggins *et al.* 1989). Conversely, in the absence of sea otters, sea urchins respond by increasing in population density, mean size, and total biomass. Large, dense urchin populations exert high grazing pressure, resulting in near-complete removal of kelps. This "urchin-dominated" system is characterized by "urchin barrens" where large, abundant sea urchins reduce algal productivity, diversity, and biomass (and associated habitat structure). The reduction of kelps, in turn, results in reduced abundance of organisms associated with, or dependent upon, foliose algae. Other species of invertebrate prey have exhibited similar trends in response to reduction in sea otter predation (*i.e.*, increasing in density, mean size, and biomass) including abalones (*Haliotis* sp.), crustaceans (*Cancer* sp.), mussels (*Mytilus* sp.), and several species of venerid clams (Lowery and Pearse 1973, Garshelis and Garshelis 1984, VanBlaricom 1988, Kvitek *et al.* 1992). In some instances humans developed commercial and subsistence fisheries for several invertebrate species that probably would not have been possible if sea otters had not been eliminated from most of their historic range.

Sea otters forage almost exclusively on benthic invertebrates, bringing their prey to the surface for consumption, allowing identification of dive function. Due to their benthic foraging, sea otter distribution is largely limited by their ability to dive to the sea floor. Therefore, the effects of sea otter predation on prey populations should be limited to depths and habitats that are within the depths frequented by foraging sea otters. However, the dive-depth distributions of foraging sea otters have not previously been estimated. Available information, largely from shore observations, on sea otter diving capacities suggest most foraging takes place in waters less than 20 m deep (Kenyon 1969, Riedman and Estes 1990), although a single record exists for a foraging dive to 97 m (Newby 1975). Due to constraints placed on divers using SCUBA, studies into the effects of sea otter predation on their prey have generally been limited to depths <10 m. However, it may be reasonable to assume that the effects of sea otter foraging on densities and sizes of benthic invertebrate prey extend throughout the depths that sea otters commonly forage. While the relation between forage depth and ecological effect is largely unknown, it is likely that the effect of sea otter predation would diminish as maximum diving capacity is approached.

We instrumented sea otters in southeast Alaska with archival time-depth recorders (TDRs) and visually monitored their diving for up to 46 d. Our objectives were to (1) classify sea otter dive types by function, (2) describe sea otter dive attributes (*e.g.*, mean dive depths, durations, and ascent/decent rates) according to function, and (3) describe the distribution of sea otter foraging dive depths.

Reintroductions of sea otters into Cross Sound, Alaska, beginning in 1965 (Jameson *et al.* 1982) led to the Port Althorp area (Fig. 1) being reoccupied by sea otters about 1977 (USGS, unpublished data). Although sea otters had been present in Port Althorp for about 20 yr at the time of this study, large areas of unoccupied, or recently occupied habitat were still available in nearby Icy Strait. Port Althorp provided sea otters access to foraging depths (*e.g.*, from 0 to >200 m) that likely included the range of their diving abilities.

In May of 1999 we captured and instrumented 21 sea otters (6 males and 15 females) in Port Althorp. Each animal was sedated (Monson *et al.* 2001), and a VHF radio transmitter (Advanced Telemetry Systems, Isanti, MN) and an archival time depth recorder (TDR) (Mark VII, Wildlife Computers, Redmond, WA) were surgically implanted in the intraperitoneal cavity (Williams and Siniff 1983). A premolar tooth was extracted and age estimates were made by Matsons Laboratory (Milltown, MT) based on cementum depositions (Bodkin *et al.* 1997). Mass and total length (nose to tip of tail) were measured on sedated animals prior to surgery. Following surgery, animals were immediately released near their capture location. VHF transmissions were used to monitor animal locations and behavior and aid in their recapture. The TDR was $69 \times 21.5 \times 23$ mm, weighed 35 g, and contained 2 MB of data storage capacity. The TDR was programmed to record depth at 2-sec intervals with an accuracy of 0.25 m for 46 consecutive days. We attempted to relocate each instrumented individual daily between the first and second capture. Visual observations were made from 8- and 16-m vessels and from shore and were aided with $10\times$ binoculars and $50\times$ telescopes (Questar Corp, New Hope, PA). During relocations we recorded the animal's location, and categorized behavior as resting, foraging, traveling, grooming, or interacting (Riedman and Estes 1990). Foraging was identified by the presence of prey consumed on the surface following a dive. In July 1999 we recaptured 14 of the 21 animals (5 males and 9 females) originally instrumented and surgically removed their instruments. One instrument was recovered from a dead animal in June 2003. One of the 15 recovered instruments, from a female, failed to record any data. Capture, handling, and surgical procedures employed were approved by the Animal Care and Use Committee of the Alaska Science Center, U.S. Geological Survey, and as permitted by the U.S. Fish and Wildlife Service under permit 766818.

Data Analysis

TDR data were downloaded and processed with zero offset software (ZOC, Wildlife Computers, Redmond, WA) to calibrate each data point relative to the sea surface (Hooker and Baird 2001). We next processed each individual's recovered data through the Dive Analysis program (DA, Wildlife Computers), which transformed the 2-sec interval depth data into individual dives. Output from DA included the following attributes for each dive: date and start time of each dive, dive duration, time at bottom, maximum depth, and mean descent and ascent rates. The proportion of the total dive time spent on the bottom was calculated for each dive by dividing time at bottom by dive duration. In this context "bottom" refers to the bottom of the dive profile (0.80 of maximum depth), not necessarily the seafloor. Due to the location of the TDR in the animal's body cavity and the instrument's accuracy (0.25 m) we included only dives greater than 2 m in our analyses. Dive duration
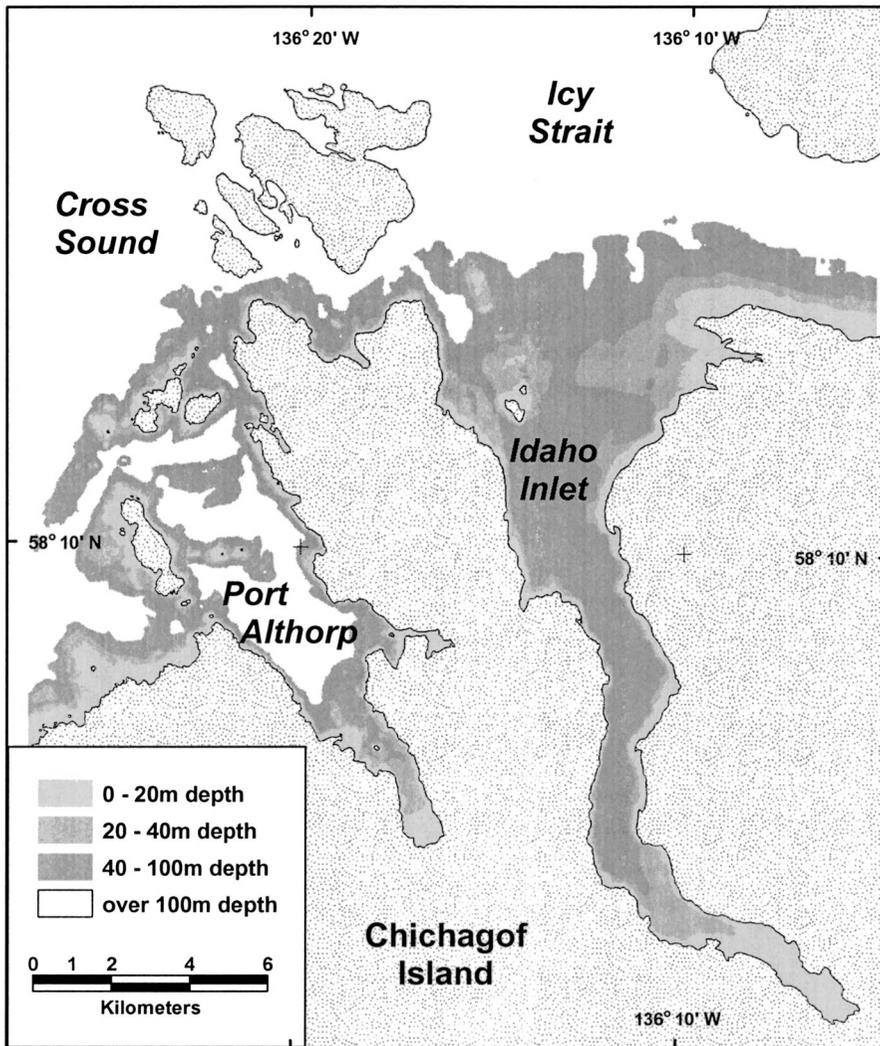
Figure 1. Study area in southeast Alaska where sea otters were captured and instrumented with TDRs in Port Althorp. All animals were relocated only within the shaded areas. Four of five males were found in Idaho Inlet and Port Althorp.

was calculated as the cumulative time between consecutive depth readings exceeding 2 m. Time at bottom was defined as the time between the first and last depth readings equal to or greater than 0.80 of the maximum dive depth. Average descent rate was calculated by subtracting the time at the beginning of the dive from the time the bottom is reached (0.80 of maximum depth), and dividing by the depth (m) at the beginning of the bottom time. Ascent rates were calculated similarly to descent rates. The variables depth (maximum during bottom time), durations, and descent and ascent rates were $\log_{10}$ transformed, and the ratio of bottom time/dive time was arcsine square root transformed to normalize distributions prior to analysis.

Dive Classification

Among the dives recorded by the TDRs was a subset of dives that we observed directly from either shore or vessels, and determined the dive function as foraging or non-foraging (including traveling, grooming, and interacting). By matching dates and times between observed and recorded dives, we assigned dive type for this subset of dives with known functions as either foraging or non-foraging. We used dive attributes from all observed dives to build a logistic model to classify unobserved dive types (PROC LOGISTIC, SAS Institute, Cary, NC), using the general logistic function:

$$\text{logit } P = \log(P/1 - P) = \alpha + \beta' x,$$

where α is the intercept parameter and β is the vector of slope parameters.

From this single logistic model we assigned TDR recorded dives of all individuals into either foraging or non-foraging dives. Known non-foraging dives were all traveling dives. Full (using all available dive attributes and potential interactions) and reduced models were developed using model selection algorithms (SAS Institute, Cary, NC), based on guidelines for model building and selection in Hosmer and Lemeshow (2000). Ten final potential models were compared, by Akaike Information Criteria (AIC) and final model selection was based on Hosmer-Lemeshow goodness-of-fit test statistics, and then on lowest AIC values.

The specific logistic model used to classify the remaining dives for each individual took the following form:

$$\text{logit } P = \alpha + (\beta_1 * k_1) \cdots + \cdots (\beta_5 * k_5),$$

where:

α = intercept
β_i = slope parameters for variables k_1 to k_i, and the variables (k):
   k_1 = dive duration,
   k_2 = bottom time/dive time,
   k_3 = average ascent rate,
   k_4 = interaction (dive duration * average ascent rate),
   k_5 = interaction (bottom time/dive time * average descent rate).

The two closest competing models had similar, but higher AIC scores (likelihood ratio test, $P > 0.1$), and were of similar form (one or both of the same interaction terms included, but with one or more main attribute variables included). The other seven models had significantly poorer fit (likelihood ratio test, $P < 0.02$ with five of the seven having significantly poor H-L goodness-of-fit test scores ($P < 0.01$). We calculated a predicted probability with the logistic equation for each dive and used a probability value of 0.5 to assign dives to either the "foraging" or "non-foraging" classification, where:

$$P = \exp(\text{logit } P)/(1 + \exp(\text{logit } P))$$

and

if $P \geq 0.5$ then dive type = foraging function (bottom) or
if $P < 0.5$ then dive type = non-foraging function (traveling).

Non-foraging function dives were predominantly traveling, but also included dives during grooming and social interactions. However, we did not have enough known non-traveling dives to build a model to differentiate traveling from

non-traveling (grooming, *etc.*) dives. Tests for differences between known dive types and among attributes by dive type were performed with MANOVA (PROC MANOVA, SAS, Institute, Cary, NC). We used two-way ANOVA to test for difference in forage dive attributes by sex and depth class (shallow *vs.* deep) and one-way ANOVA to test for difference in travel dive attributes by sex. Relations among dive attributes measured and individual weights and conditions (mass/TL) were evaluated with Bonferroni corrected correlation and linear regression.

We used our sample of 1,251 known dives to calculate error rates in our dive classification analysis. Dive classification error rates were determined using a cross validation procedure (model option "c table" within PROC LOGISTIC, SAS Institute, Cary, NC).

Following dive classification, we visually inspected forage dive depth distributions. When individual distributions were bimodal, we visually inspected the distributions for break points. We used these break points to categorize dive types as either deep or shallow foraging.

Foraging Habitat Use and Availability

We compared use of foraging habitat as determined by dive depth distributions of individuals, to the availability of foraging habitat by depth. Using NOS hydrographic data, we calculated the proportion of habitat in Port Althorp and Idaho Inlet (Fig. 1) in each of three bathymetric zones; 0–20 m, 20–40 m, and 40–100 m (ArcView, ESRI, Redlands, CA). Habitat availability was calculated for each sex and the sexes combined, based on the use of Port Althorp and Idaho Inlet by males and Port Althorp by females (Fig. 1). We calculated habitat use as the proportion of dives all individuals made within each of those bathymetric zones and compared use to availability with the resource selection program PREFER,[1] using a multiple comparison procedure (Johnson 1980).

RESULTS

Population Sample

Our sample consisted of 14 individuals, including nine females and five males (Table 1). TDRs contained 42–46 full days of continuous depth recordings at 2-sec intervals. Females ranged in age from 2 to 16 yr and were generally lighter, shorter, and weighed less per unit length than males (Table 1). Female lb/wh was pregnant at initial capture and had a pup during the study that did not survive. None of the remaining females were pregnant at either capture, and two had dependent pups during the period of data collection (pu/pu and si/si). Male ch/wh was territorial (Kenyon 1969) and remained near its capture location in Port Althorp during the study (Fig. 1). Male wh/wh was relocated only in Idaho Inlet, an area recolonized by sea otters about 1990 (Pitcher 1989)[2] in a "male aggregation" (Garshelis and

Table 1. Identification and phenotype of sample animals.

ID	Sex	Age	Mass (kg)	TL[a] (cm)	Mass/TL (g/cm)	Days of data[c]
aq/aq	F	2	23.6	118.5	199	46
re/wh	F	2	22.7	126.5	179	46
lb/lb	F	2	19.5	119.0	164	46
ch/ch	F	2	19.1	121.0	158	46
lb/wh	F	3	28.6	125.5	165[b]	43
pi/wh	F	6	23.1	127.5	181	43
pu/pu	F	9	21.3	125.5	170	46
si/si	F	11	26.3	127.0	207	46
go/wh	F	16	22.7	118.0	188	42
means		**5.9**	**23.0**	**123.2**	**186.4**	
or/or	M	5	39.0	140.0	279	46
ye/ye	M	6	38.6	135.5	285	46
re/re	M	7	41.7	141.0	296	46
ch/wh	M	7	38.1	133.0	286	46
wh/wh	M	10	38.7	141.5	273	46
means		**7.0**	**39.2**	**138.2**	**271.0**	

[a] TL = total length.
[b] Mass/TL based on recapture weight because of undetected pregnancy at capture.
[c] Total number of complete days of data collection.

Garshelis 1984, Jameson 1989) about 20 km from Port Althorp. The three remaining males traveled irregularly between Port Althorp and Idaho Inlet, but spent the majority of their time in Idaho Inlet. Based on length of occupation we assume the Port Althorp population was near equilibrium density, and the Idaho Inlet to be below.

Dive Classification

We visually observed and classified 1,251 dives of our 14 study animals as either foraging (918) or non-foraging (333) (Table 2). We observed an average of 89 known dives per individual (range 4–201). Known foraging dives were characterized by rapid descent and ascent rates (~1 m/sec), long dive and bottom times (~90 and 63 sec, respectively), with most of the dive time on the bottom (~0.72), and to relatively deep depths (Table 2). Traveling dives were characterized by slow descent and ascent rates (~0.4 m/sec), moderate dive and bottom times (~24 and 9 sec, respectively), with little of the dive time on the bottom (~0.35), and were relatively shallow (Table 2). Known forage and traveling dives were significantly different ($F_{6, 1244} = 618$, $P < 0.0001$) and all variables used in the logistic model to classify dives differed significantly ($P < 0.0001$) (Table 2).

Error rates in dive classification based on our sample of dives of known function varied between foraging and non-foraging dives. Dives of known function were correctly classified at a rate of 0.962. Twenty-five of 918 known foraging dives (0.027) were misclassified as traveling dives and 22 of 333 known traveling dives (0.066) were misclassified as foraging dives. All misclassified dives were shallow (<15 m), but within this range no bias in error assignment was evident.

Table 2. Mean (SE) values of dive attributes based on direct observation of 918 foraging dives and 333 traveling dives from 14 instrumented sea otters. All known dive attribute values used in logistic model to classify all TDR recorded dives. All values were significantly different between dive types ($P < 0.001$).

	Foraging dives	Traveling dives
Mean depth (m)	18.9 (4.6)	2.7 (0.2)
Mean duration (sec)	85 (8.8)	29 (3.2)
Mean bottom time (sec)	55 (3.2)	12 (1.8)
Bottom/dive time	0.66 (0.03)	0.27 (0.03)
Mean descent rate (m/sec)	1.0 (0.04)	0.38 (0.02)
Mean ascent rate (m/sec)	1.1 (0.06)	0.41 (0.04)

Foraging Dives

The logistic analysis identified the benthic foraging dive as the most common type (Fig. 2). Foraging dives were characterized by the greatest average depths, dive durations, and ascent/descent rates (Table 3). The average number of foraging dives among individuals was 8,365 (185/d $\pm$ 20) and ranged from 3,300 (72/d) to 13,719 (298/d) (Fig. 2). There was a significant negative correlation between the mean foraging depth and the mean number of foraging dives an individual made per day (Fig. 3). The proportion of dives foraging averaged 0.64 ($\pm$0.04) and ranged from 0.26 to 0.86 among individuals (Fig. 2).

Individuals varied both in terms of foraging dive attributes (Table 3) and the distribution of foraging dive depths (Fig. 2). Five of the 14 individuals exhibited unimodal foraging dive depths, foraging predominately in depths <25 m (Fig. 2a). Nine individuals exhibited a bimodal distribution of their foraging depths, with one mode in depths <20 m and another mode between 30 and 55 m (Fig. 2b). Sea otters foraging exclusively at shallow depths made significantly more foraging dives (11,934, $\pm$ 524) than bimodal foragers (6,158, $\pm$ 878) ($t = 4.85$, $P < 0.001$). This difference translated into an average of an additional 119 foraging dives per day for shallow foragers.

Dive attributes also varied strongly as a function of dive depth. Shallow foraging dives (mean depth 7.7 m) were significantly shorter in duration, bottom time, and surface interval, and were slower in descent and ascent rates than were deep dives (mean depth 44.4 m), while the ratio of bottom time to dive time was greater (Table 3). There were also patterns in the number of foraging dives, and forage depth distributions related to sex. All unimodal foraging divers were female, while all males and four of nine females were bimodal foraging divers (Table 3, Fig. 2). While distributions varied within bimodal foragers (Fig. 2), differences between the sexes in dive attributes were slight within the shallow or deep categories.

Female sea otters on average made significantly more foraging dives (10,429, $\pm$783) than males (4,650, $\pm$528) ($t = 5.08$, $P < 0.001$). The proportion of dives allocated to foraging averaged 0.72 for females ($\pm$0.04) and 0.48 ($\pm$0.07) for males ($t = 3.58$, $P = 0.004$). Average female dive depth was 9.7 m ($\pm$1.1) and average male dive depth was 22.4 m ($\pm$2.1). Among forage dive attributes, only the ratio of bottom time to total dive time differed by sex. Female sea otters on average spent a greater proportion of their foraging dive time on the bottom compared to males (0.74, $\pm$0.01 *vs.* 0.61, $\pm$0.03) ($t = 5.50$, $P \leq 0.001$), likely a result of shorter transit times to and from the bottom during shallow foraging dives.
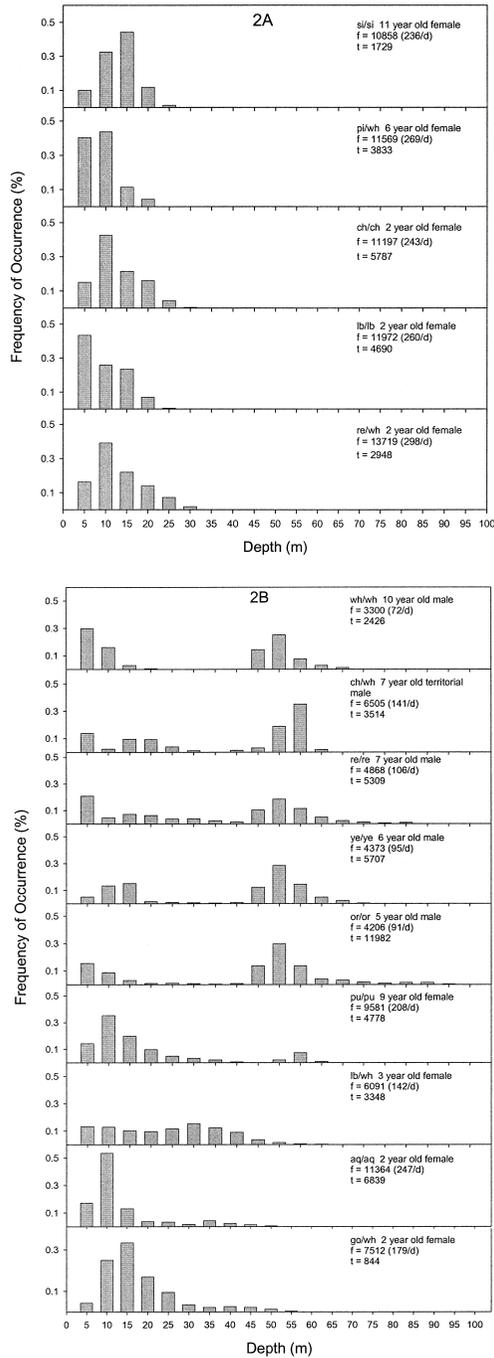
Figure 2. Forage dive depth distributions of five unimodal (A) and nine bimodal foraging sea otters (B) from SE Alaska. (f = number of foraging dives and t = number of traveling dives, number in parentheses is mean number of foraging dives per day).

Table 3.   Mean (SE) shallow and deep foraging and traveling dive attributes for 14 sea otters by sex (180,848 total dives). All forage dive attributes differed significantly between shallow and deep foraging, independent of sex ($P < 0.001$), while only the bottom/dive differed significantly between the sexes, independent of depth ($F = 6.72$, $P < 0.02$). All travel dive attributes differed significantly between the sexes ($P < 0.05$) except surface interval and descent rate.

Dive type	n	Depth (m)	Duration (sec)	Surface interval	Bottom time (sec)	Bottom/dive[a]	Descent (m/sec)	Ascent (m/sec)
Forage ♀	9	8.1	64	43	50	0.74	0.99	1.02
(shallow)		(0.7)	(3.3)	(4.6)	(2.4)	(0.006)	(0.01)	(0.04)
$n = 87,467$								
Forage ♂	5	7.1	59	48	47	0.70	0.90	0.90
(shallow)		(0.9)	(4.4)	(2.3)	(3.9)	(0.02)	(0.05)	(0.09)
$n = 6,398$								
Forage ♀	9	38.5	136	109	83	0.61	1.09	1.04
(deep)		(5.0)	(11.8)	(4.6)	(8.6)	(0.03)	(0.02)	(0.05)
$n = 9,433$								
Forage ♂	5	49.0	146	117	79	0.53	1.1	1.4
(deep)		(0.5)	(5.6)	(13.1)	(7.7)	(0.03)	(0.05)	(0.06)
$n = 13,819$								
Travel ♀	9	3.5	33	43	15	0.32	0.4	0.4
$n = 34,793$		(0.1)	(1.8)	(1.8)	(1.1)	(0.02)	(0.01)	(0.01)
Travel ♂	5	3.0	24	53	9	0.21	0.4	0.5
$n = 28,938$		(0.09)	(3.3)	(4.3)	(1.1)	(0.02)	(0.03)	(0.05)

[a] Bottom time (sec)/dive duration (sec).

Heavier individuals, and those with greater mass to total length ratios (mass/TL), generally dove deeper and longer, but not faster, than lighter individuals. We detected significant correlations between weight and condition and most dive attributes (Table 4). Mean forage depth, duration, and bottom time were positively correlated with weight and condition and negatively correlated with bottom time/dive time (Bt/Dt). No significant correlations between individual age of the sea otter and forage dive attributes were evident.

Traveling Dives

The number of traveling dives varied among individuals (Fig. 2). The mean number of traveling dives was 4,723 (± 820 range 844–11,982) and 0.35 (± 0.05 range 0.10–0.74) of all dives were traveling. Female sea otters generally made fewer (3,866 $\pm$ 633) traveling dives than males (5,788 $\pm$ 1,659) and unimodal foragers generally made fewer (3,796 $\pm$ 698) than bimodal foragers (5,238 $\pm$ 1,213), although differences were not significant. There were significant differences between the sexes in traveling dive attributes. On average, females dove deeper while traveling than males, 3.5 m *vs.* 3.0 m ($t = 2.5$, $P = 0.03$), dove longer, 33 *vs.* 24 sec ($t = 2.9$, $P = 0.01$), and had longer bottom times, 15 *vs.* 9 sec ($t = 3.4$ $P = 0.006$) while traveling, than males. While traveling, females descended slower, 0.39 *vs.* 0.49 m/sec ($t = -2.2$, $P = 0.05$), but ascended faster, 0.32 *vs.* 0.21 m/sec ($t = 3.9$ $P = 0.002$). There were no differences in traveling dive attributes between individuals exhibiting unimodal and bimodal foraging behaviors.
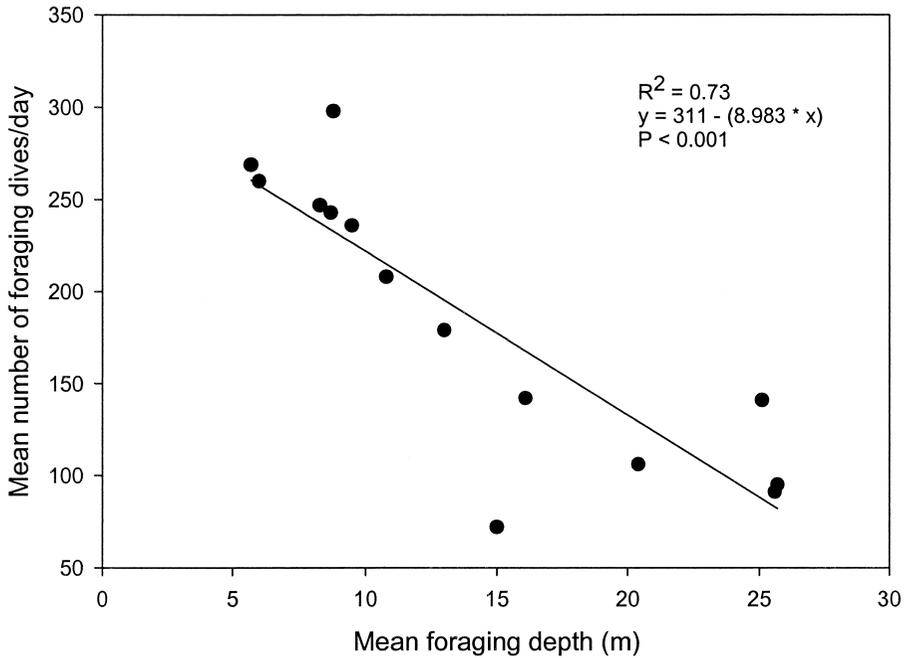
Figure 3. Relation between total number of foraging dives and mean foraging depth for 14 sea otters from SE Alaska.

Foraging Habitat Use and Availability

The distribution of observed sea otter foraging depths was not proportional to benthic habitat availability within the potential foraging depths from 0 to 100 m ($F_{2,12} = 11.42$). Females made 0.86 and males 0.37 of their dives in the 0–20-m zone, which represented 0.30 and 0.25 of the habitat available, respectively. Females made 0.10, and males 0.04 of their dives in the 20–40-m zone, which represented 0.18 and 0.21 of the habitat available, respectively. Females made 0.02, and males 0.58 of their dives in the 40–100-m zone, which represented 0.52 and 0.56 of the habitat available, respectively. For sexes combined, foraging occurred greater than availability in the 0–20-m depth range (0.69 use compared to 0.28 available, and less than availability in the 20–40-m (0.09 use to 0.19 available) and 40–100-m depths (0.22 use compared to 0.53 available). In the 40–100-m depths males used the habitat proportional to availability, while females rarely used these depths (Fig. 1, Table 5). The 0–20-m habitat was ranked as the most preferred, followed by 20–40 and 40–100-m. The 0–20-m and the 20–40-m habitat was significantly preferred by females over the 40–100-m habitat ($P < 0.05$), but habitat selection was not significant between the 0–20-m and the 20–40-m habitats by females. Males demonstrated no significant selection of foraging habitat by depth.

DISCUSSION

Behaviors of diving mammals are typically inferred from variation in patterns observed in dive attributes (*e.g.*, depth or duration) or dive profiles (Schreer and Testa

Table 4. Correlation coefficient matrix between mass (kg), mass/TL, and mean TDR dive attributes, and among dive attributes (Bonferroni corrected *P* values are below mean attribute values). Bt/Dt is bottom time/duration. NS signifies non-significant relation.

	Depth	Duration	Bottom time	Bt/Dt	Descent	Ascent
Mass	0.86	0.81	NS	−0.86	NS	NS
	<0.02	<0.02		<0.02		
Mass/TL	0.82	0.75	NS	−0.86	NS	NS
	<0.02	0.05		<0.02		
Depth		0.94	0.78	NS	NS	NS
		<0.02	0.02			
Duration			0.90	NS	NS	NS
			<0.02			
Bottom time				NS	NS	0.75
						0.05

1995, Otani *et al.* 1998, Hooker and Baird 2001, Jay *et al.* 2001). Sea otters are unusual among diving mammals in two respects related to assessing their diving behaviors. First, because they feed almost exclusively on benthic invertebrates, and typically dive close to shore, diving behaviors can be observed without disturbance effects. Secondly, because they bring their prey to the surface and exhibit foraging success rates that can exceed 90% (Estes *et al.* 1981, Kvitek *et al.* 1993, Doroff and DeGange 1994), discriminating between foraging and other dives is straightforward. The ability to simultaneously observe dives by function for instrumented sea otters provides a direct and standardized method for determining the function of unobserved dives. However, difficulty in observing sea otters far from shore could bias classification, although this did not appear to be the case, as all deep dives (> ~20m) were classified as foraging, and non-foraging dives to these depths would seem unlikely for a sea otter. Until a generalized classification model is tested among several populations, site-specific dive classifications should be derived from a sample of observed dives of known function. Future studies employing similar TDR technologies may benefit from developing models that employ dive attributes from foraging dives with known outcomes, in terms of success and prey type. Such models may eventually lead to inferences concerning foraging success and diet from TDR data alone.

Forage and traveling dives we observed were discrete and well defined by dive attributes such as depth, durations, and ascent/descent speeds (Table 2) permitting accurate classification of unknown dive types. However, intertidal foraging for prey such as mussels, (VanBlaricom 1988), or foraging in kelp forests and canopies for prey such as snails and crabs (Riedman and Estes 1990) may be problematic. Additionally, sea otter behaviors other than foraging and traveling also entail diving activity. These behaviors include grooming and social interactions such as reproduction, food stealing, and antagonism (Packard and Ribic 1982) and likely are encompassed within our travel dive category. It may be possible to further refine dive classification by observation of other known dive functions, such as canopy foraging and grooming behavior.

We detected strong negative correlations between the number of foraging dives an individual made and the depths to which they foraged. Assuming individuals are

Table 5. Comparison of available habitat in 3 bathymetric zones and the distribution of sea otter foraging depths within those zones, by sex and for sexes combined.

Bathymetric Zone	Habitat	Females	Males	Combined
0–20 m	Available	0.30	0.25	0.28
	Use	0.86	0.37	0.69
20–40 m	Available	0.18	0.20	0.19
	Use	0.11	0.04	0.09
40–100 m	Available	0.52	0.56	0.53
	Use	0.02	0.58	0.22

meeting their caloric requirements whether diving deep or shallow (based on nearly equivalent weights between captures), this relation suggests greater prey availability with increasing depth. However, diving to greater depths requires additional time and metabolic costs compared to shallow diving. Costs include potential oxygen debt from extended dives, and thermoregulatory demands as increasing pressure compresses and depletes the air layer in the pelage used as insulation (Estes and Bodkin 2002). Potential consequences of these additional costs include extended resting periods between foraging periods and additional grooming time to replace insulation. Similar to the Australian sea lions (*Neophoca cinerea*), another benthic forager, sea otters apparently attempt to maximize bottom time during deep foraging by increasing their descent and ascent rates (Costa and Gales, 2003). Although deeper dives are on average much longer in duration and bottom time, than shallow dives (Table 3), the proportion of the total dive duration actually spent searching for prey was about 33% less on deep dives, compared to shallow. The longer surface intervals detected following deep dives may be required to replenish oxygen debt, or could result from longer handling times if more or larger prey are recovered while foraging deep. Additional information on depth specific energy expenditure and foraging success, in terms of calories obtained per dive, will help clarify the observed relation between foraging depth and number of dives.

Male and female sea otters had similar dive attributes for each of the forage dive types classified (Table 3). In general, deeper foraging dives were characterized by increased dive times and increased ascent and descent rates. However, there were striking differences in the distribution of forage dive depths between the sexes (Fig. 4), with females generally foraging in shallower water than males. Although some female sea otters exhibited the ability to forage at depths up to 71 m, they rarely did. Potential explanations for the sex-related patterns in forage dive depth distributions include behavioral and physiological differences between the sexes. Traveling dives were shallower, shorter, and had ascent and descent rates much slower than foraging dives, and most attributes differed between the sexes (Table 2, 3). The greater number of traveling dives by males likely reflects movements between Idaho Inlet, where the length of sea otter occupation was less and prey abundance potentially greater, and Port Althorp, where males had reproductive opportunities (a distance of approximately 20 km).

Sea otters are sexually dimorphic, with adult males exceeding female mass by about 0.25–0.35 (Kenyon 1969, Riedman and Estes 1990). Diving ability generally increases with size and the ability to store oxygen (Costa and Williams 1999), therefore male sea otters may be effectively partitioning foraging habitat simply by exercising the ability to dive deeper than the smaller females. We detected a
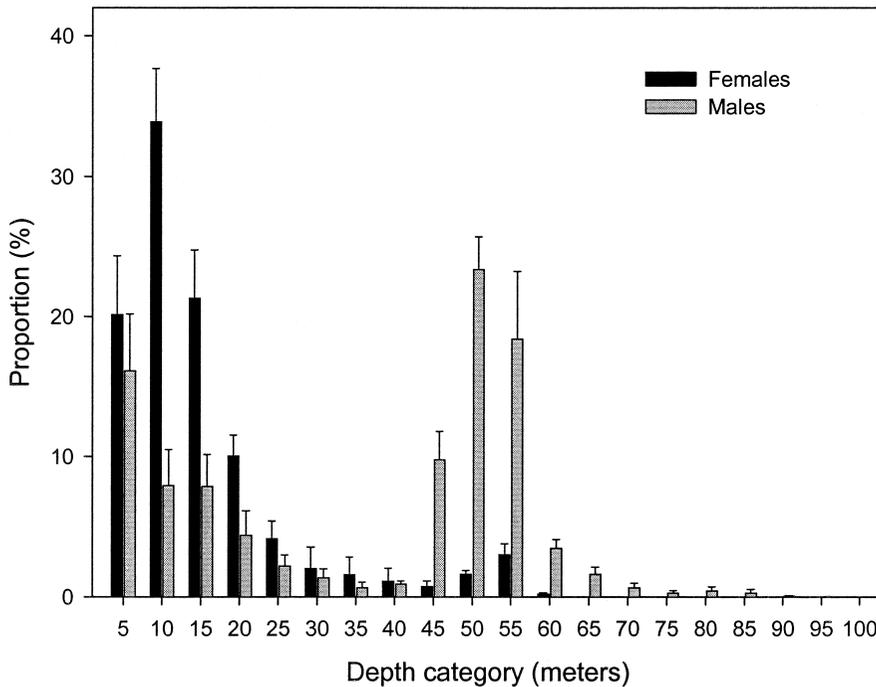
Figure 4.   Mean (SE) foraging dive depth distributions of nine female and five male sea otters from SE Alaska. Depth categories are in 5-m increments from zero. Five dives >90 m were recorded.

strong positive correlation between both weight and condition relative to mean and maximum dive depth. And although some females dove to depths approaching the maximum depths of male dives, the mean maximum female dive was 49 m compared to 82 m for males (Fig. 2).

Our finding of differences in foraging depths among individuals is consistent with individual-based preferences in foraging strategy related to diet recently described in sea otters (Estes *et al.* 2003). Although we did not obtain adequate dietary data from TDR-instrumented individuals to make meaningful contrasts, the individual forage depth distributions suggest at least two distinct foraging strategies (Fig. 2). One strategy entails foraging exclusively in shallow waters and requires a relatively large number of foraging dives, of relatively short duration, but with a high proportion of the dive searching for prey. Another strategy consists of allocating foraging effort in both shallow and deep-water habitats. Individuals displaying the latter strategy exhibit dive characteristics in shallow water similar to the exclusively shallow foraging individuals, but extend dive times more than two-fold and increase descent and ascent rates during deep foraging. The benefit of diving deeper appears to be related to a fewer number of foraging dives to obtain required calories.

It appears that relations between sea otters and their use of habitat for foraging are not proportional to availability, but include effects of sex, condition, and individual foraging strategy. Clearly sea otters in general, as well as individuals, do not forage equally over all benthic habitats that fall within their diving capacity, and while most foraging occurs in depths <20 m, significant amounts of foraging

occur in depths to 60 m. Foraging by males in depths from 40 to 100 m was proportional to availability suggesting a strong sex affect in the use of foraging habitats. Efforts to define relations between sea otter density and benthic habitat availability should consider the use of deep habitats, particularly by male sea otters.

Assuming the data from our sample of sea otters are representative of sea otter populations in general, some conclusions regarding the potential extent of sea otter effects on nearshore marine communities can be made. It appears that the distribution of forage depths we observed extend throughout the nearshore zone that supports the light-dependent attached algae that urchins could potentially overgraze. Thus, the effects of sea otter foraging in reducing urchin densities and subsequent kelp enhancement is likely limited by the depths to which kelps occur, rather than the depth limits we estimated for sea otter foraging. Sea otter effects on other components of the nearshore marine communities are likely to be limited by sea otter foraging depth. Our data suggests that prey occurring below about 55–60 m will encounter reduced sea otter predation. Examples of those taxa that sea otters consume and that occur within and beyond the effective range of sea otter foraging include echinoderms (urchins, basket stars), crustaceans (species of *Cancer*, *Chionecetes*, and *Paralithoides*), and mollusks (species of *Haliotis*, *Octopus*, and several species of bivalves). Those prey species that exhibit episodic movements from water depths >60 m to shallower depths (*e.g.*, some crabs) may become susceptible to predation in shallower water.

It is apparent that many sea otter prey populations exhibited predictable responses, in terms of increasing densities and sizes, to reduced sea otter predation during their prolonged absence throughout much of the North Pacific during the 20th century. As sea otters reoccupy these habitats, foraging at depths approaching their actual maximum may be cost effective during early recolonization. However, benefits of deeper foraging may be reduced as prey populations decline in the face of prolonged predation.

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