

**Abstract.**—During 1987 and 1988, sea otter, *Enhydra lutris*, prey composition and foraging success were studied by observing foraging otters in the northern Kodiak Archipelago. Study areas differed in the number of years in which they were occupied by sea otters and were categorized as established (occupied >25 years), intermediate (occupied 5–15 years), and frontal (occupied <5 years). Clams were the most frequently identified sea otter prey (57–67%) in all study areas, and of the clams identified to species, *Saxidomus giganteus* was the most frequently observed. Mussels, *Mytilus* spp., crabs (primarily *Telmessus* spp.), and green sea urchins, *Strongylocentrotus droebachiensis*, contributed ≤25% to the total prey within each study area. Adults did not differ in the proportion of clams, mussels, or crabs captured as prey among study areas. Adults captured clams with a greater frequency and mussels with lesser frequency than did juvenile sea otters for all study areas combined. Forage success did not differ among study areas for adults nor between adults and juveniles for all study areas combined. Adult sea otters in the established area appear to have compensated for reduced prey size by retrieving more prey items per dive; however, they obtained less clam biomass per dive than otters in the intermediate and frontal areas.

## Sea otter, *Enhydra lutris*, prey composition and foraging success in the northern Kodiak Archipelago

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The Kodiak Archipelago in south-central Alaska (Fig. 1) supported an abundant sea otter, *Enhydra lutris*, population prior to their commercial exploitation during the 18th and 19th centuries (Lensink, 1962; Kenyon, 1969). Following this period of unregulated harvesting of sea otters, which was terminated in 1911 (Kenyon, 1969), an isolated remnant population of sea otters remained at the northern tip of Shuyak Island (Schneider<sup>1</sup>). During the late 1950's through mid 1980's, episodic range expansion occurred throughout the northern Kodiak Archipelago (Lensink, 1962; Schneider<sup>1</sup>; Simon-Jackson et al.<sup>2,3</sup>).

In the absence of sea otters, dense populations of clams, crabs, sea urchins, and abalones may develop. As sea otters recolonize former habitat, shellfish densities decrease owing to sea otter predation, sometimes in combination with commercial and subsistence shellfish harvest (Garshelis et al., 1986). Sea otters have been implicated in closure of commercial and recreational fisheries in California for abalone, *Haliotis* spp. (Estes and VanBlaricom, 1985) and pismo clams, *Tivela stultorum*, (Stephenson, 1977; Miller et al.<sup>4</sup>). In Alaska, sea otters impacted

the recreational and commercial fisheries for Dungeness crab, *Cancer magister*, in Prince William Sound (Garshelis, 1983; Garshelis et al., 1986; Kimker<sup>5</sup>).

During 1987–1988 the sea otter range continued to expand near southeastern Afognak Island of the Kodiak Archipelago. The natural recolonization pattern of the archipelago provided an opportunity to study the effects of sea otters on

<sup>1</sup> Schneider, K. B. 1976. Assessment of the distribution and abundance of sea otters along the Kenai Peninsula, Kamishak Bay and the Kodiak Archipelago. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 37:527–626.

<sup>2</sup> Simon-Jackson, T., D. Taylor, S. Schliebe and M. Vivion. 1985. Sea otter survey, Kodiak Island–1984. U.S. Fish and Wildlife Service, Anchorage, Alaska. Unpubl. rep., 16 p.

<sup>3</sup> Simon-Jackson, T., M. Vivion, and D. Zwiefelsofer. 1986. Sea otter survey, Kodiak Island–1985. U.S. Fish and Wildlife Service, Anchorage, Alaska. Unpubl. rep., 11 p.

<sup>4</sup> Miller, D. J., J. E. Hardwick, and W. A. Dahlstrom. 1975. Pismo clams and sea otters. Calif. Dep. Fish and Game. Mar. Resources Tech. Rep. 31:1–49.

<sup>5</sup> Kimker, A. 1985. A recent history of the Orca Inlet, Prince William Sound Dungeness crab fishery with specific reference to sea otter predation. In B. R. Metleff (ed.), Symposium on Dungeness crab biology and management, p. 231–241. Univ. of Alaska, Alaska Sea Grant Rep. 85-3.

prey populations (Kvitek et al., 1992) and an opportunity to assess changes in sea otter foraging characteristics (prey composition, forage success, prey size and biomass) as they relate to the duration the habitat had been occupied. We describe the foraging characteristics of sea otters in relation to the length of habitat occupancy along the Kodiak Archipelago.

## Methods

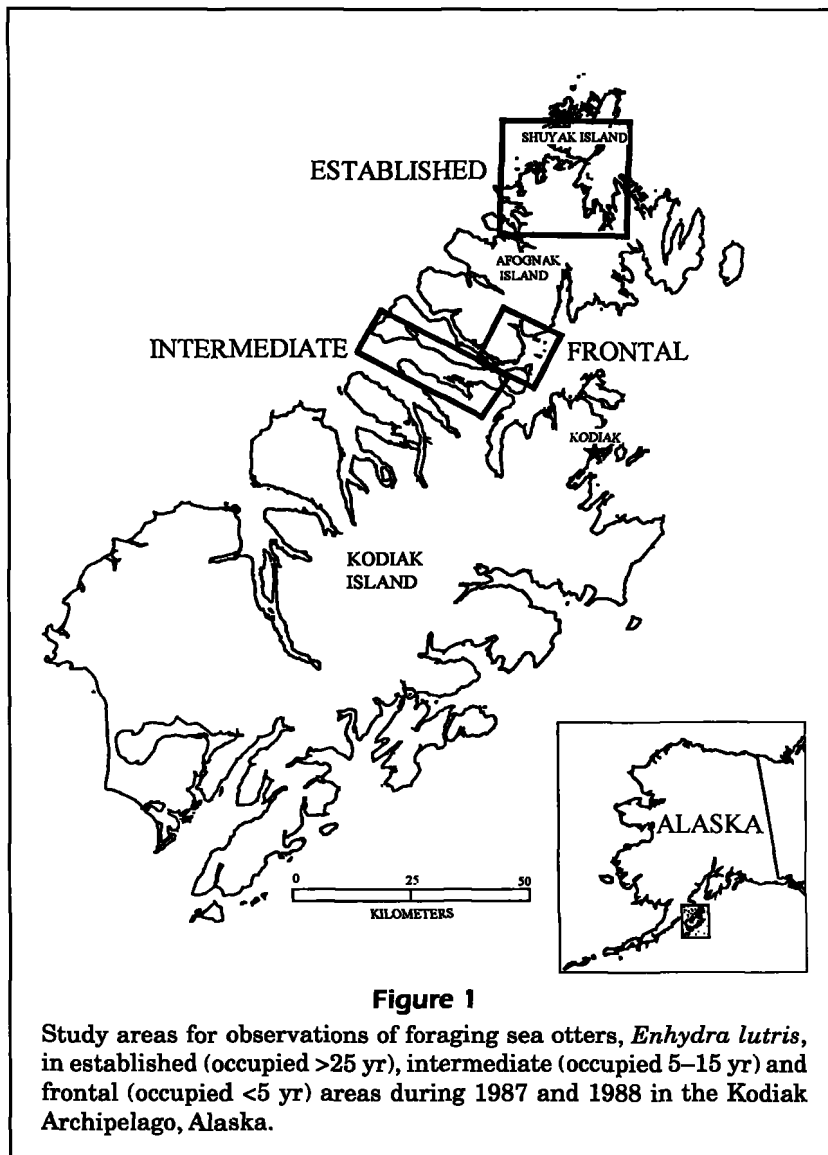
### Study area

Study areas in the Kodiak Archipelago were chosen in regions that differed in the number of years since sea otters had reoccupied the habitat (Fig. 1). We categorized the areas following Kvitek et al. (1992) as established (occupied for >25 years), intermediate (occupied for 5–15 years), and frontal (occupied for <5 years) based on sea otter surveys (Lensink, 1962; Kenyon, 1969; Schneider<sup>1</sup>; Simon-Jackson<sup>2,3</sup>; and interviews with local inhabitants). Established study sites were on southern Shuyak and northern Afognak islands, intermediate study sites were located between southern Afognak and northern Kodiak islands, and frontal study sites were southeast of Afognak and Raspberry islands. Study sites had broad expanses of shallow water (<20 m) with primarily sand and gravel sediments supporting infaunal bivalve assemblages (Kvitek et al., 1992).

### Foraging observations

Observations of foraging sea otters were made from shore with the aid of 10× binoculars and 40–80× telescopes (Questar Corp., New Hope, PA). Foraging data were collected by focal animal sampling (Altmann, 1974). Repeated dives were recorded for a focal animal while the animal remained in view and continued to forage (Calkins, 1978). All observations were made on unmarked animals that were within approximately 1 km of shore. Data were collected during June–October 1987 and during March, June, and September of 1988 during daylight hours and during various tidal states.

Data for each recorded dive included sex and age class of otter, presence of a pup, number of prey items



**Figure 1**

Study areas for observations of foraging sea otters, *Enhydra lutris*, in established (occupied >25 yr), intermediate (occupied 5–15 yr) and frontal (occupied <5 yr) areas during 1987 and 1988 in the Kodiak Archipelago, Alaska.

obtained, identification of prey (classified to lowest possible taxon), and categorization of prey size (small <5 cm, medium 5–9 cm, and large >9 cm). Size class of prey was estimated relative to the mean forepaw width (4.5 cm) and mean skull width (10 cm) for adult sea otters (Johnson<sup>6</sup>). Adult otters were classified as male, female, female with pup, or unknown sex. Juveniles that were estimated to be <2 years of age were differentiated from adults by their small body size (estimated to be <18 kg) and dark pelage. Forage data on pups still associated with their mother were not collected. Forage dives were classified as successful (prey captured), unsuccessful (no prey captured), or of unknown success (observer could not determine if prey were captured).

<sup>6</sup> Johnson, A. M. 1987. Sea otters of Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Alaska Fish and Wildlife Research Center, Anchorage, Alaska. Unpubl. rep., 87 p.

## Data partitioning

A forage record was defined as the forage data specific to a focal animal and was used as the sample unit in comparisons of prey composition, forage success, and the mean number of prey captured per dive. For assessing variation in prey composition and forage success, only forage records containing  $\geq 10$  forage dives were used; adults of unknown sex were deleted in comparisons of sex classes. Sample sizes for juveniles were small and created an unbalanced sample design in 2-way comparisons. Consequently, separate tests were conducted to assess age-class differences.

For comparisons of prey composition, we calculated the proportion of dives resulting in the capture of clams, crabs, and mussels for each forage record. Differences in the proportion of prey items captured by adult sea otters were tested among areas. Sample sizes were insufficient to test prey composition differences among areas for juveniles. Data were pooled from all study areas and the proportion of prey captured was tested by age class.

Forage success (the proportion of successful dives) was normalized by the arcsine transformation of the square root. Differences in forage success among study areas and among adult sex classes (male, female, and females with pups) were tested. Sample sizes were insufficient to test for differences among study areas for juveniles. Data were pooled for all juveniles and all adults to test age differences in forage success.

Number of prey items captured per dive was calculated by dividing the total number of prey captured by the number of forage dives per foraging record and averaging these values by sex class and area. Dives resulting in the capture of mussels (which may be difficult to count) and dives of unknown result were excluded.

We assumed mean shell lengths of 4.0, 7.0, and 10.0 cm were representative of small, medium, and large bivalve size classes, then estimated mean wet-tissue mass of *Saxidomus giganteus* by using the weight-length relationships generated by Kvittek et al. (1992). We estimated caloric gain per dive by using caloric values for this genus reported by Kenyon (1969).

## Data analysis

Kruskal-Wallis nonparametric (1-way) tests were used to assess differences in the proportion of clams, mussels, and crabs captured among study areas by adult sea otters; data were pooled for all study areas and the proportion of clams, mussels, and crabs were tested by age class. Analysis of variance (2-way ANOVA) was used to test 1) differences in forage success among study areas and

adult sex classes, and 2) differences in the mean number of prey captured per forage dive among study areas and adult sex classes. A 1-way ANOVA was used to test differences in the mean number of prey captured per dive among study areas for juvenile sea otters. A Student's *t*-test was used to test differences in forage success between adult and juvenile sea otters for all study areas combined. For all comparisons, significance was set at  $\alpha=0.05$ .

## Results

Sea otters were observed foraging on clams (57–67%), mussels (19–25%), crabs (2–4%) and green sea urchins, *Strongylocentrotus droebachiensis* (0–3%) (Fig. 2). Clams were identified to species in 23% ( $n=535$ ), 65% ( $n=957$ ), and 63% ( $n=1,060$ ) of the observations in established, intermediate, and frontal areas, respectively. The majority of clams identified were *Saxidomus* in established (98%), intermediate (89%), and frontal (96%) areas. Other clams identified (<10% per study area) were *Tresus capax*, *Mya* spp., *Protothaca staminea*, and *Entodesma macroschisma*. *Mytilus* spp. was the most common mussel observed within the study areas. Crabs were primarily *Telmessus* spp.; however, a small number of *Cancer magister*, were recorded. Other prey which contributed from <1 to 7% of the diet in each study area included *Clinocardium* spp., *Cucumaria fallax*, *Echiurus echiurus alaskensis*, *Nucella* spp., *Octopus* spp., *Pisaster* spp., *Pycnopodia helianthoides*, barnacle (class Crustacea), chiton (class Polyplacophora), tunicate

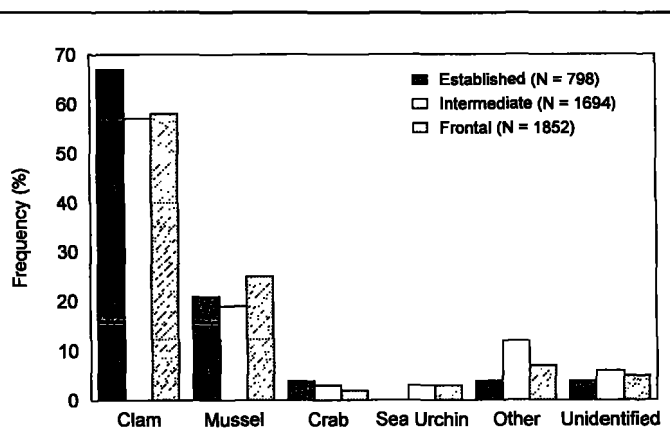


Figure 2

Frequency of occurrence of food items obtained by sea otters, *Enhydra lutris*, as determined by visual observation along the Kodiak Archipelago during 1987 and 1988 in areas of established (>25 yr), intermediate (5–15 yr), and frontal (<5 yr) sea otter forage areas.

(class Ascidiacea), and kelp (primarily kelp hold-fasts with small unidentified invertebrates attached). Unidentified prey constituted 4–6% of prey per area.

The proportion of forage dives resulting in the capture of clams, mussels, and crabs did not differ among study areas for adults. For all study areas combined, adult and juvenile sea otters differed in the proportion of forage dives capturing clams ( $\chi^2=13.35$ ,  $df=1$ ,  $P<0.001$ ) and mussels ( $\chi^2=10.40$ ,  $df=1$ ,  $P=0.001$ ) but not crabs ( $\chi^2=3.22$ ,  $df=1$ ,  $P=0.07$ ). The median proportion of dives resulting in the capture of clams ranged among study areas from 0.62 to 0.85 for adults and from 0.00 to 0.52 for juveniles. Conversely, median values for mussels ranged from 0.00 to 0.93 for juveniles and was zero for adults. Crabs were captured infrequently and the median proportion of dives capturing crabs was zero for both age classes.

Forage success did not differ among study areas ( $F=0.52$ ,  $df=2$ ,  $P=0.59$ ) nor among sex classes ( $F=2.22$ ,  $df=2$ ,  $P=0.12$ ) within areas for adults; the interaction between sex class and area was not significant ( $F=0.50$ ,  $df=4$ ,  $P=0.74$ ). Mean forage success for all study areas combined was 89% for adults and 90% for juveniles and did not differ significantly ( $t=-0.59$ ,  $df=107$ ,  $P=0.56$ ) (Table 1).

Mean number of prey captured per dive by adults in established, intermediate, and frontal areas differed among areas ( $1.6\pm 1.0$ ,  $1.1\pm 0.4$ , and  $1.2\pm 0.8$ , respectively) ( $F=3.88$ ,  $df=2$ ,  $P=0.02$ ) but not among sex class ( $F=0.98$ ,  $df=2$ ,  $P=0.38$ ); the interaction between sex class and area was not significant ( $F=1.00$ ,  $df=4$ ,  $P=0.41$ ). Juvenile sea otters, did not differ in the mean number of prey captured per dive among study areas ( $F=0.55$ ,  $df=2$ ,  $P=0.59$ ) (Table 1).

In the established area, 92% ( $n=526$ ) of the clams captured by sea otters were small (<5 cm), and 8% were medium (5–9 cm). In intermediate and frontal areas, however, only 27% ( $n=943$ ) and 38% ( $n=1,039$ ) of all clams captured were small and the majority were medium sized. The mean caloric content of *Saxidomus* captured by adult otters per forage dive in established, intermediate, and frontal areas was estimated to be 10 kcal, 21 kcal, and 21 kcal, respectively (Table 2).

## Discussion

The composition of the diet was similar for sea otters in the Kodiak Archipelago among forage areas

Table 1

Summary of foraging success and mean number of prey items per dive for juvenile and adult sea otters, *Enhydra lutris*, along the Kodiak Archipelago in established (occupied >25 years), intermediate (occupied 5–15 years), and frontal (occupied <5 years) areas.

Study area	Age and sex	No. of forage records	No. of dives	Mean % successful dives	Mean no. prey items per dive <sup>1</sup> ± SD
Established	Juvenile	3	30	83	1.0 ± 0.5
	Adult male	6	59	83	1.3 ± 0.8
	Adult female	4	63	96	2.1 ± 1.4
	Adult female w/pup	12	136	97	1.8 ± 0.9
	Adult unknown	9	93	97	1.4 ± 0.3
	Total	34	381		
Intermediate	Juvenile	16	223	93	1.0 ± 0.6
	Adult male	19	239	89	1.1 ± 0.6
	Adult female	27	343	78	1.0 ± 0.4
	Adult female w/pup	28	349	93	1.2 ± 0.4
	Adult unknown	8	92	86	1.1 ± 0.4
	Total	98	1,246		
Frontal	Juvenile	13	146	88	1.2 ± 0.6
	Adult male	25	296	96	1.4 ± 1.3
	Adult female	24	369	86	1.1 ± 0.4
	Adult female w/pup	14	272	96	1.3 ± 0.7
	Adult unknown	4	69	84	1.0 ± 0.03
	Total	80	1,152		

<sup>1</sup> Dives resulting in the capture of mussels, *Mytilus* spp., and dives of unknown result were not used in calculating mean number of prey per dive.

Table 2

Frequency and estimated biomass of *Saxidomus giganteus* retrieved per dive by adult sea otters, *Enhydra lutris*, in established (occupied for >25 years), intermediate (occupied 5–15 years), and frontal (occupied <5 years) study areas along the Kodiak Archipelago, Alaska, 1987–1988.

Study area	Size class (mm)	Proportion in sample	Mean number of prey/dive	Estimated wet-tissue weight obtained/dive (g) <sup>1</sup>	Estimated caloric content (kcal)
Established	<50	0.83	1.6	16	10
	50–90	0.17			
Intermediate	<50	0.18	1.1	33	21
	50–90	0.71			
	>90	0.11			
Frontal	<50	0.28	1.2	33	21
	50–90	0.62			
	>90	0.10			

<sup>1</sup> Wet-tissue weight =  $2.14 (10^{-4})(\text{shell length})^{2.78}$ ;  $r^2 = 0.86$  for *Saxidomus giganteus* where shell lengths equal 40, 70, and 100 mm representing small, medium, and large size classes, respectively (Kvitek et al., 1992).

irrespective of the number of years the habitat had been occupied by sea otters. Clams, particularly *Saxidomus*, were the predominant prey identified in all study areas, although 35–77% of the clams were not identified to species. Green sea urchins were absent in the diets of sea otters in established areas but were found, infrequently, in the prey composition in intermediate and frontal areas. Sea urchins were apparently locally abundant in intermediate and frontal areas prior to the initiation of our study (Kvitek et al., 1992; Stanford and Cunningham<sup>7</sup>). Sea urchin abundance had been reduced to low levels by sea otter predation in other regions of Alaska and in California (Lowry and Pearse, 1973; Estes et al., 1978; Laur et al., 1988; Kvitek et al., 1989) and it is likely that sea otter predation affected urchin populations in the Kodiak Archipelago.

Juvenile sea otter diets contained a higher proportion of mussels than that of adults. A higher occurrence of mussels in the diet of juveniles than of adult sea otters has also been demonstrated by other studies conducted in Alaska (VanBlaricom, 1988; Doroff and Bodkin, in press; Johnson<sup>6</sup>). Mussels are an easily obtainable intertidal prey, and young sea otters may rely on mussels as a food source until they become more proficient foragers (Estes et al., 1981; VanBlaricom, 1988).

Sea otters at Kodiak were highly successful in securing prey, even where prey had been reduced by years of otter predation (Kvitek et al., 1992). Therefore, forage success was not a useful criterion for discriminating among study areas that varied in the

duration of sea otter occupancy. For sea otters, forage success may vary with prey type, hunting tactics, or locality (Ostfeld, 1991) and may not be related to prey abundance or biomass (Estes et al., 1981). Ostfeld (1991) suggested, however, that forage success is a useful means of comparing forage strategies and habitat characteristics for sea otters. The lack of variation in forage success among our study areas may have resulted, in part, from similarities in habitat (Kvitek et al., 1992). Kruuk et al. (1990) recommended caution in defining and using the concept of forage success on a per dive basis and suggested that a more meaningful approach would be to examine the biomass captured per unit of effort.

We estimated the average biomass and subsequent caloric value captured on a per dive basis for sea otters. Sea otters foraging in habitat occupied an estimated 1–15 years obtained approximately twice the biomass of otters foraging in habitat occupied >25 years. This suggests that sea otters foraging in long-occupied habitat may need to compensate for reduced prey size and abundance through increased allocation of time for foraging to meet minimum daily caloric requirements (Costa, 1978; Estes et al., 1982; Estes et al., 1986; Garshelis et al., 1986). Biomass and caloric values were similar for intermediate and frontal areas. Possible explanations for the lack of disparity between intermediate and frontal areas are 1) preexisting habitat differences among study areas, 2) resilience of *Saxidomus* to sea otter predation over the short term (see Kvitek et al., 1988), or 3) an error in the classification of study areas.

We made the assumption that observed differences in foraging characteristics resulted primarily from

<sup>7</sup> Stanford, S., and W. Cunningham. Bare Island, Port Bailey, AK 99615. Personal commun., June 1987.

sea otter predation. There were likely preexisting differences in the community structure among our study areas that were not assessed, such as the distribution and abundance of bivalve species prior to sea otters re-occupying the study areas. However, we believe that comparisons of study areas are valid given the similarities in habitat and infaunal invertebrate assemblages among study areas documented by Kvitek et al. (1992).

*Saxidomus* may appear resilient to sea otter predation pressure over the short term because it is present in high densities in our study areas (Kvitek et al., 1992). *Saxidomus* was found in higher densities than was any other forage species and it was selected preferentially (based on differences between in situ population of clams and the shells discarded by foraging otters) in intermediate and frontal areas (Kvitek et al., 1992). *Saxidomus* was also the most abundant clam (in situ) in the established area; however, *Protothaca* was selected preferentially (Kvitek et al., 1992). *Protothaca* was not identified visually as sea otter prey in the established area; however, only 23% of the clams could be identified to species.

We believe the classification of our study areas and those used by Kvitek et al. (1992) were correct; however, our methods lacked the refinement needed to distinguish between intermediate and frontal areas. Kvitek et al. (1992) was also unable to detect differences between the intermediate and frontal areas by measuring prey size directly from the shells of clams consumed by sea otters. However, there were differences in the size of the in situ population of clams between areas (Kvitek et al., 1992). Newly exploited habitat in our study was represented by an area estimated to have been occupied 1–4 years by sea otters. Rapid changes may occur within the first year that sea otters occupy unexploited habitat. Garshelis et al. (1986) observed an approximate twofold decrease in kcal/dive in areas occupied by sea otters  $\leq 1$  year compared with areas occupied 1–2 years. Coincident with the change in kcal/dive was a shift in prey from crabs to clams between areas studied by Garshelis et al. (1986). In the Kodiak Archipelago, we did not observe differences in mean kcal/dive or changes in prey composition between intermediate and frontal areas. Changes in prey composition, such as the potential removal of green sea urchins from the study area, may have occurred in the frontal area during the first year and were undetected.

Adult sea otters in the established area appear to have compensated for reduced prey size by retrieving more prey items per dive. However, they still obtained less clam biomass (and subsequently less caloric intake) per dive than otters in the intermediate and frontal areas, suggesting that they may need

to forage longer to meet minimum daily caloric needs. Interestingly, juveniles in established areas did not appear to compensate for reduced bivalve prey size by increasing the number of prey captured per dive. Juveniles may be less efficient foragers and may compensate by increasing their consumption of *Mytilus* spp., which are an easily obtainable intertidal prey (Estes, 1981; VanBlaricom, 1988; Doroff and Bodkin, in press).

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