Sea Otter (*Enhydra lutris*) Prey Composition and Foraging Success in the Northern Kodiak Archipelago

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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 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.

Key words: Alaska, bivalve, Enhydra lutris, foraging, Kodiak, Saxidomus giganteus, sea otter

Introduction

The Kodiak archipelago in south-central Alaska (Figure 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[4]). During the late 1950's through mid 1980's episodic range expansion occurred throughout the northern Kodiak archipelago (Schneider[4], Simon-Jackson et al. [5,6], Lensink 1962).

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 due 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) (Miller et al.[3], Stephenson 1977). In Alaska, sea otters impacted the recreational and commercial fisheries for Dungeness crab (Cancer magister) in Prince William Sound (Kimker[2], Garshelis 1983, Garshelis et al. 1986).

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 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 (Figure 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 (Schneider[4], Simon-Jackson[5,6], Lensink 1962, Kenyon 1969, and interviews with local inhabitants). Established study sites were on southern Shuyak and northern Afognak islands, intermediate study sites were 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 using 10X binoculars and 40X-80X telescopes (Questar Corp., New Hope, PA). Foraging data were collected using 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 which 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 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[1], U.S. Fish and Wildlife unpublished data, Anchorage, AK 99503). Adult otters were classified as male, female, female with pup or unknown sex. Juveniles which 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 was not collected. Forage dives were classified as successful (prey captured), unsuccessful (no prey captured), or unknown success (observer could not determine if prey were captured).

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 when comparing 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 were tested by age class.

Forage success (the proportion of successful dives) was normalized by an 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 Kvitek *et al.* (1992). We estimated caloric gain per dive 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 equals 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%) (Figure 2). Clams were identified to species in 23% (n = 535), 65% (n = 957), and 63% (n = 1060) 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 Telemessus 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 (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 ($X^2 = 13.35$, df = 1, $P < 0.001$) and mussels ($X^2 = 10.40$, df = 1, $P = 0.001$) but not crabs ($X^2 = 3.22$, 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 = 1039) 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 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 did occur, 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 (Stanford and Cunningham[7], pers. comm., Kvitek _et al_. 1992). Sea urchin abundance had been reduced to low levels by sea otter predation in other regions of Alaska and in California

(Estes et al. 1978, Lowry and Pearse 1973, Laur et al. 1988, Kvitek et al. 1989) and it is likely 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 for adult sea otters has also been demonstrated by other studies conducted in Alaska (Johnson[1], VanBlaricom 1988, Doroff and Bodkin 1994). 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 criteria to discriminate among study areas which 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 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 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) pre-existing 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 sea otter predation. There were likely pre-existing 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 occurs in high densities in our study areas (Kvitek *et al*. 1992). *Saxidomus* occurred in higher densities than any other forage species and 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 as sea otter prey in the established area by visual observation, 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) was 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 sea otters occupy unexploited habitat. Garshelis *et al*. (1986) observed an approximate 2-fold decrease in kcal/dive from areas occupied by sea otters $\leq$1 year to 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 may have occurred in the frontal area during the first year which were undetected, such as the potential removal of green sea urchins from the study area.

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 they may need to forage longer to meet minimum daily caloric needs. Interestingly, juveniles in established areas did not appear to compensate for reduced prey size by increasing the number of prey captured per dive. Juveniles may be less efficient foragers and compensate by increasing their consumption of *Mytilus* spp., which are an easily obtainable intertidal prey (Estes 1981, VanBlaricom 1988, Doroff and Bodkin 1994).

Acknowledgments

We thank Larry Barnes, John Baird, Elizabeth Belantoni, Walt Cunningham, Dave Douglas, Dan Monson, Jay Nelson, Doug Sheperd, Annetta Smith, Susan Stanford and Shelli Vacca for assistance with data collection. Walt Cunningham and Susan Stanford graciously hosted us at their home on Bare Island. Logistic support was provided by Jay Bellinger and staff of the Kodiak National Wildlife Refuge and Al Bayer and the crew of the M\V Tiglax. Shelli Vacca and especially Bob Stehn provided computer support. For reviewing drafts of this manuscript, we thank Brenda Ballachey, Edward Bowlby, James Bodkin, Dan Esler, Dave Garshelis, Rikk Kvitek, and three anonymous reviewers.

Footnotes

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Figure 1. - Study areas for observations of foraging sea otters (*Enhydra lutris*) in established (occupied > 25 yrs), intermediate (occupied 5-15 yrs) and frontal (occupied < 5 yrs) areas during 1987 and 1988 in the Kodiak archipelago, Alaska.

Figure 2. - Frequency of occurrence of food items obtained by sea otters (*Enhydra lutris*), as determined by visual observation along the Kodiak archipelago during 1987-1988 in areas of established (> 25 yrs), intermediate (5-15 yrs) and frontal (< 5 yrs) sea otter forage areas.