Journal of Marine Animals and Their Ecology

Vol 3, No 1, 2010
Printed in Canada

Southern sea otter diet in a soft sediment community

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Abstract

Between August 2006 and February 2009, we investigated southern sea otter foraging in Elkhorn Slough, the third largest estuary in California and an important soft-sediment community for sea otters. Our study is the first peer-reviewed comprehensive account of sea otter diet in Elkhorn Slough since the 1990s and the first to look at sea otter scats in addition to visual observations. Diet and other foraging parameters were determined during 199 daytime focal observations and by collecting 115 scat samples. Foraging success was 69%, males being more successful than females. Diet included more than 21 prey items. Nineteen are found within the study area, making this the widest variety of prey items reported taken by sea otters in a soft-sediment community. Daytime prey included 78.2% *Mollusca* (clams and mussels), 11.2% *Echiurida* (inkeeper worms), 2.8% *Arthropoda* (crabs) and 7.8% undetermined prey. Scat samples contained a wider variety of prey than focal samples. Four species of crabs found in scat samples but seen during focal observations, suggest otters may also be feeding outside of the study area or feeding within the study area at night. Both prey pursuit and handling time increased with prey size but depended on prey type. Sea otters exhibited a high degree of prey specialization, most individuals being highly specialized on clams (91%). Most prey items obtained were ≤5 cm long, suggesting otters rely on greater availability or on ease of capture of this size class. [JMATE. 2010;3(1):27-36]

Keywords: California, foraging, ecology, feeding, Elkhorn Slough

Introduction

Sea otters depend on the availability of a diversity of prey items to maintain their high metabolic requirements (8, 9, 10, 12, 14 16, 29) and must consume a minimum of 25% of their body weight each day to survive (5, 11, 31, 32, 36). Their feeding behavior exerts considerable foraging pressure on benthic habitats (6, 7, 16, 31).

Although the role of sea otters as a keystone species (*sensu* 30) in rocky bottoms is well documented (9, 10), the impact of predation by sea otters in soft-bottom communities is less clear (21, 22, 23, 24, 25, 26). Deep-burrowing species appear to withstand substantial predation before declining (25).

In Monterey Bay's rocky bottom habitats, otters dive deeper and longer than the average for sea otter populations, spending up to 43% of their time feeding over a 24-hour period (33, 34, 35), which may support the hypothesis that Monterey Bay is a food-limited habitat for sea otters (35). However, soft-bottom communities in Monterey Bay, and Elkhorn Slough, a seasonal estuary at the heart the Bay, have received less attention.

Between 2006 and 2009, up to about 200 sea otters have been documented in Elkhorn Slough during a given day (Maldini unpublished data), suggesting this is an important area for the California population, which has been last estimated at approximately 2,600 individuals (USGS unpublished data). The Elkhorn Slough is unique because of its abundance of soft-bottom benthic invertebrates, its protected waters, and its lack of sea otter predators. Sea otters have been using the mouth of the Elkhorn Slough in small numbers since 1984 (1) and first moved into its upper channels in 1995 (13). The Elkhorn Slough is a core non-territorial male area at its mouth, with numbers ranging between two and 143 sea otters (53 on average) found within a single raft, depending on time of day (Maldini unpublished data). The Elkhorn Slough's main channel is a mosaic of food-rich male territories used by an average of 30 otters (mainly females and pups). Pupping occurs year-round (Maldini unpublished data). This study provides recent evidence of foraging patterns and prey preferences of sea otters in Elkhorn Slough as an invertebrate-rich, soft-bottom community in Monterey Bay. This is the first peer-reviewed comprehensive account of sea otter diet in Elkhorn Slough since the 1990s and the first to look at sea otter scats in addition to visual observations.

Received May 6, 2010; Accepted July 17, 2010
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Methods

Study Area

Elkhorn Slough is the third largest of California's estuaries (3). Designated a National Estuarine Research Reserve (NERR), it stretches 11 km eastward from Moss Landing Harbor (Figure 1). Our study area covered approximately 0.6 km^2 (0.2 km wide and 3 km long), stretching from the mouth of Moss Landing Harbor to Seal Bend (Figure 1), including mainly a non-territorial male area where females occasionally travel through to feed or rest. It is the area with the highest sea otter density within the slough (20). Moss Landing Harbor has a maximum depth of 15 m. The slough's main channel begins at the Highway One Bridge and stretches approximately 1 km east to Seal Bend (Figure 1). The channel is approximately 100 m wide at its widest point. Its depths range 1-7.5 m at Mean Lower Low Water (3). The bottom throughout Elkhorn Slough is soft mud with dense eelgrass beds (*Zostera marina*) in the shallower waters near Seal Bend. However, there are areas that feature hard substrate such as riprap, stone bridges, docks and drainage pipes, providing habitat for a variety of invertebrate assemblages (550 species and 16 phyla were reported (3)). The slough is mostly influenced by wind and tidal flux.

Data Collection

Observations were conducted between dawn and dusk, August 2006 to March 2009. Focal animals were observed from one of five shore vantage points (Figure 1) and the upper channel of the slough was sampled from a stationary vessel because there was no easy access to shore-based observation sites. Starting time and location of observations was randomly computer-generated and covered a variety of tidal conditions. Observations were conducted using Canon 10x30 Image-Stabilized binoculars and a Nikon Fieldscope ED82. The observer called observations to a data recorder to avoid losing sight of the focal animal.

All six observers participating in the study became acquainted with the study area before starting observations and were trained to recognize prey items potentially available to sea otters. We used type specimen of each prey item collected in the area, field guides and supervised observation periods to familiarize the observers with the prey and the protocols.

Focal-Animal Observations

Focal-animal observations during foraging bouts were used to determine diet composition, dive times, pursuit time, prey preferences, prey size, foraging success, and handling time. A foraging sea otter was located by scanning the study area. Unless only one forager was located, the closest sea otter to the observation point was selected for focal observation to maximize opportunities for prey identification. There are a number of flipper-tagged animals in the slough because of research, and rehabilitation efforts (28). Some of these animals were used in our focal observations and never re-sampled. We did not preferentially select animals bearing a tag, and always used the previously described method to select focal animals. Sea otters bearing no identifiable mark had a potential for being re-sampled during the study. We believe this potential was mitigated by the time span of the study (five years) and by using multiple vantage points for observations. In addition, non-territorial males in California make extensive movements along the coastline (18) and there is an influx and efflux of individuals using Elkhorn Slough over days, months, and years. Furthermore, the number of sea otters using the area during the study period averaged 53 animals during the daytime (Maldini unpublished data), making it less likely to select the same individuals for focal observations. Foraging behavior was continuously observed until the otter moved out of sight or stopped foraging. However, some potential for observing individuals multiple times remains.

Observations were continued for as long as the animal was in sight and clearly visible. Focal sessions were discontinued if: 1) the animal moved beyond the range at which reliable observations could be recorded, 2) the otter was not relocated after 15-min of search effort, or 3) the focal animal could not be reliably followed. Time at the last reliable surfacing was the end of the focal observation period.

For each focal individual, sex, presence of pup, age-class, and dive and surface intervals were recorded. Sex was determined by the presence/absence of a penile bulge, vulva, nipples, or pup. Age-class (either juvenile or adult) was estimated using body size, relative amount of grizzling (i.e., white fur) (15), and appearance of the vibrissae (short and stubby in juveniles).

Diet Composition

All observers were trained to recognize typical prey items present in Elkhorn Slough using type specimen collected in the area. A collection of specimen and prey parts was available for close examination and comparisons. Prey type during visual observations was identified to the lowest *taxon,* or marked as unknown if observations were unreliable because of distance, glare, or otter behavior.

Scat samples were collected at dawn on North Harbor Beach (36.81°N, 121.78°W; Figure 1), part of the same non-territorial male area where focal observations were conducted. Here, up to 95 sea otters regularly haul-out to rest during the night (Maldini unpublished data). This is the center of the non-territorial male area, although several females occasionally transit within it. Fresh scats were collected directly into a zip-lock plastic bag and labeled with date, time, and sample number. All scats found on the beach were collected. To minimize the possibility of re-sampling scats from the same individual, scat collection was spaced in time. Scats were collected at first light after otters hauled-out on the beach had been monitored and counted, so that the position of animals on the beach was known. Up to 95 sea otters haul-out on this beach at the same time (Maldini, unpublished data).

Samples were washed and sieved through a 3-mm mesh onto a tray for sorting. All visible prey parts were classified to the lowest *taxon* by closely examining them using a dissecting scope.

Differences in diet composition among years and sexes were assessed using Chi-Square statistics with α=0.05 for both scats and focal data.

Foraging Success, Pursuit Time, Handling Time and Prey Size

Foraging success was the proportion of successful to total dives during foraging observations. Differences in foraging success between sexes were determined using a Yates corrected z-test with α=0.05.

Pursuit time was calculated as the sum of the lengths of all unsuccessful dives completed before a prey item(s) was obtained. Handling time was calculated as the length of time spent at the surface consuming the same prey item(s). Prey size was visually estimated using the maximum length in relation to the size of an average sea otter paw (5 cm) (2, 24) and binned into one of the following size categories: ≤5 cm, 5.1<x≤10 cm, 10.1<x≤15 cm, >15 cm.

Figure 1 *– Map of the study area showing the mouth of Elkhorn Slough, the entrance of Moss Landing Harbor, and the main channel of the slough up to Seal Bend. The two white-dotted lines mark the borders of the study area, the red dots mark the position of the shore-based observation sites, and the gray area in the upper channel marks the general location of vessel-based observation.*

The statistical significance of the relationship between pursuit time and prey size, and between handling time and prey size was determined using Kruskal Wallis non-parametric statistics with Dunn's Multiple Comparisons Tests. Prey type was not added to these statistical comparisons because of the unbalanced design of the dataset caused by low sample size or because of missing categories for a particular prey type. We therefore elected to look at the trend graphically to not over-interpret the results. We used the following prey-type categories: clams, crabs, echiurids (innkeeper worms) and mussels. Each of these prey types is either a burrower (*i.e.*, clams and echiurids), epibenthic (*i.e.*, crabs) or sessile (*i.e.*, mussels) and has different handling requirements and caloric contents (19).

Dietary Specialization

The degree of dietary specialization was calculated using the Simpson's Diversity Index for broad categories of prey (*i.e.*, clams, mussels, crabs, and innkeeper worms) as follows:

$$D=1-\Sigma(ni/N)2$$

where, for each sea otter, ni is the number of individuals captured in each prey category and N is the number of prey items captured. The coefficient is a number from zero to one, zero indicating the highest level of specialization. Sea otters with a D≤0.3 were considered specialists, those with a 0.31<D≤0.6 were considered selective and those with a 0.61<D≤1 were considered generalists.

Results

From August 2006 to February 2009, 199 daytime focal observations (48 in 2006, 84 in 2007, 62 in 2008 and 5 in 2009) of foraging sub-adult and adult sea otters (12 on females, 134 on males, and 53 on unknown sex) were conducted in Elkhorn Slough. Sampling was considerably skewed toward males because the study area is a non-territorial male area and there are few females. No foraging mother/pup pairs were observed during the study.

Diet Composition

We recorded 3,098 prey items during 3,570 dives. We also identified 302 prey items in 115 scat samples. Prey items belonged to four Phyla, five Classes, five or more Orders, 15 Families, 17 Genera, and at least 21 species (Table 1). At least 12 species were recorded during focal-animal observations, whereas scat samples included ≥18 species (Table 1).

Frequency of occurrence and composition of prey was different between focal and scat samples underscoring the importance of both approaches to understanding sea otter diet (Figure 2). The frequency of occurrence of prey items observed during focal observations was 78.2% *Mollusca* (with clams 74.4% and mussels 3.8% respectively), 11.2% *Echiurida* (innkeeper worms), 2.8% *Arthropoda* (crabs) and 7.8% unidentified prey. The frequency of occurrence of prey items found in scat samples was 34.6% *Mollusca,* 59.5% *Arthropoda*, 5.6% *Echinodermata* (only sand dollars, *Dendraster excentricus*), and 0.3% unidentified.

Scat samples had a higher proportion of crab components than focal samples, and contained nine species not observed during focal observations (Table 1). Six species of crabs in the scats and the moon snail, *Polinices lewisii* are found both in the slough and in adjacent open waters. The other species in the scat, the sand dollar and the sand crab, *Emerita analoga,* are only found in adjacent open waters. At least 21% of scat samples contained these two prey types.

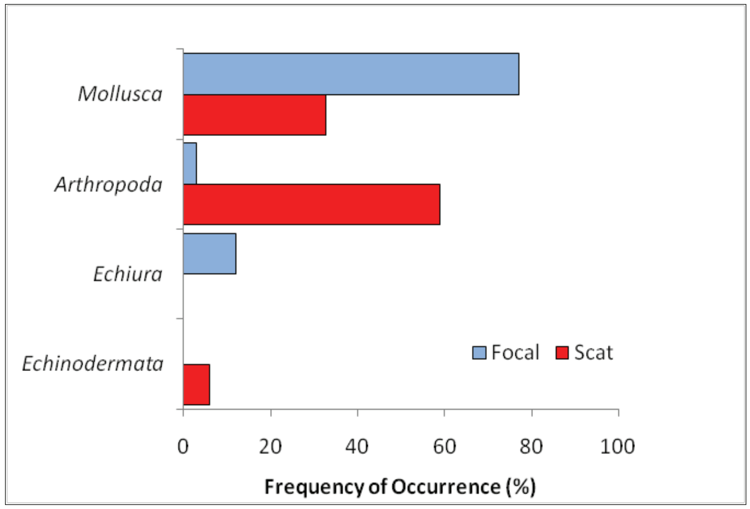

Figure 2 *- Frequency of occurrence of sea otter prey items (divided by Phylum) in focal and scat samples collected in Elkhorn Slough, California.*

Focal observations had a greater proportion of bivalves (77%) than scat samples (32%). Large clams were found only during focal sampling, while mussels and small, thin-shelled clams were more common in scat samples. In fact, sea otters tend to eat only the soft parts of large clams, while they crush and chew mussels and small clams, therefore ingesting their shells. Sea otters eat small clams and mussels fast, making them harder to detect during visual observations. Small clams are likely a large portion of unidentified prey items.

The main prey items were bivalves such as small clams (*Macoma* spp.), large clams (*Saxidomus nuttallii* and *Tresus nuttallii*) and mussels (*Mytilus californianus* and *M. galloprovincialis*), fat-innkeeper worms and several species of crab (Table 1). Diet composition varied significantly among years (χ=294.629, DF=6, P≤0.001), but 2009 was excluded from the analysis because there were only five sessions. Mussels were more common and clams less common than statistically expected in 2006, mussels and fat innkeeper worms were less common than statistically expected in 2007, and fat innkeeper worms were more common in 2008 (Figure 3).

Both females and males preferred clams (65% and 83% respectively), however their preference differed

Phylum	**Class**	**Order**	**Family**	**Species**	**Focal Obs %**	**Scat Samples %**
Mollusca	*Bivalvia*	*Veneroida*	*Veneridae*	*Saxidomus nuttallii*	13.2	0.3
				Protothaca staminea	0.8	0.8
			Mactridae	*Tresus nuttallii*	15.9	0.8
			Cardiidae	*Clinocardium nuttallii*	0.3	10.9
			Tellinidae	*Macoma* spp.	36.8	3.2
			Myidae	*Mya* spp.	0.5	-
			Mytilidae	*Mytilus* spp.	7.5	12.5
			Pharidae	*Siliqua* spp.	0.1	-
	Gastropoda		*Naticidae*	*Polinices lewisii*	-	0.8
Echiura				*Urechis caupo*	23.3	-
Echinodermata	*Echinoidea*	*Clypeasteroida*	*Dendrasteridae*	*Dendraster excentricus* (*)	-	6.9
Arthropoda	*Malacostraca*	*Decapoda*	*Cancridae*	*Cancer magister*	1	2
				Cancer antennarius	-	12.5
				Cancer anthonyi	-	0.8
				Cancer gracilis	-	6.5
				Cancer productus	-	2
			Portunidae	*Carcinus maenas*	0.1	2
			Grapsidae	*Pachygrapsus crassipes*	0.3	2.4
			Varunidae	*Hemigrapsus oregonensis*	-	0.8
			Epialtidae	*Pugettia producta*	-	0.8
			Hippidae	*Emerita analoga* (*)	-	2

Table 1 *- Sea otter diet composition in Elkhorn Slough derived from the analysis of focal-animal observations and scat samples. Species indicated with (*) are not found within Elkhorn Slough but are typical of shallow-water sandy-bottoms along the coastline of Monterey Bay.*

significantly ($\chi 2$=336.321; df=3; p=<0.001) for innkeeper worms and mussels, as males favored the former (12%) and females the latter (29%). Diving depths were comparable because all observations were taken in the same areas, and no females observed had pups.

Foraging Success, Pursuit Time, Handling Time and Prey Size

Dive times ranged between 1 sec and 5 min. Of the 3,570 dives recorded, 69% were successful in obtaining prey. We observed 2,476 dives for males, 320 for females, and 774 for individuals of unidentified sex. Success rate, calculated as average number of successful dives per focal session, was significantly different between sexes (Yates corrected, z=3.211; p=0.001), with males being more successful than females.

Pursuit time was significantly shorter for the smallest size category (≤5 cm) as compared to all other size categories (Kruskal Wallis on Ranks: H=33.569; df=3; p=≤0.001 with Dunn's Multiple Comparisons). Handling time was also significantly shorter the smaller the prey size, and all size categories were significantly different in handling time (Kruskal Wallis on Ranks: H=163.3; df=3; p=≤0.001 with Dunn's Multiple Comparisons). For clams, which had a large sample size (n=1503) and therefore influenced the statistical results, both pursuit time and handling time were shorter the smaller the clam (Figure 4). For crabs and mussels, which had low sample sizes (n=76 and n=51 respectively), the pattern showed variation, and for echiurids (n=248), pursuit time decreased with larger size and handling time was similar for all size categories (Figure 4).

Most prey items, independently of type, were ≤ 5 cm long (52%), 30% were 5.1<x<10 cm, 12% were 10.1<x≤15 cm and 7% were ≥ 15 cm long. The most frequently observed clam size was ≤ 5 cm. In fact, most clams caught by sea otters in the slough were of the genus *Macoma* (35%), which reaches maximum sizes of 7.5-12 cm, depending on the species (4). Only two species of clams, Pacific gaper and California butterclam, and one species of crab, the dungeness, reach lengths ≥ 15 cm (4). This size category represented only 5% of clams and 1% of crabs in the diet. Only echiurids (*i.e.*, innkeeper worms) were evenly distributed among size categories (Figure 5).

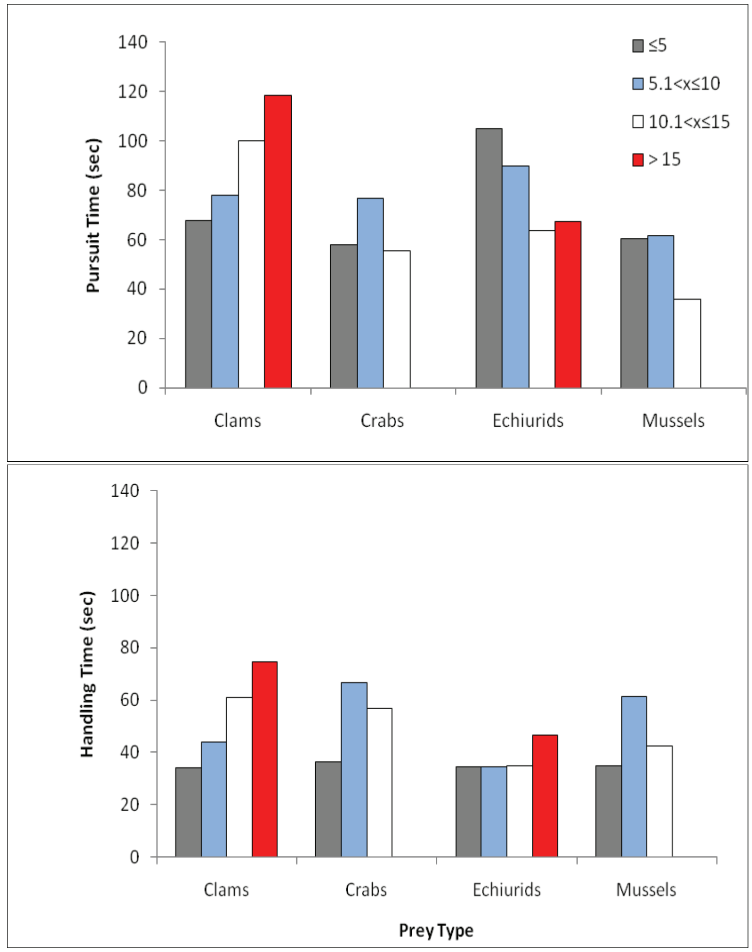

Figure 4 *- Average pursuit time and handling time (expressed in seconds) for the main four prey types eaten by sea otters in Elkhorn Slough, California, divided by size categories.*

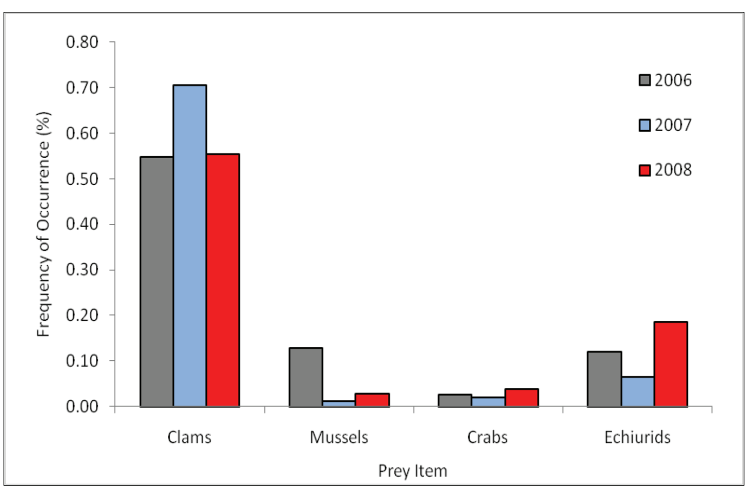

Figure 3 *– Variations in yearly occurrence of the major prey items documented during daytime sea otter focal-animal observations in Elkhorn Slough, California in the period 2006-2008.*

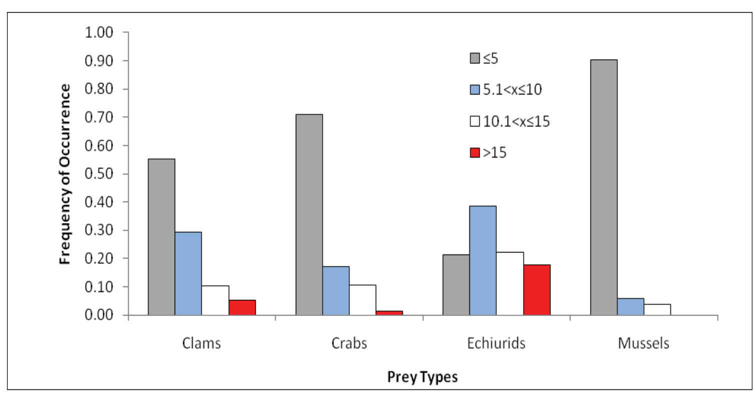

Figure 5 *– Frequency of occurrence of four size classes for the four main sea otter prey items in Elkhorn Slough, California.*

Dietary Specialization

The degree of dietary specialization was calculated for 158 individual sea otters. Most sea otters (46%) tended to fit into the 'specialist' category, generally feeding on a single prey type, while most others were considered 'selective', feeding mostly on two. Very few (9%) were generalists, feeding on three or four prey types in one feeding bout. The preferred prey by specialists was clams (91.5%).

Discussion

Our study documented a wider variety of prey items consumed by sea otters in Elkhorn Slough than previously reported. Jolly (19) found sea otters consumed at least 10 species as compared to the ≥ 21 species documented in this study. Our study relied mostly on scat samples to detect additional prey items demonstrating that both methods combined (visual and scat samples) are a powerful tool. Large clams went mostly undetected in scat samples because sea otters discarded their shells. However, large clams are easy to observe visually. Innkeeper worms are only detectable in scats by careful sieving with a fine mesh to isolate their hard-mouth-parts (missed by our sampling), but are easy to detect and recognize during focal observations. Small and medium sized clams and mussels are easily detectable in scats. Otter paws obscure them during focal observations causing their classification as unidentified prey items. Conversely, crabs are easily identifiable during both visual observations and in scats, but scats allow easier distinction to species.

Clams and innkeeper worms made up the bulk of the daytime-diet. Diet preference has remained consistent over time since the 1980s when the first studies of sea otter diet in the slough were undertaken (13, 19, 21). Innkeeper worms are considered the most abundant prey available in the slough and clams are considered very abundant (3). However, current density estimates in Elkhorn Slough are not available for any of the prey items.

Our study found a sizeable difference in the frequency of occurrence of crabs in visual observations versus scat samples. All our scat samples were collected fresh at dawn. We therefore hypothesize crabs are primarily eaten at night or eaten during the day by otters not foraging in the slough but coming back to rest here. However, all the species of crab seen in the scat samples are found in the slough, and shore crabs (*Pachygrapsus crassipes* and *Hemigrapsus oregonensis)* are particularly abundant (3). However most species of crabs found in scats are common both in open water and in the slough.

If sea otters prey on these species of crabs inside the slough, this is the first time this has been documented. Previous studies only reported *Cancer* spp. (19) as prey items in the slough. However, these studies reported a high proportion of prey items classified as unidentified that could have been crabs (19). Wilkin (37) made nighttime focal observations of feeding sea otters in Elkhorn Slough and documented a preference for crabs over other prey items commonly taken during the daytime. Because crabs are epifaunal and more active at night (27), sea otters may be more likely to detect them by touch while foraging at night (17). Crabs have a higher caloric content than most prey items, lending support to the possibility that nighttime foraging would be advantageous to sea otters and may make up a large portion of the total foraging activity budget.

Despite an increase in the number of animals using Elkhorn Slough (Maldini unpublished), sea otter predation pressure on invertebrate communities here may not have changed significantly since the first sea otter invasion of the main channel in 1995 (13). In fact, average prey-capture success rate (69%) was comparable to earlier studies (19, 21) suggesting Elkhorn Slough is an area where prey availability has remained consistent over time.

However, the quality and/or size distribution of prey items might have changed. Sea otters during our study seemed to favor prey falling within the smallest size category independent of prey type. Kvitek *et al.* (21), in the 1980s, also found sea otters in Elkhorn Slough foraged on smaller and shallow-buried gaper clams and butterclams rather than on larger items. Studies in the 1990s seemed to indicate a shift to larger prey items such as large gaper clams and butterclams (19).

In our study, smaller prey took less time to pursue, either because it was more abundant or because it took less time to obtain, or both. These different scenarios have different implications. Because more than 50 sea otters have been consistently exploiting the resources in Elkhorn Slough since 1995 (20), the size of prey available may have been reduced. This would explain why the majority of the prey captured is small. Conversely, sea otters may choose smaller prey because of the higher energetic cost of finding and obtaining larger prey, even if present. Obtaining a large prey item would only be favorable when its caloric content defrays the cost of obtaining and handling it. Without density and size distribution data for the prey patches in the slough, the answer to this question is unclear. Pursuit time for innkeeper worms decreased for larger size, possibly because larger worms are more easily detectable. Because handling time is similar for larger and smaller worms, obtaining a larger one would be advantageous. Innkeepers are very abundant in the slough but their caloric content is low.

Most sea otters using Elkhorn Slough appear to be prey specialists, at least during the daytime, focusing on a narrower selection of prey types than available. A high degree of prey specialization has been reported in multiple sea otter studies (12, 33, 34, 35). Variations in the frequency of occurrence of specific prey items in sea otter diet in the slough during specific years may depend on the degree of specialization and prey preference of individuals using the slough in a particular time-period rather than on variations in prey species abundance. In fact, most otters use the slough intermittently, and migrate to other areas along their range (K. Mayer, pers. comm.).

In summary, this study documented the widest variety of prey items so far reported for Elkhorn Slough, and results suggest forging pressure may have remained the same over time but may have caused a shift to smaller prey items. A high degree of specialization may support the food-limitation hypothesis (35) that the degree of individual specialization increases as forager populations become food-limited (34).

Acknowledgments

We thank all volunteers that helped with data collection and entry. In particular, we are grateful to Anna Janovicz, Peter Nilsson, Cyndi Browning, Mark Cotter, Andrew Walsh, Stephanie Wallace, Alessandro Ponzo, and Gary Haskins. Our gratitude also goes to Robert Scoles and Ron Eby, who joined in 2007 and were instrumental in helping us wrap-up this study. Our research was supported in part by Earthwatch Institute and in part by the first author, who contributed money and equipment out of pocket.

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