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Original Investigation

Foraging behavior and prey of sea otters in a soft- and mixed-sediment benthos in Alaska

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ABSTRACT

Sea otter (*Enhydra lutris kenyoni*) foraging behavior and prey preference were studied from June to August 2001–2004 in Simpson Bay, Prince William Sound, Alaska. The study area has an average water depth of 30 m and a benthos primarily of soft- and mixed-sediment with no canopy-forming kelps. A total of 1816 foraging dives from 211 bouts were recorded. Overall, dives ranged in depth from <5 to 82 m; most dives were less than 15 m (40%) with smaller, secondary peaks at 25–30 m (10%) and 50–55 m (7%). Average dive depth and duration were 27 m ± 19.5 and 1.89 min ± 0.88, respectively. Dive durations were all significantly different: male > unknown > female. Dive depths reflected the bathymetry (percentage of the bay within a depth range) of Simpson Bay but favored shallow areas. 87% of foraging dives were successful, and 44% of the prey was positively identified: 75% clams, 9% Pacific blue mussels, 6% crabs, 2% Reddish scallops and a variety of other invertebrates. There was no evidence for prey specialization among the sexes. Although sea otters in Simpson Bay rely heavily on bivalves, their diet has remained unchanged for the past 18 years, and the minimum summer population has been constant for at least the past nine years. It appears that bivalves are the predominant and stable component of the diet, and their productivity is sufficient to sustain a stable population of sea otters with a minimum peak summer density of 4.3 adult otters km^{-2} and an average annual density of ca. 2.9 adult otters km^{-2} for the past nine years and probably longer.

Introduction

After near extinction from commercial harvesting in the early 1800s, sea otters (*Enhydra lutris*) have reoccupied much of their former range (Estes 1990; Kenyon 1975), although fluctuations in regional populations remain dynamic (Bodkin et al. 2002; Doroff et al. 2003). Recent recolonization of areas that were historically extirpated of otters has enabled the study of top–down foraging pressure on coastal ecosystems (Estes and Duggins 1995; Kvitek et al. 1992; Estes and Bodkin 2002). Previous research on sea otter behavior and ecology has focused primarily on areas with a rocky benthos and canopy-forming kelp. In contrast, the ecological role of sea otters in soft sediment communities is less well studied (Kvitek et al. 1992; Doroff and Bodkin 1994).

To thermoregulate in the marine environment, sea otters rely on dense fur to trap an air layer next to their skin (they have little or no subcutaneous blubber) and a metabolic rate 2–3 times the allometric prediction for a terrestrial mammal of similar size (Miller 1974; Kenyon 1981; Costa 1982; Davis et al. 1988; Williams et al. 1988). To maintain this elevated metabolic rate, they consume about 25% of their body weight in food each day (Kenyon 1975). At least 150 species, mostly benthic invertebrates, are preyed on by sea otters, including mollusks, crustaceans, echinoderms, cephalopods and fin-fish, but individually they may specialize on just a few prey types (VanBlaricom 1988; Estes and Bodkin 2002; Estes et al. 2003). The degree of specialization primarily depends on the abundance of prey, and no specialization may occur if the habitat is food-rich (e.g., when otters enter a new habitat or when an area is highly productive) (Laidre and Jameson 2006; Tinker et al. 2008). In soft sediment communities, sea otters prey primarily on bivalves (Garshelis et al. 1986; Kvitek et al. 1993; Estes and Bodkin 2002). Mollusks, crustaceans and echinoderms are the main prey categories for sea otters in Prince William Sound (Calkins 1978; Garshelis 1983; Garshelis et al. 1986; Doroff and Bodkin 1994). Since these prey are benthic organisms, ocean depth is a good estimate of dive depth. On average, males dive regularly to depths of 60 m and females to 40–60 m; maximum depth is ca. 100 m (Estes and Bodkin 2002). Bodkin et al. (2004) concluded that prey below a depth of 60 m experience reduced predation and that otters do not use all habitat proportional to availability. In recently occupied areas where

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food is plentiful, routine dive depths are shallower than areas occupied for longer periods (Kvitek et al. 1992). Dive duration has been correlated with dive depth (Estes and Bodkin 2002) and with the difficulty of locating prey (Kvitek et al. 1993). Since the average depth of Simpson Bay is 30 m, most of the bay's benthos is accessible to foraging sea otters.

The purpose of this study was to examine the diving behavior and diet of sea otters in a benthic habitat of soft- and mixed-sediments. This was part of a larger, long-term study of the behavioral ecology, trophic dynamics and habitat associations of sea otters in an area of stable population that has been occupied for about 30 years (Pearson and Davis 2005; Finerty et al. 2007; Gilkinson et al. 2007; Noll et al. 2008; Gilkinson et al. 2011). Our study site (Simpson Bay), located in eastern Prince William Sound, Alaska was reoccupied by male sea otters around 1977 (Estes 1977; Garshelis et al. 1986), but is now used as a summer pupping area by females and by adult males that establish and defend territories (Garshelis 1983; Pearson and Davis 2005; Osterrieder and Davis 2009, 2011; Finerty et al. 2010). The presence of ca. 119 sea otters in Simpson Bay each summer, including females with pups and territorial males, makes it an ideal location for studying the role of an apex predator in a relatively simple food web.

Material and methods

Study area – Simpson Bay (ca. 60.6°N, 145.9°W), located in northeastern Prince William Sound, AK (Fig. 1), was used as the study site because of its protection from rough seas, reliable presence of sea otters in sufficiently high density to obtain foraging data, and easy access.

It is approximately 21 km^2 in area; 7.5 km long in the northern and western bays, 5 km long in the eastern bay, and 2.5 km wide at the entrance of the bay. The study area has an average water depth of 30 m (maximum depth 125 m) and a benthos primarily of soft sediments (mud and mixed mud and gravel) with some rocky reefs (Noll et al. 2008; Gilkinson et al. 2011). There are no large-bodied kelps (e.g., *Nereocystes*) that form canopies, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*) and sieve (*Agarum clathratum*) kelp cover the benthos in many areas of the bay from the subtidal to a depth of ca. 10 m (Davis unpub. obs.). The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983 and 1985 (Garshelis 1983; Rotterman and Simon-Jackson 1988; VanBlaricom 1988). Since 2002, it has been used during the summer (June–August) by an average, minimum of 119 ± 9.3 sea otters, including adults and subadults (91 ± 6.8) and pups (28 ± 3.8) with an average, minimum density of 5.7 otters km^{-2} (119 sea otters/21 km^{-2}; Davis, unpub. obs.). These population and density estimates were based on standard techniques using two skiffs with teams of observers moving through the entire study area at a speed of ca. 2 m s^{-1} along predetermined, parallel transects separated by ca. 600 m and counting every otter in non-overlapping areas to the starboard and port using 7–10× binoculars. This method was repeated every two weeks (ca. 7 times during the course of the summer field season) to provide an overall, minimum average for the summer. During the winter, the number of otters in the bay decreased to ca. 50 (Weltz unpub. obs. based on a single 10-m vessel moving along a predetermined transect line throughout the study area 2–3 times during the winter), although where they disperse to is poorly understood. This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

Foraging behavior – we observed the foraging behavior of sea otters between June and August of 2001–04. The study area was divided into three parts (i.e., North Bay, West Bay and East Bay; Fig. 1), each of which was surveyed separately in systematic rotation. In this manner, the entire bay was surveyed every 1–2 days depending on weather. Observations were made between 08:00 and 22:00 local time. The research team, composed of a driver, recorder and spotter, made observations from a 5-m skiff. To maximize otter encounters, no systematic vessel track was followed. Instead, the skiff approached opportunistically on search paths that minimized the possibility of encountering an otter more than once during a 3–4 h session. Foraging otters were recognized by the characteristic leap at the beginning of a dive or by the presence of a prey item at the surface. Before starting data collection, we observed the otter's behavior at a distance of ca. 100 m. Once it dove, we slowly moved the skiff to where the otter had submerged and recorded the time, location (Global Positioning System, Garmin International Inc., Olathe, KS), water depth (bathymeter, Garmin International Inc., Olathe, KS or extrapolated from a GIS bathymetric map of Simpson Bay, Gilkinson et al. 2011), and dive duration. When the otter surfaced, typically 30–50 m from the skiff, we identified each prey item to the lowest taxonomic level possible using 7–10× binoculars. This process was repeated for ca. 10 consecutive foraging dives or until the end of the feeding bout, after which we attempted to determine the animal's sex. For the sake of brevity, the term male otter refers to adult males (positively identified from presence of a penile ridge or scrotum) that may have been holding territories; the term female refers to adult females with pups ranging in age from newborn to at least several months in age; and the term unknown sex refers to otters that may have been adult or subadult males, adult females without pups, or subadult females.

Determining prey items visually from a skiff at a distance of 30–50 m instead of using a spotting scope over much longer distances from shore minimized the bias toward prey captured from nearshore areas and larger prey items (Doroff and Bodkin 1994). It also avoided the problem in determining prey composition based on scat analysis which is biased against larger prey when no hard parts are ingested. Although using a skiff may result in potential disturbance, we saw no indication that otters actively avoided the skiff or that they ceased foraging. Since small, sports fishing skiffs are relatively common in Simpson Bay, sea otters in this area are probably habituated to their presence. In most cases, they appear to ignore small boats. Finally, dive location and depth cannot be accurately determined based on shore observations, so foraging habitat is more difficult to assess.

Data analysis – dive depths and durations were analyzed using a Kruskal–Wallis and Tamhane post hoc test. We used non-parametric statistics after running a homogeneity test with the analysis and, as might be expected with sample sizes that are very different (i.e., number of observed males, females and sex unknown), equal variance could not be assumed. Foraging success and prey preference for males, females and otters of unknown sex were tested with a Chi^2 and Bonferroni post hoc test using SPSS (Version 15.0.0). Average values are shown with standard deviation. A canonical correspondence analysis was run using CANOCO (Version 4.5) to simultaneously quantify the relative influences of multiple characteristics associated with each dive. These included sex (male, female, unknown), dive depth, dive duration, prey item, month, and year. This uses a weighted averaging procedure similar to a discriminate functions analysis (Lepš and Šmilauer 2003). A preliminary analysis indicated a strong association of observations of females during a single year (2001). Therefore, we re-ran the analysis with year as a covariate so that we could better identify the relationships among sex and other explanatory variables.

Results

Depth and duration of foraging dives – a total of 1816 foraging dives from 211 bouts (26 females, 38 males and 147 unknown sex)