



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 \pm 19.5 and 1.89 min \pm 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.

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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 km² 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 Chi² 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)

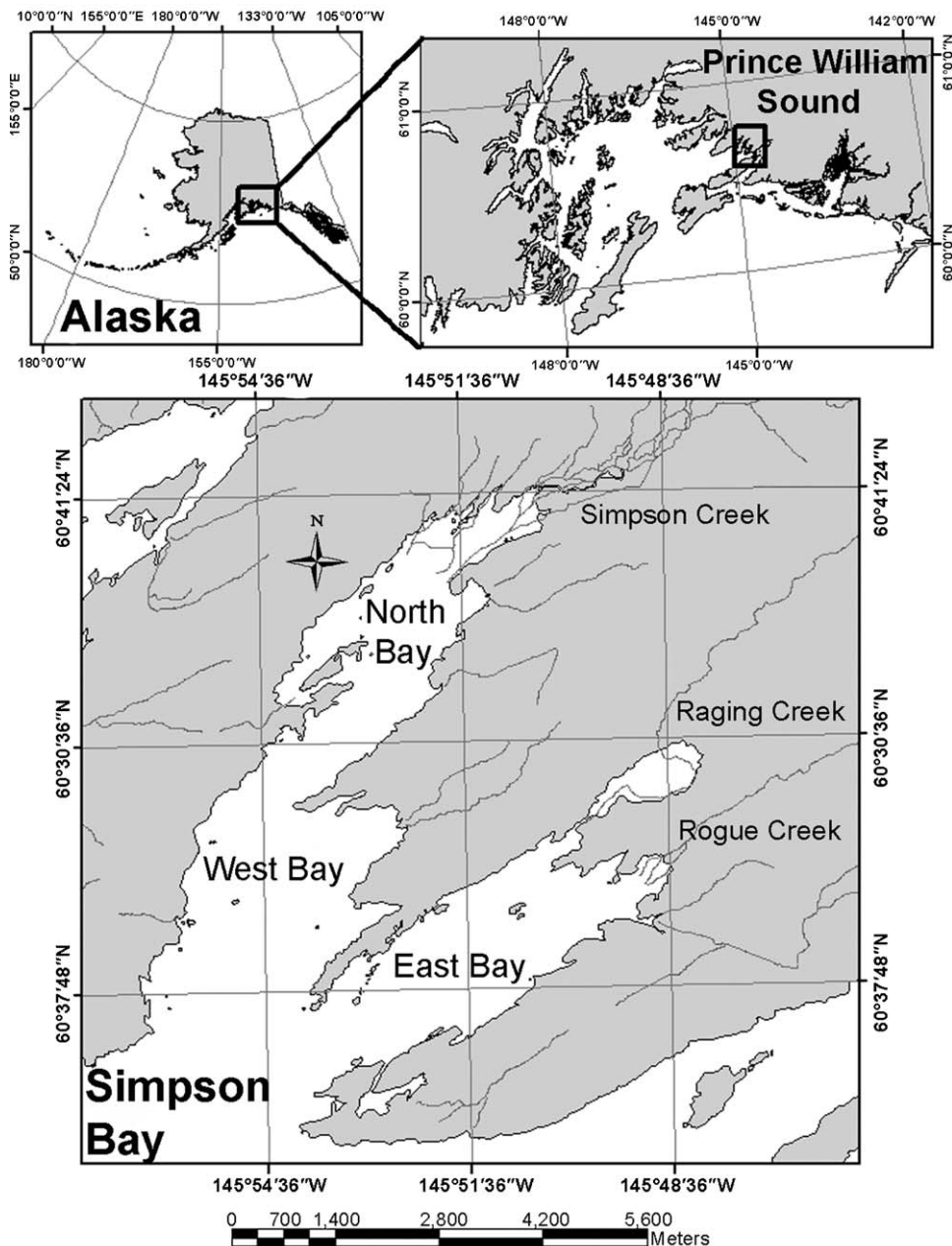


Fig. 1. Simpson Bay, Prince William Sound, Alaska (Noll et al. 2008).

were recorded. The average number of dives observed per feeding bout was 8.6; 10.2 for males, 12 for females and 7.8 for otters of unknown sex. 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%) (Fig. 2a).

Average dive depth for all otters was $27 \text{ m} \pm 19.5$; $30 \text{ m} \pm 19.7$ for males; $29 \text{ m} \pm 21.8$ for females and $25 \text{ m} \pm 18.8$ for otters of unknown sex. Adult males made significantly deeper dives than otters of unknown sex ($P < 0.001$), but there was no significant difference in average dive depths between males and females ($P = 0.124$) and females and otters of unknown sex ($P = 0.477$).

The distribution of dive depths ($N = 346$ dives) for male otters had three distinct sections: 5–15 m (32%), 25–30 m (12%) and 50–60 m (16%), with a maximum dive depth of 75–80 m (Fig. 2b). Females with pups ($N = 233$ dives) made the majority of their dives to depths shallower than 15 m (52%) but had a second peak at 50–55 m (11%) with a maximum dive depth of 75–80 m (Fig. 2c).

The distribution of dive depths for otters of unknown sex ($N = 1116$ dives) showed peaks at 5–10 (23%) and 20–30 m (20%) with a maximum dive depth of 82 m (Fig. 2d). Overall, the distribution of otter dive depths reflected the bathymetry (percentage of the bay within a depth range) of Simpson Bay indicating that all areas were used to some degree to a maximum depth of 82 m (Fig. 3). However, there was a preference for the depth ranges of 5–15 m and 25–30 m. Because the tidal range is up to 5 m during the summer, the otters could exploit most of the bay up to the maximum high tide level.

Average dive duration was $1.89 \text{ min} \pm 0.88$; $2.05 \text{ min} \pm 0.77$ for males; $1.69 \text{ min} \pm 0.84$ for females; and $1.89 \text{ min} \pm 0.90$ for otters of unknown sex. Average dive durations were significantly different: male > unknown ($P = 0.003$), male > female ($P < 0.001$) and unknown > female ($P = 0.006$). Dive durations showed a normal distribution from 0 to 4 min, peaking at 1.5–2.0 min, although adult males showed a second peak at 2–2.5 min. (Fig. 4). There was a positive relationship between dive duration and depth (Fig. 5).

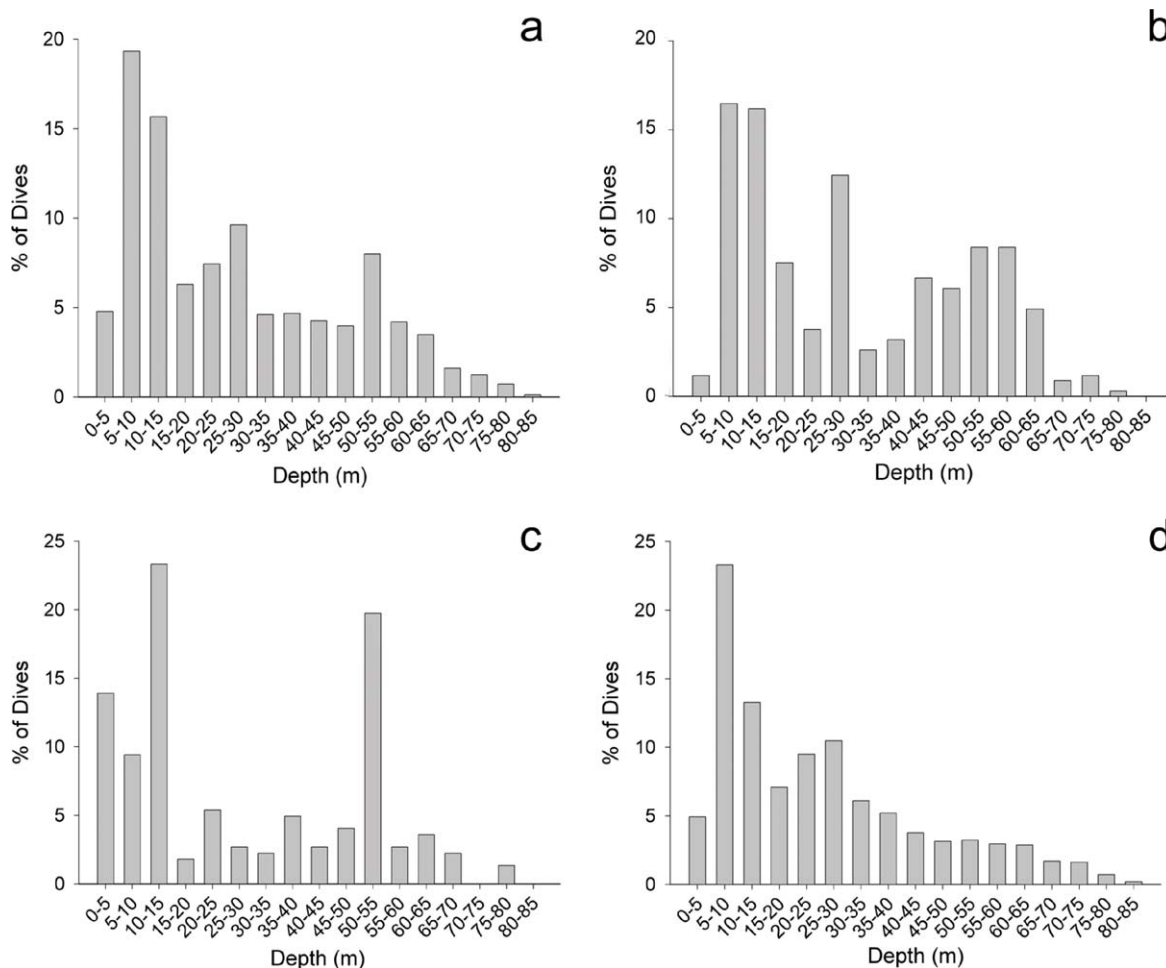


Fig. 2. Distribution of foraging dive depths: (a) all otters (211 animals, 1816 dives); (b) males (38 animals, 388 dives); (c) females (26 animals, 251 dives) and (d) sex unknown (147 animals, 1177 dives).

Prey – on average, prey was captured in at least 87% (4.3% unsuccessful and 8.7% unknown) of foraging dives, and there were no significant differences among males (86%), females (86%) and otters of unknown sex (89%) ($P=0.93$) (Table 1). Overall, 44% of prey items observed after foraging dives were positively identified to at least the taxonomic level of subclass (primarily clams) and often to the level of species (Table 1). Of these, 75% were clams (Class: Bivalvia, Subclass: Heterodonta) which could have included the Butter clam (*Saxidomus gigantea*), Pacific littleneck clam (*Protothaca staminea*), Stained macoma (*Macoma inquinata*), Bent-nose macoma (*Macoma nasuta* formally known as *Macoma staminea*), Truncate softshell clam (*Mya truncata*) and Arctic hiatella (*Hiatella arctica*): 9.4% were Pacific blue mussels (*Mytilus trossulus*): 6.3% were crabs (Class: Malacostraca, Order: Decapoda) which could have included the Dungeness crab (*Cancer magister*), Graceful rock crab (*Cancer gracilis*) and Helmet crab (*Telmessus cheiragonus*): and 2% were Reddish scallops (*Chlamys rubida*) (Fig. 6). The remaining 8% were a variety of benthic organisms, including: (1) echinoderms: Orange sea

cucumber (*Cucumaria miniata*), Purple sea star (*Pisaster ochraceus*), (2) mollusks: Alaska falsejingle (*Pododesmus macroschisma*), Nuttall cockle (*Clinocardium nuttallii*), North Pacific giant octopus (*Enteroctopus dofleini* formally known as *Octopus dofleini*) and Red octopus (*Octopus rubescens*), (3) echiurids: Fat innkeeper worm (*Urechis caupo*), and (4) skate egg cases (*Rajiformes* sp.), although none of these represented more than 2% of total prey items (Fig. 6a).

Their white shells made it easy to identify clams when they were brought to the surface by the otters. Although we could not positively identify the species of clam, the distinctive broken shells (one valve intact and the other broken near the hinge) indicative of sea otter predation of Butter clams, Pacific littleneck clams, Stained macomas, Bent-nose macomas and Truncate softshell clams were found on beaches in the study area. Arctic hiatella are generally small (length to 2.5 cm) and their contribution to the diet of sea otters is unknown but probably small. We identified Pacific blue mussels as prey both by their dark coloration and the characteristic crunching sound as the otters consumed them with the shell. Crabs

Table 1
Foraging success for male, female and unknown sex sea otters.

	Otters (N)	Dives	Successful	%	Unsuccessful	%	Unknown	%	Prey Identified	%
Male	38	388	334	86	14	3	43	11	230	59
Female	26	251	217	86	9	4	25	10	73	29
Unknown	147	1177	1049	89	70	6	58	5	530	45
Total or Ave.	211	1816	1600	87	93	4.3	126	8.7	833	44.3

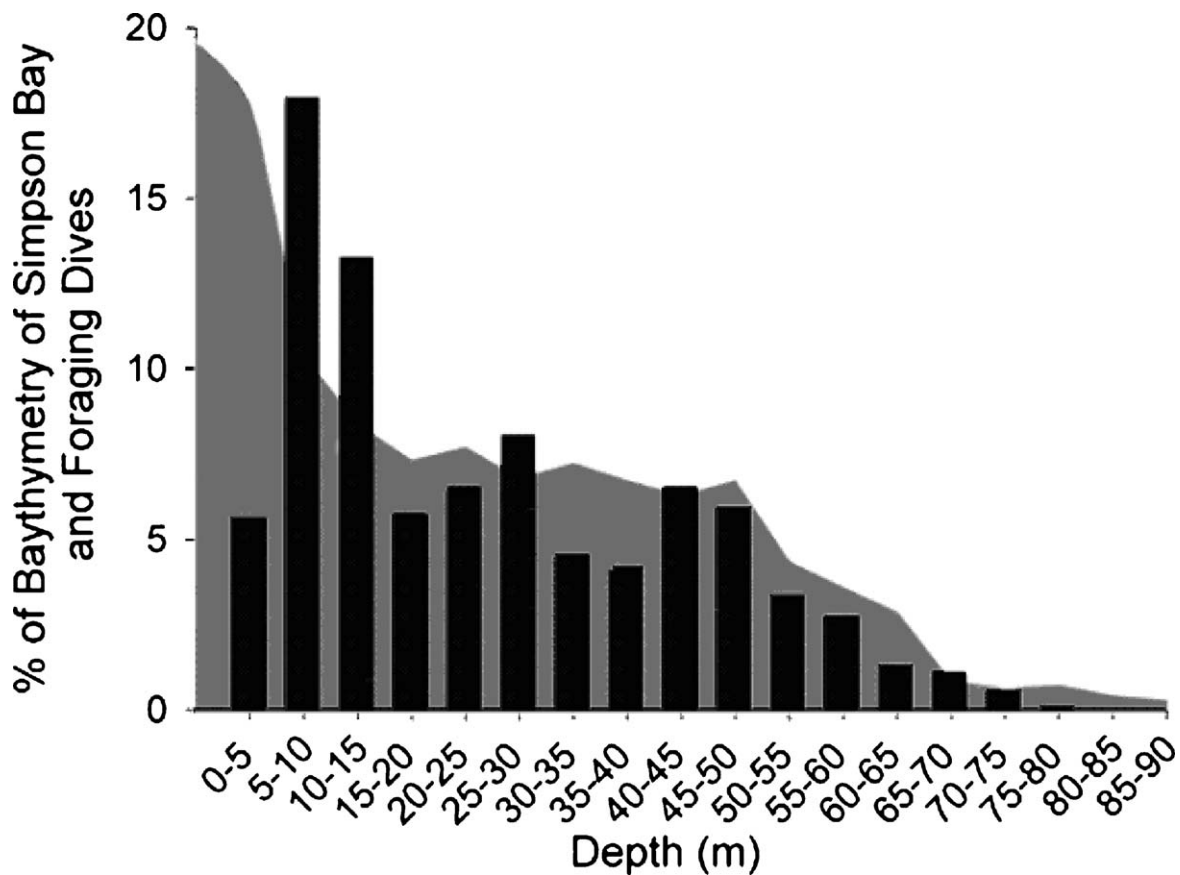


Fig. 3. Distribution of sea otter foraging dive depths (bars) and the percentage of Simpson Bay within each depth range (shaded area).

were also difficult to identify to the species level, but all appeared to be Order: Decapoda. Other prey items were distinctive enough in size, shape and coloration to enable identification.

For males, 59% of prey was identified of which 83% were clams, 11% crabs, 4% Pacific blue mussels and 3% Alaska falsejingles (Fig. 6b). For dives less than 15 m in depth, prey consisted of clams (53%), mussels (45%) and falsejingles (3%); prey for dives that were 25–30 m in depth consisted entirely of clams; prey for dives that were 40–60 m in depth consisted of clams (98%) and falsejingles (2%). For females with pups, 29% of prey was identified of which 81.7% was clams, 5.6% crabs and 5.6% sea stars; all other prey items represented less than 2% (Fig. 6c). Prey for dives less than 15 m in depth consisted of clams (77%) and crabs (23%); prey for dives that were 50–55 m in depth consisted of clams (67%), crabs (17%) and octopus (17%); at all other depths the prey was entirely clams. For otters of unknown sex, 45% of prey was identified of which 71% was clams, 13% mussels and 5% crabs (Fig. 6d). No analysis of prey at particular depths was done for this

category as it did not show the conspicuous peaks as did the other groups. For males and females, the greatest diversity of prey was seen at shallow depths (nine prey categories for dives less than 15 m in depth), clams making up an increasing percentage with deeper dives. On average, males and females captured significantly more clams ($P < 0.0001$) than otters of unknown sex, while the latter captured significantly more Pacific blue mussels ($P < 0.001$) (Table 2). Males captured significantly more crabs ($P < 0.0001$) than females and otters of unknown sex. Males also caught more falsejingles, while otters of unknown sex captured more Reddish scallops and Fat innkeeper worms (Table 2).

Canonical correspondence analysis – comparing the centroids (this is the multivariate analysis version of the mean) of the sexes (Fig. 7), females and otters of unknown sex were quite similar, which led us to conclude that the unknown sex category may be predominately females whose sex we could not positively confirm (i.e., they did not have a pup). Since Simpson Bay is a female area where territorial males aggressively exclude other males,

Table 2

Prey preferences (% occurrence of prey item in the diet) for males, females and otters of unknown sex. Only prey items making up at least 2% of the diet of any one group were included and all were significant.

Prey item	<i>P</i> -value	Bonferroni correction	<i>P</i> -value	Trend
Clams*	<0.0001			Males and females > unknown
Mussels*	0.001			Unknown > males and females
crabs*	<0.0001			Males > females and unknown
Scallop	0.022	Scallop [†]	0.003	Unknown > females
Fat innkeeper	0.029	Fat innkeeper [†]	0.004	Only in unknown
Falsejingle*	0.006			Males > unknown

* *P*-value ≤ 0.007 significant at the table-wise level.

[†] *P*-value ≤ 0.016 significant at the table-wise level.

and [†] significant at the 0.05 level.

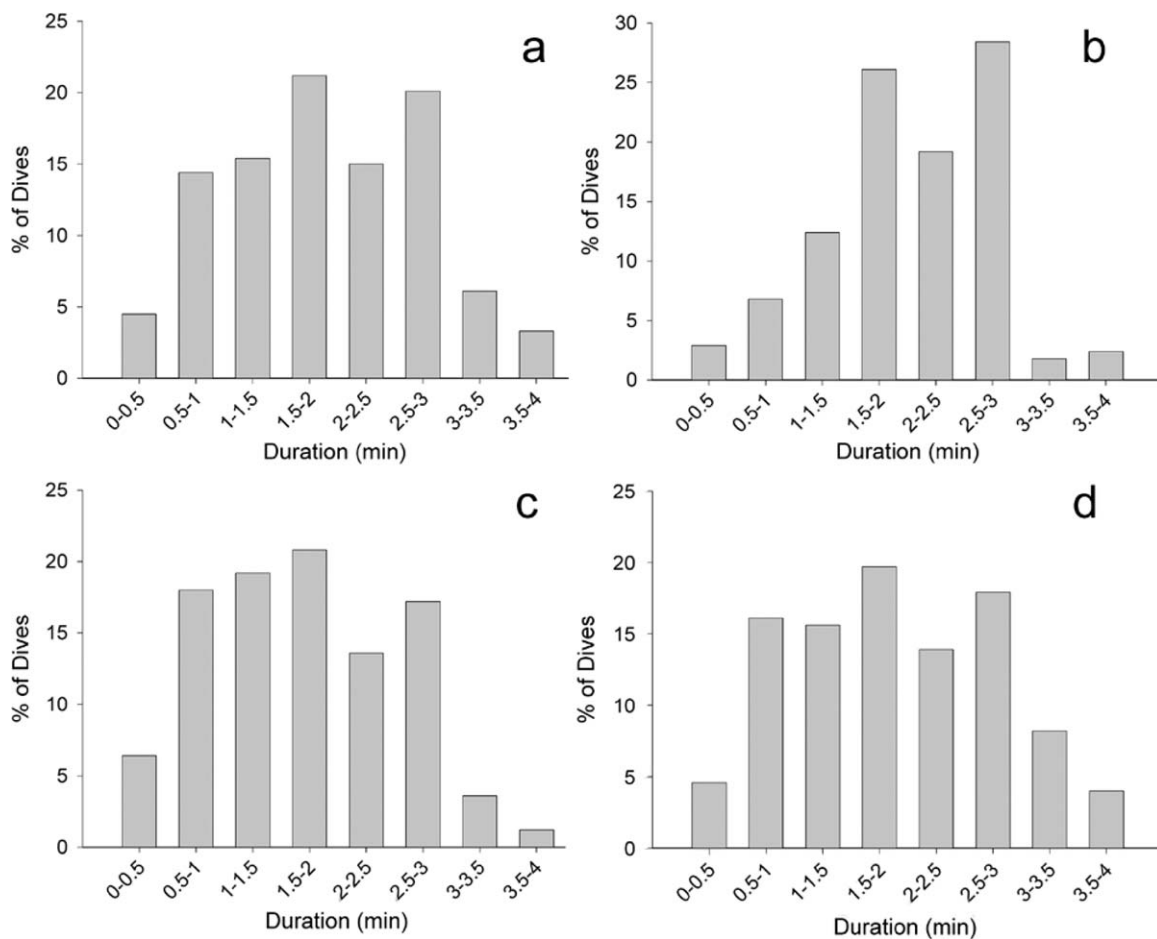


Fig. 4. Distribution of foraging dive durations: (a) all otters (209 animals, 1704 dives); (b) males (38 animals, 333 dives); (c) females (26 animals, 251 dives) and (d) sex unknown (147 animals, 1116 dives).

this assumption is plausible. The prey items (Reddish scallop, Fat innkeeper worm, skate egg case, sea star and North Pacific giant octopus) to the left of axis 1 (vertical) were eaten primarily by females and otters of unknown sex. Prey found in the diets of all three categories (clams, mussels and crabs) were near the center of the plot and did not distinguish among the sex categories well in this analysis. Males made deeper and longer dives, so their dives occurred primarily towards the top on axis 2 in the direction of

increasing values for these vectors. We included each dive in the analysis rather than taking the average over a foraging bout. Using a Monte Carlo test randomizing among individuals, we found a significant difference (F -ratio 10.09), but the explanatory variables (diet, dive depth, dive duration, and month) accounted for only 3% of the total variation. When the same test was run with the otters grouped by sex, only 0.1% was explained by the same variables, which may mean that this is a rather homogeneous system in the sense of being diverse but well mixed among individuals and across sex groups.

Discussion

Approaching the otters in a skiff to within ca. 100 m did not appear to affect their foraging behavior. Small skiffs are common in Simpson Bay during the summer, and the otters appear to be habituated to their presence. In fact, an earlier study of sea otter foraging strategies in Simpson Bay using methods similar to our study found no correlation between the distances moved by otters and the presence of a skiff (Lee et al. 2010). Hence, we think that the results from our study are representative of the undisturbed, foraging behavior of sea otters.

Our results showed little evidence of prey specialization or habitat partitioning among sex categories. This is not to say that certain individuals do not specialize, but as a group (male, female, unknown) they showed no obvious specialization. Clams of various species were the primary prey (75%), and their relatively high abundance was indicated by an average foraging success rate of 87% with no significant difference among sexes. These results are similar to

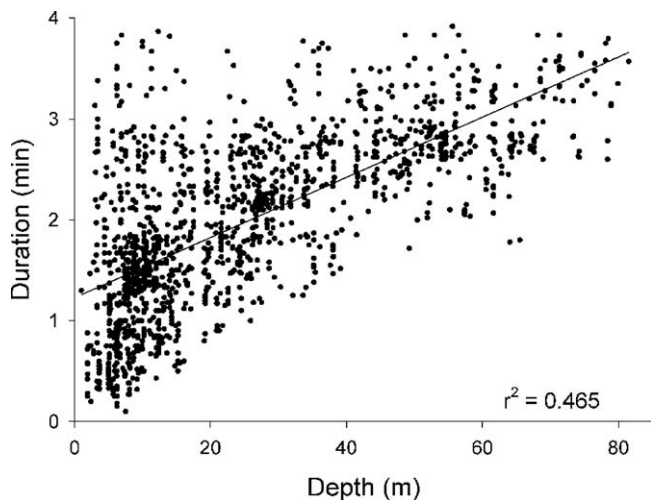


Fig. 5. Successful foraging dive depth as a function of dive duration.

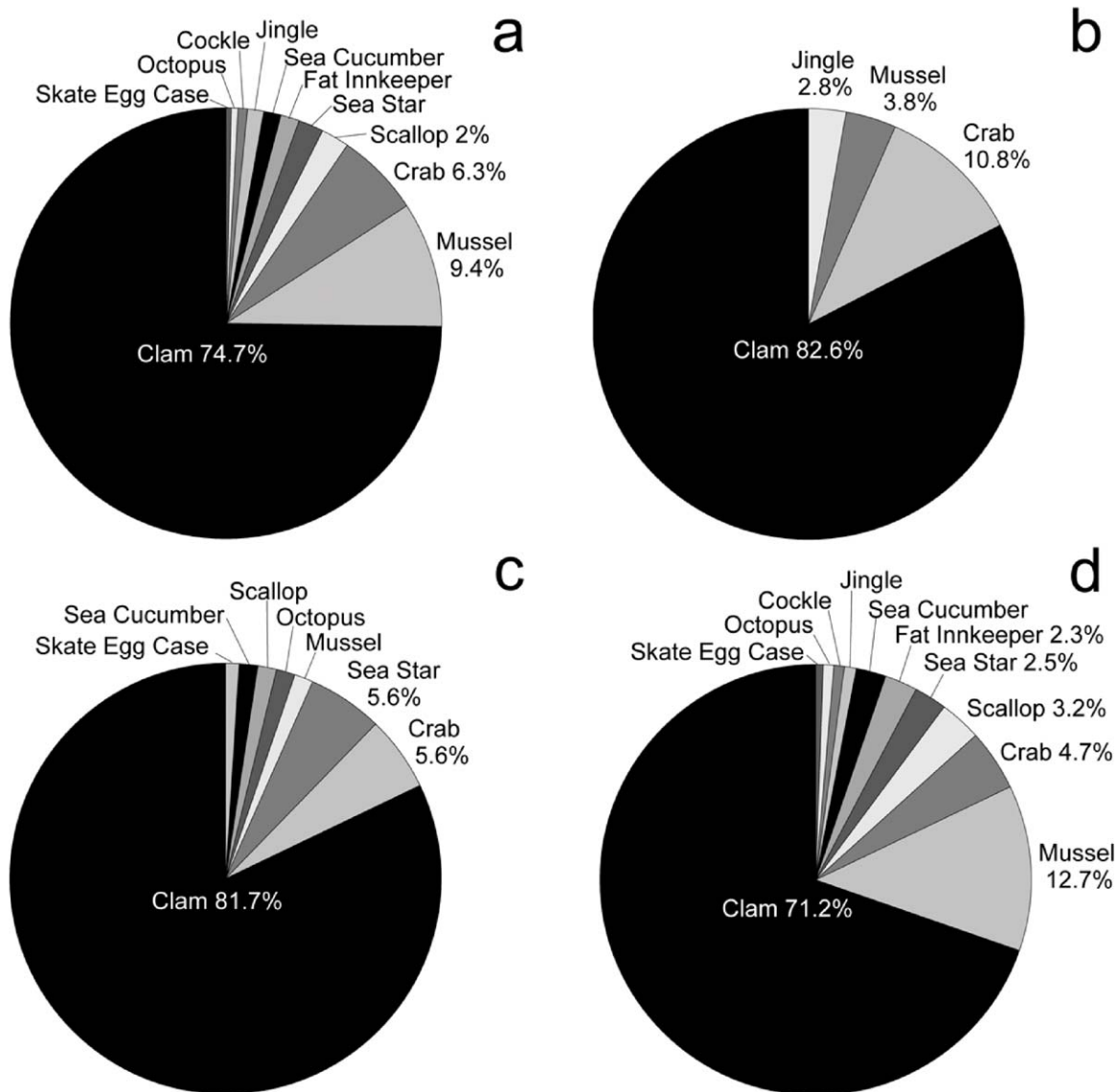


Fig. 6. Percent distribution of identified prey for (a) all otters; (b) males; (c) females and (d) sex unknown. Prey items without percentages comprise less than 2% of the diet.

previous studies at Green Island in central Prince William Sound (Garshelis 1983; Doroff and Bodkin 1994). Overall, otters exploited all of Simpson Bay proportionate to the bathymetry (i.e., percentage of the bay within a depth range) down to a depth of 82 m, although there was some preference for shallower depths in the range of 5–15 m (Fig. 3). Although sea otters have occupied Simpson Bay for over 30 years, the productivity of the bay, especially the benthic macro-invertebrate community, has been sufficient to support a stable, minimum summer (June–August) population of 119 sea otters since 2002 without a high degree of difference in prey preference among males, females with pups and otters of unknown sex, which probably includes many females without pups and younger otters. However, we cannot rule out prey specialization on an individual basis.

As all sea otters in Simpson Bay fed on benthic organisms, the depth of feeding dives depended on location within the bay. Although male otters made significantly deeper dives than otters of unknown sex (but not females with pups), the differences in average dive depth among the sex categories were small and did not indicate habitat partitioning based on depth. Males made significantly longer dives than females and otters of unknown sex, and this may reflect a greater breath-hold capacity that would give

them more time to search for prey. Alternatively, females with pups may choose to make shorter dives to reduce the amount of time the pup is unattended at the surface or to teach the pup how to dive and locate food (Osterrieder and Davis 2009). Whatever the explanation, there was no indication that females with pups were less efficient in obtaining food.

Prey – we think the percentage of prey positively identified (44%) is representative of all the prey taken in Simpson Bay. Many of the prey species making up small percentages of the diet are fairly large and recognizable (i.e., sea star, sea cucumber, octopus, crab). Of the possible prey that are typically small enough to be concealed by the otter's paws, covered in mud, or eaten quickly are small clams and Pacific blue mussels. If a bias does exist, it is likely that the clams and mussels are an even larger percentage of the diet than we observed. Identifying clams to species is a common problem when determining prey composition for sea otters using visual observation (Doroff and Bodkin 1994). Hence, we think it is best to treat hard and soft-shelled clams as a group rather than to speculate on detailed species composition.

Although a high degree of prey specialization was not apparent, males showed the narrowest range of prey with only four groups making up 99% of their diet, clams constituting 82%. Clams also

Table 3
Summary statistics for the depth of capture for various prey groups. It should be noted that the average depth of mussel capture is likely somewhat less than reported due to the difficulty of maneuvering a skiff to shallow intertidal areas.

Prey depths	Mean (m)	Standard deviation	Minimum (m)	Maximum (m)	N	Confidence level (95%)
Alaska falsejingle	15.5	16.3	0.0	58.1	10	11.6
All clams	28.5	21.0	0.0	82.0	629	1.6
Nuttall cockle	14.5	4.6	11.5	21.3	4	7.4
All crabs	30.1	21.1	3.3	74.6	52	5.9
Fat innkeeper	44.8	26.0	12.3	79.9	13	15.7
Pacific blue mussel	6.7	3.5	0.0	12.4	56	0.95
Giant octopus	35.4	19.2	8.7	50.7	4	30.6
Reddish scallop	40.7	18.0	11.0	69.2	19	8.7
Orange sea cucumber	20.0	19.5	8.6	74.1	11	13.1
Purple sea star	22.1	16.8	0.1	58.6	16	2.1

made up 82% of the female diet, but the remaining 18% was divided among seven different prey groups (Fig. 6). Otters of unknown sex had the widest variety (11 groups) of prey. Clams still comprised the majority (71%) of the diet, but mussels were a substantial portion (13%) compared to 4% for males and 1% for females. Otters of unknown sex may have included independent juveniles, and this may explain the higher percentage of mussels in their diet because they are epibenthic and found at shallow depths, thereby requiring much shorter dives (Kvitek et al. 1993). However, the comparison is complicated by the fact that this sex category may have included adult females without pups.

Of the bivalves eaten by otters, clams were the easiest to identify as a group because of their white shells, but very difficult to identify by species. The overlapping distribution of the ten species known to occur in the study area (Fig. 8a) indicates that the greatest diversity and possibly abundance of bivalves occurs in the depth range of 0–15 m (O'Clair and O'Clair 1989), which coincided with the greatest percentage (47.1%) of dives. Overall, the depth range of 0–45 m accounted for 78.6% of dives and included the average capture depth for all 10 groups of prey (Fig. 8b and Table 3).

Optimal foraging theory suggests that otters will find a balance between taking the most easily captured and energetically rich prey items (Pyke 1984). In Simpson Bay, this would be the Dungeness crab (1950 kJ for a crab with 500 g of tissue and an energy content of 3.9 kJ g⁻¹, Ensminger et al. 1994). However, large crabs may have

been depleted soon after sea otters moved into the area in 1977, and now they generally represent a small (5–11%) part of the diet, many of which are smaller (<100 g) species, probably Helmut crabs and Graceful rock crabs. Previous studies of sea otters foraging in soft sediment habitats have found clams, particularly Butter clams, to be the most common prey (43–86%; Kvitek et al. 1993). Although clams have less energy per gram of tissue than crabs (153 kJ for a clam with an average mass of 48 g [Cortez unpub. obs.] and an energy content of 3.18 kJ g⁻¹, Ensminger et al. 1994), in soft sediment communities they appear to be the most important prey and able to sustain a population for much longer periods (Garshelis et al. 1986; Kvitek and Oliver 1992; Estes and Bodkin 2002). While the mean size of clams in reoccupied areas may decrease (Kvitek and Oliver 1992), they have been able to sustain otter populations in some areas at what may be pre-fur trade historic levels (Miller 1974). Less than 10 years after sea otters re-entered Simpson Bay, Garshelis et al. (1986) found clams making up 75% of the diet and crabs 3–13%. These values are similar to what we observed 15–18 years later from 2001 to 2004, where clams constituted 75% and crabs 6% of the diet. The other 19% of the diet consisted of Pacific blue mussels, Fat innkeeper worms, sea stars, sea cucumbers, octopus and skate egg cases, similar to what we observed.

In contrast, sea otters along the central California coast eat abalone, rock crab and sea urchins in newly reoccupied areas, eventually expanding their diet to include mussels, turban snails and other less “preferred” prey (Estes et al. 1980). That study found the greatest number of prey species in California (and the fewest in Prince William Sound) because the rocky habitat supports a more diverse assemblage. This may lead to prey specialization by otters out of necessity (Tinker et al. 2007). Established populations having a broader variety of prey items (Estes et al. 1980) may not always be the case in areas with large beds of bivalves. Although sea otters in Simpson Bay rely heavily on several species of bivalves, their diet has remained unchanged for the past 18 years, and the summer population has been constant for at least the past nine years. As a result, they cannot be described as recently established.

Depth and duration of foraging dives – the average foraging dive depth for otters in Simpson Bay (27 ± 19.5 m) was similar to the average depth (30 m) of the bay (Gilkinson et al. 2011). As adult otters can regularly dive between 40 and 60 m (Estes and Bodkin 2002), most of the benthos in Simpson Bay is within easy access. While otters appeared to favor shallower depths (40% of foraging dives were ≤15 m), the distribution of foraging dives deeper than 15 m generally reflected the distribution of depths within the bay (Fig. 3). The additional peaks in foraging dive depths from 25 to 30 m and 50 to 55 m may reflect a multi-modal feeding pattern. The percentage of the bay from 10 to 50 m is fairly consistent, ranging from 8.4% (10–15 m) to 6.7% (45–50 m), so an increase in number of dives does not correspond with larger portions of the bay at these depths (Fig. 3) and may represent preferred habitat possibly driven by changes in substrate type. As a result, we hypothesize that preferred

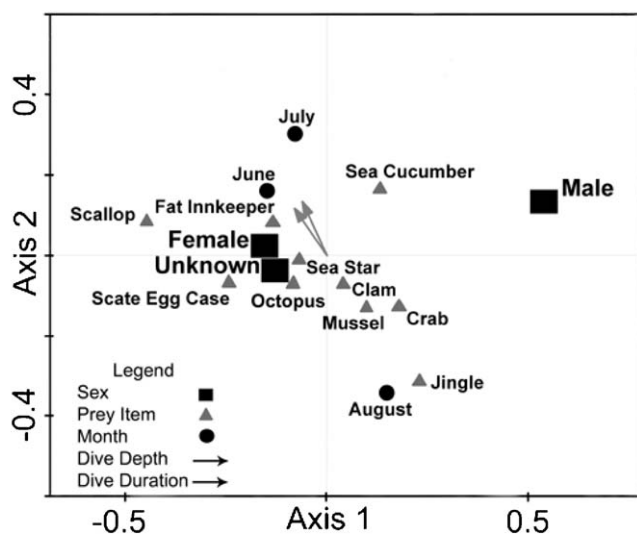


Fig. 7. Canonical correspondence analysis (with year included as a covariable) to determine characteristics that best discriminate among dives by males, females and unknown sex. This analysis measures the relative strength of ecological gradients (axes 1 and 2) that are combinations of multiple explanatory variables, which include type of prey, dive duration and dive depth (vectors as arrows point in the direction of positive correlation of these continuous variables; negative correlation is inferred for variables and individuals located in the opposite direction).

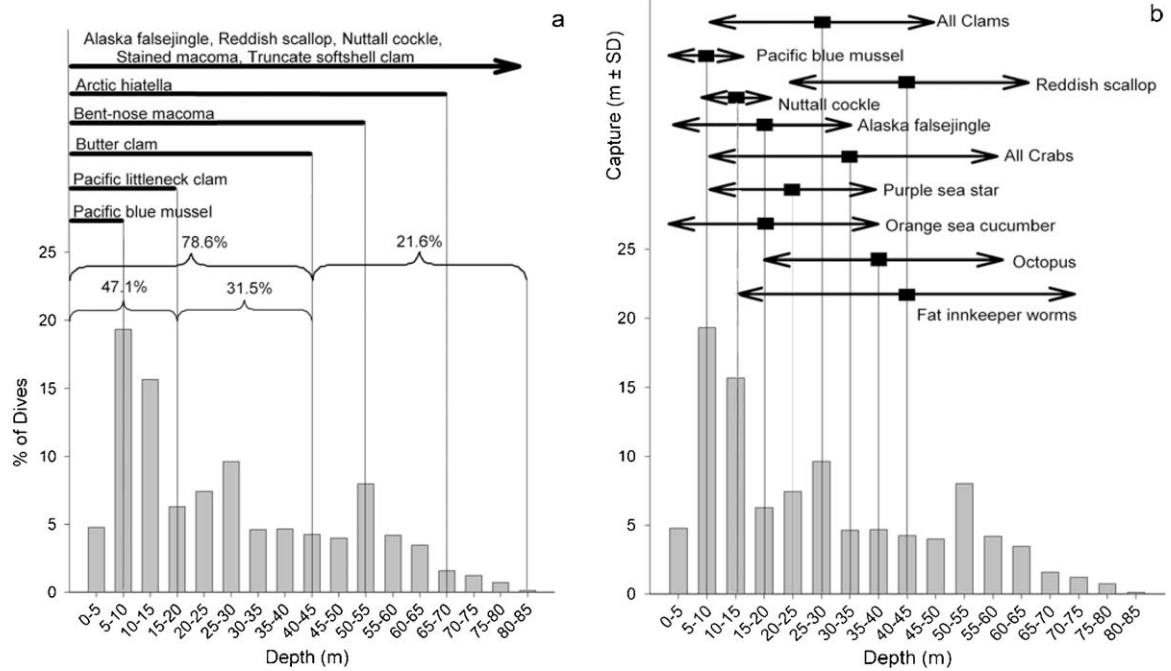


Fig. 8. (a) Reported depth ranges for bivalves and distribution of dive depths for all sea otters in this study. (b) Average depth (± 1 standard deviation) of capture for each prey group and distribution of dive depths for all sea otters in this study.

foraging depths result from the distribution and abundance of prey.

Diving ability probably influenced foraging dive depth, resulting in a multi-modal distribution for some adult males and females, but a unimodal distribution for otters of unknown sex which probably included more juvenile sea otters. A similar pattern has been described for certain California sea otters that preferentially use either shallow depths (<20 m) or deeper areas (45–55 m) with few dives at intermediate depths (Bodkin et al. 2004). However, since that study used time-depth recorders to monitor dive depth and duration, the authors could only infer that the otters were specializing on different prey. Our data do not indicate specialization on prey other than clams in Simpson Bay. The peaks at deeper dive depths made by adults may reflect the length of time (ca. 30 years) otters have reoccupied the area. Since otters will preferentially forage in shallow areas first (Kvitek et al. 1992), it may have taken several years for the otters in Simpson Bay to consume the larger clams at shallow depths (i.e., <50–60 m), and the adults, particularly males, are now working their way down to depths that previously were unused. There are potentially seven species of bivalves and three other groups of invertebrate prey that occur at these deeper (45–85 m) depths (Fig. 8b). However, the lower percentage (21.6%) of dives in this depth range may indicate that: (1) they are made primarily by adult males and some adult females and are beyond the breath-hold capability of juvenile otters (Fig. 2) or (2) the metabolic cost of diving to the benthos makes these dives less energetically efficient than shallower dives. Additional information will be needed on the metabolic cost of diving and the size, energy content and abundance of invertebrate prey to understand the energetic benefit from these deep dives.

The amount of biomass removed from Simpson Bay each year by foraging sea otters can be estimated from the minimum, average number of otters in the area and the daily food consumption per otter. The average sea otter population in Simpson Bay during the summer is 90 adults, and this decreases to about 50 adults during the remainder of the year (Davis unpub. obs.). This means that the minimum, average annual population of sea otters in Simpson Bay is ca. 60 adults. Assuming an average adult body mass of 25 kg,

an average field metabolic rate of 19 MJ day^{-1} ($0.76 \text{ MJ day}^{-1} \text{ kg}^{-1}$, Finerty et al. 2009), a metabolizable energy coefficient of 0.9, and an average energy content for prey (based on clams) of 3.18 MJ kg^{-1} , then the amount of biomass consumed annually would be $145,388 \text{ kg}$ ($[19 \text{ MJ day}^{-1} \text{ otter}^{-1} \times 60 \text{ otters} \times 365 \text{ days}] / [0.9 \times 3.18 \text{ MJ kg}^{-1}]$), of which $109,041 \text{ kg}$ (75%) are clams and $36,347 \text{ kg}$ are other species. If we divide the biomass of clams consumed by the area of Simpson Bay ($21 \times 10^6 \text{ m}^2$ assuming that the entire bay is equally productive) and assume that the wet tissue mass of an average clam is 0.048 kg (Cortez unpub. obs), then the otters are removing $0.11 \text{ clams m}^{-2} \text{ yr}^{-1}$ ($109,041 \text{ kg clam} / 0.048 \text{ kg clam}^{-1} / 21 \times 10^6 \text{ m}^2$). If this rate of removal represents less than 10% of the clam population, then the average clam density in Simpson Bay would be at least 1.1 clams m^{-2} ($1.1 \times 10^6 \text{ clams km}^{-2}$), which is not an unreasonably high density (Nickerson 1977; Cortez unpub. obs). This, along with other prey species representing the other 25% of biomass consumed, has been sufficient to sustain a stable population of sea otters with a peak summer density of $4.3 \text{ adult otters km}^{-2}$ and an average annual density of ca. $2.9 \text{ adult otters km}^{-2}$ for the past nine years and probably longer.

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