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Summer Foraging Behaviour of Female Sea Otters (*Enhydra lutris*) with Pups in Simpson Bay, Alaska

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Abstract

In altricial mammals, the mother's care and attendance are essential for the young to acquire survival skills. Not much is known about mother-pup behaviour in the sea otter population of Simpson Bay, Prince William Sound, Alaska. In this study, water depth and location of feeding females with pups of different ages were recorded. Shallow (0 to 20 m) and deep (60 to 80 m) waters were preferred for foraging over those of intermediate depths. There was no significant difference in foraging water depth relative to pup maturity, but female dive duration changed significantly with the age of the pup, likely resulting in increasing surface time for unattended pups. The range of measured dive durations increased with older pups. Dive duration was highly significantly dependent on foraging water depth.

Key Words: sea otter, *Enhydra lutris*, foraging females with pups, habitat choice, water depth, Alaska

Introduction

As in most carnivores (Starck & Ricklefs, 1998), including mustelids (Stubbe, 1993a, 1993b, and references therein), newborn sea otters are altricial. Hence, the mother-pup bond is essential for the pup to survive and acquire essential skills such as foraging and grooming. Sea otter pups usually depend on their mothers for 5 to 6 mo, but the dependency period may last as long as 12 mo (Kenyon, 1969; Riedman et al., 1994; Monnett & Rotterman, 2000). Premature weaning may lead to reduced survival (Garshelis & Garshelis, 1987; Riedman et al., 1994; Monnett & Rotterman, 2000), generally due to starvation (Garshelis, 1983).

Sea otters (*Enhydra lutris*) are benthic foragers that carry the generally single pup on the mother's abdomen, especially during the first weeks of its life (Kenyon, 1969). Pups begin to swim when they are about 3 to 4 wks old (Payne & Jameson, 1984; M. Staedler, pers. comm., 23 August 2008), and they begin to dive when approximately 6 to 10 wks old (Estes, 1980; Payne & Jameson, 1984; Faurot-Daniels, 1991). As with swimming and diving, grooming is an important milestone in a sea otter's development. Pups are kept warm in the marine environment by a dense, natal fur (lanugo) that is groomed by the mother, although they exhibit some grooming behaviour already at 1 wk of age (Kenyon, 1969; Vandevere, 1972; Hanson et al., 1993). They molt their natal pelage (highly buoyant due to a layer of air trapped within the dense fur) at about 13 wks of age (Payne & Jameson, 1984). Because of their small body size, the absence of a blubber layer, and complete reliance on fur for insulation, sea otters have a resting metabolic rate 2 to 3 times greater than a terrestrial mammal of the same body mass to maintain a stable core temperature (Costa & Kooyman, 1982). As a result, they consume *ca.* 25% of their body weight in food daily (Kenyon, 1969; Costa, 1982), and they are reliant on habitats with a high prey abundance. Pups initially rely solely on the females' milk for nourishment, but begin to eat solid food around the age of 4 to 6 wks (Payne & Jameson, 1984; Hanson et al., 1993).

Females with pups must sustain their own elevated metabolism while providing for their pups. Hence, it is likely that they obtain more food (Garshelis, 1983) and spend more time foraging than solitary adults (Garshelis, 1983; Gelatt et al., 2002). In a previous study (Gilkinson, 2004), water depth was the most significant habitat variable associated with the feeding behaviour of sea otters in Simpson Bay, Alaska. Therefore, we selected water depth as the relevant variable to investigate foraging behaviour of females with maturing pups. In this predominantly soft sediment habitat, sea otters forage on several species of molluscs, crustaceans, and echinoderms (study of 2001-2004 + 2007; R. Wolt, pers. comm., October 2008), which they collect at the sea floor (Shimek, 1977) and consume at the surface. A foraging bout mostly consists of several feeding dives (Kenyon, 1969), with prey consumption during the inter-dive intervals. A female with a pup might be constrained to a certain water depth range dependent on the pup's age. Pup behaviour, body length, and fur condition were used as a proxy for its age. The following hypotheses for the feeding behaviour of females with pups of different ages in regard to water depth were investigated:

1a. Selected water depth increases with pup age as pups learn to dive and become more independent.
1b. Selected water depth decreases with pup age to allow pups to forage themselves when they learn how to dive.
1c. Maternal diving depth is independent of pup age (null-hypothesis).
2a. Females with pups prefer very shallow (near shore) or very deep waters (closer to the middle of the bay) to either protect the pup or to support the development of its diving abilities in shallow waters or to provide sufficient nourishment from deep waters with potentially more available prey, respectively.
2b. There is no significant difference between the geographical distribution of females with pups and the distribution of available water depths (null-hypothesis).

Shallower depths might decrease the time pups are left unattended at the surface (*cf.* Estes, 1977; Estes et al., 1981; Kvitek et al., 1993; Bodkin et al., 2004), making pups less vulnerable to bald eagle predation (Sherrod et al., 1975). However, there may be advantages to foraging in deeper waters such as larger or more abundant prey with higher energy content or in lower burrowing depths (Kvitek et al., 1992, 1993). The importance of water depth might be increased by the assumptions that only in shallow waters is the pup able to obtain a (small) part of its food requirements itself and that the mother is more capable of obtaining nutrition for herself and for the pup in deeper waters.

As the pup matures and its behavioural abilities develop, the female has to adapt her behaviour relative to the pup's (e.g., the grooming and feeding needs of the pup). Not much is known about the foraging strategies (e.g., the depth of female foraging dives) of females with pups. Garshelis & Garshelis (1984) followed eight tagged females and pups in Gibbon Anchorage in central Prince William Sound, but that area is considerably shallower (generally < 12 m) than Simpson Bay. The goal of this study was to examine diving behaviour and changes in habitat preference of females with pups of different ages, while, in particular, comparing deeper with shallower areas in a predominantly soft sediment habitat.

Materials and Methods

Study Area and Otter Population

Simpson Bay (*ca.* 60.6° N, 145.9° W), located in northeastern Prince William Sound, Alaska (Figure 1), was used as the study site because of its manageable size for daily surveys, protection from rough seas, and reliable presence of sea otters, all allowing for easy and frequent observations. It is approximately 21 km² in area: 7.5 km long in the northern and western inlets, 5 km long in the eastern inlets, and 2.5 km wide at the entrance of the bay. Maximum water depth is *ca.* 125 m, with a mean depth of about 30 m. Water depths of 0 to 20 m were found in 46.4%, 21 to 40 m in 27.4%, 41 to 60 m in 20.2%, 61 to 80 m in 4.9%, and > 80 m in 1.1% of the bay. Bottom sediments consist of glacial clay, silt, and gravel, with some hard rocky reefs (Gilkinson, 2004; Noll, 2005). There are no large-bodied kelps (e.g., *Nereocystis*) that form canopies, but large fronds of sugar kelp (*Laminaria saccharina*) cover the benthos in many areas of the bay from the subtidal to a depth of *ca.* 10 m (R. Davis, pers. comm., May 2008). After the near extinction of the sea otters in the early 19th century (Estes et al., 2009), the bay was recolonized by male sea otters in 1977-1978, and females moved into the area between 1983 and 1985 (Garshelis, 1983; Garshelis & Garshelis, 1984; VanBlaricom, 1988). Since 2002, the summer (June-August) population has been fairly stable at 119 ± 9.3 SD sea otters on average, including 91 (± 6.8 SD) adults and subadults and 28 (± 3.8 SD) pups (6-y average; R. Davis, pers. obs.). During the summer of 2008 (31 May to 12 August), the average population size was 132.4 sea otters ($n = 6$ surveys) of which 97.6 were adults and subadults and 34.8 were pups. During winter, only about 50 sea otters stay in the bay, but it is unknown to what location the others disperse.

Female and Pup Diving Behaviour

We collected data on the behaviour and activity patterns of female sea otters and their pups from June through the first week of August 2008 from either a 7-m aluminium skiff or a 5-m fibreglass skiff usually with two to four people onboard. Observations were made between 0330 h and midnight and were terminated by the sea otters with the end of a feeding bout, usually consisting of several foraging dives (*cf.* Kenyon, 1969). We opportunistically approached the sea otters but avoided approaching an individual repeatedly during a (usually) 3 to 4 h session. When a female with pup was seen feeding (based on either the observed handling of prey, the characteristic leap at the beginning of a foraging dive, or a pup floating or swimming alone at the surface), both animals were monitored and, if possible, dive durations were recorded. Observations were conducted with binoculars (Nikon Eagleview 8-24×25, Nikon 7×40) to influence the sea otters as little as possible. A female with a pup was usually approached to within *ca.* 50 to 150 m and not closer than 30 m. Sea otters were left alone when they appeared to be disturbed (i.e., changed their behaviour with the appearance of the boat).

Pups were classified into three behavioural and morphological categories: Category 1, 2, and 3 (in the following C1, C2, and C3, respectively). Through combined use of behaviour, size, and fur appearance, categorizing pups was simple and consistent (see Table 1).

As soon as the mother and pup moved on, usually after stopping to feed, the mother's former diving location was approached with the aid of landmarks to obtain the GPS location (Garmin Model 126). We estimated dive depth from the water depth using the onboard bathymeter (Garmin bathymeter). As prey species are benthic and require foraging dives to the seafloor, this was a valid assumption. If the sea otters were travelling during a feeding bout, two to three GPS locations and water depths were recorded from the bathymeter, and the mean depth was used for analysis. When the location was too close to shore or too shallow for the skiff, the GPS location was either taken as close as possible (max. 5 m away) or the water depth was extracted from a detailed bathymetry map (Gilkinson, 2004) using *ArcView 9.2* (ESRI, Redlands, CA). Water depth in these cases was estimated when the bottom could be seen, but to a maximum of 5-m depth. Foraging dives were categorized into the depth classes of 0 to 20 m, 21 to 40 m, 41 to 60 m, 61 to 80 m, and over 80 m.

Statistical Analyses

A GIS program (*ArcMap 9.3*, ESRI, Redlands, CA) was used to obtain the bathymetric frequency distribution from a 10-m water depth grid map of Simpson Bay (Gilkinson, 2004). χ^2 tests were conducted separately for each pup category to compare the distribution of feeding locations with the actual distribution of available water depths (the null-hypothesis being an equal distribution according to their frequency of occurrence). Non-parametric testing was most appropriate due to the small sample sizes, especially of C1 pup observations and because of the non-normal distribution of some data. The Kruskal-Wallis test was used to test for significant differences in dive depth and dive duration in females with pups of different sizes. A linear regression was run to determine relationships between the duration of a foraging dive and water depth. For this analysis, time measurements for each observed foraging sea otter were averaged, with a minimum of at least three dives per session. Arithmetic mean values are shown with SD and medians with quartiles. Statistical analyses were conducted with *SPSS 15.0*.

Results

A total of 146 dives were recorded for females with pups (Figure 1). The median water depth of all dives was 17 m (25 to 75 percentiles: 56 to 145 m; $n = 145$), and the median dive duration was 87 s (25 to 75 percentiles: 56 to 145 s; $n = 301$). Dive duration of foraging females with pups was positively correlated with water depth (Figure 2; Regression, r = 0.861, $n = 45$, $p < 0.0005$).

There were no significant differences ($\chi^2 = 1.436$, df = 2, $p = 0.488$) between water depths for foraging dives of females with pups of different categories (medians and 25 and 75 quartiles): 13 (5.0 to 38.0) m ($n = 17$) for females with C1 pups, 16 (3.5 to 44.5) m ($n = 35$) with C2 pups, and 18.5 (7.0 to 49.1) m ($n = 94$) with C3 pups. However, dive duration varied significantly between females with pups of different ages ($\chi^2 = 6.838$, df = 2, $p = 0.033$), showing a wide range of occurring dive durations (Figure 3).

There was some selectivity in the use of Simpson Bay based on bathymetric frequency (Figure 4). Females of C1 pups did not prefer

Table 1. Characterization of C1, C2, and C3 pups

	C1	C2	C3
Behaviour			
Swimming	No	Swimming with coordinated body movements	Yes
Diving	No	Surfacing almost immediately after submerging	Yes
Size (compared to the mother)	< 1/2	1/2 - 2/3	> 2/3
Fur	Long dense fur with light brown tips	Slightly scruffy with the lanugo molting	Dark brown fur similar to adult fur

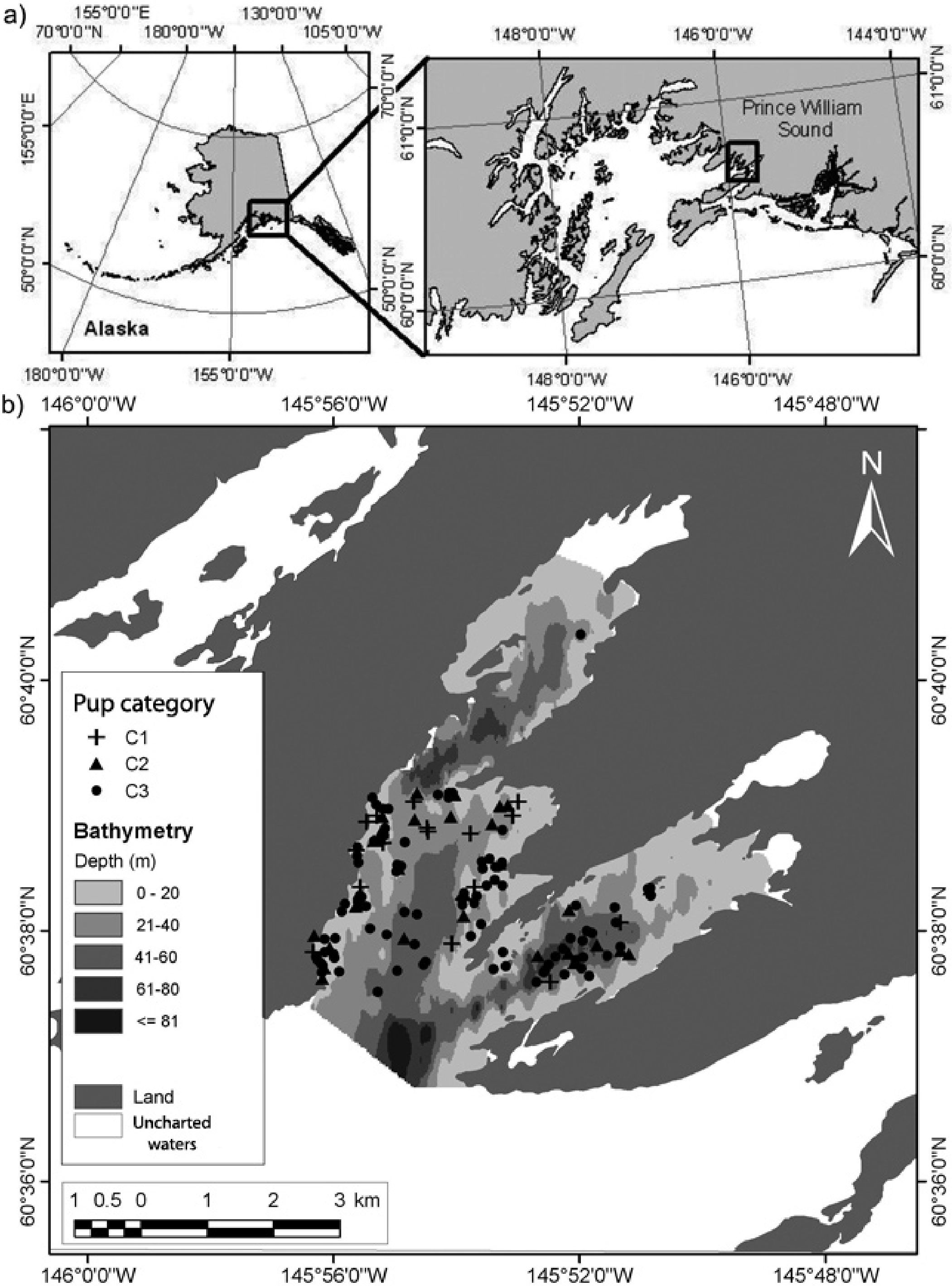

Figure 1. a) Simpson Bay in northeastern Prince William Sound, Alaska (Noll et al., 2009); and b) feeding locations of females with C1 (crosses), C2 (triangles), and C3 (dots) pups in Simpson Bay. A total of 146 foraging dives were observed. Due to mistakes in noting the proper locations, two diving locations were not plotted on this map.

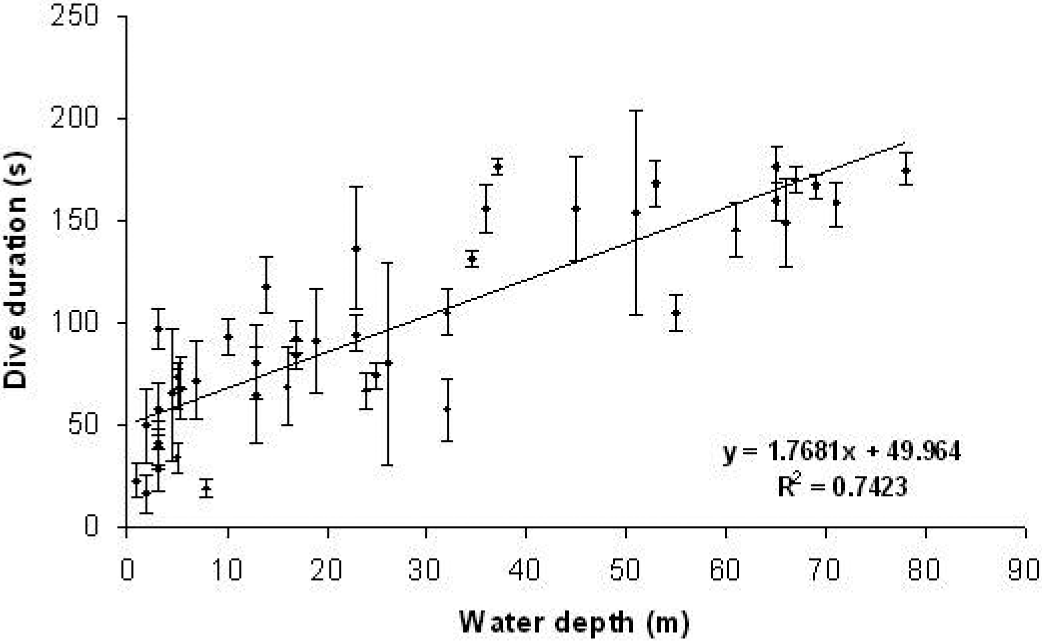

Figure 2. Relationship between dive duration and water depth (i.e., dive depth) when females with pups were foraging (r = 0.861, $n = 45$, $p < 0.0005$), including regression line

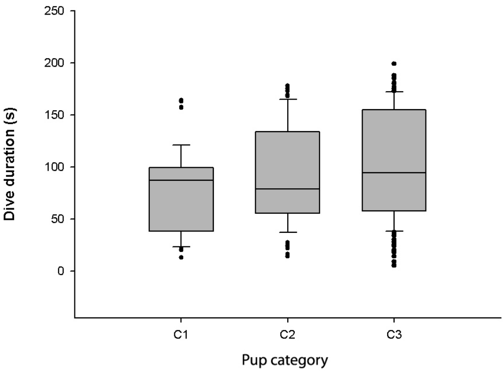

Figure 3. Box-whisker plots of dive durations for females with pups of different age categories (C1, C2, and C3), showing the medians as lines; 90th, 75th, 25th, and 10th percentiles as vertical boxes; and range bars and outliers as dots (Kruskal-Wallis Test: $\chi^2 = 6.838$, df = 2, $p = 0.033$; number of dives of females with C1 pups = 37, with C2 pups = 78, and with C3 pups =186).

foraging locations different from the available depth distribution of the bay (Table 2; $n = 17$, $\chi^2 = 3.377$, df = 3, $p = 0.337$). However, mothers of C2 and C3 pups foraged significantly differently from the available depth distribution in the bay (Table 2; $n = 35$, $\chi^2 = 9.131$, df = 3, $p = 0.028$ and $n = 94$, $\chi^2 = 28.223$, df = 3, $p < 0.0005$, respectively) and showed a preference for the depth ranges of 0 to 20 m (representing 46.4% of the bay) and 61 to 80 m (accounting for 4.9% of the bay). The nonrandomness of observation points as well as the small sample sizes, however, make a caveat regarding the statistical significance of some results necessary. In general, females with pups appeared to feed less than expected in water depths of 21 to 40 m and 41 to 60 m (which represented 27.4% and 20.2% of the bay, respectively).

Discussion

Females with pups did not significantly select for different foraging depths based on pup age, but dive durations varied significantly and showed an increase with older pups and a wider range. Females with C2 and C3 pups used water depths differing significantly from their proportionate availability in the bay, and they preferred shallow and deeper waters over intermediate depths. There was no significant difference for feeding locations regarding water depth of females with C1 pups, probably due to the small sample size.

As pups grow and their activity level increases, their energy demands rise. To provision for larger pups, females increase the proportion of their daily activity budget spent feeding (Osterrieder, 2009). Females with pups of all age categories preferred to forage in shallow water 0 to 20 m deep. Shallow water (5.0 m) was also favored in previous studies

Table 2. χ^2 results for each pup category (C1, C2, and C3) comparing the geographical distribution of observed feeding dives relative to the depth distribution of the bay

Pup category	*n*	χ^2	df	*p*
C1	17	0.337	3	0.337
C2	35	9.131	3	0.028*
C3	94	28.223	3	< 0.0005**

* significant
** highly significant

of females with pups compared to single females (7.9 m) (Garshelis, 1983) and to adult male sea otters (all females, 9.7 m; males, 22.4 m) (Bodkin et al., 2004). These areas are generally shallower than Simpson Bay.

The median feeding depths found in this study were 13.0 to 18.5 m for all females with pups. Compared with the minimal availability (6%) of deep waters (> 61 m), our results indicate that females, especially those with larger pups, used deeper water of 61 to 80 m relatively more often than shallow water. This was not significant, however, probably due to the small sample size of measured water depths.

Garshelis & Garshelis (1984) conducted their study in Gibbon Anchorage which is shallower (generally < 12 m deep) than Simpson Bay. They observed the tendency for females with larger pups to forage in shallower water and females with smaller pups to forage in deeper water outside of Gibbon Anchorage. They hypothesized that it is easier for larger pups to learn foraging behaviour in shallow water, whereas females foraging for themselves and much smaller pups may prefer deeper waters. Furthermore, it is important to keep in mind that all locations in Simpson Bay are accessible to bald eagles, posing a persistent danger to small sea otter pups (Krog, 1953; Sherrod et al., 1975; Anthony et al., 2008). Feeding outside of Gibbon Anchorage may be safer with small pups which always float on the surface, making them vulnerable to eagle predation when very young. Bald eagles are assumed to prey on pups while the mother dives for food. All pups of known age taken by bald eagles would have been C1 pups in this study (Sherrod et al., 1975). Females with older pups may prefer shallow, nearshore areas,

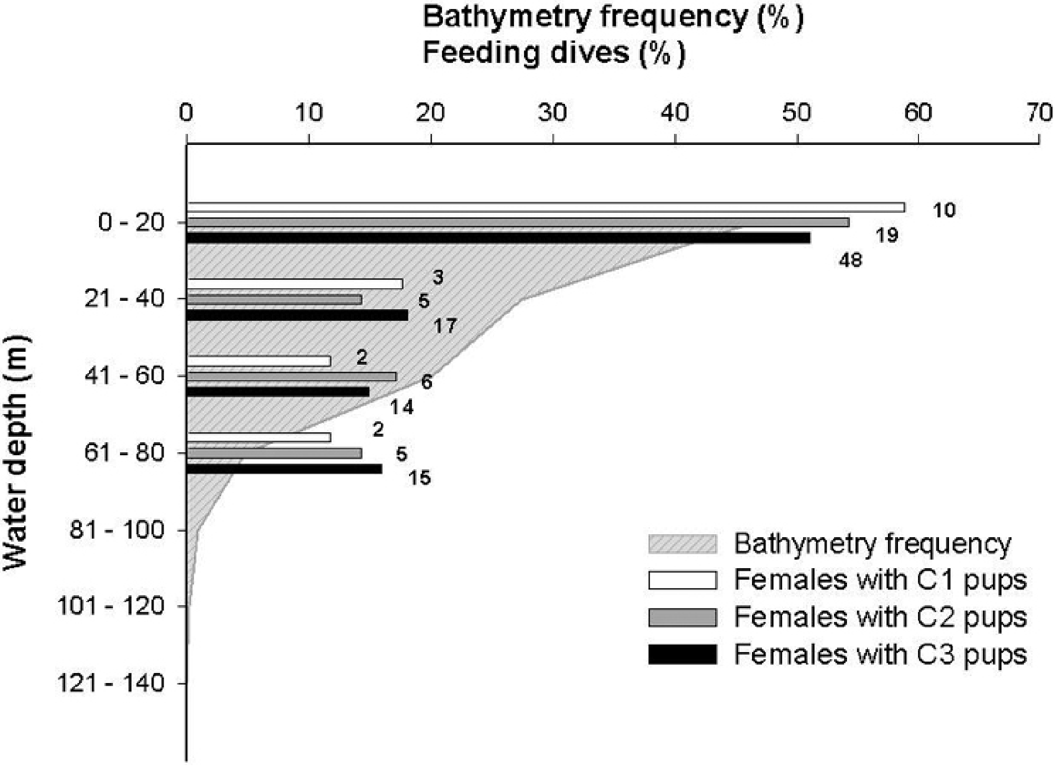

Figure 4. Percentage of foraging dives by females with different categories of pups as a function of water depth and the percentage of water depth occurrence in Simpson Bay; numbers indicate sample sizes: C1, *n* = 17; C2, *n* = 35; and C3, *n* = 94.

allowing pups to learn foraging skills. According to Garshelis & Garshelis (1984), home range size as well as distances travelled decrease with increased pup age.

Foraging dives became longer with increasing water depth (Figure 3; Estes, 1977; Estes et al., 1981; Kvitek et al., 1993; Bodkin et al., 2004) and, consequently, females left their pups unattended for longer periods at the surface while feeding in deeper water. According to other authors, variation in dive duration can be explained mostly by dive depth (Garshelis, 1983), but it is also influenced by prey type (Estes et al., 1981; Kvitek & Oliver, 1988; Kvitek et al., 1993; Laidre & Jameson, 2006). At times, sea otters in Simpson Bay were observed to feed on blue mussels (*Mytilus edulis*) from intertidal rocks (this study); and in other locations, mussels represent a large portion of the sea otter diet (Barnes, 2002). Feeding mainly on mussels, however, is not common in Simpson Bay, probably due to their small size and lower energy content per prey item relative to clams (e.g., Butter and Littleneck clams) (Garshelis, 1983). Females with pups in Simpson Bay mainly consume clams in various water depths (82%), whereas other prey, such as crabs, sea stars (each 6%), and mussels (2%), represent only a minor part of their diet (study of 2001-2004 + 2007; R. Wolt, pers. comm., October 2008). In a previous study, clams were also the primary prey in Simpson Bay (Garshelis, 1983), which agrees with other observations in other soft sediment habitats in Prince William Sound (Kvitek et al., 1988, and references therein; Kvitek et al., 1992, 1993). As these benthic prey species require foraging dives to the seabed, water depth is believed to be the dominant factor influencing dive duration in this study. Hence, the increasing dive durations for females with older pups support the assumption that they tended to forage in greater water depths.

There appears to be an advantage to feeding in deeper waters because females, especially those with large pups, fed disproportionally more in the depth range of 61 to 80 m (females with C3 pups: 16% of total foraging, but only 5% of bathymetry), although older pups were already able to dive and feed to a small degree themselves when in shallow waters (*cf.* Krebs, 1978). With females feeding in deep water, however, the pup was unlikely to reach the bottom to capture prey. Unfortunately, there are no data available on size distribution, biomass, abundance, and burrowing depths of prey species in Simpson Bay. In an earlier study in another soft sediment habitat around Kodiak Archipelago, Kvitek et al. (1992) observed a preference for large prey and a change to deeper water depths after prey depletion in shallower areas. Prey depletion is unlikely to take place in Simpson Bay as females with pups did most of their feeding dives in shallow water (0 to 20 m), indicating that prey was not yet depleted. Around Kodiak Archipelago, biomass and prey are more abundant in 10 m depth than at 5 m (Kvitek et al., 1992). Furthermore, in California, sea otters prefer to prey on infaunal bivalves with shallower burrowing depths (Kvitek et al., 1993). If at least one of these patterns is also true for Simpson Bay, then it might provide a possible explanation for the increased deep water feeding, especially with older pups. It might be that prey abundance is higher or prey size is larger and, therefore, the energy content is higher or prey has shallower burrowing depths and are thus easier to capture. To answer these hypotheses for Simpson Bay, future research will need to quantify the distribution of available prey, its caloric content in different water depths, as well as its living habits (burrowing depth).

Bodkin et al. (2004) observed that with increasing foraging depth, the number of foraging dives decreased, indicating that longer dives were offset by more energy obtained per dive. Therefore, females with C3 pups may choose a shallow area to allow their pups to practice foraging skills and at other times deeper waters to obtain sufficient nourishment to maintain their metabolism. Also, with increased pup size, bald eagle predation is less likely, allowing the female to leave the pup at the surface for longer periods while feeding in deeper water. Such complex behaviour patterns, however, have not been observed for individual females with pups yet.

A shift in prey items with different aged pups (M. Staedler, pers. comm., 12 January 2009) might also cause females to change their foraging locations. Although clams appear to be predominant in the diet in this region regardless of pup age, this hypothesis needs to be tested in future studies because of the small sample size in the study cited above (R. Wolt, pers. comm., October 2008).

In this study, female feeding behaviour showed a bimodal preference for shallow (0 to 20 m) and deep (60 to 80 m) water depths, with a trend for females with small pups (C1) to prefer shallower water. Deeper waters were used more often than expected relative to available habitat by females, especially with C3 pups.

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