ACTIVITY BUDGET, FIELD METABOLIC RATE, AND FORAGING

ECOLOGY OF FEMALE SEA OTTERS (*Enhydra lutris kenyoni*) WITH

DEPENDENT PUPS IN ALASKA

A Dissertation

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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May 2014

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Sea otter (*Enhydra lutris kenyoni*) foraging behavior and prey preference (2001-2004) and the behavior and activity budgets of females with dependent pups (2005-2010) were studied during the summer (June-August) in Simpson Bay, Prince William Sound, Alaska. Unlike most previous studies of sea otters which were conducted in coastal areas with a rocky benthos and kelp canopy, the benthic habitat in this study was primarily soft sediment (mud or mixed mud and gravel) with no canopy-forming kelps.

Foraging behavior and prey preference. A total of 1,816 foraging dives from 211 bouts were recorded. 87% of foraging dives were successful, and 44% of the prey was identified: 75% clams, 9% Pacific blue mussels, 6% crabs, 2% scallops and a variety of other invertebrates. Significantly more prey items/area were brought up from mixed mud/gravel than mud (p-value <0.0001). Sea otters in Simpson Bay have relied heavily on bivalves for the past 20 years, and the summer population has been constant for at least the past twelve 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 peak summer density of 4.3 adult otters km^{-2} for the past twelve years and probably longer.

Behavior and activity budgets of females with dependent pups. Females with dependent pups spent the greatest percentage of the day resting (42%), about equal percentages foraging (18%), grooming (15%) and swimming (15%), and the remainder

swimming slowly (8%) and interacting (2%). The estimated FMR was 12.69 MJ day^{-1}. Sea otters reoccupied the study area in the early 1980s, and the population has been stable for over a decade. However, the time spent foraging is more similar to areas that have been recently occupied. The relatively small amount of time spent foraging may indicate that geographic differences (structure of the near-shore community: substrate, water depth, kelp canopy, prey assemblage, and competitors) may play a greater role in determining the amount of time spent foraging than population status.

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INTRODUCTION

Brief History of the Sea Otter in Prince William Sound (PWS)

Sea otters (*Enhydra lutris*) historically occurred throughout most of the coastal regions of the North Pacific rim, from northern Japan to Baja California (Kenyon 1969). Total population in the early 1700's has been estimated between 150,000 (Kenyon 1969) and 300,000 individuals (Johnson 1982). Commercial harvest of sea otter pelts in North America began shortly after Russian exploration in 1741 (Larson et al. 2012, U.S. Fish & Wildlife Services, Marine Mammal Management 2011). One hundred and seventy years later, sea otters were nearly extinct throughout much of their former range. With probably fewer than 2,000 animals left, they were given protection under the International Fur Seal Treaty in 1911. Only 13 isolated remnant populations remained, one of which was in Prince William Sound (Kenyon 1969). In 1959, Lensink (1962) estimated the population in Prince William Sound at 1,000-1,500, and by 1974 the Alaska Department of Fish & Game estimated it had grown to 5,000 (Pitcher 1975). Today, sea otters have reoccupied most of their former range (Estes 1990, Kenyon 1975) although the size of regional populations remain dynamic (Bodkin et al. 2002, Doroff et al. 2003).

On March 24, 1989 the tanker Exxon Valdez ran aground on Bligh Reef, spilling 11 million gallons of crude oil which affected approximately 1,300 miles of Alaska's coast (Exxon Valdes Oil Spill Trustee Counsel 2014). Sea otters suffered the greatest

mortality among oiled mammals (Garshelis and Johnson 2013) because they rely on an air layer trapped within the fur for insulation and their behavior of resting and swimming at the surface brought them into greater contact with the oil. Before the spill, the U.S. Fish and Wildlife Service estimated the population in PWS to be 12,000 animals (2008-b). Over 2,500 animals on the western side of PWS are thought to have died as a result of the spill (Garrot et al. 1993). Although there is still debate as to the long term effects of the spill, the population in PWS is currently estimated to be close to pre-spill levels (U.S. Fish and Wildlife Service 2011).

Keystone Species

Sea otters have been considered classic examples of a keystone species (Paine 1969, Estes and Palmisano 1974, Power et al. 1996) due to their top-down influence on macro-invertebrate populations, especially sea urchins, and consequent effects on kelp forest communities. The relatively recent recolonization of areas that were historically extirpated of otters has enabled the study of this top-down foraging pressure on coastal ecosystems (Estes and Duggins 1995, Kvitek et al. 1992, Estes and Bodkin 2002).

Robert T. Paine coined the term "keystone species" and defined it as those species whose activity and abundance determined "the integrity of the community and its unaltered persistence through time . . ." (Paine, 1969). Power et al. (1996) redefined keystone species more generally as one whose overall impact on a community is disproportionately large relative to its abundance. He also noted that they are " . . . not

necessarily a dominant controlling agent in all parts of their range or at all times, but instead play keystone rolls only under certain conditions".

The impact that sea otters have on benthic invertebrates when repopulating an area is dramatic and fairly consistent because they quickly reduce the number and mean size of many prey species (Estes et al. 1982, Kvitek and Oliver 1992, Estes and Duggins 1995), especially the more easily captured, epibenthic species such as sea urchins. This predation allows large kelp beds to flourish, which are habitat for many other species. However the importance of their top-down pressure in establishing and maintaining kelp forests has been questioned. Foster and Schiel (1986), Cowen (1982), and Foster (1990) concluded that sea otters have an effect on community structure but physical disturbance is more important. Estes and Douggins (1995) used 153 sites from 7 locations from southeast Alaska and the Aleutian Islands over a period of 15 years to look at percent cover and type of near shore kelp, urchin abundance and biomass, and presence/absence or reintroduction of sea otters. They found that where otters were present, kelp densities were variable but high, and urchin biomass was consistently low. Where otters were absent, kelp densities were invariably low and urchin biomass high but variable. So, at least in the context of kelp forests, the designation of keystone species seems appropriate. Previous research on sea otter behavior and ecology has focused primarily on areas with a rocky benthos and canopy-forming kelp. However, the sea otters' range includes large areas of soft sediment with no canopy-forming kelp beds, and the ecological role of sea otters in these communities is less well studied and possibly more complex (Kvitek et al. 1992).

Foraging Behavior

To thermoregulate in the cold 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 three main prey categories for sea otters in eastern and central Prince William Sound (Calkins 1978). Clams, including butter clams (*Saxidomus gigantea*) and Pacific littleneck clam (*Protothaca staminea*), are by far the most important prey for otters in Simpson Bay comprising between 65-75% of all identified prey (Wolt et al. 2012). Research on clam species in PWS is limited to the intertidal zone, with the highest concentrations between +0.5 and -0.5m (Paul and Feder 1973, Nickerson 1977). However, from observing foraging sea otters in my study, we know clams are found throughout the bay. Gravity core sediment samples indicate that,

similar to the intertidal zone, clams in Simpson Bay are found more frequently in mixed mud/gravel than mud (I. Davis, unpubl. obs).

Since all prey species found in Simpson Bay 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 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.

Geology and Hydrology of Simpson Bay

The geology of Simpson Bay has been influenced primarily by glaciation. During the last glacial maximum (15,000 BP [Mann and Hamilton 1995]), all of Prince William Sound (PWS) was covered out to the continental shelf by the Cordilleran Ice Sheet (Calkins et al. 2001). Simpson Bay has been described as a turbid, outwash fjord with high watershed/basin surface area ratio (≈8:1), and easily erodible bedrock (Noll et al. 2009). Using side scan sonar, swath bathymetry, and seismic profiles, a detailed bathymetric map has been made, and the subsurface sediment is generally classified as

one of three categories: outcrop (hard rocky areas), mixed mud/gravel (coarse sediment) and organic-rich estuarine mud. There is an average accumulation rate of approx. 0.5 cm year^{-1}, but that this varies with fresh water input and watershed surface area (Noll et al. 2009).

Hydrographic data show generally weak subsurface currents (5–20 cm s^{-1}), while faster currents are found along shorelines, outcrops (Noll et al. 2009). These currents are generally driven by large tidal fluctuations, up to 15 feet (Gay and Vaughan 2001, NOAA Tide Tables for Cordova 2013).

Time/Energy Budget

Studies of sea otter behavior have been conducted in Alaska, California, and Washington using different methods with considerable variability in activity budgets, which were first proposed to assess the status of marine mammal populations (Eberhardt 1977). As sea otters have large energy requirements due to an elevated metabolic rate (Costa and Kooyman, 1982), previous studies focused on foraging behavior. Estes et al (1986) suggested that time spent foraging may be the best indicator of a population's status, as food is commonly the limiting resource (Kenyon 1969). Foraging time would be expected to increase as a population grows and approaches equilibrium density (Eberhardt 1977), although not all studies have shown consistent results. Some of the disparities may be attributed to the use of different methods (observation vs. tagging), constraints of study design (sample size, period of data collection) and uncertainty about

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population status (Bodkin et al. 2007). Population studies of marine mammals are difficult for a variety of reasons. Among marine mammals that breed on land (seals, sea lions, fur seals, walrus), counts during the breeding season when they gather on land or some sort of mark/tagging are common. None of these techniques is well suited for sea otters as they do not consistently spend time on land, capturing them in the water is difficult, and they readily remove tags attached to their fur or hind flippers. Fortunately, sea otters are relatively easy to observe as most of their time is spent at the surface. Behavior is usually divided into 3-5 categories: foraging, grooming, swimming and resting are the most common. Several studies used radio transmitters and/or abdominally implanted archival time-depth recorders (TDRs) to compile time budgets from a small number of animals in California and Alaska (Estes et al. 1986, Garshelis et al. 1986, Ralls and Siniff 1990, Gelatt et al. 2002, Bodkin et al. 2007). Foraging dives deeper than 2 m are easily distinguished, and data are gathered continuously for months. The disadvantage of this approach is that behavior can only be classified as foraging, resting or other (very shallow forging dives are indistinguishable from travel or grooming), so some visual observations are usually made to validate the recorded data. At the other extreme are studies that employ scan-sampling to observe as many animals as possible (Altmann 1974, Estes et al. 1982, Estes et al. 1986, Walker et al. 2008). However, this method is limited by access to suitable locations that can be reliably scanned from shore. Spatial distribution may bias samples (Gelatt et al. 2002), as some behaviors are more conspicuous than others (resting and grooming vs. foraging and swimming). In addition, the sex of the otters observed by scan sampling is often unknown.

Previous Studies of Female Sea Otter Activity Patterns

Radio Telemetry – Garshelis et al. (1986), Ralls and Siniff (1990), and Gelatt et al. (2002) used radio telemetry to determine the activity budgets of sea otters. Garshelis et al. (1986) conducted their study at Green Island (central Prince William Sound, Alaska) and Nelson Bay (one bay east of Simpson Bay) where radio transmitters were attached to the hind flippers of 26 adult female otters. Activities were categorized as foraging, resting or swimming based on the frequency and duration of interuptions of the radio signal. The authors concluded that, over a 24-h period, solitary females and females with pups allocated 37% of their time to foraging, 51% to resting and 12% to swimming for females with pups.

Gelatt et al. (2002) conducted their study around Amchitka Island, Alaska, where radio transmitters were surgically implanted in 48 adult female otters (22 had pups of various ages) that were monitored every 10 min for 24-h twice per week. Activities were categorized as foraging, resting and other. Using similar assumptions about signal patterns, the time budget from that study was similar to that of Garshelis et al. (1986) with adult female sea otters allocating 38% of their time to foraging, 48% to resting and 14% to other activities. In California, Ralls and Siniff (1990) found that over a 24- h period females with dependant pups (n=6) foraged 40% of the time, rested 44.7%, and spent 15.7% in other behaviors.

Time-Depth Recorders (TDR) – Bodkin et al. (2007) conducted their study near Cross Sound, located in southeastern Alaska. Radio transmitters and archival time-depth recorders were surgically implanted in 21 adult sea otters of which 16 were females.

Each TDR was programmed to record depth at 2 s intervals for at least 39 days. Color-coded tags were attached to the hind flippers of each individual to allow for visual recognition. Instrumented animals were observed daily from both shore and boats. Activities were categorized as foraging, resting, and other (swimming, grooming, and interacting). The females allocated 40% of their time to foraging and 52% to resting, but the authors admit that non-diving behavior may have been underrepresented.

Scan Sampling – Estes et al. (1986) used the scan-sampling method to determine the activity budget of sea otters in a rocky reef and kelp forest habitat in central California. Behavior was categorized as foraging, resting or other by sampling a group of otters in an area at 30 min intervals with binoculars. Due to low luminance and poor visibility, they could not use this method at night, so the time period for the study was dawn to dusk. The study concluded that the otters allocated 24% of their time to foraging, 59% to resting and 17% to other behaviors.

Walker et al. (2008) based their study design on the methods used by Estes et al. (1986). Scan sampling was used to determine the activity budget of translocated sea otters in rocky coastal habitat along the Olympic Peninsula in Washington State, an area known to be below equilibrium density. Sampling occurred at 30 min intervals using binoculars and a spotting scope. The study concluded that sea otters allocated 62% of their time to resting, 20% to grooming, 8% to foraging, 8% to swimming and 2% to other behaviors.

Individual Follows and Instantaneous Sampling – Pearson et al. (2005) and Finerty et al. (2009) conducted their studies in Simpson Bay, Alaska, the same location as this

study. Activities for territorial male otters only were categorized as foraging, grooming, interacting with other otters, swimming, patrolling, and resting. Pearson et al. (2005) concluded that during daylight hours, male otters allocated 30% of their time to foraging, 15% to grooming, 11% to interacting with other otters, 17% to patrolling, 18% to resting, and 9% to swimming. Finerty et al. (2009) produced a 24-h activity budget and observed the following allocation of time: foraging 14%, grooming 19%, interacting 5%, patrolling 9%, resting 27% and swimming 26%.

In the current study we used we used focal follows (Mann, 1999) with instantaneous behavioral samples (Altmann, 1974; Lehner, 1996; Mann, 1999; Pearson et al., 2005) to compile a detailed 24-h activity budget for female sea otters with pups during the summer (June to August), a period when many pups are ca. 1-3 months in age. Field Metabolic Rate (FMR) was then estimated using metabolic rates for each behavior that were measured in captive otters (Yeates et al. 2007). For the sake of brevity, the term population refers to animals in Simpson Bay with the understanding that this is a subset of the several thousand animals in Prince William Sound, and the daily and monthly movements of some animals likely encompass a much larger area.

Overview of the Current Study

My research 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, occupied for about 30 years (Gilkinson 2004, Pearson and Davis 2005, Finerty et al. 2007,

Gilkinson 2004, Noll et al. 2009). 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, Osterrieder and Davis 2010, 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 behavior and habitat

associations.

FORAGING BEHAVIOR AND PREY PREFERENCE OF SEA OTTERS

(*Enhydra lutris*) IN A PREDOMINANTLY SOFT SEDIMENT HABITAT[*]

Overview

Sea otter (*Enhydra lutris kenyoni*) foraging behavior and prey preference were studied from May-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 sediments with no canopy-forming kelps. A total of 1,816 foraging dives from 211 bouts were recorded. Overall, dives ranged in depth from < 5-82 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 was 27 m ± 19.5 and 1.89 min ± 0.88, respectively. Dive durations were all significantly different: male > unknown > female. Dive depths were correlated with bathymetry (percentage of the bay within a depth range) 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 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 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 where otters were extirpated 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).

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 three main prey categories for sea otters in eastern and central Prince William Sound (Calkins 1978). 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 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 predominately soft sediment habitat. 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 (Gilkinson 2004, Pearson and Davis 2005, Finerty et al. 2007, Gilkinson et al. 2007, Noll et al. 2009). 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, Osterrieder and Davis 2010, 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.

Materials and Methods

Study Area — Simpson Bay (ca. 60.6^o N, 145.9^o W), located in northeastern Prince William Sound, Alaska (Fig. 1), was used as the study site because of its protection from rough seas, reliable presence of sea otters 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 (Gilkinson 2004, Noll et al. 2009). There are no large-bodied kelps (e.g., *Nereocystes*) that form canopies, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*) and sieve kelp (*Agarum clathratum*) cover the benthos in many areas of the bay from the subtidal to a depth of

ca. 10 m (Davis unpub. obs.). This research was conducted under a Letter of

Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.
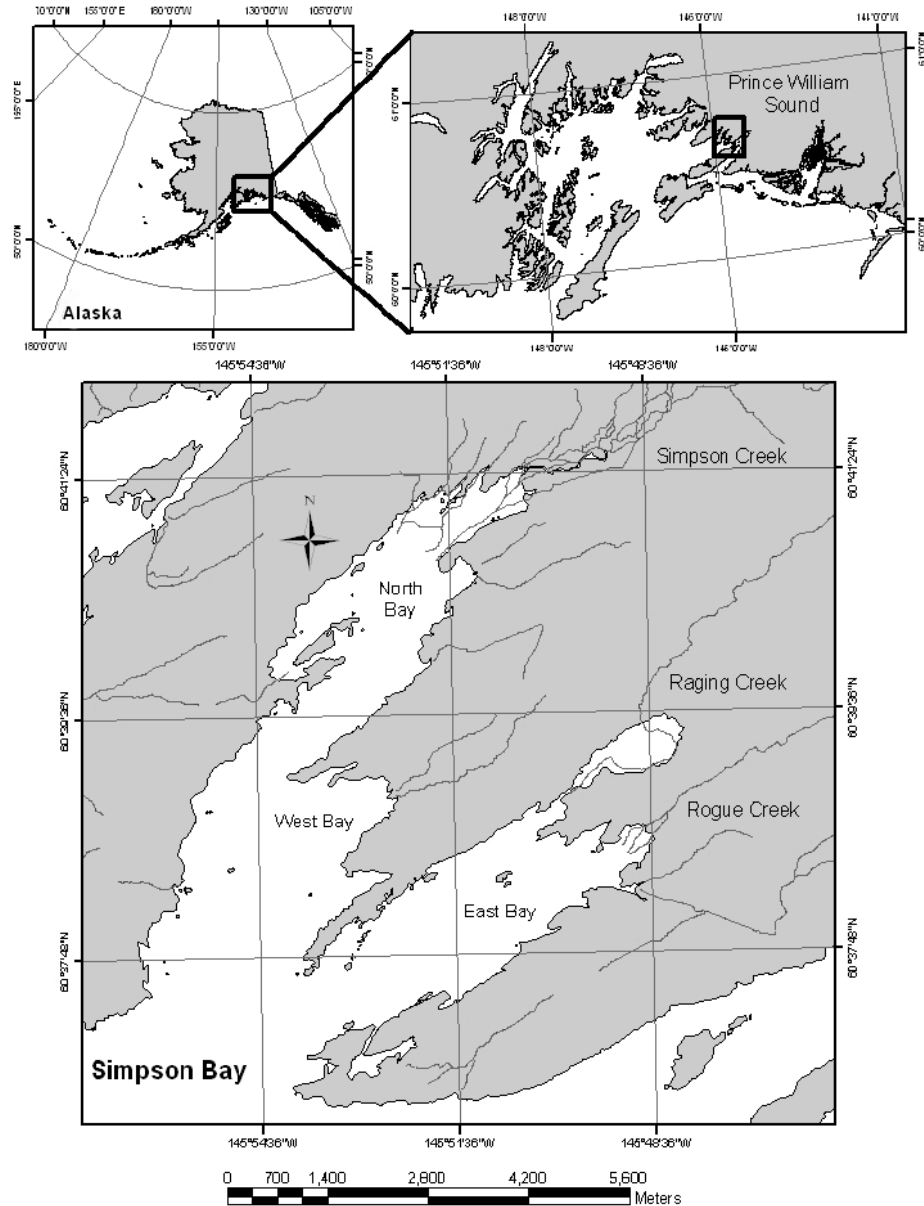
Figure 1. Simpson Bay, Prince William Sound, Alaska (Noll et al. 2005).

The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983-85 (Garshelis 1983, Rotterman and Simon-Jackson 1988, VanBlaricom 1988). Since 2002, it has been used during the summer (June-August) by an average of 119 ± 9.3 sea otters, including adults and subadults (91 ± 6.8) and pups (28 ± 3.8) with an average summer density of 5.7 otters km^{-1} (Davis, unpub. obs.). During the winter, the number of otters in the bay decreases to ca. 50 (Weltz unpub. obs.)

Foraging Behavior — We observed the foraging behavior of sea otters between June-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 working with an otter more than once during a 3-4 hr. 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, 2004]), and dive duration. When the otter surfaced, typically 30-50 m from the skiff, we

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identified each prey item to the lowest taxonomic level possible using 7-10x 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.

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 correspondance analysis was run using CANOCO (Version 4.5) to simultaneously quantify the relative influences of multiple characteristics associated with each dive (Terbraak and Verdonschot 1995). 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

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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

Dive Depth and Duration of Foraging Dives — A total of 1,816 foraging dives from 211 bouts (26 females, 38 males and 147 unknown sex) 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 < 5-82 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 m ± 19.5: 30 m ± 19.7 for males; 29 m ± 21.8 for females and 25 m ± 18.8 for otters of unknown sex. Adult males made significantly deeper dives than otters of unknown sex ($\rho < 0.001$), but there was no significant difference in average dive depths between males and females ($\rho = 0.124$) and females and otters of unknown sex ($\rho = 0.477$).
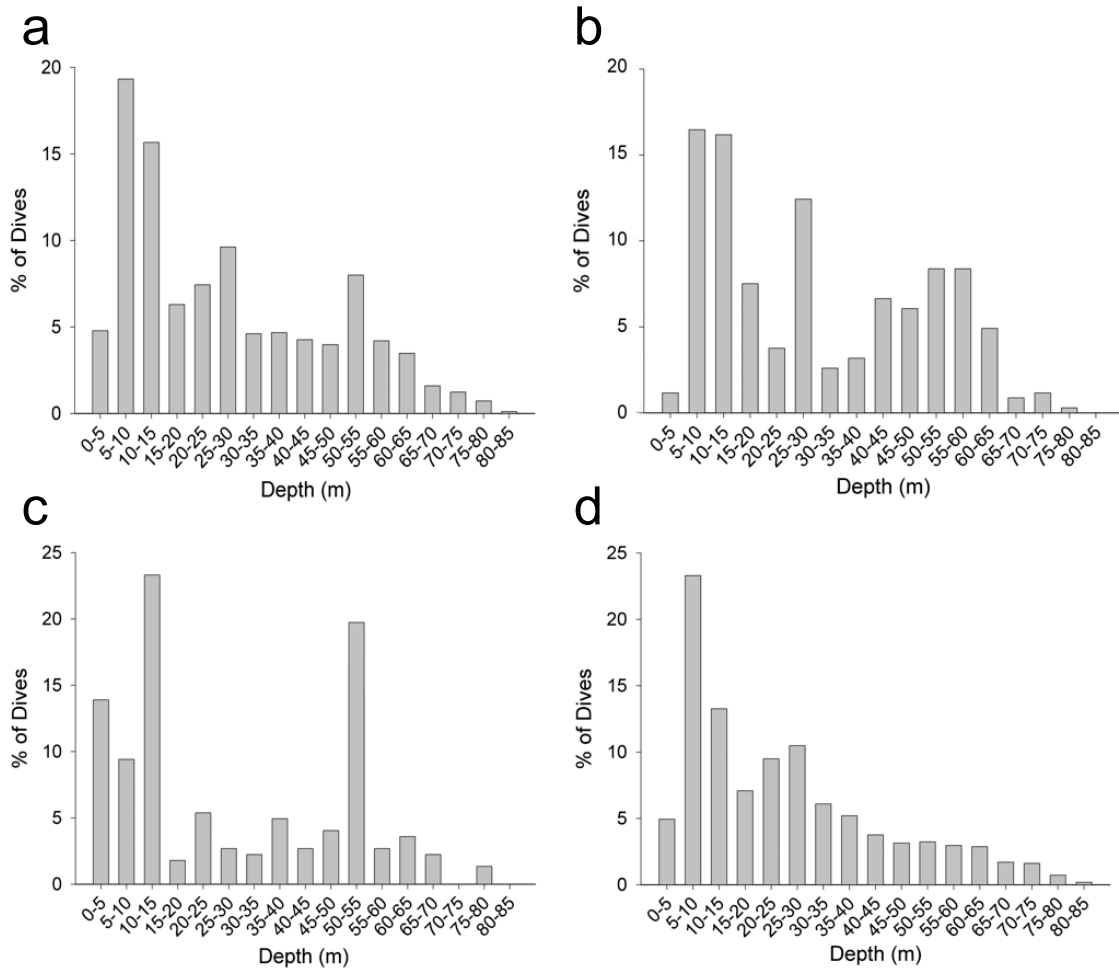
Figure 2. Distribution of foraging dive depths: (a) all otters (211 animals, 1816 dives); (b) males (38 animals, 388 dives); (c) females (26 animals, 251 dives) and (d) sex unknown (147 animals, 1177 dives).

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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 = 1,116 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 min ± 0.88; 2.05 min ± 0.77 for males; 1.69 min ± 0.84 for females; and 1.89 min ± 0.90 for otters of unknown sex. Average dive durations were significantly different: male > unknown ($\rho = 0.003$), male > female ($\rho < 0.001$) and unknown > female ($\rho = 0.006$). Dive durations showed a normal distribution from 0-4 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).
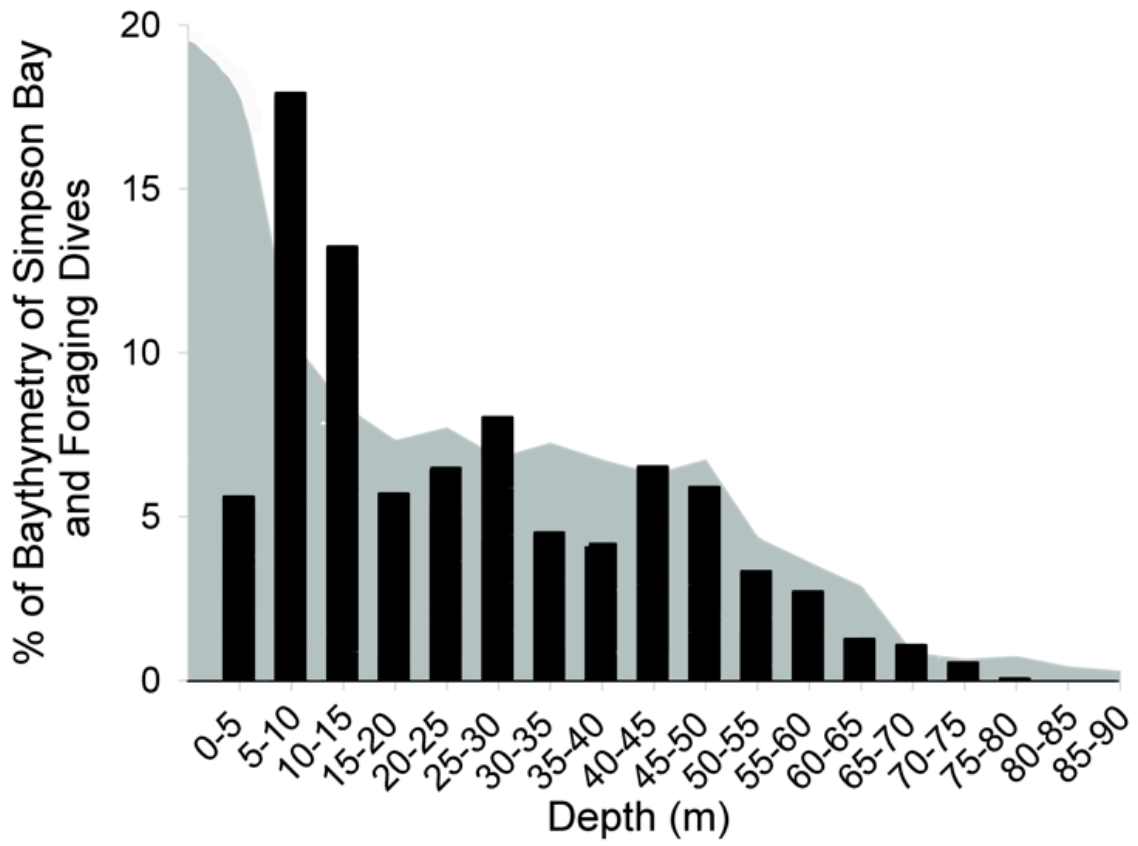
Figure 3. Distribution of sea otter foraging dive depths (bars) and the percentage of Simpson Bay within each depth range (shaded area).
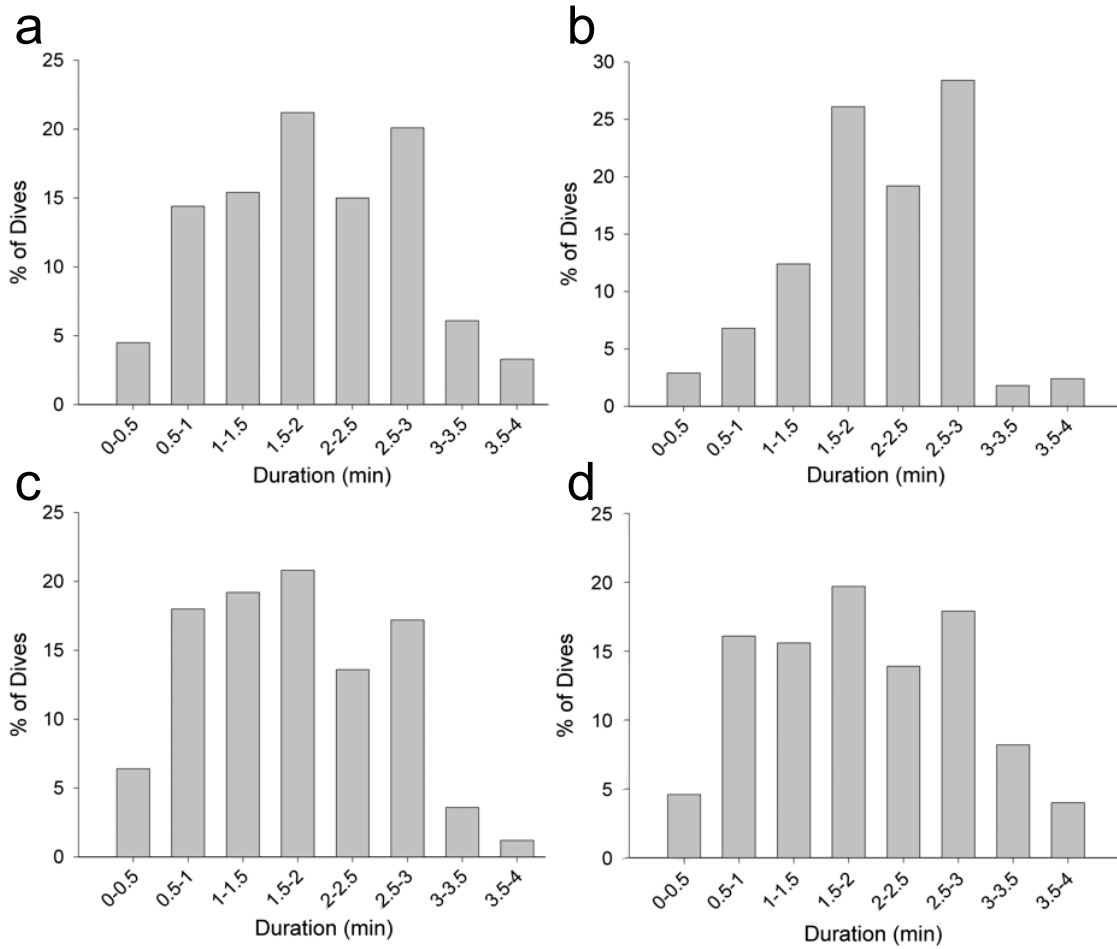
Figure 4. Distribution of foraging dive durations: (a) all otters (209 animals, 1704 dives); (b) males (38 animals, 333 dives); (c) females (26 animals, 251 dives) and (d) sex unknown (147 animals, 1116 dives).
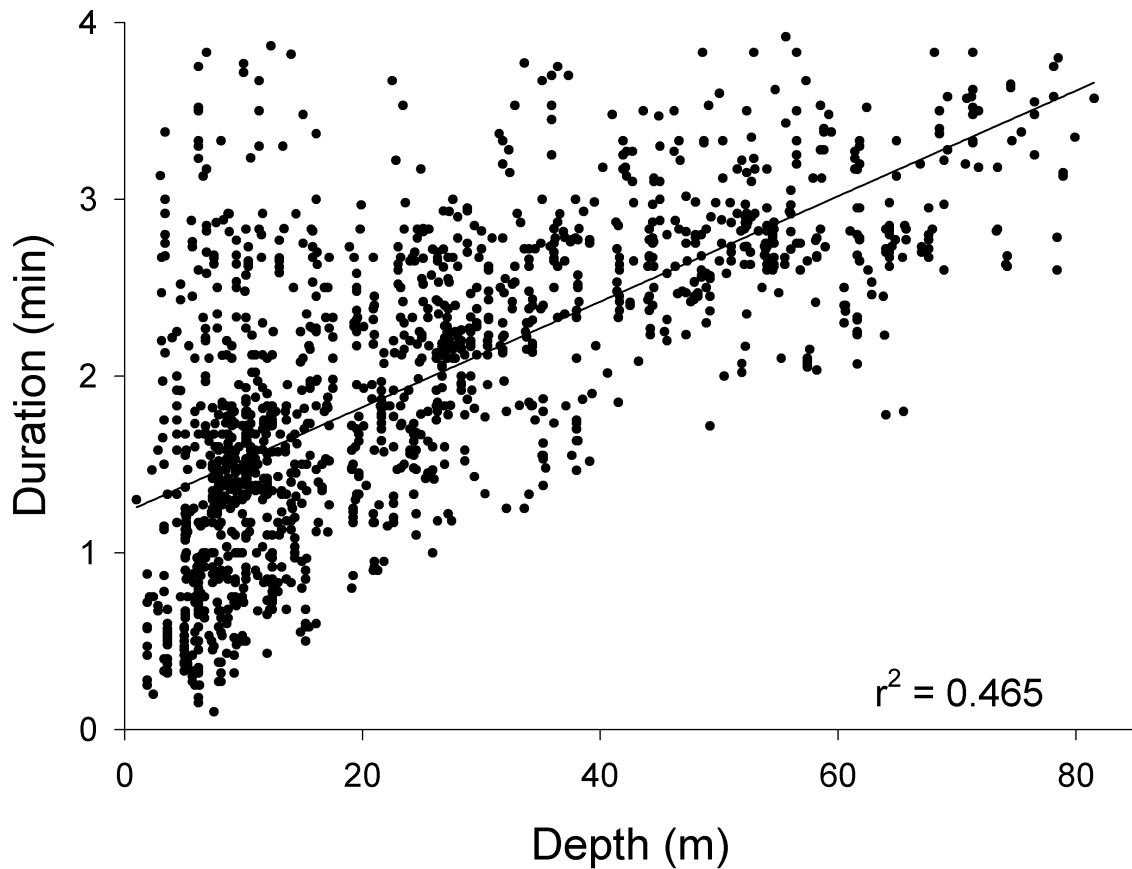
Figure 5. Successful foraging dive depth as a function of dive duration.

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%) ($\rho = 0.93$) (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*) 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).
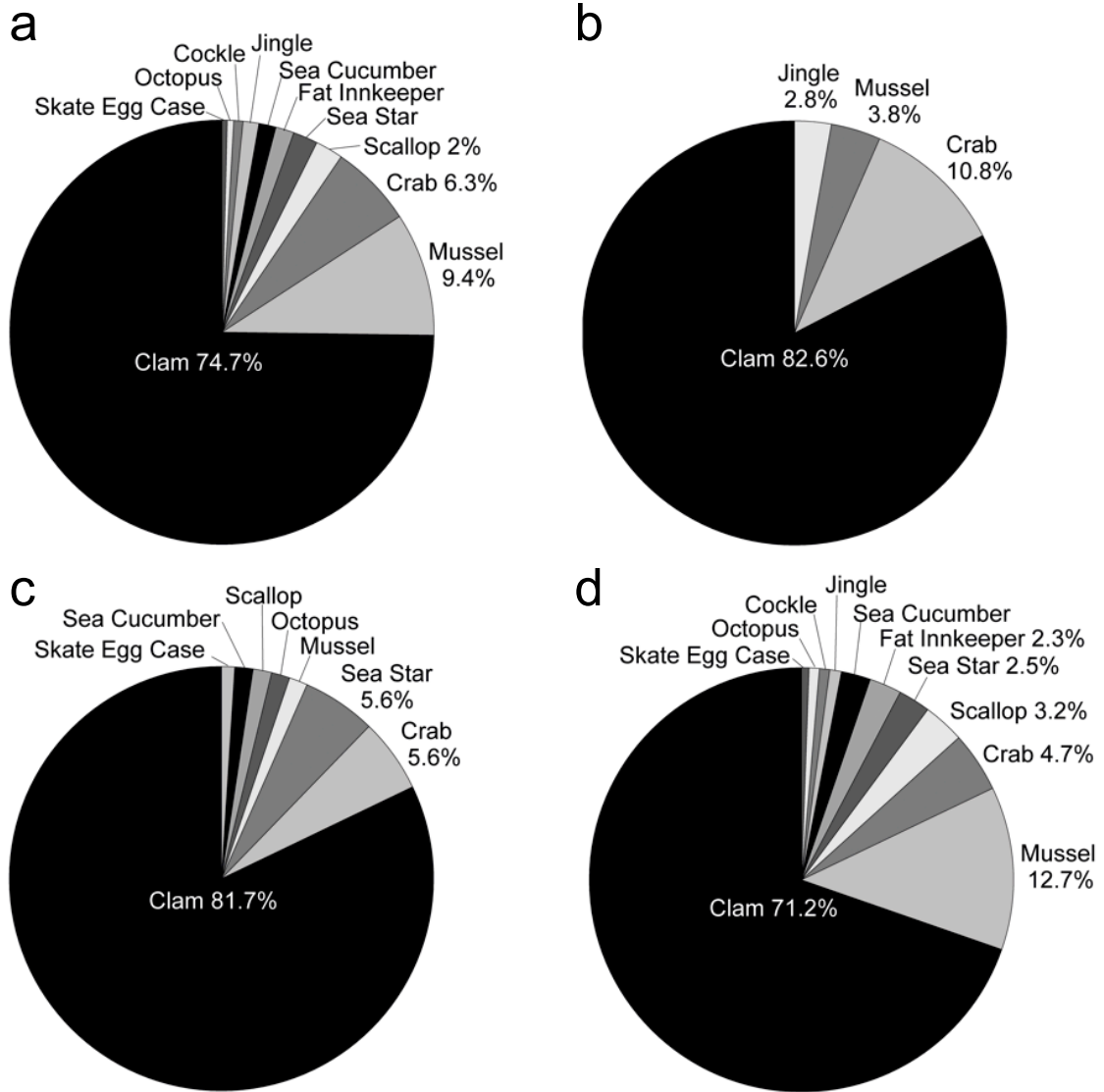
Figure 6. Percent distribution of identified prey for (a) all otters; (b) males; (c) females and (d) sex unknown. Prey items without percentages comprise less than 2% of the diet.

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	64	58	5	530	45
Total or Ave.	211	1816	1600	87	93	4.3	126	8.7	833	44.3

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 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 (ρ <0.0001) than otters of unknown sex, while the latter captured significantly more Pacific blue mussels (ρ <0.001) (Table 2). Males captured significantly more crabs (ρ <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 Correspondance 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 lead 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, 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 2 (vertical) were eaten primarily by females and otters of unknown sex. Prey found in the diets of all three categories (clams, mussels and crabs) are 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 are plotted 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 did find 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 a rather homogeneous system in the sense of being diverse but well mixed among individuals and across sex groups.
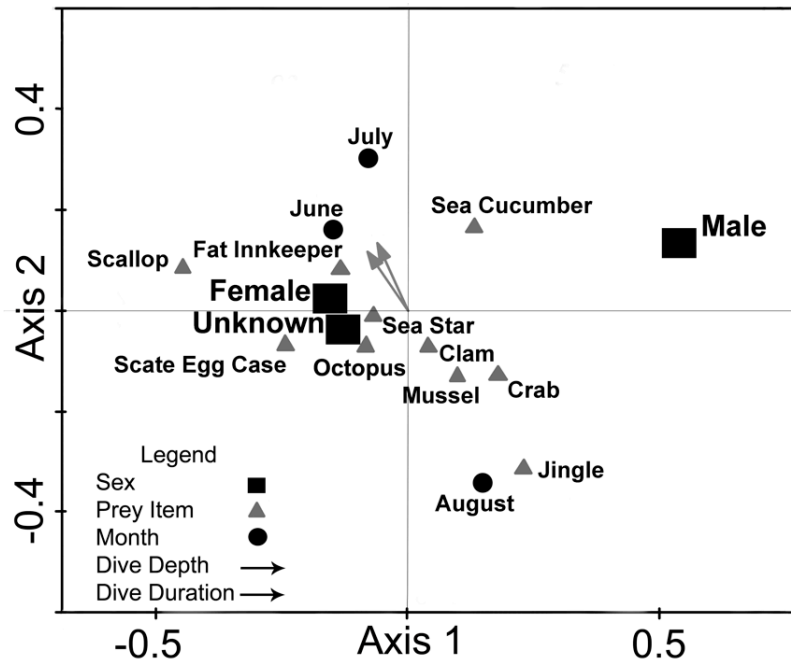
Figure 7. Canonical correspondence analysis (with year included as a covariable) to determine characteristics that best discriminate among dives by males, females and unknown sex. This analysis measures the relative strength of ecological gradients (axes 1 and 2) that are combinations of multiple explanatory 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).

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	P-value	Bonferroni correction	P-value	Trend
Clams*	<0.0001			Males & females > unknown
Mussels*	0.001			Unknown > males & females
Crabs*	<0.0001			Males > females & 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.

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. 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, summer (June-August) population of 119 sea otters since 2002 without a high degree of prey preference among males, females with pups and otters of unknown sex, which probably includes many females without pups and younger otters. However, we can not 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 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 believe the percentage of prey positively identified (44%) to be representative of 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 percent of the diet than reflected in our data.

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 made up 82% of the female diet, but the remaining 18% was divided among seven different prey groups. 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, 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 & Table 3).
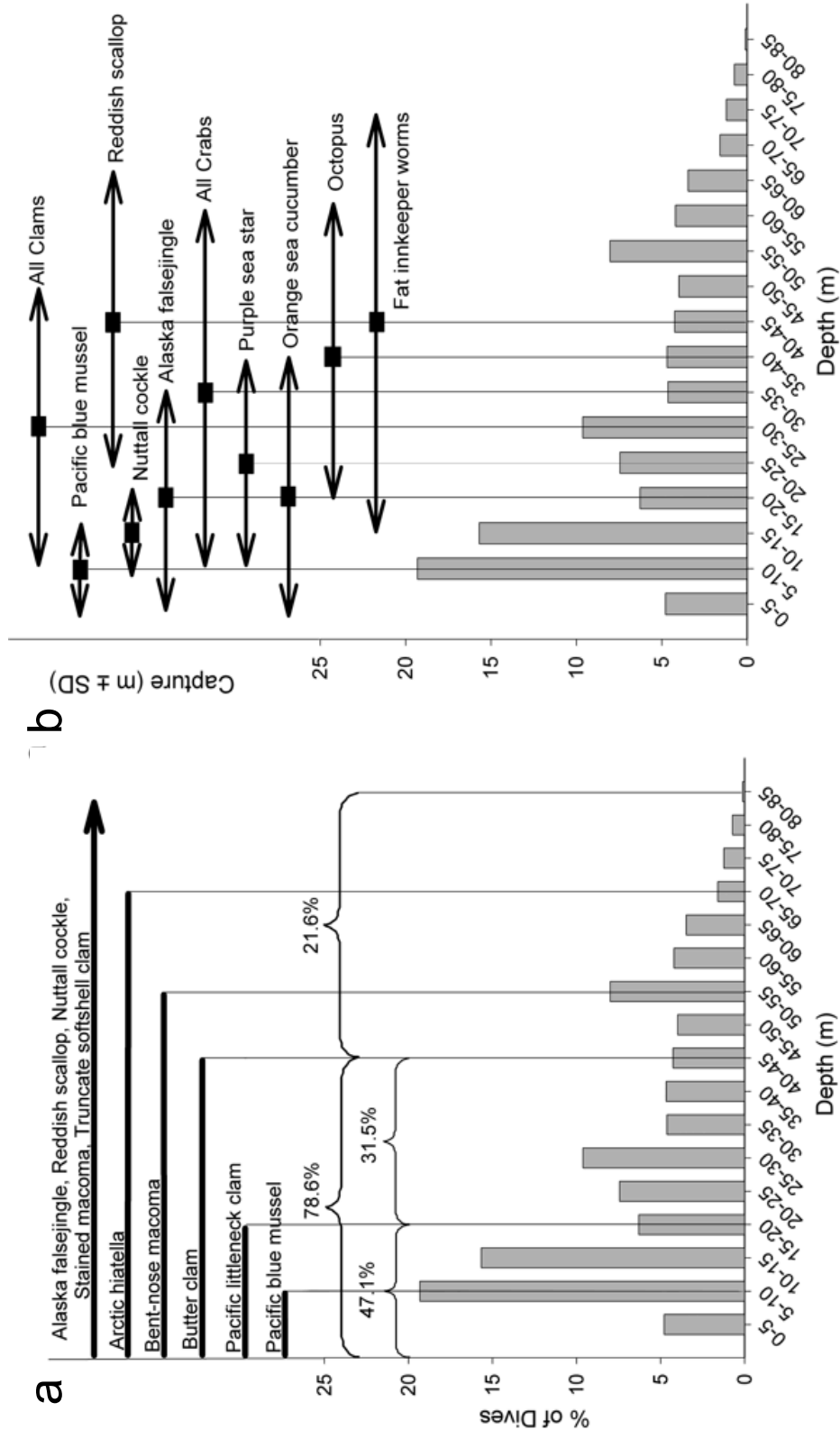
Figure 8. (a) Reported depth ranges for bivalves and distribution of dive depths for all sea otters in this study. (b) Average depth (±1 standard deviation) of capture for each prey group and distribution of dive depths for all sea otters in this study.

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

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 (1,950 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, Gershellis 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 2001-2004, 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 least the past nine years. As a result, they can not be described as recently established.

Dive 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 2004). As adult otters can regularly dive between 40-60 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 reflects the distribution of depths within the bay (Fig. 3). The additional peaks in foraging dive depths from 25-30 m and 50-55 m may reflect a multi-modal feeding pattern. The percentage of the bay from 10-50 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 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 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 unutilized. 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 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 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 MJ day^{-1} 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 kg ([19 MJ day^{-1} otter^{-1} x 60 otters x 365 days] / [0.9 x 3.18 MJ kg^{-1}]), of which 109,041 kg (75%) are clams and 36,347 kg are other species. If we divide the biomass of clams consumed by the area of Simpson Bay (21 x 10^6 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 clams m^{-2} yr^{-1} (109,041 kg clam / 0.048 kg clam^{-1} / 21 x 10^6 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 x 10^6 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 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.

HABITAT ASSOCIATIONS AMONG PREY CAPTURED BY SEA OTTERS IN

SIMPSON BAY, ALASKA

Overview

Using side scan sonar, the benthos of Simpson Bay has been classified as exposed rock, mixed mud and gravel, and mud with a high organic content. In this study data on the location and type of prey captured by sea otters were integrated with the three major categories of benthos. Foraging behavior of sea otters was observed between June and August of 2001–2013. A total of 1,775 successful foraging dives were recorded, and 1,979 prey items were identified. Of these, 1,420 had GPS positions that could be correlated with the sediment map. Most prey were found to some degree in all three benthic categories. In terms of the total number of prey items from each sediment type, all were significantly different from each other (mixed mud/gravel > mud > rock). However when the differing areas of the three sediment types are taken into account the only significant difference was between mixed mud/gravel and mud (mixed > mud p-value <0.0001). In terms of prey/area mixed sediment is significantly more productive.

Introduction

Geology and Hydrology of Simpson Bay – The surface geology of Simpson Bay has been shaped by glaciation. During the last glacial maximum (15,000 BP [Mann and Hamilton 1995]), Prince William Sound (PWS) and the coastline of south-central Alaska was entirely glaciated to the edge of the continental shelf by the Cordilleran Ice Sheet (Calkin et al. 2001). Today, Simpson Bay is a shallow, outwash fjord with high watershed/basin surface area ratio (≈8:1) and a shoreline of easily erodible bedrock (Noll et al. 2009). Using side scan sonar, swath bathymetry, and seismic profiles, the benthos of Simpson Bay has been classified as exposed rock, mixed mud and gravel, and mud with a high organic content. The average accumulation rate of sediment is ~0.5 cm year^{-1}, but this varies throughout the bay with fresh water input from various streams which depend on the size of the surrounding watershed (Noll et al. 2009).

Hydrographic studies showed generally weak subsurface currents (5–20 cm s^{-1}), while faster currents are found along the shoreline (Noll et al. 2009, Gay & Vaughan 2001). These currents are generally driven by large tidal fluctuations of up to 6 m (NOAA Tide Tables for Cordova 2013).

Prey – At least 150 species, primarily invertebrates, are known to be preyed on by sea otters (*Enhydra lutris*) including mollusks, crustaceans, echinoderms, cephalopods and fin-fish (VanBlaricom 1988; Estes and Bodkin 2002; Estes et al. 2003). Mollusks, crustaceans and echinoderms are the main prey for sea otters in PWS (Calkins 1978; Garshelis 1983; Garshelis et al. 1986; Doroff and Bodkin 1994; Wolt et al. 2012). Since

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these prey are benthic, the location of a dive can be used to determine dive depth and habitat-associations (e.g., sediment type).

Clams, including butter clams (*Saxidomus gigantea*) and Pacific littleneck clam (*Protothaca staminea*), are by far the most important prey for otters in Simpson Bay comprising between 65-75% of all identified prey (Wolt et al. 2012). Information on the distribution and abundance of clams in PWS is limited to the intertidal zone, with the highest concentrations between +0.5 and -0.5 m relative to the mean tide (Paul and Feder 1973, Nickerson 1977). However, recent research on prey preference and foraging location shows that otters forage on clams throughout the bay (Gilkinson 2004, Wolt et al. 2012). The objective of this study was to determine habitat associations of macroinvertebrates in Simpson Bay relative to benthic geomorphology. To accomplish this study, I integrated data on the location and type of prey captured by sea otters with three major categories of benthos (i.e., rock, mixed mud and gravel, and mud) that were modified from previously published data (Gilkinson 2004, Noll et al. 2005).

Methods

Study Site – Simpson Bay (ca. 60.6° N, 145.9° W), located in northeastern PWS, Alaska (Fig. 9), was used as the study site because of its protection from rough seas, reliable presence of sea otters 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.

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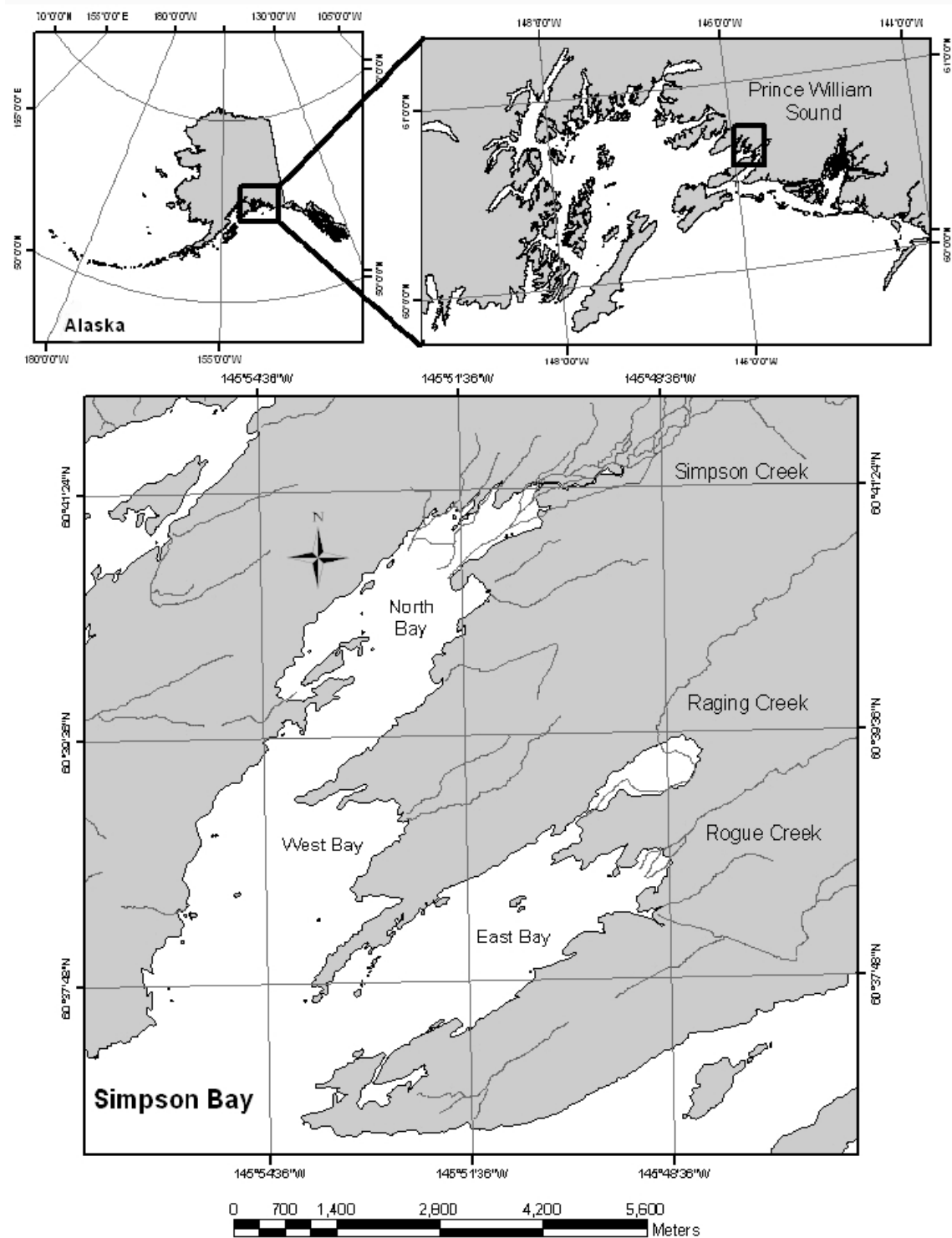
Figure 9. Simpson Bay, Prince William Sound, Alaska (Noll et al. 2005).

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 (Gilkinson 2004, Noll et al. 2005). None of the large-bodied kelps (e.g., *Nereocystis*) that form canopies are present, 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 approximately 10 m (R. W. Davis, pers. obs.). The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983-85 (Garshelis 1983, Rotterman and Simon-Jackson 1988, VanBlaricom 1988). Since 2002, it has been used during the summer (June-August) by an average of 119 ± 9.3 sea otters, including adults and subadults (93 ± 8.7) and pups (31 ± 6.9) with an average summer density of 5.9 otters km^{-1} (Wolt et al. 2012). During the winter, the number of otters in the bay decreases to ca. 50, 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 Observations – Foraging behavior of sea otters was observed between June and August of 2001–2013. 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 3–4h 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. Depending on

permitting for that year and the presence of a pup, we would either observe from a distance of ca. 30 m, or once the animal dove 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 [Noll et al. 2009, Gilkinson 2004]), and dive duration. When the otter surfaced 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.

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.

Bathymetry and Sediment – Detailed bathymetry and sediment maps were created using a towed sidescan sonar array (Noll et al. 2009). Sediment types were divided into three categories: rock outcrop (hard, rocky substrate), mixed mud and gravel, and mud (I. Davis, unpub. obs.). Foraging locations were then overlaid in GIS (Geographic Information Systems). Dives that were not located directly on the sediment map (i.e. in shallow and intertidal region) were not used.

Analysis – Chi2 and G-tests of associations, based on a null hypothesis of uniform distribution, were used to test for associations prey items and sediment type.

Results

Research Effort – A total of 1,775 successful foraging dives were recorded from

June-August, 2001-2013, and 1,979 prey items were identified (Fig. 10). Of these, 1,420

had GPS positions that could be correlated with the sediment map (Fig. 11 & Table 4).
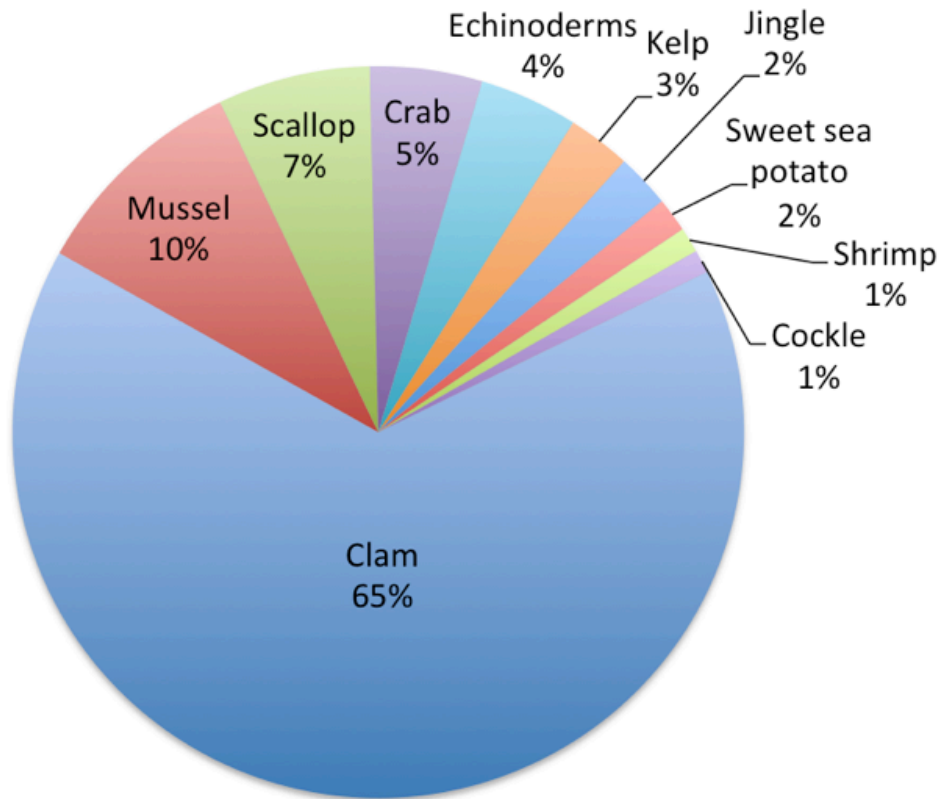
Figure 10. Identified Prey 2001-2013. Sea stars and sea cucumber are grouped
together under echinoderm. The sweet sea potato, though an echinoderm, was
separated because its preferred habitat (mud) is different from the others.
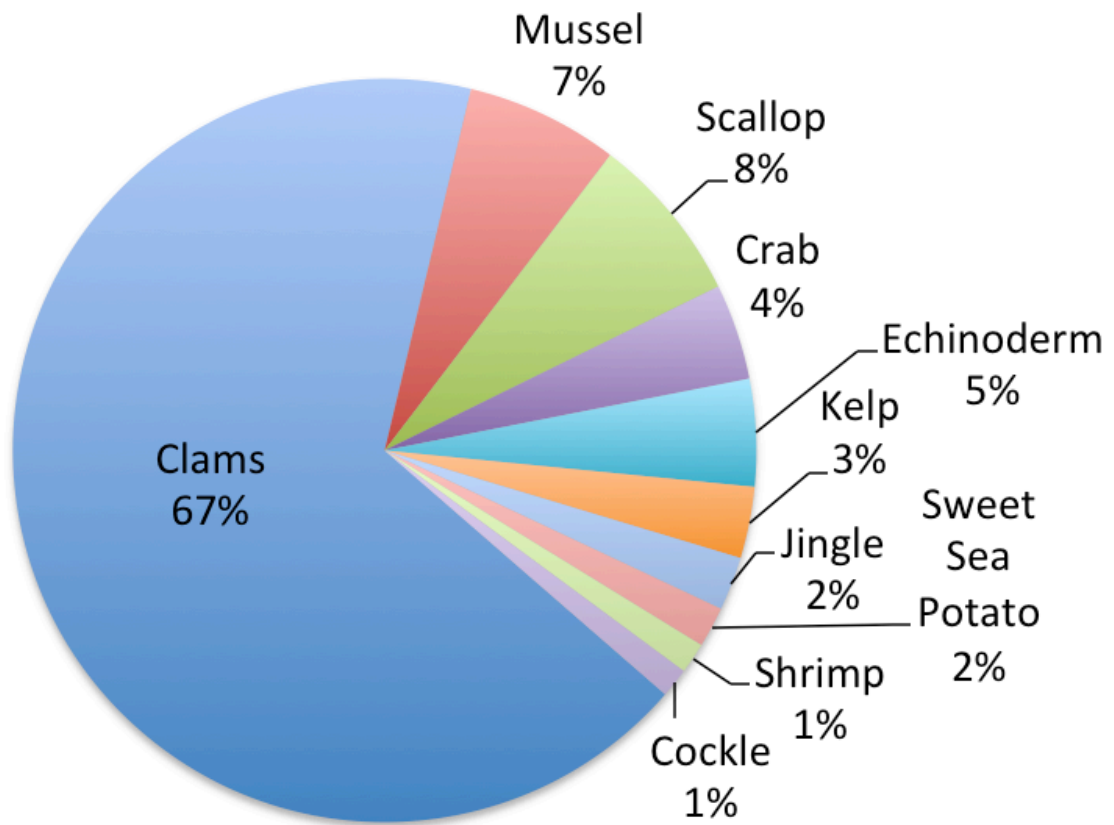
Figure 11. Prey items having a GPS location that corresponded with the side-scan sonar map.

Table 4. Prey items and sediment type.

	Rock	Mixed mud/gravel	Mud	Totals
Area km^2	0.57	9.33	7.28	17.19
All Prey	47	865	508	1420
Clams	23	570	360	953
Crab	4	31	24	59
Mussel	1	66	27	94
Scallop	4	82	18	104
Kelp*	10	23	11	44
Sweet Sea Potato	0	10	15	25
Echinoderm	1	37	28	66
Jingle	4	28	1	33
Shrimp	0	1	18	19
Octopus	0	2	3	5
Cockle	0	15	3	18

* Herring (*Clupea pallasii*) or some other fish egg spawned on the kelp.
(Lee et al. 2009)

Table 5. Chi^2 (A) and G-tests (B) for significant differences in prey taken from each sediment type. Only significant values shown, "greater then" and "less then" symbols indicate in which sediment type more prey was found.

A) Chi^2 p-value - number of each prey item taken from the three sediment types.

	Rock		Mud/gravel		Mud		Rock
All Prey	<0.0001	<	<0.0001	>			
Clam	<0.0001	<	<0.0001	>	<0.0001		
Crab			<0.0001	>			
Mussel			<0.0001	>			
Scallop	0.0003	<	<0.0001	>	0.0001		
Kelp*†	0.0001	<	<0.0001	>	<0.0001	>	0.0098
Sweet Sea Potato*			<0.0001	>			
Echinoderm*			<0.0001	>			
Jingle*		<	0.0001				
Cockle*			<0.0001	>			
Shrimp*				<	0.0051		
Octopus*†				<	0.0095		

* fewer than 50 observations so chi^2 test may be misleading

† May be statistically significant but observations in the different sediment types differ by only 1 observation.

Table 5. cont.

B) G-test p-value - taking into account the area of each sediment type.
Null H_0 = all prey are evenly distributed through all sediment types.

	Rock	Mud/gravel		Mud		Rock
All Prey		<0.0001	>			
Clam						
Crab						
Mussel		0.0017	>			
Scallop		<0.0001	>	0.048	>	
Kelp*†	<	<0.0001		<0.0001	>	
Sweet Sea Potato*						
Echinoderm*						
Jingle*		<0.0001	>		<	<0.0001
Cockle*		0.008	>			
Shrimp*				<	<0.0001	
Octopus*†						

*Williams correction for sample sizes less than 50
† May be statistically significant, but observations in the different sediment types differ by only 1 observation.

Bathymetry and Sediment – Although the shallowest areas along the shore could not be mapped with the towed array, 17.19 of the total 21 km² were mapped: rock 0.57 km² (3%), mixed mud and gravel 9.33 km² (54%), and mud 7.28 km² (43%) (Fig. 12 & 13 & 14).
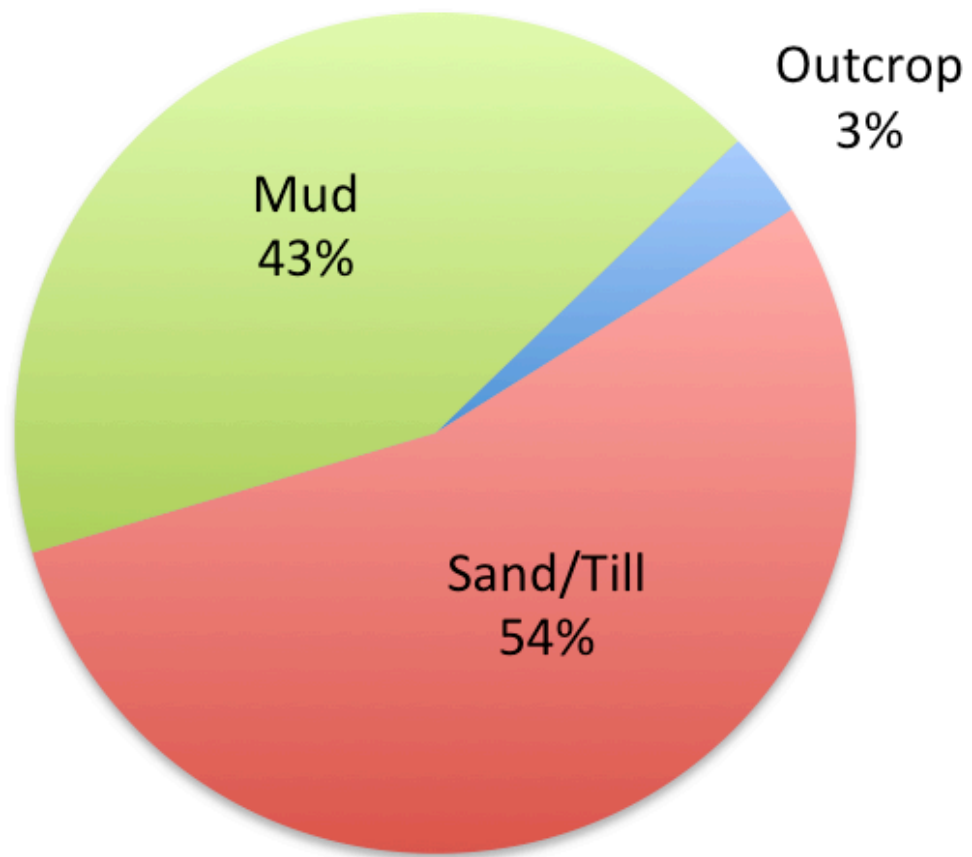
Figure 12. The percentage of sediment types in Simpson Bay deeper than ~5 m.
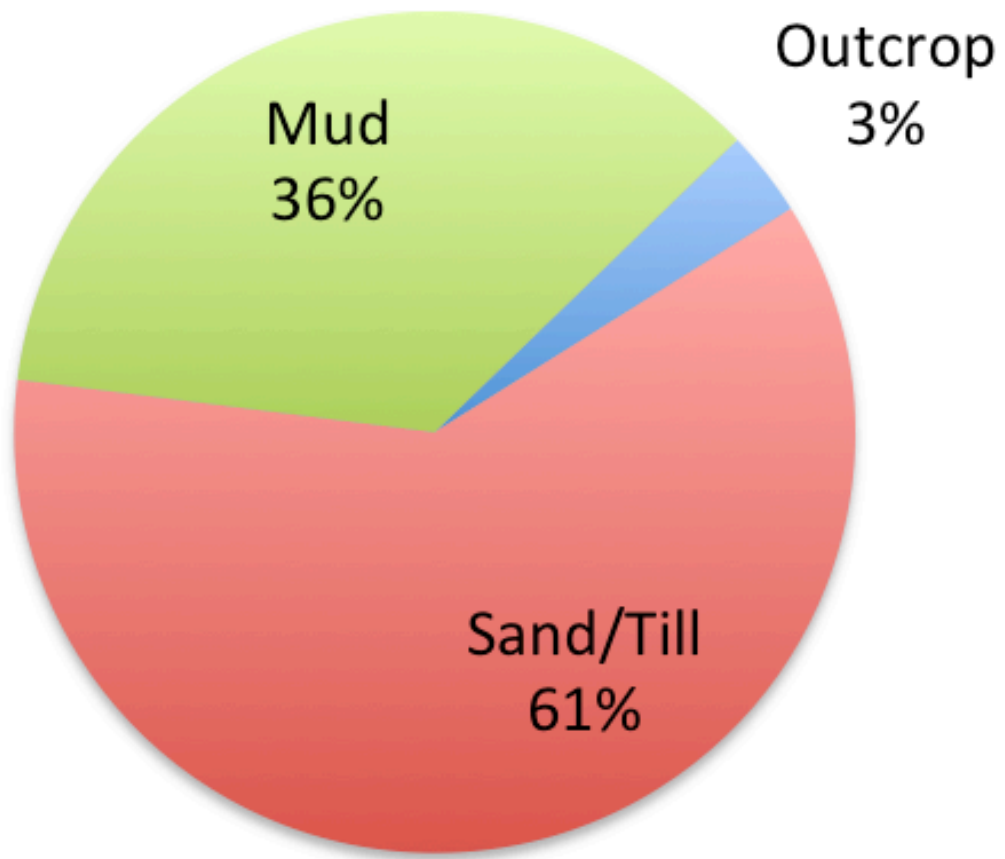
Figure 13. The percentage of prey associated with each benthic category.
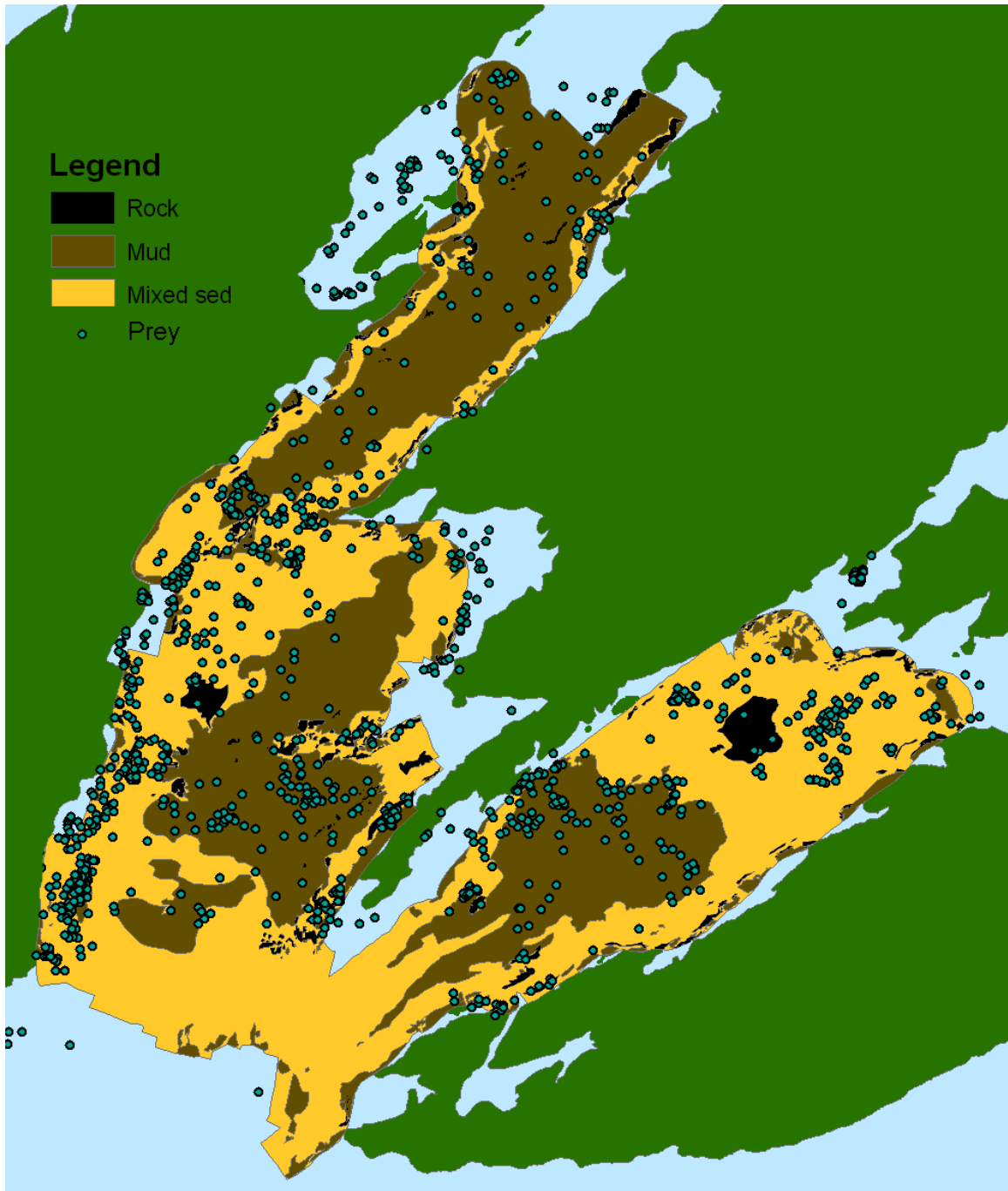
Figure 14. GIS map of sediment types in Simpson Bay.
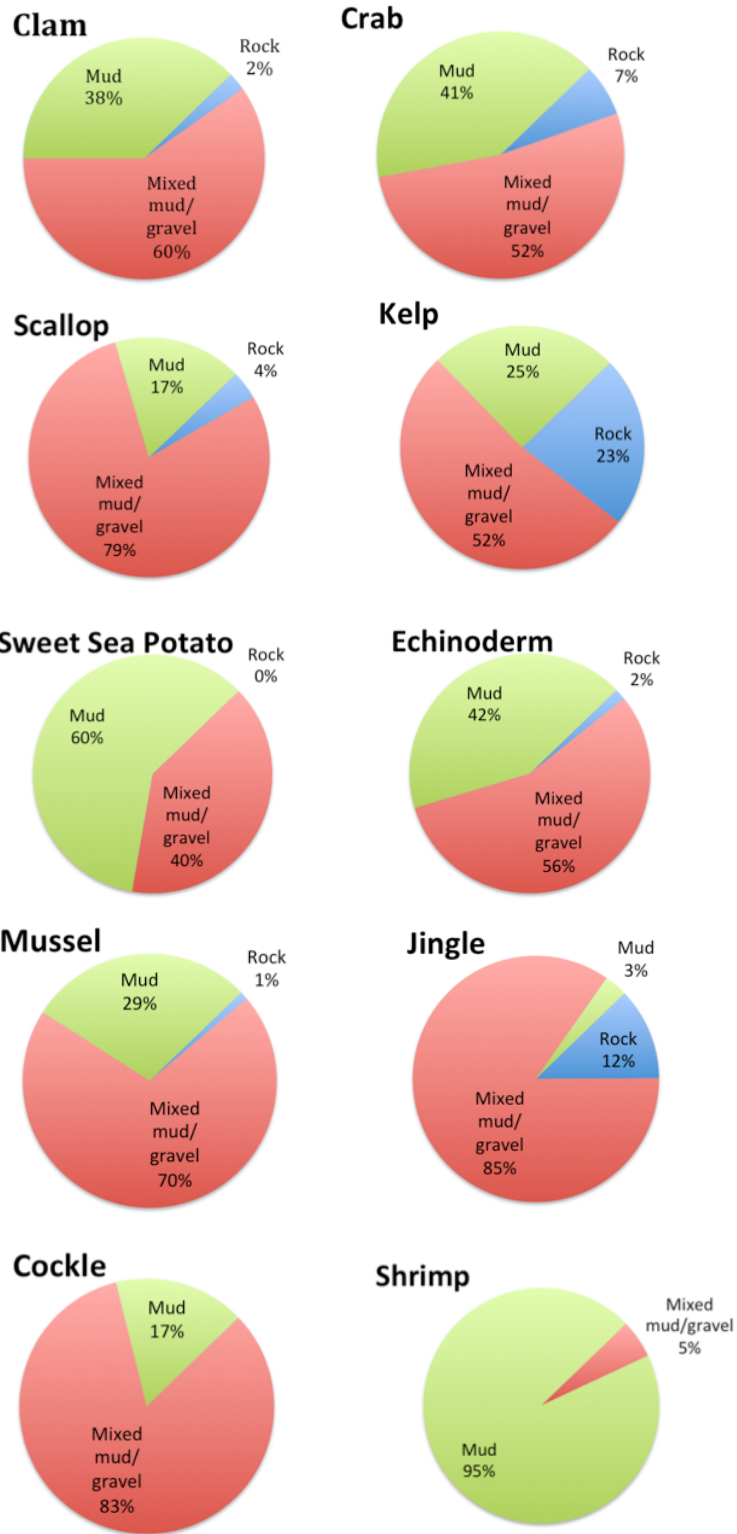
Figure 15. Percentage of each prey type associated with benthic category.

Prey Items – Most prey were found to some degree in all three benthic categories (Table 4 & Fig. 15). In terms of the total number of prey items from each sediment type, all were significantly different from each other (mixed mud gravel > mud > rock). However when the differing areas of the three sediment types are taken into account the only significant difference was between mixed mud/gravel and mud (mixed > mud p-value <0.0001). Most prey were captured over mixed mud and gravel, and in terms of prey/area mixed sediment is significantly more productive (Fig. 12 & 13 & Table 5). Although the smallest amount of prey was taken over rock, there was no significant difference between mud and rock for prey/area (p-value 0.142).

Discussion

Benthic geomorphology influences the distribution of infauna and epifauna. Mixed mud and gravel was most productive benthic category for macroinvertebrates captured by sea otters (Fig. 13, 14 & 15). Over half of each prey species, except for the sweet sea potato, were taken from this sediment type and it produced significantly more prey/area (p-value <0.0001). Clams crabs and echinoderms were distributed proportionately to the percentage of the benthos that was mud and mixed mud and gravel, though there was a small tendency (60%) for clams to be associated with mixed mud and gravel. Scallops were disproportionately (79%) associated with mixed mud and gravel [Fig. 15]). Kelp and the Alaska false jingle were the only 2 species to be found more commonly on rock as they both attach themselves to the bottom (Table 4). The only prey species to be

disproportionately associated with mud were the sweet sea potato, shrimp and octopus.

The number of observations for shrimp and octopus make any association tenuous. Mud

does seem to be the preferred habitat for the sweet sea potato, as it makes large U-shaped

burrows (O'Clair, and O'Clair, 1989). That shrimp prefer this sediment that would seem

to be lacking in refuge from predators was a little surprising until we had the opportunity

to send a small submersible down and actually see it ourselves. The muddy areas were

riddled with holes and what looked like burrows – weather made by the shrimp or

possibly the sweet sea potatoes which are amenable to sharing their excavations

(O'Clair, and O'Clair, 1989) is uncertain. Shrimp pots brought up in Simpson Bay

indicate that the coonstripe shrimp (*Pandalus hypsinotis)* is the most common demersal

species. The octopus being found frequently in mud is likely an artifact. These prey can

be large, up to 2m from tentacle tip to tentacle tip (personal observations) and may take

over 30 minutes to consume. In that time the otter has usually moved a considerable

distance, and getting a GPS point from where it first surfaced is guesswork. Mussels

being found in mud is also certainly an artifact of boat positioning. Mussels require hard

substrate to attach and are most common in shallow areas – both things usually avoided

when in a boat. We were unable to position the boat exactly where the otter had been

and so used our initial GPS location further off shore. Shallow areas of the bay that

were not mapped are used heavily by otters (Wolt et al. 2012), and rocky outcrops are

common (Noll. 2005). Mussels are underrepresented on the sediment map (comparing

Fig. 10 & 11) and probably also in terms of total prey as they are small, dark colored and

difficult to identify.

Clams are the majority of the otter's diet in Simpson Bay. The average growth rate of little neck clams in Galena Bay PWS is 2-5 mm per year (Paul and Feder 1973). If growth rate in Simpson Bay is similar, it would take over 10 years for a clam to reach the size (> 5 cm or about the size of a sea otter fore paw) preyed on by otters (Maldini et al. 2010).

Otters remove an estimated 145,388 kg of biomass annually from Simpson Bay, 109,041 kg of that being clams (Wolt et al. 2012). The relatively soft bedrock and large volume of fresh water (average of 95 inches annually, [Gay and Vaughn 2001]) over a watershed of ~168km^2 (Noll et al. 2009) contributes to the productivity of Simpson Bay which is able to sustain a stable population of sea otters (average annual density ca. 2.9 adult otters km^{-2}) for the past twelve years and probably longer.

TIME AND ENERGY ALLOCATION OF FEMALE SEA OTTERS (*Enhydra lutris*) WITH PUPS IN ALASKA

Overview

The behavior of sea otters (*Enhydra lutris kenyoni*) with dependent pups was observed between May-August of 2005-2010 in Simpson Bay, Alaska using focal follows and instantaneous sampling. Six behaviors (foraging, grooming, resting, swimming, swimming slowly and interacting) were recorded during four, 6-h time periods (dawn [05:00–11:00], day [11:00–17:00], dusk [17:00–23:00] and night [23:00–05:00]) to create a 24-h activity budget. Overall, 1,190 focal follows were conducted for a total of 595 hours. Females with dependent pups spent the greatest percentage of the day resting (42%), about equal percentages foraging (18%), grooming (15%) and swimming (15%), and the remainder swimming slowly (8%) and interacting (2%). Field Metabolic Rate (FMR) was estimated by using the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for each behavior for captive otters (Yeates et al. 2007). The estimated FMR for females with a dependent pup was 12.69 MJ day^{-1} with the following absolute and percentage allocations for each behavior: foraging 2.38 (19%), grooming 2.70 (21%), resting 3.42 (27%), swimming 2.64 (21%), swimming slowly 1.25 (10%) and interacting 0.3 (2%). The estimated weight specific FMR was 601 kJ day^{-1} kg^{-1}, similar to that reported for territorial males in the same area. The sea otter population in Simpson Bay has been stable for at least the last 12 years. It would follow then that the time spent

foraging would be similar to other areas where the population is stable, but this is not the case. In Simpson Bay, the time spent foraging is more similar to areas that have been recently occupied. The relativly small amount of time spent foraging may indicate that geographic differences (structure of the near-shore community: substrate, water depth, kelp canopy, prey assemblage, and competitors) may play a greater role in determining the amount of time spent foraging than population status.

Introduction

Studies of sea otter (*Enhydra lutris*) behavior have been conducted in Alaska, California and Washington using different methods with considerable variability in activity budgets, which were first proposed to assess the status of marine mammal populations (Eberhardt and Siniff 1977). As sea otters have large energy requirements due to an elevated metabolic rate (Costa and Kooyman, 1984), previous studies focused on foraging behavior. Estes et al (1986) suggested that time spent foraging may be the best indicator of a populations status, as food is commonly the limiting resource (Kenyon 1969). Foraging time would be expected to increase as a population grows and approaches equilibrium density (Eberhardt and Siniff 1977), although not all studies have consistent results. Some of the disparities may be attributed to the use of various methods (observation vs. tagging), constraints of study design (sample size, period of data collection) and uncertainty about population status (Bodkin et al. 2007). Population studies of marine mammals are difficult for a variety of reasons. Among the fur bearing

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marine mammals, counts during the breeding season when they gather on land or some sort of mark/tagging are common. None of these techniques work well for sea otters as they do not consistently spend time on land, capturing them in the water is difficult, and they readily remove tags attached to their fur or hind flippers. Fortunately, sea otters are relatively easy to observe as most of their time is spent at the surface. Behavior is usually divided into 3-5 categories: foraging, grooming, swimming and resting are the most common. Several studies used radio transmitters and/or abdominally implanted archival time-depth recorders (TDRs) to compile time budgets from a small number of animals in California and Alaska (Estes et al. 1986, Garshelis et al. 1986, Ralls and Siniff 1990, Gelatt et al. 2002, Bodkin et al. 2007). Foraging dives deeper than 2 m are easily distinguished, and data is gathered continuously for months. The disadvantage of this approach is that behavior can only be classified as foraging, resting or other (very shallow forging dives are indistinguishable from travel or grooming), so some visual observations are usually taken to validate the recorded data.

At the other extreme are studies that employ scan-sampling to observe as many animals as possible (Altmann 1974, Estes et al. 1982, Estes et al. 1986, Walker et al. 2008). However, this method is limited by access to suitable locations that can be reliably scanned from shore. Spatial distribution may bias samples (Gelatt et al. 2002), as some behaviors are more conspicuous than others (resting and grooming vs. foraging and swimming). In addition, the sex of the otters is often unknown.

Previous Studies of Female Sea Otter Activity Patterns

Radio Telemetry – Garshelis et al. (1986), Ralls and Siniff (1990), and Gelatt et al. (2002) used radio telemetry to determine the activity budgets of sea otters. Garshelis et al. (1986) conducted their study at Green Island (central Prince William Sound, Alaska) and Nelson Bay (one bay east of Simpson Bay) where radio transmitters were attached to the hind flippers of 26 adult female otters. Activities were categorized as foraging, resting or swimming based on the frequency and duration of interuptions of the radio signal. The authors concluded that, over a 24-h period, solitary females and females with pups allocated 37% of their time to foraging, 51% to resting and 12% to swimming for females with pups.

Gelatt et al. (2002) conducted their study around Amchitka Island, Alaska, where radio transmitters were surgically implanted in 48 adult female otters (22 had pups of varying ages) that were monitored every 10 min for 24-h twice per week. Activities were categorized as foraging, resting and other. Using similar assumptions about signal patterns, the time budget from that study was similar to that of Garshelis et al. (1986) with adult female sea otters allocating 38% of their time to foraging, 48% to resting and 14% to other activities. In California, Ralls and Siniff (1990) found that, over a 24- h period, females with dependant pups (n=6) foraged 40% of the time, rested 44.7%, and spent 15.7% in other behaviors.

Time-Depth Recorders (TDR) – Bodkin et al. (2007) conducted their study near Cross Sound, located in southeastern Alaska. Radio transmitters and archival time-depth recorders were surgically implanted in 21 adult sea otters of which 16 were females.

Each TDR was programmed to record depth at 2 s intervals for at least 39 days. Color-coded tags were attached to the hind flippers of each individual to allow for visual recognition. Instrumented animals were observed daily from both shore and boats. Activities were categorized as foraging, resting, and other (swimming, grooming, and interacting). The females allocated 40% of their time to foraging and 52% to resting, but the authors admit that non-diving behavior may have been underrepresented.

Scan Sampling – Estes et al. (1986) used the scan-sampling method to determine the activity budget of sea otters in a rocky reef and kelp forest habitat in central California. Behavior was categorized as foraging, resting or other by sampling a group of otters in an area at 30 min intervals with binoculars. Due to low luminance and poor visibility, they could not use this method at night, so the time period for the study was dawn to dusk. The study concluded that the otters allocated 24% of their time to foraging, 59% to resting and 17% to other behaviors.

Walker et al. (2008) based their study design on the methods used by Estes et al. (1986). Scan sampling was used to determine the activity budget of translocated sea otters in rocky coastal habitat along the Olympic Peninsula in Washington State, an area known to be below equilibrium density. Sampling occurred at 30 min intervals using binoculars and a spotting scope. The study concluded that sea otters allocated 62% of their time to resting, 20% to grooming, 8% to foraging, 8% to swimming and 2% to other behaviors.

Individual Follows and Instantaneous Sampling – Pearson et al. (2005) and Finerty et al. (2009) conducted their studies in Simpson Bay, Alaska, the same location as this

study. Activities for territorial male otters only were categorized as foraging, grooming, interacting with other otters, swimming, patrolling, and resting. Pearson et al. (2005) concluded that during *daylight hours*, male otters allocated 30% of their time to foraging, 15% to grooming, 11% to interacting with other otters, 17% to patrolling, 18% to resting, and 9% to swimming. Finerty et al. (2009) produced a *24-h* activity budget and observed the following allocation of time: foraging 14%, grooming 19%, interacting 5%, patrolling 9%, resting 27% and swimming 26%.

In the current study, we used we used focal follows (Mann, 1999) with instantaneous behavioral samples (Altmann, 1974; Lehner, 1996; Mann, 1999; Pearson et al., 2005) to compile a detailed 24-h activity budget for females sea otters with pups during the summer (June to August), a period when many pups are ca. 1-3 months in age. Field Metabolic Rate (FMR) was than estimated using metabolic rates for each behavior that were measured in captive otters (Yeates et al. 2007). For the sake of brevity, the term population refers to animals in Simpson Bay with the understanding that this is a subset of the animals in Prince William Sound, and the daily and monthly movements of some animals likely encompass a much larger area.

Methods

Study Site – Simpson Bay (ca. 60.6° N, 145.9° W), located in northeastern Prince William Sound, Alaska (Fig. 16), was used as the study site because of its protection from rough seas, reliable presence of sea otters 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 mud/gravel) with some rocky reefs (Gilkinson 2004, Noll et al. 2005). None of the large-bodied kelps (e.g., Nereocystis) that form canopies are present, 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 approximately 10 m (R. W. Davis, personal obs.). The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983-85 (Garshelis 1983, Rotterman and Simon-Jackson 1988, VanBlaricom 1988). Since 2002, it has been used during the summer (June-August) by an average of 124 ±14.7 sea otters, including adults and subadults (93 ± 8.7) and pups (31 ± 6.9) with an average summer density of 5.9 otters km^{-1} (Wolt et al. 2012). During the winter, the number of otters in the bay decreases to ca. 50, 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.
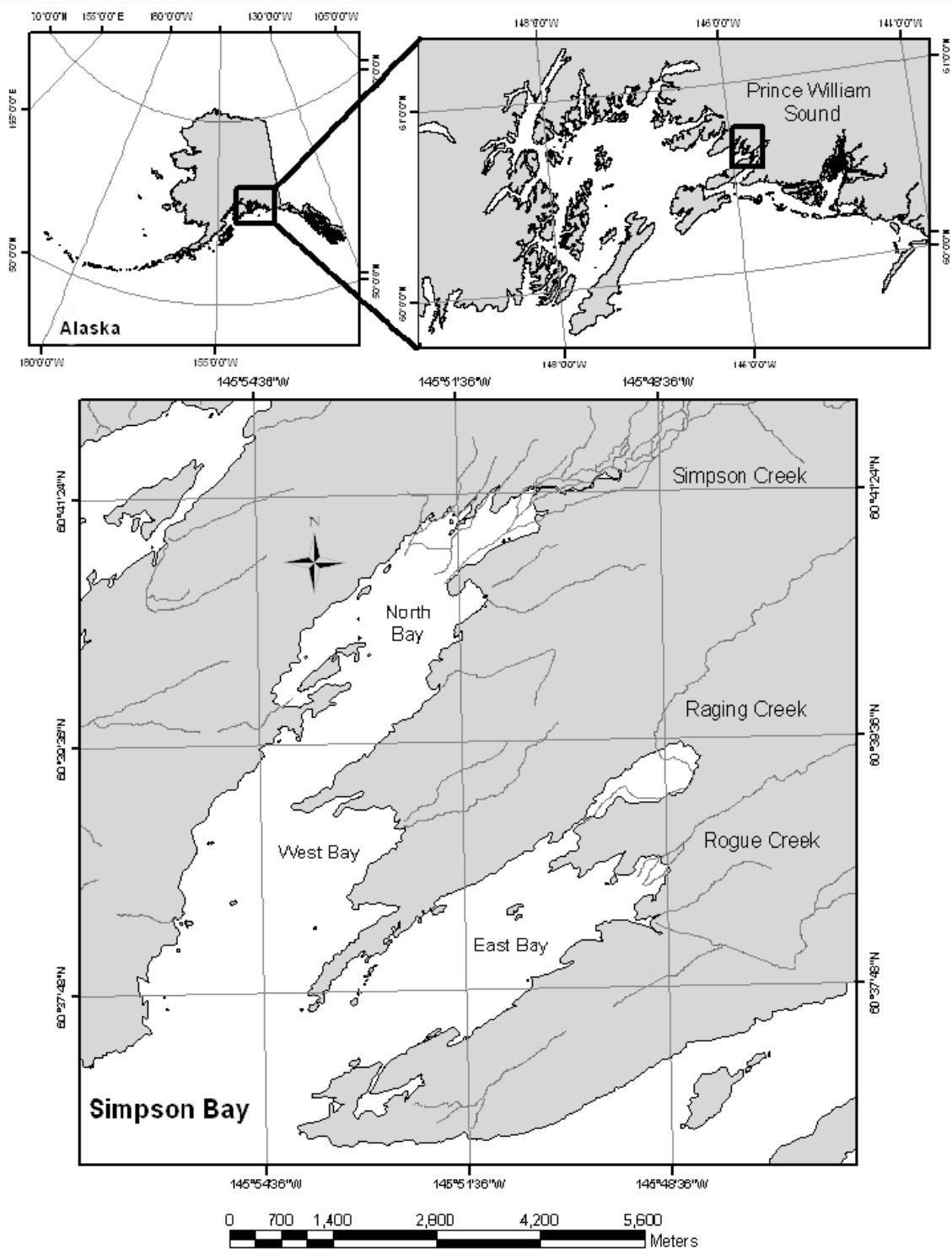
Figure 16. Simpson Bay, Prince William Sound, Alaska (Noll et al., 2005).

Focal Observations – The behavior of sea otters with dependent pups was observed from a skiff from late May to mid-August of 2005-2010. Age of the pups could not be determined, but they were newborn up to ca. three months. The high latitude made visual observations possible for nearly all 24-h which was divided into four, 6-h time periods corresponding to astronomical dawn (05:00–11:00), day (11:00–17:00), dusk (17:00–23:00) and night (23:00–05:00). Because of latitude for the study site, the level of illumination during night observations varied over the summer. From late June to mid-July, there was adequate illumination for observations throughout the night. However, by early August it was too dark to make observations around 02:00, which was astronomical midnight for this location in Alaska. As a result, we worked during periods of the night that allowed observations and avoided the darkest periods. The study area was divided into three parts (North Bay, West Bay and East Bay, Fig. 16), but no systematic vessel track was followed because the otters congregated in different locations depending on weather and other factors which are not completely understood. Instead, the skiff (with at minimum a driver and recorder/spotter) approached otters opportunistically on a search path that minimized the possibility of observing an individual otter more than once during a 3-4 h session. When an individual was sighted, the skiff was maneuvered close enough (ca. 100 m) to observe behavior with the aid of binoculars. If the individual's behavior remained unchanged once the skiff was in position, a 30 min focal follow (Mann, 1999) with 31 instantaneous samples (Altmann, 1974; Lehner, 1996; Mann, 1999; Pearson et al., 2005) was conducted.

Behaviors, based on descriptions by Packard and Ribic (1982) included foraging, grooming, resting, swimming, swimming slowly and interacting. GPS locations were taken at the beginning and the end of each observation. After the focal follow, photo-identification based on nose scars was attempted when possible at a distance $\geq$30 m (Finerty et al. 2007).

Field Metabolic Rate (FMR) – FMR was estimated by using the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for resting (13.3), feeding (21.6), grooming (29.4), swimming (29.6), and interacting (24.5) for captive otters (Yeates et al. 2007) with the activity budget for the otters in this study. Yeates et al. (2007) determined oxygen consumption in captive otters under four conditions: 1) resting on the surface, 2) grooming, 3) after serial foraging dives, and 4) after single non-foraging dives study animals were trained to dive to the bottom of a 9.1-m deep, 4-m diameter seawater tank with a metabolic dome at the surface of the water. A rocky substrate along with 3–5 kg of live crabs (*Cancer* spp.) and mussels (*Mytilus edulis*) were placed at the bottom of the tank to simulate foraging conditions in the wild. Each otter was allowed to forage by making repeated dives to the bottom to collect prey after which it surfaced beneath the metabolic dome while handling and consuming the prey. All measurements followed the methods of Williams et al. (2004b) using an open-flow respirometry for aquatic mammals (Yeates et al. 2007).

Behaviors in our study that did not fall into one of the classifications of Yeates et al. (2007) were categorized as 'other' (e.g., interacting and swimming slowly). Swimming slowly was considered to be energetically the same as "other" (24.5 vs. 29.6 ml O_2 min^{-1}

kg^{-1} for swimming) as only a single hind flipper or both intermittently were being used to propel the animal. The weight specific FMR (kJ day^{-1} kg^{-1}) was estimated as the sum of the energetic cost of each activity, the number of minutes per day spent in each activity (i.e., proportion of day in each activity times 1,440 min day^{-1}), and a conversion factor of 2.0083×10^{-2} kJ ml^{-1} O$_2$ (Schmidt-Nielsen, 1997). The total FMR (MJ day^{-1}) was calculated as the product of the weight specific FMR and the mean body mass (21.1 kg) of adult female Alaskan sea otters (Kenyon 1969) divided by 1,000 to convert kJ to MJ.

    Data Analysis – A complete 24-h time and energy budget was created, as well as for each of the four 6-h time periods. Multivariate analysis of variance (MANOVA) was used to test for differences in the relative amount of time and energy female otters spent performing each of the six behaviors (dependent variables) among the four time periods (independent variables). If a significant difference was found, an analysis of variance (ANOVA) was used to determine the source. MANOVA and ANOVA were conducted in JMP (Version 10. SAS Institute Inc., Cary, NC, 1989-2010). In addition, a canonical correspondance and canonical variates analyses were conducted using CANOCO (Version 4.5) to simultaneously quantify the relative influences of multiple characteristics associated with each time period and behavior. These included 6-h period, total time (min) spent in each behavior and year (e.g., using time of day to explain variations in behavior). This uses a weighted averaging procedure similar to a discriminate functions analysis (Lepš and Šmilauer 2003).

Results

Research Effort – Overall, 1,190 focal follows (31 min each) were conducted for a total of 595 hours; 25% (N = 291) during the dawn (05:00-11:00 h), 28% (N = 330) during the day (11:00-17:00 h), 25% (N = 303) during the dusk (17:00-23:00 h) and 22% (N = 266) during the night (23:00-05:00 h).

Activity Budget – A combined (all four time periods) 24-h activity budget showed that females with dependent pups spent the greatest percentage of the day resting (42%), about equal amounts of time feeding (18%), grooming (15%) and swimming (15%), and the remainder swimming slowly (8%) and interacting (2%) (Fig. 17). A similar allocation of time occurred among the four 6-h periods, although there were some differences (Fig. 18). Females spent a significantly greater percentage of their time resting during the dawn (52%) and less time (32%) during the day. In contrast, females spent a significantly greater percentage of their time foraging during the day (27%) and less time during the dawn (13%) and night (13%). In addition, females spent more time swimming during the night (20%) and less time during the dawn (9%). The percentage of time grooming (18-23%), interacting with other sea otters (2-3%) and swimming slowly (9-11%) did not differ significantly among the time periods.

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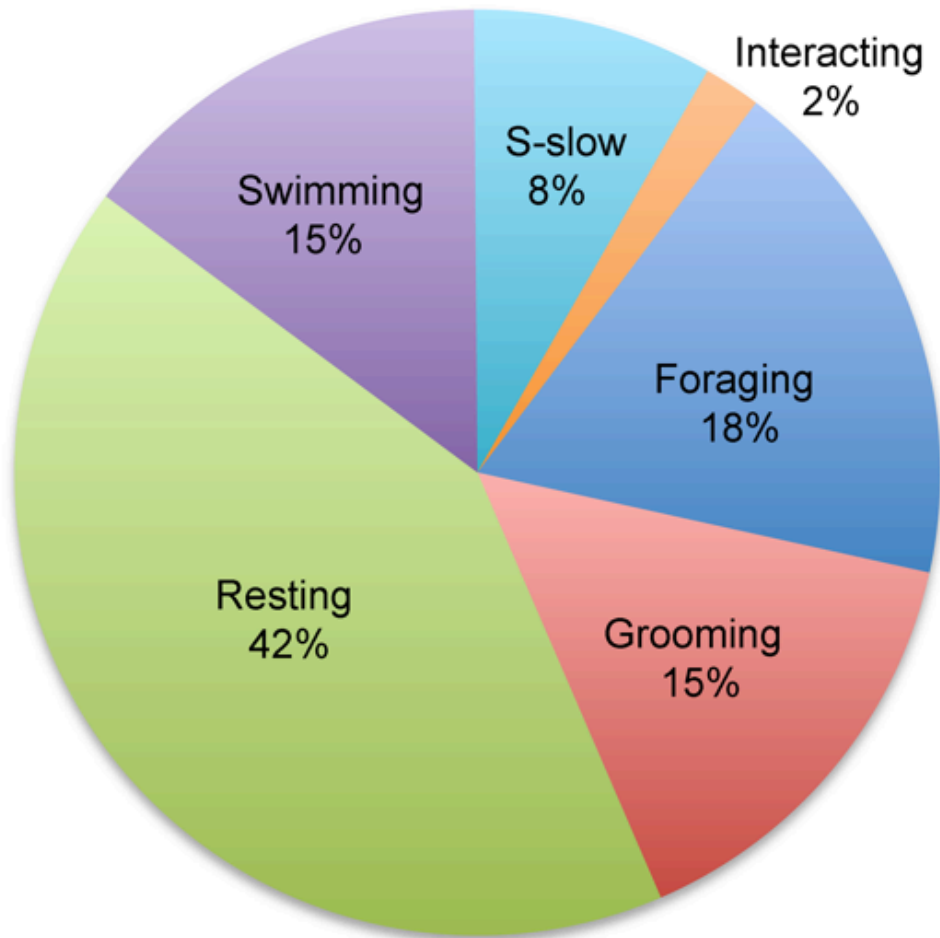
Figure 17. Twenty-four hour activity budget for adult female sea otters with dependent pups in Simpson Bay, Alaska during summers (May to August).
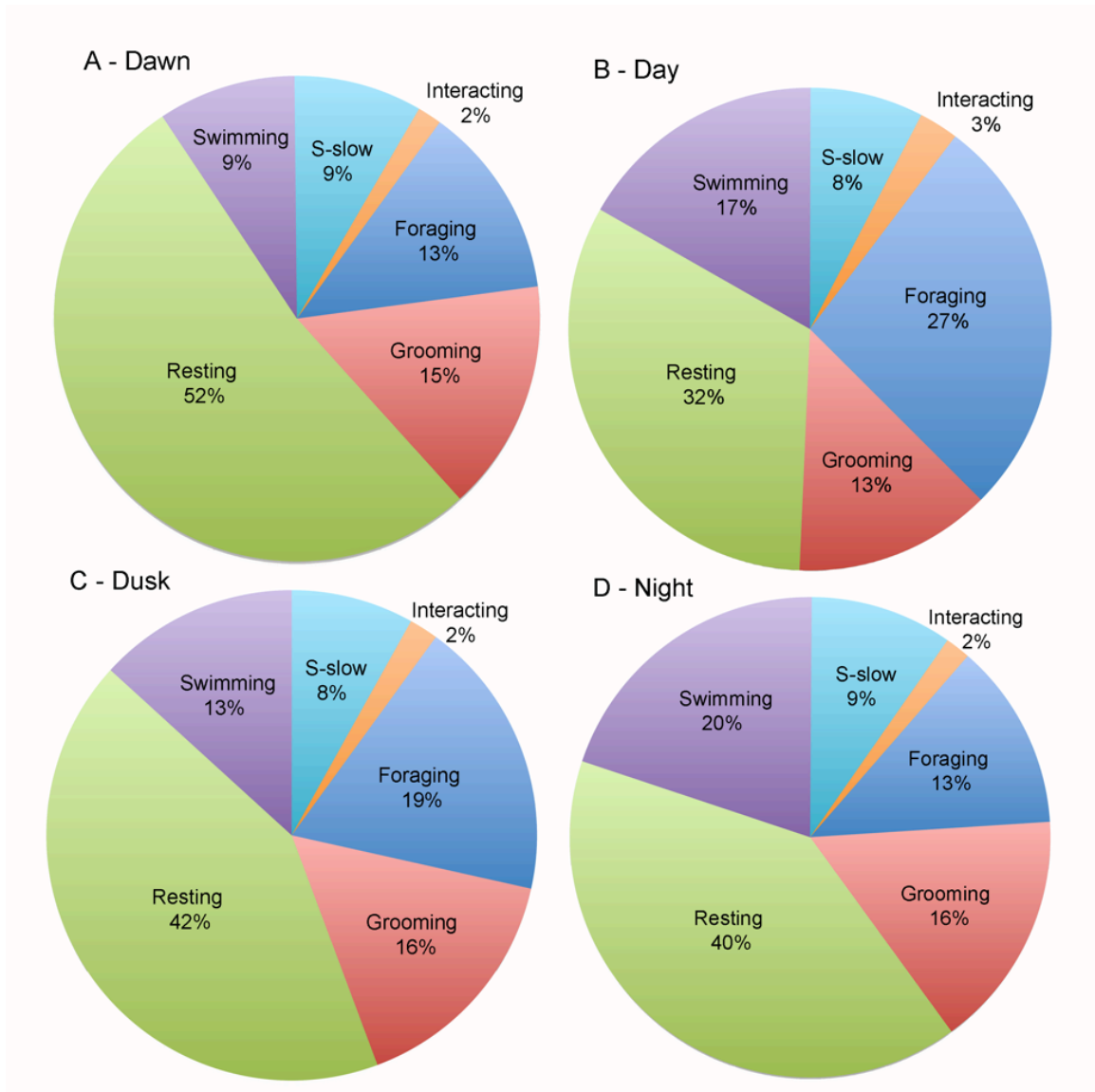
Figure 18. Six hourly (A-dawn, B-day, C-dusk, D-night) activity budgets for adult female sea otters with dependent pups in Simpson Bay, Alaska during summers (May to August).

A MANOVA showed that there was a significant difference in the percentage of time spent in at least one of the behavioral categories among the four, 6-hr time periods (Table 6). Using an ANOVA, each behavior was tested individually to identity significant differences in the amount of time spent performing each behavior among time periods (Table 7). If a significant difference was found, each time period was tested against the other three to determine which of the four were significant. Foraging, resting and swimming were found to differ significantly. Foraging was significantly different between all time periods except dusk. Resting was significantly different between dawn and day, and swimming between dawn and night.

Table 6. MANOVA testing if the relative amounts of time spent in each behavior differed by Time Period.

MANOVA Across all Behaviors	F-value	p-value
All 4 Time Periods	11.82	<0.0001
Dawn	8.21	<0.0001
Day	8.96	<0.0001
Dusk	1.18	0.32
Night	5.10	<0.0001

Table 7. ANOVA testing each behavior individually to see if there was a significant difference in the amount of time spent performing each behavior between Time Periods. Tests between time periods were conducted running each against the other three (eg. if dawn was significantly different from Day, Dusk & Night).

ANOVA	All 4 Time Periods		Dawn		Day		Dusk		Night	
	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
Foraging	13.98	<0.0001	8.81	0.003	36.75	<0.0001	0.11	0.73	9.45	0.002
Grooming	1.49	0.22								
Resting	16.85	<0.0001	36.19	<0.0001	29.62	<0.0001	0.001	0.97	0.64	0.43
Swimming	12.35	<0.0001	23.91	<0.0001	3.05	0.08	2.35	0.13	20.79	<0.0001
S-slow	0.87	0.45								
Interacting	1.98	0.11								
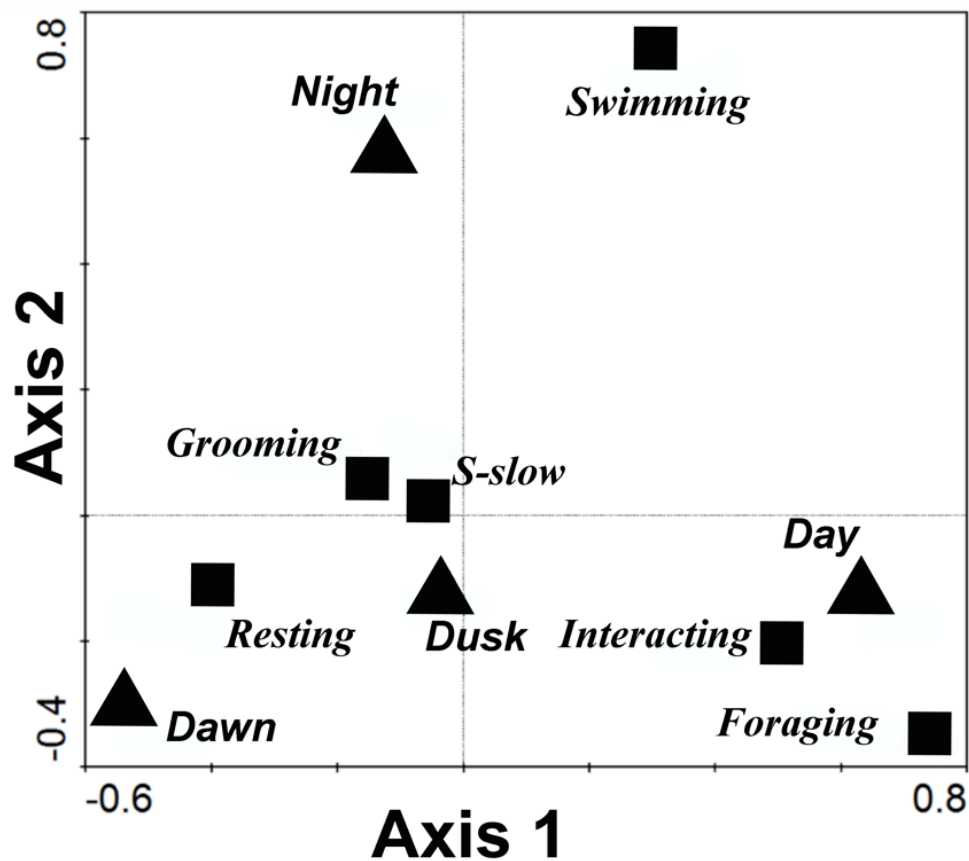
Figure 19. Canonical correspondence analysis showing associations among all
behaviors and times of day.

The canonical correspondence analysis (Fig. 19) showed dawn to be most closely associated with resting, day with interacting and foraging, and night with swimming. The percentage of time spent grooming and swimming varied the least among time periods and did not distinguish among them. While significant (p-value = 0.002), the total variation explained by time period (and year, run as a covariable) was only 4.7%, with time of day accounting for 2.4%. Canonical Variants Analysis (similar to the CCA

but using behaviors to explain time of day) showed that the greatest variation in behaviors occurred during the day (4.67%) followed by dawn (3.88%), night (2.55%) and dusk (0.54%) with 3% of the total variation explained by the 6-h time period.

Estimated Field Metabolic Rate (FMR) – The estimated FMR for a female sea otter with a dependent pup was 12.69 MJ day^{-1} with the following contribution of each behavior: foraging 2.38 (19%), grooming 2.70 (21%), resting 3.42 (27%), swimming 2.64 (21%), swimming slowly 1.25 (10%) and interacting 0.3 (2%) (Table 8 & Fig. 20 & 21).

A MANOVA showed that dusk was the only time period that did not differ significantly (Table 9). Foraging was significantly different between dawn and night (14 and 13%, respectively) compared with day (27%). The energy expended while resting differed significantly between day (20%) and dawn (36%), and for swimming between dawn (14%) and night (27%) (Table 10).

Hourly Time Budget – The 24-h activity budget plotted hour-by-hour showed an overall consistancy in behavior (Fig. 22). Although there was little periodicity, the most notable change was the gradual decrease in resting towards the afternoon with a corresponding increase in foraging (Fig. 23). Traveling increased during the night, but swimming slowly and grooming remained fairly constant throughout the 24-h cycle.

Table 8. Daily activity budget and estimated Field Metabolic Rate (FMR) for female sea otters with dependent pups in Simpson Bay.

Behavior	Activity Budget		(kJ min-1 kg-1)	Field Metabolic Rate	
	% of Day	Minutes		(MJ day-1 kg-1)	(MJ day-1)
Foraging	18.19	261.87	0.43	0.113	2.38 (18.74%)
Grooming	15.08	217.22	0.59	0.128	2.70 (21.33%)
Resting	41.64	599.66	0.27	0.162	3.42 (26.94%)
Swimming	14.70	211.72	0.59	0.125	2.64 (20.79%)
S-slowly	8.39	120.83	0.49	0.059	1.25 (9.85%)
Interacting	1.99	28.70	0.49	0.014	0.3 (2.34%)
Total	100	1440	2.86	0.60	12.69
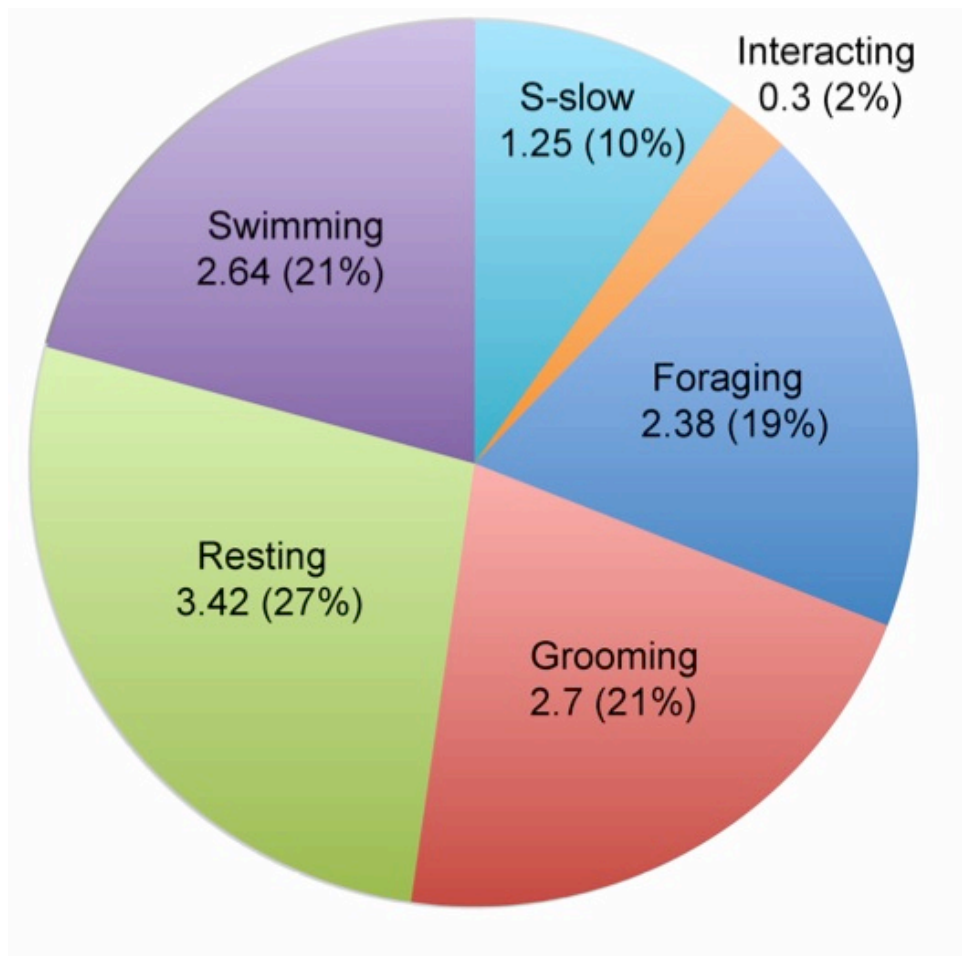
Figure 20. Contribution of each behavior to field metabolic rate (FMR) in MJ day^{-1} for adult female sea otters with dependent pups in Simpson Bay, Alaska during summers (May to August).
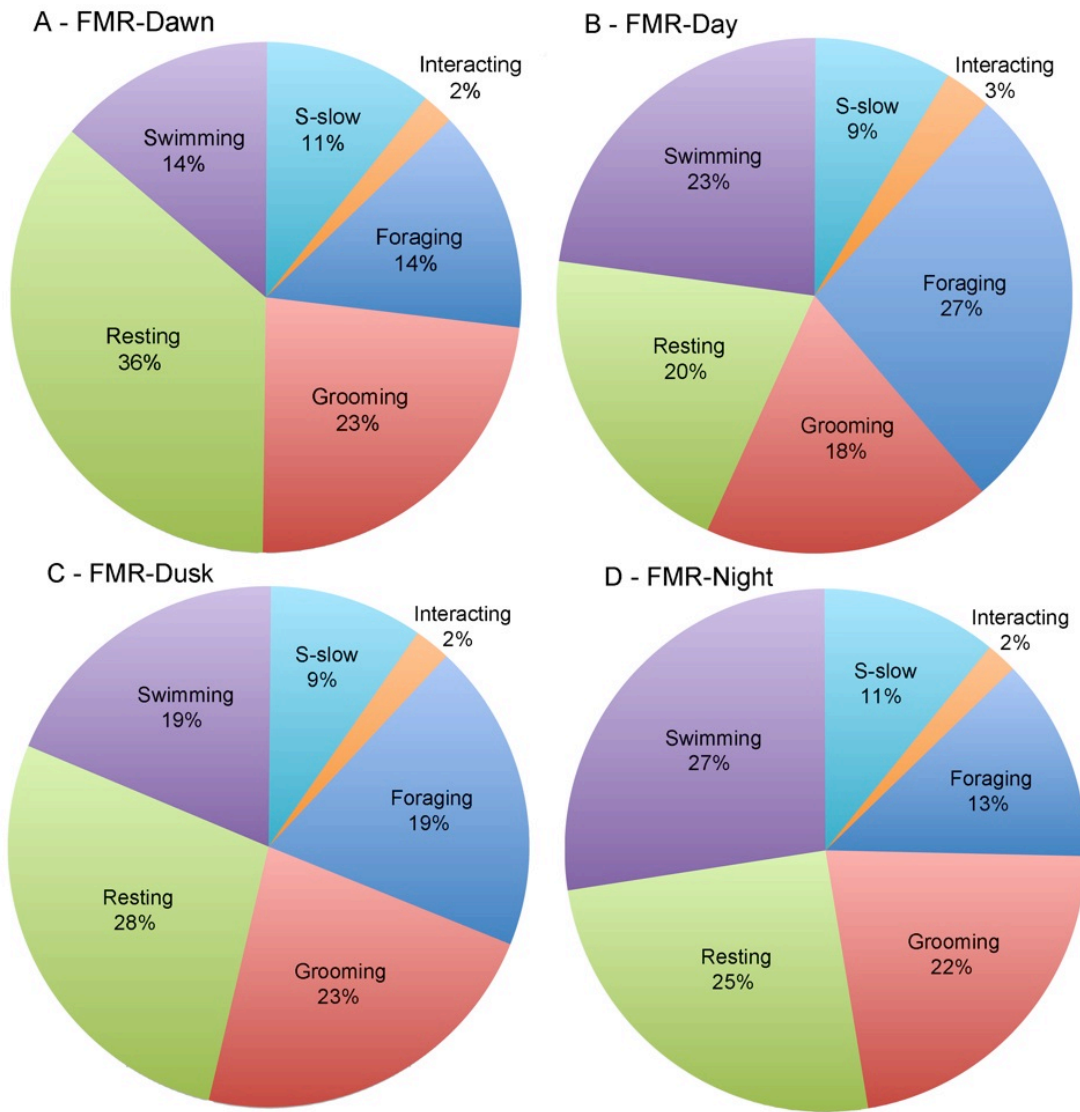
Figure 21. Six hourly (A-dawn, B-day, C-dusk, D-night) FMR for adult female sea otters with dependent pups in Simpson Bay, Alaska during summers (May to August) of 2005-10, in MJ day^{-1}.

Table 9. MANOVA testing if the relative amounts of energy spent per behavior differed by Time Period.

MANOVA Across all Behaviors	F-value	p-value
All 4 Time Periods	11.82	<0.0001
Dawn	8.21	<0.0001
Day	8.96	<0.0001
Dusk	1.17	0.32
Night	5.10	<0.0001

Table 10. ANOVA testing if there was a significant difference in the amount of energy spent per each behavior (over each 30min observation) between Time Periods. Tests between time periods were conducted running each against the other three (eg. if dawn was significantly different from Day, Dusk & Night).

ANOVA	F-value	p-value	Dawn		Day		Dusk		Night	
	All 4 Time Periods		F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
Foraging	13.98	<0.0001	8.81	0.003	36.75	<0.0001	0.11	0.73	9.44	0.002
Grooming	1.49	0.22								
Resting	16.85	<0.0001	36.19	<0.0001	29.62	<0.0001	0.001	0.97	0.64	0.43
Swimming	12.35	<0.0001	23.91	<0.0001	3.07	0.08	2.35	0.13	20.79	<0.0001
S-slow	0.87	0.45								
Interacting	1.98	0.11								

Figure 22. Activity budget of female sea otter with dependent pups in Simpson Bay during the summer (June-August) shown by hour of the day.
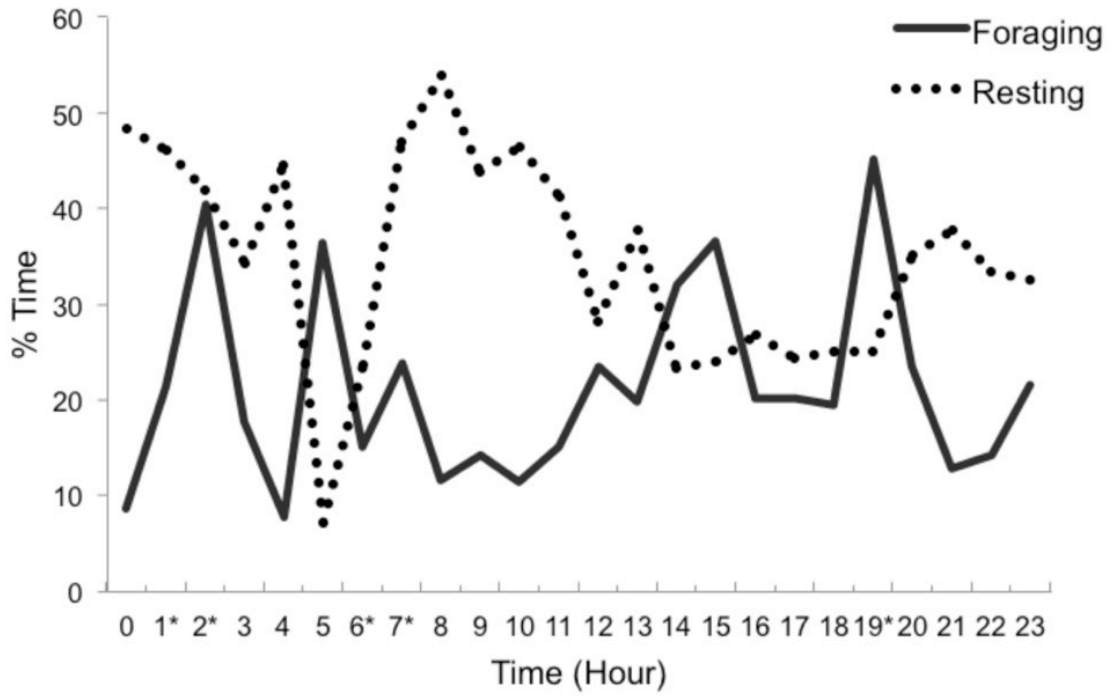
Figure 23. Percent of time spent foraging and resting shown by hour of the day. Asterisk indicates fewer than 20 observations.

Discussion

Sampling Methods – Shore-based scan sampling is the most common means of collecting time budget data for sea otters when animal-borne instrumentation is not possible, although this method has some distinct disadvantages because some behaviors are less easily identifiable visually. Estes and Jameson (1988) found that the probability of sighting a resting otter was 0.99, but only 0.77 for foraging otters. Spatial distribution of otters may also bias scan samples. Gelatt et al. (2002) found that activity was not consistent across ages and sexes and, since there is some degree of sexual segregation, a particular location will only reflect the cohort occupying that area. Scans are only possible during daylight hours depending on latitude and season, making comparisons between studies with and without night problematic. Even in areas that are in close geographic proximity (Green Island and Nelson bay which are ca. 100 km apart), sea otters have been found to forage more during the day in one location (Green Island) and at night in another (Nelson Bay) (Garshelis et al. 1986), skewing any results that assume behavior is consistent during a 24-h period. In recently occupied areas of Prince William Sound, scan sampling showed that otters spent 16% of their time foraging while with telemetry that number increased to 37%. In areas of longer occupation, scan sampling showed 62% while telemetry indicated 48% (Garshelis et al. 1990) of time spent foraging (Table 11).

Table 11. Previous sea otter activity budgets

Location	Source	Pop. Status	Method	Behavior, % of time		
				Foraging	**Resting**	**Swimming**
Prince William Sound, AK	Finerty et al. (2009)[c]	Stable	Visual – 24h	14	27	26
Washington State	Walker et al. (2008)	Increasing	Visual	8	62	8
Cross Sound, AK	Bodkin et al. (2007)	Increasing	TDR – 24h	40	52	
San Simeon, CA	Yeates et al. (2007)[c]		Telemetry – 24	36	40	8.5
Prince William Sound, AK	Pearson et al. (2005)[c]	Stable	Visual	30	18	9
Amchitka, AK	Gelatt et al. (2002)[b]	Decreasing	Telemetry – 24h	38	49	
California	Ralls & Siniff (1990)	Increasing	Telemetry – 24h	41		
California	Estes et al. (1986)	Increasing	Visual	24	59	
Prince William Sound, AK	Garshelis et al. (1986)[c]	Stable/Inc.	Telemetry – 24h	47	50	
California	Loughlin (1980)	Stable	Telemetry – 24h	34		3

[a] Row totals do not all equal 100% due to the differing categories of activities in each study.
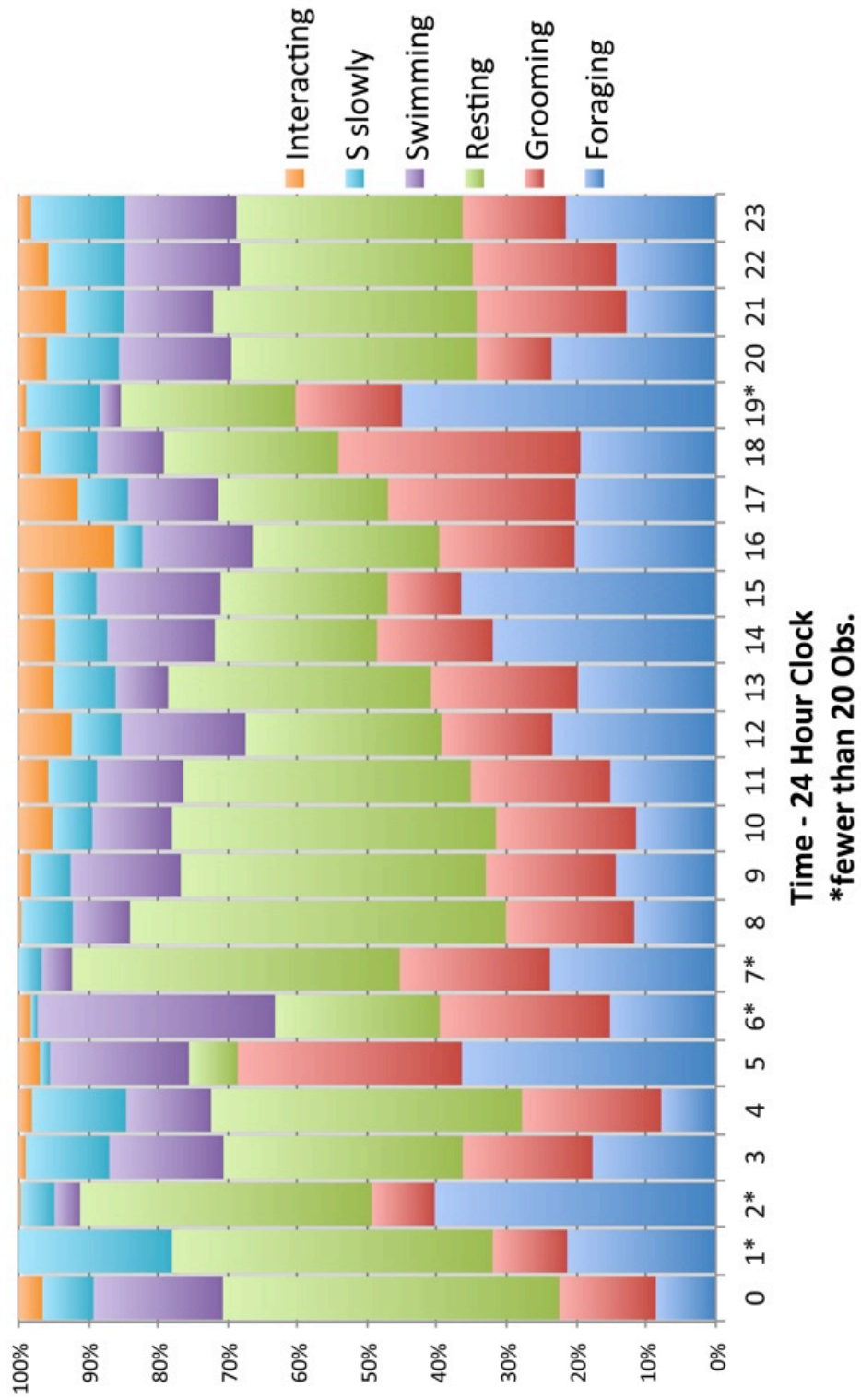[b] Females only
[c] Males only

Figure 24. Activity budget of female sea otter with dependent pups in Simpson Bay during the summer (June-August) shown by hour of the day.

Given that the data was collected at the same time of year in roughly the same locations and all within a 10-year span (most of it was much closer together in time), scan-sampling appears to be the least accurate of the two methods. Garshelis et al. (1990) concluded that scan sampling was misleading and should be abandoned.

Activity Budget – Focal animal sampling used in the current study study was the same method as that used by Pearson et al. (2005) and Finarty et al. (2009) in the same study area, extending their observations to include night and portions of dawn and dusk. Focal animal sampling (Altman, 1974; Lehner, 1996) differs from group-follows or scan sampling. In our study, we conducted "individual follows" where observers monitored a single individual regardless of whether it was solitary or in a group, which differs from a "group-follow" where an entire group of animals is monitored (Mann, 1999). In addition, we conducted "instantaneous sampling" whereby an observer recorded an individual's behavior at preselected times (i.e., every minute for 30 min). In contrast, "scan sampling" involves taking one instantaneous sample of an individual's behavior at regular intervals before moving on to the next animal, often in a group (Altmann, 1974; Mann, 1999). Scan sampling is valuable for determining behavior when individual follows are not possible or if the researcher wishes to keep track of group activities. Individual follows and the instantaneous sampling technique are better for determining time budgets (Altmann, 1974; Mann, 1999).

The percentage of time spent foraging (18%) in this study was on the low end of values reported in other studies. However it was similar to other studies of increasing populations: 15-18% (Estes et al. 1982), 11% (Bowlby et al. 1988), 21-28% (Estes et al.

1986), 24% (Shimek and Monk 1977) and to one decreasing population, 21-52% (Gelatt et al. 2002). The locations of those studies were typically exposed, high-energy coasts with rocky benthos. In southeast Alaska, where the habitat and diet are similar to Simpson Bay, Bodkin et al. (2007) reported that sea otters foraged 37% of the day (range 23-48%) using time-depth recorders. Radio transmiters were used by Garshelis et al. (1986) in Simpson and Nelson Bay from 1980-81. They found that otters foraged 37% of the day, but that study was conducted partly during the winter when the time spent foraging appears to increase.

For the 24-h period, territorial male otters in our study area spend 14% of the day foraging (Finerty et al. 2009), which was similar to that for females with pups (18%) at the same time of year. In a multivariat analysis, Finerty et al. (2009) observed that foraging was more closly associated with day (11:00-17:00h) than any other time period. Similarly, we found an increase in foraging during the day (27% versus 19% for dusk and 13% for night and dawn), although there were small peaks in foraging activity at 5:00 h and 14-15:00 h.

The number of otters in Simpson Bay during the summer has remained consistent during the summer (June-August) over the past 12 years (Wolt et al. 2012), which indicates that equilibrium density has been reached. However the time spent foraging is more similar to other areas known or thought to be below equilibrium density. It should be noted that the number of sea otter in Simpson Bay falls by almost half, to about 50 animals, during the winter (Davis and Weltz unpub. obs.). This means that the average annual population of sea otters in Simpson Bay is ca. 60 adults.

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We believe that boat-based observations do not affect otter behavior. To test this, the behavior of females with pups was recorded from five shore locations and compared to the boat-based time budget. We found no significant biological effect of the skiff on sea otter behavior. The shore-based method recorded a small decrease in resting (42% vs 50%) and a small increase in swimming (20% vs 14%). If the skiff were affecting the otter's behavior (i.e., the otter was avoiding the skiff), we would expect the opposite result. The percent of time spent foraging remained exactly the same (19%) between the two methods. Overall, there was no biological or statistical indication that boat-based observations from a distance of 100 m significantly altered the otters' behavior or gave different results from shore-based methods. Furthermore, the boat-based method provided more detailed behavior observations and could be used under lower light levels that enabled 24-hr activity budgets (Cortez et al. 2013 in review).

Females with new born pups spend suprisingly little time (2-9%) foraging (Sandegren et al. 1973, Hanson et al. 1993, Cortez in review). However, as this period only lasts a week or two, it probably did not have great effect on our results. The percentage of time spent foraging in the current study (18%) was an average based on females with pups that varied in age from new born to a couple of months. As pups mature, that energy requirements increase, so females spend more time foraging (Cortez unpub. obs.).

Resting averaged 42% of the time, ranging from 32% during the day to 52% at dawn. This is similar to or slightly below what was found in previous studies. In general, resting varied inversely with foraging (i.e., as foraging time increased resting decreased, Fig. 23). Grooming (13-16%), interacting (2-3%) and swimming slowly (8-9%) were

relatively constant across all time periods. As fur is the otters' only source of thermal insulation, frequent grooming to maintain the air layer adjacent to the skin is essential and represents a significant percentage of daily activity compared to marine mammals that use subcutaneous fat for thermal insulation. Traveling slowly may be, at least in part, a response to the large tidal changes (-2.5 to +13 feet are not uncommon, [NOAA Tide Tables for Cordova 2013]) and flow of water in and out of the bay. As there are no canopy-forming kelp in which to wrap themselves while resting, low energetic swimming may be their best means of resisting tides and currents.

Traveling averaged 15% of the time, ranging from 9% (dawn) to 20% (night). This is well below that reported for territorial males (26%) in Simpson Bay (Finerty et al. 2009) but similar (14%) to what Garshelis et al. (1986) reported, although the method of data collection was different (visual vs. telemetry). Other non-visual based studies can not distinguish among swimming, grooming and interacting and so behaviors that are not resting or foraging are lumped together as "other".

Estimated Field Metabolic Rate (FMR) – The weight specific FMR for otters in our study was 601 kJ day^{-1} kg^{-1}, and the total FMR was 12.69 MJ day^{-1} (Table 9). This is similar to the predicted FMR based on the allometric regression from other marine mammals including sea lions, fur seals and true seals (Williams et al. 2004a, 2004b). It is a little less (15.7±2.7 MJ day^{-1}) than estimated by Yeates et al. (2007) for sea otters in California, but this may be because the animals in that study were male and somewhat larger than a typical Alaskan female sea otter (21.1 kg, Kenyon 1969). Their smallest animal (22 kg) had an FMR of 12.73 MJ day^{-1} similar to our estimate. Our activity

budget differed from Yeates et al. (2007) in that our animals spent less time foraging and resting and much more time grooming and swimming.

If swimming and swimming slowly are taken together, they represent 38% of the FMR at night, more than any other category in any time period. Traveling by itself (27% of the FMR during the night) is equivalent to foraging during the day. Finerty et al. (2009) also found a large percentage of the male activity budget devoted to swimming (26% of the time and 43% of the FMR), and this was separate from territorial patrolling. It is unclear why otters in Simpson Bay spend so much time moving around. For example, during one 3-hr shore-based observation (with no possibility of our influencing the female's behavior with the presence of a boat), we observed a female with a pup swim for the entire period only to end up right back where she was when we began the observation (Cortez and Wolt personal observation).

Conclusions – Our data enabled us to examine behavior on a 24-h basis similar to telemetry studies, but without any of the assumptions about intermittent signals. As we visually observed the animals, there was no question about behavior, and our data represent an unprecedented number of observations with such high resolution. The otters in Simpson Bay show a surprising degree of homogeneity with regards to behavior throughout the 24-hr period (Fig. 22). There was a slight crepuscularity to their foraging, as has been seen to a greater degree in other locations (Estes et al. 1986, Ralls and Siniff 1990). While behavior may differ significantly among the 6-h time periods, the total variation explained by time of day was only 2.4 – 3%.

Our estimated field metabolic rate (12.69 MJ day^{-1}) was similar to that previously reported, with a small difference attributable to differences in body mass (male vs. female, and Alaska vs. California otters) and time budgets.

Time spent foraging has been the focus of most time budget studies because of its implications for population status (Eberhardt 1977, Estes et al. 1986, Ralls and Siniff 1990), although this has been questioned. While the theory behind it may be sound, there are likely many confounding variables that make comparisons among different habitats difficult. Gershelis et al. (1990) suggests that geographic differences (structure of near-shore community: substrate, water depth, kelp canopy, prey assemblage, predators and competitors) play a larger role in determining the amount of time spent foraging than population status. In California, the percentage of time foraging was similar between four study areas (21-28%) despite differences in the length of time they were occupied (Estes et al. 1986), and success rate of prey capture differed <2% between prolonged and recently occupied areas (Estes et al. 1981). For the percentage of time spent foraging to be more meaningful or useful as a proxy for population status, a complete 24-hr budget must be used and the type habitat taken into account. We suggest that our time and energy budgets are a good bench-mark for a soft and mixed sediment benthos without canopy forming kelp during the summer for a population of otters whose diet is well known and whose numbers have remained consistent for at least 12 years (Wolt et al. 2012).

SUMMARY

Activity Budget

24hr time budget – This data enabled us to examine behavior on a 24-h basis similar to telemetry studies, but without any of the assumptions about intermittent signals to interpret putative behavior. As we visually observed the animals, there was no question about their behavior, and my data represent an unprecedented number of observations with such high resolution.

The number of otters in Simpson Bay has remained consistent (119 ± 9.3, i.e. less than 10% variability about the mean) during the summer (June-August) over the past 12 years (Wolt et al. 2012), which indicates that equilibrium density has been reached. However, total numbers decreases by over half during the winter (Davis and Weltz unpub. obs.), so that the annual average annual population of sea otters in Simpson Bay is ca. 60 adults. However, the amount of time spent foraging is more similar to other areas known or thought to be below equilibrium density. Foraging success rate is higher (Watt and Siniff 2000, Estes et al. 1981) similar to increasing populations and newly reoccupied areas (Walker et al. 2008, Laidre and Jameson 2006), although a high rate of successful foraging dives is not always correlated to low numbers of otters (Ostfeld 1982). Successful foraging dives may simply indicate that Simpson Bay has a high productivity which has not changed for at least 12 years and probably much longer (Garshelis 1986).

The mean percentage of time that female sea otters with pups (age newborn to three months) spend foraging is 18% (range 13-27%). Resting averaged 42% of the time, similar to or slightly below that from previous studies. In general, the percentage of time spent resting varied inversely with foraging (i.e., as foraging time increased resting decreased). The percentages of time spent grooming (13-16%), interacting (2-3%) and traveling slowly (8-9%) were relatively constant throughout the 24-hr period. As fur is the otters' only source of thermal insulation, frequent grooming to maintain the air layer adjacent to the skin is essential and represents a significant percentage of daily activity compared to marine mammals that use subcutaneous fat for thermal insulation. Swimming may be, at least in part, a response to the large tidal changes (-2.5 to +13 feet are not uncommon, [NOAA Tide Tables for Cordova 2013]) in the bay. As there are no canopy-forming kelp in which to wrap themselves while resting, low energetic swimming may be their best means of resisting tides and currents.

Swimming occupied 15% of the activity budget (range 9% [dawn] to 20% [night]). This is well below that reported for territorial males (26%) in Simpson Bay (Finerty et al. 2009) but similar (14%) to what Garshelis et al. (1986) reported, using telemetry for data collection. Other non-visual based studies cannot distinguish among swimming, grooming and interacting, and so behaviors that are not resting or foraging are lumped together as "other".

The otters in Simpson Bay show a surprising degree of homogeneity with regards to behavior throughout the 24-hr period. While behavior may have differed significantly among the 6-h time periods, the total variation explained by time of day was only <3%.

There was a slight crepuscularity in their foraging, as has been seen to a greater degree in other locations (Estes et al. 1986, Ralls and Siniff 1990). I found an increase in foraging during the day (27% versus 19% for dusk and 13% for night and dawn), although there were small peaks in foraging activity at 5:00 h and 14-15:00 h. One possible reason for this behavior may be ease of locating a pup after the female comes up from a foraging dive. Because there are no canopy forming kelp in Simpson Bay, young pups can drift with wind and currents, and older pups can have a tendency to wander and do not always respond to the calls of the female. It may simply be easier for the females to locate their pups in daylight. Even though they have a tapetum lucidum (Riedman and Estes 1990), from my observations of them at night, the otter's eyesite in low light conditions does not seem to be much better than humans. The musculature around the eye used to contract and change the curvature of the lense for vision above and below the water may actually inhibit their ability to focus when the pupil is fully dialated, as it would be in low light conditions (Murphy et al. 1990).

Estimated Field Metabolic Rate (FMR)

The weight specific FMR for otters in my study was 601 KJ day^{-1} kg^{-1}. This is similar to the predicted FMR based on the allometric regression from other marine mammals including sea lions, fur seals and true seals (Williams et al. 2004a, 2004b). Total FMR for a typical female (21.1 kg) was 12.69 MJ day^{-1}: foraging 2.38 (19%), grooming 2.70 (21%), resting 3.42 (27%), swimming 2.64 (21%), swimming slowly

1.25 (10%) and interacting 0.3 (2%). As with the activity budget, significant differences were found among some of the 6-hr time periods, but generally there was not much variation.

If swimming and swimming slowly are combined, they represent 38% of the FMR at night, more than any other category in any time period. Swimming by itself (27% of the FMR during the night) is equivalent to foraging during the day. Finerty et al. (2009) also found a large percentage of the male activity budget devoted to swimming (26% of the time and 43% of the FMR). It is unclear why otters in Simpson Bay spend so much time moving around. For example, during one 3-hr shore-based observation (with no possibility of our influencing the female's behavior with the presence of a boat), we observed a female with a pup swim for the entire period only to end up right back where she was when we began the observation (Cortez and Wolt personal observation).

The percentage of time spent foraging has been the focus of most activity budget studies because of its implications for population status (Eberhardt 1977, Estes et al. 1986, Ralls and Siniff 1990), although this rational has been questioned. While the theory behind it may be plausible, there are likely many confounding variables that make comparisons among different habitats difficult. Garshelis et al. (1990) suggested that geographic differences (structure of near-shore community: substrate, water depth, kelp canopy, prey assemblage, predators and competitors) played a larger role in determining the amount of time spent foraging than population status. For the percentage of time spent foraging to be more meaningful or useful as a proxy for population status, a complete 24-hr activity budget must be used, and the type habitat taken into account. I

suggest that our activity and energy budgets are a good bench-mark for a soft and mixed sediment benthos without canopy forming kelp during the summer for a population of otters whose diet is well known and whose numbers have remained consistent for at least 12 years (Wolt et al. 2012).

Foraging Behavior and Prey Preference

Optimal foraging theory predicts 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 (1,950 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 (*Saxidomus gigantea*), 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 of otters for much longer periods (Garshelis et al. 1986, Kvitek and Oliver 1992, Estes and Bodkin 2002). In Simpson Bay, clams made up 65-75% of the otters' diet. They have been able to sustain otter populations in some areas at what

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may be pre-fur trade historic levels (Miller 1974). Less than 10 years after sea otters re-entered Simpson Bay, Garshellis 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 2001-2004, where clams constituted 75% and crabs 6% of the diet. No other prey specialization was apparent among the sexes, though we cannot rule out individual prey specialization.

The average foraging dive depth (27 ± 19.5 m) was similar to the average depth of the bay (ca. 30 m; Gilkinson 2004). As adult otters can easily dive to 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 reflects the distribution of depths within the bay.

Diving ability among sexes and age classes 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 2004). The deeper dives in our study 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 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 not used. The lower percentage of dives (21.6%) in the depth range of 45-85m 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 or 2) the metabolic cost of diving to these depths is 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 average number of adult animals and the daily food consumption per otter. The average sea otter population in Simpson Bay during the summer is 119 adults, and this decreases to about 50 adults during the remainder of the year (Davis unpub. obs.). This means that the 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 MJ day^{-1} 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 kg ([19 MJ day^{-1} otter^{-1} x 60 otters x 365 days] / [0.9 x 3.18 MJ kg^{-1}]), of which 109,041 kg (75%) are clams and 36,347 kg are other species. If we divide the biomass of clams consumed by the area of Simpson Bay (21 x 10^6 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 clams m^{-2} yr^{-1} (109,041 kg clam / 0.048 kg clam^{-1} / 21 x 10^6 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 x 10^6 clams km^{-2}), which is not an unreasonably high density (Nickerson 1977, Cortez unpub. obs).

The average growth rate of little neck clams in Galena Bay, also in PWS, is 2-5 mm per year (Paul and Feder 1973). If the growth rate in Simpson Bay is similar, it would take over 10 years for a clam to reach the size (> 5 cm or about the size of a sea otter fore paw) preyed on by otters (Maldini et al. 2010).

Prey and Sediment Type

Benthic geomorphology influences the distribution of infauna and epifauna. Mixed mud and gravel (MMG) was most productive benthic category for macro-invertebrates captured by sea otters. MMG produced significantly more prey per unit area (p-value <0.0001) than mud (M) and rock (R), based on a high resolution (1 m) acoustic map of the study area made using side-scan sonar. Intertidal and shallow areas (<3m) may be considerably different.

Crabs and echinoderms were distributed proportionately to the percentage of the benthos that was M and MMG, while there was a small tendency (60%) for clams to be associated with MMG.

The relatively soft bedrock and large volume of fresh water (average of 95 inches annually, [Gay and Vaughn 2001]) over a watershed of ~168 km^2 (Noll et al. 2009)

surrounding the study area may contribute to the productivity of Simpson Bay and explain why it is a pupping area for sea otters.

Future Studies in Simpson Bay

Ideally, to continue studying sea otters in Simpson Bay, we would begin to tag them. Hind flipper tags have been used in several locations and do not appear to bother most animals. An otter's ability to reach every part of its body with its forepaws, as well as its formidable dentition and use of fur for insulation make fur mounted transmitters unreliable. The implantation of intra-peritoneal transmitters has been used in the past (Monnet and Rotterman 2000), but it requires radio tracking from a boat or aircraft, which is labor intensive and expensive. In the future, intra-peritoneal satellite transmitters may enable us to track animals year round including the critical winter period.

As there are consistently 20-30 females with pups in Simpson Bay, if this group were instrumented, their movements in successive years could tell a lot about site fidelity in terms of pupping, and frequency of pupping.

If some of the females eventually return to Simpson Bay to pup, I would like to genetically compare them and their pups to territorial males from the previous season to see if the male territorial behavior actually results in successful impregnation. Theoretically, territorial behavior would not persist if it did not result in successful reproduction, but I think there may be other mating strategies. I have seen several males

who would stay in the bay for 1-2 weeks and then disappear. Is it possible they were trying to slip into the female area unnoticed by the resident territorial male? This strategy would not require the energetic investment to defend a territory; just the occasional hasty retreat when discovered. Another possibility would be to compare Simpson Bay with another, nearby location (such as Sheep Bay or Nelson Bay) with a smaller watershed to evaluate this as the driving cause of productivity.

REFERENCES

Altmann, J., 1974. Observational study of behavior - sampling methods. Behavior 49(3-4), 227-267.

Bodkin, J.L., Esslinger, G.G., Monson, D.H., 2004. Foraging depths of sea otters and implications to coastal marine communities. Marine Mammal Science 20(2), 305-321.

Bodkin, J.L., Monson, D.H., Esslinger, G.G., 2007. Activity budgets derived from time-depth recorders in a diving mammal. Journal of Wildlife Management 71(6), 2034-2044.

Bodkin, J.L., Ballachey, B.E., Dean, T.A., Fukuyama, A.K., Jewett, S.C., McDonald, L., Monson, D.H., O'Clair, C.E., VanBlaricom, G.R., 2002. Sea otter population status and the process of recovery from the 1989 'Exxon Valdez' oil spill. Marine Ecology-Progress Series 24, 237-253.

Calkin, P.E., Wiles, G.C., Barclay, D.J., 2001. Holocene coastal glaciation of Alaska. Quaternary Science Reviews 20(1–3), 449-461.

Calkins, D.G., 1978. Feeding-behavior and major prey species of sea otter (*Enhydra lutris*), in Montague Strait, Prince-William-Sound, Alaska. Fishery Bulletin 76 (1), 125-131.

Costa, D.P., 1982. Energy, nitrogen and electrolyte flux and sea-water drinking in the sea otter (*Enhydra lutris*). Physiological Zoology 55(1), 35-44.

Costa, D.P., Kooyman, G.L., 1982. Oxygen-consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, (*Enhydra lutris*). Canadian Journal of Zoology-Revue Canadienne De Zoologie 60(11), 2761-2767.

Costa, D.P., Kooyman, G.L., 1984. Contribution of specific dynamic action to heat-balance and thermoregulation in the sea otter (*Enhydra lutris*). Physiological Zoology 57(2), 199-203.

Cowen, R.K., Agegian, C.R., Foster, M.S., 1982. The maintenance of community structure in a central California giant-kelp forest. Journal of Experimental Marine Biology and Ecology 64(2), 189-201.

Davis, R.W., Williams, T.M., Thomas, J.A., Kastelein, R.A., Cornell, L.H., 1988. The effects of oil contamination and cleaning on sea otters (*Enhydra lutris*), metabolism, thermoregulation, and behavior. Canadian Journal of Zoology-Revue Canadienne De Zoologie 66(12), 2782-2790.

Doroff, A.M., Bodkin, J.L., 1994. Sea otter foraging behavior and hydrocarbon levels in prey. Marine mammals and the Exxon Valdez, T.R. Loughlin, (Eds.), Academic Press, New York, pp. 193-208.

Doroff, A.M., Estes, J.A., Tinker, M.T., Burn, D.M., Evans, T.J., 2003. Sea otter population declines in the Aleutian archipelago. Journal of Mammalogy 84(1), 55-64.

Eberhardt, L.L., Siniff, D.B., 1977. Population-dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34(2), 183-190.

Ensminger, A.H., Ensminger, M.E., Konlande, J.E., Robson, J.R.K., 1994. Food & nutrition encyclopedia. CRC Press, Inc, Boca Raton, FL, pp. 862.

Estes, J.A., 1977. Population estimates and feeding behavior of sea otters. In: Merritt, M.L., Fuller, R.G. (Eds.), The environment of amchitka island, Alaska. National Technical Information Service, Springfield, Virginia, pp. 511–526.

Estes, J.A., 1990. Growth and equilibrium in sea otter populations. Journal of Animal Ecology 59(2), 385-401.

Estes, J.A., Palmisan.Jf, 1974. Sea otters - their role in structuring nearshore communities. Science 185(4156), 1058-1060.

Estes, J.A., Jameson, R.J., 1988. A double-survey estimate for sighting probability of sea otters in California. Journal of Wildlife Management 52(1), 70-76.

Estes, J.A., Duggins, D.O., 1995. Sea otters and kelp forests in Alaska - generality and variation in a community ecological paradigm. Ecological Monographs 65(1), 75-100.

Estes , J.A., Bodkin, J.L., 2002. Otters. In: Perrin, W.F., Wursig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of marine mammals. Academic Press, San Diego, California, USA., pp. 842-858.

Estes, J.A., Jameson, R.J., M., J.A., 1981. Food selection and some foraging tactics of sea otters. In: Chapman, J.A., Pursley, D. (Eds.), Worldwide Furbearer Conference, Frostburg, Maryland, pp. 606-641.

Estes, J.A., Jameson, R.J., Rhode, E.B., 1982. Activity and prey election in the sea otter - influence of population status on community structure. American Naturalist 120(2), 242-258.

Estes, J.A., Underwood, K.E., Karmann, M.J., 1986. Activity-time budgets of sea otters in California. Journal of Wildlife Management 50(4), 626-636.

Estes, J.A., Riedman, M.L., Staedler, M.M., Tinker, M.T., Lyon, B.E., 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. Journal of Animal Ecology 72(1), 144-155.

Finerty, S.E., Hillman, G.R., Davis, R.W., 2007. Computer matching of sea otter (*Enhydra lutris*) nose scars: a new method for tracking individual otters. Aquatic Mammals, pp. 349-358.

Finerty, S.E., Wolt, R.C., Davis, R.W., 2009. Summer activity pattern and field metabolic rate of adult male sea otters (*Enhydra lutris*) in a soft sediment habitat in Alaska. Journal of Experimental Marine Biology and Ecology 377(1), 36-42.

Finerty, S.E., Pearson, H.C., Davis, R.W., 2010. Interannual assessment of territory quality for male sea otters (*Enhydra lutris*) in Simpson Bay, Prince William Sound, Alaska. Canadian Journal of Zoology-Revue Canadienne De Zoologie 88(3), 289-298.

Garshelis, D.L., 1983. Ecology of sea otters in Prince William Sound, Alaska. Ph.D. Thesis, University of Minnesota, Duluth, MN, USA.

Garshelis, D.L., Garshelis, J.A., Kimker, A.T., 1986. Sea otter time budgets and prey relationships in Alaska. Journal of Wildlife Management 50(4), 637-647.

Garshelis, D.L., Ames, J.A., Hardy, R.A., Wendell, F.E., 1990. Indexes used to assess status of sea otter populations - a comment. Journal of Wildlife Management 54(2), 260-269.

Gay, S.M., Vaughan, S.L., 2001. Seasonal hydrography and tidal currents of bays and fjords in Prince William Sound, Alaska. Fisheries Oceanography 10, 159-193.

Gelatt, T.S., Siniff, D.B., Estes, J.A., 2002. Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. Journal of Wildlife Management 66(1), 29-39.

Gilkinson, A.K., 2004. Habitat associations and photo-identification of sea otters in Simpson Bay, Prince William Sound, Alaska. Ph.D. Thesis, Texas A&M University, College Station, TX, USA.

Gilkinson, A.K., Pearson, H.C., Weltz, F., Davis, R.W., 2007. Photo-identification of sea otters using nose scars. Journal of Wildlife Management 71(6), 2045-2051.

Hanson, M.B., Bledsoe, L.J., Kirkevold, B.C., Casson, C.J., Nightingale, J.W., 1993. Behavioral budgets of captive sea otter mother pup pairs during pup developement. Zoo Biology 12(5), 459-477.

Kenyon, K.W., 1969. The sea otter (*Enhydra lutris)* in the eastern Pacific Ocean. North American Fauna (68), 1-352.

Kenyon, K.W., 1975. The sea otter in the eastern Pacific Ocean. Dover Publications, New York, USA, p. 352.

Kenyon, K.W., 1981. Sea otter, (*Enhydra lutris)*. Handbook of Marine Mammals, volume 1: the walrus, sea lions, fur seals and sea otter. Academic Press Inc., London, U.K.

Kvitek, R.G., Oliver, J.S., 1992. Influence of sea otters on soft-bottom prey communities in southeast Alaska. Marine Ecology-Progress Series 82(2), 103-113.

Kvitek, R.G., Bowlby, C.E., Staedler, M., 1993. Diet and foraging behavior of sea otters in southeast Alaska. Marine Mammal Science 9(2), 168-181.

Kvitek, R.G., Oliver, J.S., Degange, A.R., Anderson, B.S., 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecology 73(2), 413-428.

Laidre, K.L., Jameson, R.J., 2006. Foraging patterns and prey selection in an increasing and expanding sea otter population. Journal of Mammology. 87(4), 799-807.

Larson, S., Jameson, R., Etnier, M., Jones, T., Hall, R., 2012. Genetic diversity and population parameters of sea otters, (*Enhydra lutris)*, before fur trade extirpation from 1741-1911. Public Library of Science, 7: e33205.

Lee, O.A., Olivier, P., Wolt, R., Davis, R.W., Weltz, F., 2009. Aggregations of sea otters (*Enhydra lutris kenyoni*) feeding on fish eggs and kelp in Prince William Sound, Alaska. American Midland Naturalist 161(2), 401-405.

Lehner, P.N., 1996. Handbook of ethological methods. Cambridge University Press, Cambridge, U.K.

Lensink, C.J., 1962. The history and status of sea otters in Alaska. Ph.D. Thesis, Purdue University, W. Lafayette, IN., p. 188.

Lepš, J., Šmilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, U.K.

Maldini, D., Ward, C., Cecchetti, A., Riggin, J., 2010. Southern sea otter diet in a soft sediment community. Journal of Marine Animals and Their Ecology 3(1), 27-36.

Mann, D.H., Hamilton, T.D., 1995. Late pleistocene and holocene paleoenvironments of the north Pacific coast. Quaternary Science Reviews 14(5), 449–471.

Mann, J., 1999. Behavioral sampling methods for cetaceans: a review and critique. Marine Mammal Science 15(1), 102-122.

Miller, D.J., 1974. The sea otter (*Enhydra lutris)*: it's life history, taxonomic status and some ecological relationships. California Department of Fish and Game, Marine Resources Leaflet No. 7, Sacramento, CA., USA.

Monnett, C., Rotterman, L.M., 2000. Survival rates of sea otter pups in Alaska and California. Marine Mammal Science 16(4), 794-810.

Murphy, C.J., Bellhorn, R.W., Williams, T., Burns, M.S., Schaeffel, F., Howland, H.C., 1990. Refractive state, ocular anatomy, and accommodative range of the sea otter (*Enhydra lutris*). Vision Research 30(1).

Nickerson, R.B., 1977. A Study of the littleneck clam (*Protothaca staminea conrad*) and the butter clam (*Saxidomus giganteus deshayes*) in a habitat permitting coexistence, Prince William Sound, Alaska. Proceedings of the National Shellfisheries Association (67), 85-102.

Noll, C.J., Dellapenna, T.M., Gilkenson, A., Davis, R.W., 2009. A high-resolution geophysical investigation of sediment distribution controlled by catchment size and tides in a multi-basin turbid outwash fjord: Simpson Bay, Prince William Sound, Alaska. Geo-Marine Letters (29), 1-16.

Noll, C.J., IV, 2005. A high resolution geophysical investigation of spatial sedimentary processes in a paraglacial turbid outwash fjord: Simpson Bay, Prince William Sound, Alaska. Ph.D. Thesis, Texas A&M University, College Station, TX.

NOAA Tide Tables for Cordova, 2013. URL: http://tidesandcurrents.noaa.gov/noaatidepredictions/NOAATidesFacade.jsp?datatype=Annual+PDF&Stationid=9454050&text=datafiles%252F9454050%252F24102013%252F634%252F&imagename=images%2F9454050%2F24102013%2F634%2F9454050_20131025.gif&bdate=20131024&timelength=daily&timeZone=2&dataUnits=1&interval=&edate=20131025&StationName=CORDOVA&Stationid_=9454050&state=AK&primary=Harmonic&datum=MLLW&timeUnits=2&ReferenceStationName=CORDOVA&ReferenceStation=9454050&HeightOffsetLow=&HeightOffsetHigh=&TimeOffsetLow=0&TimeOffsetHigh=0&pageview=dayly&print_download=true&Threshold=&thresholdvalue=

O'Clair, R.M., O'Clair, C.E., 1989. Southeast Alaska's rocky shores. Animals Plant Press, Auke Bay, AK.

Osterrieder, S.K., Davis, R.W., 2009. Summer foraging behavior of female sea otters (*Enhydra lutris*) with pups in Simpson Bay, Alaska. Aquatic Mammals, 35(4), 481-489.

Osterrieder, S.K., Davis, R.W., 2010. Sea otter female and pup activity budgets, Prince William Sound, Alaska. Journal of the Marine Biological Association of the United Kingdom, 91(4), 883-892.

Ostfeld, R.S., 1982. Foraging strategies and prey switching in the California sea otter. Oecologia 53(2), 170-178.

Packard, J.M., Ribic, C.A., 1982. Classification of the behavior of sea otters (*Enhydra lutris*). Canadian Journal of Zoology-Revue Canadienne De Zoologie 60(6), 1362-1373.

Paine, R.T., 1969. *Pisaster tegula* interaction - prey patches, predator food preference, and intertidal community structure. Ecology 50(6), 950-961.

Paul, A., Feder, H., 1973. Growth, recruitment, and distribution of the littleneck clam, (*Protothaca staminea)*, in Galena Bay, Prince William Sound, Alaska. Fishery Bulletin 71(3).

Pearson, H.C., Davis, R.W., 2005. Behavior of territorial male sea otters (*Enhydra lutris*) in Prince William Sound, Alaska. Aquatic Mammals 31(2), 226-233.

Pitcher, K.W., 1975. Distribution and abundance of sea otters, steller sea lions and harbor seals in Prince William Sound. Alaska Department of Fish and Game, Game Division, Juneau, Alaska.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. Bioscience 46(8), 609-620.

Pyke, G.H., 1984. Optimal foraging theory - a critical review. Annual Review of Ecology and Systematics 15, 523-575.

Ralls, K., Siniff, D., 1990. Time budgets and activity patterns in California sea otters. Journal of Wildlife Management 54(2), 251-259.

Riedman, M.L., Estes, J.A., 1990. The sea otter (*Enhydra lutris)*: behavior, ecology and natural history. US Fish and Wildlife Service Biological Report 90(14), 1-126.

Rotterman, L.M., Simon-Jackson, T., 1988. Sea Otter. In: Lentfer, J.W. (Ed.), Selected marine mammals of Alaska: species accounts with research and management recommendations. Marine Mammal Commission, Washington, D.C., pp. 237-271.

Schmidt-Nielsen, K., 1997. Animal physiology: adaptation and environment. 5th edition. Cambridge University Press, Cambridge, U.K.

Shimek, S.J., Monk, A., 1977. Daily activity of sea otters off Monterey peninsula, California. Journal of Wildlife Management 41(2), 277-283.

Terbraak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57(3), 255-289.

Tinker, M.T., Bentall, G., Estes, J.A., 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proceedings of the National Academy of Sciences of the United States of America 105, 560-565.

Tinker, M.T., Costa, D.P., Estes, J.A., Wieringa, N., 2007. Individual dietary specialization and dive behavior in the California sea otter: using archival time-depth data to detect alternative foraging strategies. Deep-Sea Research Part II-Topical Studies in Oceanography 54(3-4), 330-342.

U.S. Fish & Wildlife Services, 2011. U.S. Fish & Wildlife Services, Marine Mammal Management. URL: http://www.fws.gov/alaska/fisheries/mmm/seaotters/history.htm

VanBlaricom, G.R., 1988. Effects of foraging by sea otters on mussel-dominated intertidal communities. In: VanBlaricom, G.R., Estes, J.A. (Eds.), The community ecology of sea otters. Springer-Verlag, Berlin, GER.

Walker, K.A., Davis, J.W., Duffield, D.A., 2008. Activity budgets and prey consumption of sea otters (*Enhydra lutris kenyoni*) in Washington. Aquatic Mammals 34(4), 393-401.

Watt, J., Siniff, D.B., Estes, J.A., 2000. Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska. Oecologia 124(2), 289-298.

Williams, T.M., Kastelein, R.A., Davis, R.W., Thomas, J.A., 1988. The effects of oil contamination and cleaning in sea otters (*Enhydra lutris*), thermoregulatory implications based on pelt studies. Canadian Journal of Zoology 66(12), 2776-2781.

Williams, T.M., Estes, J.A., Doak, D.F., Springer, A.M., 2004a. Killer appetites: assessing the role of predators in ecological communities. Ecology 85(12), 3373-3384.

Williams, T.M., Fuiman, L.A., Horning, M., Davis, R.W., 2004b. The cost of foraging by a marine predator, the weddell seal *Leptonychotes weddellii*: pricing by the stroke. Journal of Experimental Biology 207(6), 973-982.

Wolt, R.C., Gelwick, F.P., Weltz, F., Davis, R.W., 2012. Foraging behavior and prey of sea otters in a soft- and mixed-sediment benthos in Alaska. Mammalian Biology 77(4), 271-280.

Yeates, L.C., Williams, T.M., Fink, T.L., 2007. Diving and foraging energetics of the smallest marine mammal, the sea otter (*Enhydra lutris*). Journal of Experimental Biology 210(11), 1960-1970.