Sea Otter Carrying Capacity in a Soft- and Mixed-sediment Benthic Habitat

Ian P. Davis[1], Timothy M. Dellapenna[2], Gary E. Maale[2], Francis P. Gelwick[3], Frederick C. Weltz[4], Randall W. Davis[1*]

[1]Department of Marine Biology, Texas AM University, Galveston, TX, United States,
[2]Department of Marine Science, Texas AM University, Galveston, TX, United States,
[3]Department of Wildlife and Fisheries Science, Texas AM University, College Station TX, United States, [4]Alice Cove, Cordova, AK, United States

*Corresponding Author: Randall Davis
davisr@tamug.edu

Abstract

Identifying factors that influence sea otter (*Enhydra lutris*) population density can provide insight into why it varies spatially and temporally and when a recovering population has reached an equilibrium density because of food resources (i.e., carrying capacity *K*). Although food availability is widely recognized as an important extrinsic factor affecting sea otter density, how do we determine when a population has reached *K*? The goal of this study was to estimate *K* for Simpson Bay, Alaska by measuring the abundance of edible bivalves, the primary prey for sea otters for over 40 years. We then compared prey abundance and estimated replacement rate (i.e., the mean age of bivalves predated by sea otters) to estimated annual prey consumption based on the mean population density for the past 18 years. On average, 110 adult sea otters (5.2 km^{-2})

have occupied Simpson Bay annually since 2001 consuming an estimated 176,660 kg of bivalves. The total mass (standing stock) of the major bivalves (predominately butter clams and stained macomas) was 785,730 kg, so adult sea otters consumed about 22% annually. Based on these observations and calculations, the estimated annual number of sea otters occupying Simpson Bay appears to be at or near *K* based on the replacement rate of food resources. However, other intrinsic (e.g., male territoriality and emigration) and extrinsic (e.g., predation, disease, human-related mortality) factors may influence equilibrium density, which varies spatially and temporally, resulting in a mosaic of subpopulations with different densities, rates of growth and discontinuous distributions. Understanding the balance among these factors may be one of the most challenging ecological questions for sea otter conservation and management as populations recover from their range-wide decimation during the Maritime Fur Trade in the late 18^{th} and 19^{th} centuries.

Keywords: sea otter, population, carrying capacity, equilibrium density

1 Introduction

Sea otters are marine predators that forage primarily on large benthic invertebrates in the shallow, littoral zone of the North Pacific Rim, originally from northern Japan to central Baja California in Mexico (Fig. 1). However, their numbers were significantly reduced from ~300,000 to less than ~2,000 individuals during the Maritime Fur Trade in the late 18^{th} and 19^{th} centuries, and this allowed populations of large invertebrates (e.g. clams, crabs and urchins) to flourish in their absence (Davis et al. 2019). International protection from hunting since 1911 has allowed sea otters to recover to ~150,000, reoccupy parts of their historical habitat and restore the nearshore ecosystem, although full re-occupation is decades away. As sea otters reoccupy an area, they often experience a period of logistic population growth (10-25% yr^{-1}) such as occurred in the Aleutian Islands prior to their subsequent decline in the 1990s (Davis et al. 2019). Similar population growth rates were observed on Bering Island in eastern Russia, Southeast Alaska, British Columbia, and Washington State (Jameson et al. 1986; Estes 1990; Bodkin et al. 1999; Bodkin et al. 2000; Bodkin 2015; Tinker et al. 2019). In contrast, the population in California showed more modest growth (~5% yr^{-1} and variable), an indication that other factors influence population growth (Estes 1990; Estes et al. 2003; Bodkin 2015; Tinker 2015).

As a population approaches equilibrium density, it may fluctuate inter-annually, decadally or over longer time scales depending on intrinsic and extrinsic factors (Kenyon 1969: Estes 1990, Watt et al. 2000; Bodkin 2015). Assuming a normal reproductive rate (Monson Degange 1995), intrinsic factors include territoriality and dispersal that reduce population density, while extrinsic factors include food availability, predators, disease, human-related mortality, weather and other environmental variables that affect survival (Wolff 1997; Bodkin 2015). The impact of these factors varies spatially and temporally, resulting in a mosaic of subpopulations with different densities, rates of growth and discontinuous distributions. Hence, we cannot assume that a population of sea otters at equilibrium density (e.g., stable for >25 years or longer) is necessarily food limited and at carrying capacity (*K*) (Sutherland and Parker 1985; Fowler 1987).

Aside from its use in a logistic equation, the concept of *K* is nebulous (Sutherland Parker 1985). It may refer to the daily intake of food necessary for survival, below which animals either starve or emigrate. The poorest feeders (e.g., very young and old) are eliminated or leave while the remaining animals do well as the population approaches or hovers around *K*. In contrast, we can take a broader perspective to include other extrinsic factors that influence population equilibrium density. Here, we focus on *K* associated with food resources as the primary factor influencing equilibrium population density.

Prey abundance and availability will depend on primary production, which injects carbon and nutrients into the food web. Seasonal and interannual changes in productivity influence the abundance and growth of sea otter prey, which will have an important bottom-up effect on the carrying capacity of an area and influence local sea otter densities. Because of their elevated resting metabolic rate and food consumption (~25% of body mass per day; Costa Kooyman 1984; Yeates et al. 2007; Wolt et al. 2012), sea otters are susceptible to density-dependent competition for food. In addition, they have a top-down effect on large invertebrates, which results in a trophic cascade affecting nearshore community structure (Estes and Palmisano 1974; Kenyon 1969; Estes and Duggins 1995; Estes 2015). As sea otters reoccupy an area from which they were extirpated, populations of epifaunal prey such as sea urchins, crabs and abalone generally decline first followed by infaunal species such as bivalves depending on the type of habitat (Kimker 1982: Kvitek Oliver 1988; Kvitek et al. 1992, 1993; Bodkin et al. 2000; Coletti et al. 2016).

Although food availability is an important extrinsic factor affecting sea otter population density (Kenyon 1969, Monson et al. 2000, Monson Bowen 2015), how do we determine when a population has reached *K*? This question is relevant to predicting population trends (i.e., describing the status of populations) and developing management policies that will contribute to the full recovery of sea otters to pre-exploitation levels, reoccupation of their historical range, and restoration of nearshore ecosystems (Davis et al. 2019). Previous attempts to estimate *K* for subpopulations were based on the population density of sea otters in nearby, *long-occupied* areas, which were assumed to be at *K* (Laidre et al. 2001, 2002). For Southeast Alaska, a

Bayesian state−space model was used to analyze line transect survey data and to make probabilistic inferences about abundance, trends, and population parameters (Tinker et al. 2019). This model incorporated density−dependent population dynamics, range expansion, dispersal between sub-regions, harvest mortality, and environmental stochasticity. The average density at equilibrium, which was based on *long−occupied subregions*, was assumed to be 4.2 otters km^{-2}. However, there was considerable variation in subregional estimates of *K*, ranging from 0.7-16.6 otters km^{-2}, in part because this model did not incorporate habitat characteristics and prey availability.

In this study, we used an alternative approach to estimate *K* for sea otters in Simpson Bay, which is located in eastern Prince William Sound (PWS), Alaska. This area was reoccupied by sea otters in the late 1970s, and their numbers have been relatively stable for at least the past 18 years (Garshelis 1983; Newsome et al. 2015; Cortez et al. 2016b). Hence, we hypothesized that the population was at *K*. To test this hypothesis, we compared the abundance and replacement rate of bivalves, their primary prey, with information from our previous research on annual sea otter abundance, foraging behavior, dietary preference, prey consumption and habitat-associations (Finerty et al. 2009; Noll et al. 2009; Gilkinson et al, 2011; Wolt et al. 2012; Cortez et al. 2016b). This empirical approach, rather than modeling, provided a mechanistic basis for estimating *K*, which has not been used for most sea otter populations.

2 Methods

2.1 Study Site

Simpson Bay (60.6° N, 145.9° W) is a shallow fjord located in northeastern Prince William Sound, Alaska, with a mean water depth of ~30 m and a maximum depth < 100 m (Fig. 2). 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 shoreline is ~35 km in length consisting primarily of mud-gravel beaches and rocky intertidal. Historically, this is a well-studied site for sea otter ecology because of its easy access, protection from rough seas, and continuous presence of sea otters (Garshelis 1983; Finerty et al. 2009, 2010; Osterrieder Davis 2009, 2011; Lee et al. 2010, Gilksinson et al. 2011; Wolt et al. 2012; Cortez et al. 2016a, 2016b). After near extinction during the Maritime Fur Trade, Simpson Bay was recolonized by male sea otters in 1977, and females moved into the area in 1983 (Garshelis 1983; Rotterman Simon-Jackson 1988; VanBlaricom 1988).

Alternating periods of glaciation and deglaciation dominated the Holocene geology of Simpson Bay (Noll et al. 2009). As a result, the bay consists of sub-basins of fine sediment (mud composed of silt and clay generated by glacial erosion) and areas of higher sand and gravel content (mud-gravel), which were created as glaciers retreated, leaving behind recessional moraines (Noll 2005). Large watersheds (112 km^2 for North Bay and 52 km^2 for East Bay) drain rainwater (400 cm yr^{-1}) and glacial meltwater into creeks that deliver significant freshwater and terrigenous organic material into the bay with a mean sedimentation rate of 0.6 cm yr^{-1} (Noll et al. 2009).

Simpson Bay is oligotrophic similar to other parts of Prince William Sound (Goering et al. 1973; Ziemann et al. 1991; Quigg et al. 2013), with much less productivity than eutrophic waters such as the western Bering Sea (Springer et al., 1991). None of the large-bodied kelps (e.g., *Nereocystis* and *Macrocystis*) that elsewhere form canopies are present in Simpson Bay, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*), and sieve (*Agarum cribrosum*) kelp cover the seafloor in many areas of the bay from the lower intertidal to a depth of ~20 m based on diver surveys (Dean et al. 2000; R. Davis, pers. obs.).

2.2 Sea otter surveys

To determine the mean number of sea otters (adults and pups) occupying Simpson Bay during the summer (defined as June-August) and other times of the year (September-April), annual censuses were conducted from 2001-18. During a summer census, two skiffs with teams of 3-4 observers traveled at ~2 m s^{-1} along predetermined, parallel transects and counted every otter (adults and pups separately) in non-overlapping areas of ~300 m between the skiffs and to either shore using 7–10x binoculars. The skiffs paused or made small deviations as needed to insure an accurate count, and the slow transit speed ensured that we observed any otters surfacing after dives, which have a mean duration of about 2 min (Wolt et al. 2012). These censuses used the double-survey method in which two or more experienced counters confirmed sightings thereby reducing counting errors and the number of missed animals, (Estes Jameson 1988), although we did not estimate sighting error. This method was repeated every two weeks (~5 times) from June to August to provide an estimate of the mean abundance each summer. Hence, the summer surveys were intensive for the size of the bay.

During other times (September-April), opportunistic (based on weather, light level, and personnel availability) censuses were conducted from the bridge of a 10-m vessel (single observer) moving along a transect line similar to that used during the summer and counting every otter (adults and pups separately) using 7–10x binoculars. Pauses and deviations from the transect line were made as needed for an accurate count. From 2001-18, each month from September to April was censused at least once, and the mean was three times. Censuses were conducted only on days with good visibility and calm sea conditions. The total number of censuses conducted over 18 years totaled 112 with 87 during the summer and 25 at other times of the year.

There was no significant difference in the interannual number of sea otters over the 18-year monitoring period. We estimated the annual mean number of sea otters using the bay by assuming that the overall *mean* summer census (X) was representative of three months of the year, and the *mean* census for the remainder of the year (Y) was representative of nine months using the equation:

Eq. 1 $$[(X \text{ otters} \times 3 \text{ mo}) + (Y \text{ otters} \times 9 \text{ mo})] \div 12 \text{ mo} = \text{annual mean number of sea otters}$$

Because Simpson Bay is a pupping area, most of the adult sea otters were assumed to be females (mean body mass of 24 kg) with fewer (≤ 12) territorial males (mean body mass of 27 kg) (Garshelis et al. 1983; Ballachey et al. 2003; Pearson et al. 2006). The reproductive system of sea otters is resource defense polygyny, where males control females indirectly by defending territories or resources against conspecific males. As a result, younger, non-territorial males and those unable to defend a territory are excluded from Simpson Bay (Pearson et al. 2005). We could not distinguish between adult and subadult (> 1 yr of age) sea otters based on size, so they were included with adults. We counted dependent pups separately, which were observed either nursing or closely associated with a female (i.e., pre-weaning and < 6 months in age). See Sect. 4.1 for a discussion of survey detection bias.

2.3 Seafloor mapping and sampling stations

Before sampling benthic invertebrates, we created a seafloor sediment map based on data previously obtained using side-scan sonar imagery and simultaneous seafloor sampling to characterize sediment type and distribution (Noll et al. 2009, Gilkinson et al. 2011). The side-scan sonar was towed behind a 10-m vessel along parallel transects that covered the entire bay. It emitted wide-angle sound pulses (100 kHz) directed toward the seafloor perpendicular to the transect path. The sound pulses were reflected differentially depending on sediment composition and converted into a gray-scale from black (little or no reflectivity) to white (strong reflectivity). Images of individual transects were combined to form a sonar mosaic of the seafloor with a resolution of 1 m (Fig. 3a). We sampled seafloor sediments at predetermined locations with a box or gravity core and characterized them by grain size using standard techniques and a Shephard's Classification (Shephard 1954, Noll et al. 2009; Gilkinson et al. 2011). Dark areas on the map correlated with areas of soft sediment (primarily silt and clay), which we have labeled as mud. Lighter areas correlated with soft sediments but also contained sand and gravel, which we labeled as mud-gravel. The sonar mosaic was imported into mapping software (Arcview, ESRI, Redlands, CA), and polygons representing the sediment classes of mud, mud-gravel and rocky reef were overlayed creating a sediment map (Fig. 3b). This map was validated during this study with sediment samples (see benthic sediment analysis below) from the same box cores used to collect benthic megainvertebrates.

2.4 Sampling benthic sediments and bivalves

Based on our seafloor sediment map, we designated the locations for sampling benthic invertebrates during the summers of 2015-16 (Appendix 1). Boat-based sampling stations within the two sediment classes (mud and mud-gravel) were selected based on visually even spacing in Arcview. We used this approach instead of random sampling because it provided a sptially representative distribution in each sediment type given the logistical constraints that limited us to 40 sampling locations. Initially, twenty sampling locations were used in each of the two sediment classes with six replicates per station (Fig. 3b; Appnedix 1). This reduced any bias that may result from oversampling in one of the two sediment types. Sediment and infauna were sampled with a Gomex Box Core (cross section 25 cm x 25 cm; 180 kg mass with a maximum depth penetration of 40 cm). The corer was lowered with a winch from a 10-m vessel to the seafloor where it penetrated the sediment to a mean depth of 29 ± 4.50 *s.d.* cm in mud and 15 ± 3.80 *s.d.* cm in mud-gravel. The corer was then retracted and brought to the surface where the sample was: 1) measured for penetration depth, 2) homogenized and subsampled for sediment analysis and 3) processed by removing fine sediments and smaller organisms under moderate water pressure through a 1 cm^2 wire mesh seive. All live bivalves remaining in the sieve were collected for identification and morphometrics, and the remaining gravel and broken shell imaged *in situ* for estimating the percentage of gravel by volume. Each station was sampled six times so that 240 samples were collected from 40 locations.

2.5 Benthic sediment analysis

Each sample location was confirmed to be mud or mud-gravel based on our sediment map. Three locations originally thought to be mud were mud-gravel, so we corrected the map. Sediments were subsampled from each box core and stored in individual plastic bags until analysis at Texas AM University. The percent grain size distribution was determined using a Malvern Mastersizer 2000, which uses laser diffraction to produce a grain size distribution ranging from 0.02-200 µm. Using the particle size classification of Wentworth (1922) and Sheppard (1954), sediments were classified as clay (< 3.9 µm), silt (3.9-6.25 µm), sand (6.25-2000 µm). For analysis, each sample was solubilized with a magnetic stir bar in a solution of sodium metaphosphate (5.5 g L^{-1}). The samples were added to the Malvern until the obscuration of the lasers reached an ideal limit (15-20%) to measure the percentage of clay, silt and sand (Taylor 2007). These results were combined with the estimated volume of gravel to estimate the percentage of clay, silt, sand and gravel.

2.6 Beach mapping and sampling of sediments and bivalves

We created a catalog of images for the entire intertidal shoreline of Simpson Bay from Google Earth. Beaches were identified (based on GPS coordinates) and their lengths estimated in Google Earth using the ruler function along a series of straight lines fitted to each beach. We surveyed each beach for bivalves from a skiff at a -2.0 ft tide, which exposed all of the intertidal suitable for sampling (see below). We then selected beaches for sampling based on substrate (mud or mud-gravel) and the presence of bivalve shells.

We sampled bivalves on 12 beaches (visually spaced evenly around Simpson Bay in ArcView) in the intertidal zone from the -2 ft to +2 ft relative to mean tide level. This zone has the highest density of intertidal bivalves in Simpson Bay (Nickerson 1977; Brooks et al. 2001). A single transect perpendicular to the waterline was selected towards the middle of each beach and sampled by digging a series of five 1 m^2 holes to a depth of ~20 cm with a shovel along the *transect* line at -2, -1, 0, +1, and +2 ft relative to mean tide level. We sieved excavated sediments through 1 cm^2 wire mesh as described above for the benthic sediment samples. All living bivalves were collected for identification and morphometrics. Sediment samples were analyzed for the percentage of clay, silt, sand and gravel as described above for the benthic sediment samples. The slope of each beach was calculated across the height of the sampling zone.

2.7 Morphometrics of bivalves

Live bivalves from benthic and beach samples retained in the seive (1 cm^2 mesh) were measured for maximum length (mm) and width (mm) using digital calipers (Weymouth et al. 1931). The unfrozen, fresh (wet) mass (g) of the soft tissue (i.e., without the shell) was measured with a digital scale. Other common invertebrates such as bamboo worms (*Nicomache personata*) and brittlestars (e.g., *Amphipholis squamata*) that were brought to the surface by the Gomex corer were released on site (i.e., were not included for further analysis) because they have not been observed as prey for sea otters in Simpson Bay (Wolt et al. 2012).

2.8 Statistical Analysis

A Generalized Linear Model (binomial distribution with logit link function) was used to test (F statistic, Alpha 0.05) the explained variation (R^2) differentiating the two sediment categories (mud and mud-Gravel) among benthic samples based on the mean dry proportion of the four sediment components (clay, silt, sand, and gravel). Proportions were arcsin transformed for analysis to linearize responses and increase model fit (AIC).

A preliminary Detrended Correspondence Analysis showed 5.2 standard deviations among sample composition of bivalve species, indicating that a unimodal context for the ordination was appropriate (Ter Braak Šmilauer 2012). Therefore, a Canonical Correspondence Analysis (CCA) was used to summarize the total explained variation in abundance of bivalve species as related to the two explanatory variable groups: sediment category and arcsin proportion dry sediment composition.

Variation partitioning was used to quantify explained variation (R^2) and test (Monte Carlo simulations to calculate pseudo-F statistic, Alpha 0.05) conditional effects for each explanatory group and total explained variance of bivalve species abundances. Results were summarized in biplots showing the joint effects of the explanatory variables. All analyses were carried out using CANOCO 5.0 (Ter Braak Šmilauer 2012).

3 Results

3.1 Number of otters using Simpson Bay

During the summers (June-August) of 2001-18, we counted an overall mean of 139 ± 30.5 (95% confidence interval ±10%) sea otters including adults (102 ±18.1) and pups (37 ± 12.8) giving a mean density of 6.62 otters km^{-2} (4.86 adult otters km^{-2} and 1.76 pups km^{-2}) (Table 1). During the remainder of the year (September-April), the mean number decreased 52% to 77 ± 31.9 (95% confidence interval ±15%) sea otters including adults (69 ± 28.4) and pups (8 ± 6.3) giving a mean density of 3.67 otters km^{-2} (3.29 adult otters km^{-2} and 0.38 pups km^{-2}). There were no significant differences in the annual number of sea otters (F = 3.47, DF = 15, P = 0.08) including adults (F = 0.40, DF = 15, P = 0.54) and pups (F = 2.77, DF = 15, P = 0.12) during this 18-year period. During the summer, pups represented 27% of the population, but this decreased to 10% during other times of the year. The estimated mean *annual* number of sea otters occupying the bay based on censuses (uncorrected for detection bias; see Sect. 4.1) was 92.5 (77.3 adults and 15.3 pups; Eq. 1) with a mean *annual* density of 4.40 otters km^{-2} (3.68 adult otters km^{-2} and 0.73 pups km^{-2}). Annually, pups represented 16% of the population.

3.2 Seafloor and shoreline mapping

The seafloor of Simpson Bay is 21,000,000 m^2 of which 33.1% was estimated to be mud (6,957,300 m^2), 45.1% (9,471,000 m^2) mud-gravel and 21.8% (4,571,700 m^2) rocky substrate (Fig. 3). There are 32,445 m of intertidal shoreline suitable for bivalves (intertidal zone from the -2 ft to +2 ft relative to mean tide level) with a mean slope of 8° and a total area of 299,792 m^2. Taken together, the intertidal shoreline suitable for bivalves was 1.4% of the total area (21,299,792 m^2) of the bay.

3.3 Sediment composition

Based on the mean percent dry composition, benthic mud was composed primarily of clay (31%) and silt (66%) with little sand (2%) and gravel (1%) (Appendix 2). Benthic mud-gravel was also composed primarily of clay (29%) and silt (57%) but contained more sand (10%) and gravel (5%). The dry compositions of the two sediment types were significantly different. A

GLM (binomial with logit link function) that included an intercept term was the best-fit model to explain the two dry compositions (Parsimony 11.369 with overall test for analysis of deviance checked using quasi-likelihood approach). A Monte Carlo permutation test for all explanatory components combined was significant (pseudo-F = 50.8, P = 0.002); the model explained 88.2% of the compositional variation between the two sediment types in these samples (GLM, F = 50.789, DF = 4.31 P < 0.00001). However, no single term in the model could significantly distinguish between mud and mud-gravel sediment (P > 0.08 for each term).

Compared with the benthic sediments, beach sediments were very different and composed primarily of gravel (74%) and sand (12%) with little silt (9%) and clay (5%) (Appendix 3).

3.4 Morphometrics of bivalves

Twelve species of bivalves and a brachiopod were sampled on the seafloor and eight species along the shoreline (Table 2). The little neck clam and *Astarte sp*. were found only along the intertidal shoreline. Overall, maximum shell length and wet tissue mass ranged from 18.8 mm and 1.0 g (Nuttall cockle) to 47.7 mm and 12.9 g (butter clam), respectively. Hereafter, the single species of brachiopod (black lampshell) will be grouped with the bivalves.

3.5 Sediment composition and distribution of bivalves

Variance partitioning of the explanatory effects for species abundance showed that the two types of benthic sediment (i.e., mud and mud-gravel) together with the arcsin proportion of each of the four sediment components (silt, mud, sand, gravel) explained 16.3% of the total adjusted variation (F = 2.2, P = 0.002). Sediment components uniquely contributed 7.1% (F = 1.7, P = 0.002), sediment type uniquely contributed 2.7% (F = 1.9, P = 0.056), and an additional 6.5% of explained adjusted variation was equally attributable to (shared by) both of these variables (F = 2.2, P = 0.002).

The biplot for the first two canonical axes of the detrended correspondence analysis together accounted for 80% of the explained variation (CA 1 = 47%, P = 0.002; CA 2 = 33%, P= 0.004) (Fig. 4). The third and fourth axes contributed an additional 12% and 6%, respectively, but were not significant (P > 0.70) and are not depicted. Hard-shelled bivalves (butter clams, Nuttall cockle, smooth cockle and broad yoldia) and epibenthic bivalves (blue mussel, red scallop and false jingle) were positively correlated with mud-gravel and specifically with the sand and gravel components and negatively correlated with mud and specifically with silt and clay (Fig. 4, upper versus lower quadrant). The opposite was true for the stained macoma and bent-nose macoma (Fig. 4, lower left quadrant). The hairy cockle, black lampshell and softshell clam were positively correlated with clay (Fig. 4 lower right quadrant).

Generalized Linear Models using quasi-Poisson distribution and log link function predicted the associations of each bivalve species with each sediment component. Nine of the 12 species were significantly associated with one or more sediment components. Strongest significant associations (highest R^2, $P < 0.05$) were with clay (softshell clam = 67.2%, smooth cockle = 52.4%, and black lampshell = 45.6%). Bent-nose macoma was significantly associated with silt (35.4%), gravel (34.3%) and sand (25.3%) but not with clay (0.9%).

3.6 Abundance and density of bivalves

As a percentage of the total sample size (196), butter clams (34%) were the most abundant bivalve collected followed by the *Astarte* sp. (25%), softshell clam (14%), stained macoma (10%) and littleneck clam (5%) (Table 3). Combined, the other species represented ~13% of the total count. The majority of the butter clams (64%) were collected along the shoreline followed by subtidal mud-gravel (28%) and mud (8%). In contrast, the *Astarte sp.*, softshell clam, and the littleneck clam were found almost exclusively (99-100%) along the intertidal shoreline.

The total area sampled in subtidal mud (17 sites) and mud-gravel (23 sites) was 6.375 m^2 and 8.625 m^2, respectively. In contrast, the combined total area sampled along the intertidal shoreline (five 1-m^2 holes at each of 12 beaches) was 60 m^2, a 7 to 9-fold greater area than in subtidal mud-gravel and mud. This influenced the number of each species collected and the calculated density. The density of butter clams in mud-gravel (6.26 m^{-2}) was 2.5-fold greater than in mud (2.51 m^{-2}) and 3.0-fold greater than along the intertidal shoreline (2.1 m^{-2}) (Table 3). In contrast, the density of stained macomas in mud (4.71 m^{-2}) was 13.5-fold greater than in mud-gravel (0.35 m^{-2}) and 12.7-fold greater than along the shoreline (0.37 m^{-2}). Similarly, the density of bent-nose macomas in mud (1.41 m^{-2}) was 28-fold greater than along the shoreline, and they did not occur in mud-gravel. Black lampshells occurred exclusively in mud-gravel and had a density of 1.86 m^{-2}. Softshell clams occurred mostly along the shoreline and had a density of 1.33 m^{-2}. Likewise, the *Astarte sp*. occurred exclusively along the shoreline and had a density of 2.43 m^{-2}. All other species had densities of < 1 m^{-2}.

The abundance of edible (> 10 mm in length) blue mussels along gravel beaches and rocky shoreline was not estimated. However, intertidal edible mussels in Simpson Bay are small (mean length = 25 mm ± 5.32 *s.d*., mean fresh mass = 0.52 g, n = 450; R. Davis unpub. obs.) and sparsely distributed in clusters along the shoreline, which in total represents only 1.4% of the total area of Simpson Bay. Hence, their contribution to bivalve biomass in Simpson Bay is probably small (< 1% based on abundance and available shoreline habitat). Larger northern horse mussels (*Modiolus modiolus*) have not been identified in Simpson Bay (Nickerson 1977), and we obtained none in our benthic sampling. In addition, this species was not observed during SCUBA dives to a depth of 15 m, and its shells do not occur along the beaches (Davis unpub. obs).

3.7 Biomass of bivalves

The calculated biomass of each species in subtidal mud and mud-gravel and along the shoreline is the product of *mean* species density, the area of each habitat, and the mean tissue mass of each species (Tables 2 and 3). Since mud represented 33.1% and mud-gravel 45.1% of the total area, these two habitats contained most of the bivalve biomass. In contrast, the shoreline was only 1.4% of the total area, so it represented a small part of the total biomass for all species even though it had relatively high densities of butter clams and *Astarte sp*.

The sum of the biomasses for all species in the three habitats was 9.27 x 10^5 kg and within the foraging depth of sea otters (Table 3; Bodkin et al. 2004; Wolt et al. 2012). Butter clams (5.47 x 10^5 kg) represented 59% of the total biomass of which 76% occurred in mud-gravel, 22% in mud and 1% along the shoreline. Stained macomas (1.13 x 10^5 kg) represented 12% of the total biomass of which 91% occurred in mud and 9% in mud-gravel. Together, these two species represented 71% of the total biomass. Black lampshells (8.43 x 10^4 kg) were 9% of the total biomass of which 100% occurred in mud-gravel. The combined biomass (17.6 x 10^4 kg) of hairy cockles, broad yoldia, bent-nose macomas, smooth cockles, false jingles, reddish scallops and Nuttall cockles represented 18% of the total, most of which occurred in areas of mud-gravel except for the broad yoldia and bent-nose macoma, which occurred in mud or mud-gravel. The combined biomass of the remaining species (softshell clam, blue mussel, little neck clam and *Astarte sp*.) was < 1% of the total.

4 Discussion

4.1 Number of otters using Simpson Bay

The sea otter population in Prince William Sound is considered stable with an estimated mean density of 2.31 sea otters km^{-2} based on aerial surveys (unpublished USGS administrative report 2014; Bodkin 2015). Based on the census data uncorrected for detection bias (see below), we estimated that Simpson Bay had a mean *annual density* of 4.40 sea otters km^{-2}, which is 1.9-fold higher than the mean annual density for all of Prince William Sound. Because Simpson Bay is a part of Prince William Sound, it may be preferred habitat, especially during the summer when the density increases to 6.62 sea otters km^{-2} of which 27% are pups. The number of sea otters occupying Simpson Bay was stable from 2001-18.

At the spatial scale of Simpson Bay, this study is one the longest (18 consecutive years) conducted in Prince William Sound, which provides additional insights into population changes. Although undercounting is always possible, our standardized, double-survey method (Estes Jamison 1988) during the summer produced a consistent effort, and the use of two skiffs within this relatively small bay ensured that most sea otters were counted. The winter censuses were less rigorous because of logistical constraints (i.e., only one survey vessel, single observer and fewer censuses). As a result, we cannot be certain whether the lower mean number of sea otters in Simpson Bay between September and April resulted from undercounting (detection bias) or seasonal movement out of the bay.

Although we did not quantify detection bias, Udevitz et al. (1995) estimated a sighting probability of 70% for boat censuses of sea otters under good sighting conditions in Prince William Sound. However, sea otters avoided the skiff in that study, perhaps because they were less accustomed to small boats. Sea otters in Simpson Bay are habituated to skiffs because of the frequent occurrence of sports anglers, and pronounced avoidance behavior is uncommon unless a skiff approaches < 30 m (Davis unpub. obs). In addition, the boat speed of our censuses was half the speed in the Udevitz et al. (1995) study. Nevertheless, if we assume a detection probability of 70%, than the estimated mean annual number of sea otters in Simpson Bay was 132 (*viz*. 92.5 ÷ 0.7; Table 1) with 110 adults and 22 pups. These corrected values are similar to the mean summer census and give a corrected mean annual density of 6.3 otters km^{-2} (5.2 adults km^{-2} and 1.1 pups km^{-2}), which is 2.7-fold higher than the mean (2.31 sea otters km^{-2}) for Prince William Sound (unpublished USGS administrative report 2014; Bodkin 2015). Our corrected estimate of sea otter density was higher than the range of densities (0.92-5.2 otters km^{-2}) for a variety of coastal habitats in Southeast and Southwest Alaska (Coletti et al. 2016; Tinker et al. 2019), Washington State (Laidre et al. 2002), British Columbia (Gregr et al. 2008) and California (Laidre et al. 2001). Some of those studies assumed the sea otter population was at carrying capacity because the area had been reoccupied for at least 20 years, although prey availability and consumption was not measured. Only Dean et al. (2002; see below) and this study have attempted to determine carrying capacity based on estimates of prey availability and consumption.

4.2 Sedimentology of the seafloor and shoreline

Overall, the seafloor of Simpson Bay is composed of 33.1% mud, 45.1% mud-gravel and 21.8% rocky substrate, all of which was within a depth (< 100 m) accessible to foraging sea otters (Bodkin et al. 2004; Noll et al. 2009, Gilksinson et al. 2011; Wolt et al. 2012). Ignoring rocky substrate, 64% of the seafloor suitable for bivalves is mud-gravel and 36% is mud (Fig. 3). There is little difference in the soft sediment component (silt and clay) of mud and mud-gravel. However, mud-gravel has 5-fold more sand and gravel than mud. The mud-gravel areas are either associated with glacial moraines or are proximal to rocky promontories, rocky shorelines, or submarine outcrops. Intertidal beaches are composed primarily (86%) of gravel and sand, which is characteristic of other beaches in Prince William Sound suitable for bivalves (Brooks et al. 2001).

4.3 Bivalve habitat

In our study, the box core penetrated sediments to a mean depth of 29 ± 4.50 *s.d.* cm in mud and 15± 3.80 *s.d.* cm in mud-gravel, and the beach surveys were excavated to a depth of ~20 cm. Therefore, we likely sampled most of the bivalves present. Large butter clams can burrow as deep as 30 cm, but those that were recovered in this study (mean lenght 31 mm) were one-quarter the size of the largest clams (up to 125 mm; Dethier 2006), so they probably occurred at shallower depths in the sediment because they had shorter siphons (Kvitek Oliver 1988). The mid-sized butter clams in Simpson Bay are similar to those in areas around Kodiak Island, which are located at a sediment depth of ≤ 20 cm in areas that have been occupied by sea otters for over 25 yr (Kvitek et al. 1992). Littleneck clams occur at sediment depths of 15-20 cm (Paul Feder 1973, Dethier 2006) and cockles at sediment depths of 2-5 cm (Paul Feder 1973, Lazo 2004). Soft-shelled macomas occur at sediment depths of 10-15 cm, (Blundon Kennedy 1982). However, larger soft-shelled clams can burry as deep as 25 cm to avoid predation but at the cost of feeding efficiency (Blundon Kennedy 1982). Otter pits along the shoreline in Simpson Bay are not deeper than ~15 cm (R. Davis unpub. obs.), so our sediment sampling depths mimicked those of foraging sea otters.

Overall, the hard-shelled bivalves (butter clams, black lampshell, hairy cockle, smooth cockle, Nuttall cockle) and epibenthic bivalves (red scallop, false jingle and blue mussel) were found in or above mud-gravel sediments (or along the shoreline) and were specifically correlated with the gravel and sand components (Fig. 4). Nevertheless, some hard-shelled bivalves (butter clam, hairy cockle and smooth cockle) also occurred in mud, which may reflect a broad habitat preference or heterogeneity in our sediment map. The stained macoma and bent-nose macoma occurred primarily in mud and were specifically correlated with silt. Few or none of these two species occurred in mud-gravel. However, the broad yoldia, which ostensibly is a soft-shelled clam, occurred with nearly equal abundance in both sediment types. The little neck clam and *Astarte* sp. occurred only along the shoreline, which had a very high gravel and sand composition (74% and 12%, respectively). Of the three species of soft-shelled clams, only the softshell clam (*Mya arenaria*) occurred on the beaches and not in high abundance.

Based on the distribution of the two benthic sediment types, soft-shelled clams occurred towards the centers of the three bays in mud while hard-shelled clams occurred along the perimeter of the bays in mud-gravel or along beaches, which were predominately gravel and sand (Figs. 2 and 3). The same distribution has been described in other areas in the North Pacific. Hard-shelled clams, such as butter clams, range from the southern Bering Sea to central California and inhabit mixed substrates (sand-mud-gravel) (Kvitek et al. 1988; Bodkin et al. 2001). Truncate softshell clams (*Mya truncata*) occur intertidally and range from the Beaufort Sea to Neah Bay, Washington and inhabit sand-mud substrate (Bodkin et al. 2001). The softshell clams, which occur intertidally and range from Icy Cape, Alaska to central California, inhabit sandy and muddy substrate (Bodkin et al. 2001). In Southeast Alaska, Prince William Sound, Kodiak Island and within bays in the Yukon-Kuskokwim Delta, softshell clams are abundant in muddy sediments (Hines and Ruiz 2001). However, Simpson Bay has very few areas (< 1% of the area) of muddy intertidal shoreline, and none had broken shells on the surface indicating the presence of bivalves.

4.4 Abundance of bivalves

In terms of total biomass, butter clams were the predominant bivalve species in Simpson Bay followed by stained macomas (Table 3). Together, these two species represented 71% of the total bivalve biomass preyed on by sea otters. The shells of otter-predated butter clams and other hard-shelled bivalves are commonly found along the beaches and typically have one broken valve and one intact valve joined at the hinge. The discarded shells of otter-predated, hard-shelled clams are distinctive from those that have died from other causes (e.g., sea star predation), which have two intact valves joined with a hinge (Traiger et al. 2016). In contrast, the soft shells of otter-predated stained macomas were shattered into many pieces and often found in the subtidal mud samples using the box core.

In Simpson Bay, 75% of sea otter prey is white-shelled bivalves (Wolt et al. 2012), which is similar to the percentage (71%) of bivalves represented by butter clams and stained macomas (Table 3). These two species and the less common hard-shelled cockles and softshell clam represent 85% of the total bivalve biomass, although they cannot be distinguished reliably by species using binoculars while sea otters are feeding at the surface. However, the most common two bivalves (butter clams and stained macomas) probably constitute the majority of ingested white-shelled bivalves based on their prevalence in the subtidal. Because the shoreline represents only 1.4% of the entire bay, the biomass of butter clams in this area contributes only 1% to the total (Table 3).

Based on the location of feeding dives in Simpson Bay (Gilkinson et al. 2011) and ignoring rocky areas, sea otters spent 60% of their time foraging in mud-gravel and 40% in mud (Fig. 5). Ignoring black lamp shells, which have never been identified (visually with binoculars, in scat, or from broken shells on the beach) in the otter's diet, 64% of bivalve biomass (785,730 kg based on the butter clam, stained macoma, hairy cockle, broad yoldia, bent-nose macoma and smooth cockle) occurred in mud-gravel and 36% in mud (Table 3). Hence, sea otters appear to feed on white-shelled bivalves in proportion to their presence in the two benthic sediment types. The combined numerical density of these six bivalve species in mud (9.9 m^{-2}) was 15% greater than in mud-gravel (8.6 m^{-2}). However, the mass density (based on wet tissue mass) in mud-gravel (56.6 g m^{-2}) was 1.3-fold greater than in mud (40.5 g m^{-2}), primarily because of the higher abundance of butter clams whose mean individual mass was 2-fold greater than the mean masses of the other bivalve species (Tables 2 and 3). The overall mean numerical and mass densities of clams for the entire bay were 9.1 clams m^{-2} and 47.5 g m^{-2} adjusted for their relative occurrence in the two sediment types, respectively. The mean bivalve energy density and mean energy per unit mass of sea otters in Simpson Bay were 162 kJ m^{-2} and 1.3 x 10^3 MJ kg $otter^{-1}$, respectively:

Eq. 2 $47.5\ g\ m^{-2} \times 3.42\ kJ\ g^{-1} = 162\ kJ\ m^{-2}$

Eq. 3 $(162\ kJ\ m^{-2} \times 21 \times 10^6\ m^2 \div 1000\ kJ\ MJ^{-1}) \div (110 \times 24\ kg\ otter^{-1}) = 1.3 \times 10^3\ MJ\ kg\ otter^{-1}$

Where: 1) 47.5 g m^{-2} is the mean mass density of clams, 2) 3.42 kJ g^{-1} is the mean energy content of bivalves from Simpson Bay determined by bomb calorimetry (Cortez et al. 2016b), 3) 110 is the annual mean number of adult sea otters (see Sect. 4.1), 4) 24 kg is the mean body mass of an adult female sea otter (see Sect 2.2), and 5) 21 x 10^6 m^2 is the seafloor area of Simpson Bay (see Sect. 2.1). These estimated values are similar to those (149 kJ m^{-2} and 1.1 x 10^3 MJ kg $otter^{-1}$) for bivalves at nearby Montague Island (Dean et al. 2002), although the energy density is less (46%) than occurs in areas around Kodiak Island that have been occupied by sea otters for more than 25 years (Kvitek et al. 1992; Dean et al. 2002). Nevertheless, at these clam densities, sea otters are ~87% successful in obtaining prey during foraging dives of ~2 min in Simpson Bay, at Montague Island and in Southwest Alaska (Dean et al. 2002; Wolt et al. 2012; Coletti et al. 2016). This success rate is 2-fold higher than observed for California sea otters that exhibit a high degree of intraspecific variation in diet (i.e., high diet diversity among individuals or niche diversity) associated with density-dependent competition for food (Estes et al. 2003; Tinker et al. 2007, 2008), although this may not reflect energy consumption.

Mussels are an important dietary component for sea otters in some areas such as Green Island in Prince William Sound (Estes et al. 1981) and Kenai Fjords National Park in Southcentral Alaska (Coletti et al. 2016). In Simpson Bay, mussels numerically represent 9% of the diet (Wolt et al. 2012), but their contribution to bivalve biomass in Simpson Bay is small (Table 3). Unlike clams, sea otters eat small mussels entirely, and at least 50% of their mass is indigestible shell. As a result, whole mussels are not an energy dense food because sea otters must ingest a large quantity of shell fragments with the soft tissue, although there is seasonal variation in energy content depending on gonad growth (Bodkin et al. 2012). Shell fragments must pass through the digestive system, and this may limit the amount of mussels that can be consumed during a foraging bout. In some cases, shell fragments can cause intestinal blockage resulting in death (R. Davis, P. Tuomi and V. Gill, pers. obs.).

4.5 Estimated prey consumption and carrying capacity

After correction for detection bias, the mean *annual* number of adult sea otters in Simpson Bay was 110. Assuming a mean daily metabolic rate of 6.3 W kg^{-1} for a 24 kg adult sea otter (primarily females) and a mean energy content of 3.42 MJ kg^{-1} for clams, adult sea otters would require 5.8 kg day^{-1}, which represents 24% of their body mass (Cortez et al. 2016b; Appendix 4). However, white-shelled bivalves represent only 75% of the summer diet (and assumed to be similar for the entire year) for sea otters in Simpson Bay, so they would consume 4.4 kg day^{-1} (*viz.* 5.8 kg day^{-1} x 0.75) (Wolt et al. 2012). Mean annual consumption for 110 adult sea otters would be 176,660 kg of bivalves (*viz.* 110 sea otters x 4.4 kg day^{-1} x 365 days yr^{-1}). The total mass of the major bivalves (butter clam, stained macoma, hairy cockle, broad yoldia, bent-nose macoma and smooth cockle; Table 3) was estimated at 785,730 kg, so sea otters consume about 22% of the biomass of white-shelled bivalves in Simpson Bay annually.

Based on data from Prince William Sound, Kodiak, and Southeast Alaska, the age of subtidal butter clams (mean length 30.7 mm; Table 2) in Simpson Bay is ~4.5 years (Paul 1976; Nickerson 1977; Brooks et al. 2001). To balance the removal rate by 110 adult sea otters, clams would need to achieve a mean size of 30.7 mm in 4.5 yr (*viz*. $1 \div 22\%\ yr^{-1} \div 100$), which matches the estimated age of otter-predated clams. Hence, the estimated annual number of adult sea otters occupying Simpson Bay (i.e., 110 or 5.2 km^{-2}) appears to be at or near the carrying capacity based on food resources. That is, the annual mass of clams (i.e., mean age ~4.5 years) consumed by sea otters equals their replacement rate. In these calculations, we assume that sea otters are the principal predator of bivalves in the subtidal. Given their very high metabolic rate and prey consumption, this is probably a valid assumption (Costa and Kooyman 1984; Traiger et al. 2016). We also assume that there is sufficient prey for the other 25% of the diet, which is composed of other invertebrates such as crabs, sea cucumbers, etc. (Wolt et al. 2012).

We cannot say with certainty what factors other than prey availability have influenced sea otter population density in Simpson Bay, but we can limit the reasonable possibilities. Of the possible intrinsic and extrinsic factors, the most likely are male territoriality, emigration and Native hunting. Male territorial behavior results in ≤ 12 dominant males in Simpson Bay during the summer (Pearson et al. 2006). Younger, non-territorial males and those unable to defend a territory are excluded (emigrate) from the area. This limits the number of adult males, but has no influence on the number of females, so its effect on the mean population density in Simpson Bay is probably small. Although killer whales occur in and around Simpson Bay, the majority are not mammal eaters (Matkin et al. 1997; Matkin pers.com; Davis unpubl. obs), so predation is probably rare. In addition, there has been no evidence of widespread mortality (beach-cast carcasses) because of disease, toxins or anthropogenic pollution events. Since 2001, Native hunters have killed 2.7 sea otters annually (54% male, 46% female) in Simpson Bay (USFWS unpub. data), and this could have a small effect on the population density (Bodkin and Ballachey 2010). Despite these possible factors influencing equilibrium density, the sea otter population in Simpson Bay appears to be at carrying capacity based on prey availability and replacement.

Fundamentally, food availability strongly influences the equilibrium density of sea otter populations, and that appears to be the case in Simpson Bay. Nevertheless, each habitat will have its own combination of factors affecting the equilibrium density, and a single factor (e.g., food availability) may vary over time to produce a complex interaction among the effects of various factors (Fowler 1987; Watt et al. 2000). One example is Amchitka Island, where sea otter density was probably at carrying capacity with significant piscivory in the 1970s but is now significantly (~90%) below carrying capacity, likely because of killer whale predation (Estes et al.1998; Watt et al. 2000; Doroff et al. 2003; Estes et al. 2005). Understanding the factors that regulate sea otter density may be one of the most challenging ecological questions, which will require long-term monitoring for complete resolution. We suggest that studies such as this, when applied to a variety of littoral habitats occupied by sea otters, may provide the best approach for understanding regional carrying capacity of sea otters. In addition, this approach will provide a mechanistic assessment of *K*, which will better inform probabilistic inferences for sea otter population trends and help resource managers anticipate potential conflicts and tailor management strategies to benefit sea otters and fisheries.

Author Contributions

This article was a collaborative effort by all authors. ID collected samples, performed the data analysis as part of his Doctoral Dissertation, and participated in preparing this manuscript. TD performed the side-scan survey and analysis of the benthos. GM performed the sediment analysis. FG performed the statistical analysis. FC provided a vessel and assisted in sediment collection. RD organized and supported this project and participated in the preparation of this manuscript and previous research in Simpson Bay.

Animal Use

This study was conducted under U.S. Fish and Wildlife Permit MA84799B-0. Because the census protocol involved counting sea otters only, no Animal Use Permit was required by the Texas AM University Institutional Animal Care and Use Committee.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data Accessibility

Data will be achieved and accessible in Dryad or as Appendices to this article.

Table 1. The mean number of all sea otters, adults and pups in Simpson Bay during the summer (June-August), other times of the year (September-April), and the annual mean from 2001-18. In total, 112 censuses were conducted: 87 during the summer and 25 at other times of the year. Mean values are shown with standard deviation. These are census values uncorrected for detection bias (see Sect. 4.1).

	Mean number of sea otters		
	June-August	September -May	Annual
Adults	102 + 18.1	69 + 28.4	77.3
Pups	37 + 12.8	8 + 6.3	15.3
Adults and pups	139 + 30.5	77 + 31.9	92.5

	Mean density (sea otters m^{-2})		
	June-August	September -May	Annual
Adults	4.86	3.29	3.68
Pups	1.76	0.38	0.73
Adults and pups	6.62	3.67	4.40

Table 2. Morphometrics of bivalves and a brachiopod (black lampshell) collected using the box core (benthic specimens) during sediment sampling and from beach surveys along a transect perpendicular to the tide line. Maximum length refers to the shell, and wet mass is for tissue only.

Common name	Species name	n	Max length (mm)		Wet Mass (g)	
			Mean	sd	Mean	sd
Box core specimens						
Butter clam	*Saxidomus gigantea*	69	30.7	6.90	7.0	4.40
Stained macoma	*Macoma inquinata*	33	28.7	6.80	3.1	2.30
Broad yoldia	*Megayoldia thraciaeformis*	16	27.6	4.60	2.2	1.10
Black lampshell	*Hemithyris psittacea*	12	20.4	3.20	4.8	1.80
Bent-nose macoma	*Macoma nasuta*	9	38.1	3.90	3.0	1.10
Hairy cockle	*Clinocardium ciliatum*	6	26.9	7.70	5.3	4.10
Nuttall cockle	*Clinocardium nuttallii*	3	18.8	3.50	1.5	0.70
Smooth cockle	*Serripes laperousii*	2	33.8	3.20	7.5	2.10
False jingle	*Pododesmus macroschisma*	1	49.0	0.00	16.0	0.00
Reddish scallop	*Chlamys rubida*	1	35.0	0.00	3.0	0.00
Softshell clam	*Mya arenaria*	1	24.0	0.00	2.0	0.00
Blue mussel	*Mytilus trossolus*	1	38.9	0.00	4.0	0.00
Beach specimens						
Arctic Astarte	*Astarte sp.*	146	21.9	4.1	2.6	1
Butter clam	*Saxidomus gigantea*	126	47.7	3.56	12.9	11.20
Softshell clam	*Mya arenaria*	80	24.6	3.80	2.7	1.90
Littleneck Clam	*Leukoma staminea*	29	35.4	10.4	6.7	4.2
Stained macoma	*Macoma inquinata*	22	26.6	8.80	3.1	1.00
Bent-nose macoma	*Macoma nasuta*	3	31.9	6.00	2.0	0.00
Hairy cockle	*Clinocardium ciliatum*	1	31.1	0.00	2.0	0.00
Nuttall cockle	*Clinocardium nuttallii*	1	20.9	0.00	1.0	0.00

Table 3. Abundance and mass of bivalves larger than 1 cm from seafloor (mud, mud-gravel) and shoreline habitats in Simpson Bay. Sample size (n) is the number of individuals for each species collected in each habitat, and density is the mean number of individuals m^{-2}. The total number of individuals for each species is the product of the density and the total surface area for each habitat (shown in parentheses). Total mass (kg of fresh bivalve tissue) is the product of the total number of individuals in each habitat and the mean fresh tissue mass for each species (Table 2). The total fresh mass of bivalves for all species in Simpson Bay was 9.27 x 10^5 kg.

	Butter clam	Stained macoma	Black lampshell	Hairy cockle	Broad yoldia	Bent-nose macoma	Smooth cockle	False jingle	Reddish scallop	Nuttall cockle	Softshell clam	Blue mussel	Little neck clam	Astarte sp.
Mud (area = 6.957 x10^6 m^2)														
Sample size (n)	16	30	0	1	6	9	1	0	0	0	0	0	0	0
Density (m^{-2})	2.51	4.71		0.16	0.94	1.41	0.16							
Total number	1.75x10^7	3.27x10^7		1.09x10^6	6.55x10^6	9.82x10^6	1.09x10^6							
Total mass (kg)	1.23x10^5	1.02x10^5		5.78x10^3	1.45x10^4	2.95x10^4	8.19x10^3							
Mud-gravel (area = 9.471 x10^6 m^2)														
Sample size (n)	54	3	16	6	9	0	2	4	4	7	1	1	0	0
Density (m^{-2})	6.26	0.35	1.86	0.70	1.04		0.23	0.46	0.46	0.81	0.12	0.12		
Total number	5.93x10^7	3.29 x10^6	1.76x10^7	6.59x10^6	9.88x10^6		2.20x10^6	4.39x10^6	4.39x10^6	7.69x10^6	1.10x10^6	1.10x10^6		
Total mass (kg)	4.16x10^5	1.03x10^4	8.43x10^4	3.49x10^4	2.18x10^4		1.65x10^4	2.03x10^4	1.32x10^4	1.15x10^4	2.20 x10^3	7.58 x10^2		
Beach samples (area = 3.000 x10^5 m^2)														
Sample size (n)	126	22	0	1	0	3	0	0	0	1	80	0	29	146
Density (m^{-2})	2.10	0.37		0.02		0.05				0.02	1.33		0.48	2.43
Total number	6.30x10^5	1.10x10^5		5.00 x10^3		1.50 x10^4				5.00x10^3	4.00 x10^5		1.45 x10^5	7.30x10^5
Total mass (kg)	8.12x10^3	3.44x10^2		1.00x10^1		3.00x10^1				5.00	1.08x10^3		9.72x10^2	1.88x10^3

Grand total for Simpson Bay														
Total sample size	196	55	16	8	15	12	3	4	4	8	81	1	29	146
% total count	34%	10%	3%	1%	3%	2%	1%	1%	1%	1%	14%	0%	5%	25%
% of count in mud	8%	55%	0%	13%	40%	75%	33%	0%	0%	0%	0%	0%	0%	0%
% of count in mud/gravel	28%	5%	100%	75%	60%	0%	67%1	100%	100%	88%	1%	100%	0%	0%
% of count in shoreline	64%	40%	0%	13%	0%	25%	0%	0%	0%	13%	99%	0%	100%	100%
Total mass (kg)	5.47x10^{5}	1.13x10^{5}	8.43x10^{4}	4.07x10^{4}	3.63x10^{4}	2.95x10^{4}	2.47x10^{4}	2.03x10^{4}	1.32x10^{4}	1.15x10^{4}	3.28 x10^{3}	7.58x10^{2}	9.73x10^{2}	1.88x10^{3}
% of total mass	59%	12%	9%	4%	4%	3%	3%	2%	1%	1%	<1%	<1%	<1%	<1%
% mass in mud	22%	91%	0%	14%	40%	100%	33%	0%	0%	0%	0%	0%	0%	0%
% mass in mud-gravel	76%	9%	100%	86%	60%	0%	67%	100%	100%	100%	73%	100%	0%	0%
% mass in shoreline	1%	0%	0%	0%	0%	0%	0%	0%	0%	0%	27%	0%	100%	100%

Fig. 1. Sea otter feeding on a stained macoma (*Macoma inquinata*) in Simpson Bay. Image taken under the authority of U.S. Fish and Wildlife Service LOC MA-043219.

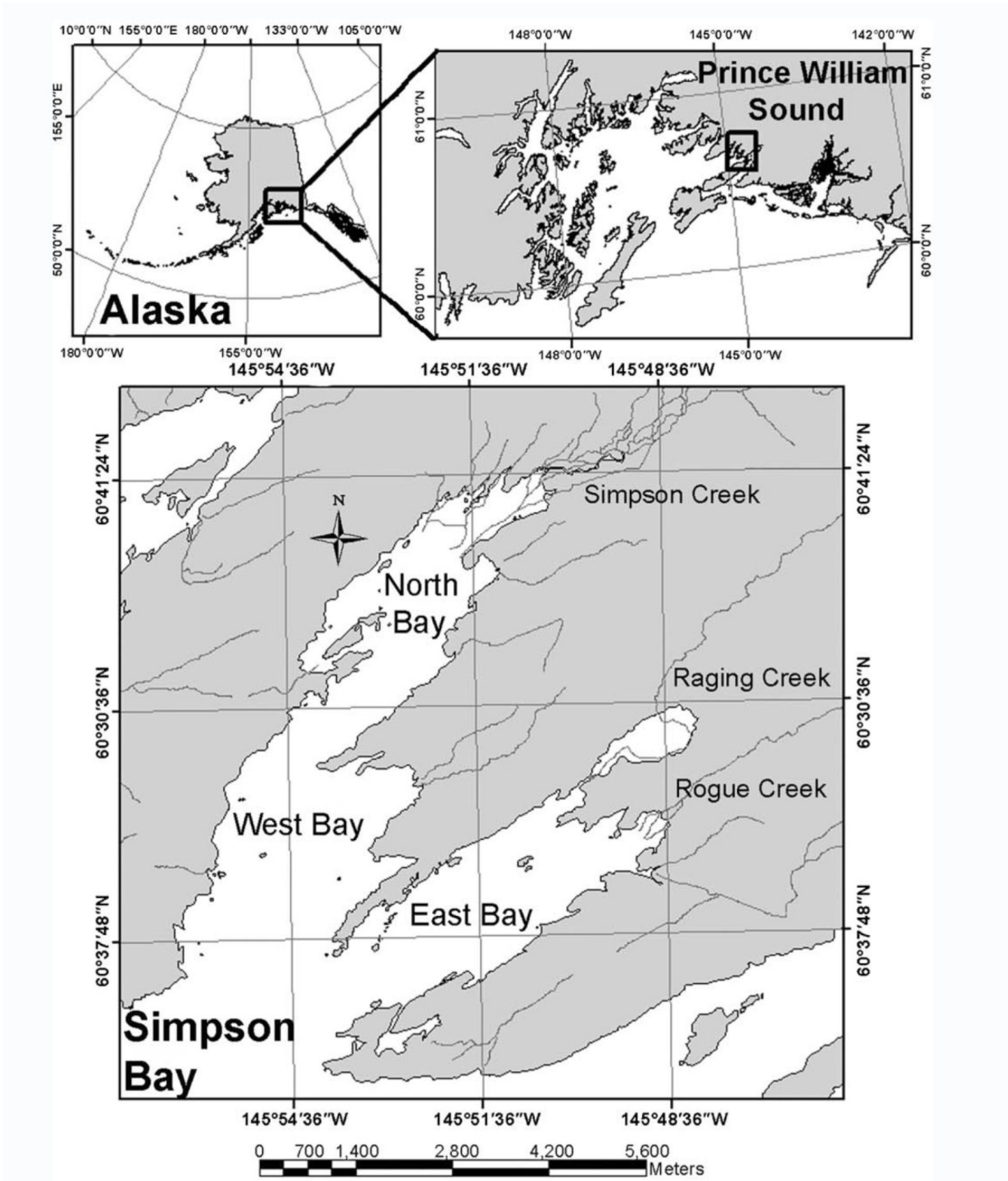

Fig. 2. Simpson Bay, Alaska

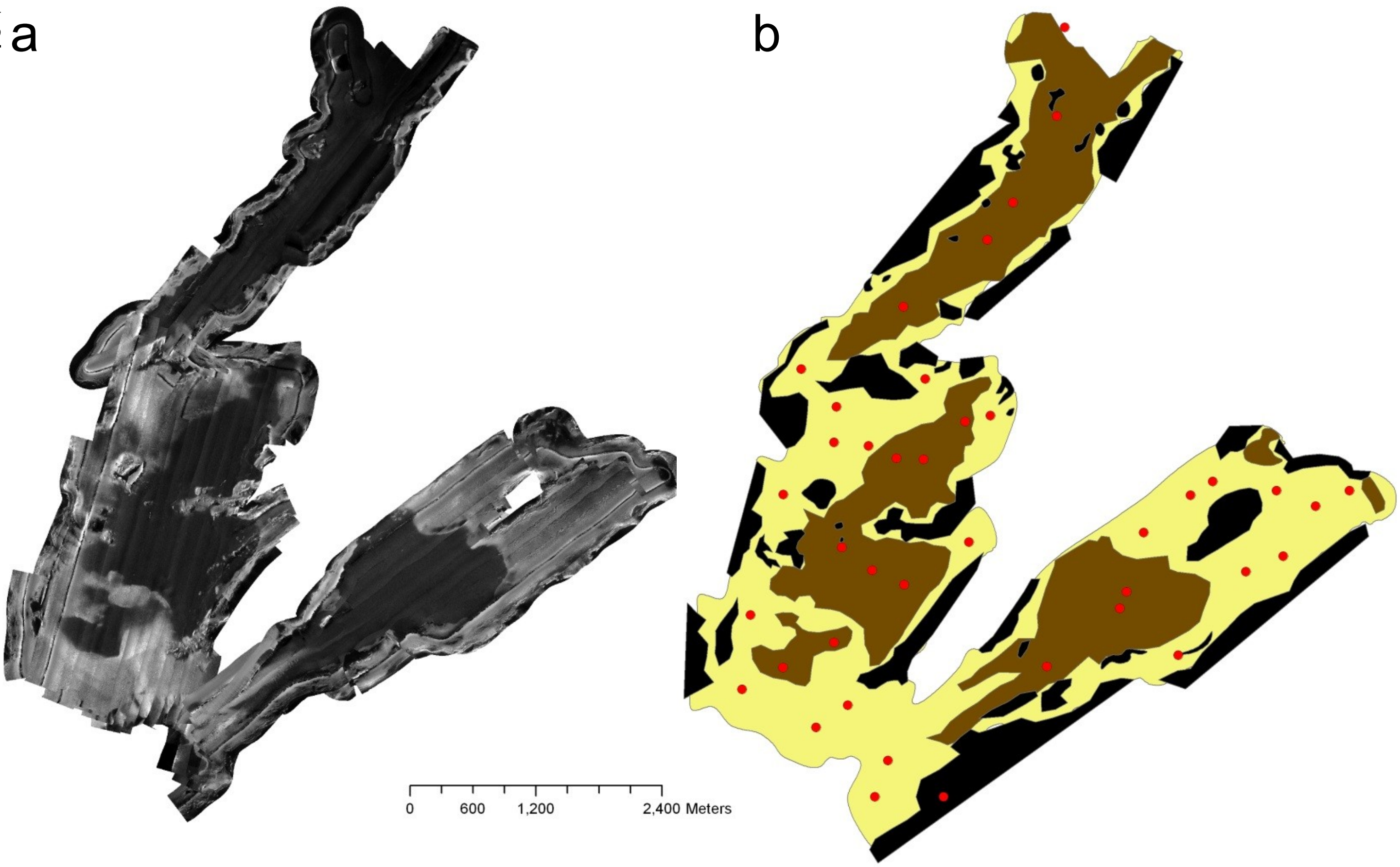

Fig.3. Two views of Simpson Bay: a) Composite side-scan acoustic survey showing areas of mud with low reflectivity (black) and areas of mud-gravel with higher reflectivity (light grey); b) Map showing areas of mud (brown), mud-gravel (yellow) and rocky reef (black) based on sediment samples and composite side scan sonar (Noll et al. 2009; Gilkinson et al. 2011). Red dots show the mean locations where benthic samples were taken with a box core (six replicates per station) to confirm sediment type and collect large invertebrates (primarily bivalves > 1 cm diameter) to estimate their distribution and abundance in areas of mud and mud-gravel.

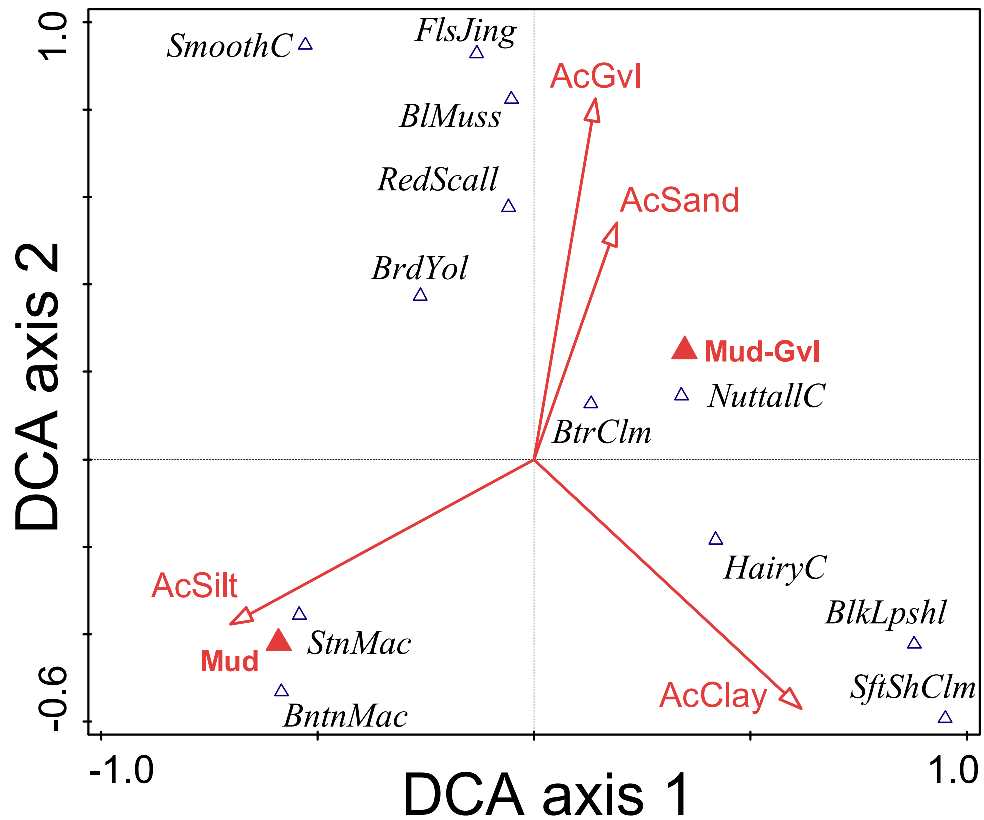

Fig. 4. Canonical Correspondence Analysis of the distribution of bivalves in seafloor mud and mud/gravel sediments. Bi-plot indicates the explained variance on the first two canonical axes for bivalve abundance among samples (CCA 1 = 47% and CCA 2 = 33%,). Arrows represent arcsine transformed values of the dry composition for each sediment characteristic and point in the direction of the steepest increase in value. Arrows also run in the opposite direction, but are not shown, which indicates the negative association (i.e., steepest decrease in value). The angle between arrows indicates the correlation between values for individual sediment characteristics. Closed triangles represent sample groups for mud and mud/gravel sediment type. Individual symbols correspond to categories, and the distance between the symbols approximates the mean dissimilarity (chi-square distance) among samples with respect to the sediment type. Open triangles represent bivalve species, and the distances among the symbols approximates the dissimilarity (chi-square distance) of their relative abundances among samples with regard to the

sediment types and characteristics. The distance between a bivalve species and a sediment type or characteristic indicates the relative preference of that species for individual sediment types; species symbols closer to arrowheads are associated with greater values for that sediment characteristic. Symbols: mud (Mud), mud/gravel (Mud-Gvl), arcsin gravel (AcGvl), arcsin sand (AcSand), arcsin clay (AcClay), arcsin silt (AcSilt), butter clam (BtrClm), stained macoma (StnMac), bent-nose macoma (BntMac), Nuttall cockle (NuttallC), Hairy cockle (HairyC), Black lampshell (BlkLpshl), soft shelled clam (SftShClm), blue mussel (BlMuss), broad yoldia (BrdYol), red scallop (RedScall), false jingle (FlsJng), smooth cockle (SmoothC).

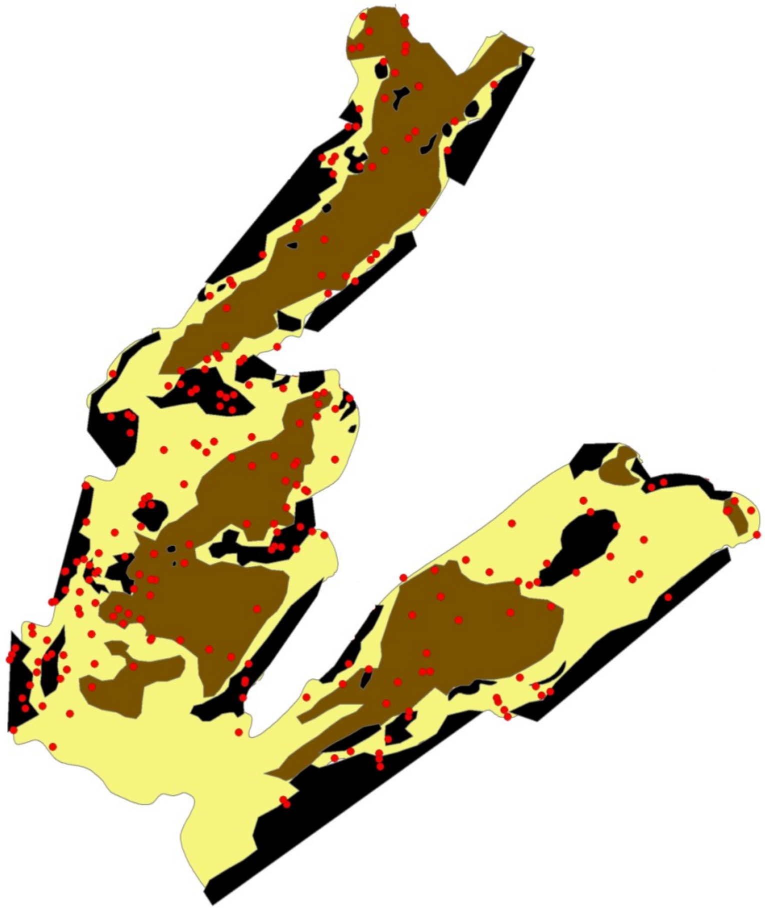

Fig. 5. Map showing areas of mud (brown), mud/gravel (yellow) and rocky reef (black) based on sediment samples and side scan sonar (Noll et al. 2009; Gilkinson et al. 2011). Red circles show sea otter feeding locations modified from Gilkinson (2011).

Appendix 1. Locations of sediment samples (six replicates per station) taken in Simpson Bay with a Gomex box core.

Sediment Type	Station	Latitude	Longitude
Mud	5	60.63256	-145.86548
Mud	8	60.62657	-145.87897
Mud	12	60.62881	-145.91441
Mud	13	60.62684	-145.92306
Mud	16	60.63661	-145.91289
Mud	17	60.63345	-145.90255
Mud	18	60.64373	-145.89900
Mud	19	60.65626	-145.90190
Mud	20	60.66467	-145.88327
Mud	21	60.67168	-145.87574
Mud	22	60.67897	-145.87413
Mud	27	60.64677	-145.89194
Mud	29	60.63121	-145.86662
Mud	30	60.63470	-145.90791
Mud	31	60.64384	-145.90352
Mud	32	60.66165	-145.88768
Mud	39	60.61611	-145.90806
Mud/Gravel	1	60.63525	-145.83915
Mud/Gravel	2	60.64065	-145.84011
Mud/Gravel	3	60.64055	-145.82788
Mud/Gravel	4	60.62730	-145.85698
Mud/Gravel	6	60.63739	-145.86241
Mud/Gravel	7	60.64149	-145.85074
Mud/Gravel	9	60.61601	-145.89657
Mud/Gravel	10	60.61906	-145.90575
Mud/Gravel	11	60.62366	-145.91230
Mud/Gravel	14	60.62508	-145.92990
Mud/Gravel	15	60.63119	-145.92830
Mud/Gravel	23	60.65129	-145.91915
Mud/Gravel	24	60.64814	-145.91337
Mud/Gravel	25	60.64490	-145.90813
Mud/Gravel	26	60.65032	-145.89844
Mud/Gravel	28	60.64722	-145.88765
Mud/Gravel	33	60.63405	-145.84545
Mud/Gravel	34	60.64041	-145.85448
Mud/Gravel	35	60.62186	-145.91768
Mud/Gravel	36	60.64103	-145.92252
Mud/Gravel	37	60.63686	-145.89163
Mud/Gravel	38	60.63932	-145.83360
Mud/Gravel	40	60.64524	-145.91390

Appendix 2. Percentage of sand, silt, clay, sand and gravel in benthic mud and mud-gravel samples after drying to remove moisture.

Sediment type	Sample Station	% clay	% silt	% sand	% gravel
Mud	5	29	68	2	1
Mud	8	32	65	2	1
Mud	12	33	64	2	1
Mud	13	33	62	3	3
Mud	16	29	68	2	1
Mud	17	31	67	2	0
Mud	18	31	68	1	0
Mud	19	33	64	2	1
Mud	20	33	65	0	1
Mud	21	30	68	1	1
Mud	22	21	67	11	1
Mud	27	28	69	1	1
Mud	29	30	69	2	0
Mud	30	30	68	2	0
Mud	31	31	67	2	0
Mud	32	32	65	2	1
Mud	39	36	62	3	0
Average		***31***	***66***	***2***	***1***
sd		*3.2*	*2.4*	*2.4*	*0.7*
Mud-gravel	1	25	57	12	7
Mud-gravel	2	28	57	7	8
Mud-gravel	3	20	64	11	5
Mud-gravel	4	29	50	15	6
Mud-gravel	6	28	61	6	5
Mud-gravel	7	21	58	11	11
Mud-gravel	9	5	25	70	0
Mud-gravel	10	36	56	3	4
Mud-gravel	11	39	60	1	0
Mud-gravel	14	38	60	2	1
Mud-gravel	15	29	54	13	4
Mud-gravel	23	34	58	3	5
Mud-gravel	24	33	55	7	5
Mud-gravel	25	28	64	3	5
Mud-gravel	26	28	53	14	5

Mud-gravel	28	29	63	3	5
Mud-gravel	33	28	58	4	10
Mud-gravel	34	21	59	14	7
Mud-gravel	35	35	59	2	3
Mud-gravel	36	31	61	4	3
Mud-gravel	37	32	62	3	3
Mud-gravel	38	23	60	7	10
Mud-gravel	40	35	61	3	1
Average		***29***	***57***	***10***	***5***
sd		*7.3*	*7.9*	*13.9*	*3.0*

Appendix 3. Percentage of sand, silt, clay, sand and gravel in beach samples after drying to remove moisture.

Sediment type	Sample Station	% clay	% silt	% sand	% gravel
Beach	1	3	4	10	83
Beach	2	2	3	27	68
Beach	3	4	8	10	78
Beach	4	9	13	7	71
Beach	5	7	10	5	78
Beach	6	2	6	14	78
Beach	7	2	2	29	67
Beach	8	4	11	7	78
Beach	9	3	6	19	72
Beach	10	4	13	9	74
Beach	11	9	11	4	76
Beach	12	12	19	3	66
Average		***5***	***9***	***12***	***74***
sd		*3.3*	*5.0*	*8.7*	*5.3*

Appendix 4. Estimated amount of clams consumed per day by a sea otter

Assumptions:

1. Average daily metabolic rate = 6.3 W kg^{-1} (Cortez 2016)

2. 86,400 s day^{-1}

3. Average body mass of an adult sea otter = 24 kg (Bellachey et al. 2003)

4. Energy content per clam = 3.42 x 10^6 J kg^{-1} (Cortez 2016)

5. Metabolizable energy coefficient = 0.9 (Costa and Kooyman 1984)

6. Digestible energy coefficient = 0.9 (Costa 1982)

7. Assimilation coefficient = 0.82 (Costa 1982)

Prey consumed (clams day^{-1}) = (6.3 x 86,400 x 24) ÷(3.42 x 10^6 x 0.9 x 0.9 x 0.82) = 5.8 kg

Prey consumed (kg) as a percentage of body mass (kg) = (5.8 ÷ 24) x 100 = 24%