Quantifying the Drivers and Mechanisms of Sea Otter (*Enhydra lutris*) Foraging Behaviour on the Central Coast of British Columbia, Canada

by

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B.Sc., Simon Fraser University, 2009

Research Project Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Resource Management

Report No. 612

in the

School of Resource and Environmental Management
Faculty of Environment

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SIMON FRASER UNIVERSITY

Fall 2014

Approval

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Degree:	**Master of Resource Management**
Report No.:	**612**
Title of Project:	***Quantifying the Drivers and Mechanisms of Sea Otter (Enhydra lutris) Foraging Behaviour on the Central Coast of British Columbia***
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Date Defended: December 10, 2014

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Abstract

As preferred prey become scarce, theory suggests that predator per-capita consumption rates decline and predator diets diversify. As a keystone predator, sea otters (*Enhydra lutris*) are known to have remarkable impacts on their macroinvertebrate prey, however, variation in the magnitude of these effects through time remain less well known. Using a space-for-time substitution, we quantified sea otter foraging behaviour at 5 rocky reef sites that fell along a gradient in otter occupation time (0.1-33 years) on British Columbia, Canada's central coast. As site occupation time increased, sea otters targeted increasingly smaller, more diverse macroinvertebrate prey suggesting the serial depletion of preferred to less valuable prey. We found strong evidence that urchin density and occupation time were important drivers of sea otter per-capita consumption rates on urchins, strongly interacting rocky reef herbivores, well known to drive the distribution and abundance of kelps. In addition, there was greater strength of evidence for prey-dependent over predator-dependent functional response models of sea otter consumption of urchins. These results have implications for nearshore productivity, commercial and subsistence shellfish fisheries and balancing the trade-offs inherent to ecosystem-based management.

Keywords: sea otters; predator-prey interactions; central coast of B.C.; sea otter occupation time; functional response; model selection

Acknowledgements

I would like to thank my senior supervisor, Dr. Anne Salomon, for intellectual support, guidance and enthusiasm throughout my Masters education. Thank you to Dr. Lawrence Dill for valuable feedback on foraging theory over the past two years. Thank you to Linda Nichol for offering expertise on sea otter natural history and for teaching me how to observe sea otters behaviour in the wild.

Many thanks to research collaborators at the Heiltsuk Integrated Resource Management Department, in particular research co-ordinator Harvey Humchitt and aquatics manager Mike Reid. Your department provided important feedback supporting this project and permitted us to conduct research in your traditional territories.

I had the pleasure of conducting a short but amazing field season, with a great field team that made the process more successful and enjoyable than I could have hoped. Angeleen Olson and Nathaniel Glickman, thank you for indulging in long days on the rocks, camping in the wilderness and for providing continual intellectual support. We also had fantastic logistical and technical support as well as delicious food provided by the Hakai Institute and their staff. Finally, it is with deep gratitude that I thank Eric Peterson and Christina Munck for steadfast support of this research and for playing an instrumental role in making it materialize.

I am also grateful for the funding support that I received from the National Science and Engineering Research Council and Simon Fraser University.

I am thankful for my colleagues and friends in the M.R.M. program who made working and learning in REM such a great experience. I am especially grateful to my friends in the Coastal Marine Ecology and Conservation Lab for making it fun and engaging to learn about sea otter-kelp forest ecosystems. Last but not least, a big thank you to my fiancé Cory Lagasse and my family for being such an incredible support system throughout my education.

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1.   Introduction

Mounting evidence suggests that the extirpation and subsequent recovery of top predators has altered the historical abundance of prey populations and caused major shifts in ecosystems worldwide (Frank et al. 2005, Estes et al. 2011, Ripple et al. 2014). Therefore the conservation and management of such ecosystems depends, in large part, on our ability to understand the ecological dynamics of top predators and the nature and strength of their trophic interactions (Soulé et al. 2005, Chadès et al. 2012). Here, we document the foraging behaviour of a recovering population of northern sea otters (*Enhydra lutris kenyoni*) and quantify the factors driving their per-capita consumption rates on sea urchins (*Mesocentrotus* spp. was *Strongylocentrotus* spp.) in a high latitude rocky reef ecosystem. Sea otters are capable of reducing the abundance and size of their shellfish prey (Breen et al. 1982, Kvitek et al. 1992, Watson and Smith 1996), many of which are commercially valuable and important as traditional food for First Nations, while simultaneously facilitating kelp growth and survivorship through their consumption of benthic herbivores (Estes and Palmisano 1974, Estes and Duggins 1995). Thus the recovery of this keystone predator can create complex ecological and social trade-offs, highlighting the need to quantify and forecast the strength and timing of sea otter-prey interactions.

Evaluating Predator-Prey Interactions

A predator's effect on ecological communities is not only a function of its abundance but its per-capita interaction strength (Paine 1969, 1980, Power et al. 1996). The per-capita impact of a predator can be influenced by predator and prey densities (Holling 1959, Arditi and Ginzburg 1989, Abrams 2001), the presence of alternative prey (Murdoch 1969) and environmental factors (Sanford 1999). Investigating a predator's rate of prey consumption in relation to prey density, the functional response (Solomon 1949), is an essential starting point for evaluating the strength of predator-prey interactions and determining the stability of predator-prey systems (Abrams and Ginzburg 2000). Holling (1959) first classified the functional response of a predator with

three basic types (Type I, Type II and III), each describing the extent to which the number of prey eaten per predator per unit time changes with prey density. These alternative models differ in how prey encounter rates and handling time vary with prey density and reflect differences in predators such as learning behaviour, whereby above a certain density of prey, predators will increase consumption of that prey. Additional models have been proposed based on the notion that predator density can also influence per-capita consumption rates and have been classified as *predator-dependent*, when the response is a function of both prey and predator populations (e.g. Beddington 1975; DeAngelis et al. 1975), and *ratio-dependent*, when the response depends on the specific ratio of prey to predator populations (e.g. Arditi and Ginzburg 1989). As predators try to maximize net energy gained from prey (Stephen and Krebs 1986), changes in the availability of high-value prey (easily captured, calorically-rich) and the presence of conspecifics are likely to exert strong influence on prey choice. Furthermore, optimal foraging theory suggests that predators should select a wider diversity of prey items as high-value prey resources become depleted (Schoener 1971). While these predictions are not widely tested on marine mammal populations, the feeding habits of sea otters, a keystone predator in temperate rocky reef ecosystems, can vary greatly and appear to depend on prey availability (Ostfeld 1982, Tinker et al. 2008).

Sea Otter Foraging Behaviour

Throughout their range, sea otters typically forage in subtidal rocky reef habitats but have also been known to frequent soft-bottom environments as well as feed at high tide on intertidal prey (Riedman and Estes 1990). Although sea otters consume a large variety of benthic marine invertebrates, empirical evidence from California suggests that sea otters exhibit different feeding habits at short versus long established sites in response to changes in abundance of their dominant prey (Tinker et al. 2008). At newly occupied sites, sea otters often target prey items that are large, energy-rich and abundant such as sea urchins (Estes et al. 1982, Ostfeld 1982, Laidre and Jameson 2006). At longer occupied sites, reduction in the size and abundance of sea urchins has been accompanied by a dietary shift and the selection of a wider array of prey items at the population level (Kvitek et al. 1993, Tinker et al. 2008) suggesting that resource availability, driven by sea otters themselves (Estes et al. 1982, Watt et al. 2000), affects differences in sea otter foraging behaviour at recent versus long-established sites. The

recovery of this keystone species in temperate rocky reef ecosystems provides a unique opportunity to test predictions from foraging theory and evaluate predator-prey dynamics across a range of prey densities, environmental conditions and stages of occupation.

Research Questions

The goal of this research was to examine sea otter feeding behaviour across a gradient of sites varying in sea otter occupation time. By directly observing sea otters we aimed to improve our predictions of otter-prey interactions, and start to illuminate when, where and how changes in prey selection and sea urchin depletion might occur as these predators recolonize rocky reef ecosystems. Specifically, we asked three questions: (1) How do sea otter diets and prey size vary with occupation time? (2) What factors best predict sea otter per-capita consumption rates on sea urchins? (3) What is the strength of evidence for alternative mechanistic models of sea otter per-capita consumption rates on sea urchins and how do consumption rates vary as a function of sea urchin density and sea otter occupation time?

Predictions

We hypothesized that sea otter occupation time would be an important factor in determining sea otter consumption rates on prey. Based on previous studies (Estes et al. 1982, Ostfeld 1982, Tinker et al. 2008) we hypothesized that as sea otter occupation time increases, sea otters would drive down the abundance of sea urchins making them more difficult to find and less likely to be eaten by otters. This would result in reduced per-capita consumption rates on sea urchins by sea otters and increased diet diversification at the population level. At the same time, size-selective foraging by sea otters would drive down the size of prey available at longer occupied sites and result in a greater proportion in the diet of smaller, less calorie-rich prey items such as chitons (Salomon et al. 2007) and intertidal mussels (Singh et al. 2013). Thus, we predicted that the length of sea otter occupation at a site may also have implications for intertidal (i.e. mussels, crabs) versus subtidal (i.e. sea urchins) foraging. Furthermore, since sea otters appear to be able to alter their feeding habits and switch to alternative prey items as sea urchins drop to low densities (Ostfeld 1982, Tinker et al. 2008) we hypothesized that

otters would exhibit a type III functional response which reflects the ability of predators to learn how to search for, attack and capture different prey types (Holling 1959).

2. Methods

Study Area

We quantified sea otter foraging behaviour on the central coast of British Columbia (B.C.), Canada during the summer of 2013 (Fig. 1AB). Sea otters were first officially recorded in this region in 1989 (BC Parks 1995), although local observations of rafts were made 10 years earlier (E. White, pers. comm). Sea otters on the central coast of B.C. appear to be descendents of otters that were intentionally translocated from Alaska to the west coast of Vancouver Island in the early 1970s (Nichol 2007). Between 1990 and 2008, the central B.C. coast population increased at a rate of 11.4% per year (Nichol et al. 2009), expanding its range northwards and southwards from Goose Island. This population is currently estimated at approximately 1000 individuals based on the 2013 Fisheries and Oceans Canada (DFO) sea otter survey (Nichol et al. in prep) and occupies exposed coastal areas characterized by a mosaic of rocky reef and sheltered soft sediment habitats.

Study Design

To determine how sea otter foraging behaviour varied with the length of time a site had been occupied by sea otters (hereafter 'sea otter occupation time'), we exploited a spatial gradient in sea otter re-establishment. We observed sea otters foraging at five sites varying from 0.1 to 33 years of occupation time (Fig. 1C). In this space for time substitution, we used raft presence (n≥ 3 individuals) as our criterion for occupation. Occupation time was estimated based on systematic sea otter surveys starting in 1990 and conducted most recently in 2013 by DFO and the Heiltsuk Integrated Resource Management Department (HIRMD) (for detailed survey methods see Nichol et al. 2009). The first year of occupation for each site was determined by the sighting of at least one raft within a three nautical miles (nm) radius of each site. Sites were separated by more than 8 nm. We assumed that sea otters did not travel between sites during the 1 month

study period and thus we did not observe the same animal at different sites. In addition, all rocky reef sites were flanked by soft sediment habitat at approximately 18m depth and may have had intrusions of soft sediment habitat interspersed between what was mostly contiguous rocky reef.

Sea Otter Foraging Observations

To quantify variation in sea otter foraging behaviour across sites, we recorded sea otter sex, foraging success, prey type, prey size, prey-specific handling time, and dive and surface intervals following previously developed focal animal sampling methods (Estes et al. 1981, Doroff and Bodkin 1994, Bodkin 2001). Specifically, individual animals were observed from shore using 10x binoculars and a 50-80x Questar telescope, at a distance of no more than 800m from the observer. Distances were estimated from Navionics 2012 navigation charts. A focal animal was observed over a sequence of foraging dives and surface intervals for as long as the animal continued to forage or until it disappeared from view. This constituted a 'foraging bout' (Calkins 1978) (Fig. S1). A foraging dive was classified as successful if one or more prey items were captured and brought to the surface for consumption, unsuccessful if no prey item was captured, or unknown when the observer could not determine the outcome. On each successful dive we identified prey to the lowest taxonomic level possible. Prey size was visually estimated based on the maximum length of prey relative to the width of a sea otter's paw (Tinker 2004) (Table S1).

At the beginning of each foraging bout, Beaufort sea state was recorded on a scale of 0-6 using WDCS Shorewatch reference sheet (2013) to approximate sea conditions. Poor sea conditions may affect an animal's ability to forage successful and/or add to potential observer error. Tidal height (m above Lowest Low Water) was also recorded at the beginning of each foraging bout. Data were collected during daylight hours and all tidal heights.

Sea Otter and Sea Urchin Density Estimates

We estimated sea otter and sea urchin density at each study site. We counted the number of sea otters up to 800 m from shore once at the beginning and once at the

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end of each observation day. Given variation in the geography of the area and presence of islands that blocked line of sight, observation areas varied between ~0.3-1 km^2. Sea otter densities were obtained by dividing the maximum number of otters observed each day by the observation area. Sea urchin density and size were estimated in subtidal rocky reef habitat (3-18m below chart datum) at each of the five study sites during July 2013 (Demes et al. in prep). At each study site, sea urchins were measured and counted to the nearest centimetre in 18 randomly stratified 1 x 1m quadrats.

Statistical Analysis

Sea otter foraging behaviour –

We quantified variation in sea otter sex, dive and surface intervals, foraging success, diet composition, prey species richness and diversity, prey size, and per-capita consumption rates on sea urchins as a function of sea otter occupation time. Dive and surface interval times were quantified by averaging across all successful dive and post-dive surface intervals at a site for comparison between study sites. Prey capture success was calculated as the total percentage of dives resulting in successful prey capture, across all dives, at each study site.

Prey selection and diet composition – To compare sea otter diet composition across sites varying in occupation time we measured the proportion of each prey type consumed by sea otters on successful foraging dives. We then averaged the proportion of prey types across all sea otters at a site. To investigate the degree to which sea otter diet diversity varied at each site, we calculated species richness (# of species) and the Shannon-Weiner index (Shannon and Weaver 1949), a measure that incorporates both species richness and evenness: $H' = -\Sigma\, p_i \ln p_i$, with *H'* being the diversity index for the diet of the population, and p_i being the relative proportion of prey item *i* in the diet.

Prey size – Based on an average sea otter paw width of approximately 5.2cm (Bodkin et al. 2010), we were able to calculate prey sizes using the maximum size of each prey category (Table S1). We then calculated the mean prey size consumed by each otter to explore prey size distributions across sites.

Per capita consumption rates on sea urchins – Sea otter per-capita consumption rates on sea urchins were calculated as the number of urchins consumed over the entire series of foraging dives that comprised a foraging bout, divided by the total duration of the bout including all dive and surface interval times for each sea otter. Each sea otter was considered an independent sample and the smallest sample unit for statistical analysis.

Factors affecting sea otter per-capita consumption rates on sea urchins –

Because sea urchins are an easily identifiable prey item and are an ecologically dominant grazer, we chose to assess the effect of various factors on sea otter per-capita consumption rates on sea urchins with generalized linear models using the *MASS* package in R (Venables and Ripley 2002). Specifically, we quantified the extent to which sea otter occupation time, sea urchin density, sea otter density, sea otter sex, tidal height and Beaufort sea state influenced sea otter consumption rates on sea urchins. We assessed potential correlation between predictors using Spearman's Rank correlation coefficient (*p*) and Pearson's correlation coefficient (*r*) and only included predictor variables in model sets where *p* and *r* were ≤ |0.5| (Booth et al. 1994, Zuur et al. 2009) (Table S4). Because sea otter occupation time was highly correlated with sea urchin density (*p*=|0.66|, *r*=|0.44|), and with otter density (*p*=|0.60|, *r*=|0.54|), we explored two model sets, the first including urchin density, sea otter density, sea otter sex, tidal height and Beaufort sea state as predictor variables and the second set including sea otter occupation time, sea otter sex, tidal height and Beaufort sea state as predictor variables. We modelled sea otter per-capita consumption on urchins as a discrete variable and included an offset term in our set of linear predictors to account for variability in the total duration of the feeding bout (offset=log(time)). To account for the high number of zeros in our data set, models were fit with a negative binomial likelihood and log link function. Additionally, we found little strength of evidence for zero-inflated models (*pscl* package in R) relative to those that did not account for zero-inflation. Lastly, we assessed the effect of different numbers of observations per-otter by weighting models by the number of dives. Because weighted models had a ΔAICc > 100 compared to non-weighted models with ΔAICc=0, final models were unweighted. All models were fit in R version 3.0.2 (R Core Team 2013).

Model selection –

To determine the strength of evidence for alternative hypothesized causal factors driving variation in per-capita sea otter consumption rates on sea urchins on B.C.'s central coast we took an information-theoretic approach (Burnham and Anderson 2002). We compared alternative candidate models with small-sample bias-corrected Akaike's Information Criterion (AICc), standardized to the most parsimonious model to produce ΔAICc. We normalized the model likelihoods to a set of positive Akaike weights (w_i), representing the strength of evidence in favour of a given model relative to the set of candidate models. From our set of top models with ΔAICc <10, we calculated multi-model averaged parameter estimates and relative variable importance (RVI) using the *MuMIn* package in R (Barton 2013). RVI for a given factor was calculated by summing the model weights across all models in the candidate set where the factor of interest occurred (Burnham and Anderson 2002). To compare factor coefficients among our candidate model set, we standardized our predictors by subtracting their mean and dividing by 2 standard deviations (Gelman 2008).

Mechanistic models of sea otter per-capita consumption rates on urchins –

To understand how sea otter consumption rates vary mechanistically as a function of sea urchin density we fit and compared alternative functional response models of sea otter per-capita consumption rates on their dominant prey, sea urchins. We fit three prey-dependent functional responses (FR): linear (Type I), hyperbolic (Type II), and sigmoid (Type III) (Holling 1959), a ratio-dependent model (Arditi and Ginzburg 1989) and one predator-dependent model (Beddington 1975, DeAngelis et al. 1975):

Eq. 1 (Type I FR) $$f(N) = aN$$

Eq. 2 (Type II FR) $$f(N) = \frac{aN}{1 + ahN}$$

Eq. 3 (Type III FR) $$f(N) = \frac{aN^2}{1 + ahN^2}$$

Eq. 4 (Ratio-dependent FR) $$f(N) = \frac{aN}{P + ahN}$$

Eq. 5 (Predator-dependent FR) $$f(N) = \frac{aN}{bN + P - C}$$

where *N* is the density of urchins available, *a* is a proportionality constant set by the rate at which predators encounter prey, *h* is the time taken by an otter to handle one urchin (estimated from the data), *P* is the density of predators, *b* and *C* are additional parameters to be estimated from the data.

To understand how sea otter per-capita consumption rates vary with sea otter occupation time, we fit alternative functional response models while accounting for the exponential decay observed in available sea urchin prey across sites (Fig. 3A) (Demes et al. in prep):

Eq. 6 $f(x) = N = be^{-mx}$

where, N is urchin density, x is otter occupation time, and b and m are parameters we estimated from the data. We then substituted Eq. 6 into Eq. 1-5 to determine alternative hypotheses for the effect of sea otter occupation time on per-capita consumption rates on urchins, where a' is now a*b from the previous equations:

Eq. 7 $f(x) = a'e^{-mx}$

Eq. 8 $f(x) = \dfrac{a'e^{-mx}}{1 + a'he^{-mx}}$

Eq. 9 $f(x) = \dfrac{a'(e^{-mx})^2}{1 + a'h(e^{-mx})^2}$

Eq. 10 $f(x) = \dfrac{a'e^{-mx}}{P + a'he^{-mx}}$

Eq. 11 $f(x) = \dfrac{a'e^{-mx}}{be^{-mx} + P - C}$

Models were fitted using the *minpack.lm* package in R (Elzhov et al. 2013) which utilizes the Levenberg-Marquardt algorithm to solve nonlinear regression. To assess the strength of evidence for each model in approach 1 and 2, we used small-sample bias-corrected Akaike's Information Criterion (AICc), as described above.

3.   Results

Sea Otter Foraging Observations

Dive Summary Statistics - We observed a total of 598 foraging dives made by 72 sea otters across the five study sites, including 29 males, 34 females and 9 otters of unknown sex (Fig. S2A). Sea otter mother and pup pairs were observed at all sites, except the most recently occupied site (Calvert 0.1 yrs). Average bout (series of dives for single otter) time ±SE for all sea otters was 17± 1.7 min and ranged from 1 to 68 min. Out of all dives of known outcome (n=585) across all study sites, 86% led to successful prey captures. Successful prey capture varied among sites, with the greatest success of 93% observed at the longest occupied site (Goose 33 yrs), and the lowest success of 76% observed at the mid-occupation time site (Simonds 4 yrs) (Fig. S2B). Mean dive intervals across all successful dives at a site varied from 53± 3 sec at the most recently occupied site (Calvert 0.1yrs), to 91± 3 sec at the intermediate occupation time site (Simonds 4yrs) (Fig. S2C) while mean surface intervals varied from 44± 2 sec to 80± 6 sec at these same sites (Fig. S2D).

Prey composition and size – Based on the 19 species we were able to identify plus one group for all unidentified prey species, sea otter diet diversity, measured by both prey species richness and H' tended to be higher at longer occupation time sites (Fig. 2AB) and prey species tended to be smaller (Fig. 2C). Furthermore, sea otter diet tended to include more intertidal invertebrates, such as mussels and shore crabs, at longer occupation sites. We categorized all identifiable prey (66% of all observations) into 13 functional prey groups based on habitat and taxonomic groupings (Table S2), including one group representing all unidentified prey. Sea urchins *(Mesocentrotus* spp.) dominated the sea otter diet (87.7± 7.0%) at the most recently occupied site, Calvert (0.1 yrs), but were much less common at Breadner (9.7± 4.9%) with just two years of sea otter occupation (Table 1, Fig. 2D). Northern abalone (*Haliotis kamtschatkana*) represented the greatest proportion of identifiable prey (22.1± 9.3%) at Breadner. With

four years of otter occupation (Simonds), geoduck (*Panopea abrupta*) represented the greatest proportion of the diet (42.2± 11.9%). After 17 years of otter occupation (McMullins), clams (Order: Veneroida) and small intertidal crabs (*Hemigrapsus* spp.) represented 28.9± 11.0% and 12.8± 6.3% of the diet respectively. After 33 years of occupation time (Goose), California mussels (*Mytilus californianus*) represented 34.1± 10.6% of the diet. Prey items that could not be identified may have represented a diversity of species that we were not able to take into account in our analysis. Small unidentified prey items represented only 4.3± 2.4% of the sea otter diet at the most recently occupied site (Calvert), but represented > 10% of the diet at all other sites with longer otter occupation time (Table 1). Uncommon prey items included an ochre sea star (*Pisaster ochraceus*) and an octopus (Family: Octopodidae). Estimated prey sizes consumed by sea otters varied from 2-16cm across all study sites. Largest median prey size (12cm), based on mean prey size consumed by each sea otter at a site, was observed at the most recently occupied site (Calvert 0.1 yrs), while the smallest median prey size (5cm) was observed at a longer occupation time of 17 years (McMullins) (Fig. 2C).

Sea Otter and Sea Urchin Density Estimates

Based on the maximum number of sea otters observed within view of each study site, we found that sea otter densities varied across sites, with the highest densities of animals observed at shorter occupation time sites (n= $19/0.5km^{-2}$ at 0.1yrs and n= $24/0.5km^{-2}$ at 4 yrs), and lowest density observed at the longest occupied site (n= $2/0.5km^{-2}$ at 33 yrs) (Table S3). Furthermore, site-specific mean urchin densities (from Demes et al. in prep) declined exponentially across sites increasing in occupation time (Fig. 3).

Factors Affecting Sea Otter Per-Capita Consumption Rates On Sea Urchins

Sea otter per-capita consumption rates on sea urchins were high at the most recently occupied site at 0.3-0.9 urchins per min, suggesting the otters could consume 20-50 urchins in one hour, relative to 0-0.1 urchins per min or 14 urchins per hour after two years of occupation.

Among alternative models of sea otter consumption rates that included urchin density, sea otter density, sea otter sex, Beaufort sea state and tidal height as predictors variables, we found strong empirical support for the effect of urchin density given that the null model of no effect (*Intercept*) was 50 to 58 ΔAICc units away from the top 14 models, all of which included urchin density as a predictor variable. Model averaging further revealed that urchin density had a positive effect on per-capita sea otter consumption rates that was 4 times greater than the negative effect of otter density (Fig. 4A). Moreover, the effect of urchin density was more important (*Urchin Density* RVI=1) in predicting sea otter consumption rates across all sites relative to the density of sea otters (*Otter density* RVI=0.39), which had a negative yet imprecise effect given its standardized coefficient's confidence intervals include zero.

Among alternative models of sea otter consumption rates that included sea otter occupation time, sea otter sex, Beaufort sea state and tidal height as predictors variables, we found strong evidence for the effect of occupation time given that the null model of no effect (*Intercept*) was 22 to 32 ΔAICc units away from the top 5 models, all of which included occupation time as a predictor variable (Table 2). Model averaging revealed that while both occupation time and tidal height were essentially equally important variables influencing otter consumption rates (RVI=1, 0.97 respectively) the negative effect of occupation time was 1.75 times the positive effect of tidal height (Fig. 4B). In addition, we found that sea otter sex was a relatively important predictor of per-capita consumption rates on sea urchins with a RVI=0.99, in that males sea otters at the earliest occupied site exhibited higher consumption rates.

Mechanistic Models of Sea Otter Per-Capita Consumption Rates On Sea Urchins

Because the previous linear models do not capture the ecological mechanisms and constraints involved in feeding behaviour (Holling 1959), we explored the relationship between per-capita consumption rates on urchins and urchin density by fitting alternative functional response models. We found strong relative evidence for prey-dependent over ratio and predator-dependent functional response models, given ΔAICc values of <2 and cumulative model weights of 90% for the 3 prey-dependent models; Type I, II and III (Table 3). However, we found no support in our data for one

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prey-dependent model over the other (ΔAICc <2 for Type I, II and III functional responses). Parameter estimates for all but the Type I model were imprecise (Table S5). The prey-dependent Type I linear model predicted that a decline in 1 urchin m^{-2} corresponded to a decrease in sea otter per-capita consumption rates on urchins by 0.03 urchins per otter per minute, or 2 urchins per hour (Fig. 5A).

When we fit alternate hypotheses of how sea otter per-capita consumption rates on urchins vary as a function of sea otter occupation time, assuming an exponential decline in urchins, we found greater strength of evidence for the prey-dependent models (ΔAICc values <2) than the ratio and predator-dependent models (Table 3). However, parameter estimates for all models, except the linear form of the prey-dependent models, did not differ significantly from zero and exhibited large standard errors, several orders of magnitude higher than the estimates (Table S5). Thus, based on parameter estimates for the linear transformation of the prey-dependent model, a one year increase in sea otter occupation time corresponded to a 70% decline in per-capita consumption rates on urchins.

4. Discussion

As sea otters expand their range in a high latitude temperate reef ecosystem, we found evidence that this keystone predator serially depleted alternative prey species and sizes, dramatically changing their diet diversity and per-capita consumption rates on one of the most important temperate reef herbivores, the sea urchin (Harrold and Pearse 1987, Estes and Duggins 1995). Across 5 sites varying in sea otter occupation time, sea urchins dominated sea otter diets at the most recently occupied site, followed by abalone and clams at mid occupation time sites, and lastly intertidal crabs and mussels at longer occupation sites (Table 1, Fig. 2D). Furthermore, sea otter diet diversity tended to be higher and prey size smaller at longer occupation time sites (Fig. 2ABC). Strong evidence suggests that variation in sea otter consumption rates of urchins can be attributed to sea otter occupation time, urchin density, sea otter sex and tidal height (Table 2, Fig. 4AB), the first three variables being highly correlated (Table S4). Specifically, we found that urchin density had a positive effect on per-capita sea otter consumption rate that was more important (RVI=1) and 4 times greater than the negative and imprecise effect of otter density (RVI=0.39) (Fig. 4A). While both occupation time and tidal height were equally important variables influencing otter consumption rates (RVI=1, 0.97 respectively), the negative effect of occupation time was 1.75 times the positive effect of tidal height. When we explored our data with mechanistic models of predation, we found greater strength of evidence for prey-dependent than predator-dependent functional response models of sea otter consumption of urchins (Fig. 5A). Furthermore, per-capita consumption rates on urchins declined exponentially with increasing sea otter occupation time (Fig.5B). Based on the most parsimonious model, we found a 70% decline in per-capita consumption rates on urchins within the first year of sea otter occupation.

Sea Otter Consumption of Sea Urchins

Results are consistent with other studies from the northeast Pacific that have shown that sea urchins likely provide an initially rich, but relatively short-term food resource for growing sea otter populations (Ostfeld 1982, Laidre and Jameson 2006, Tinker et al. 2008). While, sea urchins comprised 87.7± 7.0% of the diet of sea otters at the forefront of range expansion, after two years of occupation sea urchins comprised only 9.7± 4.9%, and continued to decline in importance in the sea otter diet (Table 1). Likewise, per-capita consumption rates on sea urchins were high at the most recently occupied site at 0.3-0.9 urchins per min, suggesting the otters could consume 20-50 urchins in one hour, relative to 0-0.1 urchins per min after two years of occupation suggesting that otters here could consume at most 14 urchins in one hour. These macroinvertebrates are conspicuous and easily captured and were abundant at the most recently occupied site (Calvert 0.1 yrs) (Demes et al. in prep). In contrast, at sites with longer otter occupation time, easily captured prey like sea urchins were not readily available (Fig. 3). Thus, our data demonstrates that shifts in sea urchin availability were in turn reflected in sea otter diets, suggesting that sea otters eat urchins in proportion to their availability. It is important to note that by exploring consumption rates on urchins across sites with varying occupation time, we are assuming that study sites offer similar habitat and risks, and that sea otters across sites are making the same foraging decisions based on profitability and availability of prey.

Diet Diversification, Serial Depletion & Changes in Habitat Use

While sea urchins were targeted at the most recently occupied site (Calvert 0.1 years), we found that different prey items dominated the sea otter diet at each site with increasing occupation time, suggesting this top predator is progressively depleting marine resources. Abalone, geoduck clams, other small clams, intertidal crabs and mussels were targeted in sequence of increasing occupation time (Fig.2D). This pattern of serial depletion of marine invertebrates has been observed in Alaska and attributed in part to the recovery of sea otters (Salomon et al. 2007). In addition, our results are consistent with predictions that predators diversify their diets and target less valuable prey as easily captured, calorically-rich, and abundant prey (i.e. sea urchins) are

depleted (Schoener 1971, Ostfeld 1982). In addition to optimal foraging, variation and complexity of habitat around each site in our study helps explain the selection of both rocky and soft-bottom prey types by sea otters as they make energy maximizing decisions.

Geoduck clams (*Panopea abrupta)* represented a large portion of the sea otter diet (42± 11%) after 4 years of otter occupation at Simonds. While increased effort is required to capture these deeply buried prey (Kvitek et al. 1993), the benefit of higher caloric content may have counterbalanced the cost of capture. Contrary to our findings, in southeast Alaska at sites where sea urchins were very rare, researchers found that sea otters targeted smaller butter clams in soft-sediment habitat, rather than abundant geoduck clams (Kvitek et al. 1993). However, Kvitek et al. (1993) hypothesized that sea otters may not have recognized geoduck as a profitable prey since food preferences are influenced by maternal transmission and this population had been relocated twenty years earlier from a region outside of the geoduck range. In our study, we observed both adult males and mothers with pups consuming geoduck. Since geoduck clams were likely available across the central coast study region due to the patchy nature of habitat, it is likely that sea otters learned to identify this novel prey once easily accessed prey items such as sea urchins were depleted.

California mussels *(Mytilus californianus)* were a high proportion of identifiable prey in the sea otter diet after 33 years of otter occupation at Goose. This prey can be easily obtained because they occur in the intertidal and require little effort to capture (VanBlaricom 1988), however they also have little nutritional value (Garshelis 1983). Estes et al. (1981) observed that mussels may be used by either young animals as a food source until they become more proficient foragers, or by females with dependent pups. Indeed we observed a higher proportion of unidentified sea otters at Goose that have been young animals. It is likely that as higher-value prey items were depleted, young animals and females were left to forage on this easily obtainable intertidal prey. At both sites, we observed sea otters spending more time foraging at higher tides when intertidal prey items were presumably accessible, suggesting that more subtidal prey had been depleted or were inaccessible at higher otter occupation time sites.

Furthermore, small unidentified prey items and intertidal crabs (Genus: *Hemigrapsus*) made up the greatest proportion of sea otter diets at three of our sites representing 2 (Breadner), 17 (McMullins) and 33 (Goose) years of sea otter occupation time, suggesting that higher value prey items had been depleted. Unidentified prey are represented in our analysis as one prey category, whereas they may represent a more diverse selection of species, leading to a degree of uncertainty in our diet diversity (H' and species richness) results. However, it is more likely that we underestimated rather than overestimated diversity in sea otter diets at the population level where we observed a larger proportion of unidentified prey.

Urchin Density and Occupation Time Drive Consumption Rates on Sea Urchins

We detected strong evidence that sea urchin density is a better predictor of per-capita consumption rates on sea urchins than otter density, sea otter sex or environmental variables (Table 2, Fig.4). Optimal foraging theory predicts that prey resource availability will influence prey selection and thus consumption rates; if high-value (easily captured, calorically-rich) prey items are greatly reduced in abundance, this will increase search time leading predators to select alternate prey (Ostfeld 1982). Our results are consistent with the notion that strong top-down pressure by otters triggers changes in prey availability and encounter rates, thus resulting in changes in diet (Estes et al. 1982).

Among alternative models of sea otter per-capita consumption rates that included sea otter occupation time, sea otter sex, Beaufort sea state and tidal height as predictors variables, we found strong evidence for the negative effect of occupation time (Table 2, Fig. 4). Increased sea otter occupation time represents predation pressure from a population of sea otters over time. While few other studies have explored a gradient in occupation time, they have shown drastic differences in consumption on sea urchins at early versus long established sites (Estes et al. 1982, Laidre and Jameson 2006, Tinker et al. 2008). We may not have seen as strong relative support for occupation time as predicted, because this factor represents a more indirect effect of sea otter predation on urchins, as compared to urchin densities that directly affect consumption of urchins. We also made various assumptions in our methods of estimating occupation time, such as

that higher occupation times represent consistent occupation and predation pressure by sea otters. While DFO sea otter surveys show that sea otters were observed at a site on consecutive survey years, we do not know if these sites are being used consistently throughout the year.

Our results also suggest that sea otter sex and tidal height are important predictors of consumption rates on sea urchins in addition to occupation time. Male sea otters tended to occupy newly occupied sites (Calvert 0.1 yrs) (Fig. S2), consistent with patterns of sea otter range expansion observed in other regions of the Pacific coast (Garshelis et al. 1984, Riedman and Estes 1990). Our observation of sea otter sex distribution and diet (Fig.2) suggest that males deplete urchin resource before female sea otters and pups arrive. In addition, territorial males may have a negative effect on female foraging success at sites in the core of the sea otter range due to food stealing and harassing (Riedman and Estes 1990). Tidal height may have come out as an important predictor with a positive effect on consumption rates because a greater area of habitat is available to exploit at higher tides. In addition other studies have found that foraging activity can vary greatly between sites throughout the day (Estes et al. 1982), thus during our three week study period, tidal observations may have been somewhat correlated with time of day.

The Functional Response of Sea Otters to Sea Urchins

Our non-linear models appear to capture the steep declines evident in per-capita consumption rates on sea urchins with increasing occupation when fit to empirical data (Fig. 5B). Thus, these mechanistic models allowed us to predict rates of change in sea otter per-capita consumption rates on urchins with time, such that based on the most parsimonious model, we found a 70% decline in per-capita consumption rates on urchins within the first year of sea otter occupation.

This is the first study to explore the functional relations between sea otters and their dominant prey, sea urchins. Our results suggest that the functional response of sea otters to sea urchins is likely strongly prey-dependent (Table 3). While we predicted a Type III functional response due to evident learning behaviour in sea otters and prey switching which can lead to this response (Murdoch 1969), we were unable to discern

between Type I, II or III functional response models. It is likely that we did not have enough data across a range of urchin densities to detect strong evidence for one prey-dependent FR model over another. However, the decline of sea urchin density with sea otter occupation time (Fig. 3) occurs so rapidly that the exact shape of the response may not be as important to resource managers as identifying *when* and *where* depletion of prey resources may occur.

Conversely, Vucetich et al. (2002) found that wolf consumption on moose was largely explained by predator-dependent functional response models. Various factors may lead to predator-dependent per-capita consumption rates such as predator or prey behaviours (including interference among predators), limitation of predator populations by something other than prey, or allocation of prey among predators (Vucetich et al. 2002). In our study, sea otter-prey interactions did not appear to be characterized by the factors expected to generate predator-dependent responses. For example, social interactions did not appear to dampen or enhance foraging success in a density dependent manner; at the most recently occupied site (Calvert 0.1 yrs) we observed large groups of sea otters foraging successfully in close proximity to one another. In addition, sea otters may not be the typical large carnivore. They have a very high metabolic rate and are able to consume the equivalent of 1/3 of their body weight each day (Kenyon 1981). Furthermore, the prey resource, sea urchins, are sessile, readily available and easy to grab off the sea floor at unoccupied rocky reef sites, thus unlike other large predators in pursuit of prey (i.e wolves), sea otters do not need to employ group hunting tactics. Thus strong prey-dependency makes sense based on sea otter natural history. However, Abrams and Ginzburg (2000) argue that both prey and predator density should influence predator consumption of prey. With a greater number of foraging observations or an alternate method of obtaining estimates of predator density we might detect some predator-dependency in sea otter foraging.

Other factors can influence consumption of prey by predators that were not captured in our data. Predators may not only influence their prey through consumption, but by altering prey behaviour (e.g. Lima and Dill 1990). Watson and Estes (2012) made observations of sea urchins fleeing when broken urchin tests were dropped by sea otters. Sea urchins also tend to be found in cracks and crevices when predators are present (Tegner and Levin 1981, Shears et al. 2008). In addition, predators have the

potential to be frightened by other predators, such that foraging individuals may optimize energy gain and safety from predators by spending less time in more profitable but dangerous sites (Wirsing et al. 2008). Thus it is possible that interspecific interactions between sea otters and other predators such as killer whales (*Orcinus orca*) and pinnipeds (see Estes et al. 1998, Fisher et al. 2014) may influence site selection, foraging behaviour, and per-capita consumption rates on sea urchins.

Broader Implications of Sea Otter Consumption of Shellfish to Management

Sea otter populations on the central coast of B.C. are still recovering from years of overexploitation during the maritime fur trade (COSEWIC 2007). As sea otters recover, empirical evidence suggests that there are two major consequences to marine systems: first, by consuming large quantities of prey, sea otters are capable of altering the abundance of species such as sea urchins (Estes et al. 1982), northern abalone (Watson and Smith 1996), clams (Kvitek et al. 1992) and sea cucumbers (Larson et al. 2013); second, by driving down the size and abundance of sea urchins, sea otters limit herbivory by this dominate grazer and allow perennial kelps to re-grow (Estes and Palmisano 1974, Watson and Estes 2011). Increased predation pressure on culturally and commercially important marine invertebrate species may lead to potential conflict where sea otter range overlaps with commercial and First Nations Food, Social and Ceremonial (FSC) invertebrate fisheries (COSEWIC 2007), but also result in potential benefits associated with kelp forest recovery.

Accounting for interactions between sea otters and their prey –

Northern sea otters (*Enhydra lutris kenyoni*) are listed as a species of *Special Concern* under the *Species at Risk Act* in Canada (COSEWIC 2007), thus recovery targets and management strategies should be developed with consideration of strong interactions between sea otters and their prey. However, the main recovery goal for sea otters in Canada is that the population be able to naturally expand and grow to the extent that threats, such as oil spills, would be unlikely to cause extirpation or diminish the population (Sea Otter Recovery Team 2007). Chadès et al. (2012) argue that the status quo of managing species in silos and setting recovery targets without considering strong interactions between species can lead to inefficient management, waste of

resources and risk of extinction. In a study to examine how different management actions might impact population dynamics of both, sea otters and northern abalone (*Haliotis kamtschatkana*), an endangered species in Canada, Chadès et al. (2012) found that the type of functional response (FR) had the largest effect on abalone density in the presence of sea otters. While in our study we were not able to discern the exact prey-dependent FR of sea otters to changing sea urchin densities, our methods do provide insight into how these measurements might be obtained. Further work is required to better discern the functional response of sea otters to changing sea urchin densities, and could likely be obtained by observing sea otters at a single site during the first several years of occupation.

Implications for commercial and subsistence sea urchin fisheries –

Harvest of red sea urchins in traditional territories is important for coastal First Nations for food, social and ceremonial (FSC) purposes. Fisheries and Oceans Canada identifies FSC allocation which takes place throughout the B.C. coast as the first priority after conservation (DFO 2012). Over the past 100 years commercial fisheries have been able to develop in the absence of sea otters, due to a hyper-abundance of their prey (Estes 1996). However, in recent years there has been increasing concern by fishermen and coastal First Nations for the sustainability of sea urchin fisheries where sea otters and urchin harvesting sites coexist (DFO 2012). Quotas for red sea urchins have already been reduced on the west coast of Vancouver Island, where sea otters have been established for over forty years (DFO 2012). Indeed, our data suggest that sea otter consumption rates of urchins (which reflects availability) can decline dramatically within the first year of sea otter occupation, suggesting that sea urchin harvesters on the central coast of B.C. need to prepare for large reductions in sea urchin availability as sea otters expand their range. Furthermore, by removing the largest size classes of sea urchins, the impact of sea otters on fisheries may be further magnified.

Potential implications to kelp forest recovery –

Although it is evident sea otters can, and have, reduced the abundance of many benthic invertebrate populations, leading to potential losses of livelihood, they also play an important role in enhancing kelp forest productivity and fisheries. In the Northeast Pacific, sea otters have been shown to exert strong ecological effects in the habitats

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they occupy, playing an important role in limiting herbivory by sea urchins and structuring kelp forest communities (Estes and Palmisano 1974, Estes and Duggins 1995, Watson and Estes 2011). The recovery of sea otters can also have positive indirect effects on other species that use kelp forests. For example, fish communities may use kelp forests as habitat for juveniles, for shelter from predation, or to feed on other species that inhabit the kelp. By comparing areas with and without sea otters, researchers have shown that sea otters have positive indirect effects on juvenile and adult rockfish (Markel 2011, Szpak et al. 2013) and rock greenling (Reisewitz et al. 2006).

Collaboration in Sea Otter Management

As the sea otter population on the central coast of B.C. continues to expand and grow, it is likely that they will continue to target sea urchins and other commercially and culturally important shellfish as they occupy new nearshore habitats, thus driving ecosystem change in rocky reef environments. An improved understanding of predator-prey interactions and functional relations will reduce uncertainty about the magnitude and timing of these effects and improve our ability to develop effective management goals and conservation strategies. Local First Nations and resource managers can then be armed with the information they need for making decisions about the management of marine resources in their territories and communities. Management of coastal marine resources can be further improved with efforts to balance economic, socio-cultural, and environmental values and priorities and increase collaboration between scientists, local community members, government agencies and First Nations resource managers.

5.   Tables

Table 1.   Percent occurrence of main prey items captured by northern sea otters (*Enhydra lutris kenyoni)* at study sites varying in sea otter occupation time (in brackets) on the central coast of British Columbia, Canada. Occurrences are averaged by prey type across otters with +/- SE for each site. Identifiable prey types representing the greatest proportion of the otter diet are bolded.

Study Site	Sea Urchin	Abalone	Geoduck	Unid. clam	Shore crab	Mussel	Unidentified
Calvert (0.1 yrs)	**87.7±7.0**	0.0	0	0	0	0.0	4.3±2.4
Breadner (2 yrs)	9.8±4.9	**22.1±9.3**	0	0	0	0.0	42.4±10.2
Simonds (4 yrs)	5.3±4.6	0.0	**42.2±11.9**	**31.1±11.8**	0.1± 0.1	0.0	19.6±7.9
McMullins (17 yrs)	1.2±1.2	0.0	1.7±1.7	**27.2±11.2**	**12.8± 6.3**	0.0	35.7±8.0
Goose (33 yrs)	6.5±5.1	0.0	0	6.7±6.9	0.6±0.7	**34.1± 10.6**	37.1±8.2

Table 2.   Strength of evidence for alternative models of northern sea otter (*Enhydra lutris kenyoni*) per-capita consumption rates on sea urchins. Models with varying numbers of parameters (K), were compared with small sample corrected Akaike's Information Criterion (AICc), differences in AICc (ΔAICc = AICc$_i$-minAICc), and Akaike model weights (w_i) indicating the weight of evidence in favour of model i.

Model	K	AICc	ΔAICc	w_i
Model Set 1				
Urchin Density	3	168.09	0.00	0.27
Urchin Density + Otter Density	4	168.97	0.88	0.18
Urchin Density + Sea State	4	170.12	2.03	0.10
Urchin Density + Tide	4	170.22	2.13	0.09
Urchin Density + Sea State + Otter Density	5	170.88	2.79	0.07
Urchin Density + Tide + Otter Density	5	171.04	2.95	0.06
Urchin Density + Sex	5	171.15	3.06	0.06
Urchin Density + Otter Density + Sex	6	172.02	3.93	0.04
Urchin Density + Sea State + Tide	5	172.35	4.26	0.03
Urchin Density + Sea State + Sex	6	173.45	5.36	0.02
Urchin Density + Sea State + Otter Density + Sex	7	174.28	6.19	0.01
Urchin Density + Tide + Otter Density + Sex	7	174.28	6.19	0.01
Urchin Density + Sea State + Tide + Sex	7	175.65	7.56	0.01
Urchin Density + Otter Density + Sea State + Tide + Sex	8	176.45	8.36	0.00
Tide + Sea State + Sex	6	212.56	44.47	0.00
Otter Density	3	214.19	46.10	0.00
Tide + Otter Density	4	214.71	46.62	0.00
Sea State + Tide + Otter Density	5	216.14	48.05	0.00
Tide + Sea State	4	221.44	53.35	0.00
Sea State	3	222.17	54.08	0.00
Tide	3	225.10	57.01	0.00
Intercept Model	2	226.30	58.21	0.00
Model Set 2				
Occupation Time + Tide + Sex	6	194.54	0.00	0.72
Occupation Time + Sea State + Tide + Sex	7	196.79	2.25	0.24
Occupation Time + Sex	5	201.39	6.85	0.03
Occupation Time + Sea State + Sex	6	203.66	9.12	0.01
Occupation Time + Tide + Sea State	5	204.05	9.51	0.01
Occupation Time + Tide	4	205.40	10.86	0.00
Sex	4	209.56	15.03	0.00
Tide + Sex	5	210.37	15.84	0.00
Occupation Time + Sea State	5	210.62	16.08	0.00
Occupation Time	4	211.72	17.20	0.00
Sea State + Sex	6	211.74	17.18	0.00
Sea State + Tide + Sex	3	212.56	18.02	0.00
Tide + Sea State	4	221.44	26.90	0.00
Sea State	3	222.17	27.63	0.00
Tide	3	225.10	30.56	0.00
Intercept	2	226.30	31.76	0.00

Table 3.   Strength of evidence for alternative mechanistic models of per-capita consumption rates on sea urchins by northern sea otters (*Enhydra lutris kenyoni*) as a function of A) urchin density (N) and B) otter occupation time (x) while accounting for observed exponential decay rates in available sea urchin prey. Models with varying numbers of parameters (K), were compared with small sample corrected Akaike's Information Criterion (AICc), differences in AICc (ΔAICc = AICc$_i$-minAICc), and Akaike model weights (w$_i$) indicating the weight of evidence in favour of model i.

Response and Model		K	AICc	ΔAICc	w$_i$
Per-Capita Consumption Rate on Urchins					
Type I FR	aN	2	-105.34	0.00	0.31
Type II FR	$\dfrac{aN}{1+ahN}$	3	-105.29	0.04	0.30
Type III FR	$\dfrac{aN^2}{1+ahN^2}$	3	-105.18	0.16	0.28
Predator-dependent FR	$\dfrac{aN}{bN+P-C}$	4	-103.06	2.28	0.10
Ratio-dependent FR	$\dfrac{aN}{P+ahN}$	4	-11.24	94.10	0.00
Per-Capita Consumption Rate on Urchins					
Type I FR + Exp. decay urchins	$a'e^{-mx}$	3	-104.42	0.00	0.47
Type II FR+ Exp. decay urchins	$\dfrac{a'e^{-mx}}{1+a'he^{-mx}}$	4	-102.64	1.79	0.19
Type III FR + Exp. decay urchins	$\dfrac{a'(e^{-mx})^2}{1+a'h(e^{-mx})^2}$	4	-102.51	1.92	0.18
Ratio-dependent FR+ Exp. decay urchins	$\dfrac{a'e^{-mx}}{P+a'he^{-mx}}$	4	-100.97	3.45	0.08
Predator-dependent FR + Exp. decay urchins	$\dfrac{a'e^{-mx}}{be^{-mx}+P-C}$	5	-100.54	3.89	0.07

6.   Figures
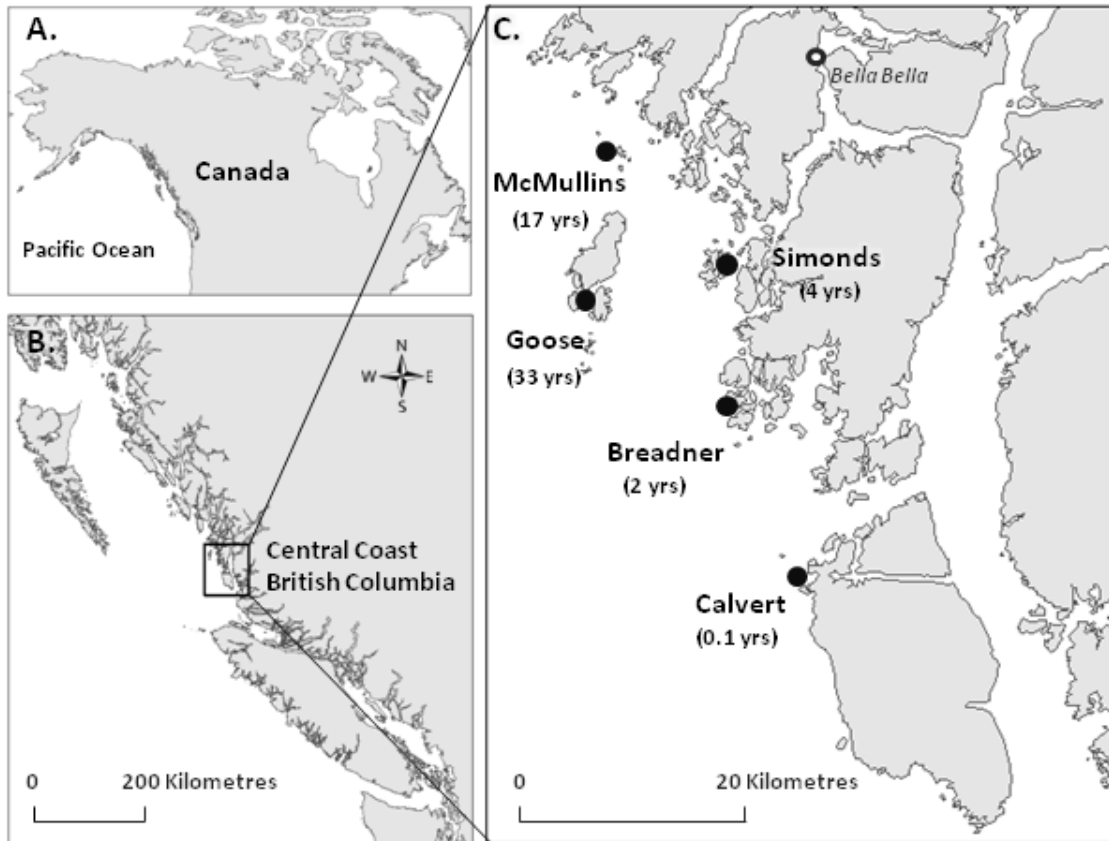
Figure 1.   We quantified northern sea otter (*Enhydra lutris kenyoni*) foraging behaviour on the central coast of British Columbia, Canada (A and B) at 5 sites (C) varying in sea otter occupation time (in brackets).
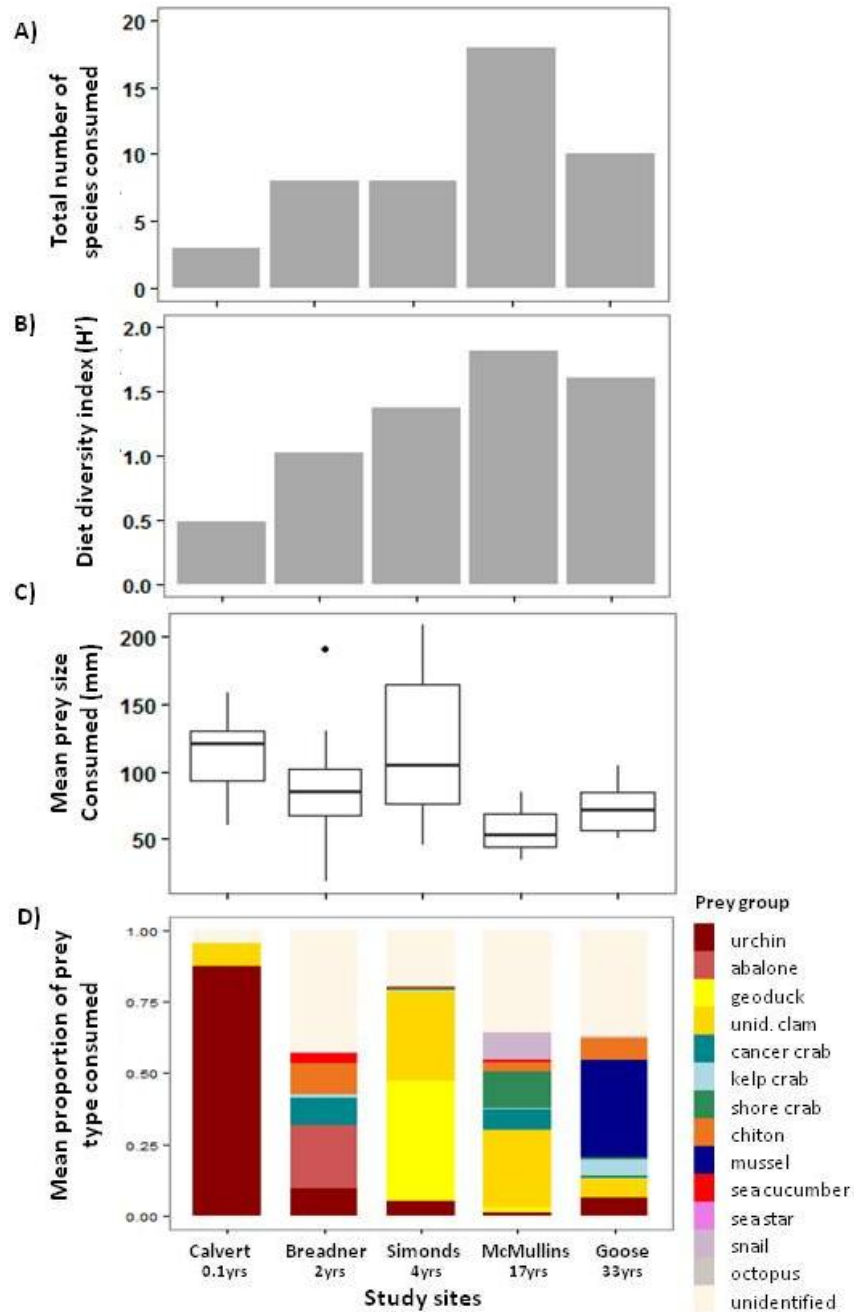
Figure 2. Prey selection by northern sea otters (*Enhydra lutris kenyoni)* on the central coast of British Columbia, Canada, at sites varying in sea otter occupation time. (A) Prey species richness calculated as total number of prey species observed across all dives at a site; (B) Diet diversity calculated using Shannon-Weiner Index - H' based on percent occurrence of prey species in the sea otter diet and averaged across the site; (C) Range of prey sizes at a site, averaged by otter, showing the median, 1st and 3rd quartiles, ± 1.5*IQRs; (D) Sea otter diets calculated as the proportion (by #) of prey types consumed by each sea otter and averaged across each site.
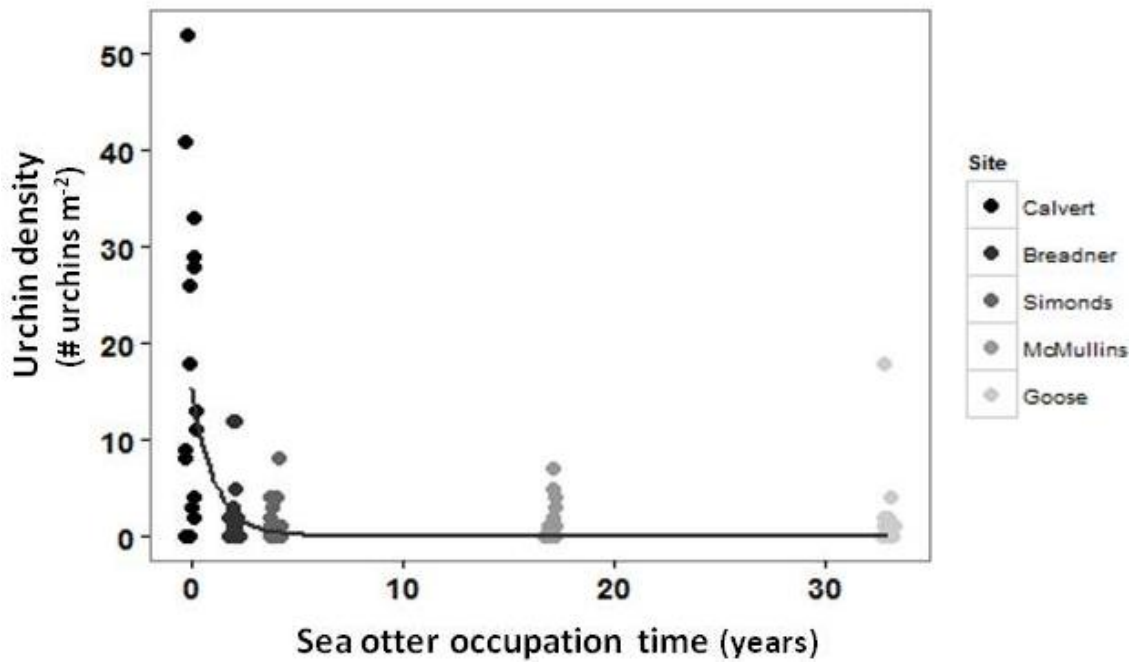
Figure 3.   Variation in sea urchin (*Mesocentrotus* spp*.)* density as a function of sea otter occupation time along British Columbia, Canada's central coast. Urchin densities found at n=18 quadrats at each study site (n=5), from Demes et al. in prep. Exponential decline fit to empirical data. Data points are jittered.

Factors Affecting Per-Capita Consumption Rates on Sea Urchins

A)
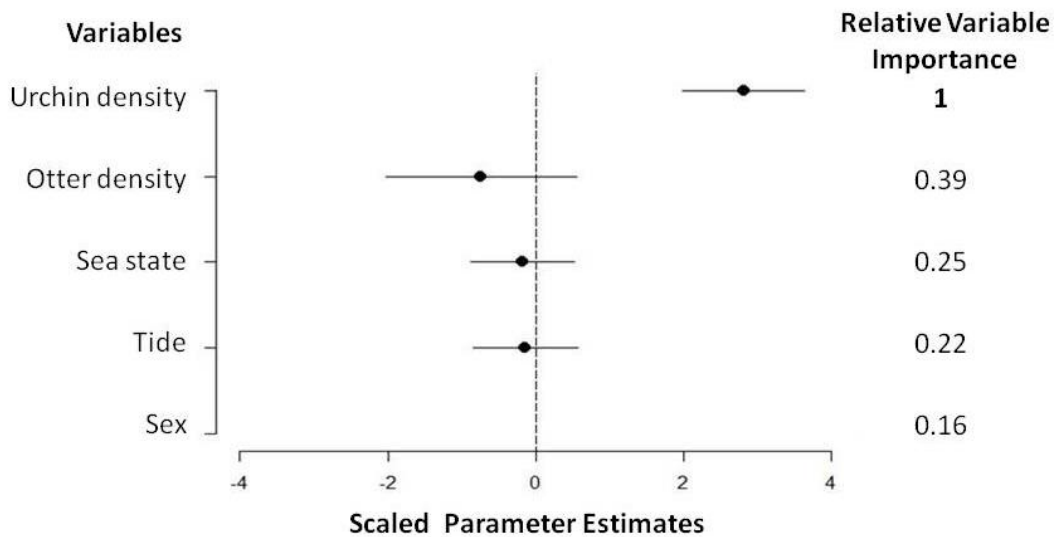
B)
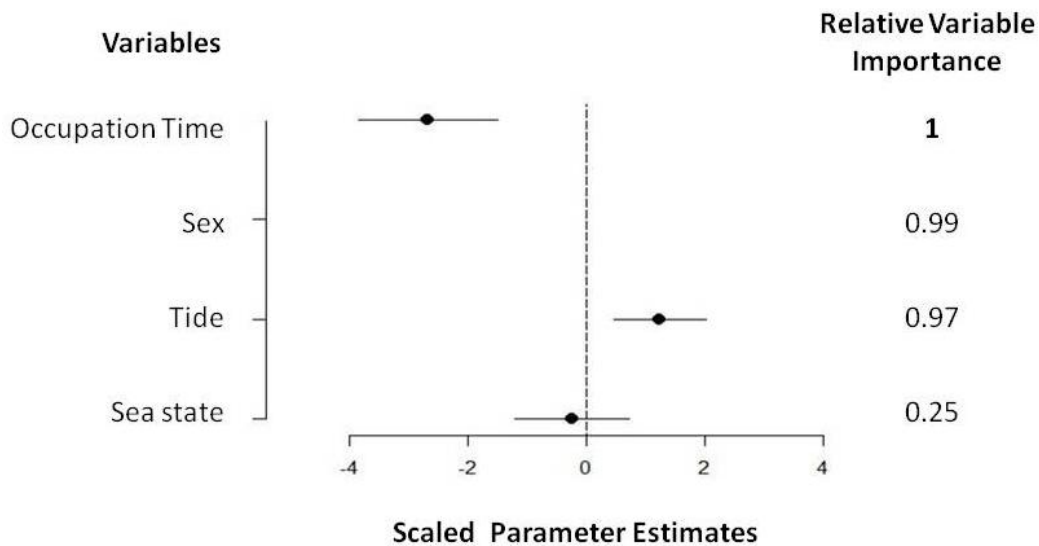
Figure 4.   Scaled parameter estimates (circles) and 95% confidence intervals (lines) of biological and physical variables thought to drive variation in sea otter consumption rates on sea urchins along British Columbia, Canada's central coast. Variable "sex" is a factor with three levels and does not have a single scaled parameter estimate. Variables within two model sets A) and B) are ranked in decreasing order of relative importance on a scale of 0 to 1. Model averaging results are based on all models within ΔAICc <10.

A)

Per-capita consumption rate on urchins (# urchins otter^{-1} min^{-1})

Type I Prey $\quad aN$

Type II Prey $\quad \dfrac{aN}{1+ahN}$

Type III Prey $\quad \dfrac{aN^2}{1+ahN^2}$

Ratio $\quad \dfrac{aN}{P+ahN}$

Predator $\quad \dfrac{aN}{bN+P-C}$

Mean urchin density (# urchins m^{-2})

B)

Per-capita consumption rate on urchins (# urchins otter^{-1} min^{-1})

Type I Prey $\quad a'e^{-mx}$

Type II Prey $\quad \dfrac{a'e^{-mx}}{1+a'he^{-mx}}$

Type III Prey $\quad \dfrac{a'(e^{-mx})^2}{1+a'h(e^{-mx})^2}$

Ratio $\quad \dfrac{a'e^{-mx}}{P+a'he^{-mx}}$

Predator $\quad \dfrac{a'e^{-mx}}{be^{-mx}+P-C}$

Sea otter occupation time (years)

Figure 5. Alternative mechanistic models fit to field data of per-capita sea otter consumption rates on sea urchins as a function of (A) site-specific mean urchin density (m^{-2}), and (B) sea otter occupation time (years).

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References

Abrams, Peter A. 2001. "Describing and quantifying interspecific interactions: a commentary on recent approaches." *Oikos* 94(2): 209–218.

Abrams, Peter A., and L.R. Ginzburg. 2000. "The nature of predation: prey dependent, ratio dependent or neither?" *Trends in ecology & evolution* 15(8): 337–341.

Arditi, Roger, and L.R. Ginzburg. 1989. "Coupling in predator-prey dynamics: ratio dependence." *Journal of Theoretical Biology* 139(3): 311–326.

Barton, K. 2013. MuMIn: Multi-model inference. R package version 1.9. 5.

British Columbia Parks. 1995. (Ministry of the Environment). *Sea Otter Management Plan, for Hakai Recreation Area*. [Unpublished report prepared by J.C. Watson] British Columbia Ministry of Water, Land and Air Protection, Parks and Protected Areas Branch.

Beddington, J.R. 1975. "Mutual interference between parasites or predators and its effect on searching efficiency." *Journal of Animal Ecology* 44(1): 331–340.
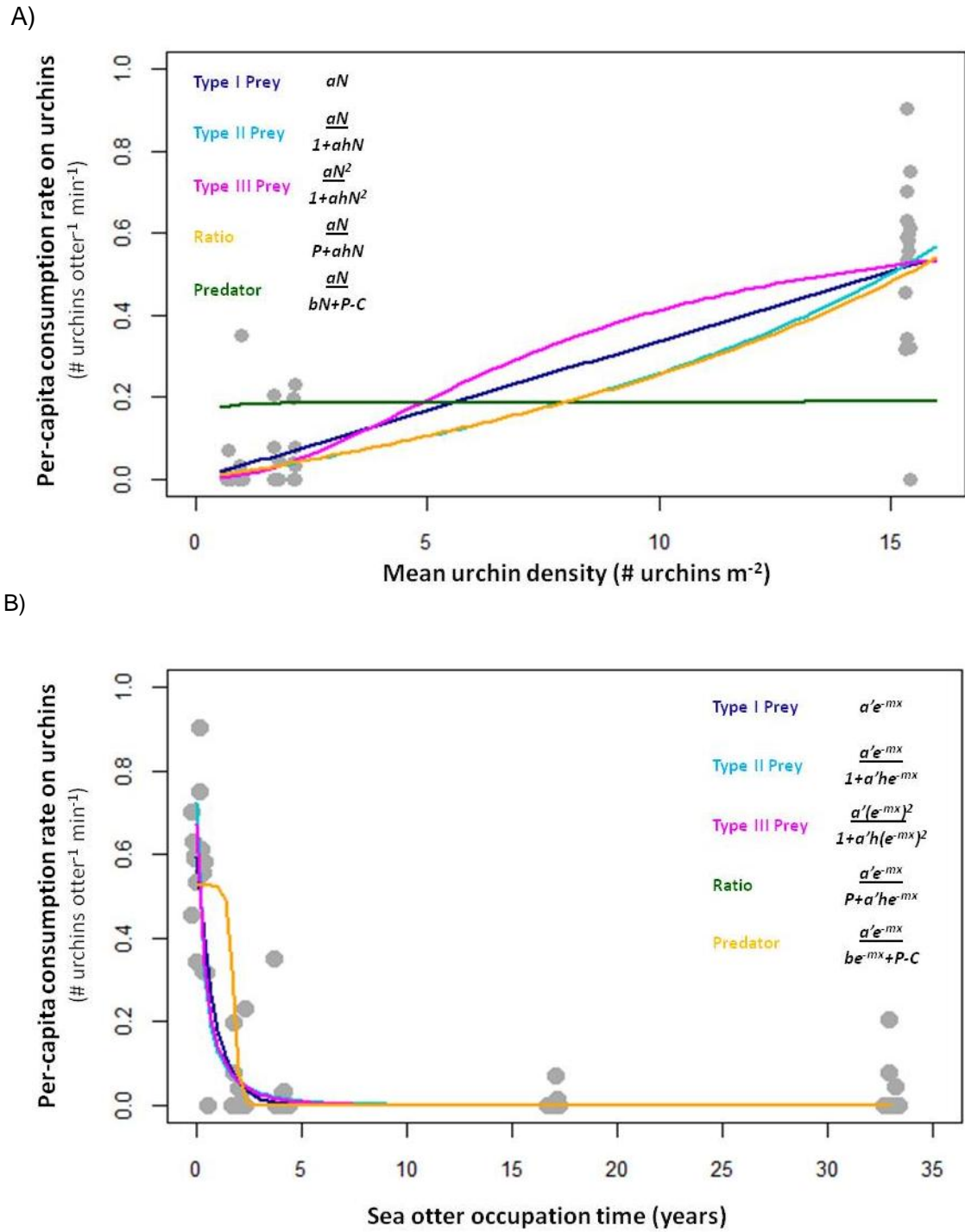
Bodkin, J.L., K.A. Kloecker, G.G. Esslinger, D.H. Monson, and J. D. DeGroot. 2001. Sea otter studies in Glacier Bay National Park and Preserve: Aerial surveys, foraging observations, and intertidal clam sampling: 2000 Annual Report. United States Geological Survey, Alaska Biological Science Center, Anchorage, AK, USA.

Booth, G.D., M.J. Niccolucci. and E.G. Schuster. 1994. "Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation." *Research Paper INT-470*. USA.

Breen, Paul A, Trudy A Carson, J Bristol Foster, and E Anne Stewart. 1982. "Changes in Subtidal Community Structure Associated with British Columbia Sea Otter Transplants." *Marine Ecology* 7(1): 13–20.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer.

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

Chadès, Iadine, Janelle M R Curtis, and Tara G Martin. 2012. "Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone." *Conservation Biology* 26(6): 1016–25.

COSEWIC. 2007. COSEWIC assessement and update status report on the sea otter Enhydra lutris in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 36 pp. URL, www.sararegistry.gc.ca/status/stauts_e.cfm

DeAngelis, D.L., R.A. Goldstein, and R.V. O'Neill. 1975. "A model for trophic interaction." *Ecology* 56(4):881–892.

Doroff, A.M. and J.L. Bodkin. 1994. "Sea otter foraging behavior and hydrocarbon levels in prey." In *Marine mammals and the Exxon Valdez*, edited by T. Loughlin, 193-208. San Diego, CA: Academic Press.

Elzhov, T.V., K.M. Mullen, A. Spiess, and B. Bolker. 2013. Minpack.lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds. R package version 1.1-8.

Estes, James A. 1996. Predators and ecosystem management. *Wildlife Society Bulletin* 390-396.

Estes, James A., and David O Duggins. 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., R.J. Jameson, and A.M. Johnson. 1981. Food selection and some foraging tactics of sea otters. In *Proceedings from the Worldwide Furbearer Conference Vol. 1*, edited by J. Chapman and D. Pursley. Frostburg, Maryland: University of Maryland Press.

Estes, James A., R.J. Jameson, and Elaine B. Rhode. 1982. "Activity and prey election in the sea otter: influence of population status on comminty structure." *The American Naturalist* 120(2): 242–258.

Estes, James A., and John F. Palmisano. 1974. "Sea otters: their role in structuring nearshore communities." *Science* 185(4156): 1058–1060.

Estes, James A., M.T. Tinker, T.M. Williams, and D.F. Doak. 1998. "Killer whale predation on sea otters linking oceanic and nearshore ecosystems." *Science* 473(282): 473–476.

Estes, James A., John Terborgh, Justin S. Brashares, Mary E. Power, Joel Berger, William J Bond, Stephen R. Carpenter, Timothy E. Essington, Robert D. Holt, Jeremy B.C. Jackson, Robert J. Marquis, Lauri Oksanen, Tarja Oksanen, Robert T. Paine, Ellen K. Pikitch, William J. Ripple, Stuart A. Sandin, Marten Scheffer, Thomas W. Schoener, Jonathan B. Shurin, Anthony R.E. Sinclair, Michael E. Soulé, Risto Virtanen, and David A. Wardle. 2011. "Trophic downgrading of planet Earth." *Science* 333(6040): 301–6.

Fisher, Jason T., Chris Pasztor, Amanda Wilson, John P. Volpe, and Bradley R. Anholt. 2014. "Recolonizing sea otters spatially segregate from pinnipeds on the Canadian Pacific coastline: The implications of segregation for species conservation." *Biological Conservation* 177: 148–155.

DFO (Fisheries and Oceans Canada). 2012. *Integrated Fisheries Management Plan red sea urchin: August 1, 2012 to July 31, 2013*. URL: http://www.pac.dfo-mpo.gc.ca/fm-gp/mplans/2012/red_urchin-oursin_rouge-2012-eng.pdf

Frank, Kenneth T., Brian Petrie, Jae S. Choi, and William C. Leggett. 2005. "Trophic cascades in a formerly cod-dominated ecosystem." *Science* 308(5728): 1621–3.

Garshelis, A., A.M. Johnson, and J.A. Garshelis. 1984. "Social organization of sea otters in Prince William Sound, Alaska." *Canadian Journal of Zoology* 62(12): 2648–2658.

Garshelis, David L. 1983. "Ecology of sea otters in Prince William Sound, Alaska." PhD, University of Minnesota.

Gelman, Andrew. 2008. "Scaling regression inputs by dividing by two standard deviations." *Statistics in Medicine* 27(15): 2865–2873.

Harrold, C., and J. S. Pearse. 1987. The ecological role of echinoderms in kelp forests. In *Echinoderm studies* edited by J. M. Lawrence, 137–233 Rotterdam, The Netherlands: A.A. Balkema.

Holling, C.S. 1959. "The components of predation as revealed by a study of small-mammal predation of the European pine sawfly." *Canadian Entomologist* 91(05): 293–320.

Kenyon, K.W. 1969. "The sea otter in the eastern Pacific ocean." *North American Fauna* (68): 1–352.

Kenyon, K.W. 1981. "Sea otter, Enhydra lutris." In *Handbook of marine mammals, volume 1: the walrus, sea lions, fur seals and sea otter, edited by* S.H. Ridgway and R.J. Harrison, 209-224. London: Academic Press Inc.

Kvitek, Rikk G., C. Edward Bowlby, and Michelle M. Staedler. 1993. "Diet and foraging behavior of sea otters in southeast Alaska." *Marine Mammal Science* 9(2): 168–181.

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

Laidre, Kristin L., and Ronald J. Jameson. 2006. "Foraging patterns and prey selection in an increasing and expanding sea otter population." *Journal of Mammalogy* 87(4): 799–807.

Larson, Sean D., Zachary N. Hoyt, Ginny L. Eckert, and Verena A. Gill. 2013. "Impacts of sea otter (Enhydra lutris) predation on commercially important sea cucumbers (Parastichopus californicus) in southeast Alaska." *Canadian Journal of Fisheries and Aquatic Science* 70(10): 1498–1507.

Lima, S.L., and M. Dill. 1990. "Behavioral decisions made under the risk of predation: a review and prospectus." *Canadian Journal of Zoology* 68(4): 619–640.

Markel, R.W. 2011. "Rockfish recruitment and trophic dynamics on the west coast of Vancouver Island: fishing, ocean climate, and sea otters." PhD, Department of Zoology, Vancouver, B.C: University of British Columbia.

Murdoch, William W. 1969. "Switching in general predators: experiments on predator specificity and stability of prey populations." *Ecological Monographs* 39(4): 335–354.

Nichol, L.M. 2007. "Recovery potential assessment for sea otters (Enhydra lutris) in Canada." *Canadian Science Advisory Secretariat Research - Document 2002/034 - Fisheries and Oceans Canada* 3848.

Nichol, L.M., M.D. Boogaards, and R. Abernethy. 2009. "Recent trends in the abundance and distribution of sea otters (Enhydra lutris) in British Columbia." *Canadian Science Advisory Secretariat Research Document 2009/016 Fisheries and Oceans Canada, Nanaimo, British Columbia* 3848.

Ostfeld, Richard S. 1982. "Foraging strategies and prey switching in the California sea otter." *Oecologia* 53(2): 170–178.

Paine, Robert T. 1969. "The pisaster-tegula Interaction: prey patches, predator food preference, and intertidal community structure." *Ecology* 50(6): 950–961.

Paine, Robert T.. 1980. "Food webs: linkages, interaction strength and community infrastructure." *Journal of Animal Ecology* 49(3): 666–685.

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

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for statistical Computing. Vienna, Austria.

Reisewitz, Shauna E., James A. Estes, and Charles A. Simenstad. 2006. "Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago." *Oecologia* 146(4): 623–631.

Riedman, M.L., and James A. Estes. 1990. "The sea otter (Enhydra lutris): behavior, ecology, and natural history." *Biological report (USA). no. 90 (14)*.

Ripple, William J., James A. Estes, Robert L. Beschta, Christopher C. Wilmers, Euan G. Ritchie, Mark Hebblewhite, Joel Berger, Bodil Elmhagen, Mike Letnic, Michael P. Nelson, Oswald J. Schmitz, Douglas W. Smith, Arian D. Wallach, and Aaron J. Wirsing. 2014. "Status and ecological effects of the world's largest carnivores." *Science* 343(6167): 1241484.

Salomon, Anne K., Nick M. Tanape Sr, and Henry P. Huntington. 2007. "Serial depletion of marine invertebrates leads to the decline of a strongly interacting grazer." *Ecological Applications* 17(6): 1752–1770.

Sanford, Eric. 1999. "Regulation of keystone predation by small changes in ocean temperature." *Science* 2095(283): 10–13.

Schoener, Thomas W. 1971. "Theory of Feeding Strategies." *Annual Review of Ecology and Systematics* 2: 369–404.

Sea Otter Recovery Team. 2007. Recovery Strategy for the Sea Otter (*Enhydra lutris*) in Canada. *Species at Risk Act* Recovery Strategy Series. Fisheries and Oceans Canada, Vancouver. vii + 56 pp.

Shannon, C.E., W. Weaver. 1949. T*he mathematical theory of communication*. Urbana, Illinois: University of Illinois Press.

Shears, Nick T., Russell C. Babcock, Anne K. Salomon, and Ecological Applications. 2008. "Context-dependent effects of fishing: variation in trophic cascades across environmental gradients." *Ecological Applications* 18(8): 1860–1873.

Singh, Gerald G., Russell W. Markel, Rebecca G. Martone, Anne K. Salomon, Christopher D.G. Harley, and Kai M.A. Chan. 2013. "Sea otters homogenize mussel beds and reduce habitat provisioning in a rocky intertidal ecosystem." *PloS one* 8(5): e65435.

Solomon, M.E. 1949. "The natural control of animal population." J*ournal of Animal Ecology* 18(1):1-35.

Soulé, Michael E., James A. Estes, Brian Miller, and Douglas L. Honnold. 2005. "Strongly Interacting Species : Conservation Policy , Management , and Ethics." *BioScience* 55(2): 168–176.

Stephens, D.W., and J.R. Krebs. 1986. *Foraging theory.* Princeton, NJ: Princeton University Press.

Szpak, Paul, Trevor J. Orchard, Anne K. Salomon, and Darren R. Gröcke. 2013. "Regional ecological variability and impact of the maritime fur trade on nearshore ecosystems in southern Haida Gwaii (British Columbia, Canada): evidence from stable isotope analysis of rockfish Sebastes spp.) bone collagen." *Archaeological and Anthropological Sciences* 5(2): 159–182.

Tegner, M., and L.A. Levin. 1981. "Spiny lobster and sea urchins: analysis of a predator-prey interaction." Journal of Experimental Marine Biology and Ecology 73(2): 125-150.

Tinker, M. Tim, Gena Bentall, and James A. Estes. 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(2): 560–565.

Tinker, M. T. 2004. Sources or variation in the foraging and demography of the sea otter, *Enhydra lutris.* PhD, University of California Santa Cruz, Santa Cruz, CA.

VanBlaricom, G.R. 1988. Effects of foraging by sea otters on mussel-dominated intertidal communities. In *The community ecology of sea otters,* edited by G.R. VanBlaricom and James A. Estes*,* 48-91. Springer Berlin Heidelberg.

Venables, W.N., and B.D. Ripley. 2002. *Statistics Complements to Modern Applied Statistics with S-Plus.* 4th ed. New York: Springer.

Vucetich, J.A., R.O. Peterson, and C.L. Schaefer. 2002. "The effect of prey and predator densities on wolf predation." *Ecology* 83(11): 3003–3013.

Watson, J.C., and James A. Estes. 2011. "Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada." *Ecological Society of America* 81(2): 215–239.

Watson, J.C., and T.G. Smith. 1996. "The effects of sea otters on invertebrate fisheries in British Columbia: a review." *Canadian Technical Report of Fisheries and Aquatic Sciences* 2089: 262–303.

Watt, Jon, Donald B. Siniff, and James A. Estes. 2000. "Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska." *Oecologia* 124(2): 289–298.

WDCS Shorewatch. 2013. Beafort Sea States. URL, http://www.wdcs.org/submissions_bin/WDCS_Shorewatch_Seastate.pdf

Wirsing, Aaron J., Michael R. Heithaus, Alejandro Frid, and Lawrence M. Dill. 2008. "Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals." *Marine Mammal Science* 24(1): 1–15.

Appendix A.

Supplementary Tables

Table S1.   Prey size categories estimated in the field relative to a sea otter's paw of average width 5.2cm (from Bodkin et al. 2010). Each prey that was 1-4 times the size of a sea otter's paw was further broken down into thirds resulting in 12 size classes.

Size class Estimated in Field	Max length (cm)
1- 1a	1.7
2- 1b	3.5
3- 1c	5.2
4- 2a	6.9
5- 2b	8.7
6- 2c	10.4
7- 3a	12.1
8- 3b	13.9
9- 3c	15.6
10- 4a	17.3
11- 4b	19.1
12- 4c	20.8

Table S2.   Prey items captured by northern sea otters (*Enhydra lutris kenyoni*) on successful foraging dives along the central coast of British Columbia, Canada.

Prey Group	Common name	Latin name
Urchin	Red urchin	*Mesocentrotus franciscanus*
	Green urchin	*M. droebachiensis*
	Purple urchin	*M. purpuratus*
Abalone	Northern abalone	*Haliotus kamtschatkana*
Clam	Geoduck clam	*Panopea abrupta*
	Butter clam	*Saxidomus gigantea*
	Horse clam	*Tresus* spp.
	Rock scallop	*Crassadoma gigantea*
	Unidentified clams	
Cancer crab	Dungeness crab	*Cancer magister*
	Red rock crab	*Cancer productus*
Kelp crab	Northern kelp crab	*Pugettia productus*
Shore crab	Shore crabs	*Hemigrapsus* spp.
Chiton	Gumboot chiton	*Cryptochiton stelleri*
Mussel	California mussel	*Mytilus californianus*
Sea Cucumber	California sea cucumber	*Parastichopus californicus*
	Burrowing sea cucumber	*Cucumaria miniata*
	Unidentified sea cucumber	
Sea star	Ochre sea star	*Pisaster ochraceus*
Snail	Unidentified snails	Class: Gastropoda
Octopus	Unidentified octopus species	Family: Octopodidae
Unidentified	Unidentified prey species	

Table S3.   Northern sea otter (*Enhydra lutris kenyoni*) densities (per 0.5 km^2) observed at study sites on the central coast of British Columbia, Canada, July 2013. Given variation in the geography of the region, survey areas varied between ~0.3-1 km^2.

Site	Date	Estimated Area Surveyed (km^2)	Max # Otters Observed	Otter Density per 0.5 km^2
Calvert	Jul-20	0.67	50	19
Calvert	Jul-21	0.67	50	19
Breadner	Jul-10	0.33	3	2
Breadner	Jul-11	1.01	16	4
Breadner	Jul-12	1.01	9	2
Breadner	Jul-29	1.01	9	2
Simonds	Jul-27	2.01	15	2
Simonds	Jul-28	1.01	95	24
Simonds	Jul-29	1.01	95	24
McMullins	Jul-15	0.50	10	5
McMullins	Jul-16	0.50	30	15
McMullins	Jul-17	0.50	20	10
Goose	Jul-22	1.01	2	0
Goose	Jul-23	1.01	3	1
Goose	Jul-24	1.01	4	1
Goose	Jul-25	1.01	5	1

Table S4.   Correlation matrices for potential predictors of northern sea otter (*Enhydra lutris kenyoni*) per-capita consumption rate on sea urchins at the otter-level based on (A) Pearson's correlation coefficient (*r*) and (B) Spearman's rank correlation coefficient (*p*). Predictors were only included in a model together if *p* or *r* ≤|0.5| (Booth et al. 1994, Zuur et al. 2009). Highlighted values are those where *r* or *p*>|0.5|.

A. Pearson's

	Occupation Time	Otter density	Urchin density	Tidal height	Sea state
Occupation time	1	-0.54	-0.44	0.20	0.14
Otter density	-0.54	1	0.49	-0.13	-0.47
Urchin density	-0.44	0.49	1	0.29	-0.28
Tidal height	0.20	-0.13	0.29	1	-0.03
Sea state	0.14	-0.47	-0.28	-0.03	1

B. Spearman's

	Occupation Time	Otter density	Urchin density	Tidal height	Sea state
Occupation time	1	-0.60	-0.66	0.04	0.15
Otter density	-0.60	1	0.05	-0.19	-0.45
Urchin density	-0.66	0.05	1	0.28	-0.15
Tidal height	0.04	-0.19	0.28	1	0.03
Sea state	0.15	-0.45	-0.15	0.03	1

Table S5. Parameter estimates for alternative mechanistic models of northern sea otter (*Enhydra lutris kenyoni*) per-capita consumption rates on sea urchins as a function of (A) sea urchin density and (B) sea otter occupation time assuming an exponential decline of sea urchins with increasing occupation time (Eq. 7-12).

Models		Parameter	Estimate	Std. Error
A)				
Eq. 1	aN	a	0.03	0
Eq. 2	$\underline{aN}$	a	0.02	0.01
	1+ahN	h	-1.74	2.15
Eq. 3	$\underline{aN^2}$	a	0.01	0.01
	$1+ahN^2$	h	1.52	0.26
Eq. 4	$\underline{aN}$	a	1.09	0.84
	P+ahN	h	3.88	1.13
Eq. 5	$\underline{aN}$	a	3.67	74.15
	bN+P-C	b	-7.36	128.52
		C	-201.73	4146.6
B)				
Eq. 7	$a'e^{-mx}$	a	0.59	0.04
		m	1.20	0.32
Eq. 8	$\underline{a'e^{-mx}}$	a	0.09	0.44
	$1+a'he^{-mx}$	m	0.46	11.39
		h	-9.71	55.47
Eq. 9	$\underline{a'(e^{-mx})^2}$	a	0.16	0.75
	$1+a'h(e^{-mx})^2$	m	0.33	0.79
		h	-4.68	29.47
Eq.10	$\underline{a'e^{-mx}}$	a	7.62E+04	4.17E+09
	$P+a'he^{-mx}$	m	6.37	2.73E+04
		h	1.90	24.5
Eq.11	$\underline{a'e^{-mx}}$	a	2.43	21.98
	$be^{-mx}+P-C$	m	0.12	1.42
		b	-220.72	1998.08
		C	-203.74	1985.97

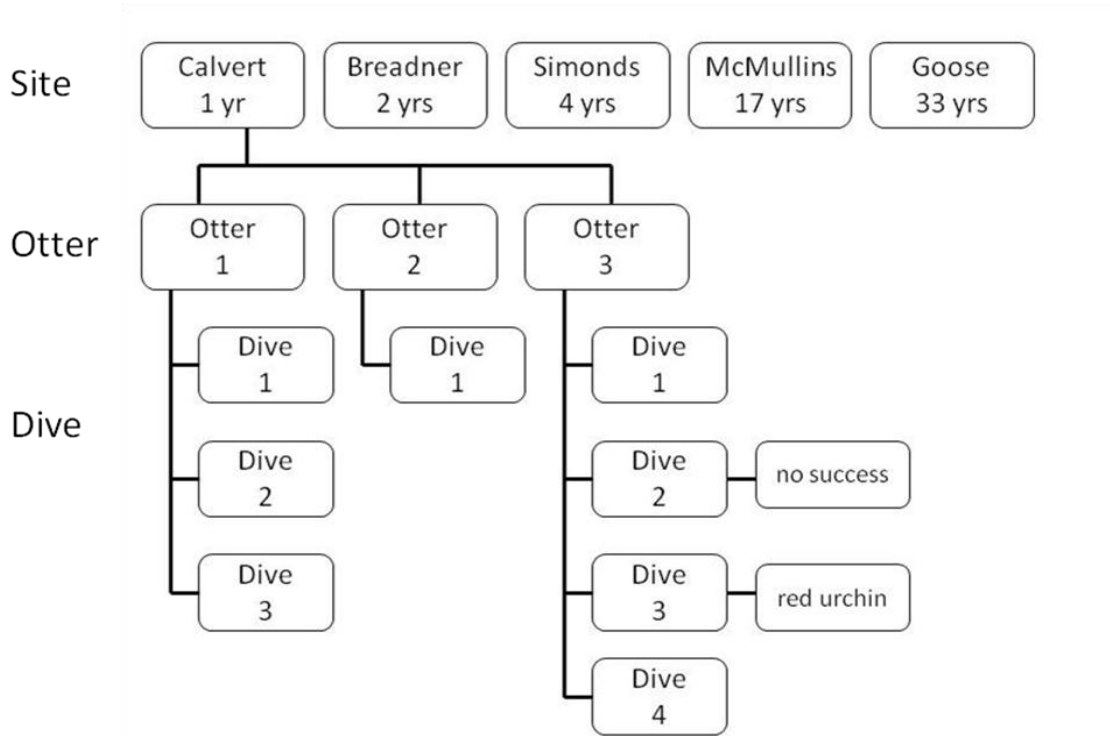# Appendix B.

Supplementary Figures

Figure S1.   Hierarchical structure of northern sea otter (*Enhydra lutris kenyoni)*
foraging data collected on the central coast of British Columbia, Canada
in July 2013. Multiple foraging dives were nested within a focal sea otter,
representing a foraging 'bout' (Calkins 1978). Multiple sea otters were
nested within five study sites, which varied across a gradient of sea otter
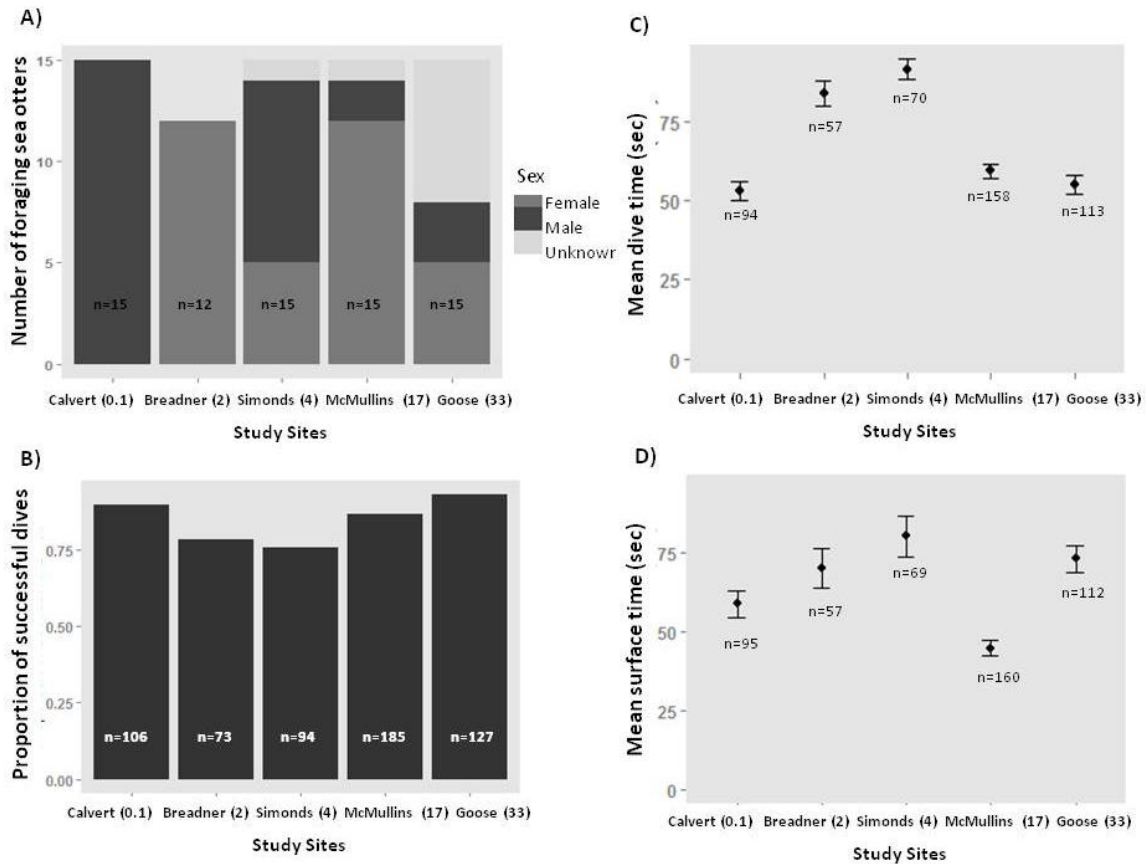occupation time. Mock dive data examples shown here.

Figure S2.   Summary data on northern sea otter (*Enhydra lutris kenyoni*) sex and
dives across sites varying in sea otter occupation time (years in brackets)
A) number of foraging males, females and otters of unknown sex
observed at each site (n=total # otters observed); B) proportion of dives
resulting in successful prey capture across all dives of known outcome at
each site; C) mean dive intervals +/- SE calculated across all successful
dives at a site; and D) mean surface intervals +/- SE calculated across all
surfacings after successful dives at a site. B, C, D, n=total # dives
observed.