Title
Effects Of Sea Otter Colonization On Soft-Sediment Intertidal Prey Assemblages In Glacier Bay, Alaska

Author
Weitzman, Benjamin Phillip

Publication Date
2013

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

EFFECTS OF SEA OTTER COLONIZATION ON SOFT-SEDIMENT INTERTIDAL PREY ASSEMBLAGES IN GLACIER BAY, ALASKA

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF ARTS

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Benjamin P. Weitzman

March 2013

The Thesis of Benjamin Weitzman
is approved:

Professor Laurel Fox, chair

Professor Pete Raimondi

Professor M. Tim Tinker

Professor James Estes

James L. Bodkin, USGS

Tyrus Miller
Dean of Graduate Studies

Table of Contents

INDEX OF TABLES & FIGURES

Effects of sea otter colonization on soft-sediment intertidal prey assemblages in Glacier Bay, Alaska

Benjamin P. Weitzman

Abstract

The influence of sea otters (*Enhydra lutris*) on nearshore marine communities has been widely studied in kelp-forest ecosystems, however less is known about their impacts in other systems. In Southeast Alaska, the recolonization by sea otters into areas where they have been long absent (~100 years), provides a natural experiment with which to examine the response of soft-substrate intertidal prey communities to the return of a top predator. Sea otter abundance in Glacier Bay, Alaska increased from zero in 1993 to >8,500 individuals in 2012. Their aggregated diet from intertidal foraging bouts consisted predominantly of clam (56%), horse mussels (15%) and urchins (18%) and was found to diversify over space and time as sea otters colonized and persisted. To assess intertidal community response to sea otters 45 intertidal sites were sampled prior to, or concurrent with sea otter colonization, and again up to 12 years later. Using GIS and aerial surveys I estimated the cumulative density of the sea otters at each site. At a sea otter density of roughly 6-otters/km^2 clam populations were found to have 50% probability of population decline, and preferred prey species such as *Saxidomus giganteus* were found to likely decline at sea otter densities <2-otters/km^2. At sites where sea otters were at low densities or absent, clam biomass generally remained unchanged or increased. Energy recovery rates decreased significantly with cumulative otter density from roughly 20 kcal/min at 0.36 otters/km^2 to 9 kcal/min at 4.54 otters/km^2, requiring individual otters to increase the amount of effort they expend foraging. The effect of sea otters on intertidal clam populations in soft-sediment was consistent with findings in other habitats, where reduced densities and sizes of prey were documented. This study established the occurrence of top-down structuring in soft-sediment systems over a multi-decadal time scale.

Acknowledgements

I would like to thank everyone who ever worked on this project for their countless efforts and hard work over the years:

Jim Bodkin, George Esslinger, Kim Kloecker, Tim Tinker, Jim Estes, Dan Monson, Brenda Ballachey, Heather Coletti, Greg Snedgen, Ken Vicknair, Joe Tomoleoni, Nicole LaRoche, Gena Bentall, Jessica Fuji, Michelle Staedler, Zac Hoyt, Eric Wood, Heidi Herter, Corey Oldham, Casey Clark, Alexis Walker, Michael Weitzman, Marc Blouin, Stephen Jewett, Julie Stewart, Calum Tinker, Lee Bodkin, Mike Lee, Jennifer DeGroot, Mike Kenner, Brian Hatfield, Dr. Mike Murray, Janet Neilsen, Noel Farvaag, Jim de la Bruere, and numerous Park Service Rangers & Staff!

Sea otter studies in Glacier Bay National Park have been a historically collaborative effort between the U.S. Geological Survey and National Park Service, I thank the NPS for their support of in this project of its duration and thank the USGS-Alaska Science Center for sponsoring me to conduct the terminus of this research endeavor.

I want to especially thank my co-advisory team: Tim Tinker, Jim Estes, and Jim Bodkin, as well as my other committee members: Pete Raimondi & Laurel Fox.

This work would not have been possible without the dedication put forth by Jim Bodkin and his team from USGS who initiated sea otter research studies in Glacier Bay in the early 1990's and made it possible for me to present this work today. To Jim, Jim, Tim, George & Kim, thanks for everything, you have been instrumental as researchers, colleagues, and mentors over the years.

Introduction: The Return of a Top Predator

Effective resource management requires not only information on population dynamics but also an understanding of the underlying interactions within an ecosystem. Trophic interactions, particularly between top predators and their prey may greatly alter the state and function of a system when a shift in the distribution and/or abundance of apex consumers occurs (Estes et al. 1998, Estes *et al.* 2011). The direct effects of a single high-level, or "keystone" species (Paine 1966) can greatly influence species composition and community structure (Connell 1961, Power et al. 1996, Terborgh and Estes 2010). Most studies have documented the effects of the presence or absence of a keystone species in a single ecosystem, however it is not well understood whether that same species will have a keystone effect across multiple ecosystems (Kvitek et al. 1992, Menge et al. 1994, Estes and Duggins 1995, Vicknair and Estes 2012).

The northeast Pacific marine environment is highly diverse and the status and state of a particular system can often be influenced by the presence or absence of a keystone predator (Paine 1974, Duggins 1980, Paine 1980) such as the sea otter (*Enhydra lutris*) (Estes *et al.* 1978). Sea otters and kelp forests provide one of the early and best documented examples of this process (Estes and Palmisano 1974). Sea otters are capable of exerting substantial effects on community structure and dynamics by virtue of their large energetic requirements – consuming 25% of their body weight in food per day (Morrison *et al.* 1974, Williams and Yeates 2004, Yeates et al. 2007) consisting primarily of macro-invertebrate prey (Estes et al. 1981).

The most well known effect of sea otter predation is the trophic cascade extending from sea otters to herbivorous sea urchins to kelps and fleshy macroalgae. This trophic cascade can cause a phase shift between kelp-dominated and deforested urchin-dominated ecosystem states in hard-substrate habitats (Estes and Palmisano 1974). When sea otters are rare or absent, urchins can intensely graze down macroalgae, creating a system known as an urchin barren, characterized by large, abundant urchins and sparse algal cover. Where sea otters are abundant they directly reduce urchin biomass and grazing intensity, allowing macroalgae to flourish resulting in a kelp dominated system (Estes and Duggins 1995). Despite this paradigm, the impact of sea otters on community structure and productivity varies considerably across sea otter dominated and sea otter free phase-states in rocky-bottomed ecosystems (Steneck et al. 2002, Estes et al. 2010).

While the effects of sea otter predation are well documented in hard-substrate systems, few studies have rigorously examined the role of this predator in soft and mixed-substrate environments (Kvitek et al. 1992, Jolly 1997, Maldini et al. 2008, Gilkinson et al. 2011, Wolt et al. 2012), leaving many questions about their structuring effects in these ecosystems. Sea otters forage from the submerged intertidal to depths over 100m, but dives seldom exceed more than 10-40m in depth (Bodkin et al. 2004b) and intertidal foraging may account for up to roughly one-third of feeding bouts in some areas (Bodkin et al. 2012). In mixed or unconsolidated substrate habitats (hereafter referred to as soft-sediments), sea otter diet is dominated by filter feeding infaunal invertebrates including bivalve mollusks (Estes et al. 1981, Kvitek et al. 1989, Bodkin et al. 2007a). These resources are often very patchy in nature and rarely occur uniformly or continuously throughout the environment (Zajac et al. 1998). In contrast, sea otter diets in hard-bottom systems dominated by macroalgae primarily consist of herbivorous epibenthic invertebrates (Calkins 1978, Estes et al. 1982). The otters' dependence on two functionally different prey guilds between these systems may result in very different dynamics.

Previous work in soft-sediment ecosystems show the response of prey populations to sea otter predation in these environments is similar to that reported in hard-substrate systems, with significant declines in abundance and mean size (Miller et al. 1975, Kvitek et al. 1992, Jolly 1997). Compared to the acute response in hard substrate systems, these trends appear to take longer to manifest in soft-sediment communities, often requiring a decade or more before the effect becomes apparent (Kvitek et al. 1992). However to date, the hypothesis that prey responses will be similar between hard-bottom, rocky-reef and mixed or unconsolidated substrate habitat has only been tested in subtidal environments. At higher latitudes in the North Pacific, the intertidal environment is vast and can be incredibly productive, with physical energy generated by large tidal swings (>8m), and may support dense invertebrate resources that are utilized by sea otters as well as a variety of other marine and terrestrial consumers, including humans (Miller et al. 1975, Bodkin et al. 2012).

There has yet to be a thorough investigation of the generality of sea otter effects in soft-sediment communities, or indeed what these effects may be for intertidal communities. The fundamental difference in community structure and trophic organization between rocky substrate and unconsolidated environments highlights the importance of understanding sea otter effects in intertidal soft-sediment habitats. Furthermore, this information is vital to the appropriate management of resources in soft or mixed-substrate habitat, and in understanding the role of a keystone predator across different habitats.

A Natural Experiment: Sea Otters in Glacier Bay

Sea otters narrowly escaped complete extirpation throughout their range from the Pacific maritime fur trade (Kenyon 1969). Since they were afforded protection under the International Fur Seal Treaty in 1911, otters have been recolonizing their historic range in the Pacific through natural expansion and translocations (Jameson et al. 1982). Between 1966 and 1969, 403 sea otters were translocated from Prince William Sound and Amchitka Island to six locations in Southeast Alaska, one of which was the outer coast of Cross Sound between Cape Spencer and Yakobi Island (Burris and Mcknight 1973, Esslinger and Bodkin 2009). From this founding colony of 55 animals, sea otters began to reoccupy the waters of Cross Sound and Icy Strait (Figure 1).

By the mid 1990s, it was apparent that the expanding sea otter population in Cross Sound would soon spread into the waters of Glacier Bay National Park & Preserve. In 1993, researchers and resource managers with the US Geological Survey and National Park Service recognized the opportunity to document the changes that might occur due to the sea otter colonization event. In addition to providing resource managers with information on potential effects sea otters might have in Glacier Bay, it also presented the chance to ask ecologically meaningful questions about sea otters in soft and mixed-substrate habitat. Bodkin et al. (2001) determined that three kinds of data would be required to properly assess changes incurred by sea otter colonization in Glacier Bay: changes in the abundance and distribution of sea otters; information on the sea otter's diet and foraging behavior and information on the structure and function of the coastal marine communities. In establishing a study design, it was recognized that two distinct approaches have proven effective in efforts to document changes caused by sea otters on prey communities, (Estes and Van Blaricom 1988, Kvitek et al. 1992, Estes and Duggins 1995). One approach is to contrast prey communities at particular sites over time, before and after their colonization by sea otters; the other approach is based on spatial contrasts between areas with and without sea otters (Bodkin et al. 2007a). Both of these approaches were used in the Glacier Bay study (Bodkin et al. 2001).

Beginning in 1993, aerial census surveys were conducted on an annual basis to assess sea otter abundance and distribution within Glacier Bay. Foraging observations were made from 1993-2011 as sea otters expanded their range throughout the Bay. Finally, the abundance, biomass, and population structure of intertidal prey species were characterized at particular sites before, during and after they were colonized by sea otters, and between areas with and without sea otters. I used this information to address the following questions:

Q1) What were the effects of sea otters on the available biomass of intertidal prey species?

> In areas that have been colonized by sea otters, I expected there to be a significant reduction in the biomass of prey species, with the magnitude of this reduction at any particular site related to both time and the number of otters present.

Q2) How did sea otters influence the size distributions of intertidal prey species in a soft-sediment habitat?

> I expected the mean size and skewness towards larger individuals to be reduced in areas utilized by sea otters.

Q3) How did sea otter diet vary through space and over time in relation to available resources in the intertidal zone?

> I expected that sea otters would consume a high proportion of infaunal bivalves that would result in a reduction of the mean size of consumed bivalves.

Methods

Study Area

Glacier Bay National Park and Preserve (58°24’ N; 135°59’ W) is located in Southeast Alaska, approximately 90 km west of the city of Juneau. The dynamic landscape was declared a national monument in 1925 after Dr. William S. Cooper’s seminal work on successional changes in terrestrial ecosystems (Cooper 1923). Over a century before Cooper, when Captain George Vancouver sailed through Icy Strait in 1794, Glacier Bay was buried beneath a sheet of ice that extended more than 160 km north to the St. Elias range. Since then the glacier has retreated rapidly, more than 50 km by 1879 and more than 95 km by 1916 (Cooper 1923, Larsen et al. 2004).

Glacier Bay was an ideal natural laboratory to evaluate the effects of sea otters in a soft-sediment ecosystem. There were few visitors to most of the park each year, and thus little direct anthropogenic disturbance in the environment. Since many of the large glaciers that carved Glacier Bay have retreated, invertebrate populations have colonized and existed in the absence of sea otters for over 200 years in some areas. Without sea otters in the system, a lack of "top-down" predatory regulation has allowed prey species to flourish; reaching sizes that would not likely be present when sea otters are abundant (Estes et al. 1981).

Overall, the substratum of Glacier Bay was unconsolidated and spatially heterogeneous, varying from rocky boulder points to mud bottomed lagoons and long sandy shoals. Varying degrees of suitable infaunal clam habitat exist, even at smaller spatial scales (Wilson 1990, Thrush et al. 1994). This patchiness may be exacerbated by glacially-derived dynamics in the upper Bay (Etherington et al. 2007) resulting in significant environmental and biological variability throughout Glacier Bay.

Aerial Surveys & GIS

Aerial surveys provide a measure of the treatment effect, the spatially explicit natural colonization of sea otters in Glacier Bay through time. To describe the pattern of sea otter colonization in Glacier Bay, two types of surveys were conducted, one to determine distribution and the other to estimate abundance. Distribution surveys were flown parallel to the coastline at an altitude of 152 m, observers scanned out to the 100m bathymetric contour and counted all sea otters observed (Bodkin et al. 2007a). Beginning in 1993, the distribution surveys were conducted annually, excluding the years 1994, 2007, and 2008. In 2005 and 2006, monthly distribution surveys were conducted to assess seasonal changes, and while small scale movements were found to occur, the overall pattern of distribution remained constant (Beck 2010). Abundance surveys were flown at an altitude of 91 m, along predetermined 400 m strip transects throughout Glacier Bay, and included correction factors for sightability of otters in the estimate; only otters on transect were counted [see Bodkin and Udevitz (1999) for details]. Abundance surveys were flown in 1999-2004, 2006, and 2012, with 3-5 replicates flown per year to acquire a more accurate estimate of the sea otter population in Glacier Bay. Despite differences between counts, the trend in population growth is similar for the survey methods, thus I used the distribution data for my spatial analysis, as it was more complete time-series.

To investigate the level of impact at a given site in Glacier Bay, I used the aerial distribution data to create a continuous smoothed 2-D surface representing the cumulative sea otter density. Each aerial survey yielded spatially referenced data points that were analyzed in a GIS (ESRI ArcDesktop10). Using a kernel density estimator (KDE) tool, I created a density map in raster format with cell size of 25 m^2, smoothed across all points within the survey area. A kernel-smoothing window of 5 km was used for this model as this is the appropriate distance sea otters travel between resting and foraging locations (Beck 2010). Once a density surface was generated for each survey year, these were summed over years to establish a cumulative sea otter density through time. To establish the values of predicted otter impact at intertidal sites, I extracted the value of each raster cell for a corresponding intertidal site in each year of sampling. In this sense, I expected a site sampled in 1998, 2005, and 2010 to have an increasing level of sea otter effect at each time step if the treatment was continuously applied. Conversely, I expected extremely low to no otter presence at "control" sites. I also assigned the time period of occupation as the first year in which sea otters appeared to be within 5 km of a site. This method generates two important metrics – i) the length of time that sea otters were using resources at a site and, ii) the overall number of sea otters that were exploiting resources at a site. With these data, I monitored the response of intertidal prey populations as a function of increased sea otter impact (cumulative density and time of occupation) at control sites (beyond the sea otter range) and treatment sites (within the sea otter's range); before, during, and after the treatment was applied, effectively creating a before/after control/impact (BACI) design (Stewart-Oaten et al. 1986).

Foraging Observations

Foraging observations were made concurrent with sea otter colonization events and aerial surveys using a standardized observation protocol (Dean et al. 2002, Tinker et al. 2008). Briefly, dietary data observations of individual foraging sea otters were made using high-powered telescopes (Questar, Field Model 3.5) from shore or a stable vessel platform. A focal sea otter was observed for up to 20 sequential dives (defined as a feeding bout) and the date, site, start and end time, observer location, otter location, sex, reproductive status, and estimated age were recorded for each bout. For each dive, observers recorded dive time, surface interval, prey handling and consumption times, dive success, identification of prey to the lowest taxon, number of prey recovered, and estimated prey size (categorical, based on size relative to otter paw width). Sea otter locations were determined using a handheld GPS.

For all comparisons of foraging observations to prey community statistics, I limited analysis to bouts recorded from otters feeding intertidally, defined as being within the 10 m bathymetric contour. I determined this using observed sea otter locations superimposed over a bathymetric map of Glacier Bay in a GIS. Foraging bouts were further designated to blocks containing neighboring intertidal sites to account for the variability of diet composition within Glacier Bay (Bodkin et al. 2001) and to ensure that comparative analyses would be from similar areas. Foraging data were analyzed in a program designed to evaluate a complex foraging dataset, using a Monte Carlo based simulation approach to account for incomplete data records using a re-sampling algorithm, thereby accounting for various sources of uncertainty and potential sampling bias in estimating species-specific prey consumption rates. This approach has been previously described in analyses of similar sea otter foraging data sets (Dean et al. 2002, Tinker et al. 2008, Tinker et al. 2012). Algorithm output included estimates of diet composition (frequency distribution of prey types), feeding rates (mass/min), and energy recovery rates (energy gain in kcal/min), as well as uncertainty estimates of each. All foraging observations were categorized by location and time period of otter occupation – i.e., early (the first five years of occupation), mid (5-10 years of occupation), and late (10 years or more of occupation). Sea otter occupation was defined as the years since sea otters first began to forage within 5 km to an intertidal site.

The dietary analysis of sea otters within Glacier Bay is based on >6,759 successful feeding dives observed within the intertidal zone between 1993 and 2011. These data come from a total of >14,580 observations collected throughout Glacier Bay.

Intertidal Prey Site Selection & Sampling Chronology

Invertebrate prey communities were sampled intertidally following a sampling protocol established by Bodkin and Kloecker (1999). The intertidal sampling sites were randomly selected throughout Glacier Bay. Additional high density clam sites (hereafter referred to as PCH, "preferred clam habitat") were later added to reflect areas with higher resource densities (Bodkin et al. 2001). To select random intertidal monitoring sites, this study utilized the results of the aerial portion of the Glacier Bay Inventory and Monitoring Protocol (Irvine 1998). The coastline of Glacier Bay was split into 5,545 - 200 m segments, from which every 23rd section was selected if it met the criteria for a soft-sediment clam site, until 48 randomly selected sites were identified (Bodkin and Kloecker 1999). Because random selection resulted in very few sites with high clam densities, twelve PCH sites were established to augment the randomly selected sites. PCH sites were identified based on presence of clam siphons and squirts at low tide, along with obvious shell litter deposition (Bodkin et al. 2001).

Of the 48 random and 12 PCH sites initially sampled, 45 were subsequently resampled at least twice over the course of sea otter colonization (1998-2011). Fifteen random sites were excluded from analysis due to Park-induced access restrictions during the post-treatment sampling, or because of concerns that resampling would have other negative impacts on the site. Of the 45 resampled sites, eighteen were excluded from the analysis because they lacked prey species of clams at any sampling event and were thus assumed to be unsuitable habitat for clams (Table 2) (Zuur et al. 2009).

To ensure that sites were resampled at the same location, a handheld GPS was used to navigate to the selected site coordinates (accuracy ≤±24m). A 200 m transect was positioned from the start point horizontally along the beach at 0 MLLW tide. Using a randomly selected starting location on the transect for each sampling event, ten 0.25 m^2 quadrats were placed 20 m apart along the transect and excavated to 25 cm depth (or deeper if necessary) to extract all clams. Prior to and during excavation the primary and secondary substrate types were characterized using the Wentworth Scale to determine sediment grain size (Bodkin and Kloecker 1999). Unearthed sediment was then sieved through 10mm mesh sieve. All clams recovered were identified to the lowest possible taxon, counted, and measured to the nearest millimeter using dial calipers. Urchins were also collected from the quadrat prior to excavation, counted, and their test diameters measured.

All 45 intertidal sites were first sampled between 1998 and 2000, prior to or near the initial colonization of sea otters, and again in 2010 and 2011, after ten years or more of occupation, and some of these sites were opportunistically resampled during the interim to examine natural variation. Sampling events, together with the status of cumulative sea otter density at each point of sampling are provided in Table 2.

Intertidal Prey Community Analysis

Intertidal sites were compared using community level statistics on prey populations as they varied with cumulative sea otter density and time of occupation. I assessed prey assemblage composition and calculated species diversity at sites using the Shannon Wiener Index (H'). I determined H' and H_{max}, the maximum possible diversity in the observed community when all species are known, and compared sites before and after sea otter colonization. The sites were categorized as controls (not colonized over the course of study), and treatment (where sea otters became established). I further categorized the treatment sites into three groups (low, medium, or high sea otter density; see table 2 for grouping level definitions). I compared the average biomass per quadrat (grams wet weight [gwwt.] /$0.25m^2$) and the average maximum length or diameter (mm) of common prey species using two-way ANCOVA before and after sea otter colonization at control and treatment sites, with substrate and time since deglaciation as covariates. I compared mean size and size frequency distributions of prey species and used skewness and kurtosis to evaluate the change in shape of distributions.

Analyzing data collected over the course of study as a continuous time-series allowed me to assess the functional relationship between sea otters and intertidal prey assemblages while accounting for natural variation due to time since deglaciation, distance to freshwater input, substrate grain size, and initial biomass at a site. I used the response variable of proportional change in edible biomass, λ_{bmass}, from one sampling time step to the next to evaluate change in biomass as a function of increasing sea otter foraging pressure. Proportional biomass was established as a similarity from one sampling event to the next (calculated as Eqn. 1), and is bounded by -1 and 1. Thus, a site that has $\lambda_{bmass}=0$ experienced no change in mean biomass, and a positive or negative value signifies a respective increase or decline in the population.

To better describe the functional relationship between the intensity of sea otter predation and prey abundance, I used a binary multiple logistic regression to examine the probability of increase of intertidal prey species biomass as a function of increasing sea otter foraging pressure (cumulative density) across sites through time. For this analysis I converted proportional change of prey species biomass into a binary form of either growing (1, positive λ_{bmass}) or not growing (0, negative or zero λ_{bmass}) and assessed the best model fit using Akaike Information Criteria (AIC). Physical parameters were either recorded in situ at time of sampling or by using a GIS. I considered the pattern of glacial retreat (time since deglaciation) particularly important as previous work has shown that key ecosystem parameters, such as temperature, salinity, and productivity can be influenced by proximity to glacial inputs such as nutrients and sediments (Etherington et al. 2007), as well as through the effects of isostatic rebound (Larsen et al. 2004). Time since deglaciation was obtained using GIS and records provided by the U.S. Geological Survey (USGS) and National Park Service on glacial retreat. Distance to freshwater input was thought to be an important source of potential variation in nutrients, sediment deposition, temperature, and salinity. Distance to freshwater was also calculated using a GIS with data layers on major streams and watersheds in Glacier Bay, provided by USGS. Substrate type was thought to be a potentially important source of habitat complexity. Substrate grain size for each site was evaluated using the Wentworth Scale in situ and later converted into the numerical Krumbein Phi Scale (Krumbein 1936, Williams et al. 2006). The phi score was averaged among quadrats within sites to establish values ranging from -8 (largest grain size) to 8 (smallest grain size). Initial prey biomass was included in the model because preliminary analysis showed sites with a high prey biomass were suspected of attracting sea otters (and other predators) and therefore potentially undergoing a greater change over time. All remaining variation is subsumed as error in the random site effect

I compared models of best fit by AIC with a criteria difference of 5 points. I compared all models with the simplified intercept model and tested the most likely models based on expert opinion. I used *Saxidomus giganteus* as the model species because of its high abundance and prevalence in sea otter diet. I evaluated significance of effects using p-values, significant under $p < 0.10$, for all parameters included in the best-fit model. (Table 6).

Equation 1. The proportional change in biomass bounded by -1 and 1.

$$\lambda_{bmass\ ij} = \frac{(bmass_i - bmass_j)}{(bmass_i + bmass_j)}$$

Equation 2: Multiple Logistic Regression of Change in Biomass

$$\lambda_{spp} = logit[K + \beta_1 bmass_i + \beta_2 OttMag_j + \beta_6 TSD + \beta_7 phi + \beta_8 FW +] + \varepsilon_{ij}$$

Where

λ_{spp} = probability of increase in biomass of a given species

K = constant

bmass = site biomass at the previous sampling (gwwt/0.25m^2)

OttMag = cumulative sea otter density

TSD = time since deglaciation

Phi = enumerated substrate grain size

FW = distance (m) to nearest freshwater input

ε = residual error

Results

Sea Otter Distribution and Density

The sea otter population in Glacier Bay grew exponentially, from 0 in 1993 to 8508 (SE=2243) individuals by 2012 (Table 1). Sea otters were first seen in Glacier Bay proper (defined as the area north of Sitakiday Narrows) in 1995; remaining at low densities until about 2004. Otters established a reproducing population near Boulder Island in the central part of the Bay by 1998, achieving high densities before expanding west to Fingers Bay and north to Leland Island and Sandy Cove. Range expansion continued into the upper Bay at Geikie Rock and Sturgess Island by 2010, and into the arms of Glacier Bay by 2012 (Figure 3).

The density of sea otters across sites over time ranged from zero to 10 otters/km^2 during the course of study (Table 1). The cumulative density, summed over years, was used as the metric of treatment level and ranged from zero to 1otters/km^2 over the course of study. Of 45 intertidal sites in Glacier Bay, 17 remained unoccupied by otters throughout the study, 8 supported <1.0 otters/km^2, and most of the high and medium impact sites supported densities that ranged from approximately 1-2 otters/km^2 at pre-treatment sampling to between 2 - 73 otters/km^2 at post-treatment sampling (Table 4). The highest cumulative density at an intertidal site during sampling was 73.4 otters/km^2 at Boulder Island in 2010.

Sea Otter Foraging Observations

Overall, sea otters in Glacier Bay consumed 42% clam, 21% urchins, 25% horse mussel, 7% crab, 3% snail, and 2% other prey types (chitons, worms, and stars). When restricted to intertidal foraging observations sea otters were observed to consume a total of 37 identified species (Table 3a) these lumped dietary contributions changed were 56% clam, 18% urchins, 15% horse mussel, 6% crab, 4% snail, and 1% other (Figure 4). Clams were the primary prey item and feeding rates decreased over time from 62% to 46% of clams in the sea otter diet (Figure 4); 8 species of clams were observed being consumed at the following proportions: 31.15% *Saxidomus giganteus,* 5.49% *Serripes groenlandicus*, 2.24% *Mya spp.,* 2.05% *Clinocardium* *nuttali*, 1.35% *Leukoma staminea*, <1.00% a combination of *Entodesma navicula, Mactromeris polynyma, Macoma spp.*, and 13.76% unidentified clam species (Figure 5).

The rate of energy recovery (energy gain in kcal/min) also decreased over time as sea otters depleted preferred high energy and large prey (Figure 6). Throughout Glacier Bay energy recovery rates dropped from 18.01±2.12, to 15.08±1.74, to 9.21±1.34 kcal/min over early, mid, and late periods of occupation respectively. Intertidal energy recovery was highest in the early years at 19.14±2.29, dropping significantly to 12.19±1.45 and 9.63±1.22 kcal/min in the mid and late periods of occupation. The average sea otter density within Glacier Bay at early, mid, and late periods was 0.36, 1.19, and 4.54 otters/km^2 respectively (Table 1).

Figures 6a and 7 display the frequency of size classes consumed by sea otters in early, mid, and late time periods superimposed over the size frequency distributions of *Saxidomus giganteus* and *Mya spp* at our intertidal treatment sites from pre and post-treatment sampling events. Sea otters preferentially consume larger clams where they are present and as they deplete the abundance of larger clams they begin to consume smaller clams at a higher proportion of the diet. Figure 7b shows the expected trend in size distribution from control sites for *Mya spp.* where sea otters have no effect and there is an increase in the abundance of larger clams. As sea otters consumed *S. giganteus* over time, the median size consumed and maximum size clam eaten decreased over time, reflecting the distribution of available resources in the system as noted by the depression over the central mode from pre to post-treatment sampling (Figure 8).

Intertidal Prey Community Response

Species Diversity and Community Composition

Over the course of study I observed 14 identifiable species of infaunal bivalves and one species of sea urchin (Table 3b). In the pretreatment sampling period H_{max} was determined to be 3.6, increasing to 3.9 in the post-treatment sampling. None of the sites approached H_{max}, thus indicating a lack of evenness in population abundance among species. The highest observed diversity was H=1.5 at Leland Island (site-221) in 1999; the mean observed diversity through time was H=0.78. Diversity was higher at treatment sites and is also correlated with time since deglaciation (Figure 9).

Of all species encountered, *Macoma spp.* (a lumped group of *M. nasuta, M. balthica, M. oblique,* and *M. inquinata*) as well as *Hiatella spp.* were numerically the most abundant bivalves at intertidal sites but comprised a small portion of the available biomass and were not observed being eaten by sea otters (Bodkin et al. 2007a). In terms of biomass consumed, the predominant intertidal prey species were *Mya spp.*, *Leukoma staminea*, and *Saxidomus giganteus,* which comprised the majority of edible biomass in the intertidal zone. *Mya truncata* is the dominant *Mya* species within Glacier Bay, however *Mya arenaria*, though uncommon in the Bay, may have been present in samples as juveniles.

Size Distributions

I analyzed the size distributions of *Saxidomus giganteus, Mya spp., Leukoma staminea,* and *Strongylocentrotus droebachiensis* from pre and post treatment sampling at multiple treatment levels: i.e. among control, low, medium, and high impact sites, as previously explained. At medium and high impact sites, the size distributions of all these species or species groups changed significantly ($p<0.005$, Table 4 and Figures 13-16). See Table 5 for a complete list of statistics for skewness and kurtosis, as well as abundance and median size observed for each species.

Saxidomus giganteus exhibited the most dramatic change in size distribution with a strongly left shifted skew, fewer large clams, and a reduced median size (from 65.0 mm to 43.5 mm) at high impact sites (Kruskal-Wallis [K-W], U=10834.5, $p<0.000$). Similar patterns were seen at the medium impact sites although the changes were not as extreme (75 mm to 70 mm, K-W, U=70490.5, p=0.001). Size distributions also differed significantly at low impact sites although this change is probably more a consequence of the aging of a young cohort than the influence of sea otter predation, as abundance of larger clams did not appear to have a decrease. Overall, the influence of sea otter predation on the size distribution of *Saxidomus giganteus* is a shift toward right skew, with more individuals in smaller size classes (Δskew = 0.6800, 0.443, 1.318 at low, medium, and high sites). Kurtosis also decreased with the increasing cumulative impact of sea otter effects, as indicated by a flattening of the size distributions (Δkurt = -1.661, -0.960, -1.932 at low, medium, high sites). *Saxidomus giganteus* was relatively uncommon at the control sites.

However, skewness and kurtosis at these sites trended in the opposite direction to the treatment sites (K-W, U=9, p=0.806, Δskew = -0.874, Δkurt = 0.994).

The size distributions of *Mya spp.* changed through time at the treatment sites (p<0.05), although the nature of this change differed from that seen for *S. giganteus*. At high impact sites there was a decline in the number of larger individuals and a pulse of incoming smaller clams, and a resulting reduction in the median size from 34 mm to 22.5 mm (K-W, U=3437, p<0.000, Δskew = 0.932). At medium impact sites the distributions were similar at both time steps, however there was a slight reduction in the abundance of larger individuals and an increase in the number of smaller clams (K-W, U=85248, p=0.006, Δskew = 0.072). Sea otters appear to have little or no effect on *Mya spp*. at low impact sites. However, clam abundance increased significantly (K-W, U=113325.5, p<0.000) and their size distribution shifted to the right (increased median size from 39mm to 47mm).

Leukoma staminea experienced significant declines in abundance and mean size throughout Glacier Bay over the course of my study. This observation is consistent with reports of widespread mortality in *L. staminea* throughout the Gulf of Alaska (Dennis Lees, pers. Comm.). Thus, the patterns I observed are not likely the result of sea otter colonization and predation, but are due to factors not measured in this study and would confound any attempt of interpretation.

As an apparent consequence of a probable recruitment pulse, the smaller size classes of green sea urchin, *Strongylocentrotus droebachiensis,* increased in abundance between pre and post treatment sampling. Because of this, the size distributions differed significantly, as did skew (K-W, U=236842.5, $p<0.000$, Δskew = -2.262). Increases were greater at low impact sites and occurred even at sizes above 25mm, whereas increases were not observed at size over 25 mm at medium or high impact sites.

Change in Biomass

Mean edible biomass of clams (gwwt/0.25m^2) varied greatly across the intertidal sites in Glacier Bay. At sites where clams occurred, mean biomass of clams observed being consumed by sea otters ranged from 0.07 to 1790.38 gwwt./0.25m^2. Prey species were much more abundant in the lower Bay than the upper Bay and there was a disproportionately higher biomass density of clams in both the pre and post treatment sampling of treatment sites in the lower bay.

I first compared the mean pooled biomass density of *S. giganteus, L. staminea,* and *Mya spp.* at control and treatment sites, pre and post-treatment. Biomass increased at the control sites although this increase was not significant (ANCOVA, F=1.36, p=0.274). In contrast, the pooled biomass decreased significantly at treatment sites (ANCOVA, F=3.25, p=0.080) (Figure 10a). Sea urchin biomass density increased at both control and treatment sites but the change was not statistically significant (Figure 10b).

To examine the functional response of intertidal clam biomass to sea otter colonization I examined the more continuous relationship between intertidal clam biomass and cumulative sea otter impact among the sites (Figure 11). High prey biomass density occurred commonly at the pre and intermediary treatment sampling, whereas biomass density was more uniformly low across sites in the post treatment. These data indicate little or no effect of sea otter predation below a cumulative otter density of about 6 otters/km^2, whereas above this value clam biomass was more likely to decline. There was a clear species specific negative response in the biomass density of *S. giganteus* compared *to L. staminea,* and *Mya spp.* over time at these latter sites.

Figure 17 shows the functional relationship between sea otter cumulative effect and probability of increasing clam biomass for each of the four primary prey species, with other variables (time since deglaciation, substrate grain size, distance to freshwater input, and initial biomass) held constant at their mean observed values. I found that sea otter magnitude had a strong negative effect on the proportional change in biomass of *Saxidomus giganteus* over time (Z=-2.701, p=0.007), and the probability of declines in biomass were >50% for cumulative sea otter densities of <2 otters/km^2. There was a declining trend in the population growth of *Mya spp.*, however, the relationship was not statistically significant (Z=-0.849, p=0.396). For *L. staminea,* growth was very unlikely and sea otters had little effect, though this result is confounded by mortality not associated to sea otter predation. In the case of *Strongylocentrotus droebachiensis,* there *was* a weakly positive (Z=0.423, p=0.672) relationship between cumulative sea otter density and the probability of increasing biomass.

Discussion

Sea otters have increased rapidly in Glacier Bay National Park and Preserve since the mid-1990s, with intrinsic growth rates far exceeding those previously reported anywhere throughout the species range. In fact, an average annual growth rate of 42% per year from 1995-2012 far exceeds the theoretical maximum intrinsic rate of population increase of 24% per year for this species (Estes 1990), suggesting high reproduction but also demonstrating the immigration of sea otters from outside Glacier Bay (Bodkin et al. 2007a, Esslinger and Bodkin 2009). The pattern of colonization of Glacier Bay by sea otters has been rapid but also spatially variable, possibly due to associated variation in resource availability, physical characteristics of the environment, and/or conspecific social influences (Ralls et al. 1996, Laidre et al. 2009). In soft and mixed-sediment systems with limited kelp canopy, sea otters may congregate in large resting rafts over open water (Gilkinson et al. 2011), which may explain why high densities of otters have not become permanently established in the convoluted island groups or coves in Glacier Bay and may only use that habitat for foraging excursions. Thus, fine scale movements may play a crucial role in how sea otters influence prey communities in Glacier Bay. I used the asymmetrical pattern of colonization to elucidate the effects of predation by sea otters at intertidal sites through time. Certain areas, even within the treatment zone, maintained low otter densities whereas other areas experienced exponential population growth. Despite rapid population growth and continued range expansion of sea otters in

Glacier Bay, large areas of apparently suitable habitat remained incompletely or unoccupied by 2012.

Sea otter diet from observed intertidal feeding bouts throughout Glacier Bay consisted predominantly of infaunal bivalves. However, over the course of continued occupation, feeding rates of clams decreased. *Saxidomus giganteus* was by far the most important prey item of sea otters in Glacier Bay, which likely explains why this species exhibited the most dramatic response to sea otter colonization. The presence of *Serripes groenlandicus* in the intertidal diet of sea otters was surprising as this is typically a subtidal clam species (Khim 2001) and was rarely recovered in the sampling of intertidal sites. A likely explanation for this apparent discrepancy stems from the grouping method used in the GIS analysis. That is, bathymetry maps may not capture the fine scale variation in nearshore depth and so the classification of intertidal foraging bouts inside of the 10 m isobath may actually include some foraging observations on the border of the subtidal zone. *Mya spp.* was relatively uncommon in both our intertidal samples and in the sea otter's diet, which may explain why the prey species displayed such a weak response to sea otter colonization. It became apparent that prey selection may be a driving factor in the response elicited by a given species, and that sea otters rely on high densities of large clams in Glacier Bay.

Intertidal prey communities were most diverse in the lower Bay. The majority of control sites occurred in the upper Bay, in most cases characterized by the absence of bivalves or domination by a single non-prey species such as small *Macoma spp.* or

Hiatella spp. Treatment sites, in contrast, were widely distributed across the lower and middle Bay where diversity varied. Although there are too many unmeasured environmental variable to determine the causes of variation in diversity across sites, there was no apparent effect of sea otter abundance or occupation on intertidal clam diversity. However at several control sites in the upper Bay, increasing diversity was documented over the course of the study, as indicated by increases in the presence and abundance of *Saxidomus giganteus, Mya spp.,* and other clams between pre and post-treatment sampling. Dead clam assemblages (clams dead in place) were observed at several sites. This may have been a result of changes in temperature, salinity, or isostatic rebound – the uplift resulting from glacial retreat. Parts of Southeast Alaska were found to uplift at rates approaching >10 mm/year (Larsen et al. 2004) and may have incurred a similar result to the dead clam assemblages observed after rapid uplift from the 1964 earthquake in Prince William Sound, Alaska (Baxter 1964). Dead clam assemblages observed in Glacier Bay often consisted of large individuals of *Mya spp.* in the upper and middle Bay. This may also have been caused by a cohort senescing without continued recruitment to replace the dying population.

It is clear that sea otters significantly influenced the size structure of intertidal prey communities in Glacier Bay but the effect was variable through space and across species. Contrary to the expected result, I observed quite different responses from the two dominant species of infaunal prey, *Mya spp.* and *Saxidomus giganteus.* Sea otters had a weak effect on the size and biomass of *Mya spp.* at high treatment levels, and opposite trends of increasing size and biomass were observed at medium and low impact sites. Conversely, *S. giganteus* showed consistent reductions in size and biomass at all treatment levels. The preference in sea otter diet for feeding on *S. giganteus* results in the species being more sensitive to sea otter predation than other, less-consumed species of clam. Additionally, the distribution of *S. giganteus* may have played an important role in the pattern of colonization and habitat-use by sea otters in Glacier Bay.

These species-specific response between prey species of clam may have resulted from four potential mechanisms. (1) The primary factor is that Sea otters preferentially consumed *Saxidomus giganteus.* This species was the dominant source of edible biomass in the middle and lower Bay and it was relatively rare in the upper bay compared to other prey species such as *Mya spp.* Perhaps consumption rate would have been a valuable parameter to include in explaining the variance across species, as the direct foraging pressure on a given population is likely a primary driver for the differential response of these species to sea otter predation. (2) Sea otters exert a strong influence by selectively removing larger individuals of infaunal species and altering the balance of pre- and post-settlement survival. *S. giganteus* is a particularly long lived clam, >20 years, that can attain sizes of nearly 140 mm (Fraser and Smith 1928, Goong and Chew 2001). They are the dominant large infaunal organism at intertidal sites in Glacier Bay and comprise the majority of edible biomass available to sea otters in this system. At high densities, *S. giganteus* and other large infauna compete for space in the benthos and may consume recruiting bivalve larvae through suspension feeding (Ólafsson et al. 1994). Thus, removal of large *S. giganteus* and other large suspension feeding infauna may reduce inter- and intra- specific competition for space and reduce larval mortality, thereby increasing the diversity and number of smaller size individuals observed in a population. (3) Recruitment potential likely varied among sites and has been show to vary greatly throughout Glacier Bay for other larval species, being more limited with increasing distance from the mouth of Glacier Bay (Herter and Eckert 2008). Infaunal bivalve species will spawn and recruit sporadically through time and recruitment is greatly influenced by hydrodynamics in the ecosystem (Eckman 1983), which we did not measure. Patterns witnessed in the size distributions at intertidal sites were likely influenced by recruitment variation, but available data do not document these events nor indicate the scale at which they may have occurred. (4) Sediment grain size also varied among sites, *Mya spp.* prefers finer grain substrate and *S. giganteus* prefers coarser grain substrate. Most low and medium impact sites were located in the middle/upper Bay or in protected coves where finer substrate was more prevalent. *Mya spp.* may thus have increased at many of the low and medium sites both because of reduced predation and the preferable finer grain substrate at these sites. Additionally, competition for space may have been reduced as *S. giganteus* occurred infrequently compared with *Mya spp.* in the upper Bay possibly due to habitat characteristics. Thus it was more likely to witness an increase in *Mya spp.* in the absence of sea otters because of the predation and habitat type interaction. This interaction may also be a primary factor influencing spatial-use patterns of sea otters, as it is clear that sea otters preferentially consume *S. giganteus* and are more likely to forage in an area with higher densities of *S. giganteus.*

Sea otters are believed to forage optimally, selecting resources that offer the highest rates of energy return given their size, abundance, ease of acquisition, and caloric content (Ostfeld 1982). In the early years of their occupation in Glacier Bay, sea otters foraged primarily on large clams. Later, as they depleted those resources, they had to expand their diet and began to forage more extensively on medium and small sized clams. The result of this shift is exemplified in the energy recovery rates, which declined significantly over time in Glacier Bay. During the initial phase of colonization of Glacier Bay, sea otters displayed energy recovery rates similar to those measured in other systems with abundant prey resources, around 20 kcal/min (USGS unpub. data). These high rates dropped to approximately 9 kcal/min in later stages of occupation similar to other sea otter populations estimated to be at equilibrium densities (USGS unpub. data). The more than 2-fold decline in energy recovery has several implications. At sites where resources became less available or scarce, the otters need to spend more time foraging in order to meet their daily caloric requirements (Bodkin et al. 2007b). The otters were also able to expand their range into other parts of the lower Bay, where prey resources remained abundant, which likely helps explain their initial colonization in the Bay. However at some point, sea otters will reach a point of resource limitation. Energy recovery rates at sites that had been occupied for >10 years were similar to those observed in resource limited systems (USGS unpub. data), thus suggesting that parts of Glacier Bay may already be at or near a local carrying capacity. The observed reduction in energy recovery rates translates into the need of an individual otter to expend more time and energy foraging per day to meet its caloric demands.

In soft-substrate systems, recolonizing sea otters preferentially prey upon the most abundant and available resources, in this case primarily infaunal organisms. While we did not directly quantify the presence of all invertebrate assemblages at our sites, we did note the presence of large epibenthic invertebrates such as large green sea urchins (*Strongylocentrotus droebachiensis*), and various large snail and crab species at sites in the pre-treatment that were absent by the post-treatment sampling. The absence of many large epibenthic invertebrates at intertidal sites suggests that habitat ideal for rich infaunal communities may be inferior habitat for urchins and other grazing invertebrates. Urchins encountered tended to be small and sea otters do not often consume sea urchins much smaller than 25 mm (Estes and Duggins 1995), thereby providing the urchins a size refuge from predation. Another factor influencing the size distribution in sea urchins is recruitment. While we can only infer these events from size distributions, urchins are known to recruit episodically in southeast Alaska (Estes and Duggins 1995, Bodkin et al. 2004a) so the observed peak of small individuals in the size frequency data is most likely the result of a large recruitment event. Lastly, at treatment sites a noted increase in habitat complexity was observed due to sea otters excavating for infaunal prey and leaving a layer of shell litter on the benthos. The creation of a more rugose and complex substrate may provide habitat and refuge for smaller epibenthic invertebrates.

The response of intertidal prey communities to sea otter colonization in Glacier Bay is a complex story that is still unfolding as a multi-decadal event for which the patterns and dynamics may not be fully manifested for years to come. Contrary to my expectations of a stronger and more uniform response of the intertidal community to sea otter predation, the response was in fact quite variable amongst treatment sites. This variation may be due in large part to the temporal transitioning of sea otter diet as well as variability in prey distributions through out the Bay. Previous work in soft and mixed substrate has shown that sea otters can have an effect within about five years of occupation, but full effects may not be manifested until 20 years or more (Kvitek et al. 1992, Jolly 1997).

The gradual nature of intertidal soft-sediment prey community response to sea otter colonization highlights a key difference between Glacier Bay and other systems. The intertidal zone in this environment is vast in its extent, perhaps in part explaining the low response rate. Furthermore, intertidal habitat may provide a quasi-refuge from sea otter predation for several reasons. Large cobble or boulders armor many beaches, and in some cases the interstitial substratum has amalgamated into a hard packed layer that is difficult to excavate. Both features may provide a physical barrier between predator and prey. Other predators can exploit the intertidal zone during low tide, however sea otters seldom do this and instead forage subtidally until the tide rises. Thus, resources in the intertidal are accessible only part of the time to sea otter predation. Additionally, organisms inhabiting the intertidal undergo greater physiological stress due to greater fluctuations in temperature and salinity, as well as times without access to resources during low tide. These factors may limit the growth and proliferation of an intertidal population and may explain why change is more gradual in intertidal prey communities, taking longer to detect a response.

Characterizing the gradual change in a soft-sediment ecosystem is difficult as there is little known about the indirect interactions among species in this system. This situation is in contrast with the effects of sea otters in hard-substrate, where ecosystem phase-state shifts often result from the direct and indirect effects of sea otters that cascade through the ecosystem. Similarly important indirect effects may occur in unconsolidated systems, but any such effects would be intrinsically more difficult to characterize because soft-sediment habitats are highly variable, the system cannot be directly observed without extensive disturbance, and there is no *a-priori* expectation as to what changes to look for as a result of indirect interactions. However, one might at least speculate on what some of these indirect effects might be. One possibility is increased habitat complexity and resource availability for other consumers as a result of excavation during foraging activities in soft-sediments (Oliver et al. 1985, Kvitek et al. 1992, Thrush 1999, Hodges et al. 2008). By removing many large filter-feeding organisms and re-suspending sediments during foraging, sea otters may influence the dynamics of sediment and nutrient transport as well as changes in turbidity and water quality as seen in other systems following the addition or removal of abundant filter-feeding bivalves (Newell 1988, MacIsaac 1996). It is likely that through bioturbation and shell deposition, sea otters are fundamentally changing the physical structure in Glacier Bay. While diving several subtidal sites within Glacier Bay in 2011, researchers from USGS observed dense algal turf mats attached to discarded shells from sea otter foraging, along with some areas being covered by shell litter nearly 10 cm deep over the substrate. This observation may help explain anecdotal reports by other researchers and National Park Service personnel of the appearance of large kelp beds between 2000 and 2010 in parts of lower Glacier Bay where they had been previously non-existent.

Although my Masters research has focused on the direct effects of a recovering sea otter population on intertidal prey assemblages, the ecological influences of otters on soft-sediment systems in Glacier Bay and elsewhere likely extend far beyond the documented response through direct and indirect effects on other species and processes. As sea otters continue to recolonize regions of coastal North America where they have been long absent, their influence will become manifested, however we cannot at this time generalize their effects between systems. Continued monitoring of the effects of sea otters in Glacier Bay National Park and Preserve could serve as a model system in describing the changes caused by the return of a top predator in a soft-sediment ecosystem. This knowledge will be crucial to properly inform the management of valued recreational, commercial, and social resources in the face of continuing sea otter recolonization.

Tables & Figures

Table 1. Results from Aerial surveys in Glacier Bay, 1993-2012. Displays: Results from distribution surveys, abundance estimates with SE from abundance surveys. The calculated sum of distribution surveys over time (cumulative count). The baywide density of otters in and the maximum cumulative density over time within Glacier Bay.

Year	Distrib. Count	Abundance Estimate±SE	Cumulative Count	BayDensity Otters/km^2	MaxMag. Otters/km^2
1993	68	0*	68	0.08	2.77
1995	106	5*	174	0.20	6.55
1996	129.5	39*	303.5	0.34	10.18
1997	68	21*	371.5	0.42	12.20
1998	308.5	209*	680	0.76	17.31
1999	63.2	384±111	743.2	0.83	17.36
2000	98.25	554±97	841.45	0.95	17.46
2001	323.4	1238±143	1164.85	1.06	17.56
2002	251.6	1266±196	1416.45	1.35	17.66
2003	347	1866±458	1763.45	1.74	17.68
2004	360.75	2381±594	2124.2	2.15	24.49
2005	1138	.	3262.2	3.45	34.99
2006	470.25	2785±361	3732.45	3.98	41.75
2009	1780	.	5512.45	5.97	68.87
2010	1061	.	6573.45	7.17	74.73
2012	2333	8508±2243	8906.45	9.77	105.18

***early abundance estimates excluded points around the entrance of Glacier Bay, distribution counts do not.**

Table 2. Values of cumulative sea otter density (otters/km2) extracted at a site for a given year of sampling. Low-lighted sites (in grey) were those excluded from analysis due to their identification as unsuitable clam habitat.

		Year of Sampling									
Site	Treatment level	1998	1999	2000	2004	2005	2006	2007	2010	2011	Sample Count
5*	Control	.	.	0.00	.	.	.	.	0.00	.	2
10*	Control	.	.	0.00	.	.	.	.	0.00	.	2
24	Control	.	.	0.00	0.00	0.00	.	.	0.00	.	4
27*	Control	.	.	0.00	.	.	.	.	0.00	.	2
83*	Control	.	.	0.00	.	.	.	.	0.00	.	2
86	Control	.	.	0.00	0.00	0.00	.	.	0.00	.	4
117*	Control	.	.	0.00	.	.	.	.	0.00	.	2
120*	Control	.	.	0.00	.	.	.	.	0.00	.	2
138*	Control	.	.	0.00	.	.	.	.	0.00	.	2
141*	Control	.	.	0.00	.	.	.	.	0.00	.	2
142*	Control	.	.	0.00	.	.	.	.	0.00	.	2
159*	Control	.	.	0.00	0.00	0.00	.	.	0.00	.	4
167*	Control	.	.	0.00	.	.	.	.	0.00	.	2
176*	Control	.	.	0.00	.	.	.	.	0.00	.	2
179*	Control	.	.	0.00	0.00	0.00	.	.	0.00	.	4
Sundew_PCH	Control	.	.	0.00	0.00	0.00	.	.	0.00	.	4
211	Control	.	.	0.00	.	.	.	.	0.00	.	2
Geikie_PCH	Control	.	.	0.00	.	.	0.00	.	0.02	.	3
95*	Control	.	.	0.00	.	.	.	.	.	0.09	2
91*	Low	.	0.00	.	.	.	.	.	0.17	.	2
170	Low	.	.	0.00	.	.	.	.	0.20	.	2
37	Low	.	.	0.00	.	.	.	.	0.23	.	2
71	Low	.	0.05	.	.	.	.	.	0.31	.	2
30	Low	.	0.00	.	.	.	.	.	0.77	.	2
Berg_PCH	Low	0.09	.	.	.	0.14	0.18	.	0.79	.	4
58	Low	.	0.09	.	.	.	.	.	1.12	.	2
46	Low	.	0.78	.	0.81	.	0.92	.	1.12	.	4
67	Low	0.07	.	.	.	.	.	.	1.42	.	2
74*	Low	.	1.31	.	.	.	.	.	2.57	.	2
52	Med	.	.	0.18	.	.	.	.	2.68	.	2
43	Med	.	1.5	.	1.58	.	1.97	.	.	3.11	4
55	Med	.	0.19	.	0.84	1.28	.	.	4.47	.	4
Secret_PCH	Med	.	.	0.30	1.08	1.67	.	.	5.53	.	4
PCH_230	Med	1.64	.	.	1.65	1.70	.	.	6.03	.	4
Fingers_PCH	Med	1.04	.	.	.	1.07	1.07	.	7.85	.	4
77*	Med	0.99	.	.	.	1.02	1.02	.	8.09	.	4
221	Med	.	0.24	.	2.46	5.04	5.33	.	9.48	.	5
64*	Med	.	0.99	.	.	.	.	.	10.29	.	2
40	Med	.	2.97	.	.	.	.	.	14.36	.	2
Rush_PCH	Med	.	.	1.36	1.89	2.79	.	.	17.44	.	4
233	Med	.	1.07	.	.	.	.	.	18.33	.	2
236	Med	.	1.78	.	2.08	.	3.11	.	.	.	3
Triangle_PCH	High	.	.	2.70	.	.	.	18.66	34.51	.	3
229	High	.	2.80	.	.	.	.	.	39.03	.	2
Boulder_PCH	High	.	2.31	.	.	.	.	40.60	73.39	.	3

Table 3a. List of species observed being consumed by sea otters foraging intertidally in Glacier Bay over the course of study.

Group	Scientific Name	Common Name
Bivalves		
Clam	*Clinocardium nuttalli*	Nuttall's heart cockle
Clam	*Entodesma navicula*	Ugly clam
Clam	*Mactromeris polynyma*	Arctic surf clam
Clam	*Macoma spp.*	Macoma
Clam	*Mya spp.*	Soft shell clam
Clam	*Leukoma staminea*	Pacific littleneck clam
Clam	*Saxidomus gigantea*	Butter clam
Clam	*Serripes groenlandicus*	Greenland cockle
Clam	*Unidentified Clam*	Cam
Mussel	*Modiolus modiolus*	Horse mussel
Mussel	*Mytilus trossulus*	Blue mussel
Mussel	*Unidentified Mussel*	Mussel
Scallop	*Chlamys rubidis*	Red Scallop
Scallop	*Unidentified scallop*	Scallop
Bivalve	*Unidentified Bivalve*	Bivalve
Crustaceans		
Crab	*Cancer magister*	Dungeness crab
Crab	*Cancer productus*	Red rock crab
Crab	*Chionoecetes bairdi*	Tanner crab
Crab	*Hyas lyratus*	Pacific Lyre crab
Crab	*Paralithodes camtschaticus*	Red king crab
Crab	*Pugettia gracilis*	Graceful kelp crab
Crab	*Pugettia spp.*	Kelp crabs
Crab	*Telmessus cheiragonus*	Helmet crab
Crab	*Unidentified Crab*	Crab
Shrimp	*Pandalus spp.*	Prawn
Gastropods		
Snail	*Euspira lewisii*	Moon snail
Snail	*Fusitriton oregonensis*	Hairy triton
Snail	*Neptunea spp.*	Lyre whelk
Snail	*Unidentified snail*	Snail

Asteroidea		
Sea Star	*Crossaster papposuss*	Rose Star
Sea Star	*Gorgonocephalus caryi*	Basket star
Sea Star	*Pteraster tesselatus*	Snotty sea star
Sea Star	*Pycnopodia helianthoides*	Sunflower star
Sea Star	*Solaster spp.*	Sun star
Sea Star	*Unidentified sea star*	Sea Star
Echinoidea		
Urchin	*Strongylocentrotus droebachiensis*	Green sea urchin
Polyplacophora		
Chiton	*Unidentified Chiton*	Chiton
Chiton	*Cryptochiton stelleri*	Gumboot chiton
Other		
Barnacle	*Balanus spp.*	Barnacle
Cephalopoda	*Octopus dofleini*	Giant Pacific Octopus
Holothuroidea	*Cucumber spp.*	Sea cucumber
Holothuroidea	*Cucumaria fallax*	Large black sea Cucumber
Holothuroidea	*Cucumaria miniata*	Embedded cucumber
Ophiuroidea	*Ophiuroid spp.*	Brittle star
Worm	*Echiurus spp.*	Fat inkeeper worm
Worm	*Unidentified worm*	Worm
Fish	*Unidentified fish*	Fish
Unidentified	*Unidentified Prey Item*	Unknown

Table 3b. Abundance of all clam and urchin species encountered over course of study at intertidal sites.

Species	Count
Clams	
Unidentified Clam	5
Clinocardium nuttali	186
Entodesma navicula	1
Gari californicum	1
Hiatella spp.	12935
Humilaria kennerlyi	3
Mactromeris polynyma	4
Macoma spp.	29108
Mya spp.	3943
Panomya ampla	4
Leukoma staminea	4292
Pseudopythina compressa	277
Saxidomus giganteus	3062
Serripes groenlandicus	2
Ziphaerea pilsbryi	4
Urchins	
Stronglyocentrotus droebachiensis	8446

Table 4. Results from Kruskal-Wallis (Mann-Whitney) test of size distributions of prey species pre and post treatment at sites.

Species	**Zone**	**median Pre**	**median Post**	**U score**	**N Pre**	**N Post**	**p-val**
S. giganteus	Control	64	70	9	4	5	**0.806**
S. giganteus	Low	82	73	73	105	137	**0.003**
S. giganteus	Med	75	70	70490.5	486	335	**0.001**
S. giganteus	High	65	43.5	10834.5	347	162	**0.000**
M. truncata	Control	19	28	60.5	14	5	**0.018**
M. truncata	Low	39	47	113325.5	350	533	**0.000**
M. truncata	Med	39	38	85284	438	436	**0.006**
M. truncata	High	34	22.5	3437	94	108	**0.000**
L. staminea	Control	44.5	40	8	22	1	**0.650**
L. staminea	Low	48	45	16755.5	494	67	**0.868**
L. staminea	Med	40	46	101118.5	1373	125	**0.001**
L. staminea	High	34	37	4603	362	25	**0.885**
S. droebachiensis	Control	17	14	64.5	14	16	**0.047**
S. droebachiensis	Low	46	45	236842.5	349	2015	**0.000**
S. droebachiensis	Med	17	14	733503.5	1048	1905	**0.000**
S. droebachiensis	High	15	14	54276.5	319	423	**0.000**

Table 5. Size distribution statistics (Min, Max, Median, Mean±StD in mm) and change in skewness and kurtosis pre and post treatment at control, low, medium, and high impact sites.

Species	Period	Treatment	N	Min	Max	Median	Mean	±SD	*Skew.*	skewSE	*Kurt.*	Kurt SE	Δskew	Δkurt
SAG	Pre	Low	105	20	105	**82**	78.505	17.742	***-1.108***	0.236	***1.210***	0.467	.	.
SAG	Post	Low	137	15	114	**73**	70.423	21.652	***-0.428***	0.207	***-0.451***	0.411	0.680	-1.661
SAG	Pre	Med	486	15	113	**75**	72.560	20.196	***-0.607***	0.111	***0.074***	0.221	.	.
SAG	Post	Med	335	14	122	**70**	67.519	22.348	***-0.164***	0.133	***-0.886***	0.266	0.443	-0.960
SAG	Pre	High	347	14	100	**65**	62.490	15.351	***-1.002***	0.131	***1.227***	0.261	.	.
SAG	Post	High	162	14	84	**43.5**	43.907	15.510	***0.316***	0.191	***-0.705***	0.379	1.318	-1.932
SAG	Pre	Control	4	57	74	**64**	64.750	8.098	***0.267***	1.014	***-3.931***	2.619	.	.
SAG	Post	Control	5	53	73	**70**	64.800	9.524	***-0.607***	0.913	***-2.936***	2.000	-0.874	0.994
MYS	Pre	Low	350	14	70	**39**	38.643	11.980	***0.028***	0.130	***-0.664***	0.260	.	.
MYS	Post	Low	533	15	82	**47**	44.242	15.438	***-0.031***	0.106	***-1.079***	0.211	-0.059	-0.416
MYS	Pre	Med	438	14	70	**39**	40.103	12.480	***0.059***	0.117	***-0.987***	0.233	.	.
MYS	Post	Med	436	15	73	**38**	37.732	12.634	***0.131***	0.117	***-0.980***	0.233	0.072	0.007
MYS	Pre	High	94	14	55	**34**	33.138	9.149	***-0.048***	0.249	***-0.493***	0.493	.	.
MYS	Post	High	108	14	67	**22.5**	27.667	11.741	***0.883***	0.233	***-0.025***	0.461	0.932	0.468
MYS	Pre	Control	14	15	39	**19**	22.143	7.564	***1.530***	0.597	***1.301***	1.154	.	.
MYS	Post	Control	5	23	49	28	33.400	11.459	***0.708***	0.913	***2.038***	2.000	-0.821	-3.339
LES	Pre	Low	494	14	69	**48**	42.887	13.997	***-0.464***	0.110	***-1.059***	0.219	.	.
LES	Post	Low	67	14	65	**45**	43.970	12.089	***-0.777***	0.293	***0.088***	0.578	-0.313	1.148
LES	Pre	Med	1,373	14	102	**40**	39.194	12.585	***-0.012***	0.066	***-0.518***	0.132	.	.
LES	Post	Med	125	14	64	**46**	42.680	12.485	***-0.752***	0.217	***-0.290***	0.430	-0.740	0.228

LES	Pre	High	362	14	59	**34**	33.080	10.628	***-0.064***	0.128	***-0.950***	0.256	.	.
LES	Post	High	25	15	52	**37**	33.080	11.317	***-0.117***	0.464	***-1.465***	0.902	-0.053	-0.515
LES	Pre	Control	22	25	57	**44.5**	42.091	8.944	***-0.496***	0.491	***-0.519***	0.953	.	.
LES	Post	Control	1	40	40	**40**	40.000	.	**.**	.	**.**	.	.	.
STD	Pre	Low	349	11	46	**17**	17.716	5.091	***2.082***	0.131	***5.990***	0.260	.	.
STD	Post	Low	2,015	11	45	**14**	15.719	5.090	***1.598***	0.055	***2.697***	0.109	-0.484	-3.293
STD	Pre	Med	1,048	11	43	**17**	18.637	6.256	***0.945***	0.076	***0.439***	0.151	.	.
STD	Post	Med	1,905	11	43	**14**	16.046	5.169	***1.509***	0.056	***2.441***	0.112	0.564	2.002
STD	Pre	High	319	11	38	**15**	16.313	5.084	***1.167***	0.137	***1.189***	0.272	.	.
STD	Post	High	423	11	33	**14**	14.478	3.612	***1.681***	0.119	***3.655***	0.237	0.514	2.466
STD	Pre	Control	14	11	53	**17**	19	10.318	***3.1***	0.597	***10.694***	1.154	.	.
STD	Post	Control	16	11	21	**14**	14.375	2.705	***0.838***	0.564	***0.766***	1.091	-2.262	-9.928

Table 6. Significance of model terms from best fit model (Equation 2).

λ = *logit*[1+PREVBM+LOTTMAG+TSD+PHI+FWM]					AIC=74.58	
Saxidomus Giganteus				Overall Model Fit p-value =		**0.007**
Parameter	**Estimate**	**Std. Error**	**Z**	**p-Value**	**Lower C.I.**	**Upper C.I.**
CONSTANT	**-8.619264**	5.075378	-1.69825	***0.089***	-18.566823	1.328296
PREVBM	**-0.001691**	0.000786	-2.1524	***0.031***	-0.003231	-0.000151
LOTTMAG	**-1.622745**	0.600804	-2.700956	***0.007***	-2.800298	-0.445191
TSD	**0.058697**	0.033412	1.756762	***0.079***	-0.006789	0.124182
PHI	**-0.158036**	0.088623	-1.783236	***0.075***	-0.331735	0.015662
FWM	**0.000683**	0.000329	2.07809	***0.038***	0.000039	0.001327
Mya Spp.				Overall Model Fit p-value =		**0.694**
Parameter	**Estimate**	**Std. Error**	**Z**	**p-Value**	**Lower C.I.**	**Upper C.I.**
CONSTANT	**-0.732535**	2.285408	-0.320527	*0.749*	-5.211852	3.746783
PREVBM	**-0.004846**	0.003402	-1.424439	*0.154*	-0.011514	0.001822
LOTTMAG	**-0.379363**	0.446785	-0.849094	*0.396*	-1.255046	0.496321
TSD	**0.007466**	0.015784	0.473041	*0.636*	-0.02347	0.038403
PHI	**0.015116**	0.072524	0.208432	*0.835*	-0.127028	0.157261
FWM	**0.000271**	0.000269	1.010312	*0.312*	-0.000255	0.000798
Strongylocentrotus droebachiensis				Overall Model Fit p-value =		**0.090**
Parameter	**Estimate**	**Std. Error**	**Z**	**p-Value**	**Lower C.I.**	**Upper C.I.**
CONSTANT	**5.339729**	2.983624	1.789679	***0.074***	-0.508066	11.187524
PREVBM	**-0.029267**	0.014691	-1.992258	***0.046***	-0.05806	-0.000474
LOTTMAG	**0.192816**	0.455718	0.423105	*0.672*	-0.700374	1.086007
TSD	**-0.031207**	0.019751	-1.580012	*0.114*	-0.069918	0.007504
PHI	**-0.151614**	0.079774	-1.900534	***0.057***	-0.307969	0.004741
FWM	**-0.00011**	0.000267	-0.411058	*0.681*	-0.000634	0.000414
Leukoma staminea				Overall Model Fit p-value =		**0.111**
Parameter	**Estimate**	**Std. Error**	**Z**	**p-Value**	**Lower C.I.**	**Upper C.I.**
CONSTANT	**1.791726**	2.468095	0.725955	*0.468*	-3.045652	6.629105
PREVBM	**-0.008675**	0.005739	-1.511757	*0.131*	-0.019923	0.002572
LOTTMAG	**-0.172163**	0.531012	-0.324217	*0.746*	-1.212927	0.868601
TSD	**-0.011504**	0.017602	-0.653587	*0.513*	-0.046003	0.022995
PHI	**-0.025764**	0.086199	-0.298896	*0.765*	-0.194711	0.143182
FWM	**-0.000195**	0.000358	-0.544448	*0.586*	-0.000898	0.000507

Table 7. Model selection of multiple logistic regression of probability of population growth with increasing sea otter density. Gray values beyond the dashed margin are outside of the 5 point criteria.

Overall Model Model Support		Model Parameters								
AIC	constant	PrevBM	PrevBM^2	Log(OttMag)	OttMag	OttOcc	TSD	PHI	FWM	Interaction Terms
74.58	1	x		x			x	x	x	
74.70	1	x		x			x	x	x	TSD*PrevBM
74.93	1	x		x			x	x	x	Log(OttMag)*PrevBM + TSD*PrevBM
75.45	1	x		x			x	x	x	Log(OttMag)*PrevBM
76.19	1	x	x	x			x	x	x	
76.23	1	x			x		x	x	x	
77.50	1	x		x			x	x		
78.77	1	x		x			x			
79.30	1	x	x		x		x	x		
79.84	1	x	x		x	x	x	x	x	
79.93	1	x		x				x		
80.77	1	x		x		x	x			
80.77	1	x	x	x			x			
81.35	1	x			x	x	x	x		
82.18	1	x		x					x	
83.17	1	x		x						
104.63	1			x						
109.82	1			x				x		
110.09	1			x			x	x		

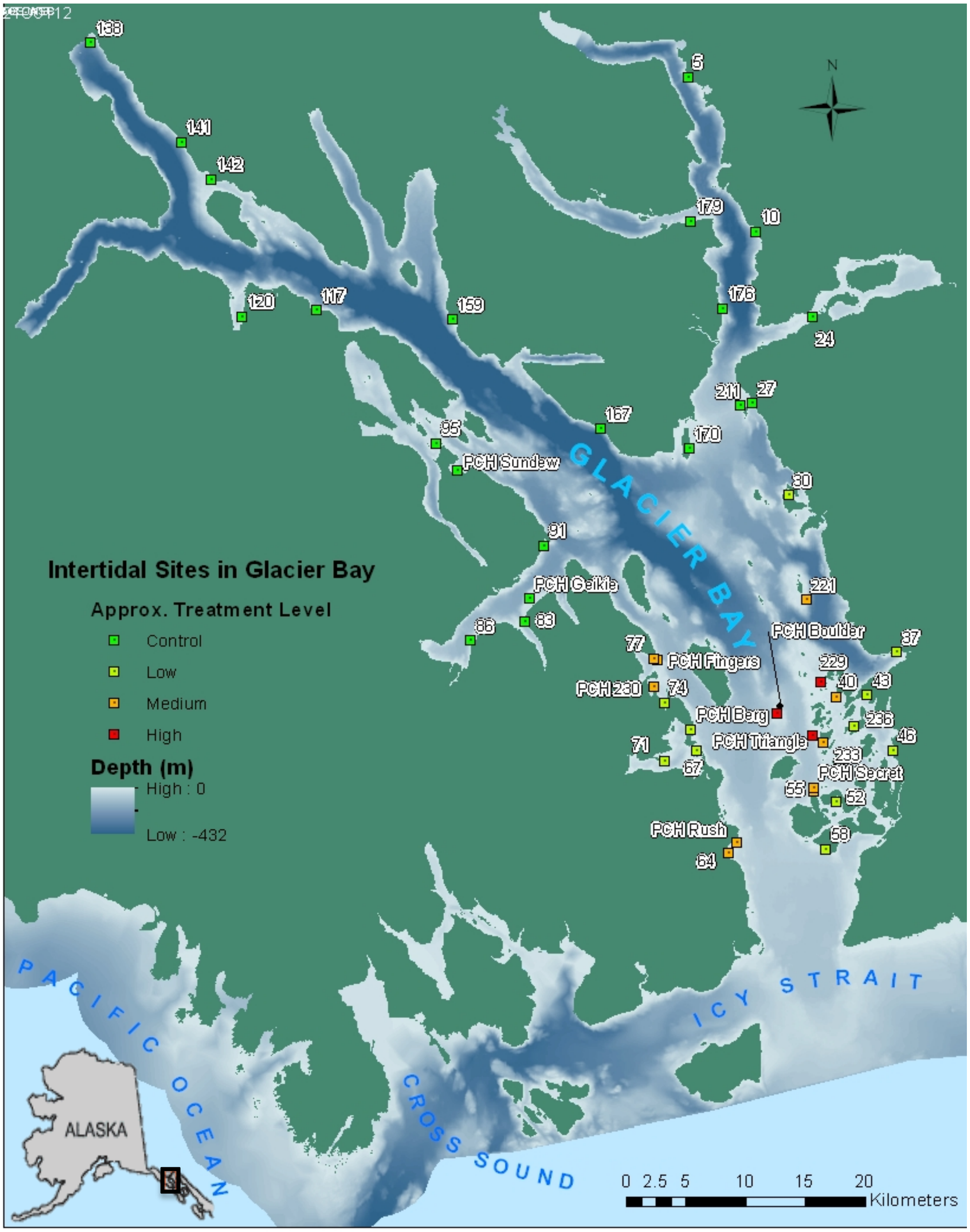

Figure 1. Glacier Bay National Park & Preserve in Southeast Alaska, shown with bathymetry and intertidal sites. Sites are categorized into their treatment levels by color: control, low, medium, and high, explained in detail in this study.

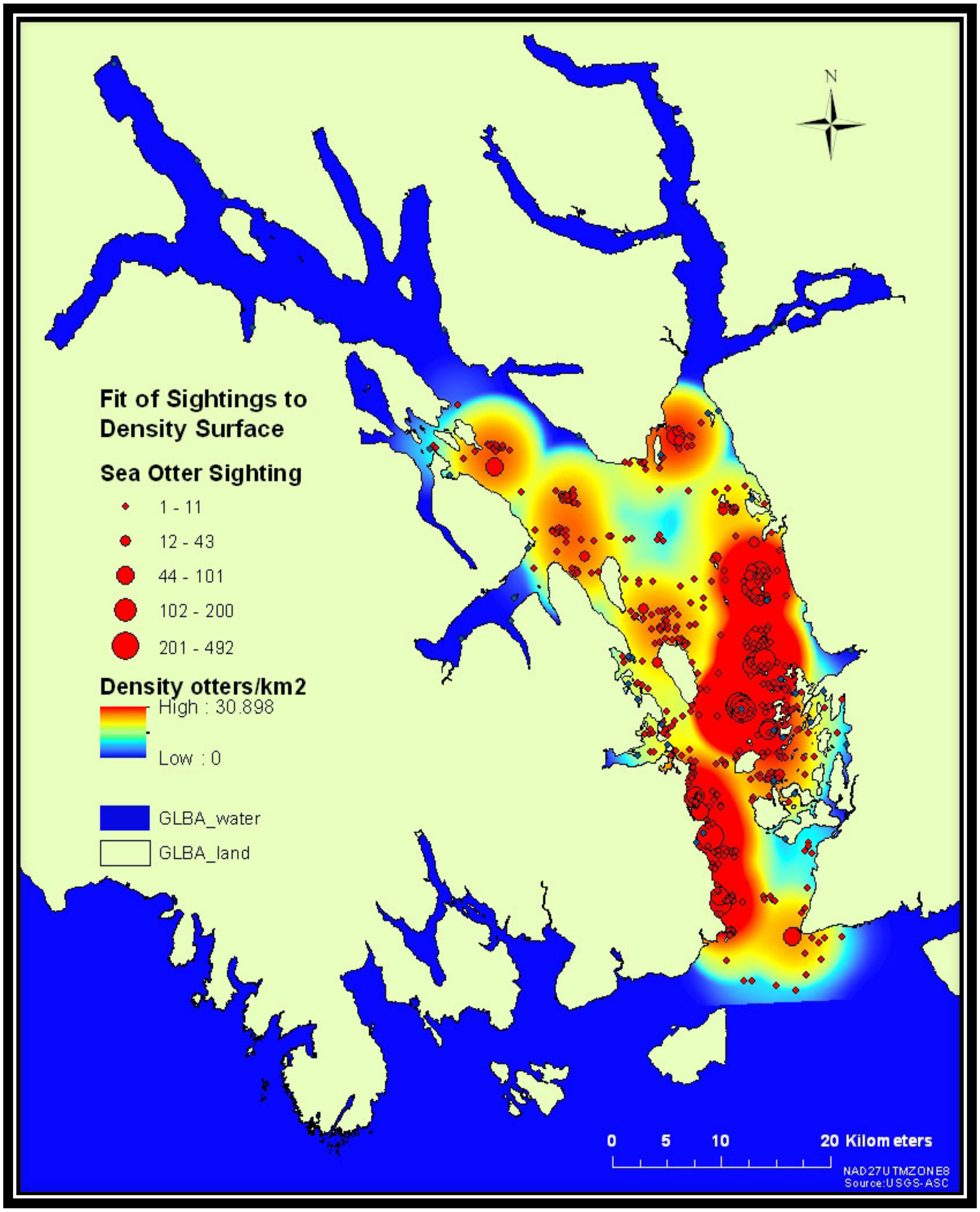

Figure 2. The fit of survey points over the smoothed density surface using KDE from 2012 survey data, high densities of points result in “hot spots”. A smooth surface was generated for each survey and then summed over years to establish a cumulative sea otter density over time.

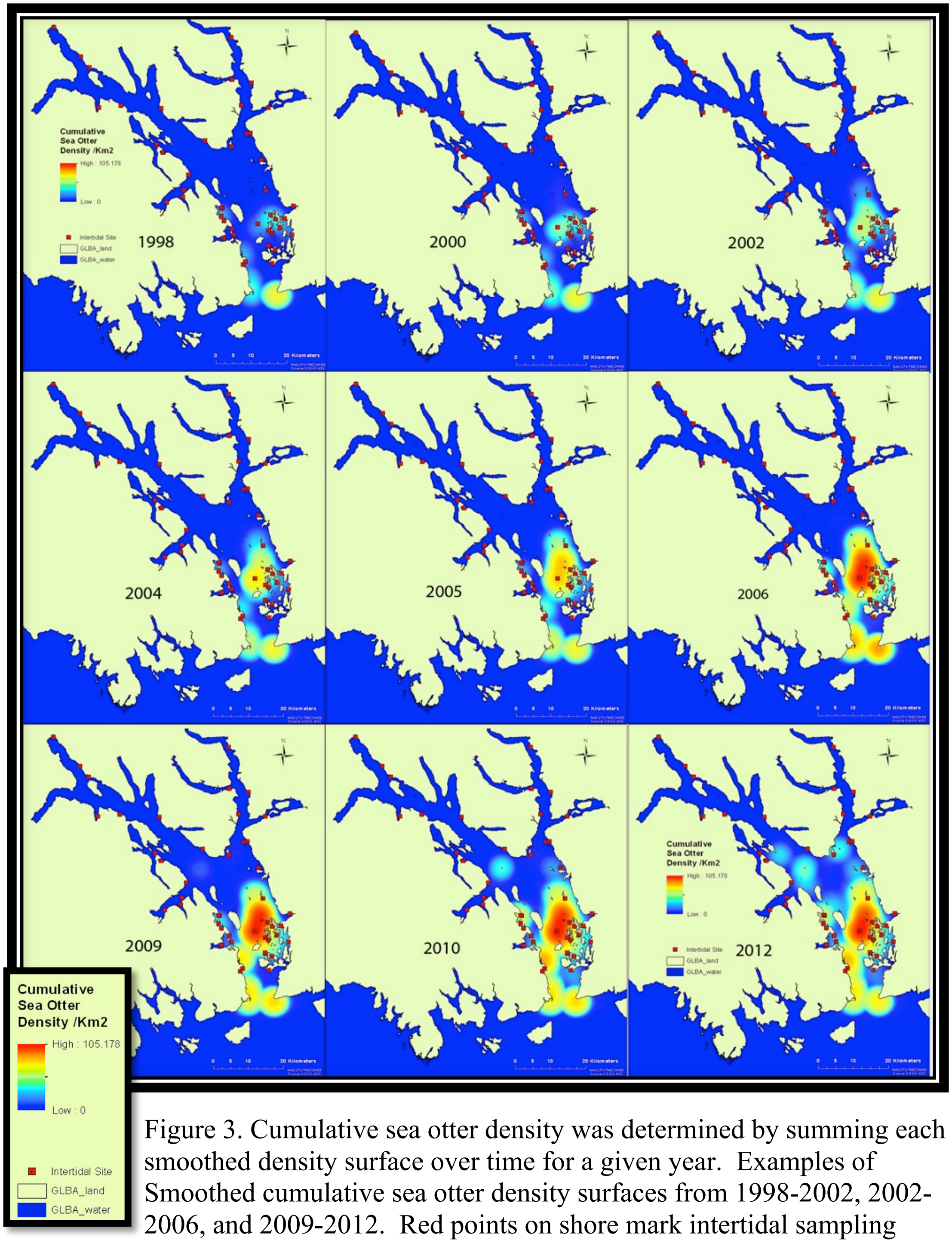

Figure 3. Cumulative sea otter density was determined by summing each smoothed density surface over time for a given year. Examples of Smoothed cumulative sea otter density surfaces from 1998-2002, 2002-2006, and 2009-2012. Red points on shore mark intertidal sampling sites. Analysis included years 1993, 1995-2006, 2009, 2010, 2012.

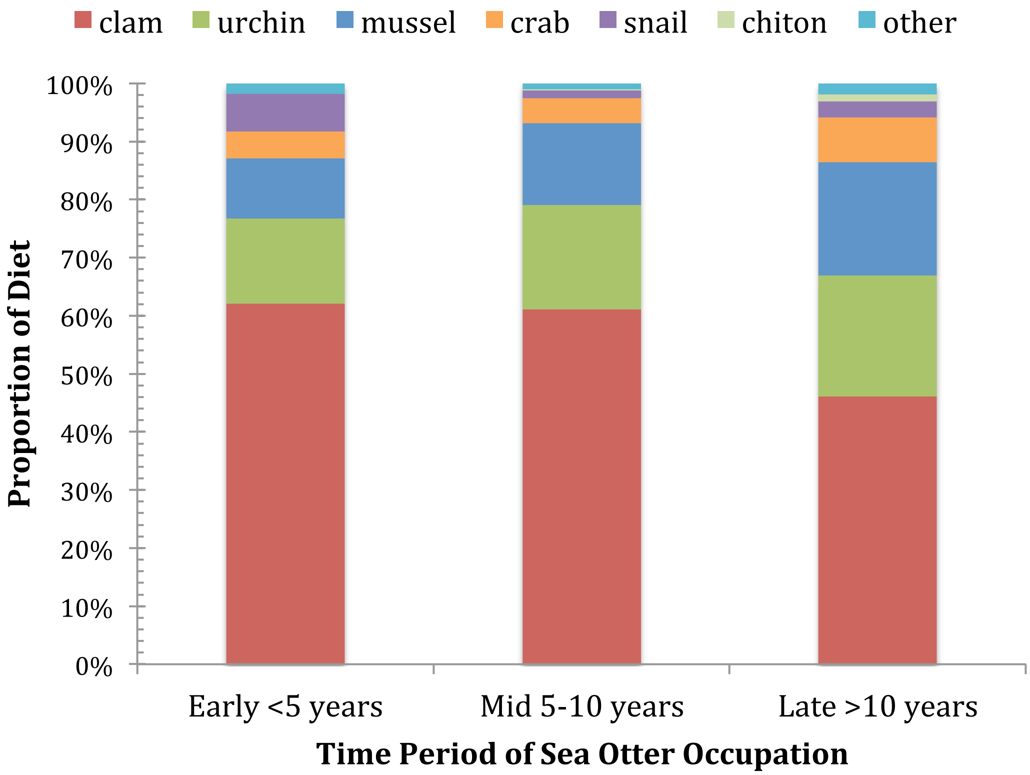

Figure 4. Sea otter diet composition from observed intertidal foraging dives at early, mid, and late time period of sea otter occupation. Clams were observed to be the primary prey in sea otter diet from intertidal foraging bouts.

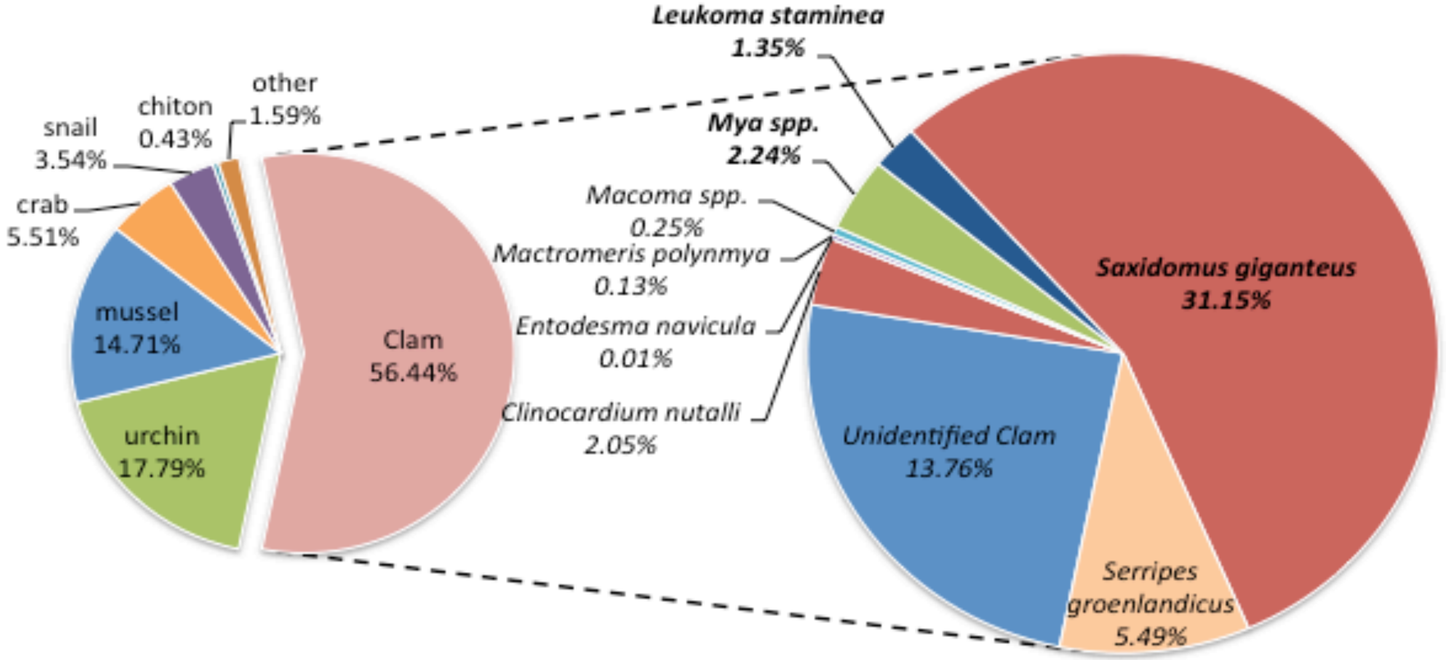

Figure 5 Sea otter diet composition from intertidal feeding dives aggregated through time and expanded to show composition of clams consumed in the diet. *Saxidomus giganteus* was the most widely consumed prey item in Glacier Bay.

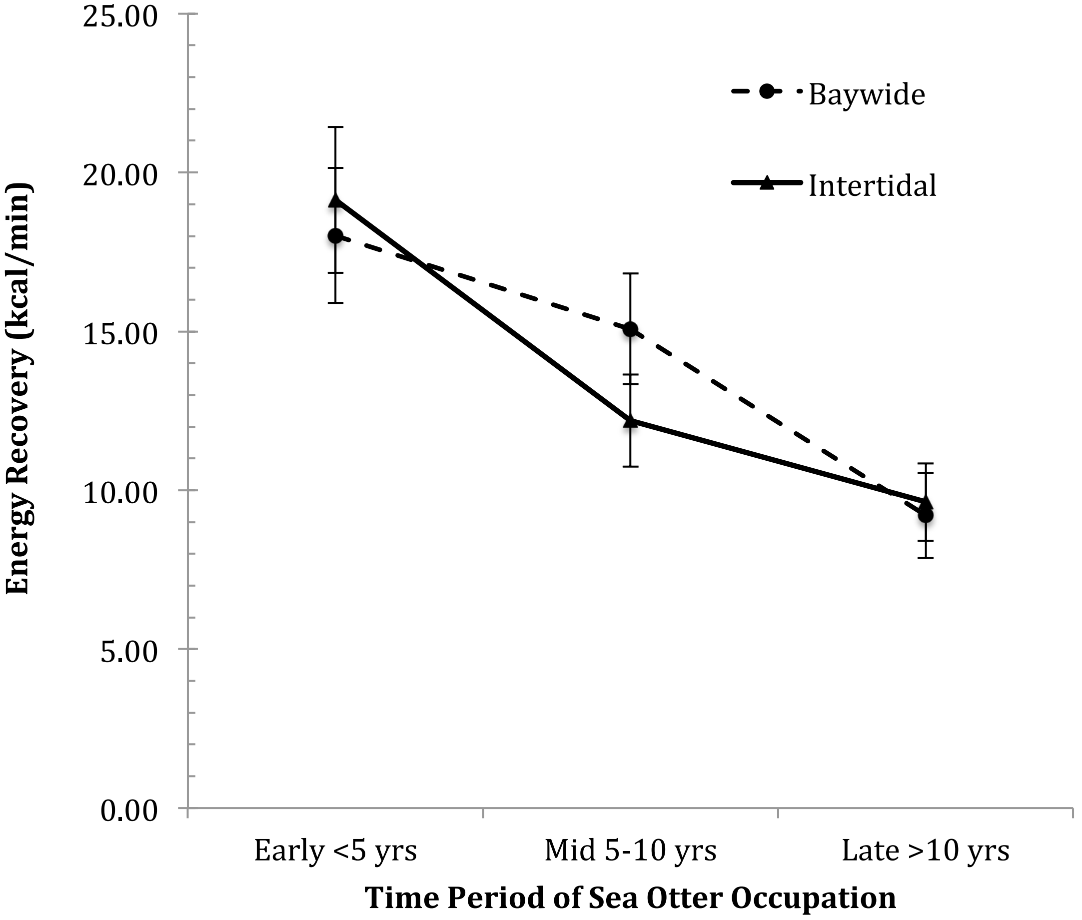

Figure 6. Energy recovery rates In Glacier Bay, overall and from intertidal feeding dives, through time. A decrease in energy recovery results in fewer calories gained per unit time expended foraging, thus sea otter activity patterns would change over time as they must spend more time foraging to meet daily caloric requirements.

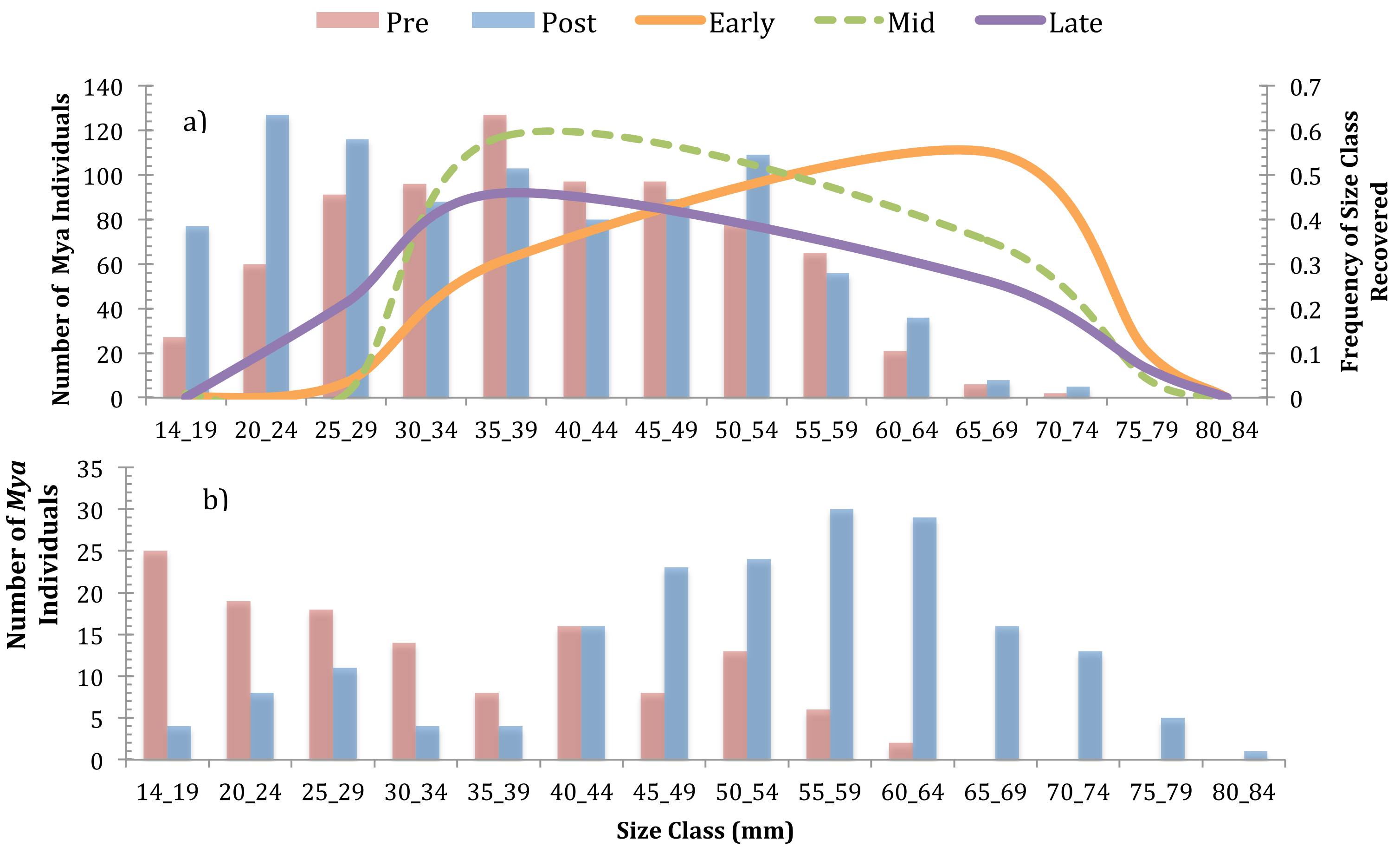

Figure 7. a) The frequency of *Mya spp*. size classes recovered by sea otters during intertidal foraging dives in Early (<5 years), Mid (5-10 years), and Late (>10 years) otter occupation periods over the observed size frequency distributions at intertidal sites at pre and post treatment samplings. b) The size frequency distributions at intertidal sites, pre and post-treatment at control sites were sea otters were not observed.

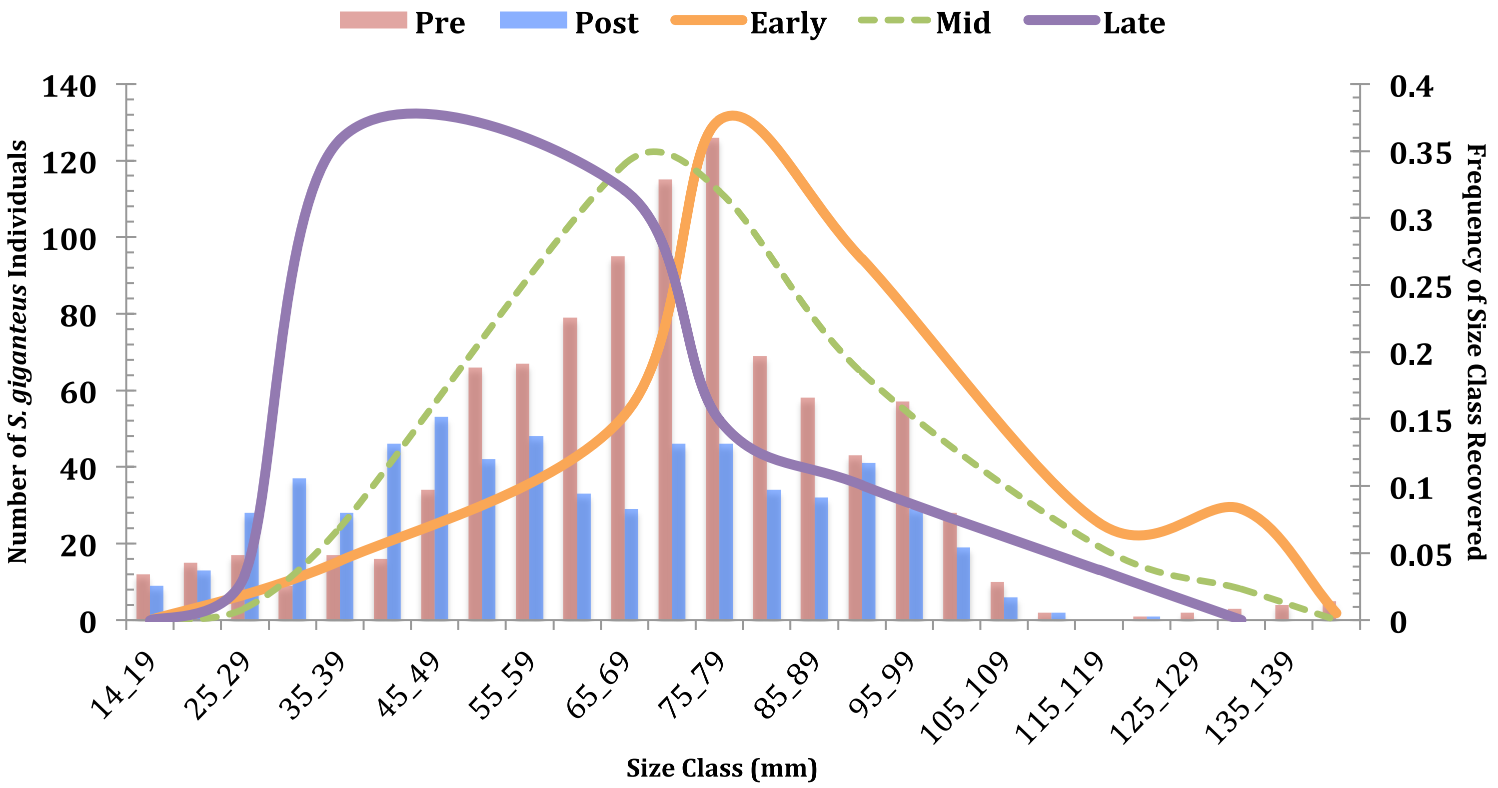

Figure 8. The frequency of *Saxidomus giganteus* size classes recovered by sea otters during intertidal foraging dives in Early (<5 years), Mid (5-10 years), and Late (>10 years) otter occupation periods over the observed size frequency distributions at intertidal sites at pre and post treatment samplings.

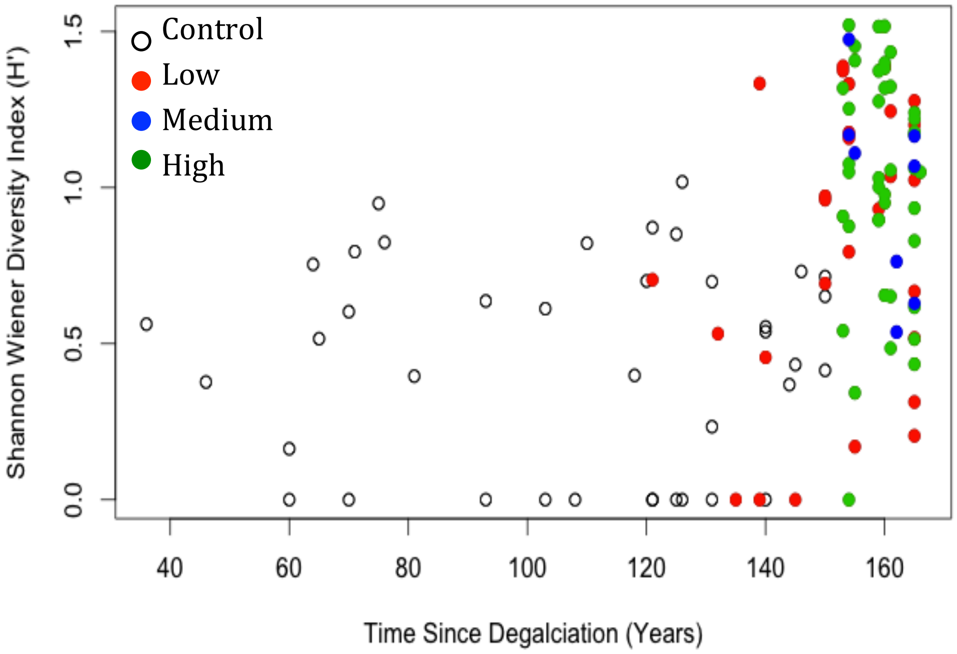

Figure 9. Species diversity (H') as a function of time since deglaciation at intertidal sampling sites (p<.0001). The hollow dots indicate control sites, and the red, blue, and green dots show treatment sites. The control sites were located in the upper Bay arms. H' of zero is a mono-species community.

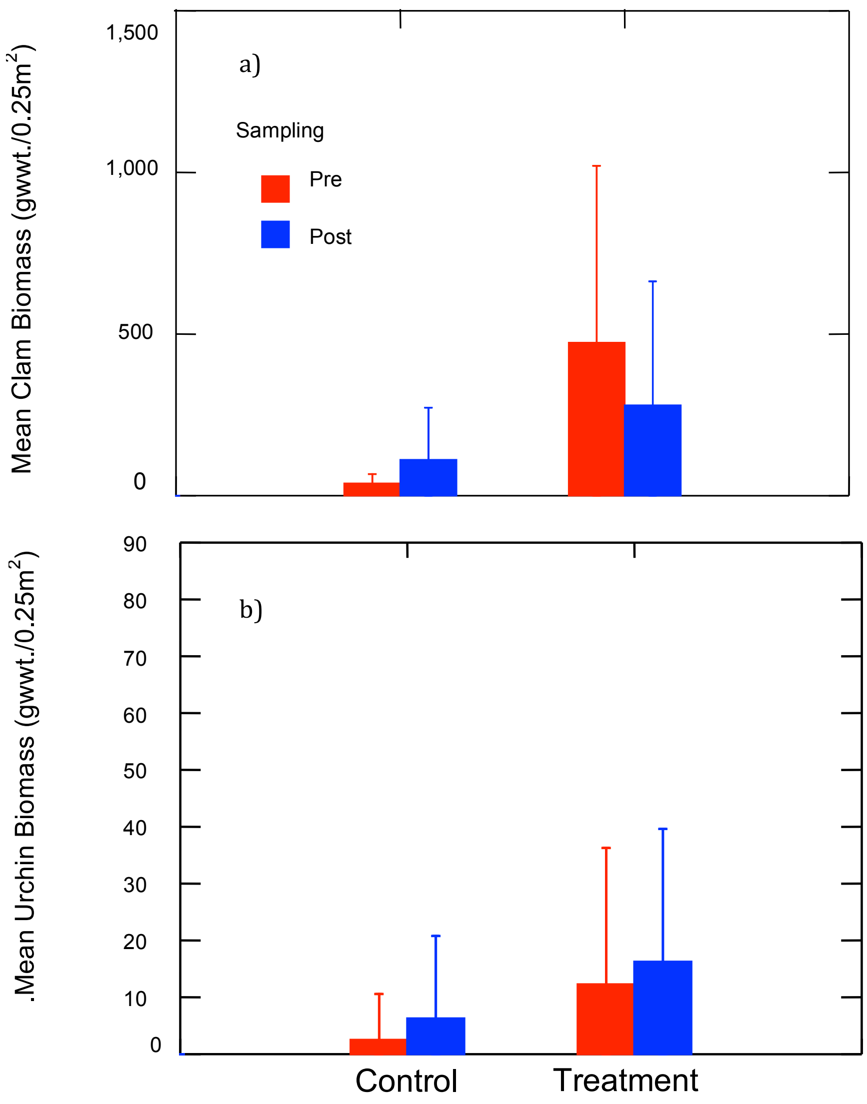

Figure 10. Mean biomass of clam prey species pooled (a) and sea urchins (b) at control and treatment sites before and after the colonization of sea otters.

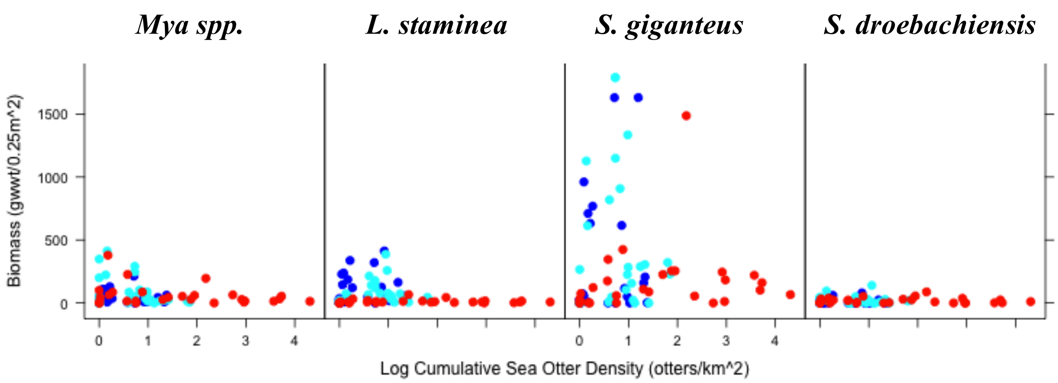

Figure 11. Observed biomass at intertidal sites over the estimated cumulative sea otter density values during pre (Light Blue), intermediary (Dark Blue), and post-treatment sampling (Red).

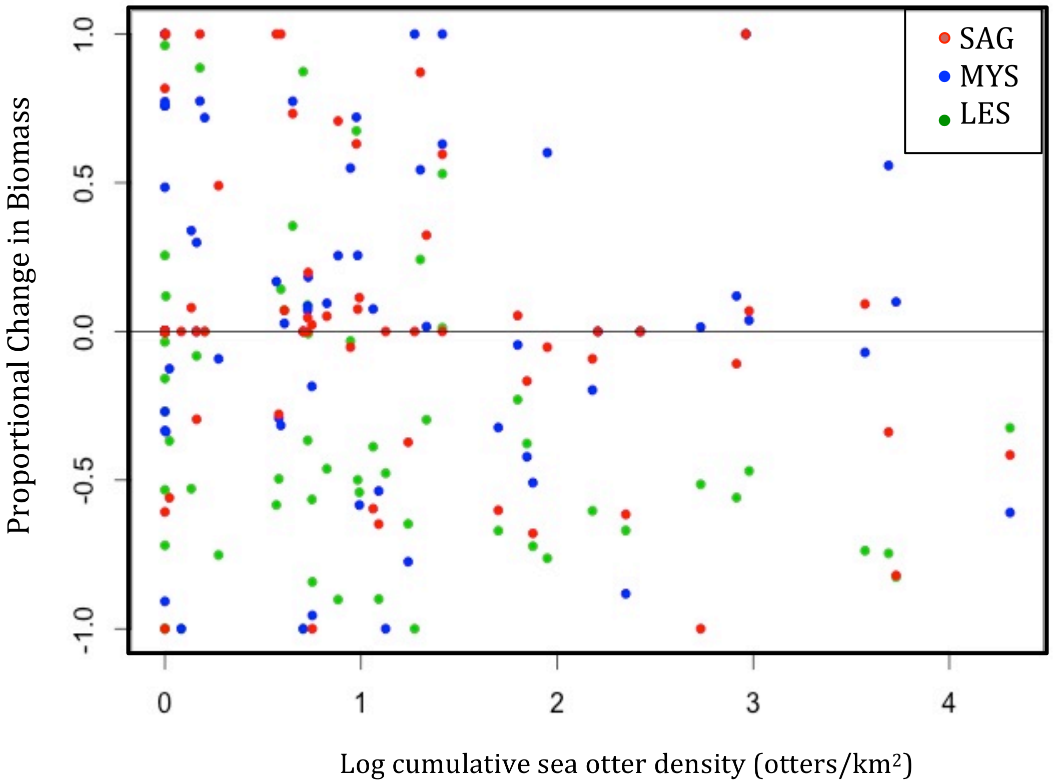

Figure 12. The proportional change in biomass as increasing or decreasing between sampling events as a function of increasing cumulative sea otter density (log scale) for *Saxidomus giganteus, Mya spp., and Leukoma staminea*. At an approximate cumulative density of 6 otters/km^2 we see that intertidal clam populations are much less likely to grow. If sea otters had little to no effect you expect a consistent pattern with increasing density or point to remain focal around 0.

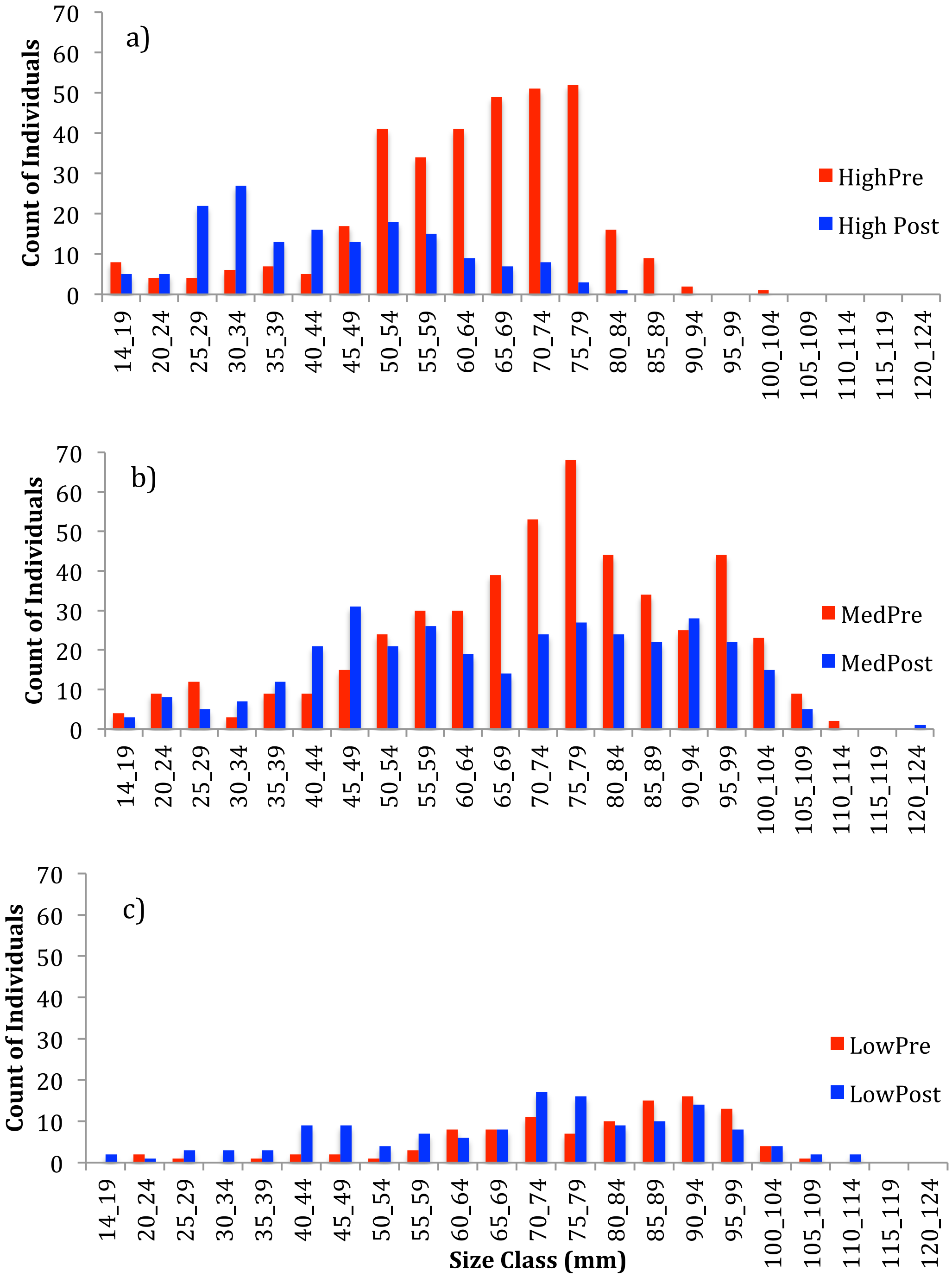

Figure 13. Size distributions of Saxidomus giganteus at a) High, b) Medium, and c) Low impact treatment sites at pre and post-treatment sampling.

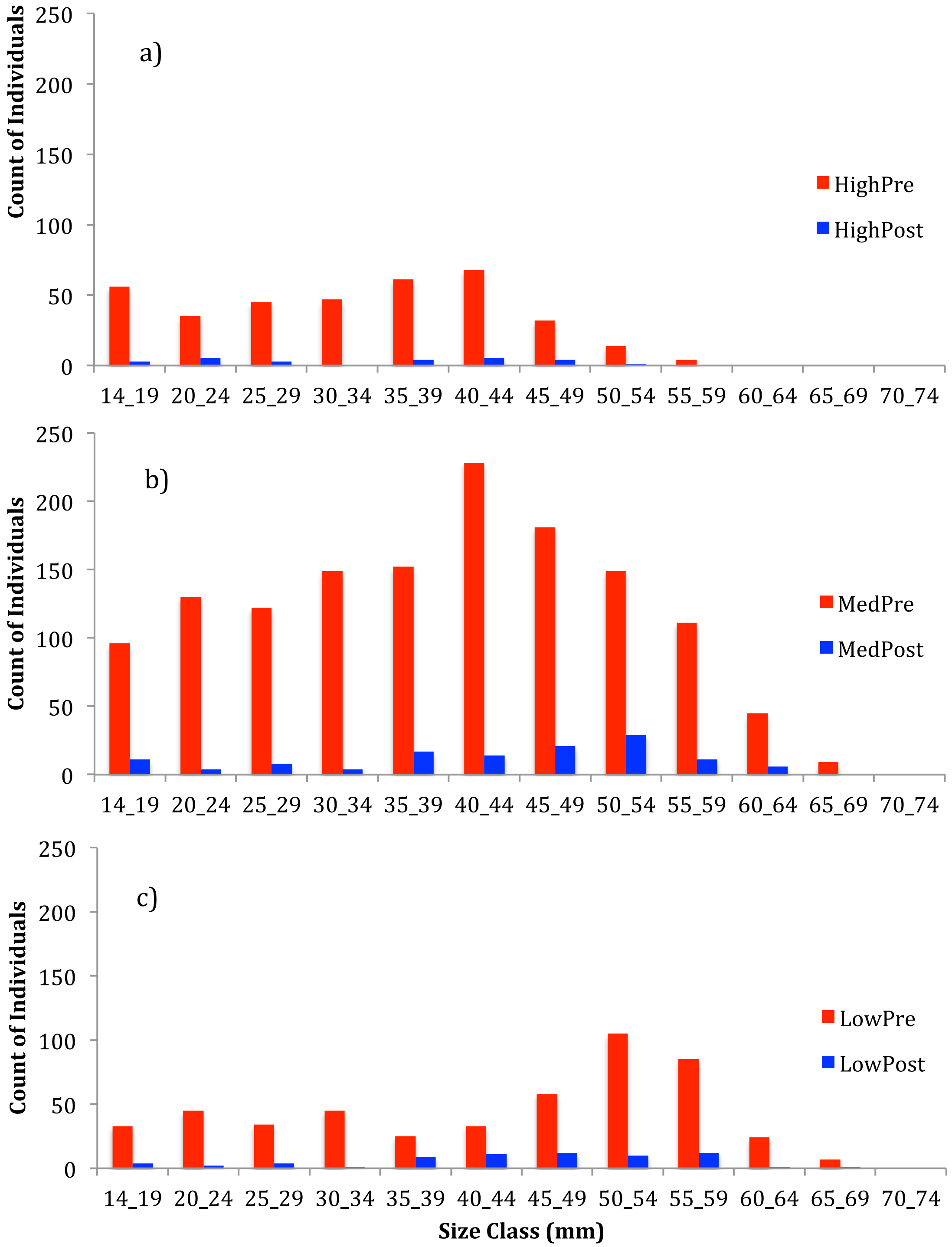

Figure 14. Size distributions of Mya spp. at a) High, b) Medium, and c) Low impact treatment sites at pre and post-treatment sampling.

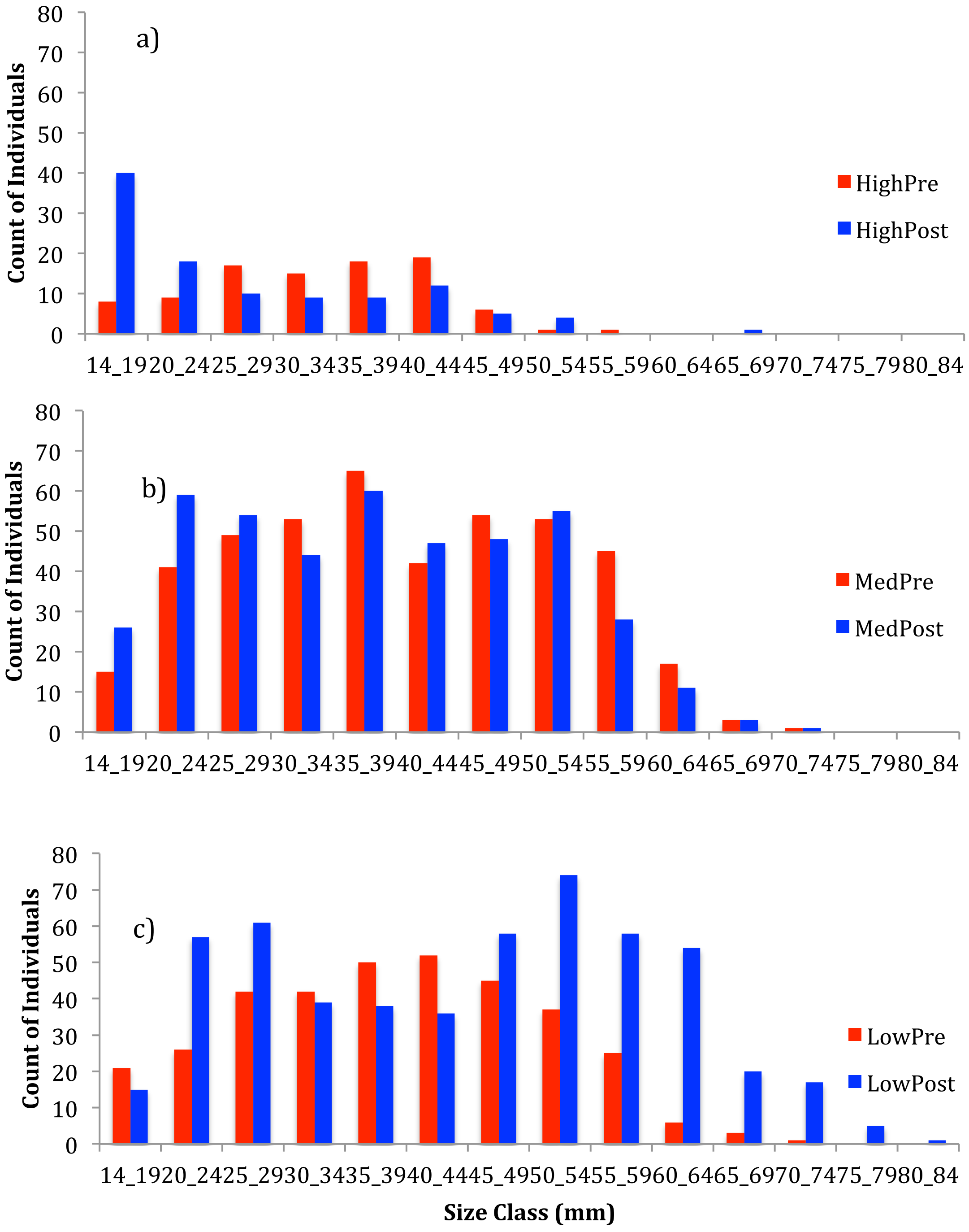

Figure 15. Size distributions of Leukoma staminea at a) High, b) Medium, and c) Low impact treatment sites at pre and post-treatment sampling.

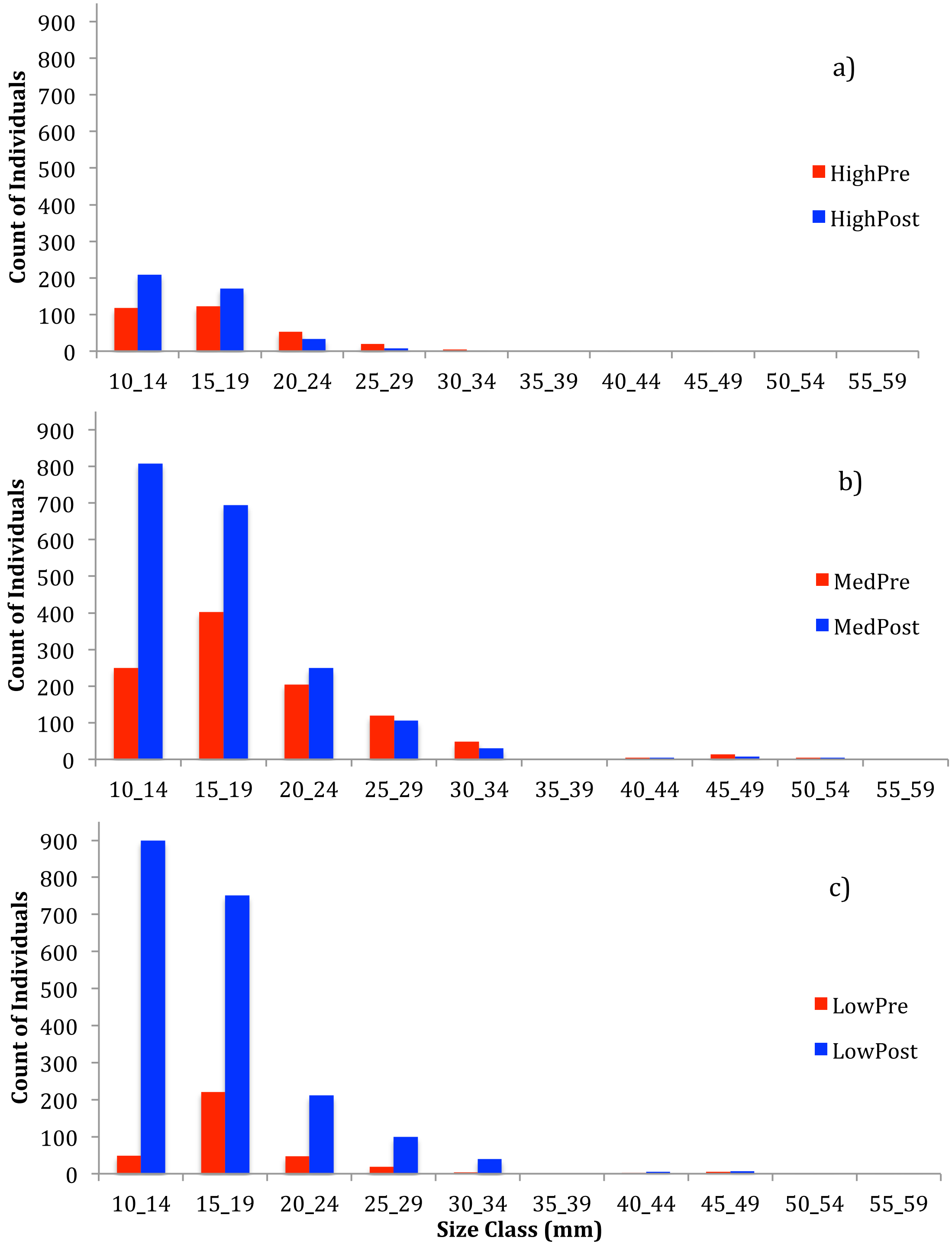

Figure 16. Size distributions of Strongylocentrotus droebachiensis at a) High, b) Medium, and c) Low impact treatment sites at pre and post-treatment sampling.

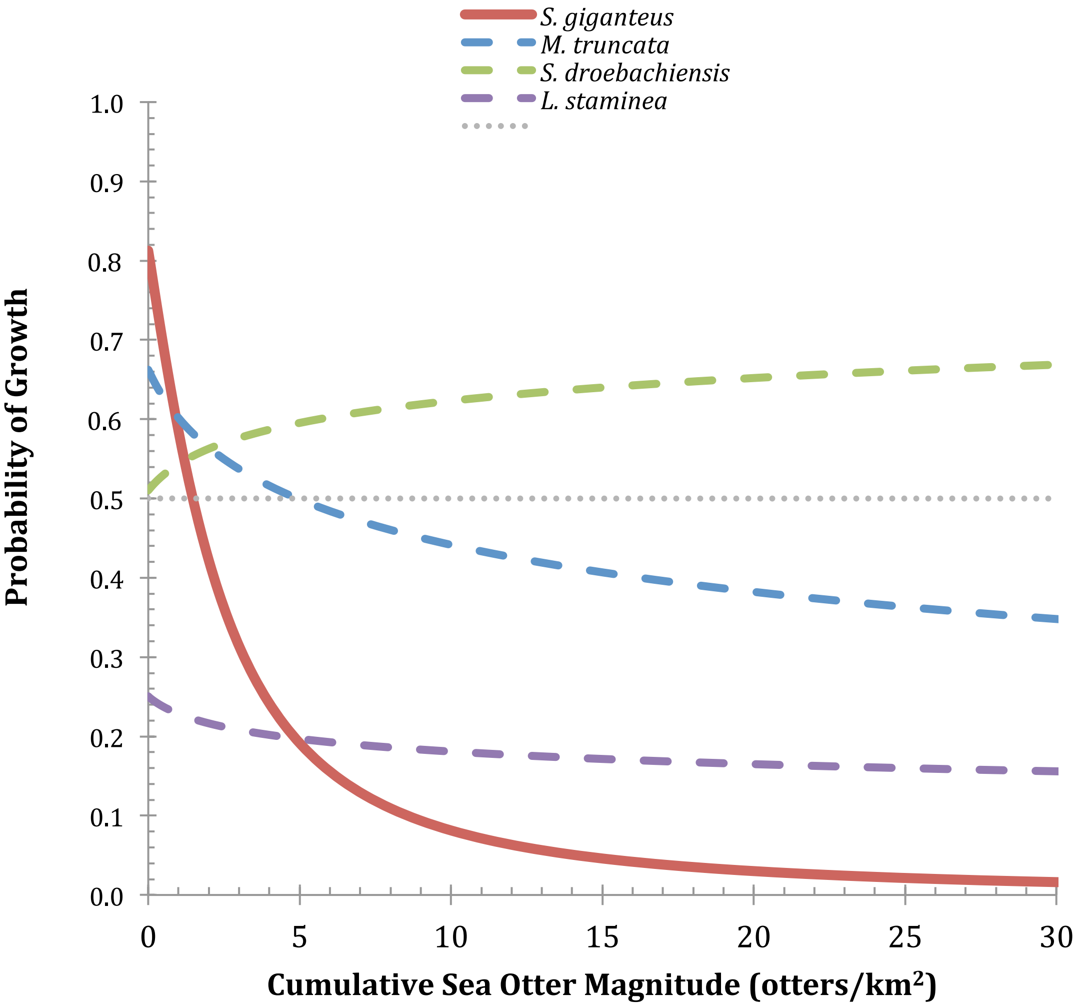

Figure 17. Probability of prey population increase as a function of increasing sea otter density determined by multiple logistic regression of the four primary intertidal prey species. A solid line indicates a significant relationship ($p<0.1$) and a dashed line indicates non-significance ($P>0.1$). The dashed grey line marks 50% probability of growth threshold.

References

Baxter, R. 1964. Earthquake Effects on Clams of Prince William Sound. Pages 238-245 The Great Alaska Earthquake of 1964. National Academy of Sciences, Washington, DC.

Beck, A. L. 2010. Geospatial Analysis of Sea Distribution and Proximity to Intertidal and Subtidal Sites in Glacier Bay, Alaska. University of Arkansas at Little Rock, Little Rock, AR.

Bodkin, J., K. Kloecker, G. Esslinger, D. Monson, and J. DeGroot. 2001. Sea Otter Studies in Glacier Bay National Park and Preserve, Annual Report 2000. U.S. Geological Survey, Alaska Science Center, Anchorage, AK.

Bodkin, J. L., B. E. Ballachey, H. A. Coletti, G. G. Esslinger, K. A. Kloecker, S. D. Rice, J. A. Reed, and D. H. Monson. 2012. Long-term effects of the , Exxon Valdez, oil spill: sea otter foraging in the intertidal as a pathway of exposure to lingering oil. Marine Ecology Progress Series 447:273-287.

Bodkin, J. L., B. E. Ballachey, G. G. Esslinger, K. A. Kloecker, D. H. Monson, and H. A. Coletti. 2007a. Perspectives on an Invading Predator—Sea Otters in Glacier Bay. Pages p. 133-136 *in* Proceedings of the Fourth Glacier Bay Science Symposium. U.S.Geological Survey Scientific Investigations Report.

Bodkin, J. L., B. E. Ballachey, K. A. Kloecker, G. G. Esslinger, D. H. Monson, H. A. Coletti, and J. A. Estes. 2004a. Sea Otter Studies in Glacier Bay National Park and Preserve, 2003 Annual Report. U.S. Geological Survey, Alaska Science Center, Anchorage, AK.

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

Bodkin, J. L. and K. A. Kloecker. 1999. Intertidal Clam Diversity, Size, Abundance, and Biomass In Glacier Bay National Park & Preserve, 1999 Annual Report. U. S. Geological Survey, Alaska Science Center, Anchorage, AK.

Bodkin, J. L., D. H. Monson, and G. G. Esslinger. 2007b. Activity Budgets Derived From Time□Depth Recorders in a Diving Mammal. The Journal of Wildlife Management 71:2034-2044.

Bodkin, J. L. and M. S. Udevitz. 1999. An aerial survey method to estimate sea otter abundance. Marine Mammal Survey and Assessment Methods. Balekema, Rotterdam, Netherlands:13-26.

Burris, O. E. and D. E. Mcknight. 1973. Game Transplants in Alaska: Sea Otters. Alaska Dept. Fish & Game, Anchorage, AK.

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

Connell, J. H. 1961. Effects of Competition, Predation by Thais lapillus, and Other Factors on Natural Populations of the Barnacle Balanus balanoides. Ecological Monographs:61-104.

Cooper, W. S. 1923. The Recent Ecological History of Glacier Bay, Alaska: The Interglacial Forests of Glacier Bay. Ecology 4:93-128.

Dean, T. A., J. L. Bodkin, A. K. Fukuyama, S. C. Jewett, D. H. Monson, C. E. O'Clair, and G. R. VanBlaricom. 2002. Food limitation and the recovery of sea otters following the'Exxon Valdez'oil spill. Marine Ecology Progress Series 241:255-270.

Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. Ecology:447-453.

Eckman, J. E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnology and Oceanography:241-257.

Esslinger, G. G. and J. L. Bodkin. 2009. Status and trends of sea otter populations in Southeast Alaska, 1969-2003. U. S. Geological Survey, Anchorage, AK.

Estes, J. and G. Van Blaricom. 1988. The community ecology of sea otters.

Estes, J. A. 1990. Growth and equilibrium in sea otter populations. The Journal of Animal Ecology:385-401.

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

Estes, J. A., R. J. Jameson, and A. M. Johnson. 1981. Food selection and some foraging tactics of sea otters.*in* Worldwide Furbearer Conference Proceedings, Frostburg, Maryland.

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

Estes, J. A. and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science (New York, NY) 185:1058.

Estes, J. A., C. H. Peterson, and R. Steneck. 2010. Some effects of apex predators in higher-latitude coastal oceans. Pages 37–53 *in* T. J and J. Estes, editors. Trophic cascades: predators, prey, and the changing dynamics of nature. . Island Press, Washington, DC.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, and J. B. C. Jackson. 2011. Trophic downgrading of planet earth. Science 333:301-306.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473-476.

Estes, J. E., N. S. Smith, and J. F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology:822-833.

Etherington, L. L., P. N. Hooge, E. R. Hooge, and D. F. Hill. 2007. Oceanography of Glacier Bay, Alaska: implications for biological patterns in a glacial fjord estuary. Estuaries and Coasts 30:927-944.

Fraser, C. and G. M. Smith. 1928. Notes on the Ecology of the Butter Clam, Saxidomus giganteus. Transactions of the Royal Society of Canada, Series 3:271-291.

Gilkinson, A. K., S. E. Finerty, F. Weltz, T. M. Dellapenna, and R. W. Davis. 2011. Habitat associations of sea otters (Enhydra lutris) in a soft-and mixed-sediment benthos in Alaska. Journal of Mammalogy 92:1278-1286.

Goong, S. A. and K. K. Chew. 2001. Growth of butter clams, Saxidomus giganteus Deshayes, on selected beaches in the state of Washington. Journal of Shellfish Research 20:143-148.

Herter, H. and G. L. Eckert. 2008. Transport of Dungeness crab Cancer magister megalopae into Glacier Bay, Alaska. Marine Ecology Progress Series 372:181-194.

Hodges, J. I., D. J. Groves, and B. P. Conant. 2008. Distribution and abundance of waterbirds near shore in southeast Alaska, 1997-2002. Northwestern Naturalist 89:85-96.

Irvine, G. 1998. Development of Coastal Monitoring Protocols and Process-Based Studies to Address Landscape-Scale Variation in Coastal Communities of Glacier Bay National Park and Preserve,Katmai National Park and Preserve, and Wrangell-St. Elias National Park and Preserve. Phase II: Development and Testing of Monitoring Protocols for Selected Intertidal Habitats and Assemblages., U.S. Geological Survey, Anchorage, AK.

Jameson, R. J., K. W. Kenyon, A. M. Johnson, and H. M. Wight. 1982. History and status of translocated sea otter populations in North America. Wildlife Society Bulletin:100-107.

Jolly, J. M. 1997. Foraging ecology of the sea otter, *Enhydra lutris*, in a soft-sediment community. University of California Santa Cruz, Santa Cruz, CA.

Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. US Bureau of Sport Fisheries and Wildlife Washington, DC, USA.

Khim, B. K. 2001. Stable isotope profiles of Serripes groenlandicus shells. II. Occurrence in Alaskan coastal water in south St. Lawrence Island, northern Bering Sea. Journal of Shellfish Research 20:275-282.

Krumbein, W. C. 1936. The use of quartile measures in describing and comparing sediments. American Journal of Science 32:98-111.

Kvitek, R., J. Oliver, A. DeGange, and B. Anderson. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecology:413-428.

Kvitek, R. G., D. Shull, D. Canestro, E. C. Bowlby, and B. L. Troutman. 1989. Sea otters and benthic prey communities in Washington State. Marine Mammal Science 5:266-280.

Laidre, K. L., R. J. Jameson, E. Gurarie, S. J. Jeffries, and H. Allen. 2009. Spatial habitat use patterns of sea otters in coastal Washington. Journal of Mammalogy 90:906-917.

Larsen, C. F., R. J. Motyka, J. T. Freymueller, K. A. Echelmeyer, and E. R. Ivins. 2004. Rapid uplift of southern Alaska caused by recent ice loss. Geophysical Journal International 158:1118-1133.

MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist 36:287-299.

Maldini, D., C. Ward, A. Cecchetti, and J. Riggin. 2008. Southern sea otter diet in a soft sediment community. Journal of Marine Animals and Their Ecology 3.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64:249-286.

Miller, D. J., J. E. Hardwick, and W. A. Dahlstrom. 1975. Pismo Clams and Sea Otters. California Department of Fish & Game.

Morrison, P., M. Rosenmann, and J. A. Estes. 1974. Metabolism and thermoregulation in the sea otter. Physiological zoology 47:218-229.

Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, Crassostrea virginica. Understanding the estuary: advances in Chesapeake Bay research 129:536-546.

Ólafsson, E. B., C. H. Peterson, and W. G. Ambrose Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre-and post-settlement processes. Oceanography and marine biology: An annual review 32:65-109.

Oliver, J. S., R. G. Kvitek, and P. N. Slattery. 1985. Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. Journal of Experimental Marine Biology and Ecology 91:233-246.

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

Paine, R. 1974. Intertidal community structure. Oecologia 15:93-120.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist:65-75.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of animal ecology 49:667-685.

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

Ralls, K., T. C. Eagle, and D. B. Siniff. 1996. Movement and spatial use patterns of California sea otters. Canadian Journal of Zoology 74:1841-1849.

Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29:436-459.

Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental Impact Assessment:" Pseudoreplication" in Time? Ecology 67:929-940.

Terborgh, J. and J. A. Estes. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press.

Thrush, S. F. 1999. Complex role of predators in structuring soft□sediment macrobenthic communities: Implications of changes in spatial scale for experimental studies. Australian Journal of Ecology 24:344-354.

Thrush, S. F., R. D. Pridmore, and J. E. Hewitt. 1994. Impacts on soft-sediment macrofauna: the effects of spatial variation on temporal trends. Ecological Applications:31-41.

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

Tinker, M. T., P. R. Guimarães Jr, M. Novak, F. M. D. Marquitti, J. L. Bodkin, M. S. Staedler, G. B. Bentall, and J. A. Estes. 2012. Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. Ecology letters 15:475–483.

Vicknair, K. and J. A. Estes. 2012. Interactions among sea otters, sea stars, and suspension-feeding invertebrates in the western Aleutian archipelago. Marine Biology:1-9.

Williams, S. J., M. A. Arsenault, B. J. Buczkowski, J. A. Reid, J. G. Flocks, M. A. Kulp, S. Penland, and C. J. Jenkins. 2006. Surficial sediment character of the Louisiana offshore Continental Shelf region: a GIS Compilation. U.S. Geological Survey Open-File Report 2006-1195.

Williams, T. M. and L. Yeates. 2004. The energetics of foraging in large mammals: a comparison of marine and terrestrial predators. Pages 351-358 *in* International Congress Series. Elsevier.

Wilson, W. H. 1990. Competition and predation in marine soft-sediment communities. Annual Review of Ecology and Systematics:221-241.

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

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

Zajac, R. N., R. B. Whitlatch, and S. F. Thrush. 1998. Recolonization and succession in soft-sediment infaunal communities: the spatial scale of controlling factors. Hydrobiologia 375:227-240.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer.