Estimating Historic Sea Otter Prevalence from Archaeological and Contemporary California Mussel Size Structure

by
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BSc, Queen’s University, 2015

Project Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Resource Management in the School of Resource and Environmental Management Faculty of Environment

Report No. 727

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Spring 2019

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Degree: Master of Resource Management
Report No: 727
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Date Defended/Approved: April 24, 2019
Abstract

Along the northeastern Pacific, the extirpation and subsequent recovery of sea otters generated profound changes in coastal social-ecological systems. Today, most conservation targets for sea otter recovery are formulated on pre-fur trade population estimates reflecting ecosystems devoid of humans. However, evidence suggests that for millennia prior to European contact, complex hunting and management protocols by Indigenous communities limited sea otters at sites of high human occupation in order to enhance local access to shellfish. To make inferences about relative sea otter prevalence in deep time, we compared the size structure of ancient California mussels (*Mytilus californianus*) from five archaeological sites on the Northwest Coast of North America to modern mussels at locations with and without sea otters. To estimate mussel shell length from archaeological umbo fragments, we established a morphometric regression between modern mussel umbo thickness and maximum shell length. We also quantified modern mussel size distributions from eight locations on the central coast of British Columbia, Canada, varying in sea otter occupation time. Comparisons of modern and ancient mussel size revealed that pre-fur trade mussel size distributions are more similar to modern mussel size distributions in the absence of sea otters, suggesting that sea otters prior to the maritime fur trade were maintained below carrying capacity as a result of human intervention. These findings provide broader insight into the conditions under which humans and sea otters persisted over millennia, and potential solutions for their coexistence in the future.

**Keywords:** Historical ecology; sea otter, mussel; *Mytilus californianus*; Indigenous knowledge; shifting baselines
Acknowledgements

I would first like to acknowledge and express my gratitude to the skwx wú7mesh (Squamish), sel̓íwətulh (Tsleil Waututh), Stó:lō (Sto:lo), and xwməθkwəy̓əm (Musqueam) Nations for remaining stewards of the land I’m lucky enough to work and live on during my graduate studies at Simon Fraser University. I would also like to thank members of the Heiltsuk, Nuu-chah-nulth and Haida Nations who have shared their knowledge both directly and indirectly to guide this project.

This work was logistically supported by the Tseshaht, Heiltsuk, and Wuikinuxv First Nations, Pacific Rim National Park Reserve, Bamfield Marine Sciences Centre, and the Hakai Institute. I thank Seonaid Duffield for providing access to samples from EjTa-13, John Maxwell, Ted Knowles, Duncan McLaren, Jennifer Walkus, Denis St. Claire, Wanda Robinson, Erin Rechsteiner, Eric Peterson, and Christina Munck for logistically supporting this work in the field. Thank you to research assistant Anne Tuominen for measuring mussels from the central BC Coast and UVic archaeology field school students for screening archaeological mussel shell samples from Barkley Sound. I was supported by an NSERC Canada Graduate Scholarship. This work was funded by NSERC Discovery grants to IM (531246) and AKS (2016-04492) and a Canadian Foundation for Innovation grant to AKS.

To my supervisors Anne Salomon and Iain McKechnie, it has truly been a gift to work with the two of you. Your commitment to your work and to your students is commendable, and I cannot thank you enough for your mentorship, guidance and patience through this incredible learning process. This project has led me to many new experiences and relationships that have shaped who I am, and I have you both to thank for this.

To Erin Rechsteiner, it was a pleasure working with you and I’ve learned a ton from our time in the field and our conversations since. Thank you for so graciously inviting me to join you in the field, and for the experience, relationships, support and guidance you facilitated. To the rest of the sea otter team at the Hakai Institute, thank you for taking time out of your days to work with me, you made the time and the work pass more quickly.
Thank you to my field teammates in Bella Bella, Markus Thompson, Sachi Ouchi and Hannah Kobluk. You all kept me safe, fed, and sane, followed me onto questionable terrain, all the while making mussel measuring one of my favourite memories. I hope we’ll have more like these to share in the future. Hannah and Markus, I can never repay you for your brave work transporting and storing decaying mussels on my behalf, but I will continue to try.

Finally, this work could not have been completed without the many relationships that kept me going throughout the past 2 and a half years. To my lab mates in the coastal marine ecology and conservation lab, I would not be where I am without you. Sachi Ouchi, Hannah Kobluk, Carolyn Prentice, Natasha Salter, Markus Thompson, Lynn Lee, Jenn Burt, Gabby Pang, Skye Augustine, Heather Earle and Nicky Roberts – you have helped me with everything from getting out of bed in the morning to producing the final figure of my thesis, and for that and everything in between I am forever grateful.

To my REM cohort, you are simply the best. I couldn’t have dreamt up a more supportive group of nerds to share this experience with. Thank you for the endless talks, questions and beers we’ve shared. To Taylor Clark, thank you for getting me out in the wilderness when I needed it most. To Hannah Kobluk, Jess Gill and Tash Salter, thank you for convincing me of my own abilities when I couldn’t.

Finally, to my family, for providing me with a safe space to explore and grow as a person, and for loving and supporting me in every way possible to make this happen. You taught me to be curious and gave me the tools to use it. For this and more I am eternally grateful.
Table of Contents

Introduction .................................................................................................................. 1

Methods .................................................................................................................... 4
  Experimental design .............................................................................................. 4
  Archaeological sites .............................................................................................. 4
  Modern locations ................................................................................................. 4

Historical context ..................................................................................................... 5

Estimating ancient mussel shell length .................................................................. 6

Modern mussel field sampling ............................................................................. 7

Statistical analysis .................................................................................................. 8
  Modern vs. ancient mussel size comparison ..................................................... 9
  Modern mussel size structure ........................................................................... 9

Results ..................................................................................................................... 10
  Modern umbo-shell length regression ............................................................ 10

Modern vs. ancient mussel size comparison ..................................................... 10

Modern mussel size structure ........................................................................... 11

Discussion .............................................................................................................. 13
  Larger ancient mussel size reflects lower sea otter predation in ancient times .... 13
  Modern mussel size cannot be attributed exclusively to sea otter occupation .... 15
  Indigenous management to maintain resource diversity .................................. 16

Archaeological uncertainties .............................................................................. 18

Implications of long-term data in managing human-mediated ecosystem interactions ... 19

Figures .................................................................................................................... 21

Tables ..................................................................................................................... 25

References ............................................................................................................. 27

Appendix ............................................................................................................... 38
List of Tables

Table 1  Results of ANCOVAs testing the effect of A) ecological context (modern with sea otters, modern without sea otters, ancient) and B) occupation time (years) on the relationship between California mussel length and the log proportion of California mussels on the south and central coasts of North America. Significant effects are starred. .......................................................... 25

Table 2  Results of Tukey’s post hoc pairwise comparisons of the relationship between California mussel length (mm) and log transformed proportion of mussels (slopes of each size spectra), between each A) ecological context and B) occupation time on the south and central coasts. Significant results are starred. ................................................................. 26
List of Figures

Figure 1  A) Size of modern and ancient California mussels (*Mytilus californianus*) were compared within two regions (south coast and central coast) along the west coast of North America (see insets). Modern mussels were sampled from intertidal locations (n=12, blue circles) with (closed circle) and without (open circle) sea otters. Ancient mussels were sampled from the faunal remains of archaeological sites (n=5, grey triangles). B) Within the Central Coast region specifically, we sampled mussels from 8 locations along an established gradient of sea otter occupation time spanning 0-37 yrs........................................21

Figure 2  A) Modern California mussel (*Mytilus californianus*) umbo thickness and total shell length were measured to establish (B) a linear relationship between these two morphometrics (n=313 mussels, filled orange squares from this study, all other symbols from McKechnie et al. 2015). 95% confidence interval of the mean is represented by the grey band around the curve. (C) Ancient California mussel umbos were recovered from shell middens, measured and their total shell length estimated from the relationship established in B). .................................................22

Figure 3  Size distributions and size spectra of California mussels (*Mytilus californianus*) from the south coast (A, B) and central coast (C, D) of North America. Modern mussel sizes at locations with sea otters present for 20-40 years (blue filled bars and circles) and without (unfilled bars and circles). Ancient mussel sizes (grey bars and triangles) estimated from mussel umbos collected from archaeological sites. Mean mussel sizes (vertical black lines). 95% confidence interval of the mean is represented by the coloured bands around size spectra lines. ....................................23

Figure 4  Size spectra of California mussels (*Mytilus californianus*) from all modern locations on the A) south and B) central coasts of North America, grouped by sea otter occupation time. Open triangles represent locations occupied by sea otters for 5 years of less, while closed triangles represent locations occupied for more than 5 years. See appendix table 3 for further location information. 95% confidence interval of the mean is represented by the coloured bands around size spectra lines. ........................................24
Introduction

In 1998, Paul Dayton, Mia Tegner, and colleagues identified a challenge at the crux of endangered species management; population baselines cannot be defined without considering potential ecological ‘ghosts’ that served formerly consequential roles in marine ecosystems. Resource managers and coastal harvesting communities have since been challenged in establishing an extended baseline from which to measure ecosystem change, and increasingly acknowledge the importance of archaeological and paleobiological data to broaden perspectives and identify changes beyond the time scales of direct ecological observation which typically only span recent decades (Dayton et al., 1998; Pauly, 1995; Rick & Erlandson, 2009). Long-term datasets are particularly important in marine systems where keystone predators have been eliminated (James A Estes et al., 2011) or have had their ecological role greatly diminished before inclusion in modern management and restoration targets (Dayton et al., 1998; Jackson et al., 2001). There is also a growing acknowledgement of the functional role that humans have played in food webs globally (Salomon et al., 2010; Worm & Paine, 2016), particularly the resource harvesting practices of Indigenous populations over millennia that have greatly diminished since European contact, contributing to misperceptions of ecological baselines (Bliege Bird & Nimmo, 2018; Boivin et al., 2016; Power et al., 2018).

In Canada, an emerging conflict exists between the recovery and protection status of a shellfish predator and the constitutionally protected rights of Indigenous people to access those same shellfish; and the conservation and management solutions hinge on our perspective of baseline and the role humans once played in coastal ecosystems (Pinkerton et al., 2019; Salomon et al., 2015). Currently, sea otters (Enhydra lutris) in Canada are protected under the federal Fisheries Act (R.S.C., 1985), and their recovery is defined as occurring when their "long term persistence in the wild is secured” (Sea Otter Recovery Team, 2007). Functionally, their conservation status is determined by either a positive population trend over 10 yrs or 3 generations, whichever is longest (COSEWIC, 2007; 2015). Population baseline estimates from which ‘pre-exploitation’ sea otter population estimates are informed by early maritime trade pelt landings (Fisher, 1940; Mackie, 1997; Nichol et al., 2015; Rickard, 1947; Sloan & Dick, 2012), and habitat suitability models (COSEWIC, 2007; Gregr et al., 2008). However, the applicability of these estimates as a representation of ‘natural baselines’ is limited, given
that they are based on data and observations of sea otter ecology from recent centuries. A further limiting factor is that this time scale does not reflect the long-term coexistence of sea otters with humans dating back to the early Holocene (Fedje et al., 2005; Szpak et al., 2012).

Archaeological data, specifically shifts in abundance, size and age of faunal remains in ancient assemblages, are increasingly being used to explore population baselines and illuminate changes in food webs in deep time (Braje et al., 2017; Dunne et al., 2016; Haas et al., 2019; Jerardino, 1997; Lotze et al., 2011; Steneck et al., 2002; Steneck et al., 2004). This method can be extended to investigate changes in food web interactions between humans, sea otters and invertebrate prey. In kelp forest ecosystems along the Northwest Coast of North America, spatial and temporal comparisons of the size of zooarchaeological remains has been used to understand how sea otters were managed by coastal peoples. Sea otters are known to serially reduce the size and abundance of their invertebrate prey over time where established populations reside (Estes & Palmisano, 1974; Fanshawe, et al., 2003; Kvitek et al., 1992; Salomon et al., 2007). With an understanding of such size shifts in contemporary food webs, one can draw inferences on the magnitude of predation by sea otters from the size structure of ancient sea otter prey. For example, in the Aleutian Islands, the presence of sea urchins exceeding sizes that can be sustained in areas foraged by sea otters suggests that sea otter populations were kept below carrying capacity by human influence (Corbett et al., 2008; Simenstad et al., 1978). These findings are consistent with zooarchaeological data and isotopic analyses (Szpak et al., 2012) from British Columbia (BC), and indigenous oral histories from the coast of BC and Alaska, where hunters limited sea otters from valued shellfish resources (Ibarra et al. 2017; Salomon et al., 2017; Salomon et al., 2015).

On the Northwest Coast of North America, California mussels (*Mytilus californianus*) provide a prime candidate as a size-based indicator for sea otter predation. Singh and colleagues (2013) found that both mean and maximum mussel size at locations occupied by re-introduced sea otters for 20 years or more were significantly smaller than in regions where re-introduced sea otters were absent. Moreover, ancient California mussels are ubiquitous in archaeological sediments along the Northwest Coast of North America (Jones & Richman, 1995; McKechnie, 2013, 2015; Moss, 1993) throughout the Holocene. Their ubiquity had led to the quantification of several
morphometric relationships (McKechnie et al., 2015), allowing full shell length to be derived from shell fragments, enabling the reconstruction of past mussel size structure (Braje et al., 2018).

Here, we make inferences about the relative magnitude of sea otter predation in deep time based on comparison between ancient California mussel size structure and modern mussels at locations with and without sea otters. We also compared modern mussel size structure across eight locations varying in sea otter occupation time from 0-37 years on the central coast of BC, to investigate variation in the magnitude of the effect of sea otter foraging on modern mussel size. Contrary to the general perception that sea otters were near carrying capacity throughout their range prior to the maritime fur trade, our results suggest that sea otters were well below this maximum abundance near sites of human occupation.
Methods

Experimental design

To establish the relationship between sea otter presence and California mussel (*Mytilus californianus*) size, we measured modern mussel sizes in locations of varying sea otter occupation time on the central coast of British Columbia (BC), Canada to accompany an existing dataset from the south coast of BC and northern Washington, USA (Fig. 1). Ancient mussel size structure was estimated from 6 archaeological sites within these two regions (Table A-1 for site details).

Archaeological sites

We collected shellfish assemblages containing abundant California mussel fragments from 6 archaeological sites from separate ancient Indigenous villages spanning a range of time periods from 2,500 years ago up until approximately AD 1900 on the south coast and 6000-300 cal BP on the central coast (Fig.1, Table A-1). On the south coast, samples come from 4 sites within the Broken Group Island archipelago, in the territory of the modern Tseshalt First Nation, ranging in age from 2500 to 100 BP (McKechnie, 2013, 2015; McKechnie et al., 2019; McMillan & St. Claire., 2005; Smith et al., 2012). Central coast samples come from two sites in the territories of the Hailtzaq (Heiltusk) and Wuikinuxv First Nations. Both sites (Borden numbers EjTa-13 and EjTa-4) have a longer occupation history than the south coast, spanning the mid-late Holocene (Table A-1; Duffield 2017).

Shellfish assemblages from archaeological sites were extracted using several methods, including vibracore (Duffield, 2017), auger (McKechnie, 2013, 2015), column samples (Gilchrist, 2017) and hand collection from exposed midden (Table A-1). All samples were screened through 2mm mesh and nothing below this size was measured (Table 1).

Modern locations

In the south coast region modern mussel sizes were measured in 2009 by Singh et al. (2013). This study used a space for time substitution approach, using the
expanding margins of the sea otter’s range to define four regions varying in sea otter occupation time – the minimum length of time a region had been observed to have been occupied by otters. These four regions represent four temporal categories of occupation time: Kyuquot Sound (40 years), Neah Bay (20 years), Clayoquot Sound (<5 years), and Barkley Sound (no otters).

In the central coast region, we also used a space for time substitution (Pickett, 1989) to represent a gradient of sea otter occupation from our 8 sample locations. A location was considered occupied by the presence of a raft (>3 otters) within 5.5 km of a location (Stevenson et al., 2016). Raft presence was recorded during range-wide population surveys conducted every five years from 1990-2013, augmented by surveys and reports of sea otter rafts in between these surveys (Nichol et al. 2009; Nichol et al., 2015; Nichol et al., 2005), and observations from colleagues (Lee, Burt pers comm).

We used sea otter occupation time over population abundance as a proxy for sea otter predation intensity on mussels because sea otter range expansion is observed to occur first through the expansion of male sea otters, who tend to establish new high-density rafts in previously unoccupied territory (Garshelis et al., 1984), followed by smaller rafts of females and pups. Moreover, the serial depletion of benthic invertebrates by sea otters has been documented in similar habitats elsewhere, whereby more economically valuable subtidal prey are consumed at early recently-occupied locations followed by less-valued intertidal species (such as mussels) at longer-occupied locations (Honka, 2014; Salomon et al., 2007; Tinker et al., 2008).

**Historical context**

Prior to the maritime fur trade which began in the late 18th century, sea otters ranged from Japan, north through the Aleutian Islands and down the Pacific coast of North America to Baja California (Barabash-Nikiforov, 1947; Kenyon, 1969; Lensink, 1962). Sea otters were ecologically extirpated from the Northwest Coast of North America by the mid 1800s (Kenyon, 1969; Sloan & Dick, 2012). Following over a century of their functional absence, sea otters were reintroduced to the south coast of BC on the west coast of Vancouver Island and to northern Washington via translocations from Aleutian Islands between 1969-1972 (Bigg & MacAskie, 1978; Kenyon, 1970).
Populations were documented as reaching the central coast of BC in 1989, assumed to have originated from the reintroduced population in BC.

Today, sea otter population size and growth trajectories vary spatially and temporally across the Northwest Coast North America. Surveys conducted by Fisheries and Oceans Canada in 2013 counted 5,612 individuals in the south coast region and 1,142 individuals on the central coast, with estimates of the Washington, US population at 1,753 animals based on 2015-2017 surveys (Jeffries et al., 2017; Sato, 2018). Since their reintroduction, the population growth rate of sea otters in the south coast of Canada has declined from 19% per year between 1977 and 1995, to 8.4% per year between 2004 and 2008, and to a most recent estimate of 7.12% per year from 2008-2013 (Nichol et al., 2015). On the central coast however, the population growth rate of sea otters decreased from 12.4% from 1990-2004, to 4.22% per year between 2004-2008, and then increased to 12.56% per year between 2008 and 2013 as further range expansion occurred (Nichol et al., 2015, 2005). The Washington population has been growing since 1989 at an overall growth rate of 9.5% per year (Sato, 2018).

**Estimating ancient mussel shell length**

To determine total California mussel shell length from fragmentary ancient specimens, we expanded on an existing valve length to umbo thickness relationship established for modern mussels by linear regression analysis (McKechnie et al., 2015). We expanded the upper size range of this dataset with large mussel shells (n = 50) collected from Barkley Sound, BC in 2018. This contemporary morphometric relationship was chosen to estimate ancient shell length because umbos are the most robust portion of the mussel preserved in midden deposits, and represent the origin of shell growth, a strong predictor of full shell length (Ford et al., 2010; Seed, 1968). Umbo thickness was measured from the tip of the umbo to the inside of the hinge using digital calipers (Fig 2A), while shell length was measured from the outer umbo to the point on the shell’s end that measures the longest linear dimension. See McKechnie et al. (2015), and Singh and McKechnie (2015) for detailed methods

We then fit a saturating curve to these data using the *nls()* function in R, using a least squares method, predicting shell length from umbo thickness (Fig. 2B; Equation 1).
\[ y = \frac{544.81x}{24.75+x} \quad (1) \]

This equation was used to estimate all total shell length values representing our archaeological (ancient) data. Confidence intervals around the saturating curve were computed using Monte Carlo simulation of the normal distribution around each predictor value using the `predictNLS()` function in the `propagate` package in R.

In order to explore the nature of the relationship between umbo thickness and total shell length, we also fit a linear regression to our umbo thickness-total shell length data \( y = 13.3 + 14.5x \), using the `lm()` function in R. We chose between the linear and saturating models based on the amount of variation they explained and their potential to overestimate total shell length values (see further justification under Results, p. 10)

Site and sampling details regarding all archaeological data can be found in Table A-1. Inter-observer measurement discrepancy and error were minimized by using a consistent measurement approach, carried out by two trained observers.

**Modern mussel field sampling**

In the south coast region, California mussels were sampled by Singh et al. (2013) at 3 intertidal mussel beds in each of our four regions representing different sea otter occupation times, from ten 25x25 cm quadrats randomly placed along a horizontal transect at the middle and lower regions of a mussel bed. From each quadrat, 15-50 individuals were randomly selected and measured along their longest linear dimension.

On the central coast region, we recorded California mussel size from 8 intertidal areas on the central coast of BC, varying in sea otter occupation time from 0 - 37 years (Fig. 1B). At each location, we measured mussels from six 25x25 cm quadrats randomly placed along a 30m horizontal transect at the middle \( n=3 \) and lower \( n=3 \) regions of the mussel bed. Rather than taking a subset as Singh et al. (2013) did, we collected and measured all mussels along their longest linear dimension.

We also measured a random subset of unprocessed California mussels in 2017 that had been harvested for consumption by two members of the Tseshahat Beachkeepers, who patrol the Broken Group Islands in the summer. We collected a random subset from the bin of all harvested mussels by closing our eyes and extracting
aggregated clumps of mussels until we filled two smaller buckets (n=261). After measuring the longest linear dimension of all mussels from this subset with calipers, we compiled this mussel length data to produce a size-frequency distribution (Fig. A-5).

**Statistical analysis**

We compiled size frequency distributions of both modern and ancient mussel size by site/location, and converted them to size spectra - linear descriptions of the abundance of individuals per size class in a population or community (Edwards et al., 2005; Sheldon & Parsons, 1967; Sheldon et al., 1972). Specifically, size spectra are linear models fit to size frequency data, providing a slope to describe the relationship between abundance and body size class.

Prior to this analysis, we eliminated all mussel sizes below 20mm in order to create more comparable samples between modern mussels, which represent samples of the intertidal population, and archaeological data, which represent mussels selectively harvested for food by humans. This cut-off was selected because it represents the smallest estimated shell length from our archaeological data apart from a single outlier (18mm), representing an approximate lower detection limit for archaeological mussels. Furthermore, mussels below 20mm are unreliably detected and measured in both modern and archaeological samples. Though 20mm is below the size of mussels typically consumed, examination of the size structure of a modern mussel haul in 2017 demonstrates that mussels in this size range are often represented in the bycatch of a mussel harvest (Fig. A-5), and are thus represented in archaeological deposits. We grouped shell lengths into 10mm bins to capture the range of values needed to fit a relationship without small scale variability interfering with detection of the overall trend. The proportion of values in each bin was then calculated, and the midpoint of each bin was plotted against the log transformed proportion of their abundance, converting size-frequency distributions to size spectra. Confidence intervals for each size spectra were generated based on the standard error around the mean estimate of the response variable.

We also produced size spectra with centered x axes (Fig. A-3,A-4), by subtracting the midpoint of each length bin by the mean midpoint value on the x axis of each size spectra, producing an x axis that is centered around 0. This returns a model
coefficient representing the proportion of mussels at 0 on the centered x axis (see Fig.A-3,A-4), which provides an index of population abundance of mussels (Graham et al., 2005). However, we found this representation less useful for interpreting shifts in actual mussel size than non-centered size spectra.

**Modern vs. ancient mussel size comparison**

To test for the effect of sea otter presence on the relative proportion of modern and ancient mussel sizes, we ran an ANCOVA with ecological context (modern mussels with sea otters, modern mussels without sea otters, ancient mussels) as a fixed effect and mussel length as a covariate (Table 1). We then used post hoc Tukey pairwise comparisons between the slopes of size spectra for each ecological context to test for differences among specific ecological contexts (Table 2).

To represent the ecological context “modern with sea otters”, on the south coast we combined modern mussel lengths from locations with sea otter occupation times of 20 and 40 years, and on the central coast from two locations with sea otter occupation times of 21 and 37 years. The ecological context “modern without sea otters” is represented on the south and central coasts by mussel size from all sample locations where sea otters were absent (occupation time = 0 years). All archaeological mussel size data from each region were included to represent “ancient” ecological context (aka. prior to the maritime fur trade).

**Modern mussel size structure**

To test for an effect of sea otter occupation time on modern mussel size we ran an ANCOVA with occupation time as a fixed effect and mussel length as a covariate (Table 1) and post hoc Tukey pairwise comparisons between the slopes of size spectra for each occupation time (Table 2).
Results

Modern umbo-shell length regression

With the additional data added to McKechnie et al. (2015)’s previously-established regression, we found a significant linear relationship between modern mussel umbo thickness and total shell length (Fig 2B, p < 2.2e-16, n=313 mussels). Specifically, umbo thickness explained 87% of the variation in total shell length (Fig. A-1, y=13.26 + 14.52x, R²=0.87), improving upon the previous regression by 3% (McKechnie et al. 2015; R²=0.84). However, residuals are larger at larger umbo thickness values, making predictions at the larger size range more uncertain. We also found a significant saturating relationship between modern mussel umbo thickness and total shell length (Fig. 2B, p=1.07e-8). As expected, the saturating curve explained slightly more variation (Fig. 2B, y=(544.81*x)/(24.75+x), R²=0.89) than did the linear relationship. We chose to use the saturating curve to estimate the total shell length of our archaeological mussel fragments, due to its stronger R² value and the more conservative estimates that predicted at larger umbo thickness values. We chose this more conservative model because large mussel length values have a strong influence on the slope of size spectra, creating the potential for large estimates of mussel length to have a disproportionate influence on our comparisons of modern and ancient mussel size.

Modern vs. ancient mussel size comparison

Overall, we observed smaller California mussels in modern areas with sea otters compared to modern areas without sea otters, on both the south and central coasts. We also observed that ancient mussel size distributions most resembled modern mussel size distributions at locations without established populations of sea otters on both the south and central coasts (Fig 3, Table 2A). Specifically, along the south coast, the size distribution of modern mussels at localities occupied by sea otters was truncated in comparison with both the size distribution of mussels at modern locations lacking sea otters and the ancient mussel size distribution (Fig 3A). Modern mussels at locations occupied by sea otters had smaller mean and maximum shell lengths (Table A-3A, 47.91±0.38mm, 103mm respectively) compared to locations without sea otters (Table A-
In our size spectra analysis on the south coast, we found a significant effect of ecological context (modern with-, without sea otters, ancient) on the relationship between mussel length and the log transformed proportion of mussels (Table 1A; F=5.54, p= 0.005). We detected a significantly steeper slope of size spectra at locations with sea otters than in both ancient mussel size spectra (Table 2A; Tukey adjusted slope comparison: p=0.003), and size spectra from locations without sea otters (Table 2A; p=0.008). In contrast, we did not detect a significant difference in this rate between locations without sea otters and ancient data (Table 2A, p=0.72).

We found similar patterns, although less pronounced in the central coast region (Fig 3C, Table 3), with a smaller difference between mean mussel size at locations with sea otters (Table A-3B 39.40±0.22mm) compared to locations without sea otters (Table A-3B, 45.56±0.35mm) and ancient mussel size (Table A-3B 73.94±1.40mm). Maximum mussel size was smaller at locations with sea otters (132 mm), than at locations without sea otters (182 mm) and ancient mussel size (166.00±4.25mm).

We also found a significant effect of ecological context on the relationship between mussel length and log-transformed proportion of mussels on the central coast (Table 1A; F=8.98, p=0.001). Again, we detected a significantly steeper slope of size spectra at location with sea otters than in both ancient mussel size spectra (Table 2A; Tukey slope comparison: p=0.0009), and size spectra from locations without sea otters (Table 2A; p=0.034). However, we did not see a significant difference between this rate at locations without sea otters compared to ancient data (Table 2A, p=0.13).

**Modern mussel size structure**

On the south coast, the slope of modern size spectra decreased with increasing occupation time (absent to 40 years; Fig. 4, Table A-3A). Building on the observations of Singh et al. (2013), this trend suggests that larger mussels are more common at locations where otters are absent and get smaller as their occupation time increases. However, this effect of occupation time on the relationship between mussel length and the log-transformed proportion of mussels is not significant (Table 1B; F=1.89, p=0.15),
and pairwise comparisons of these slopes at each occupation time revealed no significant differences (Table 2B).

On the central coast, where we have more finely resolved modern occupation time and spatial information, we observe a significant effect of occupation time on the relationship between mussel length and the log-transformed proportion of mussels (Table 1B; F=15.92, p= 2.33e-08). Locations with sea otters tended to have steeper size spectra slopes than locations without sea otters. However, in contrast to the south coast, we did not observe a consistent increase in slope with each increase in occupation time (Appendix Table 3). The shallowest slope of size spectra from our modern central coast data was found where otters were absent (occupation time = 0 years; Table A-3B: slope = -0.00057). However, the steepest slope value from our length-proportion size spectra was found at 21 years of occupation (Table A-4B: slope = -0.0025), and unexpectedly, slope was shallower at our longest-occupied location (37 years; Table A-4B: slope = -0.00081). Through pairwise comparisons, we found that only the slope at 21 years of occupation varied significantly from all other locations (Table 2B, p<0.0001).

From the harvest profile of mussels collected by the Tsersaht Beachkeepers in 2017, we found that mussel size ranged from 11mm to 170mm, with a mean length of 76.33±2.18mm (n=261; Fig. A-5).
Discussion

Our results provide further evidence supporting the hypothesis (Szpak et al., 2012) that on the Northwest Coast of North America prior to the maritime fur trade, sea otters existed below carrying capacity in proximity to human settlements. That is, indigenous communities prior to the maritime fur trade maintained access to significantly larger mussels than those found at modern locations with sea otters (Fig. 3, Table 2). We suggest that these findings are indicative of a human-mediated limitation of sea otters where humans harvested mussels during the late-Holocene on the Northwest Coast of North America.

In the contemporary environment, we found that the relationship between sea otter occupation time and modern mussel size varied within and between regions. The change in the proportion of mussels across its length range varied significantly with sea otter occupation time on the central coast, but not the south coast (Fig 4, Table 1,2, Fig.A-2). These findings modulate the inferences we can make regarding sea otter populations exclusively based on archaeological mussel size.

Though uncertainties remain regarding the relationships between sea otters, humans, and the nearshore environment, it is only through continued exploration of a variety of information sources and time scales that this picture will become clearer. Collectively, our use of data extending beyond the time scales of the written record has expanded and enriched our understanding of how sea otters persisted in the context of human occupation of the Northwest Coast of North America prior to the maritime fur trade.

**Larger ancient mussel size reflects lower sea otter predation in ancient times**

Our archaeological data suggest that the effect of sea otter predation on mussel size was limited in areas in proximity to human settlements which were places where mussels were regularly harvested during the pre-contact era (Fig. 3). Though many factors affect the growth rate and size of intertidal and subtidal invertebrate species (discussed below), sea otters have been documented to exert strong foraging pressure resulting in the reduced average size of their prey throughout their current geographic
range, and across a variety of habitats and environmental conditions (Burt et al., 2018; Estes & Palmisano, 1974; Fanshawe et al., 2003; Hale et al., 2019; Kvitek et al., 1992; Lee et al., 2016; Salomon et al., 2007; Singh et al., 2013). In some cases, environmental variation affecting growth rates have been ruled out or found to have minimal effect in comparison to sea otter predation. For example, in Prince William Sound, Alaska, the closely related mussel *Mytilus trossulus* (formerly *M. edulis*) was smaller where sea otter occupation time was longer, and predator exclusion experiments confirmed that this difference was not due to location-level environmental growth factors (VanBlaricom, 1988).

Sea otter occupation time can also be evaluated through diet diversification among individuals (Estes et al., 2003; Newsome et al., 2009; Tinker et al., 2008), which occurs over time as initial populations of high-value prey species become diminished and individuals turn to a wider variety of less valued prey items (Estes et al., 1981; Laidre & Jameson, 2006; Ostfeld, 1982; Rechsteiner et al., 2019). As a less-valued prey item, mussels are typically consumed by territorial males and females at locations that have been occupied (previously by males) near equilibrium population densities long enough to reduce the abundance of preferred prey (Honka, 2014; Rechsteiner et al., 2019; Singh et al., 2013; VanBlaricom, 1988), and may therefore provide an indication of their population status. Prey size response to sea otter foraging pressure, as well as diet diversification, have been investigated in archaeological invertebrate assemblages, where smaller size distributions of prey (Corbett et al., 2008; Erlandson et al., 2005; Simenstad et al., 1978), and less diverse sea otter diets reflected in isotopic niche widths (Szpak et al., 2012) suggested that sea otters were absent or below carrying capacity in earlier time periods.

However, given that our samples of ancient mussels come from human collection, we must consider that humans as predators can also affect the mussel sizes found in middens, through both selection for larger sizes, and resource depression (Botkin, 1980; Braje et al., 2018). Although the larger mussels found in our archaeological assemblages may reflect a bias toward collection of larger shells in the field, the occurrence of these large mussels can only occur if they are available and haven't been eliminated by sea otter foraging.
Finally, it is important to consider that top-down control by predators is not the only factor influencing mussel size and growth rates. Control of mussel growth has been shown to be strongly influenced by bottom-up factors such as upwelling events, nutrient input (e.g. Menge, 2000), which can in turn increase the strength of top-down effects. Mussel recruitment and growth rates have been found to vary with oceanographic factors at scales from 100s to 10s of kms (Menge, 2000), even differing within the same upwelling zone (Menge et al., 1997; Menge et al., 1994). These bottom-up influences in productivity have been associated with increased recruitment rates and food availability (Menge et al., 1997; Menge et al., 2009; Menge et al., 1994), while other factors such as water temperatures (Blanchette et al., 2007; Menge et al., 2008) and weather during low tide (Blanchette et al., 2007) have also been linked to mussel growth. Interestingly, sea otter reintroduction and associated reestablishment of kelp forests have also been associated with increased mussel growth rates due to higher levels of kelp-derived carbon (Duggins et al., 1989). While it is not possible to quantify all of these factors over the vast time scales that our archaeological data represents, further paleoecological and archaeological research across larger and multiple spatial and temporal scales may help further tease these factors apart.

**Modern mussel size cannot be attributed exclusively to sea otter occupation**

Our investigation of modern mussel size (Fig 4) suggests that the effect of sea otter occupation time on mussel size varies spatially. While locations on the south coast show a clear trend of increasing mussel size as sea otter occupation time increases, this pattern is less clear on the central coast. While 21 years of sea otter occupation is associated with the smallest reported mean mussel size, our longest-occupied location (37 years) contradicted our expectations, with the largest mean mussel size of all locations, the opposite of the effect seen on the south coast. Though we attempted to control for environmental factors such as wave exposure, aspect, slope and rugosity that are known to affect mussel size, limited time and ability to estimate these factors in the field may have resulted in location-level variation in previously-mentioned environmental growth factors that explain some of the variation we found on the central coast.

Alternatively, this variation in mussel response to sea otter occupation time may also be associated with variations in sea otter diet and foraging intensity. The degree to
which sea otter predation can affect the size structure of a prey species varies as a function of top-down factors such as diet composition and prey selection, rate of capture, and predator population density, which are in turn affected by bottom-up factors such as variability in habitat productivity. Though our measure of sea otter occupation time captures some of the variation in top-down factors, other variables may be influencing sea otter foraging behaviour and dynamics on the central coast more so than on the south coast. In Canada, the current population size of sea otters on the central coast (1,142 individuals) is substantially lower than that of the south coast population (5,612 individuals). Recent foraging observations on the central coast have noted a trend toward smaller and more diverse prey sources with increasing occupation time, noting that small and large mussels are the most observed prey harvested at 27-30 years of occupation (Rechsteiner et al., 2019), and the effects of sea otter occupation time have also been noted on species such as sea urchins and abalone (Burt et al., 2018; Lee et al., 2016; Stevenson et al., 2016). However, it is possible that the population density of sea otters is not high enough to have a significant effect on mussel size structure. It is also possible that mussel populations are experiencing a rebound in growth following size depression by sea otters, as has been observed by Honka (2014) and VanBlaricom (1988).

Furthermore, even at similar occupation histories and population densities, sea otter diet is also strongly influenced by habitat type and shoreline complexity (Hale et al., 2019; Hessing-Lewis et al., 2017; Hoyt, 2015). The south coast study area contains a much more linear coastline in comparison to the central coast, consisting of a multitude of small islands and more broadly dispersed coastline. With the availability and proximity of suitable foraging habitat, it is possible that sea otter populations on the central coast are expanding their foraging range to access available and preferred species prior to having a strong negative effect on mussel populations.

**Indigenous management to maintain resource diversity**

A growing body of evidence in the form of archaeological, ethnographic and historical ecological research supports the notion that indigenous communities maintained deliberate systems of resource management prior to European contact (Jackley et al., 2016; Lepofsky & Caldwell, 2013; Moss, 2011; Salomon et al., 2017). Our findings provide further support for this hypothesis, specifically that communities were
managing sea otters in part to maintain access to shellfish resources on the Northwest Coast of North America.

Though it has often been assumed that sea otters were abundant throughout their range, our investigation of archaeological prey size yields similar findings to those of Simenstad et al. (1978) and Corbett et al. (2008), finding larger size ranges of urchins that are unlikely to persist at locations with long-term, highly dense sea otter occupation. The ubiquity of sea otter remains in archaeological middens in BC has also allowed for exploration of their diet composition through stable isotope analysis, revealing that their prey composition was consistent with populations below carrying capacity (Szpak et al., 2012).

This evidence, along with the knowledge that sea otter hunting was technically complex and widespread among coastal indigenous communities (Corbett et al., 2008; Fedje et al., 2005; McKechnie & Wigen, 2011; Orchard, 2009; Szpak et al., 2012), has led to the hypothesis that sea otters were deliberately limited by humans from accessing shellfish in close proximity to sites that were targeted or cultivated for human shellfish harvesting. There are many examples in recent history of conflicts between sea otters and humans over their shared use of shellfish prey (Pinkerton et al., 2019; Sloan, 2004; Thomas, 2018; Watson, 2000). Oral histories and ethnographies from coastal British Columbia and elsewhere recall the practice of otter exclusion from areas protected for shellfish harvest in the millennia preceding the maritime fur trade (Ibarra et al., 2017; Salomon et al., 2017; Salomon et al., 2011). This human-mediated spatial mosaic of high and low density sea otter populations has been proposed elsewhere (Corbett et al., 2008; Erlandson et al., 2008; Szpak et al., 2012) and in other species including sea lions (Lyman, 2003) on the Pacific coast of North America, and may provide an alternative approach to managing the conflict between human access to shellfish and sea otter conservation today (Pinkerton et al., 2019; Salomon et al., 2015).

There are, however, some caveats when interpreting factors influencing archaeological mussel size structure. The scope of this project limited our exploration of archaeological data to 5 sites and a sample size of 1236 mussels split between two regions, making it challenging to determine whether there was any shift in mussel size across time periods within our archaeological assemblages. However, other studies have associated consistent size of midden shellfish species over time with sustainably
managed resource use by indigenous communities (e.g. Erlandson et al. 2008). It follows then, that other studies have associated reductions in shellfish size with resource depression by increasing human harvest pressure (Braje et al., 2017; Erlandson et al., 2011). However, others argue that such changes are associated with shifts in harvest strategies and the tidal height at which foraging occurs, rather than overall reduction in the size of available shellfish (Thakar et al., 2017; Thakar et al., 2017). Given the limited spatial scale of our data, it is difficult to determine whether our observations of mussel size would persist across more of the BC coast than in the localized regions we investigated. We therefore cannot distinguish between these two hypotheses based on our data.

**Archaeological uncertainties**

The nature of investigations using archaeological data to make ecological inferences in deep time means that a number of methodological limitations and uncertainties must be addressed (Orton, 2016). The following section will describe these limitations and uncertainties, and our attempts to minimize them.

Archaeological mussel fragments came from several different sources with various sampling methods, including vibracore, auger, column sample and hand collection from exposed shell midden. Vibracore, auger, and column samples yield a smaller-volume sample of midden matrix than unit excavation, with the logistical benefit of allowing a greater number of sampling locations and depth range within and between midden deposits. While this improves our ability to represent spatial heterogeneity, the smaller samples yield an assemblage of *Mytilus umbos* that is sparse in comparison to a conventional excavation. However, several studies have demonstrated that fine-screen auger and column samples provide an accurate reflection of the taxa represented in a given shell midden (Casteel, 1976; McKechnie, 2005), and are commonly used to sample hyperabundant shellfish taxa (e.g. Cannon et al. 2008, Martindale et al. 2009). However, this sampling method is less representative when separated by time period (McKechnie, 2005). Due to the relatively small sample size per site, we collapsed all of our data into a single region-level observation of mussel size variation, which analytically precludes an assessment of temporal variability or chronological shifts in mussel size but ensures a wide range of ecological circumstances.
Although our saturating curve predicting total shell length from umbo thickness captures 89% of the variation in total mussel length, this predictability varies across umbo thickness values, with greater uncertainty at larger umbo thickness (Fig. 2B). Further sampling of modern California mussels across their range of size and in varying growth conditions may increase precision of the uncertainty around our prediction of total mussel length from umbo thickness. Furthermore, at small sizes, it is difficult to distinguish between *M. californianus* and the morphologically similar blue mussel *Mytilus trossulus*, found within the same geographic range as *M. californianus*, typically in less wave exposed habitats. Though it is possible that some of our smaller measurements were *M. trossulus*, Singh and McKechnie (2015; pp. 180) found that the relationship between umbo thickness and total shell length is similar between the two species.

Finally, the limited spatial variability of our samples hinders our ability to make broadly generalizable predictions about indigenous mussel harvest size across the Northwest Coast of North America. Though our use of multiple auger, vibracore and column samples provide greater within-site variability, our observations are still limited to two regions: the Broken Group Islands on the South Coast, and Kwakshua Channel on the Central Coast. With increasing calls for a greater spatial breadth of sampling efforts to make legitimate interpretations about Northwest Coast cultural practices (Cannon, 2001; Moss, 2012), we suggest that further investigations of ancient mussel size along the Northwest Coast will provide refined insight into the variability required to fully demonstrate a spatial mosaic in sea otter abundance that we hypothesize about here.

**Implications of long-term data in managing human-mediated ecosystem interactions**

With growing evidence of the long-established alterations humans have made to our surrounding ecosystems globally (Estes et al., 2011), it has become clear that establishing “natural” baselines requires us to extend our investigations beyond the most recent century and broaden our view of what constitutes an ecosystem’s natural state. For example, evidence of millennia-old clam gardens on the coast of BC suggest that clam growth and abundance were enhanced by tending practices and habitat alteration by coastal indigenous peoples, a practice that was diminished or halted following contact (Groesbeck et al., 2014; Lepofsky et al., 2015; Lepofsky & Caldwell, 2013; Salter, 2018; Smith et al., 2019).
In the case of sea otters along the Pacific coast of North America, the conventional method for estimating baseline regional carrying capacity is to calculate the density of individuals within the total suitable habitat area in the region, with the assumption that sea otters would occur at carrying capacity everywhere within this area (Burn et al., 2003; Gregr et al., 2008; Laidre et al., 2002; Laidre, 2001). These current estimates likely contribute to what has been considered a “small” population when justifying the reasoning for sea otters’ current listing as “Special Concern” in Canada (COSEWIC, 2007). However multiple archaeological studies have now indicated that it is unlikely that sea otters were at carrying capacity throughout their range prior to the maritime fur trade.

Our results provide evidence toward a growing movement in ecosystem management and conservation that places humans as an integral part of ecosystems (Salomon et al., 2010; Worm & Paine, 2016). Archaeological and ethnographic research has demonstrated that humans, sea otters and shellfish coexisted for millennia on the coast of BC (e.g. Cannon and Burchell 2009, Salomon et al. 2015), yet interactions between coastal indigenous peoples and sea otters are currently limited by and at the discretion of colonial governing authorities (Pinkerton et al., 2019; Thomas, 2018).

There is already a desire by coastal indigenous communities to play a more active role in managing sea otters, which has led to a proposed sea otter management plan by the Nuu-chah-nulth Tribal Council on the west coast Vancouver Island (Nuu-chah-nulth Tribal Council, 2012; Pinkerton et al., 2019; Thomas, 2018). Examination of such past social-ecological management systems can provide alternative pathways for future management of conflicting species. By broadening the time scale and socioecological scope within which we examine the persistence of a given species, we can create opportunities for solutions that involve greater power and agency in the hands of those most affected by its management, thus creating more socially just outcomes that protect the future of coastal environments.
Figure 1. A) Size of modern and ancient California mussels (*Mytilus californianus*) were compared within two regions (south coast and central coast) along the west coast of North America (see insets). Modern mussels were sampled from intertidal locations (n=12, blue circles) with (closed circle) and without (open circle) sea otters. Ancient mussels were recovered from archaeological sites (n=5, grey triangles). B) Within the Central Coast region specifically, we sampled mussels from 8 locations along an established gradient of sea otter occupation time spanning 0-37 yrs.
Figure 2. A) Modern California mussel (*Mytilus californianus*) umbo thickness and total shell length were measured to establish (B) a saturating relationship between these two morphometrics (n=313 mussels, filled orange squares from this study, all other symbols from McKechnie et al. 2015). 95% confidence interval of the mean is represented by the grey band around the curve. (C) Ancient California mussel umbos were recovered from shell middens, measured and their total shell length estimated from the relationship established in B).

Bottom left photo by Iain McKechnie
Figure 3. Size distributions and size spectra of California mussels (*Mytilus californianus*) from the south coast (A, B) and central coast (C, D) of North America. Modern mussel sizes at locations with sea otters present for 20-40 years (blue filled bars and circles) and without (unfilled bars and circles). Ancient mussel sizes (grey bars and triangles) estimated from mussel umbos collected from archaeological sites. Mean mussel sizes (vertical black lines). 95% confidence interval of the mean is represented by the coloured bands around size spectra lines.
Figure 4. Size spectra of California mussels (*Mytilus californianus*) from all modern locations on the A) south and B) central coasts of North America, grouped by sea otter occupation time. Open triangles represent locations occupied by sea otters for 5 years or less, while closed triangles represent locations occupied for more than 5 years. See appendix table 3 for further location information. 95% confidence interval of the mean is represented by the coloured bands around size spectra lines.
Tables

Table 1. Results of ANCOVAs testing the effect of A) ecological context (modern with sea otters, modern without sea otters, ancient) and B) occupation time (years) on the relationship between California mussel length and the log proportion of California mussels on the south and central coasts of North America. Significant effects are starred.

<table>
<thead>
<tr>
<th>Model Region</th>
<th>Interaction Term</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Modern-Ancient</td>
<td>Log10(Proportion) of mussels ~ Length + Context + Length*Context</td>
<td></td>
<td></td>
</tr>
<tr>
<td>South coast</td>
<td>Length*Context</td>
<td>5.22</td>
<td>0.005*</td>
</tr>
<tr>
<td>Central coast</td>
<td>Length*Context</td>
<td>6.09</td>
<td>0.001*</td>
</tr>
<tr>
<td>(B) Modern</td>
<td>Log10(Proportion) of mussels ~ Length + Occupation time + Length*Occupation time</td>
<td></td>
<td></td>
</tr>
<tr>
<td>South coast</td>
<td>Length*Occupation time</td>
<td>1.89</td>
<td>0.15</td>
</tr>
<tr>
<td>Central coast</td>
<td>Length*Occupation time</td>
<td>15.92</td>
<td>2.33e-08*</td>
</tr>
</tbody>
</table>
Table 2. Results of Tukey’s post hoc pairwise comparisons of the relationship between California mussel length (mm) and log transformed proportion of mussels (slopes of each size spectra), between each A) ecological context and B) occupation time on the south and central coasts. Significant results are starred.

<table>
<thead>
<tr>
<th>Model Region</th>
<th>Pairwise Comparison</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Modern-Ancient</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Log10(Proportion) of mussels ~ Length + Context + Length*Context*

| South coast | Modern without Sea Otters - Ancient | 0.72  |
|            | Modern with Sea Otters - Ancient    | 0.003*|
|            | Modern with Sea Otters - Modern without Sea Otters | 0.008*|

| Central coast | Modern without Sea Otters - Ancient | 0.13  |
|              | Modern with Sea Otters - Ancient    | 0.0009*|
|              | Modern with Sea Otters - Modern without Sea Otters | 0.034*|

(B) Modern

*Log10(Proportion) of mussels ~ Length + Occupation time + Length*Occupation time*

| South coast | 0 - <5 | 0.99 |
|            | 0 - 20 | 0.42 |
|            | 0 - 40 | 0.24 |
|            | <5 - 20 | 0.54 |
|            | <5 - 40 | 0.30 |
|            | 20 - 40 | 0.90 |

| Central coast | 0 - 4 | 0.015*|
|              | 0 - 6-8 | 0.18 |
|              | 0 - 21 | <0.0001*|
|              | 0 - 37 | 0.35 |
|              | 4 - 6-8 | 0.82 |
|              | 4 - 21 | <0.0001*|
|              | 4 - 37 | 0.64 |
|              | 6-8 - 21 | <0.0001*|
|              | 6-8 - 37 | 0.10 |
|              | 21 - 37 | <0.0001*|
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### Appendix.

#### Table A-1.
Archaeological mussel umbos from collections in the (A) South Coast and (B) Central Coast regions, compiled by region and sampling effort.

<table>
<thead>
<tr>
<th>Site</th>
<th>Site/unit number</th>
<th>Core</th>
<th>Screen Size</th>
<th>Sample type</th>
<th>n</th>
<th>Site Date Range (yrs cal BP)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) South Coast</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Keith Island</td>
<td>306T7C</td>
<td>&gt;6.35mm</td>
<td>Column Sample</td>
<td>69</td>
<td>500-100</td>
<td></td>
</tr>
<tr>
<td></td>
<td>306T8C</td>
<td>&gt;6.35mm</td>
<td>Column Sample</td>
<td>44</td>
<td>800-200</td>
<td></td>
</tr>
<tr>
<td></td>
<td>306T8D</td>
<td>&gt;6.35mm</td>
<td>Column Sample</td>
<td>11</td>
<td>800-200</td>
<td></td>
</tr>
<tr>
<td></td>
<td>306T10A</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>11</td>
<td>1180-500</td>
<td></td>
</tr>
<tr>
<td></td>
<td>306T9A</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>46</td>
<td>1500-200</td>
<td></td>
</tr>
<tr>
<td>Nettle Island</td>
<td>305T1</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>76</td>
<td>2700-200</td>
<td></td>
</tr>
<tr>
<td>Lower Dicebox</td>
<td>83T11A</td>
<td>&gt;2mm</td>
<td>Auger</td>
<td>42</td>
<td>800-150</td>
<td></td>
</tr>
<tr>
<td></td>
<td>83T6A</td>
<td>&gt;2mm</td>
<td>Auger</td>
<td>92</td>
<td>800-150</td>
<td></td>
</tr>
<tr>
<td></td>
<td>83T7C</td>
<td>&gt;2mm</td>
<td>Auger</td>
<td>81</td>
<td>500-150</td>
<td></td>
</tr>
<tr>
<td>Wouwer</td>
<td>206T12D</td>
<td>&gt;2mm</td>
<td>Auger</td>
<td>69</td>
<td>2500-1200</td>
<td></td>
</tr>
<tr>
<td></td>
<td>206T19B</td>
<td>&gt;2mm</td>
<td>Auger</td>
<td>69</td>
<td>2500-1300</td>
<td></td>
</tr>
<tr>
<td></td>
<td>206T20B</td>
<td>&gt;2mm</td>
<td>Auger</td>
<td>74</td>
<td>800-150</td>
<td></td>
</tr>
<tr>
<td>(B) Central Coast</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hecate Island</td>
<td>EjTa-13</td>
<td>&gt;6.35mm</td>
<td>Hand collection</td>
<td>62</td>
<td>6,000 to 300</td>
<td></td>
</tr>
<tr>
<td>Calvert Island</td>
<td>EjTa-4</td>
<td>&gt;6.35mm</td>
<td>Hand collection</td>
<td>177</td>
<td>6,000 to 300</td>
<td></td>
</tr>
<tr>
<td>Hecate Island</td>
<td>EjTa-13</td>
<td>VC 7</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>18</td>
<td>3,370-390</td>
</tr>
<tr>
<td></td>
<td>EjTa-13</td>
<td>VC 5</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>17</td>
<td>5,830-380</td>
</tr>
<tr>
<td></td>
<td>EjTa-13</td>
<td>VC 4</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>75</td>
<td>5,650-490</td>
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<tr>
<td></td>
<td>EjTa-13</td>
<td>VC 1</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>1</td>
<td>3,450-3,390</td>
</tr>
<tr>
<td></td>
<td>EjTa-13</td>
<td>VC 2</td>
<td>&gt;2mm</td>
<td>Vibracore</td>
<td>54</td>
<td>Not dated</td>
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</tbody>
</table>

*Chronological data obtained from Duffield 2017 and McKechnie 2013.
Figure A-1. Linear regression curve fitted to total shell length as a function of umbo thickness (n=313 mussels, filled orange squares were collected for this study, all other symbols are from McKechnie et al. 2015). 95% confidence interval of the response mean is represented by the pink band around the regression line.
Figure A-2. Mussel size (A,C) and slope of size spectra (B,D) grouped by occupation time of sea otters at each location sampled on both the A,B) south and C,D) central coasts of British Columbia.
Figure A-3. Size distributions and centered size spectra of mussels from two regions of coastal British Columbia: south coast (A,B) and central coast (C,D). Centered length midpoints were calculated by subtracting each midpoint value from the mean midpoint each distribution. Blue filled bars and circles represent grouped modern locations with sea otters present from 20-37 years, while unfilled bars and circles represent locations not yet occupied by sea otters. Grey bars and triangles represent all archaeological data. 95% confidence interval of the mean is represented by the coloured bands around size spectra lines.
Figure A-4. Centered size spectra from the a) south and b) central coasts of northwestern North America. Centered length midpoints were calculated by subtracting each midpoint value from the mean midpoint each distribution. Thickness of lines indicate increasing time the location has been occupied by sea otters. 95% confidence interval of the mean is represented by the coloured bands around size spectra lines.
Figure A-5. Size-frequency distribution of mussel length (mm) from California mussels collected by Tseshahaht beachkeepers during single harvesting effort at Gilbert Island, BC in July, 2017.
Figure A-6. Size distributions and size spectra of California mussels (*Mytilus californianus*) from the south coast (A, B) and central coast (C, D) of North America, with Ancient mussel sizes predicted using linear predictor (Appendix Fig.1). Modern mussel sizes at sites with sea otters present for 20-40 years (blue filled bars and circles) and without (unfilled bars and circles). Ancient mussel sizes (grey bars and triangles) estimated from mussel umbos collected from archaeological sites. Mean mussel sizes (vertical black lines).
Table A-2. Summary of sample location information and associated mussel length arranged by region and by occupation time (for modern samples). Smallest values are underlined, while largest values are bold. Note: occupation time (years) recorded from date of collection.

<table>
<thead>
<tr>
<th>Location</th>
<th>Lat, Long</th>
<th>Occupation Time (yr)</th>
<th>N</th>
<th>Min (mm)</th>
<th>Max (mm)</th>
<th>Median (mm)</th>
<th>Mean (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A) Modern – South Coast</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barkley Sound</td>
<td>48.83, -125.20</td>
<td>0</td>
<td>1357</td>
<td>20</td>
<td>206</td>
<td>67</td>
<td>71</td>
</tr>
<tr>
<td>Clayoquot Sound</td>
<td>41.14, -125.93</td>
<td>&lt;5</td>
<td>486</td>
<td>20</td>
<td>181</td>
<td>63</td>
<td>67</td>
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<tr>
<td>Neah Bay</td>
<td>48.36, -124.63</td>
<td>20</td>
<td>425</td>
<td>20</td>
<td>103</td>
<td>53</td>
<td>52</td>
</tr>
<tr>
<td>Kyuquot Sound</td>
<td>50.01, -127.42</td>
<td>40</td>
<td>996</td>
<td>20</td>
<td>87</td>
<td>46</td>
<td>46</td>
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<tr>
<td><strong>B) Modern – Central Coast</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>7th Beach</td>
<td>51.64, -128.15</td>
<td>0</td>
<td>4170</td>
<td>20</td>
<td>182</td>
<td>41</td>
<td>46</td>
</tr>
<tr>
<td>8th Beach</td>
<td>51.64, -128.15</td>
<td></td>
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</tr>
<tr>
<td>2nd Beach</td>
<td>51.65, -128.15</td>
<td>4</td>
<td>1250</td>
<td>20</td>
<td>125</td>
<td>37</td>
<td>44</td>
</tr>
<tr>
<td>Triquet</td>
<td>51.80, -128.24</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Spider</td>
<td>51.84, -128.25</td>
<td>6-8</td>
<td>4692</td>
<td>20</td>
<td>132</td>
<td>42</td>
<td>47</td>
</tr>
<tr>
<td>Simmonds</td>
<td>51.93, -128.24</td>
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<td>McMullins</td>
<td>52.07, -128.41</td>
<td>21</td>
<td>3321</td>
<td>20</td>
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<td>32</td>
<td>34</td>
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<tr>
<td>Gosling</td>
<td>58.90, -128.45</td>
<td>37</td>
<td>1833</td>
<td>20</td>
<td>132</td>
<td>47</td>
<td>49</td>
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<tr>
<td><strong>C) Ancient – South Coast</strong></td>
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<td></td>
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</tr>
<tr>
<td>Keith Island</td>
<td>48.91, -125.29</td>
<td>--</td>
<td>281</td>
<td>29</td>
<td>220</td>
<td>78.00</td>
<td>82.39</td>
</tr>
<tr>
<td>Nettle Island</td>
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<td>94</td>
<td>23</td>
<td>133</td>
<td>50.50</td>
<td>54.15</td>
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<tr>
<td>Wouwer Island</td>
<td>48.86, -125.36</td>
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<td>211</td>
<td>20</td>
<td>185</td>
<td>77.000</td>
<td>79.10</td>
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<tr>
<td>Dicebox Island</td>
<td>48.86, -125.33</td>
<td>--</td>
<td>215</td>
<td>22</td>
<td>141</td>
<td>82.00</td>
<td>82.95</td>
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<tr>
<td><strong>D) Ancient – Central Coast</strong></td>
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<tr>
<td>Calvert Island</td>
<td>51.66, -128.08</td>
<td>--</td>
<td>436</td>
<td>25</td>
<td>166</td>
<td>70.50</td>
<td>73.93</td>
</tr>
<tr>
<td>Hecate Island</td>
<td>51.66, -128.10</td>
<td></td>
<td></td>
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</table>
Table A-3. Linear regression coefficients and goodness of fit for fitted size spectra predicting log(proportion) from mussel length midpoints. Values are grouped by time period and sea otter presence (Fig. 3). Midpoint height values relate to centered y-intercept values (Fig. 6).

<table>
<thead>
<tr>
<th>Occupation time/period</th>
<th>Slope</th>
<th>Y-int</th>
<th>Midpoint height</th>
<th>R²</th>
<th>Mean length (mm) ± SE</th>
<th>Max length (mm)</th>
<th>Median length (mm)</th>
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<tbody>
<tr>
<td><strong>A) South Coast</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modern without sea otters</td>
<td>-0.00032</td>
<td>0.058</td>
<td>0.022</td>
<td>0.61</td>
<td>70.47±0.74</td>
<td>206.00</td>
<td>66.70±0.74</td>
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<tr>
<td>Modern with sea otters</td>
<td>-0.0011</td>
<td>0.058</td>
<td>0.044</td>
<td>0.59</td>
<td>47.91±0.38</td>
<td>103.00</td>
<td>47.01±0.38</td>
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<tr>
<td>Ancient</td>
<td>-0.00024</td>
<td>0.050</td>
<td>0.022</td>
<td>0.42</td>
<td>78.35±1.00</td>
<td>220.00</td>
<td>76.00±1.00</td>
</tr>
<tr>
<td><strong>B) Central Coast</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modern without sea otters</td>
<td>-0.00058</td>
<td>0.084</td>
<td>0.025</td>
<td>0.72</td>
<td>45.56±0.35</td>
<td>182.00</td>
<td>41.00±0.35</td>
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<tr>
<td>Modern with sea otters</td>
<td>-0.0011</td>
<td>0.12</td>
<td>0.033</td>
<td>0.78</td>
<td>39.40±0.22</td>
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<td>Ancient</td>
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<td>0.030</td>
<td>0.36</td>
<td>73.94±1.40</td>
<td>166.00</td>
<td>70.50±1.40</td>
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</table>
Table A-4. Summary of linear regression statistics for ALL modern mussel size spectra, arranged by occupation time on the South (A) and Central (B) coasts. Midpoint height values relate to centered y-intercept values from figure 6 centered size spectra. For each region, largest slope is bold, while smallest slope is underlined. Note: occupation time (years) recorded from date of collection.

<table>
<thead>
<tr>
<th>Location</th>
<th>Occupation time</th>
<th>N</th>
<th>Slope</th>
<th>Y-intercept</th>
<th>Midpoint Height</th>
<th>R²</th>
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<tr>
<td><strong>A) South Coast</strong></td>
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<td></td>
</tr>
<tr>
<td>Barkley Sound</td>
<td>0</td>
<td>1357</td>
<td>-0.00032</td>
<td>0.058</td>
<td>0.022</td>
<td>0.59</td>
</tr>
<tr>
<td>Clayoquot Sound</td>
<td>&lt;5</td>
<td>486</td>
<td>-0.00037</td>
<td>0.062</td>
<td>0.024</td>
<td>0.41</td>
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<td>Neah Bay</td>
<td>20</td>
<td>425</td>
<td>-0.00081</td>
<td>0.097</td>
<td>0.045</td>
<td>0.50</td>
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<td>Kyuquot Sound</td>
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<td>996</td>
<td>-0.0012</td>
<td>0.12</td>
<td>0.056</td>
<td>0.32</td>
</tr>
<tr>
<td><strong>B) Central Coast</strong></td>
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<tr>
<td>7th and 8th Beach</td>
<td>0</td>
<td>4488</td>
<td>-0.00058</td>
<td>0.084</td>
<td>0.025</td>
<td>0.72</td>
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<td>1340</td>
<td>-0.0011</td>
<td>0.12</td>
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<td>0.85</td>
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<td>Simmonds, Spider, Triquet</td>
<td>6-8</td>
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<td>0.92</td>
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<td>1918</td>
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<td>0.10</td>
<td>0.34</td>
<td>0.94</td>
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