

**Assessing late Holocene variability in sea otter
prevalence in two areas of coastal British Columbia
using archaeological and isotopic data**

**by
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BSc, University of Victoria, 2016

Thesis 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

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FALL 2020

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Abstract

Keywords: zooarchaeology, historical ecology, marine ecology, shifting baselines, sea otters, isotope analysis, keystone species, trophic cascade

The historic extirpation and subsequent recovery of sea otters, a well-recognized keystone predator, has generated far-reaching changes in nearshore ecosystems across the Northeast Pacific. What remains unclear, is how coastal food webs were structured over the Holocene, when people and sea otters co-existed. Mounting archaeological evidence indicates that sea otter populations were lower in the vicinity of human shellfish harvesting sites and that their prevalence varied across regional scales. We used zooarchaeological data, stable isotope analysis, and a social-ecological lens to investigate differences in late Holocene sea otter prevalence in two areas of coastal British Columbia: Barkley Sound and southern Gwaii Haanas. We assessed differences in the isotopic signatures of ancient coastal consumers, sea otter diets, and shellfish prey assemblages to draw inferences on their relative abundance and how nearshore food webs differed in these two areas over the late Holocene. We show that the size and consistency of archaeological shellfish prey, as well as the overall low-trophic level of sea otter diets, suggest that sea otters were reduced or absent in the vicinity of harvesting sites in both southern Gwaii Haanas and Barkley Sound. Moreover, several lines of evidence suggest a greater prevalence of sea otters in southern Gwaii Haanas with coastal consumers showing enriched levels of ^{13}C and ^{15}N and sea otter diets exhibiting a more diverse prey base compared to Barkley Sound. Other lines of evidence were inconclusive or suggested the opposite with no difference in the size of some shellfish between areas and with the relatively greater occurrence of urchins, a preferred sea otter prey, in Gwaii Haanas archaeological deposits. Our findings add to the large body of evidence documenting thousands of years of interactions and coexistence between people and sea otters while revealing a degree of geographic variation in this relationship. This work emphasizes the need for spatially explicit sea otter recovery targets that account for the longstanding role of humans as interacting components of coastal ecosystems and offers insights into practices that could support the coexistence between people, sea otters, and seafood.

Dedication

To my mother and her great capacity for delight.

Acknowledgements

I would first like to acknowledge and express my gratitude to the Tseshaht and Haida Nations for sharing their knowledge both directly and indirectly to guide this project. It's been a privilege to explore the history of these ancestral peoples.

This research was made possible by the Tseshaht First Nation, Pacific Rim National Park Reserve, the Bamfield Marine Sciences Centre, the Keith Island Archaeological project, Gwaii Haanas National Park Reserve and Haida Heritage Site, and the University of Victoria. I am grateful to the Keith Island project co-director, Denis St. Claire, as well as Wanda Robinson, the Tseshaht Beach Keepers, and the HECA field school students. For access to samples from SGang Gwaii, I am grateful to Gwaii Hannas and Parks Canada staff Jenny Cohen and Quentin Mackie as well as Kii'iljuus (Barbara Wilson). Thank you to Victoria Otton and David Qu at Simon Fraser University for facilitating access to various equipment without which I could not have successfully extracted bone collagen. Thank you to Dr. Russ Markel for sharing modern shellfish isotopic data from Barkley Sound as well as the CMEC lab for modern isotopic data from Gwaii Haanas. Thank you to the HECA lab at the University of Victoria for facilitating access to Barkley Sound zooarchaeological samples. I was supported by an NSERC Canada Graduate Scholarship as well as SFU scholarships and fellowships. Isotopic analyses and travel for this research was funded in part by NSERC Discovery grants to IM (531246) and AKS (2016-04492).

Permissions: Archaeological Fieldwork that enabled this research and laboratory analyses was provided by Tseshaht First Nation council resolution and a Parks Canada Research and Collection permit issued to Keith Island project co-directors Iain McKechnie and Denis St. Claire. Similarly, access to samples for analysis from Gwaii Haanas was enabled by a Gwaii Haanas Archipelago Management board approved research and collection permit issued to Jenny Cohen (Parks Canada) and Dr. Quentin Mackie (University of Victoria).

I lucked out with an exceptional committee to guide me through this research. I am so grateful to my supervisors, Dr. Anne Salomon and Dr. Iain McKechnie, for the opportunity to learn and grow from your knowledge, guidance, and most of all, your

passion for this work. Thank you for taking me on as a student and for investing so much time into making me a stronger ecologist and archaeologist.

There are a number of people who have been a huge help to me and this project by sharing their knowledge and time. I am very grateful to Dylan Hillis for always being a friendly voice on the other end of the phone while I was making sense of stable isotope analysis and mixing models. Likewise, I am thankful to Erin Slade who shared her time and support to help me navigate such an interdisciplinary project. Thank you to Dr. Chris Darimont for sharing your thoughts on mixing models and trophic discrimination factors. Thank you to Megan Wong for patiently showing me how to extract collagen.

To my peers in REM – thank you for being the best. I feel so lucky to have had such a smart, fun, and thoughtful group of people to go through this degree with. Likewise, I am so grateful to my CMEC lab mates and their endless support. To Erin Slade, Skye Augustine, Gabby Pang, Hannah Kobluk, Emily Stewart, Danielle Denley, Kelsey Miller, Meredith Fraser, Maya Guttman, Sachi Ouchi, Jenn Burt, Nicky Roberts, and Kim-Ly Thompson – I am so fortunate to have been surrounded by such an insightful, generous, and fun group of people. Thank you for sharing your knowledge, laughs, code, and time in the amazing places we were lucky to find ourselves in.

To my family, thanks for all of the cold swims and the lifetime of support. I am especially grateful to Rosie, for putting me up, even if it was only to ruin me at crib.

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Introduction

The critical role of apex predators in shaping the world's ecosystems is well established, as are the cascading effects of their widespread declines (Estes et al., 2011). It is typically assumed that these human-induced losses are a recent phenomenon (McCauley et al., 2015) and that if humans are removed, ecosystems will recover to their original pristine state. Yet humans have been interacting with predators for millennia (Stiner, 2002) resulting in reciprocal relationships that have co-evolved through time (Berkes & Folke, 2008). Consequently, our understanding of the 'natural' baselines against which we assess modern populations can be greatly distorted by both the short time frame over which species interactions are typically considered (Jackson et al., 2001; Pauly, 1995) and our perception of humans as external disruptors to an otherwise pristine nature (Gelcich et al., 2010). Fortunately, historical ecology offers a critical opportunity to expand the time horizon over which these relationships are examined (McClenachan et al., 2012; Rick & Erlandson, 2009) and a social-ecological systems approach widens analyses to consider humans as dynamic and adaptive components of nature. Here, we pursue multiple lines of archaeological evidence to explore the relationship between people, sea otters (*Enhydra lutris*), and coastal consumers in two areas of the Northeast Pacific during the late Holocene and showcase how investigating social-ecological dynamics through a deep time lens can inform conservation and management objectives, targets, and practices today.

Historical ecology operates across disciplinary boundaries, drawing on historical, paleoecological, and archaeological datasets to expand ecological timelines and chart a deep history of change. These efforts have been particularly enlightening in marine systems, where a growing body of work has revealed the magnitude of changing ocean ecosystems (Lotze & Worm, 2009) as well as the long and dynamic role of humans in driving these changes (Braje et al., 2017). Historic data, including catch records and photo archives, show declines far beyond previous estimates in the size and biomass of highly valued marine species over recent centuries (Holm, 2005; McClenachan, 2009; Ravier, 2001; Rosenberg et al., 2005). Archaeological investigations further expand timelines with ancient faunal remains chronicling millennia of human interactions with coastal ecosystems (Rick & Erlandson, 2009) that had measurable impacts on the

distribution, abundance, and size of marine species (Braje & Rick, 2011; Erlandson & Rick, 2008). These investigations have been a powerful means of illuminating ancient patterns of marine resource depletion, management, and enhancement that varied through space and time (Braje et al., 2009; McKechnie et al., 2014; Sanchez, 2020; Toniello et al., 2019).

Archaeological approaches have revealed thousands of years of interactions between humans and marine mammals, such as pinnipeds and sea otters, identifying long-term changes in their abundance, biogeography, and behaviour that challenge contemporary ecological thinking (Braje & Rick, 2011; McKechnie & Wigen, 2011; Moss et al., 2006; Newsome et al., 2007). For example, elephant seals (*Mirounga angustirostris*) are currently among the most numerous pinnipeds in California, but their remains are sparse among archaeological sites, suggesting that they were rare over much of the preceding 10,000 years. Sea otters, a species exploited to near extinction during the maritime fur trade, occur regularly in archaeological deposits along the west coast of North America, indicating a history of wide-spread human use that spanned the late Holocene (Elliott Smith et al., 2020; Fedje & Mathewes, 2005; Moss, 2020) and calling into question current notions that this predator was present near carrying capacity along coastlines prior to European contact (Estes, 1990; Davis et al., 2019;)

Evidence from archaeological research and Indigenous knowledge suggest that ancient humans suppressed sea otter populations in proximity to coastal village sites to moderate predation and maintain access to productive shellfisheries (Corbett et al., 2008; Erlandson et al., 2005; Salomon et al., 2015, 2018; Simenstad et al., 1978; Slade et al., in review; Szpak et al., 2012). For example, archaeological data from the Aleutian Islands suggests people may have reduced sea otter populations in areas close to village sites, consequently increasing the size and abundance of this keystone predator's principal prey, sea urchins, also harvested in the shallow subtidal and deep intertidal by people for food (Corbett et al., 2008; Simenstad et al., 1978). Moreover, the reduction in sea otters likely altered the structure and function of kelp forest ecosystems (Corbett et al., 2008; Simenstad et al., 1978). Isotopic analysis of sea otter remains in British Columbia (BC) reveal that late Holocene sea otter diets exhibited lower variability, suggesting that intraspecific competition was low and that these populations existed well below carrying capacity (Szpak et al., 2012). Using the archaeological remains of

California mussels (*Mytilus californianus*), a sea otter shellfish prey, Slade et al. (in review) found that ancient mussel size distributions in British Columbia more closely resemble those from shorelines that lack sea otters today compared to shorelines where sea otters have been present for over 50 years. This evidence, in addition to the frequent presence of sea otter bones within and across archaeological sites spanning the past 5000 years (McKechnie & Wigen, 2011; Szpak et al., 2012), also suggests that these predators may have been kept below carrying capacity by human disturbance and hunting. Given the broad distribution of archaeologically recorded human settlement sites, it is also possible that sea otters may not have had a uniform distribution along the west coast of North America prior to the maritime fur trade but, rather, were less abundant in proximity to areas of high human settlement, likely resulting in a spatial mosaic of kelp forests and shellfish beds along ancient coastlines (Corbett et al., 2008; Erlandson et al., 2005; Salomon et al., 2015, 2018; Szpak et al., 2012). The suppression of sea otters would have driven a diversity of community and ecosystem-level effects.

Decades of contemporary ecological research have provided a firm grasp of the keystone role that sea otters occupy in controlling herbivorous grazers, indirectly fostering the growth of kelp forests, and altering the structure and function of rocky reef food webs. In areas with otters, kelp forests are considerably deeper and more expansive (Watson & Estes, 2011) supporting greater trophic complexity (Markel & Shurin 2015; Pang 2018) by exponentially increasing both three-dimensional structural habitat as well as kelp-derived organic carbon to nearshore food webs (Duggins et al., 1989; Markel & Shurin, 2015). As sea otters increase in number, they reduce the size and abundance of their preferred prey (Estes & Palmisano, 1974; Kvitek et al., 1992; Salomon et al., 2007) leading to increased dietary diversity at the population level (Estes, 1990; Estes et al., 2003; Laidre & Jameson, 2006; Newsome et al., 2009; Tinker et al., 2008). Calorically rich benthic invertebrates, such as sea urchins or abalone, are a primary target when available (Estes et al., 1982; Laidre & Jameson, 2006; Ostfeld, 1982) with the eventual inclusion of a wider variety of more energetically expensive macroinvertebrates and even fish when populations are near equilibrium density (Estes et al., 1981, 1982). Consequently, piscivory, dietary variability, and higher trophic level foraging by sea otters has been suggested as an indicator of long sea otter occupation times and high relative density (Estes et al., 1982; Ostfeld, 1982; Szpak et al., 2012). While these modern studies have greatly expanded our understanding of the ecological

role of sea otters, they centre on relict and recovering populations protected from industrial-scale human harvest by international legislation. As such, marine scientists lack understanding of the longer-term ecological relationships between sea otters and humans and how these relationships varied through time and space.

While mounting evidence suggests that sea otters existed in numbers well below carrying capacity along some stretches of shoreline (Corbett et al., 2008; Slade et al., in review; Szpak et al., 2012), differences exist in the relative and absolute number of sea otter bones from archaeological sites across the northeastern Pacific (McKechnie et al., n.d.). The degree to which their abundance might have varied regionally over the late Holocene remains unclear. To investigate this, we assessed zooarchaeological data from ancient settlement sites in two areas of the British Columbia coast: southern Haida Gwaii, in the traditional territory of the Kunghit Haida, where sea otter bones are abundant relative to all other mammals and in absolute terms (Orchard, 2009; Orchard & Szpak, 2015; Szpak et al., 2012; McKechnie et al., n.d.) and Barkley Sound in Nuu-chah-nulth territories on southwest Vancouver Island where sea otter bones are fewer and represent a much lower proportion of mammal bones in both relative and absolute terms (McKechnie and Wigen 2011; McKechnie et al., n.d.). What remains unknown is whether these observed differences in the archaeological record reflect demographic differences in the prevalence of sea otters between these two areas, a difference in the cultural hunting traditions and preferences among the people inhabiting them, or some combination of the two. While the relative and absolute number of sea otter bones are suggestive as standalone proxies for sea otter prevalence, these data can be strengthened when combined with additional indicators that are influenced by sea otter density such as ancient prey size, the temporal patterns of shellfish harvesting by humans, and the magnitude of kelp-derived organic carbon assimilated by nearshore consumers. Collectively, these multiple lines of evidence can illuminate the general structure of rocky reef food webs and thus the prevalence of sea otters during the late Holocene (ca. 2500 years). Given that sea otters have been shown to truncate prey size distributions, reduce prey densities that would otherwise be available for human harvest, and indirectly cause the expansion of kelp forests, increasing detrital and dissolved kelp-derived organic carbon, we look for archaeological evidence of these other indicators to draw stronger inferences about variability in sea otter prevalence.

To gain insight into the observed disparities in the abundance of archaeological sea otter remains between Gwaii Haanas and Barkley Sound (McKechnie et al., n.d.), we asked: 1) To what extent do the isotopic signatures of ancient coastal consumers differ between southern Haida Gwaii and Barkley Sound? 2) How did the variability and trophic level within ancient sea otter diets differ between these two areas? And 3) is there a difference in the size and temporal continuity of archaeological shellfish prey between areas? Although it is likely that sea otters were kept below carrying capacity by humans in both areas, we hypothesize that sea otters were more prevalent in Gwaii Haanas than Barkley Sound over the late Holocene and hypothesize that this difference will be reflected in our findings with the following: 1) Gwaii Haanas coastal consumers enriched in both ^{13}C and ^{15}N compared to Barkley Sound; 2) Truncated shellfish prey size distributions in Gwaii Haanas; 3) Reduced occurrence in shellfish prey through time in Gwaii Haanas and 4) A greater degree of dietary variability and trophic position in ancient Gwaii Haanas sea otter diets.

Methods

Study Areas

We compiled various zooarchaeological data from two areas within coastal British Columbia, Canada: Barkley Sound and southern Haida Gwaii (Figure 1). Barkley Sound, a 30 km wide coastal embayment containing hundreds of islands, is situated on the southwest coast of Vancouver Island where there is a wide continental shelf. This area is within the northern reach of the California Current and is characterized by strong, wind-driven seasonal upwelling facilitating high pelagic productivity (Hickey & Banas, 2008; Thomson, 1981). Gwaii Haanas National Park Reserve and Haida Heritage Site (hereafter Gwaii Haanas), a collection of islands and islets in southern Haida Gwaii, is flanked by a very narrow continental shelf on the West and the relatively shallow Hecate Strait to the East. Oceanographically, this region is situated in a transition zone between downwelling to the North, associated with the Alaska Gyre, and upwelling to the South, associated with the California Current (Peterson et al., 2007). Sea otters were extirpated from both areas during the maritime fur trade (DFO, 2015; Watson & Estes, 2011) but have been observed in recent years in small numbers in both areas. In 2017 a mother and pups were sighted off the coast of Haida Gwaii (Salomon et al., 2020) and there have been various sightings of small groups of sea otters in Barkley Sound since 2007 (Okerlund, 2007). We examined isotopic data from nine archaeological sites in Barkley Sound, within the territory of the modern day Tseshaht First Nation, and seven archaeological sites within Gwaii Haanas in the territory of the Kunghit Haida (Figure 1). We obtained existing archaeological shellfish data from the same areas from 16 sites in Gwaii Haanas (Keen 1990) and 10 sites in Barkley Sound (Sumpter et al., 2005; McKechnie 2014).

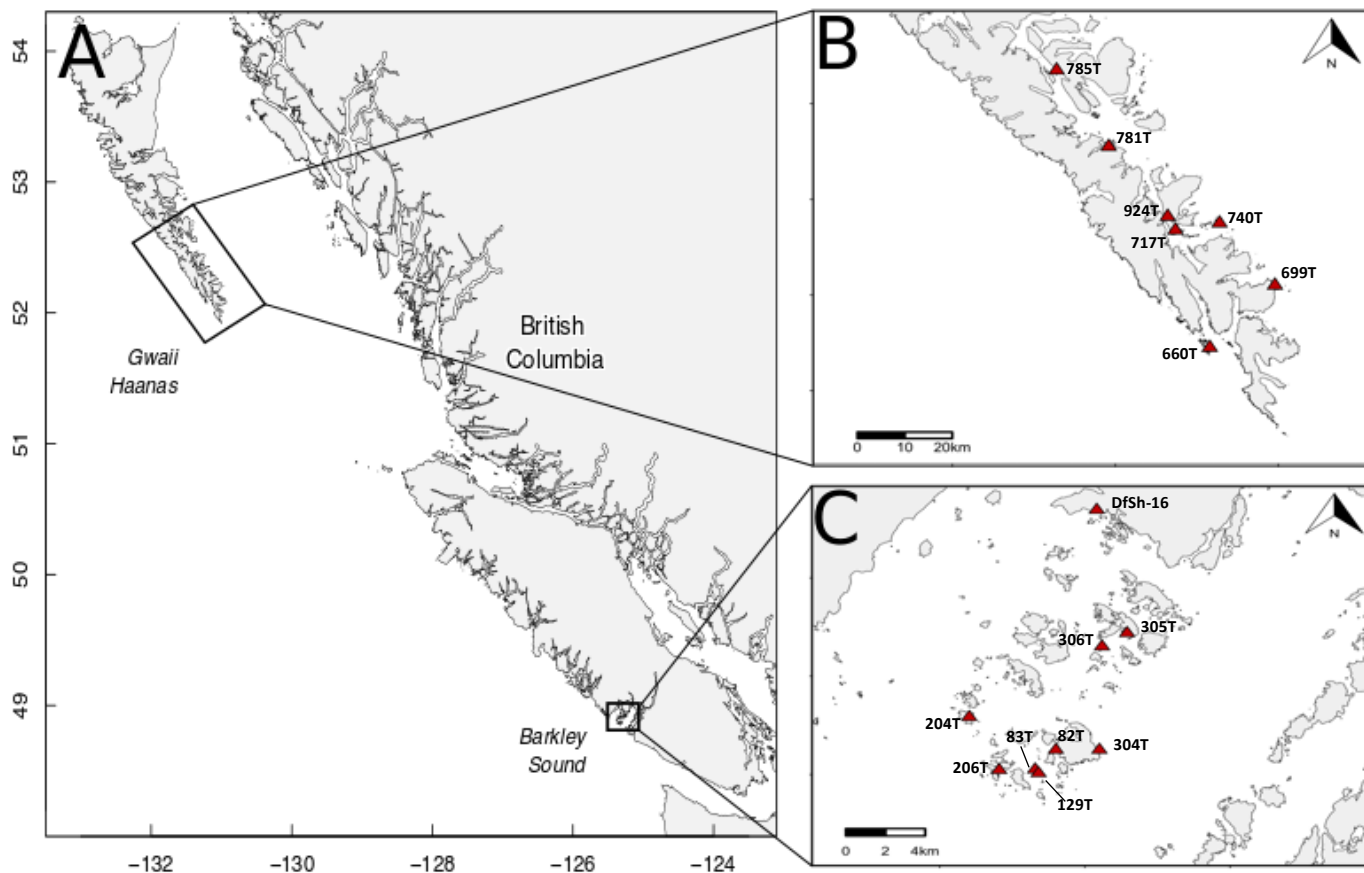


Figure 1. A) Isotopic archaeological data were assessed from two areas in coastal British Columbia, Canada: B) Gwaii Haanas (Szapak et al., 2009, 2012 2013; Szpak and Orchard 2011; Orchard and Szpak 2015; this study) and C) Barkley Sound (Hillis et al., 2020; this study).

Isotopic Comparison of Ancient Coastal Consumers

Experimental Design and Zooarchaeological Data

We compared the carbon and nitrogen isotopic signatures of ancient coastal consumers from archaeological faunal remains collected from Gwaii Haanas and Barkley Sound. Isotopic values were derived from bone collagen extracted from skeletal remains that were identified to genus or species by specialists using a zooarchaeological comparative collection at the University of Victoria. We selected species in the archaeological record known to rely on kelp forest habitat including sea otters, rockfish (*Sebastes* sp.), greenling (*Hexagrammos* sp.), lingcod (*Ophiodon elongatus*), harbour seal (*Phoca vitulina*) (Estes et al., 2009; Estes, 2016; Koenigs et al., 2015; Markel & Shurin, 2015;

Olson et al., 2019; von Biela et al., 2016), as well as Pacific herring (*Clupea pallasii*), and northern fur seal (*Callorhinus ursinus*), two species that are known to be more pelagic, foraging offshore (Newsome et al., 2007; McKechnie et al., 2014).

Zooarchaeological Data

Our isotopic dataset is compiled from existing values derived from archaeological bone collagen from a variety of published studies for Gwaii Haanas (Orchard & Szpak, 2015; Szpak & Orchard 2011; Szpak et al., 2009, 2012, 2013) and Barkley Sound (Hillis et al. 2020; Newsome et al., 2007; Moss et al. 2006) (Tables A1, A2). To increase the sample size and taxonomic representation for both areas, we extracted collagen from archaeofaunal remains from one additional site in Gwaii Haanas as well as two additional sites in Barkley Sound (Table A2). Chronological information including radiocarbon dates indicate that samples from Gwaii Haanas approximately span the time period between 2000 calibrated years BP to AD 1880 (Acheson, 1995; Mackie et al., 2001; Orchard, 2004). Isotopic samples from Barkley Sound date between approximately 3,000-200 cal yr BP (Hillis et al., 2020; McKechnie, 2014, 2015; McKechnie et al., 2019; McMillan & St. Claire, 2005) with the majority of samples coming from well prior to the historic era maritime fur trade (ca. AD 1778-1850).

Collagen Extraction

To ensure isotopic data were consistent across previous studies, we followed standard bone collagen extraction and calibration methods (Guiry et al., 2016; Szpak et al., 2017). Specifically, we cleaned bones of surface residue by brushing and washing them with tap water, rinsing with Milli-Q water, and air drying them. We took 50-100 mg subsamples from dried specimens for collagen extraction. To account for potential lipid contamination in fish bones (Szpak, 2011), we placed fish samples in an ultrasonic bath while soaking in 5-10 ml 2:1 chloroform-methanol for 15-45 minutes (solution refreshed every 15 minutes until no colour change observed) (Guiry et al., 2016). We demineralized bone samples with 0.5 M Hydrochloric acid (HCl) at 4°C for ~12-15 hours. We then rinsed the samples with Mili-Q water to neutrality. We removed humic acids by soaking the samples in 0.1 M Sodium hydroxide (NaOH) at room temperature in an ultrasonic bath for successive 15-minute periods (until the solution remained clear). We

then rinsed the samples to neutrality with Milli-Q water once again. We solubilized our samples in 10^{-3} M HCl (pH 3), heating them to 75°C for 48 hours. After lyophilizing the gelatinized collagen, we weighed ~1 mg samples and placed them into tin capsules for isotopic and elemental analysis.

Stable Isotope Analysis

These samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer by the Stable Isotope Facility at the University of California Davis. Isotopic results are expressed as δ values in parts per thousand (‰) relative to international known standards, Vienna-Pee Dee Belemnite limestone (VPDB) for carbon and atmospheric N₂ for nitrogen:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \right] \quad (1)$$

Where X equals ¹³C or ¹⁵N and R = ¹³C/¹²C or ¹⁵N/¹⁴N, respectively, capturing the relative enrichment of heavy to light isotope. Carbon and nitrogen isotopic compositions were calibrated to glutamic acid standards, USGS40 ($\delta^{13}\text{C} = -26.39$ ‰; $\delta^{15}\text{N} = -4.52$ ‰) and USGS41 ($\delta^{13}\text{C} = +36.55$ ‰; $\delta^{15}\text{N} = +47.57$ ‰) or USGS41a ($\delta^{13}\text{C} = -36.55$ ‰; $\delta^{15}\text{N} = +47.55$ ‰). Uncertainty was monitored using standards with well-characterized isotopic compositions and standard uncertainty was determined to be ± 0.04 ‰ for $\delta^{13}\text{C}$ and ± 0.03 ‰ for $\delta^{15}\text{N}$.

Statistical Analysis

To assess the strength of evidence for an effect of *Area* on consumer isotopic signatures, we took an information theoretic and model selection approach (Burnham & Anderson, 2002). We compared generalized linear models of consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as a function of *Area* (Barkley Sound vs. Gwaii Haanas) as a fixed effect, to null models with no effect of *Area* (*Intercept*). Models assumed a Gaussian error distribution and were fit via maximum likelihood with the stats package in R (v. 3.6.3, R Core Team, 2020). We then compared alternative models with small-sample corrected Akaike Information Criterion (AIC_c) standardized to the most parsimonious model to produce

ΔAIC_c and normalized Akaike weights (w_i) (Burnham & Anderson, 2002) calculated with the dredge function within the MuMin package in R (Bartoń, 2018). We determined that there was empirical support for a model when the next most parsimonious model had a ΔAIC_c value greater than 2. Note the variation in sample sizes among species and between Areas (Table A1).

Estimating Sea Otter Diet with MixSIAR

We used an open source Bayesian stable isotope mixing model (MixSIAR, v 3.1) that employs Markov Chain Monte Carlo methods to estimate the proportional contribution of isotopically distinct sources to a mixture while accounting for uncertainty in model inputs (Phillips et al., 2014; Stock et al., 2018; Stock & Semmens, 2016). We estimated the contribution of four prey sources to the diet of late Holocene sea otters in the two areas. We ran three replicate chains (each with 3,000,000 draws) with a burn-in of 1,500,000 and a thinning rate of 500. We used both the Gelman-Rubic diagnostic and the Geweke diagnostic to assess model convergence. We focus on the median (50%) and interquartile range (25–75%) of estimated dietary contributions based on mixing model outputs. We completed all MixSIAR modelling in R (v 3.6.3).

MixSIAR Inputs

We used isotopic values from ancient sea otter collagen as described in the previous section (Tables A1, A2) as the consumer. We included samples from species representing two broad categories of prey: lower trophic level macroinvertebrates represented by California mussels (*Mytilus Californianus*) and red sea urchins (*Strongylocentrotus franciscanus*); and higher trophic level finfish represented by greenling (*Hexagrammos sp.*) and rockfish (*Sebastes sp.*) (Table B1). Invertebrate isotopic values were derived from modern tissue samples (Berger & Jelinski, 2008; Markel, 2011; Pang, 2018; von Biela et al., 2016) and fish isotopic values from archaeological bone collagen (Hillis et al., 2020; Orchard & Szpak, 2015; Szpak et al., 2009, 2013). Ideally, consumer and prey samples would be contemporaneous, but the variation in trophic position and isotope signature is unlikely to vary for the relationships queried in the model using the best available source data. Therefore, following Hillis et al. (2020), we opted for a combination of archaeological and modern source inputs,

recognizing that there is potential for isotopic variation between preindustrial and modern time periods. To address this uncertainty, we additionally estimated ancient sea otter diet using only modern prey values by substituting archaeological fish values with modern kelp greenling (*Hexagrammos decagrammus*) and black rockfish (*Sebastes melanops*) (Pang, 2018; von Biela et al., 2016). See Table B1 for a summary of all models.

Correction Factors

To standardize prey inputs across tissue types (bone collagen and muscle), we adjusted fish bone collagen values by -1.1 ‰ for $\delta^{13}\text{C}$ and +2.3 ‰ for $\delta^{15}\text{N}$, reflective of the difference between bone collagen and muscle in fish according to previous work (Sholto-Douglas et al., 1991). We corrected modern invertebrate data for the Suess effect using the following equation, after Hilton et al. (2006) and modified by Misarti et al. (2009) to allow for the comparison between modern and pre-historic values:

$$\text{Suess Effect Correction Factor} = a * \exp(b * 0.027) \quad (2)$$

Where a is the maximum annual rate of $\delta^{13}\text{C}$ decrease in the North Pacific (-0.014); b is the year of animal death or collection minus AD 1850 (a commonly used benchmark for the onset of the industrial revolution); and 0.027 represents the exponential curve established by Gruber et al. (1999) for the change in $\delta^{13}\text{C}$ of the global oceans between 1945 and 1970. See Table B2 for a summary of all correction factors applied to model inputs.

Trophic Discrimination Factors

We used trophic discrimination factors (TDFs) to correct for isotopic differences between consumer tissues and diet that occur during assimilation and excretion processes (Phillips et al., 2014). Currently, there are no published diet-collagen TDFs for sea otters, therefore we adapted sea otter vibrissae-diet values established by Newsome et al. (2010) in a wild population of sea otters (2.2 ± 0.7 ‰ for $\delta^{13}\text{C}$ and 3.5 ± 0.6 ‰ for $\delta^{15}\text{N}$). We applied a correction factor to these values to account for differential diet-tissue discrimination between keratin and collagen resulting from differences in biochemical

composition, routing of dietary components, and timing of nutrient incorporation (Bocherens et al., 2014). We used the median values from a range of differences between hair and collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in mammals from various studies (Bocherens et al., 2014; Crowley et al., 2010; Fox-Dobbs et al., 2007; O'Connell et al., 2001; Tieszen et al., 1983; Vogel, 1978). This resulted in corrections of +1.4 for $\delta^{13}\text{C}$ and +0.6 for $\delta^{15}\text{N}$ and final TDFs of 3.6 ± 0.7 ‰ for $\delta^{13}\text{C}$ and 4.1 ± 0.6 ‰ for $\delta^{15}\text{N}$. These values are similar to those used for sea otters by Szpak et al. (2012) (3.7 ± 1.6 ‰ for $\delta^{13}\text{C}$ and 3.6 ± 1.3 ‰ for $\delta^{15}\text{N}$) which are based on mean values from a summary of published mammalian bone collagen TDFs. We ran two additional models to assess the uncertainty surrounding TDFs and the robustness of our model design by examining the implications of adjusting the standard deviations for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table B1).

Shellfish Size Structure and Temporal Ubiquity

California Mussel Size Structure

In order to compare the size structure of harvested mussels from Gwaii Haanas to those previously estimated from Barkley Sound (Slade et al., in review), we estimated the length of fragmentary archaeological mussels (*Mytilus californianus*) from SGang Gwaay (660T) an important Haida village and world heritage site (UNESCO 2020). This enables a comparison of the level of sea otter predation between areas using a size-based shellfish proxy. We used an existing valve length to umbo thickness relationship established by saturating regression analysis (Slade et al., in review) to estimate mussel shell length from fragmentary specimens which maximizes sample size. We measured the thickness of all mussel umbos found within four column samples from site 660T taking measurements from the tip of the umbo to the inside of the hinge using digital calipers (Figure C1). Estimated shell lengths represent the distance from the outer umbo to the point on the shell's end which is its longest linear dimension (Figure C1). We combined these estimates into a size frequency distribution in order to compare our data from Gwaii Haanas and data from four sites in Barkley Sound (83T, 206T, 305T, 306T) as reported in Slade et al. (in review). We compared the size frequency distributions of estimated mussel shell lengths between areas using a Kolmogorov-Smirnov test in R. To assess the strength of evidence for an effect of *Area* on the size of California mussels,

we compared a linear model of mussel shell length as a function of *Area* to a null model with no effect of *Area* (Intercept). Models assumed gaussian error distributions and were compared with Akaike's Information Criterion (AIC) and normalized Akaike weights in R.

Red Turban Snail Size Structure

Red turban snails (*Astraea gibberosa*) are marine snails whose opercula are found abundantly in archaeological deposits in Barkley Sound (Earle, 2019; Sumpter, 2005, 2012). We used a pre-established operculum-shell length relationship (Earle 2019) to estimate the size of red turban snails from archaeological opercula (Appendix C). We measured all opercula retrieved from three excavation units (7, 8, and 10) representing a temporal range of approximately 3000 years of occupation at site 306T in Barkley Sound (McKechnie et al., 2019). We measured along the longest axis of each opercula which we used to estimate the length of the longest portion of the base of the shell (Figure C2). We compiled these estimates into size frequency distributions for each unit and conducted pairwise comparisons using Kolmogorov-Smirnov tests in R. To assess the strength of evidence for an effect of *Unit* on red turban snail size, we compared linear models of shell length as a function of *Unit*, to null models with no effect of *Unit* (Intercept). Models assumed gaussian error distributions and were compared with Akaike's Information Criterion (AIC) and normalized Akaike weights in R. While we do not have a similar dataset from Gwaii Haanas to compare these results to, this provides an additional size and abundance-based proxy for a commonly consumed sea otter prey item to infer the potential for human mediated foraging limitations for sea otters in Barkley Sound.

Urchin Ubiquity Through Time

We assessed the ubiquity of urchin remains in archaeological contexts in both Gwaii Haanas and Barkley Sound. Here, we define ubiquity as the percentage of temporally and depositionally unique contexts (in this case individual levels within auger and column samples) in which urchins are present or absent (McKechnie 2014; McKechnie and Moss 2016; Lambrides et al. 2019). We calculated this metric, roughly characterizing the frequency of use, from archaeological shellfish data from a report by Keen (1990) which documents urchin abundance by level across 250 depositional contexts from 20 column samples at 16 archaeological sites in southern Gwaii Haanas

(Table C1). Each column sample level represents ~5 cm of depth for which we noted the presence or absence of urchin remains. Using data from McKechnie (2013) and Sumpter (2005), we conducted the same analysis in Barkley Sound using data representing 383 depositional contexts from 10 sites in the Broken Group Islands spanning 5,000 years (Table C1). To assess the strength of evidence for an effect of *Area* on the proportion of depositional contexts in which sea urchins were present, we fit a generalized linear mixed-effects model (GLMM) with the proportion of contexts as a function of *Area*, as a fixed effect, and *Site* nested within *Area* as a random effect using a beta likelihood and logit link function. We then compared this model to a null model of no effect with small-sample corrected Akaike Information Criterion (AIC_c) standardized to the most parsimonious model to produce ΔAIC_c and normalized Akaike weights (w_i) (Burnham & Anderson, 2002). These models were built within the glmmTMB package in R (Brooks et al., 2017).

Results

Isotopic Comparison of Ancient Coastal Consumers

We observed a consistent pattern of isotopic enrichment among coastal consumers from Gwaii Haanas relative to Barkley Sound for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figure 2). The one exception to this was in harbour seals which had relatively lower $\delta^{13}\text{C}$ in Gwaii Haanas compared to those from Barkley Sound. Specifically, we found strong evidence for an effect of *Area* on the $\delta^{13}\text{C}$ values of northern fur seals, sea otters and rockfish (Figure 2, Table A3). Specifically, these consumers were more enriched in $\delta^{13}\text{C}$ in Gwaii Haanas compared to Barkley sound. We did not detect an effect of *Area* on the $\delta^{13}\text{C}$ values of harbour seal, greenling, lingcod, or herring. (Figure 2, Table A3).

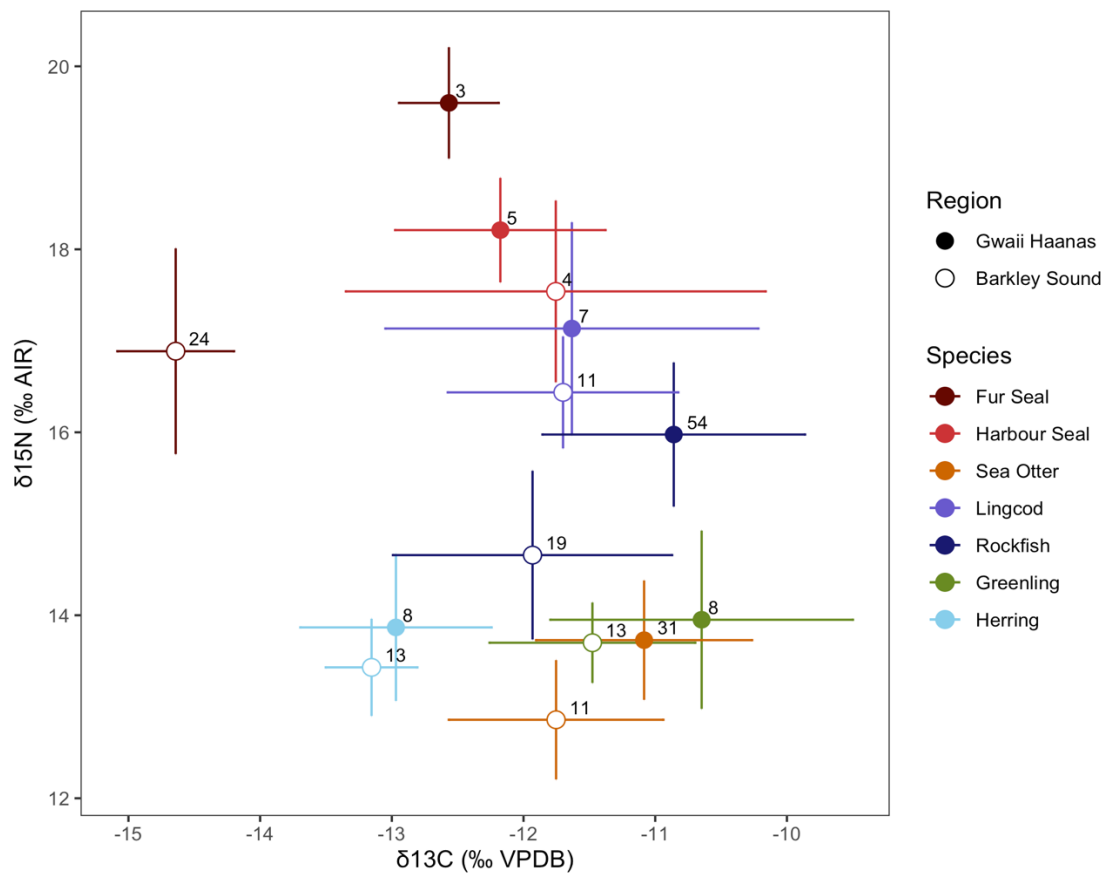


Figure 2: Mean \pm SD of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for archaeological coastal species in Barkley Sound and Gwaii Haanas.

Similarly, there is a consistent enrichment in ^{15}N across consumers from Gwaii Haanas compared to Barkley Sound, and we found strong evidence for an effect of *Area* on the $\delta^{15}\text{N}$ values of northern fur seals, sea otters, and rockfish (Figure 2, Table A3). However, we did not detect an effect of *Area* on the $\delta^{15}\text{N}$ of harbour seals, lingcod, greenling, or herring.

Ancient Sea Otter Diet

Our model estimates indicate that ancient sea otter diets were dominated by low trophic level macroinvertebrates in both Barkley Sound and Gwaii Haanas during the late Holocene (Figure 3). Focusing on the median and interquartile range (50%, 25-75%) of estimated dietary contributions, we detected a relatively high probability that sea otter diets in Barkley Sound were dominated by California mussels (83%, 78 – 87%) with relatively minimal contribution of red sea urchins (12%, 8 – 17%), rockfish (3%, 1 – 5%) and greenling (4%, 2 – 6%). In Gwaii Haanas, we detected a high probability that sea otter diets encompassed both California mussels (52%, 49 – 58%) and red urchins (38%, 36 – 41%) in medium proportions, with relatively small contribution of rockfish (5%, 2 – 7%) and greenling (5%, 2 – 9%). The contribution of fish to sea otter diets is estimated to be low for both areas, but especially in Barkley Sound (Figure 3, Table S8). Overall, sea otter diets in Gwaii Haanas are estimated to be slightly more diverse, including a greater proportion of higher trophic level prey (fish) than those in Barkley Sound. We see consistency across models (which varied in prey type and TDF uncertainty, Table B1) with similar estimates of source contributions to sea otter diet (Table B3, Figures 3 and B1 – B3). We focus on outputs from model 1 (Figure 3) which represents the most refined of the four models, three of which were used to evaluate the robustness of our design.

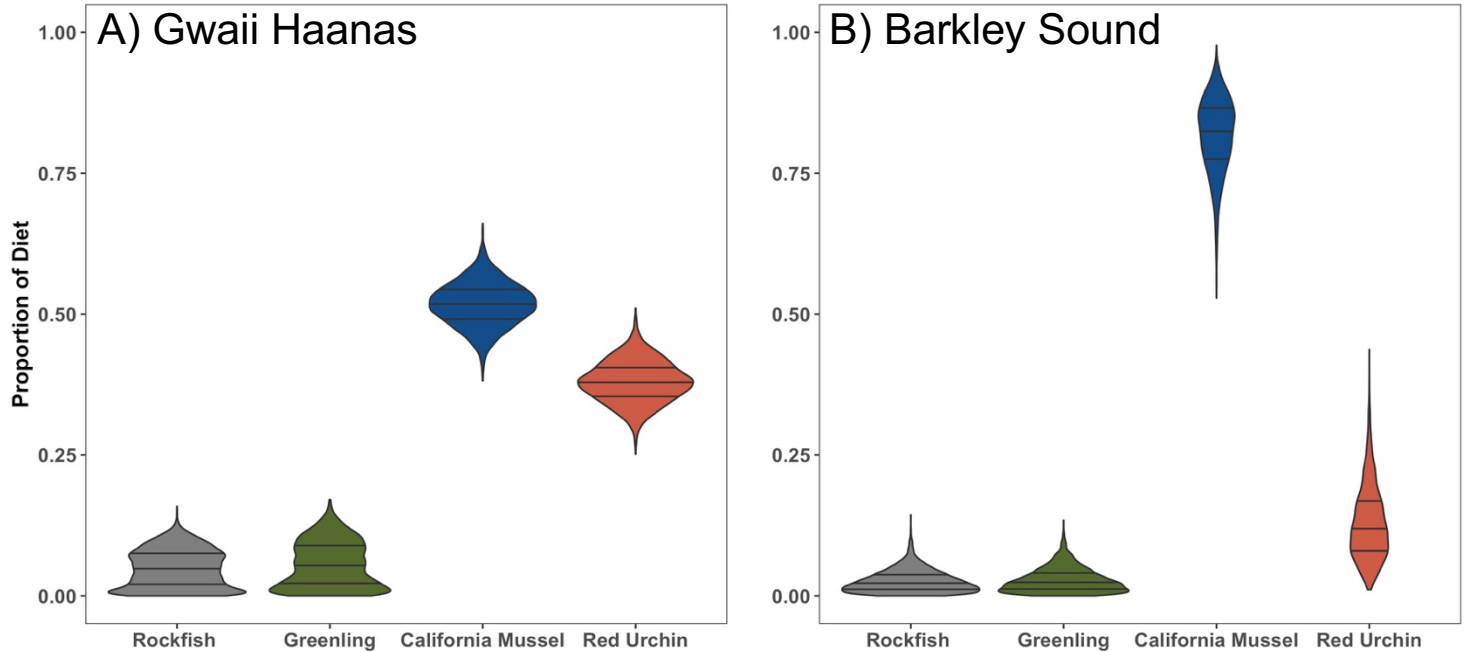


Figure 3. Violin plots representing posterior distributions of the relative proportion of different prey types assimilated by late Holocene sea otters in A) Gwaii Haanas (n=31) and B) Barkley Sound (n=11). Bars within violins indicate the median, 25, and 75 percentile estimates.

Shellfish Size Structure and Ubiquity

California Mussel Size Structure

The size structure of ancient California mussels harvested in Gwaii Haanas and Barkley Sound were relatively similar (Figure 4). For mussels from Gwaii Haanas, we observed a mean estimated mussel length of 96.5 ± 22.8 mm with a maximum estimated length of 164.01 mm. We detected statistically significant differences in the size distributions of mussels between Barkley Sound and Gwaii Haanas study areas (K-S D = 0.30997 $p = 1.07e-07$). We also found evidence for an effect of Area on mussel shell length (Table C2) with larger mussels in Gwaii Haanas. In both study areas we observed that a considerable proportion of shell length estimates exceed 10 cm (21% in Barkley Sound and 45% in Gwaii Haanas, (Figure 4) which we note in the context of work by Singh et al. (2013) who document few, if any, modern mussels larger than 10 cm in locations where sea otters have been present for 20 years or longer.

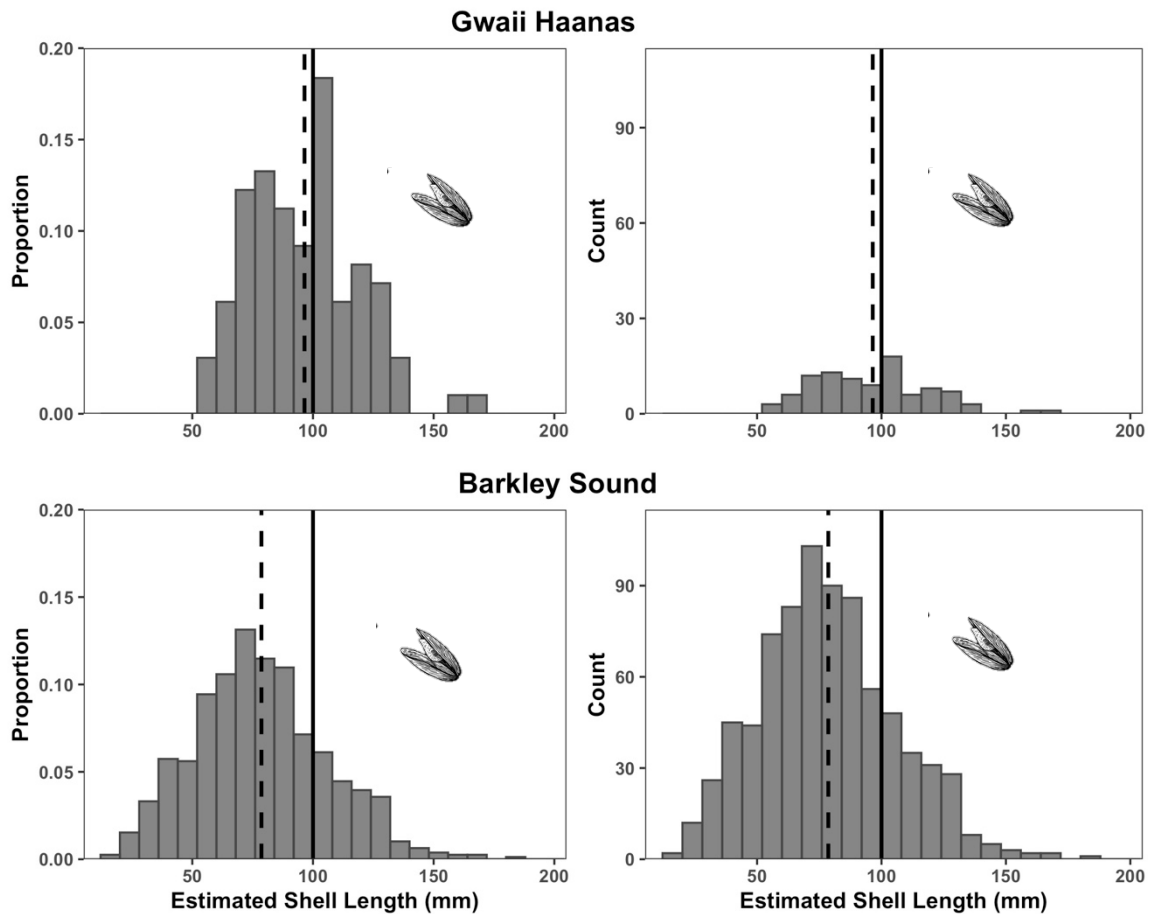


Figure 4. Size frequency distributions of California mussel shell lengths estimated from Gwaii Haanas ($n=98$) and Barkley Sound ($n=785$). Dotted vertical lines represent mean estimated shell length and solid lines show 10 cm threshold, above which Singh et al. (2013) found few modern mussels in areas where sea otters were present for 20 years or longer.

Red Turban Snail Size Structure

Visually, our measurements of red turban snails in Barkley Sound produce very similar size frequency distributions with very similar means (44.7, 45.93, and 44.5 mm) across three excavation units (*Unit*) dating to different time periods on Keith Island (Figure 5). Across units, estimated shell lengths ranged between 12.8 and 65.1 mm. We detected significant differences in size distributions between two units, 7 and 10 (K-S D:0.08, $p = 0.15$) and no statistically significant differences between Units 7 and 8 ($D = 0.08$, $p = 0.06$) or 8 and 10 ($D = 0.12$, $p = 0.03$). We did not, however, find evidence for an effect of

Unit on the length of red turban snails in Barkley Sound (Table C2). Consequently, red turban snails harvested and brought to the Keith Island village site appear to be consistent in size over an approximate 2300-year period.

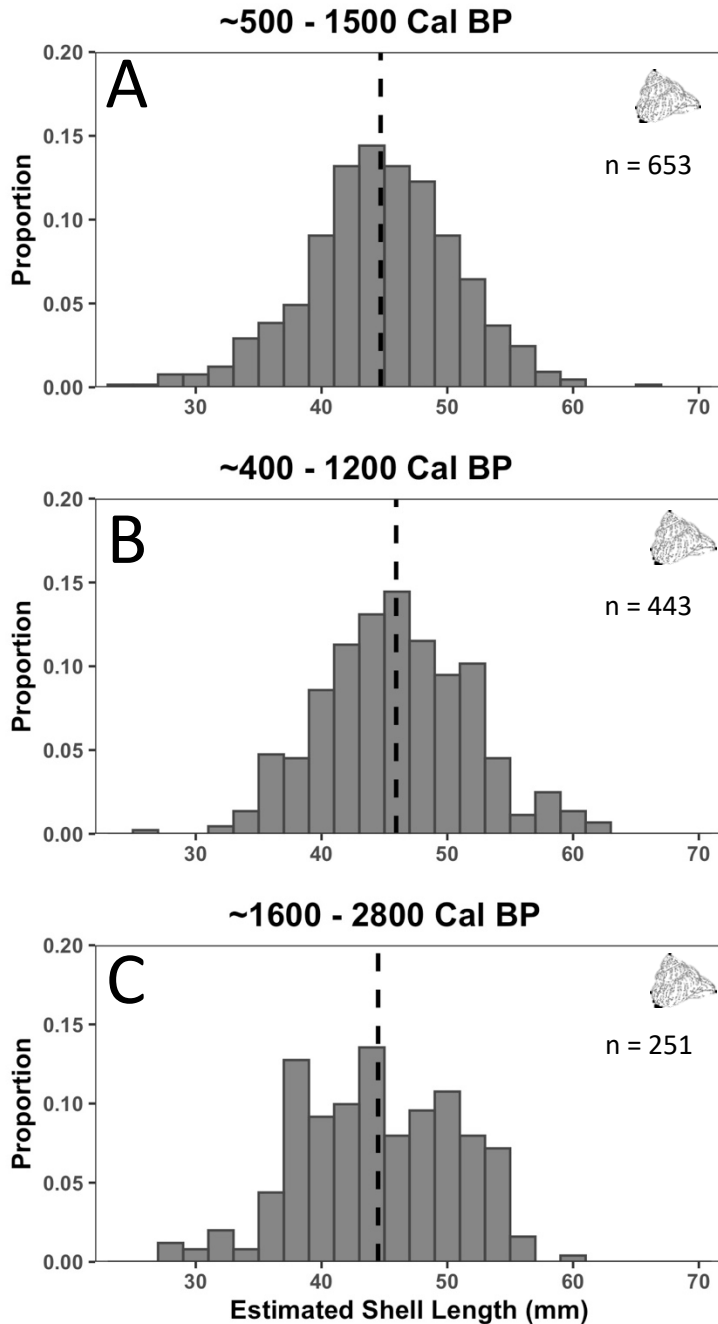


Figure 5. Size frequency distribution for estimated red turban snail shell lengths from A) unit 7, B) unit 8, and C) unit 10 at site 306T in Barkley Sound. Dotted lines represent mean estimated shell lengths.

Urchin Ubiquity Through Time

We apply the simple metric of ubiquity, or frequency of occurrence, to the greatest number of sampled contexts within archaeological sites to calculate that urchin ubiquity ranges from 0% and 53% in the Broken Group Islands, with urchins present in 24% across all 383 contexts (Figure 6, Table C1). In Gwaii Haanas, urchins are present in 50% of all contexts from all sites and ranges from 0% to 100% for different sites (Figure 6). We found strong evidence for an effect of *Area* (Barkley Sound, Gwaii Haanas) on the proportion of depositional contexts in which urchins were present (Table C2).

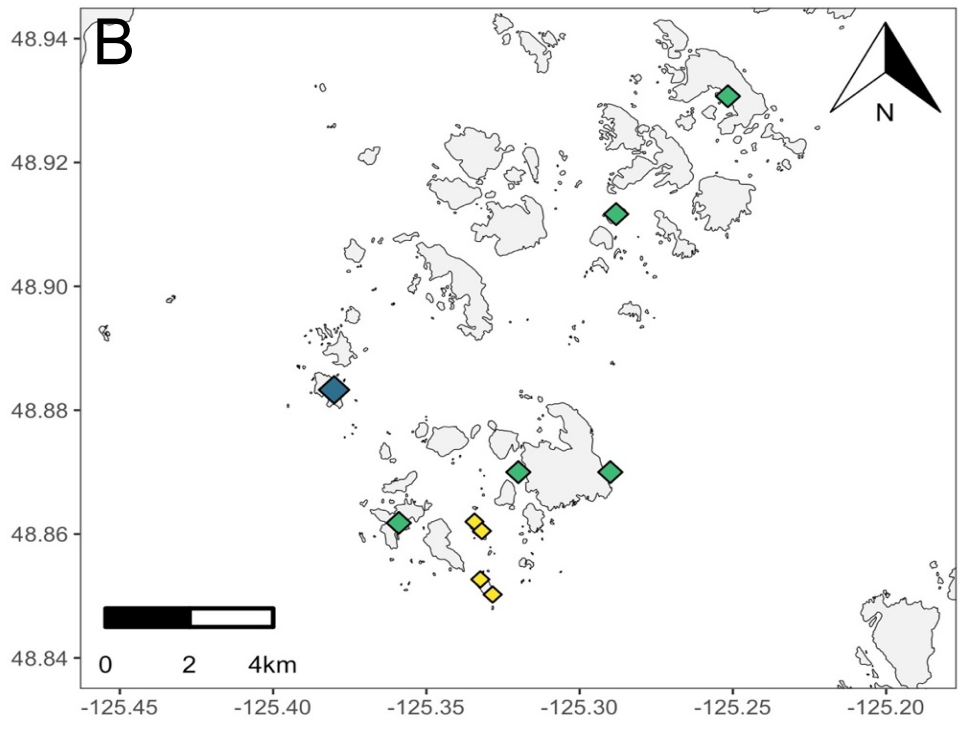
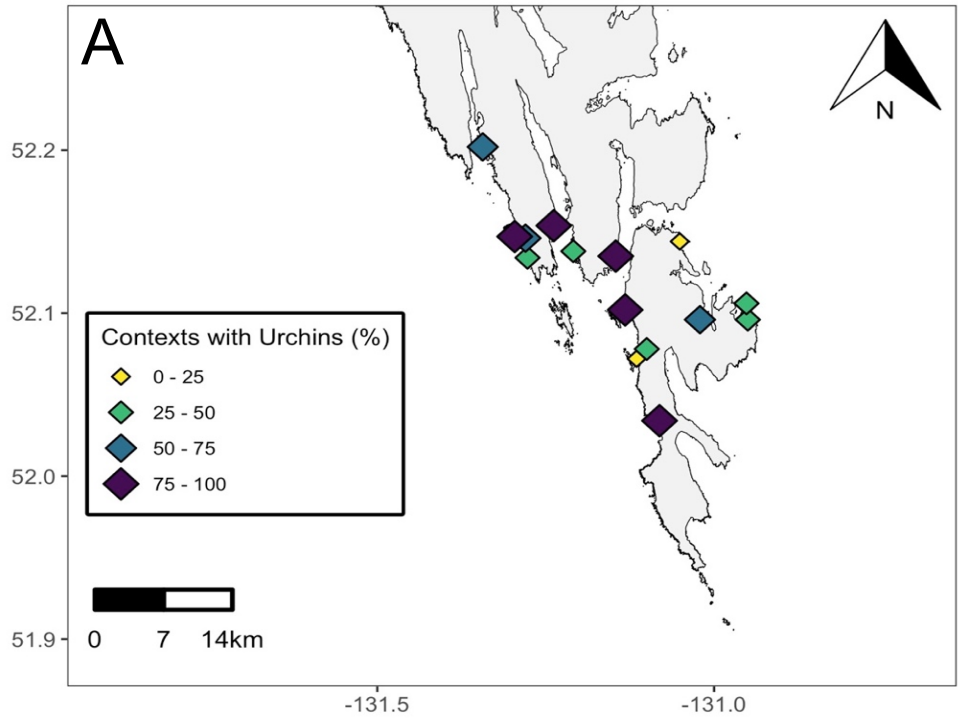


Figure 6. Percentage of temporal contexts (column and auger sample levels) by site containing urchin remains in A) Gwaii Haanas (Keen 1990) and B) Barkley Sound (McKechnie 2014; Sumpter 2005).

Overall, our findings provide several forms of evidence in support of hypotheses surrounding the suppression of sea otters in proximity to village sites, as well as the notion that sea otter prevalence varied between different areas of the coast (Table 1).

Table 1. Main findings and the degree of support for the hypotheses that, in the late Holocene, A) sea otters were below carrying capacity along some stretches of shoreline and B) sea otter prevalence varied regionally such that Gwaii Haanas encompassed greater relative abundances.

Line of Evidence	Finding	A) Evidence that sea otters were below carrying capacity along some stretches of coastline	B) Evidence that there were more sea otters in Gwaii Haanas than Barkley Sound
Isotopic signatures of coastal consumers	↑ ¹³ C and ¹⁵ N in consumers from Gwaii Haanas	NA	YES ↑ Kelp-derived organic carbon and ↑ trophic level is associated with ↑ sea otter prevalence
Sea otter diets	Sea otter diets overall dominated by benthic invertebrates. But, slightly more diverse and higher trophic level in Gwaii Haanas	YES Macroinvertebrate dominated diets indicate low sea otter prevalence	YES Slightly more diverse/higher trophic level diets are associated with ↑ sea otter prevalence
California mussel size distributions	Mussel size distributions include large harvestable individuals in both Gwaii Haanas and Barkley Sound	YES Sea otters not in sufficient numbers to truncate size distributions	NO Slightly larger mussels from one site in Gwaii Haanas may indicate ↓ sea otter prevalence
Sea urchin ubiquity through time	Urchins consistent through archaeological contexts, especially in Gwaii Haanas	YES Urchins consistently available to human harvesters through time suggesting exclusion of sea otters from these areas	NO ↑ urchin ubiquity may indicate ↓ sea otters and/or ↑ secondary production in Gwaii Haanas
Red turban snail size distributions through time in Barkley Sound	Red turban snails consistent in size and occurrence through time at one site in Barkley Sound	YES Indicates sustained access by people and lack of effect of sea otter predation in the vicinity of this site	NA Lacking comparable data in Gwaii Haanas

Discussion

In this study, we integrate multiple lines of evidence to provide new insight into late Holocene sea otter prevalence in two areas on the west coast of British Columbia. Collectively, our results suggest that sea otter populations existed below carrying capacity in both Barkley Sound and Gwaii Haanas, which supports the hypothesis that this keystone predator was suppressed in proximity to human settlements and shellfish harvesting sites on the Northwest coast of North America (Table 1A) (Corbett et al., 2008; Slade et al., in review; Szpak et al., 2012). Specifically, we found that the remains of shellfish consumed by both sea otters and people occur consistently throughout the highest level of temporal resolution recovered from excavated archaeological contexts suggesting that people had sustained access to these resources through time and that sea otter predation on shellfish was limited in these areas. Moreover, the observed consistency in the size of red turban snails in Barkley Sound over 2,300 years alongside the proportion of mussels larger than 10 cm in both Barkley Sound and Gwaii Haanas are indicative of nearshore environments in which the effects of sea otter predation were diminished (based on Singh et al., 2013). These patterns are further corroborated by our model estimates of sea otter diet which were dominated by sea otters' preferred macroinvertebrate prey and so suggest these populations were below carrying capacity. Our evidence for regional differences in sea otter prevalence, however, is less clear cut.

While some lines of evidence suggest a higher relative abundance of sea otters in Gwaii Haanas compared with Barkley Sound, other sources of evidence may suggest the opposite (Table 1B). For example, in Gwaii Haanas we found higher levels of ^{13}C and ^{15}N in the remains of coastal consumers which, along with estimates of more diverse and higher trophic level sea otter diets, suggest that sea otters were more abundant in this area. However, our mussel size investigation indicates that there were larger mussels in Gwaii Haanas suggesting a decreased effect of sea otter predation in this area (Table C2). We also detected a greater ubiquity of sea urchin remains in Gwaii Haanas archaeological contexts compared to Barkley Sound (Figure 6, Table C2), which may indicate that sea urchin populations were very productive and not recruitment limited or that the Haida were effective at keeping sea otters away from urchin harvesting sites near villages. We discuss these findings in further detail below. Despite not meeting the expectations of two hypotheses (regarding archaeological mussels and

sea urchin remains), our findings, in combination with previous observations of geographic differences in sea otter abundance (McKechnie et al., n.d.), suggest a degree of spatial variation in the prevalence of late Holocene sea otters.

Evidence of regional variation in late Holocene sea otter prevalence

We detected greater levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in several ancient consumers from Gwaii Haanas relative to Barkley Sound (Figure 2, Table A3) suggesting that there were regional differences in the structure of late Holocene rocky reef food webs. Three alternative but not mutually exclusive mechanisms could be driving this pattern: (i) Regional differences in the isotopic composition of primary producers may have existed and driven differences in consumer signatures at higher trophic levels; (ii) Differences in regional oceanographic productivity between these areas may have affected the relative contribution of kelp-derived subsidies to nearshore food webs; and (iii) Differences in the number of sea otters between these areas, and their cascading effects on kelp forest extent may have resulted in an increase of kelp-derived subsidies to rocky reef consumers as well as longer and more complex nearshore food chains.

Although the isotopic composition of pelagic primary producers is known to vary geographically (Burton & Koch, 1999; Cherel & Hobson, 2007), we consider this the least likely explanation of the three alternative mechanisms. It has been demonstrated that the isotopic signatures of pelagic primary producers vary latitudinally; however, there tends to be a poleward depletion in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Burton & Koch, 1999; Rau et al., 1982; Saino & Hattori, 1987), which is not reflected in our data (Figure 2) with the exception of harbour seals. We do not see a poleward depletion in these isotopes in northern fur seals or herring, two species that forage along the continental shelf edge and would be expected to exhibit these pelagic patterns. Nonetheless, the overall inverse trend in our data from established latitudinal isotopic gradients may suggest an even stronger isotopic signal from the effects of sea otter predation in Gwaii Haanas, which supports our third hypothesis.

Oceanographically, our two study areas differ in important ways which may be driving the availability of pelagic primary productivity and causing differential uptake of kelp-derived carbon in nearshore food webs between areas. Barkley Sound is influenced by strong, wind-driven, seasonal upwelling producing high pelagic productivity which is further amplified by local factors such as submarine canyons, freshwater inputs, and a wide continental shelf (Allen et al., 2001; Hickey & Banas, 2008). In contrast, wind-driven upwelling is relatively rare on the west side of Gwaii Haanas although weak seasonal upwelling does occur in Hecate Strait and along the east coast of Gwaii Haanas where the majority of our study sites are located. Satellite imagery using chlorophyll as a proxy for primary productivity indicates that the marine waters around Gwaii Haanas experience lower pelagic productivity than Barkley Sound although seasonal blooms do occur in the bays and channels along eastern Gwaii Haanas (Jackson et al., 2015; Peterson et al., 2007; Robinson et al., 2004). Despite potential variations in paleoclimate, we infer that these different conditions were largely consistent over the late Holocene. Therefore, it is possible that the higher pelagic productivity in Barkley Sound may have offset potential benefits of kelp-derived organic carbon to consumers in this area, whether it was magnified by sea otters or not. When pelagic production is not limiting, the uptake of kelp-derived detrital carbon may be relatively minimal in nearshore food webs (Salomon et al., 2008) which may explain the relative depletion of $\delta^{13}\text{C}$ in consumers from Barkley Sound. In contrast, consumers in Gwaii Haanas may have been capitalizing on elevated kelp-derived food sources amidst a relative scarcity of pelagic subsidies, which may explain the elevated levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ observed in Gwaii Haanas consumers. However, the persistent enrichment in $\delta^{15}\text{N}$ across Gwaii Haanas consumers seems to indicate that elevated $\delta^{13}\text{C}$ levels in these consumers are related to differences in feeding ecology, rather than differences at the base of the food web (Szpak et al., 2013), which aligns with our third hypothesis that sea otter prevalence varied between these two areas during the late Holocene.

Previous work demonstrates that kelp-associated consumers in areas with more sea otters, and thus more expansive kelp forests, exhibit higher levels of not only $\delta^{13}\text{C}$ from kelp-derived carbon subsidies (Duggins et al., 1989), but also $\delta^{15}\text{N}$ due to expanded trophic niches attributed to an increase in the availability of higher-trophic level prey (Markel & Shurin, 2015; Olson et al., 2019; Pang, 2018; Szpak et al., 2013). In our study, we observed persistent enrichment in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in Gwaii Haanas, suggesting

there may have been greater sea otter presence in this area relative to Barkley Sound. Our isotopic modelling estimates of sea otter diet further support this interpretation, with a more diverse and slightly higher-trophic level prey base in Gwaii Haanas sea otter diets (Figure 3). While this evidence lends the greatest support to our third hypothesis that there was variable sea otter prevalence between areas, it is also possible that the isotopic differences we observe result from a combination of both bottom-up and top-down forces. Differing oceanographic conditions and varying sea otter prevalence may have influenced the isotopic signatures in late Holocene consumers (Szpak et al., 2013). Interestingly, regional variation in sea otter prevalence during the late Holocene was not supported by all of our lines of evidence (Table 1B).

Multiple lines of evidence advance our understanding of late Holocene nearshore social-ecological systems

Given that sea otters are known to serially reduce the size and abundance of their invertebrate prey (Estes & Palmisano, 1974; Kvitek et al., 1992; Salomon et al., 2007), we anticipated that archaeological shellfish from Gwaii Haanas, where sea otters are hypothesized to have been relatively more prevalent, would be characterized by reduced occurrence and size through time compared to Barkley Sound. Counter to our expectations, we detected smaller archaeological mussels in Gwaii Haanas (Figure 4, Table C2) and found that sea urchin remains were more ubiquitous in archaeological contexts in Gwaii Haanas (Figure 6, Table C2). These findings may indicate that sea otter predation on mussels and sea urchins was lower in Gwaii Haanas relative to Barkley Sound, challenging the inferences we draw from isotopic evidence. However, our study included archaeological mussels from only a single, relatively exposed site in Gwaii Haanas compared to four sites in Barkley Sound which may influence the observed size differences. Similarly, our comparison of sea urchin ubiquity data includes two heavily sampled defensive fortress sites in Barkley Sound (83T and 129T) which have similarly low urchin ubiquity values (6%, Table C1). This likely influences the relatively lower sea urchin ubiquity values observed in Barkley Sound in comparison with Gwaii Hannas (Table C1). In either case, the frequent occurrence of urchins in both study areas as well as numerous mussels larger than 10 cm suggests that sea otter predation on sea urchins and mussels was not limiting human harvests in either Barkley Sound or Gwaii Haanas for much of the late Holocene. Therefore, these findings may

support the notion that sea otters were excluded from or avoided the proximity of village sites (Corbett et al., 2008; Szpak et al., 2012) which would have enabled sustained human access to these sizes and abundances of shellfish while the prevalence of sea otters may still have varied at a regional scale beyond settlement sites.

A growing body of evidence suggests that sea otter populations were maintained below carrying capacity in proximity to village settlements, in part to maintain access to shellfish resources for which humans and sea otters directly compete (Corbett et al., 2008; Salomon et al., 2015, 2018, 2020; Simenstad et al., 1978; Slade et al., in review; Szpak et al., 2012). Our findings further support this hypothesis, with our investigations of archaeological prey depicting shellfish sizes and abundances that are unlikely to occur in areas with sustained, high-densities of sea otters, as found in similar studies (Corbett et al., 2008; Erlandson et al., 2005; Simenstad et al., 1978; Slade et al., in review). Our findings also hint at the temporal depth of sea otter management by humans, with sea urchin remains occurring consistently in archaeological deposits in both study areas and remarkably similar size distributions of red turban snails across three excavation units representing approximately 2,300-years at one site in Barkley Sound (Figure 5, Table C2). Finally, our estimates of sea otter diet expand on work by Szpak et al. (2012), revealing sea otter diets in both Gwaii Haanas and Barkley Sound characterized by a high reliance on a small number of low-trophic level prey, consistent with populations kept below carrying capacity. Combined with oral histories and ethnographic accounts, this body of evidence has led to the hypothesis that sea otters existed within a spatial mosaic of high- and low-density populations, mediated by humans, along the Pacific coast of North America (Corbett et al., 2008; Erlandson et al., 2005; Salomon et al., 2018; Slade et al., in review). While we provide further evidence of this spatial mosaic along the west coast of Canada, we also detect a degree of geographic variation in how this mosaic presented, with the prevalence of sea otters varying at a regional scale.

With multiple lines of evidence, we are able to add context to observed spatial disparities in the relative and absolute abundance of archaeological sea otter remains and by extension the variable influence of Indigenous peoples on nearshore ecosystems (McKechnie et al., n.d.). While catch records are often used as a proxy for biomass when other indicators are unavailable, these two variables can also be orthogonal,

particularly when management restrictions cause a reduction in catch leading to greater biomass of the target species in the wild (Pauly et al., 2013). Although data on the abundance of sea otter remains may indicate differences in late Holocene sea otter prevalence, it remains unclear whether this reflects actual demographic differences or an effect of differing cultural hunting traditions. In combining these data with additional proxies indicative of sea otter prevalence, we strengthen this interpretation which provides greater insight into the structure of late Holocene nearshore social-ecological systems. Our findings suggest that the relative abundance of archaeological sea otter bones in Gwaii Haanas reflects a greater biomass of these predators in this area over the late Holocene with subsequent ecological impacts that we detect in the archaeological record today.

While the combination of stable isotopes, diet modelling, and zooarchaeological analyses represents a powerful means of illuminating previous ecological states, certain methodological limitations and uncertainties exist in our study design. Although not uncommon of isotopic studies in archaeology (Burton et al., 2001; Moss et al., 2006; Szpak et al., 2012; Hillis et al., 2020), limited and uneven sample sizes for some species and prey groups in our study lower the degree of confidence with which we can make inferences, especially amidst high within-species isotopic variability. This variability may also be a product of other factors known to influence the isotopic signature of consumers such as gape size of fish species (Olson et al., 2019), wave exposure (Szpak et al., 2013), sex and age-at-harvest (Newsome et al., 2007). Future work will benefit from additional bone collagen samples for species such as northern fur seals, harbor seals, and lingcod (Figure 2). Likewise, additional archaeological mussel and snail samples from Gwaii Haanas would further strengthen our analysis and enable a more robust size distribution comparison (see Slade et al., in review) as we only had mussels from one site in this area and no red turban snails. Finally, a considerable source of uncertainty in our MixSIAR outputs are the limited number of prey sources included in our analysis, especially for a generalist consumer such as sea otters. Although common in isotope mixing model approaches (Hillis et al., 2020), the limited number of prey categories, can result in other dietary sources being over-represented in model outputs (Phillips et al., 2014), which may be the case in our study. Future diet reconstructions would be strengthened with additional prey sources important to sea otters such as clams, crabs, and abalone, preferably from archaeological contexts. Despite these uncertainties and

despite the variation in clarity and precision in our proxies, we detect the same ecological signals using multiple indicators of late Holocene sea otter prevalence, which increases our confidence in our results.

Bottom-up and top-down drivers of variable sea otter prevalence

The differences late Holocene sea otter prevalence that we detect may have been driven by a variety of interacting ecological and oceanographic forces. In the absence of top-down predation from orcas (*Orcinus orca*), white sharks (*Carcharodon carcharias*), and humans, it is understood that sea otter density is largely determined by habitat characteristics and bottom-up prey productivity, specifically invertebrate prey recruitment and growth rates (Hale et al., 2019; Tinker, Gill, et al., 2019; Tinker, Tomoleoni, et al., 2019). In terms of the latter, oceanographic differences may contribute to variations in sea otter prevalence between areas as regions that experience persistent wind-driven offshore transport of surface waters (Ekman transport) have been shown to receive decreased recruitment of benthic invertebrates as their planktonic larvae are swept seaward (Broitman et al., 2008; Menge et al., 2003, 2004). Although greater pelagic productivity from wind-driven upwelling in Barkley Sound likely benefits filter feeding invertebrates, the associated Ekman transport may decrease recruitment of a number of species such as sea urchins, mussels, barnacles, and crabs (Broitman et al., 2008; Miller & Emllet, 1997). This may indicate an overall net decrease in prey biomass available to sea otters in this Barkley Sound. In contrast, areas with weaker upwelling, such as Gwaii Haanas (Peterson et al., 2007), may see more intermittent shoreward transport of surface waters with greater recruitment of benthic invertebrates (Broitman et al., 2008). This line of thinking may also shed light on the regional patterns we observed in archaeological shellfish data, specifically in Gwaii Haanas where urchin remains were more ubiquitous and mussels larger (Table 1B and C2), despite higher sea otter prevalence in this area compared to Barkley Sound. Although patterns of larval recruitment are influenced by drivers beyond upwelling intensity such as temperature, reproductive timing, and regional circulation patterns (Broitman et al., 2008), differences in offshore seawater transport may be one of the major factors determining invertebrate recruitment (Harrold & Pearse, 1987) and driving differential sea otter prey productivity, and thus sea otter prevalence, in our study areas.

Extent and complexity of nearshore habitat is also known to influence prey abundance and by proxy, sea otter prevalence (Gregar et al., 2008; Hale et al., 2019; Tinker, Gill, et al., 2019). Sea otters typically forage at depths between 2 and 30 metres with greater energetic expenditure for deeper dives (Bodkin et al., 2004). Along the outer coast of Washington, offshore foraging may be of particular importance to sea otters where a large shallow shelf exists with depths of less than 40 metres extending more than 10 kilometres offshore, significantly increasing the amount of usable habitat for sea otters (Laidre et al., 2009). Although the bathymetry within our study areas is variable, on the East coast of Gwaii Haanas, where all but one of our study sites are situated, the 20-metre contour extends several kilometres further offshore than the 20-metre contour in the vicinity of our sites in Barkley Sound (FLNRO, 2011). This may produce more expansive foraging habitat and thus greater sea otter carrying capacity in Gwaii Haanas, as has been found on the outer coast of Washington (Hale et al., 2019). Though Gregor et al. (2008) predicted low optimum sea otter habitat in Gwaii Haanas relative to Barkley Sound using complexity-based models, they suggest that coastal characteristics in the Haida Gwaii area overall are likely poorly captured in their model. Increased coastline and bottom complexity are hypothesized to provide higher quality sea otter foraging habitat (Gregor et al., 2008), although low resolution bathymetric data limits our ability to apply a spatial comparison. We suspect that regional oceanographic and bathymetric differences interact to produce differing sea otter carrying capacities and are among the factors driving differing sea otter prevalence over the late Holocene.

Sea otter prevalence would have also been impacted by top-down forces such as human harvest which likely varied across environmental and cultural contexts. Archaeological, ethnographic, and historic data affirm the importance of sea otters to coastal Indigenous groups up and down the west coast of North America (Erlandson et al., 2005; Salomon et al., 2015; Moss 2020). Evidence from this study suggests a particular emphasis on sea otter harvest by ancestral Haida, likely sustained by a relatively greater availability of this predator compared to other areas. The observed archaeological differences in sea otter remains (McKechnie et al. n.d.) align with historical accounts which recall exceptionally high pelt landings from Haida Gwaii which was a trading destination for 50 years longer than elsewhere on the coast (Dixon, 1789; Howay, 1973; Lillard, 1989; Sloan & Dick, 2012). In comparison, on the West coast of Vancouver Island, archaeological evidence suggests that northern fur seals were a focus

of Indigenous hunting for at least 5,000 years and ethnographic reports detail specialized fur seal hunting traditions among Nuu-chah-nulth peoples (McKechnie and Wigen 2011). This suggests that Indigenous harvesting practices and traditions in our two study areas were shaped by the differing environmental contexts in which they evolved leading to an emphasis on sea otters by the Kunghit Haida and on northern fur seals by the Tseshaht. This variability in sea otter harvest pressure would have contributed to the differences we detect in sea otter prevalence with top-down hunting by humans working in tandem with the bottom-up oceanographic and ecological drivers described above to shape the structure of rocky reef ecosystems along late Holocene coastlines.

Rethinking contemporary sea otter management

Marine historical ecology plays a pivotal role in treating symptoms of sliding baselines, where magnitudes of change are based on relatively short time frames and often ignore the antiquity and intentionality of humans as protagonists among coastal food web interactions (Lotze & McClenachan 2013). Conventional descriptions of historic sea otter populations generally assume a continuous and undisturbed distribution of animals over the full extent of their potential range (Davis et al., 2019; Estes, 1990). Moreover, estimates of coastal carrying capacity, developed under the context of guiding recovery targets, are based on the maximum number of sea otters that could be sustained in a given area (Burn et al., 2003; Gregr et al., 2008; Laidre et al., 2001). This contrasts significantly with the large body of evidence showing that late Holocene sea otters were harvested and managed by coastal First Nations and distributed discontinuously along coastlines with a degree of spatial variation in their prevalence, as indicated by this study. With that, there is a critical need to reconceptualize prehistoric sea otter baselines and to adapt our current management approach to encompass spatially explicit recovery targets that recognize the role of humans in altering nearshore ecosystems (Corbett et al., 2008; McKechnie and Wigen 2011; Moss, 2020; Salomon et al., 2018; Slade et al., in review).

Indigenous people have co-existed with sea otters for millennia (Erlandson et al., 2005; Moss 2020) with ethnographies recounting ancient governance protocols that incorporated diverse technologies to manage and conserve coastal resources within

defined marine tenure systems (Salomon et al., 2015, 2020). With sea otters protected from hunting under federal legislation, Indigenous peoples in Canada have been prevented from harvesting sea otters and managing this predator as they once did (Burt et al., 2020; Pinkerton et al., 2019). As such, the recovery of sea otters along the west coast of Canada brings considerable challenges to social-ecological systems, directly impacting Indigenous food systems, economies, and cultural traditions (Burt et al., 2020). Revitalizing ancient practices and governance protocols could allow both predators to thrive (Burt et al., 2020; Pinkerton et al., 2019) and return agency to those most affected by sea otter management, thus creating more diverse, just, and resilient coastal ecosystems.

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Appendix A – Isotopic Comparison of Ancient Coastal Consumers

Table A1: Isotopic values (Mean \pm SD) derived from archaeological bone collagen of coastal species in Barkley Sound (BS) and Gwaii Haanas (GH).

Species	Region	n	$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	References
Fur Seal	BS	24	-14.64 ± 0.4	16.88 ± 1.1	1, 2, 3
	GH	3	-12.57 ± 0.4	19.6 ± 0.6	4
Harbour Seal	BS	5	-11.76 ± 1.6	17.54 ± 1.0	3
	GH	4	-12.18 ± 0.8	18.21 ± 0.6	3
Sea otter	BS	11	-11.75 ± 0.8	12.86 ± 0.7	1, 3
	GH	31	-11.08 ± 0.8	13.73 ± 0.7	2, 5
Lingcod	BS	11	-11.70 ± 0.9	16.44 ± 0.6	1
	GH	7	-11.63 ± 1.4	17.13 ± 1.2	2, 4
Rockfish	BS	19	-11.93 ± 1.1	14.66 ± 0.9	1
	GH	54	-10.86 ± 1.0	15.98 ± 0.8	2, 4, 6, 7
Greenling	BS	13	-11.48 ± 0.8	13.7 ± 0.4	1
	GH	8	-10.65 ± 1.1	13.95 ± 1.0	2, 4, 6
Herring	BS	13	-13.15 ± 0.3	13.43 ± 0.5	1
	GH	8	-12.97 ± 0.7	13.86 ± 0.8	4, 6

References: (1) Hillis et al. 2020 (2) This study, (3) Newsome et al. 2007, (4) Szpak et al. 2009, (5) Szpak et al. 2012, (6) Szpak & Orchard 2011, (7) Szpak et al. 2013

Table A2: Isotope values and elemental data for archaeological bone collagen from Barkley Sound and Gwaii Haanas used in this work. All of the 31 samples processed in this study produced percentages of carbon and nitrogen as well as collagen yields characteristic of well-preserved collagen (Ambrose, 1990; Szpak, 2011). All except two of the samples produced C:N ratios within the acceptable range of 2.9-3.6 for unaltered bone collagen (Ambrose, 1990). NR = not recorded.

Sample Number	Area	Site	Taxon	$\delta^{13}\text{C} \text{‰}$	$\delta^{15}\text{N} \text{‰}$	Col Yield %	%C	%N	C:N	Source
4446	Barkley Sound	206T	<i>Enhydra lutris</i>	-11.9	12.9	14	40.6	14.5	3.3	Hillis et al. 2020
4447	Barkley Sound	206T	<i>Enhydra lutris</i>	-12.3	13.9	14.1	42.4	15	3.3	Hillis et al. 2020
4448	Barkley Sound	206T	<i>Enhydra lutris</i>	-11.4	13.3	9.4	42.7	14.9	3.3	Hillis et al. 2020
4449	Barkley Sound	206T	<i>Enhydra lutris</i>	-11.8	13.4	9.7	41.9	14.4	3.4	Hillis et al. 2020
4458	Barkley Sound	129T	<i>Enhydra lutris</i>	-11.8	13.2	4.7	41.1	14.6	3.3	Hillis et al. 2020
6511	Barkley Sound	306T	<i>Enhydra lutris</i>	-11.5	12.5	unk	39.1	13.5	3.4	Hillis et al. 2020
10	Barkley Sound	DfSh-16	<i>Enhydra lutris</i>	-10.51	13.42	2.2	31.6	10.9	3.38	This study
12	Barkley Sound	DfSh-16	<i>Enhydra lutris</i>	-11.86	11.9	7.3	39.2	13.7	3.33	This study
13	Barkley Sound	DfSh-16	<i>Enhydra lutris</i>	-11.7	12.45	9.2	36.9	12.8	3.36	This study

Sample Number	Area	Site	Taxon	$\delta^{13}\text{C} \text{‰}$	$\delta^{15}\text{N} \text{‰}$	Col Yield %	%C	%N	C:N	Source
14	Barkley Sound	DfSh-16	<i>Enhydra lutris</i>	-10.83	12.59	7.3	36	12.8	3.27	This study
15	Barkley Sound	DfSh-16	<i>Enhydra lutris</i>	-13.68	11.88	2.5	30.3	9.6	3.67	This study
NR	Gwaii Haanas	781T	<i>Enhydra lutris</i>	-11.1	13.5	8.9	34.48	11.65	3.45	Szpak et al. 2012
NR	Gwaii Haanas	781T	<i>Enhydra lutris</i>	-11.2	13.3	10.2	34.77	12.56	3.23	Szpak et al. 2012
NR	Gwaii Haanas	781T	<i>Enhydra lutris</i>	-11	13.5	11.1	37.02	13.56	3.19	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-11.2	14.1	9.6	35.41	13.07	3.16	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-10.4	13.7	10.8	34.4	12.6	3.19	Szpak et al. 2012
NR	Gwaii Haanas	781T	<i>Enhydra lutris</i>	-10.9	14.6	13.5	35	12.81	3.19	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-10.9	13.3	12.5	38.76	14.06	3.22	Szpak et al. 2012
NR	Gwaii Haanas	781T	<i>Enhydra lutris</i>	-10.5	14	9.4	32.15	11.72	3.2	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-11.2	13.5	6.9	31.6	11.44	3.22	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-10.5	12.8	5.8	33.31	12.22	3.19	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-10.7	13.4	13.5	39	13.5	3.37	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-10.8	13.9	8	35.6	12.1	3.43	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-11	14.3	6.8	37.2	12.6	3.46	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-10.7	13.5	18.4	41	15.1	3.17	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-12.5	13.2	7.8	36.7	13.4	3.19	Szpak et al. 2012
NR	Gwaii Haanas	717T	<i>Enhydra lutris</i>	-10.5	13.3	10.5	37.7	13.2	3.32	Szpak et al. 2012
NR	Gwaii Haanas	717T	<i>Enhydra lutris</i>	-10.5	14.3	13	37.7	14	3.15	Szpak et al. 2012
NR	Gwaii Haanas	717T	<i>Enhydra lutris</i>	-11.1	14.6	12.8	33.9	12.4	3.18	Szpak et al. 2012
NR	Gwaii Haanas	740T	<i>Enhydra lutris</i>	-10.4	13.7	10.9	31.6	11.4	3.23	Szpak et al. 2012
NR	Gwaii Haanas	740T	<i>Enhydra lutris</i>	-11.8	13.6	10.8	29.6	10.7	3.23	Szpak et al. 2012
NR	Gwaii Haanas	740T	<i>Enhydra lutris</i>	-10.7	14.5	9	34.6	12.5	3.24	Szpak et al. 2012
NR	Gwaii Haanas	785T	<i>Enhydra lutris</i>	-11.4	13.6	13.5	36.6	12.2	3.49	Szpak et al. 2012
NR	Gwaii Haanas	785T	<i>Enhydra lutris</i>	-10.5	14.3	7.2	36.1	13.1	3.2	Szpak et al. 2012
NR	Gwaii Haanas	785T	<i>Enhydra lutris</i>	-10.5	14.4	10.5	33	12.2	3.17	Szpak et al. 2012
NR	Gwaii Haanas	924T	<i>Enhydra lutris</i>	-10.4	13.5	13.5	36.5	12.7	3.35	Szpak et al. 2012
NR	Gwaii Haanas	924T	<i>Enhydra lutris</i>	-11.4	12.8	7.2	34.8	12.7	3.21	Szpak et al. 2012
NR	Gwaii Haanas	699T	<i>Enhydra lutris</i>	-14.3	13.2	5.5	35.9	12.2	3.44	Szpak et al. 2012
22	Gwaii Haanas	660T	<i>Enhydra lutris</i>	-11.49	12.59	4.8	25.8	9	3.34	This study
26	Gwaii Haanas	660T	<i>Enhydra lutris</i>	-12.6	13.31	7.1	50.4	18.2	3.23	This study
33	Gwaii Haanas	660T	<i>Enhydra lutris</i>	-10.33	15.78	10.3	32.7	11.5	3.32	This study
1	Barkley Sound	306T	<i>Phoca vitulina</i>	-10.78	18.55	5.6	33.69	12.03	3.27	This study
2	Barkley Sound	306T	<i>Phoca vitulina</i>	-14.11	16.23	2.1	28.24	9.9	3.33	This study
3	Barkley Sound	306T	<i>Phoca vitulina</i>	-10.77	17.39	3.1	26.13	9.01	3.38	This study
17	Barkley Sound	306T	<i>Phoca vitulina</i>	-11.36	17.99	7	29	10.2	3.32	This study
18	Gwaii Haanas	660T	<i>Phoca vitulina</i>	-13.16	17.48	8.3	40.5	14.6	3.23	This study
19	Gwaii Haanas	660T	<i>Phoca vitulina</i>	-11.64	18.1	6.8	32.3	11.1	3.41	This study

Sample Number	Area	Site	Taxon	$\delta^{13}\text{C} \text{‰}$	$\delta^{15}\text{N} \text{‰}$	Col Yield %	%C	%N	C:N	Source
21	Gwail Haanas	660T	<i>Phoca vitulina</i>	-11.41	18.23	6.1	35.3	12.5	3.29	This study
24	Gwail Haanas	660T	<i>Phoca vitulina</i>	-11.76	18.16	8.7	32.9	11.2	3.43	This study
34	Gwail Haanas	660T	<i>Phoca vitulina</i>	-12.91	19.08	6.3	32.5	11.5	3.29	This study
4459	Barkley Sound	83T	<i>Callorhinus ursinus</i>	-14.9	18.3	4	42.6	14.8	3.4	Hillis et al. 2020
4460	Barkley Sound	129T	<i>Callorhinus ursinus</i>	-15	15	unk	37.4	13.4	3.3	Hillis et al. 2020
4527	Barkley Sound	206T	<i>Callorhinus ursinus</i>	-15	17.8	3.9	39	13	3.5	Hillis et al. 2020
4531	Barkley Sound	82T	<i>Callorhinus ursinus</i>	-14.8	17.8	3	42.6	14.4	3.5	Hillis et al. 2020
4546	Barkley Sound	306T	<i>Callorhinus ursinus</i>	-15.2	17.3	0.6	25	8.6	3.4	Hillis et al. 2020
5	Barkley Sound	306T	<i>Callorhinus ursinus</i>	-14.21	18	2.3	20.63	6.72	3.58	This study
6	Barkley Sound	306T	<i>Callorhinus ursinus</i>	-13.47	18.67	3.6	38.02	13.53	3.28	This study
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.1	16.6	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.4	17.8	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14	17.1	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.4	18.7	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.7	16.1	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.9	16.2	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.8	15.1	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-15.2	15.1	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.8	16.3	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.4	17.3	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.9	18.3	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.7	16.2	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-15.3	15.6	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.6	16.9	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14	16.6	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.7	16.3	unk	unk	unk	unk	Newsome et al. 2007
NR	Barkley Sound	204T	<i>Callorhinus ursinus</i>	-14.9	16.2	unk	unk	unk	unk	Newsome et al. 2007
NR	Gwail Haanas	699T	<i>Callorhinus ursinus</i>	-12.4	20	9.8	33.17	12.16	3.18	Szpak et al. 2009
NR	Gwail Haanas	740T	<i>Callorhinus ursinus</i>	-13	19.9	6.9	33.07	12.26	3.15	Szpak et al. 2009

Sample Number	Area	Site	Taxon	$\delta^{13}\text{C} \text{‰}$	$\delta^{15}\text{N} \text{‰}$	Col Yield %	%C	%N	C:N	Source
NR	Gwail Haanas	699T	Callorhinus ursinus	-12.3	18.9	11.4	31.67	11.65	3.17	Szpak et al. 2009
4152	Barkley Sound	306T	<i>Sebastes sp.</i>	-11	15.1	10.5	30.7	11	3.3	Hillis et al. 2020
4157	Barkley Sound	306T	<i>Sebastes sp.</i>	-13	13.7	5.4	33.5	12	3.3	Hillis et al. 2020
4167	Barkley Sound	306T	<i>Sebastes sp.</i>	-13.3	14.1	2.2	44	15.7	3.3	Hillis et al. 2020
4174	Barkley Sound	306T	<i>Sebastes sp.</i>	-12.3	14.6	4.9	38.6	13.9	3.2	Hillis et al. 2020
4176	Barkley Sound	306T	<i>Sebastes sp.</i>	-10.6	14.5	18.8	41.9	15.8	3.1	Hillis et al. 2020
4179	Barkley Sound	306T	<i>Sebastes sp.</i>	-13.2	14.2	2.7	34.2	12.5	3.2	Hillis et al. 2020
4181	Barkley Sound	306T	<i>Sebastes sp.</i>	-11.4	15.1	unk	44.6	16.6	3.1	Hillis et al. 2020
4188	Barkley Sound	306T	<i>Sebastes sp.</i>	-12.7	13.3	9.4	36.3	13.2	3.2	Hillis et al. 2020
4194	Barkley Sound	306T	<i>Sebastes sp.</i>	-11	14.3	3.3	34.8	12.5	3.3	Hillis et al. 2020
4199	Barkley Sound	306T	<i>Sebastes sp.</i>	-10.8	14.1	2.9	37.9	13.6	3.2	Hillis et al. 2020
4204	Barkley Sound	306T	<i>Sebastes sp.</i>	-11.3	14.9	3.7	41.6	15.3	3.2	Hillis et al. 2020
4207	Barkley Sound	306T	<i>Sebastes sp.</i>	-10.5	15.5	2.4	41.1	14.9	3.2	Hillis et al. 2020
4208	Barkley Sound	306T	<i>Sebastes sp.</i>	-11.9	14.5	4.2	37.7	13.7	3.2	Hillis et al. 2020
4209	Barkley Sound	306T	<i>Sebastes sp.</i>	-11.6	16.7	4.8	37.8	13.6	3.2	Hillis et al. 2020
4443	Barkley Sound	83T	<i>Sebastes sp.</i>	-10.8	15.8	6.5	42.7	15.1	3.3	Hillis et al. 2020
4536	Barkley Sound	306T	<i>Sebastes sp.</i>	-13.2	13.4	5.1	42.9	14.7	3.4	Hillis et al. 2020
6392	Barkley Sound	306T	<i>Sebastes sp.</i>	-13.5	13.6	unk	42.2	14.7	3.3	Hillis et al. 2020
6394	Barkley Sound	306T	<i>Sebastes sp.</i>	-13.2	15	unk	41.5	14.7	3.3	Hillis et al. 2020
6395	Barkley Sound	306T	<i>Sebastes sp.</i>	-11.4	16.1	unk	43.2	15.5	3.2	Hillis et al. 2020
NR	Gwail Haanas	699T	<i>Sebastes sp.</i>	-11.3	15.7	10.8	43.02	14.63	3.43	Szpak et al. 2009
NR	Gwail Haanas	699T	<i>Sebastes sp.</i>	-11.4	15.6	4.4	37.97	12.54	3.54	Szpak et al. 2009
NR	Gwail Haanas	699T	<i>Sebastes sp.</i>	-9.9	16.3	10.4	36.35	12.88	3.29	Szpak et al. 2009
NR	Gwail Haanas	699T	<i>Sebastes sp.</i>	-11.4	15.1	7.8	32.09	11	3.4	Szpak et al. 2009
NR	Gwail Haanas	2008T	<i>Sebastes sp.</i>	-11.66	16.05	4.56	42.04	14.81	3.31	Szpak & Orchard 2011
NR	Gwail Haanas	2008T	<i>Sebastes sp.</i>	-11.37	14.57	5.39	42.51	15.22	3.26	Szpak & Orchard 2011
NR	Gwail Haanas	2008T	<i>Sebastes sp.</i>	-11.54	14.39	5.08	43.19	15.38	3.27	Szpak & Orchard 2011
NR	Gwail Haanas	699T	<i>Sebastes sp.</i>	-13.6	15.3	2.1	unk	unk	3.81	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-13.1	15.5	1.4	unk	unk	3.25	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-11.5	15.3	8.7	unk	unk	3.21	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-11.1	17	5.6	unk	unk	3.33	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-12.1	15.5	7.7	unk	unk	3.13	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-13.1	15.5	9.7	unk	unk	3.47	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-11.5	15.3	6.5	unk	unk	3.39	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-11.1	17	4.7	unk	unk	3.16	Szpak et al. 2013
NR	Gwail Haanas	740T	<i>Sebastes sp.</i>	-12.1	15.5	6.1	unk	unk	3.36	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.5	16.5	10.7	unk	unk	3.35	Szpak et al. 2013

Sample Number	Area	Site	Taxon	$\delta^{13}\text{C} \text{‰}$	$\delta^{15}\text{N} \text{‰}$	Col Yield %	%C	%N	C:N	Source
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.4	16.7	10.4	unk	unk	3.31	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.4	18.3	7.9	unk	unk	3.39	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-11.2	16.8	8.5	unk	unk	3.28	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.1	16	5.4	unk	unk	3.35	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.1	15.7	4.3	unk	unk	3.36	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10	16.5	11.2	unk	unk	3.32	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.3	15.7	6.8	unk	unk	3.36	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.3	16.6	9.3	unk	unk	3.34	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.5	16.8	5.5	unk	unk	3.31	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.2	16	1.6	unk	unk	3.56	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.3	16.1	11.6	unk	unk	3.55	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.7	15.8	6	unk	unk	3.09	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-11.2	14	8.6	unk	unk	3.28	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.2	15.5	12	unk	unk	3.36	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.1	16.2	8	unk	unk	3.3	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.5	15.9	2.8	unk	unk	3.45	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-9.4	17.6	6.7	unk	unk	3.15	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.5	16.3	4.2	unk	unk	3.17	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-9.8	16.6	7.7	unk	unk	3.4	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-9.8	15.9	8	unk	unk	3.38	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.8	15.4	7.4	unk	unk	3.1	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.4	15	6.6	unk	unk	3.15	Szpak et al. 2013
NR	Gwail Haanas	781T	<i>Sebastes sp.</i>	-10.4	15.4	8	unk	unk	3.06	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-10.8	16.7	7	unk	unk	3.37	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-9.5	17.1	8	unk	unk	3.46	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-10.4	16.7	6.1	unk	unk	3.42	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-9.6	16.1	10.8	unk	unk	3.33	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-8.6	15.3	8.3	unk	unk	3.35	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-11	16.3	5.9	unk	unk	3.38	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-10.6	16.7	7.2	unk	unk	3.33	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-10	16.5	4.4	unk	unk	3.38	Szpak et al. 2013
NR	Gwail Haanas	785T	<i>Sebastes sp.</i>	-10.3	16.5	11.5	unk	unk	3.19	Szpak et al. 2013
NR	Gwail Haanas	924T	<i>Sebastes sp.</i>	-11.6	15	7.9	unk	unk	3.11	Szpak et al. 2013
NR	Gwail Haanas	699T	<i>Sebastes sp.</i>	-11	16.1	7.4	40.55	13.91	3.4	Szpak et al. 2009
20	Gwail Haanas	660T	<i>Sebastes sp.</i>	-12.31	15.47	4.1	36.9	12.8	3.37	This study
25	Gwail Haanas	660T	<i>Sebastes sp.</i>	-11.95	15.96	9.1	35.3	12.9	3.19	This study
32	Gwail Haanas	660T	<i>Sebastes sp.</i>	-12.87	15.35	10	17.5	6.3	3.25	This study
4153	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-11.3	13.3	2.8	39.2	13.9	3.3	Hillis et al. 2020

Sample Number	Area	Site	Taxon	$\delta^{13}\text{C} \text{‰}$	$\delta^{15}\text{N} \text{‰}$	Col Yield %	%C	%N	C:N	Source
4159	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-11.1	13.2	3.9	30.3	10.6	3.3	Hillis et al. 2020
4166	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-11.4	13.6	2.9	42.9	15.9	3.1	Hillis et al. 2020
4171	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-11.3	13.7	6.7	41.1	15.2	3.2	Hillis et al. 2020
4178	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-11.8	13.9	5.2	39.5	14.3	3.2	Hillis et al. 2020
4185	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-12.6	13.1	unk	42.1	15.5	3.2	Hillis et al. 2020
4201	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-11.9	13.7	2.6	32.2	11.3	3.3	Hillis et al. 2020
4521	Barkley Sound	129T	<i>Hexagrammos sp.</i>	-10.4	14.2	9.4	42.3	15.5	3.2	Hillis et al. 2020
6399	Barkley Sound	93T	<i>Hexagrammos sp.</i>	-11.7	13.2	unk	40.6	14.1	3.3	Hillis et al. 2020
6400	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-10.3	14.4	unk	39.7	14.3	3.2	Hillis et al. 2020
6403	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-12.9	13.6	unk	39.3	13.2	3.5	Hillis et al. 2020
6404	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-10.6	14.4	unk	39.3	13.8	3.3	Hillis et al. 2020
6405	Barkley Sound	306T	<i>Hexagrammos sp.</i>	-11.9	13.8	unk	40.3	14	3.4	Hillis et al. 2020
NR	Gwaii Haanas	2008T	<i>Hexagrammos sp.</i>	-10.46	13.56	5.17	42.6	15.12	3.29	Szpak & Orchard 2011
NR	Gwaii Haanas	699T	<i>Hexagrammos sp.</i>	-11.4	14.2	9.2	34.1	12.19	3.26	Szpak et al. 2009
NR	Gwaii Haanas	781T	<i>Hexagrammos sp.</i>	-10	15	5.8	38.65	14.19	3.18	Szpak et al. 2009
23	Gwaii Haanas	660T	<i>Hexagrammos sp.</i>	-9.36	14.07	8.6	32.2	11.8	3.19	This study
29	Gwaii Haanas	660T	<i>Hexagrammos sp.</i>	-8.88	15.63	7.2	35	12.9	3.18	This study
30	Gwaii Haanas	660T	<i>Hexagrammos sp.</i>	-11.46	13.1	12.2	43.9	15.3	3.34	This study
31	Gwaii Haanas	660T	<i>Hexagrammos sp.</i>	-12	13.19	8.1	38.2	13.7	3.25	This study
26	Gwaii Haanas	660T	<i>Hexagrammos sp.</i>	-11.62	12.86	11.1	35.5	13.1	3.17	This study
4155	Barkley Sound	306T	<i>Clupea pallasii</i>	-12.6	13.2	70	28.8	10.2	3.3	Hillis et al. 2020
4160	Barkley Sound	306T	<i>Clupea pallasii</i>	-13.1	13.3	14.3	33.9	12	3.3	Hillis et al. 2020
4170	Barkley Sound	306T	<i>Clupea pallasii</i>	-13.2	14	3.1	34.5	12	3.3	Hillis et al. 2020
4172	Barkley Sound	306T	<i>Clupea pallasii</i>	-13.5	13.2	4.8	34.9	12.2	3.3	Hillis et al. 2020
4177	Barkley Sound	306T	<i>Clupea pallasii</i>	-13.5	13.3	12.5	33.4	11.6	3.4	Hillis et al. 2020
4189	Barkley Sound	306T	<i>Clupea pallasii</i>	-12.7	13.1	10	34.3	12.1	3.3	Hillis et al. 2020
4192	Barkley Sound	306T	<i>Clupea pallasii</i>	-13.5	14.1	2.6	38.4	13.5	3.3	Hillis et al. 2020
4197	Barkley Sound	306T	<i>Clupea pallasii</i>	-13.3	13.1	16.7	33.6	12	3.3	Hillis et al. 2020
4210	Barkley Sound	306T	<i>Clupea pallasii</i>	-13.6	14.5	3.4	34.3	11.9	3.4	Hillis et al. 2020
4440	Barkley Sound	83T	<i>Clupea pallasii</i>	-13.1	12.8	12.1	42.2	14.8	3.3	Hillis et al. 2020
4441	Barkley Sound	83T	<i>Clupea pallasii</i>	-13	12.9	10.7	43.4	15.1	3.4	Hillis et al. 2020

Sample Number	Area	Site	Taxon	$\delta^{13}\text{C} \text{‰}$	$\delta^{15}\text{N} \text{‰}$	Col Yield %	%C	%N	C:N	Source
4442	Barkley Sound	83T	<i>Clupea pallasii</i>	-12.6	13.1	12.1	42.8	15.8	3.2	Hillis et al. 2020
6379	Barkley Sound	93T	<i>Clupea pallasii</i>	-13.3	14	unk	40.6	14.5	3.3	Hillis et al. 2020
NR	Gwaii Haanas	924T	<i>Clupea pallasii</i>	-12.79	13.05	4.79	44.43	15.51	3.34	Szpak & Orchard 2011
NR	Gwaii Haanas	924T	<i>Clupea pallasii</i>	-12.58	12.95	3.63	41.65	15.53	3.13	Szpak & Orchard 2011
NR	Gwaii Haanas	924T	<i>Clupea pallasii</i>	-12.64	15.02	4.15	43.3	16.03	3.15	Szpak & Orchard 2011
NR	Gwaii Haanas	924T	<i>Clupea pallasii</i>	-12.68	14.8	5.99	44.36	16.79	3.08	Szpak & Orchard 2011
NR	Gwaii Haanas	924T	<i>Clupea pallasii</i>	-12.26	14.52	4.9	43.7	16.19	3.15	Szpak & Orchard 2011
NR	Gwaii Haanas	785T	<i>Clupea pallasii</i>	-12.7	13.4	11.5	35.43	13.1	3.15	Szpak et al. 2009
NR	Gwaii Haanas	924T	<i>Clupea pallasii</i>	-14.5	13.7	1.6	28.12	9.41	3.49	Szpak et al. 2009
NR	Gwaii Haanas	781T	<i>Clupea pallasii</i>	-13.6	13.5	7.8	34.97	12.68	3.22	Szpak et al. 2009
4158	Barkley Sound	306T	<i>Ophiodon elongatus</i>	-10.8	15.2	5	34.7	12.7	3.2	Hillis et al. 2020
4165	Barkley Sound	306T	<i>Ophiodon elongatus</i>	-11.8	16.3	5.2	39.9	14.6	3.2	Hillis et al. 2020
4202	Barkley Sound	306T	<i>Ophiodon elongatus</i>	-11.8	16.4	3	38.2	13.8	3.2	Hillis et al. 2020
4203	Barkley Sound	306T	<i>Ophiodon elongatus</i>	-11	16.9	5.9	41.1	15	3.2	Hillis et al. 2020
4444	Barkley Sound	83T	<i>Ophiodon elongatus</i>	-11	16.1	6	42	15.1	3.2	Hillis et al. 2020
4453	Barkley Sound	129T	<i>Ophiodon elongatus</i>	-11.9	16	10.7	41.9	15.4	3.2	Hillis et al. 2020
4454	Barkley Sound	129T	<i>Ophiodon elongatus</i>	-13.3	16.8	1.5	40.4	13.2	3.6	Hillis et al. 2020
4455	Barkley Sound	129T	<i>Ophiodon elongatus</i>	-13.1	16	1.8	41.4	13.9	3.5	Hillis et al. 2020
4457	Barkley Sound	206T	<i>Ophiodon elongatus</i>	-11	17.3	17.7	42.1	16.2	3	Hillis et al. 2020
6397	Barkley Sound	306T	<i>Ophiodon elongatus</i>	-12.1	16.6	unk	41.8	15.2	3.2	Hillis et al. 2020
6398	Barkley Sound	306T	<i>Ophiodon elongatus</i>	-10.9	17.2	unk	39.9	14	3.3	Hillis et al. 2020
NR	Gwaii Haanas	785T	<i>Ophiodon elongatus</i>	-9.5	17.9	8.5	37.19	14.03	3.09	Szpak et al. 2009
NR	Gwaii Haanas	781T	<i>Ophiodon elongatus</i>	-10.7	16.9	7.3	34.52	12.95	3.11	Szpak et al. 2009
NR	Gwaii Haanas	699T	<i>Ophiodon elongatus</i>	-10.9	16.7	11.7	37.75	14.09	3.13	Szpak et al. 2009
35	Gwaii Haanas	660T	<i>Ophiodon elongatus</i>	-12.51	16.48	5.6	25.39	8.92	3.32	This study
36	Gwaii Haanas	660T	<i>Ophiodon elongatus</i>	-12.29	16.29	7.8	31.8	11.54	3.22	This study
37	Gwaii Haanas	660T	<i>Ophiodon elongatus</i>	-11.69	16.23	3.2	32.69	11.94	3.19	This study
28	Gwaii Haanas	660T	<i>Ophiodon elongatus</i>	-13.84	19.44	8.6	28.6	9.2	3.63	This study

Table A3. Strength of evidence for alternative models assessing the effect of *Area* on consumer isotopic signatures. Models with varying numbers of parameters (*K*) were compared using log-likelihood (*LL*), small sample bias corrected Akaike's Information Criterion (*AIC_c*), *AIC_c* differences (ΔAIC_c), normalized Akaike weights (*W_i*) and adjusted R squared (*R² adj*). The intercept model represents the null model of no effect of *Area*.

Model	<i>K</i>	<i>n</i> (BS)	<i>n</i> (GH)	<i>LL</i>	<i>AIC_c</i>	ΔAIC_c	<i>w_i</i>	<i>R² adj</i>
(A) $\delta^{13}C$								
Fur Seal $\delta^{13}C$								
Area	2	24	3	-15.01	37.1	0.0	1.00	0.78
Intercept	1			-31.48	67.5	30.4	0.00	0.00
Harbour Seal $\delta^{13}C$								
Intercept	1	15	5	-13.494	33	0.0	0.90	0.00
Area	2			-13.324	37.4	4.5	0.10	0.39
Sea Otter $\delta^{13}C$								
Area	2	11	31	-50.181	107	0.0	0.82	0.13
Intercept	1			-52.843	110	3.0	0.18	0.00
Lingcod $\delta^{13}C$								
Intercept	1	11	7	-26.358	57.5	0.0	0.81	0.00
Area	2			-26.35	60.4	2.9	0.19	0.00
Rockfish $\delta^{13}C$								
Area	2	19	54	-103.54	213.4	0.0	1.00	0.19
Intercept	1			-110.85	225.9	12.4	0.00	0.00
Greenling $\delta^{13}C$								
Area	2	13	8	-27.304	62	0.0	0.64	0.18
Intercept	1			-29.268	63.2	1.2	0.36	0.00
Herring $\delta^{13}C$								
Intercept	1	13	8	-15.369	35.4	0.0	0.74	0.00
Area	2			-15.352	37.5	2.1	0.26	0.03
(B) $\delta^{15}N$								
Fur Seal $\delta^{15}N$								
Area	2	24	3	-39.65	86.30	0.00	0.996	0.41
Intercept	1			-46.48	97.50	11.12	0.004	0.00
Harbour Seal $\delta^{15}N$								
Intercept	1	15	5	-10.36	26.70	0.00	0.811	0.00
Area	2			-9.41	29.60	2.91	0.189	0.21
Sea Otter $\delta^{15}N$								
Area	2	11	31	-40.61	87.80	0.00	0.995	0.30
Intercept	1	11	31	-47.09	98.50	10.64	0.050	0.00
Lingcod $\delta^{15}N$								
Area	2	11	7	-23.24	51.30	0.00	0.500	0.00
Intercept	1			-21.78	51.30	0.00	0.500	0.16
Rockfish $\delta^{15}N$								
Area	2	19	54	-88.44	183.20	0.00	1.000	0.36
Intercept	1	19	54	-103.39	211.00	27.73	0.000	0.00
Greenling $\delta^{15}N$								
Intercept	1	13	8	-21.22	47.10	0.00	0.734	0.00
Area	2			-20.86	49.10	2.03	0.266	0.04
Herring $\delta^{15}N$								
Intercept	1	13	8	-20.72	46.10	0.00	0.547	0.00
Area	2			-19.54	46.50	0.37	0.453	0.21

Appendix B – Estimating Sea Otter Diets with MixSIAR

Table B1: MixSIAR models with associated prey inputs and TDFs.

	Prey Type	Trophic Discrimination Factors (‰)	
		$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$
Model 1	Ancient & Modern	3.6 ± 0.7	4.1 ± 0.6
Model 2	Modern Only	3.6 ± 0.7	4.1 ± 0.6
Model 3	Ancient & Modern	3.6 ± 0.95	4.1 ± 0.85
Model 4	Ancient & Modern	3.6 ± 1.2	4.1 ± 1.1

Table B2: Modern and ancient prey isotope data and associated corrections for Barkley Sound (BS), Gwaii Haanas (GH), and Clayoquot Sound (CS).

Species	Region	Age	n	Collagen-Muscle Correction (‰)		Collection Year	Suess Correction (‰)	Corrected Isotope Values (‰)		References
				$\delta^{13}\text{C}$	$\delta^{15}\text{N}$			$\delta^{13}\text{C} \pm \text{SD}$	$\delta^{15}\text{N} \pm \text{SD}$	
<i>S. franciscanus</i>	BS	Modern	18	NA	NA	2005	0.92	-13.08 ± 0.9	10.20 ± 0.1	1
<i>S. franciscanus</i>	GH	Modern	36	NA	NA	2009	1.02	-12.33 ± 1.1	8.06 ± 0.5	2
<i>M. californianus</i>	BS	Modern	19	NA	NA	2005 - 2008	0.96	-15.39 ± 1.4	8.48 ± 0.9	3
<i>M. californianus</i>	GH	Modern	135	NA	NA	2011	1.08	-17.05 ± 1.4	9.23 ± 0.6	2
<i>H. decagrammus</i>	CS	Modern	53	NA	NA	2010/2011	1.07	-14.23 ± 0.4	15.50 ± 0.4	4
<i>H. decagrammus</i>	GH	Modern	23	NA	NA	2009/2010	1.04	-15.29 ± 1.1	15.18 ± 0.5	2
<i>S. melanops</i>	CS	Modern	55	NA	NA	2010/2011	1.07	-15.13 ± 0.4	14.90 ± 0.4	4
<i>S. melanops</i>	GH	Modern	34	NA	NA	2009/2010	1.04	-16.72 ± 0.8	14.11 ± 0.7	2
<i>Hexagrammos sp.</i>	BS	Ancient	13	-1.1	+2.3	NA	NA	-12.58 ± 0.8	16.00 ± 0.4	5, 6
<i>Hexagrammos sp.</i>	GH	Ancient	8	-1.1	+2.3	NA	NA	-11.75 ± 1.1	16.25 ± 1.0	6, 7, 8
<i>Sebastes sp.</i>	BS	Ancient	19	-1.1	+2.3	NA	NA	-13.03 ± 1.1	16.96 ± 0.9	5, 6
<i>Sebastes sp.</i>	GH	Ancient	54	-1.1	+2.3	NA	NA	-11.96 ± 1.0	18.28 ± 0.8	6, 7, 8, 9

References: (1) Berger and Jelinski (2008); (2) Salomon unpublished data; (3) Markel (2011); (4) Von Biela et al. (2016); (5) McKechnie unpublished data; (6) Szpak et al. (2009); (7) Szpak & Orchard (2011); (8) This study; (9) Szpak et al. (2013).

Table B3: 25%, 50%, and 75% percentile estimates of the contribution of different prey to sea otter diets in Barkley Sound (n=11) and Gwaii Haanas (n=31) for each MixSIAR model output. Note that for model 2 'rockfish' are specifically black rockfish, and 'greenling' are specifically kelp greenling.

	Region	Rockfish			Greenling			California Mussels			Red Urchins		
		25%	50%	75%	25%	50%	75%	25%	50%	75%	25%	50%	75%
Model 1	Barkley Sound	1.1	2.2	3.7	1.1	2.3	4.0	77.6	82.5	86.5	8.0	11.9	16.8
	Gwaii Haanas	1.7	4.6	7.4	1.9	5.1	8.8	49.2	51.8	58.0	35.5	37.9	40.5
Model 2	Barkley Sound	1.4	2.9	4.8	1.7	3.5	5.8	74.7	79.5	83.9	8.6	12.6	17.4
	Gwaii Haanas	2.2	6.6	10.9	2.8	8.4	14.3	35.1	38.8	42.5	42.4	45.4	48.2
Model 3	Barkley Sound	1.0	2.1	3.5	1.2	2.4	4.0	77.6	82.4	86.6	8.1	11.9	16.9
	Gwaii Haanas	1.6	4.3	7.1	1.9	5.4	9.0	49.4	51.9	54.6	35.3	37.8	40.3
Model 4	Barkley Sound	1.0	2.1	3.6	1.2	2.0	4.1	77.6	82.4	86.4	8.0	12.0	16.8
	Gwaii Haanas	1.7	4.4	7.3	1.9	5.0	8.9	49.3	51.9	54.5	35.4	37.9	40.3

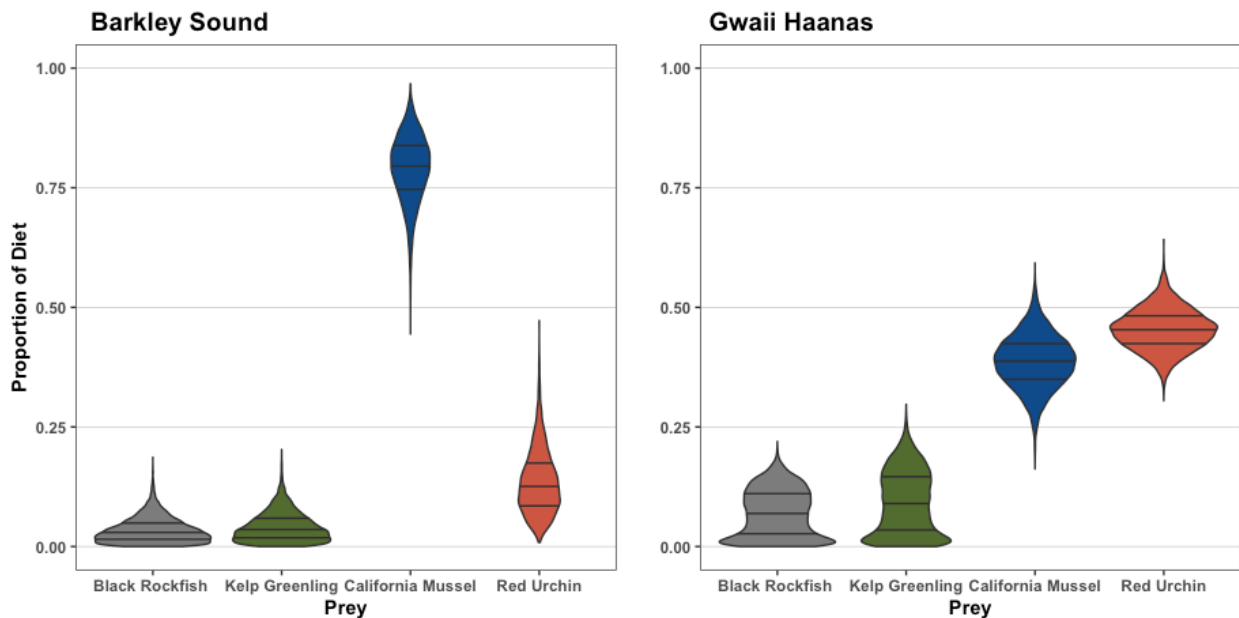


Figure B1: Violin plots representing MixSIAR estimates of sea otter diet from Model 2 for archaeological specimens from Barkley Sound (n = 11) and Gwaii Haanas (n = 31).

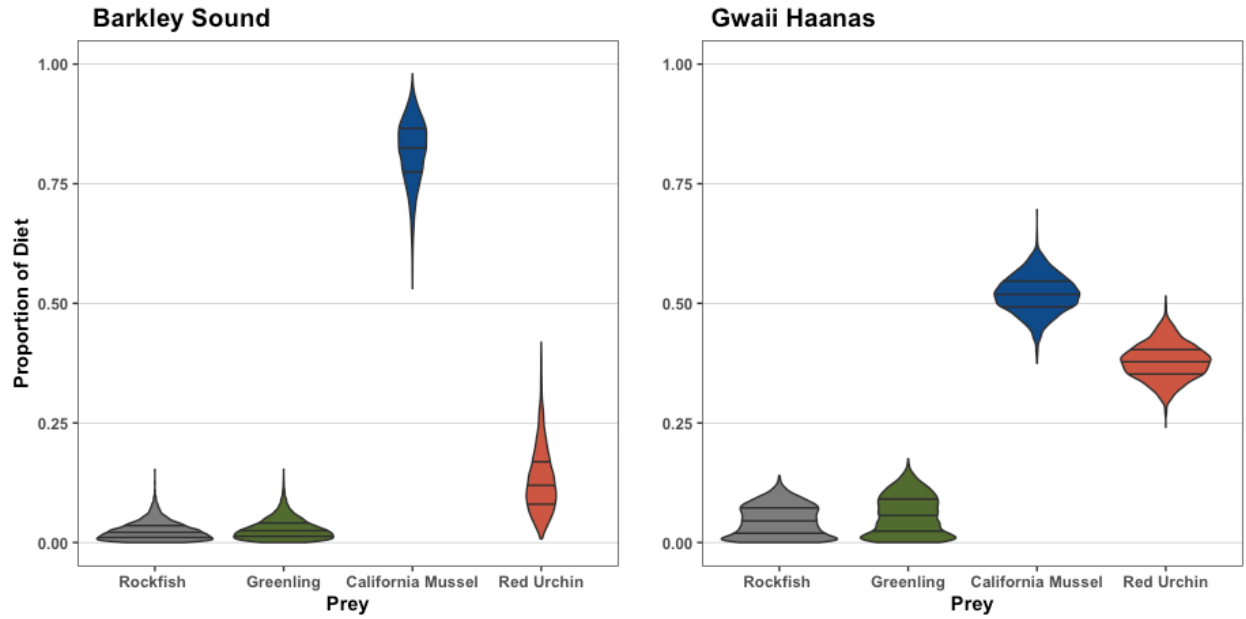


Figure B2: Violin plots representing MixSIAR estimates of sea otter diet from Model 3 for archaeological specimens from Barkley Sound (n = 11) and Gwaii Haanas (n = 31).

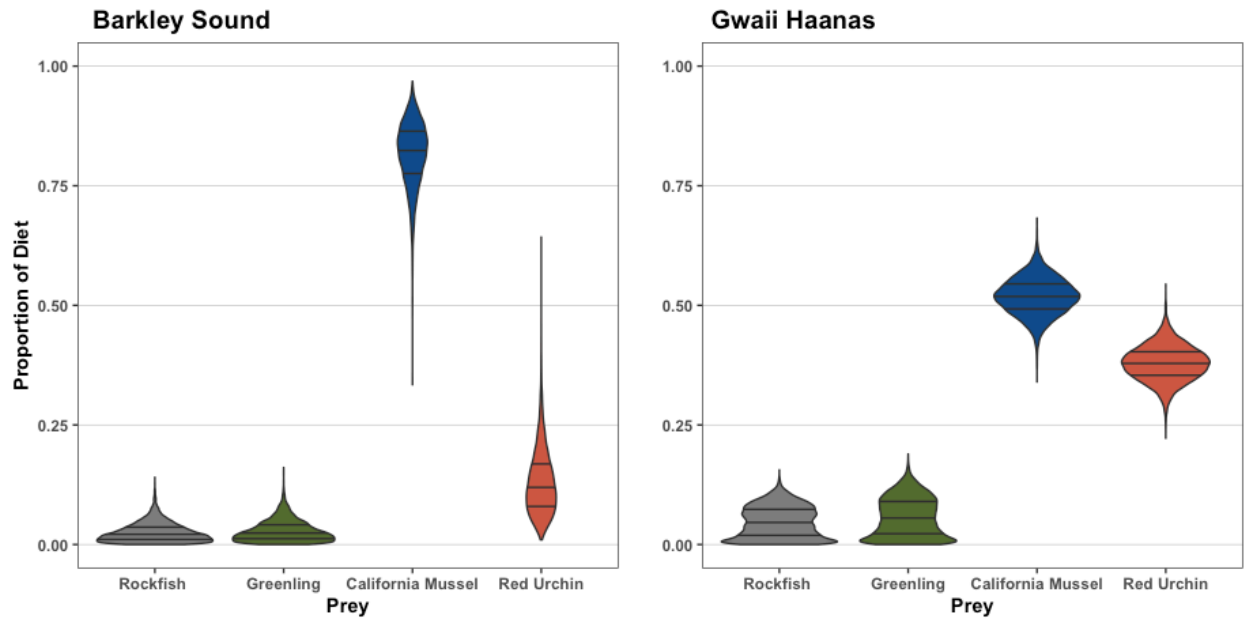


Figure B3: Violin plots representing MixSIAR estimates of sea otter diet from Model 4 for archaeological specimens from Barkley Sound (n = 11) and Gwaii Haanas (n = 31).

Appendix C – Shellfish Size Structure and Temporal Ubiquity

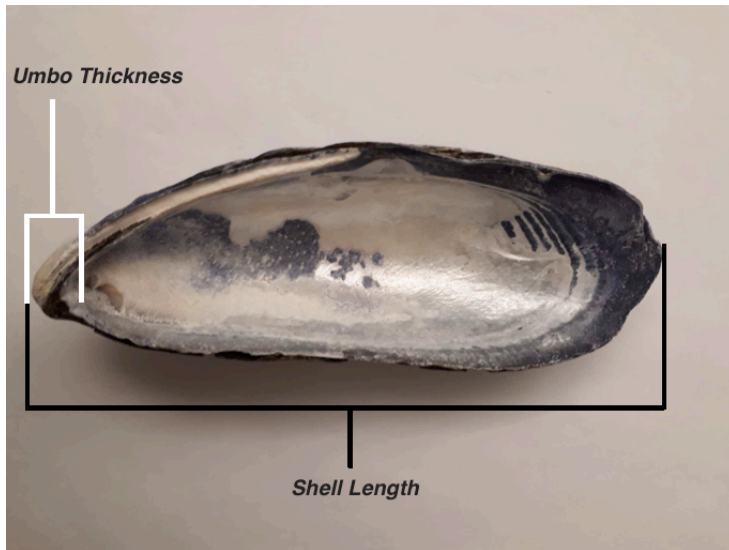


Figure C1. Measurement of California mussel umbo thickness and estimated shell length dimension.

Supplementary Information - Modern red turban snail collection and regression analysis

We collected 29 live red turban snails, ranging in size, from the Ross Islets in the Deer Group Islands within Barkley Sound. For each snail, we measured the longest part of the base of the shell (hereafter, length) and the longest axis of the operculum (operculum length) (Figure A1). We used these measurements to establish a simple linear regression between operculum length and shell length ($y = -0.7628 + 2.6386x$, $R^2 = 0.88$). More details available in Earle (2019).

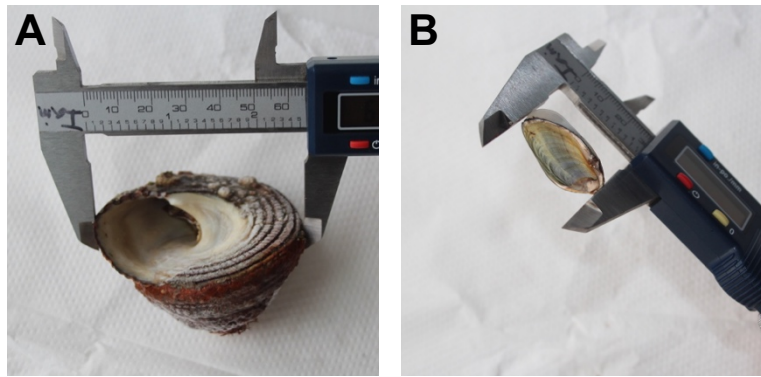


Figure C2. Red turban snail shell length (A) and operculum length (B) measured with digital calipers.

Table C1. Percentage of archaeological contexts containing urchin remains at sites in Barkley Sound and Gwaii Haanas.

Region	Site Number	Number of contexts analyzed	Number of contexts with urchins	Urchin Ubiquity at site	Reference
Gwaii Haanas	FaTr-3	18	5	28%	Keen 1990
Gwaii Haanas	FaTs-1	7	6	86%	Keen 1990
Gwaii Haanas	FaTs-3	10	2	20%	Keen 1990
Gwaii Haanas	FaTs-17	11	11	100%	Keen 1990
Gwaii Haanas	FaTs-20	16	8	50%	Keen 1990
Gwaii Haanas	FaTs-27	3	3	100%	Keen 1990
Gwaii Haanas	FaTs-31	5	0	0%	Keen 1990
Gwaii Haanas	FaTs-35	7	5	71%	Keen 1990
Gwaii Haanas	FaTt-9	45	13	29%	Keen 1990
Gwaii Haanas	FaTt-16	17	7	41%	Keen 1990
Gwaii Haanas	FaTt-20	8	7	88%	Keen 1990
Gwaii Haanas	FaTt-22A	18	13	72%	Keen 1990
Gwaii Haanas	FaTt-23	11	10	91%	Keen 1990
Gwaii Haanas	FaTt-28	50	22	44%	Keen 1990
Gwaii Haanas	FaTt-31	8	2	25%	Keen 1990
Gwaii Haanas	FbTu-5	16	12	75%	Keen 1990
Barkley Sound	206T	99	36	36%	McKechnie 2014
Barkley Sound	304T	62	17	27%	McKechnie 2014
Barkley Sound	82T	37	14	38%	McKechnie 2014
Barkley Sound	83T	77	5	6%	McKechnie 2014
Barkley Sound	129T	77	5	6%	McKechnie 2014
Barkley Sound	131T	6	0	0%	McKechnie 2014
Barkley Sound	132T	8	0	0%	McKechnie 2014
Barkley Sound	306T	5	2	40%	McKechnie 2014
Barkley Sound	204T	30	16	53%	Sumpter 2005
Barkley Sound	305T	7	2	29%	McKechnie 2014

Table C2. Strength of evidence for alternative models assessing the effect of *Area* (mussels) and *Unit* (red turban snails) on shellfish size as well as *Area* and *Site* nested within *Area* on the proportion of archaeological levels with urchins. Models with varying numbers of parameters (K) were compared using log-likelihood (LL), Akaike's Information Criterion (AIC) and small sample bias corrected AIC (AIC_c), AIC differences (ΔAIC), normalized Akaike weights (W_i) and adjusted R squared (R^2). The intercept model represents the null model of no effect of *Area/Unit*.

Model	K	n (BS)	n (GH)	LL	AIC	ΔAIC	w_i	R^2 adj
Astraea Shell Length								
Unit	2	1344	NA	-4294.61	8597.2	0.0	0.992	0.01
Intercept	1			-4301.43	8606.90	9.65	0.008	0.00
Mussel Shell Length								
Area	2	785	98	-13.494	33	0.0	0.90	0.40
Intercept	1			-13.324	37.4	4.5	0.10	0.00
	K	n (BS)	n (GH)	LL	AIC_c	ΔAIC_c	w_i	R^2 adj
Proportion of Levels with Urchins								
Area + Area:Site	2	10	16	5.23	-0.56	0.0	0.81	0.86
Intercept	1			1.73	3.63	4.19	0.109	0.00