Sea otter effects on soft-sediment flora and fauna, and within ancient Indigenous maricultural systems

By

Erin U. Foster
B.Sc., Vancouver Island University, 2009
M.Sc., University of British Columbia, 2012

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of
DOCTOR OF PHILOSOPHY
In the Department of Geography

Sea otter effects on soft-sediment flora and fauna, and within ancient Indigenous maricultural systems

By

Erin U. Foster

B.Sc., Vancouver Island University, 2009

M.Sc., University of British Columbia, 2012

Supervisory Committee:

Dr. Chris Darimont, Co-supervisor

Department of Geography, University of Victoria

Dr. M. Tim Tinker, Co-supervisor

Department of Geography, University of Victoria

Dr. Anne Salomon, Outside member

Department of Resource and Environmental Management, Simon Fraser University

Dr. Jane Watson, Outside member

Department of Biology, Vancouver Island University

Abstract

Most of what is known about the ways in which strongly interacting species affect ecological communities stems from changes to community structure revealed in contemporary research. However, trophic downgrading has limited the temporal extent to which inferences can be drawn. The aim of my Dissertation was to expand on the strongly interacting species concept by examining species interactions at a historical scale, in a textbook example of a strongly interacting and keystone predator. The sea otter, *Enhydra lutris*, was driven to near-extinction but is recovering in parts of its range, providing a mosaic of areas with and without sea otters. This mosaic allowed for a series of natural experiments, which I conducted using behavioural observations, genetic tools, and archaeological methods, to examine sea otter effects spanning contemporary (last ~40 yrs.), and late-Holocene (~3500-150 yrs. ago) timeframes, and on an evolutionary scale that inferred middle-Pleistocene interactions. In Chapter 2, my coauthors and I found that sea otter use of clam-based niches increased as occupancy-time increased, and that bachelor groups of male otters primarily inhabited these niches, findings that informed and inspired subsequent questions. In Chapter 3, we found that where sea otters were established for 20-30 years, the disturbance to eelgrass (*Zostera marina*), caused by sea otters digging for clams and other infaunal prey, was correlated with ~25% greater eelgrass allelic richness than where otters were present <10 yrs, or absent. We posit that sea otter digging has long-influenced the genetic diversity and resilience of eelgrass – perhaps since the middle Pleistocene. In Chapter 4, we asked how two strongly interacting species – people and sea otters – co-existed for millennia where they both consumed clams. We used assemblages of live and otter-cracked butter clams (*Saxidomus gigantea*), to confirm the ecological effects that sea otters exert today. We measured clams from archaeological assemblages in areas densely populated with clam gardens – terraced beaches that enhance clam habitat and productivity – and found that sea otters reduced the sizes of ancient clams, acting as ecologically effective predators in the mid-to-late Holocene. However, clam harvests were stable for thousands of years, with or without otters. We suggest that clam gardening supported coexistence of people and otters in the past, and could function the same way today. Collectively, we found that a few, perhaps long-forgotten, interactions increased the breadth of the strongly interacting species concept. In Chapter 5, I suggest that such rediscoveries could occur in other systems. Many large vertebrates have suffered population declines, but the most insidious losses accompanying these, are the losses of ecological interactions that become unknowable, and thus cannot be intentionally restored. By searching out ancient interactions, long-forgotten relationships have the potential to be recovered, and to inform our understanding of contemporary systems.

Table of Contents

List of Tables

List of Figures

Acknowledgements

I would not have had the opportunity to conduct this research without the support of Drs. Eric Peterson and Christina Munck at the Hakai Institute. The time you gave me to look, think, and appreciate the complexities of nearshore communities and sea otter behaviour was transformative. To all my colleagues at the Hakai Institute: science, maintenance, house-keeping, and kitchen teams, I thank you for your friendship, your input, and the knowledge you shared with me.

To my colleagues who embarked on long field days watching sea otters and sampling eelgrass on the central coast, I thank you for being stalwart friends and collaborators. Matthew Morgan Henderson, Christie McMillan, Marie Fournier, Mike DeRoos, Rian Dickson, Carly Janusson, Meghan Humchitt, Keith Holmes, Angeleen Olson, Rebecca Piercey, Hannah Hall, Jessie Hale, Jess Fujii, Gena Bentall, Michelle Staedler, Linda Nichol, Jane Watson, and many others – thank you for enriching our sea otter surveys, bringing humour to long days, embarking on a variety of zodiac- kayak- and canoe-based camping trips, and chilly winter "snorkels" for sea otter prey. Your company and optimism regarding the number of bouts we were going to come home with kept me motivated. We spent more than 20 months in the field over 5 years, and made 20 thousand sea otter foraging observations. I am proud of our collective efforts.

To Jane and Linda – I am so grateful for your mentorship. You seeded the ideas we pursued during my PhD work. You have been supportive friends, sounding boards, and guides throughout this process. Thank you for sharing your several decades more than "20 months" of sea otter, kelp, and eelgrass knowledge with me. Jane, Leah Saville, Gina Lemieux, and Graeme Ellis, thank you for the time you spent and investments you made in conducting all the Vancouver Island observations and eelgrass collections that we used. Jane, thank you for teaching me how to do all of this – beginning in my early undergrad days – and continuing to help see things through now. My trips with you built a foundation that I will always be grateful for.

I have had the most supportive PhD committee that any student could hope for. Thank you to Chris Darimont, Anne Salomon, Tim Tinker, and Jane Watson for expanding the way I think about the world. Chris, I am grateful for our many laps of ring-road - the insights you shared with me, and your unwavering support – even when I moved back to Quadra Island and had a child. Tim, you have pushed me quantitatively and hopefully I can now pass as "not an 80 year old" in terms of my statistical prowess – though I'm sure there is a ways yet to come. Thank you for hosting me in California when I first started at Hakai, and helping me learn the ropes. Anne, thank you for mentoring me in socio-ecological approaches and ways of thinking about ecology. You have influenced how I see the world. Jane, I don't think I would have embarked on a PhD without your support. You have role modeled, among many things, the importance of Natural History. I especially enjoyed reading your clam sampling field notes and working with you on those data (and am grateful that I wasn't diving for those clams!).

One of the dynamics of fieldwork at Hakai, is the meeting of people from different disciplines. My meetings with "the archaeologists" have also been transformative. Duncan McLaren, Dana Lepofsky, Iain McKechnie, and Becky Wigen, thank you for the time you spent teaching me the basics of archaeology. Duncan, thanks for leading me down the path to the Broughton excavations and braving a global pandemic to access the bowels of the campus and schlep 40+ boxes of shell midden to my car! Becky, I am so grateful that you cared for boxes upon boxes of faunal remains for 50 years, and the insights you patiently shared with me. To Midori Nicolson, thank you for taking a chance on me and sharing your knowledge of the people and the ecology of your homelands. Barb, the ideas you shared with me at the PEW meeting at Hakai were very influential. Midori, Barb, and Chris, your enthusiasm, time, and inputs to thinking through the ancient people-clam-otter relationships were invaluable.

I'd like to extend my thanks to others who have shaped my thinking. Thank you to Jim Estes for many foundational conversations and guidance – the weeks I spent with you when I first started at Hakai cultivated many ideas. Thank you to Lance Barrett-Lennard for instructive ideas about how we might use genetic tools to examine sea otter effects – and of course for the Tsitika!! Thanks to Graeme Ellis for putting up with constantly tied up phone lines – and more seriously, for sharing your natural history observations with me over the years. To Stan Hutchings and Karen Hansen, thank you for all of the visits, engaging conversations, and for repairing our boat that evening in Sans Peur Pass! To the ACS lab, thank you for being such an inspirational group of scientists to work with. To Sara Wickham, Megan Adams, Lauren Hanson, Katie Davidson, Heather Bryan, Aerin Jacob, and Jenn Burt, thank you for the many coffee dates and walks. Thank you to the Tula Foundation, NSERC Vanier, and UVIC for financial support.

Thank you to my family. To my parents for instilling a curiosity and appreciation for nature, and to my Mum and Mike for the days they took Eli on city-adventures while I went to campus. To Matt, for doing pretty much every single job that owning a house and parenting a toddler requires – the bath times, bed times, dinners, dishes, firewood, chickens, honey bees, cats…. I owe you a very big holiday and without you I never would have had time to write. Thank you to Eli, who kept my dissertation in perspective, and made sure I got outside to play, rain or shine; I will try not to worry that he pretends to be a sea otter eating clams when he wants to get my attention.

Dedication

To my Grandma, Dr. Doreen Kilpatrick.

Co-authorship Statement

Chapters 2 through 4 of this dissertation were co-authored. Authorship was shared among all without whom the study would not have been completed, including technicians and volunteers. The following outlines my contributions and that of my co-authors.

Chapter 2

Rechsteiner[*], E. U., Watson, J. C., Tinker, M. T., Nichol, L. M., Morgan Henderson, M. J., McMillan, C. J., DeRoos, M. , Fournier, M. C. , Salomon, A. K., Honka L. D. , Darimont, C. T. 2019. Sex and occupation time influences the niche space of a recovering keystone predator. *Ecology and Evolution*, 9: 3321-3334.

EUR, JCW, MTT, LMN, AKS, LDH and CTD conceived the ideas and designed the methodology. EUR, JCW, MMH, CJM, MDR, MCF, and LMN collected the data. EUR and MTT analyzed the data. EUR led the writing of the manuscript. All authors contributed to writing.

Chapter 3

Foster, E. U., Watson, J. C., Lemay, M. A., Tinker, M. T., Estes, J. A., Piercey, R. S., Henson, L., Ritland, C., Miscampbell, A., Nichol, L. M., Hessing Lewis, M., Salomon, A., Darimont, C. T. *In revision.* Physical disturbance by recovering sea otter populations increases eelgrass genetic diversity. *Science*.

EUF, JCW idea conception. CTD, LMN, MTT, JAE, MHL, AKS, and MAL hypothesis development and methodology. EUF led fieldwork. RSP, CR, AM led lab work. EUF, CR, AM, MTT, MAL, LH conducted data analyses. All authors contributed to writing.

Chapter 4

Foster, E. U., Lepofsky, D., McKechnie, I., McLaren, D., Nichol, L. M., Nicolson, M., Puckett, M., Roberts, C., Salomon, A. K., Testani, A., Tinker, M. T., Toniello, G., Watson, J. C., Wigen, R., K̲ii’iljuus, B. J. W., Darimont, C. T. *In preparation.* Clam gardens and Indigenous stewardship supported ancient clam harvests, even where sea otters were ecologically effective.

EUF, JCW, LMN, BJWK, AKS, DM, IM, idea conception. EUF, DL, IM, DM, MN, CR, AKS, MTT, JCW, RW, BJWK, CTD, idea development and study design. DL led fieldwork at Quadra. RW and IM curated samples from the Broughton Archipelago. EUF, AT, MP, GT measured clams. EUF conducted the statistical analyses. All authors contributed to writing. Except first and last author, authorship order is alphabetical.

---

[*] now Foster

Chapter 1. Introduction

1.1. Strongly interacting species

That some species interact more strongly than others within ecological communities is not a new idea, but it has important ramifications for ecological systems. The label *strongly interacting species* can be generally applied to any species with a disproportionate influence on an ecological community (Soulé *et al.* 2005). A species' interaction strength is defined, in essence, as the difference in abundances of each of the species comprising an ecological community when a it is present vs. absent (Paine 1969; Estes *et al.* 2016). Although generally measured *per capita*, interaction strength is influenced by species' densities (Berlow *et al.* 1999). A species whose ecological effects are large, and disproportionately large relative to the species' abundance, is known as a *keystone species* (Paine 1969; Power *et al.* 1996). Strongly interacting and keystone species can be the primary driver of community structure when they occur at ecologically effective densities – that is, at densities or abundances sufficient to exert ecological effects (Soulé *et al.* 2002).

Much of what is known about how keystone species can influence ecological communities arises from trophic effects exerted via predation. Direct predation, a consumer-mediated interaction, can cause declines in prey populations, with associated changes in community structure (Hairston *et al.* 1960; Paine 1969; Estes & Palmisano 1974; Power 1990; Ripple & Beschta 2012; Rosenblatt *et al.* 2013), and community interactions (Estes *et al.* 2011; Dorresteijn *et al.* 2015; Estes *et al.* 2016; Lee *et al.* 2016). Fear of predation, a trait-based interaction, can also change communities (Lima & Dill 1990) and species interactions (Smith *et al.* 2021). Evolutionary pressures have favoured vigilance and predator avoidance strategies such that a landscape of fear can affect community interactions, generally increasing the effects of top-predators on prey populations by further limiting prey (Power *et al.* 1985; Schmitz *et al.* 1997; Ford *et al.* 2014; Suraci *et al.* 2016; Suraci *et al.* 2019). By altering the prevalence of various phenotypes, survival of attempted predation can affect evolutionary processes. For example, phenotypic traits that allow prey to elude predation can increase in abundance through natural selection (e.g., shell strength, Vermeij 1982; phlorotannins, Estes & Steinberg 1988). Although predation-associated interactions are important to community interactions, the influences of strongly interacting species on ecological and evolutionary processes can occur through other pathways.

Disturbance is an important agent of ecological and evolutionary processes, and can provide a pathway for species interactions. Disturbance can alter the ecological (Connell 1978; Power *et al.* 2008; Pringle *et al.* 2015) and genetic (Banks *et al.* 2013; Davies *et al.* 2016) diversity of populations. For example, African elephants (*Loxodonta africana*) induce a change from forest to open savannah communities by trampling and toppling trees (Laws 1970) - a disturbance effect that is greater than those of both fire and frost (Holdo 2007). Disturbance from gray whales (*Eschrichtius robustus*), which feed on infaunal invertebrates by sucking large amounts of sediment from the sea floor, alter sediment size composition and subsequent infaunal community structure (Oliver & Slattery 1985). Notably, variation in rainfall regimes (e.g., flood and drought disturbance) increased the genetic diversity of the grass *Andropogon gerardii*, which promoted adaptation to changing environments (Avolio & Smith 2013).

Disturbance is arguably one of the most important determinants of genetic diversity (Nevo 2001; Banks *et al.* 2013; Davies *et al.* 2016). However, the mechanisms underlying how disturbance affects genetic diversity are less well understood (Davies *et al.* 2016; Messa *et al.* 2013). In the case of organisms that can produce both sexually and asexually, theory predicts that asexual reproduction should be favoured in a stable environment if parents are well-adapted, because a genetically-identical offspring should also be well adapted (Williams 1975). In contrast, sexual reproduction should be favoured in a disturbed environment, because the likelihood of adaptation through natural selection is higher with greater genetic diversity (Williams 1975). During ecological stress or disturbance, a switch from asexual to sexual reproduction and an associated increase in genetic diversity has been observed across various taxa: including invertebrates (Grapputo *et al.* 2005), fungi (Chen & McDonald 1996), and plants (Wilk *et al.* 2009). Strongly interacting species can disturb plants through herbivory (Deng *et al.* 2014), trampling (Elson & Hartnett 2017), digging (Eldridge *et al.* 2009), and bioengineering (Jones *et al.* 1994; Estes *et al.* 2016). Yet, with the exception of herbivory (Estes & Steinberg 1988; Agrawal *et al.* 2012), the effects of these disturbances on genetic diversity of recipient species, are relatively unstudied.

The predation- and disturbance-related effects that a species can impose on ecological processes are determined by the suite of biotic and abiotic interactions that together comprise its niche. A species niche can be defined as the place an animal occupies in the biotic environment – including its relationships with food and enemies (Elton 1927). A species' niche space considers all the abiotic and biotic variables that can determine whether or not a species can survive and reproduce, often mapping these in *n*-dimensional space (Hutchinson 1957). Understanding the breadth of relationships that a single species influences within its *n*-dimensional niche space is integral in predicting what interactions it may elicit across ecological communities.

Although the concept of the ecological niche has generally been considered to be static, it is increasingly recognized that niche spaces, and by association, ecological interactions, are dynamic (Newsome *et al.* 2015; Baudrot *et al.* 2016; Ingram *et al.* 2018). Factors such as life stage and habitat use (Polis 1984; Power 1984), intraspecific competition (Newsome *et al.* 2015) and sex (Shine 1989; Shine & Wall 2005) all affect niche variation within species or populations. An in-depth consideration of the dynamic interactions that strongly interacting species can impose could broaden our understanding of species interactions.

Many strongly interacting species include predators that have suffered widespread population declines. Globally, the extirpation of predators and large herbivores is known to have ecological consequences (Jackson 2001; Estes *et al.* 2011; Dirzo *et al.* 2014; Ripple *et al.* 2015; Estes *et al.* 2016), but the study of the roles these species play in structuring ecological communities often occurs following reintroduction and subsequent recovery. As predators become re-established, they may occupy seemingly new habitats, or broaden their diet, leading to increased diversity in niche space that appears novel to scientists but is in fact a re-occupancy of pre-exploitation niche space (Silliman *et al.* 2018).

The effects of strongly interacting species on ecological communities often extend to humans. Where humans have become accustomed to trophically-downgraded systems, predator recovery can cause conflict (Redpath *et al.* 2013). Conversely, people may rely on predator-mediated ecological interactions, that, if predator populations decline below ecologically effective numbers, can negatively impact people (Estes *et al.* 2011; McCain *et al.* 2016).

For much of the Holocene, humans have acted as a strongly interacting species, influencing many top-down and bottom-up effects. Humans tend to mediate top-down effects by harvesting predators (Darimont *et al.* 2015; Worm & Paine 2016), which can affect trophic linkages in food webs synergistically (by creating a landscape of fear) where fear drives the behaviour of species to avoid interactions with people (Suraci *et al.* 2019). Humans today are considered hyper-keystone species (Worm & Paine 2016) in part because of their disproportionately strong limitation of large vertebrates (Darimont *et al.* 2015). Yet in some places and times people have coexisted with an abundance of other large-bodied vertebrates (Stothert *et al.* 2003). Human mediated bottom-up processes can also influence the extent to which people can co-exist with other consumers. For example, by altering food and habitat availability through forest management, agriculture, cultivation, and other forms of land-use (Foley *et al.* 2005), people can influence entire food webs (Dorresteijn *et al.* 2015). Despite the importance of socio-ecological interactions, the details of these linkages are often poorly understood, particularly as they apply through, and prior to, the Holocene.

1.2. Sea otters as strongly-interacting species

Sea otters are a textbook example of a strongly interacting and keystone species. They are best-known for inducing ecological changes in nearshore rocky reef communities. By limiting sea urchins and other marine herbivores, sea otters initiate a cascade of ecological changes, transforming ecological communities from urchin barrens to kelp forests (Estes & Palmisano 1974; Estes & Duggins 1995; Watson & Estes 2011). Sea otters also influence soft-sediment communities via their predation on crabs (Garshelis *et al.* 1986; Hughes *et al.* 2013; Hessing Lewis *et al.* 2018) and clams (Kvitek *et al.* 1988; Kvitek *et al.* 1992; Weitzman 2013). Recent work documented a trophic cascade, exerted by sea otters in eelgrass communities; otters limited crabs and their predatory effects, which increased epiphyte-grazers that reduced epiphyte cover on eelgrass, and increased eelgrass biomass (Hughes *et al.* 2013). Taken together, the predation-induced effects of sea otters influence many ecological communities.

Much of what is known about sea otter interactions stems from their effects as predators, however they also impose disturbances in both rocky-intertidal and soft-sediment communities. In the rocky intertidal, sea otters expose bare patches of mussels (VanBlaricom 1988) which may in turn increase diversity of shorebird diets (Berg 2015). In soft sediments, sea otters excavate clams and other infaunal prey, altering sea star and crab foraging behaviour (Kvitek *et al.* 1992). Based on decades of sea otter observations (Watson *pers. obs.*), we hypothesized that disturbance from sea otter digging in eelgrass (*Zostera marina*) meadows could be sufficient to influence eelgrass life history traits and thus genetic diversity. Eelgrass is a marine angiosperm with the ability to reproduce both asexually by sprouting clones via rhizome mats, or sexually through flowering and aquatic pollination. Several species of seagrasses are known to increase flowering efforts and reduce clonal reproduction when disturbed by both digging and grazing (Alexandre *et al.* 2005; Hughes & Stachowicz 2011; Henderson & Hacker 2015; Ruiz *et al.* 2018). Biotic disturbances in seagrass meadows are widespread, and common agents of disturbance include herbivory by sirenians, turtles, and waterfowl (Thayer & Engel 1982; Williams 1988; Preen 1995; Jackson 2001; Hughes & Stachowicz 2004) and digging by rays (Short & Wyllie-Echeverria 1996) and people (Alexandre *et al.* 2005; Cullis-Suzuki *et al.* 2015). Sea otter digging breaks up rhizome mats, creates pits, and leaves bare patches. Understanding how sea otter disturbance affects genetic diversity is important because such effects may enhance ecological resilience in changing environments, and inform the historical interactions that drive eelgrass adaptive potential.

Sea otters tend to occupy eelgrass habitats after years-to-decades of occupancy in an area, as the niche spaces occupied by- and ecological effects imposed by- sea otters vary. In some cases, dynamic niches arise due to sea otter legacy effects. Legacy effects in this context, refer to the types of ecological effects a species exerts, that change the ecological community they are a part of, and consequentially change their role in that community. For example, as sea otter predation of herbivores induces a system-change from urchin barrens to kelp forest, the diversity of fauna supported in the system increases, with a consequential increase in sea otter diet diversity (Estes *et al.* 2003). As sea otter occupancy increases, their niche space expands at a population level, yet individuals sometimes specialize on prey to increase foraging efficiency (Tinker *et al.* 2008a; Newsome *et al.* 2015). Sea otters segregate by sex, with mature males and females generally occupying discrete areas throughout the range (Riedman & Estes 1990). Groups of bachelor (non-reproductive or non-territorial) males pioneer range expansion, often settling in urchin-rich areas at the range-edge (Lafferty & Tinker 2014). Female groups later replace bachelor male groups, at which point they tend to occupy the same areas for decades or more (Lafferty & Tinker 2014; Nichol *et al.* 2015). In some areas, differences between male and female niches have been observed (Elliot Smith *et al.* 2015). In a polygynous species such as the sea otter, the niche used by males – and the associated effects on survival – may be less important to population productivity than the niche used by females, because individual females contribute more to population recovery than males (Emlen & Oring 1977; Tarjan 2016). Thus, a better understanding of sex- and occupancy- related difference in sea otter niches could influence conservation directives.

Like many large animals, sea otters were heavily hunted, interrupting our understanding of the ecological roles they mediate. Before the 18-19th century Maritime Fur Trade, sea otters numbered about 300,000 animals, ranging from Japan to California. Across their range, hunting reduced them to about a dozen remnant groups, together comprising fewer than 1000-5000 individuals across their range (Kenyon 1969; Riedman & Estes 1990). On the BC coast, fur traders reported vast numbers of sea otters in the late-1700s (Robinson 1996; Orchard 2007; Sloan & Dick 2012), yet by 1820-1850 sea otters were ecologically extinct, meaning they occurred at numbers below the threshold at which they would have had any ecological effect (Watson 2000; Sloan & Dick 2012). Much of what is currently known about sea otters today, stems from contemporary studies made after sea otters recovered in specific areas, yet many of the ecological interactions driven by sea otters have been lost or overlooked because of their extirpation (Silliman *et al.* 2018).

The Maritime Fur Trade triggered changes in the socio-ecological relationships between northwest coast Indigenous peoples and sea otters. Sea otters were harvested to a greater extent than they previously had been, and because the fur-trade economy benefited people adept at harvesting sea otters, less emphasis was put on other traditional practices (Lightfoot 1995). The spatial distribution of village sites was re-shaped as people moved nearer to trading centres, and these re-distributions resulted the abandonment of “productive” (e.g. cultivated) sites in favour of sites from which furs could more easily be acquired (Lightfoot 1995; Marsden & Galois 1995). By the mid-to-late 1800s, Indigenous people were being relocated on to Reservations, and this further prevented people from accessing their traditional lands and resources (Government of British Columbia, 1875 *cited in* Turner et al. 2008). Colonization, warfare, and disease reduced northwest coast Indigenous populations to approximately one tenth of their pre-colonization abundance (Ames & Maschner 1999). With these reductions, and the colonial governance of resources, came further losses of socio-ecological interactions that had influenced ecological and evolutionary processes during the past 14,000 years (Turner *et al.* 2008; Turner & Turner 2008). Given the long history of northwest coast Indigenous peoples in shaping ecological and evolutionary processes, rediscovery of ancient interactions could provide insights to the structuring of contemporary ecological and socio-ecological systems.

Today, the recovery of sea otters imposes strong effects on contemporary socio-ecological systems. Sea otters can enhance ecosystem services (Wilmers *et al.* 2012; Hessing Lewis *et al.* 2018), and tourism and fin-fishery based livelihoods (Gregr *et al.* 2020). Yet, they can also exert negative effects on invertebrate fisheries. Sea otter extirpation allowed for the expansion of commercial invertebrate harvests; in BC, the ages of harvested geoduck (to 152 years, Reidy & Cox 2013) and surveyed urchins (to 200 years, Ebert & Southon 2003) correspond to when sea otters were considered to be ecologically extinct (1820-1850; Watson 2000; Sloan and Dyck 2012). However, as sea otters have recovered in parts of their range, declines in shellfish availability have precluded some commercial (Miller *et al.* 1975) and food-social-ceremonial (Salomon *et al.* 2015; Burt *et al.* 2020) fisheries. Understanding and recovering the human-mediated ecological interactions that may have enabled co-existence of people and sea otters in the past, could build resilience in socio-ecological systems today (Burt *et al.* 2020).

Sea otters and otter-associated communities provide an excellent model system to investigate how ancient and contemporary interactions shape(d) ecological and socio-ecological communities. In many parts of the Pacific Rim, including parts of BC, sea otter populations are recovering after overexploitation, providing a mosaic of areas where otters are absent, have recently re-occupied, or are long-established. Such spatial variation lends itself well to natural experiments. In addition, because sea otters have inhabited the coastal regions of the Pacific Ocean since at least the middle-Pleistocene (Boessenecker 2016), they provide a model to think about how a predator might have structured ecological interactions before people arrived to the Americas, through the Holocene (parts of which supported high populations of Indigenous people), and to contemporary times, following sea otter extirpation and recovery. Sea otters are just one of many strongly interacting species whose numbers and distributions have changed through the Holocene and again over the past two centuries. Using sea otters as a model that could be widely applied to other recovering species, my coauthors and I used the spatial mosaic and deep temporal history of sea otter occurrences to examine three major questions in my PhD Dissertation.

1.3. Dissertation scope and objectives

In my Dissertation, I consider the strong-interaction of sea otters over time - from the middle Pleistocene to present-day. I infer from contemporary studies how sea otter and eelgrass interactions evolved before humans arrived to the northwest coast, then I examine how sea otters and humans interacted as common (and perhaps competing) predators of clams during the mid- to late-Holocene. I address how sea otters and the ecological interactions they trigger have changed following their extirpation in 18th and 19th century Maritime Fur Trade and ongoing recovery. To consider these broad effects of sea otters in time and space, I took an interdisciplinary approach, drawing on ecological, population genetic, and archaeological domains, which were influenced and guided by members of my co-authorship teams. Our work is based largely on natural-experiment frameworks that compare ecological interactions in areas where sea otters were established vs. absent, and across an occupancy gradient using a *space-for-time* design (Picket 1989).

Collectively, my research chapters highlight how ancient ecological and socio-ecological interactions involving sea otters may have driven ecological and evolutionary processes, and how the legacy effects of sea otter occupancy inform our understanding of these processes today. In my concluding chapter, I bring these different interactions together to reflect upon the losses of sea otter-mediated and human-mediated interactions once common in many northwest coast ecosystems. Finally, I suggest that for many large-bodied fauna, the majority of which have suffered from widespread population declines, rediscovering forgotten interactions could inform our understanding of today's ecological communities.

In Chapter 2, published in *Ecology & Evolution* (Rechsteiner et al. 2019 – I was the lead author, this chapter was published prior to changing my surname to Foster) my coauthors and I made direct observations of foraging sea otters across an occupancy gradient from places where sea otters had arrived during the past year, to areas where they had been present ~35 years. Our observations, conducted over four years, reveal how sea otter niche space changes over the course of their recovery, and in relation to sex. We found that, as elsewhere, sea otter niche space expanded as recovery progressed. Differences in sea otter niche spaces among sites with varying occupancy times arose due to the legacy of effects that sea otters exert on ecological communities as they recover; a combination of declining abundances of the initial prey that sea otters target, and changing vegetation (i.e. kelp forest growth) that support diverse prey populations, which in turn support sea otters over the course of otter recovery. Additionally, we found that while female and territorial male otters generally occupied kelp forest and intertidal niches, where they consumed small and diverse prey, males that occupied male-only rafting areas foraged over open water, where their diet was clam-based. The potential for sea otters to exert strong interactions in ecological communities while occupying clam-based niches at long-occupied mother-and-pup areas, and in male-dominated areas, informed and inspired the questions I asked in subsequent chapters.

In Chapter 3 (*in revision, Science*), my coauthors and I examined the effects of sea otter substrate disturbance (i.e. digging for infaunal prey such as clams), on microevolutionary processes in a marine angiosperm, eelgrass (*Zostera marina*). We hypothesized that disturbance to eelgrass, caused by sea otters routinely digging for clams and other infaunal prey, should drive increased sexual vs. vegetative reproduction in eelgrass, which would lead to higher genetic diversity in areas with sea otters than in areas without sea otters. We evaluated this hypothesis using a natural experiment that we replicated across two genetically-differentiated eelgrass populations (Vancouver Island and the central BC coast). In both eelgrass populations, we found eelgrass allelic richness was ~25% higher where sea otters were established (20-30 yrs) compared to where they had recently arrived (<10 yrs) or were absent (>100 yrs). Otter occupancy was the most important predictor of eelgrass allelic richness relative to depth, latitude, temperature and meadow size, and otter occupancy together with meadow size were the most important predictors of genotypic diversity. These findings have far-reaching conservation implications because genetic diversity increases the adaptive potential of *Z. marina* populations, which enhances resilience and resistance to perturbations. We inferred that the genetic associations between sea otters and eelgrass have been occurring since at least the middle-Pleistocene. Similar interactions may be common in other communities where they have previously been overlooked because of the losses of large-bodied animals and their associated effects.

In Chapter 4 (*in preparation*), my coauthors and I further develop our understanding of the strongly interacting species concept by examining how two such species – sea otters and people – co-occurred on the northwest coast of North America for some 14,000 years, both consuming clams. We first conducted a contemporary natural experiment, and found that butter clams (*Saxidomus gigantea)* were smaller in areas with sea otters than in areas without. We examined otter-cracked clam shells, and found that otters consumed, on average, butter clams that were twice as large as the average available sizes. These contemporary measurements emphasized the effects sea otters have on the size structure of ecologically available clams. Next, we designed a natural experiment in areas where sea otters were historically (i.e., for the past 3500 years) absent vs. present, but where environmental conditions and Indigenous maricultural practices were similar. In this context, we found that sea otters influenced the size structure of two culturally-important clam species (the butter clam, and the littleneck clam, *Leuconoma staminea*). Taking into account other factors that may have influenced clam sizes, we demonstrated that butter clams were significantly smaller from archaeological assemblages with sea otters than those without sea otters, and that size distributions of butter and littleneck clams were truncated in areas with sea otters. Despite the ecological effects sea otters had on clams, people harvested from stable and predictable clam resources for four millennia – a testament to Indigenous maricultural practices that allowed for people and sea otters to coexist. Our work adds to a body of evidence showing how ancient interactions can inform our understanding, and potentially the restoration, of socio-ecological relationships today.

In Chapter 5, I reflect on how a few, perhaps long-forgotten, ecological and socio-ecological interactions can increase the breadth of the strongly interacting species concept. Understanding the ecological function of any species in nature relies upon characterizing the linkages it elicits, and understanding the dynamic nature of such linkages (Estes *et al.* 2016). I applied this idea to a variety of temporal scales to capture the historical contexts within which we study keystone species. I suggest that lost interactions are waiting to be rediscovered as species recover, or in ancient data that illuminates past species interactions. Following the Maritime Fur Trade, most remnant populations of sea otters occurred along the outer coast of the Pacific Rim. Thus, much of the foundational work on sea otter ecology comes from a limited ecological context—that of otters in rocky substrate and kelp forest habitats (Silliman *et al.* 2018). Like sea otters, many large vertebrates have suffered widespread population declines. Such declines have influenced our understanding of species interactions in contemporary food webs. Estes et al. (2011) argue that loss of unknown ecological interactions is the most insidious part of losing a species. In this dissertation I have tried to re-illuminate some of these ancient ecological and socio-ecological interactions in sea otters systems. A better understanding of past community interactions will inform the ways in which contemporary communities interact, and in many cases could build resilience in a changing environment.

Chapter 2. Sex and occupancy time influence niche space of a recovering keystone predator

Chapter 2 is adapted from Rechsteiner et al. (2019).

2.1 Abstract

Predators exert strong effects on ecological communities, particularly when they re-occupy areas after decades of extirpation. Within species, such effects can vary over time and by sex, and cascade across trophic levels. We used a space-for-time substitution to make foraging observations of sea otters (*Enhydra lutris*) across a gradient of re-occupancy (1-30 yrs), and nMDS analysis to ask if 1) sea otter niche space varies as a function of occupancy time, and 2) if niche space varies by sex. We found that niche space varied among areas of different sea otter occupancy times. Dietary niches at short occupancy times were dominated by urchins (*Mesocentrotus* and *Strongylocentrotus* spp; >60 % of diets) in open habitats at 10-40 m depths. At longer occupancy times niches were dominated by small clams (Veneroida; >30% diet), mussels (*Mytilus* spp; >20% diet), and crab (Decapoda; >10% diet) in shallow (<10 m) kelp habitats. Diet diversity was lowest (H' = 1.46) but energy-rich (~37 kcal/min) at the earliest occupied area and highest, but energy-poor (H' = 2.63, ~9 kcal/min) at the longest occupied area. A similar transition occurred through time at a recently occupied area. We found that niche space also differed between sexes, with bachelor males consuming large clams (>60%), and urchins (~25%) from deep waters (>40 m), and females and territorial males consuming smaller, varied prey from shallow waters (<10 m). Bachelor male diets were less diverse (H' = 2.21) but more energy-rich (~27 kcal/min) than territorial males (H' = 2.54, ~13 kcal/min) and females (H' = 2.74, ~11 kcal/min). Given that recovering predators require adequate food and space, and considering the ecological interactions they elicit, we emphasize the importance of investigating niche space over the duration of recovery, and considering sex-based differences in these interactions.

2.2 Introduction

The effects of predators on ecological processes are determined by the suite of biotic and abiotic interactions that together comprise their niche space. The multi-dimensional niche space of a species (Hutchinson 1957) can be examined by mapping a species' biotic and abiotic requirements, and then used to predict what interactions a species may have within a larger community (Holt 2009). Recently nutrition, physiology, and behaviour have also been used to better-characterize niche breadth and predict a species' trophic interactions (Machovsky-Capuska *et al.* 2018). Although once viewed as static, niche space is no longer seen as a fixed property, but one that can change as a function of intraspecific variation (Newsome *et al.* 2015; Baudrot *et al.* 2016; Ingram *et al.* 2018). Factors such as life stage and habitat use (Polis 1984; Power 1984), intraspecific competition (Newsome *et al.* 2015) and sex (Shine *et al.* 1998; Shine & Wall 2005) all affect niche variation within species or populations. For example, niche space can change with catfish (Loricariidae) growth, where juveniles are limited, by fear of predation from larger fish, to ecologically ineffective densities in shallow areas, and large catfish occur at ecologically effective densities deeper waters – avoiding the shallows due to fear of bird and mammal predators (Power 1984). Niche space can also change as a population reaches carrying capacity, reflecting increased intraspecific competition (Newsome *et al.* 2015). This has important implications for recovering populations of predators whose niche space may change over the course of recovery.

Globally, the extirpation of predators is known to have ecological consequences (Jackson 2001; Estes *et al.* 2011), but an understanding of the roles of these predators in structuring ecological communities often occurs following reintroduction and subsequent recovery (e.g., Ripple *et al.* 2014). When high trophic-level species recover, they may have substantial effects on the trophically-downgraded systems to which they return. As predators become re-established, they may occupy new habitats, or broaden their diet, leading to increased diversity in niche space (Silliman *et al.* 2018). Recovering predator populations can also induce ecological changes that exert feedback on prey or habitat availability, further diversifying or expanding the predator's niche-space (Estes *et al.* 1982; Tinker *et al.* 2008a).

Population diversification and expansion in niche space may reflect intraspecific differences in trophic interactions and habitat use brought about by sex-specific constraints. Sex-based differences in niche space may include body size differences or reproductive demands (Ruckstahl & Clutton-Brock 2005), or differing nutritional requirements (Machovsky-Capuska *et al.* 2016). If the sexes occupy different niche space, their ecological needs and interactions might likewise vary. Thus understanding how niche space is used by both sexes will provide a more comprehensive insight into the ecological effects and conservation needs of a species.

Sea otters (*Enhydra lutris*) provide a useful model to examine changes over time and sex-related differences in niche space in a keystone predator recovering from near extinction. Owing to the Maritime Fur Trade that lasted from the mid 1700s to the early 1900s, sea otters were likely ecologically extinct in British Columbia, Canada, by 1820–1850 (Watson 2000; Sloan & Dick 2012). Sea otters were re-introduced to Canada's west coast in the late 1960s and early 1970s (Bigg & MacAskie 1978). Sea otters segregate by sex with non-territorial males and adult females generally occupying discrete areas throughout the range (Riedman & Estes 1990). As sea otter populations recover and recolonize habitats, groups of males pioneer range expansion, typically settling in urchin-rich areas at the range-edge (Lafferty & Tinker 2014). Female-dominated groups later replace male groups. This transition often occurs after the ecological community has changed from urchin- to kelp-dominated as a result of sea otter foraging on sea urchins, an important reef herbivore (Watson & Estes 2011; Lafferty & Tinker 2014). As sea otter occupancy time increases, kelp forest communities are further altered by the effects of otter foraging, and sea otter diets may become more diverse at the population level (Ostfeld 1982; Tinker *et al.* 2008a).

Here we use sea otters as a model to pose two broad questions about niche space within recovering carnivore populations. We made direct observations of sea otter foraging at five areas spanning a gradient of sea otter occupancy time from 1-30 years to ask 1) how does the niche space of a predator change as the population recovers from extirpation and; 2) how does niche space vary between females and males? Our findings yield insight into how ecological interactions exerted by predators vary during recovery, and how these interactions can differ between female and male predators.

2.3 Methods

Field methods. We observed sea otter foraging from 2014-2017 on the central coast of British Columbia in five *occupancy areas,* where sea otters arrived at different periods: Gosling Rocks (1980s, occupied ~27-30 yrs.), McMullin Islands (~1996, occupied ~18-21 yrs.), Simond Islands, (~2009, occupied ~5-8 yrs.), Breadner Islands, (~2011, occupied ~3-6 yrs.), and Calvert Island (2013, occupied 1-4 yrs.). We estimated the arrival time of sea otters in an area based on the first reported observations of a raft of otters that occupied the area for a minimum of one year (Nichol *et al.* 2015). We used a space-for-time design to estimate temporal changes in niche space (Pickett 1989). At the most recently occupied area (Calvert), which was colonized by sea otters during our study, we divided longitudinal data into *initial* (1 year occupied) and *established* (2-4 years occupied) periods to examine potential changes in niche within an occupancy area through time, thereby complementing the space-for-time design.

We collected data on diet and foraging behavior using well-established, standardized observation methods (Estes *et al.* 1982; Tinker *et al.* 2008a; Tinker *et al.* 2012). Data were collected from 2014-2017 in winter (January and February) and summer (June, July, August) by trained observers stationed at locations on shore within 1000 m of foraging otters. Locations from which observers collected sea otter foraging data are called *observation sites* and were visited repeatedly throughout the four-year study period (Fig. 2.1).

We used a 50-80x magnification Questar telescope (Field model 3.5, Questar Corp., Pennsylvania, USA) to observe individual otters (identified by sex, age and unique markings such as percent grizzled or blonde fur, animal size, and nose scarring patterns) over a contiguous sequence of dives, referred to as a foraging bout. For each dive we recorded the duration of dive and surface intervals, dive outcome (i.e., whether prey were captured), prey type (identified to lowest taxon possible), and the number of items and size class of prey (relative to sea otter paw-width, Fig. 2.S1). We collected a minimum of 50 foraging bouts at each occupancy area in each season and year, with the exception of the exposed Gosling Rocks site in winter (due to inclement weather), where we collected 60 bouts across all winters combined. Using species accumulation curves, we determined that a sample of 50 bouts accounted for ~95% of sea otter diet variability (Figure 2.S2). Dean *et al.* (2014) reported a similar sample size for sea otters in Alaska. We made observations within 1000 m of large (>50-200 individuals) sea otter rafts; we worked at sites with many otters to increase the likelihood that 50 foraging bouts would include diverse individuals. We used individual markings to reduce the probability of recording multiple bouts in the same site and season by the same individual. Individual bouts were averaged to the observation site-level, which was used as the replicate in all statistical models avoiding the risk of pseudo-replication.

Quantifying habitat use. We recorded several habitat parameters at each sea otter's surfacing location for each foraging dive. We used direct observation of floating canopy kelps (*Macrocystis pyrifera* or *Nereocystis leutkeana*) to determine the presence or absence of kelp where sea otters surfaced with prey. Seagrass (*Zostera* spp.) coverage was established through video-tows made throughout the study area when underwater visibility was adequate (Hakai 2014). Sea otter surface locations were spatially joined to seagrass polygons *post hoc* using ArcGIS (ESRI 2017). The water depth foraged over by sea otters was determined *post hoc* using ArcGIS (ESRI 2017) and was based on chart datum data obtained from the Canadian Hydrographic Service (CHS 2016 – license 2016-03-01-1290-H). Foraging depths were categorized as intertidal (<0 m below chart datum), shallow (0-10 m below chart datum), mid (10-40 m below chart datum) and deep (>40 m below chart datum).

Data analyses overview. Our analyses of foraging ecology and niche space variation in sea otters involved several steps. First, we used established analytical methods to quantify diet composition (i.e., frequency of occurrence representation of various prey taxa and size classes in sea otter diets), and rate of energy gain and diet diversity from observational foraging data (Tinker *et al.* 2008a; Tinker *et al.* 2012).

We then combined foraging data for each occupancy area with environmental parameters (habitat, depth) and analyzed the multivariate data set using nonmetric multidimensional scaling analysis (nMDS) to examine whether there were groupings that correlated with occupancy area or sex class. We used a similarity percentage analysis (SIMPER) to determine the diet items most strongly influencing similarities within groups (by frequency of occurrence), and employed a hierarchical clustering analysis with group average linking to check for corroboration with nMDS results. Finally, we used an Analysis of Similarity (ANOSIM) test to determine whether or not differences among groups were significant. These analyses are described in detail below.

Foraging data analysis. We used direct observations of foraging behaviour combined with a Monte Carlo algorithm to analyze sea otter foraging data (Tinker *et al.* 2008a; Tinker *et al.* 2012). Prey functional groups were defined by both taxa and size class (Table 2.1) and were limited to prey that comprised at least 5% of overall diets by frequency of occurrence. The proportion of each prey group and mean prey size from foraging bouts at the same observation site were averaged to provide site-specific values for all prey groups. We then calculated the Shannon index of diversity (Shannon 1948) for each occupancy area. For the occupancy area data, we limited consideration to observation sites with ≥ 25 bouts (n = 26 observations sites: 4 from Gosling, 6 from McMullins, 4 from Simonds, 4 from Breadners, 4 from Calvert *established* and 4 from Calvert *initial*). For the sex class data, we further limited consideration to sites where ≥10 bouts were observed for at least one sex class. Sex classes were defined as *female* (n = 13 sites; all females regardless of reproductive status), *territorial male* (n = 11 sites; males holding territories), or *bachelor male* (n = 12 sites; males aggregated in large male-only rafts, which in our study existed both in the range-centre and at the range-edge). In California (Jameson 1989; Tinker *et al.* 2008b; Tarjan 2016) and Alaska (Garshelis & Garshelis 1984) some males move between bachelor groups and female areas where they may become territorial males seasonally, and we suspect this is also the case in British Columbia. Therefore, classifications of *territorial* or *bachelor* male in our study apply to the otter at the time and location it was observed foraging.

Energy intake rates can be used to infer the abundance and quality of prey resources for sea otter populations (Tinker 2015). Because population growth in sea otters is usually determined by prey abundance, energy intake provides a useful index of status with respect to carrying capacity (Tinker 2015). Data on size-specific edible biomass and caloric content of most sea otter prey items is available from an earlier study (Oftedal *et al.* 2007). These data can be combined with observational foraging data to estimate energy intake rates for sea otters. Sea otters are almost unique in their tractability for foraging studies, because their feeding dives are conducted close to shore and prey are consumed at the surface, where prey species, size, and handling time can be readily observed. However, recording all relevant parameters is subject to the challenges of direct observation, and missing information tends to be biased towards smaller prey, shorter handling times, or more distant sea otters (Tinker *et al.* 2012; Tinker 2015). To account for this potential bias, we used a Monte Carlo algorithm used in many previous studies (e.g., Tinker *et al.* 2012; Newsome *et al.* 2015; Hessing Lewis *et al.* 2018). This process-based model replicated the recorded foraging bouts and iteratively assigns missing parameters by drawing randomly from appropriate probability distributions while maintaining observed covariance patterns between dive parameters (details in Tinker *et al.* 2012; Tinker 2015). The results of the analysis include estimates of energy intake rates (kcal consumed per minute of time spent feeding) for sea otters at each observation site.

Niche space analysis. We quantified niche space along multiple dimensions corresponding to prey selection and habitat and depth-use variables. As with the foraging data, variables were first quantified at the bout-level and then averaged at the site level with each site average becoming an individual point in the nMDS analysis. Variables used in the nMDS analysis included the proportional representation of prey functional groups, dive habitat (open, kelp canopy, seagrass) and depth (intertidal, shallow, mid, deep) over which sea otters foraged.

We used PRIMER-e V7 (Clarke & Gorley 2015) to calculate a resemblance matrix of sea otter niche space at each observation site and for each site-sex class pair, using Bray-Curtis dissimilarities of square root transformed diet, habitat, and depth variables (Clarke *et al.* 2014). To include the three different data types (diet, habitat, and depth) in the resemblance matrices, we square root transformed all data and then rescaled the habitat and depth variables such that the mean values across sites were equal to the mean of the transformed prey values; this procedure prevented any single data type (diet, habitat or depth) from having an exaggerated influence on the nMDS analysis (Clarke *et al.* 2014; Kenner & Tinker 2018).

The resemblance matrices were then used to perform non-metric multi-dimensional scaling (nMDS) in PRIMER-e (Clarke & Gorley 2015). We incorporated environmental data (depth and habitat), mean prey size, diet diversity, energy intake rate, and occupancy time as vectors in our nMDS plots *post hoc*. Correlations between each of these vectors and the ordination axes were calculated with the Pearson correlation coefficient (Clarke *et al.* 2014). Vectors with correlation coefficients ≥ 0.50 were included on the nMDS plots. The nMDS converged in two dimensions with stress values of 0.12

(occupancy areas) and 0.13 (sex). An nMDS with stress values below 0.20 can provide a useful 2-dimensional interpretation, but if stress is >0.10 the plot should be superimposed with results from cluster analyses to assess agreement (Clarke *et al.* 2014). Thus, for each resemblance matrix we also performed hierarchical clustering using group average linking of replicate sites at each occupancy area or for each sex (Clarke *et al.* 2014).

We used an Analysis of Similarity (ANOSIM) test to determine whether groups (occupancy areas, sex classes) were significantly different (Clarke *et al.* 2014). If significant differences were detected in the global ANOSIM test, pair-wise comparisons were made. We used a similarity percentage analysis (SIMPER) to determine which prey and environmental metrics contributed most to similarities within clusters identified by nMDS, and included the most influential prey groups in bubble plots to help interpret nMDS results (Clarke *et al.* 2014).

2.4 Results

Sea otter foraging data. We observed 19,535 foraging dives in 1,983 bouts. Of these, 12,922 foraging dives from 1,330 bouts were collected from observation sites where we had observed ≥ 25 bouts. Individual bouts ranged from 3-81 dives (mean 10.10 ± 0.22 dives SE), and from 2.4 min to 162 min (mean 20.8 ± 0.48 min SE). We identified the sex of the otter in 968 (~73%) of these bouts, which were used for the nMDS analysis with sex. Prey sizes and energy intake are reported as mean ±SE.

Diet varied among sites with different occupancy times. Sea otters at the Calvert *Initial* area consumed ~60% large urchins (*Mesocentrotus* and *Strongylocentrotus* spp.) while large urchins composed only ~20% of otter diets at Calvert *Established* and Breadners (3-6 years occupied), ~10% of diets at Simonds (5-8 years occupied), and less than 2% of diets at the McMullins (18-21 yrs) and Gosling (27-30 yrs) (Fig. 2.2). The proportion of clams (Veneroida), including geoduck (*Panope generosa*), comprised <25% of the diet at Calvert *Initial* and Breadners but was >50% of the diet at Calvert *Established*, Simonds, and McMullins (Fig. 2.2). Sea otter diets at Gosling Rocks were composed mostly of mussels (*Mytilus* spp. ~40%), clams (~10%), urchins (~10%) and kelp crabs (*Pugettia* spp. ~10%) (Fig. 2.2). Mean prey size declined from 12.17 ± 0.41 cm at the Calvert *Initial*, to 9.73 ± 0.33 cm at Gosling Rocks (Fig. 2.2). Shannon indices showed lowest diversity (H’ = 1.46) at Calvert *Initial* and higher diversity (H’ = 2.07–H’ = 2.63) at all other occupancy areas (Fig. 2.2). Monte Carlo analysis indicated that the mean energy intake rate declined from 37.04 ± 12.02 kcal/min consumed at Calvert *Initial*, to 9.61 ± 1.45 kcal/min at Gosling Rocks (Fig. 2.2).

Sea otter diets also differed by sex. Bachelor males consumed ~30% urchins, and >50% clams, whereas territorial males and females consumed ~15% urchins, ~20% each of small and large clams, >10% each of small crabs and mussels, and ~10% snails (Turbinidae; Fig. 2.3). Mean prey size was highest for bachelor males (13.34 ± 0.37 cm) and lower for territorial males (10.03 ± 0.26 cm) and females (9.94 ± 0.26 cm) (Fig. 2.3). Shannon indices showed lowest diversity in bachelor male diets (H' = 2.21) and higher diversity in territorial male and female diets (H' >2.50; Fig. 2.3). Monte Carlo analysis indicated that the mean energy intake rate was highest for bachelor males (26.67 ± 4.72 kcal/min) and lower for territorial males (12.89 ± 1.72 kcal/min) and females (11.29 ± 0.63 kcal/min) (Fig. 2.3).

Sea otter niche space. Otters from different occupancy areas strongly diverged in niche space. Cluster analysis showed groupings with 63% similarity by occupancy area, and by *Initial* and *Established* sites at the Calvert occupancy area (Fig. 2.4). Results of the nMDS showed two-dimensional stress of 0.12 and dissimilarities among occupancy areas (Fig. 2.5a). The results of the ANOSIM supported statistically significant differences in niche space among occupancy areas (ANOSIM, R = 0.74, P <0.001). All but two pairwise comparisons were significantly different from one another (Table 2.S1). Bubble plots depict the prey species most important in driving similarities within occupancy areas, as identified by SIMPER (>8% contribution to within-group similarity; Fig. 2.5b). We found that niche space similarities within occupancy areas were determined primarily by urchins, clams, geoduck, mussels, small crabs, open water (i.e., absence of kelp canopy) and shallow water (Table 2.S2). *Post hoc* vector correlations indicated that use of intertidal, shallow, and kelp canopy areas were correlated with longer occupancy times whereas use of deep, mid, and open areas, large prey sizes and higher rates of energy intake were correlated with shorter occupancy times (Fig. 2.5a, Table 2.S3).

Sexes also showed strong divergence in niche space. Cluster analysis identified groupings by sex class with 45% similarities (Fig. 2.6). Results of the nMDS showed two-dimensional stress of 0.13 and dissimilarities among females and territorial males, and bachelor males (Fig. 2.7a). The results of the ANOSIM confirmed that niche space significantly differs among sex classes (ANOSIM, R = 0.36, P <0.001). Pairwise comparisons revealed that females and territorial males used a different niche space than bachelor males (Table 2.S4). Bubble depicting the variables most important in driving similarities within sex classes, as identified by SIMPER (>8% contribution to within-group similarity; Fig. 2.7b) illustrate differences in niche space were driven by urchins, clams, geoduck, small crabs, open water and shallow water (Table 2.S5). *Post hoc* vector correlations indicated that higher diet diversity and use of intertidal, shallow, kelp canopy, and seagrass areas were correlated with females and territorial males, whereas use of deep, mid, and open areas, and larger prey sizes were correlated with bachelor males (Fig. 2.7a, Table 2.S6).

2.5 Discussion

The dynamics of sea otter niche space. In this study, we used sea otters as a model to evaluate support for the hypotheses that a) predator niche space changes during population recovery, and b) niche space varies between sexes. We found that across a gradient of occupancy times, sea otters on the BC central coast occupied different niche spaces, initially foraging on large urchins in open water, before transitioning to soft-sediment habitats to forage on clams in deep waters, and then to kelp canopy and intertidal areas where smaller and more diverse invertebrates were acquired. Both mean prey size and energy intake rates were lower in long-occupied areas. These niche space differences among sites with varying occupancy times likely reflect sea otter behavioural responses to variation in prey availability – a legacy of the effects they exert on benthic prey communities as they recover (i.e., Estes *et al.* 2003; Tinker *et al.* 2008a). The pattern we observed at a single occupancy area over the four-year study period offers evidence to support this hypothesis, with sea otter diets changing from urchin-dominated (>60%) to clam-dominated (~50%) after only ~1 year of occupancy.

Niche space also varied among female, territorial male, and bachelor male sea otters. Bachelor males at recent and <10 yrs. occupancy areas (i.e., 1-8 yrs) foraged predominantly in open (no kelp canopy or seagrass) habitats, using deeper waters than females, and consumed ~70% clams. In contrast, females and territorial males exhibited higher diet diversity, and used kelp canopy, seagrass, and shallow and intertidal waters to forage on a diverse suite of smaller prey. Together, these findings suggest that the niche occupied by sea otters on the central coast of BC is context-specific, depending on both occupancy time, and sex.

Although niche space has not been thoroughly examined in sea otters (but see Silliman *et al.* 2018), sea otter diets have been well-studied. In British Columbia (Breen *et al.* 1982; Honka 2014; Hessing Lewis *et al.* 2018), Washington (Laidre & Jameson 2006; Hale *et al.* 2019), California (Estes *et al.* 1982; Estes *et al.* 2003; Tinker *et al.* 2008a; Tinker *et al.* 2012), and Alaska (Kvitek *et al.* 1992; Weitzman 2013; Hoyt 2015), sea otter diets differ among recently and long-occupied areas. The ecological interactions driven by sea otter foraging can also differ due changing otter diets; one example from our study area was that sea otter foraging provisioned large red urchins to Harlequin ducks, *Histrionicus histrionicus* but only where otter occupancy was <1 yr. (Rechsteiner & Olson 2016). In California, where individual sea otters have been observed for decades, sea otter diets diversify at the population level as occupancy time increases (Estes *et al.* 1982). In Washington State, sea otter diets do not vary with occupancy time and density as much as they vary with kelp habitat (Hale *et al.* 2019). On the exposed Washington coast, kelp habitats may be an important source of food, as well as providing shelter from storms and predators (Thometz *et al.* 2016), whereas in BC the role of kelp may be less important because there is more shelter provided by islands and inlets (Hessing Lewis *et al.* 2018).

Differences in the diets of female and male sea otters have also been noted in other parts of the sea otter's range. In California, individual males over 1.5 years consumed more diverse prey than females, though this likely included males in transition between bachelor and territorial stages (Elliot Smith *et al.* 2015). In our study, bachelor males had the least diverse diets. We also observed that large groups of bachelor males (n = 50-150 individuals) in our study areas regularly undertook local movements (i.e., within ~1500 m) *en masse*, arriving to new rafting and foraging sites regularly within each occupancy area, usually where prey were large. Additionally, females may restrict their diets to increase time spent at the surface with their pups (Thometz *et al.* 2016). The different niches used by male and female sea otters is important because there are many large bachelor male groups spanning recent- to long-occupied areas on the BC and Alaska coasts, and the ecological role of these large male groups has previously been overlooked.

Study limitations. Our study indicates that changes occur in sea otter niche space with increasing occupancy time, changes that are likely a product of the ecological effects exerted by the sea otters themselves. However, the inherent weakness of space for time frameworks lies in determining the extent to which differences are a function of predator recovery and occupancy time, or reflect variation among sites in the absence of predator recovery. Our observational design addresses this limitation to some extent. We used multiple observation sites (n = 4-6) within each occupancy area to replicate occupancy time and monitored changes within each occupancy area over the four-year study period. Only Calvert, the most recently occupied area, showed any indication of niche change, and we suspect this is because initial changes happen rapidly, whereas further changes take longer than 4 years to observe. To interpret whether, for example, sea otter diets at longer occupancy times transition from clam-dominated to mussel- and smaller invertebrate- dominated (as appears to be the case when comparing McMullins to Gosling), we would need to observe otters and the associated prey communities in each occupancy area on a time-scale of decades. This would also confirm whether the changes detected from our space for time design are indeed a factor of the ecological effects of sea otters on the prey community (e.g., Tinker *et al.* 2008a; Tinker *et al.* 2012).

Our study focused on the energy intake, diet, and habitat-use of sea otters. Sea otters, lacking the insulating blubber of most marine mammals, have high metabolic rates and consume ~25% of their bodyweight daily (Costa & Kooyman 1982). Previous research suggests that most critical macro- and micronutrients are well represented in sea otter diets, and that energy is the primary resource driving sea otter prey selection (Oftedal 2007). However, variability in macronutrient composition among prey species can be an important driver of diet choice and niche space (Machovsky-Capuska *et al.* 2016; 2018). Accordingly, including data on the macronutrient content of prey may enhance our characterization of niche space, but quantifying macronutrient profiles for the diverse suite of prey that sea otters consumed was beyond the scope of this study. However, future work should include a more comprehensive examination of nutritional dimensions to sea otter prey selection.

Energy intake was approximated by an established analytical framework used in many sea otter foraging studies (e.g., Tinker *et al.* 2008a; 2012; Hessing Lewis *et al.* 2018). This analysis makes use of a published data set on prey edible biomass and caloric content from 76 taxa collected in all seasons over a 4-year period at multiple sites in California and Alaska (see Oftedal *et al.* 2007; Tinker 2015 for more details). Although these data are broadly representative, we recognize their limitation for assessing fine-scale variation in prey quality. While such fine scale variation is undoubtedly important, our study was designed to examine coarse-scale patterns of niche use. Because we collected data over a 4-year period, we believe that we captured variation in sea otter diets and energy intake at the scale of interest.

Disentangling the relative effects of sex and occupancy time in sea otter niche space is difficult because the two are linked via the natural history of sea otters. On the central coast of BC, groups of bachelor males (typically n = >100 males in each raft) occurred at the range edge (Calvert *initial* and *established*) and in the range center (Simonds). Unpublished data (50 foraging bouts) collected over a two-week period in August 2016 by EUR and JCW in Kyuquot Sound (50.0° N, 127.4° W; >200 km south of the central coast of BC), in an area occupied by bachelor male sea otters since the 1980s, corroborated our findings: this bachelor male group foraged primarily on small clams (~70% of diet) in open waters. Further unpublished data (50 foraging bouts) collected over a two-week period in July 2017 by LMN and CJM in the Nuchatlitz Islands (49.8° N, 126.9° W; ~40 km south of Kyuquot Sound), at an area occupied by sea otters since the 1990s, similarly found that the diet of bachelor males was comprised mostly of clams (~70%). Our findings indicate that even at long-occupancy times, bachelor males predominantly used a soft-sediment, open water niche space where they feed on clams, however at longer occupancy times clams were small and energy intake rates were likely lower than on the central coast of BC.

Ecological and conservation implications of changing niche space in sea otters. Sex-related differences in feeding ecology and habitat use are rarely considered in habitat management or ecological interactions, despite these differences having potentially major effects (Du Toit 2005). In a polygynous species such as the sea otter, the niche used by males – and the associated effects on survival – may be less important to population productivity than the niche used by females, because individual females contribute more to population recovery than males (Emlen & Oring 1977; Tarjan 2016). Our finding that females gain less energy per minute of foraging than bachelor males indicates that they must spend more time foraging than males. Moreover, the high cost of lactation (Thometz *et al.* 2016) and parental care may put females at a greater conservation risk than males. This finding suggests that site-fidelity in females, even to lower-energy prey areas, is important, perhaps to avoid predators or due to other reproductive constraints. Thus, recovery planning should consider that females and territorial males may require different prey and habitat than bachelor males.

Understanding how prey selection and the range of habitats used by sea otters varies over the course of recovery has important implications for sea otter conservation, and affects our understanding of the recovery process in a predator that has traditionally been studied in a limited context (Silliman *et al.* 2018). Although dietary changes have been noted within and among sea otter populations, only limited research has examined niche variation across space and time. Following the Maritime Fur Trade, most remnant populations of sea otters occurred along the outer coast of the Pacific Rim. Thus, much of the foundational work on sea otter ecology comes from a limited ecological context – that of otters in open, exposed rocky substrate and kelp forest habitats (Estes & Palmisano 1974; Estes & Duggins 1995; Watson & Estes 2011). Although research has focused on the role of sea otters in hard substrate areas, they use soft substrate areas as well, at both recent- and long-occupied sites (Kvitek *et al.* 1992; Weizman 2013) and particularly in stormy weather (Garshelis & Garshelis 1984). Only recently have the effects of sea otters in estuaries and salt marshes been examined (Hughes *et al.* 2013; Hughes *et al.* 2016; Hessing Lewis *et al.* 2018), and such habitats are beginning to be considered essential, and historically important, to sea otters (Silliman *et al.* 2018). In our study, we found that use of soft sediment habitat becomes more important over the course of recovery, and that soft sediment communities may be more important to bachelor males than females.

Although the ecological effects of sea otters foraging on urchins at exposed rocky sites are well-known (see Estes *et al.* 2016 for a review), their effects on other habitat types and prey communities are less well understood. Sea otter interactions in contexts other than urchin-kelp communities include serial depletion of macroinvertebrate prey (Salomon *et al.* 2007), homogenization of mussel beds (Singh *et al.* 2013), and clearing patches in mussel beds that provides space for diverse invertebrate recruits (VanBlaricom 1988), which can in turn affect shorebird diets (Berg 2015). In soft sediment areas, sea otters can reduce large size classes of clams and alter benthic community structure as their occupancy time increases (Kvitek *et al.* 1992; Weizman 2013). Sea otter predation on clams may have further effects in seagrass communities: digging can act as a source of disturbance to plants (Alexandre *et al.* 2005) and invertebrates (Kvitek *et al.* 1992). Recently, the role of sea otter predation on crabs in seagrass communities has been shown to initiate a trophic cascade that increases seagrass biomass (Hughes *et al.* 2013). Ecological effects of sea otters can sometimes transcend marine-terrestrial boundaries (Rechsteiner *et al.* 2018). Together, these studies show that sea otter community interactions are context-dependent, and that the ecological consequences of alternative niche-use patterns may be important to consider in terms of beneficial conservation impacts, fisheries interactions, and other management and conservation priorities (Silliman *et al.* 2018).

The dynamics of niche space in recovering predators. Most of the world's large predators have suffered widespread extirpation, limiting our understanding of how ecological communities function with intact predator populations (Jackson 2001; Estes *et al.* 2011; Silliman *et al.* 2018). Thus the interactions among predators, herbivores, and primary producers, and the habitat and food requirements of recovering predators, are difficult to predict. Over the course of recovery, many predators have expanded their ecological niche, often surprising ecologists with the different ecological interactions that they can elicit (Silliman *et al.* 2018).

Niche partitioning, once seen as a static species characteristic (Hutchinson 1957), is now viewed as a dynamic property driven by intraspecific differences in traits such as age and sex (Polis 1984; Shine 1989), as well as factors such as population size (Newsome *et al.* 2015), and historical context (Jackson 2001; Silliman *et al.* 2018). We used a re-introduced sea otter population to examine these ideas, and found that niche space differed between sexes, and changed over time as sea otter recovery progressed. These results have implications for depleted or recovering predator populations because sex-related differences and temporal changes in characteristics such as feeding ecology and habitat use will affect the recovery process. If ecologists treat niche space as being dynamic and intraspecifically-partitioned they will be better equipped to predict the conservation needs and ecological interactions of recovering predators, and to consider more broadly the ecological interactions that may have been driven by predators historically.

2.6 Acknowledgements

We thank Drs. Eric Peterson and Christina Munck for supporting this work through the Tula Foundation. EUR was supported by NSERC Vanier. AKS was supported by an NSERC Discovery Grant. CTD was supported by NSERC Discovery Grant (435683). We thank the field observers that contributed to this study: Robin Abernethy, Gena Bentall, Mykelti Berg, Dustin Chappel, Rian Dickson, Jessica Fujii, Jessie Hale, Hannah Hall, Keith Holmes, Stacey Hrushowy, Megan Humchitt, Carly Janusson, Zachary Monteith, David Norwell, Angeleen Olson, Rebecca Piercey, Nelson Roberts, Leah Saville, Michelle Staedler, Alanna Vivani, and Brianna Wright. Rachel Barclay, Blake Dixie, Karen Hansen, Stan Hutchings, Adam Turner and Rod Wargo assisted with field logistics. Matthew Foster assisted with data management. We thank two anonymous reviewers for their feedback on this manuscript. We thank the Heiltsuk Integrated Resource Management Department, the Heiltsuk Nation, and the Wuikinuxv Nation for their support and permitting of research in their traditional territories. Sea otters were observed under Parks Use Permit 107314, Fisheries and Oceans Canada License XMM-9-2015, and the University of Victoria Animal Care Permit AUP2017-007.

2.7 Tables and Figures

Table 2. 1. Prey groups used in nMDS and Cluster analyses.

Common name	Lowest taxon	Size (paw)	Apx. size (cm)	Prey group	Prey group abbreviation
urchin	*Mesocentrotus* spp., *Strongylocentrotus* spp.	1a-1c	<2-5	small urchin	urc_sm
		2a-4c	7-20	large urchin	urc_lrg
clam	Veneroida	1a-1c	<2-5	small clam	clam_sm
		2a-4c	7-20	large clam	clam_lrg
chiton	Polyplacophora	1a-1c	<2-5	small chiton	chit_sm
		2a-2c	7-10	medium chiton	chit_med
		2a-6c	7-30	large chiton	chit_lrg
abalone	*Haliotis kamtschatkana*	1a-1c	<2-5	small abalone	aba_sm
		2a-3c	7-15	large abalone	aba_lrg
cucumber	Holothuroidea	1a-1c	<2-5	small cucumber	cuc_sm
		2a-2c	7-10	medium cucumber	cuc_med
		2a-8c	7-40	large cucumber	cuc_lrg
crab	unknown crabs	1a-1c	<2-5	small crab	crab_sm
		2a-4c	7-20	large crab	crab_lrg
Cancer crab	*Cancer* spp.	1a-1c	<2-5	small cancer crab	can_sm
		2a-4c	7-20	large cancer crab	can_lrg
geoduck	*Panopea generosa*	1a-2c	<2-10	small geoduck	geo_sm
		3a-3c	12-15	medium geoduck	geo_med
		4a-4c	17-20	large geoduck	geo_lrg
kelp crab	*Pugettia* spp.	1a-1c	<2-5	small kelpcrab	kelpcrab_sm
		2a-3a	7-12	large kelpcrab	kelpcrab_lrg
mussels	*Mytilus* spp.	1a-1c	<2-5	small mussel	mus_sm
		2a-4c	7-20	large mussel	mus_lrg
scallop	Crassadoma	1a-1c	<2-5	small scallop	scal_sm
		1c-4a	5-17	large scallop	scal_lrg
snail	Turbinidae	1a-1c	<2-5	small snail	sna_sm
		2a-3c	7-15	large snail	sna_lrg
octopus	Octopoda	all	all	octopus	oct
shore crab	*Hemigrapsus* spp.	all	all	shorecrab	shorecrab

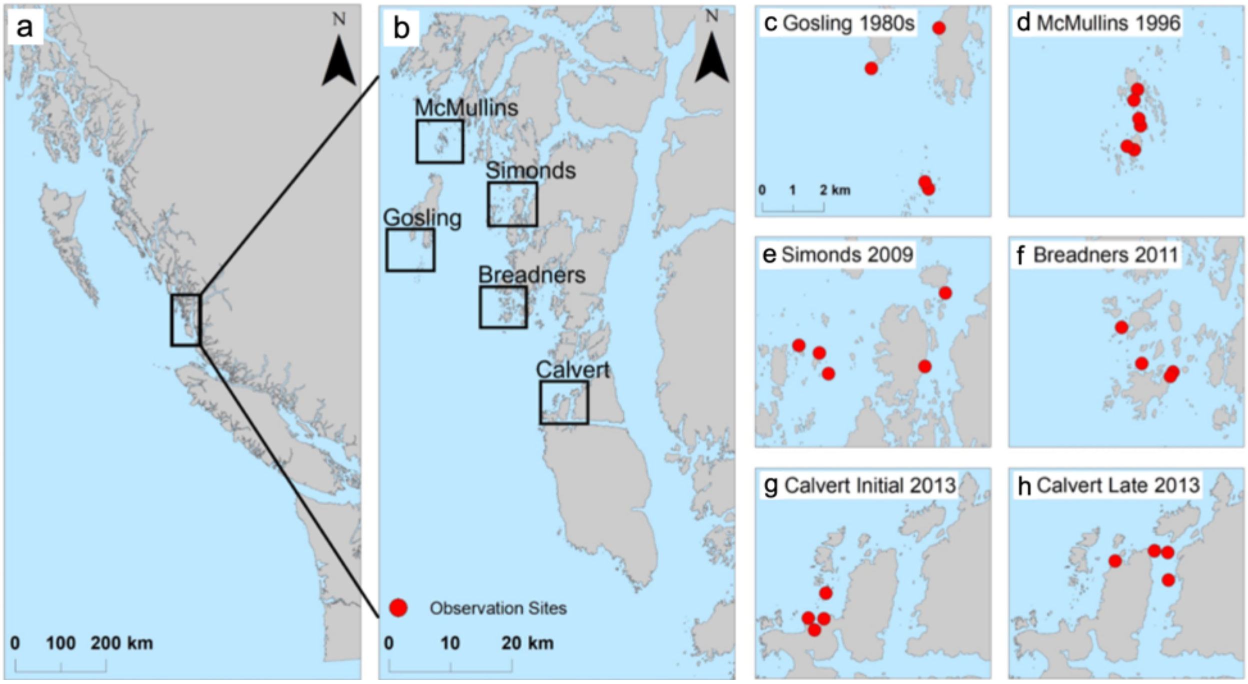


Fig. 2. 1. Map of British Columbia shoreline (a) and central coast study area (b) with occupancy areas (c-h) and observation sties (red circles).

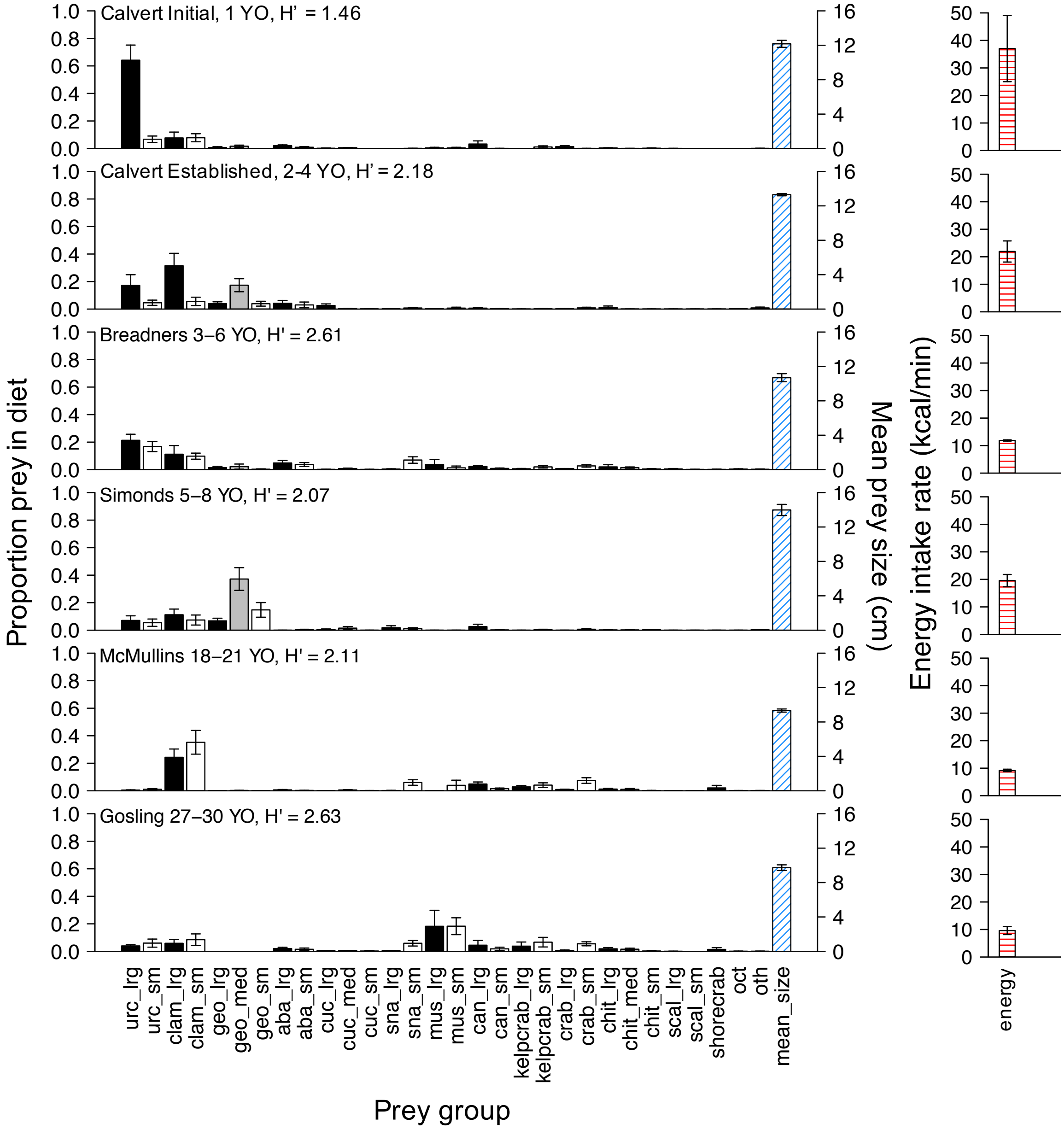


Fig. 2. 2. Prey consumed by sea otters at occupancy areas from 1-30 years occupied (YO) as proportion of diet by frequency of occurrence. Black bars show large prey, grey bars show medium prey, and white bars show small prey. Blue cross-hatched bars indicate mean size of prey. Red cross-hatched bars show energy intake. Error bars are SEM, n = 4 for all occupancy areas except McMullins where n = 6. H’ is Shannon Index of Diversity. For prey group abbreviations, see Table 2.1.

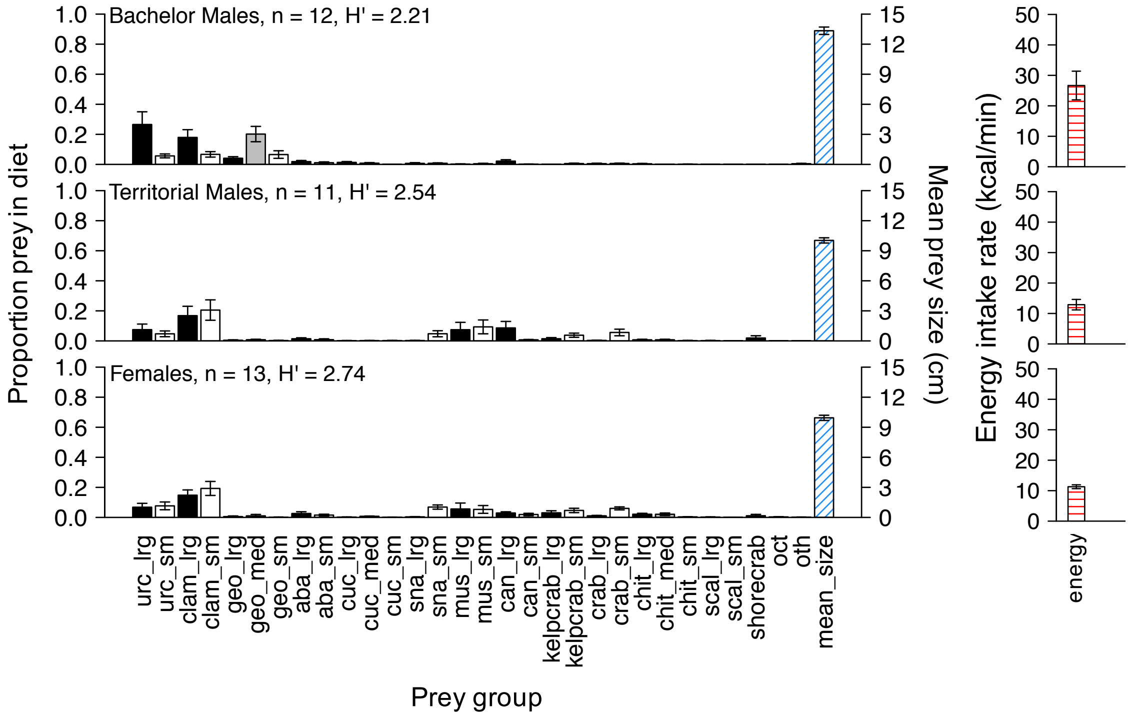


Fig. 2. 3. Prey consumed by sea otters of each sex class as proportion of diet by frequency of occurrence. Black bars show large prey, grey bars show medium prey, and white bars show small prey. Blue cross-hatched bars indicate mean size of prey. Red cross-hatched bars show energy intake. Error bars are SEM, n is number of sites, H’ is Shannon Index of Diversity. For prey group abbreviations, see Table 2.1.

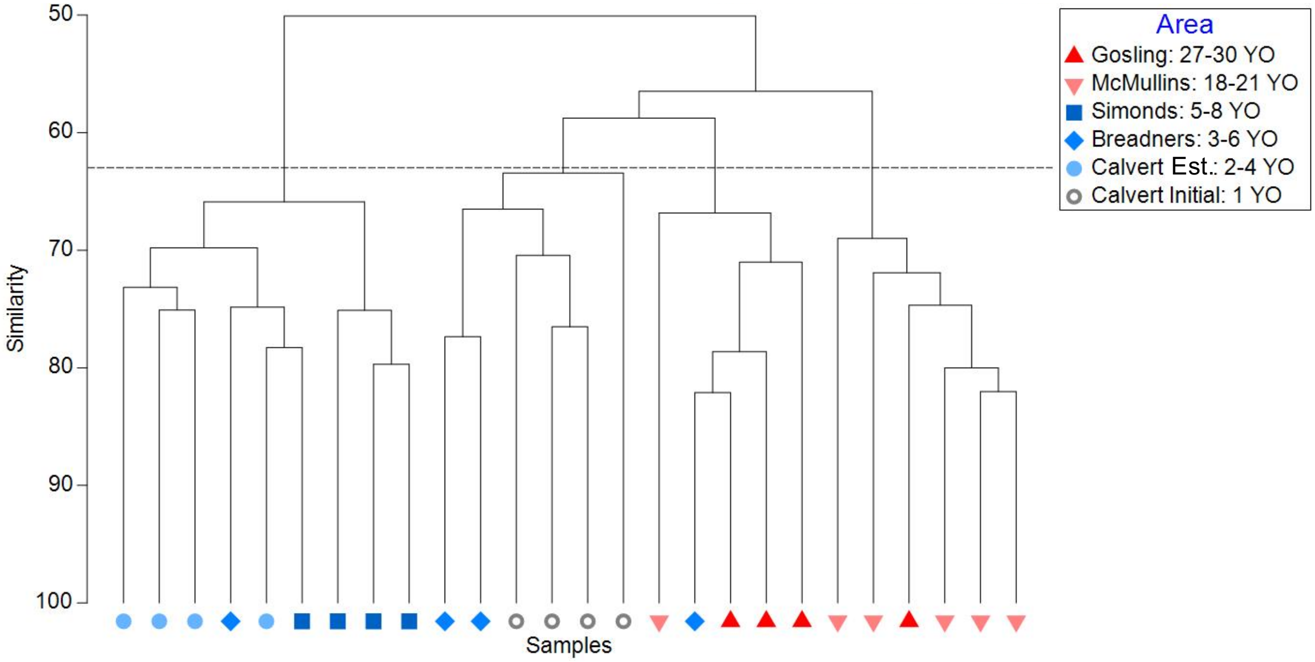


Fig. 2. 4. Dendrogram of hierarchical clustering of replicate observation sites at each occupancy area, based on Bray-Curtis dissimilarity matrix. Dotted line shows 63% similarity. Grey symbols correspond to the shortest occupancy time, blue symbols to medium occupancy times, and red symbols to longest occupancy times.

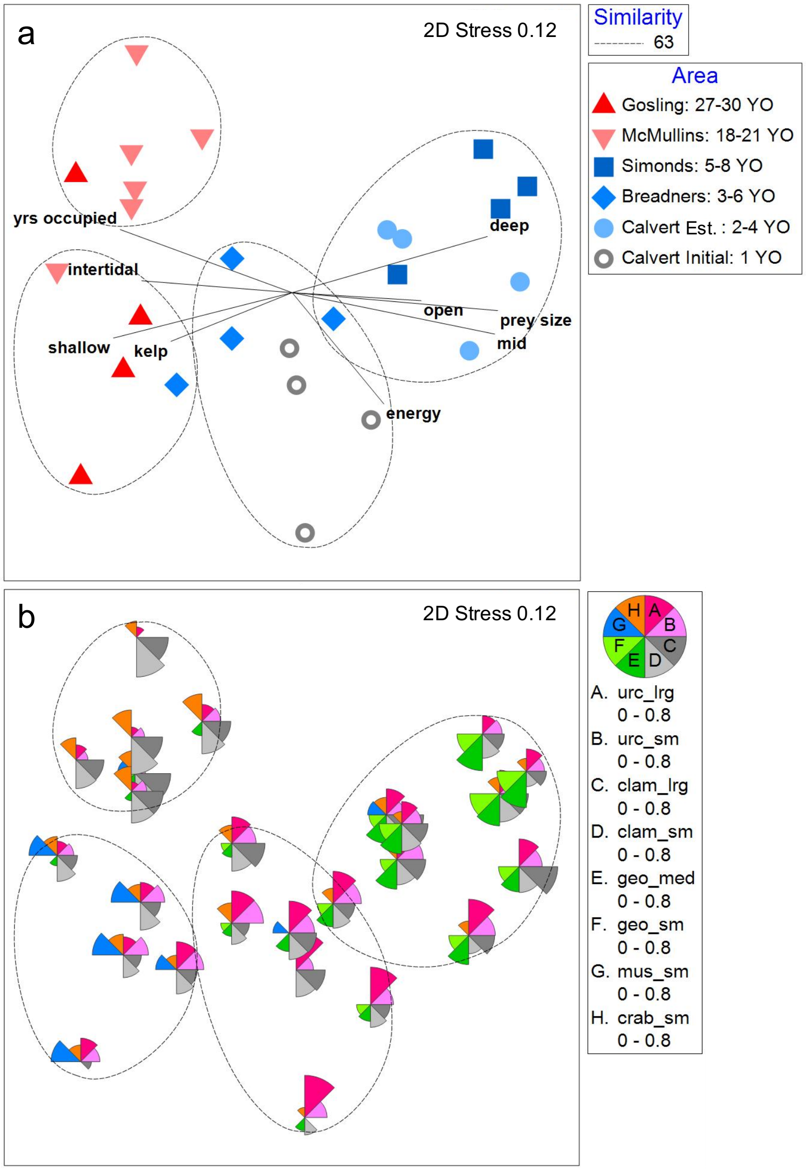


Fig. 2. 5. nMDS plot of sea otter niche space with a) clusters identified in Figure 4 with 63% similarity, and environmental vectors with ≥ 0.5 correlation to dissimilarities, and b) bubble plots depicting the most common prey groups, with bubble segments approaching sizes of segments in the legend representing ~80% of the diet by frequency of occurrence.

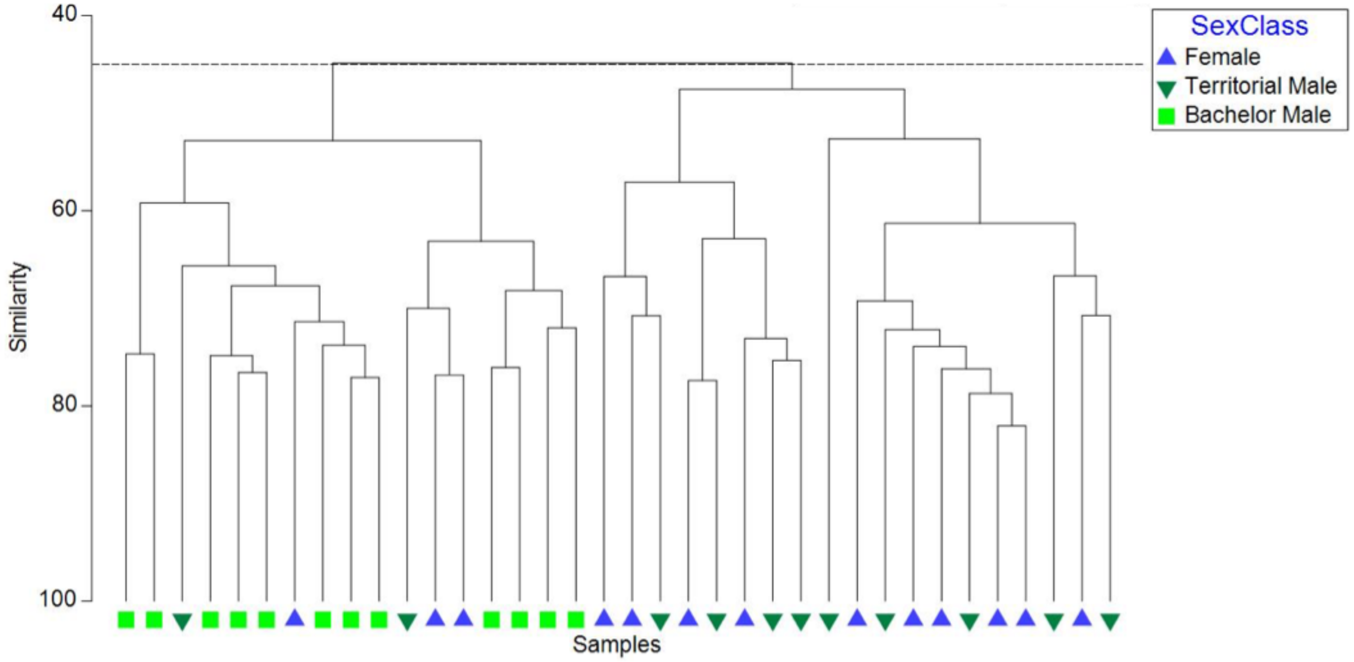


Fig. 2. 6. Dendrogram of hierarchical clustering of replicate observation sites for each sex, based on Bray-Curtis dissimilarity matrix. Dotted line shows 45% similarity.

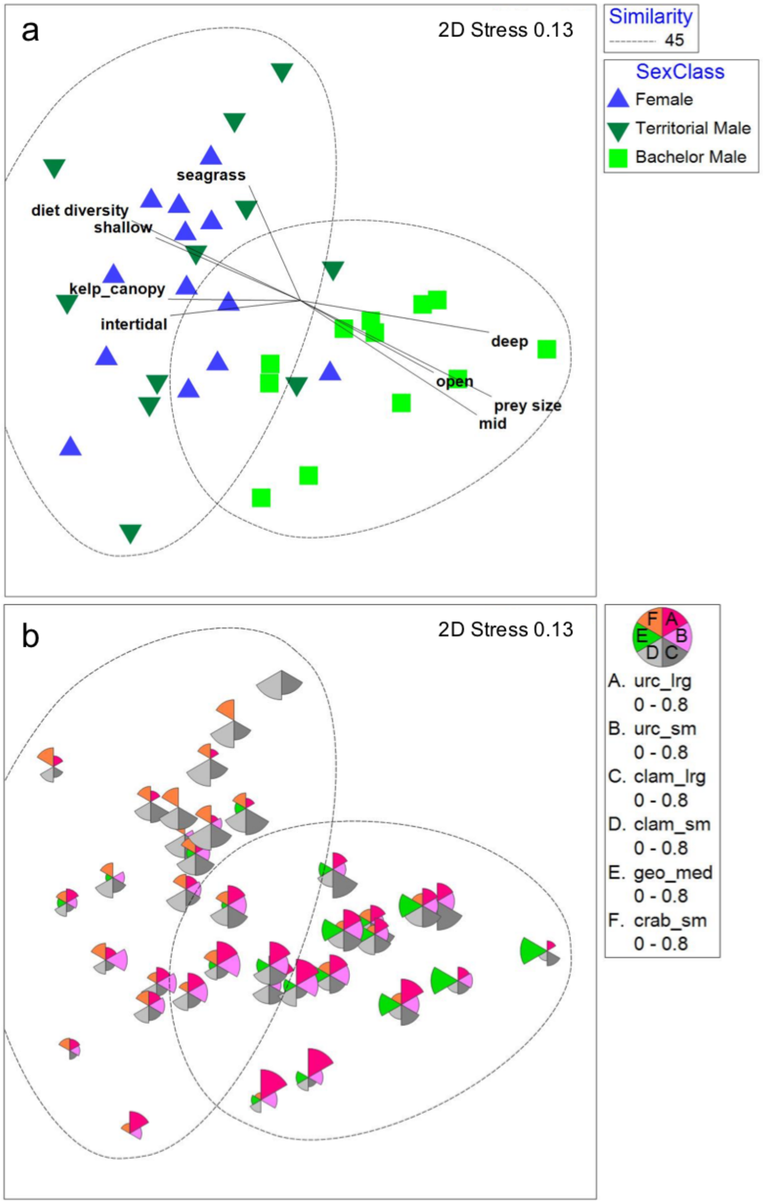


Fig. 2. 7. nMDS plot of sea otter niche space with a) clusters identified in Figure 6 with 45% similarity, and environmental vectors with ≥ 0.5 correlation to dissimilarities, and b) bubble plots depicting the most common prey groups, with bubble segments approaching sizes of segments in the legend representing ~80% of the diet by frequency of occurrence.

2.8 Supplementary Materials

Supplemental Tables and Figures

Table 2.S1. R-statistics and p-values from pair-wise comparisons of occupancy areas assessed by ANOSIM.

	Gosling: 27-30 YO	**McMullins: 18-21 YO**	**Simonds: 5-8 YO**	**Breadners: 3-6 YO**	**Calvert Established: 1 YO**
McMullins: 18-21 YO	R=0.429; P=0.024*	X	X	X	X
Simonds: 5-8 YO	R=0.958; P=0.029*	R=0.988; P=0.005*	X	X	X
Breadners: 3-6 YO	R=0.354; P=0.057	R=0.702; P=0.010*	R=0.875; P=0.029*	X	X
Calvert Established: 2-4 YO	R=0.896; P=0.029*	R= 0.980; P=0.005*	R=0.323; P=0.143	R=0.875; P=0.029*	X
Calvert Initial: 1 YO	R=0.760; P=0.029*	R=0.948; P=0.005*	R=0.938; P=0.029*	R=0.740; P=0.029*	R=0.917; P=0.029*

*denotes significant different between groups based on a = 0.05

Table 2.S2. Diet, habitat, and depth groups contributing to >8% within group similarity (proportion by frequency of occurrence) at each occupancy area, as identified by SIMPER analysis.

Area	Average similarity	Species	Contribution
Gosling: 27-30 YO	65.35	mus_sm	8.23
McMullins: 18-21 YO	70.76	clam_sm	18.51
		clam_lrg	14.91
		shallow	8.71
		crab_sm	8.22
Simonds: 5-8 YO	71.64	geo_med	19.00
		geo_sm	9.60
		clam_lrg	9.39
		open	8.16
		urc_lrg	8.09
Breadners: 3-6 YO	72.53	urc_lrg	11.89
		urc_sm	10.26
Calvert Established: 2-4 YO	72.29	clam_lrg	14.58
		geo_med	13.06
		urc_lrg	10.92
		open	8.10
Calvert Initial: 1 YO	69.25	urc_lrg	27.41
		clam_sm	10.65
		urc_sm	9.05
		open	8.52

Table 2.S3. Pearson's correlations of nMDS vectors for occupancy areas. Multiple correlation coefficients ≥ 0.50 bolded.

	Intertidal	**Shallow**	**Mid**	**Deep**	**Open**	**Kelp**	**Seagrass**	**Yrs occupied**	**Diet diversity**	**Prey size**	**Energy intake**
nMDS1	-0.652	-0.776	0.879	0.847	0.559	-0.526	-0.331	-0.746	-0.350	0.89	0.40
nMDS2	0.052	0.197	-0.180	0.243	-0.035	-0.211	0.333	0.274	0.139	-0.078	-0.48
Multiple	**0.655**	**0.800**	**0.897**	**0.881**	**0.561**	**0.567**	0.469	**0.795**	0.377	**0.895**	**0.625**

Table 2.S4. R-statistics and p-values from pair-wise comparisons of sexes assessed by ANOSIM.

	Female	**Territorial Male**
Female	X	R=0.036 P=0.254
Bachelor Male	R=0.602 P=0.001*	R=0.419 P=0.001*

*denotes significant different between groups based on *α* = 0.05

Table 2.S5. Diet, habitat, and depth groups contributing to >8% within group similarity (proportion by frequency of occurrence) of each sex class, as identified by SIMPER analysis.

Sex	**Average similarity**	**Species**	**Contribution**
Female	**60.05**	clam_sm	11.18
		clam_lrg	9.83
		shallow	8.67
		crab_sm	8.05
Territorial Male	**48.23**	clam_sm	15.31
		shallow	12.73
		clam_lrg	10.76
		open	9.95
Bachelor Male	**59.12**	urc_lrg	14.99
		clam_lrg	10.84
		geo_med	10.82
		open	9.45
		clam_sm	9.42
		urc_sm	8.09

Table 2.S6. Pearson’s correlations of nMDS vectors for different sexes. Multiple correlation coefficients ≥ 0.50 bolded.

	Intertidal	Shallow	Mid	Deep	Open	Kelp	Seagrass	Diet diversity	Prey size	Energy intake
nMDS1	0.494	0.667	-0.867	-0.793	-0.633	0.526	0.375	0.749	-0.898	-0.351
nMDS2	0.253	-0.033	0.189	-0.155	0.086	0.191	-0.377	-0.027	0.096	0.320
Multiple	**0.555**	**0.667**	**0.887**	**0.808**	**0.639**	**0.560**	**0.532**	**0.749**	**0.903**	**0.475**

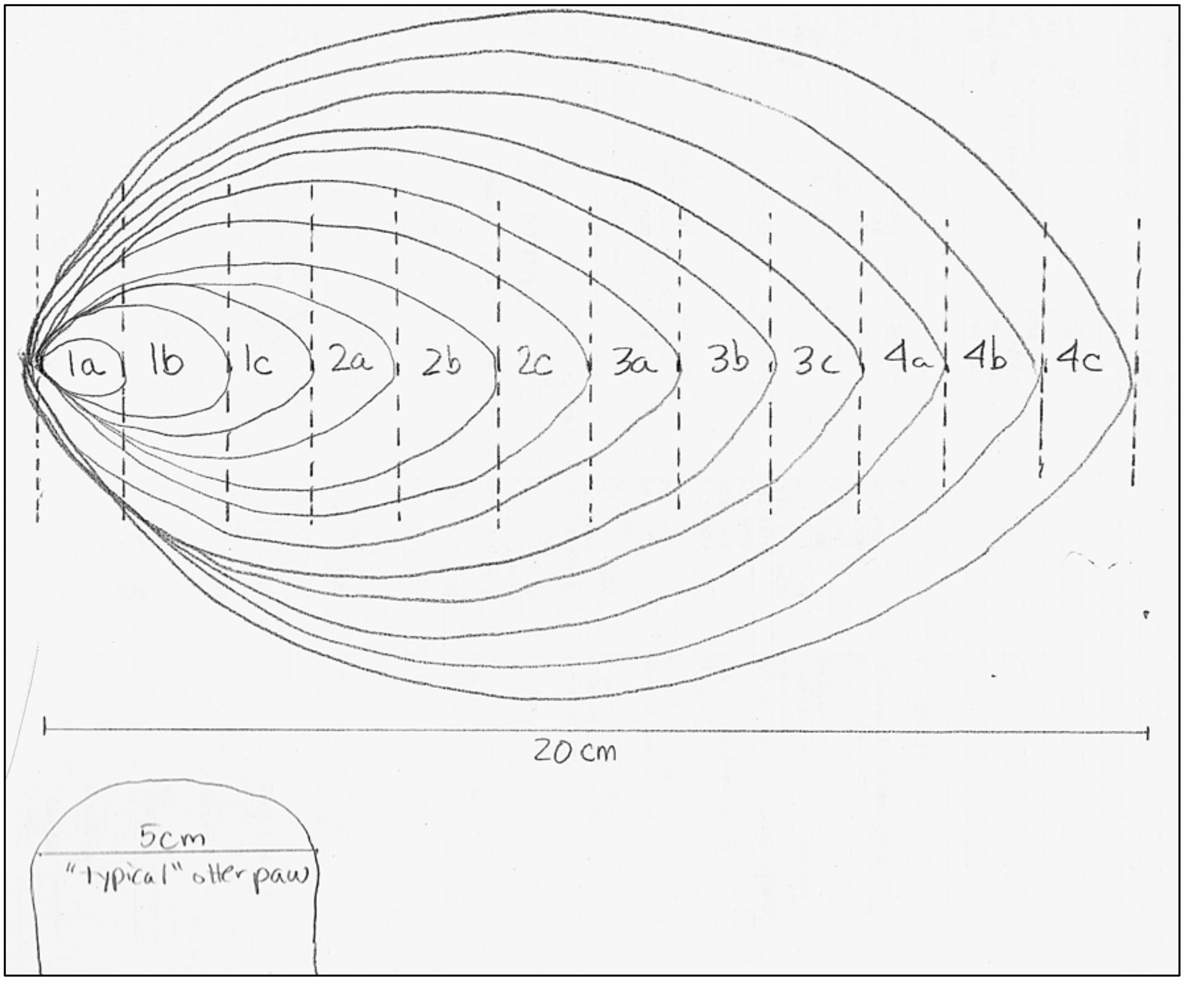


Fig. 2.S1. The size classes of sea otter prey using relative size of focal otter's paw. Sketch by LMN.

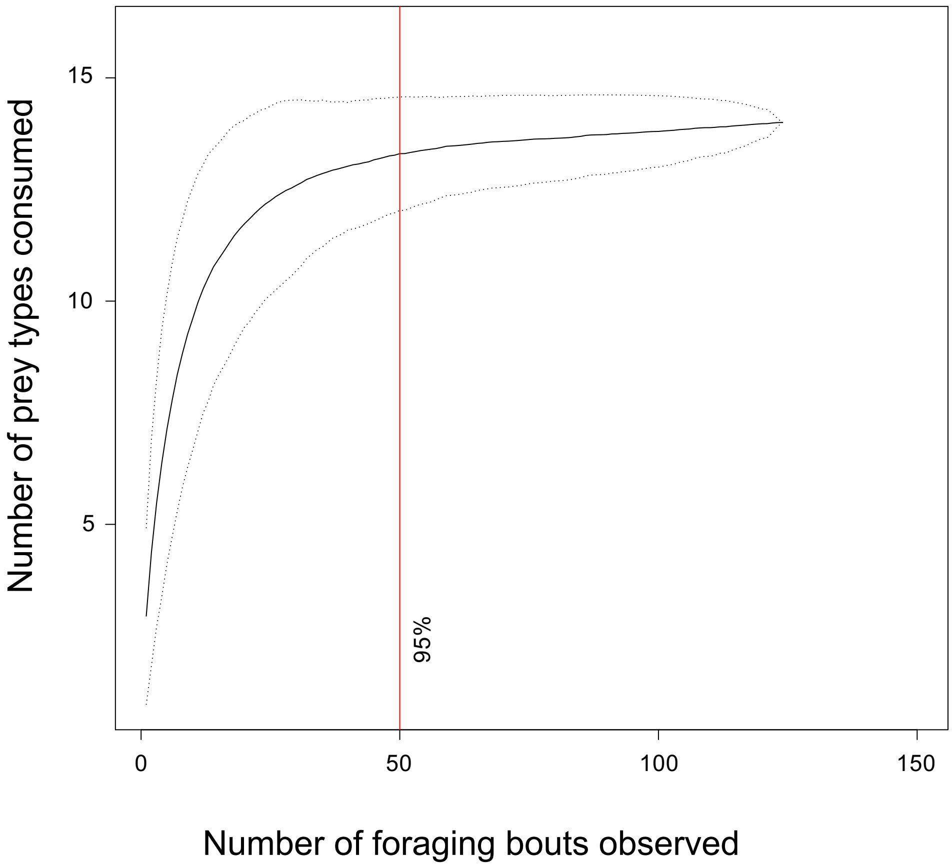


Fig. 2.S2. The number of bouts required to observe 95% of diet variability in sea otters.

Chapter 3. Physical disturbance by recovering sea otter populations increases eelgrass genetic diversity

Chapter 3 is currently in revision. Table and Figure numbers have been reformatted in this Dissertation, however this chapter has largely been left as-formatted for Science. *Most of the detail for this chapter is reported within the* Supplementary Materials*, which follow the* Main Text*, below.*

3.1 Abstract

Most knowledge about the role of predation in the workings of nature is ecological, focused on changes to community structure. Here, we report how disturbance by sea otters (*Enhydra lutris*) digging for commonly-sought infaunal prey, increases eelgrass (*Zostera marina*) genetic diversity by promoting conditions for sexual reproduction. Eelgrass allelic richness was 25% higher where otters were established (20-30 yrs) compared to where they had recently arrived (<10 yrs) or were absent (>100 yrs). There were 75% fewer eelgrass clones in meadows with otters than without. Otter occupancy was the most important predictor of eelgrass allelic richness and genotypic diversity relative to depth, temperature and meadow size. Our findings reveal an underappreciated evolutionary process by which large fauna contribute to genetic diversity and associated ecological resilience.

3.2 Main Text

Predators can profoundly affect ecosystems, but most of what is known about these effects stems from changes in community structure brought about by trophic interactions (Estes *et al.* 2011; Estes *et al.* 2016). In contrast, non-trophic genetic and evolutionary consequences of predation on ecosystems have rarely been examined (Janzen & Martin 1982; Estes & Steinberg 1988). Disturbance is an established driver of genetic diversity (Banks *et al.* 2013), and is often a consequence of foraging activity (e.g., Oliver & Slattery 1985). Yet, most inquiry into the genetic consequences of disturbance center on abiotic forces that enhance diversity by removing barriers to gene flow (Templeton *et al.* 2011), or reduce diversity by diminishing effective population size (Potvin *et al.* 2017). Moreover, the known evolutionary consequences of biotic disturbances to plants are limited to direct effects of herbivores and pathogens (Agrawal *et al.* 2012); indirect effects have rarely been considered (Estes *et al.* 2013). Here, we describe genetic changes in a plant (eelgrass, *Zostera marina*) that result from substrate disturbance caused by a foraging predator (sea otter, *Enhydra lutris*).

Otters regularly dig for infaunal prey in eelgrass (Hessing Lewis *et al.* 2018), breaking up rhizome mats, creating pits in the seafloor (Traiger *et al.* 2016), and leaving bare patches where seeds can settle (Fig. 3.1). Eelgrass meadows can consist of both clonal perennial plants, which propagate vegetatively through rhizomes, and sexually-reproducing annual plants that produce flowers and seeds (Blok *et al.* 2018). Most contemporary populations of *Z. marina* are perennial (Blok *et al.* 2018), but sexually-reproducing annual plants, which increase genetic variation through recombination, are favoured in disturbed environments (Cabaço & Santos 2012). We thus hypothesized that sea otter digging would influence the life history strategy and genetic diversity of eelgrass.

History provides an opportunity to test this hypothesis. Sea otters, which once existed across the North Pacific rim but were hunted to near-extinction in the maritime fur trade, are recovering from extirpation in British Columbia (BC), Canada, and occur over gradients of occupancy ranging from long-absent (i.e., >100 years) to long-established (i.e., several decades; Nichol *et al.* 2015). To test the prediction that eelgrass genetic diversity was enhanced by otter-imposed disturbance, we considered this occupancy gradient a natural experiment, replicated across two geographic regions and eelgrass populations (Vancouver Island, Central Coast; Fig. 2). We documented the extent of eelgrass disturbance by otters, and collected eelgrass shoots (n = 462) for genetic analyses from meadows (n = 15) where sea otters had been absent for over a century, arrived within the past few years, or present for decades (hereafter *absent, recent*, or *established*, areas, respectively; *Supplementary Materials*). We also accounted for meadow size, water temperature, latitude, and depth: factors that can influence eelgrass reproduction and genetic diversity (Blok *et al.* 2018; see *Supplementary Materials*). We used two Bayesian modelling frameworks to assess the relative magnitude and effect-size of each predictive variable on the response variables: allelic richness and genotypic diversity.

Allelic richness and genotypic diversity can be related to processes associated with disturbance. Allelic richness was our primary measure of genetic diversity because it is the most-prone to influencing the adaptive capacity of populations (Petit *et al.* 1998; Leberg 2002; Caballero & Garcia-Dorado 2013). Allelic richness is also sensitive to demographic events (Widmer & Lexer 2001; Leberg 2002). In seagrass, allelic richness increases with sexual reproduction (Ruiz *et al.* 2018). Together, these traits make allelic richness the measure of genetic diversity that is most useful to assessing a population’s resilience potential (Massa *et al.* 2013). Genotypic diversity has also been shown to effect resilience (Hughes & Stachowicz 2004; Arnaud-Haond *et al.* 2007; Ehlers *et al.* 2008). Genotypic diversity can sometimes be correlated with allelic richness, however their correlative nature is not systematic in the wild (Massa *et al.*

2013). In a study that de-coupled the influences of allelic richness and genotypic diversity as they related to resilience, allelic richness was associated with higher resistance and resilience to disturbance, whereas there was no clear relationship with genotypic diversity (Massa *et al.* 2013).

Our results indicate that disturbance from foraging sea otters increases eelgrass genetic diversity. About 5% of the area of eelgrass meadows in *established* areas was disturbed by otters, which – because foraging pits are ephemeral (Blok *et al.* 2018) – provides a temporal snap-shot of the actual extent of disturbance (Traiger *et al.* 2016). The mean number of alleles in *established* areas (46, range 42-50) was 21-44% greater than in *recent* or *absent* areas (32, range 31-34 and 38, range 34-45, respectively; Fig. 3a). Allelic richness was greater in meadows with *established* otters than without otters – a result replicated in both regions (Fig. 3.3b). Allelic richness was best predicted by otter occupancy (RVI = 0.99) and water depth (RVI = 0.90), and the effect of established otters on allelic richness had roughly twice the magnitude of depth (over a ~2.5 m range; Fig. 3.4a). The marginal means of allelic richness in *established* areas (4.27, 95% CI = 3.43-5.32) were ~25% greater than in *absent* areas (3.28, 95% CI = 2.61-4.09). Allelic richness was greater in deeper meadows (3.89, 95% CI = 3.06-4.89) compared with intertidal meadows (2.95, 95% CI = 2.32-3.70; Fig. S1), a pattern that aligns with 68% of 342 observed otter foraging dives in eelgrass occurring at subtidal compared to intertidal depths (Rechsteiner *et al.* 2019, *Supplementary Materials*). *Established* areas had 75-76% fewer clones (mean 1.17, range 0-2) compared with *recent* (mean 4.6, range 0-10) and *absent* areas (mean 4.8, range 0-7; Table 3.S1). The genotypic diversity of meadows with *established* otters was greater than meadows without otters in both regions (Fig. 3.3c). Genotypic diversity was best predicted by the model including meadow size, otter occupancy, and temperature (RVIs 0.79, 0.76, 0.63, respectively). The marginal means of genotypic diversity in *established* areas (0.98, 95% CI = 0.94-0.99) were significantly greater than in *absent* areas (0.93, 95% CI = 0.84-0.97); this effect had approximately twice the magnitude of meadow size (0.02-3.90 km^2) or temperature (3.5-7.2 °C; Figs. 3.4c, 3.4d, 3.S2). Allelic richness and genotypic diversity were moderately correlated (R^2=0.62, p<0.01; Fig3.S3a), however the slope was driven by a single meadow where genotypic diversity was uncharacteristically low, as predicted by Massa *et al.* 2013. Without this meadow, the correlation was insignificant (R^2=0.49, p = 0.08; Fig3.S3b). The only parameter shared by the top models predicting both allelic richness and genotypic diversity was sea otter occupancy.

The relationship between disturbance, flowering, and seed-set is well-established, but uniquely, we implicate digging megafauna in this process. Globally, eelgrass meadows subjected to sediment disturbance exhibited up to 5-fold increases in flowering (Cabaço & Santos 2012), and increased seed-set

(Blok *et al.* 2018). In our study, digging disturbance was correlated with years of otter occupancy (R^2 = 0.86, p <0.01; Fig. 3.S4). Where otters were *absent*, eelgrass rhizomal mats were largely undisturbed (0-0.5% of meadow area) and clones were up to 50 m long (Table S1). We could not directly measure flowering rates because flowering periods are too geographically and temporally variable at the scale of our study (Blok *et al.* 2018).

Sea otters have probably exerted evolutionary and ecological effects on eelgrass meadows of the North Pacific since at least the mid-Pleistocene (~600-700 kya; Coyer *et al.* 2013; Boessenecker 2016). Digging by otters likely stimulated sexual reproduction and increased seed-set in eelgrass, a micro-evolutionary interaction that unraveled when sea otters were extirpated. The resulting diminished disturbance regime likely favoured clonal growth, initiating a decline in eelgrass allelic diversity. Traditional harvesting of *Z. marina* rhizomes by BC Indigenous peoples may have also promoted flowering and genetic diversity in eelgrass (Cullis-Suzuki *et al.* 2015), a practice that declined with the arrival of Europeans. The return of otters, and the subsequent spatio-temporal pattern of disturbance, provides insights into how genetic diversity can be affected when relationships between strongly-interacting species (Soulé *et al.* 2005) are lost.

These findings have far-reaching conservation implications. Genetic diversity increases the adaptive potential of *Z. marina* populations, which enhances resilience (Reusch *et al.* 2005) and resistance (Hughes & Stachowicz 2004) to perturbations. Thus, the recovery of sea otters confers both genetic and ecological (i.e., Hughes *et al,.* 2013) benefits to foundational eelgrass communities.

Such non-trophic effects on genetic diversity, caused by animal-induced disturbance, could be widespread. Large-bodied animals can have profound genetic and evolutionary effects on other species owing to the biomass they consume and excrete (Janzen & Martin 1982), their extensive space-use, and the mechanical engineering exerted as they move and forage (Estes *et al.* 2016). Gomphotheres – abundant during the Pliocene – had strong evolutionary interactions on associated flora, which purportedly determined fruit and nut qualities, reproductive traits, and dispersal patterns (Janzen & Martin 1982). Today, Bison (*Bison bison*) trampling and wallowing increases flower and seed production in forbs (Elson & Hartnett 2017), and trampling ungulates 'plant' seeds, thereby increasing germination rates (Eichberg & Donath 2018). In the ocean, large fauna disturb swaths of sediment foraging on buried prey (Oliver & Slattery 1985). Such disturbances may influence genetic diversity in non-target populations, and where such influential animals have recovered, these interactions may be restored, as with the otter-eelgrass system we present here. This suggests a heretofore unrecognized role for megafauna – as agents of disturbance with potentially cascading genetic effects – a process lost and over-looked in the many places where large-bodied animals have disappeared from land- and seascapes.

3.3 Acknowledgements

We thank the Tula Foundation/Hakai Institute for support and the Ka:'yu:'k't'h'/Che:k:tles7et'h' (Kyuquot/Checleset), Huu-ay-aht, Haíłzaqv **(**Heiltsuk**),** and Wuikinuxv Nations in whose territories we worked. R. Hughes, K. Kay, J. Maron, M. Peterson, D. Rasher and T. Williams reviewed early versions of our manuscript. We thank the Hakai Nearshore Team, G. Ellis, G. Lemieux, M. Humchitt, and L. Saville for lab and field involvement. L. Barrett-Lennard, B. Cameron, C. Crossman, R. Gryba, T. Hanley, R. Hughes, R. Joy, C. Kellogg, N. Kollars, J. Olsen and J. Stachowicz advised us. L. Reshitnyk and K. Holmes provided geospatial support, and M. Foster and M. Morgan Henderson managed data. Funding: EUF was supported by NSERC Vanier and the Tula Foundation, and CTD by an NSERC Discovery Grant.

3.4 Tables and Figures

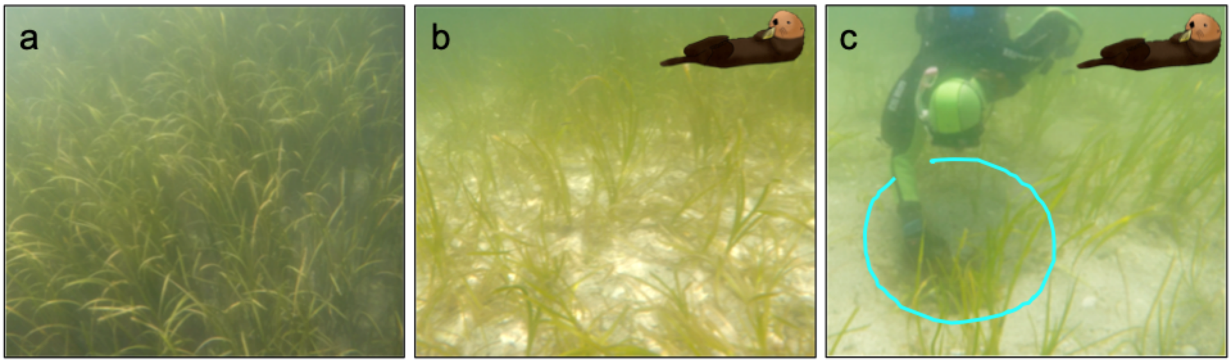


Fig. 3. 1. *Zostera marina* meadows where sea otters are absent (a) and established (b). Sea otter foraging pit outlined in turquoise (c).

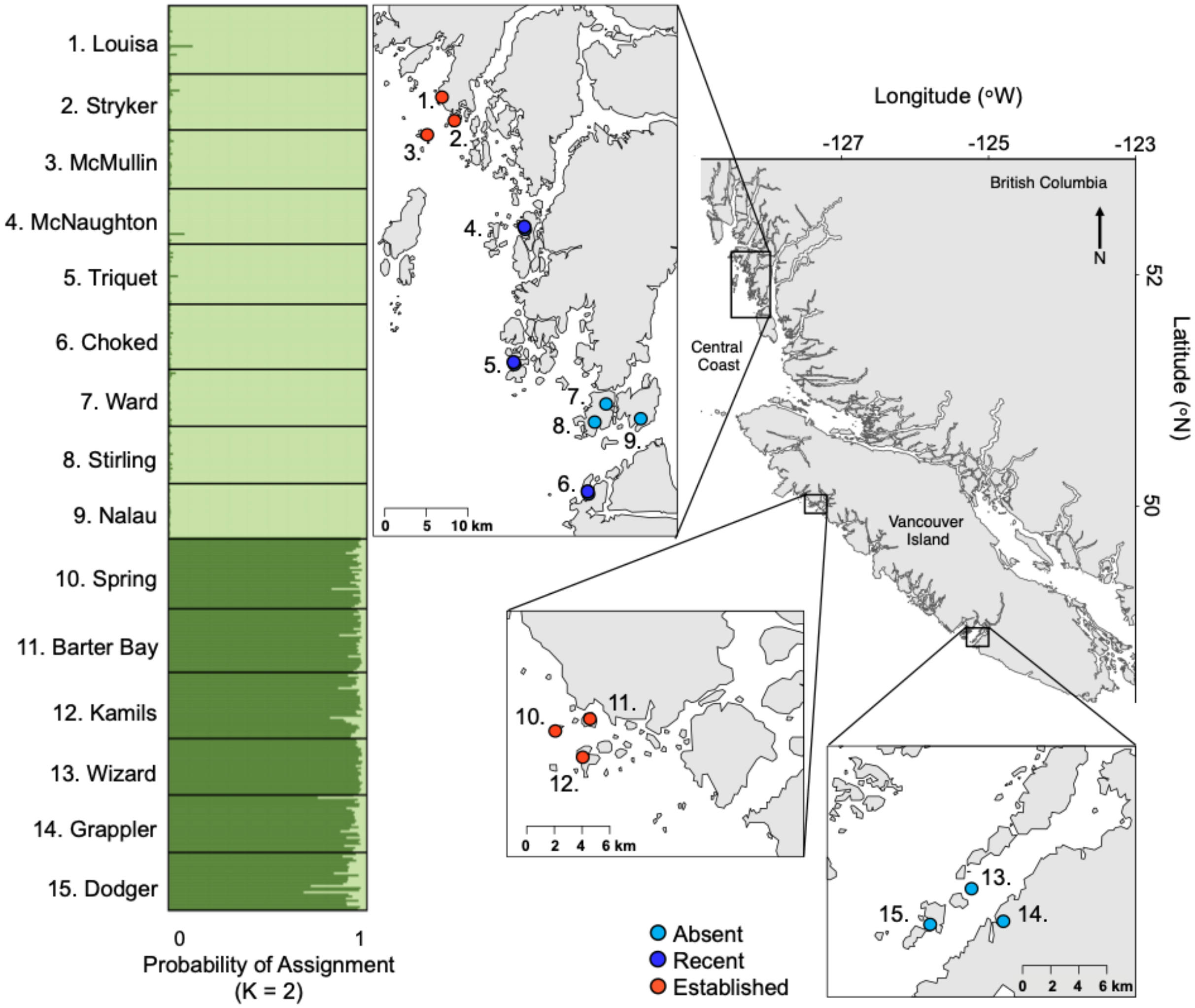


Fig. 3. 2. Locations of *Zostera marina* meadows on the Central Coast (CC) and Vancouver Island (VI), BC. Sea otters *absent* (pale blue circles), *recent* (<10 yrs., dark blue circles), and *established* (20-30 yrs., red circles). STRUCTURE analyses identified two eelgrass populations (K = 2; CC and VI), providing additional replication (i.e. spatial and genetic) in *established* and absent sea otter treatments; pale- and dark- green bars show the probability of individual population assignment.

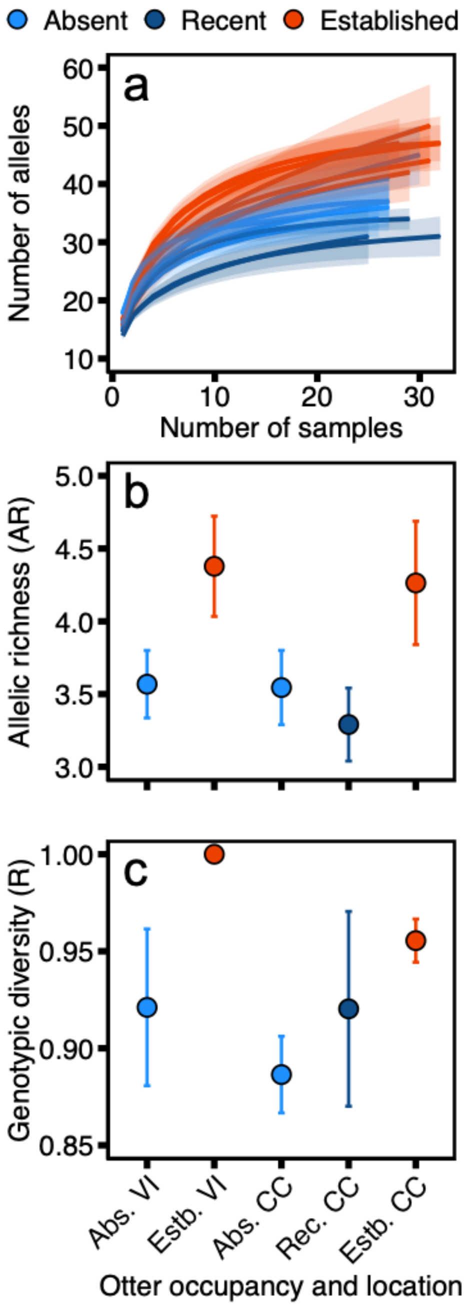


Fig. 3. 3. Allele discovery curves for each eelgrass meadow (a), color codes as in Fig. 2. Shaded areas show 95% confidence intervals. Means (circles) and SE (vertical lines) of allelic richness (b) and genotypic diversity (c). Abs. = otters absent, Rec. = otters recent, Estb. = otters established, VI = Vancouver Island, CC = Central Coast.

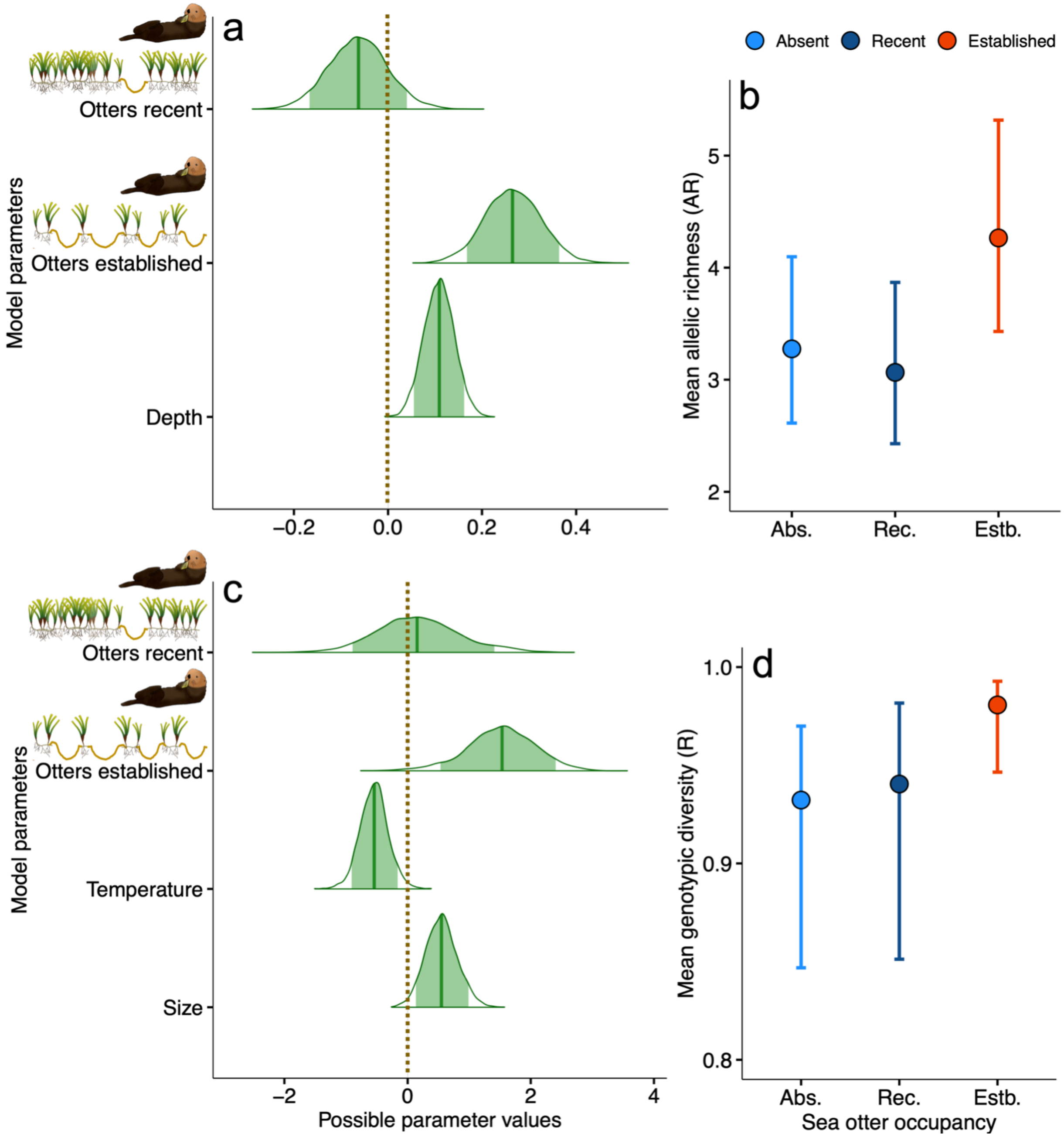


Fig. 3. 4. Posterior distributions of estimated parameters from the best-supported model predicting eelgrass allelic richness (a) and genotypic diversity (c). Shaded areas show 90% credible intervals (CI). Marginal means of sea otter effects on allelic richness (b) and genotypic diversity (d); bars indicate 95% CI. Color codes and abbreviations as in Fig. 3.3.

3.5 Supplementary Materials

Study design and sample collection. Sea otters (*Enhydra lutris*) were ecologically extinct in BC by 1820s-1850 (*32, 33*), extirpated by the early 1900s, and re-introduced in 1969-72 (Bigg & MacAskie 1978). To test the hypothesis that genetic diversity of eelgrass (*Zostera marina*) varied between areas where otters were long reestablished (20-30 yrs.) and areas where they have been absent for over a century (Nichol *et al.* 2015), we collected 50 eelgrass blades from each of 15 eelgrass meadows (Fig. 3.2). Our experimental design used a space-for-time approach (Pickett 1989), and was replicated in two regions: the Central Coast of BC, and the west coast of Vancouver Island, BC (Fig. 3.2). On the Central Coast we were able to test the additional effect of recently arrived (<10 yrs) otters on the genetic diversity of eelgrass.

We collected samples by SCUBA, under BC Parks permit #107190 (Hakai Institute). In each meadow, we laid 3-5 transects up to 200 m long, perpendicular to shore from the intertidal to subtidal meadow edge. Transects were spaced equidistantly across the shoreward margin of the meadows. We measured the proportion of each transect line that was disturbed by sea otter digging, which provides a recent snap-shot of disturbance, and was used to complement rather than replace our sea otter occupancy categories because of potential inconsistencies in pit visibility and persistence (Traiger *et al.* 2016). We collected eelgrass blades from 50 evenly spaced locations within the meadow (mean spacing distance = 5.47 m; range = 2.5-10 m). For each sample, we recorded location on the transect and *in situ* depth, the latter standardized to chart datum. We removed the newest leaf from each eelgrass shoot and dried it in silica within 12 hours of collection for later genetic analysis.

Genetic methods. We extracted Genomic DNA from ~8 mg of dried leaf tissue per sample, using a DNeasy Plant DNA extraction kit (Qiagen, USA). A subset of approximately 30 (mean 30.8, range 28–33) eelgrass samples was randomly selected from each meadow and we genotyped these at 13 microsatellite loci (Table 3.S2) previously identified in *Z. marina* (*36-39*). We included 6-7 individuals from each seagrass meadow on each 96-well extraction plate.

We amplified DNA using polymerase chain reactions (PCR) targeting 13 loci with a Bio-Rad T100 Thermal Cycler (Bio-Rad Laboratories Inc. Hercules, CA, USA) in 10ul reaction volumes consisting of 2 pmol dNTP (New England Biolabs, Ipswich, MA, USA), 1X PCR buffer, 1.5 units of Paq5000 (Stratagene, La Jolla, CA, USA), 1 pmol each forward and reverse primer (Eurofins MWG Operon, Louisville, KY, USA), 0.3 pmol M13 IRDye® labelled primer (Integrated DNA Technologies, Skokie, IL, USA), with 5-15ng DNA template. PCR conditions were as follows: 94°C for 3 min, 27 cycles of 94°C for 40 sec, 56°C for 40 sec (except for primer GA2 = 58°C), 72°C for 1 min, with a final extension of 72°C for 30 min.

Amplified products were denatured and run on a 5% polyacrylamide gel electrophoresed for 2.5 hours on a LI-COR 4300 automated sequencer (LICOR Inc., Lincoln, NE, USA) with a minimum of four size standards (50-350 bp or 50-700 bp LICOR) per 64-well gel. We scored gels using SAGA 3.3 Microsatellite Analysis software (LICOR Inc., Lincoln, NE, USA). The scorer was blind to sample location and sea otter occupancy.

Data quality. Prior to analysis, we took several steps to ensure data quality. Eelgrass individuals (genets) are composed of many shoots (ramets), which are genetically identical clones that can extend several meters (Olsen *et al.* 2014). We used the R package *poppr* (Kamvar *et al.* 2014) to identify identical multi-locus genotypes (MLGs; Table 3.S1) and assess the probability of identical genotypes arising by chance due to sexual reproduction (P_{sex}; Parks & Werth 1993). The mean P_{sex} for all meadows was 0.00009 (range 0-0.007), suggesting all identical genotypes in our samples as probable clonemates. We recorded the minimum distance (m) between each identical genotype (herein referred to as *clone length;* Table S1) and removed all but one of each identical genotype to prevent resampling clones for subsequent analyses (Kim *et al.* 2017; Connolly *et al.* 2018).

After removing clones, the remaining data were screened for null alleles, stuttering, and allelic dropout using Microchecker (version 2.2.3; van Oosterhout *et al.* 2004). For three of the markers (ZMC12075, ZME02125 and GA2) possible null alleles were suggested at four meadows (Wizard, Kamils, Dodger and Ward). We checked the data for possible technical errors but did not find any signs of excess homozygotes or excessive stuttering causing artifacts. Thus, we did not remove any of these data.

We assessed deviations from Hardy-Weinberg Equilibrium (HWE) using the exact test (Guo & Thompson 1992) with GenePop (Rousset 2008), and investigated all loci for linkage disequilibrium (LD). To mitigate the occurrence of Type 1 errors, potential deviations from HWE and LD were tested with a sequential Bonferonni adjustment (Rice 1989). Loci at Dodger (4), Wizard (1), Stirling (1), Stryker (1), and Triquet (1) had significant probabilities of deviation from HWE (Table 3.S3). However, there was variability in which loci contributed to potential deviations from HWE. Owing to this inconsistency, we included all meadows in our analyses. Of the 13 loci we analyzed for linkage disequilibrium, one locus, CL853 Contig1, deviated in 9 meadows and was removed from all analyses. GA23/GA12 showed linkage disequilibrium in 3 populations, and several other loci showed disequilibrium in one or two populations (Table 3.S4). As no other patterns emerged in LD occurrences we used the remaining 12 loci in all analyses.

We used the R (version 3.2.4, 2018) package iNEXT (Chao *et al.* 2014; Hsieh *et al.* 2019) to interpolate allele discovery curves for each seagrass meadow, which indicated the total number of alleles in each meadow, and evaluated if sample sizes were sufficient to assess variation in genetic diversity among seagrass meadows in areas with different sea otter occupancy times (Fig. 3.3a).

Prior to testing our hypothesis that sea otters affect genetic diversity, we evaluated the assumption that broad-scale genetic population structure of eelgrass meadows on the Central Coast and Vancouver Island was not correlated with sea otter occupancy. We used a Bayesian population assignment model (STRUCTURE; Pritchard *et al.* 2000) to estimate likelihood of varying numbers of population clusters in our data. We set the STRUCTURE parameters with a locprior of Vancouver Island and Central Coast, as LOCPRIOR = 1, and the remaining parameters set to: USEPOPINFO = 0, MAXPOPS = 20, NOADMIX = 0, ALPHA = 1. We ran 5 iterations of 100,000 burn-ins and 500,000 MCMC repetitions at each value of K. We then used delta K to select the best approximation of K (Evaano *et al.* 2005) in Structure Harvester (Earl & Vondoldt 2012). We repeated the STRUCTURE analysis with all of the same parameters but without setting prior locations of VI and CC (i.e. with LOCPRIOR = 0). To corroborate STRUCTURE results, we used a spatial principle component analysis (sPCA) with the R package *adegenet* (Jombart 2008) with a Delauney triangulation, eigenvalues chosen interactively, and data not scaled to unit variance. We calculated the presence of private alleles in each seagrass bed using GenAlEx (Peakall & Smouse 2012), and calculated F_{st} values for each pair-wise comparison of seagrass meadows and between VI and CC in Arelequin. We tested F_{st} values for significance with a Bonferonni adjustment (Rice 1989).

Both the Bayesian and frequentist methods we used to assess population structure supported the inference that distinct populations were not confounded with sea otter occupancy. Results from both of our STRUCTURE analyses identified two populations, one comprised of the eelgrass meadows on Vancouver Island (VI), and another consisting of the eelgrass populations on the Central Coast (CC; Figs. 3.2, 3.S4). When LOCPRIOR was included, all VI meadows were assigned to one population and all CC meadows to a second population; mean assignment probabilities were 0.39, range 0.003-0.98 (pop 1, largely VI individuals; Fig 3.2), and 0.61, range 0.02-0.99 (pop 2, largely CC individuals; Fig. 3.2). When a LOCPRIOR term was not included, one meadow on VI was assigned to the same population as all meadows from CC (Fig. 3.S5), and mean assignment probabilities were 0.57, range 0.01-0.99 (pop 1; Fig. 3.S5) and 0.43, range 0.01-0.99 (pop 2, Fig 3.S5). Results from the sPCA generally corroborated the STRUCTURE results and showed population differentiation was strongest among CC and northern VI (Kyuquot), with southern VI (Barkley Sound) showing admixture from both the CC and Kyuquot populations (Fig. 3.S6). Eigenvalues show strong global structure and weak local structure (Fig. 3.S7). Private alleles occurred in 12/15 meadows (Table 3.S5). F_{st} values among all except one pairwise comparison were significant; F_{st} between CC and VI samples was low (0.025) and significant (Table 3.S6).

Genetic and Genotypic diversity. We calculated genetic diversity using allelic richness (*AR*), heterozygosity (expected [H_e] and observed [H_o]), and genotypic diversity (*R*). *AR* was calculated at the locus and population level with the R (version 3.2.4, 2018) package *popgenreport* (Adamack & Gruber 2014) using methods by El Mousadik and Petit (1996), which employs rarefaction to account for differences in sample sizes and genotyping success, standardizes to the smallest sample size of any site, and uses the smallest number of alleles encountered in any sample across all populations and loci. We calculated effective alleles, H_e and H_o, using GenAlEx (Peakall & Smouse 2012). We calculated genotypic diversity (*R*), the proportion of unique multi-locus genotypes in each population, as $(N_G - 1)/(N - 1)$, where N_G is number of unique multi-locus genotypes detected, and N is number of samples collected (Dorken & Eckert 2001).

Seagrass reproduction (vegetative vs. sexual) and genetic diversity can be affected by disturbance (Connolly *et al.* 2018; Alexandre *et al.* 2005), meadow size (Kim *et al.* 2017), temperature (Ruiz *et al.* 2018; Marin-Guirao *et al.* 2019), latitude (Olsen *et al.* 2004), and depth (Fain *et al.* 1992; Reynolds *et al.* 2017), each of which provide alternative hypotheses to explain differences in genetic diversity. We limited our suite of explanatory factors to these five fixed effects, based on the literature and our *a priori* knowledge of eelgrass systems in our study areas (Burnham & Anderson 2002). To evaluate our competing hypotheses, we used sea otter occupancy time as a proxy for disturbance.

We used three methods to map eelgrass (*Zostera marina*) meadows. The three eelgrass meadows sampled in Kyuquot were mapped using SCUBA and snorkeling. Snorkelers followed the shoreward edge and divers swam the seaward perimeter of each meadow. A 3 m boat followed the snorkelers or divers and recorded GPS waypoints using Arc Collector (ESRI 2017). To delineate the seaward edge of the meadow, divers surfaced every 3 minutes or each time the bed changed direction, and the points were plotted. On the Central Coast, six of the eelgrass meadows we sampled (McMullin, McNaughton, Choked, Ward, Nalau and Stirling) were mapped using drones (DJI Phantom 3/4 Pro). Drone survey flights occurred during the morning low tide when weather was suitable for flying (winds <20 kn, no rain, tide <1 m). Drone operators used a grid pattern survey design to ensure adequate coverage. Orthomosaics of each site were created using a Structure from Motion Multi-View Stereo (SfM-MVS) workflow within Pix4Dmapper software (Version 2.1.61, Pix4D) in Windows 10. The extent of eelgrass from each orthomosaic was delineated using object-based image analysis (OBIA) with eCognition Developer software (eCognition Developer 9, 2014). Depending on site and water conditions, it can be difficult to discern the subtidal edge of eelgrass from RPAS imagery (Nahirnick *et al.* 2018). Accordingly, georeferenced towed underwater video (SplashCam Pro) data were used to provide ground-truth the aerial analysis. When reviewing the video, one analyst classified substrate and vegetation over a 4 second period, which represents approximately 2 m across the seafloor using a hierarchical habitat classification scheme (Reshitnyk *et al.* 2014). We obtained meadow size for the remaining three seagrass meadows on the Central Coast and in Barkley sound from maps produced by British Columbia Marine Conservation Analysis (https://bcmca.ca). We found the mean meadow area was 86,000 m^2 (range 2,108-389,329 m^2). We used HOBO Pendant ® loggers to record temperature every 30 min at 5 m below chart datum for one year and calculated the temperature range for each meadow (mean 5.9 °C, range 3.5-7.2 °C). We calculated the median depth of each sample to obtain a single depth value for each meadow (median = 0.66 m below chart datum, mean = 0.78 m, range = 5.13 below datum to 1.6 m above datum, across all meadows).

We used an information theoretic approach to assess the relative importance of the putative fixed effects (sea otter occupancy, depth, latitude, bed size, and temperature) in predicting genetic diversity as measured by allelic richness. A suite of Bayesian Generalized Linear Mixed-Effects Models (GLMER) were built in R (version 3.2.4, 2018), with a gamma distribution and log link, and using the package *rstanarm* (Goodrich *et al.* 2018). We constructed 31 models that encompassed all pair-wise comparisons of our five fixed effects, as well as a null model (Table 3.S7). All models included the random effect of locus. We used un-informative priors for all estimated parameters, and evaluated r-hat statistics to ensure model convergence (r-hat <1.1). We calculated and compared Widely Applicable Information Criterion (WAIC) scores for each model, and WAIC weights were used to calculate the Relative Variable Influence (RVI; Burnham & Anderson 2002) for each fixed effect, over the full suite of 31 models. To evaluate goodness of fit of the best-supported model, we used the R packages *bayesplot* (Gabry & Mahr 2019) and *ggplot2* (Wickham 2009) to conduct posterior predictive checks, examining kernel density curves of observed and simulated data, and histograms of statistical skew from the posterior predictive distribution (Gabry *et al.* 2019); the model fit the data well. Finally, we used our top model to calculate marginal means, standard errors, and density plots of the posterior distributions of fitted effects.

The above methods were replicated for a second suite of models with genotypic diversity as the response variable, with a few differences. Because genotypic diversity is calculated based on the individual plant, rather than across loci (i.e. plants are either a unique multilocus genotype, or a clone), these models did not include any random effects. Also, unlike allelic richness, the response variable (genotypic diversity) was constrained to a 0-1 range, and thus not well described by a gamma distribution. We therefore constructed a suite of 31 Generalized Linear Models (GLM) using a beta distribution and logit link (beta regression; Table 3.S8) in predicting genotypic diversity.

The influence of alternative hypotheses on genetic diversity. Other than sea otters, other agents of biotic disturbance occur on the BC coast. Indigenous people may have historically affected eelgrass reproduction and genetic diversity through the disturbance created when harvesting rhizomes (Cullis-Suzuki *et al.* 2015). In the closely related *Z. noltii,* digging by clam harvesters disturbs rhizome mats and induces flowering, thereby increasing sexual reproduction (Alexandre *et al.* 2005). Elsewhere, *Z. marina* is subjected to shoot loss via vertebrate grazers (Hughes & Stachowicz 2004). We did not see evidence of biotic disturbances (i.e., harvests, disease, vertebrate grazers), other than sea otter digging, at any of the meadows we examined, suggesting that where alternative biotic agents of disturbance occur, the present-day effects are minimal.

We quantified abiotic conditions known to affect eelgrass genetic diversity. Meadow size can increase diversity where larger populations are more likely to include variety in genotypes (Kim *et al.* 2017). Temperature is a stressor in other seagrasses (Ehlers *et al.* 2008) and can lead to increased sexual reproductive efforts in *Z. marina* (Cabaço & Santos 2012). Latitude also effects the likelihood that meadows are mostly vegetative vs. sexual (due to glaciation histories; (Olsen *et al.* 2004). At the geographic scale we were interested in, latitude was considered as a proxy for photoperiod (Kim *et al.* 2014).

Comparison of Bayesian GLMER models identified sea otter occupancy time as the strongest predictor of eelgrass allelic richness. Relative Variable Influence (RVI) was 0.99 for sea otter occupancy, and this effect was, respectively, 1.1, 2.5, 3.2, and 3.5 times more likely to appear in the best-supported model than depth (0.90), size (0.39), temperature (0.31), and latitude (0.28). Model weight (0.27) gave support for a single top-model, which included the effects of sea otter occupancy and depth (Table 3.S7). Posterior predictive distributions showed that the effect of depth was weak but significant, whereas the established sea otter occupancy effect influenced allelic richness twice as much as depth. To help interpret the effect of depth, we used data from (Rechsteiner *et al.* 2019) to quantify the proportion of sea otter foraging dives made at subtidal vs. intertidal depths, and found that, when foraging over eelgrass meadows, sea otters feed 68% of the time in the subtidal as opposed to 32% in the intertidal.

Thus it is possible that the depth effect we found in our model is amplified by the effect of otter disturbance, which is greater in deeper water.

Comparison of Bayesian GLM models identified meadow size, sea otter occupancy, and temperature as the strongest influencers of genotypic diversity (Fig. 3.4c). Model weight (0.27) supported a single top-model (Table 3.S8). RVIs were highest for meadow size (0.79) and sea otter occupancy (0.76), followed by temperature range (0.63), latitude (0.49), and depth (0.28).

Considering alternative measures of genetic diversity. We investigated alternative measures of genetic diversity, including the number of effective alleles in each meadow, and expected and observed heterozygosity. Effective allele number showed a similar pattern to allelic richness (Fig. 3.S8a). We found no patterns with time of sea otter occupancy in measures of heterozygosity (Fig. 3.S8b-c). The discrepancy between measures of allele diversity and heterozygosity is not surprising, as similar discrepancies have been noted in terrestrial angiosperms (Comps *et al.* 2001) and have been found elsewhere in the marine angiosperm *Z. marina* (Hughes & Stachowicz 2009). Such discrepancies can be common in clonal organisms (Arnaud-Haond *et al.* 2007). While heterozygosity measures act on the individual level (i.e., an individual plant is homo- or heterozygotic at each locus), allelic richness considers the total number of alleles at each locus across the population (Hughes & Stachowicz 2009). Allele-diversity metrics (e.g., allelic richness) are more informative than gene-frequency measures (e.g., heterozygosity) in predicting the long-term adaptive potential of populations (Caballero & Garcia-Dorado 2013). The resilience imparted by long-term evolutionary potential may be particularly consequential to *Z. marina,* given that meadows are typically monospecific (Procaccini *et al.* 2007; Talbot *et al.* 2016). The weaker effect of sea otter disturbance relative to meadow size in predicting genotypic diversity is similarly unsurprising. Our field methods, designed to sample the entire bed but rely on similar sample sizes among beds, resulted in larger beds having larger spacing between sample collections, thus decreasing the likelihood of sampling clones. Further, genotypic diversity is not typically correlated with allelic richness in the wild, and the factors that act on genotypic diversity in the wild are inconsistent among studies (Massa *et al.* 2013). Our finding that allelic richness is greater where sea otters are established than where they are absent indicates that eelgrass communities with established populations of sea otters have greater adaptive potential than do eelgrass communities where the functional roles of sea otters have been lost. Given the global trophic downgrading of ecosystems (Estes *et al.* 2011), we expect such linkages between large-bodied predators and long-term evolutionary potential in plant communities to occur broadly where megafauna occur at ecologically effective densities.

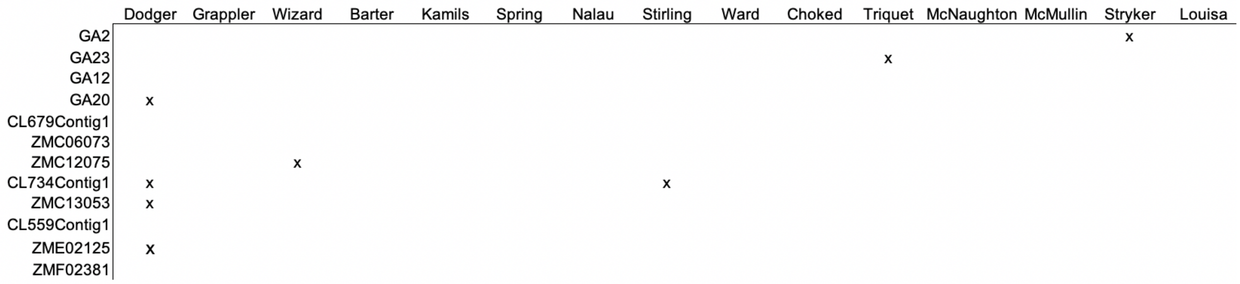
Table 3.S1. Eelgrass (*Zostera marina*) samples collected from Vancouver Island (VI) and the Central Coast (CC) where otters were absent, recent, or established. Horizontal lines through the four right-hand columns denote identical genotypes (i.e. genetic clones).

Area	Otters	Meadow	Total samples	No. identical genotypes	Sample ID	Transect	Metre mark	Est. length
VI	Absent	Wizard	30	6	b015	3	60	10
					b017	3	70	
					b031	1	17.5	5
					b032	1	22.5	
					b037	1	10	7.5
					b041	1	2.5	
		Dodger	31	6	b105	1	5	35
					b149	1	40	
					b131	2	50	
					b108	3	50	
					b146	1	30	25
					b109	3	55	
		Grappler	31	0			na	
	Established	Barter	32	0			na	
		Kamils	31	0			na	
		Spring	32	0			na	
CC	Absent	Stirling	31	6	h088	1	27.5	25
					h126	2	2.5	
					h113	2	10	15
					h117	2	15	
					h120	2	25	
					h080	3	20	
		Nalau	28	4	h136	2	30	50
					h152	2	80	
					h149	2	85	5
					h145	2	90	
		Ward	31	7	h409	3	0	10
					h381	5	10	
					h426	1	2.5	7.5
					h416	1	10	
					h417	1	12.5	10
					h420	1	15	
					h407	1	5	
	Recent	Triquet	31	4	h460	2	50	5
					h462	2	45	
					h474	2	0	15
					h477	2	15	
		McNaughton	30	10	h291	1	12.5	7.5
					h289	4	20	
					h329	2	7.5	2.5
					h294	4	10	
					h315	3	0	40
					h297	4	40	
					h295	4	45	42.5
					h318	5	2.5	
					h308	1	7.5	2.5
					h319	5	10	
		Choked	32	0			na	
	Established	Stryker	29	2	h219	1	2.5	25
					h231	1	27.5	
		Louisa	33	2	h238	1	90	10
					h247	1	80	
		McMullins	31	3	h333	1	20	17.5
					h337	1	2.5	
					h341	1	10	

Table 3.S2. Forward and Reverse primer labels used at each loci, including expected and actual size (bp), annealing temperature, and number of alleles.

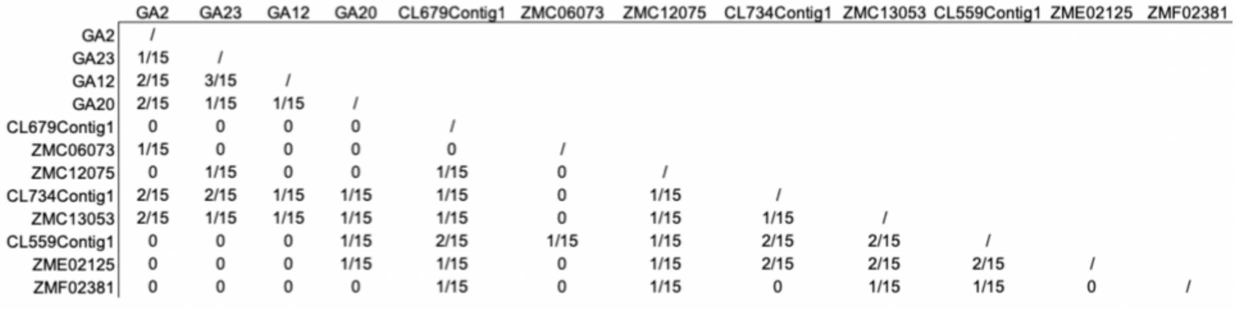
Locus	Reference	Forward Primer	Reverse Primer	Repeat size	Expected size (bp)*	Size (bp) this study	Ta (ºC)	No. Alleles	Results
GA2	Reusch *et al.* 1999	TGAAGAAATCCCAGAAATCCC	AGACCCGTAAAGATACCACCG	2	106-134	100-136	58	13	462 samples analyzed
GA23	Reusch *et al.* 1999	GGCAGCGATCTAATACAATTAAGG	ACGTCACATCTTTTCACGACC	2	147-185	155-171	56	9	463 samples analyzed
GA12	Jahnke *et al.* 2018	CGTTCATCTTGTCCTCGTCC	TTTCATTTCCATTTCCCACC	2	112-160	132-148	56	10	464 samples analyzed
GA20	Jahnke *et al.* 2018	TGGAAGGAGTTTCGATGTATCC	GGGAGATTTGCAGTGTAGAATTTAG	2	78-170	136-156	56	9	465 samples analyzed
CL853Contig1	Oetjen & Reusch 2007	CATTCCATTCAAGAGCAGCA	CAACAAATCAATCAATCATTCACTC	4	124-140	126-298	56	42	466 samples analyzed
CL679Contig1	Oetjen & Reusch 2007	ATAAAAACCGGCCTGATCG	CACACACACAGACGATCGAA	2	86-92	86-94	56	6	467 samples analyzed
ZMC06073	Oetjen & Reusch 2007	CGAATCCTCCTGCGTCTTT	ACGCACCGGATTTTATGCT	3	86-93	93-119	56	3	468 samples analyzed
ZMC12075	Oetjen & Reusch 2007	CCTCTTTTTTCCTCTCTCTCTCTCT	CTTCTGCGAATGATGCCATA	2	100-114	94-118	56	11	469 samples analyzed
CL734Contig1	Oetjen & Reusch 2007	TGGTCTTCTTCACTCGCTCA	AGCGACGATTCTTCAGCATT	3	75-96	69-141	56	20	470 samples analyzed
ZMC13053	Oetjen & Reusch 2007	CCCCATCTTTTGAGTTTGGA	TCATCATTTCTTGCAATTTGAATC	2	86-102	88-104	56	6	471 samples analyzed
CL559Contig1	Oetjen *et al.* 2010	CCACTTCCGTAGTTGCTGTT	CGATGAGGACGATGAGGAAT	2	171-177	171-181	56	6	472 samples analyzed
ZME02125	Oetjen *et al.* 2010	CGTTCAACTCAACACGCATT	GGTGACGAAAAGAAGCGAAG	**	**	109-119	56	6	473 samples analyzed
ZMF02381	Oetjen *et al.* 2010	GTGCAGGCGATCGAGTTATC	AAATTCGAGCTCTCAACTTCAA	**	**	132-153	56	8	474 samples analyzed
			Genotyped using pilot data only (n = 120 samples)						
GA17D	Jahnke *et al.* 2018	TTTTCATTTATCCAATAGTTTGCC	GATTCTCATCGGAGATTGAGG	2	96-180		55		monomorphic
GA6	*Reusch et al. 1999*	AGAAACCCTAATGTGATGAAATG	TGTTGGTTAATTCTCTTCTAATCTTG	2	108-120		55		messy amplification, wrong product size
ZMC19017	Oetjen & Reusch 2007	TCGTCGAGAAAGAGGAGGAA	TGTTCTGATTCCGTTCTCCA	3	75-99		56		possibly monomorphic, faint amplification
ZMC02023	Oetjen & Reusch 2007	TCGTTGGATACTGCACTTCTC	GAATCCAACCAATTATTTAAATACC	2	134-148		56		possibly monomorphic, poor results
ZMC19089	Oetjen & Reusch 2007	AGTGAAAAAACAAAGAAAGAAAGAGAA	CGTCGTCAGGTAGGCTCAA	2	88-96		56		monomorphic
CL412Contig1	Oetjen & Reusch 2007	GTACACCCGTTGCGTTCATT	GATTCCGTAGACTTGCGTCTG	2	240-260		56		monomorphic
CL11Contig1	Oetjen *et al.* 2010	GTGGAGGAAAGTGTGGGTGT	CTTGCATCCACCTTCATTTG	**	**		56		monomorphic
ZMC05062	Oetjen *et al.* 2010	GAAGCCAACTTAATTCAACATCG	TTAATATAAATCCGAGACACAGACTC	**	**		56		monomorphic

Table 3.S3. Identification of loci that significantly deviated from Hardy-Weinberg equilibrium, marked “x”.



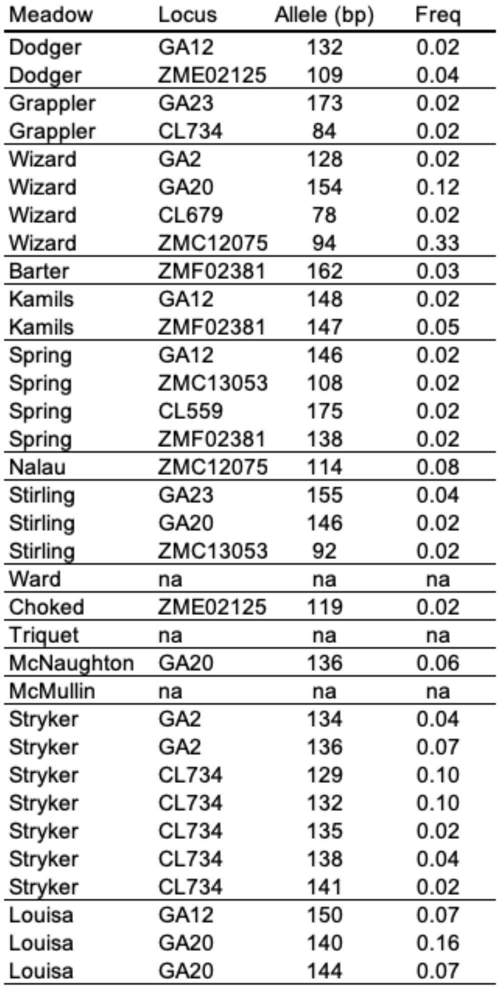
	Dodger	Grappler	Wizard	Barter	Kamils	Spring	Nalau	Stirling	Ward	Choked	Triquet	McNaughton	McMullin	Stryker	Louisa
GA2														x	
GA23											x				
GA12															
GA20	x														
CL679Contig1															
ZMC06073															
ZMC12075			x												
CL734Contig1	x							x							
ZMC13053	x														
CL559Contig1															
ZME02125	x														
ZMF02381															

Table 3.S4. Number of populations where pairs of loci exhibited linkage disequilibrium.



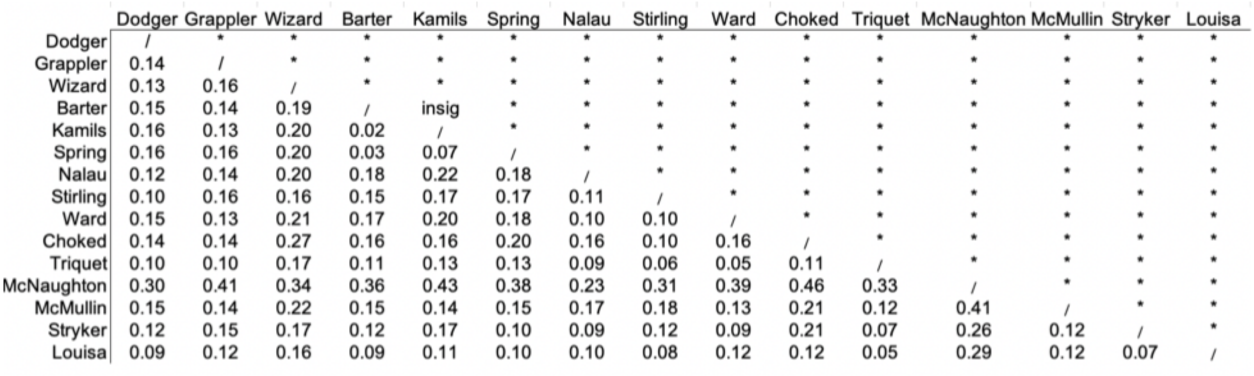
	GA2	GA23	GA12	GA20	CL679Contig1	ZMC06073	ZMC12075	CL734Contig1	ZMC13053	CL559Contig1	ZME02125	ZMF02381
GA2	/											
GA23	1/15	/										
GA12	2/15	3/15	/									
GA20	2/15	1/15	1/15	/								
CL679Contig1	0	0	0	0	/							
ZMC06073	1/15	0	0	0	0	/						
ZMC12075	0	1/15	0	0	1/15	0	/					
CL734Contig1	2/15	2/15	1/15	1/15	1/15	0	1/15	/				
ZMC13053	2/15	1/15	1/15	1/15	1/15	0	1/15	1/15	/			
CL559Contig1	0	0	0	1/15	2/15	1/15	1/15	2/15	2/15	/		
ZME02125	0	0	0	1/15	1/15	0	1/15	2/15	2/15	2/15	/	
ZMF02381	0	0	0	0	1/15	0	1/15	0	1/15	1/15	0	/

Table 3.S5. Private alleles identified in each eelgrass meadow.



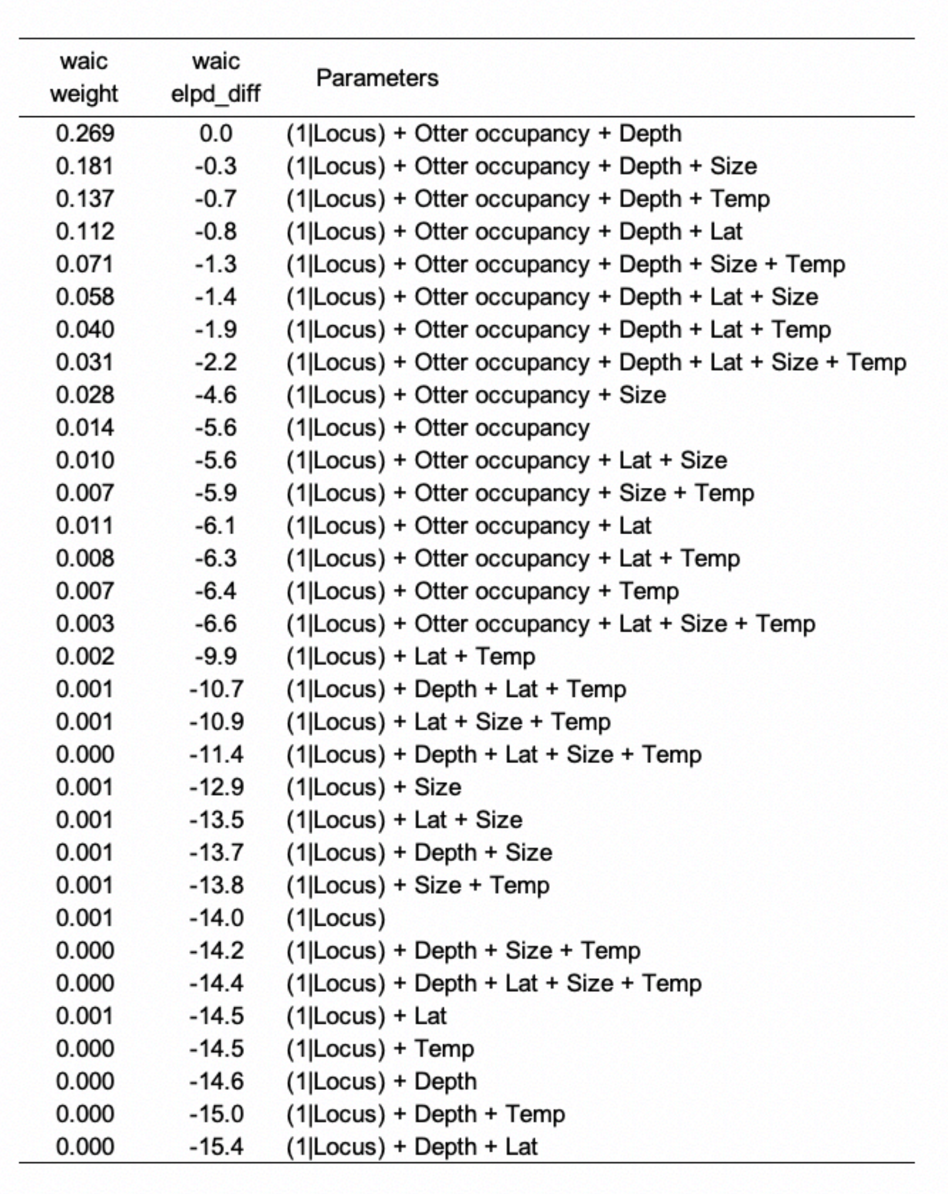
Meadow	Locus	Allele (bp)	Freq
Dodger	GA12	132	0.02
Dodger	ZME02125	109	0.04
Grappler	GA23	173	0.02
Grappler	CL734	84	0.02
Wizard	GA2	128	0.02
Wizard	GA20	154	0.12
Wizard	CL679	78	0.02
Wizard	ZMC12075	94	0.33
Barter	ZMF02381	162	0.03
Kamils	GA12	148	0.02
Kamils	ZMF02381	147	0.05
Spring	GA12	146	0.02
Spring	ZMC13053	108	0.02
Spring	CL559	175	0.02
Spring	ZMF02381	138	0.02
Nalau	ZMC12075	114	0.08
Stirling	GA23	155	0.04
Stirling	GA20	146	0.02
Stirling	ZMC13053	92	0.02
Ward	na	na	na
Choked	ZME02125	119	0.02
Triquet	na	na	na
McNaughton	GA20	136	0.06
McMullin	na	na	na
Stryker	GA2	134	0.04
Stryker	GA2	136	0.07
Stryker	CL734	129	0.10
Stryker	CL734	132	0.10
Stryker	CL734	135	0.02
Stryker	CL734	138	0.04
Stryker	CL734	141	0.02
Louisa	GA12	150	0.07
Louisa	GA20	140	0.16
Louisa	GA20	144	0.07

Table 3.S6. F_{st} values of all pairwise contributions as calculated in Arlequin. F_{st} value for all VI compared with all CC was significant at 0.025.



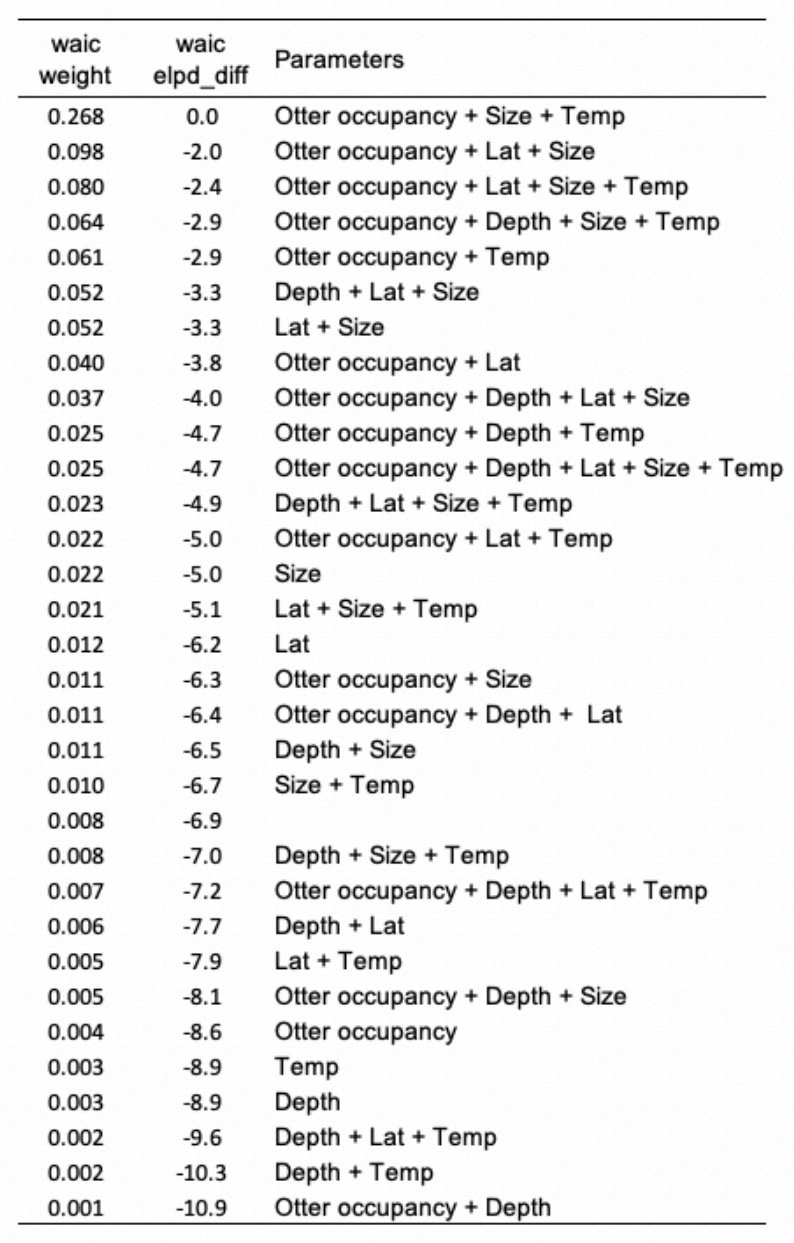
	Dodger	Grappler	Wizard	Barter	Kamils	Spring	Nalau	Stirling	Ward	Choked	Triquet	McNaughton	McMullin	Stryker	Louisa
Dodger	/	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Grappler	0.14	/	*	*	*	*	*	*	*	*	*	*	*	*	*
Wizard	0.13	0.16	/	*	*	*	*	*	*	*	*	*	*	*	*
Barter	0.15	0.14	0.19	/	insig	*	*	*	*	*	*	*	*	*	*
Kamils	0.16	0.13	0.20	0.02	/	*	*	*	*	*	*	*	*	*	*
Spring	0.16	0.16	0.20	0.03	0.07	/	*	*	*	*	*	*	*	*	*
Nalau	0.12	0.14	0.20	0.18	0.22	0.18	/	*	*	*	*	*	*	*	*
Stirling	0.10	0.16	0.16	0.15	0.17	0.17	0.11	/	*	*	*	*	*	*	*
Ward	0.15	0.13	0.21	0.17	0.20	0.18	0.10	0.10	/	*	*	*	*	*	*
Choked	0.14	0.14	0.27	0.16	0.16	0.20	0.16	0.10	0.16	/	*	*	*	*	*
Triquet	0.10	0.10	0.17	0.11	0.13	0.13	0.09	0.06	0.05	0.11	/	*	*	*	*
McNaughton	0.30	0.41	0.34	0.36	0.43	0.38	0.23	0.31	0.39	0.46	0.33	/	*	*	*
McMullin	0.15	0.14	0.22	0.15	0.14	0.15	0.17	0.18	0.13	0.21	0.12	0.41	/	*	*
Stryker	0.12	0.15	0.17	0.12	0.17	0.10	0.09	0.12	0.09	0.21	0.07	0.26	0.12	/	*
Louisa	0.09	0.12	0.16	0.09	0.11	0.10	0.10	0.08	0.12	0.12	0.05	0.29	0.12	0.07	/

Table 3.S7. Bayesian GLMER model weights, WAIC differences, and parameters included for all models run where allelic richness was the response variable. Locus was included as a random effect in all models whereas sea otter occupancy (*absent*, *recent*, *established*), depth, size, latitude, and temperature were included as fixed effects.



waic weight	waic elpd_diff	Parameters
0.269	0.0	(1|Locus) + Otter occupancy + Depth
0.181	-0.3	(1|Locus) + Otter occupancy + Depth + Size
0.137	-0.7	(1|Locus) + Otter occupancy + Depth + Temp
0.112	-0.8	(1|Locus) + Otter occupancy + Depth + Lat
0.071	-1.3	(1|Locus) + Otter occupancy + Depth + Size + Temp
0.058	-1.4	(1|Locus) + Otter occupancy + Depth + Lat + Size
0.040	-1.9	(1|Locus) + Otter occupancy + Depth + Lat + Temp
0.031	-2.2	(1|Locus) + Otter occupancy + Depth + Lat + Size + Temp
0.028	-4.6	(1|Locus) + Otter occupancy + Size
0.014	-5.6	(1|Locus) + Otter occupancy
0.010	-5.6	(1|Locus) + Otter occupancy + Lat + Size
0.007	-5.9	(1|Locus) + Otter occupancy + Size + Temp
0.011	-6.1	(1|Locus) + Otter occupancy + Lat
0.008	-6.3	(1|Locus) + Otter occupancy + Lat + Temp
0.007	-6.4	(1|Locus) + Otter occupancy + Temp
0.003	-6.6	(1|Locus) + Otter occupancy + Lat + Size + Temp
0.002	-9.9	(1|Locus) + Lat + Temp
0.001	-10.7	(1|Locus) + Depth + Lat + Temp
0.001	-10.9	(1|Locus) + Lat + Size + Temp
0.000	-11.4	(1|Locus) + Depth + Lat + Size + Temp
0.001	-12.9	(1|Locus) + Size
0.001	-13.5	(1|Locus) + Lat + Size
0.001	-13.7	(1|Locus) + Depth + Size
0.001	-13.8	(1|Locus) + Size + Temp
0.001	-14.0	(1|Locus)
0.000	-14.2	(1|Locus) + Depth + Size + Temp
0.000	-14.4	(1|Locus) + Depth + Lat + Size + Temp
0.001	-14.5	(1|Locus) + Lat
0.000	-14.5	(1|Locus) + Temp
0.000	-14.6	(1|Locus) + Depth
0.000	-15.0	(1|Locus) + Depth + Temp
0.000	-15.4	(1|Locus) + Depth + Lat

Table 3.S8. Bayesian GLM model weights, WAIC differences, and parameters included for all models run where genotypic diversity was the response variable. Sea otter occupancy (*absent, recent, established*), depth, size, latitude, and temperature were included as fixed effects.



waic weight	waic elpd_diff	Parameters
0.268	0.0	Otter occupancy + Size + Temp
0.098	-2.0	Otter occupancy + Lat + Size
0.080	-2.4	Otter occupancy + Lat + Size + Temp
0.064	-2.9	Otter occupancy + Depth + Size + Temp
0.061	-2.9	Otter occupancy + Temp
0.052	-3.3	Depth + Lat + Size
0.052	-3.3	Lat + Size
0.040	-3.8	Otter occupancy + Lat
0.037	-4.0	Otter occupancy + Depth + Lat + Size
0.025	-4.7	Otter occupancy + Depth + Temp
0.025	-4.7	Otter occupancy + Depth + Lat + Size + Temp
0.023	-4.9	Depth + Lat + Size + Temp
0.022	-5.0	Otter occupancy + Lat + Temp
0.022	-5.0	Size
0.021	-5.1	Lat + Size + Temp
0.012	-6.2	Lat
0.011	-6.3	Otter occupancy + Size
0.011	-6.4	Otter occupancy + Depth + Lat
0.011	-6.5	Depth + Size
0.010	-6.7	Size + Temp
0.008	-6.9	
0.008	-7.0	Depth + Size + Temp
0.007	-7.2	Otter occupancy + Depth + Lat + Temp
0.006	-7.7	Depth + Lat
0.005	-7.9	Lat + Temp
0.005	-8.1	Otter occupancy + Depth + Size
0.004	-8.6	Otter occupancy
0.003	-8.9	Temp
0.003	-8.9	Depth
0.002	-9.6	Depth + Lat + Temp
0.002	-10.3	Depth + Temp
0.001	-10.9	Otter occupancy + Depth

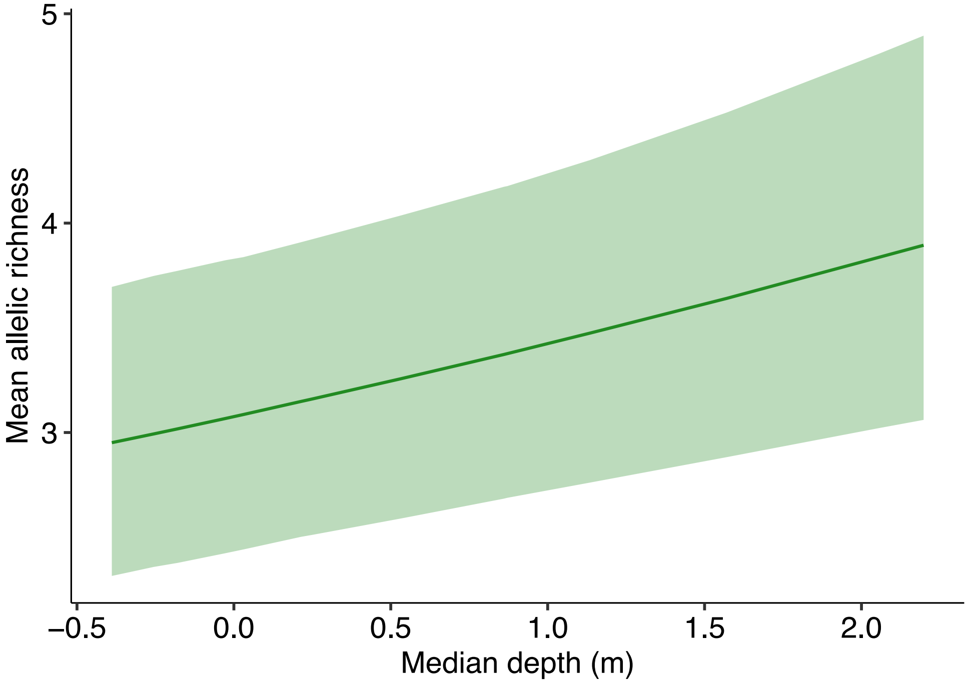


Fig. 3.S1. Bayesian GLMER output showing the effect of meadow depth on allelic richness.

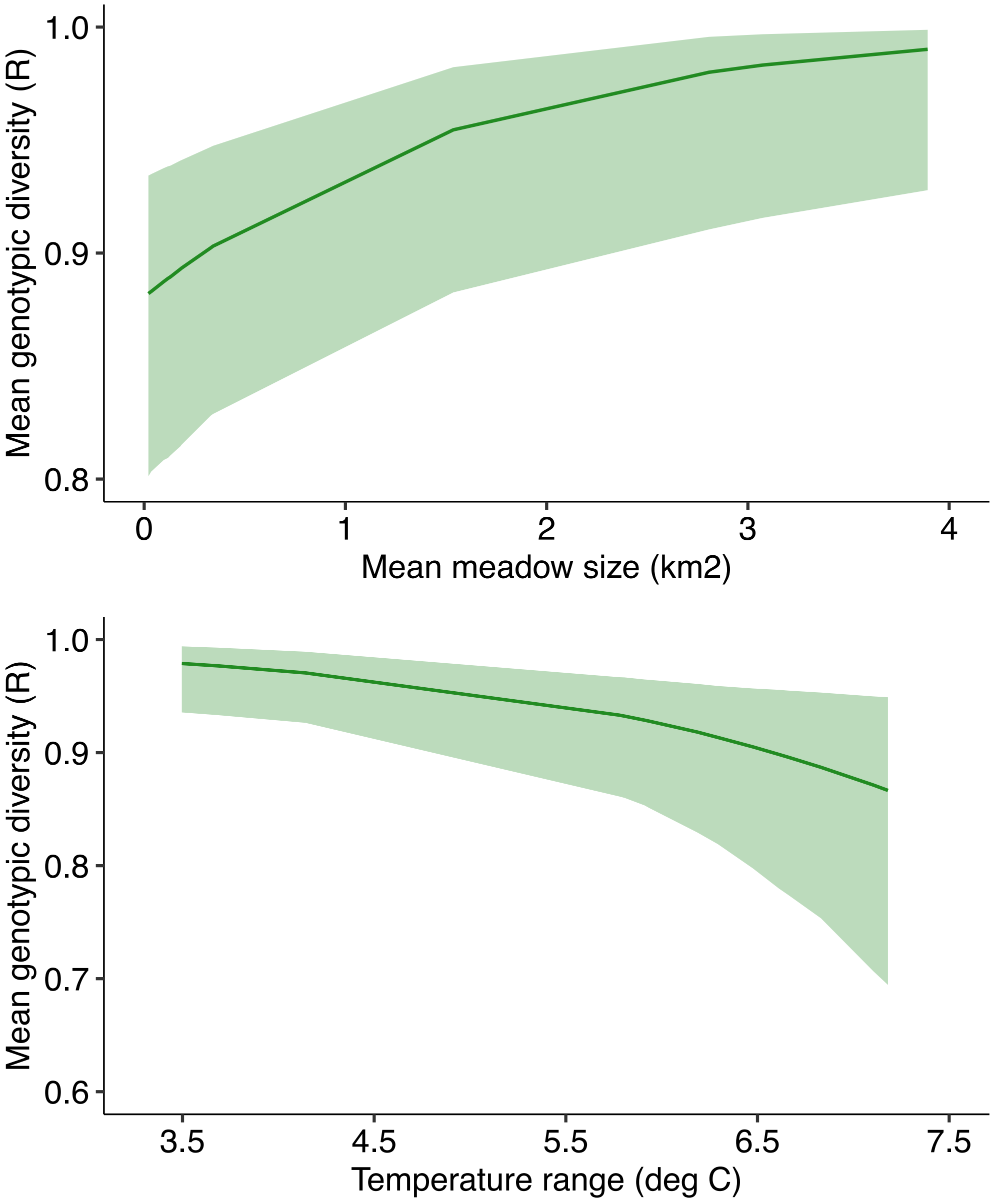


Fig. 3.S2. Bayesian GLM output showing the effects of meadow size and temperature range on genotypic diversity of *Zostera marina*.

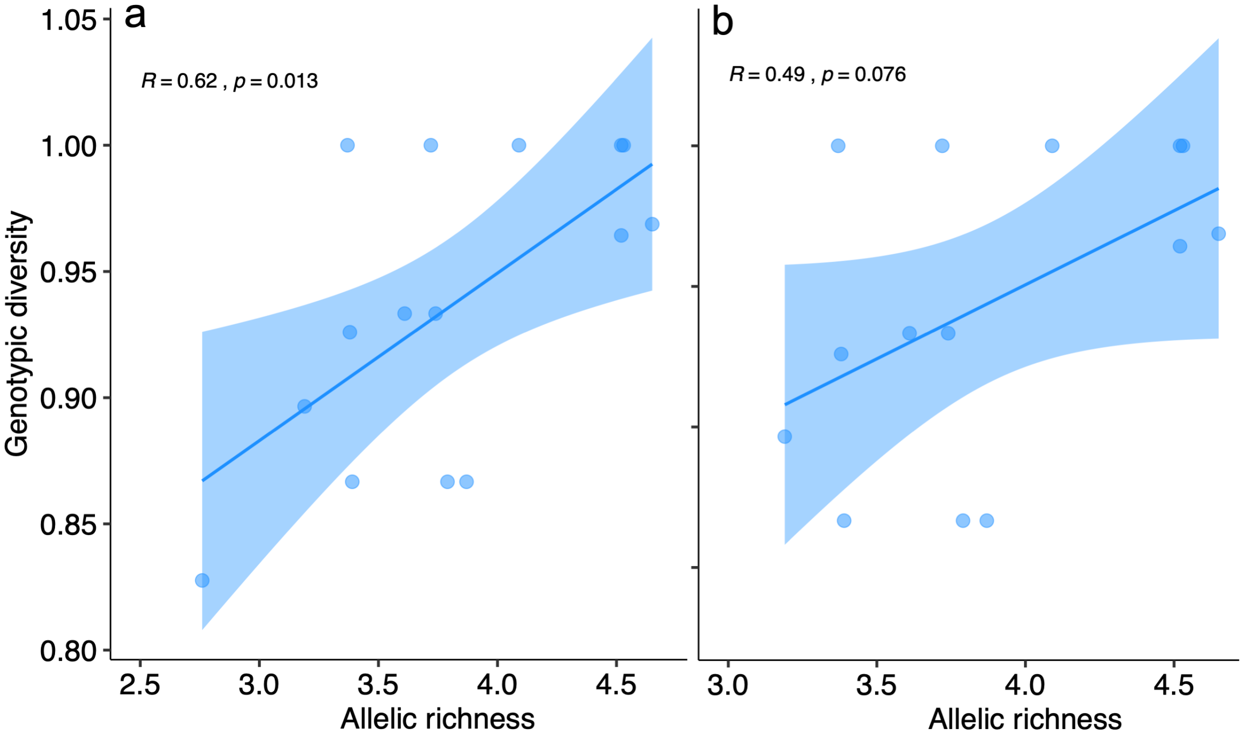


Fig. 3.S3. The relationship between allelic richness and genotypic diversity in the 15 *Zostera marina* meadows we examined (a) and with the meadow with low genotypic diversity removed (b). Shaded area represents 95% confidence interval.

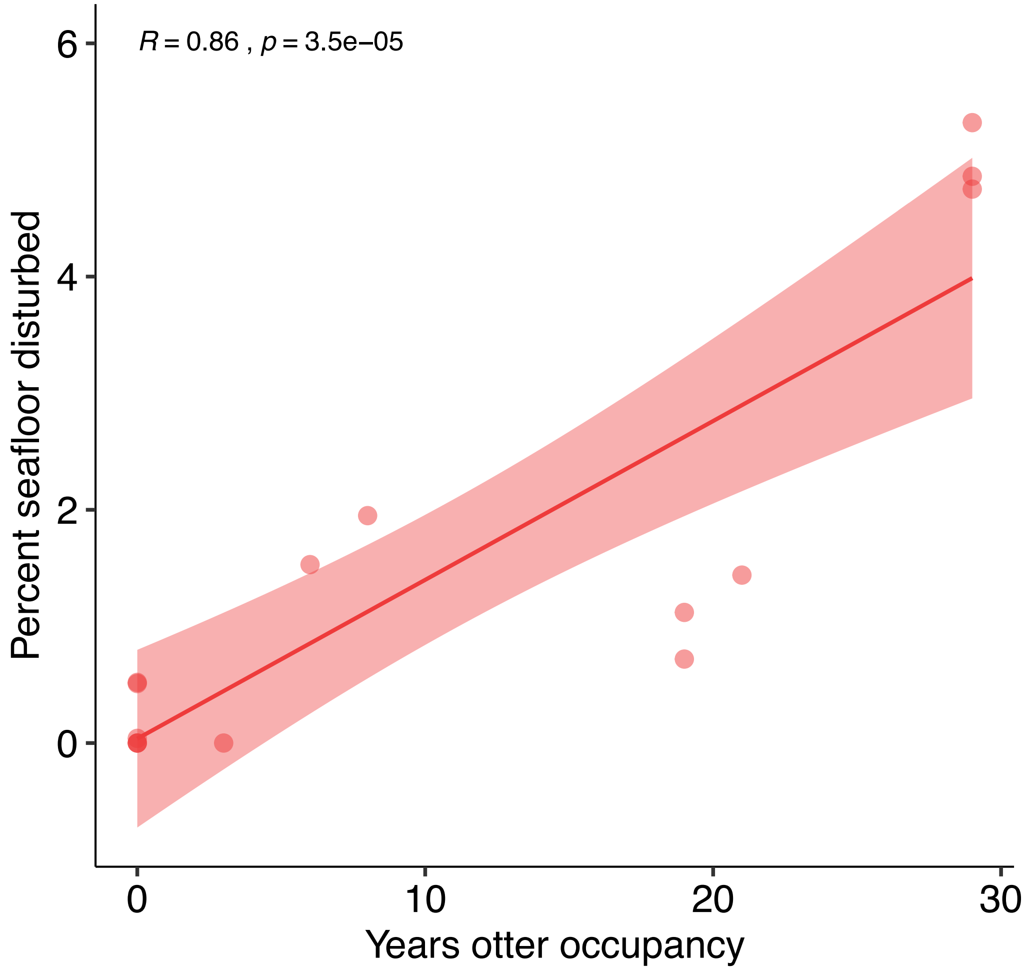


Fig. 3.S4. The number of years since sea otter arrival to each eelgrass meadow area, and the percent disturbance, measured as a proportion of the transect line that was dug. Shaded area represents 95% confidence interval.

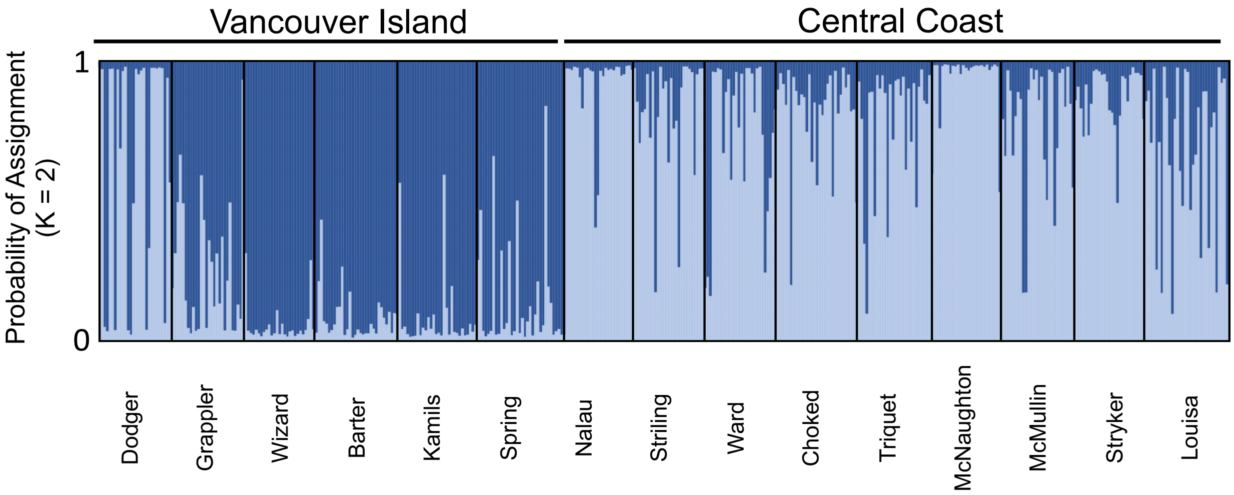


Fig. 3.S5. Population assignment results from STRUCTURE where LOCPRIOR = 0 and K = 2. Pale- and dark-blue bars show the probability of individual population assignment at K = 2, where K is the number of populations present.

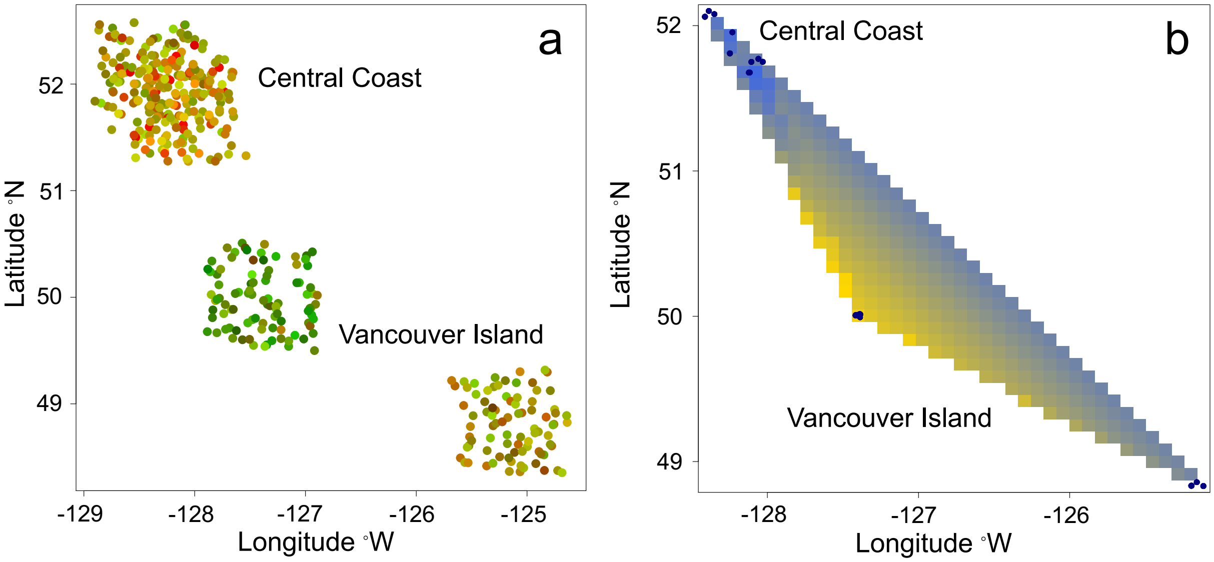


Fig. 3.S6. Representation of the first global score of the sPCA analysis including geographic coordinates, where each point represents an individual seagrass genotype and its sampling location (a) or meadow via an interpolated map of individual sPCA scores, showing genetic clines (b).

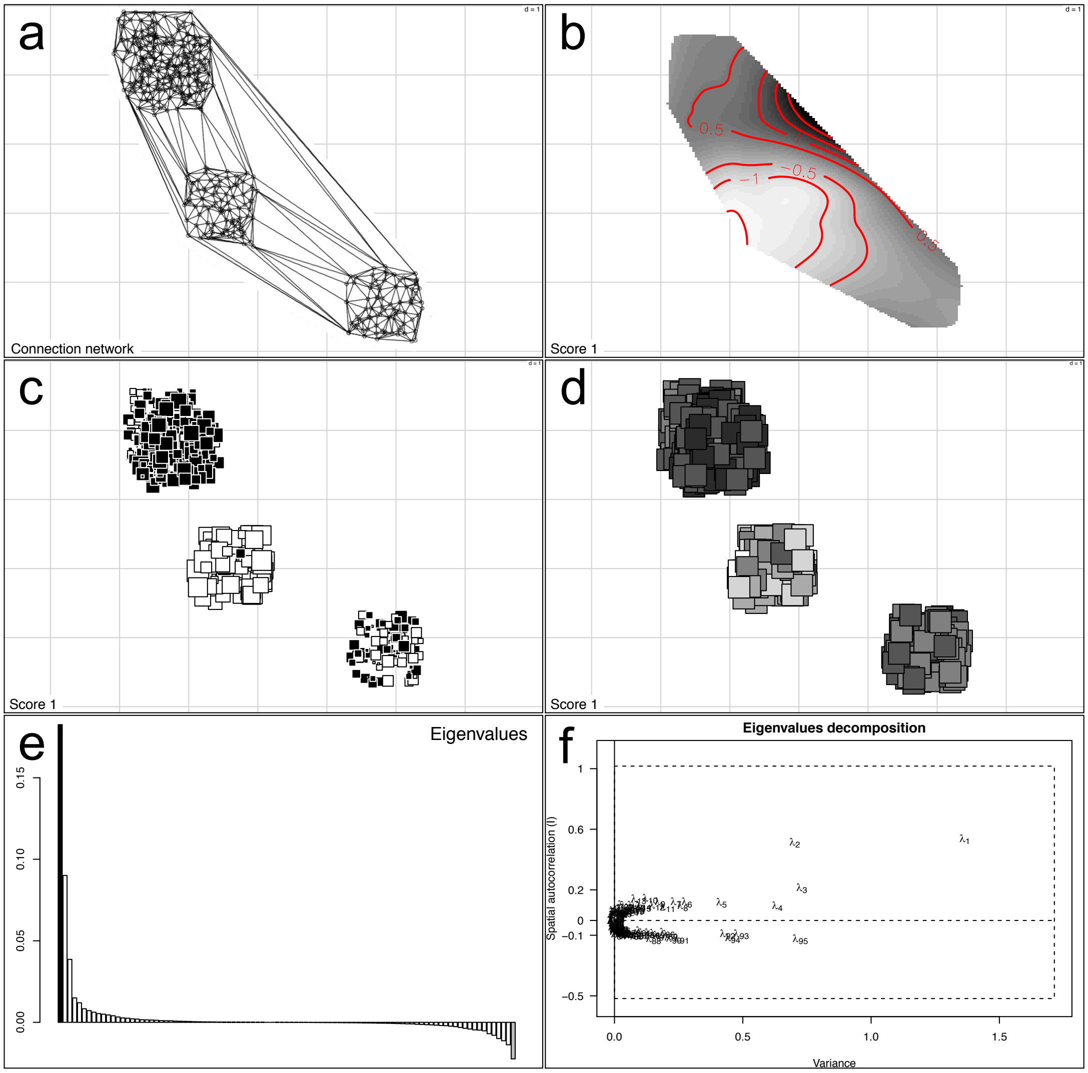


Fig. 3.S7. sPCA results showing the connection network used to define spatial weighting (a), representations of scoring of spatial entities where white symbols are negative and black symbols are positive (b-d). Local interpolation of global scores are shown in (b), where closer contour lines denote strongest genetic differentiation. Sizes of squares (c) show different absolute values (i.e. large black squares are very different from large white squares, but small squares are more similar), with (d) being similar to (c) but using a grey scale to denote differences. Panel (e) shows eigenvalues, with positive values (bars to the left) showing global differentiation and negative values (bars to the right) showing local differentiation. Panel (f) shows eigenvalues of sPCA (denoted λ_i with i = 1, . . . , r, where λ_1 is the highest positive eigenvalue, and λ_r is the highest negative eigenvalue). Here, λ_1 is the largest value and shows that the first global structure is the best interpretation.

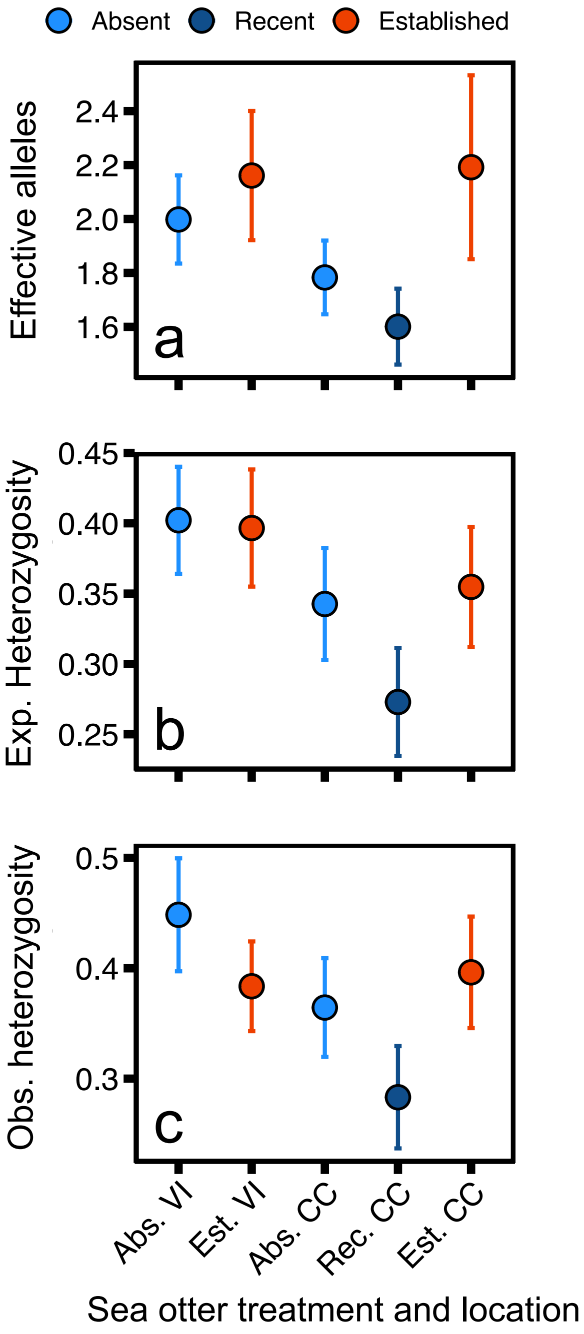


Fig. 3.S8. Mean and SE of the number of effective alleles, expected heterozygosity, and observed heterozygosity in eelgrass (*Zostera marina*) meadows where otters were absent, recently arrived, and long established, on Vancouver Island (VI) and the central BC coast (CC).

Chapter 4. Clam gardens and Indigenous stewardship support ancient clam harvests where sea otters were ecologically effective predators.

4.1 Abstract

Apex predators are known to play an important role in structuring ecological communities, but few studies have examined how these interactions might change across human-dominated landscapes. We hypothesized that clam gardens – human-made, terraced beaches used for clam cultivation – enabled coexistence among people and sea otters where both consumed clams. We examined contemporary effects of sea otters on intertidal butter clams (*Saxidomus gigantea*) on the west coast of Vancouver Island, Nuu-chah-nulth territory. We found that median butter clam lengths were significantly smaller in areas with sea otters (42 mm) than in areas without sea otters (77 mm; $W = 18478$, $p < 0.001$), yet the median lengths of otter-cracked clams were 87 mm. These contemporary data demonstrate the significant effect that sea otter foraging has on the size-structure of clam populations. Accounting for environmental effects, we examined the lengths of clams in archaeological assemblages from 3500-150 years ago, in areas with the highest known concentrations of clam gardens, but where sea otters were present or absent. Median butter clam lengths and size distributions were significantly smaller in the Broughton Archipelago, Musgamagw Dzawada'enuxw territory, where sea otters were present, than at Quadra Island, Laich-kwil-tach and northern Coast Salish territory, where sea otters were absent (~55 mm vs. ~68 mm; $W = 10633$, $p < 0.001$). A smaller species, littleneck clams (*Leuconoma staminea*), had indistinguishable median lengths, but significantly different length distributions ($D = 0.1768$; $p < 0.001$) between areas with and without sea otters; similar median lengths indicate similar size-at-harvest prescriptions were used in both areas, whereas truncated length distributions in the Broughton Archipelago suggest an apparent effect of sea otter predation. Despite the ecological effects of sea otters on clams, clam sizes in archaeological assemblages from both areas were stable, spanning periods of coast-wide human population growth and clam garden development. Clam gardening may have enabled stable clam harvests by increasing clam productivity, and limiting otter access by elevating beach heights out of otter-accessibility, and excluding sea otters from harvesting areas. Given the array of cultivation and management practices among Coastal Peoples, we suggest that mariculture might have produced stable harvests of other invertebrates. Widespread changes have occurred in social-ecological systems since European colonization. Here we show that rediscovery of ancient socio-ecological interactions can inform contemporary management of culturally important species.

4.2 Introduction

Cultivation is an important aspect of how people manage resources. The cultivation of plants and animals is an ecologically consequential practice that facilitates increases in food availability, and tends to allow higher human populations than can be otherwise sustained (Ellis 2015). Cultivation provides predictable food harvests (e.g., Hoffmann *et al.* 2016), and products with desired traits via selective breeding (e.g., large roots/bulbs, particular fruit qualities; Lepofsky & Lertzman 2008). Additionally, it reduces competition with other consumers (Green & Woodruff 1988; Deur *et al.* 2015), which is important when they exert strong ecological effects on shared prey, and thus influence what is available for people to harvest.

People of the northwest coast of North America cultivate clams and other invertebrates. Clam gardens, rock-walled terraces built in the low intertidal zone (Harper *et al.* 1995; Williams 2006; Lepofsky *et al.* 2015) date back at least 3500 years (Smith *et al.* 2019). By reducing beach slope and expanding clam habitat at the tidal height at which clams grow and survive best, clam gardens enhance clam biomass and productivity (Groesbeck *et al.* 2014; Jackley *et al.* 2016; Lepofsky *et al.* 2020). As sediment accumulates behind the rock wall it increases habitat area and productivity for butter (*Saxidomus gigantea*) and littleneck (*Leuconoma staminea*) clams, which were among the bivalves most commonly harvested by coastal people for millennia (e.g., Deur *et al.* 2015). Clam growth is further enhanced by gardening practices such as aerating substrate and adding shell hash and gravel to facilitate clam growth and recruitment, and beaches were cleared of cobbles and woody debris (Ellis & Wilson 1981; Deur *et al.* 2015; Lepofsky *et al.* 2015). As a result, butter and littleneck clams grow at least twice as fast, and can be raised at 2-4 times higher densities in clam gardens, compared to non-walled beaches (Groesbeck *et al.* 2014; Jackley *et al.* 2016). Although clam gardening was common in parts of the BC coast by the mid-to-late-Holocene, clam gardening practices were largely interrupted following European colonization (Toniello *et al.* 2019).

One of the consequences of clam gardening, in addition to enhancing clam habitat and productivity, may have been to reduce the extent to which non-human consumers could impact clams. Although Indigenous practices today and in the past include deliberate sharing of foods with non-human consumers (Gunther 1926; Brown & Brown 2009; Adams *et al.* in revision), practices also evolved to minimize losses to consumers that can influence the availability of shared resources. In clam gardens, people deterred, removed or harvested sea ducks (Hogg 1985; Deur *et al.* 2015), sea stars (Asteroidea), crabs (*Cancer* spp.), and likely sea otters, *Enhydra lutris* (Salomon *et al.* 2018; Salomon *et al.* 2020), probably reducing predatory impacts on clams and thus maximizing the benefits of clam gardens to people.

Of the consumers influencing sizes and abundances of clams available for people to harvest, sea otters were probably the most influential. Contemporary data show that sea otters severely reduce clam abundances and sizes across their range (Kvitek *et al.* 1988; Kvitek & Oliver 1992; Kvitek *et al.* 1992; Weitzman 2013; Hale *et al.* 2019; Rechsteiner *et al.* 2019). Much of what is known about the contemporary ecological effects of sea otters comes from scientific studies following their recovery after widespread extirpation during the 18th and 19th century Maritime Fur Trade. Butter clams (which today, can reach lengths to 130 mm; Harbo 2007) were among the first clam species to decline in both size and abundance as sea otters recovered in southeast Alaska (Kvitek *et al.* 1992; Kvitek *et al.* 1993; Weitzman 2013). As butter clams become less accessible to sea otters (*e.g.,* remaining individuals are buried deeper or are rejected by sea otters for being too small) sea otter diets shift to include large individuals from smaller species of clams, including littleneck clams (which today, can reach lengths to 80 mm; Harbo 2007) (Weitzman 2013). Today, in the absence of intensive clam garden practices or sea otter harvesting, sea otter predation reduces the sizes and abundances of clams that Indigenous Peoples can harvest, affecting subsistence invertebrate fisheries (Burt *et al.* 2020). Yet, people and sea otters have co-occurred across much of coastal BC since the early Holocene (Lyman 2011; McKechnie & Wigen 2011), and over a period of increasing clam garden development (Smith *et al.* 2019).

Here, we consider the possibility that clam garden technology and associated maricultural practices mitigated the potential effects of sea otters on clam sizes and abundances. This idea was proposed by Indigenous knowledge holders and ecologists during a recent transdisciplinary workshop (Salomon *et al.* 2018), where knowledge holders described how clam gardens comprised part of a suite of management protocols to protect and maintain reliable access to local shellfish resources (Salomon *et al.* 2018; Salomon *et al.* 2020). We focus on the sizes of butter clams harvested by people during the last four millennia, reasoning that clam sizes can inform our understanding of past interactions among sea otters, clams, and people in two important dimensions. First, any size differences in ancient clams harvested in areas with and without sea otters, which are known to target large clams, would provide insight into the ecological effects of sea otters and the availability of large clams for people to harvest. Additionally, the sizes of harvested clams within any one region over time can indicate the consistency and efficacy of clam management. Specifically, with resource depression, sizes of individual clams should decline over time, as has been observed for bivalves and fish in some pre-contact archaeological assemblages (e.g., McKechnie 2007; Erlandson *et al.* 2008; Erlandson *et al.* 2011). In contrast, if the sizes of clams are consistent over time, the inference is that clam gardens and associated maricultural practices produced a stable and predictable supply of clams.

Our multidisciplinary team of ecologists, archaeologists, and Indigenous knowledge holders drew on multiple sources of information to examine the dynamics of human-clam-sea otter interactions through the past four millennia. Accounting for environmental forces that could also influence differences in clam sizes over space and time, we used a series of natural experiments set primarily in areas with some of the highest known densities of clam gardens, with and without sea otters, and in ancient (3500 to 150 years ago) and contemporary (30 to 40 years ago) time periods, to examine the following hypotheses:

1. Sea otters are known to reduce the sizes of invertebrates through size-selective predation. We thus predicted that present-day butter clam lengths should be significantly smaller in areas subjected to sea otter foraging compared to areas without sea otters.
2. Given these effects, we predicted that if sea otters functioned as ecologically effective predators over the past several thousand years, ancient butter clam lengths in archaeological assemblages should be smaller in areas with sea otters compared with where they are absent.
3. Littleneck clams are smaller than butter clams and are less sought after by sea otters. Thus, we predicted that the archaeological sample of littleneck clams should exhibit similar size distributions in areas with and without sea otters, assuming that the harvesting preferences of people were similar between areas, and that sea otter foraging pressure was not sufficient to affect littleneck clam sizes.
4. We predicted that if clam gardening and its associated management practices enabled co-existence between people and sea otters, the lengths of clams in archaeological assemblages within areas (with vs. without sea otters) should remain stable or increase, through the mid to late Holocene, as clam garden technology developed.

In addition to informing our hypotheses, Indigenous knowledge shared by members of our coauthor team and in recent transdisciplinary workshops (Salomon *et al.* 2018; Salomon *et al.* 2020) informed and expanded our understanding of Indigenous management practices (Reid *et al.* 2020). Our approach allows for insights into past interactions among people, predators, and shared prey, and illustrates how a comprehensive rediscovery of ancient interactions could influence future management.

4.3 Methods

4.3.1 Data sources and study areas

Data sources. Our data sources came from more than 50 years of scientific and archaeological research, and millennia of cultural and traditional (which includes scientific) knowledge. The first dataset we examined came from clam surveys in the 1990s, conducted by JW on the west coast of Vancouver Island, Nuu-chah-nulth territory, to evaluate the effect that contemporary sea otter predation has on butter clam lengths on the west coast of Vancouver Island. Next, we measured clams in shell middens from sites inhabited by people, from 3500-150 years before present (= archaeological assemblages), in two areas: where sea otters were present (Broughton Archipelago) or absent (Quadra Island) (Fig. 4.1). Our hypotheses about the size structure of ancient clams from shell middens, were informed by traditional knowledge held by MN, CR, and KBW, which guided our thinking in how clams were selected and harvested, how sea otters were used by Coastal Peoples, and in the specific ways in which clam gardening technology may have allowed stable clam harvests even where sea otters could have affected the ecological availability of clams. We used unpublished archaeological data (DL, IM, RW) to describe fauna from previously collected excavations and improve our understanding of where sea otters may have been absent for the past four millennia. In the Broughton Archipelago, Musgamagw Dzawada'enuxw territory, archaeological excavations were led in the 1970s by the late Don Mitchell, and faunal remains from these excavations were identified by RW and colleagues in the 1980s, and typically included sea otter bones (Hogg 1985). At northern Quadra Island, Laich-kwil-tach and northern Coast Salish territory, archaeological excavations were led by DL in the 2010s and zooarchaeological analysis by AT in 2020, and sea otter bones were absent. To evaluate contemporary differences in clam lengths and growth rates in the same areas the archaeological samples came from, but following sea otter extirpation from British Columbia (BC), we used contemporary clam measurements from Fisheries and Oceans Canada (DFO; 1980s-2000s) and GT (Toniello *et al.* 2019) (Fig. 4.1).

Study areas and sea otter presence. Contemporary sea otter occupancy in BC was determined by surveys of the full sea otter range, conducted from 1977 to 1993 (Bigg & MacAskie 1978; Watson 1993). Through this time period, the majority of the sea otter population in BC occurred on the northwestern coast of Vancouver Island, with a small group of sea otters inhabiting the central BC coast (Nichol et al. 2015). In 1993, sea otters were established in Checleset Bay for 2-3 decades, after their re-introduced in the 1960s and 1970s (Bigg & MacAskie 1978; Watson 1993), but were absent from Barkley Sound

(*Supplementary Materials*; Fig. 4.1). These two broad areas, with and without sea otters in 1993, formed the basis for our contemporary natural experiment.

To design a natural experiment using ancient clams, we first located areas that could be defined as *sea otters present*, or *sea otters absent* during the past several thousand years. To this end, we used zooarchaeological identifications of vertebrate skeletal remains from five previously collected archaeological assemblages in each of the Broughton Archipelago and Quadra Island. For sites in the Broughton Archipelago, up to 28% of non-cetacean marine mammal bone fragments (n = 34 of 118; all sites reported in Fig. 4.1) from the archaeological assemblages, were sea otter (Hogg 1985). In contrast, on Quadra Island, we examined all of the vertebrate remains in the smaller-volume column samples, and detected no sea otter bones (Fig. 4.1). The patterns in these zooarchaeological analyses were corroborated by patterns spanning a greater geographic extent, which indicated that sea otters were generally absent in the Strait of Georgia (in which Quadra Island occurs; Hanson & Kusmer 2001; McKechnie & Wigen 2011; Caldwell 2015), despite being typically present in archaeological assemblages elsewhere, across the BC coast (McKechnie & Wigen 2011; Szpak *et al.* 2012).

Our designation of sea otters present vs. absent at ancient sites aligns with historical records and traditional knowledge. Archibald Menzies, a naturalist with Captain George Vancouver in 1792, noted the presence of sea otters during their exploration of the BC coast. Although they did not encounter live sea otters in the Strait of Georgia, Menzies noted that when he visited Cape Mudge, on southern Quadra Island, otter skins were rarely worn by the Indigenous People; he surmised sea otters were uncommon. However, when in western Johnstone Strait (near the Broughton Archipelago), Menzies noted that villages had a “great abundance of Sea Otter Skins” and wrote, “we were visited by a great number of Natives in their Canoes from the Village, and a small traffic commenced for Sea Otter Skins”. These pelts could have arrived via trade routes across Vancouver Island (Layland 2016), or could have been hunted locally, because a few days later, just outside Fife Sound, which borders the Broughton Archipelago, the ship ran aground, and in this area Menzies encountered: “A great number of Sea Otters which we disturbed and frightened off the rock when we landed” (Menzies 1792).

Further evidence indicates there were sea otters in the Broughton Archipelago. By the 1800s fur traders were frequenting the Broughton Archipelago, as revealed by pictographs of trade ships throughout the territory (Hill 1985; M. Nicolson pers. comm.). Further evidence that sea otters were once prevalent in Musgamagw Dzawada’enuxw territory comes from their presence in historical stories and regalia (Boas & Hunt 1905; Galois 1994), the use of adzes that were specifically made with sea otter bones and used for canoe construction, sea otter art, sea otter fur clothing and blankets, and specific sea otter-hunting arrows (Boas & Hunt 1905; Boas 1909). Taken together, the zooarchaeological analysis, written records, ethnographic literature, and traditional knowledge indicate that sea otters were present around the Broughton Archipelago but ecologically absent at Quadra Island during the late Holocene.

4.3.2 Contemporary effects of sea otters on butter clam lengths

Overview. We made several comparisons to examine the relationship between sea otter presence and clam lengths. First, we measured lengths of live butter clams sampled in 1993, from areas with and without sea otters, collected within park and protected area boundaries. Second, we measured butter clam shell lengths to assess the size of clams preyed on by sea otters, which were identified by the distinct break patterns caused when sea otters crack open clams (Kvitek *et al.* 1992). Lastly, we evaluated nearshore substrate disturbance in the form of distinctive pits left by foraging sea otters (e.g., Traiger *et al.* 2016), to determine if the intensity of sea otter predation varied by tidal height. We took this step because the rock terraces of clam gardens increase beach elevation (Williams 2006; Lepofsky *et al.* 2020), which makes clams landward of the rock wall inaccessible to sea otters for several hours of the day (*i.e.* when tide is too low – sea otters require 2m of water to excavate clams; Thometz *et al.* 2016; Tinker *et al.* 2019).

Live clams. We dug butter clams from the intertidal and subtidal zones, using 10-20 randomly-placed 0.25 m^2 quadrats (0.5 x 0.5 m) in each zone (*Supplementary Materials*). We measured butter clam lengths (Fig. 4.S1) using Vernier calipers. Clams <25 mm were not measured because they could not be reliably collected, especially while sampling underwater. We pooled sites within regions, and used a Wilcoxon Rank-Sum test to examine if median live butter clam lengths were significantly different between the intertidal and subtidal zones within each area. We used a Kolmogorov-Smirnov test to examine if length distributions were different (*Supplementary Materials*). We then pooled measurements from clams collected in the intertidal and subtidal zones, and used a Wilcoxon Rank-Sum and a Kolmogorov-Smirnov test to examine whether median lengths or length-distributions of the butter clams differed between areas with and without otters.

Shell collections. At each of the sites in Checleset Bay, we collected butter clam shells from the surface of the sea floor, using 100 haphazardly placed 1m x 1m quadrats placed in each of the intertidal (0-20 ft.), shallow subtidal (20-30 ft.), and deep subtidal (30-40 ft.) zones. We measured left valve lengths to the nearest mm. Sea otter predation was inferred by distinctive single-valve breakage, where one of two valves is smashed, which occurs when otters smash clams open by hitting one clam with another or with a rock (Kvitek *et al.* 1992) (Fig. 4.S2a). We pooled clams from all depths, and then used a Wilcoxon Rank-Sum test to compare the median lengths of otter-cracked shells with live butter clams, and a Kolmogorov-Smirnov test to compare length distributions.

Substrate disturbance. To determine whether sea otter predation pressure on clams varied with depth, we used sediment disturbance as a proxy. Specifically, we assessed the percent area of the seafloor that was disturbed at sites occupied by sea otters (Fig. 4.S2b-c; *Supplementary Materials*).

4.3.3 Ancient butter clam lengths at otter-present and otter-absent sites 3500-150 years ago

Overview. We measured previously collected ancient butter clams from archaeological assemblages in two areas with some of the highest-known densities of clam gardens (Harper *et al.* 1995; Lepofsky *et al.* 2015; Lepofsky *et al.* 2020). Where whole shells were present, we established a regression equation to predict clam length from umbo thickness, so that we could evaluate archaeological butter clam fragments with an intact umbo (e.g., Singh & McKechnie 2015; Slade 2019). We then compared archaeological butter clam lengths in areas with and without sea otters, across four ecologically- and socially-relevant time periods (*Supplementary Materials*). For insight into how small changes in clam length affected individual clam biomass, we fit a power function to individual length and biomass (*Supplementary Materials*).

Excavation stratigraphy and radiocarbon dating. We digitized the archaeological stratigraphy from each excavation that we sampled shell assemblages from, and submitted two sets of radiocarbon dates, the first to determine broad midden accumulation rates, and the second to select specific layers for refined dating (Table 4.S1). Charcoal was preferentially chosen for dating over shell, due to uncertainties of comparability of marine reservoir effects in shells from the two areas. We used radiocarbon dates to group clams into socially, ecologically, and environmentally relevant time periods (*Supplementary Materials*; *Appendix A*, Figs. 4.A1- 4.A9).

Estimating ancient butter clam lengths. Sediment samples were screened through 6.4 mm mesh, and we did not measure shell fragments below this size. We measured butter clam umbo thickness and shell length (Fig. 4.S1), discarding measurements from clams <25 mm because clams that small may have arrived in the shell midden via the stomach contents of other prey species (e.g., scoters, *Melanitta* spp. or other sea ducks), and were not reliably encountered (n = 11 of 1351 clams). Of 1351 butter clams with an intact umbo, we could confidently measure the shell length of 225. We regressed umbo thickness and shell length to determine how well umbo thickness predicted length (*Supplementary Materials*). We evaluated inter-observer measurement discrepancies, and found a mean (± SD) of 0.014 (± 0.31) mm for umbo thickness. When this error was incorporated into the regression (Equation 1; *Supplementary Materials*) variation in the predicted clam length was negligible (Fig. 4.S3a-d).

We used Planned Paired Contrasts to test for differences in butter clam shell lengths between Quadra Island and the Broughton Archipelago within each time period (3500-1500; 1500-1000; 1000-500; 500-150 cal BP; see *Supplementary Materials*), and within each area we compared clam sizes from the 3500-1500 time period to the 1500-1000 year time period, as well as from the 1500-1000 year time period to the 500-150 year time period (total of 8 pairwise-comparisons). We used Wilcoxon Rank-Sum and Kolmogorov-Smirnov tests with Bonferonni adjustments ($\alpha = 0.05/8 = 0.006$) to test if median butter clam lengths or length distributions were significantly different between areas or time periods.

We used allometric relationships from clam surveys led by DFO in Fishery Areas 12 and 13 (Fig. 4.1), from 1990-2004, to predict individual clam biomass from individual clam length (*Supplementary Materials*). We note that individual biomass estimates cannot be scaled up to population biomass estimates, as we lack sufficient data on archaeological clam densities and abundance, but made these comparisons to better-understand how small changes in clam length affected individual clam sizes.

4.3.4 Ancient littleneck clam lengths at otter-present and otter-absent sites 3500-150 years ago

We compared measurements of littleneck clams between areas with and without sea otters, to inform the intensity of sea otter predation on clams in archaeological assemblages and the extent to which harvest prescriptions (e.g., the clam lengths selected by harvesters) among people living in the two areas were similar for littleneck clams. We compared previously measured ancient littleneck clam lengths from 3500-150 years ago from shell middens on Quadra Island (Testani 2017; Lepofsky and Puckett unpublished) and in the Broughton Archipelago. As with butter clams, we did not include clams <25 mm. We did not use umbo thickness-to-clam length regressions in these analyses because only the Broughton samples would have been subjected to regressions (there were 653 whole littlenecks from Quadra sites, compared with 111 whole shells plus 517 clam fragments with an intact umbo from Broughton sites). Sample sizes for littleneck clam lengths were too small to analyze across all four time-periods (4 out of 8 groups where $n < 30$). Accordingly, we pooled samples into two time periods: 3500-1500 and 1500-150 cal BP. We used Wilcoxon Rank-Sum, and Kolmogorov-Smirnov tests with Bonferonni adjustments ($\alpha =$

0.05/4 = 0.0125) to test if littleneck clam median lengths or length-distributions were significantly different between areas or time periods.

4.3.5 Environmental and biological differences between areas, not related to sea otters.

We used contemporary clam measurements to assess the contribution of environmental factors, such as primary productivity and temperature, that could affect clam lengths in the same areas as the archaeological assemblages, but when sea otters are absent from both areas (Nichol et al. 2015). Butter clams were collected from Fishery Areas 12 (incl. Broughton Archipelago), 13 (incl. Quadra), and 25 (west coast Vancouver Island, between Checleset Bay and Barkley Sound) between 1982 and 2002 as part of Intertidal Clam Monitoring Program at DFO, and additional surveys were conducted on Quadra Island in 2013 (Toniello *et al.* 2019; Fig. 4.1). Butter clam lengths were measured (Fig. 4.S1) and ages were determined by counting annuli (Quayle & Bourne 1972; Toniello *et al.* 2019). We constructed von-Bertalanffy growth curves to examine length-at-age relationships at Quadra Island and the Broughton Archipelago to examine how comparable growth, and the factors that influence it (predominantly productivity and temperature), were between areas; we later compared these with growth curves from the west coast of Vancouver Island. We used a Wilcoxon Rank-Sum test to examine differences in contemporary median butter clam lengths, and a Kolmogorov-Smirnov test to examine differences in length distributions, between Quadra and the Broughton Archipelago (when otters were absent from both areas). For the latter two analyses, only butter clams >25 mm were used, following DFO protocols surrounding the lack of reliability of sampling clams <25 mm (Gillespie & Kronlund 1999).

4.3.6 Analyses and visualizations

All analyses and visualizations were completed in *R* version 3.6.1, using the tidyr (1.0.0; Wickham & Henry 2019), dplyr (0.8.3; Wickham *et al.* 2019), car (3.0-8; Fox & Weisberg 2019), propagate (1.0-6; Spiess 2018), and ggplot2 (3.3.2; Wickham 2009) packages. In reporting clam-size distributions we state the median length followed by 75th percentile value (PC_{75}) in parentheses.

4.4 Results

4.4.1 Contemporary effects of sea otters on butter clam lengths

Contemporary median butter clam length in Barkley Sound, where sea otters were absent, was 77 mm (PC_{75} = 85), which was significantly larger than in Checleset Bay, where sea otters were present

(42 mm [$PC_{75} = 67$]; $W = 18478$, $p < 0.001$); length distributions were also significantly different between areas with and without sea otters ($D = 0.63$; $p < 0.001$) (Fig. 4.2a). The median size of available butter clams in Checleset Bay (42 mm) was less than half the median size of otter-cracked butter clams (median = 87 mm, $PC_{75} = 99$, $W = 4420$, $p < 0.001$), suggesting strong size-selectivity by sea otters (Fig. 4.2b). Butter clam length distributions of available and otter-cracked clams were also significantly different ($D = 0.61$; $p < 0.001$).

The proportion of substrate disturbed by sea otters among the three depth categories we measured was not significant ($F = 0.94_{[2,22]}$, $p = 0.40$), although there was a weak trend of increased disturbance in deeper water than in shallower water (Fig. 4.S4).

4.4.2 Ancient butter clam lengths at otter-present and otter-absent sites 3500-150 years ago

Ancient butter clams were larger in archaeological assemblages from Quadra Island, where sea otters were absent, than from the Broughton Archipelago, where sea otters were present. However, clam sizes either increased or were stable within each area through time. Pairwise comparisons demonstrated that for all but one time period, clams were significantly larger on Quadra Island than in the Broughton Archipelago (Table 4.1). At their maximum differences, which occurred in the 500-150 years ago time period, butter clam lengths were 68 mm ($PC_{75} = 78$) mm on Quadra Island, where otters were absent, and were 55 mm ($PC_{75} = 61$) in the Broughton Archipelago where otters were present ($W = 9535$, $p < 0.008$; Table 4.1). Butter clam length distributions were significantly different in the same time periods (Table 4.1); length distributions were truncated in areas with sea otters but were up to 25 mm larger in areas where sea otters were absent (Fig. 4.3). Within each area, butter clam lengths significantly increased from the earliest (3500-1500 cal BP) to next oldest (1500-1000 cal BP) time periods, and then stabilized (Fig. 4.3). On Quadra Island, where sea otters were absent, median butter clam lengths increased from 49 mm ($PC_{75} = 62$) to 63 mm ($PC_{75} = 73$; $W = 17893$, $p < 0.006$) and then stabilized for over a thousand years – to the end of our data series, when they were 68 mm ($PC_{75} = 78$). In the Broughton Archipelago, where sea otters were present, median lengths increased from 49 mm ($PC_{75} = 56$) to 55 mm ($PC_{75} = 61$; $W = 6420$, $p < 0.006$) and then stabilized until the end of our data series where they remained at median 55 mm ($PC_{75} = 61$ mm) (Table 4.1).

Like most species, clam biomass increases as a power function of length (Fig. 4.S5). Thus, a 10 mm increase in butter clam length from 55-65 mm, which approximates the differences in median clam lengths from archaeological assemblages with and without sea otters, is associated with a 30 g (67%)

increase in individual clam biomass, from 45 to 75 g. This result highlights that the small but significant effects of sea otters on individual clam length equate to exponentially larger effects on individual clam biomass (Fig. 4.S5) however the biomass available for harvest would have depended upon clam density. Clam densities could not be derived from archaeological data in this study, so differences in overall clam biomass in each area cannot be calculated.

4.4.3 Ancient littleneck clam lengths at otter-present and otter-absent sites 3500-150 years ago

Median lengths in littleneck clams did not differ between areas with and without sea otters, but they did differ in size distributions, and, like butter clams, the median sizes of littlenecks increased between the 3500-1500 and 1500-150 year time periods. Median littleneck clam lengths were 42 mm in both the Broughton Archipelago and on Quadra Island ($PC_{75} = 45$ and $PC_{75} = 46$; $W = 587$; $p = 0.62$). As with butter clams, littleneck clam length distributions were truncated with the larger sizes missing in areas with sea otters when compared to areas without sea otters in all time periods, and distributions were significantly different in the 1500-150 years ago time period ($D = 0.1768$; $p = <0.0125$; Fig. 4.4). Littleneck clam lengths were 37 mm ($PC_{75} = 42$) in the 3500-1500 cal BP time period, and 41 mm ($PC_{75} = 47$) in the 1500-150 cal BP time period at Quadra Island ($W = 20592$ $p < 0.0125$), but did not significantly increase through time in the Broughton Archipelago (Table 4.2).

4.4.4 Environmental and biological differences between areas, not related to sea otters.

Contemporary butter clam lengths and distributions, collected from the same general areas as the archaeological assemblages, but after sea otters had been extirpated from the Broughton Archipelago, did not differ between Fishery Area 13 (incl. Quadra Island; 69 mm [$PC_{75} = 73$]) and Fishery Area 12 (incl. the Broughton Archipelago; 67 mm [$PC_{75} = 76$]; $W = 11422$, $p = 0.94$; $D = 0.13$, $p = 0.27$; Fig. 4.5a). Growth curves were not significantly different between Fishery Area 13 (incl. Quadra Island) and 12 (incl. Broughton Archipelago (Fig. 4.5b), but growth curves were significantly different in Fishery Area 25 (west coast of Vancouver Island) where butter clams grew faster and to larger asymptotic lengths than in Fishery Areas 12 and 13; Fig. 4.S8).

4.5 Discussion

Apex predators and their associated strong ecological interactions are known to play an important role in structuring ecological communities. However, much of what is known about these interactions come from areas where humans are considered ecologically absent (Dorresteijn *et al.* 2015).

Ecological interactions can differ in human-dominated landscapes when compared with landscapes (or time periods) were humans are not as influential (Dorresteijn *et al.* 2015). In this study, we considered how an ancient Indigenous maricultural practice, clam gardening, may have mitigated the ecological effects of sea otters, and allowed humans and sea otters to coexist where both consumed clams. Our contemporary ecological data indicate that sea otter predation can reduce the size of butter clams significantly. However, the archaeological records suggest that although harvested butter clams were smaller in areas exposed to sea otters, compared to those without otters, the size of harvested clams remained stable or increased over millennia – regardless of the presence of sea otters. Surprisingly, this effect extended to a clam species less preferred by otters, because of its small size. Although the median size of ancient littleneck clams from shell middens was the same in areas with or without sea otters, the larger-size classes were missing from the archaeological assemblage in areas with sea otters. The absence of large ancient clams from areas with sea otters, combined with sea otters' strong size-selectivity in our contemporary ecological data, together infer that foraging sea otters removed large clams from ancient clam populations. We infer from these data that sea otters remained ecologically effective predators (Soule *et al.* 2002), whose size-selective foraging reduced the sizes of clams available for people to harvest, but that clam gardens and associated Indigenous management protocols, facilitated coexistence among people, and sea otters where sea otters were present.

Allometric relationships between the length and biomass of individual clams provides further insight into the ecological effects of sea otter predation on clams. The difference in median butter clam lengths that we observed between areas (~13 mm), are equivalent to 55-67% differences in individual clam biomass. Although smaller clams have less biomass individually, the density of these smaller clams was likely higher and produced similar total clam biomass on beaches in both areas, which seems likely, given the stability in harvests for millennia. Given the median sizes of littleneck clams and their prevalence in shell middens, people did not seem to avoid small clams (once they reached permissible harvesting size).

Although we used contemporary butter clam measurements from the west coast of Vancouver Island to infer the strong ecological effect that sea otters have on clam size distributions, we cannot make direct comparisons on the sizes of butter clams between the contemporary ecological data and the archaeological record for several reasons. First, our contemporary butter clam measurements are taken from random samples of clam populations, whereas our ancient butter clam measurements come from clams harvested by people, in a non-random sample (fishery-catch data), which is often size-selective. Second, the growth curves of contemporary butter clams on the west coast of Vancouver Island are not comparable to those from Quadra Island or the Broughton Archipelago; present day clams grow faster and reach larger sizes on the west coast of Vancouver Island, compared with contemporary Broughton Archipelago and Quadra Island clams (*Supplementary Materials*, Fig. 4.S8). Third, the intensive Indigenous management that enhanced clam productivity (and likely the carrying capacity of intertidal habitat for clams) from 3500 to 150 years ago was largely interrupted following European colonization – making it difficult to interpret how contemporary clam populations and productivity might compare to ancient Indigenous-managed populations, with or without sea otters. Thus the contemporary ecological data are used only to inform hypotheses regarding how the effects of sea otters were ameliorated by people and ancient clam management.

We interpret our results in light of several previous studies that use invertebrate sizes and changes in community composition, to infer the influences of sea otters in ancient human-otter-invertebrate food webs. In the Aleutian Islands, alternating stable states in ecological communities from sea-otter-dominated to shellfish-dominated archaeological assemblages supported the hypothesis that people excluded sea otters in some time periods, but that otters were prevalent in other time periods (Simenstad *et al.* 1978). Shell middens in the Aleutian Islands have also shown that sea urchins were larger than where contemporary sea otters are abundant, inferring that otter populations were low in the past (Corbett *et al.* 2011). In California, paleo-ecological studies have found that shell middens tended to be dominated either by kelp-forest fauna or by large invertebrates, the latter of which were assumed to occur only if sea otters were rare, or ecologically ineffective (Erlandson *et al.* 2005). On the British Columbia coast, Clarke and Clarke (1980) speculated that clams were only available to be harvested in large quantities at Yuquot (Nootka Sound) once sea otters were extirpated, given the rarity of butter clams found in the shell midden at this location prior to the Maritime Fur Trade. More recent research, conducted on the central and south coast of BC, found that ancient California mussels (*Mytilus californianus*) from archaeological assemblages dating back 6000 years, were generally larger than would have been expected if sea otters were abundant (Slade 2019).

In contrast, our study shows that people harvested clams from areas where sea otter predation was sufficient to alter clam size distributions and average clam lengths, yet people made consistent harvests of clams, where sea otters were both present and absent. Our study is unique in its design of comparing ancient areas with otters to ancient areas without otters, over the same time periods. An additional feature of our study is that we focus on areas within the densest aggregations of ancient clam gardens that we know of. Within this context, we found that clams from shell middens in areas with sea otters were smaller than expected if sea otter foraging had not affected clam sizes through the past four millennia, but that these size differences did not affect the stability of clam harvesting by people, suggesting these ancient maricultural practices promoted coexistence between people and sea otters.

Because clam gardening increases clam habitat, productivity, and recruitment (Groesbeck *et al.* 2014; Jackley *et al.* 2016; Slater 2018; Lepofsky *et al.* 2020), and reduces sea otter access to clams by elevating the beach height clams are accessible at, we hypothesized that clam gardening allowed for sustainable clam harvests for people, even where sea otter predation affected clam sizes. Additional Indigenous management practices probably further limited sea otter effects on clams. Sea otters were harvested across much of the northwest coast of North America (Orchard 2007; Corbett *et al.* 2011; McKechnie & Wigen 2011; Szpak *et al.* 2012; Salomon *et al.* 2018; Salomon *et al.* 2020). Therefore, a fear of being hunted and the use of scare-tactics likely further-reduced the impacts sea otters had on clams in gardens. We discuss the implications of our findings below, after evaluating alternative hypotheses to explain the size differences we observed in clams from areas with and without sea otters.

Alternative hypotheses. We evaluated several alternative hypotheses for the differences we observed in clam sizes between areas with and without sea otters. We consider how the sizes of clams recovered in archaeological assemblages reflect 1) fishery-catch data, influenced by what was ecologically available, 2) Indigenous management practices, and 3) human harvest pressure on resources.

Ecological availability. Environmental conditions affect the sizes of clams available for harvest, and may have differed between areas. We found, however, that in the 1990-2010s, more than a century after sea otters were extirpated from the BC coast (Nichol *et al.* 2015), and after severe declines in traditional maricultural practices due to European colonization (Toniello *et al.* 2019), median butter clam lengths from the Broughton Archipelago and Quadra Island (67 and 69 mm respectively) and size distributions were indistinguishable between the two areas. Moreover, contemporary butter clam growth rates were also indistinguishable. Although we used contemporary growth rates, Toniello *et al.* (2019) measured length-at-age in butter clams from archaeological assemblages on Quadra Island through the Holocene, and found that butter clam growth curves from 4200-2900, 2800-2300, and 500-250 years ago were indistinguishable, suggesting that climatic changes over that 4000 year period did not affect clam growth on Quadra Island. This evidence makes spatial and temporal environmentally-induced effects affecting clam sizes in our data, unlikely.

We used data from contemporary species-interactions to consider how other clam predators could have affected the sizes of clams available for harvest. Of the significant clam predators in coastal BC waters today, sea ducks generally consume clams in the 25-45 mm range (Lewis *et al.* 2007), and red rock crabs (*Cancer productus*) select clams <45 mm (Boulding 1984). Clams buried below 40-50 mm typically escape sea star predation (Doering 1982) and even the largest sea stars on the northwest coast, sunflower stars (*Pycnopodia helianthoides*), consume smaller (10-40 mm) clams than sea otters (40-70 mm) (Traiger *et al.* 2016). Bears (*Ursus* spp.) and racoons (*Procyon lotor*) also consume clams (generally softer-shelled species), but do not prey on large sizes (Smith & Partridge 2004; Simmons *et al.* 2014). River otters (*Lutra canadensis*) and mink (*Neovision vision*) typically consume few clams (Hatler 1976; Stenson *et al.* 1984). Taken together, it seems unlikely that predators other than people or sea otters, affected the size distributions of clams available for harvest.

Indigenous management practices. The extent to which clam management differed between Indigenous groups, as it applied to the sizes of clams in archaeological assemblages, is unknown. The differences in butter clam sizes between areas could be due to cultural differences in butter clam management strategies, where people in the Broughton Archipelago selected smaller clams than the people of Quadra Island, for a reason not related to sea otters. We reason however, that clam harvesters in both areas were affected by similar constraints and used common technologies. For example, when selecting beaches, people would find places that were not affected by waves and were easy to land at in winter (K̲ii'iljuus Barb Wilson, *pers. comm.*). Moreover, butter and littleneck clams are considered cultural keystone species (*sensu* Garibaldi & Turner 2004) because they are integral to the health and wellbeing of Indigenous and ecological communities (Barber *et al.* 2019), suggesting there were clam conservation and sustainability priorities.

Human harvest pressure on resources**.** There is a possibility that more people were sustained per linear km of shoreline in the Broughton Archipelago than Quadra Island, or vice versa. Previous work examining invertebrate sizes in archaeological assemblages has sometimes found that sizes decline as human populations increase (e.g., Erlandson *et al.* 2011), thus, smaller clams might occur where human populations were larger and harvest pressure was greater. A population census from 1830 has been used to hind-cast pre-contact population sizes of Indigenous People in specific areas of the BC coast, including Quadra Island and the Broughton Archipelago (Harris 1994). However, these estimates, although predicting similar population sizes after adjusting for smallpox epidemics (~2000 men in each area) apply only to the recent pre-contact period and cannot be used to infer population sizes over the past 3500 years. To this end, volumes of shell middens have sometimes been used to estimate ancient population sizes (e.g., Ascher 1959). Alternatively, an inventory of human-modified shoreline features (Caldwell *et al.* 2012) can infer historical population sizes. There are no estimates of the size of Indigenous populations in the study areas for the past 3500 years, although both areas have exceptionally high densities of clam gardens (Harper *et al.* 1995; Lepofsky *et al.* 2020) compared to anywhere else on the northwest coast or elsewhere (Lepofsky *et al.* 2015). The lack of differences we found in median littleneck clam sizes between the two areas, and the fact they do not decline through time in either area, suggests that human pressures on clams were relatively constant and did not differ between areas to the extent that they affected harvested clam sizes.

While the smaller sizes of clams from archaeological assemblages in the Broughton Archipelago compared with Quadra Island could arise from differences in Indigenous management practices, or human population sizes/harvesting pressures, the major ecological difference that we know of between the two areas was the presence vs. absence of sea otters. Butter and littleneck clam size distributions from the Broughton Archipelago both lack the larger-sized clams found in the size distributions from Quadra Island. This pattern suggests that in the Broughton Archipelago, the larger clams found at Quadra Island were not available to people harvesting clams, having already been removed from the clam populations by sea otters.

Signals of stability in Indigenous clam harvests over millennia. Ancient butter clam lengths from shell middens indicated people were able to continuously harvest clams from a stable clam population up to as recently as 150 years ago, and as long ago as 3500 years, even in the presence of sea otters. Butter clam sizes increased in both areas from the 3500-1500 year to 1500-1000 year time periods, over a period of clam garden development (e.g., Smith *et al.* 2019; Toniello *et al.* 2019) and when human populations along the BC coast were increasing exponentially (Ames & Maschner 1999). Clam sizes in the archaeological record were then stable for 1500 years, despite peaks in human populations that were thought to occur about 1000 years ago, coast-wide (Ames & Maschner 1999). Such stability indicates that that a consistent clam supply was available, despite the pressures exerted by both sea otters and people. The highly productive clam habitat created by clam gardens may have allowed for a consistent clam harvests despite the ecological effects of sea otters. Detailed radiocarbon dating from multiple levels in each of the shell-middens we examined (n= 37 radiocarbon dates) allowed us to evaluate clam size within the context of changing climatic conditions over the past 3500 years, and from a period including the oldest dated clam gardens yet documented, to when gardens were widespread. Despite differences in temperature regimes over this period, the size of harvested clams remained consistent. Clam gardens increase the habitat, productivity, recruitment, and abundance of clams (Groesbeck *et al.* 2014; Jackley *et al.* 2016; Slater 2018; Lepofsky *et al.* 2020), thereby promoting stable clam populations for harvest.

Management of clams in areas with sea otters likely required different harvest prescriptions than in areas lacking sea otters. For example, because sea otters remove large clams, harvest strategies might have accommodated smaller clams in areas with otters than without; a hypothesis that our data supported. Our length-at-age curves demonstrated that butter clams, like most species, grow much faster at younger ages (and associated smaller sizes) than at older ages (and associated larger sizes). Consequently, a managed clam-beach subjected to sea otter foraging, may have produced a great number of clams of smaller sizes, and resulted in shorter turnover rate (or time until the next cohort of clams reaches harvestable size). Furthermore, the combined pressure of sea otter predation and clam harvesting by people may have driven selection for size at first reproduction. Smaller size at first reproduction may be selected for where mortality is high for large individuals, given that fitness depends on individuals reproducing before they are harvested (e.g., Watson 2000; Lee *et al.* 2016). In contrast, where mortality occurs at a smaller size, selection should favor individuals that grow rapidly when they are small, and reproduce at a larger size, when fecundity is greater (Endler 1986).

Limiting clam consumption by sea otters. Given that sea otters consume up to 30% of their bodyweight in prey each day (Costa & Kooyman 1982; Thometz *et al.* 2016), how did people limit the effects of sea otters on clams? One dimension relates to the physical constraints imposed on otters by the engineering of clam gardens. Clam gardens may partially exclude sea otters because clam garden walls raise beach elevation and increase the hours clams are accessible to humans but are inaccessible to otters. Sea otters require require >2 m of water to dig for clams (Thometz *et al.* 2016; Tinker *et al.* 2019), so we estimated how many hours a walled clam beach would be accessible to sea otters on the largest and smallest tides in the Broughton Archipelago (Canadian Hydrographic Service, 2021) . In the Broughton Archipelago, the average height of low intertidal clam garden walls was 1.3 m above chart datum (range 1.03-1.58 m, n = 5 clam gardens measured; Harper 1995). Thus, a 3.3 m tide would be needed for a sea otter to access clams in a clam garden whereas a 2 m tide would allow access to clams at the same tide height on a non-walled beach. Thus, on the highest tidal exchange in 2021 in the Broughton Archipelago (May 27th, 5.2 m), sea otters could have accessed non-walled beaches for 19 hours out of a 24 hr period whereas walled clam gardens were accessible for 10.75 hours. Similarly, on the day with the smallest tidal exchanges of 2021 (May 20th, up to 2.4 m), otters could have accessed non-walled beaches for 20 hours out of a 24 hr period, whereas clam gardens were accessible for 10 hours. Thus, clam gardens may have reduced sea otter access to clams in gardens by up to 50% compared to non-walled beaches.

Today, sea otter influences on butter clams extend beyond changes to shell lengths. Where sea otters and clams co-occur, clam population biomasses (a measure that accounts for changes in individual clam sizes as well as the relative abundances of different size classes available in live-clam assemblages) can be heavily reduced compared to where sea otters are absent (Kvitek *et al.* 1992; Weitzman 2013). Extensive Indigenous Knowledge reveals that people actively limited sea otters' access to clams, probably reducing these effects. Northwest coast oral histories and ethnographies indicate that sea otter exclusion from shellfish harvesting areas was practiced (Salomon *et al.* 2015; Salomon *et al.* 2018; Salomon *et al.* 2020). Because otters were widely hunted for their furs, fear alone might have limited sea otter access to defended areas, such as clam gardens. People may have additionally hunted sea otters specifically to control their access to harvesting areas (Salomon *et al.* 2018; Burt *et al.* 2020; Salomon *et al.* 2020). If sea otters were afraid of humans, the smell of campfire smoke and the presence of people on the landscape may have acted as a deterrent (Salomon *et al.* 2018). Guarding clam beaches from sea otters was probably easiest in winter, because the high tides occur in the day time and otters could have been easily-deterred during daylight hours. Overnight, the tides are low and the clams are inaccessible to sea otters. In a recent transdisciplinary workshop, Indigenous Knowledge Holders shared that people used scarecrows – for example, a skinned sea otter moored at clam beaches – to deter sea otters (Hup n yook Tom Happynook and K̲ii'iljuus Barbara Wilson in Salomon et al. 2018). In addition to scarecrows, dogs may have also been used to guard clam beds (Salomon *et al.* 2018). The utility of dogs would have further mitigated sea otter effects on clams if dogs were left at village sites at times when village residency was low (e.g., if the village seasonally relocated to harvest other resources). Given the importance of village dogs to Indigenous Peoples for millennia (Hillis *et al.* 2020; McKechnie *et al.* 2020), their use to assist with resource protection is plausible.

Recent scientific research provides evidence complementary to Indigenous Knowledge. For example, where sea otters are hunted today, there is compelling data indicating their avoidance of people. Around the community of Kake, southeast Alaska, within two years of increased sea otter hunting, sea otter occurrences were reduced by 25% (Hoyt 2015). A similar reduction in local sea otter abundance occurred in Sitka Sound following a period of intensified hunting (Raymond *et al.* 2019). Additionally, recent work has shown how the sound of a recorded dog barking can cause racoon predators to avoid beaches (Suraci *et al.* 2016). The efficacy of dogs as a deterrent for otters would arise from a long co-evolutionary relationship with wolves; recent work suggests that wolves may prey on sea otters (Roffler *et al.* 2021). The combined effects of clam cultivation, walled-beaches, sea otter harvesting, and scare-tactics could have produced a nearshore seascape that promoted stable clam harvests for millennia, even with sea otter predation reducing clam sizes (Fig. 4.6).

Indigenous knowledge holders have shared that people managed shellfish resources not only to protect clams from sea otters, but also to protect the sea otters themselves (Salomon *et al.* 2018; Salomon *et al.* 2020). Sea otters were harvested for their furs, which were used for bedding, clothing, and regalia by Musgamagw Dzawada'enuxw, in the Broughton Archipelago (Boas 1909), whereas, on Quadra Island, Laich-kwil-tach and Coast Salish people raised wool dogs, the wool of which was used for bedding and clothing (Howay 1918; Olsen 2010; McKechnie *et al.* 2020). Indigenous Knowledge Holders suggest a human-mediated spatial mosaic of ancient coastal ecosystems, whereby sea otter densities varied from place-to-place (Salomon *et al.* 2015; Salomon *et al.* 2018; Salomon *et al.* 2020); an idea also supported by the scientific literature (e.g., Corbett *et al.* 2011; Szpak *et al.* 2012; Slade 2019).

Conclusions and implications. We have identified, using complementary insights from ecology, archaeology, history, and Indigenous knowledge, a novel benefit to clam gardening – it enabled consistent clam harvests in the presence of a strongly-interacting predator. In the decades following sea otter reintroduction to British Columbia, conflicts have arisen between Indigenous fisheries sustainability and sea otter conservation, calling for alternative management objectives to mitigate conflict (Salomon *et al.* 2015; Pinkerton *et al.* 2019; Burt *et al.* 2020). Clam gardening has been suggested as a step towards coexistence between people and sea otters (Salomon *et al.* 2018; Burt *et al.* 2020). Based on contemporary studies of currently unmanaged ancient clam gardens, productivity was more than double that of non-modified beaches (Groesbeck *et al.* 2014; Jackley *et al.* 2016). It is likely that if these same gardens were actively managed, their productivity would be greater, declines in traditional management, combined with the effects of logging and siltation that affect clam beaches today, have reduced the capacity of clam beaches compared to the past (Toniello *et al.* 2019). Over the past ~3500 years, tended clam gardens were more productive than untended areas in any-other period during the Holocene (Toniello *et al.* 2019). The resurgence of clam gardening – now well underway – is already providing people with improved access to culturally-important clams (Augustine & Dearden 2014) and may provide additional benefits where other strongly-interacting consumers prey on clams.

Given the sustained clam harvests clam gardens allowed even in the presence of sea otters, it is likely that other invertebrates were similarly cultivated to improve access and harvest yields. For example, California mussels (*Mytilus californianus*; lengths to 255 mm, Harbo 2007), which typically inhabit exposed shorelines, have been observed in sheltered high-current areas usually dominated by blue mussels (*Mytilus edulis*; lengths to 110 mm, Harbo 2007), where people remembered transplanting them (Haida Gwaii; Ellis & Wilson 1981). Frequent mussel-harvests provided space and increased recruitment in the rocky intertidal – and mussel harvesting techniques in Haida Gwaii have been described as a *semi-cultivated* maricultural system (Ellis & Wilson 1981). On the west coast of Vancouver Island, people only harvested mussels from patches that they re-visited, because places that hadn't been previously harvested were "no good" (Ellis & Swan 1986). Similar descriptions of mussel cultivation also come from California, where people used mussel stripping techniques to clear the rocks every ~24 months; this reduced short-term yields, but increased mussel productivity and the stability of longterm harvests (Whitaker 2008). Taken together, these management techniques may have influenced the sizes of mussels to which people had access, particularly if mussel beds were protected from other consumers. Other examples of seafood cultivation may include the rock walls used to terrace clam gardens, which were used to harvest fish, crabs, snails, seaweeds, and additional marine-species typically associated with rocky-reef communities. Such diverse harvests indicate that use of the term "seagarden" is most appropriate in reference to cultivation within soft-sediment terraces and along boulder walls (Thorne 2016; Black *et al.* 2018).

Across the northwest coast of North America, Indigenous peoples have been tending and cultivating gardens for millennia. Examples of terrestrial gardening practices are well known (reviewed by, Lepofsky & Lertzman 2008; Turner *et al.* 2013; Turner 2014; Mathews & Turner 2017) and include soil tilling, mulching, and transplanting (Deur 2002, 2005; Turner *et al.* 2013), fertilizing with fish and kelp (Brown & Brown 2009; Turner *et al.* 2013), prescribed burning (Lepofsky *et al.* 2005; Hoffman *et al.* 2017), terracing (Deur 2002, 2005; Turner *et al.* 2013), among others. People tended gardens of wapato (*Sagittaria latifolia*), camas (*Camassia* spp.), springbank clover (*Trifolium wormskioldii*) and Pacific silverweed (*Potentilla egedii*), orchards of Pacific crabapple (*Malus fusca*) and hazelnut (*Corylus cornuta*), and patches of riceroot (*Friteillaria camschatecensis*), stinging nettle (*Urtica dioica*), berry bushes (Lepofsky & Lertzman 2008; Turner *et al.* 2013; Turner 2014), and even eelgrass (*Zostera marina*) meadows (Cullis-Suzuki *et al.* 2015). Camas (*Camassia quamash*) were sustainably cultivated and predictably harvested for at least the past 3500 years, despite climate variability (Carney *et al.* 2021). Large wapato fields at least 3800 years old, preserved in-context with more than 150 tips of broken digging sticks and nearly 4000 tubers (Turner 2014; Hoffmann *et al.* 2016; Lyons *et al.* 2021), further illustrate the investments of extensive growing practices. Diverse, ancient *forest gardens* show how these cultivation systems extended to large terrestrial communities, enhancing functional diversity and resource availability (Armstrong *et al.* 2021). Given the extensive expertise Indigenous people hold in terrestrial gardening, it is likely that there were many forms of marine “gardening” that were managed to support a coastline densely populated with people.

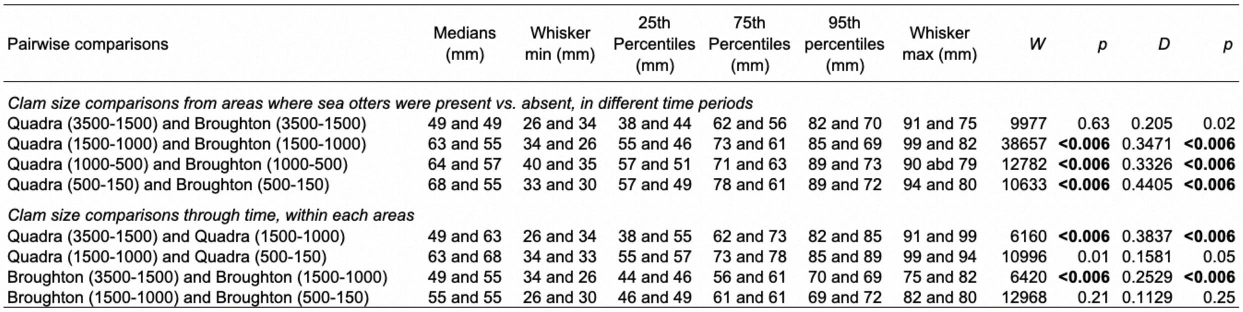
Throughout the Holocene, changes in human population densities and management practices have affected myriad ecological interactions (Boivin *et al.* 2016; Armstrong *et al.* 2021; Carney *et al.* 2021). However, since European colonization of the Americas, there has been a loss of the traditional practices that mediated socio-ecological interactions. Rediscovery of Indigenous Knowledge and the ancient interactions that were once common among people and their environments could mitigate interactions with other species and increase resource availability. Clam gardens are clearly one of the sophisticated cultivation techniques within the food production systems used by coastal peoples for millennia; their restoration could recover ancient interactions and promote resilience in a changing environment.

4.6 Acknowledgements

We thank the communities of Kyuquot and Bamfield, the Bamfield Marine Sciences Centre, the Ka:’yu:’k’t’h’/Che:k:tles7et’h’ (Kyuquot/Checleset) and Huu-ay-aht, Tsehaht, and Uchucklesaht First Nations, Friends of the Ecological Reserves, Bob Redhead, Rick Harbo, and Jim Boutillier for supporting our work on the west coast of Vancouver Island in the 1990s; we thank Leah Saville, Gregr Back, Debbie Lacroix, Don Dempster, and Graeme Ellis for their capabilities preparing for and conducting fieldwork. We thank the Musgamagw Dzawada’enuxv Fisheries Group for permission to use the archaeological samples collected in Musgamagw Dzawada’enuxv territory, in the 1970s. We thank the We Wai Kum and We Wai Kai Nations for their permission and support to conduct the archaeological work on Quadra Island in 2016. We thank the late Dr. Don Mitchell for the body of archaeological work and excavations we relied on, and for leaving us with detailed field notes. We thank the men and officers of C and D Company, 3rd Battalion Princess Patrician Canadian Light Infantry, the BC Provincial Museum’s Archaeology and Conservation Division, the Archaeological Sites Advisory Board, and all who assisted with the 1973 excavations. Genevieve Hill at the Royal BC Museum accessed additional information about these excavations. We thank the archaeologists and all others who assisted with excavations on Quadra Island from 2014-2016: Travis Crowell, Nicole Smith, Louie Wilson, Christina Neudorf, Bryn Letham, Daryl Fedje, Quentin Mackie, Joanne McSporran, Travis Gingerich, Susan Kidwell, Kate Lansley, Mark Wunsch, Richard Chia, Colton Vogelaar, and Emily Purcell. We thank Krystal Groves for assistance with clam measurements, and Sage Vanier for accessing shell samples from SFU. Q̓íx̌itasu Elroy White, Cal Humchitt, Megan Humchitt, and Kirsten Rowsell shared engaging and thoughtful conversations that helped us approach this research. Dominic Bureau, Leslie Barton, Rob Flemming, Michelle Bigg, and Sarah Dudas provided data and assistance with its interpretation. Andrew Edwards and Hannah Kobluk advised statistical approaches. JCW was supported with funding from the Nestucca Trust Fund, EUF was supported by an NSERC Vanier scholarship, and CTD was supported with an NSERC Discovery Grant.

4.7 Tables and Figures

Table 4. 1. Butter clam measurements and statistical results for pair-wise comparisons. Test statistics from Wilcoxon Rank-Sum and Kolmogorov-Smirnov tests are reported as *W* and *D*, respectively. Differences were considered statistically significant where $p < \alpha = 0.006$ (adjusted for multiple comparisons), and are bolded where significant.



Pairwise comparisons	Medians (mm)	Whisker min (mm)	25th Percentiles (mm)	75th Percentiles (mm)	95th percentiles (mm)	Whisker max (mm)	*W*	*p*	*D*	*p*
Clam size comparisons from areas where sea otters were present vs. absent, in different time periods										
Quadra (3500-1500) and Broughton (3500-1500)	49 and 49	26 and 34	38 and 44	62 and 56	82 and 70	91 and 75	9977	0.63	0.205	0.02
Quadra (1500-1000) and Broughton (1500-1000)	63 and 55	34 and 26	55 and 46	73 and 61	85 and 69	99 and 82	38657	**<0.006**	0.3471	**<0.006**
Quadra (1000-500) and Broughton (1000-500)	64 and 57	40 and 35	57 and 51	71 and 63	89 and 73	90 abd 79	12782	**<0.006**	0.3326	**<0.006**
Quadra (500-150) and Broughton (500-150)	68 and 55	33 and 30	57 and 49	78 and 61	89 and 72	94 and 80	10633	**<0.006**	0.4405	**<0.006**
Clam size comparisons through time, within each areas										
Quadra (3500-1500) and Quadra (1500-1000)	49 and 63	26 and 34	38 and 55	62 and 73	82 and 85	91 and 99	6160	**<0.006**	0.3837	**<0.006**
Quadra (1500-1000) and Quadra (500-150)	63 and 68	34 and 33	55 and 57	73 and 78	85 and 89	99 and 94	10996	0.01	0.1581	0.05
Broughton (3500-1500) and Broughton (1500-1000)	49 and 55	34 and 26	44 and 46	56 and 61	70 and 69	75 and 82	6420	**<0.006**	0.2529	**<0.006**
Broughton (1500-1000) and Broughton (500-150)	55 and 55	26 and 30	46 and 49	61 and 61	69 and 72	82 and 80	12968	0.21	0.1129	0.25

Table 4. 2. Littleneck clam measurements and statistical results for pair-wise comparisons. Test statistics from Wilcoxon Rank-Sum and Kolmogorov-Smirnov tests are reported as *W* and *D*, respectively. Differences were considered statistically significant where $p < \alpha = 0.006$ (adjusted for multiple comparisons), and are bolded where significant.

Pairwise comparisons	Medians (mm)	Whisker min (mm)	25th Percentiles (mm)	75th Percentiles (mm)	95th percentiles (mm)	Whisker max (mm)	*W*	*p*	*D*	*p*
Clam size comparisons from areas where sea otters were present vs. absent, in different time periods										
Quadra (3500-1500) and Broughton (3500-1500)	37 and 42	26 and 35	33 and 38	42 and 45	57 and 48	51 and 49	282	0.05	0.4326	0.07
Quadra (1500-150) and Broughton (1500-150)	41 and 42	25 and 26	36 and 36	47 and 45	60 and 49	63 and 55	34182	0.39	0.1768	**<0.013**
Clam size comparisons through time, within each areas										
Quadra (3500-1500) and Quadra (1500-150)	37 and 41	26 and 25	33 and 36	42 and 47	57 and 60	51 and 63	20592	**<0.013**	0.2516	**<0.013**
Broughton (3500-1500) and Broughton (1500-150)	42 and 42	35 and 26	38 and 36	45 and 45	48 and 49	49 and 55	587	0.62	0.1991	0.86

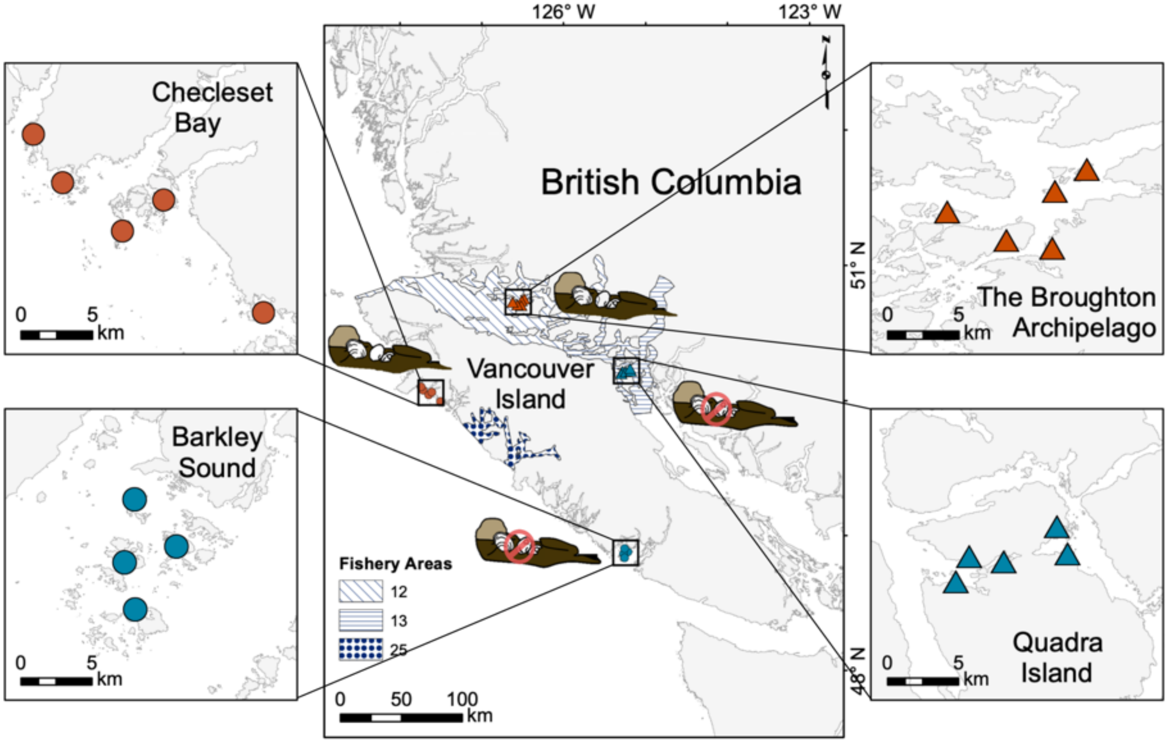


Fig. 4. 1. Study areas used to evaluate the effects of sea otters on contemporary and ancient clam lengths. Circles show contemporary sites and triangles show ancient sites. Red circles show sites where otters were present and blue circles show sites were otters were absent. At each of the filled circles in Checleset Bay and Barkley Sound, contemporary live clams, clam shells, and sea otter pits were measured. At each of the filled triangles in the Broughton Archipelago and on Quadra Island, ancient clams in archaeological assemblages were measured. The archaeological site designations (or Borden numbers, each corresponds with a filled triangle) are listed below, from west to east, along with sea otter bones, as a percentage of non-cetacean marine mammal bones in brackets: Broughton Archipelago; EeSp-95 (28%); EeSp-48 (absent); EeSo-1 (5%); EeSo-19 (absent); EeSo14C (1.5%). Quadra Island; EbSh-14 (absent); EbSh-13 (absent); EbSh-8 (absent); EbSh-21 (absent); EbSh-87 (absent). Fishery areas are shown with striped polygons, where contemporary clam samples and data were collected by Fisheries and Oceans Canada from 1980s-2000s after sea otters had been extirpated from the Broughton Archipelago.

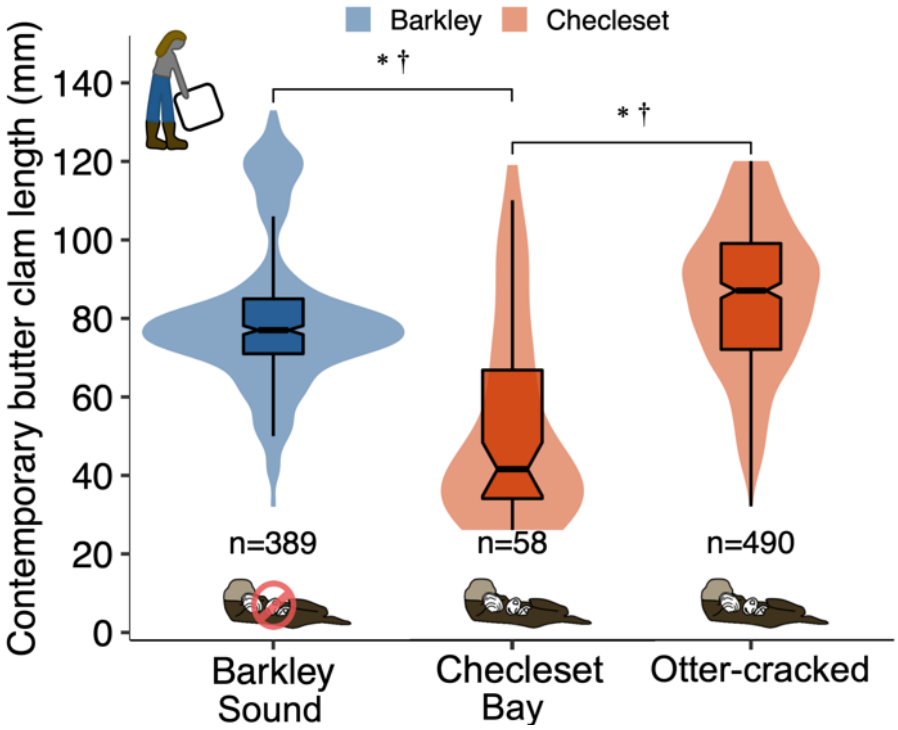


Fig. 4. 2. Contemporary butter clam (*Saxidomus gigantea*) lengths from Barkley Sound, where sea otters were absent (blue) and in Checleset Bay, where sea otters were present (red), and otter-cracked clams where otters were present. Box plots depict median length (center line), and 25th and 75th percentiles (box edges). Whiskers extend to the largest and smallest values within 1.5 times the interquartile range above (below) the 75th (25th) percentiles. Shaded violin plots depict kernel density estimates based on *Silverman's rule of thumb* (Silverman 1986) and show a vertical, smoothed, histogram of the raw data, and do not extend past data points. Asterisks denote statistical significance based on Wilcoxon Rank-Sum tests where α was 0.05, and obelisks denote statistical significance based on Kolmogorov-Smirnov tests, where α was 0.05.

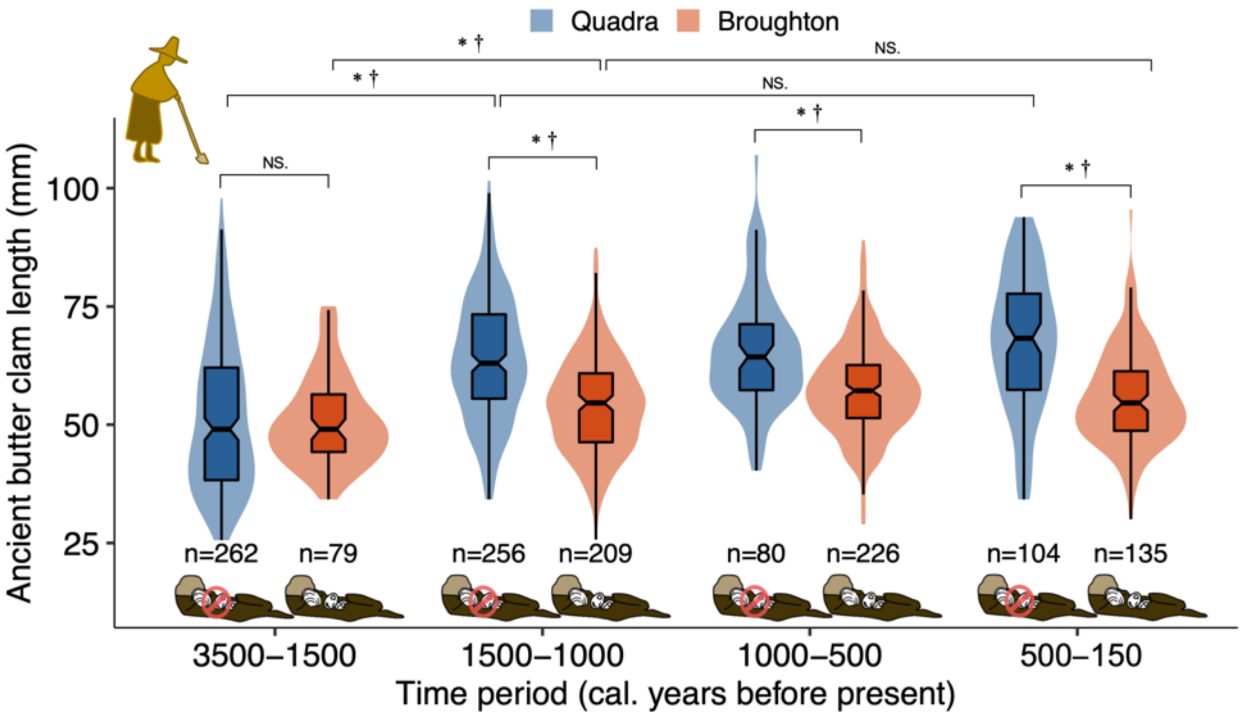


Fig. 4. 3. Ancient butter clam (*Saxidomus gigantea*) lengths from archaeological assemblages on Quadra Island, where sea otters were absent (blue) and in the Broughton Archipelago, where sea otters were present (red). Box plots depict median length (center line), and 25th and 75th percentiles (box edges). Whiskers extend to the largest and smallest values within 1.5 times the interquartile range above (below) the 75th (25th) percentiles. Shaded violin plots depict kernel density estimates based on *Silverman's rule of thumb* (Silverman 1986) and show a vertical, smoothed, histogram of the raw data, and do not extend past data points. Asterisks denote statistical significance based on Wilcoxon Rank-Sum tests where α was 0.006 and obelisks denote statistical significance based on Kolmogorov-Smirnov tests where α was 0.006.

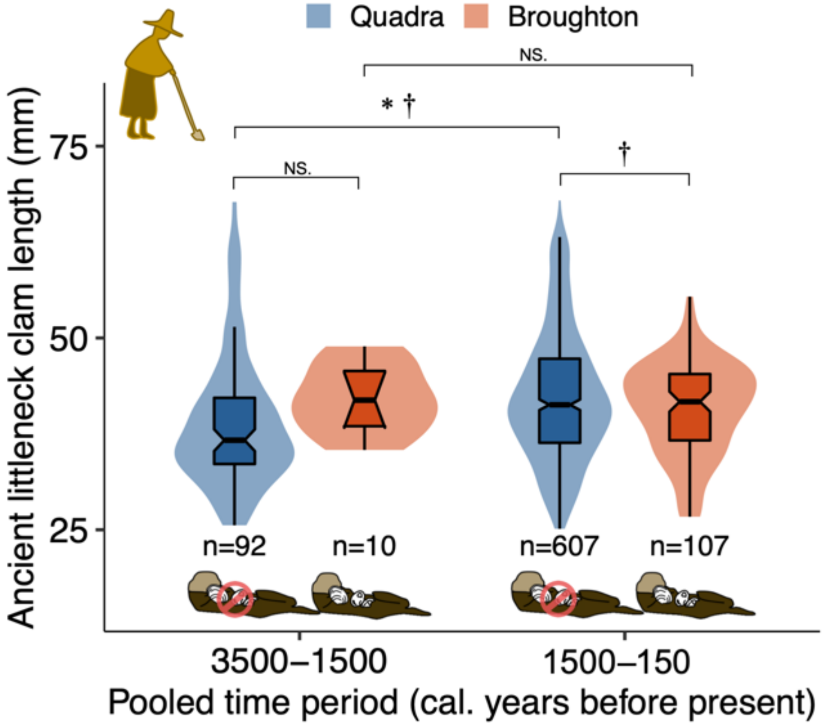


Fig. 4. 4. Ancient littleneck (*Leuconoma staminea*) clam lengths from archaeological assemblages on Quadra Island, where sea otters were absent (blue) and in the Broughton Archipelago, where sea otters were present (red). Box plots depict median length (center line), and 25th and 75th percentiles (box edges). Whiskers extend to the largest and smallest values within 1.5 times the interquartile range above (below) the 75th (25th) percentiles. Shaded violin plots depict kernel density estimates based on *Silverman's rule of thumb* (Silverman 1986) and show a vertical, smoothed, histogram of the raw data, and do not extend past data points. Asterisks denote statistical significance based on Wilcoxon Rank-Sum tests where α was 0.00125 and obelisks denote statistical significance based on Kolmogorov-Smirnov tests where α was 0.00125.

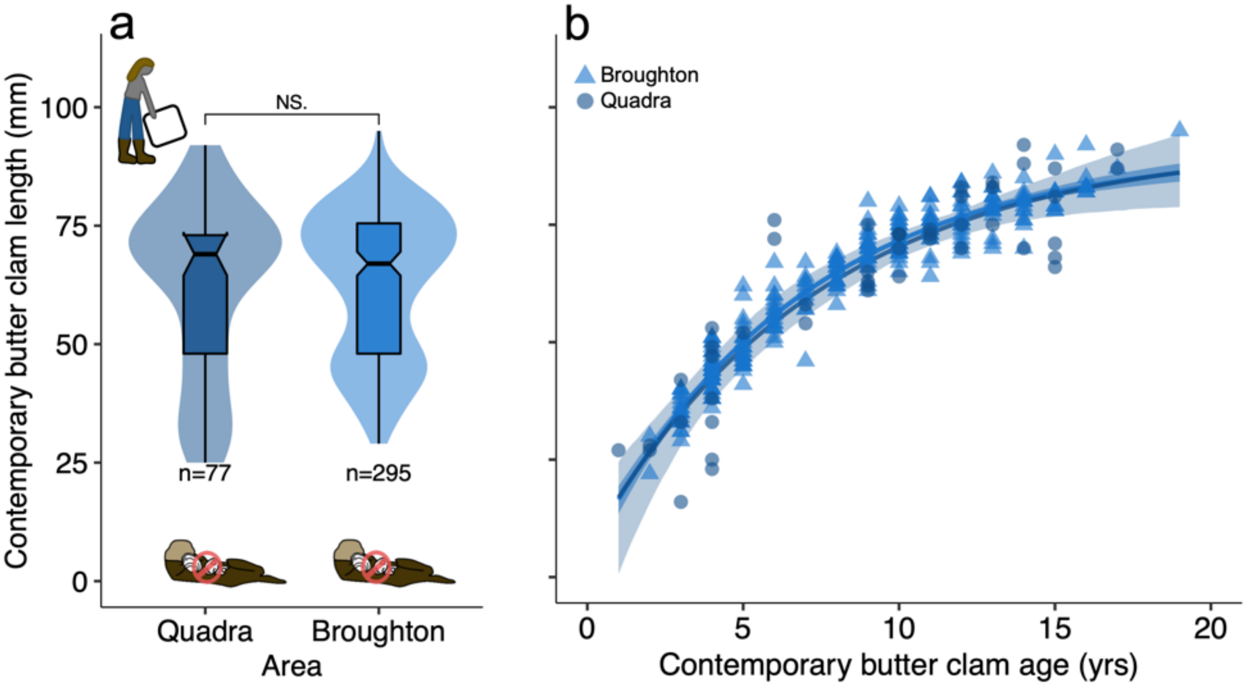


Fig. 4. 5. Panel (a) shows contemporary butter clam (*Saxidomus gigantea*) measurements made from 1982-2013 in Fishery Areas 12 and 13, which include the Broughton Archipelago and Quadra Island, respectively. When these contemporary measurements were made, sea otters were absent from Quadra Island (as they were in archaeological assemblages) and had been extirpated from the Broughton Archipelago for more than 100 years (as opposed to being present there, as in the archaeological assemblages). Shaded violin plots depict kernel density estimates based on *Silverman's rule of thumb* (Silverman 1986) and show a vertical, smoothed, histogram of the raw data, and do not extend past data points. The same data, plus clam measurements <25 mm, were used to model von Bertalanffy growth curves in panel (b). Shaded areas show the 95% confidence intervals around the contemporary clam growth curves; curves from the two areas are nearly indistinguishable.

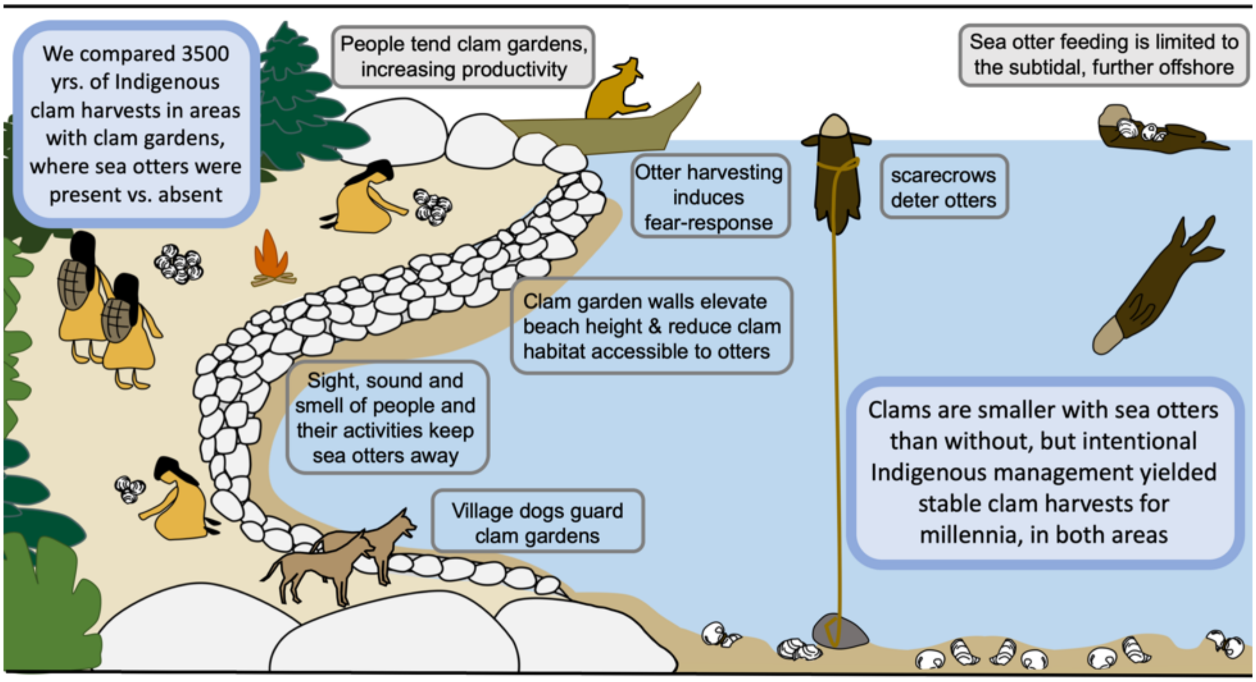


Fig. 4. 6. An illustration of intentional ancestral practices that limited sea otter access to clams. The clam garden walls elevate the lowest intertidal beach habitat, expanding the area of ideal clam habitat and making it more accessible to people, and less accessible to sea otters. Clam cultivation and tending of clam gardens increased productivity of the clam garden (Groesbeck et al. 2014; Jackley et al. 2016). Human-mediated enrichment of sediments enhanced recruitment of clam larvae and post recruitment survival (Slater 2018). Sea otters were relegated to subtidal habitats, further offshore, whereas people harvested clams in the intertidal. Dogs, active hunting, and dead sea otters intentionally anchored just offshore from valuable harvesting sites (i.e., scarecrows) were used to deter otters (Hup n yook Tom Happynook and K̲ii’iljuus Barbara Wilson in Salomon et al. 2018). Activities associated with humans, such as campfires, contributed to a landscape of fear, further deterring sea otters. Illustration by EUF.

4.8 Supplementary Materials

Methods and Results

Contemporary associations between sea otter presence and butter clam lengths

Study areas and sea otter treatments. We sampled butter clams from five sites within Ecological Reserve 109, in Checleset Bay, which was (and remains) an area occupied by sea otters since their reintroduction in the late 1960s, and four sites in the Broken Group Island region of Pacific Rim National Park Reserve, in Barkley Sound, which was (and remains) an area without sea otters (Fig. 4.1).

Live clam sampling. Clams in the intertidal zone were sampled by digging quadrats at low tide, whereas a water stream was used to excavate quadrats underwater. The quadrat was a bottomless welded-aluminum box, pushed into the sediment to 15 cm depth and held in place by four steel pins. In subtidal samples, divers used a 3 HP Honda fire pump to excavate quadrats to 50 cm sediment depth. Water was pumped through 35 m of flexible fiberglass fire hose, and 5 m of reinforced PVC hose. A 1 m length of PVC pipe with a gate valve at the end was used to direct and regulate water flow – similar to equipment used by surface-supplied commercial geoduck (*Panopea generosa*) divers. The water stream was used to excavate the sediment and all clams were collected as they "floated" to the sediment surface.

Substrate disturbance. We swam 1-3 transects from the upper intertidal to 30 ft (~10 m) depth at each site in Checleset Bay, and measured each sea otter pit we encountered within 2 m of the transect. Sea otter pits were identified by the piling of sediment to one end of the pit (Fig. 4.S2b-c), which allowed us to distinguish sea otter pits from those left by sea ducks, sea stars (Asteroidia), or crabs (*Cancer* spp.). Transects were laid out roughly perpendicular to the beach and covered three depth categories (0-10 ft.; 10-20 ft.; and 20-30 ft.). We recorded the total transect length in each depth category 498 m at 0-10 ft; 931 m at 10-20 ft., and 728 m at 30 ft. We measured the longest axis of each sea otter pit we encountered. We calculated disturbance as a proportion of total m pits out of the total m surveyed at each depth on each transect (n = number of transects per depth category). We used a one-way ANOVA on arc-sin transformed data to ask whether or not sea otter disturbance differed significantly by depth category.

Butter clam lengths in relation to depth. In both Barkley Sound and Checleset Bay, live butter clams were smaller in the intertidal zone than in the subtidal zone. In Barkley Sound, median (PC_{75})

intertidal butter clam lengths were 75 mm (PC_{75} = 80), which was significantly smaller than the median lengths of subtidal butter clams 115 mm (PC_{75} = 121; W = 2408, p <0.001). Butter clam size distributions were also significantly different between intertidal and subtidal depths (D = 0.78; p <0.001) (Fig. 4.S6a). Similarly, in Checleset Bay, intertidal butter clams were 39 mm (PC_{75} = 50), which were significantly smaller than subtidal butter clams, which were 96 mm (PC_{75} = 104; W = 19.5, p <0.001), and size distributions were significantly different (D = 0.82; p <0.001) (Fig. 4.S6b). Because sea otters feed on clams in both the intertidal and subtidal areas, we pooled clam measurement across both these depths for subsequent contemporary analyses.

Ancient butter clam lengths between otter-present and otter-absent sites 3500-150 years ago

Archaeological column samples and radiocarbon dating. Stratigraphic profiles were available for all but one excavation (EeSo-1, E.U.2, 5.9 m deep). A single piece of charcoal (~0.5 x 0.5 x 0.25 mm) sampled from the top and bottom of each column, was radiocarbon dated using Accelerator Mass Spectrometry (AMS) at the André E. Lalonde AMS Laboratory, University of Ottawa. Additional charcoal samples were subjectively selected for dating where there were high concentrations of clams in a layer, or if there was more than 1 m of undated shell midden accumulation, with most columns receiving 3 to 5 dates (Figs. 4.A1-9).

We categorized clams into socially, ecologically, and climatically relevant time periods that also ensured adequate sample sizes and replication across columns. We grouped clams into the following time periods: 3500-1500; 1500-1000; 1000-500; 500-150 calibrated years before present (cal BP); “present” refers to 1950 AD, the end of the radiocarbon curve. The earliest period, 3500-1500 cal BP, includes some of the oldest as-yet dated clam gardens on Quadra Island (Smith *et al.* 2019), and covers period of exponential increases in human settlements detected on the BC coast (Ames & Maschner 1999) as well as increasing human-mediated ecological interactions on Quadra Island (Toniello *et al.* 2019). In this period, SST in the northeast Pacific oscillated from 9-11 °C (Kienast & McKay 2001). The next time period, 1500-1000 cal BP, includes the *Medieval Warm Period*, and SST in the northeast Pacific was steady at ~10.5 °C (Kienast & McKay 2001); this time period includes the peak abundance of coastal settlements (Ames & Maschner 1999). The more recent time period, 1000-500 cal BP, includes the start of the *Little Ice Age* and recent glacial maxima in nearby mountain ranges (Lewis & Smith 2004; Koch *et al.* 2007) with SST in the northeast Pacific declining fairly steadily from 10.5 to 10 °C (Kienast & McKay 2001). The most recent time period, 500-150 cal BP, is a mixed sample, complicated by the flatness of the radiocarbon curve

(Reimer *et al.* 2020) smallpox epidemics (Boyd 1994; Harris 1994), declines in traditional resource management (Deur *et al.* 2015; Toniello *et al.* 2019) as well as the ecological extinction (by ~1820-1850 AD) of sea otters in BC (Watson 2000; Sloan & Dick 2012); and continued cooling SST (to 9.5 °C; Kienast and McKay 2001).

Butter clam umbo thickness to shell length regression. To predict clam length from umbo thickness, we fit a saturating curve in the *nls()* function in *R*, using the least squares method (Equation 4.1 and Fig. 4.S7). We estimated confidence intervals around the saturating curve using the *predictNLS()* function in the *propagate* package in R.

Equation 4.1. $$\text{Length} = (369.21 \times \text{umbo thickness}) / (29.38 + \text{umbo thickness})$$

This equation was used to estimate the lengths of butter clams that could not be directly measured. We used the 225 clams with an intact umbo and lengths from the archaeological assemblages to fit this regression, and also included 115 contemporary butter clams collected from Quadra Island and the central BC coast in 2015-2016 (n = 340 total clams in regression) to expand the length ranges from those that were prevalent in archaeological samples (e.g., Slade 2019).

Observer measurement discrepancies. We limited inter-observer measurement discrepancies by having two authors measure 96% of the clams we used (AT: 72%, and EF: 23%). However, to include multiple time periods at EbSh-13 and EbSh-14, we used previously measured clam lengths from MP, which totaled an additional 68 whole butter clams (5%). We estimated differences between measurements made by AT and EF by randomly subsampling 70 (5.3% of total) whole butter clams and each measuring the same individuals. We calculated the absolute differences in our replicated measurements and examined these for positive or negative skews (Fig. 4.S3a-b). We also regressed our individual measurements of umbo thickness to umbo thickness and length to length (R^2 = 0.97 and 0.99 respectively; Fig. 4.S3c-d).

Allometric relationship of contemporary butter clam length to biomass. We examined the relationship between butter clam length and mass from collections made by DFO in Fishery Areas 12 and 13 from 1990-2002 (methods for measuring clam biomass differed in the 1980s compared to the 1990s). Individual clams were weighed in the lab after being frozen in the field (Gillespie & Kronlund 1999) and lengths were measured as in Fig. 4.S1. We fit a power function with the *nls()* function in *R* (Equation 4.2).

Equation 4.2. $$\text{Mass} = 7.5\text{e-}5 * \text{Length}^{(3.31)}$$

We estimated confidence intervals around the saturating curve using the *predictNLS()* function from the *propagate* package in R.

Research Permits.

We conducted no new fieldwork for this research but list relevant permissions related to all data sets we used. Permissions were granted to JW in 1993 to conduct clam research in Pacific Rim National Park. Excavations from the Broughton Archipelago were completed under permit #1973-6. Archaeological excavations from Quadra Island were completed under HCA Permit #2014-0095. We collaborated with the Musgamagw Dzawada'enuxw Fisheries Group to access and interpret the archaeological samples previously collected from the Broughton Archipelago.

Supplementary Figures & Tables

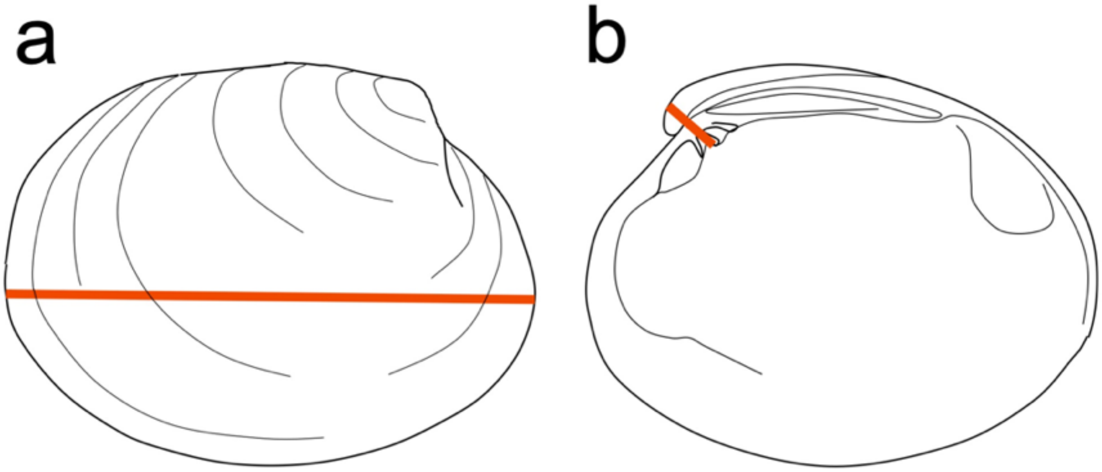


Fig. 4.S1. Panel (a) shows the measurement axis for clam length. Panel (b) shows the measurement axis for umbo thickness. Illustration by Alessandra Testani.

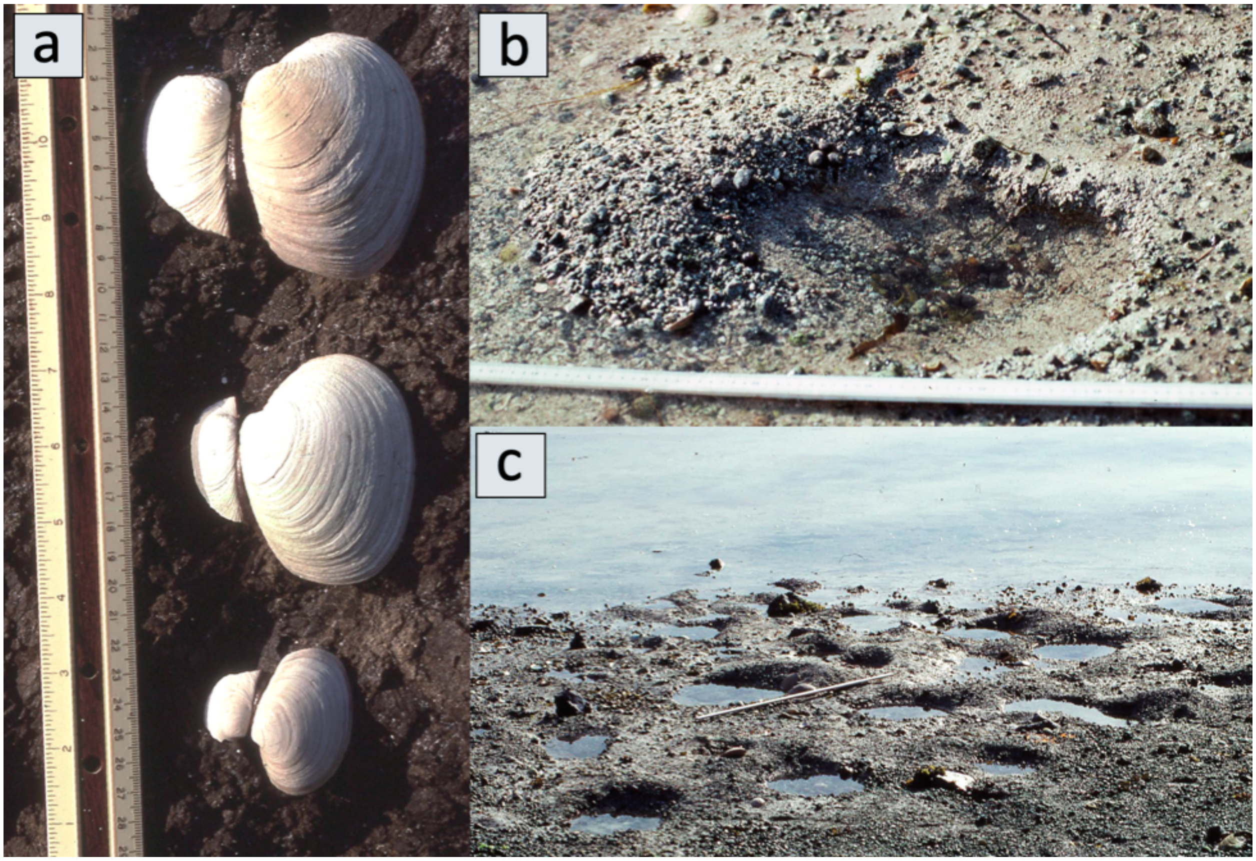


Fig. 4.S2. Panel (a) shows butter clam (*Saxidomus gigantea*) shells categorized as otter-cracked based on distinctive single-valve breakage (Kvitek et al. 1992). Panel (b) shows a sediment pile and a pit that was dug by an otter – sediment piling was used to discern pits dug by sea otters from those dug by sea ducks, sea stars (Asteroidia), or crabs (*Cancer* spp.). Panel c shows part of a substrate-disturbance transect with average pit densities. Photographs by Jane Watson and Leah Saville, in Checleset Bay, 1993.

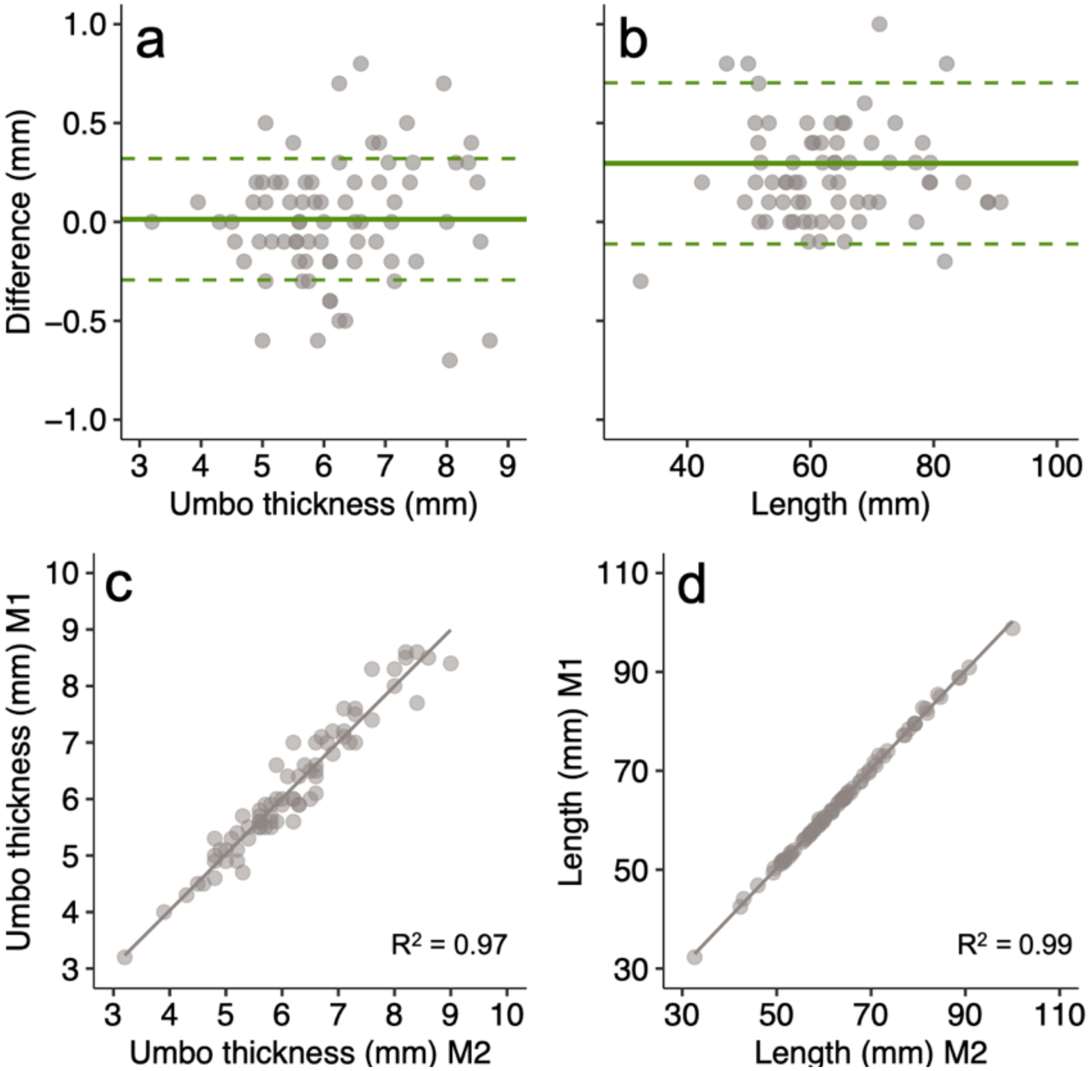


Fig. 4.S3. Differences between observer measurements of umbo thickness (a) and length (b), and regressions of umbo thickness between observers (c) and regressions of length between two observers (d). M1 = measurer 1 and M2 = measurer 2.

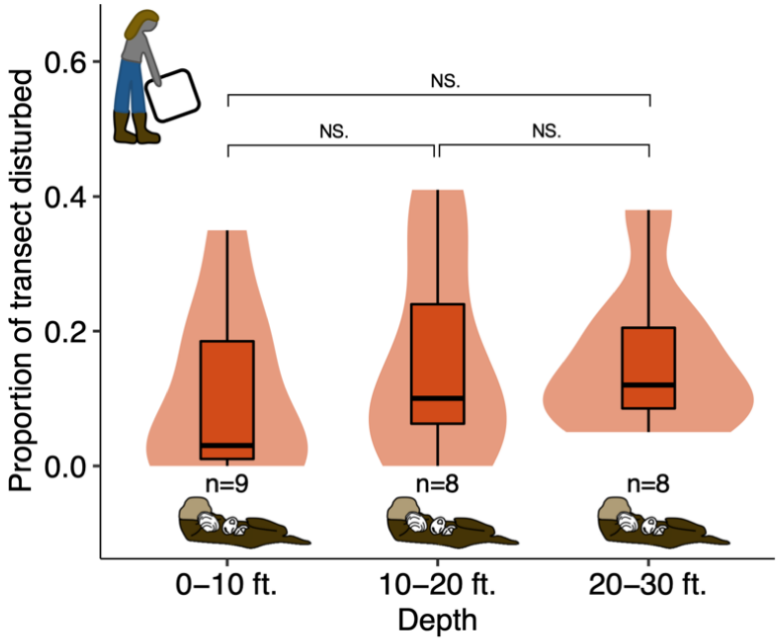


Fig. 4.S4. Proportion of the transect area disturbed by foraging sea otters in Checleset Bay, in 1993, where sea otters were established. Differences were insignificant. The thick centre line on boxplots shows the median length, box edges show the 25th and 75th percentiles. Whiskers extend to the largest and smallest values within 1.5 times the interquartile range above (below) the 75th (25th) percentiles. Shaded violin plots depict kernel density estimates based on *Silverman's rule of thumb* (Silverman 1986) and show a vertical, smoothed, histogram of the raw data, and do not extend past data points.

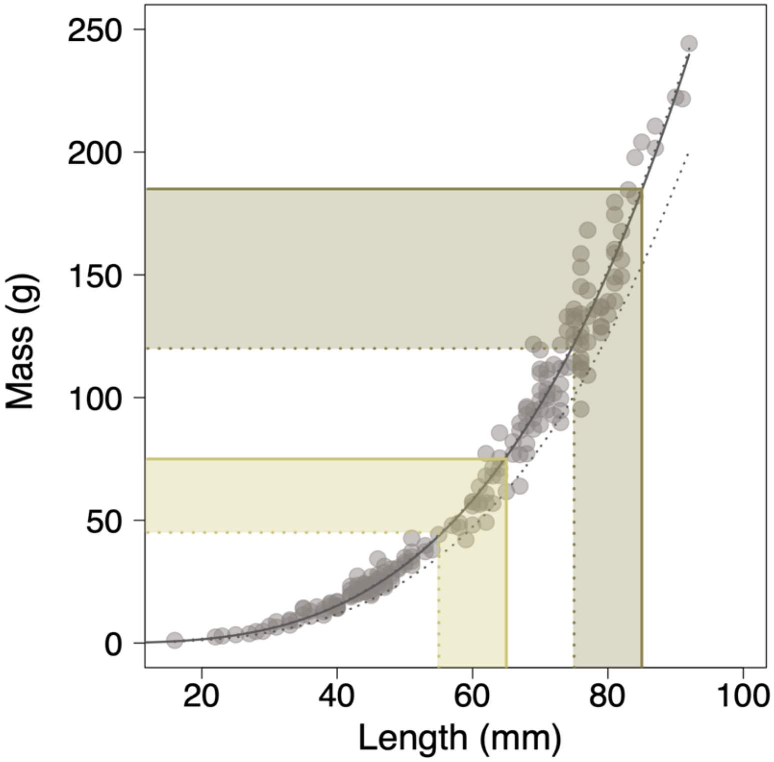


Fig. 4.S5. Allometric relationship of length and mass of butter clams (*Saxidomus gigantea*) collected from Fishery Areas 12 and 13 from 1990-2004. Light green shading represents the mass differences associated with a 10 mm increase in length from 55-65 mm, which approximates differences in ancient median clam lengths from areas with and without otters. Dark green shading represents the mass differences associated with a 10 mm increase in length from 75-85 mm, which approximates differences in ancient 75th percentile clam lengths from areas with and without otters. Dotted lines around the curve represent the 95% Confidence Interval.

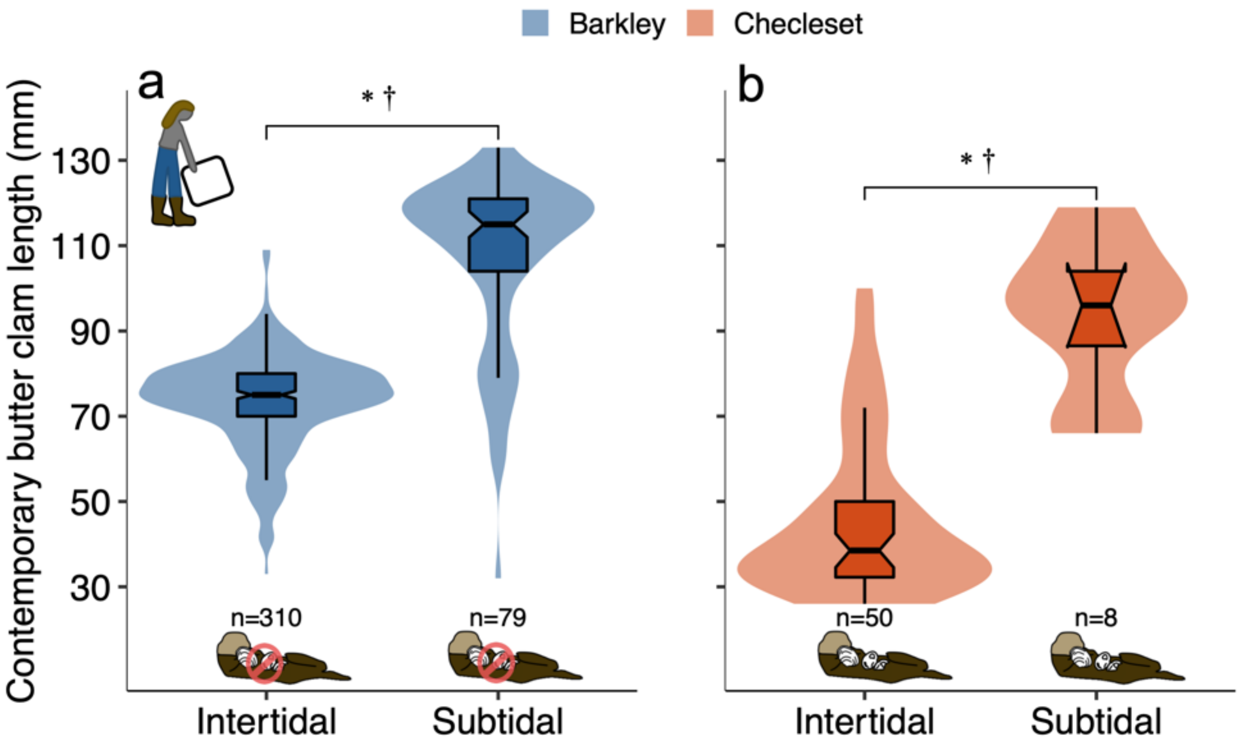


Fig. 4.S6. Butter clam (*Saxidomus gigantea*) lengths from collections made in 1993, in Barkley Sound, where sea otters were absent (blue, panel [a]) and in Checleset Bay, where sea otters were present (red, panel [b]). Asterisks denote statistical significance based on Wilcoxon Rank-Sum tests where α was 0.05, and obelisks denote statistical significance based on Kolmogorov-Smirnov tests where α was 0.05. Thick centre line on boxplots shows the median length, box edges show the 25th and 75th percentiles. Whiskers extend to the largest and smallest values within 1.5 times the interquartile range above (below) the 75th (25th) percentiles. Shaded violin plots depict kernel density estimates based on *Silverman's rule of thumb* (Silverman 1986) and show a vertical, smoothed, histogram of the raw data, and do not extend past data points.

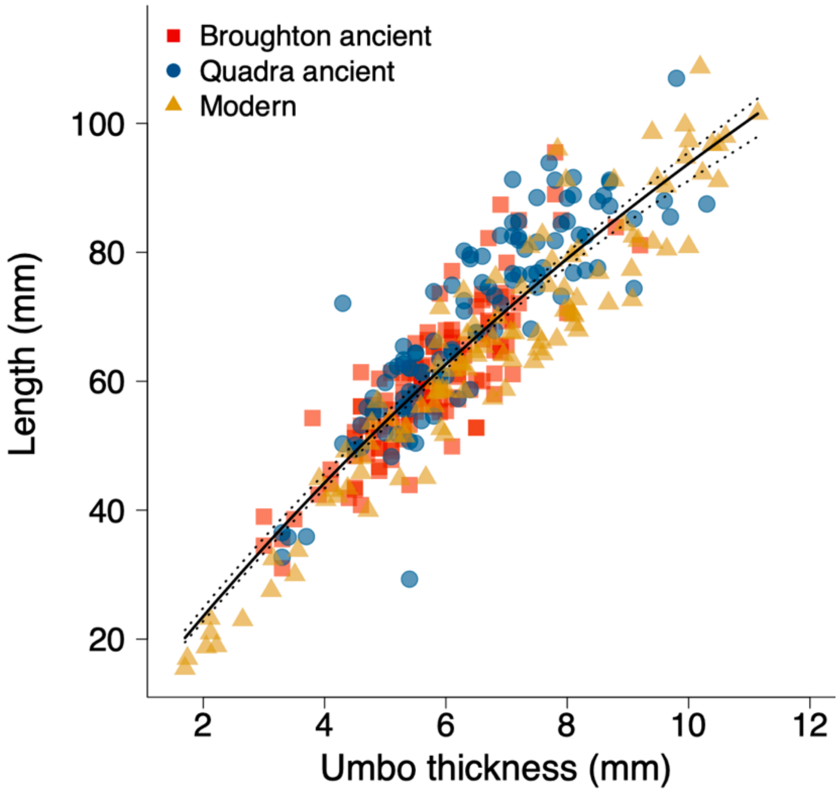


Fig. 4.S7. Saturation curve showing regression between butter clam (*Saxidomus gigantea*) umbo thickness and clam length where both axes could be measured. The curve was generated using the nls() function in R 3.6.1 (R Core Team, 2019) and the 95% confidence intervals of the curve were calculated with the *predictNLS()* function in the *propagate* package. Equation of the saturating curve is *Length = (369.21 x umbo thickness) / (29.38 + umbo thickness)*.

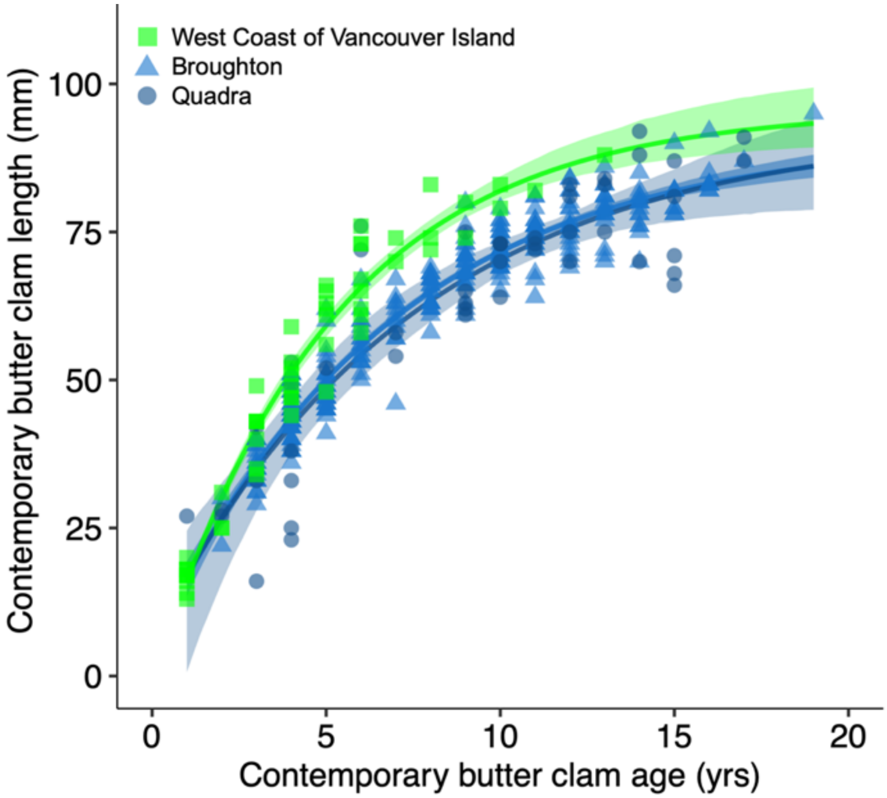


Fig. 4.S8. Comparison of butter clam (*Saxidomus gigantea*) growth curves using length-at-age measurements from 1990-2002 (collected by Fisheries and Oceans Canada) and 2013 (collected by GT), in Fishery Areas 12 (incl. Broughton Archipelago), 13 (includes Quadra Island), and 25 (between Checleset Bay and Barkley Sound, west coast of Vancouver Island). This figure shows the same data as shown in Figure 4.5b, but includes data from the west coast of Vancouver Island where clam-growing conditions differ from those in the Broughton Archipelago and Quadra Island. Shaded areas show the 95% confidence intervals around the growth curves.

Table 4.S1. Radiocarbon calibration and errors (1σ). Calibration was performed using OxCal v4.4 (Bronk Ramsey, 2009) and the IntCal20 calibration curve (Reimer et al., 2020).

Lab ID	Borden number	Column ID	Label/Depth	Material	14C yr BP	±	cal BP	Median Probability cal BP	Published
Broughton Archipelago									
UOC-13580	EeSo-1	EU2	A/080-090	charcoal	180	27	293-255 (19.4%) 226-138 (52.7%) 112-73 (4.7%) <35 (18.7%)*	**183**	This study
UOC-13980	EeSo-1	EU2	A/120-130	charcoal	1468	30	1391-1303 (95.4%)	**1348**	This study
UOC-13581	EeSo-1	EU2	A/170-180	charcoal	1603	29	1535-1406 (95.4%)	**1472**	This study
UOC-13582	EeSo-1	EU2	A/260-270	charcoal	1722	27	1700-1655 (28.8%) 1640-1541 (66.6%)	**1608**	This study
UOC-13981	EeSo-1	EU2	A/360-370	charcoal	2159	28	2305-2229 (36.3%) 2202-2199 (0.3%) 2181-2046 (57.1%) 2020-2007 (1.8%)	**2147**	This study
UOC-13583	EeSo-1	EU2	A/570-580	charcoal	2948	28	3209-3190 (3.7%) 3184-2999 (91.8%)	**3108**	This study
UOC-13586	EeSo-14c	EU2 west wall	FS01	charcoal	217	26	308-266 (35.9%) 217-146 (52.3%) <22 (7.3%)*	**191**	This study
UOC-13978	EeSo-14c	EU2 west wall	FS07	charcoal	351	27	491-421 (40.8%) 410-315 (54.6%)	**391**	This study
UOC-13587	EeSo-14c	EU2 west wall	FS12	charcoal	610	28	651-547 (95.4%)	**603**	This study
UOC-13584	EeSo-14c	EU4 east wall	SS02	charcoal	161	27	287-248 (16.5%) 230-165 (33.6%) 158-134 (9.8%) 118-60 (15.4%) <43 (20.1%)*	**172**	This study
UOC-13979	EeSo-14c	EU4 east wall	SS05	charcoal	581	27	645-585 (66.5%) 567-535 (28.9%)	**603**	This study
UOC-13585	EeSo-14c	EU4 east wall	SS10	charcoal	667	26	671-630 (51.2%) 593-560 (44.2%)	**633**	This study
UOC-13982	EeSo-19	south wall	A/000-060	charcoal	679	26	674-633 (58.9%) 591-562 (36.6%)	**648**	This study
UOC-13576	EeSo-19	south wall	A/060-075	charcoal	377	27	501-426 (59.6%) 391-319 (35.9%)	**446**	This study
UOC-13577	EeSo-19	south wall	A/200-215	charcoal	795	26	732-675 (95.4%)	**705**	This study
UOC-13578	EeSo-19	south wall	A/270-285	charcoal	1302	27	1290-1176 (95.4%)	**1227**	This study
UOC-13579	EeSo-19	south wall	A/320-340	charcoal	1350	26	1308-1260 (74.5%) 1254-1248 (1.1%) 1209-1176 (19.9%)	**1284**	This study
UOC-13976	EeSp-48	TC1 east wall	A/000-020	charcoal	954	27	921-792 (95.4%)	**849**	This study
UOC-13588	EeSp-48	TC1 east wall	A/020-040	charcoal	955	28	922-792 (95.4%)	**850**	This study
UOC-13589	EeSp-48	TC1 east wall	A/080-100	charcoal	1220	27	1248-1210 (14.0%) 1179-1064 (81.4%)	**1137**	This study
UOC-13977	EeSp-48	TC1 east wall	A/200-210	charcoal	1277	26	1286-1173 (92.1%) 1159-1149 (1.8%) 1140-1131 (1.6%)	**1225**	This study
UOC-13983	EeSp-95	TC2 south wall	A/402-412	charcoal	156	27	285-242 (16.4%) 232-166 (30.7%) 157-130 (9.9%) 119-57 (18.8%) <45 (19.7%)	**155**	This study
UOC-13573	EeSp-95	TC2 south wall	A/428-429	charcoal	155	27	285-241 (16.4%) 232-166 (29.8%) 156-129 (9.9%) 119-57 (19/8%)*	**151**	This study
UOC-13574	EeSp-95	TC2 south wall	A/488-498	charcoal	352	26	490-421 (40.9%) 409-315 (54.6%)	**391**	This study
UOC-13575	EeSp-95	TC2 south wall	A/586-596	charcoal	508	27	551-505 (95.4%)	**528**	This study

table con't

Lab ID	Borden number	Column ID	Label/Depth	Material	14C yr BP	±	cal BP	Median Probability cal BP	Published
Quadra Island									
UOC-13974	EbSh-8	Col3-2016	70-78 DBD	charcoal	191	26	300-257 (22.7%) 225-139 (56.5%) <33 (16.3%)	**184**	This study
UOC-14125	EbSh-8	Col3-2016	166-185 DBD	charcoal	298	28	453-350 (68.9%) 337-294 (26.5%)	**388**	This study
UOC-14126	EbSh-13	Col2-2016	25-40 cm DBD	charcoal	1276	29	1286-1174 (88.9%) 1160-1129 (6.6%)	**1223**	This study
AMS#-182891	EbSh-13	Col2-2016	115-125 cm DBD	shell	2700	15	1809-2275 (100%)	**2014**	*Crowell 2016*
UOC-14127	EbSh-14	Col4-2016	90-100 cm DBS	charcoal	2515	29	2730-2670 (23.6%) 2656-2611 (18.8%) 2601-2492 (53.0%)	**2587**	This study
UOC-14128	EbSh-14	Col4-2016	152-162 cm DBS	charcoal	2886	30	3150-3091 (9.7%) 3081-2927 (84.1%) 2900-2885 (1.7%)	**3017**	This study
UOC-14129	EbSh-14	Col4-2016	210-220 cm DBS	charcoal	2889	27	3150-3091 (10.2%) 3081-2933 (85.3%)	**3021**	This study
UOC-13971	EbSh-21	Col5-2016	20-30 cm DBD	charcoal	1509	25	1468-1459 (1.1%) 1414-1341 (90.6%) 1331-1311 (3.7%)	**1377**	This study
UOC-13972	EbSh-21	Col5-2016	81-91 cm DBD	charcoal	923	25	915-772 (92.2%) 759-746 (3.3%)	**847**	This study
UOC-14130	EbSh-87	Col1-2016	45-55 cm DBD	charcoal	369	28	497-424 (52.7%) 395-318 (42.8%)	**433**	This study
AMS#-182775	EbSh-87	Col1-2016	75-80 cm DBD	charcoal	705	15	656-679 (100%)	**669**	*Crowell 2016*
UOC-13973	EbSh-87	Col1-2016	168-173 DBD	charcoal	1365	25	1342-1330 (2.2%) 1312-1267 (87.8%) 1205-1191 (4.8%) 1183-1179 (0.7%)	**1292**	This study

4.9 Appendix A

Figures 4.A1-4.A9; stratigraphic profiles of archaeological excavations with associated radiocarbon dates.

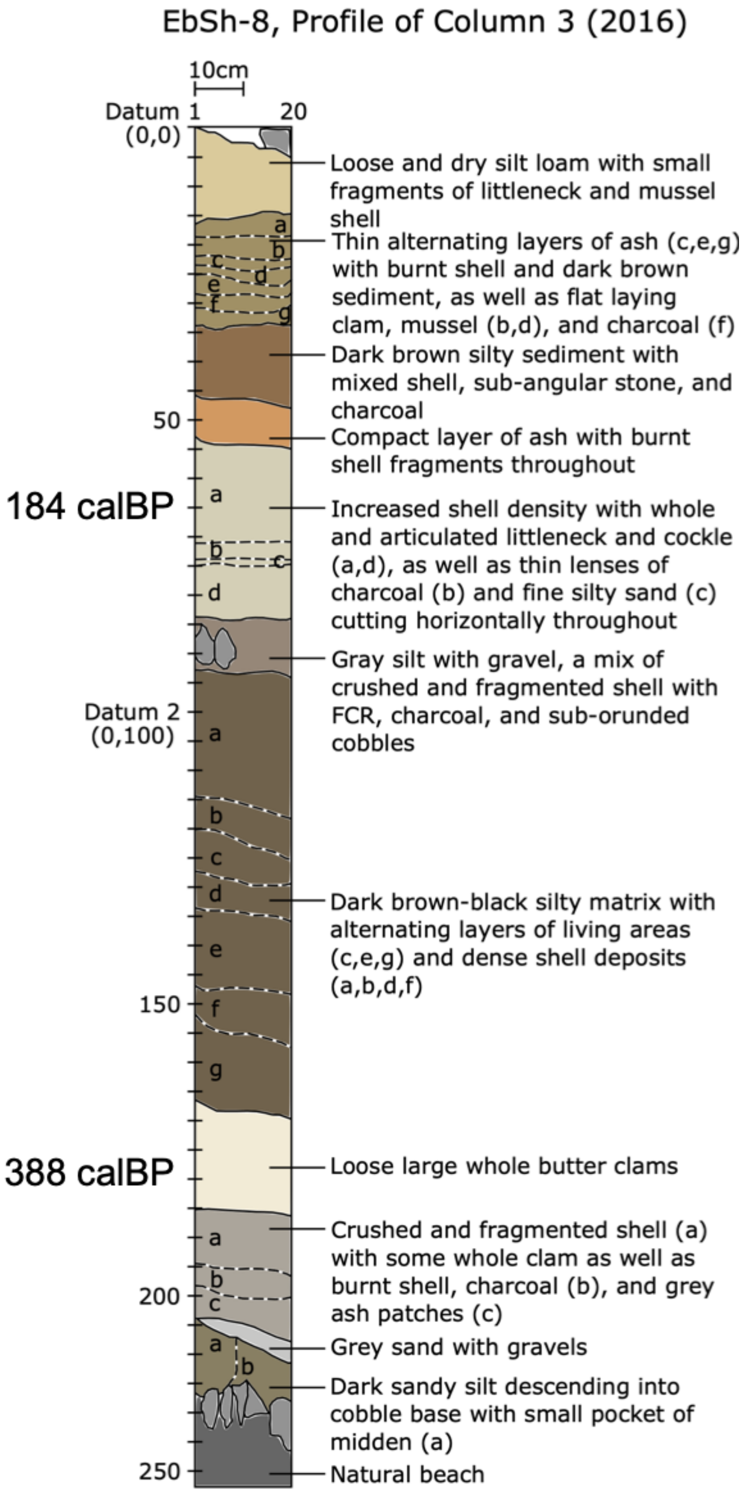


Fig. 4.A1. Quadra Island Column Profile from EbSh-8, Column 3-2016. Median calibrated radiocarbon dates shown along left margin. Adapted from Toniello and Crowell (2020). Digitized Illustration by Madison Skala.

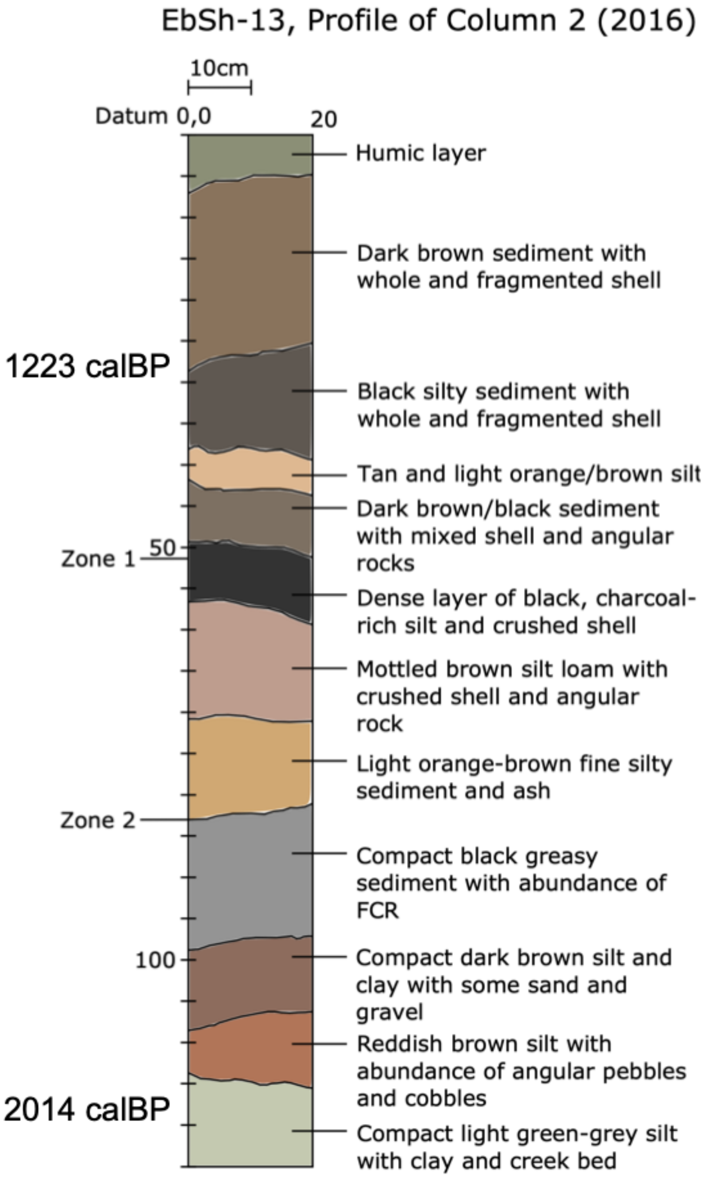


Fig. 4.A2. Quadra Island Column Profile from EbSh-13, Column 2-2016. Median calibrated radiocarbon dates shown along left margin Adapted from Toniello and Crowell (2020). Digitized Illustration by Madison Skala.

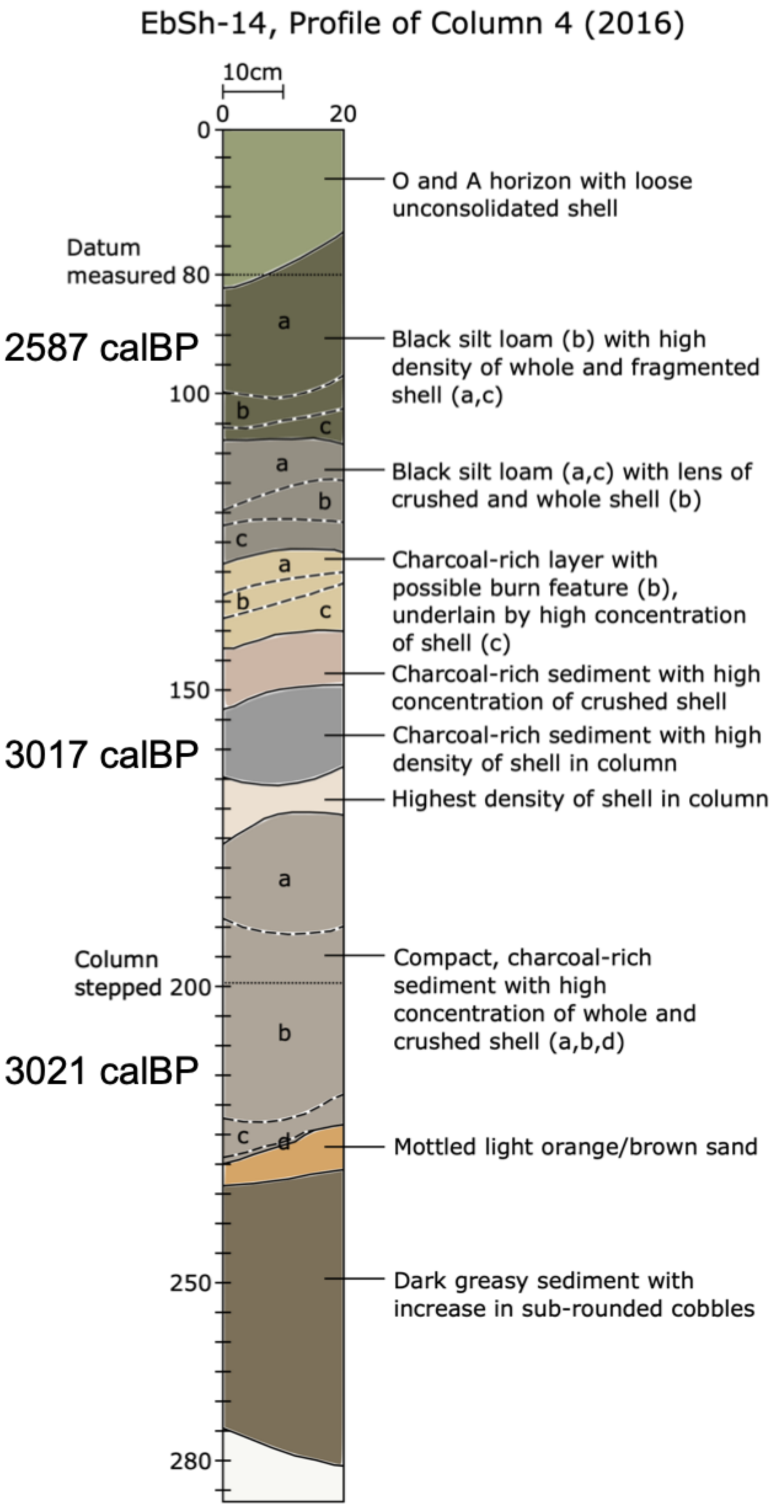


Fig. 4.A3. Quadra Island Column Profile from EbSh-14, Column 4-2016. Median calibrated radiocarbon dates shown along left margin. Adapted from Toniello and Crowell (2020). Digitized Illustration by Madison Skala.

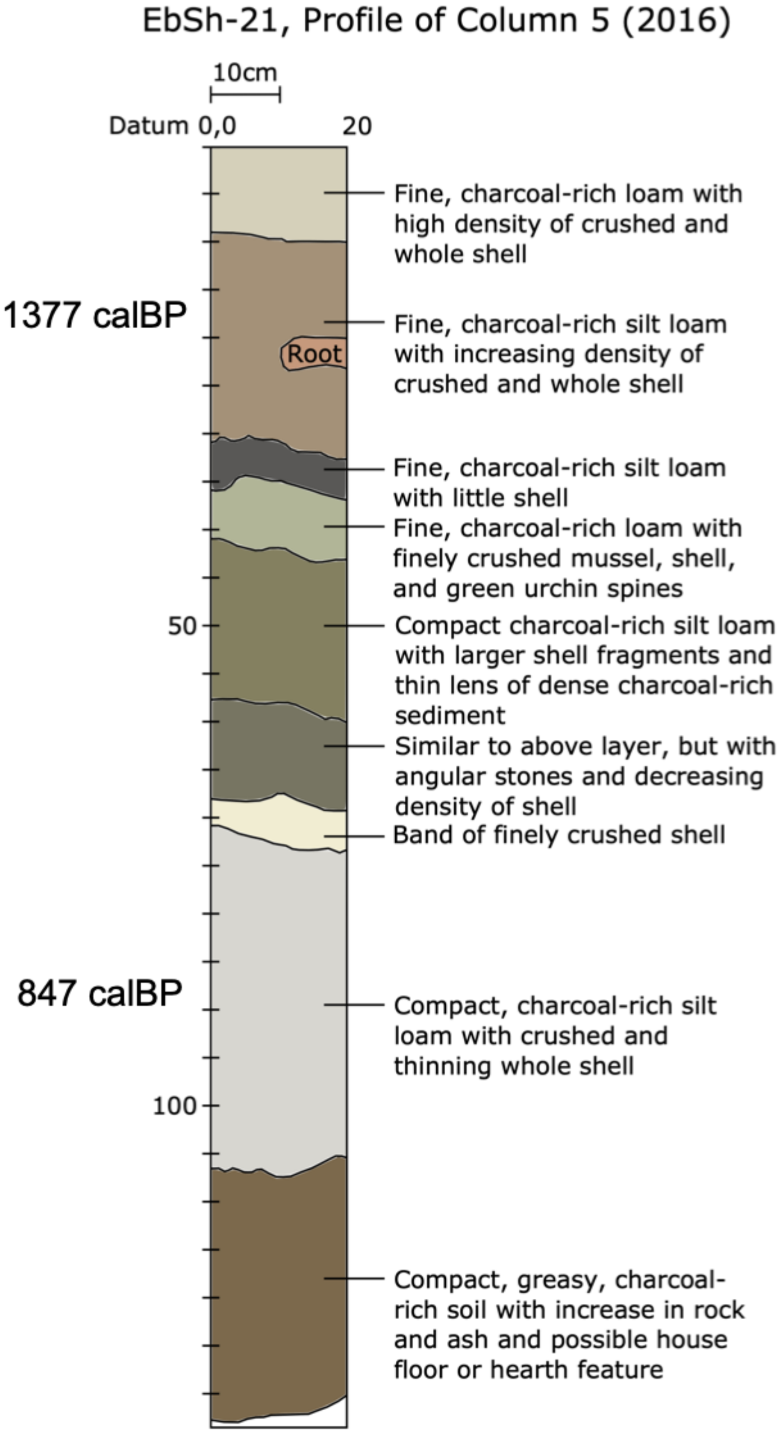


Fig. 4.A4. Quadra Island Column Profile from EbSh-21, Column 5-2016. Median calibrated radiocarbon dates shown along left margin. Adapted from Toniello and Crowell (2020). Digitized Illustration by Madison Skala.

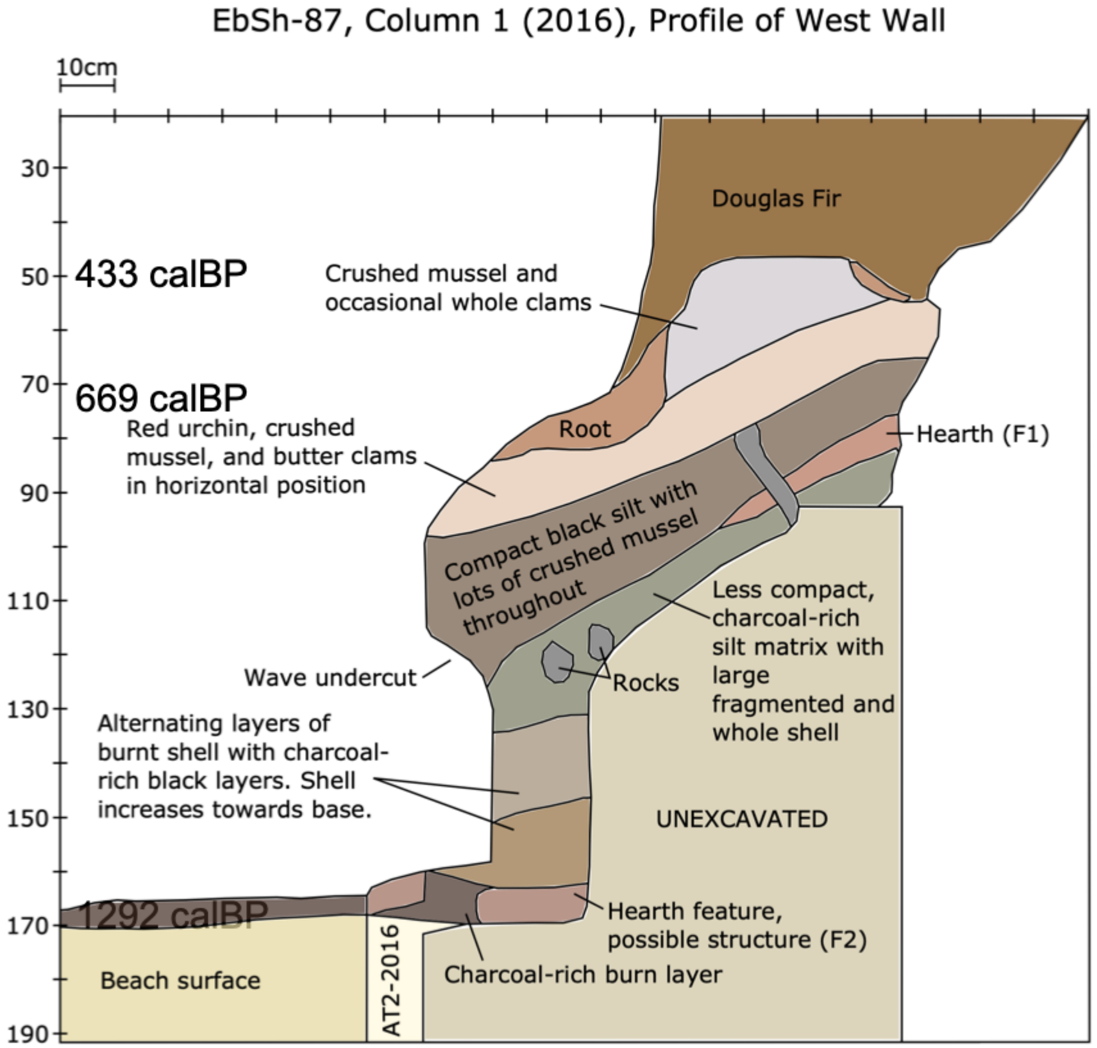


Fig. 4.A5. Quadra Island Column Profile from EbSh-87, Column 1-2016. Median calibrated radiocarbon dates shown along left margin. Adapted from Toniello and Crowell (2020). Digitized Illustration by Madison Skala.

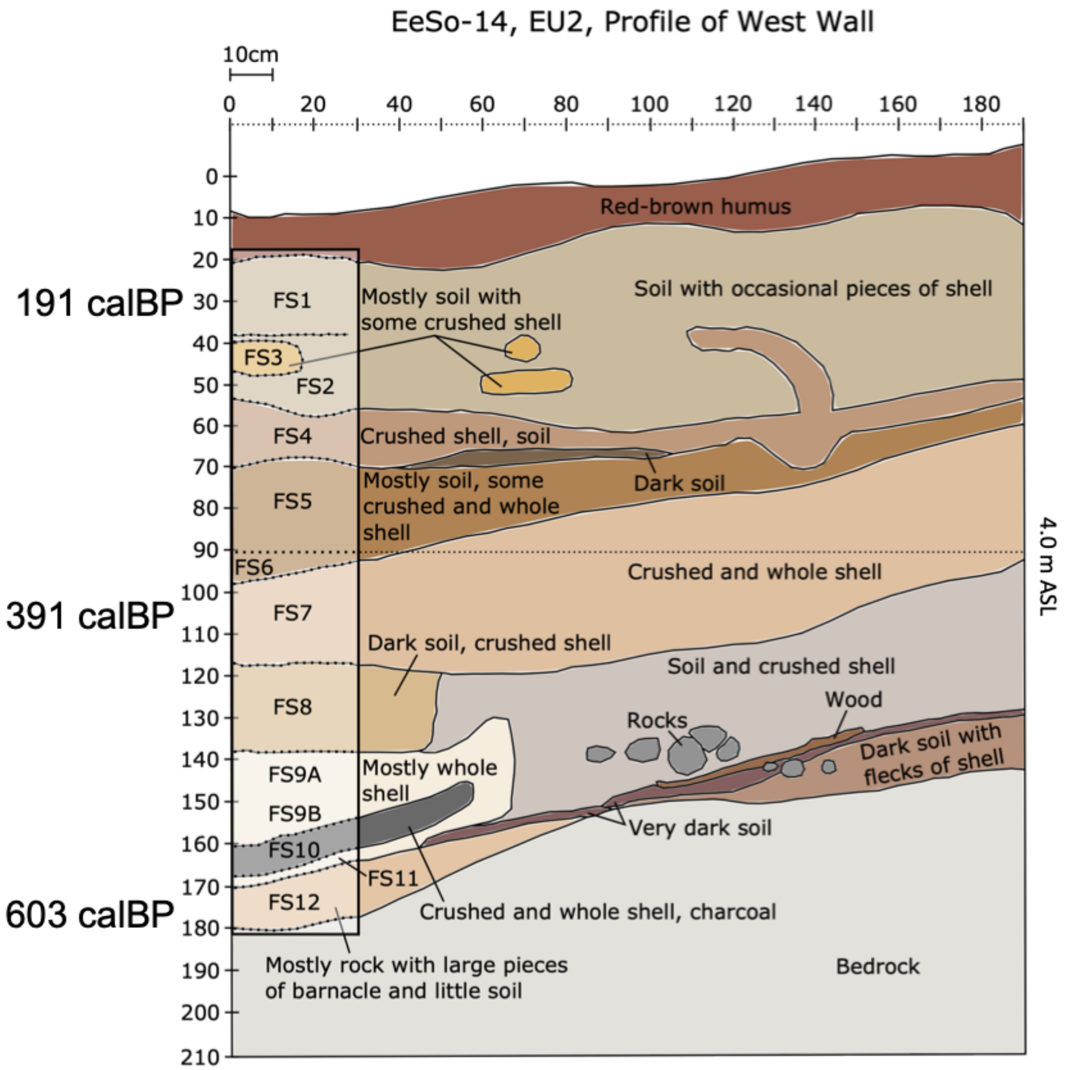


Fig. 4.A6. Broughton Archipelago Excavation Unit and Column Profiles from EeSo14C, EU2, west wall. Median calibrated radiocarbon dates shown along left margin. Adapted from field sketches made in 1973, by Don Mitchell's excavation teams. Digitized Illustration by Madison Skala.

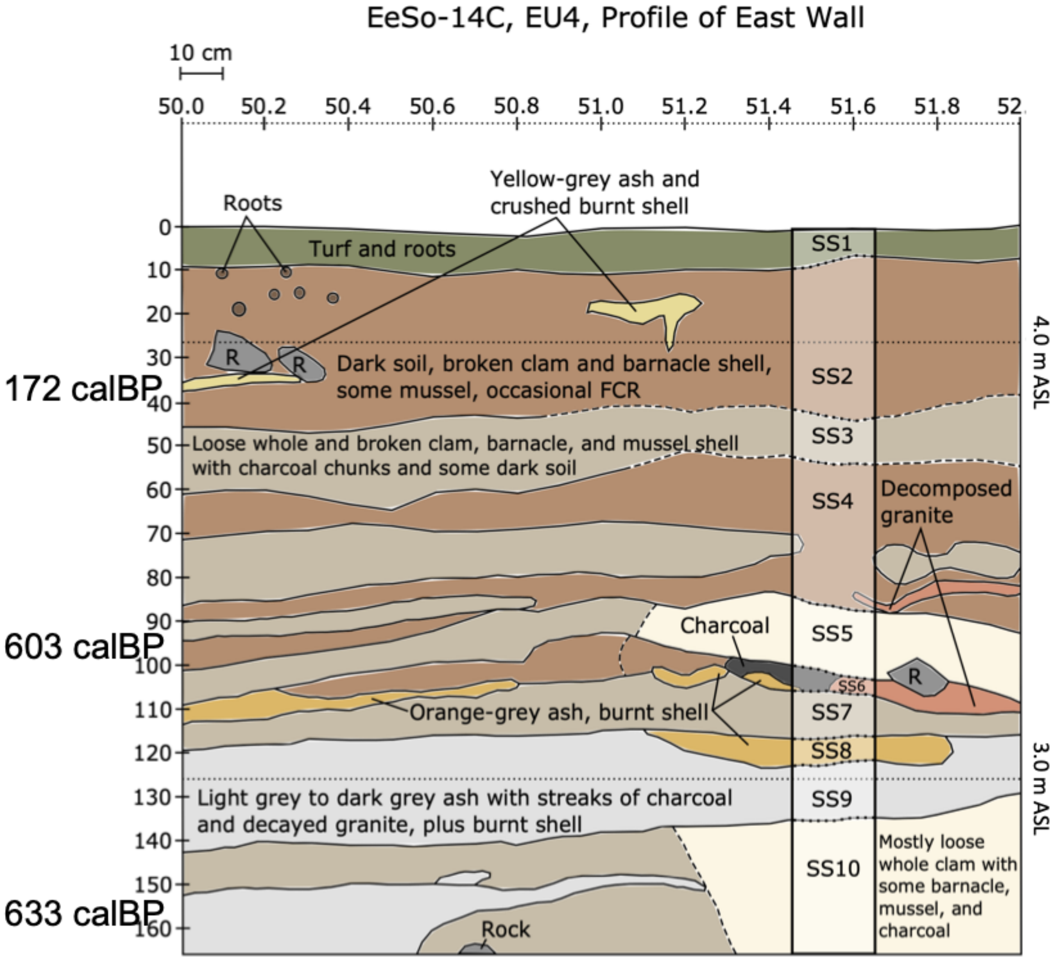


Fig. 4.A7. Broughton Archipelago Excavation Unit and Column Profiles from EeSo14C, EU4, east wall. Median calibrated radiocarbon dates shown along left margin. Adapted from field sketches made in 1973, by Don Mitchell's excavation teams. Digitized Illustration by Madison Skala.

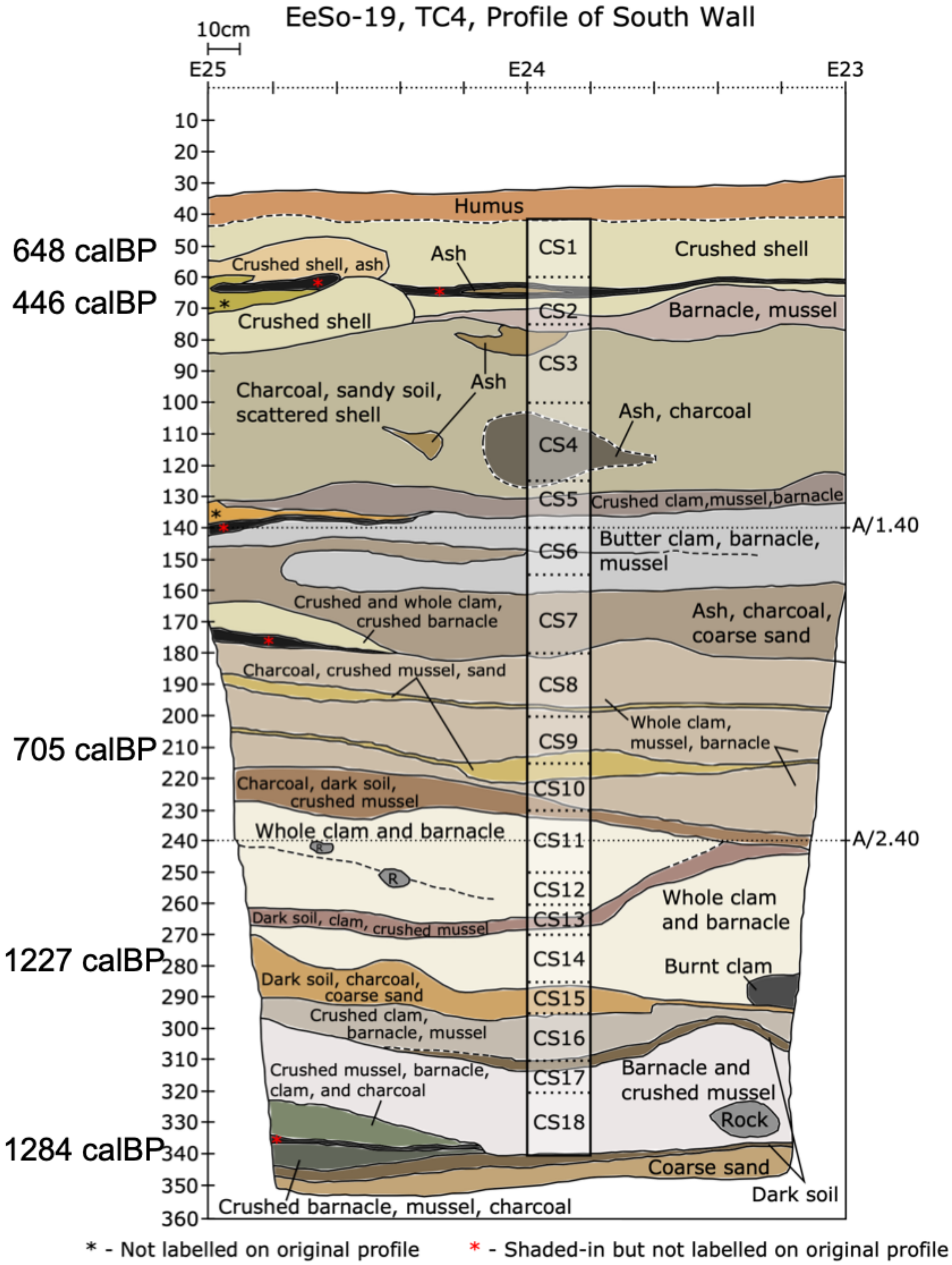


Fig. 4.A8. Broughton Archipelago Excavation Unit and Column Profiles from EeSo19, TC4, south wall. Median calibrated radiocarbon dates shown along left margin. Adapted from field sketches made in 1973, by Don Mitchell's excavation teams. Digitized Illustration by Madison Skala.

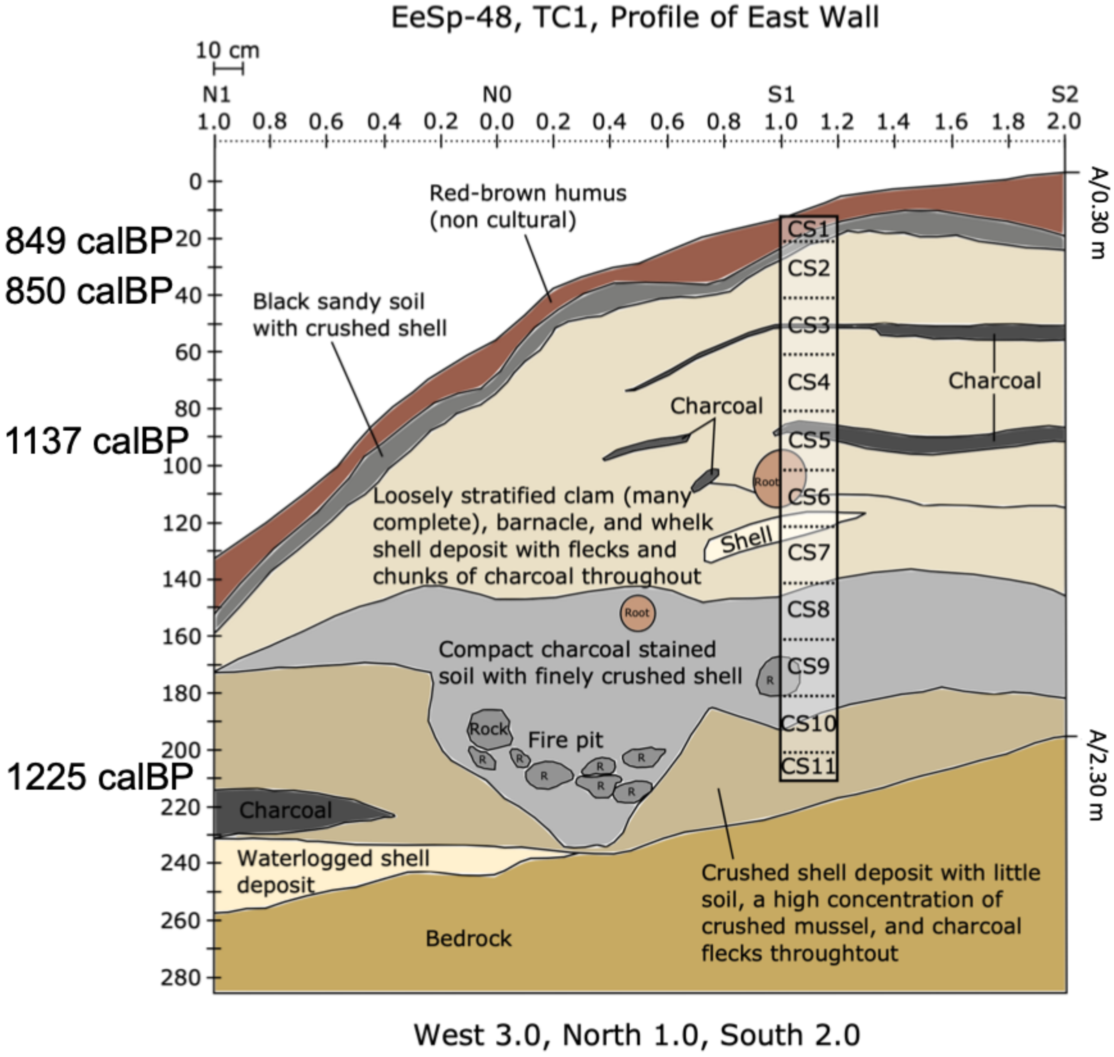


Fig. 4.A9. Broughton Archipelago Excavation Unit and Column Profiles from EeSp-48, TC1, east wall. Median calibrated radiocarbon dates shown along left margin. Adapted from field sketches made in 1973, by Don Mitchell's excavation teams. Digitized Illustration by Madison Skala.

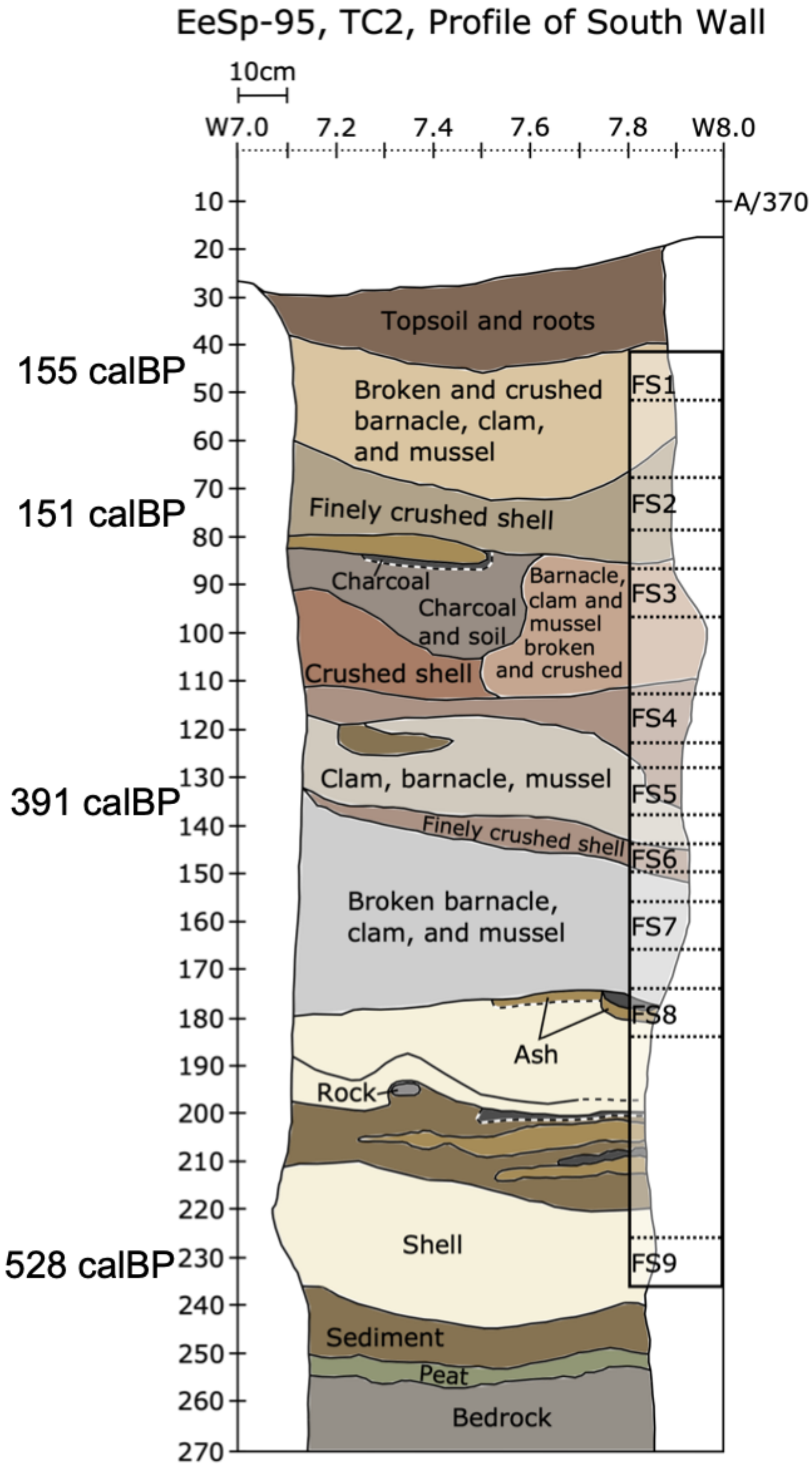


Fig. 4.A10. Broughton Archipelago Excavation Unit and Column Profiles from EeSp-95, TC2, south wall. Median calibrated radiocarbon dates shown along left margin. Adapted from field sketches made in 1973, by Don Mitchell's excavation teams. Digitized Illustration by Madison Skala.

Chapter 5. Discussion

5.1 Summary of research findings

Understanding the needs and influences of strongly interacting species is important for a number of reasons. First, many such species include large-bodied predators that have suffered widespread population declines during the past century (Jackson 2001; Estes *et al.* 2011; Ripple & Beschta 2012; Rosenblatt *et al.* 2013; Dirzo *et al.* 2014; Estes *et al.* 2016); where their recovery is possible, success will be determined in part by understanding species' dynamic conservation requirements. Second, given the ability of strongly interacting species to alter both ecological and socio-ecological processes, a comprehensive understanding of these effects is essential in determining the breadth of interactions that contribute to community structure and function (Estes *et al.* 2016; Rasher *et al.* 2020). Finally, due to widespread losses in species, and species interactions, many of the ecological interactions that drove past ecological processes have been lost (Jackson 2001; Estes *et al.* 2011; Dirzo *et al.* 2014; Estes *et al.* 2016). Rediscovery of long-forgotten interactions can reveal pathways by which contemporary ecological relationships can be restored.

In this Dissertation, I expanded upon the scope and scale under which we consider the effects of strongly interacting species. Based on investigations of the community interactions that were driven by sea otters in a variety of habitats and time periods, my coauthors and I uncovered species-interactions that were not previously described. We found that vegetated soft-sediment habitats and clam-based diets were underappreciated niche spaces occupied by sea otters as they recovered in BC waters. By examining sea otter interactions in this niche space, we found evidence that the disturbance caused by sea otters digging for infaunal prey increased eelgrass genetic diversity, and infer that such effects may date to the middle Pleistocene. We used assemblages of live, and otter-cracked butter clams, to confirm the ecological effects that sea otters exert on the size structure of clams today – contemporary effects which often cause conflict between people and otters (Reidy 2011; Burt *et al.* 2020; Ibarra 2021). We used archaeological data to examine the relationships between two strongly interacting species – sea otters and people – over the past four millennia, and found that sea otters exerted ecological effects on ancient clams, but that Indigenous maricultural practices supported sustainable clam harvests whether sea otters were present or absent. This result suggests that clam gardening could restore some of the socio-ecological interactions that enabled coexistence of people and sea otters today, supporting stable clam harvests for both people and ecologically effective (Soule 2003) populations of sea otters. Taken together, our results emphasize the potential for rediscovering lost interactions in ecological and socio-ecological communities, and indicate that restoring such interactions could build diversity and resilience in contemporary ecosystems.

To understand the role of any species in nature requires describing the linkages it experiences and elicits, and characterizing the dynamic nature of such linkages (Estes et al. 2016). My coauthors and I took the approach of comparing areas with and without otters, and along gradients of otter occupancy time, to examine how some components of ecosystem structure and function varied under different levels of sea otter influence. The natural experiment approaches that we took, were effective in elucidating several previously unrecognized interactions that have likely affected sea otter co-evolution with clams, plants, and people. Our findings raise more questions: What is the scope of the additional, as-yet un-realized interactions occurring in sea otter communities, that may have been historically important? How and where might we rediscover ancient ecological and socio-ecological interactions in the many other communities where keystone predators have been lost or reduced to ecologically ineffective densities?

5.2 The rediscovery of ancient species interactions

Our research illustrates some of the ways in which ancient relationships can contribute to an understanding of historical baselines in species interactions. Many ecological interactions have been lost or overlooked where large-bodied animals have disappeared from land- and seascapes (Jackson 2001; Estes *et al.* 2011; Dirzo *et al.* 2014; Estes *et al.* 2016); such losses can be at least as important as species-losses (Estes *et al.* 2011). Among these, ancient socio-ecological interactions have also been lost and overlooked (e.g., Turner *et al.* 2008; Turner & Turner 2008). For example, socio-ecological interactions, common on the northwest coast in the late-Holocene, declined during and following the Maritime Fur Trade (Lightfoot 1995; Marsden & Galois 1995) and with European colonization of the Americas (Turner *et al.* 2008; Turner & Turner 2008; Toniello *et al.* 2019). A rediscovery of historical ecological and socio-ecological interactions can inform our understanding of contemporary ecolological and socio-ecological relationships.

In BC, sea otters were extirpated by the early 1900s, after suffering widespread population declines across their entire north Pacific range. Following the Maritime Fur Trade, most remnant otter populations occurred along the outer coast of the Pacific Rim (Silliman *et al.* 2018). Thus, much of the foundational work on sea otter and associated community ecology came from a context of otters inhabiting rocky-reef systems where they limited grazers and indirectly promoted kelp forests (but see, Miller *et al.* 1975; Kvitek *et al.* 1988; Kvitek & Oliver 1992; Kvitek *et al.* 1992; Weitzman 2013). Over the past few decades, however, scientists have begun to appreciate that sea otter effects extend to eelgrass and saltmarsh systems – which are now considered to have been historically important habitats (Hughes *et al.* 2013; Hughes *et al.* 2016; Eby *et al.* 2017; Espinosa 2018; Hessing Lewis *et al.* 2018; Silliman *et al.* 2018; Hughes *et al.* 2019). Encompassing the full breadth of a species' interactions – including the variety of communities they influence – has conservation implications, particularly where niche expansions include habitat that could be critical to species recovery (Estes *et al.* 2016; Silliman *et al.* 2018). We found, like elsewhere, that soft-sediment habitats formed one of many important foraging habitats for sea otters. We additionally found that the use of such habitats increased over the course of sea otter recovery and in male-dominated areas. Given the increasing importance of soft-sediment communities to sea otters, as occupancy-time increases, we infer that such interactions were also historically important. A focus on these historically-important interactions influenced subsequent research chapters.

Observations of sea otter behaviour in soft-sediment environments revealed that otters often dug for infaunal prey in eelgrass (*Zostera marina*) meadows, leaving large pits in their wake. Sea otters disturb eelgrass rhizome mats when foraging, and decades of observations of these routine disturbances suggested that eelgrass might respond by increasing its investment in sexual vs. asexual reproduction. To indirectly assess changes in eelgrass life-history strategies, but capture potential microevolutionary effects, we measured the genetic response of eelgrass to sea otter disturbances. We found that sea otter digging increased the genetic diversity of eelgrass by ~25% – a finding that was replicated in two genetically different eelgrass populations. We posit that sea otter digging for infaunal prey has long-influenced the life history strategies, genetic diversity, and resilience, by creating conditions that favour sexual reproduction and seed set. Our discovery builds on previous research linking sea otter effects to the evolutionary processes of primary producers. For example, in the north Pacific Ocean – where kelps co-evolved with sea otters – energetically costly chemical adaptations in kelps, that prevent grazing, are rare. In contrast, in temperate Australia, where there are no known grazer predators of comparable influence to sea otters, phlorotannins – chemical grazing deterrants – are nearly three times as prevalent in kelps, as they are in the north Pacific (Estes & Steinberg 1988). Our work, and that of Estes and Steinberg (1988), support the hypothesis that sea otters have exerted strong evolutionary effects on plant and alga evolutionary processes since at least the middle Plesitocene (Boessenecker 2016). The kelp highway hypothesis (Erlandson *et al.* 2007) also suggests that sea otter influences over kelp could have occurred in the Pleistocene. Abundant kelp forests provided sheltered waters and plentiful food-resources that facilitated the peopling of the Americas via a coastal route from Asia (Erlandson *et al.* 2007). It may be impossible to know the extent of sea otter effects as they occurred several hundred thousand years ago, but paleoecological and archaeological studies can help to illuminate some of these ancient relationships.

Using archaeological methods, we found that sea otters influenced the ecological availability of clams to northwest coast Indigenous peoples from the middle to late Holocene, and that sea otter effects were ameliorated by people. Much like recent work that suggested humans dampen the effects of apex predators in terrestrial systems (Dorresteijn *et al.* 2015), stable sizes of ancient clams in shell middens, whether at small sizes in sea otter areas or large sizes in otter-free areas, indicated that Indigenous peoples in the middle to late Holocene dampened the effects of sea otters on clams, and – ultimately – themselves. We suggest that three ancient interactions facilitated co-existence between people and sea otters: 1) clam gardening practices enhanced clam habitat and productivity, creating more clams which could in turn support more consumers than could be supported by unmanaged beaches (Harper *et al.* 1995; Williams 2006; Groesbeck *et al.* 2014; Jackley *et al.* 2016; Toniello *et al.* 2019; Lepofsky *et al.* 2020); 2) Sea otter access to clam gardens was limited by the height of the terrace walls which raised beach height and reduced the hours per day that clams were accessible to sea otters, by up to 50% (Chapter 4); and 3) People further modified sea otter behaviour by using techniques such as mooring dead otters outside harvesting areas to deter live otters, and by harvesting sea otters and creating a landscape of fear (Salomon *et al.* 2015; Salomon *et al.* 2018; Salomon *et al.* 2020) that probably restricted sea otters to primarily subtidal foraging areas. We suspect many other socio-ecological links between keystone predators and Indigenous peoples were important in structuring ancient systems, and future research could reveal some of these relationships.

5.3 Future work

Like most PhD students, my dissertation has left me with more questions than answers. To build upon our findings regarding the dynamic and sex-based nature of sea otter niche space, future work could investigate seasonal components in niche occupancy. In many species, recovery can be limited by a poor understanding of year-round habitat needs. A better understanding of winter sea otter habitat-requirements has been suggested as a way to enhance recovery, and to potentially mitigate the effects of oil spills (Watson 1990; COSEWIC 2007). Sea conditions that are most-likely to cause oil spills are prevalent in the winter months, and responding to oiled otters will require knowledge of where they are rafting and foraging. Despite the efforts my colleagues and I exerted over five winters (Jan-Feb annually) were only able to routinely access three rafting areas in rough weather. The *West Beach* rafting area was abandoned mid-way through the first winter after sea otter arrival, and has not been reoccupied (7 years). I suspect that this site was abandoned due to inclement sea conditions and lack of shelter, as sea otter energy intake rates were still ~50-60 kcal per minute at the time of relocation – and energy intake rates were roughly the same when sea otters arrived to the new site in *Choked Passage* (Foster, *unpub. data*). The abandoned area was regularly exposed to high seas that made both resting and foraging look difficult, but *Choked Passage* was generally calm even when seas <500 m away were rough (Foster, *pers. obs.*). In one of the female-dominated areas, we found that rafting areas often relocated (<2km) between sheltered and exposed shorelines, that were (anecdotally) weather-dependent. Weather-related distribution patterns have been reported for sea otters elsewhere (Garshelis & Garshelis 1984). The ability to observe sea otter behaviour in winter might reveal additional prey or habitat-reliances than those we have characterized here.

Several additional studies that could increase the strength of our conclusions regarding the effects of sea otter digging on *Zostera marina* (eelgrass) genetic diversity. Although we attempted to measure flowering rates of eelgrasses, the timing of flowering was too variable to capture flowering shoots over the three week period and geographic extent of the meadows we surveyed (central BC coast to southwestern Vancouver Island). I considered experimentally applying disturbance effects to eelgrass to induce flowering, but I was not convinced that I could replicate the disturbance frequency and intensity that sea otters impose. Future work could improve upon our findings by using a before-after-control-impact (BACI) design, under which eelgrass flowering rates and genetic diversity are measured before, during, and after sea otter recovery in the same meadows. Such a study might also address the threshold of disturbance needed to enhance genetic diversity. There are many conservation initiatives designed to mitigate disturbances to eelgrass – preventing large and small disturbances alike (i.e. shading from log booms, anchoring of boats). At some level, disturbance effects destroy eelgrass meadows (Short & Wyllie-Echeverria 1996; Nahirnick *et al.* 2019). However, our work suggests that where eelgrass co-evolved with sea otters – and perhaps other biological agents of disturbance, such as skates, rays, ducks, turtles, and grey whales – it may be well-adapted to disturbance, perhaps relying upon disturbance to reach levels of genetic diversity sufficient to promote resilience.

Examining the synergistic effects of human- and predator-caused disturbances on eelgrass provides another avenue for future research. Specifically, how did Indigenous-management of eelgrass meadows influenced eelgrass genetic diversity? Northwest coast Indigenous people harvested eelgrass rhizomes throughout much of the Holocene, and Cullis-Suzuki *et al.* (2015) posited that such disturbance could have enhanced the genetic diversity of eelgrass meadows. In the Gulf of California, Mexico, *Zostera marina* seeds are one of the most important food sources to Indigenous Seri Tribes, which suggests that conditions in this area supported sexual (flowers and seeds) reproduction – perhaps via a disturbance-induced pathway. The Seri have language describing April moons as *Xnois i?aat íiSSaaX ’Xnóis* (when-there-is moon – taken to mean when there is eelgrass grain ready to harvest moon), and eelgrass harvesting is called *kapóee* (a time of happiness), indicating that eelgrass harvests are culturally important (Felger & Moser 1973). Eelgrass seeds provided essential starches and nutrients; seeds were ground into flour and made into a gruel that was favoured with sea turtle oil (Felger & Moser 1973). Sea turtles – at historical abundances – are strongly interacting grazers in eelgrass meadows (e.g., Jackson 2001). Seri language also references a species of duck, seen to foretell the success of eelgrass seed harvest (Felger & Moser 1973). Today, grazing by ducks and geese can affect eelgrass reproductive efforts (Hughes & Stachowicz 2004), and it is likely that grazing turtles do this as well. Taken together, ethnographic histories suggest there were many ancient interactions among humans, eelgrass-consumers, and seed production, which might extend to socio-ecological systems including fauna that exert digging disturbances in eelgrass. Capturing such interactions may help advance our collective understanding of the ideal conditions required for thriving, resilient, eelgrass meadows.

Given our finding that clam gardening practices ameliorated the ecological effects of sea otters on clams, and ultimately on people, future research could evaluate how restoring such practices might allow people and otters to coexist today, where otters are ecologically effective and where both people and otters consume clams. Clam garden restoration is already underway (Augustine & Dearden 2014). Future efforts could occur in areas with and without sea otters, and examine how clam gardening and associated cultivation practices affect the relative availability of clams to people, where otters co-occur. Ideally, a BACI design could be used in areas without otters, but where otters are predicted to re-establish within ~10 years, to investigate changes in clams size and abundance as otter occupancy increases. Enhancing clam productivity, use of garden terraces, and consumer- or trait-mediated limitation of sea otter access to clams, may restore the ancient interactions that promoted coexistence between people and otters.

In addition to recovery of clam gardening practices, future research could seek to understand other ancient socio-ecological relationships. Given our understanding of the many terrestrial cultivation practices that northwest coast peoples have practiced for at least the past four millennia, and that increased diversity and accessibility of resources (Mathews & Turner 2017; Armstrong *et al.* 2021; Carney *et al.* 2021), we posit in Chapter 4, that cultivation of marine invertebrates was probably more widespread than currently appreciated. Future research that includes Indigenous knowledge of invertebrate cultivation strategies may support modern initiatives that could in turn support food-social-ceremonial fisheries even where other invertebrate consumers occur at ecologically effective densities. Ancient socio-ecological interactions that allowed for sustainable invertebrate harvesting could help people re-imagine the ways in which marine foods managed to build resilience into socio-ecological systems.

More broadly, future work could compare how the effects of people have varied through the Holocene. In today's world, humans are a hyperkeystone species because we influence nearly every species-interaction, and drive community composition (Worm & Paine 2016). Globally, contemporary humans function as so-called 'super predators', owing to our ability to exploit other predators at exceptionally high rates, and target adult-individuals (the reproductive capital of populations). Compared to humans, other predators have smaller ecological effects because they tend to target lower trophic-levels and immature individuals (Darimont *et al.* 2015). The effects of humans on large vertebrates have often been invoked to explain the Pleistocene megafaunal extinctions. The overkill hypothesis posits that N and S American megafaunal extinctions by the late-Pleistocene occurred because of overhunting of naïve prey by expanding human populations (Martin 1973). However, recent work indicates that the synergistic effects of climate and people (Meltzer 2015; Broughton & Weitzel 2018) or perhaps climate alone (Stewart *et al.* 2021) caused these extinctions. The results of Chapter 4 indicate that in the late-Holocene otter-clam-human system, human-mediated interactions allowed for ecologically effective populations of sea otters, prior to the Maritime Fur Trade. Future study examining ages and sexes of harvested vertebrates from the end of the Pleistocene through the Holocene could ask if the ages, or sexes or harvested animals varied through time. This could inform some of the ways in which people and large-bodied vertebrates interacted in the past.

5.4 Concluding remarks

I have found that a few, perhaps long-forgotten, ecological and socio-ecological interactions triggered by sea otters can increase the breadth of the strongly interacting species concept. I suggest that such lost interactions are waiting to be rediscovered as species return to ecosystems, or in ancient data that illuminates past species interactions. Like sea otters, many large vertebrates suffered widespread population declines that have influenced our understanding of species interactions in contemporary food webs. Over the course of recovery, more than 21 strongly interacting species expanded their ecological niche, often surprising ecologists with the different interactions they elicited (Silliman *et al.* 2018). Silliman *et al.* (2018) argue that much of what we know about recovering species is influenced by historical accidents – that research has focused overwhelmingly on the initial habitats that species re-occupied where they began to recover. In many of these cases, species recovered into ecological communities where their interactions had been lost for decades to centuries – these can be different from the communities they were extirpated from. Scientists do not always appreciate these "ghosts of predators past" when investigating ecological relationships of today (Silliman *et al.* 2018). Estes *et al.* (2011) argues that the most insidious losses accompanying species-losses are the losses of ecological interactions that become unknowable, and thus cannot be intentionally restored. In this dissertation I have tried to re-illuminate some of these forgotten interactions in systems occupied by sea otters.

Most of the research conducted on strongly interacting species to-date, has not considered the interactions driven by human behaviour. Given the widespread impacts that people have on ecosystems globally (Darimont *et al.* 2015; Dorresteijn *et al.* 2015; Boivin *et al.* 2016; Worm & Paine 2016), it is unclear today whether or not apex predators can achieve ecologically effective population sizes outside wilderness and protected areas (Dorresteijn *et al.* 2015; Silliman *et al.* 2018); this is important where species are being re-introduced to restore ecological interactions. The wealth of knowledge regarding ancient socio-ecological interactions, held in Indigenous histories, has suffered from great losses over the past several hundred years (Turner *et al.* 2008; Turner & Turner 2008), but could be an integral part of predicting contemporary interactions among people and other strongly interacting species. Restoring ancient socio-ecological interactions, and better-characterizing contemporary interactions, has implications if we are to successfully restore strongly-interacting species for particular ecological roles. If human behaviour is not adequately considered, the strength of non-human predator effects will be difficult to predict.

Long-forgotten species interactions are important, yet they are often underappreciated. As species recover, they often demonstrate expanding and dynamic niche breadth the longer they occupy a system. By examining forgotten species interactions, and the associated socio-ecological systems they occurred in, we may be able to mitigate the cost of the lost ecological interactions that occur when species decline or are lost from a system. A better understanding of past ecological and socio-ecological interactions will inform the ways in which contemporary communities interact, and in many cases build resilience in a changing environment.

Literature Cited

Adamack, A.T. & Gruber, B. (2014). PopGenReport: simplifying basic population genetic analyses in R. *Methods in Ecology and Evolution*, 5, 384-387.

Adams, M., Connors, B., Levi, T., Shaw, D., Walkus, J., Rogers, S. *et al.* (in revision). Local values and data empower culturally-guided ecosystem-based fisheries management of the Wuikinuxv bear-salmon-human system. *Marine and Coastal Fisheries*.

Agrawal, A.A., Hastings, A.P., Johnson, M.T.J., Maron, J.L. & Salminen, J.P. (2012). Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science*, 338, 113-116.

Alexandre, A., Santos, R. & Serrão, E. (2005). Effects of clam harvesting on sexual reproduction of the seagrass *Zostera noltii*. *Marine Ecology Progress Series*, 298, 115-122.

Ames, K.M. & Maschner, H.D.G. (1999). *Peoples of the Northwest Coast*. Thames and Hudson, London, England.

Armstrong, C.G., Miller, J.E.D., McAlvay, A.C., Ritchie, P.M. & Lepofsky, D. (2021). Historical Indigenous land-use explains plant functional trait diversity. *Ecology and Society*, 26, 6.

Arnaud-Haond, S., Duarte, C.M., Alberto, F. & Serrao, E.A. (2007). Standardizing methods to address clonality in population studies. *Molecular Ecology*, 16, 5115-5139.

Ascher, R. (1959). A prehistoric population estimate using midden analysis and two population models. *Southwestern Journal of Anthropology*, 15, 168-178.

Augustine, S. & Dearden, P. (2014). Changing paradigms in marine and coastal conservation: a case study of clam gardens in the Southern Gulf Islands, Canada. *The Canadian Geographer / Le Géographe canadien*, 58, 305-314.

Avolio, M.L. & Smith, M.D. (2013). Mechanisms of selection: phenotypic differences among genotypes explain patterns of selection in a dominant species. *Ecology*, 94, 953-965.

Banks, S.C., Cary, G.J., Smith, A.L., Davies, I.D., Driscoll, D.A., Gill, A.M. *et al.* (2013). How does ecological disturbance influence genetic diversity? *Trends in Ecology and Evolution*, 28, 670-679.

Barber, J.S., Ruff, C.P., McArdle, J.T., Hunter, L.L., Speck, C.A., Rogers, D.W. *et al.* (2019). Intertidal clams exhibit population synchrony across spatial and temporal scales. *Limnology and Oceanography*, 64, S284-S300.

Baudrot, V., Perasso, A., Fritsch, C., Giraudoux, P. & Raoul, F. (2016). The adaptation of generalist predators’ diet in a multi-prey context: insights from new functional responses. *Ecology*, 97, 1832-1841.

Berg, M. (2015). Black Oystercatcher (*Haemotopus bachmani*) diet on the central coast of BC and the influences of sea otter (*Enhydra lutris*) occupation. BSc thesis. Vancouver Island University Nanaimo, BC.

Berlow, E.L., Navarrete, S.A., Briggs, C.J., Power, M.E. & Menge, B.A. (1999). Quantifying variation in the strengths of species interactions. *Ecology*, 80, 2206-2224.

Bigg, M.A. & MacAskie, I.B. (1978). Sea otters reestablished in British Columbia. *Journal of Mammalogy*, 59, 874-876.

Black, M., Dudas, S. & Juanes, F. (2018). Marine macrofaunal communities of First Nations' clam gardens. In: *Ecological Society of Australia* Brisbane, AUS.

Blok, S.E., Olesen, B. & Krause-Jensen, D. (2018). Life history events of eelgrass *Zostera marina* L. populations across gradients of latitude and temperature. *Marine Ecology Progress Series*, 590, 79-93.

Boas, F. (1909). *The Jesup north Pacific expedition, memoir of the American Museum of Natural History. Part II: Kwakiutl of Vancouver Island*. Leiden EJ Brill Ltd. Printers and Publishers, New York, NY.

Boas, F. & Hunt, G. (1905). *Kwakiutl texts*. Kessinger Publishing, Whitefish, Montana.

Boessenecker, R.W. (2016). A middle pleistocene sea otter from northern California and the antiquity of *Enhydra* in the Pacific Basin. *Journal of Mammalian Evolution*, 25, 27-35.

Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M. *et al.* (2016). Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Science USA*, 113, 6388-6396.

Boulding, E.G. (1984). Crab-resistent features of shells of burrowing bivavles: decreasing vulnerabiliy by increasing handling time. *Journal of Experimental Marine Biology and Ecology*, 76, 201-223.

Boyd, R. (1994). Smallpox in the Pacific Northwest. *BC Studies*, 101, 5-40.

Breen, P.A., Carson, T.A., Foster, B.J. & Stewart, A.E. (1982). Changes in subtidal community structure associated with British Columbia sea otter transplants. *Marine Ecology Progress Series*, 7, 12-20.

Broughton, J.M. & Weitzel, E.M. (2018). Population reconstructions for humans and megafauna suggest mixed causes for North American Pleistocene extinctions. *Nature Communications*, 9, 5441-5453.

Brown, F. & Brown, Y.K. (2009). *Staying the course, staying alive: coastal First Nations fundamental truths: biodiversity, stewardship and sustainability*. Biodiversity BC, Victoria, British Columbia.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, USA.

Burt, J.M., K̲ii'ijuus, Wilson, B.J., Malchoff, T., Wii-tsts-koom, Mack, A. *et al.* (2020). Enabling coexistence: navigating predator-induced regime shifts in human-ocean systems. *People and Nature*, 2, 557-574.

Cabaço, S. & Santos, R. (2012). Seagrass reproductive effort as an ecological indicator of disturbance. *Ecological Indicators*, 23, 116-122.

Caballero, A. & Garcia-Dorado, A. (2013). Allelic diversity and its implications for the rate of adaptation. *Genetics*, 195, 1373-1384.

Caldwell, M.E. (2015). Northern Coast Salish marine resource management. PhD thesis. Univeristy of Alberta Edmonton, AB.

Caldwell, M.E., Lepofsky, D., Combes, G., Washington, M., Welch, J.R. & Harper, J.R. (2012). A Bird's Eye View of Northern Coast Salish Intertidal Resource Management Features, Southern British Columbia, Canada. *The Journal of Island and Coastal Archaeology*, 7, 219-233.

Canadian Hydrographic Service (2021). Canadian tide and current tables, 2021. Volume 6: Discovery Passage and west coast of Vancouver Island. *Fisheries and Oceans Canada*.

Carney, M., Tushingham, S., McLaughlin, T. & d'Alpoim Guedes, J. (2021). Harvesting strategies as evidence for 4000 years of camas (*Camassia quamash*) management in the North American Columbia Plateau. *Royal Society Open Science*, 8, 5361979.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, H., Colwell, R.K. *et al.* (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45-67.

Chen, R.S. & McDonald, B.A. (1996). Sexual reproduction plays a major role in the genetic structure of populations of the fungus *Mycosphaerella graminicola*. *Genetics*, 142, 1119-1127.

Clarke, K.R. & Gorley, R.N. (2015). PRIMER v7. Primer-E Ltd.

Clarke, K.R., Gorley, R.N., Somerfield, P.J. & Warwick, R.M. (2014). *Change in marine communities: an approach to statistical analysis and interpretation, 3rd edition*. PRIMER-E, Plymouth, NZ.

Clarke, L.R. & Clarke, A.H. (1980). Zooarchaeological analysis of mollusc remains from Yuquot, British Columbia. In: *The Yuquot Project, Vol III* (eds. Folon, WJ & Dewhirst, J). Parks Canada, Canadian Government Publishing Services. Hall, Quebec, pp. 37-57.

Comps, B., Gömöry, D., Letouzey, J., Thiébaut, B. & Petit, R.J. (2001). Diverging trends between heterozygosity and allelic richness during postglacial colonization in the European beech. *Genetics*, 157, 389-397.

Connell, J.H. (1978). Diversity in tropical rainforests and coral reefs. *Science*, 199, 1302-1310.

Connolly, R.M., Smith, T.M., Maxwell, P.S., Olds, A.D., Macreadie, P.I. & Sherman, C.D.H. (2018). Highly disturbed populations of seagrass show increased resilience but lower genotypic diversity. *Frontiers in Plant Science*, 9, 894.

Corbett, D.G., Causey, D., Clementz, M., Koch, P.L., Doroff, A., Levèvre, C. *et al.* (2011). Aleut hunters, sea otters, and sea cows: three thousand years of interactions in the western Aleutian Islands, Alaska. In: *Human impacts on seals, sea lions, and sea otters*. University of California Press Berkeley, CA.

COSEWIC (2007). Assessment and update status report on the sea otter (*Enhydra lutris*) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 36 pp.

Costa, D.P. & Kooyman, G.L. (1982). Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. *Canadian Journal of Zoology*, 60, 2761-2767.

Coyer, J.A., Hoarau, G., Kuo, J., Tronholm, A., Veldsink, J. & Olsen, J.L. (2013). Phylogeny and temporal divergence of the seagrass family Zosteraceae using one nuclear and three chloroplast loci. *Systematics and biodiversity*, 11, 271-284.

Cullis-Suzuki, S., Wyllie-Echeverria, S., Dick, K.A., Sewid-Smith, M.D., Recalma-Clutesi, O.K. & Turner, N.J. (2015). Tending the meadows of the sea: a disturbance experiment based on traditional indigenous harvesting of *Zostera marina* L. (Zosteraceae) the southern region of Canada's west coast. *Aquatic Botany*, 127, 26-34.

Darimont, C.T., Fox, C.H., Bryan, H.M. & Reimchen, T.E. (2015). The unique ecology of human predators. *Science*, 349, 858-860.

Davies, I.D., Cary, G.J., Landguth, E.L., Lindenmayer, D.B. & Banks, S.C. (2016). Implications of recurrent disturbance for genetic diversity. *Ecology and Evolution*, 6, 1181-1196.

Dean, T.A., Bodkin, J.L. & Coletti, H. (2014). Protocol narrative for nearshore marine ecosystem monitoring in the Gulf of Alaska. Natural Resource Report NPS/SAN/NRR-2014/756. National Park Service, Fort Collins, Colorado.

Deng, L., Sweeney, S. & Shangguan, Z.P. (2014). Grassland responses to grazing disturbance: plant diversity changes with grazing intensity in a desert steppe. *Grass and Forage Science*, 69, 524-533.

Deur, D. (2002). Plant cultivation on the Northwest Coast: a reconsideration. *Journal of Cultural Geography*, 19, 9-35.

Deur, D. (2005). Tending the garden, making the soil. In: *Keeping it living: traditions of plant use and cultivation on the northwest coast of North America* (eds. Deur, DE & Turner, NJ). University of Washington Press Seattle, Washington.

Deur, D., Dick, A., Recalma-Clutesi, K. & Turner, N.J. (2015). Kwakwaka'wakw "Clam Gardens". *Human Ecology*, 43, 201-212.

Dirzo, R., Young, H.S., Baletti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401-406.

Doering, P.H. (1982). Reduction of sea star predation by the burrowing response of the hard clam *Mercenaria mercenaria* (Mollusca: Bivavlvia). *Estuaries*, 5, 310-315.

Dorken, M.E. & Eckert, C.G. (2001). Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *Journal of Ecology*, 89, 339-350.

Dorresteijn, I., Schultner, J., Nimmo, D.G., Fischer, J., Hanspach, J., Kuemmerle, T. *et al.* (2015). Incorporating anthropogenic effects into trophic ecology: predator-prey interactions in a human-dominated landscape. *Proceedings of the Royal Society B*, 282, 20151602.

Du Toit, J.T. (2005). Sex differences in the foraging ecology of large mammalian herbivores. In: *Sexual segregation in vertebrates: ecology of the two sexes* (eds. Ruckstahl, KE & Neuhaus, P). Cambridge University Press Cambridge, pp. 35-52.

Earl, D. & Vondoldt, B. (2012). Structure Harvester: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, 4, 359-361.

Ebert, T.A. & Southon, J.R. (2003). Red sea urchins (*Strongylocentrotus franciscanus*) can live over 100 years: confirmation with A-bomb 14 carbon. *Fishery Bulletin*, 101, 915-922.

Eby, R., Scoles, R., Hughes, B.B. & Wasson, K. (2017). Serendipity in a salt marsh: detecting frequent sea otter haul outs in a marsh ecosystem. *Ecology*, 98, 2975-2977.

Ehlers, A., Worm, B. & Reusch, T.B.H. (2008). Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Marine Ecology Progress Series*, 355, 07369.

Eichberg, C. & Donath, T.W. (2018). Sheep trampling on surface-lying seeds improves seedling recruitment in open sand ecosystems. *Restoration Ecology*, 26, 211-219.

El Mousadik, A. & Petit, R.J. (1996). High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. *Theoretical and Applied Genetics*, 92, 832-839.

Eldridge, D.J., Whitford, W.G. & Duval, B.D. (2009). Animal disturbances promote shrub maintenance in a desertified grassland. *Journal of Ecology*, 97, 1302-1310.

Elliot Smith, E.A., Newsome, S.D., Estes, J.A. & Tinker, M.T. (2015). The cost of reproduction: differential resource specialization in female and male California sea otters. *Oecologia*, 178, 17-29.

Ellis, D.W. & Swan, L. (1986). *Teachings of the tides: uses of marine invertebrates by the Manhousat people*. Theytus Books Ltd., Nanaimo, BC.

Ellis, D.W. & Wilson, S. (1981). *The knowledge and usage of marine invertebrates by the Skidegate Haida people of the Queen Charlotte Islands*. The Queen Charlotte Islands Museum Society, Skidegate, British Columbia.

Ellis, E.C. (2015). Ecology in an anthropogenic biosphere. *Ecological Monographs*, 85, 287-331.

Elson, A. & Hartnett, D.C. (2017). Bison increase the growth and reproduction of forbs in tallgrass prairie. *American Midland Naturalist*, 178, 245-259.

Elton, C.S. (1927). *Animal Ecology*. University of Chicago Press, Chicago, Illinois.

Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215-223.

Endler, J. (1986). *Natural selection in the wild*. Princeton University Press, Princeton, NJ.

Erlandson, J.M., Braje, T.J., Rick, T.C., Jew, N.P., Kennett, D.J., Dwyer, N. *et al.* (2011). 10,000 years of human predation and size changes in the owl limpet (*Lottia gigantea*) on San Miguel Island, California. *Journal of Archaeological Science*, 38, 1127-1134.

Erlandson, J.M., Graham, M.H., Bourque, B.J., Corbett, D., Estes, J.A. & Steneck, R.S. (2007). The kelp highway hypothesis: marine ecology, the coastal migration theory, and the peopling of the Americas. *The Journal of Island and Coastal Archaeology*, 2, 161-174.

Erlandson, J.M., Rick, T.C., Braje, T.J., Steinberg, A. & Vellanoweth, R.L. (2008). Human impacts on ancient shellfish: a 10,000 year record from San Miguel Island, California. *Journal of Archaeological Science*, 35, 2144-2152.

Erlandson, J.M., Rick, T.C., Estes, J.A., Graham, M.H., Braje, T.J. & Vellanoweth, R.L. (2005). Sea otters, shellfish, and humans: 10,000 years of ecological interaction on San Miguel Island, California. *Journal of Archaeological Science*, 38, 1127-1134.

Espinosa, S. (2018). Predictors of sea otter salt marsh use in Elkhorn Slough, California. MA thesis. University of California at Santa Cruz Santa Cruz, CA.

ESRI (2017). ArcGIS Version 10.1.

Estes, J.A., Brashares, J.S. & Power, M.E. (2013). Predicting and detecting reciprocity between indirect ecological interactions and evolution. *American Naturalist*, 181, S76-99.

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

Estes, J.A., Heithaus, M., McCauley, D.J., Rasher, D.B. & Worm, B. (2016). Megafaunal impacts on structure and function of ocean ecosystems. *Annual Review of Environment and Resources*, 41, 83-116.

Estes, J.A., Jameson, R.J. & Rhode, E.B. (1982). Activity and prey election in the sea otter: influence of population status on community structure. *The American Naturalist*, 120, 242-258.

Estes, J.A. & Palmisano, J.F. (1974). Sea otters: their role in structuring nearshore communities. *Science*, 185, 1058-1060.

Estes, J.A., Riedman, M.L., Staedler, M., Tinker, M.T. & Lyon, B.E. (2003). Individual variation in prey selection by sea otters: patterns, causes and implications. *Journal of Animal Ecology*, 72, 144-155.

Estes, J.A. & Steinberg, P.D. (1988). Predation, herbivory, and kelp evolution. *Paleobiology*, 14, 19-36.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011). Trophic downgrading of planet Earth. *Science*, 333, 301-306.

Evaano, G., Regnaut, S. & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, 14, 2611-2620.

Fain, S.R., DeTomaso, A. & Alberte, R.S. (1992). Characterization of disjunct populations of *Zostera marina* (eelgrass) from California: genetic differences resolved by restriction-fragment length polymorphisms. *Marine Biology*, 112, 683-689.

Felger, R. & Moser, M.B. (1973). Eelgrass (*Zostera marina* L.) in the Gulf of California: discovery of its nutritional value by the Seri Indians. *Science*, 181, 355-356.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. *et al.* (2005). Global consequences of land use. *Science*, 309, 570-574.

Ford, A.T., Goheen, J.R., Otieno, T.O., Bidner, L., Isbell, L.A., Palmer, T.M. *et al.* (2014). Large carnivores make savanna tree communities less thorny. *Science*, 346, 346-349.

Fox, J. & Weisberg, S. (2019). An {R} companion to applied regression, third edition. Thousand Oaks, CA.

Gabry, J. & Mahr, T. (2019). Bayesplot: plotting for Bayesian models. R package version 1.7.9.

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M. & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A*, 182, 389-402.

Galois, R. (1994). *Kwakwa̱ka̱’wakw settlements 1775-1920: a geographical analysis and gazeteer*. UBC Press, Vancouver, BC.

Garibaldi, A. & Turner, N. (2004). Cultural keystone species: implications for ecological conservation and restoration. *Ecology and Society*, 9, 1.

Garshelis, D.L. & Garshelis, J.A. (1984). Movements and management of sea otters in Alaska. *Journal of Wildlife Management*, 48, 665-678.

Garshelis, D.L., Garshelis, J.A. & Kimker, A.T. (1986). Sea otter time budgets and prey relationships in Alaska. *The Journal of Wildlife Management*, 50, 637-347.

Gillespie, G.E. & Kronlund, A.R. (1999). A manual for intertidal clam surveys. *Canadian Technical Report of Fisheries and Aquatic Sciences.* Fisheries and Oceans Canada Nanaimo, BC.

Goodrich, B., Gabry, J., Ali, I. & Brilleman, S. (2018). Rstanarm: Bayesian applied regression modeling via Stan. R package version 2.17.4.

Grapputo, A., Kumpulainen, T., Mappes, J. & Parri, S. (2005). Genetic diversity in populations of asexual and sexual bag worm moths (Lepidoptera: Psychidae). *BMC Ecology*, 5, 1-11.

Green, J.S. & Woodruff, R.A. (1988). Breed comparisons and characteristics of use of livestock guarding dogs. *Journal of Range Management*, 41, 249-251.

Gregr, E.J., Christensen, V., Nichol, L., Martone, R.G., Markel, R.W., Watson, J.C. *et al.* (2020). Cascading social-ecological costs and benefits triggered by a recovering keystone predator. *Science*, 368, 1243-1247.

Groesbeck, A.S., Rowell, K., Lepofsky, D. & Salomon, A.K. (2014). Ancient clam gardens increased shellfish production: adaptive strategies from the past can inform food security today. *PLoS One*, 9, e91235.

Gunther, E. (1926). An analysis of the first salmon ceremony. *American Anthropologist*, 28, 605-617.

Guo, S.W. & Thompson, E.A. (1992). Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics*, 48, 361-372.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *The American Naturalist*, 94, 421-425.

Hakai (2014). Eelgrass extent 2014, Central Coast. [Data file]. Available from Hakai Institute website: https://hecate.hakai.org/geonetwork/srv/eng/catalog.search#/ metadata/51171738 -7556-48f1-8757-658d99fa25dd.

Hale, J.R., Laidre, K.L., Tinker, M.T., Jameson, R.J., Jeffries, S.J., Larson, S.E. *et al.* (2019). Influence of occupation history and habitat on Washington sea otter diet. *Marine Mammal Science*, 35, 1369-1395.

Hanson, D.K. & Kusmer, K.D. (2001). Sea otter (*Enhydra lutris*) scarcity in the Strait of Georgia, British Columbia. In: *People and wildlife in northern North America: essays in honor of R. Dale Guthrie* (eds. Gerlach, SC & Murray, MS). Archaeopress Oxford, UK.

Harbo, R. (2007). *Shells and shellfish of the Pacific Northwest*. Harbor Publishing, Madeira Park, British Columbia.

Harper, J., Haggarty, J. & Morris, M. (1995). Broughton Archipelago clam terrace survey. Coastal and Ocean Resources, Inc. Sidney, BC, p. 39.

Harris, C. (1994). Voices of disaster: smallpox around the Strait of Georgia in 1782. *Ethnohistory*, 41, 591-626.

Hatler, D.F. (1976). The coastal mink on Vancouver Island, British Columbia. PhD thesis. In: *Zoology*. University of British Columbia Vancouver, BC.

Henderson, J. & Hacker, S.D. (2015). Buried alive: an invasive seagrass (*Zostera japonica*) changes its reproductive allocation in response to sediment disturbance. *Marine Ecology Progress Series*, 532, 123-136.

Hessing Lewis, M., Rechsteiner, E.U., Hughes, B.B., Tim Tinker, M., Monteith, Z.L., Olson, A.M. *et al.* (2018). Ecosystem features determine seagrass community response to sea otter foraging. *Marine Pollution Bulletin*, 134, 134-144.

Hill, B. (1985). *Upcoast Summers*. Horsdal and Schubart Publishers Ltd, Ganges, BC.

Hillis, D., McKechnie, I., Guiry, E., St Claire, D.E. & Darimont, C.T. (2020). Ancient dog diets on the Pacific northwest coast: zooarchaeological and stable isotope modelling evidence from Tseshaht territory and beyond. *Scientific Reports*, 10, 15630.

Hoffman, K.M., Lertzman, K.P. & Starzomski, B.M. (2017). Ecological legacies of anthropogenic burning in a British Columbia coastal temperate rain forest. *Journal of Biogeography*, 44, 2903-2915.

Hoffmann, T., Lyons, N., Miller, D., Diaz, A., Homan, A., Huddlestan, S. *et al.* (2016). Engineered feature used to enhance gardening at a 3800-year-old site on the Pacific Northwest Coast. *Science Advances*, 2, e1601282.

Hogg, R.S. (1985). An investigation into the Aboriginal substistence patterns in the eastern Queen Charlotte Strait. In: *Anthropology*. University of Victoria Victoria, p. 40.

Holdo, R.M. (2007). Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications*, 17, 558-568.

Holt, R.D. (2009). Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 19659-19665.

Honka, L.D. (2014). Quantifying the drivers and mechanisms of sea otter (*Enhydra lutris*) foraging behaviour on the Central Coast of British Columbia, Canada. Simon Fraser University Burnaby, BC, p. 44.

Howay, F.W. (1918). The dog's hair blankets of the Coast Salish. *The Washington Historical Quarterly*, 9, 83-92.

Hoyt, Z. (2015). Resource competition, space use and forage ecology of sea otters, *Enhydra lutris*, in southern southeast Alaska. PhD thesis. University of Alaska, Fairbanks.

Hsieh, T.C., Ma, H. & Chao, A. (2019). iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.19.

Hughes, A.R. & Stachowicz, J.J. (2004). Genetic diveristy enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences USA*, 101, 8998-9002.

Hughes, A.R. & Stachowicz, J.J. (2009). Ecological impacts of genotypic diversity in the clonal seagrass *Zostera marina*. *Ecology*, 90, 1412-1419.

Hughes, A.R. & Stachowicz, J.J. (2011). Seagrass genotypic diversity increases disturbance response via complementarity and dominance. *Journal of Ecology*, 99, 445-453.

Hughes, B.B., Eby, R., Van Dyke, E., Tinker, M.T., Marks, C.I., Johnson, K.S. *et al.* (2013). Recovery of a top predator mediates negative eutrophic effects on seagrass. *Proceedings of the National Academy of Sciences USA*, 110, 15313-15318.

Hughes, B.B., Hammerstrom, K.K., Grant, N.E., Hoshijima, U., Eby, R. & Wasson, K. (2016). Trophic cascades on the edge: fostering seagrass resilience via a novel pathway. *Oecologia*, 182, 231-241.

Hughes, B.B., Wasson, K., Tinker, M.T., Williams, S.L., Carswell, L.P., Boyer, K.E. *et al.* (2019). Species recovery and recolonization of past habitats: lessons for science and conservation from sea otters in estuaries. *PeerJ*, 7, e8100.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Monograph Series*, 22, 415-427.

Ibarra, S.N. (2021). Addressing complex resource conflict: humans, sea otters, and shellfish in southeast Alaska. PhD thesis. University of Alaska, Fairbanks.

Ingram, T., Costa-Pereira, R. & Araujo, M.S. (2018). The dimensionality of individual niche variation. *Ecology*, 99, 536-549.

Jackley, J., Gardner, L., Djunaedi, A.F. & Salomon, A.K. (2016). Ancient clam gardens, traditional management portfolios, and the resilience of coupled human-ocean systems. *Ecology and Society*, 21, 20.

Jackson, J.B.C. (2001). What was natural in the coastal oceans? *Proceedings of the National Academy of Sciences, USA*, 98, 5411-5418.

Jameson, R.J. (1989). Movements, home range, and territories of male sea otters off central California. *Marine Mammal Science*, 5, 159-172.

Janzen, D.H. & Martin, P.S. (1982). Neotrophical anachronisms: the fruits the Gomphotheres ate. *Science*, 215, 19-27.

Jombart, T. (2008). Adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24, 1403-1405.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373-386.

Kamvar, Z.N., Tabima, J.F. & Grünwald, N.J. (2014). Poppr: an R package for genetic analysis of populations with clonal, partiallly clonal, and/or sexual reproduction. *PeerJ*, 2.

Kenner, M.C. & Tinker, M.T. (2018). Stability and change in kelp forest habitats at San Nicholas Island. *Western North American Naturalist*, 78, 1-11.

Kenyon, K. (1969). The sea otter in the eastern Pacific Ocean. *North American Fauna*, 68.

Kienast, S.S. & McKay, J.L. (2001). Sea surface temperatures in the subarctic northeast Pacific reflect millennial-scale climate oscillations during the last 16 kyrs. *Geophysical Research Letters*, 28, 1563-1566.

Kim, J.H., Kang, J.H., Jang, J.E., Choi, S.K., Kim, M.J., Park, S.R. *et al.* (2017). Population genetic structure of eelgrass (*Zostera marina*) on the Korean coast: Current status and conservation implications for future management. *PLoS One*, 12, e0174105.

Kim, S.H., Kim, J.H., Park, S.R. & Lee, K.S. (2014). Annual and perennial life history strategies of *Zostera marina* populations under different light regimes. *Marine Ecology Progress Series*, 509, 1-13.

Koch, J., Clague, J.J. & Osborn, G.D. (2007). Glacier fluctuations during the past millennium in Garibaldi Provincial Park, southern Coast Mountains, British Columbia. *Canadian Journal of Earth Sciences*, 44, 1215-1233.

Kvitek, R.G., Bowley, C.E. & Staedler, M. (1993). Diet and foraging behavior of sea otters in southeast Alaska. *Marine Mammal Science*, 9, 168-181.

Kvitek, R.G., Fukayama, A.K., Anderson, B.S. & Grimm, B.K. (1988). Sea otter foraging on deep-burrowing bivalves in a California coastal lagoon. *Marine Biology*, 98, 157-167.

Kvitek, R.G. & Oliver, J.S. (1992). Influence of sea otters on soft-bottom prey communities in southeast Alaska. *Marine Ecology Progress Series*, 82, 103-113.

Kvitek, R.G., Oliver, J.S., DeGange, A.R. & Anderson, B.S. (1992). Changes in Alaskan soft-bottom prey communties along a gradient in sea otter predation. *Ecology*, 73, 413-428.

Lafferty, K.D. & Tinker, M.T. (2014). Sea otters are recolonizing southern California in fits and starts. *Ecosphere*, 5, 50.

Laidre, K.L. & Jameson, R.J. (2006). Foraging patterns and prey selection in an increasing and expanding sea otter population. *Journal of Mammalogy*, 87, 799-807.

Laws, R.M. (1970). Elephants as agents of habitat and landscape change in East Africa. *Oikos*, 21, 1-15.

Layland, M. (2016). *A perfect Eden: encounters by early explorers of Vancouver Island*. Touchwood Editions, Victoria, BC.

Leberg, P.L. (2002). Estimating allelic richness: effects of sample size and bottlenecks. *Molecular Ecology*, 11, 2445-2449.

Lee, L.C., Watson, J.C., Trebilco, R. & Salomon, A.K. (2016). Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator. *Ecosphere*, 7, e01604.

Lepofsky, D., Hallett, D., Washbrook, K., McHalsie, A., Lertzman, K. & Mathewes, R. (2005). Documenting precontact plant management on the northwest coast: an example of prescribed buring in the central and upper Fraser Valley, British Columbia. In: *Keeping it living: traditions of plant use and cultivation on the northwest coast*. University of Washington Press Seattle, Washington.

Lepofsky, D. & Lertzman, K. (2008). Documenting ancient plant management in the northwest of North America. *Botany*, 86, 129-145.

Lepofsky, D., Smith, N.F., Cardinal, N., Harper, J., Morris, M., White), G.E. *et al.* (2015). Ancient shellfish mariculture on the northwest coast of North America. *American Antiquity*, 80, 236-259.

Lepofsky, D., Toniello, G., Earnshaw, J., Roberts, C., Wilson, L., Rowell, K. *et al.* (2020). Ancient anthropogenic clam gardens of the northwest coast expand clam habitat. *Ecosystems*, 24, 248-260.

Lewis, D.H. & Smith, D.J. (2004). Little Ice Age glacial activity in Strathcona Provincial Park, Vancouver Island, British Columbia, Canada. *Canadian Journal of Earth Sciences*, 41, 285-297.

Lewis, T.L., Esler, D. & Boyd, S. (2007). Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. *Marine Ecology Progress Series*, 329, 131-144.

Lightfoot, K.G. (1995). Culture contact studies: redefining the relationship between prehistoric and historical archaeology. *American Antiquity*, 60, 199-217.

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

Lyman, R.L. (2011). A history of paleoecological research on sea otters and pinnipeds of the eastern Pacific rim. In: *Human impacts on seals, sea lions, and sea otters: integrating archaeology and ecology in the northeast Pacific* (eds. Braje, TJ & Rick, TC). University of California Press Berkeley and Los Angeles, California.

Lyons, N., Hoffmann, T., Miller, D., Martindale, A., Ames, K.M. & Blake, M. (2021). Were the ancient Coast Salish farmers? A story of origins. *American Antiquity*, 1-22.

Machovsky-Capuska, G.E., Miller, M.G.R., Silva, F.R.O., Amiot, C., Stockin, K.A., Senior, A.M. *et al.* (2018). The nutritional nexus: linking niche, habitat variability and prey composition in a generalist marine predator. *Journal of Animal Ecology*, 87, 1286-1298.

Machovsky-Capuska, G.E., Senior, A.M., Benn, E.C., Tait, A.H., Schuckard, R., Stockin, K.A. *et al.* (2016). Sex-specific macronutrient foraging strategies in a highly successful marine predator: the Australasian gannet. *Marine Biology*, 163.

Marin-Guirao, L., Entrambasaguas, L., Ruiz, J.M. & Procaccini, G. (2019). Heat-stress induced flowering can be a potential adaptive response to ocean warming for the iconic seagrass *Posidonia oceanica*. *Molecular Ecology*, 28, 2486-2501.

Marsden, S. & Galois, R. (1995). The Tsimshian, the Hudson's Bay Company, and the geopolitics of the northwest coast fur trade 1787-1840. *The Canadian Geographer / Le Géographe canadien*, 39, 169-181.

Martin, P.S. (1973). The discovery of America. *Science*, 179, 969-974.

Massa, S., Paulino, C.M., Serrão, E.A., Duarte, C.M. & Arnaud-Haond, S. (2013). Entangled effects of allelic and clonal (genotypic) richness in the resistance and resilience of experimental populations of the seagrass *Zostera noltii* to diatom invasion. *BMC Ecology*, 13, 39.

Mathews, D.L. & Turner, N.J. (2017). Ocean cultures: northwest coast ecosystems and Indigenous management. In: *Conservation for the Anthropocene ocean* (eds. Levin, P & Poe, M). Academic Press, Elsiever San Diego, CA, pp. 169-206.

McCain, J.S.P., Cull, D.J., Schneider, D.C. & Lotze, H.K. (2016). Long-term shift in coastal fish communities before and after the collapse of Atlantic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 73, 1415-1426.

McKechnie, I. (2007). Investigating the complexities of sustainable fishing at a prehistoric village on western Vancouver Island, British Columbia, Canada. *Journal for Nature Conservation*, 15, 208-222.

McKechnie, I., Moss, M.L. & Crockford, S.J. (2020). Domestic dogs and wild canids on the northwest coast of North America: animal husbandry in a region without agriculture? *Journal of Anthropological Archaeology*, 60, 101209.

McKechnie, I. & Wigen, B. (2011). Toward a historical ecology of pinniped and sea otter hunting traditions on the coast of southern British Columbia. In: *Human impacts on seals, sea lions, and sea otters: integrating archaeology and ecology in the northeast Pacific* (eds. Braje, TJ & Rick, TC). University of California Press Berkeley and Los Angeles, California.

Meltzer, D.J. (2015). Pleistocene overkill and North American mammalian extinctions. *Annual Review of Anthropology*, 44, 33-53.

Menzies, A. (1792). *Menzies' journal of Vancouver's Voyage, April to October 1792. Edited, with botanical and ethnological notes, by C.F. Newcombe, and a biographical note by J. Forsyth, 1923*. BC Historical Books: William H. Cullin, Printer to the King's Most Excellent Majesty, Victoria BC.

Miller, D.J., Hardwick, J.E. & Dahlstrom, W.A. (1975). Pismo clams and sea otters. In: *Marine Resources Technical Report*. Marine Resources Technical Report No. 31. California Department of Fish and Game.

Nahirnick, N.K., Costa, M., Schroeder, S. & Sharma, T. (2019). Long-term eelgrass habitat dhange and associated human impacts on the west coast of Canada. *Journal of Coastal Research*, 36, 30-40.

Nahirnick, N.K., Reshitnyk, L., Campbell, M., Hessing-Lewis, M., Costa, M., Yakimishyn, J. *et al.* (2018). Mapping with confidence; delineating seagrass habitats using Unoccupied Aerial Systems (UAS). *Remote Sensing in Ecology and Conservation*, 10.1002/rse2.98.

Nevo, E. (2001). Evolution of genome-phenome diversity under environmental stress. *Proceedings of the National Academy of Sciences, USA*, 98, 6233-6240.

Newsome, S.D., Tinker, M.T., Gill, V.A., Hoyt, Z.N., Doroff, A., Nichol, L. *et al.* (2015). The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. *Oecologia*, 178, 45-59.

Nichol, L.M., Watson, J.C., Abernethy, R., Rechsteiner, E. & Towers, J. (2015). Trends in the abundance and distribution of sea otters (*Enhydra lutris*) in British Columbia updated with 2013 survey results. In: *DFO Canadian Science Advisory Secretariat Research Document*, p. vii + 31 p.

Oftedal, O.T., Ralls, K., Tinker, M.T. & Green, A. (2007). Nutritional constraints of the southern sea otter in the Monterey Bay National Marine Sanctuary.

Oliver, J.S. & Slattery, P.N. (1985). Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecology*, 66, 1965-1975.

Olsen, J.L., Coyer, J.A. & Chesney, B. (2014). Numerous mitigation transplants of the eelgrass *Zostera marina* in southern California shuffle genetic diversity and may promote hybridization with *Zostera pacifica*. *Biological Conservation*, 176, 133-143.

Olsen, J.L., Stam, W.T., Coyer, J.A., Reusch, T.B., Billingham, M., Bostrom, C. *et al.* (2004). North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. *Molecular Ecology*, 13, 1923-1941.

Olsen, S. (2010). *Working with wool: a Coast Salish legacy and the Cowichan sweater*. Sono Nis Press, Winlaw, BC.

Orchard, T. (2007). Otters and urchins: continuity and change in Haida economy during the Late Holocene and maritime fur trade periods. PhD thesis. University of Toronto Toronto, Ontario.

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

Paine, R.T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103, 91-93.

Peakall, R. & Smouse, P.E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research - an update. *Bioinformatics*, 28, 2537-2539.

Petit, R.J., el Mousadik, A. & Pons, O. (1998). Identifying populations for conservation on the basis of genetic markers. *Conservation Biology*, 12, 844-855.

Pickett, S.T.A. (1989). Space for time substitution as an alternative to long-term studies. In: *Long-term studies in ecology* (ed. Likens, GE). Springer-Verlag New York, pp. 110-135.

Pinkerton, E., Salomon, A.K. & Dragon, F. (2019). Reconciling social justice and ecosystem-based management in the wake of a successful predator reintroduction. *Canadian Journal of Fisheries and Aquatic Sciences*, 76, 1031-1039.

Polis, G.A. (1984). Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *The American Naturalist*, 123, 541-564.

Potvin, D.A., Parris, K.M., Smith Date, K.L., Keely, C.C., Bray, R.D., Hale, J. *et al.* (2017). Genetic erosion and escalating extinction risk in frogs with increasing wildfire frequency. *Journal of Applied Ecology*, 54, 945-954.

Power, M.E. (1984). Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology*, 65, 523-528.

Power, M.E. (1990). Effects of fish in river food webs. *Science*, 250, 811-814.

Power, M.E., Matthews, W.J. & Stewart, A.J. (1985). Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology*, 66, 1448-1456.

Power, M.E., Parker, M.S. & Dietrich, W.E. (2008). Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs*.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, S. *et al.* (1996). Challenges in the quest for keystones. *Bioscience*, 46, 609-620.

Preen, A. (1995). Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Marine Ecology Progress Series*, 124, 201-213.

Pringle, R.M., Kimuyu, D.M., Sensenig, R.L., Palmer, T.M., Riginos, C., Veblen, K.E. *et al.* (2015). Synergistic effects of fire and elephants on arboreal animals in an African savanna. *Journal of Animal Ecology*, 84, 1637-1645.

Pritchard, J.K., Stephens, M. & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, 155, 945-959.

Procaccini, G., Olsen, J.L. & Reusch, T.B.H. (2007). Contribution of genetics and genomics to seagrass biology and conservation. *Journal of Experimental Marine Biology and Ecology*, 350, 234-259.

Quayle, D.B. & Bourne, N. (1972). The clam fisheries of British Columbia. *Fisheries Research Board of Canada*, 179, 1-73.

Rasher, D.B., Steneck, R.S., Halfar, J., Kroeker, K.J., Ries, J.B., Tinker, M.T. *et al.* (2020). Keystone predators govern the pathway and pace of climate impacts in a subarctic marine ecosystem. *Science*, 369, 1351-1354.

Raymond, W.W., Tinker, M.T., Kissling, M.L., Benter, B., Gill, V.A. & Eckert, G.L. (2019). Location-specific factors influence patterns and effects of subsistence sea otter harvest in Southeast Alaska. *Ecosphere*, 10, e02874.

Rechsteiner, E.U. & Olson, A.M. (2016). Harlequin ducks (*Histrionicus histrionicus*) scavenge sea urchin fragments from foraging sea otters (*Enhydra lutris*). *Canadian Field Naturalist*, 130, 91-98.

Rechsteiner, E.U., Watson, J.C., Tinker, M.T., Nichol, L.M., Morgan Henderson, M.J., McMillan, C.J. *et al.* (2019). Sex and occupation time influence niche space of a recovering keystone predator. *Ecology and Evolution*, 9, 3321-3334.

Rechsteiner, E.U., Wickham, S.B. & Watson, J.C. (2018). Predator effects link ecological communities: kelp created by sea otters provides an unexpected subsidy to bald eagles. *Ecosphere*, 9, e02271.

Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A. *et al.* (2013). Understanding and managing conservation conflicts. *Trends in Ecology and Evolution*, 28, 100-109.

Reid, A.J., Eckert, L.E., Lane, J.F., Young, N., Hinch, S.G., Darimont, C.T. *et al.* (2020). “Two-Eyed Seeing”: an Indigenous framework to transform fisheries research and management. *Fish and Fisheries*, 22, 243-261.

Reidy, R.D. (2011). The potential impact of sea otters (*Enhydra lutris*) on the British Columbia geoduck clam (*Panopea abrupta*) fishery. In: *School or Resource and Environmental Management*. Simon Fraser University Vancouver, BC.

Reidy, R.D. & Cox, S.P. (2013). Geoduck clam (*Panopea abrupta*) demographics and mortality rates in the presence of sea otters (*Enhydra lutris*) and commercial harvesting. *The Open Fish Science Journal*, 6, 28-40.

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C. *et al.* (2020). The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon*, 62, 725-757.

Reshitnyk, L., Robinson, C.L.K. & Dearden, P. (2014). Evaluation of WorldView-2 and acoustic remote sensing for mapping benthic habitats in temperate coastal Pacific waters. *Remote Sensing of the Environment*, 153, 7-23.

Reusch, T.B., Ehlers, A., Hammerli, A. & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences, USA*, 102, 2826-2831.

Reynolds, L.K., Stachowicz, J.J., Hughes, A.R., Kamel, S.J., Ort, B.S. & Grosberg, R.K. (2017). Temporal stability in patterns of genetic diversity and structure of a marine foundation species (*Zostera marina*). *Heredity*, 118, 404-412.

Rice, W.R. (1989). Analyzing tables of statistical tests. *Evolution*, 43, 223-225.

Riedman, M. & Estes, J.A. (1990). The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. U.S. Fish and Wildlife Service, U.S. Department of the Interior Washington, D.C.

Ripple, W.J. & Beschta, R.L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, 145, 205-213.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M. *et al.* (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484-1241411.

Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M. *et al.* (2015). Collapse of the world's largest herbivores. *Science Advances*, 1, e1400103.

Robinson, M.P. (1996). *Sea Otter Chiefs*. Bayeux Arts, Calgary AB.

Roffler, G.H., Allen, J.M., Massey, A. & Levi, T. (2021). Metabarcoding of fecal DNA shows dietary diversification in wolves substitutes for ungulates in an island archipelago. *Ecosphere*, 12, e03297.

Rosenblatt, A., Heithaus, M., Mather, M., Matich, P., Nifong, J., Ripple, W. *et al.* (2013). The roles of large top predators in coastal ecosystems: new insights from long term ecological research. *Oceanography*, 26, 156-167.

Rousset, F. (2008). Genepop'007: a complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources*, 8, 103-106.

Ruckstahl, K.E. & Clutton-Brock, T.H. (2005). Sexual segregation and the ecology of the two sexes. In: *Sexual segregation in vertebrates: ecology of the two sexes* (eds. Ruckstahl, KE & Neuhaus, P). Cambridge University Press Cambridge, pp. 3-10.

Ruiz, J.M., Marin-Guirao, L., Garcia-Munoz, R., Ramos-Segura, A., Bernardeau-Esteller, J., Perez, M. *et al.* (2018). Experimental evidence of warming-induced flowering in the Mediterranean seagrass *Posidonia oceanica*. *Marine Pollution Bulletin*, 134, 49-54.

Salomon, A.K., Burt, J.M., Ḵii'iljuus, B.J.W. & McKechnie, I. (2020). Coastal voices: lessons learned and recmmendations on revitalizing our relationship with sea otters, kelp forests, and coastal fisheries. Burnaby, British Columbia.

Salomon, A.K., Burt, J.M., Ḵii'iljuus, B.J.W., Roberts, N., Wood, L. & Honka, L. (2018). Visioning the future of kelp forest, sea otter, and human interactions; workshop summary report. Burnaby, British Columbia.

Salomon, A.K., Ḵii'iljuus, B.J.W., Xanius, E.W., Tanape Sr., N. & Happynook, T.M. (2015). First Nations perspectives on sea otter conservation in British Columbia and Alaska: insights into coupled human-ocean systems. In: *Sea otter conservation* (eds. Bodkin, JL & Larson, SE). Elsevier San Diego, CA.

Salomon, A.K., Tanape Sr., N.M. & Huntington, H.P. (2007). Serial depletion of marine invertebrates leads to the decline of a strongly interacting grazer. *Ecological Applications*, 17, 1752-1770.

Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, 78, 1388-1399.

Shannon, C.E. (1948). A mathematical theory of communication. *The Bell System Technical Journal*, 27, 379-423.

Shine, R. (1989). Ecological causes for the evoluation of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology*, 64, 419-461.

Shine, R., Harlow, P.S. & Boedi (1998). The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology*, 12, 248-258.

Shine, R. & Wall, M. (2005). Ecological divergence between the sexes in reptiles. In: *Sexual Segregation in Vertebrates*. Cambridge University Press New York.

Short, F.T. & Wyllie-Echeverria, S. (1996). Natural and human-induced disturbance of seagrasses. *Environmental Conservation*, 23, 17-27.

Silliman, B.R., Hughes, B.B., Gaskins, L.C., He, Q., Tinker, M.T., Read, A. *et al.* (2018). Are the ghosts of nature's past haunting ecology today? *Current Biology*, 28, 532-537.

Silverman, B.W. (1986). *Density estimation for statistics and data analysis*. Chapman and Hall, London, UK.

Simenstad, C.A., Estes, J.A. & Kenyon, K.W. (1978). Aleuts, sea otters, and alternate stable-state communities. *Science*, 200, 403-411.

Simmons, B.L., Sterling, J. & Watson, J.C. (2014). Species and size-selective predation by raccoons (*Procyon lotor*) preying on introduced intertidal clams. *Canadian Journal of Zoology*, 92, 1059-1065.

Singh, G.G., Markel, R.W., Martone, R.G., Salomon, A.K., Harley, C.D. & Chan, K.M. (2013). Sea otters homogenize mussel beds and reduce habitat provisioning in a rocky intertidal ecosystem. *PLoS One*, 8, e65435.

Singh, G.G. & McKechnie, I. (2015). Making the most of fragments: a method for estimating shell length from fragmentary mussels (*Mytilus californianus* and *Mytilus trossulus*) on the Pacific Coast of North America. *Journal of Archaeological Science*, 58, 175-183.

Slade, E. (2019). Estimating historic sea otter prevalence from archaeological and contemporary California mussel size structure. MRM thesis. Simon Fraser University Burnaby, BC.

Slater, N. (2018). Ancient clam gardens magnify bivavle production by moderating ambient temperature and enchancing sediment carbonate. MRM thesis. Simon Fraser University Burnaby, BC.

Sloan, N.A. & Dick, L. (2012). *Sea otters of Haida Gwaii: icons in human-ocean relations*. Gwaii Haanas Archipelago Management Board and Haida Gwaii Museum, Skidegate.

Smith, J.G., Tomoleoni, J., Staedler, M., Lyon, S., Fujii, J. & Tinker, M.T. (2021). Behavioral responses across a mosaic of ecosystem states restructure a sea otter-urchin trophic cascade. *Proceedings of the National Academy of Sciences, USA*, 118, e2012493118.

Smith, N.F., Lepofsky, D., Toniello, G., Holmes, K., Wilson, L., Neudorf, C.M. *et al.* (2019). 3500 years of shellfish mariculture on the Northwest Coast of North America. *PLoS One*, 14, e0211194.

Smith, T.S. & Partridge, S.T. (2004). Dynamics of intertidal foraging by coastal brown bears in southwestern Alaska. *Journal of Wildlife Management*, 68, 233-240.

Soulé, M.E., Estes, J.A., Berger, J. & Martinez del Rio, C. (2002). Ecological effectiveness: conservation goals for interactive species. *Conservation Biology*, 17, 1238-1250.

Soulé, M.E., Estes, J.A., Miller, B. & Honnold, D.L. (2005). Strongly interacting species: conservation policy, management, and ethics. *Bioscience*, 55, 168-176.

Spiess, A.-N. (2018). Propogate: propagation of uncertainty. R package version 1.0-6.

Stenson, G.B., Badgero, G.A. & Fisher, H.D. (1984). Food habits of the river otter *Lutra canadensis* in the marine environment of British Columbia. *Canadian Journal of Zoology*, 62, 88-91.

Stewart, M., Carleton, W.C. & Groucutt, H.S. (2021). Climate change, not human population growth, correlates with Late Quaternary megafauna declines in North America. *Nature Communications*, 12, 965-980.

Stothert, K.E., Piperno, D.R. & Andres, T.C. (2003). Terminal Pleistocene/early Holocene human adaptation in coastal Ecuador: the Las Vegas evidence. *Quaternary International*, 109-110, 23-43.

Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D. & Zanette, L.Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, 7, 10698.

Suraci, J.P., Clinchy, M., Zanette, L.Y. & Wilmers, C.C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22, 1578-1586.

Szpak, P., Orchard, T.J., McKechnie, I. & Gröcke, D.R. (2012). Historical ecology of late Holocene sea otters (*Enhydra lutris*) from northern British Columbia: isotopic and zooarchaeological perspectives. *Journal of Archaeological Science*, 39, 1553-1571.

Talbot, S.L., Sage, G.K., Rearick, J.R., Fowler, M.C., Muniz-Salazar, R., Baibak, B. *et al.* (2016). The structure of genetic diversity in eelgrass (*Zostera marina* L.) along the north Pacific and Bering sea coasts of Alaska. *PLoS One*, 11, e0152701.

Tarjan, L.M. (2016). Space use and reproductive success of male sea otters. PhD thesis. University of California at Santa Cruz.

Templeton, A.R., Brazeal, H. & Neuwald, J.L. (2011). The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology*, 92, 1736-1747.

Testani, A. (2017). The effects of clam gardens on ancient subsistence practices on Quadra Island: a zooarchaeologicla analysis. BA thesis. Simon Fraser University Burnaby, British Columbia.

Thayer, G.W. & Engel, D.W. (1982). Evidence for short-circuiting of the detritus cycle of seagrass beds by the green turtle, *Chelonia mydas*, L. *Journal of Experimental Marine Biology and Ecology*, 62, 173-183.

Thometz, N.M., Staedler, M.M., Tomoleoni, J.A., Bodkin, J.L., Bentall, G.B. & Tinker, M.T. (2016). Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behavioral Ecology*, 27, 1552-1566.

Thorne, K. (2016). Stutul’na’mut report: caring for our beaches. Hul’q’umi’num-Gulf Islands National Park Reserve Committee Sidney, BC.

Tinker, M.T. (2015). The use of quantitative models in sea otter conservation. In: *Sea otter conservation* (eds. Bodkin, JL & Larson, SE). Elsevier San Diego, CA.

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

Tinker, M.T., Doak, D.F. & Estes, J.A. (2008b). Using demography and movement behavior to predict range expansion of the southern sea otter. *Ecological Applications*, 18, 1781-1794.

Tinker, M.T., Tomoleoni, J.A., Weitzman, B.P., Staedler, M., Jessup, D., Murray, M.J. *et al.* (2019). Southern sea otter (*Enhydra lutris nereis*) population biology at Big Sur and Monterey, California - investigationg the consequences of resource abundance and anthropogenic stressors for sea otter recovery. In: *US Geological Survey Open-File Report*, p. 225 p.

Tinker, T.M., Guimaraes, P.R., Jr., Novak, M., Marquitti, F.M., Bodkin, J.L., Staedler, M. *et al.* (2012). Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. *Ecology Letters*, 15, 475-483.

Toniello, G. & Crowell, T. (2020). Simon Fraser University Quadra Island archaeological clam garden and settlement project: 2014-2016 fieldwork in Kanish and Waiatt Bays. HCA Permit#2014-0095.

Toniello, G., Lepofsky, D., Lertzman-Lepofsky, G., Salomon, A.K. & Rowell, K. (2019). 11,500 y of human-clam relationships provide long-term context for intertidal management in the Salish Sea, British Columbia. *Proceedings of the National Academy of Sciences, USA*, 116, 22106-22114.

Traiger, S.B., Konar, B., Doroff, A. & McCaslin, L. (2016). Sea otters versus sea stars as major clam predators: evidence from foraging pits and shell litter. *Marine Ecology Progress Series*, 560, 73-86.

Turner, N.J. (2014). *Ancient pathways, ancectral knowledge: ethnobotany and ecological wisdom of Indigenous peoples of northwestern North America*. McGill-Queens University Press, Montreal.

Turner, N.J., Deur, D. & Lepofsky, D. (2013). Plant management systems of British Columbia's first peoples. *BC Studies*, 179, 107-133.

Turner, N.J., Gergory, R., Brooks, C., Failing, L. & Satterfield, T. (2008). From invisibility to transparency: identifying the implications. *Ecology and Society*, 13, 7.

Turner, N.J. & Turner, K.L. (2008). "Where our women used to get the food": cumulative effects and loss of ethnobotanical knowledge and practice; case study from coastal British Columbia. *Botany*, 86, 103-115.

van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M. & Shipley, P. (2004). MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, 4, 535-538.

VanBlaricom, G.R. (1988). Effect of foraging by sea otters on mussel-dominated intertidal communities. In: *Ecological studies 65: the community ecology of sea otters* (eds. VanBlaricom, GR & Estes, JA). Springer-Verlag Berlin, pp. 48-91.

Vermeij, G.J. (1982). Unsuccessful predation and evolution. *The American Naturalist*, 120, 701-720.

Watson, J. (2000). The effects of sea otters (*Enhydra lutris*) on abalone (*Haliotis* spp.) populations. In: *Workshop on Rebuilding Abalone Stocks in British Columbia* (ed. Campbell, A). Canadian Special Publication Fisheries and Aquaculture Science, pp. 123-132.

Watson, J. & Estes, J.A. (2011). Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. *Ecological Monographs*, 81, 215-239.

Watson, J.C. (1990). The effects of the *Nestucca* oil spill on the British Columbia sea otter population and its environment. Ecological Reserves Collection. Government of British Columbia, Victoria BC. 24 pp.

Watson, J.C. (1993). The effects of sea otter (*Enhydra lutris*) foraging on shallow rocky communities of northwestern Vancouver Island, British Columbia. PhD thesis. University of California, Santa Cruz Santa Cruz, CA.

Weitzman, B.P. (2013). Effects of sea otter colonization on soft-sediment intertidal prey assembladges in Glacier Bay, Alaska. University of California at Santa Cruz.

Whitaker, A.R. (2008). Incipient aquaculture in prehistoric California? Long-term productivity and sustainability vs. immediate returns for the harvest of marine invertebrates. *Journal of Archaeological Science*, 35, 1114-1123.

Wickham, H. (2009). Ggplot2: elegant graphics for data analysis. Springer-Verlag New York.

Wickham, H., François, R., Henry, L. & Müller, K. (2019). Dplyr: a grammar of data manipulation. R package version 0.8.3.

Wickham, H. & Henry, L. (2019). Tidyr: tidy messy data. R package version 1.0.0.

Widmer, A. & Lexer, C. (2001). Glacial refugia: sanctuaries for allelic richness, but not for gene diversity. *Trends in Ecology & Evolution*, 16, 267-269.

Wilk, J.A., Kramer, A.T. & Ashley, M.V. (2009). High variation in clonal vs. sexual reproduction in populations of the wild strawberry, *Fragaria virginiana* (Rosaceae). *Annals of Botany*, 104, 1413-1419.

Williams, G.C. (1975). *Sex and Evolution*. Princeton University Press, Princeton, New Jersey.

Williams, J. (2006). *Clam gardens: Aboriginal mariculture on Canada's west coast*. New Star Books, Vancouver, British Columbia.

Williams, S.L. (1988). *Thalassia testudinum* productivity and grazing by green turtles in a highly disturbed seagrass bed. *Marine Biology*, 98, 447-455.

Wilmers, C.C., Estes, J.A., Edwards, M., Laidre, K.L. & Konar, B. (2012). Do trophic cascades affect the storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and the Environment*, 10, 409-415.

Worm, B. & Paine, R.T. (2016). Humans as a hyperkeystone species. *Trends in Ecology and Evolution*, 31, 600-607.