Navigating coexistence: Ecological drivers and social implications of predator-induced regime shifts in the Northeast Pacific

by

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Faculty of Environment

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## Approval

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Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

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Abstract

Societies are greatly challenged by regime shifts, when ecosystems undergo fundamental changes that are rapid, unexpected, and difficult to reverse. In order to better navigate these transitions, we need information on the drivers, species interactions, and feedbacks that influence ecosystem dynamics, and an understanding of how human communities are adapting to the profound shifts in ecosystem resources. My thesis applies this social-ecological system lens to an iconic regime shift – the recovery of sea otters (*Enhydra lutris*) in the Northeast Pacific that is triggering a trophic cascade which causes sea urchin and shellfish-dominated rocky reefs to become productive macroalgae-dominated forests. To examine how predation and herbivory interactions affect the structure, function, and resilience of reef communities on the central coast of British Columbia (BC), I conducted four years of subtidal surveys and experiments. These data confirm the critical role of sea otter predation in suppressing urchin populations, but also demonstrate for the first time, that complementary predation by mesopredators (i.e. sunflower sea star *Pycnopodia helianthoides*) further enhance the resilience of kelp forests by consuming smaller-sized urchins that are otherwise unconsumed by otters. I also experimentally quantified how numerical and behavioural factors collectively influence herbivory rates that maintain alternative reef states. Kelp consumption rates showed a positive but non-linear relationship with urchin biomass, whereas food subsidies and predator-avoidance behaviour reduced urchin grazing rates. Next, to understand how sea otter recovery influences coastal Indigenous communities, I worked in a collaborative Indigenous partnership to host workshops and conduct survey-interviews in a comparative case study. We identified 22 social-ecological conditions that can influence Indigenous peoples’ ability to adapt to otters, and revealed how perceptions and adaptive capacity differed between a BC First Nations community and an Alaska Sugpiaq Tribe. These quantitative and qualitative data suggest that coexistence with sea otters could be improved through strengthening Indigenous agency and authority and enabling collaborative adaptive otter management grounded in traditional knowledge and western science. As a whole, this thesis highlights the complexities, surprises, and contextual nuances that characterize sea otter recovery in tightly coupled social-ecological systems, and provides the foundations for a road map to improve future human-otter coexistence.
Keywords: tipping points; social-ecological regime shift and resilience; predator-prey interactions; Indigenous governance and knowledge; adaptive co-management
To all those seeking or embarking on a challenge.

“Whatever you can do, or dream you can do, begin it. Boldness has genius, power, and magic in it.”

- von Goethe -
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Filled with learning, tears, and laughter, as the years have gone by.
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My mentor and teacher, colleague, friend, co-conspirer.
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---

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Chapter 1.

Introduction

Regime shifts, resilience, and social-ecological systems

Ecosystems and human social systems are inherently interconnected, linked through complex feedbacks and evolving systems of management that influence how humans interact with, and steward natural resources (Berkes & Folke 1998; Brown & Brown 2009). Recognizing these linkages is especially important given that ecosystems and social systems do not always behave in predictable ways, but are often unpredictable in time and space (Paine et al. 1998; Scheffer et al. 2001; Berkes et al. 2003; Folke et al. 2004; Hughes et al. 2013). Whether one examines fluctuating market trends within economics, swings in election results within political science, or complex species interactions in ecology, it is evident that understanding these systems’ dynamics requires moving beyond simple linear models, acknowledging both non-linear patterns and uncertainty. This understanding of complex systems behaviour has evolved over time, from a period dominated by the concept of “nature in equilibrium”, to a period beginning in the 1960s where the existence of stability in natural systems was challenged and debated (Fig. 1: Lewontin 1969; Holling 1973; Sutherland 1974). In the 1970s, the idea emerged that ecological systems could exist in alternative states: the same species might be present, but in vastly different abundances, with different interactions and feedbacks that persist through time (Noy-Meir 1975; May 1977; Scheffer et al. 2001). The often rapid, unpredictable, and dramatic shifts between alternative ecological configurations became known as “regime shifts,” and have been documented across the world’s major biomes in terrestrial (e.g., grasslands to shrublands), aquatic (e.g., clear lakes to turbid lakes), and marine ecosystems (e.g., coral-dominated to algal-dominated reefs, or kelp forests to urchin barrens) (see citations in Fig. 1). Overall, the growing awareness of regime shifts presents a multi-faceted challenge to society and scholars alike – to better understand the ecological dynamics and social adaptations of regime shifts and seek improved approaches to resource management that respond to these complex and interconnected system dynamics. This is the focus of my thesis.
Figure 1.1. Evolution of the scholarly literature that has advanced the ecological and social-ecological theory on regime shifts and their implications for management and conservation. ‘Lightbulbs’ demark key themes that define an era of scholarly literature, green/orange/blue text are themes ongoing in the present. Within each theme seminal papers are listed by author and title (full citations under ‘References’).
With the realization that shocks and disturbances can trigger rapid and dramatic ecosystem shifts, the concept of “resilience” emerged as a way to understand the capacity of ecosystems to absorb change (Holling 1973). An ecological community with high resilience can maintain a state where key relationships (e.g., processes and variables that control system behaviour) persist when the system is subject to perturbation, whereas a community with lower resilience might be pushed over a threshold causing it to shift into an alternative configuration (Holling 1996). Resilience theory has also been applied to social systems applications (e.g., Berkes & Folke 1998; Lebel et al. 2006; Marshall & Marshall 2007; Nelson et al. 2007; O’Brien et al. 2009; Adger et al. 2011; Cote & Nightingale 2012; Berkes & Ross 2013), where social resilience can be defined as “the ability of [human] communities to cope with external stresses and disturbances as a result of social, political, and environmental change” (Adger 2000, p.374). The concept of resilience is useful in the context of ecological regime shifts because it is critical to understand the mechanisms that either reinforce, or erode the stability of alternative community configurations (e.g., Konar & Estes 2003; Ling et al. 2015). This is the focus of chapters 2 and 3. Similarly, it is useful to draw on key factors and conditions identified through social resilience theory (e.g., having social capital, community leadership, diverse knowledge systems, agency and power) to contextualize how individuals and groups are adapting to environmental change (Nelson et al. 2007; Cote & Nightingale 2012). Such an approach has not been applied within the context of regime shifts, and this is the broad focus of Chapter 4.

As humans manage ecosystems and resources it is clear that ecological and social resilience are related, and that a natural extension is to think in terms of “social-ecological systems.” Social-ecological systems are those in which humans and the environment are intertwined, linked through complex feedback mechanisms (Berkes & Folke 1998). This integrative concept has been inherently recognized in Indigenous worldviews throughout the world for millennia, whereby humans are not considered as external disrupters of ecosystems but rather as an integral part of the system dynamics (Trosper 2003; Berkes 2008; Brown & Brown 2009). Similar notions today underpin the modern fields of sustainability science (Kates et al. 2001), political ecology (Escobar 1998), ecological economics (Daly 2005), environmental ethics (Norton & Hannon 1997), common pool resource theory (Ostrom 2009), resilience thinking (Walker & Salt 2012), and planetary boundaries (Rockström et al. 2009). A social-ecological system framing is
highly relevant in the context of regime shifts given that many of them are triggered, at least in part, by human actions (Hicks et al. 2016), and because dramatic ecological changes have significant implications for human communities (Steneck et al. 2011; Cumming et al. 2014; Rocha et al. 2015; Nayak & Armitage 2018). Essentially, drivers of, and responses to regime shifts are a complex integrated cycle of feedbacks between social and ecological components and processes. For this reason, much of the literature since the 1990s uses a social-ecological system framing to conceptualize management approaches for regime shifts (Fig. 1: Folke et al. 2004; Hughes et al. 2005, 2013; Selkoe et al. 2015; Nayak & Armitage 2018), as well as management approaches for complex natural resource systems more generally (Armitage et al. 2009; Ostrom 2009; Biggs et al. 2012; Crépin et al. 2012).

**Ecological and social interactions in kelp forest regime shifts**

Kelp forests are recognized globally as ecosystems that collapse and recover rapidly in response to environmental and biological perturbations. On temperate rocky reefs around the world, grazing by herbivorous sea urchins can drive regime shifts between productive macroalgae-dominated forests and unproductive ‘barrens’ dominated by encrusting corallines (Steneck et al. 2002; Filbee-Dexter & Scheibling 2014; Ling et al. 2015). Kelp forest and urchin barren alternative states tend to be persistent because the transitions exhibit hysteresis (i.e., the threshold density/biomass of sea urchins that initiates destructive grazing is greater than that which enables kelp recovery), and both states have associated feedback mechanisms which function to stabilize a particular community configuration (reviewed in Filbee-Dexter & Scheibling 2014; Ling et al. 2015).

Across regions and time scales, different factors are known to control sea urchin populations and thus drive barren-to-kelp or kelp-to-barren regime shifts. The overharvest of predatory fishes releasing top-down control on urchins is noted as a key driver of kelp forest collapse in the Gulf of Maine, France, New Zealand, the Mediterranean, and California (Sala & Zabala 1996; Babcock et al. 1999; Tegner & Dayton 2000; Lafferty 2004; Filbee-Dexter & Scheibling 2014). Climate-facilitated urchin range expansion triggered destructive grazing of kelp forests in Australia and Tasmania (Johnson et al. 2005; Ling 2008). Conversely, urchin disease outbreaks have facilitated kelp forest recovery in Nova Scotia, Norway, and Ireland (Filbee-Dexter & Scheibling
2014), while human harvest of urchins allowed kelp to recover in the Gulf of Maine and California (Steneck et al. 2002). One of the most widely known drivers of kelp forest regime shifts is the trophic cascade triggered by the recovery of sea otters (Enhydra lutris) in the Northeast Pacific. Trophic cascades are indirect species interactions that are initiated by predators and spread downward through food webs, requiring top-down effects of one species on another through at least one intermediary species (Paine 1980; Ripple et al. 2016). In the Aleutian Islands of Alaska, Estes and Palmisano (1974) discovered the keystone role of sea otters controlling urchins, and thus indirectly controlling algal abundance and distribution. Since that time, the documented changes that occur with the recovery of sea otters along the Pacific coast have become a “poster child” example of a trophic cascade-triggered regime shift that affects kelp forest collapse and recovery (Estes & Duggins 1995; Watson & Estes 2011; Estes et al. 2016). However, the generality of this otter-centric cascade has also been subject to debate, where authors have strongly suggested the need for more explicit recognition of spatial and temporal variation in the diversity of factors that influence kelp forest dynamics (Foster & Schiel 1988).

Research on kelp forest regime shifts tends to focus on changes in the abundance of key predators, consumers, and resources. For example, in a global review of sea urchin-triggered regime shifts spanning rocky reefs in 11 regions across both hemispheres, the regime shift dynamics are presented through graphs showing a distinct ‘discontinuous’ relationship between sea urchin and kelp abundance (Ling et al. 2015). However, the same authors acknowledge there is high variability across urchin-grazing systems, and a deeper exploration is needed of the processes and rates of predation, herbivory, and production that determine regime shift dynamics. Another literature review echoes this sentiment, noting that “there is still a high degree of uncertainty with regard to the factors that control sea urchin consumption rates,” particularly within field settings (Suskiewicz & Johnson 2017). Understanding the key trophic interactions and rates in a system, and the factors that influence them, is important because they provide the mechanistic pathways through which observed abundances shift or remain balanced (e.g., Noy-Meir 1975; May 1977), and they also dictate the magnitude and response time of system changes (Meadows 2009; Salomon et al. 2010). In chapters 2 and 3, I use a population model and field experiments to examine the key rates of predation and
Regime shifts can cause substantial changes in ecosystems that affect the lives of humans (Rocha et al. 2015). Regime shifts in kelp forests are no exception. Along the Northeast Pacific, the recovery and range expansion of sea otters following their extirpation in the 19th century fur trade is triggering a regime shift that presents considerable social challenges and trade-offs (Sloan & Dick 2012; Larson et al. 2015). When sea otters are absent, urchins, crabs, clams, abalone and other shellfish are abundant, which supports significant commercial fisheries (Larson et al. 2013; Carswell et al. 2015) and subsistence harvest in coastal communities (Salomon et al. 2007; Lee et al. 2018). When sea otters occupy reefs, there is a substantial reduction in shellfish density and size (reviewed in Estes et al. 2016), but kelp forests flourish, which supports marine biodiversity (reviewed in Teagle et al. 2017), expanded habitat for some fish (reviewed in Bertocci et al. 2015), recreation and tourism (Loomis 2006), and carbon sequestration (Wilmers et al. 2015). These trade-offs in ecosystem services are further challenged by the cultural and political context of sea otter recovery along the coast of British Columbia (BC) and Alaska, where otter populations are recovering within the traditional territories of coastal Indigenous First Nations and Tribes.

Indigenous peoples across the Northeast Pacific have valued, hunted, used, controlled and traded sea otters for millennia (Simenstad et al. 1978; Erlandson et al. 2005; Szpak et al. 2012; Salomon et al. 2015). But these relationships, economies, and resource management systems have shifted with colonial settlement and laws (Salomon et al. 2015). As sea otters are now recovering and expanding their range along the coast, Indigenous communities have raised many issues with regard to reduced shellfish food security, traditional use and stewardship of otters, and marine mammal co-management (Gardner 2003a, b; Sloan & Dick 2012; Salomon et al. 2015). However, to date, these issues have been largely neglected, following a historic pattern where Indigenous peoples have been marginalized in the marine management decision-making processes that directly affect their well-being (Langton 2002; Carothers 2010; Bennett et al. 2018). To confront the complex challenges associated with sea otter recovery, there is a pressing need to better understand Indigenous perspectives, identify conditions and strategies that enable coexistence with sea otters, and identify the types of management
and governance structures that can help communities navigate the shift between alternative social-ecological states. This is the focus of Chapter 4.

Navigating this thesis

The overarching goal of this thesis is to advance our understanding of how the sea otter triggered-regime shifts influence both ecological and human communities in the Northeast Pacific (Fig. 1.2). Within this goal, my first objective was to determine how sea otter recovery influences key trophic interactions that affect the structure, function, and resilience of alternative rocky reef communities on the central coast of BC. Chapter 2 focuses on quantifying the magnitude of and variation in predation rates among an apex and mesopredator whereas Chapter 3 focuses on quantifying herbivory by a dominant reef grazer and the factors that alter its strength. My second objective was to examine what influences people’s ability to adapt to sea otter recovery within coastal Indigenous communities, and stemming from this, my third objective is to identify a suite of actions

Figure 1.2. The framework for my thesis spans ecological, social, and management domains (boxes) around an overarching goal (blue text) and three main objectives (1-3).
that might improve Indigenous communities’ capacity to coexist with otters. I use the lens of resilience theory (Holling 1973; Berkes et al. 2003), as it emphasizes understanding the interactions that affect the persistence or adaptability of ecological and human communities in the face of disturbance (e.g., the recovery of keystone predators). I also use a combination of ecological and social science methods to achieve my objectives, including scuba surveys, subtidal experiments, quantitative modeling, facilitated workshops, community member interviews, and qualitative analyses. As such, my thesis takes on a social-ecological systems framing and approach (Berkes & Folke 1998), in that it uses the tools necessary to focus on interactions within rocky reef ecosystems and understand how changes in these systems influence coastal communities and systems of resource management (Fig. 1.2).

The chapters are written as papers for submission. Chapter 2 has been published in Proceedings of the Royal Society B (Burt et al. 2018), and chapters 3 and 4 are in preparation for submission.

In Chapter 2, I examine the roles of apex and mesopredators in shaping rocky reef ecosystem dynamics. Specifically, I assess the relative roles of sea otters and the co-occurring sunflower sea star (*Pycnopodia helianthoides*) in controlling sea urchin abundance and size, and thereby kelp abundance on rocky reefs. I use the empirical data from four years of reef scuba surveys and a Bayesian model of urchin population dynamics to reveal the size-structured instantaneous urchin mortality rates attributable to both predators. I also examine how urchin densities and size structure, total annual urchin mortality rates, urchin grazing capacities, subtidal kelp density, and aerial kelp cover vary as a function of sea otter presence.

In Chapter 3, I examine the factors that influence rates of herbivory on rocky reefs. I conducted grazing trials on subtidal reefs that spanned a natural gradient of sea urchin densities and sizes to examine how kelp consumption varied as a function of urchin biomass, and how this relationship was influenced by other ecological conditions, specifically: cryptic urchin behaviour, drift kelp availability, and a sea otter-associated predator cue. In combining the results of multiple field experiments, this chapter provides a mechanistic basis for how differences in grazing activity might reinforce either forested or deforested community configurations on rocky reefs.
In Chapter 4, I explore how sea otter recovery is being navigated in coastal Indigenous communities spanning from BC to Alaska, and examine what influences people’s ability to adapt to the dramatic changes sea otters bring. I worked within a collaborative Indigenous partnership and conducted surveys with people from the Kyuquot-Checleset First Nations and the Port Graham and Nanwalek Sugpiaq Tribes in Southcentral Alaska—communities among the first to experience sea otter recovery. Drawing from the outputs of a large workshop with multiple coastal Indigenous communities from BC to Alaska and my comparative case study, I examine the social-ecological conditions that enable people’s ability to adapt to living with sea otters and how people’s perceptions of these conditions, and their attitudes toward sea otters, differ between communities. I discuss my results drawing on examples from other resource systems to illustrate ways that current sea otter management system could shift to increase local Indigenous authority and enable community-based collaborative management grounded in traditional knowledge and western science.

Finally, in Chapter 5 I conclude this thesis with a synthesis of key findings and how they have advanced our knowledge of kelp forest regime shifts, sea otter management specifically and social-ecological resilience theory more broadly. I also discuss the limitations of my work, which spur promising opportunities for future research and collaboration. My hope is that this work will inspire curiosity in future researchers wishing to study reef ecology, provide new information for resource managers about the complexity of trophic interactions, and catalyze constructive dialogue relating to sea otter recovery, social justice, and Indigenous management and rights in British Columbia and beyond.

References


Chapter 2.

Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts

Abstract

While changes in the abundance of keystone predators can have cascading effects resulting in regime shifts, the role of mesopredators in these processes remains underexplored. We conducted annual surveys of rocky reef communities that varied in the recovery of a keystone predator (sea otters *Enhydra lutris*) and the mass mortality of a mesopredator (sunflower sea star *Pycnopodia helianthoides*) due to an infectious wasting disease. By fitting a population model to empirical data, we show that sea otters had the greatest impact on the mortality of large sea urchins, but that *Pycnopodia* decline corresponded to a 311% increase in medium urchins and a 30% decline in kelp densities. Our results reveal predator complementarity in size-selective prey consumption strengthens top-down control on urchins, affecting the resilience of alternative reef states by reinforcing the resilience of kelp forests and eroding urchin barrens. We reveal previously underappreciated species interactions within a ‘classic’ trophic cascade and regime shift, highlighting the critical role of middle-level predators in mediating rocky reef state transitions.

Introduction

The knowledge that ecological communities can abruptly shift between alternative states (i.e., dynamic community configurations maintained by feedbacks, Sutherland 1974), has made illuminating the mechanisms that induce these shifts a core focus in ecology (Holling 1973; Scheffer *et al.* 2001). Although there are diverse examples of ecosystems worldwide that exhibit multiple system states (Folke *et al.*

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empirical data elucidating processes that shape transition dynamics are less common because regime shifts occur rapidly, unexpectedly, and over different scales of space and time. Similarly, it can be difficult to identify the mechanisms that confer or erode community configurations through time because the relevance of key species interactions may only be revealed following a significant disturbance event (Paine 1969; Doak et al. 2008).

Shifts in top-down control of herbivore abundance and size can trigger the reorganization of entire ecosystems (Shurin et al. 2002; Estes et al. 2011). When predation is size-dependent, predators exacerbate shifts in the size-structure of prey populations, which can strongly influence the net effect of herbivory (Brooks & Dodson 1965; Sousa 1993). Predator species often vary dramatically in the range of prey size they target as a result of gape limitation, optimizing foraging efficiency, and prey reaching size-refugia (Schoener 1971; Paine 1976; Ostfeld 1982). As such, the same prey species may be subject to predation pressure from different predators during different life history stages and/or different size classes (Werner & Gilliam 1984; De Roos et al. 2008). Moreover, because individual body size is an important determinant of grazing capacity (Stevenson et al. 2016), for many herbivorous prey, the abundance of different size-selective predators could have differential cascading impacts on primary producers.

While food-web ecology has focused extensively on the direct and indirect effects of apex predators on community structure and stability (Paine 1969; Estes & Palmisano 1974; Beschta & Ripple 2009; Estes et al. 2011), there has been less consideration of how co-occurring middle-level predators, or mesopredators, influence systems that exhibit regime shifts. Mesopredator release can cause unanticipated declines in lower trophic levels (Ritchie & Johnson 2009), but fewer studies investigate food webs where apex and mesopredators share the same prey species, or track cascading effects of mesopredator abundance to primary producers. More generally, it has been shown that predator diversity can alter the strength of a trophic cascade when one predator mediates the consumptive effects of another, either reducing (e.g., intraguild predation, Finke & Denno 2004; Sitvarin & Rypstra 2014) or enhancing (e.g., predator complementarity, Byrnes et al. 2006; Snyder et al. 2006) the net effect on herbivorous prey. Many of these studies focus on guilds of predators occupying similar trophic levels,
but the degree to which community structure may be differentially affected by apex and mesopredators in a system prone to trophic cascades remains largely underexplored.

On temperate rocky reefs around the world, grazing by herbivorous sea urchins can drive regime shifts between productive macroalgae-dominated forests and unproductive “barrens” dominated by encrusting corallines (Steneck et al. 2002; Filbee-Dexter & Scheibling 2014; Ling et al. 2015). Kelp forest and urchin barren alternative states are persistent because the transitions tend to exhibit hysteresis (i.e., the threshold biomass of sea urchins initiating destructive grazing is greater than that which enables kelp recovery), and both states have associated feedback mechanisms that contribute to stabilizing that particular community configuration (reviewed in Filbee-Dexter & Scheibling 2014; Ling et al. 2015). In one of the most well-known examples, sea otters (*Enhydra lutris*) in the northern Pacific exert strong top-down control on sea urchins and facilitate regime shifts from urchin barrens to kelp forests (Estes & Palmisano 1974; Estes & Duggins 1995; Watson & Estes 2011). Whereas global reviews emphasize the role that apex predators play in influencing catastrophic regime shifts caused by urchin overgrazing (Steneck et al. 2002; Ling et al. 2015), these reviews contain little information about other less-prominent urchin consumers (e.g., sea stars and decapods) that may influence the resilience of alternative rocky reef states (Duggins 1983; Bonaviri et al. 2012, 2017).

Here, we examine the relative roles of an apex predator (sea otters) and a co-occurring mesopredator (sunflower sea star *Pycnopodia helianthoides*, hereafter *Pycnopodia*) in controlling sea urchin abundance and size, and thereby the degree of kelp abundance on high latitude rocky reefs. We focus on *Pycnopodia* because in 2013 an epidemic of sea star wasting disease (SSWD) spread across the Northeast Pacific, causing a precipitous decline in sea stars, including *Pycnopodia* (Montecino-Latorre et al. 2016; Schultz et al. 2016). We hypothesized this could affect kelp forest dynamics as a growing body of literature has demonstrated *Pycnopodia* are effective urchin predators throughout their range (Tegner & Dayton 1981; Duggins 1983; Schultz et al. 2016; Bonaviri et al. 2017). We took advantage of the SSWD event co-occurring with sea otter recovery to analyze a unique time series of dominant rocky reef consumers and producers across sites that varied in sea otter occupation, both before and after the mass mortality of *Pycnopodia*. Using empirical data and a size-structured Bayesian model of urchin population dynamics, we examine how urchin densities and size
structure, total annual urchin mortality rates, net size-specific urchin grazing capacities, and kelp density vary as a function of sea otter and *Pycnopodia* presence/absence. Finally, we explore how the loss of *Pycnopodia* influenced the resilience of alternative kelp-dominated and urchin-dominated rocky reef community configurations.

**Methods**

**Field surveys**

We conducted annual subtidal surveys at 11 sites on the central coast of British Columbia, Canada (Figure 2.1), where sea otter populations have been recovering (since ~1980) from extirpation due to the fur trade (Nichol et al. 2009). We selected sites by identifying subtidal rocky reefs that shared similar physical characteristics (i.e., wave exposure, depth range, aspect, and topography) but varied in sea otter occupation. Five sites had a documented history of sea otter occupation (i.e., rafts of foraging otters),

![Sea otter distribution map](image)

**Figure 2.1.** Subtidal rocky reef survey sites along the central coast of British Columbia (BC), Canada, varying in sea otter occupation: present (green squares), absent (pink circles), and “newly arrived” in 2013 (orange triangles). Box shows region of aerial kelp canopy mapping.
whereas six sites had no recorded observations of otter rafts (Nichol et al. 2009). Shortly after our first survey in July 2013, a large raft of sea otters arrived and began foraging at three of the six “otters absent” sites, changing their sea otter status from “absent” to “present” (Fig. 2.2). At each site we measured *Pycnopodia* density and size within six 30 x 2 m transects within two depth ranges (3-6 m, 9-12 m), then calculated and sum the total *Pycnopodia* biomass/10m² (Appendix Table A1). We measured the density of sea urchins and all adult kelps (order Laminariales, stipe length >15 cm to exclude recruits) in 18 stratified random 1 m² quadrats (depths 4-15 m). Although three urchin species are found in the study region, our analyses focus on red urchins (*Mesocentrotus franciscanus*) because this species constituted 88% of the regional abundance and 98% of the regional urchin biomass (Appendix Table A2). We calculated mean kelp stipe density at depths available to urchin grazing (i.e., below ~5 m) because wave-generated surge and ‘whiplashing kelp’ at shallower depths create a kelp refuge from urchin grazing (Konar & Estes 2003). Our time series encompasses two years prior, and two years post the onset of SSWD in the region (Jan. 2015), during which *Pycnopodia* populations dramatically declined (Fig. 2.2b; Appendix Figure A3).

Urchins were measured to the nearest centimeter and grouped into three size categories (“large”, “medium”, “small”) based on demarcations evident in our size distributions (Appendix Figure A4) and sea urchin natural history. “Large” red urchins (≥ 8 cm) generally attain a size-escape from sea star predation (Tegner & Dayton 1981; Duggins 1983), but are the preferred size range for foraging sea otters (Tinker et al. 2008; Stevenson et al. 2016). “Medium” urchins (4-7 cm) are easily handled and consumed by otters and *Pycnopodia*, but are generally too large to seek refuge under larger urchin spine canopies (Tegner & Dayton 1981; Duggins 1983). “Small” urchins (1-3 cm) represent the population recruits – individuals that settle successfully and can avoid predation by sheltering under the spines of large adults (Tegner & Dayton 1977).

**Bayesian modelling framework**

Mortality rates were not directly observed in our surveys; rather, they are latent unobserved processes that we estimated by fitting our survey observations to an ecological process model. We fit a size-structured population dynamics model in a
Figure 2.2. Annual changes in (a) sea otter presence, (b) total Pycnopodia biomass, (c) mean red sea urchin density, and (d) mean adult kelp stipe density across subtidal rocky reef sites varying in sea otter occupation status: otters continuously present (green squares), continuously absent (pink circles), and “newly arrived” during summer 2013 (orange triangles). Orange arrows indicate the timing of sea otter arrival at three sites; white arrows indicate the onset of sea star wasting disease.

A hierarchical Bayesian state-space framework to estimate instantaneous mortality rates for small, medium, and large urchins due to sea otters and *Pycnopodia*, while accounting for stochastic variation in baseline mortality rates across sites and years (see Appendix Table A5 describing all model elements). The Bayesian state-space framework allows us
to 1) estimate and account for both process and observation error inherent in survey data that may otherwise bias parameter estimates; 2) leverage prior information on, and incorporate uncertainty in parameters that impact model fit but are not directly of interest; and 3) develop a mechanistic understanding of key demographic processes in this system, specifically the role of size-specific predation in driving urchin population dynamics and thus shifts in community state.

Population state dynamics

The demographic process of interest, instantaneous mortality ($\gamma$) was assumed to represent the combined effects of sea otter and *Pycnopodia* predation, plus all other sources of mortality (hereafter “baseline mortality”). We combined recruitment ($R_t$), growth (i.e., size-class transition probabilities, $G_i$), and instantaneous mortality to calculate the dynamics of each urchin size class (small, medium, large) in discrete annual time steps:

\begin{equation}
N_{1,j,t+1} = [N_{1,j,t} (1 - G_1) + R_t] \exp[-\gamma_{1,j,t} \exp(\epsilon_{1,j,t} - \sigma_e^2 / 2)]
\end{equation}

\begin{equation}
N_{2,j,t+1} = [N_{2,j,t}(1 - G_2) + N_{1,j,t} G_1] \exp[-\gamma_{2,j,t} \exp(\epsilon_{2,j,t} - \sigma_e^2 / 2)]
\end{equation}

\begin{equation}
N_{3,j,t+1} = [N_{3,j,t} + N_{2,j,t} G_2] \exp[-\gamma_{3,j,t} \exp(\epsilon_{3,j,t} - \sigma_e^2 / 2)]
\end{equation}

where $N_{i,j,t}$ represents abundance of urchins in size class $i$ at site $j$ and time $t$ (where urchins in $N_{i=1} = 1-3$ cm, $N_{i=2} = 4-7$ cm, and $N_{i=3} \geq 8$ cm), $\gamma_{i,j,t}$ represents instantaneous mortality rate for size class $i$ at site $j$ and time $t$, and $\epsilon_{i,j,t}$ represents Gaussian error in log-scale mortality due to annual environmental stochasticity, $\epsilon_{i,j,t} \sim N(0, \sigma_e^2)$. The estimated recruitment parameter ($R_t$) represents the combined effects of successful larval settlement and subsequent survival to 1 cm, while size class transition probabilities ($G_i$) were specified parameters with fixed values derived from a published red urchin growth model (Appendix A6). At all sites, we initialize the population at time 0 (one year before observations) at the equilibrium abundance and size distributions conditional on estimated parameters.
We estimated independent size-specific parameters for urchin mortality due to sea otters and *Pycnopodia*. From equations 1-3 above, the instantaneous mortality rate ($\gamma$) for an individual urchin of size class $i$ at site $j$ during time step $t$ was estimated by:

$$
\gamma_{i,j,t} = (\alpha_{O,i} \ast O_{j,t}) + (\alpha_{P,i} \ast P_{j,t}) + \delta_{i,j}
$$

(4)

where $\alpha_{O,i}$ and $\alpha_{P,i}$ are fitted parameters that represent the instantaneous mortality rate of size class $i$ attributable to predation by sea otters and *Pycnopodia*, respectively. We did not fit a mortality rate parameter for sea otters consuming small urchins ($\alpha_{O,i=1}$) based on extensive foraging observations showing otters rarely consume this size class (Tinker et al. 2008). $O_{j,t}$ and $P_{j,t}$ are variables that come from the survey data; otter presence/absence (1 or 0) and the measured biomass of *Pycnopodia* (per kg/10m$^2$).

Baseline mortality ($\delta_{i,j}$) was estimated as a hierarchical random effect to account for unexplained differences in mortality across sites associated with variation in habitat quality and/or other environmental factors. We assumed that conditions at a site would tend to be more/less favourable for urchins of all sizes, and thus deviations from average mortality rates would be correlated across size classes. Accordingly, mortality for small urchins at site $j$ ($\delta_{1,j}$) was drawn from a normal distribution with mean $\bar{\delta}_1$ and standard deviation $\sigma_\delta$ (a fitted parameter determining the magnitude of variation across sites) and mortality values for medium and large urchins were then scaled relative to small urchin mortality ($\delta_{2,j} = \beta_2 \ast \delta_{1,j}$ and $\delta_{3,j} = \beta_3 \ast \delta_{1,j}$), where $\beta_2$ and $\beta_3$ were fitted parameters.

We linked observations ($C_{i,j,t,k} =$ counts of urchins of size class $i$ at site $j$ during year $t$ in quadrat $k$) to the hidden state dynamics using a negative binomial (NB) likelihood, with a mean value corresponding to the estimated “true” abundance of urchins at a given site ($N_{i,j,t}$) and dispersion parameter ($r$) that controls variance relative to the mean:

$$
C_{i,j,t,k} \sim \text{NB}(r / [r + N_{i,j,t} \ast \theta], r)
$$

(5)

For small urchins ($i=1$), we included a fitted “observability” parameter ($\theta$, where $0<\theta<1$) to account for imperfect detection of this size class (i.e., patchy distribution and cryptic individuals). For medium and large urchins ($i=2$ or 3) we assume $\theta=1$. 
We estimated model parameter posteriors using Gibbs sampling. Details on prior specification, posterior distribution sampling, prior-posterior comparisons, output parameter estimates, Gelman-Rubin diagnostics, and posterior predictive checks are provided in Appendix A7. To examine the model’s ability to reproduce observed urchin dynamics, we ran iterated deterministic simulations over the four-year study period to project the density of urchins in each size class through time under four scenarios of predator status: 1) Both predators absent; 2) Pycnopodia present but otters absent; 3) Otters present but Pycnopodia absent; and 4) Both otters and Pycnopodia present (Appendix A8).

**Relative predator impacts on urchins and kelp at the reef scale**

To further explore the cascading effects of sea otters and Pycnopodia, we used the four predator scenarios (described above) to examine the relative differences in size-specific rates of urchin mortality, urchin grazing, and empirical density estimates of urchins and kelp. We calculated total annual urchin mortality as $1 - e^{-\gamma}$ by using equation 4 to yield ($\gamma$) for the four different combinations of predators along with the size-specific parameters and baseline mortality estimates sampled from our model posteriors. To examine how predator scenarios influenced urchin size structure, we summarized mean urchin densities ($\pm$SE) for site and year combinations where the appropriate predators were present or absent. To evaluate the kelp grazing capacity of different urchin densities and size structures, we calculated the maximum potential kelp consumption (kg/m$^2$/yr) by multiplying mean urchin densities by size-specific per-capita feeding rates for red urchins (Stevenson et al. 2016). Finally, for each predator scenario we plotted the distribution of mean kelp density.

**Documenting kelp forest regime shifts at a regional scale**

We used aerial imagery to quantify changes in the spatial extent and density of kelp canopy cover in the region where sea otters arrived in 2013 (~ 6 km$^2$ and over 40 km of shoreline; boxed area in Fig 2.1). We obtained two high-resolution orthophotos captured prior to sea otter occupation and generated three additional orthophotos using aerial surveys (details in Appendix A9) in the three years following otter arrival. We compared the total aerial coverage (km$^2$) of canopy kelp (mostly Nereocystis luetkeana)
of high and low-density (≥ or < 10 plants per 10 m², respectively) across five years that encompass pre- and post-otter arrival and the onset of SSWD. We also show the mean density (±SE) of perennial understory species (*P. californica, L. setchellii, S. latissima, S. groenlandica*) from three reef sites within the “new otter arrival” region.

Lastly, to examine how the decline in *Pycnopodia* influenced rocky reef community states across the BC central coast region, we plotted mean urchin density vs. kelp density for all sites in the years before and after the onset of SSWD to examine shifts in alternative reef states (as in Estes *et al.* 2010; Ling *et al.* 2015).

Statistical parameters calculated directly from empirical data are reported ±1 standard deviation, while Bayesian-estimated parameters are reported with 95% credible intervals. All analyses were conducted using JAGS (Plummer 2017) and R (R Core Team 2017).

**Results**

**Trends in dominant reef consumers**

Sea urchin densities decreased at sites where sea otters returned (n=3), but also increased at 10 out of 11 sites following SSWD (Fig. 2.2a-c) with concurrent declines in kelp stipe density at macroalgae-dominated sites (n=8, Fig. 2.2d). Notably, sea otter presence and *Pycnopodia* biomass influenced the density and biomass of different size classes of urchins (Fig. 2.3a-f). Sea otters had the greatest impact on large urchins; otter arrival at three unoccupied sites resulted in an 89-98% decrease in the mean density of large urchins within one year (from 4.4 ± 1.3 to 0.2 ± 0.3 urchins/m²), to similar densities recorded at previously otter-occupied sites (0.2 ± 0.3 urchins/m²). Conversely, *Pycnopodia* decline corresponded to increases in the density of medium and small sized urchins. Following two years of SSWD, the average density of medium urchins across all sites increased from 0.9 ± 0.9 to 3.7 ± 1.7 urchins/m², representing a 311% increase irrespective of sea otter occupation (Fig 2.3b). Compared to abundance, the increase in medium urchin biomass was less dramatic, increasing by 73% from 0.08 ± 0.08 to 0.3 ± 0.1 kg/m² (Fig. 2.3e). While the densities of small urchins were variable across sites and years (Fig. 2.3c), 10 out of 11 sites showed a small net increase (+0.5 urchins/m² on average) following two years of SSWD.
Size-specific effects of sea otters and *Pycnopodia* predation on mean red sea urchin density (a-c) and mean biomass (d-f) for large, medium, and small urchin size classes at sites with different otter sea otter status (otters absent = pink circles, otters present = green squares, newly arrived = orange triangles). (g-i) Additive increase in instantaneous mortality rate (mean posterior parameter estimate ± 95% CI) within each urchin size class due to the presence of sea otters or a 1 kg/10m$^2$ increase in *Pycnopodia* biomass. Violin plots show the smoothed posterior distributions for the predator- and size-specific instantaneous mortality rate estimates.

**Predator-specific size-structured sea urchin mortality rates**

Our model converged well (all psrf values ≤1.01), satisfied posterior predictive checks (met model assumptions), resulted in posterior distributions dramatically different from priors (sufficient data to inform the model), and was able to reproduce through simulations comparable urchin densities to those observed under various scenarios of predator abundance (all details in Appendix 7).
Model results suggest that *Pycnopodia* have a substantial size-specific predatory effect on urchins that is complementary to that of sea otters. Specifically, instantaneous urchin mortality rates attributed to sea otters were estimated as 1.46 (0.76-2.82) and 0.53 (0.07-1.23), for large and medium size classes respectively (Fig. 2.3g,h), whereas *Pycnopodia* imposed instantaneous mortality rates of 0.070 (0.0-0.16), 1.27 (0.32-2.65) and 0.83 (0.03-2.52) on large, medium and small urchins respectively (Fig. 2.3g,h,i) – having more than double the effect on medium urchins compared to sea otters (Fig. 2.3h).

Estimates of size-specific total annual urchin mortality revealed notable differences in relative predator effects (Fig. 2.4a). The estimated total annual mortality of large urchins was low when otters were not present (2 and 9% when *Pycnopodia* were absent and present, respectively) and high when otters were present (74 and 76%). Medium urchin mortality depended on which predators were present in the system: total annual mortality was moderate (51%) for sites with only sea otters, was 1.5 times higher when only *Pycnopodia* were present (74%), and was highest when both predators co-occurred (84%). Given these rates and the average change in *Pycnopodia* biomass that occurred after two years of SSWD, we estimated that SSWD resulted in a 166% increase in the annual survival of medium urchins at a given site. Small urchins had the highest and most variable baseline mortality rate (60%), which increased in the presence of *Pycnopodia* (80%). Overall, estimated mortality rates reflect similar patterns to observed urchin densities (Fig. 2.4b).

**The cascading effects of sea otters and *Pycnopodia***

Different predator combinations had notably different kelp grazing capacities (Fig. 2.4c): estimated kelp consumption by urchins when no predators were present (32 kg kelp/m²/year) was 16 times greater than when both sea otters and *Pycnopodia* were present (2 kg kelp/m²/year) (Fig. 2.4c). Due to the higher per-capita grazing rate of large urchins that are targeted by otters, estimated kelp consumption was primarily determined by sea otter presence (Fig. 2.4c). However, when otter-occupied kelp forest sites did not have *Pycnopodia*, there was 3.5 times more kelp consumption capacity (7 kg kelp/m²/year) due to more abundant medium urchins relative to when both predators were present.
Figure 2.4. Estimated total annual mortality (mean ± 95% CI) for small, medium, and large urchins corresponding to a given predator status: no predators, only *Pycnopodia* predators, only sea otter predators, and both predators present. (b) Observed size-specific mean urchin density (± SE). (c) Estimated size-specific maximum kelp consumption by urchins. (d) Observed mean density of adult kelp stipes at each survey site (n, triangles). Box plots show the median (solid line), mean (dotted line), 25th and 75th percentiles (outer box) and inter-quartile range.
Subtidal kelp density was positively associated with the presence of *Pycnopodia* as well as sea otters (Fig. 2.2d, 2.4d). Subtidal kelp densities were high when otters were present at sites (1.3–10.4 stipes/m²) and low when otters were absent (0–1.6 stipes/m², with the exception of one outlier) (Fig. 2.4d). However, at otter-occupied sites, mean kelp stipe density was higher in the presence of *Pycnopodia* (7.3 ± 1.4 stipes/m²). We calculate that the loss of *Pycnopodia* from otter-occupied kelp forests due to SSWD corresponded to a 30% decline in mean stipe density (to 5.1 ± 2.7 stipes/m²) and higher variation in kelp density across sites. Observations made by divers at these forested sites included sightings of medium-sized urchins consuming kelp blades and climbing up or pulling down kelp stipes (photos in Appendix Figure A10).

A rapid and large-scale expansion in the spatial extent and density of canopy kelp occurred in the region where sea otters recovered in 2013 (Fig. 2.5; see aerial kelp maps in Appendix Figure A11). The year following sea otter arrival, kelp canopy was 2.9 times greater (covering 1.0 km²) than it was the year prior. Kelp beds were also more dense in the years following sea otter return (92%, 82%, 70% of beds ‘high density’ in 2014, 2015, 2016, respectively) compared to the years prior (45% and 46% of beds ‘high density’ in 2006 and 2012, respectively). Aerial extent of canopy cover was reduced in 2015-2016, corresponding to the simultaneous increase in perennial understory species and the onset of SSWD (Fig. 2.5).

![Figure 2.5.](image)

**Figure 2.5.** Annual changes in the spatial extent and density of kelp canopy cover in relation to sea otter recovery and the onset of sea star wasting disease (grey arrows). Points and lines show changes in mean perennial understory kelps (± SE) across three subtidal survey sites within the mapping region (~6 km²).
The loss of *Pycnopodia* due to SSWD was associated with less distinct ‘kelp dominated’ reef states (Fig. 2.6). Following the near elimination of *Pycnopodia*, sea otter-occupied kelp forest sites had higher and wider ranging urchin densities, slightly increased urchin biomass, and lower kelp densities with greater variation within and among sites (Fig. 2.6b). During SSWD years, the coefficient of variation for kelp density across sites increased from 20% to 54%.

**Figure 2.6.** Mean red urchin and adult kelp stipe density (± SE) for all rocky reef survey sites (a) two years before SSWD, 2013-2014, and (b) two years after SSWD, 2015-2016. Point sizes are scaled to the mean biomass of urchins at each site. Dark green circles indicate sites occupied by sea otters, red symbols indicate sites where sea otters are absent. The trophic interactions between species are illustrated for each scenario; solid lines show direct negative interactions, dashed lines show indirect positive interactions.
Discussion

Our results show that complementarity between a mesopredator and an apex predator in their prey size selection can enhance top-down regulation of a strongly interacting herbivore, with cascading impacts on primary producers. In this study, the unpredictable events of SSWD in conjunction with sea otter range expansion provided a unique opportunity to disentangle the responses of sea urchin prey to both a keystone and mesopredator. Overall, our findings provide strong evidence that *Pycnopodia* predation on small and medium urchins helps reinforce kelp-dominated reef states, and may facilitate the rapid transitions from urchin barrens to kelp forests that follow sea otter reintroduction.

Complementary size-structured predation

There are several mechanisms by which multiple predators can exhibit complementarity to successfully exploit the same prey species. Predators can target the same prey species in different habitats (Vonesh & Osenberg 2003), life history stages (De Roos *et al.* 2008), via different feeding strategies (Galasso *et al.* 2015), or by consuming different size-classes (Duplisea 2005). In this study, sea otters and *Pycnopodia* differentially impact prey sizes based on unique feeding strategies and constraints. Sea otters’ high metabolic rate and inability to store energy necessitate that they maximize energy intake per unit of foraging time (Ostfeld 1982). Conversely, sea stars are slower acting invertebrate predators constrained by the size of prey they can physically digest (Mauzey *et al.* 1968; Duggins 1983). Sea otters select large urchins when they are highly abundant and easily obtainable, but then switch prey species rather than consume smaller-sized urchins that require increased foraging effort for lower caloric gain (Ostfeld 1982). Our data support this foraging theory, showing that large red urchins were only abundant at sites unoccupied by sea otters, and that upon otter arrival, large urchins suffered the most dramatic declines. Our estimates of urchin mortality from sea otter predation are consistent with published reports of high attack rates by sea otters on the largest size class of urchins in the years following sea otter re-colonization (Tinker *et al.* 2008) and another study from this region showing the median size of red urchins dropped by 63% following sea otter arrival (Stevenson *et al.* 2016). While *Pycnopodia* are also capable of consuming large red urchin prey (Mauzey *et al.*
1968), they typically avoid larger individuals because their long spines render them difficult to consume (Moitoza & Phillips 1979; Duggins 1983). Similar to other invertebrates that exhibit size escape from sea star predation (Paine 1976), our data show large red urchins can form extensive barrens on rocky reefs despite high abundance and biomass of *Pycnopodia*.

Building on other studies, our results demonstrate that *Pycnopodia* are effective consumers of small and medium-sized (0-7 cm) urchins (Duggins 1983; Schultz *et al.* 2016; Bonaviri *et al.* 2017). When *Pycnopodia* are present at a given site, the estimated annual mortality rate for medium urchins was 4.1 times higher than the natural mortality rate in the absence of predators, and 1.5 times higher compared to sites with only sea otter predators. These results are supported by several lab studies showing that *Pycnopodia* actively consume smaller urchin prey (Moitoza & Phillips 1979; Freeman 2006; Nishizaki & Ackerman 2007), and even target small red urchins over other urchin species (Nishizaki & Ackerman 2007). Correspondingly, the behavioural tendency for small red urchins to seek refuge under the spines of larger conspecifics is suggested to be a direct adaptation to minimize predation risk (Breen *et al.* 1985; Freeman 2006; Nishizaki & Ackerman 2007).

**Indirect effects on kelp forests**

Consistent with previous studies on northern Pacific temperate reefs, we found that sea otters had a large positive indirect influence on subtidal kelp abundance (Estes & Palmisano 1974; Breen *et al.* 1982; Estes & Duggins 1995; Watson & Estes 2011; Markel & Shurin 2015; Stevenson *et al.* 2016). Unlike those studies however, we show that complementary predation by *Pycnopodia* contributes to these indirect effects: mean kelp densities at otter-occupied sites were 1.4 times higher in the presence of *Pycnopodia*. Sea otters have dramatic indirect effects on kelp due to their rapid consumption of large high biomass urchins, which due to metabolic scaling laws, have almost three times the kelp consumptive capacity of medium urchins (Fig. 2.4c Stevenson *et al.* 2016). Nonetheless, we show the increased abundance of medium urchins following *Pycnopodia* decline had sufficient consumptive capacity to reduce standing kelp abundance. This is consistent with studies where *Pycnopodia* are the primary controlling force on smaller-sized *S. purpuratus* and *S. droebachiensis* urchin species, and where *Pycnopodia* declines were correlated with increased kelp abundance.
(Schultz et al. 2016; Bonaviri et al. 2017). Because *Pycnopodia* are reported to suppress the grazing rates in urchins (Byrnes et al. 2006; Freeman 2006), we note that the observed kelp declines following SSWD could reflect both a numerical (more urchins) and behavioural (increased per capita grazing rates) response.

Our data demonstrate that the indirect effects of two key predators on kelp abundance at individual reefs scale up to influence regional-scale patterns in aerial kelp canopy extent. However, kelp abundance and distribution are also well known to be influenced by environmental factors (Parnell et al. 2010; Cavanaugh et al. 2011) and successional processes (Duggins 1980; Watson & Estes 2011). For example, water temperature is negatively correlated with the nutrients required for kelp growth (Dayton et al. 1999). While SSWD was first observed in southern BC in 2013 (Schultz et al. 2016), its sudden appearance on BC’s central coast may be in part due to an anomalous marine heatwave that affected the region in 2015 and 2016 (Hunt et al. 2016). Although our data and diver observations suggest destructive grazing by medium urchins was a key factor, it is possible the co-occurrence of warmer ocean temperatures contributed directly to the observed kelp decline. While summer average sea surface temperatures in this region (see Appendix Figure A12) during the ‘heatwave’ years did not exceed levels where nutrient limitation affects kelp sporophytes [>16°C; Dayton et al. 1999], winter temperatures were 1-2°C warmer than historical averages which may have negatively affected kelp reproduction and gametophyte stages (Harley et al. 2012).

At sites where sea otters returned, post-disturbance successional processes that occur within kelp forests likely also contributed to canopy kelp declines following SSWD. The patterns we observed are similar to other studies that have shown a large regional expansion in *N. luetkeana* kelp canopy following rapid sea urchin removal, followed by a decline in canopy cover concordant with an increase in subtidal perennial species that suppress annuals by dominating light and space resources (Duggins 1980; Breen et al. 1982; Watson & Estes 2011).

**Mechanisms of species interactions**

While natural removal experiments are a powerful way to demonstrate the effect one species has on others in the system, a limitation is that they do not reveal specific mechanisms. Our population model is framed in terms of lethal consumptive effects of
sea otters and *Pycnopodia* on urchins; however, both predators are known to elicit behavioural responses from their herbivore prey (Lowry & Pearse 1973; Moitoza & Phillips 1979; Duggins 1983). As such, it is likely some of the increases in medium urchins we observed following SSWD reflected vulnerable individuals emerging from hiding or migrating into surveyed habitat in the absence of *Pycnopodia* (Schultz *et al.* 2016). This would not change the visible trends in our empirical data, and indeed is consistent with our model formulation as we assume that the alpha parameters represent “apparent mortality”, including both consumptive and behavioral effects.

Another limitation of our model is the assumption of a linear functional response between predators and urchins, which results in an estimated urchin mortality rate by otters that may underestimate high predation rates when sea otters arrive at a new site (high urchin availability) and overestimate low urchin predation rates at sites with long sea otter occupation (reduced urchin availability). A more elaborate model, which would require longer time series to fit, could account for prey-switching with a type 3 functional response, whereby per capita urchin mortality would decline with reduced urchin availability (Ostfeld 1982). Similarly, greater kelp habitat complexity might increase urchin survival via crypsis, and also increase the amount of drift in the system that can augment urchin growth rates via bottom-up effects (Ebert 1968). Under such conditions urchins typically switch from actively grazing kelp to consumption of drift algae, thus weakening their influence on attached kelp abundance (Harrold & Reed 1985). Future ecosystem models could examine the implications of multiple and interacting ecological phenomena well known to occur in kelp forest systems.

**Implications for the resilience of alternative states in systems prone to trophic cascades**

Many different stabilizing feedback mechanisms can maintain the persistence of macro-algae dominated states: high spore production facilitates kelp recruitment, whiplashing macro-algae limits urchin grazing, abundant kelp detritus promotes passive feeding by urchins, and macro-algae provides habitat for predators that limit urchin populations (Filbee-Dexter & Scheibling 2014; Ling *et al.* 2015). While predator-induced mortality of sea urchins has been considered a key mechanism contributing to the stability of kelp forests (Ling *et al.* 2015), most empirical studies are focused on the mortality of adult urchins, with less known about the role of predators suppressing
smaller size classes. Notable exceptions include algal forests in the Mediterranean, where abundant ‘micropredators’ (primarily decapods) consume post-settled urchins and are thought to be an important mechanism stabilizing algae-dominated reefs (Bonaviri et al. 2012). Similarly, predation intensity on juvenile *S. droebachiensis* by crabs and fish in Atlantic Canada is considered a key factor regulating urchin populations at an important demographic bottleneck, which in turn influences kelp abundance (Scheibling & Hamm 1991). Our findings suggest that on the Pacific coast of Canada, complementary predation on small and medium red urchins by *Pycnopodia* at sea otter-occupied reefs is an important factor contributing to the resilience of kelp forests (i.e., maintaining structure and function in the face of disturbance, Holling 1973). We show that while sea otters dictate alternative community configurations, the absence of *Pycnopodia* leads to higher urchin grazing, reduced kelp densities and increased spatial patchiness within and among sites.

Suppression of small-to-medium sea urchin densities by *Pycnopodia* likely also affects the rate of algal recovery following sea otter-induced trophic cascades. We observed that when sea otters arrived at new reefs and removed most large urchins, kelp recovery occurred rapidly (within 1 year). While equally rapid transitions are reported in Southeast Alaska, slower transitions are observed in the Aleutian Islands (Estes & Duggins 1995), which are beyond the range limit of *Pycnopodia*. On Aleutian reefs, high densities of unconsumed smaller *S. polycanthis* urchins (< 3 cm) are sufficient to prevent the recolonization of kelp sporophytes for years, even decades after the initial arrival of foraging otters (Estes & Duggins 1995). While higher and more consistent urchin recruitment rates are considered key factors driving high densities of small urchins in the Aleutians (Estes & Duggins 1995), our data suggest that suppression of smaller urchins by *Pycnopodia* may be an important factor facilitating more rapid otter-induced regime shifts in BC and Southeast Alaska. By facilitating kelp recovery in the face of a sea otter ‘disturbance,’ *Pycnopodia* presence may reduce the resilience of urchin barrens. Our current data are insufficient to fully test this hypothesis, however the arrival of sea otters to new reefs in the wake of SSWD may present this opportunity in the future.

Ecological surprises are important in ecology because they are catalysts for reformulating views of community dynamics (Paine et al. 1998; Doak et al. 2008). The unanticipated event of SSWD helped reveal the important role of a mesopredator,
Pycnopodia, in enhancing the top-down control on urchins, a functional role that would have remained underappreciated without this perturbation. Overall, this study expands our knowledge of the dominant species interactions operating within a ‘classic’ regime shift that affects one of the world’s most productive ecosystems, and provides critical information helpful to managing these systems which may be subject to more compound perturbations in an increasingly unpredictable world.

Authors’ contributions

JMB, AKS, KWD designed the field study, JMB, KWD, KH, AKS collected data, TMT, DKO, JMB designed and performed modelling, JMB, TMT, DKO, KWD, AKS analyzed output data, JMB, KH performed mapping and GIS analysis, JMB created species icons in figures, JMB wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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References


Chapter 3.

Herbivore biomass, food availability, and fear affect grazing rates that drive a temperate reef regime shift

Abstract

Identifying the factors driving variation in grazing rates is critical for predicting where, when, and under what conditions herbivores can trigger shifts between alternative community states. While globally documented regime shifts between kelp forests and urchin barrens tend to focus on changes in urchin abundance, a mechanistic understanding of the factors influencing urchin herbivory in complex reef environments is less clear. We conducted grazing trials on subtidal reefs on the coast of British Columbia, Canada, that spanned a natural gradient of sea urchin (*Mesocentrotus franciscanus*) densities and sizes to examine how kelp consumption varied as a function of urchin biomass, and how this relationship was influenced by cryptic urchin behaviour, drift kelp availability, and a sea otter-associated predator cue. We found a saturating relationship between plot-level urchin biomass and total grazing rate indicative of intraspecific competition, and that accounting for available drift kelp further explained variability in kelp consumption. Grazing rates were also significantly lower at sea otter occupied sites, which were characterized by low urchin biomass, mostly cryptic urchins, and higher densities of attached kelp. When experimentally exposed to eviscerated conspecifics – a sea otter predation cue – urchins were not deterred from grazing kelp, but grazing rates were reduced by 27% and were dependent on patch-scale urchin biomass. Overall, our findings show that because herbivore abundance, size structure, food-availability, and predator-avoidance behavior all contribute substantially to modulate grazing rates on kelp, adequately understanding and predicting kelp forest regime shifts requires a shift from considering any of these in isolation, to considering their integrated dynamics.

Introduction

Understanding key factors that influence herbivory has been a long-standing aim in community ecology (Hairston *et al.* 1960; Noy-Meir 1975; Lubchenco & Gaines 1982),
especially when changes in grazing intensity drive regime shifts between alternative community configurations (Estes & Palmisano 1974; Walker et al. 1981; Knowlton 1992). Because quantifying species interactions is more elusive than counting species themselves, studies on regime shifts tend to focus on changes in the abundance of key consumers and resources, rather than changes in the trophic rates and behavioural interactions that drive ecosystem-level change. However, community structure and primary productivity are known to be influenced by more than just consumer abundance; for example, in various systems the intensity of herbivory is affected by herbivore size-structure (Atkins et al. 2015; Stevenson et al. 2016), herbivore behavior (Dill et al. 2003; Schmitz et al. 2004), and food availability (Werner & Peacor 2003). In turn, these herbivory-influencing factors have been proposed as key mechanisms maintaining ecological communities in alternative vegetation-suppressed versus -abundant states (Wolf et al. 2007; Filbee-Dexter & Scheibling 2014). As such, a useful approach to understanding regime shifts is to focus attention on the factors that influence key trophic rates, and in particular, the determinants of variation in herbivore grazing intensity (Burkepile 2013; Holbrook et al. 2016). Here we focus on the numerical and behavioural factors that influence the grazing rates of a globally important marine herbivore – the sea urchin – to illuminate key mechanisms that maintain forested or deforested states on temperate rocky reefs.

The intensity or extent of herbivore grazing is commonly considered to be a function of numerical factors such as herbivore abundance and size. For example, the population-level effect of grazers on a resource is often assumed to scale linearly with density, implying that per capita effects are constant and can be multiplied by species density (Wootton 1997; Berlow 1999). This assumption was made in early field experiments measuring interaction strength at a single predator density (Paine 1992). Since then, this assumption was challenged by research revealing the prevalence of non-linear species interactions (Abrams & Ginzburg 2000; Novak & Wootton 2008). For example, competitive, interfering, and facilitative interactions between consumers that result in density dependence have been observed in freshwater (Helgen 1987; Fussmann et al. 2005; Klemmer et al. 2012) and marine systems (Ruesink 1998; Atkins et al. 2015). For sea urchins on rocky reefs, studies have revealed density-dependent facilitative grazing (Breen & Mann 1976; Lauzon-Guay & Scheibling 2007a) and threshold effects in destructive grazing (Wright et al. 2005; Lauzon-Guay & Scheibling
Along with abundance, the intensity of grazing interactions can also depend on herbivore size (Bakker et al. 2006; Atkins et al. 2015). Given the greater per capita grazing effects of larger individuals (Belovsky 1986), several studies have found that measures of herbivore body size in addition to density determine the strength of consumer-resource interactions (Hillebrand et al. 2009; Atkins et al. 2015) and best predict observed vegetation abundance (Stevenson et al. 2016).

The intensity of herbivory can also be critically influenced by herbivore behaviour via non-lethal predator-induced effects (Dill et al. 2003) and shifts in foraging linked to resource availability (Werner & Peacor 2003). The presence of predators for instance, can cause reduced rates of grazing when herbivore prey species adopt more risk-averse foraging (Ripple et al. 2001), seek refuge (Nelson & Vance 1979; Trussell et al. 2003), or reduce overall feeding activity (Kats & Dill 1998; McKay & Heck 2008). These predator-induced responses occur often in aquatic systems as prey are exposed to waterborne predator cues (Kats & Dill 1998). Moreover, by altering herbivore grazing, predators can trigger behaviourally-mediated trophic cascades that indirectly affect primary producers and ecosystem function (Schmitz et al. 2004; Rasher et al. 2017; Haggerty et al. 2018). Many consumers will also adjust their foraging behaviour based on resource supply. For example, the browsing behaviour and foraging rate of moose and other ungulates can shift depending on the available herbage and saplings (Vivas & Saether 1987). On temperate reefs, the intensity of sea urchin herbivory can depend on the availability of algal food supply: individuals actively scavenge and form destructive grazing fronts when there is minimal drift kelp to feed on, but remain more stationary if they can passively feed on abundant drift kelp (Dean et al. 1984; Ebeling et al. 1985; Harrold & Reed 1985). While many of these predator-induced and resource-dependent effects on herbivore grazing rates have been shown in laboratory and mesocosm experiments, the magnitude and variation in these effects are less well known under field conditions.

Here, we examine the effects of numerical and behavioural factors on sea urchin herbivory, a key trophic rate known to drive transitions between forested and deforested rocky reef states. We conducted sea urchin grazing trials on subtidal reefs that spanned a gradient of naturally-occurring sea urchin densities and sizes, to ask: (1) How does the rate of total kelp consumed vary as a function of urchin biomass? (2) Is this relationship influenced by urchin crypsis and resource availability? and (3) Does a sea otter-associated predator-cue affect kelp consumption rates by sea urchins? We hypothesized
that sea urchin grazing rates would be positively related to urchin biomass, but that this relationship might approach a limit where high urchin biomass results in intraspecific interference (Parnell et al. 2017). Alternatively, high urchin biomass could stimulate aggressive feeding and enhance kelp consumption (Lauzon-Guay & Scheibling 2007a). Moreover, we predicted that accounting for cryptic urchin behaviour (Nelson & Vance 1979) and alternative resource availability (i.e., drift and attached kelp, Harrold & Reed 1985) would help explain variation in observed grazing rates. Finally, we hypothesized that grazing rates would be reduced at sites with sea otter predators (Steinberg et al. 1995), and in response to a sea otter-associated predator-cue (Watson & Estes 2011). We quantify the evidence for these hypotheses to advance our understanding of the mechanisms that maintain forested and deforested states on temperate reefs (Filbee-Dexter & Scheibling 2014).

**Methods**

**Study design and location**

We conducted sea urchin grazing trials in May 2014 and 2015 on shallow subtidal rocky reef sites (n=8) located on the central coast of British Columbia (BC), Canada (Fig. 3.1). Sites were chosen specifically to span a natural range in sea urchin densities, resulting in rocky reefs ranging from urchin- to kelp-dominated (Fig. 3.2a-d), depending on the presence of sea otters (*Enhydra lutris*), a well-recognized urchin predator whose populations are expanding their range following historical extirpation (Waston and Estes 2011, Nichol et al. 2015). Urchin species were predominantly red sea urchins (*Mesocentrotus franciscanus*, 96.5% and 99.6% of total urchin abundance and biomass respectively), while the rest were green sea urchins (*Strongylocentrotus droebachiensis*).

**Field grazing trials**

*Effects of numerical and behavioural factors on sea urchin grazing rate*

To examine the effects of urchin density, biomass, crypsis, and available kelp resources on sea urchin grazing rates, we transplanted pre-weighed damp-dried blades of *Macrocystis pyrifera* (n=8, Fig. 3.2a) in replicate 6 m2 plots (n=5) at each rocky reef
Figure 3.1. Grazing trial sites on the central coast of British Columbia (B.C.), Canada. Circles are sites where sea otters are absent, triangles are sites with observed sea otter rafts and foraging. Experimental predator-cue grazing trials took place at two sites (•).

site (n=8). Plots were established between 4-13 m depth by placing 3 m long pieces of anchor chain on the reef to which blade transplants were attached. To avoid confounding urchin density with site effects, we exploited urchin patchiness within a site and established plots in areas of varying urchin density, spaced > 5 m apart. In each plot, we measured all urchins to the nearest cm within four 1 m² quadrats, then used a length-to-mass conversion (Lochead et al. 2015) to calculate and sum urchin biomass (per m²). We recorded urchin behaviour as ‘exposed’ (out in the open) or ‘cryptic’ (hiding in cracks, under rocks) and whether individual urchins were eating/holding drift kelp. If present, drift kelp was removed from urchins and from the plot at the start of the trial. Finally, for each plot we recorded the depth, dominant substrate type (0-5 scale ranging from bedrock to large boulders), relief (0 = flat, 4 = high relief terrain) and stipe counts of all attached adult kelp species (order Laminariales, > 15cm in length).
Urchins were left to graze for 24 hours and the remaining kelp material was retrieved and re-weighed back in the lab (Fig. 3.2f). We calculated tissue loss \((g)\) for each blade as the difference between the initial and final kelp blade weights, and the plot-level blade consumption rate as the mean blade loss over the duration of the grazing trial \((g/24 \text{ h})\). We chose mean blade loss rate as our response variable as it encompasses the variation in blade consumption within a plot, reflecting the naturally patchy distribution of urchins even within a small area of substrate. Where we found a blade was entirely consumed upon retrieval, we could not calculate the time period over which to estimate a consumption rate, therefore, we excluded these blades from our mean plot-level grazing rate estimates. When more than 4 of 8 transplanted blades were completely consumed (i.e., in eight plots with very high urchin biomass, 4000-6000 g/m\(^2\)), we chose to exclude these plots from our analyses due to their low blade sample size.

**Effect of sea otter predator cue on sea urchin kelp consumption**

To examine whether sea urchin predator-avoidance behaviour influences *in situ* grazing rates, we conducted an experiment to test the hypothesis that consumption of kelp by urchins is reduced in the presence of a sea otter predation cue. We conducted
grazing trials (as above) at two urchin barren sites: one site with high urchin biomass (mean ± SD: 5534 ± 2131 g urchins/m² or 18 ± 6 urchins/m²) and one site with low urchin biomass (1393 ± 876 g urchins/m² or 5 ± 3 urchins/m²). We established 12 plots per site, randomly assigning half the plots as ‘treatments’ and the remaining as ‘controls’ (one control and one treatment plot were lost upon retrieval at the high-biomass site, n=10). When transplanted kelp blades were attached, we added three small mesh bags each containing three freshly eviscerated conspecific (M. franciscanus) urchin tests to each treatment plot. These eviscerated tests are similar to what foraging sea otters discard after consuming urchin prey and have been observed to trigger a ‘flee’ response in another study (Watson and Estes 2011). In the control plots we attached the same mesh bags containing old clam shell fragments free of any organic material or living tissue.

Grazing trials in this experiment ran for six hours, after which urchin number and size were resurveyed (in anticipation of urchin movement), and the remaining kelp material was retrieved and re-weighed in the lab. This experimental duration ensured there was measurable kelp biomass in all plots at the end of the trial (especially high biomass plots).

### Statistical analyses

**Modeling the relationship between urchin biomass and grazing rate**

To determine the relationship between indices of sea urchin biomass and the rate of kelp consumption we fit alternative mechanistic mixed-effect models and assessed the relative strength of evidence for the competing models using an information-theoretic approach (Burnham and Anderson 2002). We focused on the total rates of kelp consumption as opposed to per capita rates given that we did not maintain an ambient density of urchins at a particular number throughout the duration of our trials. Moreover, we used urchin biomass as a key predictor to account for variation in urchin sizes (Ling et al. 2015) and because incorporating size-structure rather than density alone has been shown to better predict kelp abundance (Stevenson et al. 2016). We fit three basic linear models (shown in Table 1) and a non-linear saturating model (Eq.1) derived from a Holling Type II functional response (Holling 1959):
where plot-level mean kelp blade loss \( y_{ij} \) within a site \((j)\) is a function of urchin biomass \((x_{ij})\) and the parameters \(a\) and \(b\) define slope and saturation of the curve, respectively. We used exponentiated parameters to return positive grazing rates along with an additive error term to account for random blade loss in addition to the potential for blade growth (i.e., negative loss). In all models, where they appear, the parameters \(a\) and \(b\) were allowed to vary by site as correlated random effects for the \(j^{th}\) site. The models were fit by maximum likelihood and the fixed effects compared using small sample bias-corrected Akaike’s Information Criterion (\(AIC_c\)). We also report the positive Akaike weights \((w_i)\), representing the strength of evidence in favour of a given model relative to the set of candidate models. We plotted the best-fit model with a 95% confidence interval.

*Testing the relative effects of urchin biomass, density, behaviour, and drift kelp*

To determine the relative importance of sea urchin biomass, density, exposed vs. cryptic behaviour, and the presence of drift kelp affecting kelp consumption rates, we compared the fits of non-linear mixed-effect models (Eq.1) that used different metrics of urchin abundance representing different biological hypotheses. For example, if urchin size plays a role in affecting grazing rates, then we would expect the model using urchin biomass as the predictor variable to have a better fit compared to urchin density. Similarly, if only ‘exposed’ urchins are contributing to the observed plot-level kelp consumption (i.e., cryptic urchins not grazing), we would expect that models using the density or biomass of ‘only exposed’ urchins to have an improved fit over models using ‘all urchins’ which includes cryptic urchins. If urchins already eating drift at the start of the grazing trial were not consuming the transplanted kelp, we would expect that modeling only ‘non-drift-eating’ urchins to better predict grazing rates. Finally, our last two models used the density or biomass of ‘only exposed, non-drift eating’ urchins as the predictor variables. We used this approach because it was the most parsimonious way to test different hypotheses using comparable predictor variables in a series of non-linear saturating mixed effect models, and we lacked the data to build and test more complex models. We assessed the strength of evidence for these different candidate models using \(AIC_c\) as described above.
Examining the influence of sea otters on urchin grazing rates

As sea otter predation in this region is the primary mechanism driving shifts in urchin abundance and behaviour, we examined the overall difference in kelp consumption between sites where sea otters were absent (n=6) and present (n=2). We fit a linear mixed-effects model where kelp consumption was a function of sea otter presence (fixed effect), allowing a random effect of ‘site’. We then conducted a likelihood ratio test to determine the effect of sea otter presence on kelp consumption rates and plotted the distribution of kelp consumption rates within sea otter present/absent categories, and as a function of attached adult kelp density.

Testing the effect of a sea otter predator cue on urchin grazing rates

To determine whether the mean rate of transplanted kelp blade consumption was influenced by exposure to eviscerated urchin conspecifics (experimental treatment), we fit a linear regression model allowing the slopes of the fixed effects for urchin biomass versus blade consumption relationship to vary by ‘treatment’. In this model, we used the biomass of ‘exposed’ urchins to best reflect individuals that could access the kelp blade transplants (i.e., excluded the few urchins in cracks or under boulders). All analyses were conducted in R (R Core Team 2017), using the packages nlme (Pinheiro et al. 2017) for the mixed-effect modeling.

Results

Non-linear relationship between urchin biomass and grazing rate

We found the strongest support for a saturating relationship between kelp consumption rates and sea urchin biomass ($w_i = 1.0$), relative to the competing linear models ($w_i = 0$, Table 3.1). As plot-level urchin biomass increased, so did the consumption rate of transplanted blades, but at a decelerating rate. (Fig. 3.3a). In several plots with very low to no urchin biomass, we observed net kelp growth (negative kelp consumption rates in Fig. 3.3).
Table 3.1. Relative strength of support for alternative linear and non-linear models of kelp consumption rates (grazerate) as various functions of urchin biomass. Models compared via differences in Akaike’s Information Criterion (AICc) corrected for small sample sizes, (ΔAICc), and the normalized Akaike’s weight (wi). K is the number of parameters, log(L) is the likelihood of the model given the data.

<table>
<thead>
<tr>
<th>Model</th>
<th>Equation</th>
<th>K</th>
<th>log(L)</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saturating</td>
<td>$grazerate \sim \frac{biomass}{e^{-a} + e^{-b} \cdot biomass}$</td>
<td>6</td>
<td>-0.4</td>
<td>16.2</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Linear</td>
<td>$grazerate \sim a + b \cdot biomass$</td>
<td>6</td>
<td>-5.6</td>
<td>26.6</td>
<td>10.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Linear 0 intercept</td>
<td>$grazerate \sim b \cdot biomass$</td>
<td>3</td>
<td>-10.0</td>
<td>27.0</td>
<td>10.7</td>
<td>0.0</td>
</tr>
<tr>
<td>Null</td>
<td>$grazerate \sim a$</td>
<td>3</td>
<td>-13.0</td>
<td>32.8</td>
<td>16.6</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Additional factors influence urchin grazing rate

The consumption of drift kelp by urchins had a detectable influence on the grazing rate of transplanted blades (Table 3.2). When we excluded urchins that were recorded as eating a piece of drift kelp at the beginning of the grazing trial (up to 16 out of 33 urchins in one plot), this measure of urchin abundance provided the most parsimonious model of observed grazing rates (Wi = 0.9, Table 3.2) and explained 62% of the variance in the data relative to the null model. Additionally, there was greater overall support for models of kelp consumption that used urchin biomass as a predictor compared to those using urchin density (Table 3.2).

Plots within the sites where sea otters were absent had significantly higher rates of kelp consumption compared to sites where sea otters were present (Fig. 3.3b, $\chi^2$ = 15.7, df=1, p<0.001). The mean grazing rate was nine times higher (median was 40 times higher) in the deforested ‘sea otter absent’ plots (18.2 ± 8.5 g/24 h, median: 19.2 g/24 h) compared to the forested ‘sea otter present’ plots (2.0 ± 5.8 g/24 h, median: 0.5 g/24 h). Within deforested ‘sea otter absent’ sites, urchin biomass in plots was high (459 - 3035 g/m²), 55-100% of urchins in each plot were exposed (or 763 out of 804 total urchins counted across plots were exposed, 95%), and there were mostly no attached adult kelp present (Fig. 3.3c). Two notable outliers include a plot with only one urchin and considerable adult kelps, and a plot with 1.3 kelp stipes/m² despite high urchin
Figure 3.3. Numerical and behavioural factors influencing urchin grazing rates. (a) Saturating relationship (line) and 95% confidence interval (grey band) between urchin biomass and total rate of kelp consumption. (b) Difference in kelp consumption rate between sites with and without sea otters. Boxplots show median (solid line), mean (dashed line), and 25th/75th percentiles. (c) Consumption of transplanted kelp as a function of the density of naturally-occurring attached adult kelp in each plot. In all figures, data points represent a single experimental plot: shape of point indicates sea otter absent (circles) vs. present (triangles) and fill colour reflects proportion of urchins within the plot that were exposed (i.e., not cryptic). Data points without fill indicate plots with no urchins. Points below zero indicate net blade growth.
**Table 3.2.** Relative strength of support for alternative models of kelp consumption rate as a function of urchin density, biomass, and behaviour (exposed vs. cryptic; not eating vs. eating drift kelp). Models are compared via differences in Akaike's Information Criterion (AIC<sub>c</sub>) corrected for small sample sizes, (ΔAIC<sub>c</sub>), and the normalized Akaike's weight (w<sub>i</sub>). K is the number of fixed and random parameters, log(L) is the likelihood of the model given the data.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>K</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>Log(L)</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass of urchins not eating drift</td>
<td>6</td>
<td>9.1</td>
<td>0.0</td>
<td>3.1</td>
<td>0.9</td>
</tr>
<tr>
<td>Biomass of all urchins</td>
<td>6</td>
<td>16.2</td>
<td>7.1</td>
<td>-0.4</td>
<td>0.03</td>
</tr>
<tr>
<td>Density of urchins not eating drift</td>
<td>6</td>
<td>16.6</td>
<td>7.5</td>
<td>-0.6</td>
<td>0.02</td>
</tr>
<tr>
<td>Biomass of exposed urchins not eating drift</td>
<td>6</td>
<td>20.1</td>
<td>11.0</td>
<td>-2.4</td>
<td>0.004</td>
</tr>
<tr>
<td>Density of all urchins</td>
<td>6</td>
<td>20.3</td>
<td>11.2</td>
<td>-2.5</td>
<td>0.004</td>
</tr>
<tr>
<td>Biomass of exposed urchins</td>
<td>6</td>
<td>23.7</td>
<td>14.6</td>
<td>-4.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Density of exposed urchins not eating drift</td>
<td>6</td>
<td>25.1</td>
<td>16.0</td>
<td>-4.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Density of exposed urchins</td>
<td>6</td>
<td>26.1</td>
<td>17.0</td>
<td>-5.4</td>
<td>0.0</td>
</tr>
<tr>
<td>Null model</td>
<td>3</td>
<td>32.8</td>
<td>23.7</td>
<td>-13.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Biomass (Fig. 3.3c), which may have been related to an unusually high density (8 per m<sup>2</sup>) of *Desmarestia* spp. (a seaweed containing high concentrations of sulfuric acid which act as a chemical defense against herbivory; Gagnon et al. 2006). Among forested ‘sea otter present’ sites, urchin biomass in plots was low (0 - 391 g/m<sup>2</sup>), urchins were mostly cryptic (46 out of 49 total urchins counted across plots, 94%), there were higher densities of attached kelp (1.25 - 7.25 stipes/m<sup>2</sup>), and the rate of transplanted kelp consumption was zero to low (0 - 6.1 g / 24 h), including four plots where blades actually grew slightly during the trial (Fig. 3.3). One notable outlier with an unusually high grazing rate (16.3 g / 24 h) was due to four transplanted blades falling near the opening of a rock crevasse where several cryptic urchins were hiding.

Some variation in our measured grazing rates was also attributable to random site effects. The standard deviation in the random effects due to site was moderate relative to the fixed effect slope parameter (a = -6.7, σ<sub>a</sub> = 0.6), and exceedingly small relative to the fixed effect saturation parameter (b = 0.41, σ<sub>b</sub> < 0.0001).
Sea otter predation cue reduces urchin grazing rate

We detected a significant effect of our predator-cue (mimicking sea otter predation discards) on kelp consumption rates by sea urchins but this effect was mediated by ambient urchin biomass ($F_{2,20} = 202.6$, $p < 0.001$). Kelp consumption rates were reduced in treatment plots with eviscerated urchin tests, but this difference was greater in plots with higher urchin biomass (Fig. 3.4). For a given urchin biomass, the predicted grazing rate was 27% lower in plots containing eviscerated urchin tests compared to plots without this predator cue.

Discussion

Our study provides field evidence of numerical, size-related, and behavioural factors that influence the rate of *in situ* kelp consumption by sea urchins on temperate
rocky reefs. As we hypothesized, we found that urchin kelp consumption was positively related to patch-scale urchin biomass, reflecting both the density and body size of this key grazer. However, negative density-dependence, the presence of drift kelp, urchin crypsis and a sea otter predator-cue all functioned to reduce the intensity of grazing on transplanted kelp blades. Overall, these findings provide a mechanistic basis for how differences in grazing activity might reinforce either forested or deforested community configurations on temperate rocky reefs.

**Density dependence in grazing rates**

Although many studies have reported how kelp abundance on reefs varies with observed sea urchin abundance (reviewed in Ling *et al.* 2015), only a handful of studies have quantified how *in situ* grazing rates vary as a function of urchin density or biomass (Suskiewicz & Johnson 2017). Whereas studies showing positive density-dependence in urchin grazing rates are most common (Breen & Mann 1976; Schiel 1982; Lauzon-Guay & Scheibling 2007a), our data revealed a saturating relationship between the total rate of kelp consumption and red urchin biomass. We also found that urchin biomass was a better predictor of observed grazing rates than urchin density, reflecting the importance of urchin size as a determinant of *in situ* consumptive capacity (Stevenson *et al.* 2016; Suskiewicz & Johnson 2017). Theory suggests predator-dependence can be due to intraspecific interference (Hassell & Varley 1969, Beddington 1975), which may be the case for red urchins given their large size, long spines, and behavioural observations of ‘jamming’ and crowding that lead to density-dependent movement inhibition, even in the absence of bottlenecks (Parnell *et al.* 2017). Red urchins also commonly aggregate (Russo 1979; Duggins 1981a), which has been shown in other species to increase the likelihood of inter-individual encounters (Kratina *et al.* 2008). However, negative density-dependence among consumers can also be attributed to the depletion of resources (Fussmann *et al.* 2005), typically observed over longer timescales or experimental durations. In our experiment, a combination of interference competition and the more rapid depletion of kelp transplants in high urchin biomass plots over the 24-hour grazing trial likely contributed to the observed saturation in grazing rates. These results are consistent with a behavioural field study on red urchins that found responses to algal food subsidies were increasingly limited with increasing localized densities (Parnell *et al.* 2017).
The implications of density-dependence in sea urchin grazing are contingent on the ecological context. For green sea urchins in eastern Canada, increasing densities when food resources are limited contribute to a synergistic feeding effect (i.e., elevated per capita grazing) that leads to the destruction of adjacent kelp beds (Breen & Mann 1976; Lauzon-Guay & Scheibling 2007a). These authors postulated that a threshold biomass of ~2000 g/m² was required to initiate destructive grazing in order to weigh down kelp blades and prevent them from dislodging urchins. In contrast to these studies, we measured urchin grazing rates across a gradient of urchin biomass in already-established urchin barren and kelp forest contexts. While the observed negative density dependence in grazing rates is an indication of elevated competition for limited food resources in urchin barrens, we suggest this phenomenon has minimal significance for regime shift transitions in this system because our data show that attached kelp in urchin barrens is low to zero across a wide range of urchin biomass (450 – 3000+ g/m², Fig. 3.3a) and associated grazing rates (5 – 32 g consumed/24 h, Fig.3.3c). As others have found, our study supports the idea that food limitation in urchin barrens (Konar & Estes 2003) is a key condition driving active grazing which, even across considerable variation in consumptive pressure, ensures any palatable kelp resources are quickly devoured (Duggins 1981b; Harrold & Reed 1985; Watanabe & Harrold 1991; Byrnes et al. 2013) and deforested states remain deforested.

**Drift subsidies**

Drift algae are known to influence the foraging behavior of sea urchins, in turn determining whether passive feeding or destructive grazing allows kelp forests to thrive or collapse, respectively (Dean et al. 1984; Ebeling et al. 1985; Harrold & Reed 1985). While our experiments differ from these studies that focus on how drift subsidies influence urchin foraging mode, our results support similar conclusions that the presence of drift algae reduces urchin consumption of ambient kelp resources. Interestingly, the presence of drift kelp helped explain variation in grazing rates mostly within urchin barren plots, where some had up to half the individuals recorded as ‘eating drift’. While drift subsidies are an important food source in barrens (Kelly et al. 2012) and can improve the condition of urchins (Lowe et al. 2014), they are however ephemeral and vary across space and time (Britton-Simmons et al. 2009). Consequently, the presence of drift kelp in barrens does not support a lasting behavioural shift in foraging from destructive to passive grazing that would permit the recolonization of kelp. On these
resource-limited reefs, a substantial and sustained food subsidy is required in order to diffuse grazing pressure and permit kelp recruitment, survival and growth (Duggins 1981b).

**Sea otter predation**

By creating persistent spatial variation in the abundance, size-structure, or foraging efficiency of herbivores, predators can generate significant spatial variation in the intensity of herbivory (Ripple & Beschta 2004; Schmitz *et al.* 2004; Watson & Estes 2011). Consistent with our expectations, the net rate of kelp consumption was low or zero at forested sites where sea otters were present, with a mean grazing rate 9 times higher (median was 40 times higher) in deforested urchin barrens where otters were absent. While studies that measure urchin herbivory *in situ* are rare, a similar difference in magnitude of grazing rates was observed for urchins (*S. polyacanthus*) in the Aleutians, where average total kelp consumption rates were 30-100 times greater at two islands without sea otters compared to one that was otter-occupied (Steinberg *et al.* 1995). Our data suggest that net kelp consumption by herbivorous urchins at sites affected by sea otter predation is collectively influenced by reduced urchin density, size truncation, and behavioral modifications (i.e., crypsis). Moreover, at these ‘sea otter sites,’ there were higher densities of attached kelp that are a source of food and algal drift for urchins. While our experiments did not test these separate contributions explicitly, we provide evidence to demonstrate these are distinguishing differences between sea otter present/absent sites and their associated rates of herbivory.

Many species respond to predators through flight or shelter-seeking behaviour that reduces predation risk at the expense of food acquisition (Dill *et al.* 2003; Trussell *et al.* 2003; Werner & Peacor 2003; Preisser *et al.* 2005). Accordingly, predator avoidance is viewed as a primary reason that sea urchins occupy cryptic habitats (Lowry & Pearse 1973; Nelson & Vance 1979; Bernstein *et al.* 1981; Scheibling & Hamm 1991; Sala *et al.* 1998; Spyksma *et al.* 2017), similar to cryptic/hiding behaviour observed in other species (Lima & Dill 1990; Sih 1997; Kats & Dill 1998; Werner & Peacor 2003). Moreover, urchins’ ability to employ a sit-and-wait foraging strategy when drift algae is abundant further facilitates cryptic behaviour in kelp forests (Ebeling *et al.* 1985; Harrold & Reed 1985). Our data showed a clear distinction between the total proportion of urchins exposed versus cryptic in plots located in sea otter-absent urchin barrens (95%
exposed) and sea otter-occupied kelp forests (94% cryptic). While our field experiments were not designed to explicitly test how exposed versus cryptic urchin behaviour influences grazing rates, our results correspond with other studies that show that cryptic urchins on reefs with predators typically graze less of the ambient algal resources compared to exposed urchins on predator-free reefs (Nelson & Vance 1979; Carpenter 1984; Shears & Babcock 2003; Hereu 2005). What remains unclear is whether crevice-seeking is simply the result of sea otter predators removing exposed urchins (e.g., our data do show cryptic urchins in barren grounds), or a behavioural response to increased food supply or sea otter predator cues, or a combination thereof. For example, a mesocosm experiment demonstrated that *Evechinus chloroticus* urchins in New Zealand sought shelter in response to damaged conspecifics (a cue for lobster predation) but not increased drift supply (Spyksma *et al.* 2017).

Chemotaxis and alarm responses to the physical presence of predators or injured conspecifics (a predator cue) are key to species’ developing adaptive behavioural responses (reviewed in Kats & Dill 1998). Our results show a response of red urchins to eviscerated conspecifics that mimic a predation cue of sea otter foraging. Previous laboratory studies have shown that strongylocentrotid sea urchins greatly reduce foraging rates on kelp in response to predator cues from crabs (McKay & Heck 2008), spiny lobster (Matassa 2010), and sea stars (Freeman 2006). However, experiments in field conditions showed that green urchins did not refrain from consuming kelp in the presence of decapod predators (Scheibling & Hamm 1991; Harding & Scheibling 2015). Our results are consistent with both of these findings, whereby urchins in our field grazing trials openly consumed kelp in the presence of eviscerated conspecifics, but reduced their feeding rate relative to controls when urchin biomass was high. Interestingly, red urchins showed very different behaviour to the same sea otter predator cue in a field experiment by Watson and Estes (2011), whereby urchins consistently showed a flee response, moving rapidly out of urchin barren plots with eviscerated conspecifics. The provision of kelp resources in our experiment may explain this discrepancy, as other studies have shown that predator-avoidance behaviours can be subordinate to the attraction of kelp, particularly for large sea urchins in food-limited settings such as lab tanks or urchin barrens (Vadas *et al.* 1986; Scheibling & Hamm 1991; Harding & Scheibling 2015).
Herbivory rates in alternative states

Variation in the rate of herbivory has important consequences for community structure. This is particularly relevant in ecosystems that shift between alternative community configurations based on the intensity of herbivory; for example, by fishes on coral reefs (Holbrook et al. 2016), by deer in terrestrial riparian areas (Ripple et al. 2001), and by livestock in savannas (Walker et al. 1981). Our study provides a link between urchin grazing and alternative forested or deforested states on temperate reefs by illustrating the ways in which urchin biomass, food availability, and behaviour in the presence/absence of sea otter predation influence the rates of kelp consumption. However, we were limited in our ability to quantify how physical and environmental factors might have explained variation in grazing rates across different sites. This presents an opportunity for future studies to consider how the pathways that influence herbivory we examined might interact with additional factors recognized to influence urchin movement, behaviour, and grazing; for example, wave turbulence and storm surge (Lauzon-Guay & Scheibling 2007b; Shears et al. 2008), substrate microtopography (Parnell et al. 2017), the availability of cryptic habitat (Scheibling & Hamm 1991), temperature (Kawamata 1997), salinity (Himmelman et al. 1984), and pH (Rodríguez et al. 2018). Overall, our focus on identifying the factors that influence grazing rates across rocky reefs is important in light of regime shifts because system change is brought about by alterations to flows (i.e., rates of predation, herbivory) in advance of detectable changes in system elements (i.e., consumer and producer numbers) (Meadows 2009). Given that herbivore abundance, size structure and behavior all contribute substantially to impact grazing rates on primary producers, adequately understanding and predicting kelp forest regime shifts requires a shift from considering any of these in isolation, to considering their integrated dynamics.

Authors’ contributions

J.M.B., A.K.S. and K.W.D. designed the field study; J.M.B. and O.P. collected data; J.M.B., D.K.O., K.W.D. and A.K.S. performed or advised statistical analyses; J.M.B wrote the manuscript and all authors contributed substantially to revisions.
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References


Chapter 4.

Enabling coexistence: Navigating predator-induced regime shifts in human-ocean systems

Abstract

Rapid system-wide changes triggered by predators can pose considerable challenges to human communities. In the Northeast Pacific, the recovery of sea otters (*Enhydra lutris*) following the 19th century fur trade is driving a social-ecological regime shift with profound implications. While the ecological consequences of this shift are well documented, very little research has examined the conditions that enable or constrain people’s ability to adapt to the social, economic, and cultural changes that transpire. Through a collaborative partnership and workshops with Indigenous knowledge holders spanning Alaska to British Columbia, along with quantitative and qualitative interviews in two Indigenous communities among the first to experience sea otter recovery, we examined people’s perceptions of the social-ecological conditions that affect their ability to adapt to these changes. We found that communities differed in their relative rankings of adaptation-enabling conditions, however, four broad strategies were perceived as critical to improving coexistence with sea otters: (1) strengthening Indigenous governance authority, (2) promoting adaptive co-management, (3) weaving Indigenous knowledge and western science into management plans, and (4) establishing learning platforms. In contrast, both communities identified that increased livelihood options and financial assistance would not compensate for lost food security. Lastly, we found diverse attitudes towards sea otters exist within and across communities, indicating people’s perceptions are influenced by the social-ecological context in which otter recovery occurs. Our study suggests that enhancing Indigenous peoples’ ability to adapt to predator-induced regime shifts will require a transformation in current resource governance systems if we are to navigate towards an ecologically sustainable and socially just operating space. Overall, this work highlights the need for more Indigenous voice, authority, and leadership in addressing predator-induced regime shifts in complex and tightly coupled human-ocean systems.
Introduction

Human communities and systems of resource management are greatly challenged by social-ecological regime shifts, when linked systems of people and nature cross tipping-points and undergo changes that are unexpected, dramatic, and difficult to reverse (Scheffer et al. 2001; Nayak & Armitage 2018). For example, regime shifts triggered by the recovery of keystone predators generate considerable social and ecological management challenges. In ecological systems, changes in top-down predation can result in cascading effects that fundamentally alter ecosystem functions and processes, causing a transition to an alternative state (Beschta & Ripple 2009; Estes et al. 2011). In social systems, rapid changes associated with predator-induced regime shifts can entail difficult psychosocial adjustments (Russell et al. 2013; Treves & Bruskotter 2014), involve trade-offs and unequal distributions of negative impacts and benefits (Selkoe et al. 2015; Marshall et al. 2016), and deeply challenge traditional institutions and systems of governance (Clark et al. 2014; Marshall et al. 2016). While the ecological changes associated with predator-induced regime shifts are often well documented, less information is available on how human communities are navigating and adapting to the interconnected transformations in food systems, livelihoods, and resource management. Recognizing these challenges, there is a growing need to better understand what enables people’s ability to adapt to new social-ecological system configurations and coexist with apex predators that trigger profound change (Carter & Linnell 2016).

In coastal communities around the world, many people rely heavily on marine resources that are highly influenced by apex predators and susceptible to regime shifts (Estes et al. 2016). In a famous example, the collapse of Atlantic cod (Gadus morhua) predators triggered a regime shift from groundfish-dominated to invertebrate-dominated fisheries that profoundly influenced maritime livelihoods, culture, demographics, and economies (Hamilton & Butler 2001). However, the impacts of shifting predator populations and marine regime shifts are especially challenging for coastal Indigenous communities for several reasons: Indigenous worldviews, subsistence, and cultures are closely tied to ocean resources (McNiven 2004; Lepofsky & Caldwell 2013); their communities have relatively high rates of food insecurity (Power 2008); and they are frequently marginalized in marine management decision-making processes that directly affect their well-being (Langton 2002; Carothers 2010; Bennett et al. 2018). While
Indigenous knowledge of marine species and predator management is increasingly documented (Berkes 2008; Huntington 2011; Salomon et al. 2015), there is a pressing need to work with coastal Indigenous communities to better understand their unique capacities for adaptive strategies in response to rapid environmental change (Berkes & Jolly 2001; Ford et al. 2009; Galloway 2009; Reid et al. 2014).

Adaptation refers to adjustments in social-ecological systems that are carried out to reduce damaging impacts, or to take advantage of new opportunities that result from observed or anticipated changes (Smit & Wandel 2006). Similarly, ‘adaptive capacity’ is the latent potential for adaptation. But decision-making about adaptation is challenging, particularly at local scales, where people are often divided about what should be done and how it should be implemented. Moreover, people’s worldviews and values influence their perceptions of change and determine their desired courses of action (Wolf et al. 2013; Reid et al. 2014). In addition to theoretical advancements in adaptation research, there are consistent calls to use adaptive governance approaches (Folke et al. 2005) to enhance a community’s capacity to manage change on the ground (Smit & Wandel 2006; Whitney et al. 2017). One approach is to elicit perceptions of adaptation strategies from individuals who are experiencing rapid change to identify and prioritize adaptive measures tailored to the needs of a community and a particular stressor (Marshall & Marshall 2007; Ford et al. 2009; Wolf et al. 2013). In Indigenous communities, studies have further shown that if adaptation planning, management, and policy are to be perceived as legitimate, adaptation research has to include Indigenous knowledge, values and rights (Berkes & Jolly 2001; Pinkerton & John 2008; Wolf et al. 2013; Reid et al. 2014).

Along the northeastern Pacific coast, one of the most iconic predator-induced regime shifts is occurring in the traditional territories of coastal Indigenous peoples. The recovery and range expansion of sea otters (*Enhydra lutris*) following their extirpation in the 18-19th century fur trade are triggering both a dramatic ecological transformation and considerable social challenges (Salomon et al. 2007, 2015; Sloan & Dick 2012, Lee et al. 2018). As keystone predators and major architects of marine ecosystems (Estes & Palmisano 1974), the return of sea otters involves significant trade-offs. When otters are absent, sea urchins, crabs, clams, abalone and other shellfish are abundant, supporting commercial and subsistence fisheries (Salomon et al. 2007; Larson et al. 2013; Carswell et al. 2015). In contrast, when sea otters are present, there is a substantial reduction in
shellfish density and size (reviewed in Estes *et al.* 2016) reducing human access to these species, but kelp forests flourish, which support marine biodiversity (Estes & Palmisano 1974), expanded habitat for some fish (Bertocci *et al.* 2015), recreation and tourism (Loomis 2006), and carbon sequestration (Wilmers *et al.* 2012). However, despite the prevalence of recovering sea otter populations in Indigenous territories, issues of co-management, traditional use and stewardship of otters, and reduced food security have been largely neglected (Salomon *et al.* 2015; Levine *et al.* 2016; Pinkerton *et al.* 2019). Furthermore, in Canada, sea otter recovery has implications for Indigenous rights where the federal constitution protects Indigenous access to fisheries for food, social and ceremonial purposes (R. v. Sparrow 1990). To confront the complex challenges associated with sea otter recovery, there is a pressing need to identify conditions and strategies that enable coexistence with sea otters, and the types of governance structures that can help communities navigate the shift between alternative social-ecological states.

Here, we examine the conditions that affect people’s ability to adapt to the social-ecological regime shift triggered by sea otter recovery. We worked within a collaborative Indigenous partnership led by Hereditary Chiefs spanning south central Alaska through British Columbia (BC), to ask: 1) What social-ecological conditions are perceived to enable people’s ability to adapt to sea otter recovery, and which are most enabling?; 2) How do perceptions of these conditions differ between communities?; and 3) How variable are people’s attitudes toward sea otters and what factors might influence this? We examined these questions through workshops with Indigenous knowledge holders, along with survey-interviews in two Indigenous communities where we hypothesized that people’s perspectives would be influenced by the length of time they have been exposed to sea otter recovery, and the federal regulations that govern sea otter management. Our study aims to identify a suite of possible actions that improve Indigenous communities’ capacity to coexist with sea otters, and insights for natural resource agencies seeking to design socially just and environmentally sustainable ecosystem management more broadly.
Methods

Research co-production

To uphold Indigenous rights and governance protocols, we acquired free, prior and informed consent (UN 2007) from the Hereditary Chief Councils of three coastal Indigenous groups; the Nuu-chah-nulth, Haida and Heiltsuk First Nations before we began our research. We then established a collaborative partnership with an elected steering committee of Hereditary Chiefs, knowledge holders, and cultural advisors to guide our collaborative approach (Salomon et al. 2018a: www.CoastalVoices.net). This approach ensured that the co-production of research (see Davidson-Hunt & O’Flaherty 2007; Salomon et al. 2018b) followed each Nation’s protocols, was grounded in Indigenous values, and was supported by participating communities. Critically, it gave joint decision-making authority over the specific research questions pursued. Members of the steering committee and cultural advisors participated in all components of the research, including the design and implementation of workshops, community visits and surveys.

Survey design

We used a two-step, inductive and deductive process to design an interviewer-administrated survey that assessed people’s perceptions of the social-ecological conditions that enable their ability to adapt to sea otter recovery. We use the term ‘social-ecological conditions’ broadly to refer to social, institutional, management, regulatory, or ecological circumstances that influence the context in which people experience sea otter recovery. First, we identified social-ecological conditions relevant to sea otter adaptation from the dialogue generated during a 4-day workshop: “Visioning the future of kelp forest, sea otter and human interactions” (June 17-20, 2016). The workshop was attended by 21 Indigenous leaders and knowledge holders from 12 coastal communities across BC and Alaska and was structured by themes and questions that were addressed in break-out groups with facilitators, along with semi-structured interviews with select Chiefs and knowledge holders. We conducted an emergent content analysis (Stemler 2001) of the workshop transcripts using NVivo11 Qualitative Research software to identify 18 social-ecological conditions that were stated to influence people’s ability to coexist with otters (Table 4.1).
Table 4.1. Social-ecological conditions identified by knowledge holders as influencing an individual's or community's ability to adapt to sea otter recovery. Conditions with a * were identified from the literature. Actions illustrate how each condition might enable adaptation, except ‘climate change’, which was considered to reduce ↓ adaptation. Details in Appendix Table B1.

<table>
<thead>
<tr>
<th>Theme</th>
<th>Conditions Identified to Influence Adaptation</th>
<th>Actions that Enable Adaptation to Sea Otter Recovery</th>
</tr>
</thead>
<tbody>
<tr>
<td>Management</td>
<td>Incorporate Traditional Knowledge</td>
<td>• Weave traditional knowledge and stewardship with Western management approaches</td>
</tr>
<tr>
<td></td>
<td>Local Management Plan</td>
<td>• Design and implement a local management plan for sea otters, shellfish, and kelp</td>
</tr>
<tr>
<td></td>
<td>Experiment with Management</td>
<td>• Experiment with otter exclusions, spatial harvests, shellfish transplants, aquaculture, kelp harvest, etc.</td>
</tr>
<tr>
<td>Governance</td>
<td>More Local Indigenous Authority</td>
<td>• Increase decision-making power in local management of otters, shellfish, kelp and all nearshore resources</td>
</tr>
<tr>
<td></td>
<td>Community Leadership</td>
<td>• Support effective leaders that communicate, build trust, and play a key role in local resource management</td>
</tr>
<tr>
<td></td>
<td>Trust &amp; Respect Across Governments</td>
<td>• Enhance trust, legitimacy and cooperation between Indigenous and Federal/State governments</td>
</tr>
<tr>
<td></td>
<td>Federal Regulations</td>
<td>• Have federal regulations that can enable local hunting/harvesting of sea otters</td>
</tr>
<tr>
<td>Knowledge &amp; Learning</td>
<td>More Traditional Knowledge</td>
<td>• Gather traditional knowledge relating to the use, stewardship, and governance of otters, shellfish, kelp</td>
</tr>
<tr>
<td></td>
<td>Learning from Other Communities</td>
<td>• Exchange info with other communities adapting to sea otter recovery (their experience, their advice, etc.)</td>
</tr>
<tr>
<td></td>
<td>Monitoring Information</td>
<td>• Monitor information on the abundance/locations of otters, shellfish, kelp and harvest activity</td>
</tr>
<tr>
<td>Social Capital</td>
<td>Within Community</td>
<td>• Hold gatherings, groups, and social exchanges that are forums for communication or support</td>
</tr>
<tr>
<td></td>
<td>Between Communities</td>
<td>• Enhance reciprocity and exchange with adjacent communities to expand access to important resources</td>
</tr>
<tr>
<td>Perceived Resilience</td>
<td>Willingness to Embrace Change</td>
<td>• Have a positive or accepting attitude toward change</td>
</tr>
<tr>
<td></td>
<td>Experience from Other Changes</td>
<td>• Utilize experience from navigating other shocks/shifts that involved re-organization and learning</td>
</tr>
<tr>
<td>Livelihoods &amp; Financial Security</td>
<td>Novel Livelihood Opportunities</td>
<td>• Create sea otter-focused tourism opportunities</td>
</tr>
<tr>
<td></td>
<td>* Employment Options</td>
<td>• Expand alternative livelihood opportunities in the community to better cope with uncertainty</td>
</tr>
<tr>
<td></td>
<td>* Individual Occupational Mobility</td>
<td>• Expand people’s capacity/willingness to engage in alternative livelihoods making them more flexible</td>
</tr>
<tr>
<td></td>
<td>* Household Occupational Multiplicity</td>
<td>• Have multiple household incomes to enhance flexibility and income security</td>
</tr>
<tr>
<td></td>
<td>* Access to Financial Support</td>
<td>• Facilitate access to loans from the bank or other community sources to help with financial security</td>
</tr>
<tr>
<td>Ecosystem Resilience</td>
<td>Redundancy of Harvest Sites</td>
<td>• Have multiple locations where community members can harvest shellfish, urchins, crab, etc.</td>
</tr>
<tr>
<td></td>
<td>More Kelp Habitat Created</td>
<td>• Become aware of positive trade-offs: More kelp may provide greater fish habitat and other benefits</td>
</tr>
<tr>
<td></td>
<td>Climate Change</td>
<td>• Warming ocean temperatures and ocean acidification are additional system stressors</td>
</tr>
</tbody>
</table>

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Second, we reviewed the literature on adaptive capacity and social resilience to provide each social-ecological condition with a theoretical basis and predicted direction of influence (Appendix Table B1). This allowed us to group the 18 conditions into seven social-ecological themes grounded in adaptation and resilience theory (e.g., Adger 2003a; Folke et al. 2003; Armitage et al. 2009; Biggs et al. 2012; additional references in Appendix Table B1). Although only one condition was identified in relation to people’s livelihoods (i.e., sea otter tourism opportunities), several studies have identified that having alternative livelihood options, occupational mobility and multiplicity, and access to financial support are critical factors influencing communities’ adaptive capacity (Allison & Ellis 2001; Marschke & Berkes 2006; Cinner et al. 2009a, b; Badjeck et al. 2010; Blythe et al. 2014). Consequently, we incorporated these conditions into our survey for a total of 22 social-ecological conditions (Table 4.1 and B1) framed to enable adaptation to sea otters, with negative responses identifying potential constraints.

The final survey asked respondents to rank each social-ecological condition on a 9-point Likert scale from “greatly reduces” (−4) to “does not influence” (0) to “greatly improves your ability to adapt to living with sea otters in your territory” (+4). Interviewers recorded respondent comments associated with each condition to provide contextual qualitative information that we used to help interpret our ‘adaptation response score’. We also asked participants to rank their attitude toward the presence of sea otters on a 9-point scale ranging from “very negative” (−4) to “neutral” (0) to “very positive” (+4). Covariates such as participants’ age, gender, occupation, economic status (monthly cost of living) were collected along with a self-assessed ranking (none=0, low=2, medium=4, high=6, very high=8) for knowledge of sea otters/shellfish/kelp, level of trust between their community and federal marine governing institutions, and level of power in resource decision-making. Survey questions and administration were pilot-tested with cultural advisors and approved by the project steering committee and Simon Fraser University’s office of research ethics.

**Case study communities**

We used a community-based comparative case study approach that focused on two Indigenous communities that were among the first to experience sea otter recovery in the northeastern Pacific (Fig. 4.1). The communities were chosen because they are comparable in population size, geographic isolation (only accessed by boat or small
aircraft), socio-economic status (locally-based livelihoods, low average incomes, and high unemployment), and strong subsistence culture. Yet they differ in the length of time they have experienced sea otter recovery (~60 vs ~45 years), the manner in which sea otters recovered (natural recolonization vs. active re-introduction), and the federal regulations that govern sea otter protection and management.

![Map of Northeast Pacific coast with village locations for the Port Graham and Nanwalek Sugpiaq Tribes and Kyuquot/Chekleset First Nations with the approximate range of sea otter populations (current and pre-fur trade). Locations of remnant otter colonies (yellow dots) and translocated otter populations post maritime fur trade (green dots). Modified from Bodkin (2015).](image)

**Figure 4.1.** Northeast Pacific coast with village locations for the Port Graham and Nanwalek Sugpiaq Tribes and Kyuquot/Chekleset First Nations with the approximate range of sea otter populations (current and pre-fur trade). Locations of remnant otter colonies (yellow dots) and translocated otter populations post maritime fur trade (green dots). Modified from Bodkin (2015).

**The Sugpiaq Tribes**

In southcentral Alaska, on the tip of the Kenai Peninsula, the Sugpiaq people in the adjacent villages of Port Graham (population ~178) and Nanwalek (population ~300) have experienced sea otter recovery since the late 1950s when otters naturally
expanded their range into the area (Fig. 4.1; Salomon et al. 2007, 2011). Due to their close proximity (1km apart) and shared history, family relations, and experience of sea otter recovery, we considered these villages to represent a single Sugpiaq community in our analyses. Subsistence activities have always been and remain an essential part of these village economies; most households exchange and rely on subsistence harvest of salmon, halibut, seal, sea lion, as well as intertidal invertebrates and algae (Salomon et al. 2007, 2011). Following the return of sea otters, the Sugpiaq people observed a serial decline of highly valued shellfish species, which they attributed to both to sea otter predation and intensified local subsistence and commercial harvests (Salomon et al. 2007, 2011). As Alaska Natives, the Sugpiaq are legally permitted to hunt sea otters through a waiver to the federal Marine Mammal Protection Act (MMPA 1972), which places a moratorium on the take of all marine mammals. Locally hunted otters must be processed, tagged, and tanned, then “culturally modified” before sea otter products can be traded and sold (MMPA 1972).

**The Kyuquot/Chekleset First Nations**

The people of the Ka:'yu:'k't'h'/Che:k'tles7et'h’ First Nations, in English the Kyuquot/Chekleset (used hereafter), are members of the broader Nuu-chah-nulth First Nations that live along the west coast of Vancouver Island, British Columbia. The Kyuquot/Chekleset people have experienced sea otter recovery since the early 1970s when a coordinated federal government effort actively translocated 89 otters into their traditional territory just north of the village of Kyuquot (population ~172) (Bigg & MacAskie 1978; Fig. 4.1). The sea otter population on the west coast of Vancouver Island grew at a rate of 19.0% per year between 1977 and 1995 (Nichol et al. 2015), corresponding to a dramatic decline in sea urchins and other shellfish that residents harvested and relied on for food, social and ceremonial purposes (Gardner 2003a; Watson & Estes 2011). Kelp beds also expanded in areas where urchins declined (Watson & Estes 2011). Sea otters were listed as ‘Endangered’ in 1978 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and regulations under the Fisheries Act (1985), then the BC Wildlife Act (1996), and eventually their legal listing in 2003 as ‘Threatened’ under the Species at Risk Act - SARA (2002), protected sea otters from being captured, killed, or disturbed, and prohibited anyone from possessing an otter pelt (Nichol 2015). As the annual population growth rate slowed to 8.4% from 1996 to 2008 and 7.1% from 2009 to 2013 (Nichol et al.
In 2015, sea otters were down-listed in 2009 and remain a species of ‘Special Concern’ under SARA (Nichol 2015). As the SARA prohibitions don't apply to the ‘Special Concern’ designation, this enables First Nations to apply for a license under the Aboriginal Communal Fishing License Regulations, in turn under the Fisheries Act, to hunt otters for food, social, or ceremonial purposes. However, to date, such a licence has yet to be applied for (R. Dunlop, Uu-a-thluk, Nuu-chah-nulth Fisheries Program, pers. comm., Jan. 2019).

**Data collection**

Surveys were carried out through invited visits to our case study communities in spring 2016 and included convenience sampling of as many adult residents (≥19 years old) as possible during our stay. Effort was made to capture a representative sample covering a range of ages (19-96) and occupations, and balancing male/female respondents. Survey interviews were conducted one-on-one in-person and lasted 1-1.5 hr. Recorded responses were verified with the participant to ensure the qualitative statements and intended interpretations were accurately captured. Within the Kyuquot/Chelkis and Sugpiaq communities, we conducted 39 and 35 survey-interviews, representing ~34% and ~15% of the resident adult population, respectively. In addition to conducting survey-interviews, the project team (including hereditary Chiefs on the steering committee) and community leaders co-hosted town meetings to more broadly inform community members of the research project, facilitate dialogue, and encourage members to participate more formally.

**Data analyses**

To examine which social-ecological conditions most enabled people’s ability to adapt to sea otter recovery and how they differed between communities, we used a nested ordinal logistic mixed-effect model with a cumulative link function (details in Appendix B3). We used likelihood ratio tests to evaluate the influence of the main fixed effects (‘Social-ecological condition’ and ‘Community’) and their interaction, and we conducted pair-wise contrasts to evaluate whether ‘Condition’ differed in mean response score by ‘Community’ (p-values adjusted via Tukey method). We plotted the response distributions for each social-ecological condition within the two communities along with the median response score and 25th/75th percentiles. We then delineated the most
influential (enabling or constraining) conditions for each community as those with median response scores $\geq 3$, or $\leq -2$.

Second, we reviewed and summarized the qualitative information from the survey responses to interpret and contextualize the quantitative results (Marshall and Marshall 2007). We selected key statements related to each of the 22 social-ecological conditions to illustrate the range of responses (Appendix Table B2).

Finally, we examined if respondents’ attitude towards sea otters differed between communities and could be explained by socio-demographic covariates. Covariates were selected a priori based on hypotheses derived from the literature and a posteriori based on informative univariate relationships with sea otter attitude (Appendix B4). We fit ordinal regression models of ‘Otter Attitude’ including two-way interactions of independent covariates and compared their relative strength of evidence using small sample adjusted Akaike’s Information Criterion (AICc) and likelihood ratio tests (Appendix B5). We also examined the relative proportions of positive, neutral, and negative qualitative statements in response to ‘Otter Attitude’. Analyses were conducted using the ordinal and lsmeans packages in R (Lenth 2016; R Core Team 2017; Christensen 2018).

Results

Social-ecological conditions that enable adaptation differ between communities

The relative ranking of social-ecological conditions perceived to influence respondents’ ability to adapt to sea otters varied between communities (Fig. 4.2; $\chi^2 = 182.83$, df=21, $p < 0.001$). Overall, the adaptation response scores of respondents from Kyuquot/Chekleset in BC were lower than those of the Sugpiaq in Alaska, suggesting that the former community perceived fewer conditions would enable their ability to adapt to sea otter recovery in their territory. Specifically, the Kyuquot/Chekleset had only six conditions with a median response score $\geq 3$, whereas the Sugpiaq had 14 (yellow points, Fig. 2).
Figure 4.2. Relative rankings of social-ecological conditions nested within seven themes that are perceived to influence the Sugpiaq and Kyuquot/Chekleset peoples’ ability to adapt to sea otters. Coloured bars show response proportions (top axis); points show median response score (bottom axis) with 25th/75th quantiles; yellow points the most influential conditions perceived to improve or reduce adaptation (median ≥ 3, or ≤ -2, respectively). Conditions in bold green text have the greatest influence across both communities. Stars represent a significant difference (*<0.05, **<0.005, ***<0.001) in least squared means between communities.
Several social-ecological conditions were perceived differently by the two communities with respect to their influence on adaptation (Fig. 4.2). For example, federal regulations governing Indigenous hunting or possession of sea otter pelts were viewed as ‘reducing’ Kyuquot/Chekleset respondents’ ability to adapt (62%), whereas the majority of Sugpiaq respondents felt they ‘improved’ or ‘greatly improved’ (71%) their ability to adapt. Qualitative responses strongly suggest this is tied to the Canadian federal regulations that have restricted the Kyuquot/Chekleset from hunting otters. In contrast, the Sugpiaq value their legal ability to harvest sea otters under US federal legislation (Table 4.2, B2). Kyuquot/Chekleset respondents expressed that being restricted in their traditional use of sea otters, not being able to play an active role in sea otter management, and the general disregard for traditional systems of natural resource governance constrained their ability to adapt (Table 4.2, B2).

We also detected differences between Sugpiaq and Kyuquot/Chekleset respondents in their perceptions of ‘social capital’ within their community (i.e., the value of community events, forums, meetings) and between communities (i.e., the value of exchanging seafood with adjacent communities). The Sugpiaq viewed both social capital conditions as ‘improving adaptation’, whereas the Kyuquot/Chekleset perceived them as ‘not’ or only ‘slightly’ improving adaptation (Fig. 4.2). The Sugpiaq expressed that social exchanges and community meetings helped “bring people onto the same page”, reduce internal conflicts, and "let people know about marine system components". In contrast, the Kyuquot/Chekleset commented that exchanges and meetings about sea otters were repetitive, did not offer solutions or lead to actions, and were dominated by negative voices and opinions (Appendix Table B2).

Last, the magnitude by which human-induced climate impacts were perceived to affect respondent’s ability to coexist with sea otters differed between communities. In general, the Sugpiaq perceived climate change to greatly reduce their ability to coexist with sea otters (median= -2) whereas the Kyuquot/Chekleset perceived no influence (median = 0) (Table 4.2, B2). Sixty-nine percent of Sugpiaq respondents gave specific comments about the negative effects of climate change on the local ecosystem and subsistence harvest, compared to only 28% of Kyuquot/Chekleset (Table B2).
Conditions that most enable coexistence with sea otters

Seven social-ecological conditions were perceived in both communities to have the greatest influence on enabling adaptation to sea otters (Fig. 4.2, Table B2). Respondents in both communities perceived that ‘incorporating traditional knowledge into management of sea otters’ (#1), in addition to ‘having more traditional knowledge’ (#2) relating to the use, stewardship, and governance of sea otters, shellfish, and kelp would greatly improve people’s ability to coexist with otters. Survey respondents and Indigenous knowledge holders from the initial workshop expressed their perception that traditional knowledge provided important information about “when to hunt otters, how to hunt otters, how to prepare to hunt otters,” how otters/shellfish were used and managed in the past, and how stewardship values of respectful, non-wasteful harvest are important to emphasize and teach the younger generations (Table 4.2, B2). Similarly, it was expressed that place-based traditional knowledge provides important local-scale system understanding, that traditional stewardship values should be the foundation of any active sea otter management, and that the ideal scenario is “traditional, local, and current knowledge all combined in one pot” (Table B2).

Respondents in both communities felt that ‘implementing a local management plan’ (#3) for sea otters, shellfish, and kelp would greatly improve people’s ability to live with otters in their territory. In the Sugpiaq community in Alaska, respondents expressed that the draft management plan helps keep hunting and crafting alive but ensures overharvesting does not occur. Moreover, community members familiar with the plan, or the process to generate the plan expressed that it “triggered us getting involved” in sea otter management and “getting a seat at the table” alongside federal and state management agencies (Table 4.2). Respondents also emphasized that the management plan has to be co-created with the active participation of local people and would only be helpful if it was properly implemented with adequate capacity to be maintained. Both communities also identified the need to ‘experiment with different active management approaches’ (#4), for example, trying to spatially manage sea otters (e.g., keeping them out of key shellfish areas by hunting them and using a variety of deterrents), rebuilding shellfish populations (e.g., transplants, aquaculture, rebuilding ancient clam gardens), and initiating kelp harvesting (Table 4.2, B2). While many respondents commented that different ‘experiments’ their community had tried resulted in improved system
Table 4.2. Select quotes illustrating the highest-ranked social-ecological conditions perceived to enable adaptation to sea otter recovery. Additional quotes and attributions in Appendix Table B2.

<table>
<thead>
<tr>
<th>Key Social-Ecological Conditions</th>
<th>Perspectives from Indigenous Leaders &amp; Community Members</th>
</tr>
</thead>
</table>
| (1) Incorporate traditional knowledge into management | • “The traditional knowledge has to be the basis of the [sea otter management] plan.”  
• “I think it’s important that we combine traditional knowledge and scientific knowledge. It gives us a better understanding of what we can prepare for.”  
• “It is important that our ancient management knowledge come forth in current practice because our people live there. Connection to place is needed to effectively manage.” |
| (2) Gather more traditional knowledge | • “The greater knowledge we have of traditional values and cultural roles helps us be able to adapt to change. Traditional values focus on balance - and harvesting in a responsible, non-wasteful manner.”  
• “We have a cultural responsibility to the sea otter. There are specific rules… for example, when to hunt otters, how to hunt otters, how to prepare to hunt otters.”  
• “My traditional knowledge gives me the information about what we had before. It can guide us in making policies and decisions on what needs to be done.” |
| (3) Implement a local management plan for otters, shellfish, & kelp | • “Having a plan helps to keep the traditions alive but ensure that we don’t overharvest.”  
• “The management plan triggered us getting involved - having our people go out and harvest [otters] and utilize the furs. It wasn’t until we started to devise an otter management plan that the villages got a seat at the table.”  
• “[A management plan for sea otter] has got to be co-created, not created for us.” |
| (4) Experiment with different management approaches | • “[Management experiments] might be useful to know if any methods have worked or not. Shellfish transplants, clam gardens, kelp harvests are some of the things that would be so good to have done.”  
• “There needs to be an experimental approach to human control of sea otters on a small spatial scale. The objective would be to manage for local resources - certain clam beaches/bays - site specific management!”  
• “You can apply the knowledge you gain in one experiment to another system that might not even be linked to sea otters. You’ll expect one thing, but there will be more other surprises and things you learn.” |
| (5) Federal regulations on traditional hunting of otters | • “It’s hard to live with the [Federal] restrictions. We used to play a more active role in management.”  
• “They [Federal Government] have taken away our people’s ability to manage this resource. Our Hereditary Chiefs had a management plan in their governing system.”  
• “[Being allowed to harvest otters] is keeping our hunting and our traditions alive - that’s what we survived on, it’s how we adapted.” |
| (6) Indigenous authority in marine resource decision making | • “It doesn’t really work very well when outside people come in and impose their values on a system they don’t understand.”  
• “We need to have authority so we can manage this situation to benefit all, including the sea otter, our resources, and us as a people.”  
• “You have to get a seat at the table. We had to fight for that. I would say to other communities that it’s important to sit at the table, so you have a voice.” |
| (7) Learn from communities who have experienced sea otter recovery | • “[Learning from others] is necessary in these adapting times. The best is to communicate what is working and not working with each other.”  
• “[Sharing information] gives us a better understanding of what we can prepare for…. We’re looking at other communities that have management plans for otters and apply it to here.”  
• “I would like to see the Alaskan people come share information about sea otter management.” |
understanding and learning, some respondents were more skeptical because they felt the community had spent valuable time and resources on trying things that did not work.

Having ‘federal regulations that support Indigenous hunting of sea otters’ (#5) was perceived to improve coastal communities’ ability to coexist with otters. Sugpiaq respondents in Alaska, expressed that they valued being able to “control local otter populations”, “keep hunting/crafting traditions alive”, and use and sell otter pelts (Table 4.2, B2). In 14 of the 26 comments, the Sugpiaq explicitly mentioned that only a very limited number of otters were hunted in their community due to the limited number of people who actively hunt, the prohibitive cost of processing and tanning pelts, the rules which constrain the commercialization of pelts, the enforcement consequences that exist if people over-harvest, the sentiment that hunting large numbers of otters is unnecessary and inappropriate, and that unlike seals and sea lions, sea otters are not hunted for food.

Respondents in both communities felt that having ‘increased local Indigenous authority in resource decision-making’ (#6) would improve people’s ability to coexist with otters. Both communities ranked their current authority as being just above “low”, with an average rank (from 0 to 8) of 3.3 (± 2.5 SD) and 2.5 (± 2.5 SD) among Sugpiaq and Kyuquot/Chekleset respondents, respectfully. Similarly, mean perceived levels of trust between the communities and federal marine governing institutions were “low” (Sugpiaq = 2.5 ± 1.6 SD, Kyuquot/Chekleset = 2.2 ± 2.0 SD). Respondents in both communities felt that resource decisions were being made by governments that had little understanding of the local context (“how we actually live”, “our way of life”), and suggested that having increased power in decision-making would help people become more aware of Indigenous people’s commitment to conservation, would encourage more young people to join advisory committees, would “give communities a voice”, and could help legitimize local enforcement (Table 4.2, B2).

Finally, both communities perceived that adaption to sea otter-induced changes would improve if they could ‘learn from other communities experiencing sea otter recovery’ (#7). They suggested this would help them better understand anticipated changes, help them be better prepared, and that sharing information (i.e., what has worked, what has not) would be useful to inform ongoing management strategies and plans (Table 4.2, B2).
Conditions that least enable coexistence with sea otters

Having household occupational multiplicity, individual occupational mobility, and access to financial support were among the least influential conditions influencing both Sugpiaq and Kyuquot/Chekleset respondents’ ability to adapt to sea otter recovery (Fig. 4.2). While having alternative employment options in the community was recognized by some people in both communities as being beneficial, many of the comments indicated that employment, additional incomes, and bank loans could not be considered a substitute for the loss of local shellfish subsistence resources: “Having jobs doesn't bring fresh seafood” (Table 4.3).

Table 4.3. Select comments from the survey-interview questions pertaining to ‘livelihoods and financial security’ in the Sugpiaq versus Kyuquot/Chekleset communities. Additional quotes and attributions in Appendix Table B2.

<table>
<thead>
<tr>
<th>Community Perspectives: Food Security in the Context of Livelihoods and Financial Security</th>
</tr>
</thead>
<tbody>
<tr>
<td>• &quot;Any community needs jobs to help the economy, but jobs don't help people deal with otters.&quot;</td>
</tr>
<tr>
<td>• &quot;Your body will lead you back to trying to find food. Jobs are not as important.&quot;</td>
</tr>
<tr>
<td>• &quot;If people have a part-time job or full-time job, they still need subsistence harvest. And the otters affect subsistence harvest.&quot;</td>
</tr>
<tr>
<td>• &quot;Having access [to loans or financial support] in certain situations may be helpful, but the subsistence is more important.&quot;</td>
</tr>
</tbody>
</table>

| • "[If we had a variety of employment opportunities], we would still miss our seafood." | Kyuquot/Chekleset |
| • "Having more [income] sources would not help because there is still no seafood." |
| • "I don't think [access to financial support] makes a difference, because it's the food we want back." |
| • "The otter has depleted valuable traditional foods that we have been able to trade like abalone, sea cucumber, clams, etc." |

Diverse attitudes toward otters exist between and within communities

The majority (68%) of Sugpiaq respondents felt either positive (31%) or neutral (37%) towards the presence of sea otters in their territory. In contrast, 51% of Kyuquot/Chekleset respondents had a negative attitude towards sea otters (Fig. 4.3). This pattern was also reflected in the qualitative data (Fig. 4.3) whereby the Sugpiaq had more positive (39%) or neutral (29%) comments, expressing a general acceptance of sea otters and appreciation for being able to hunt them, with fewer comments (32%)
Figure 4.3. Quantitative and qualitative responses to the question: “How would you rank your general attitude toward the presence of sea otters in your territory?” (A) Bars show response proportions and points show the median response score with 25th/75th quantiles, with n = community sample size. (B) The relative proportions (% and reflected in box size) of qualitative comments with select illustrative quotes, n = number of respondents who provided commentary.

raising negative otter sentiments. In contrast, the majority of Kyuquot/Chekleset comments were negative (57%), expressing their frustration with the “forced” re-introduction of otters, having witnessed the loss of shellfish resources within one’s
lifetime, the younger generation having no access to traditional shellfish foods, and the lack of Indigenous involvement in sea otter management (Fig. 4.3, Table B2).

Although a wide range of perspectives on sea otters was expressed in both communities (Fig. 4.3), we could not attribute this variability to respondent age, economic status, occupation, or level of knowledge associated with the use/stewardship of otters, shellfish, and kelp (Appendix B4). However, we did detect a small effect of gender on Kyuquot/Ch'ekleset attitudes towards sea otters, but not among the Sugpiaq ($\chi^2= 6.33$, df=1, p<0.01, Appendix B5). Among the Kyuquot/Ch'ekleset, female respondents had a more negative attitude toward sea otters then males (p<0.01). However, models including ‘Community’ and ‘Gender’ only explained 16% of the variation in ‘otter attitude’.

**Trade-offs elicit polarized perspectives**

Conditions commonly cited as being positive gains that accompany sea otter-induced regime shifts – sea otter tourism and increased kelp habitat – elicited polarized responses in both communities (Fig. 4.2). Some respondents in both communities felt that the opportunity for sea otter tourism would be “a boost to the economy,” “a sustainable source of income”, “an ecotourism asset”, and a way to “create jobs” (Table B2). In contrast, some Sugpiaq respondents expressed that tourist values might clash with their traditional hunting values: “Tourists wanting to see the otters would make it harder to hunt them. Most people who want to see them are the ‘save the whales’ type people” (Table B2). Similarly, some Kyuquot/Ch'ekleset respondents felt “tourism would only benefit the [mostly non-Indigenous] lodges” in the area. Other Kyuquot/Ch'ekleset respondents expressed that while tourism could be beneficial, there was not sufficient information, resources, or training within the community to develop such ventures (Table B2). Perspectives about kelp were also mixed. There were positive comments from Kyuquot/Ch'ekleset respondents who felt more kelp was “good for herring,” or “good for rockfish”, but also comments that too much kelp made it difficult for navigation, or that having more kelp didn’t matter because “the fish are being fished out.” Sugpiaq respondents were more negative about kelp, expressing that “having more kelp makes it harder to get around using small outboard motors” and that kelp is “not good for salmon”, a predominant subsistence food, because they observe adult salmon avoid swimming in kelp beds and also kelp fouls their salmon gill nets.
Discussion

Our study identifies seven key social-ecological conditions that influence the ability of Indigenous communities to coexist with sea otters and the profound social-ecological changes they elicit. Our findings also show that while communities differed in their relative rankings of adaptation-enhancing conditions, four broad themes were perceived as the most important for improving coexistence with sea otters; (1) strengthening Indigenous governance authority, (2) promoting active and adaptive otter management, (3) acquiring and incorporating Indigenous knowledge in management, and (4) learning from others. While our results highlight that adapting to sea otter recovery is strongly influenced by the degree to which Indigenous communities have decision-making authority and agency in marine resource management, we also show that local food security is a primary concern which is not compensated for by having greater livelihood opportunities or financial stability. Finally, we reveal that diverse attitudes towards sea otters exist within and across communities, suggesting that people’s perceptions of predators and the regime shifts they trigger are highly context dependent. Overall, our findings point to a number of specific strategies and a more collaborative governance approach to improve the adaptive capacity of coastal Indigenous communities that are currently, or will soon be navigating the transformations triggered by recovering sea otters.

Social-ecological context

Our findings echo other studies that show that people’s perceptions of environmental change and their ability to adapt are influenced by their individual experiences within a broader social-ecological context (Marshall & Marshall 2007; Coulthard 2012; Wolf et al. 2013; Cinner & McClanahan 2014). In our study, the Sugpiaq Tribes tended to have a more ‘positive’ overall perception of sea otter recovery and their ability to adapt, compared to the Kyuquot/Chelkeset First Nations who were overall more ‘negative’ (Fig. 4.2, 4.3). One explanation for this may be due to the different lengths of time each community has been exposed to sea otter-induced regime shifts and the legacy effects of ‘shifting baselines’ (sensu Pauly 1995), whereby human perceptions of ecological systems change due to loss of knowledge and experience about past conditions. Given that sea otters recovered in Sugpiaq territory in the late 1950s, most of the participants we surveyed have grown up in the presence of sea otters with only a few
remaining Elders having memories of a ‘pre-otter’ ecosystem. In contrast, many adult Kyuquot/Chekleset respondents can recall harvesting abundant shellfish before sea otters were re-introduced in their territory in the 1970s, and stated that younger generations “don’t know what we’re missing.” Others from Kyuquot/Chekleset commented that “a lot of people don’t eat our traditional foods, so they don’t care [about otters]” which indicates changing social and cultural norms may also influence how people perceive ecological change (Adger 2003b; Turner & Turner 2008). Contrary to the often negative implication of shifting baselines (Papworth et al. 2009), our findings suggest that human adaptation to predator recovery may improve with time:

“There are different viewpoints on [sea otter recovery] and it depends on how you’re raised and what your current ecological timeline in the reintroduction of the sea otters is… We [Sugpiaq] are a little ahead on the ecological timeline… - they’re neither a benefit or a detriment. But currently in British Columbia they are nuisance and they are not looked highly upon.” (J. Anahonak)

While the temporal context is important, our data suggest that a more influential element relates to the level of agency and power that communities have during their experience of sea otter recovery. Since 1969 when sea otters were translocated to Kyuquot/Chekleset territory without prior consultation and subsequently protected under federal and provincial laws, residents have lost their access to local shellfish resources and been given little opportunity to participate in decision-making around sea otter management (Pinkerton et al. 2019). By comparison, the agency of the Sugpiaq Tribes has been higher, given they have federally-granted ‘operational access rights’ (sensu Schlager & Ostrom 1992) to hunt marine mammals, and Indigenous-led institutions such as The Alaska Sea Otter and Sea Lion Commission which have promoted Tribal involvement in policy decisions, research, and otter stewardship (TASSC 2018). That these different social contexts of agency and power influence people’s attitudes and ability to adapt reflect the findings from Nayak et al. (2016) who showed that social-ecological regime shifts in two coastal lagoons had a disproportionally negative impact on disempowered and marginalized communities. Social structures of power are shown to shape adaptation actions, such that ‘powerlessness’ reduces adaptive capacity (Marshall & Marshall 2007; McLaughlin & Dietz 2008; Adger 2016), and having ‘agency’ – the ability of people to have free choice in actively shaping their future – is essential for building adaptive capacity (Cinner et al. 2018) and resilience (Coulthard 2012). Our work highlights that it is critical to consider how agency and power shape adaptive capacity,
determine the perceptions of impacts, and influence the ability for resource-dependent communities to be involved in the decisions and interventions required to navigate difficult environmental change (McLaughlin & Dietz 2008; Adger 2016; Nayak et al. 2016; Whitney et al. 2017; Cinner et al. 2018).

**Access to local seafood and social justice**

While sea otter recovery is an acknowledged threat to commercial shellfish-based fishery livelihoods (Larson et al. 2013; Carswell et al. 2015), our work with Indigenous communities highlights a foundational concern less frequently discussed in the adaptation literature: subsistence harvest and local food security. These issues are rarely examined in many coastal studies that focus on adaptation in fishing livelihoods subject to various stressors (Allison & Ellis 2001; Marschke & Berkes 2006; Badjeck et al. 2010; Cinner et al. 2012a; Coulthard 2012; Blythe et al. 2014), in which the adaptive capacity of fisherfolk is often tied to occupational diversity, multiplicity, mobility, and access to credit, among other factors. In contrast to a focus on livelihoods, Indigenous workshop participants and survey respondents strongly emphasized how sea otter recovery affected their access to locally-obtained shellfish food sources that are critical to people’s diets and health, to social bonding and cultural continuity, and to local food sovereignty given their remote locations. These strong values around place-based food access and complex ties to well-being are widely acknowledged in other studies with coastal Indigenous people (Turner et al. 2000; Turner & Turner 2008; Poe et al. 2013), and help explain why having more livelihood options and greater financial security were not considered very influential in improving coexistence with otters (Fig. 4.2, Table 4.3). Another reason why livelihoods may have been less of a priority is that very few people in either community are actually employed in commercial fisheries. This is largely due to the legacy of federal “fleet rationalization” and privatization policies that have resulted in reduced Indigenous access rights to most commercial fisheries along the coast (Carothers 2010; Pinkerton & Silver 2011).

In Canada, because Indigenous access to fisheries for food, social, and ceremonial (FSC) purposes is a protected right in the Canadian constitution, the recovery of sea otters in Indigenous traditional territories raises issues of social justice (Pinkerton et al. 2019). While there is increasing research interest in the integration of law and social-ecological resilience (Garmestani et al. 2013; Green et al. 2015), there
remains limited empirical work that focuses on regime shifts in relation to social-environmental injustices (Nayak et al. 2016). Based on the information shared by our respondents, forward-thinking strategies and interventions that might improve people’s ability to coexist with sea otters will involve directly addressing power imbalances and social injustices through redistributions of governance authority, establishing collaborative management arrangements, and finding new ways to integrate Indigenous knowledge and objectives (Plagányi et al. 2013).

**Enabling coexistence**

**Strengthen Indigenous governance and authority**

Power sharing and the devolution of management rights to promote increased local-level participation and agency are key components of adaptive governance (Folke et al. 2005). This is especially relevant for Indigenous Peoples who are seeking to reinstate the Indigenous governance and stewardship systems that were heavily eroded through colonization (Johannes 1978, Mulrennan 2014, Pinkerton et al. 2019). In a broader international movement toward recognizing Indigenous rights (UNDRIP: UN 2007), Indigenous peoples are increasingly playing a central role in the governance of marine resources in their traditional territories; for example, in Indigenous-owned marine protected areas (Butterly 2013), state-recognized customary tenure systems (Hickey 2006), and through power sharing on fishery co-management boards (Armitage 2005; Jones et al. 2017; Snook et al. 2018). In our study, both communities perceived their current authority in marine resource management to be “low” and felt that adapting to sea otter recovery would be improved if they had increased participation and agency in marine resource decision-making – “a voice and seat at the table”.

Several multi-level collaborative governance arrangements in North America illustrate that power sharing in marine mammal management is possible. In northern Alaska, the Inupiat (“people of the whale”) are part of a two-tiered cooperative management agreement between the Alaska Eskimo Whaling Commission and the US National Oceanic and Atmospheric Association (NOAA) that uses customary laws and contemporary science to manage subsistence take of endangered bowhead whales (Chiropolos 1994; Huntington 2000). In the Canadian Beaufort Sea, the federal government and industry support the community-based management of beluga whales
by the Inuvialuit people, which was enabled by establishing their harvest and management rights in the Inuvialuit Final Agreement in 1984 (FJMC 2013). While no such power-sharing governance arrangements exist for sea otters in Canada, Alaska Tribes have benefited from active participation in The Alaska Sea Otter and Sea Lion Commission, which has operated through a Memorandum of Agreement (1994) with the US Fish and Wildlife Service, enabling Tribal involvement in sea otter management planning, policy decisions, research, and population monitoring (TASSC 2018). All the above examples are highly relevant in adapting to regime shifts, given their polycentric arrangements of shared power help provide institutional structures for cross-cultural communication, managing conflict, and enhancing self-organization and learning – conditions which in turn enhance adaptive capacity and social-ecological resilience (Folke et al. 2003; Armitage 2005; Biggs et al. 2012).

Information from our study supports findings that suggest decentralizing resource governance and establishing Indigenous co-management present both challenges and opportunities (Armitage 2005; Spaeder & Feit 2005; Snook et al. 2018). One major barrier we identified is a deep lack of trust between Indigenous communities and state/federal management agencies, whereby respondents felt that their communities were undermined in negotiations, that traditional knowledge was not always used or respected, and that there remained a general lack of consultation, information sharing, and open communication (Appendix Table B2). This is a core issue that will need addressing as studies have shown that relationships of trust and respect help promote the cooperation, cross-scale linkages, and perceived legitimacy of management actions that become key when resolving conflict and adapting to changing environmental conditions (Adger 2003a; Cinner et al. 2009b; Young et al. 2016). In Canada, there is an opportunity for continued progress to build better “Nation to Nation” relationships through the federal government’s commitments to reconciliation (TRC 2015). In other First Nations communities along the BC coast, fisheries with long histories of mistrust and conflict are beginning to move toward new relationships of negotiation and co-management (e.g., Jones et al. 2017).

*Establish community-based and adaptive management*

Nested multi-level structures of resource co-management that include strong local-level engagement benefit from place-based system understanding and can have
higher levels of monitoring and compliance due to perceived legitimacy (Pinkerton & John 2008; Armitage et al. 2009; Cinner et al. 2012b; Quimby & Levine 2018). Our study suggests that Indigenous peoples’ ability to coexist with sea otters can be improved when they are able to actively hunt and adaptively manage their use of otters in their traditional territories, as evidence suggests they have done for millennia (Simenstad et al. 1978; Szpak et al. 2012; Salomon et al. 2015). In a contemporary context, this pertains to having the legal authority to hunt sea otters, the ability to implement a locally-designed management plan for otters (along with shellfish and kelp), and the ability to experiment with different management approaches that might help sustain local shellfish resources or provide economic opportunities. The Sugpiaq people already implement several aspects of their Tribal management plan as community members engage in the non-wasteful hunting of otters (mostly adult males), tag and monitor their harvest, do hunter-implemented bio-sampling, and use otter pelts for cultural handicrafts that provide economic benefit to the community. In contrast, the Canadian federal government maintains exclusive responsibility over sea otter management planning and monitoring in BC (DFO 2014), largely ignoring the cultural, economic, and ecological sea otter relationships that First Nations people wish to revitalize (Salomon et al. 2015; Pinkerton et al. 2019). However, in 2012 the Nuu-chah-nulth Tribal Council Fisheries Department, Uu-a-thluk, drafted a comprehensive management plan for K‘akwatl (sea otters), with the desire to provide ceremonial use of sea otters for First Nation communities (NCN 2012). This draft management plan contains quantitative estimates for an annual allowable harvest rate in addition to details on the spatial boundaries, harvest permitting and protocols, bio-sampling, population and compliance monitoring, joint federal-First Nation enforcement, and a commitment to work collaboratively with all levels of government and relevant agencies. While this draft remains under review by the Nuu-chah-nulth Tribal Council, its future implementation would represent a paradigm shift towards recognizing Indigenous rights and authority in ecosystem management in BC and improving First Nations coexistence with sea otters.

Developing the capacity for communities to learn from their own experiences is an important part of building adaptive management institutions that are beneficial for dealing with complex social-ecological change and conflict (Folke et al. 2005; Armitage et al. 2009; Cinner et al. 2018). In our study, there was strong support in both communities for experimenting with different sea otter, shellfish and kelp management strategies and general acknowledgement of the benefits of experiential learning. This
may be an important element in the development of Indigenous participation in sea otter management, as natural and social scientists emphasize the importance of treating new policies and management arrangements as ‘learning experiments’ that need to be monitored, evaluated and adapted over time (Walters & Holling 1990; Ostrom 2005). For example, following the Nunavut Final Agreement that transferred decision-making power to Inuit communities in northern Canada, a new community-based narwhal management plan was first treated as a 3-year experimental process and reviewed by a multiparty committee who made recommendations that were endorsed by the Nunavut Wildlife Management Board and the Canadian federal fisheries minister (Armitage 2005). Importantly, respondents in our study also highlighted that thoughtful planning must go into any new ‘experiments’ in ecosystem management (e.g., spatial exclusion of otters, shellfish seeding or transplants, restoring ancient clam gardens (Groesbeck et al. 2014), small-scale kelp harvest, etc.), as they can be time and resource-consuming, and do not always produce the desired outcomes.

Overall, it is acknowledged that many challenges can arise in implementing community-based resource management, raising caution that the success of such arrangements hinges on providing significant and sustained local capacity building, efficient administration, effective monitoring and enforcement of new rules, and successfully bridging different knowledge systems (Dietz 2003; Berkes 2004; Armitage 2005; Armitage et al. 2009; Mistry & Berardi 2016). For example in Alaska, many of the successful programs for sea otter management planning, monitoring, and research implemented as a result of a co-operative agreement between the Tribal-led Alaska Sea Otter and Sea Lion Commission and the US federal Fish and Wildlife Service have ceased to run since 2007/08 due to insufficient available funding and political conflicts that couldn’t be reconciled (P. Norman, Vice-Chair TASSC, Chief of Port Graham, pers. comm., Dec. 2018).

**Acquire and incorporate Indigenous knowledge in management**

Interactions between Indigenous peoples and their environments over millennia have resulted in detailed knowledge and place-based stewardship practices that enable adaptation to social-ecological changes (Turner & Berkes 2006; Berkes 2008; Brown & Brown 2009; Mulrennan 2014). As such, communities adapting to regime shifts can benefit from mobilizing, making use of, and connecting Indigenous knowledge to other
knowledge systems in ways that can generate new insights, understandings, and innovations to manage complex adaptive systems (Berkes et al. 2000; Folke et al. 2003; Tengo et al. 2014; Ban et al. 2017). In the context of sea otter recovery, this will involve gaining a greater understanding for how sea otters and shellfish were managed by Indigenous people in the past to inform potential practices for contemporary management (Salomon et al. 2015, 2018). Moreover, because monitoring regime shifts is acknowledged as being key to increasing communities’ ability to anticipate and respond to rapid change (Danielsen et al. 2005; Selkoe et al. 2015), there is great potential to enhance the use of Indigenous knowledge and participation in community-based marine mammal monitoring (e.g., Huntington 2000; Berkes & Jolly 2001; FJMC 2013). Finally, finding ways to uphold and use Indigenous knowledge and western science has the opportunity to generate new insights and shared understandings about social-ecological regime shifts (Lee et al. 2018). Several examples from Canada and Alaska already demonstrate how bridging these ways of knowing enhances our understanding of social-ecological change in coastal settings and reinforces the legitimacy of each contributing knowledge system (Huntington 2000; Salomon et al. 2007; Armitage et al. 2011; Housty et al. 2014; Atlas et al. 2017; Ban et al. 2017).

Indigenous knowledge is also importantly underpinned by cultural values, principles, and protocols (e.g., Brown & Brown 2009), which become highly important for framing collaborative governance relationships, policies, and management institutions (Jones et al. 2010; Artelle et al. 2018). As an example, the Nuu-chah-nulth concepts of ‘Hishuk’ish Ts’awalk’ (everything is one) and ‘Isaak’ (respect with caring) are core principles in the guiding strategic plan of the West Coast Aquatic Management Board – Canada’s first aquatic co-management program following the 1997 Ocean’s Act (WCA 2012). These same two principles are central in the Nuu-chah-nulth draft sea otter management plan, framing the overarching vision and stated objectives (NCN 2012). These examples, among others globally, illustrate the opportunity for “values-based management” to act as a platform to build respectful cross-cultural relationships and advance effective stewardship practices (Artelle et al. 2018).

**Learning platforms and knowledge co-production**

Learning from other’s experiences of navigating ecosystem change can reduce social uncertainties and enable communities to better plan and prepare for shocks and
disturbances (Folke et al. 2003; Berkes 2009; Armitage et al. 2011; Cinner & McClanahan 2014). Echoing this sentiment, both Sugpaiq and Kyuquot/Chekleset respondents stated that learning from other communities who are experiencing sea otter recovery would greatly improve their ability to adapt (Table 4.2, B2). Fortunately, there is great potential for information exchange as multiple Indigenous communities are in different stages of sea otter recovery across BC and Alaska. The opportunity for these communities to share experiences, knowledge, as well as successful and unsuccessful management strategies could provide important understanding and insight, in addition to providing a broad network of support, communication and potential resources. As an example, the successful proliferation of community-based marine reserves in Kenya was attributed in part to the development of ‘learning platforms’ – regular visits to neighbouring communities and annual forums to share information about management outcomes (Cinner & McClanahan 2014).

Many elements of this research also demonstrate the potential benefits for sea otter recovery learning platforms. Indigenous knowledge holders and scientists who attended our initial workshop from across BC and Alaska expressed that the gathering (and subsequent film and website: www.CoastalVoices.net) had expanded their understanding and preconceived notions of sea otter recovery. Similarly, through their active participation in the workshop, research presentations, and community visits, Hereditary Chiefs on the project steering committee are now transmitting their learnings within their respective communities. Just as social learning has become a recognized catalyst in climate change adaptation (Cinner et al. 2018), our research suggests that ongoing efforts to support information exchange about sea otter recovery has the potential to transform how different actors (the public, coastal communities, managers, policy-makers) perceive predator-induced regime shifts and the types of governance and management systems required to enhance communities’ adaptive capacity.

**Plurality of perspectives**

People’s perceptions of predators and environmental change are ultimately shaped by individual values and experiences (Marshall & Marshall 2007; Wolf et al. 2013; Treves & Bruskotter 2014; Pooley et al. 2017). In both communities there was a high degree of individual variation in people’s ranking of enabling conditions (Fig. 4.2) and their attitudes toward otters (Fig. 4.3). This plurality of sea otter attitudes within
communities, and also between different societal groups (e.g., conservation professionals, Stewart 2005), is common in situations of predator recovery globally, where research shows people's differing core values, risk perceptions, personal experiences, and social-cultural norms all contribute to the way they view coexisting with predators (reviewed in Pooley et al. 2017). Moreover, our study revealed that this plurality of attitudes is not always visible; while negative ‘otter attitudes’ dominated in Kyuquot/Chekleset community meetings, one-on-one interviews revealed several individuals with neutral or positive perspectives. This is common in regime shift scenarios where public discourse centered on an extreme position can create significant social inertia that makes it harder to explore options for policy and management action (Lynham et al. 2017). Another interesting result was that female Kyuquot/Chekleset respondents tended to have more ‘negative’ attitudes toward otters than males. This aligns with evidence that women are the predominant harvesters of shellfish (Turner 2003) and attribute higher value to shellfish relative to other ecosystem components (Levine et al. 2016). Additionally, both Indigenous communities were highly polarized in their perspectives about sea otter-based tourism. While many different reasons for supporting/opposing otter tourism were cited, several Sugpiaq respondents were concerned that the values of tourists (i.e. otter enthusiasts) would not align with the Sugpiaq value of hunting otters. These disparities in values are common in situations of predator recovery, and it has been argued that the failure to directly address differences in human attitudes, worldviews, and knowledge about predators undermines coexistence (Carter & Linnell 2016).

Conclusion

Navigating predator-induced regime shifts that profoundly affect both ecological and human communities is a substantial challenge globally. These regime shifts disproportionally impact remote Indigenous communities that are reliant on subsistence food sources (Turner & Turner 2008; Lee et al. 2018), constrained in economic opportunities (Langton 2002), and frequently marginalized in natural resource decision-making (Bennett et al. 2018). Based on our empirical data combined with adaptation and social resilience theory, it is evident that enhancing Indigenous coexistence with sea otters will require a transformation in current environmental governance systems that increases local Indigenous authority and enables community-based management grounded in traditional knowledge and practice. Successful examples of where such
transformations have produced multi-level, adaptive governance and Indigenous co-management of marine mammals provide proof that it is possible (Chiropolos 1994; Armitage 2005; FJMC 2013).

On the Pacific coast of Canada, while there are significant barriers to more collaborative sea otter management, there are also growing opportunities to support change (e.g., a federal commitment to reconciliation, new collaborative marine planning initiatives, and the draft Nuu-chah-nulth sea otter management plan). In Alaska, although Alaska Natives enjoy operational access rights to harvest sea otters, there remains a need for strengthened authority through formalized co-management agreements and a renewal of sustained federal engagement and funding. More broadly, our work suggests that a greater awareness of the diversity in values tied to apex predators could help promote relationship building, enhance cross-cultural understanding, and facilitate people learning together more collaboratively. Overall, this work highlights the need for more Indigenous voice, authority and leadership in generating socially just and ecologically sustainable management options to address predator-induced regime shifts within complex and tightly coupled human-ocean systems.

**Authors’ contributions**

J.M.B. A.K.S, and K.B.W. conceived the ideas and all authors designed the methodology; J.M.B and A.K.S led, and all other authors assisted in workshops and data collection; J.M.B analysed the data; J.M.B led the writing of the manuscript with assistance from A.K.S. All authors contributed critically to the drafts and gave final approval for publication.

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This project was a collaborative partnership supported by the Nuu-chah-nulth Council of Ha’wiih, Nuu-chah-nulth Tribal Council, Council for the Haida Nation Hereditary Chiefs Council, Heiltsuk Hemas, Heiltsuk Tribal Council. We are deeply thankful to Wigvihba Wakas H. Humchitt, Hup-in-Yook T. Happynook, and the late Nick Tanape Sr. for their roles and guidance on the steering committee, and also to Tony Hanson, Pat Norman, and John Kvasnikoff for inviting us to their communities. We thank Geetla E. White for his role as a cultural advisor, L. Wood for her coordination, and I.
Herb for his artistic documentation. N.K. Ban, E. Pinkerton, and S. Ibarra provided helpful reviews, D. Okamot o reviewed the statistical models, and L. Nichol, J. Watson, T. Tinker, and E. Rechsteiner shared their insights on sea otter ecology. We thank the Hakai Institute for hosting the first workshop and supporting J.M.B with a graduate fellowship. This research was funded by a Pew Fellowship to A.K.S. and a SFU Community Engagement Grant to J.M.B. and A.K.S.

References


Coulthard, S. (2012). Can we be both resilient and well, and what choices do people have? Incorporating agency into the resilience debate from a fisheries perspective. Ecol. Soc., 17, 4


Chapter 5.

Conclusion

“You can’t manage out of ignorance; you have to know what species do, whom they eat, and what role these prey species play. When you know that, you can begin to make some intelligent decisions.”

(Bob Paine, Seattle Times, 2013)

“We’re facing rapid changes and we’ve been facing rapid changes for some time now. We don’t really know what to expect from it, but we have to prepare ourselves.”

(Harvey Humchitt, Heiltsuk Hereditary Chief, 2014)

The discovery of “keystone species,” “trophic cascades,” and the recognition of “regime shifts” in ecological communities have changed the way we understand ecosystem dynamics. The former two concepts opened our eyes to the fact that strongly-interacting species can have disproportionate effects on the structure and function of ecological communities (Paine 1966, 1980; Ripple et al. 2016). Similar – yet distinct – ecological regime shifts demonstrate how systems can cross ‘tipping points’ and undergo dramatic non-linear change to an alternative state that persists over time due to reinforcing feedbacks (Scheffer et al. 2001; Folke et al. 2004; Hughes et al. 2005). My thesis links these concepts through its focus on a “classic” regime shift on rocky reefs triggered by the recovery of sea otters, a notorious keystone predator, and their cascading effects (Estes & Palmisano 1974). Using scuba surveys, subtidal experiments, quantitative modeling, facilitated workshops, community member interviews, and qualitative analyses, I examined both the ecological dynamics and social-ecological adaptations linked to sea otter-triggered regime shifts taking place along the coast of British Columbia (BC), and drawing some comparisons to south central Alaska. My investigation of the patterns and processes on rocky reefs where sea otters are recovering reveals new insights into the trophic interactions that contribute to the resilience of alternative kelp forest and urchin barren states. My work through a collaborative Indigenous partnership also highlights the factors that enable and constrain coastal Indigenous communities in navigating the changes that sea otters trigger, and shines a light on important issues of Indigenous rights and social justice, currently
underexplored in the context of regime shifts and social-ecological resilience research. As a whole, this thesis highlights the complexities, surprises, and contextual nuances that characterize sea otter recovery in tightly coupled human-ocean systems, and provides the foundations for a road map to improve future human-otter coexistence. I review these ideas in more detail below, beginning with a summary of how my research meets the core objectives I initially outlined (Table 5.1), followed by a discussion of my scholarly contributions framed within two cross-cutting themes that span all three research chapters, and concluding by 'looking ahead' with a summary of how my work might inform ongoing dialogues, research, and management of this complex social-ecological system.

Table 5.1. Summary of research outcomes in relation to initial thesis objectives.

<table>
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<tr>
<th>Domain</th>
<th>Objective</th>
<th>Research Outcomes</th>
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<tr>
<td>Ecosystem</td>
<td>1. How does sea otter recovery influence key trophic interactions that affect reef community structure, function and resilience?</td>
<td>(Ch. 2) I quantified the magnitude and variation in predation rates among an apex predator (sea otters) and mesopredator (<em>Pycnopodia</em>) on sea urchins, and provided data that demonstrate the indirect effects of both predators on kelp forest community structure and resilience. (Ch. 3) I quantified the <em>in situ</em> herbivory rates of a dominant reef grazer (sea urchins) and the factors that alter these rates, which collectively influence the maintenance of alternative forested and deforested reef states.</td>
</tr>
<tr>
<td>Social System</td>
<td>2. What influences coastal Indigenous communities’ ability to adapt to sea otter recovery?</td>
<td>(Ch. 4) I worked with leaders and knowledge holders from 12 Indigenous communities from southern BC to central Alaska to identify 22 social-ecological conditions that influence coastal Indigenous communities’ ability to adapt to sea otter recovery. I identified potential theoretical mechanisms for each of these conditions based on research from adaptive capacity and resilience scholarship. (Ch. 4) Results from my survey-interviews in two Indigenous communities provide in-depth quantitative and qualitative data on how and why people perceived these conditions to influence their ability to adapt to sea otters.</td>
</tr>
<tr>
<td>Management System</td>
<td>3. Identify strategies that might improve Indigenous communities’ capacity to coexist with otters.</td>
<td>(Ch. 4) Four key strategies emerge from my comparative case study as being highly influential in improving Indigenous community’s capacity to coexist with sea otters. I discuss these strategies drawing on examples and research from other marine mammal management systems to highlight the opportunities and challenges associated with shifting current sea otter management to a system that is more adaptive, collaborative, and socially just. * I helped create the Coastal Voices website as a platform for sharing this these Indigenous perspectives, and research outcomes more widely.</td>
</tr>
</tbody>
</table>
Cross-cutting themes and novel contributions

Conferring ecological and social resilience

Resilience in both ecological and social contexts is linked to having system properties that enable key relationships to persist in the face of disturbance (Holling 1996; Adger 2000). In all three of my thesis chapters, my research has identified novel mechanisms that contribute to both ecological and social resilience in the context of sea otter recovery. On nearshore rocky reefs, the resilience of either kelp forests and urchin barrens can be attributed to a combination of feedback mechanisms that act to reinforce a given community configuration. For example, macroalgal dominance in kelp forests is maintained by increased spore production and recruitment (Johnson & Mann 1988; Keats 1991), increased kelp detritus which minimizes urchin grazing on attached stipes (Ebeling et al. 1985; Harrold & Reed 1985), increased biogenic habitat for predators that keep urchin populations suppressed (Steneck et al. 2002; Ling et al. 2015), and kelp whiplashing that physically inhibits urchin grazing (Konar & Estes 2003). In Chapter 2 however, I provided empirical data to support a previously underappreciated mechanism that influences the resilience of kelp forests – size-structured complementary predation on urchins by a sea star mesopredator (*Pycnopodia helianthoides*, hereafter *Pycnopodia*). While the ability of *Pycnopodia* to control sea urchin abundance, and to affect trophic cascades, has been previously recognized on rocky reefs in the absence of other predators (Tegner & Dayton 1981; Duggins 1983; Schultz et al. 2016; Bonaviri et al. 2017), *Pycnopodia*’s unique role in a reef system thought to be mostly controlled by keystone predators remained elusive. On the central coast of BC, this study showed that regime shift dynamics are triggered by the cascading effects of sea otter predators who prefer to consume the largest-sized (≥ 8 cm) red urchins (*Mesocentrotus franciscanus*), and that the presence of *Pycnopodia* plays a key role in controlling the small and medium size-classes of urchins (< 8 cm) (Fig. 5.1a, Burt et al. 2018). We provide an estimate of *Pycnopodia*’s urchin consumption rate relative to sea otters, which is a novel contribution in quantifying the relative predation rates of both a keystone and mesopredator species. What this work illustrates more broadly is the importance of predation on urchins in smaller size classes (or earlier life history stage) as a mechanism to reinforce the resilience of kelp forests. With the exception of one study that highlights how predation by ‘micropredators’ (decapods, crustaceans) may be a potential stabilizing process on rocky reefs in the Mediterranean (Bonaviri et al. 2012), very little
attention has been paid to how less conspicuous predators in kelp forests may be contributing to the mortality of smaller urchin size classes and early recruits, despite the knowledge that this is a critical urchin population bottleneck (Pearse & Hines 1987; Watanabe & Harrold 1991; Scheibling 1996). Given my research showed that the absence of complementary predation by *Pycnopodia* corresponded to increased urchin abundances that destructively grazed kelp, it suggests that future research on predation interactions with smaller urchin size classes would be of great value.

Similar to kelp forests, the resilience of urchin barrens is linked to predation processes. With broad-reaching implications, my research suggests that the presence of *Pycnopodia* on rocky reefs may play a critical role in determining how regime shifts from urchin barrens to kelp forests unfold following the arrival of sea otter predators. Although my data were insufficient to test this hypothesis, they are strongly suggestive that *Pycnopodia* suppression of small and medium urchin size classes within red urchin barrens contributes to these reefs having populations of predominantly large-sized urchins – those most susceptible to predation by sea otters. *Pycnopodia* presence can thus be conceptualized as ‘eroding’ the resilience of an urchin barren state to a sea otter ‘perturbation’, because after otters rapidly remove most large urchins (e.g., Honka 2014), insufficient urchin biomass remains to suppress algal recruitment – and a kelp forest is born. As such, the natural range of *Pycnopodia* may help explain regional differences in the speed of sea otter-triggered regime shifts, whereby rapid barrens-to-kelp transformations occur as sea otters recover in BC and Southeast Alaska (Duggins 1980; Watson & Estes 2011; Burt et al. 2018), compared to relatively slow transitions in the Aleutian Islands where *Pycnopodia* are absent (Estes & Duggins 1995). This is similar to the hypothesis that functional redundancy in urchin predators (e.g., lobsters and wrasse in southern California) is the reason why sea otter recovery in California does not always trigger the same cascading regime shifts as is observed at higher latitudes (Steneck et al. 2002). Overall, these findings underscore the critical importance of trophic interactions and ecological context in conferring the resilience of alternative temperate reef states.

Along with trophic-mediated indirect interactions, sublethal predator-induced effects can influence consumer behaviour which results in indirect effects on the consumer’s prey (Dill et al. 2003; Schmitz et al. 2004, 2014; Wissing et al. 2008). In
Figure 5.1. Trophic- and behaviour-mediated interactions between predators, herbivorous sea urchins, and kelp. (a) Complementary size-structured predation on urchins by sea otters and *Pycnopodia* sea stars lead to indirect positive effects on kelp. Thicker arrows denote stronger direct negative effects (solid arrows) or indirect positive effects (dashed arrows). (b) Urchins exhibit hiding (crypsis) in the presence of predators or a predator-cue (eviscerated conspecifics), which reduces their grazing rate on kelp. More attached kelp increases the production of drift kelp which provides food for urchins, reducing their grazing on attached kelp.

Chapter 3 I provide empirical data that illustrate behaviourally-mediated urchin responses that reduce the intensity of herbivory, which I propose act collectively as mechanisms to confer kelp forest resilience (Fig. 5.1b). In addition to the numerical reduction in urchin biomass (abundance and size) on reefs occupied by urchin predators (Fig. 5.1a), my experiments showed the rate of kelp consumption by urchins is reduced when urchins are cryptic (i.e., hiding in cracks/crevices), exposed to a sea otter predator cue (i.e., eviscerated conspecifics), and when urchins can consume available drift kelp (Fig. 5.1b). While many of these mechanisms have been previously identified in the literature (Nelson & Vance 1979; Ebeling et al. 1985; Harrold & Reed 1985; Spyksma et al. 2017), my findings are a significant contribution because very few studies actually quantify urchin grazing rates associated with these herbivory-influencing factors (Suskiewicz & Johnson 2017), and even fewer quantify kelp consumption rates within field settings (but see Estes & Steinberg 1988). One notable gap which neither Chapter 2 nor 3 explore is the predator-avoidance behaviour of urchins due to *Pycnopodia* (as
shown in Fig. 5.1b). However, a revisualization of my survey data from 2013-2016 is suggestive that higher proportions of urchins were 'exposed' (i.e., possibly emerged from cryptic hiding) following the loss of *Pycnopodia* on reefs due to Wasting Disease (Fig. 5.2). This behaviour change was also hypothesized to contribute to urchin explosions following Wasting Disease in southern BC (Schultz et al. 2016). Taken together, these findings illustrate that sea otter-triggered regime shifts on rocky reefs are initiated and maintained by numerical and behavioural factors acting collectively, and that the complex behavioural changes induced by predators merit further exploration in future experiments and field studies.

![Figure 5.2](image-url)  
*Figure 5.2. Urchin density and behaviour (proportion 'exposed' versus 'cryptic') at subtidal rocky reefs sites (n=11) surveyed before (2013-2014) and after (2015-16) the loss of *Pycnopodia* due to Sea Star Wasting Disease (SSWD).*

Where coastal Indigenous communities are navigating sea otter-triggered changes, my research findings suggest there are ways to enhance social resilience (i.e., the capacity of individuals and the collective community to adapt to changes). In Chapter 4, I worked with Indigenous leaders and knowledge holders from southern BC to central
Alaska to identify 22 social-ecological conditions (see Table 4.1) that influence coastal Indigenous communities’ ability to adapt to sea otter recovery. Importantly, each of these conditions was mapped onto social mechanisms supported by adaptive capacity and resilience theory (Appendix Table B1), connecting their relevance and application more broadly to conditions that build resilience and adaptability across many forms of social-ecological change. The results from the comparative case study in Chapter 4 then highlight which of these social-ecological conditions are most relevant to the Kyuquot-Checkleset First Nations on the west coast of British Columbia and the Sugpiaq Tribes on the Alaska Kenai Peninsula – two Indigenous communities among the first to experience sea otter recovery in the Northeast Pacific. We found that while each community differed in their relative rankings of enabling conditions, there were four key themes perceived as critical to improve community coexistence with otters: (1) strengthen Indigenous governance authority, (2) promote active and adaptive otter management, (3) acquire and integrate Indigenous knowledge, and (4) establish learning platforms. These themes can in turn be treated as strategies to guide future actions toward improving human-otter coexistence. While the strategies 1-3 are challenging and likely require a major shift in current systems of resource management and governance (see Chapter 4 discussion and section below: Navigating toward improved human-otter coexistence), the 4th strategy to establish platforms for learning, communication, and information exchange has already begun as part of this thesis work. This includes the 4-day workshop I helped facilitate in 2014 that brought Indigenous and western science knowledge holders together, and my work with collaborators to establish the Coastal Voices website (www.CoastalVoices.net, Salomon et al. 2018a) and Facebook page (Coastal Voices) to share and amplify Indigenous perspectives on sea otter recovery more widely. Among diverse media and scientific resources, the website includes a ‘Video room’ that hosts short interview clips sharing perspectives from Indigenous leaders, knowledge holders, and scientists on the past, present, and future of sea otter recovery. Efforts should continue building on this initiative, establishing other channels for communication (e.g., committees, workshops, regular meetings, networks, listserves) among communities who are navigating sea otter recovery, and between Indigenous and non-Indigenous researchers, knowledge holders, and resource managers.
Context, complexity, and surprise

While my research provides additional support for the pivotal role of sea otters influencing both ecological and human communities, it also emphasizes the critical importance of context and uncertainty. Following a slew of papers in the 1970-80s documenting the principal role of sea otters in structuring kelp forest communities on rocky reefs, a provocative paper by Foster and Scheil (1988) proposed the following:

“a hierarchical view of kelp forest organization, with sea otters ameliorating the pervasive grazing effects of echinoids, may be appealing in its simplicity, but it has the disadvantage of depreciating the importance of many other factors known to influence the presence of macroalgae and the structure of nearshore communities” (p. 106).

My findings from Chapter 2 speak to this statement, in that they reveal a surprisingly strong indirect effect of a sea star mesopredator on kelp. An important thing this highlights is that rocky reef regime shifts are context dependent; trophic cascades that result in kelp forest collapse or recovery will depend on what predators and urchin species are in the system. For example, on reefs where urchin species don’t reach size escape (e.g., purple and green urchins, S. purpuratus and droebachiensis, respectively) and sea otters are absent, Pycnopodia are shown to be a keystone predator that can trigger a trophic cascade that influences kelp abundance (Schultz et al. 2016; Bonaviri et al. 2017). Presently, the collapse of Pycnopodia across reefs is one of several factors making national news headlines in association with the ongoing explosion of urchin populations and dramatic kelp forest declines (The New York Times 2018). Anomalous marine heatwaves are also part of this reported “perfect storm” (CDFW 2016).

Collaborative work I was part of shows warm temperature anomalies are a driver of Pycnopodia decline from California to Southeast Alaska (Harvell et al. 2019) and other studies show how temperature anomalies have direct negative effects on kelp (Wernberg et al. 2013, 2015; but see Reed et al. 2016). This suggests my research and the above message from Foster and Scheil (1988) may be even more relevant for kelp forest dynamics in the Anthropocene – an era defined by increasing mass mortality events, temperature anomalies, intense storms, along with general climate warming and ocean acidification (Fey et al. 2015; Steffen et al. 2015; Oliver et al. 2018). In the same way that my work shows how discrete alternative states may be weakened following the sudden and unanticipated loss of a key mesopredator (see Figure 2.6), it’s possible that current and future sea otter-triggered regime shifts may unfold in different ways than
they have in the past. For example, a recent study documenting 30 years of sea otter recovery in Washington shows that kelp area trends in the last decade have become decoupled from both sea otters and urchin abundance (Shelton et al. 2018). The title of this paper says it all, remarking how the ecosystem consequences of sea otter reintroduction have shifted “From the predictable to the unexpected.”

Just as context dependency is important in ecological systems, the capacity for individuals or communities to adapt to change must be understood in the context of how cultural values, institutional dynamics, history, and other local nuances influence human-environment relations (Smit & Wandel 2006; Cote & Nightingale 2012). The importance of this is revealed in Chapter 4 which shows how sea otter recovery in the Sugpiaq and Kyuquot/Chécleset communities is occurring within different cultural contexts and involves different federal regulations, management institutions, and ecological timelines. Our findings show that the social-ecological conditions perceived to improve the ability of people to adapt to sea otters in one community, are not necessarily perceived the same way in another. This has implications for the applicability of our research, where it becomes important to recognize that a “one size fits all” approach is unrealistic for enabling adaptation to sea otter recovery. For example, our survey-interviews were limited to the perspectives from two communities and it is certain that if we visited others, different views would be shared. It is also likely that if we revisited communities over time, we would observe shifts in how people perceive their adaptive capacity (e.g., Cinner et al. 2015). Indeed, my Chapter 4 findings show how people’s perceptions of sea otter recovery are subject to shifting baselines (sensu Pauly 1995). Overall this underscores the value of engaging in place-specific collaborative research and policy dialogues (ideally over time), where the pathways to navigate social-ecological regime shifts can be determined through ongoing work with people experiencing change on-the-ground, using methods that align with local and cultural protocols. This social context dependency also highlights that if management or policy changes are made at regional, provincial/state, or national scales, they may not be sensitive to local nuances and be received in the same way across communities or across time.

Different contexts of political agency and social relations of power are also important for understanding how people, groups, and communities are able to adapt to environmental change (McLaughlin & Dietz 2008; Brown & Westaway 2011; Coulthard 2012; Reid et al. 2014; Nayak et al. 2016; Cinner et al. 2018). For example, it has been
globally acknowledged that “Indigenous peoples have suffered from historic injustices as a result of their colonization and dispossession of their lands, territories and resources, thus preventing them from exercising, in particular, their right to development in accordance with their own needs and interests” (UNDRIP: UN 2007). Around the world, failure to recognize this legacy of systematic marginalization has led to conservation and resource management initiatives that have discounted Indigenous knowledge systems or disregarded issues of rights and the equitable use of resources (Davis & Jentoft 2001; Langton 2002; Allison et al. 2012; Brondizio & Tourneau 2016; Mistry & Berardi 2016; Bennett et al. 2018; Salomon et al. 2018b). These issues of social justice and the legitimacy of knowledge systems are relevant as coastal Indigenous communities navigate sea otter recovery in a context where state/provincial and federal agencies make most of the regulations and decisions that dictate sea otter management. Indeed, an important contribution of our collaborative research is that it illuminates how varying degrees of agency and power within Indigenous communities can influence people’s perceptions of sea otters and people’s ability to adapt to the changes they bring. Survey respondents from the Sugpiaq in Alaska who have federally-granted rights to hunt otters, Indigenous-led management institutions (i.e., The Alaska Sea Otter and Sea Lion Commission), and have experienced a longer period over which to adapt to otter recovery were more optimistic about human-otter coexistence compared to the Kyuquot/Chemliset respondents in BC who expressed more negativity and constraints in their ability to play a role in otter management. While the critical function of agency and power in shaping adaptive capacity has been recognized in the context of climate change adaptation (reviewed in Cinner et al. 2018), disaster response (reviewed in Brown & Westaway 2011), shifting fisheries livelihoods (e.g., Coulthard 2012; Bennett et al. 2015) and environmental change more generally (e.g., McLaughlin & Dietz 2008), this remains a research frontier within the literature on regime shifts (Nayak et al. 2016; Nayak & Armitage 2018). Ultimately, our findings indicate that crafting effective management and governance models in response to regime shifts will require careful attention to issues of social justice and Indigenous rights, the distribution of benefits and costs in alternative regimes, divergent and evolving views on ecosystem change, and the degree to which affected communities are involved in decision-making.
Looking ahead: Navigating toward improved human-otter coexistence

In addition to advancing the scholarly literature on regime shifts, my PhD research can be boiled down to three major outcomes that are important for informing future dialogues, planning, and management decisions:

1. Most broadly, my work emphasizes the importance of considering sea otter recovery as a “social-ecological regime shift (SERS)”, defined by Nayak & Armitage (2018) as “abrupt, long-term and significant changes in linked systems of people and nature with uncertain implications for ecosystem services and human wellbeing.” Future plans and decisions need to recognize the fundamental role of humans as active agents in marine food webs and consider how social relations of power and Indigenous rights play a role in ecosystem management.

2. My research reveals previously underappreciated trophic interactions (i.e., complimentary predation by a mesopredator and behaviourally-mediated interactions that influence the strength of herbivory, Fig. 2.6) that contribute to the resilience of alternative kelp forest and urchin barren states. This knowledge helps inform our understanding of regional differences in the way sea otter-triggered regime shifts unfold and should be considered in the development or expansion of rocky reef monitoring programs.

3. My work done in partnership with First Nations and Alaska Tribes highlights several factors that enable and constrain coastal Indigenous communities in navigating regime shifts and identifies four general strategies that can be used as a road map to improve future human-otter coexistence as these predators continue to expand their range. This can help governments and coastal communities shift from ‘reactionary’ to more adaptive and ‘forward thinking’ in their approaches to managing sea otter recovery.
With regard to the latter outcome, there is currently a window of opportunity as the Canadian government is “committed to achieving reconciliation with Indigenous peoples through a renewed, nation-to-nation, government-to-government, and Inuit-Crown relationship based on recognition of rights, respect, co-operation, and partnership as the foundation for transformative change” (Canada Department of Justice 2017). As the findings from Chapter 4 suggest, enhancing Indigenous coexistence with sea otters will indeed require such “transformative change” in current environmental governance to increase local Indigenous authority and enable community-based management models that are grounded in traditional knowledge and western science. This will require the Government of Canada to consider new approaches to sea otter management, such as those proposed in the Nuu-chah-nulth k’ak’atl (sea otter) Management Plan (NCN Tribal Council 2012), that will involve a greater degree of power sharing, joint decision-making, and community involvement. It will also require sustained relationship building and financial support. While the Tribal-led Alaska Sea Otter and Sea Lion Commission (TASSC) has been a successful model to engage Tribes in policy decisions, research, and sea otter stewardship, it has recently collapsed due to diminished funding and political conflicts (Pat Norman, Vice-Chair TASSC, Chief of Port Graham, pers. comm., 2018). This example, along with other cases of marine mammal co-management in the Arctic (reviewed in Armitage et al. 2011) serve as a testament to the fact that navigating new pathways for Indigenous involvement in marine mammal management and governance will not likely be easy. Challenges will include overcoming historically hierarchical relationships and a lack of trust between federal and Indigenous resource management actors and agencies (Ansell & Gash 2007; Armitage et al. 2011; Pinkerton et al. 2014); handling public concerns over animal welfare if sea otter harvest occurs; being aware of livelihood pressures and ongoing market integration in Indigenous communities that can alter motivations and marine mammal harvest incentives (Armitage 2005); building capacity in Indigenous communities to lead local management, enforcement, and monitoring activities (Gutiérrez et al. 2011; Pinkerton et al. 2014); establishing mechanisms for conflict management (Castro & Nielsen 2001); and building new management and governance institutions that are sufficiently stable and yet flexible enough to allow actors to modify practices as needed (e.g., as new information, opportunities, or technologies becomes available, or as institutional learning occurs) (Folke et al. 2005; Armitage et al. 2011). But where there is challenge, there is opportunity. The work from this thesis is part of a growing momentum of research and
dialogue (e.g., www.CoastalVoices.net) that is drawing attention to the ecological and social complexities associated with predator-induced regime shifts. It is also part of a growing chorus of voices calling for change – highlighting the need for more Indigenous engagement, authority, and leadership in generating socially just and ecologically sustainable strategies to address not only sea otter-triggered regime shifts, but issues of marine resource management and conservation more broadly.

References


Coulthard, S. (2012). Can we be both resilient and well, and what choices do people have? Incorporating agency into the resilience debate from a fisheries perspective. Ecol. Soc., 17, 4


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Appendix A.

All supplementary tables, figures, and appendices for Chapter 2
### Table A1. Length-biomass relationships for converting individual sea star lengths (longest diameter across) and urchin test diameters to biomass.

<table>
<thead>
<tr>
<th>Species</th>
<th>Length-biomass relationship</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea stars</td>
<td>yields biomass (g)</td>
<td></td>
</tr>
<tr>
<td><em>Crossaster papposus</em></td>
<td>exp(-2.454)*(length.cm^2.5226)</td>
<td>Vicknair &amp; Estes 2012</td>
</tr>
<tr>
<td><em>Dermasterias imbricata</em></td>
<td>0.045*(length.cm)^2.835</td>
<td>R. Martone, unpublished data</td>
</tr>
<tr>
<td><em>Evasterias troschellii</em></td>
<td>exp(-2.8661)*(length.cm^2.4038)</td>
<td>Vicknair &amp; Estes 2012 (for <em>Evasterias retifera</em>)</td>
</tr>
<tr>
<td><em>Henricia leviuscula</em></td>
<td>0.082*(length.cm^2.159)</td>
<td>R. Martone, unpublished data</td>
</tr>
<tr>
<td><em>Mediaster aequalis</em></td>
<td>0.045*(length.cm)^2.735</td>
<td>Used relationship for <em>Dermasterias</em>, the closest in morphology</td>
</tr>
<tr>
<td><em>Orthasterias koehleri</em></td>
<td>exp(-2.8661)*(length.cm^2.4038)</td>
<td>Used relationship for <em>Evasterias</em>, similar in morphology</td>
</tr>
<tr>
<td><em>Pisaster brevapinus</em></td>
<td>0.002*(length.mm)^2.147</td>
<td>Reed et al. 2016</td>
</tr>
<tr>
<td><em>Pycnopodia helianthoides</em></td>
<td>exp(-3.9989)*length.cm^3.133</td>
<td>Lee et al. 2016</td>
</tr>
<tr>
<td><em>Solaster spp.</em></td>
<td>exp(-3.9989)*length.cm^2.9</td>
<td>Used relationship for <em>Evasterias</em>, the closest in morphology</td>
</tr>
<tr>
<td><em>Stylasterias forreri</em></td>
<td>exp(-2.8661)*(length.cm^2.4038)</td>
<td>Used relationship for <em>Evasterias</em>, similar in morphology</td>
</tr>
<tr>
<td>Sea urchins</td>
<td>yields biomass (g)</td>
<td></td>
</tr>
<tr>
<td><em>S. droebachiensis</em></td>
<td>11.2181*(test.diameter.mm/30)^2.754085</td>
<td>Lochead et al. 2015</td>
</tr>
<tr>
<td><em>M. franciscanus</em></td>
<td>0.0010169*(test.diameter.mm)^2.7787</td>
<td>Lochead et al. 2015</td>
</tr>
<tr>
<td><em>S. purpuratus</em></td>
<td>0.00051*(test.diameter.mm)^2.9035</td>
<td>Oftedal et al. 2007</td>
</tr>
</tbody>
</table>

### References


Table A2. Total count and biomass (kg) for the three urchin species summed across all eleven rocky reef sites on the central coast of BC. The proportion of total urchin count and biomass that is M. franciscanus also given.

<table>
<thead>
<tr>
<th></th>
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<tr>
<td>S. purpuratus</td>
<td>2</td>
<td>0.1</td>
<td>0</td>
<td>0.0</td>
<td>2</td>
<td>0.3</td>
<td>13</td>
<td>0.8</td>
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<td>S. droebachiensis</td>
<td>93</td>
<td>2.6</td>
<td>21</td>
<td>0.8</td>
<td>212</td>
<td>2.0</td>
<td>183</td>
<td>7.2</td>
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<tr>
<td>M. franciscanus</td>
<td>873</td>
<td>189.2</td>
<td>514</td>
<td>113.3</td>
<td>925</td>
<td>150.8</td>
<td>1139</td>
<td>159.0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Proportion</th>
<th>2014</th>
<th>2015</th>
<th>2016</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. franciscanus</td>
<td>90.2%</td>
<td>96.1%</td>
<td>95.2%</td>
</tr>
</tbody>
</table>

**Total average proportion M. franciscanus:** 88.2% (count) 97.9% (biomass)
Figure A3. The decline of *Pycnopodia helianthoides* relative to other sea star species following the onset of sea star wasting disease (SSWD) on the central coast of British Columbia. Species’ biomass for each survey year is averaged over 11 subtidal rocky reef sites in the region. Both plots show the same data, except the bottom plot is graphed on a log scale to reveal variation among species with lower biomass.
Figure A4. Urchin size-frequency histograms for sites grouped by sea otter presence. The dotted lines show the demarcation of our selected urchin size classes, small (<3 cm), medium (4-7 cm), and large (> 8 cm). The smoothed curves show the kernel density estimate, using a Gaussian kernel with bandwidth equal to the standard deviation.
Table A5. Descriptions and specification for all elements within the state-space model.

<table>
<thead>
<tr>
<th>Model Element</th>
<th>Description</th>
<th>Specified by</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Parameters Estimated by the Model</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\alpha_{o,i}$</td>
<td>Size-specific sea otter predation effect: The additive increase in instantaneous mortality rate of size class $i$ associated with the presence of sea otters</td>
<td>Uniform(0.0001, 5)</td>
</tr>
<tr>
<td>$\alpha_{p,i}$</td>
<td>Size-specific $Pycnopodia$ predation effect: The additive increase in instantaneous mortality rate of size class $i$ associated with a unit increase in $Pycnopodia$ biomass</td>
<td>Uniform(0.0001, 5)</td>
</tr>
<tr>
<td>$\delta_1$</td>
<td>Mean baseline mortality parameter for small urchins ($i=1$) across sites (due to sources other than predation by sea otters or $Pycnopodia$)</td>
<td>Uniform(0.0001, 10)</td>
</tr>
<tr>
<td>$\beta_i$</td>
<td>Size-specific mortality adjustment parameter: scales baseline mortality rates (mortality from sources other than predation by sea otters or $Pycnopodia$) for medium ($i=2$) and large ($i=3$) urchin relative to small ($i=1$) urchins</td>
<td>Beta(1, 2)</td>
</tr>
<tr>
<td>$\sigma_\delta$</td>
<td>Spatial variation in baseline urchin mortality (standard deviation across sites) for small urchins due to site-specific conditions or habitat</td>
<td>Uniform(0.001, 10)</td>
</tr>
<tr>
<td>$\sigma_\varepsilon$</td>
<td>Temporal variation in urchin mortality due to environmental stochasticity (standard deviation across years)</td>
<td>Uniform(0.001, 10)</td>
</tr>
<tr>
<td>$\theta$</td>
<td>Observability parameter, describing the probability of detecting small urchins (1-3 cm) in surveys (“nuisance parameter”)</td>
<td>Beta(1.5, 1.5)</td>
</tr>
<tr>
<td>$r$</td>
<td>Overdispersion parameter for the negative binomial distribution describing observation error in urchin counts at a site</td>
<td>Gamma(1.1, 0.1)</td>
</tr>
<tr>
<td><strong>Varies by Site</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\delta_{1,j}$</td>
<td>Site-specific baseline mortality parameter for small urchins, $i=1$ (mortality due to sources other than predation by otters or $Pycnopodia$). Prior informed by hyperparameter $\sigma_\delta$</td>
<td>Normal($\delta_1$, $\sigma_\delta^2$)</td>
</tr>
<tr>
<td><strong>Varies Across Years</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R_t$</td>
<td>Annual regional “effective” recruitment (urchins recruiting to the 1cm size class) in years $t=1$-$4$. Weakly informed prior results in a range of possible values between 1-20 (mean $\approx$ 5) recruits/m$^2$/year, as informed by reported empirical recruitment data from BC (Sloan et al. 1987, Atkins et al. 2006, Zhang et al. 2011)</td>
<td>Lognormal(1.4, 0.67)</td>
</tr>
<tr>
<td><strong>Varies Across Sites and Years</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\varepsilon_{i,j,t}$</td>
<td>Error in urchin mortality due to annual environmental stochasticity for size class $i$, at site $j$, in year $t$. Prior informed by hyperparameter $\sigma_\varepsilon$</td>
<td>Normal(0, $\sigma_\varepsilon^2$)</td>
</tr>
<tr>
<td><strong>Specified Parameters</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$G_i$</td>
<td>Size class transition probabilities give the proportion of urchins transitioning from size class small to medium ($G_1$) or from medium to large ($G_2$)</td>
<td>$G_1 = 0.52$, $G_2 = 0.09$ Estimated via simulations using urchin growth model (see Appendix A6)</td>
</tr>
<tr>
<td><strong>Variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$C_{i,j,k}$</td>
<td>Density of urchins in size class $i$, at site $j$, in year $t$, in quadrat $k$ (where urchins in $N_{i=1} = 1$-$3$ cm, $N_{i=2} = 4$-$7$ cm, and $N_{i=3} \geq 8$ cm)</td>
<td>Number per 1m$^2$ quadrat</td>
</tr>
<tr>
<td>$O_{j,t}$</td>
<td>Sea otter presence ($O = 1$) or absence ($O = 0$) at a given site $j$ and year $t$</td>
<td>Recorded sea otter presence</td>
</tr>
<tr>
<td>$P_{j,t}$</td>
<td>Biomass of $Pycnopodia$ at a given site $j$ and year $t$</td>
<td>kg per 10m$^2$ survey area</td>
</tr>
</tbody>
</table>
References


Appendix A6. Methods and the associated outputs for the analysis of size class transition probabilities using the Zhang et al. 2008 growth model.

To model transitions between urchin size classes we required estimates of size-specific growth rates, which we obtained from a recently published red urchin growth model from British Columbia (Zhang et al. 2008). In summary, we converted the growth function into stage-specific transition probabilities using a simulation model that tracked the growth of individual urchins drawn randomly from our empirically derived size distribution (combined for all sites, all years), calculated annual growth according to the published model (including stochasticity), and then computed transition probabilities as the proportion of individuals from size class $i$ that transitioned to size class $i + 1$ after one year. See equations and graphs below.

Zhang et al. (2008) use a Tanaka growth function within a Bayesian framework to model the growth of red sea urchins *Mesocentrotus franciscanus* ($D$) based on tag-recapture data and abundance surveys conducted in four locations on the coast of British Columbia:

$$D_{t+1} = \frac{1}{\sqrt{f}} \log \left( \left[ 2f \left( \frac{E}{4f} - \frac{a}{E} + 1 \right) + 2 \sqrt{f^2 \left( \frac{E}{4f} - \frac{a}{E} + 1 \right) + f \ast a} \right] + d + \epsilon \right)$$

$$E = \exp \left( \sqrt{f \left( D_t - d \right)} \right)$$

where $\epsilon$ is a normal variate $\epsilon \sim N(0, \sigma^2)$, and with other area-specific parameters defined as follows (we chose the Price Island area closest to our survey region):

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Area where data derived</th>
<th>Mean parameter estimate from Zhang et al. 2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>Price Island</td>
<td>0.00539</td>
</tr>
<tr>
<td>$d$</td>
<td>Price Island</td>
<td>118.2</td>
</tr>
<tr>
<td>$f$</td>
<td>Price Island</td>
<td>0.00342</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Price Island</td>
<td>1.21</td>
</tr>
</tbody>
</table>

We used above equations and parameter values to simulate one year of growth for 5000 individual urchins (Figure A6.1a), where the initial size of urchins were drawn randomly from our empirically-derived size distribution (we combined data from all sites, all years). We then used these simulated growth trajectories to calculate stage-specific
“growth transition probabilities” ($G_i$). Specifically, we computed the proportion of individuals that began the year in the “small” size class (1-3 cm) and transitioned to the “medium” size class (4-7 cm) by the end of the year ($G_1$), and the proportion of individuals that began the year in the “medium” size class and transitioned to the “large” size class ($\geq 8$ cm) by the end of the year ($G_2$). To quantify uncertainty, we bootstrapped the above analyses 1000 times and plotted the distribution of estimated growth transition values (Figure A6.1b). We used the median values of growth transitions ($G_1=0.52$ and $G_2=0.09$) to parameterize our urchin population model.

![Figure A6.1](image.png)

**Figure A6.** (A) Simulated growth increment over one year for all individual urchins measured over the course of our four years of dive surveys. The blue line is a fitted smoothing spline. (B) Estimated growth transition probabilities are shown as the proportion of urchins that transition from the small to medium size class (left) and medium to large size class (right). Box plots show the median value with the interquartile range, with whiskers showing the distance to the furthest values.
Appendix A7. Bayesian model diagnostics and outputs, including information on posterior distribution sampling (below), prior-posterior comparisons and trace plots (Fig. A7.1), posterior predictive checks (Fig. A7.2), and output parameter estimates with Gelman-Rubin diagnostics (Table A7.3).

Posterior Distribution Sampling

Our model was run using JAGS 4.3.0 (Plummer 2017) and the runjags package in R (Denwood 2016). To obtain posterior distributions we allowed the model to burn-in for 2000 samples, then saved every 5th sample to total 1000 samples from the posterior distribution for each of 25 chains, for a total of 25,000 replicates.

References


Figure A7.1  Posterior distributions (grey histograms), prior distributions (black lines), and trace plots (in colour) for parameters in the Bayesian state-space model.
Figure A7.2 Posterior predictive checks illustrating observed vs expected test-statistics for model assumptions and fit (Gelman et al. 2014). X-axes show the observed values, which are a single realization from the model posterior, and y-axes show expected values, which are a random draw from the model posterior prediction. Metrics include (a) $\chi^2$ goodness of fit-test statistics, (b) Kolmogorov-Smirnov test statistics checking adequacy of the negative binomial likelihood function, and (c) Pearson rank correlation testing for correlation between residuals and predicted values. Dramatic departures from the 1:1 line illustrate more or less extreme values than assumed under the model structure and parameterization. P-values are proportions of observe test-statistic values more extreme than expected.

References

Table A7.3  Model-estimated values and associated statistics for fitted parameters. The mean, standard deviation (sd), and 95% credible interval (CI) are given for each parameter (refer to Appendix Table A5 for full parameter descriptions). Potential scale reduction factor (psrf) of the Gelman-Rubin statistic estimates the potential decrease in the between-chains variability with respect to the within-chain variability. A psrf < 1.1 indicates convergence was reached (Brooks and Gelman 1997).

<table>
<thead>
<tr>
<th>Model Params.</th>
<th>Short form description</th>
<th>Mean</th>
<th>sd</th>
<th>95% CI</th>
<th>psrf</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_{o,2}$</td>
<td>Medium urchin instantaneous mortality rate (otters)</td>
<td>0.53</td>
<td>0.30</td>
<td>0.067 : 1.23</td>
<td>1.01</td>
</tr>
<tr>
<td>$\alpha_{o,3}$</td>
<td>Large urchin instantaneous mortality rate (otters)</td>
<td>1.46</td>
<td>0.54</td>
<td>0.75 : 2.82</td>
<td>1.00</td>
</tr>
<tr>
<td>$\alpha_{p,1}$</td>
<td>Small urchin instantaneous mortality rate ($Pycnopodia$)</td>
<td>0.83</td>
<td>0.68</td>
<td>0.035 : 2.52</td>
<td>1.01</td>
</tr>
<tr>
<td>$\alpha_{p,2}$</td>
<td>Medium urchin instantaneous mortality rate ($Pycnopodia$)</td>
<td>1.27</td>
<td>0.60</td>
<td>0.32 : 2.66</td>
<td>1.01</td>
</tr>
<tr>
<td>$\alpha_{p,3}$</td>
<td>Large urchin instantaneous mortality rate ($Pycnopodia$)</td>
<td>0.070</td>
<td>0.037</td>
<td>0.0097 : 0.16</td>
<td>1.00</td>
</tr>
<tr>
<td>$\delta_1$</td>
<td>Mean (across sites) baseline mortality for small urchins</td>
<td>1.09</td>
<td>0.71</td>
<td>0.065 : 2.72</td>
<td>1.01</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>Adjustment of baseline mortality (medium urchins)</td>
<td>0.21</td>
<td>0.18</td>
<td>0.00 : 0.59</td>
<td>1.01</td>
</tr>
<tr>
<td>$\beta_3$</td>
<td>Adjustment of baseline mortality (large urchins)</td>
<td>0.020</td>
<td>0.02</td>
<td>0.00 : 0.064</td>
<td>1.00</td>
</tr>
<tr>
<td>$\sigma_6$</td>
<td>Variation in baseline mortality (across sites)</td>
<td>0.65</td>
<td>0.35</td>
<td>0.090 : 1.36</td>
<td>1.01</td>
</tr>
<tr>
<td>$\sigma_x$</td>
<td>Variation in baseline mortality (across years)</td>
<td>1.15</td>
<td>0.17</td>
<td>0.83 : 1.48</td>
<td>1.00</td>
</tr>
<tr>
<td>$\varphi$</td>
<td>Probability of observing small urchins</td>
<td>0.20</td>
<td>0.041</td>
<td>0.13 : 0.28</td>
<td>1.00</td>
</tr>
<tr>
<td>$r$</td>
<td>Dispersion parameter for negative binomial</td>
<td>0.42</td>
<td>0.026</td>
<td>0.37 : 0.47</td>
<td>1.00</td>
</tr>
<tr>
<td>$R$</td>
<td>Mean (across years) urchin recruitment</td>
<td>7.71</td>
<td>1.98</td>
<td>4.27 : 11.60</td>
<td>1.01</td>
</tr>
</tbody>
</table>

* These parameter estimates have undergone a bias correction to account for the fact that the mean of the lognormal process error with sd $\sigma^2_x$ is not zero but $\exp(\sigma^2_x/2)$ (see model equations in main text). In practice the model is not estimated with this bias correction, so it is conducted following estimation. The adjusted means, sd, and CIs were calculated after multiplying each iteration in the posterior by $\exp(\sigma^2_x/2)$.

References

Appendix A8. Examining model performance by comparing model-simulated and observed mean urchin densities. Methods overview and outputs.

Methods overview

We ran iterated simulations using our population model over the four-year study period starting with the mean values for size-specific urchin counts in 2013 (at sites without sea otters). Using parameter estimates drawn from posterior distributions, we iterated simulations of urchin dynamics using equations (1) to (3) in the main text (but without site variation in baseline mortality or environmental stochasticity) to project the abundance of urchins in each size class through time under four scenarios varying in “predator status”: 1) Both predators absent; 2) Pycnopodia present but otters absent; 3) Otters present but Pycnopodia absent; and 4) Both predators present. We then compared these estimated size-specific mean urchin densities with the observed mean urchin density at site/year combinations corresponding to each predator status category (Fig. A8.1 below).
Figure A8.1 Comparison of model-simulated and observed mean urchin densities. a) Estimated size-specific mean urchin densities (± 90% credible interval) for comparison with the, b) Observed mean urchin densities (± s.e.) at site/year combinations corresponding to each predator status category, and c) A table summarizing the mean values in panels a) and b).
Appendix A9. Methods for generating, processing, and classifying aerial kelp canopy imagery.

Obtaining aerial imagery prior to sea otter arrival

We opportunistically obtained aerial imagery for two years (2006 and 2012) prior to the arrival of sea otters in the Northwest Calvert Island region in 2013 captured from the British Columbia air photo archives in 2006 (www2.gov.bc.ca/gov/content/data/about-data-management/geobc) and a terrestrial lidar survey which included nearshore waters in 2012 commissioned by the Hakai Institute (details and metadata available at https://hecate.hakai.org/).

Because the 2006 and 2012 images were captured at higher tide heights compared to the 2014, 2015, 2016 images generated in our aerial surveys (where all tides < +1.0 m), we applied a correction factor to compensate for tide-related underestimates of kelp canopy extent prior to sea otter arrival. Data to calculate the correction factor was generated in 2015: We selected a 20 hectare sub-sample within the study region that contained a mix of high and low density kelp beds of variable sizes and used drones to generate aerial imagery (see methods below) captured at three tide heights: 0.25 m, 2.5 m, and 3.0 m. We performed a simple linear regression using the total area of kelp cover (m²) observed at these three tide heights (Fig. A9.1). With this relationship, we calculated the percent reduction in canopy kelp area between the imagery tide heights and a +0.25 m tide height (23% reduced at a 2.5 m tide in 2006, 16% reduced at a 1.8 m tide in 2012). We then multiplied the extent of all kelp beds from the 2006 and 2012 by the equivalent correction factors, 1.23 and 1.16, respectively.

![Figure A9.1](image-url)  
**Figure A9.1** Linear regression of tide height vs. extent of kelp canopy cover.
Annual aerial surveys post sea otter arrival

Starting in 2014, we conducted annual aerial surveys of the surface canopy kelp in the Northwest Calvert Island region. In 2014, 2015, and 2016, the aerial surveys were conducted in the first low tide sequence in August, which is within the seasonal time period (August – October) that corresponds to maximum canopy extent in British Columbia. All imagery capture occurred during low tide cycles at tide heights below +1.0 m and during periods where environmental conditions were favorable: calm seas (sea state less than 1.5 m swell), clear visibility (no fog or low-lying cloud), and low winds (less than 15 knots).

In 2014, we obtained kelp canopy imagery taken from a helicopter using a Canon EOS MarkII camera with a Canon EF 16-35mm f/2.8L II USM lens. The images were taken at 800 m altitude over a period of 25 minutes. We then processed the images into a mosaic using the program Autostitch v.2.2 (http://matthewalunbrown.com/autostitch/autostitch.html). After stitching was complete the mosaic was georeferenced in ARC GIS 10.0 to the 2012 reference imagery using a spline transformation.

In 2015 and 2016, we conducted aerial kelp canopy surveys using DJI Phantom 3 professional Unmanned Aerial Vehicles (UAVs or drones) equipped with a commercial grade 12 megapixel 4k f 2.8 lens RGB camera to capture imagery. We conducted a continuous series of UAV flights from a small research vessel moving in a pre-planned grid formation through the study region and operated the UAV and camera using the DJI Capture software application connected to a tablet. Flights ranged from 12 – 17 minutes at a flight level of approximately 200-250 m (results in images 8-12 cm in spatial resolution), which allowed an area of 1.5 x 1.5 km to be covered in one flight. We captured adjacent images with a minimum overlap of 85% to ensure sufficient coverage and to give us the flexibility to select out images of poor quality.

Imagery processing

We gathered and stored the UAV images with relevant field condition metadata (date, time, location, pilot, weather, tide, flight elevation, grid size, UAV application used, notes). We used Pix4D image processing software to mosaic and project the UAV images into a .tiff file format. Within Pix4D, we selected the images to produce a full image report which we checked to ensure no gaps or major errors were transferred to
the final map product. Finally, we digitally stamped the fully processed image mosaic with the time, compass bearing, and GPS location and loaded it into ARC GIS 10.2 for georeferencing. For all the survey image mosaics produced, we used the 2012 orthophoto imagery at 25 cm spatial resolution as the georeference. The 2012 imagery was validated with a survey grade GPS to ensure that all images georeferenced to it achieved a sub meter accuracy.

**Manual classification of kelp beds:**

We loaded the time series of aerial images into ARC GIS 10.2 and manually classified the kelp extents. Classification resulted in a shapefile layer (.shp) of kelp bed polygons with a number of associated attributes: species (*M. pyrifera* or *N. luetkeana*), bed area (m$^2$), mapper name, mapper confidence (high, medium, low), and bed density (high or low). We applied the following decision rules during the mapping process: 1) Individual kelp beds are delineated areas of consistent kelp density: either ‘high density’ (≥10 plants per 10m$^2$) or ‘low density’ (< 10 plants/fronds per 10m$^2$) based on the BC Province’s Kelp Inventory Method (Foreman 1975), 2) A “kelp bed” consists of at least three adjacent plants/fronds, and 3) Individual kelp beds are considered distinct if they are separated by a gap larger than 5 m whereas kelp plants or patches within 5 m of each other are considered part of the same bed. Following initial kelp bed classification, the final classified polygon layers were quality control checked by the same individual who utilized field notes and corresponding high-resolution imagery confirm kelp beds classified with ‘low confidence’.

**References**

Figure A10. Images of field observations (all photos except A-B by Jenn Burt). A) The raft of sea otters that arrived and foraged at three previously unoccupied rocky reef sites in 2013 (photo: Grant Callegari), B) Sea otter eating a large red sea urchin (photo: Erin Rechsteiner), C) Piles of discarded red urchin tests accumulated at a rocky reef site following sea otter arrival, D-E) Large Pycnopodia at rocky reef sites before SSWD, F) Pycnopodia from photo “D” eating a medium-sized red urchin, G-H) Survey quadrats at sea otter-occupied sites, I-J) Survey quadrats at sites not occupied by sea otters, K) Kelp forest site following the onset of SSWD and an increased abundance of medium urchins (white arrows show locations of medium urchins, which are difficult to see in the image), L) Medium urchins grazing kelp (Pterygophora californica) at a site occupied by sea otters.
Figure A11. (a) Aerial surveys for canopy kelp were conducted in three mapping blocks within the region of Northwest Calvert Island where sea otters returned in 2013 (refer to Figure 2.1 for overall map). Red triangles show the location two subtidal survey sites. (b) Changes in the spatial extent of canopy kelp within one mapping block (2 km$^2$) and red circles show the location and approximate size of one rocky reef survey site (~180 m$^2$).
Figure A12. Sea surface temperature at the Egg Island Lighthouse Station (51.25°-127.833° Lat/Long) located on the outer coast just south of this study’s rocky reef survey sites. The blue line shows the monthly average (±SD) sea surface temperature during the study period (2013-2016) and the black line shows the historical mean temperature (monthly average between 1970-2016). Arrows depict the start (S) and dissipation (D) of an anomalous marine heatwave affected the study region between Oct. 2015 and summer 2016 (Hunt et al. 2016). These data are available on-line from Fisheries and Oceans Canada (http://open.canada.ca/data/en/dataset/719955f2-bf8e-44f7-bc26-6bd623e82884, accessed Dec. 20, 2017).
Appendix B.

All supplementary tables, figures, and appendices for Chapter 3
Table B1. Theoretical foundations linked to 22 social-ecological conditions identified to influence community’s ability to sea otter recovery. A theoretical rationale for how each condition (within seven themes) might influence a community’s adaptive capacity or resilience is provided with the supporting literature. The assumed direction of influence in our study (increase or decrease ability to adapt) for each condition is provided, recognizing that in many cases there are examples of where the opposing direction is possible.

<table>
<thead>
<tr>
<th>Theme</th>
<th>Condition</th>
<th>Theoretical Rationale (and assumed direction)</th>
<th>Supporting Literature</th>
<th>Survey Question</th>
</tr>
</thead>
<tbody>
<tr>
<td>Management</td>
<td>Incorporating Indigenous Knowledge</td>
<td>Efforts to mobilize, make use of, and connect different knowledge systems can generate new insights, understandings, and innovations to manage complex adaptive systems and deal with uncertainty.</td>
<td>(Berkes et al. 2000; Folke et al. 2003, 2005; Lebel et al. 2006; Armitage et al. 2011; Tengo et al. 2014)</td>
<td>Would including traditional knowledge, local knowledge, and stewardship protocols into management of sea otter, shellfish, and kelp affect your ability to adapt to sea otters in your territory?</td>
</tr>
<tr>
<td>Management</td>
<td>Local Management Plan</td>
<td>Local-level management can capitalize on place-based knowledge (traditional and local) and context-specific system understanding (ecological and social) and may benefit from higher levels of monitoring and compliance.</td>
<td>(Wilson et al. 1994; Folke et al. 2003; Ostrom 2009; Biggs et al. 2012)</td>
<td>Would implementing a [local] management plan for sea otter, shellfish and kelp affect your ability to adapt to sea otters in your territory?</td>
</tr>
<tr>
<td>Governance</td>
<td>More Local Indigenous Authority</td>
<td>Adaptive governance involves power sharing and the devolution of management rights to promote increased local-level participation and greater local agency to make decisions and actively respond to change.</td>
<td>(Wilson et al. 1994; Allison &amp; Ellis 2001; Berkes &amp; Jolly 2001; Folke et al. 2005; Hughes et al. 2005; Stringer et al. 2006; Biggs et al. 2012)</td>
<td>Would having Indigenous authority in marine resource decision making affect your community’s ability to adapt to sea otters in your territory?</td>
</tr>
<tr>
<td>Governance</td>
<td>Community Leadership</td>
<td>Effective leaders build trust, manage conflict, link actors, compile and communicate knowledge, and mobilize support for management initiatives and self-organization.</td>
<td>(Folke et al. 2005; Lebel et al. 2006; Olsson et al. 2006; Ostrom 2009; Westley et al. 2013)</td>
<td>Does community leadership affect your ability to adapt to sea otters in your territory?</td>
</tr>
<tr>
<td>Governance</td>
<td>Trust/Respect Across Governments</td>
<td>Relationships of trust and respect help build vertical linkages between local actors/organizations and state governments and promote cooperation, perceived legitimacy, tighter feedback loops, and novel institutional arrangements to respond to changing conditions.</td>
<td>(Adger 2003a, b; Lebel et al. 2006; Cinner et al. 2009b; Armitage et al. 2011)</td>
<td>Would an increased level of trust and respect between First Nations and Federal marine resource governing institutions affect your community’s ability to adapt to sea otters in your territory?</td>
</tr>
<tr>
<td>Governance</td>
<td>Federal Regulations</td>
<td>Centralized authorities establish the top-down regulatory context in which communities operate, enabling (↑) or constraining (↓) their agency and scope for management decision-making and action in times of change.</td>
<td>(Folke et al. 2005; Gelcich et al. 2006; Marin &amp; Berkes 2010; Biggs et al. 2012)</td>
<td>Do the current federal regulations on hunting sea otters affect your ability to adapt to sea otters in your territory?</td>
</tr>
<tr>
<td>Table Heading</td>
<td>Description</td>
<td>References</td>
<td>Implications</td>
<td></td>
</tr>
<tr>
<td>---------------</td>
<td>-------------</td>
<td>------------</td>
<td>--------------</td>
<td></td>
</tr>
<tr>
<td>More Traditional Knowledge</td>
<td>Intricate interactions between local peoples and their environments (over millennia) has resulted in detailed knowledge and place-based stewardship practices that enable continual adaptation to social-ecological changes.</td>
<td>(Berkes et al. 2001; Berkes &amp; Jolly 2001; Turner &amp; Clifton 2009; Fernández-Llamazares et al. 2015)</td>
<td>Would greater knowledge of the traditional use and stewardship of sea otters, shellfish and kelp affect your ability to adapt to sea otters in your territory?</td>
<td></td>
</tr>
<tr>
<td>Learning from Other Communities</td>
<td>Learning from other’s experiences, successes, mistakes and innovations linked to navigating change/shocks can reduce social uncertainties and enable communities to better plan and prepare.</td>
<td>(Folke et al. 2003, 2005; Olsson et al. 2004; Lebel et al. 2006; Geleij et al. 2010)</td>
<td>Would learning from other communities who are adapting to sea otters affect your ability to adapt to sea otters in your territory?</td>
<td></td>
</tr>
<tr>
<td>Monitoring Information</td>
<td>Ecological monitoring can enhance communities’ system knowledge, provide information for adaptive management, and help detect early signals of environmental change – allowing for preparation or preventative actions.</td>
<td>(Berkes &amp; Jolly 2001; Danielsen et al. 2005; Lebel et al. 2006)</td>
<td>Does having monitoring information on sea otter numbers, locations and their effects in your territory affect your ability to adapt to sea otters in your territory?</td>
<td></td>
</tr>
<tr>
<td>Within Community (Bonding Social Networks)</td>
<td>Social relationships are strengthened through social interactions, kinship ties, and community groups, which enhances communities’ communication and capacity to organize, act collectively and cope with adversity in times of change.</td>
<td>(Allison &amp; Ellis 2001; Adger 2003a, b; Folke et al. 2005; Marschke &amp; Berkes 2006; Cinner et al. 2009a; Ostrom 2009)</td>
<td>Does having community events and other social exchanges (e.g., gatherings, Elders groups, Facebook groups) affect your ability to adapt to sea otters in your territory?</td>
<td></td>
</tr>
<tr>
<td>Between Communities (Bridging Social Networks)</td>
<td>Networks of reciprocity and exchange are important for obtaining access to resources, which enhances security and may provide some insurance in times of scarcity or disturbance.</td>
<td>(Biggs et al. 2012; Westley et al. 2013; Bennett et al. 2014)</td>
<td>Does the ability to exchange shellfish and fish within and between communities affect your ability to adapt to sea otters in your territory?</td>
<td></td>
</tr>
<tr>
<td>Willingness to Embrace Change</td>
<td>Determination, perseverance, having a positive outlook or the ability to 'bounce back' from adversity can promote individual and community resilience and strengthen social cohesion to support collective action.</td>
<td>(Marshall &amp; Marshall 2007; Hegney et al. 2008; Buikstra et al. 2010; Berkes &amp; Ross 2013)</td>
<td>Does having a positive attitude towards change affect your ability to adapt to sea otters in your territory?</td>
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<tr>
<td>Experience from Other Changes</td>
<td>Actors/communities that are experienced in navigating change may have better capacity to plan, learn and reorganize in new situations and develop a greater openness to change and adapting.</td>
<td>(Folke et al. 2003; Fazey et al. 2007; Marshall &amp; Marshall 2007)</td>
<td>If your community has experience planning and responding to other changes (e.g., social, political, environmental changes), does this affect your ability to adapt to sea otters in your territory?</td>
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<tr>
<td>Novel Livelihood Opportunities (Tourism Jobs)</td>
<td>The emergence of new occupational sectors provides alternative livelihood opportunities that can reduce sensitivity to rapid change affecting traditional livelihoods.</td>
<td>(Mcclanahan et al. 2008; Badjeck et al. 2010; Cinner et al. 2012a)</td>
<td>If sea otters create tourism opportunities for your community, would this affect your ability to adapt to sea otters in your territory?</td>
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<tr>
<td>Employment Options in the Community</td>
<td>Having diverse employment options provides the capacity to pursue alternative livelihood opportunities during times of uncertainty, changing social-ecological conditions, or due to resource seasonality.</td>
<td>(Marschke &amp; Berkes 2006; Cinner et al. 2009a; Badjeck et al. 2010; Cinner et al. 2011; Blythe et al. 2014)</td>
<td>Would having a variety of alternative employment opportunities in the community affect your ability to adapt to sea otters in your territory?</td>
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<td>Individual Occupational Mobility</td>
<td>Individuals who are more able/willing to change occupations (i.e. diverse skills, lower attachment, open to change, etc.) have higher adaptive capacity when faced with changes that influence livelihoods.</td>
<td>(Allison &amp; Ellis 2001; Cinner et al. 2009a, c, 2011; Badjeck et al. 2010)</td>
<td>Would being able to change jobs affect your ability to adapt to sea otters in your territory?</td>
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<td>Household Occupational Multiplicity</td>
<td>Multiple household income sources help enhance flexibility and income security during times of uncertainty, changing social-ecological conditions, or due to resource seasonality.</td>
<td>(Allison &amp; Ellis 2001; Cinner et al. 2009a, c; Badjeck et al. 2010)</td>
<td>How would having more sources of income (i.e. a variety of jobs) in your household affect your ability to adapt to sea otters in your territory?</td>
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<tr>
<td>Access to Financial Support</td>
<td>Having access to financial assets during times of change or sudden shocks can help individuals and households cope with and manage adversity.</td>
<td>(Allison &amp; Ellis 2001; Marschke &amp; Berkes 2006; Badjeck et al. 2010; Blythe et al. 2014)</td>
<td>Would having access to financial support, such as loan from the bank or another source, affect your ability to adapt to sea otters in your territory?</td>
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<tr>
<td>Ecosystem Resilience</td>
<td>Redundancy of, and connectivity between habitat patches (harvest areas) in the larger seascape can provide “insurance” for resource provisioning the face of disturbance and system changes.</td>
<td>(Elmqvist et al. 2003; Folke et al. 2004; Biggs et al. 2012)</td>
<td>If there were other locations where community members could go to harvest abundant shellfish (such as urchins, abalone, clams, cockles, crabs), would this affect your ability to adapt to sea otters in your territory?</td>
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<tr>
<td>Redundancy of Harvest Sites</td>
<td>Regime shifts in ecological systems will cause an increase in certain system elements (e.g., kelp), which may provide new ecosystem services (e.g., habitat for fish), while other system elements will decrease and remove ecosystem services.</td>
<td>(Steneck et al. 2002; Folke et al. 2004; Hughes et al. 2005)</td>
<td>If sea otters caused more kelp, and thus more fish habitat in your territory, would this affect your ability to adapt to sea otters in your territory?</td>
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<tr>
<td>More Kelp Habitat Created (system trade-offs)</td>
<td>Additional large-scale drivers of change can interact with, and exacerbate changes already being experienced by communities, reducing the capacity to adapt.</td>
<td>(Perry et al. 2010; Biggs et al. 2012; Bennett et al. 2016; Kaplan-Hallam et al. 2017)</td>
<td>Does climate change (e.g., warming ocean temperatures and ocean acidification) affect your ability to adapt to sea otters in your territory?</td>
<td></td>
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</tbody>
</table>

**References**


Cinner, J.E., Folke, C., Daw, T. & Hicks, C.C. (2011). Responding to change : Using scenarios to understand how socioeconomic factors may influence amplifying or dampening exploitation feedbacks among Tanzanian fishers. Glob. Environ. Chang., 21, 7–12


### Table B2

**Key quotes from coastal Indigenous peoples in reference to social-ecological conditions that influence adaptation to sea otter recovery.** Quotes in the left column were obtained from the workshop (“Visioning the Future of Kelp Forest, Sea Otter & Human Interactions”) with Chiefs and knowledge holders from 12 Indigenous communities in British Columbia and Alaska. Quotes on the right were obtained from qualitative responses recorded during one-on-one survey-interviews with members of the Kyuquot/Chekleset First Nations (British Columbia) and the Sugpiaq Tribes of Port Graham and Nanwalek (Alaska). The quote attribution (if permission given) lists the English name, and Indigenous Nation/Tribe.

<table>
<thead>
<tr>
<th>Condition that Influences Adaptation</th>
<th>Quotes from Coastal Indigenous Leaders and Knowledge Holders from BC and Alaska</th>
<th>Quotes from Survey Responses in the Sugpiaq and Kyuquot/Chekleset communities</th>
</tr>
</thead>
</table>
| **Incorporating Traditional Knowledge Integration in Species and Ecosystem Management** | • “I think it’s important that we combine traditional knowledge and scientific knowledge. It gives us a better understanding of what we can prepare for.” (Harvey Humchitt, Heiltsuk)  
• “It is important that our ancient management knowledge come forth in current practice because our people live there. Connection to place is needed to effectively manage.” (Tom Happynook, Huu-ay-aht)  
• “The dialog between different people [knowledge holders] is useful to each one of them...I think that the more information that you have the closer we are going to being able to come to figure out what’s best for everything.” (Guujaaw, Haida) | • “The traditional knowledge has to be the basis of the [management] plan.” (Priscilla Evans, Sugpiaq)  
• “The more the elders get together and talk, the more it helps us with our subsistence life style. [For example,] you go out and hunt in the wintertime because that is when the [sea otter] fur is at its best.” (Lydia McMullen, Sugpiaq)  
• “Protocol to include [in management] are - Don't waste. Don't overharvest. Take only what you need. Be mindful of the other creatures.” (Nancy Radtke, Sugpiaq)  
• “[The best scenario is] traditional, local and current knowledge all combined into one pot.” (John Ardenia, Sugpiaq) |
| **Local management plan for sea otters, shellfish, kelp** | • “The management plan triggered us getting involved - having some of our people go out and harvest them [otters] and utilize the furs. It wasn’t until we started to devise an otter management plan that the villages got a seat at the table.” (Violet Yeaton, Sugpiaq)  
• “There is an opportunity to pay more attention to our role as managers and re-think the way we think about our management systems - thinking about how we contribute to the balance, instead of just taking. In the context of sea otters, trying to get an understanding of how we can manage them in a way that | • “[A management plan for sea otter] has got to be co-created, not created for us.” (anonymous, Sugpiaq)  
• “Having a plan helps to keep the traditions [hunting and crafting] alive but ensure that we don't overharvest.” (Priscilla Evans, Sugpiaq)  
• “There is a draft management plan here but it hasn't been adopted. It is based around language and regulation to say no harvest limit, but not to be done in a wasteful manner. Not to take females with pups, pregnant females, and focus harvest of sub-adult and white-headed males. The use [of otters] is for arts and crafts; it provides financial resources for individual community members. It is not explicit in the plan, but |
isn’t perceived as killing them because they’re a nuisance, but managing them as other predators interacting within the system.” (anonymous)

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<tr>
<th>harvesting otters</th>
<th>gives us the ability to control otters in our bay.”</th>
<th>(Pat Norman, Sugpiaq)</th>
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<tr>
<td>“[A sea otter management plan] has to be about balance. It might show the feds that we’re managing our resources in our own traditional way.”</td>
<td>(Nancy Radtke, Sugpiaq)</td>
<td></td>
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<tr>
<td>“I believe that [implementing a management plan] would have prevented the devastation and depletion of other natural resources in our territory.”</td>
<td>(Therese Smith, Kyuquot/Chekleset)</td>
<td></td>
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<tr>
<td>“I think having a management plan would help because if someone wanted to grow kelp for harvesting, they could, it would be in the management plan.”</td>
<td>(Anonymous, Kyuquot/Chekleset)</td>
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| “There needs to be an experimental approach to human control of sea otters on a small spatial scale. The objective would be to manage for local resources - certain clam beaches and bays - site specific management!...In order for it to be applied at a larger, coast-wide approach, there would need to be major shifts in legislative frameworks to allow for it to happen.” | (Anonymous) |
| “There have been people [in Kyuquot] that have experimented with different ways of excluding otters from the beaches.” | (Tony Hanson, Kyuquot/Chekleset) |
| “[There is a desire to] convince leadership on the west coast of Vancouver Island to try mechanisms that have been used before; for example, transplanting urchins; doing things with the [traditional] knowledge we have.” | (Anonymous) |
| “You can apply the knowledge you gain in one experiment to another system that might not even be linked to sea otters. You’ll expect one thing, but there will be more other little surprises and things you learn.” | (Tim Malchoff, Sugpiaq) |
| “It is helpful to try techniques to keep otters off heavy subsistence beaches.” | (John Ardenia, Sugpiaq) |
| “[Management experiments] are time consuming and resource consuming - so it is important to choose wisely which to do.” | (Alex Hatrick, Sugpiaq) |
| “We tried to plant shellfish in ‘sea otter proof’ cages and it didn't work. We tried to transplant shellfish, but it didn't work. Someone tried to do shellfish aquaculture here, but it didn’t work.” | (Jeff McMullen, Sugpiaq) |
| “[Management experiments] might be useful to know if any methods have worked or not. Shellfish transplants, clam gardens, kelp harvests are some of the things that would be so good to have done.” | (Teresa Smith, Kyuquot/Chekleset) |
| “Experiencing might help us learn things we didn't even think of.” | (Brenda Leo, Kyuquot/Chekleset) |
| “We need these studies, in a semi-controlled, full-controlled and uncontrolled environments to see what works, what doesn't work, or what we need to do.” | (Russell Hanson, Kyuquot/Chekleset) |

<p>| “It doesn’t really work very well when outside people [non-local or non-Indigenous] come in and impose their values on a system they don’t understand.” | (Cliff Atleo Sr., Ahousaht) |
| “You have to be at the table. You have to get a seat at the table. We had to fight for that. I would say to other communities that it’s important to sit at the table, so you have a voice. When you start to develop a sea otter management plan, it will be your plan, not someone else’s plan.” | (Violet Yeaton, Sugpiaq) |
| “Even though there is an Aboriginal right, and successful court cases have been won by First Nations, the DFO continue to manage the resource without acknowledgement of Aboriginal rights and cases that have been” | (Anonymous) |
| “Need to get local management. Local management works a lot better than State or Federal.” | (Wally Kvasnikoff, Sugpiaq) |
| ”We need more of our people to sit on the decision-making boards to advocate for our community and who we are.” | (Nancy Yeaton, Sugpiaq) |
| “I don’t know why [marine resource decision making] is controlled by people who don’t understand our way of life. They don’t come out and see how we actually live.” | (John Kvasnikoff, Sugpiaq) |
| “Policing by local governing bodies would help keep harvesting numbers low and the resources abundant.” | (Kevin Seville, Sugpiaq) |
| “You do have to walk together. If you're actively involved with them [the State government] it helps to get your voice heard.” | (Gwen Kvasnikoff, Sugpiaq) |</p>
<table>
<thead>
<tr>
<th>Local Community Leadership</th>
<th>Trust and Respect Across Governments</th>
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<tbody>
<tr>
<td>• “Leadership is really important; leaders take responsibility and consult carefully with community before making final decisions” (anonymous)</td>
<td>• “Since the early 50s, kids were taken off to residential school to ‘take the Indian out of the Indian.’ Distrust of government is deep.” (anonymous)</td>
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<tr>
<td>• “The challenge is getting our people to stand up. The people who stand up are the Hereditary Chiefs. It’s going to build, I can see that more and more.” (Cliff Atleo Sr., Ahousaht)</td>
<td>• “We get so frustrated with DFO [Department of Fisheries and Oceans] who come from other places and make management rules here. Managers have less knowledge of the intricacies of these local systems, or ignore them, and make management decisions that are not appropriate to the local context.” (anonymous)</td>
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<tr>
<td>• “The leadership, the strength of leadership, and how that leadership is not just about an individual person but it’s about generations of trained individuals who consult with their tribal members about decisions that affect all of them. And that’s the responsibility to carry out the planning and decision-making and to adapt to different changing conditions based on informed decision making from their people.” (Nancy Turner, Indigenous knowledge scholar)</td>
<td>• “Even if you talk nicely with them [Dept. of Fisheries and Oceans], they don’t care. They have an agenda. DFO are the enemy. They are not open to working with us.” (Cliff Atleo, Ahousaht)</td>
</tr>
<tr>
<td>• “The role of leadership is to make wise decisions and to stand up to Fish and Game [State management].” (Lydia McMullen, Sugpiaq)</td>
<td>• “Traditional forms of governance can work because they are based on respect, inclusion of people. You want to manage and govern the way that you have been taught.” (Cliff Atleo, Ahousaht)</td>
</tr>
<tr>
<td>• “Leadership need to have cultural awareness in order to represent the community.” (Nancy Radtke, Sugpiaq)</td>
<td>• “I wish the trust could be more, but I don't think it can happen.” (Roberta Moonin, Sugpiaq)</td>
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<td>• “[The community] leadership had the [sea otter] tags that tell you how many [otters] you can get. They limit you.” (Nina Kvasnikoff, Sugpiaq)</td>
<td>• “Sharing information is challenging. They say one thing, but then they use it against us.” (Tim Malchoff, Sugpiaq)</td>
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<td>• “There can be other non-council leadership that is important [for living with sea otters]. These leaders teach the kids and youth about traditions and hunting.” (Anonymous, Sugpiaq)</td>
<td>• “It would be nice to have both governments come together to meet government-to-government and work on an agreement on how to work together, and not overpower each other.” (Priscilla Evans, Sugpiaq)</td>
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<tr>
<td>• “The leadership has to listen to what people are saying, and the people must listen to what the leader is saying and not always expecting the leader can change everything.” (Maralyn Short, Kyuquot/Chekleset)</td>
<td>• “We can't go into other Native territories and boss them around. You have to respect their ways. And yet, Fish and Game do that to us. That's a way to break down trust.” (anonymous)</td>
</tr>
<tr>
<td>• “The role of being the leaders is to bring the voice of the community to higher levels of government.” (Jennifer Hanson, Kyuquot/Chekleset)</td>
<td>• “We are constantly focused on bringing up the past instead of working together to build a true co-management structure.” (Pat Norman, Sugpiaq)</td>
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<td>• “It's up to the leadership to negotiate with government about community rights. (Peter Hanson, Kyuquot/Chekleset)</td>
<td>• “[Increased trust might be possible] if we were given rights to manage [resources].” (Jennifer Hanson, Kyuquot/Chekleset)</td>
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<td>• “A good leader will bring DFO [Federal management] to the table on how to manage otters.” (Lana Jules, Kyuquot/Chekleset)</td>
<td>• “[Increased trust might be possible] if they ever took in local knowledge and used it, instead of always thinking theirs was a better way.” (Terese Smith, Kyuquot/Chekleset)</td>
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<td>• “The leader has to listen to what people are saying, and the people must listen to what the leader is saying and not always expecting the leader can change everything.” (Maralyn Short, Kyuquot/Chekleset)</td>
<td>• “We need to have authority so we can manage this situation to benefit all, including the sea otter, our resources and us as a people.” (Russel Hanson, Kyuquot/Chekleset)</td>
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The biggest struggle is getting them [Federal government] to relinquish power.” (Harvey Humchitt, Heiltsuk)
<table>
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<tr>
<th>Federal Regulations on communities’ ability to hunt otters</th>
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<tr>
<td>• “The Kyuquot/Chekleset people weren’t allowed to take the sea otters when they were coming in, and manage them so they wouldn’t eat all of the crabs. I feel like when you take our [First Nations] role out of the system, that is when things go out of balance. We’ve learned that lesson now from the sea otters - we haven’t been able to fulfill our role in the balance of life…That is part of the lesson we are talking about now - the role of humans as predators in the system.” (Tom Happynook, Huu-ay-aht)</td>
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<td>• “It was probably the case that historical management was a mosaic of places with lots of sea otters, and places with not so many. A goal might be to manage for that – mechanically, it’s not impossible, but politically it may be difficult. The biggest barrier is you can’t have harvest while otters are listed [Federal Species at Risk Act].” (anonymous)</td>
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<td>• “When they [the local government/community] started managing the sea otters I saw a vested interest of the community members wanting to do it right. They took only what was allocated. And the pelts were sent away and processed. They were able to make hats and different arts and crafts from the pelts. Beautiful, beautiful…” (Violet Yeaton, Sugpiaq)</td>
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<tr>
<th>More Traditional Knowledge (otters, kelp, shellfish)</th>
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<td>• “My traditional knowledge gives me the information about what we had before. It can guide us in making policies and decisions on what needs to be done. (Harvey Humchitt, Heiltsuk)</td>
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<td>• “For our culture [Sugpiaq], sea otters were really important, they were used for furs, clothing… We’ve lost a lot of information about how to tan the hides, how to make the traditional items.” (Violet Yeaton, Sugpiaq)</td>
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<td>• “You can’t just kill them [otters] to kill them - you have to give value to them. In our case, they were chiefly robes of high value, very high-ranking chiefs could wear the sea otter capes.</td>
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<th>bring together all stakeholders to reach consensus about best way forward.” (Violet Yeaton, Sugpiaq)</th>
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<tr>
<td>• “[Skeptical increased trust can help] “If they [government] ever treated us with equality…maybe.” (Marilyn Short, Kyuquot/Chekleset)</td>
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<tr>
<td>• “[Skeptical increased trust can help] “If government would listen to the needs of our people, and the knowledge that we have to share about the management of resources.” (Natalie Jack, Kyuquot/Chekleset)</td>
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<th>• “The rules around commercialization of pelts is restricting. It doesn't give us full usage.” (Pat Norman, Sugpiaq)</th>
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<td>• “They have taken away our people's ability to manage this resource. Our hereditary chiefs had a management plan in their governing system.” (Theresa Smith, Kyuquot/Chekleset)</td>
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<tr>
<td>• “It's hard to live with the [Federal] restrictions. We used to play a more active role in management. Our way was that if anything was harming the way we were living, if there was too much otters, we would hunt them, if there were too many wolves, we would shoot them.” (Velina Vincent, Kyuquot/Chekleset)</td>
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<td>• “[A barrier to adapting to sea otters is] not having any say in how they can be managed in our territory.” (Russel Hanson, Kyuquot/Chekleset)</td>
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<td>• “A major barrier is the fact that they [otters] are a protected species. There is no management in the amount of otters in our territory, therefore they are depleting our shellfish.” (Natalie Jack, Kyuquot/Chekleset)</td>
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<td>• “I would like to have some pelts for my regalia.” (anonymous, Kyuquot/Chekleset)</td>
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<td>• “To teach tradition and culture is very important. It's what brings the community together. Tightens the bond.” (Cecil Moonin, Sugpiaq)</td>
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<td>• “Another skill that's disappearing is how to skin and treat pelts.” (Priscilla Jack, Kyuquot/Chekleset)</td>
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<tr>
<th>• “Hunting provides an opportunity for people to make money. It's a very positive thing for Native people to be able to use otter skin for arts and crafts.” (Nancy Yeaton, Sugpiaq)</th>
</tr>
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<tr>
<td>• “It's nice to be able to control the population if needed. You have to tag what you kill. Hunting doesn't happen that often. Only when they [otters] become a problem.” (Eric Kvasnikoff, Sugpiaq)</td>
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<td>• “A major barrier is the fact that they [otters] are a protected species. There is no management in the amount of otters in our territory, therefore they are depleting our shellfish.” (Natalie Jack, Kyuquot/Chekleset)</td>
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<td>Learning from Other Communities Experiencing Sea Otter Recovery</td>
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<td>---------------------------------------------------------------</td>
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<td>• “[Sharing information] gives us a better understanding of what we can prepare for…. We’re looking at other communities that have management plans for otters and apply it to what we have here.” (Harvey Humchitt, Heiltsuk)</td>
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<td>• “There are different viewpoints on it [sea otter recovery] and it depends on how you're raised and what your current ecological timeline in the reintroduction of the sea otters is….We are a little ahead on the ecological timeline in Port Graham, how we are currently level with sea otters - they're neither a benefit for a detriment. But currently in British Columbia they are nuisance and they are not looked highly upon.” (Joshua Anahonak, Sugpiaq)</td>
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<td>• “We should share information across Nations and across generations.” (anonymous)</td>
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<th>Monitoring Information (otters, shellfish, kelp, fish)</th>
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<td>• “[Researchers] coming in to study the behaviour of sea otters and other things has been a great benefit to the community… We need more of our people to become scientists.” (Elroy White, Heiltsuk)</td>
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<td>• “It’s vitally important that they [federal government] involve the communities in the research... Getting the locals involved [reporting, tagging, sampling, monitoring otters], it’s a sense of empowerment. So that you can have some knowledge and awareness to be able to participate in the decision-making process.” (Violet Yeaton, Sugpiaq)</td>
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<td>• “[In Alaska] we have to tag and tan every animal. We primarily have tribal taggers (not all) and they have a good relationship with Fish &amp; Wildlife Service. At the end of the year, Fish &amp; Wildlife can do a quick summary of how many...” (Peter Hanson, Kyuquot/Chekleset)</td>
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<th>Monitoring Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>• “Knowledge is golden! There is an urgency to learn because our elders are fewer today.” (Therese Smith, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “The younger people go hunting/fishing no matter what the season, whenever, wherever... because they don’t know the traditional stewardship.” (Marilyn Short, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “Chiefs used valuable pelts for their regalia, also trade. The value is in the thickness of the pelt.” (Peter Hanson, Kyuquot/Chekleset)</td>
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</tbody>
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<table>
<thead>
<tr>
<th>Learning from Other Communities Experiencing Sea Otter Recovery</th>
</tr>
</thead>
<tbody>
<tr>
<td>• “[Learning from other communities] is necessary in these adapting times. The best is to communicate what is working and not working with each other.” (Anonymous, Sugpiaq)</td>
</tr>
<tr>
<td>• “You have to have the local understanding for each place - what we eat, what our environment is, etc. It is helpful to get information from elsewhere, but you have to understand how it applies here.” (Alex Hetrick, Sugpiaq)</td>
</tr>
<tr>
<td>• “This is the first time I'm learning about other communities. It's always helpful to learn.” (Roberta Moonin, Sugpiaq)</td>
</tr>
<tr>
<td>• “Having extra information would be helpful for me. If someone from another community came and said, ‘this is what we did,’ it would be better than sitting watching them [otters] eat and crying.” (Nina Kvasnikoff, Sugpiaq)</td>
</tr>
</tbody>
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<tr>
<td>• “It’s too late for our community now. But I think it would have helped us be aware and prepare more.” (Anonymous, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “I would like to see the Alaskan people come share information about sea otter management.” (Danny Short, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “We should have had them [people in Alaska] come in and let us know what we were gonna go through.” (Chris Jules, Kyuquot/Chekleset)</td>
</tr>
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<tr>
<td>• “Scientific information can help make informed decisions. But it would work best if we could use the information to make our own decisions. Let us take the available information and make rules that work best for us.” (anonymous, Sugpiaq)</td>
</tr>
<tr>
<td>• “It’s important to monitor. It’s important to survey historical numbers and locations of where sea otters are. We need to look at other shifts too. For example, recording temperature changes.” (Nancy Radke, Sugpiaq)</td>
</tr>
<tr>
<td>• “I think monitoring information is important, but I'm always worried that it will be used against us.” (Anonymous, Sugpiaq)</td>
</tr>
</tbody>
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<tr>
<td>• “[Monitoring information] would be helpful, but we didn’t have it.” (Daisy Hanson, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “It’s helpful, but the information has to get used.” (Peter Hanson, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “Monitoring has been going on for a few decades now and the otter has been protected as long! We need training for our people to be biologists.” (Therese Smith, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>Social Capital within Communities (exchanges, groups, gatherings, support)</td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>• “When we share and we listen to each other with respect and with regard for the things around us, we are more likely to get through everything.” (Barb Wilson, Haida)</td>
</tr>
<tr>
<td>• “When you bring the harvest back, you share it with the community, whether it’s through culture or through arts and crafts, or through giving it to your elders.” (Violet Yeaton, Sugpiaq)</td>
</tr>
<tr>
<td>• “Clans and families were monitored in terms of their actions. [Taught] through a lot of stories and taboos and the way that you are raised. Those stories with the conservation and ethic in them are incredible – share properly, be respectful – some of those we are forgetting, and we have to start living that way again and showing it again.” (Dolly Garza, Haida/Tlingit)</td>
</tr>
<tr>
<td>• “[Chiefs] gain respect by how much they give away. It’s a good system. It would put them into debt and cause other chiefs to go into debt to do potlatches to reciprocate.” (Guujaaw, Haida)</td>
</tr>
<tr>
<td><strong>Social Capital Between Communities (exchanging resources between communities)</strong></td>
</tr>
<tr>
<td>• “Haida and Heiltsuk and Nuu-chah-nulth are people who changed as requirements changed. We had training and treaties to find ways to get food. There would be negotiations between areas to offset resource imbalances.” (Anonymous)</td>
</tr>
<tr>
<td>• “Ha’houlthee [traditional territories belonging to hereditary chiefs] leads to resilience - if one community is struggling, another one will help.” (Anonymous)</td>
</tr>
<tr>
<td>• “For responding [to otter introduction], we got some urchins from adjacent areas and give them to the elders in order to keep the tradition and the taste. Which doesn’t really address the issue [the loss of urchins in our territory].” (Tony Hanson, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “The relationship between Nations has changed. There used to be more inter-Nation trade...but land claims and the reserve system have shifted these relationships… these relationships used to be integral to the resource management.” (Anonymous)</td>
</tr>
<tr>
<td>• “Communication is extremely helpful. The fastest communication is Facebook to let the community know what's going on.” (Gwen Kvasnikoff, Sugpiaq)</td>
</tr>
<tr>
<td>• “[Having social exchanges] keeps the conflict between people down. Real face time not Facebook.” (Priscilla Evans, Sugpiaq)</td>
</tr>
<tr>
<td>• “Having time for connection is important. Also, sharing information let's people know about marine system components.” (Pat Norman, Sugpiaq)</td>
</tr>
<tr>
<td>• “Communication is super important. We do better when we're all on the same page. We all go our own ways, but then we have a crisis or an issue that brings us all together.” (Anonymous, Sugpiaq)</td>
</tr>
<tr>
<td>• “We had meetings, but you just hear the same stuff, &quot;it's going to balance out, it's going to balance out.” (Anonymous, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “It helps everybody to voice their opinions, but they’re usually negative.” (Jennifer Hanson, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “They're not really helpful because we can't do anything about it [sea otter recovery].” (Marilyn Short, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “Having community and social exchanges hasn’t helped. People talk talk talk and nothing ever happens.” (Leo Jack, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “This meeting [during research visit] was the first time we had a positive meeting.” (Lucy Pavio, Kyuquot/Chekleset)</td>
</tr>
</tbody>
</table>

Kept all text in table format. Added one table row for any text that went off in a column, including one table row for the last sentence of each quote. All text was presented in natural language.
<table>
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<tr>
<th>Having a Positive Attitude Toward Change</th>
</tr>
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<tr>
<td>• “The best way to adapt to change is to be positive. To utilize the strengths of the people.” (Elroy White, Heiltsuk)</td>
</tr>
<tr>
<td>• “Our teachings talk about adapting to change, and not being afraid to change, but actually figuring out how you fit into that change.” (Tom Happynook, Hiuu-ay-aht)</td>
</tr>
<tr>
<td>• “I’m optimistic as a young person… I think things are going to be ok… so a lot of people can be kind of negative in terms of oh there’s no hope…but I’m one of those people who thinks we have the ability to create change, it’s just a matter of doing it, and doing it together.” (Ken Watts, Tseshaht)</td>
</tr>
<tr>
<td>• “We’ve got a chain of educated people coming down the pipe. We have marine and fisheries biologists coming. The optimism is never going to go away. It’s allowing that to filter into everyone’s way of thinking.” (Cliff Atleo, Ahousaht)</td>
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<td>• “We’re facing rapid changes and we’ve been facing rapid changes for some time now. We don’t really know what to expect from it, but we have to prepare ourselves.” (Harvey Humchitt, Heiltsuk)</td>
</tr>
<tr>
<td>• “Coastal communities have experienced dramatic and cultural change.” (Anonymous)</td>
</tr>
<tr>
<td>• “In the old days, pressures weren’t like they are today – habitat destruction, full scale fishing and other factors. International markets are now driving demand, not local.” (Gajajaw, Haida)</td>
</tr>
<tr>
<td>• “Our social systems are changing. There is a lot of technology today. The youth today are not engaged in the process of sustaining themselves from the resources.” (Mel Innes, Heiltsuk)</td>
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<tr>
<th>Novel Livelihood Opportunities</th>
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<td>(sea otter-focused tourism)</td>
</tr>
<tr>
<td>• [RE: opportunities associated with sea otter recovery] “Invest in sea otter tourism.”</td>
</tr>
<tr>
<td>• “Sea otter tourism – you expect to have a positive benefit for communities with sea otters.” (Jennifer Walkus, Wuikinuxv)</td>
</tr>
<tr>
<td>• “There is sea otter tourism in Katchemat Bay.” (Violet Yeaton - Sugpiaq)</td>
</tr>
<tr>
<td>• “Getting people to think forward about benefits of the new system to prepare for change. Getting people to invest in otter</td>
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<td>• “You can't expect change with a negative attitude. You need a positive attitude to bring change. Negative attitudes make controversy and conflict. It’s hard to get people to change from their old ways. It’s the older generations that have a harder time adapting to change.” (John Ardenia, Kyuquot/Chekleset)</td>
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<td>• “I think you have to work toward having a positive attitude. Sea otters are competition for food. But there is a positive - we can hunt them or use them for arts and crafts.” (Mary Malchoff, Sugpiaq)</td>
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<td>• “It’s good to be positive, but it’s good to be realistic. Being positive doesn't always fix things.” (Anonymous, Sugpiaq)</td>
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<td>• “There is so much negativity around otters. Not everybody sees it the way we see it. We’ve adapted over the years. We’re pretty open-minded for ‘Mr. otter.’” (Brenda Leo, Kyuquot/Chekleset)</td>
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<td>• “We’ve allowed so much to happen. We need more than a positive attitude, we need a stronger attitude.” (Theresa Smith, Kyuquot/Chekleset)</td>
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<tr>
<td>• “I don’t think that after seeing how the otters ate all our seafood there has ever been a positive attitude about them.” (Paul Vincent, Kyuquot/Chekleset)</td>
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<td>• “There are a lot of things that we have a hard time adapting to. We have to build up our resiliency to adapt to changes because time doesn't stand still.” (Mandy Wood, Sugpiaq)</td>
</tr>
<tr>
<td>• “We’re adapting all the time. It’s all we do. We have so many changes, it’s overwhelming. The changes are coming regardless. When you are offered a challenge, the goal is to overcome it. But we’re not overcoming them. We’re just coping to get by. We never clear our plate. Fighting back is all we can do.” (Anonymous, Sugpiaq)</td>
</tr>
<tr>
<td>• “There is so many changes to adapt to. I get frustrated with it.” (Anonymous, Sugpiaq)</td>
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<tr>
<td>• “Change is a hard thing no matter what. People around here are scared of change, younger people less so.” (Anonymous, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “I think lots of things are changing. (e.g., Technology). A lot of people don't eat our traditional foods. So they don't care [about otters].” (Marilyn Short, Kyuquot/Chekleset)</td>
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tourism. Need to educate people about why there needs to be harmony.” (Elroy White, Heiltsuk)
- “The viability of sea otter tourism depends how accessible your community is, ease of travel.” (anonymous)
- “In Sitka had issues with tourism to make sure people did not hunt in certain places during certain times.” (Dolly Garza, Haida/Tlingit)
- “I'd rather see no tourism in here. Keep it a little secluded.” (Tim Malchoff, Sugpiaq)
- “Tourists don't understand we hunt them. They especially don't understand us living on the land.” (Wally Kvasnikoff, Sugpiaq)
- “Tourists wanting to see the otters would make it harder to hunt them. Most people who want to see them are the ‘save the whales’ type people.” (John Kvasnikoff, Sugpiaq)
- “The sea otters in my experience are a big asset to us as eco-tourism.” (Russell Hanson, Kyuquot/Chekleset)
- “People from around the world come to see otters. There could be a lot more [tourism] around here, mountain biking, hiking trails, etc.” (Anonymous, Kyuquot/Chekleset)
- “There is no knowledge of how to start something like that [otter tourism] up. If there was information available in the community it could be good.” (Anonymous, Kyuquot/Chekleset)
- “I think that tourism would only benefit the lodges, but it wouldn't help people over here.” (Paul Vincent, Kyuquot/Chekleset)
- “[Tourism is] an opportunity for seasonal work but sea otters are here year round. It's not that easy to do, it takes a lot bucks to get something started.” (Peter Hanson, Kyuquot/Chekleset)
- “There needs to be a business plan together. Can't just go out there and expect people to do it.” (Marilyn Short, Kyuquot/Chekleset)
- “It does not make a difference because we've still got to eat off the land. It's not about jobs...it's about our way of life.” (Nina Kvasnikoff, Sugpiaq)
- “If people have a part time job or a full time job, they still need subsistence harvest. And the otters affect subsistence harvest.” (Jeff McMullen, Sugpiaq)
- “Your body will lead you back to trying to find food. Jobs are not as important.” (Nancy Yeaton, Sugpiaq)
- “Any community needs jobs to help the economy, but jobs don't help people deal with otters.” (John Ardenia, Sugpiaq)
- “We're limited in jobs. [Having more employment opportunities] would take the strain off.” (Anonymous, Sugpiaq)
- “Having jobs doesn't bring fresh seafood.” (Anonymous, Kyuquot/Chekleset)
- “[Alternative employment opportunities] would not affect the ability to adapt. Still no seafood.” (Peter Hanson, Kyuquot/Chekleset)
- “[If we had a variety of employment opportunities], we would still miss our seafood.” (Anonymous, Kyuquot/Chekleset)
- “Flexibility is important for dealing with changes.” (Sperry Moonin, Sugpiaq)
- “Flexibility is important. The subsistence calendar doesn't match nature's calendar.” (Anonymous, Sugpiaq)
- “I've had 6 different jobs, so I have been flexible.” (Christalina Jager, Sugpiaq)
<table>
<thead>
<tr>
<th>Household Occupational Multiplicity</th>
<th>NA</th>
</tr>
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<tbody>
<tr>
<td>“It's hard to transition jobs because not much is available. People really hold on to their positions.” (Gwen Kvasnikoff, Sugpiag)</td>
<td></td>
</tr>
<tr>
<td>“We’ve had to change occupations in winter ie: clam digging - to non-seafood gathering occupations (forestry, office administration).” (Russell Hanson, Kyuquot/Chekleset)</td>
<td></td>
</tr>
<tr>
<td>“Changing jobs would not affect the ability to adapt to seafood.” (Peter Hanson, Kyuquot/Chekleset)</td>
<td></td>
</tr>
<tr>
<td>“A lot of jobs are seasonal, so have to be able to change or deal with no work.” (Anonymous, Kyuquot/Chekleset)</td>
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<tr>
<th>Financial Support</th>
<th>NA</th>
</tr>
</thead>
<tbody>
<tr>
<td>“It doesn't make a difference because we have to have subsistence anyway.” (Jeff McMullen, Sugpiag)</td>
<td></td>
</tr>
<tr>
<td>“When subsistence is low, having money to buy from the store is helpful.” (Anonymous, Sugpiag)</td>
<td></td>
</tr>
<tr>
<td>“Because the cost of living is way higher so more income that comes in, the better for the family and the community.” (Lydia McMullen, Sugpiag)</td>
<td></td>
</tr>
<tr>
<td>“[If we had more sources of income], we still wouldn't have seafood or shellfish.” (Anonymous, Kyuquot/Chekleset)</td>
<td></td>
</tr>
<tr>
<td>“Having more [income] sources would not help because there is still no seafood.” (Peter Hanson, Kyuquot/Chekleset)</td>
<td></td>
</tr>
<tr>
<td>“Sea otters are still here, I still don't have seafood.” (Anonymous, Kyuquot/Chekleset)</td>
<td></td>
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<tr>
<td>“We are changing and adjusting and not dealing with the problem at hand.” (Russel Hanson, Kyuquot/Chekleset)</td>
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<p>| Redundancy of Harvest Sites | “Likely there was a mosaic of areas along the coast with otter free areas created by people hunting sea otters close to village sites and other important shellfish resources, along with areas with more abundant sea otters. Abundant sea otters and abundant people. Midden records from the Aleutians support this mosaic idea over space and time.” (Anonymous) |
| “The problem is, we want to be able to harvest locally! It's not helpful if you have to go to other locations to get food.” (Pat Norman, Sugpiag) |
| “[Harvest sites] would be nice. It would be hard to keep them [otters] out. It's just not feasible.” (Nina Kvasnikoff, Sugpiag) |</p>
<table>
<thead>
<tr>
<th>Habitat Created</th>
<th>Climate Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>• “Territories were under the responsibility of clan’s and families; different resources with different times of the year in different locations. This idea of a mosaic of different kinds of habitat in whole area.” (anonymous)</td>
<td>• “The weather is changing. We don’t get to harvest as much as we used to before.” (Nina Kvasnikoff, Sugpiag)</td>
</tr>
<tr>
<td>• “Within a territory, we had different places where resources were harvested or used each year so that they could ensure resources were plentiful. For example, rotating use of clam beds.” (anonymous)</td>
<td>• “The window we harvest in is smaller. More red tides.” (Wally Kvasnikoff, Sugpiag)</td>
</tr>
<tr>
<td>• [RE: traditional resource management] “There was spatial management and careful stewardship of resources, also traditions and rituals with consequences, roles of respect, also knowledge and ability to be selective. For example, clam gardens.” (anonymous)</td>
<td>• “There are areas like this [with abundant shellfish], but you need a barrel of fuel to get there and back which is expensive. The distance to harvesting areas matters.” (Gwen Kvasnikoff, Sugpiag)</td>
</tr>
<tr>
<td>• “Trade-offs” (Trade-offs)</td>
<td>• “[It would help a lot] if we had areas where we were able to keep them [otters] out of, where we could still harvest abalone, or urchins, or butter clams.” (Anonymous, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>More Kelp Habitat Created (system trade-offs)</td>
<td>• “I think it would have helped a lot if we had been allowed to somehow hunt them [otters] out of some areas. If I had to go somewhere else to harvest seafoods, it would be costly.” (Therese Smith, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “If you have less shellfish, might have more finfish habitat [kelp forests]; if they [community members] can see trade-offs they may have more patience with otters.” (Jennifer Walkus, Wuikinuxv)</td>
<td>• “Depends on how far we have to go. It [shellfish] used to be right there in front of us. If the harvest areas are far, it does not help.” (Al Vincent, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “Indirect effects – ecosystem services, kelp as a carbon sink - are generally underappreciated. Maybe it’s worth trying to communicate these better.” (anonymous)</td>
<td>• “If that would help save it [shellfish], then yes, that would be something that neighbouring tribes should do. Guard that place.” (Velina Vincent, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “Kelp is important habitat for more small fish (but very hard to trace this to direct impacts on salmon or rockfish).” (anonymous)</td>
<td>• “We have to go to Campbell River to get tutsup [red urchins], which is really far.” (Anonymous, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>• “We’ve seen the case where it [otters] might have a good counter balancing effect to the carbon in the oceans and those things that are becoming a global problem. The atmospheric effects of sea otter aren’t something that you can see, but it is really helpful to get the whole picture and to be able to weigh those sorts of things out.” (Guujaaw, Haida)</td>
<td>• “From what I know, the otters can go anywhere and get the food…so not sure it would work.” (Jennifer Hanson, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td>More Kelp Habitat Created (system trade-offs)</td>
<td>• “More kelp would be a problem. When the nets get fouled, the salmon see it and don’t swim into it. The kelp is negative for the salmon, but positive to other fish.” (Tim Malchoff, Sugpiag)</td>
</tr>
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<td>• “If we had less shellfish, might have more finfish habitat [kelp forests]; if they [community members] can see trade-offs they may have more patience with otters.” (Jennifer Walkus, Wuikinuxv)</td>
<td>• “In areas with lots of kelp, the salmon don't go there because they like to school and the kelp breaks them up. The kelp is like a wall; they go around. The benefits of kelp depend on where your net is!” (Sperry Moonin, Sugpiag)</td>
</tr>
<tr>
<td>• “Indirect effects – ecosystem services, kelp as a carbon sink - are generally underappreciated. Maybe it’s worth trying to communicate these better.” (anonymous)</td>
<td>• “Having more kelp makes it harder to get around using small outboard motors.” (Priscilla Evans, Sugpiag)</td>
</tr>
<tr>
<td>• “Kelp is important habitat for more small fish (but very hard to trace this to direct impacts on salmon or rockfish).” (anonymous)</td>
<td>• “Kelp is good for rockfish - that's their habitat - but not for salmon. Salmon don't go into the kelp forest because ling cod will eat them.” (Lydia McMullen, Sugpiag)</td>
</tr>
<tr>
<td>• “We’ve seen the case where it [otters] might have a good counter balancing effect to the carbon in the oceans and those things that are becoming a global problem. The atmospheric effects of sea otter aren’t something that you can see, but it is really helpful to get the whole picture and to be able to weigh those sorts of things out.” (Guujaaw, Haida)</td>
<td>• “[More otters] are good for the herring and for other little fish. There was a pass that didn't have any kelp and now it's thick with kelp - and last year we saw a herring spawn on it.” (Richard Gillette, Kyuquot/Chekleset)</td>
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<td>• “More kelp would be a problem. When the nets get fouled, the salmon see it and don’t swim into it. The kelp is negative for the salmon, but positive to other fish.” (Tim Malchoff, Sugpiag)</td>
<td>• “[The otters returning] has been good for rockfish.” (Therese Smith, Kyuquot/Chekleset)</td>
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<td>• “If we had less shellfish, might have more finfish habitat [kelp forests]; if they [community members] can see trade-offs they may have more patience with otters.” (Jennifer Walkus, Wuikinuxv)</td>
<td>• “The fish are being fished out by humans. Maybe in the past more kelp would have been more useful.” (Leo Jack, Kyuquot/Chekleset)</td>
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<td>• “Indirect effects – ecosystem services, kelp as a carbon sink - are generally underappreciated. Maybe it’s worth trying to communicate these better.” (anonymous)</td>
<td>• “There are places we can't travel anymore because there is so much kelp. We have to change navigation.” (Paul Vincent, Kyuquot/Chekleset)</td>
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<tr>
<td>• “Kelp is important habitat for more small fish (but very hard to trace this to direct impacts on salmon or rockfish).” (anonymous)</td>
<td>• “More kelp would be a problem. When the nets get fouled, the salmon see it and don’t swim into it. The kelp is negative for the salmon, but positive to other fish.” (Tim Malchoff, Sugpiag)</td>
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<td>(an additional ecosystem stressor)</td>
<td>prepare ourselves for anything that might come from climate change and any of the changes that we can foresee.” (Harvey Humchitt, Heilsuk)</td>
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<td></td>
<td>“It’s a little scary, things are happening around the world with climate change that concern me and that I think should concern everybody…We live in a really interesting time right now, there’s so much happening in terms of climate change and global warming.” - (Ken Watts, Tseshaht)</td>
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<td></td>
<td>“I’m worried about losing subsistence. We live off our land and sea.” (Stacey Hetwick, Sugpiaq)</td>
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<td></td>
<td>“Climate change is making things a lot worse. It’s throwing off the ecosystem.” (Tim Malchoff, Sugpiaq)</td>
</tr>
<tr>
<td></td>
<td>“It [climate change] happens slowly, so the impact is not so bad.” (anonymous, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td></td>
<td>“We're noticing clam declines not related to otters or ducks.” (anonymous, Kyuquot/Chekleset)</td>
</tr>
<tr>
<td></td>
<td>“Climate change is giving us less opportunity to harvest shellfish.” (Russel Hanson, Kyuquot/Chekleset)</td>
</tr>
</tbody>
</table>
Appendix B3. Details on the ordinal logistic mixed-effect model.

We used an ordinal logistic mixed-effect model with a cumulative link function (Christensen 2018a, b) to examine which social-ecological conditions most enabled people’s ability to adapt to sea otter recovery and how they differed between communities. Our model estimated the probability that each social-ecological condition, within each community, was ranked at or below a particular ordinal ‘adaptation response score’ (9-point scale). Because each respondent answered 22 questions and the data derived from those questions were not independent, we treated ‘respondent ID’ as a random effect. Mathematically this is represented by:

$$P(Y_i \leq j) = \dfrac{1}{1 + e^{\beta_1 \text{Condition} + \beta_2 \text{Community} + \beta_3 (\text{Condition} \times \text{Community}) - \mu(\text{ID})}}$$

where the $Y_i$ is the index of all response score observations (n=1610, groups=74), $j$ represents a given response score (1,…,J=9), $\theta_j$ is the threshold parameter, $\beta_{1,2,3}$ are the parameters for the fixed effects (‘Social-ecological condition’, ‘Community’, and their interaction), and $\mu(\text{ID})$ represents the random effects of individual respondent ID, which we assume are normally distributed $\mu(\text{ID}) \sim N(0, \sigma^2_{\mu})$.

References


NOTE: “Occupation’ and ‘Gender’ are significantly associated with one another irrespective of community ($\chi^2 = 33.4, \text{df}=6, p = 8.9 \times 10^{-6}$), and also when tested within Sugpiaq ($\chi^2 = 18.5, \text{df}=6, p = 0.005$) and Kyuquot/Chekleset ($\chi^2 = 25.7, \text{df}=6, p = 2.5 \times 10^{-4}$) communities. Otter attitude is not influenced by occupation in the Sugpiaq Tribes, but graphs and paired contrasts reveal Kyuquot/Chekleset respondents in ‘Education’ and ‘Homemakers’ had significantly more negative attitudes toward otters. However, a large part of this relationship appears related to the respondents in those occupations being entirely female. As such, we consider the ‘Occupation’ effect an artifact of gender tendencies in those occupations, rather than a true effect of occupation. See gender model in Appendix B5.
Appendix B5. Figures and statistics associated with respondent ‘Gender’ and ‘Occupation’ that explain some of the variation in ‘Otter Attitude Response Score’. (A) Table shows ordinal logistic regression models. The most parsimonious model (lowest AICc) is highlighted in grey. (B) Graph shows ‘Otter Attitude Response Score’ is influenced by respondent gender in Kyuquot/Chekleset, but not for the Sugpiaq Tribes.

A)

<table>
<thead>
<tr>
<th>Ordinal Regression Models and Associated Statistics</th>
<th>Significance of Individual Factors from Likelihood Ratio Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>model</td>
<td>k</td>
</tr>
<tr>
<td>Com + Gen + Com:Gen</td>
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</tr>
<tr>
<td>Com</td>
<td>1</td>
</tr>
<tr>
<td>Com + Gen</td>
<td>2</td>
</tr>
</tbody>
</table>

Community = Com, Gender = Gen, Occupation = Occ, k = number of estimable parameters, AICc = small sample adjusted Akaike’s Information Criterion, ΔAICc = difference in AICc scores between the top-ranked model, r² = Nagelkerke’s pseudo r-squared is a measure of goodness-of-fit.

B)

The significant ‘Community’ by ‘Gender’ interaction can be visualized graphically. Pair-wise contrasts (with p-values adjusted via Tukey method) show male and females did not have different otter attitudes in the Sugpiaq community (p = 0.59), whereas males and females’ attitudes were significantly different in the Kyuquot/Chekleset community (p = 0.0037).