Advancing abalone conservation by revealing change in predator-prey interactions and social-ecological resilience through time

by

Lynn Chi Lee

B.Sc., University of British Columbia, 1992

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

in the
School of Resource and Environmental Management
Faculty of Environment

SIMON FRASER UNIVERSITY
Summer 2018

Approval

Name:	**Lynn Chi Lee**
Degree:	**Doctor of Philosophy**
Title:	**Advancing abalone conservation by revealing change in predator-prey interactions and social-ecological resilience through time**
Examining Committee:	**Chair:** Clifford Atleo Assistant Professor

Anne K. Salomon
Senior Supervisor
Associate Professor

Murray Rutherford
Supervisor
Associate Professor

Jane Watson
Supervisor
Emeritus Professor Vancouver Island University

Norm Sloan
Supervisor
Emeritus Parks Canada Agency

Isabelle Coté
Internal Examiner
Professor
Department of Biological Sciences

Andrea Sáenz-Arroyo
External Examiner
Professor
Dept. de Conservacion de la Biodiversidad
El Colegio de la Frontera Sur

Date Defended/Approved: August 14, 2018

Ethics Statement

Abstract

Species conservation remains challenged by paucity of long-term data on how human use and environmental factors have shaped species abundance and trends. Further, as humanity pushes against limits of the biosphere, sustainable environmental governance could benefit from understanding factors that conferred resilience to enduring coupled social-ecological systems (SESs). Along Canada's west coast, northern abalone (*Haliotis kamtschatkana*) and coastal indigenous peoples (First Nations) have co-evolved for millennia. Yet within a half-century, commercial overfishing under centralized fisheries management caused closure of all abalone fisheries and subsequent listing of abalone as endangered. While loss of this cultural keystone species profoundly affected coastal First Nations and recent abalone recovery fuels interest in restoring traditional fisheries, concurrent recovery of a key predator, sea otters (*Enhydra lutris*), poses a conservation conundrum. I aim to advance abalone conservation by illuminating key changes in components and interactions within this SES through time. To understand ecological effects of sea otter recovery on abalone, I conducted field surveys in three regions of coastal British Columbia, representing four decades of sea otter occupation and varying environmental conditions. While sea otters caused abalone density decline, indirect effects improved habitat conditions and altered abalone behaviour and distribution, thereby mediating predation effects. Next, I synthesized multiple knowledge sources to demonstrate how ecological extirpation of sea otters caused social-ecological regime shifts allowing abalone to obtain higher historical abundances than were likely prior to European contact. This shifted baseline and continuing declines amplified perceptions of abalone extinction risk. However, if abalone are not truly endangered, society is morally obligated to conserve abalone and restore sustainable traditional fisheries for reasons of social justice. Finally, I explored how fisheries sustainability might be achieved using traditional knowledge of past governance and management protocols. Although polycentric institutions for abalone recovery today might support future co-management, key issues of power asymmetries, trust and funding remain barriers to address. By broadening our understanding of the abalone SES in western Canada, my thesis provides insights into how weaving indigenous knowledge of past resource management with contemporary western science can inform ecologically sustainable and socially just approaches to coastal fisheries today.

Keywords: adaptive co-management; northern abalone; predator-prey interactions; sea otter; social-ecological system resilience; traditional knowledge

To my loving and well-loved family.

My eternal gratitude for sharing fine adventures beside, on and under the ocean.

Acknowledgements

When I was 8, I dreamt I could breathe underwater. I learned to SCUBA dive, became a marine biologist, and revelled in swimming with the fishes! I moved to Haida Gwaii and found myself engaged in marine science and stewardship work with the Haida Nation. Along the way, I thought I would do a PhD. The opportunity presented itself almost a decade ago when I invited Anne to Haida Gwaii with her colleague, Sugpiaq Elder Nick Tanape, to speak about their work weaving together traditional and scientific knowledge to better understand coastal changes in Alaska. Here is the rest of the story!

My deepest gratitude goes out to Anne for persevering with me as her first and rather unconventional 'older' PhD student, and for the phenomenal support she has provided along the way, particularly in this last push to get it done! To my entire committee, thank you for steadfastly believing in me. Anne, Jane, Murray, Norm (and Paul Dayton), what a great privilege to work with such a talented and inspiring group of ecologists who have and continue to do innovative and enduring marine conservation work, each in your unique way. Learning from your diverse expertise in field and experimental work, data analyses, social science, and how to write a good scientific paper, has been a grand adventure that will continue. I have learned much from you, including that there is ever more to learn. Thanks to Isabelle Coté and Andrea Sáenz-Arroyo for respectively being my internal and external examiners. Your approaches to marine conservation research inspire me – it is an honour to have you on my committee.

Aside from the academic challenge, one of my motivations for going 'back to school' was to get my young son, then seven, out on the boat with us. The extensive underwater fieldwork we did for this thesis was only possible through the amazing support from Anne's Coastal Marine Ecology and Conservation lab, Heiltsuk Integrated Resource Management Department (HIRMD), Council of the Haida Nation Haida Fisheries Program and Haida Oceans Technical Team, Fisheries and Oceans Canada (DFO), Gwaii Haanas Archipelago Management Board, Pacific Rim National Park Reserve, Hakai Institute, and MTE Inc, with funding from NSERC, SFU, DFO, Hakai, Gwaii Trust Society, and Gwaii Haanas. Special mention to Leandre Vigneault, Taimen Lee Vigneault, Rowan Trebilco, Alejandro Frid, Eric White, Hannah Stewart, Matt Drake, Stu Humchitt, Leah Saville, Erin Rechsteiner, Jane Watson, Joanne Lessard, Seaton

Taylor, Mike Atkins, Joel White, Twylabella Frid, Gail Lotenberg, Julie Carpenter, Brooke Davis, Mark Wunsch, Sharon Jeffery, Rod at Hakai, Stan Hutchings and Karen Hansen, with whom I spent many enjoyable and memorable hours, days and weeks on and under the water. Your subtidal survey skills and above water expertise were invaluable! Thanks to those on land who also provided invaluable advice and logistical assistance with field planning and lab experiments including Linda Nichol, Rebecca Martone, Dominque Bureau, Juanita Rogers, Tammy Norgard, Claudia Hand and Holly Hicklin. A shout out goes to Rowan Trebilco, Sean Anderson and Joe Thorley for your 'mad' statistical skills. Thanks, too, to the many I did not name who contributed along the way.

My particular gratitude to Mike Reid, Jennifer Carpenter, Harvey Humchitt, Ross Wilson and Gary Wilson from the HIRMD, who provided their support and collaborated to conduct traditional knowledge interviews with Heiltsuk abalone experts. Walas Giaxsixa (thanks) to *Gitla* (Elroy White) who co-interviewed with me – without you, many of the stories told by experts may not have been shared. To Gus Brown, Bill Gladstone Sr, George and Gary Housty, Howard Humchitt, Sonny Hunt, Mike Reid, Tony and Emma Reid, Fred Reid, Davie Wilson, and three anonymous experts, Walas Giaxsixa for so generously sharing your time and knowledge – along with dried seaweed, herring roe on hemlock branches, eulachon grease and halibut. Special haawa (thanks) to Russ Jones, Terri-Lynn Williams-Davidson, the participants in the Haida Marine Traditional Knowledge Study, and Janet Winbourne for facilitating the contribution of Haida traditional knowledge of abalone ecology and stewardship practices. I came to Haida Gwaii in 1993 from big Canadian cities without any real knowledge of First Nations. I am humbled by what all of you, and the innumerable other people I have been fortunate to work with in the Haida, Heiltsuk, Gitga'at and Metlakatla Nations, have taught me over the decades about what it means to live with the land and sea.

Finally, thanks to my family and friends for your unwavering support, humour, love, and encouragement. Although I can't name you all here, know that I feel so fortunate to call you friend! Special thanks to Lucy, Sonia, Jean-Louis and Sylvie, Jenn, Lindsay, Rowan, Alejandro, Marco and Julia, Robyn and Joe, David, and Vernal for sharing your time, your thoughts and your homes, especially on this final stretch. Lastly to my amazing spouse Leandre who can make anything happen, and my wonderfully independent son, now teenager – your adventure is just beginning!

Table of Contents

Approval ii
Ethics Statement iii
Abstract iv
Dedication vi
Acknowledgements vii
Table of Contents ix
List of Tables xii
List of Figures xiii
List of Plates xvi
List of Acronyms xvii

Chapter 1. Introduction 1
People are intertwined with the biosphere 1
  Trophic cascades can trigger social-ecological regime shifts 2
  Historical knowledge of social-ecological change is critical for conservation 3
  21st century environmental governance regimes 5
  Exploring the nexus between abalone, coastal ecosystems and social justice 6
Context for the thesis 8
Navigating the thesis 8
References 10

Chapter 2. Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator 21
Abstract 21
Introduction 22
Methods 24
  Study site context and field survey design 24
  Lab predation experimental design 29
  Statistical analysis 30
Results 33
  Biotic and abiotic factors influence abalone distribution and abundance 33
  Abalone behavioral class shifts with sea otter occupation 42
  Biotic and abiotic factors may mediate predation outcomes 43
  Indirect benefits of sea otters for abalone 44
Discussion 46
  Abalone behavior may reduce predation effects 46
  The importance of habitat characteristics 48
  Mesopredator effects 49
  Ocean conditions and human influence 50
  Implications for interacting species of conservation concern 51
Acknowledgements 54

References 55

Chapter 3. Shifting baselines driven by social-ecological transformations alter perceptions of species status and trends 65
Abstract 65
Introduction 66
Methods 68
  Study area 68
  Zooarchaeological, historical and fisheries data 68
  Traditional knowledge 68
  Western knowledge 69
  Population model of abalone abundance 69
Results 70
  Drivers of the abalone social-ecological system 70
  Causes of recent abalone decline in Heiltsuk territory 73
  Abalone population trends estimated from traditional and western knowledge 74
  Changes in abalone size structure 75
Discussion 76
  Multiple lines of evidence illuminate abalone social-ecological system transformations 76
  Traditional and western knowledge broaden views of abalone trends 78
  Cultural resilience underpins governance transformations 79
  Shifting baselines alter perceptions of abalone status: implications for conservation 79
Acknowledgements 81
References 81

Chapter 4. Designing adaptive co-management to foster resilient and socially just coastal fisheries 87
Abstract 87
Introduction 88
Social-ecological system description 90
  Study area, components and interactions 90
  Governance regimes 92
Methods 95
  Evaluating the resilience of indigenous and federal fisheries governance regimes 95
  Improving conservation using an adaptive co-management approach 95
Resilience assessment of abalone fisheries governance regimes 96
  Principle 1. Maintain diversity and redundancy 96
  Principle 2. Manage connectivity 100
  Principle 3. Manage slow variables and feedbacks 102
  Principle 4. Foster complex adaptive thinking 103
  Principle 5. Encourage learning and experimentation 104
  Principle 6. Broaden participation 105
  Principle 7. Promote polycentric governance 107
Building an adaptive co-management approach for abalone governance 108

Current conditions that can foster successful adaptive co-management 110
Addressing underlying power dynamics and trust 112
Restoring traditional abalone fisheries 114
Conclusion 116
Acknowledgements 118
References 118

Chapter 5. Conclusions 130
Trophic cascades and trait-mediated interactions can reduce predation effects on weakly-interacting alternative prey 130
Shifting baselines affect perceptions of species status and trends 133
The future of marine conservation and management for coastal British Columbia 135
References 138

Appendix A. Length-mass relationships, substrate complexity scoring, and list of kelp species included in field survey data analyses 145

Appendix B. Saturated models for field and lab experimental analyses 147

Appendix C. Field survey data: Region, site- and transect-level bivariate relationships between abalone density and biomass, and biotic and abiotic environmental factor 150

Appendix D. Field survey analyses: Strength of evidence for alternative candidate models of abalone density, presence, length and biomass 155

Appendix E. Field survey analyses: Strength of evidence for alternative candidate models of sunflower star presence and biomass, urchin presence and biomass, and kelp stipe density 160

Appendix F. Interactions between predatory sunflower stars and their prey, abalone and sea urchins, in the Haida Gwaii seascape and in laboratory tanks 163

Appendix G. Model results for lab experiment investigating the effects of substrate complexity and availability of alternate prey on predation of abalone by sunflower stars 166

Appendix H. Supplementary materials for Chapter 3 167

List of Tables

Table 2.1 Best models of the effects of biotic and abiotic factors on density, presence, length, and biomass of total, exposed, covered, and cryptic, abalone from field surveys. 37

Table 2.2 Strength of evidence for alternative candidate models of the effects of sea otter occupation time on the proportion of exposed, covered, and cryptic, abalone by site. 43

Table 3.1 Representative observations of abalone use and ecology by decade from Heiltsuk traditional knowledge interviews. 72

Table 4.1 Summary of key characteristics of historical First Nations traditional and Canadian federal fisheries governance regimes for abalone in relation to seven foundational principles identified to enhance the resilience of coupled social-ecological systems (Biggs *et al.* 2012). 98

Table 4.2 Traditional indigenous abalone harvesting practices and stewardship protocols specified by Heiltsuk First Nation experts. Equivalent modern fishing regulations in [*italics*]. 99

Table 4.3 Scale of ecological features for abalone compared with scale of management practices (Sloan and Breen 1988; Farlinger 1990; Lee *et al.* 2016). 101

Table 4.4 Examples of traditional ecological knowledge about abalone shared by Heiltsuk experts. 106

List of Figures

Figure 2.1 Subtidal rocky reef study sites (open diamonds) along the coast of British Columbia, Canada, in three regions: Haida Gwaii (n = 23), Central Coast (n = 19) and West Coast Vancouver Island (n = 18), with the range of sea otter occupation at the time of surveys highlighted in bold black lines.... 26

Figure 2.2 Bivariate relationships between density of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone and three factors: sea otter occupation time, region and depth. Symbols represent regions: Haida Gwaii (HG; open circles), Central Coast (CC; open triangles) and West Coast Vancouver Island (WCVI; open diamonds). Error bars are site means ± SE. Closed symbols (region panel) are the mean of site means by region. Lines are LOWESS smoothers (otter occupation time and depth panels). 35

Figure 2.3 Size frequency histograms of shell length for (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone for each of three surveyed regions of BC. Sample sizes (n) are given in sequence: sites, transects, abalone. Number of sample sites and transects are the same within regions, but differ across regions. Bin sizes are 10 mm except for covered abalone in CC and WCVI that are 20 mm........ 36

Figure 2.4 Standardized coefficients and 95% confidence intervals for relationships of biotic and abiotic factors with the density, length and biomass of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone from averaged models within ΔAIC_c <2. Factors without coefficient and relative variable importance (RVI) values were absent from final model sets. 38

Figure 2.5 Predicted abalone densities from best model parameters for (A) total, (B) exposed, (C) covered, and (D) cryptic (note different scale bar), abalone on Haida Gwaii as a function of sea otter occupation time at two depths, 0 m and the average survey depth of 4.3 m, when other biotic and abiotic factors are held at their mean surveyed values........ 41

Figure 2.6 Proportion of (A) exposed, (B) covered, and (C) cryptic, abalone in each behavioral class by site. Symbols are as in Fig. 2.2. Shaded areas represent confidence intervals about best-fit relationships: (A) non-linear exponential decay, (B) intercept, and (C) linear. 42

Figure 2.7 (A) Successful (black) and unsuccessful (gray) attacks by sunflower stars on hatchery-raised abalone in lab predation trials (n = 4 per treatment). Trials with no circles indicate no attacks. (B) Escape speeds of abalone and red urchins, and attack speed of sunflower stars, measured in the lab and field. (C) Capture efficiency, (D) handling time and (E) feeding rate of sunflower stars by treatment (mean ± SE). 44

Figure 2.8 Bivariate relationships (left) and standardized coefficients and 95% confidence intervals from averaged models within ΔAIC_c <2 (right) for relationships between (A) sunflower star biomass, (B) urchin biomass, and (C) kelp stipe density, and sea otter occupation time. For bivariate plots, symbols represent regions: Haida Gwaii (HG; open circles), Central Coast (CC; open triangles) and West Coast Vancouver Island (WCVI;

open diamonds). Error bars are site means ± SE. Lines are LOWESS smoothers. 45

Figure 2.9 Conceptual models of habitat and abalone conditions with (A) no sea otters, (B) short sea otter occupation time (≤6 yr), and (C) long sea otter occupation time (≥10 yr), illustrating multiple mechanisms by which sea otter recovery may facilitate abalone persistence at low densities. Moving from panel A to C demonstrates: (1) increased extent and depth of kelp cover, including growth of longer-lived kelp species, providing abalone with increased access to food and protection from predators that visually detect prey; (2) behavioral shift to higher proportions of cryptic abalone due to increased predation risk and/or drift kelp food supply; (3) distributional shift in abalone from concentration at the low intertidal/shallow subtidal kelp line to dispersion across deeper depths with increased depth of kelp forests; (4) increased abalone fertilization success due to gamete retention within kelp forests and crevices, potentially reducing Allee effects at low overall abalone densities; and (5) increased retention of short-lived abalone larva (3–12 d; Sloan and Breen 1988) to facilitate settlement within kelp forests (also see Watson 2000). Potential lower abundance and smaller size of mesopredators (e.g., sunflower stars, octopus, crabs) due to decreased prey availability and/or direct predation by sea otters, and higher abalone growth rates within kelp forests, may also indirectly benefit abalone. Arrows at the bottom of each panel illustrate expected retention of gametes and larva in urchins barrens, kelp forest and crevice habitats, with increasing spirals indicating higher retention. Drawings by Lynn Lee. 53

Figure 3.1 Historical social-ecological timeline for northern abalone in British Columbia, Canada, highlighting key governance and management systems, events, and resource uses driving system change within three social-ecological system regimes – sea otters present, absent, and recovering – from start of the Holocene to present. 71

Figure 3.2 (a) Map of the British Columbia coast, including the communities of Kyuquot in Nuu-chah-nulth traditional territory and Bella Bella in Heiltsuk traditional territory. Sea otters were re-introduced near Kyuquot from 1969-72. A sea otter raft was first documented in the Goose Islands in the 1980s. Proportional change in densities of abalone, urchins and kelp by region: (b) Nuu-chah-nulth traditional territory on the west coast of Vancouver Island and (C) Heiltsuk traditional territory on the central coast. Means of site means from transects within sites are plotted by decade of sea otter occupation. 73

Figure 3.3 Examples of abalone abundance and size reconstructions by decade from Heiltsuk traditional knowledge interviews with: (a) George and Gary Housty from 1940s-1980s, and (b) Davie Wilson from 1970s-2000s. 74

Figure 3.4 Density of large ≥70 mm and small <70 mm abalone: (a, c) by decade from Heiltsuk traditional knowledge interviews, and (b, d) by year of federal fisheries agency population index site monitoring surveys. Black lines represent abalone density estimates from the most-supported population growth model for: (a, b) large abalone using data from traditional and western knowledge (WSK), and (d) small abalone using data from WSK only. Dotted lines indicate 95% credible intervals. 75

Figure 3.5 Proportion of abalone in each length-class in Heiltsuk territory: (a) by decade from traditional knowledge interviews, and (b) by year from federal fisheries population index site monitoring surveys. 76

Figure 4.1 Study area showing locations of communities where abalone harvesting practices and stewardship protocols were drawn from: Bella Bella where we conducted our primary research of collaborative interviews with Heiltsuk Nation abalone experts; Old Massett and Skidegate where the Haida Nation conducted interviews for the Haida Marine Traditional Knowledge Study (Haida Marine Traditional Knowledge Study participants et al. 2011a); and Kitkatla and surrounding territory where published Gitxaala Nation knowledge was documented (Menzies 2010, 2015). 91

Figure 4.2 Key components (orange rectangles), drivers (green ovals), direct linkages (solid arrows) and feedbacks (dashed arrows) in the northern abalone social-ecological system, including currently active (dark orange) and formerly active (light orange) components. Illegal fishing during and after the commercial fishery also affected the three legal fisheries, and commercial overfishing led to closure of the recreational and First Nations traditional fisheries. Photo credit left to right: The McNeill family of Skidegate, Haida Gwaii; Lynn Lee; Guy White, former commercial abalone fisher; and Fisheries and Oceans Canada. 93

Figure 4.3 Timeline of key events and changes in the northern abalone social-ecological system, including abalone use, major fisheries governance regimes and interim periods, and ecological regimes (also see Lee *et al*. 2016). 94

Figure 4.4 Actors, institutions and multi-scale linkages governing abalone recovery in coastal BC: (A) Locally, First Nations Constitutions and governance oversee abalone recovery initiatives and First Nations natural resource organizations communicate and learn within and among each other; (B) Local-scale multi-interest and/or multi-species working groups led by First Nations organizations develop and implement community-based action plans; (C) Regionally, the technical advisory Abalone Recovery Implementation Group, initiated by Canada's federal fisheries agency, engages in regional learning by sharing knowledge and information related to abalone recovery; (D) Nationally, the Department of Fisheries and Oceans Canada, along with Parks Canada Agency and Environment Canada, are mandated to protect and conserve abalone under federal legislation; (E) First Nations governments that often communicate and learn between and among nations and are guided by their respective worldviews and ethics and values; and (F) Internationally, Canada's endorsement of the Convention on Biological Diversity, Convention on the International Trade of Endangered Species and United Nations Declaration on the Rights of Indigenous Peoples, establish overarching expectations for Canada's decision-making related to species conservation and First Nations. 109

List of Plates

Plate 2.1 Abalone in different behavioral classes: (A) three exposed abalone in urchin barrens habitat, (B) two covered abalone under Laminarian kelp in an area occupied by sea otters for three years, and (C) two cryptic abalone capturing drift kelp in an area occupied by sea otters for six years. Natural history observations: (D) red urchins capturing bull kelp in an urchin barrens, (E) nine abalone moving in to feed on kelp captured by red urchins, (F) abalone shell and urchin test expelled following digestion by a sunflower star in habitat with high complexity substrate, and (G) cryptic abalone in a kelp forest occupied by sea otters. Images by Lynn Lee.... 28

List of Acronyms

AbRIG	Abalone Recovery Implementation Group
ACM	Adaptive co-management
AICc	Akaike Information Criterion (corrected for small samples sizes)
BC	British Columbia
CBD	Convention on Biological Diversity
CC	Central coast (of British Columbia)
CHN	Council of the Haida Nation
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
DFO	Department of Fisheries and Oceans Canada
DMI	Density-mediated interaction
GLMM	Generalized linear mixed effects models
HG	Haida Gwaii
HGMSG	Haida Gwaii Marine Stewardship Group
HIRMD	Heiltsuk Integrated Resource Management Department
IUCN	International Union for the Conservation of Nature
RVI	Relative variable importance
SARA	Species at Risk Act
SES	Social-ecological systems
TK	Traditional knowledge
TMI	Trait-mediated interaction
UN	United Nations
VIF	Variance inflation factor
WCVI	West coast of Vancouver Island
WSK	Western scientific knowledge

Chapter 1. Introduction

People are intertwined with the biosphere

That people are part of an ecosystem is inherently recognized in indigenous societies throughout the world, and Canada is no exception (e.g., Turner 2005, Council of the Haida Nation 2007, Brown and Brown 2009, Jones et al. 2010, Stephenson et al. 2014). Yet western knowledge systems created a construct of wilderness as "an area where the earth and its community of life are untrammelled by man, where man himself is a visitor who does not remain" (US Wilderness Act 1964). In the United States of America, this idea was borne in the early 1900s from the preservationist ideals of John Muir who inspired the establishment of America's National Parks. At the same time, the utilitarian ideals of Gifford Pinchot led to conservation through responsible use of lands for recreation, profit and learning, inspiring the creation of the US Forest Service. Almost a century later, these differences in worldview continue to spur debate about how conservation of the land and sea should operate. Advocates of biodiversity-based traditional conservation supported use of conventional conservation tools like protected areas and species at risk listings to protect biodiversity for its own sake (Soule 1985, 2013), while advocates for 'new conservation' promoted "… seek[ing] to enhance those natural systems that benefit the widest number of people, especially the poor," with assumptions that poverty-alleviation would lead to improved conservation outcomes for nature (Kareiva and Marvier 2012). Between these extremes lie indigenous management systems "whose knowledge and practices reflect a long history of co-evolving and interdependent social-ecological systems" (Stephenson et al. 2014), where people have been part of ecosystems that sustained biological and cultural diversity over millennia (Lepofsky and Lertzman 2008, Lepofsky et al. 2015, Mathews and Turner 2017).

In today's age of the Anthropocene (Vitousek et al. 1997, Waters et al. 2016) where the impact of humanity is pushing against the safe operating space of the earth's biosphere (Rockstrom et al. 2009, Raworth 2012, Dearing et al. 2014, Steffen et al. 2015), it is increasingly difficult to see people as separate from ecosystems. In spite of global commitments to the United Nations Convention on Biological Diversity (1992), global and local biodiversity loss on land and in the ocean is growing as are the number of species at risk (Worm et al. 2006, Butchart et al. 2010, Hoffmann et al. 2010, Hutchings et al. 2012, Tittensor et al. 2014, although see Cardinale et al. 2018), having negative impacts on ecosystem function that are on par with habitat loss, climate change and pollution (Hooper et al. 2012, Young et al. 2016). Evidence suggests that conventional conservation efforts including protected areas are not sufficient to halt continuing biodiversity decline (Mora and Sale 2011, Gonzalez et al. 2016). When loss of biodiversity includes decline or loss of top or keystone predators, this can have disproportionately large consequences for ecosystem structure and function because these strongly-interacting species can regulate and alter ecosystem dynamics through direct consumptive and indirect behavioural effects on their prey, often initiating trophic cascades (Estes and Duggins 1995, Pace et al. 1999, Preisser et al. 2005, Heithaus et al. 2008, Estes et al. 2011, Rosenblatt et al. 2013, Beschta and Ripple 2016).

Trophic cascades can trigger social-ecological regime shifts

Trophic cascades, a key concept in community ecology, are “indirect species interactions that originate with predators and spread downward through food webs,” requiring top-down effects of one species on another through at least one intermediary species (Ripple et al. 2016). Early conceptualizations focused on the direct effects of keystone predators on their prey and subsequent indirect effects on those prey’s resources, primarily related to the direct effects of strongly-interacting predators (e.g., Estes and Palmisano 1974, Paine 1980, Pace et al. 1999). Innovative experiments and empirical observational evidence in more recent decades provided evidence that indirect trait-mediated interactions (TMIs) between predator and prey could have equivalent or in some cases stronger ecosystem consequences than direct effects (Preisser et al. 2005, Rudman et al. 2016). For example, experimental arenas showed that systems controlled by predatory spiders, with or without the actual physical ability to eat grasshopper prey, had equal positive effects on growth of old field plants and no detectable difference in grasshopper densities, demonstrating that TMIs changed prey behaviour to reduce grazing pressure (Schmitz et al. 1997). Indirect TMI effects of predation continue to be observed in a multitude of marine, freshwater and terrestrial systems (Lima and Dill 1990, Schmitz et al. 1997, Preisser et al. 2005). Through direct and indirect mechanisms, including TMIs, top predators can have significant impacts on their prey that cascade through ecosystems, as I demonstrate in Chapter 2. These impacts can have consequent effects on coupled social-ecological systems (SESs), linked systems of people and nature (Berkes and Folke 1998, Liu et al. 2007) as I show in Chapter 3.

Trophic cascades embedded in SESs can be key drivers of ecological regime shifts (e.g., Scheffer et al. 2001, Casini et al. 2009). Ecological regime shifts can occur when multiple stable states characterized by different species composition and feedbacks exist within a system. Classic examples include freshwater lakes that flip between clear and turbid states, temperate rocky reefs that flip between forested kelp and deforested urchin-dominated states, and coral reefs that flip between coral- and algae-dominated states (Hughes et al. 2005). These systems exhibit non-linear response to disturbance including hysteresis, which occurs when the critical threshold for switching from one stable state to the other differs depending on which direction the system is moving in (Scheffer et al. 2001). Thus if thresholds into an undesirable state are crossed, shifting back to a desired state can be more challenging because the thresholds back require going further beyond the one that was crossed. When regime shifts occur, they alter the structure and function of ecosystems and can have significant consequences for social systems (e.g., Folke et al. 2004, Hughes et al. 2005).

Historical knowledge of social-ecological change is critical for conservation

As I show in Chapter 3, regime shifts, often triggered by human activities, can extend back centuries or more. For example, archaeological evidence has demonstrated multiple shifts over millennia in the relative abundance of urchins in the Aleutians (Simenstad et al. 1978) and abalone in California (Braje et al. 2009), both likely related to human hunting of sea otters and ecological effects linked to trophic cascades (Estes and Palmisano 1974). Predation by sea otters greatly reduces the abundance of their prey including urchins and abalone. When people hunt sea otters to low densities for sufficient periods of time, the reduced predation pressure allows their prey species to flourish and this fluctuation in prey abundance can be observed in the archaeological record.

Increasingly, marine conservation science is acknowledging the need to understand SES changes over long historical timescales to fully appreciate the magnitude of change that has occurred prior to modern fisheries records or ecological monitoring (e.g., Dayton et al. 1998, Jackson et al. 2001, Pandolfi et al. 2003, Baum and Myers 2004, Lotze and Milewski 2004, Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2006, Saenz-Arroyo and Roberts 2008, Early-Capistran et al. 2018). Elucidating these historical changes therefore requires acceptance of unconventional data sources, previously considered ‘anecdotal’, as a valid source of ‘scientific’ data (Pauly 1995). Such sources include the observations of early explorers and naturalists recorded in ships’ logbooks, historical charts, newspaper clippings, and interview data from local resource users including fishers, recreational operators, and community members (e.g., Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2006, Salomon et al. 2007, Saenz-Arroyo and Roberts 2008, Beaudreau and Levin 2014, Thurstan et al. 2015, Buckley et al. 2017, McClenachan et al. 2017, Thurstan et al. 2017, Early-Capistran et al. 2018, Salomon et al. 2018). These intergenerational changes can lead to ‘shifting baselines syndrome’ where each human generation accepts the ecosystem condition and species abundances in which they were raised as being normal (Pauly 1995, Costanza et al. 2012).

In most cases, shifting baselines have been diagnosed for declining species where older generations’ perceptions of high abundance is much greater than that of younger generations, leading to loss of understanding about the real magnitude of species decline (Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2005b, Soga and Gaston 2018). Declining, often non-linear, trends in species abundance through time have been well documented in a multitude of marine ecosystems throughout the world. Examples include serial depletion of different abalone species by commercial fisheries (Rogers-Bennett et al. 2002), and persistence of Pacific herring over millennia then decline following advent of modern commercial fisheries (McKechnie et al. 2014). Globally, overfishing has caused loss of large predatory fish and marine biodiversity with associated ecosystem impacts (Jackson et al. 2001, Myers and Worm 2003). Finally, declining trends in abundance and size of Gulf groupers and abundance of East Pacific sea turtles in Mexico due to intensified fishing, followed by turtle population recovery following fisheries closure and other conservation actions (Saenz-Arroyo et al. 2005a, Early-Capistran et al. 2018), and reduction in abundance and size along with changes in dietary niche of California sheephead due to overfishing (Braje et al. 2017b), are among the many cases. Adaptive and innovative governance and management approaches are needed to address marine conservation issues in the context of these complex shifting SES baselines.

21st century environmental governance regimes

Within the biosphere's safe operating space lies room for environmental governance that can achieve both social justice and ecological sustainability, particularly for people who are marginalized in an increasingly 'western' and interconnected world (Raworth 2012, Dearing et al. 2014, Folke et al. 2016). As the rapid pace of global industrialization accelerates the impacts of humanity on the earth, less densely populated places and the indigenous people who continue to live there are being re-discovered as areas crucial to conservation (Brondizio and Le Tourneau 2016). Acknowledgement of the important role of place-based local and indigenous knowledge systems in land- and sea-scape governance may spur innovative and respectful institutional approaches that address power asymmetries (Turner et al. 2013, Brondizio and Le Tourneau 2016, Mistry and Berardi 2016) and promote social-ecological system resilience and sustainability. As I demonstrate in Chapter 4, opportunities are ripe for bridging new relationships with indigenous peoples through novel and innovative hybrid indigenous-state governance institutions that build on the time-tested resilience of pre-contact indigenous governance and management systems.

Operationalizing innovative governance that can lead to social justice and ecological sustainability is less well-trodden ground. However, recent meta-analyses suggest that co-management presents a useful process for indigenous-state governance that has proven effective for meeting social and ecological objectives (Cinner et al. 2012), and can additionally address issues of power sharing and engagement of indigenous knowledge systems and other knowledge sources (Carlsson and Berkes 2005). Further, applying an adaptive co-management approach addresses key foundational principles of SES resilience, particularly by fostering complex adaptive thinking and encouraging learning and experimentation. Co-management approaches in Canada and elsewhere have encountered successes and barriers that provide important lessons for the future. Internationally, Target 18 of the United Nations (UN) Convention on Biological Diversity (CBD) Strategic Plan for Biodiversity 2011-2020 (UN CBD 2010) specifies that by 2020, "the traditional knowledge, innovations and practices of indigenous and local communities relevant for the conservation and sustainable use of biodiversity, and their customary use of biological resources, are respected," in ways that have "the full and effective participation of indigenous and local communities, at all relevant levels." In Chapter 4, I suggest some governance approaches that may promote human well-being while supporting foundations of the biosphere to foster long-term sustainability (*sensu* Westley et al. 2011, Fischer et al. 2015).

Exploring the nexus between abalone, coastal ecosystems and social justice

In this thesis, I explore these interconnected social-ecological system concepts and interactions using the case study of the northern abalone social-ecological system in the traditional territories of the Haida, Heiltsuk and Nuu-chah-nulth First Nations located in coastal British Columbia (BC), Canada. Five key components and their complex interactions comprise this SES: (1) **people**, who hunted sea otters, fished abalone and used kelp, (2) **sea otters**, keystone predators that eat macroinvertebrates including abalone and sea urchins among many others, (3) **sea urchins**, voracious grazers of kelp and other algae and important cultural and commercial species, (4) **abalone**, a grazer of kelp, cultural keystone species for indigenous peoples in coastal BC, and formerly important commercial and recreational fisheries species, and (5) **kelps**, productive primary producers that can form extensive kelp forest habitat for many marine and coastal species. Sea otter recovery in rocky reef ecosystems is well known to trigger trophic cascades that cause ecological regime shifts and alter prey behavior (Estes and Palmisano 1974, Watson 2000, Watson and Estes 2011, Lee et al. 2016, Stevenson et al. 2016).

For sea otters and abalone, the situation is even more complex because this predator and prey are both listed as species at risk in Canada (Sea Otter Recovery Team 2007, Fisheries and Oceans Canada 2012). Recovery of sea otters, a species of special concern, could place their endangered abalone prey in further peril. I explore and advance our understanding of the key nuances of their interactions and their magnitude of effect in Chapter 2. Historically, the maritime fur trade caused ecological extirpation of sea otters, resulting in ecological regime shifts that altered abalone abundance baselines. In Chapter 3, I explore the consequences of these shifting baselines on perceptions of abalone status and trends. Increasing colonial influence initiated by the maritime fur trade caused governance regime shifts that reduced resilience of the abalone SES and resulted in closure of all BC abalone fisheries in 1990. The ensuing current period of abalone recovery, along with increasing assertion of indigenous rights and title in BC, hold promise for transformation into an indigenous-state governance system for abalone management that fosters cultural, social and ecological resilience and sustainability, which I explore in Chapter 4. Indigenous environmental governance and management conferred resilience under social-ecological conditions very different from today's, therefore a hybrid of indigenous and modern governance systems is likely needed to foster SES resilience into the future. Multiple and sometimes conflicting social and ecological objectives within SESs will ultimately lead to trade-offs in management decision-making that will benefit from consideration of the multiple perspectives offered by interdisciplinary research such as this.

The complex SES interactions explored in my thesis take place within larger-scale oceanographic contexts, including past ocean regime shifts and current climate-driven changes. These can have potentially large effects on the abalone SES that I did not fully consider in my thesis. However, current knowledge can provide some insights for future governance and management. For example, lab studies showed that ocean acidification can impair northern abalone larval development and survival (Crim et al. 2011), and red abalone fertilization success, growth and survival (Kim et al. 2013, Boch et al. 2017). Field experiments also showed that local environmental conditions strongly affected juvenile green abalone growth and survival, highlighting the need for local-scale management (Boch et al. 2018). Growth of kelp that provides food and habitat for abalone can also be negatively affected by warming oceans with consequent SES effects (e.g. Krumhansl et al. 2017). Fortunately, establishment of well-placed marine reserves can help enhance abalone population persistence in the face of climate change, preserve genetic diversity, and support coastal fisheries (Micheli et al. 2012, Munguia-Vega et al. 2015, Rossetto et al. 2015).

Past human marine resource use has shaped sometimes long-lasting and cascading effects in SESs, with influences on food webs that can persist today. For example, hunting of large whales and other marine mammals has been proposed as the mechanism driving killer whale predation on sea otters in the Aleutian Islands, leading to significant sea otter decline and associated trophic cascades and ecological regime shifts in some areas (Springer et al. 2003, Estes et al. 2004, Laidre et al. 2006, Estes et al. 2009). These cascading effects would have influenced, and will continue to have effects, on abalone population dynamics and species interactions through time. Understanding effects of these and other historical SES alterations will also be important considerations for future abalone SES governance and management.

Context for the thesis

My motivation for this thesis was nurtured by decades of marine conservation work within the Haida First Nation and other coastal communities of Xaayda Gwaayaay (Haida Gwaii) – Islands of the People – an archipelago of remote islands perched on the continental shelf of northern British Columbia. I followed my heart and moved here in 1993 and I call this place home. Xaayda Gwaayaay is a place that has co-evolved with the Haida indigenous people over at least 13,500 years (Fedje et al. 2005). Strengthening Haida cultural reclamation continues to shape and inspire positive conservation outcomes for the land, sea and people. Over my two and a half decades here, I have been privileged to play a small and diverse part in taking care of the land and sea. My diverse roles have included being an active member of multi-interest land and marine planning tables supporting development of the Haida Gwaii Land Use Plan and Marine Use Plan, a marine biologist and marine planner for the Council of the Haida Nation, and a local marine coordinator for World Wildlife Fund Canada. Currently, I am the marine ecologist for Gwaii Haanas National Park Reserve, National Marine Conservation Area Reserve, and Haida Heritage Site, Canada's first park reserve to be jointly co-managed by a federal agency and First Nation. In this thesis, I draw from these decades of personal experience and local knowledge of people and place, as well as scientific and narrative knowledge stemming from both traditional and western knowledge systems.

Navigating the thesis

The overarching objective of this thesis was to explore how we can meet the needs of abalone and people on the BC coast within a complex, adaptive social-ecological system. Specifically, I used a SES resilience lens (Walker and Salt 2006, Biggs et al. 2012, Folke et al. 2016) to frame and evaluate the system and consider temporally and spatially dynamic relationships between key ecological and social components across multiple scales. The chapters are written as papers for submission.

Chapter 2 has been published in Ecosphere (Lee et al. 2016), Chapter 3 is currently under review by Conservation Letters and revisions are in progress (Lee et al. *in review*), and Chapter 4 will be submitted to the journal Marine Policy.

In Chapter 2, I explore predator-prey interactions between sea otters and abalone within the theoretical framework of food web dynamics, trophic cascades, and trait-mediated interactions. Recognizing the importance of local environmental conditions and prey behaviour in mediating these interactions, I use linear models to assess the effects of sea otters and environmental variables on the density, size and biomass of abalone in three behavioural classes: exposed, cryptic and covered. I find that although sea otters have an overall negative effect on abalone density reducing densities by upwards of 16 fold, they also have a measurable positive indirect effect resulting from increased depth and extent of kelp forest habitat due to the sea otter-induced trophic cascade (Lee et al. 2016).

By weaving together traditional knowledge (TK) of the Heiltsuk First Nation and western scientific knowledge (WSK) in Chapter 3, I use historical ecology techniques (Costanza et al. 2012, Thurstan et al. 2015) and a multiple evidence-based approach (Tengo et al. 2014), to broaden our understanding of how relative abundance of key components in the abalone SES – kelp, abalone, urchins, sea otters and people – have changed over millennia. I construct an abalone population exponential growth model using a Bayesian framework that integrates TK and WSK to extend the timeframe of abalone trends beyond that available from WSK alone. I find that dynamic and shifting baselines of abundance can significantly alter our perceptions of abalone conservation status and trends.

In Chapter 4, I use the foundational principles of social-ecological system resilience (Biggs et al. 2012) to assess and compare traditional Heiltsuk and Haida indigenous and Canadian federal governance regimes for abalone fisheries. I find that First Nations governance systems demonstrate a greater alignment with these resilience principles than centralized federal systems. Consequently, I propose a hybrid indigenous-state model (Armitage et al. 2012) for future governance of abalone. This model would encompass First Nations worldviews, ethics and values, and traditional harvesting practices and stewardship protocols, to foster future resilience and sustainability within the modern governance context. Further, given the need for sharing of power and responsibility in abalone management with First Nations, I propose how we can advance an adaptive co-management approach (Armitage et al. 2009) that builds on potentially innovative abalone recovery governance structures.

Finally, Chapter 5 concludes the thesis with a synthesis of key findings from the previous three chapters, their implications for conservation of species at risk, and my perspectives on promising directions for future research and change in governance and management. My hope is for this work to further illuminate how we might collectively navigate towards socially just and ecologically sustainable abalone fisheries in BC, Canada, a case study that is emblematic of coastal fisheries worldwide.

References

1964. Wilderness Act. Public Law 88-577 (16 U.S. C. 1131-1136), United States of America.

1992. Convention on Biological Diversity. 1760 UNTS 79; 31 ILM 818, United Nations.

Armitage, D., R. de Loe, and R. Plummer. 2012. Environmental governance and its implications for conservation practice. Conservation Letters **5**:245-255.

Armitage, D. R., R. Plummer, F. Berkes, R. I. Arthur, A. T. Charles, I. J. Davidson-Hunt, A. P. Diduck, N. C. Doubleday, D. S. Johnson, M. Marschke, P. McConney, E. W. Pinkerton, and E. K. Wollenberg. 2009. Adaptive co-management for social-ecological complexity. Frontiers in Ecology and the Environment **7**:95-102.

Baum, J. K., and R. A. Myers. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecology Letters **7**:135-145.

Beaudreau, A. H., and P. S. Levin. 2014. Advancing the use of local ecological knowledge for assessing data-poor species in coastal ecosystems. Ecological Applications **24**:244-256.

Berkes, F., and C. e. Folke. 1998. Linking social and ecological systems: management practices and social mechanisms for building resilience. Cambridge University Press, Cambridge, UK.

Beschta, R. L., and W. J. Ripple. 2016. Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. Biological Conservation **198**:93-103.

Biggs, R., M. Schluter, D. Biggs, E. L. Bohensky, S. BurnSilver, G. Cundill, V. Dakos, T. M. Daw, L. S. Evans, K. Kotschy, A. M. Leitch, C. Meek, A. Quinlan, C. Raudsepp-Hearne, M. D. Robards, M. L. Schoon, L. Schultz, and P. C. West. 2012. Toward Principles for Enhancing the Resilience of Ecosystem Services. Pages 421-+ *in* A. Gadgil and D. M. Liverman, editors. Annual Review of Environment and Resources, Vol 37.

Boch, C. A., S. Y. Litvin, F. Micheli, G. De Leo, E. A. Aalto, C. Lovera, C. B. Woodson, S. Monismith, and J. P. Barry. 2017. Effects of current and future coastal upwelling conditions on the fertilization success of the red abalone (*Haliotis rufescens*). ICES Journal of Marine Science **74**:1125-1134.

Boch, C. A., F. Micheli, M. AlNajjar, S. G. Monismith, J. M. Beers, J. C. Bonilla, A. M. Espinoza, L. Vazquez-Vera, and C. B. Woodson. 2018. Local oceanographic variability influences the performance of juvenile abalone under climate change. Scientific Reports **8**.

Braje, T. J., J. M. Erlandson, T. C. Rick, P. K. Dayton, and M. B. A. Hatch. 2009. Fishing from past to present: continuity and resilience of red abalone fisheries on the Channel Islands, California. Ecological Applications **19**:906-919.

Braje, T. J., T. C. Rick, P. Szpak, S. D. Newsome, J. M. McCain, E. A. Elliott Smith, M. Glassow, and S. L. Hamilton. 2017. Historical ecology and the conservation of large, hermaphroditic fishes in Pacific Coast kelp forest ecosystems. Science Advances **3**.

Brondizio, E. S., and F. M. Le Tourneau. 2016. Environmental governance for all. Science **352**:1272-1273.

Brown, F., and Y. K. Brown. 2009. Staying the Course, Staying Alive - Coastal First Nations fundamental truths: biodiversity, stewardship and sustainability. Biodiversity BC, Victoria, British Columbia, Canada.

Buckley, S. M., R. H. Thurstan, A. Tobin, and J. M. Pandolfi. 2017. Historical spatial reconstruction of a spawning-aggregation fishery. Conservation Biology **31**:1322-1332.

Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno, K. E. Carpenter, G. M. Carr, J. Chanson, A. M. Chenery, J. Csirke, N. C. Davidson, F. Dentener, M. Foster, A. Galli, J. N. Galloway, P. Genovesi, R. D. Gregory, M. Hockings, V. Kapos, J. F. Lamarque, F. Leverington, J. Loh, M. A. McGeoch, L. McRae, A. Minasyan, M. H. Morcillo, T. E. E. Oldfield, D. Pauly, S. Quader, C. Revenga, J. R. Sauer, B. Skolnik, D. Spear, D. Stanwell-Smith, S. N. Stuart, A. Symes, M. Tierney, T. D. Tyrrell, J. C. Vie, and R. Watson. 2010. Global biodiversity: Indicators of recent declines. Science **328**:1164-1168.

Cardinale, B. J., A. Gonzalez, G. R. H. Allington, and M. Loreau. 2018. Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. Biological Conservation **219**:175-183.

Carlsson, L., and F. Berkes. 2005. Co-management: concepts and methodological implications. Journal of Environmental Management **75**:65-76.

Casini, M., J. Hjelm, J. C. Molinero, J. Lovgren, M. Cardinale, V. Bartolino, A. Belgrano, and G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proceedings of the National Academy of Sciences of the United States of America **106**:197-202.

Cinner, J. E., T. R. McClanahan, M. A. MacNeil, N. A. J. Graham, T. M. Daw, A. Mukminin, D. A. Feary, A. L. Rabearisoa, A. Wamukota, N. Jiddawi, S. J. Campbell, A. H. Baird, F. A. Januchowski-Hartley, S. Hamed, R. Lahari, T. Morove, and J. Kuange. 2012. Comanagement of coral reef social-ecological systems. Proceedings of the National Academy of Sciences of the United States of America **109**:5219-5222.

Costanza, R., S. van der Leeuw, K. Hibbard, S. Aulenbach, S. Brewer, M. Burek, S. Cornell, C. Crumley, J. Dearing, C. Folke, L. Graumlich, M. Hegmon, S. Heckbert, S. T. Jackson, I. Kubiszewski, V. Scarborough, P. Sinclair, S. Sorlin, and W. Steffen. 2012. Developing an Integrated History and future of People on Earth (IHOPE). Current Opinion in Environmental Sustainability **4**:106-114.

Council of the Haida Nation. 2007. Towards a marine use plan for Haida Gwaii: A discussion paper. Pages 1-8. Council of the Haida Nation, Haida Gwaii, British Columbia, Canada.

Crim, R. N., J. M. Sunday, and C. D. G. Harley. 2011. Elevated seawater CO2 concentrations impair larval development and reduce larval survival in endangered northern abalone (*Haliotis kamtschatkana*). Journal of Experimental Marine Biology and Ecology **400**:272-277.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts and reduced expectations in kelp forest communities. Ecological Applications **8**:309-322.

Dearing, J. A., R. Wang, K. Zhang, J. G. Dyke, H. Haberl, M. S. Hossain, P. G. Langdon, T. M. Lenton, K. Raworth, S. Brown, J. Carstensen, M. J. Cole, S. E. Cornell, T. P. Dawson, C. P. Doncaster, F. Eigenbrod, M. Floerke, E. Jeffers, A. W. Mackay, B. Nykvist, and G. M. Poppy. 2014. Safe and just operating spaces for regional social-ecological systems. Global Environmental Change-Human and Policy Dimensions **28**:227-238.

Early-Capistran, M. M., A. Saenz-Arroyo, J. G. Cardoso-Mohedano, G. Garibay-Melo, S. H. Peckham, and V. Koch. 2018. Reconstructing 290 years of a data-poor fishery through ethnographic and archival research: The East Pacific green turtle (Chelonia mydas) in Baja California, Mexico. Fish and Fisheries **19**:57-77.

Estes, J. A., E. M. Danner, D. F. Doak, B. Konar, A. M. Springer, P. D. Steinberg, M. T. Tinker, and T. M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. Bulletin of Marine Science **74**:621-638.

Estes, J. A., D. F. Doak, A. M. Springer, and T. M. Williams. 2009. Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. Philosophical Transactions of the Royal Society B-Biological Sciences **364**:1647-1658.

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

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. Science **185**:1058-1060.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet earth. Science **333**:301-306.

Fedje, D. W., A. P. Mackie, R. J. Wigen, Q. Mackie, and C. Lake. 2005. Kilgii Gwaay: An early maritime site in the south of Haida Gwaii. Pages 187-203 *in* D. W. Fedje and R. W. Mathewes, editors. Haida Gwaii: Human History and Environment from the Time of the Loon to the Time of the Iron People UBC Press, Vancouver, British Columbia, Canada.

Fischer, J., T. A. Gardner, E. M. Bennett, P. Balvanera, R. Biggs, S. Carpenter, T. Daw, C. Folke, R. Hill, T. P. Hughes, T. Luthe, M. Maass, M. Meacham, A. V. Norstrom, G. Peterson, C. Queiroz, R. Seppelt, M. Spierenburg, and J. Tenhunen. 2015. Advancing sustainability through mainstreaming a social-ecological systems perspective. Current Opinion in Environmental Sustainability **14**:144-149.

Fisheries and Oceans Canada. 2012. Action Plan for the Northern Abalone (*Haliotis kamtschatkana*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Folke, C., R. Biggs, A. V. Norstrom, B. Reyers, and J. Rockstrom. 2016. Social-ecological resilience and biosphere-based sustainability science. Ecology and Society **21**.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics **35**:557-581.

Gonzalez, A., B. J. Cardinale, G. R. H. Allington, J. Byrnes, E. K. Arthur, D. G. Brown, D. U. Hooper, F. Isbell, M. I. O'Connor, and M. Loreau. 2016. Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. Ecology **97**:1949-1960.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol Evol **23**:202-210.

Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Bohm, T. M. Brooks, S. H. M. Butchart, K. E. Carpenter, J. Chanson, B. Collen, N. A. Cox, W. R. T. Darwall, N. K. Dulvy, L. R. Harrison, V. Katariya, C. M. Pollock, S. Quader, N. I. Richman, A. S. L. Rodrigues, M. F. Tognelli, J. C. Vie, J. M. Aguiar, D. J. Allen, G. R. Allen, G. Amori, N. B. Ananjeva, F. Andreone, P. Andrew, A. L. A. Ortiz, J. E. M. Baillie, R. Baldi, B. D. Bell, S. D. Biju, J. P. Bird, P. Black-Decima, J. J. Blanc, F. Bolanos, W. Bolivar, I. J. Burfield, J. A. Burton, D. R. Capper, F. Castro, G. Catullo, R. D. Cavanagh, A. Channing, N. L. Chao, A. M. Chenery, F. Chiozza, V. Clausnitzer, N. J. Collar, L. C. Collett, B. B. Collette, C. F. C. Fernandez, M. T. Craig, M. J. Crosby, N. Cumberlidge, A. Cuttelod, A. E. Derocher, A. C. Diesmos, J. S. Donaldson, J. W. Duckworth, G. Dutson, S. K. Dutta, R. H. Emslie, A. Farjon, S. Fowler, J. Freyhof, D. L. Garshelis, J. Gerlach, D. J. Gower, T. D. Grant, G. A. Hammerson, R. B. Harris, L. R. Heaney, S. B. Hedges, J. M. Hero, B. Hughes, S. A. Hussain, J. Icochea, R. F. Inger, N. Ishii, D. T. Iskandar, R. K. B. Jenkins, Y. Kaneko, M. Kottelat, K. M. Kovacs, S. L. Kuzmin, E. La Marca, J. F. Lamoreux, M. W. N. Lau, E. O. Lavilla, K. Leus, R. L. Lewison, G. Lichtenstein, S. R. Livingstone, V. Lukoschek, D. P. Mallon, P. J. K. McGowan, A. McIvor, P. D. Moehlman, S. Molur, A. M. Alonso, J. A. Musick, K. Nowell, R. A. Nussbaum, W. Olech, N. L. Orlov, T. J. Papenfuss, G. Parra-Olea, W. F. Perrin, B. A. Polidoro, M. Pourkazemi, P. A. Racey, J. S. Ragle, M. Ram, G. Rathbun, R. P. Reynolds, A. G. J. Rhodin, S. J. Richards, L. O. Rodriguez, S. R. Ron, C. Rondinini, A. B. Rylands, Y. S. de Mitcheson, J. C. Sanciangco, K. L. Sanders, G. Santos-Barrera, J. Schipper, C. Self-Sullivan, Y. C. Shi, A. Shoemaker, F. T. Short, C. Sillero-Zubiri, D. L. Silvano, K. G. Smith, A. T. Smith, J. Snoeks, A. J. Stattersfield, A. J. Symes, A. B. Taber, B. K. Talukdar, H. J. Temple, R. Timmins, J. A. Tobias, K. Tsytsulina, D. Tweddle, C. Ubeda, S. V. Valenti, P. P. van Dijk, L. M. Veiga, A. Veloso, D. C. Wege, M. Wilkinson, E. A. Williamson, F. Xie, B. E. Young, H. R. Akcakaya, L. Bennun, T. M. Blackburn, L. Boitani, H. T. Dublin, G. A. B. da Fonseca, C. Gascon, T. E. Lacher, G. M. Mace, S. A. Mainka, J. A. McNeely, R. A. Mittermeier, G. M. Reid, J. P. Rodriguez, A. A. Rosenberg, M. J. Samways, J. Smart, B. A. Stein, and S. N. Stuart. 2010. The impact of conservation on the status of the world's vertebrates. Science **330**:1503-1509.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature **486**:105-U129.

Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution **20**:380-386.

Hutchings, J. A., I. M. Cote, J. J. Dodson, I. A. Fleming, S. Jennings, N. J. Mantua, R. M. Peterman, B. E. Riddell, A. J. Weaver, and D. L. VanderZwaag. 2012. Is Canada fulfilling its obligations to sustain marine biodiversity? A summary review, conclusions, and recommendations. Environmental Reviews **20**:353-361.

Jackson, C. A., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**:629-637.

Jones, R., C. Rigg, and L. Lee. 2010. Haida Marine Planning: First Nations as a Partner in Marine Conservation. Ecology and Society **15**.

Kareiva, P., and M. Marvier. 2012. What Is Conservation Science? BioScience **62**:962-969.

Kim, T. W., J. P. Barry, and F. Micheli. 2013. The effects of intermittent exposure to low-pH and low-oxygen conditions on survival and growth of juvenile red abalone. Biogeosciences 10:7255-7262.

Krumhansl, K. A., J. N. Bergman, and A. K. Salomon. 2017. Assessing the ecosystem-level consequences of a small-scale artisanal kelp fishery within the context of climate-change. Ecological Applications **27**:799-813.

Laidre, K. L., J. A. Estes, M. T. Tinker, J. Bodkin, D. Monson, and K. Schneider. 2006. Patterns of growth and body condition in sea otters from the Aleutian archipelago before and after the recent population decline. Journal of Animal Ecology **75**:978-989.

Lee, L. C., J. Thorley, J. Watson, M. Reid, and A. K. Salomon. *in review*. Diverse knowledge systems reveal historical social-ecological and species abundance changes for gauging conservation status. Conservation Letters.

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

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

Lepofsky, D., N. F. Smith, N. Cardinal, J. Harper, M. Morris, Gitla, R. Bouchard, D. I. D. Kennedy, A. K. Salomon, M. Puckett, and K. Rowell. 2015. Ancient shellfish mariculture on the northwest coast of North America. American Antiquity **80**:236-259.

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

Liu, J. G., T. Dietz, S. R. Carpenter, M. Alberti, C. Folke, E. Moran, A. N. Pell, P. Deadman, T. Kratz, J. Lubchenco, E. Ostrom, Z. Ouyang, W. Provencher, C. L. Redman, S. H. Schneider, and W. W. Taylor. 2007. Complexity of coupled human and natural systems. Science **317**:1513-1516.

Lotze, H. K., and I. Milewski. 2004. Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecological Applications **14**:1428-1447.

Mathews, D. L., and N. J. Turner. 2017. Ocean Cultures: Northwest Coast ecosystems and indigenous management systems. Pages 169-206 *in* P. S. Levin and M. R. Poe, editors. Conservation for the Anthropocene Ocean: Interdisciplinary Science in Support of Nature and People. Academic Press, USA.

McKechnie, I., D. Lepofsky, M. L. Moss, V. L. Butler, T. J. Orchard, G. Coupland, F. Foster, M. Caldwell, and K. Lertzman. 2014. Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. Proceedings of the National Academy of Sciences of the United States of America **111**:E807-E816.

McClenachan, L., G. O'Connor, B. P. Neal, J. M. Pandolfi, and J. B. C. Jackson. 2017. Ghost reefs: Nautical charts document large spatial scale of coral reef loss over 240 years. Science Advances **3**.

Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza Montes, M. Rossetto, and G. A. De Leo. 2012. Evidence that marine reserves enhance resilience to climatic impacts. Plos One **7**.

Mistry, J., and A. Berardi. 2016. Bridging indigenous and scientific knowledge. Science **352**:1274-1275.

Mora, C., and P. F. Sale. 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. Marine Ecology Progress Series **434**:251-266.

Munguia-Vega, A., A. Saenz-Arroyo, A. P. Greenley, J. A. Espinoza-Montes, S. R. Palumbi, M. Rossetto, and F. Micheli. 2015. Marine reserves help preserve genetic diversity after impacts derived from climate variability: Lessons from the pink abalone in Baja California. Global Ecology and Conservation **4**:264-276.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423**:280-283.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol **14**:483-488.

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

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science **301**:955-958.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol Evol **10**:430.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology **86**:501-509.

Raworth, K. 2012. A safe and just space for humanity: Can we live within the doughnut? , Oxfam, Oxford, UK.

Ripple, W. J., J. A. Estes, O. J. Schmitz, V. Constant, M. J. Kaylor, A. Lenz, J. L. Motley, K. E. Self, D. S. Taylor, and C. Wolf. 2016. What is a trophic cascade? Trends Ecol Evol **31**:842-849.

Rockstrom, J., W. Steffen, K. Noone, A. Persson, F. S. Chapin, E. F. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sorlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen, and J. A. Foley. 2009. A safe operating space for humanity. Nature **461**:472-475.

Rogers-Bennett, L., P. L. Haaker, T. O. Huff, and P. K. Dayton. 2002. Estimating baseline abundances of the abalone in California for restoration. CalCOFI Report **43**:97-111.

Rosenblatt, A. E., M. R. Heithaus, M. E. Mather, P. Matich, J. C. Nifong, W. J. Ripple, and B. R. Silliman. 2013. The roles of large top predators in coastal ecosystems: New insights from long term ecological research. Oceanography **26**:156-167.

Rossetto, M., F. Micheli, A. Saenz-Arroyo, J. A. E. Montes, and G. A. De Leo. 2015. No-take marine reserves can enhance population persistence and support the fishery of abalone. Canadian Journal of Fisheries and Aquatic Sciences **72**:1503-1517.

Rudman, S. M., J. Heavyside, D. J. Rennison, and D. Schluter. 2016. Piscivore addition causes a trophic cascade within and across ecosystem boundaries. Oikos **125**:1782-1789.

Saenz-Arroyo, A., and C. M. Roberts. 2008. Consilience in fisheries science. Fish and Fisheries **9**:316-327.

Saenz-Arroyo, A., C. M. Roberts, J. Torre, and M. Carino-Olvera. 2005a. Using fishers' anecdotes, naturalists' observations and grey literature to reassess marine species at risk: the case of the Gulf grouper in the Gulf of California, Mexico. Fish and Fisheries **6**:121-133.

Saenz-Arroyo, A., C. M. Roberts, J. Torre, M. Carino-Olvera, and R. R. Enriquez-Andrade. 2005b. Rapidly shifting environmental baselines among fishers of the Gulf of California. Proceedings of the Royal Society B-Biological Sciences **272**:1957-1962.

Saenz-Arroyo, A., C. M. Roberts, J. Torre, M. Carino-Olvera, and J. P. Hawkins. 2006. The value of evidence about past abundance: marine fauna of the Gulf of California through the eyes of 16th to 19th century travellers. Fish and Fisheries **7**:128-146.

Salomon, A. K., K. Lertzman, K. Brown, K. B. Wilson, D. Secord, and I. McKechnie. 2018. Democratizing conservation science and practice. Ecology and Society **23**.

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

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591-596.

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

Sea Otter Recovery Team. 2007. Recovery Strategy for the Sea Otter (*Enhydra lutris*) in Canada. *Species at Risk Act* Recovery Strategy Series. Fisheries and Oceans Canada, Vancouver, British Columbia, Canada.

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

Soga, M., and K. J. Gaston. 2018. Shifting baseline syndrome: Causes, consequences, and implications. Frontiers in Ecology and the Environment **16**:222-230.

Soule, M. E. 1985. What is conservation biology? BioScience **35**:727-734.

Soule, M. E. 2013. The "New Conservation". Conservation Biology **27**:895-897.

Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences of the United States of America **100**:12223-12228.

Steffen, W., K. Richardson, J. Rockstrom, S. E. Cornell, I. Fetzer, E. M. Bennett, R. Biggs, S. R. Carpenter, W. de Vries, C. A. de Wit, C. Folke, D. Gerten, J. Heinke, G. M. Mace, L. M. Persson, V. Ramanathan, B. Reyers, and S. Sorlin. 2015. Planetary boundaries: Guiding human development on a changing planet. Science **347**.

Stephenson, J., F. Berkes, N. J. Turner, and J. Dick. 2014. Biocultural conservation of marine ecosystems: Examples from New Zealand and Canada. Indian Journal of Traditional Knowledge **13**:257-265.

Stevenson, C. F., K. W. Demes, and A. K. Salomon. 2016. Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. Ecology and Evolution **6**:1041-1053.

Tengo, M., E. S. Brondizio, T. Elmqvist, P. Malmer, and M. Spierenburg. 2014. Connecting diverse knowledge systems for enhanced ecosystem governance: The multiple evidence base approach. Ambio **43**:579-591.

Thurstan, R. H., E. Game, and J. M. Pandolfi. 2017. Popular media records reveal multi-decadal trends in recreational fishing catch rates. Plos One **12**.

Thurstan, R. H., L. McClenachan, L. B. Crowder, J. A. Drew, J. N. Kittinger, P. S. Levin, C. M. Roberts, and J. M. Pandolfi. 2015. Filling historical data gaps to foster solutions in marine conservation. Ocean & Coastal Management **115**:31-40.

Tittensor, D. P., M. Walpole, S. L. L. Hill, D. G. Boyce, G. L. Britten, N. D. Burgess, S. H. M. Butchart, P. W. Leadley, E. C. Regan, R. Alkemade, R. Baumung, C. Bellard, L. Bouwman, N. J. Bowles-Newark, A. M. Chenery, W. W. L. Cheung, V. Christensen, H. D. Cooper, A. R. Crowther, M. J. R. Dixon, A. Galli, V. Gaveau, R. D. Gregory, N. L. Gutierrez, T. L. Hirsch, R. Hoft, S. R. Januchowski-Hartley, M. Karmann, C. B. Krug, F. J. Leverington, J. Loh, R. K. Lojenga, K. Malsch, A. Marques, D. H. W. Morgan, P. J. Mumby, T. Newbold, K. Noonan-Mooney, S. N. Pagad, B. C. Parks, H. M. Pereira, T. Robertson, C. Rondinini, L. Santini, J. P. W. Scharlemann, S. Schindler, U. R. Sumaila, L. S. L. Teh, J. van Kolck, P. Visconti, and Y. M. Ye. 2014. A mid-term analysis of progress toward international biodiversity targets. Science **346**:241-244.

Turner, N. J. 2005. The Balance between Humans and Nature. The Earth’s Blanket: Traditional Teachings for Sustainable Living. Douglas & McIntyre, Vancouver, BC.

Turner, N. J., F. Berkes, J. Stephenson, and J. Dick. 2013. Blundering Intruders: Extraneous Impacts on Two Indigenous Food Systems. Human Ecology **41**:563-574.

UN CBD. 2010. X/2. The Strategic Plan for Biodiversity 2011-2020 and the Aichi Biodiversity Targets. United Nations Environment Programme, Convention on Biological Diversity, Nagoya, Japan.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Mellilo. 1997. Human domination of the earth's ecosystems. Science **277**:494-499.

Walker, B., and D. Salt. 2006. Resilience thinking: sustaining ecosystems and people in a changing world. Island Press, Washington DC, USA.

Waters, C. N., J. Zalasiewicz, C. Summerhayes, A. D. Barnosky, C. Poirier, A. Galuszka, A. Cearreta, M. Edgeworth, E. C. Ellis, M. Ellis, C. Jeandel, R. Leinfelder, J. R. McNeill, D. D. Richter, W. Steffen, J. Syvitski, D. Vidas, M. Wagreich, M. Williams, Z. S. An, J. Grinevald, E. Odada, N. Oreskes, and A. P. Wolfe. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. Science **351**:137-+.

Watson, J. C. 2000. The effects of sea otters (*Enhydra lutris*) on abalone (*Haliotis* spp.) populations. Canadian Special Publication of Fisheries and Aquatic Sciences **130**:123-132.

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

Westley, F., P. Olsson, C. Folke, T. Homer-Dixon, H. Vredenburg, D. Loorbach, J. Thompson, M. Nilsson, E. Lambin, J. Sendzimir, B. Banerjee, V. Galaz, and S. van der Leeuw. 2011. Tipping toward sustainability: Emerging pathways of transformation. Ambio **40**:762-780.

Worm, B., E. B. Barbier, N. Beaumont, E. Duffy, C. Folke, B. S. Halpern, J. B. Jackson, H. K. Lotze, F. Micheli, K. A. Selkoe, J. J. Stachowicz, and K. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science **314**:787-790.

Young, H. S., D. J. McCauley, M. Galetti, and R. Dirzo. 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. Pages 333-358 *in* D. J. Futuyma, editor. Annual Review of Ecology, Evolution, and Systematics, Vol 47.

Chapter 2. Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator[1]

Abstract

Managing for simultaneous recovery of interacting species, particularly top predators and their prey, is a longstanding challenge in applied ecology and conservation. The effects of sea otters (*Enhydra lutris kenyoni*) on abalone (*Haliotis* spp.) is a salient example along North America's west coast where sea otters are recovering from 18th and 19th century fur trade while efforts are being made to recover abalone from more recent overfishing. To understand the direct and indirect effects of sea otters on northern abalone (*H. kamtschatkana*) and the relative influence of biotic and abiotic conditions, we surveyed subtidal rocky reef sites varying in otter occupation time in three regions of British Columbia, Canada. Sites with sea otters had lower densities of exposed abalone than those without otters (1.38 ± 0.51/20m^{-2} versus 7.56 ± 0.98/20m^{-2}), but higher densities of cryptic abalone (2.96 ± 0.75/20m^{-2} versus 1.31 ± 0.20/20m^{-2}) and higher proportions of cryptic abalone (53.35 ± 0.07% versus 16.47 ± 0.03%). Abalone densities were greater in deeper versus shallower habitats at sites with sea otters compared to sites without otters. Sea otter effects on exposed abalone density were three times greater in magnitude than that of any other factor, whereas substrate and wave exposure effects on cryptic abalone were six times greater than that of sea otters. While higher substrate complexity may benefit abalone by providing refugia from sea otter predation, lab experiments revealed that it may also lead to higher capture efficiency by sunflower stars (*Pycnopodia helianthoides*), a ubiquitous mesopredator, compared to habitat with lower complexity. Sea otter recovery indirectly benefitted abalone by decreasing biomass of predatory sunflower stars and competitive grazing sea urchins, while increasing stipe density and depth of kelp that provides food and protective habitat. Importantly, abalone persisted in the face of sea otter recovery, albeit at lower densities of smaller and more cryptic individuals. We provide empirical

---

[1] A version of this chapter has been published as: Lee, L.C., Watson, J.C., Trebilco, R., Salomon, A.K. (2016) Indirect effects and prey behavior mediate interactions between an endangered prey and recovering predator. *Ecosphere* **7**.

evidence of how complex ecological interactions influence the effects of recovering predators on their recovering prey. This ecosystem-based understanding can inform conservation trade-offs when balancing multifaceted ecological, cultural and socio-economic objectives for species at risk.

Introduction

Disentangling the direct and indirect effects of predators on their prey, and how these effects are mediated by environmental conditions, is a longstanding challenge in ecology. This understanding is particularly important in the context of predator recovery from overexploitation, and even more so when both predator and prey are of conservation concern (Soulé et al. 2005, Marshall et al. 2016). While re-establishing populations of strongly interacting top predators can trigger a cascade of indirect effects that may restore ecological functions, it can also put already vulnerable prey in further peril (Estes 1996, Soulé et al. 2003, 2005, Estes et al. 2011, Ripple et al. 2014). Fortunately, a clear understanding of the factors that mediate predator-prey interactions and alter their effects on prey density, size and behavior, can inform trade-offs in conservation objectives elicited by food web interactions. Here, we examined the ecological factors that mediate the interaction between endangered northern abalone (*Haliotis kamtchatkana*) and recovering sea otter (*Enhydra lutris kenyoni*) populations along the west coast of British Columbia (BC).

Predators induce both changes in prey abundance and behavior. Consequently, as predator populations recover, prey depletion through time varies as a function of predator per capita attack rates including search time and handling time (Holling 1959), and prey behavioral response to changes in predation risk. Prey can reduce their risk of predation by becoming increasingly cryptic (hiding in refugia), reducing the proportion of time they spend out in the open (exposed) to acquire food (Sih 1980, Lima 1998, Preisser et al. 2005). Risk-averse behavior may also entail selection of lower-risk but lower quality habitat, or reduced activity levels to minimize predator detection (Sih 1982, Lima 1998). Importantly, the strength of these anti-predator behaviors can differ depending on temporal and spatial variation in predation risk and the availability of refugia (Orrock et al. 2013). Predators themselves can also mediate outcomes of predator-prey interactions when they affect the abundance of alternate predators and/or indirectly increase food availability, habitat quality, and/or refugia for their prey.

Determining the relative influence of direct and indirect effects of predators on their prey, and context-dependent effects, remains a challenge. Multiple top-down (consumer-driven) and bottom-up (resource-driven) factors can drive complex ecological interactions across different spatial and temporal scales, varying in magnitude with biotic and abiotic conditions to affect prey recovery in multiple ways (Polis and Strong 1996, Thrush and Dayton 2010). Furthermore, these forces are affected by historical and contemporary food web alterations (Simenstad et al. 1978, Salomon et al. 2007) and linked social-ecological systems (Liu et al. 2007, Salomon et al. 2015). Consequently, understanding the effects of predators on prey within their ecological and social context is particularly important for informing the conservation trade-offs involved in the recovery of interacting species-at-risk (Sloan 2004).

Sea otters are keystone predators (Paine 1969, Power et al. 1996) whose re-introduction and range expansion on the Pacific Coast of North America exemplify how successful recovery of one species-at-risk can have important ecological consequences for another (Sloan 2004). By the early 20th century, ecological extirpation of sea otters released their macroinvertebrate prey from high predation pressure, allowing prey populations including abalone to flourish (Tegner and Dayton 2000, Watson 2000, Sloan and Dick 2012). Northern abalone, a gastropod mollusc that grazes primarily on drift kelp, became a ubiquitous and abundant species on intertidal and shallow subtidal temperate rocky reefs in BC (Watson 2000, Sloan 2004). An intensive commercial dive fishery from the 1960s to 1980s dramatically reduced mature abalone abundance, leading to closure of all BC abalone fisheries in 1990 (Farlinger 1990, Fisheries and Oceans Canada 2012). Abalone surveys continued to show little evidence of recovery 20 years later (COSEWIC 2009), a conservation challenge reflected in abalone species worldwide (Hobday et al. 2001, Micheli et al. 2008). Meanwhile, sea otters re-introduced to BC between 1969 and 1972 (Bigg and MacAskie 1978) were successfully re-establishing and expanding their range. By 2009, sea otters had been legally down-listed from their original status of *endangered* to *special concern* under Canada's *Species at Risk Act* (Fisheries and Oceans Canada 2014), whereas northern abalone had been up-listed from *threatened* to *endangered* status by 2011 (Fisheries and Oceans Canada 2012).

In spite of strong interactions, abalone and sea otters are both currently managed using a single-species approach (Fisheries and Oceans Canada 2007, Sea

Otter Recovery Team 2007), leading to conservation objectives and recovery targets that are unlikely to be simultaneously achieved (Chadès et al. 2012). Previous empirical studies of abalone have considered a subset of the key biotic and abiotic factors known to affect abalone abundance and distribution, but only in the absence of sea otters (Sloan and Breen 1988, Tomascik and Holmes 2003, Lessard and Campbell 2007, Campbell and Cripps 1998). Only one study in BC has explicitly considered the effects of sea otters on abalone but without accounting for other biotic and abiotic factors (Watson 2000), limiting our empirical understanding of sea otter-abalone interactions under varying environmental conditions (for interactions between sea otters and other abalone species in California, see Fanshawe et al. 2003, Raimondi et al. 2015).

Here, we took advantage of spatial gradients of sea otter recovery along the west coast of Canada to investigate the direct and indirect effects of predator recovery on abalone density, size, biomass and behavior. We concurrently evaluated the effect of other key biotic and abiotic factors known to affect abalone: substrate, depth, wave exposure, kelp density, sea urchin biomass and sunflower star (*Pycnopodia helianthoides*) biomass. To explore the possible role of mesopredator release on abalone mortality in areas that remain otter free, we conducted laboratory experiments to test how substrate complexity (spatial refugia) and the presence of alternative prey (red sea urchins; *Mesocentrotus franciscanus*) may mediate predation outcomes between a ubiquitous mesopredator, the sunflower star, and abalone. Finally, we discuss the conservation trade-offs that occur when predator recovery has both negative direct and positive indirect effects on an endangered prey.

Methods

Study site context and field survey design

Our study was conducted in three regions across British Columbia, Canada, varying in broad-scale patterns of sea otter recovery and abundance, latitude, oceanographic context, and human influence (Fig. 2.1). During the spring and summer of 2010 and 2011, we surveyed subtidal rocky reef sites on Haida Gwaii (HG; n = 23), BC’s central coast (CC; n = 19) and the west coast of Vancouver Island (WCVI; n = 18). Within each region, we selected sites based on: (1) presence of suitable abalone habitat (semi wave-exposed to highly wave-exposed rocky reefs), (2) previously reported abalone occurrence (summarized in Sloan and Breen 1988), and (3) local expert knowledge. Sites were selected across gradients of sea otter occupation time spanning from 0–38 years in a space-for-time substitution (Pickett 1989, Hargrove and Pickering 1992) in the two regions where sea otters are recovering (CC and WCVI). Across all three regions, sites also varied in a suite of biotic and abiotic factors known to influence abalone abundance, size and distribution: wave exposure and transects within sites varied in depth, kelp stipe density, substrate complexity, sea urchin biomass, and sunflower star biomass (Sloan and Breen 1988, Campbell and Cripps 1998, Tomascik and Holmes 2003, Lessard and Campbell 2007). Abalone, other macroinvertebrates and transect-level abiotic factors were quantified using 10 m x 2 m belt transects placed parallel to shore, with the ends of each transect at least 5 m apart. Replicate transects were surveyed at each site (n = 6–9) with three transects in each of two or three depth ranges (0–2 m, 2–5 m, 5–10 m below chart datum) to capture the subtidal range for the majority of abalone (Sloan and Breen 1988).

Sea otter occupation time. Sea otter occupation time on the CC was determined from the first year of sighting of an otter raft (≥3 individuals together) within a 3 nautical mile radius of the site (Nichol et al. 2009, 2015). For WCVI sites, sea otter survey data and published records were used to determine occupation time (Watson 1993, Nichol et al. 2009, Watson and Estes 2011, Nichol et al. 2015). Sea otters, which were re-introduced to northern WCVI, included approximately 5000 individuals along the WCVI at the time of our survey with a regional growth rate of about 7% per year (Nichol et al. 2015). Along the CC, groups of sea otters were first recorded in 1989 and at the time of our survey included approximately 800 individuals with a regional growth rate of about 13% per year (Nichol et al. 2015). Both CC and WCVI have sea otter-free areas (no observations of 3 or more individuals in a group or raft, following Nichol et al. 2009) and HG has remained sea otter-free since otters were extirpated, although 17 confirmed sightings of individual sea otters were recorded between 1970 and 2012 (Sloan and Dick 2012).

Abalone. All abalone visible to the observer without turning over rocks and removing algae were counted and their length measured to the nearest millimeter. We classified observed abalone sheltering behavior (i.e., behavioral class) as exposed (visible out in the open; Plate 2.1A), covered (under kelp, other algae, seagrass and urchin spine canopies; Plate 2.1B), or cryptic (in a crevice or between boulders; Plate

2.1CG). Abalone biomass was calculated from an established length-mass regression (Zhang et al. 2007; Appendix A: Table A1).

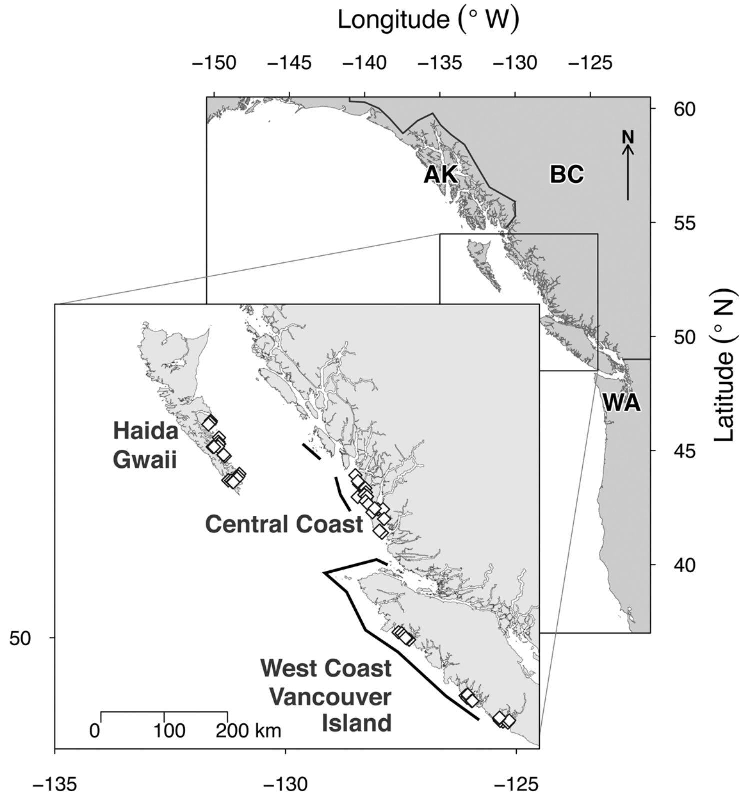

Figure 2.1 **Subtidal rocky reef study sites (open diamonds) along the coast of British Columbia, Canada, in three regions: Haida Gwaii (n = 23), Central Coast (n = 19) and West Coast Vancouver Island (n = 18), with the range of sea otter occupation at the time of surveys highlighted in bold black lines.**

Sea urchin and sunflower star biomass. Sea urchins were counted and test diameters measured to the nearest centimeter, including red urchin, *Strongylocentrotus purpuratus* (purple urchin) and *S. droebachiensis* (green urchin). For transects with >10 urchins/m^2, we measured a random sample of at least 50 urchins per species per transect and counted the remainder. For a subset of 25 transects on the CC in 2010, some red urchins were classified and counted in three test diameter size classes: small <5 cm, medium 5–9 cm, and large >9 cm. Urchin biomass was estimated from established length-mass regressions for each species (Appendix A: Table A1). For red urchins counted in size classes, we used the median value of each size class for length to biomass conversions (small = 4 cm, medium = 7 cm, large = 10 cm). For urchins that were counted but not measured, missing lengths were randomly sampled from measured urchins of the same species along each transect. We counted and measured the diameter of sunflower stars to the nearest centimeter and estimated biomass from an established length-mass regression (Appendix A: Table A1).

Kelp stipe density. We quantified kelp stipe density of individuals >0.15 m in height within five randomly placed 1 x 1 m quadrats along each transect (see Appendix A: Table A2 for kelp species list). At seven sites on the CC, we sampled five random quadrats in 2011 within the same depth range as each transect with quadrats missing from 2010 surveys.

Substrate complexity. We classified substrate types using a modified Wentworth scale: sand, shell, pea gravel (2–16 mm diameter (D)), gravel (16–64 mm D), cobble (64–256 mm D), small boulder (256–500 mm D), medium boulder (500–1000 mm D), large boulder (>1000 mm D), smooth bedrock, lumpy bedrock, or creviced bedrock. Substrate type was recorded at two spatial scales: (1) transect-level – primary and secondary substrates determined by percent cover over the entire transect; and (2) abalone-level – substrate the abalone was using. To account for substrate suitability (stable rock) and availability of cryptic habitat, each substrate type was assigned a score for substrate complexity. We determined complexity by summing scores accounting for three criteria: stability (0–3), presence/absence of cryptic habitat (1/0) and relative amount of cryptic habitat (0–3), for a maximum score of 7 (Appendix A: Table A3). To account for differences in the contribution of secondary substrate to overall complexity, transect-level complexity values were determined by weighting the primary substrate score by 70% and secondary substrate score by 30% (based on mean percent cover of primary and secondary substrate from previous surveys in abalone habitat; L. Lee, *unpublished data*).

Wave exposure and depth. We represented wave exposure as average fetch for 5° compass bearing intervals measured in ArcGIS 9.3 to a maximum single fetch length of 200 km (following Ekebom et al. 2003). We used average fetch from combined southeast (90–180°) and northwest (270–360°) bearings to represent prevailing southeast winter storms and northwest summer winds (Thomson 1981). Depths were tide-corrected to chart datum based on the time of survey and closest tidal station with NobelTec Lite Version 2.1.

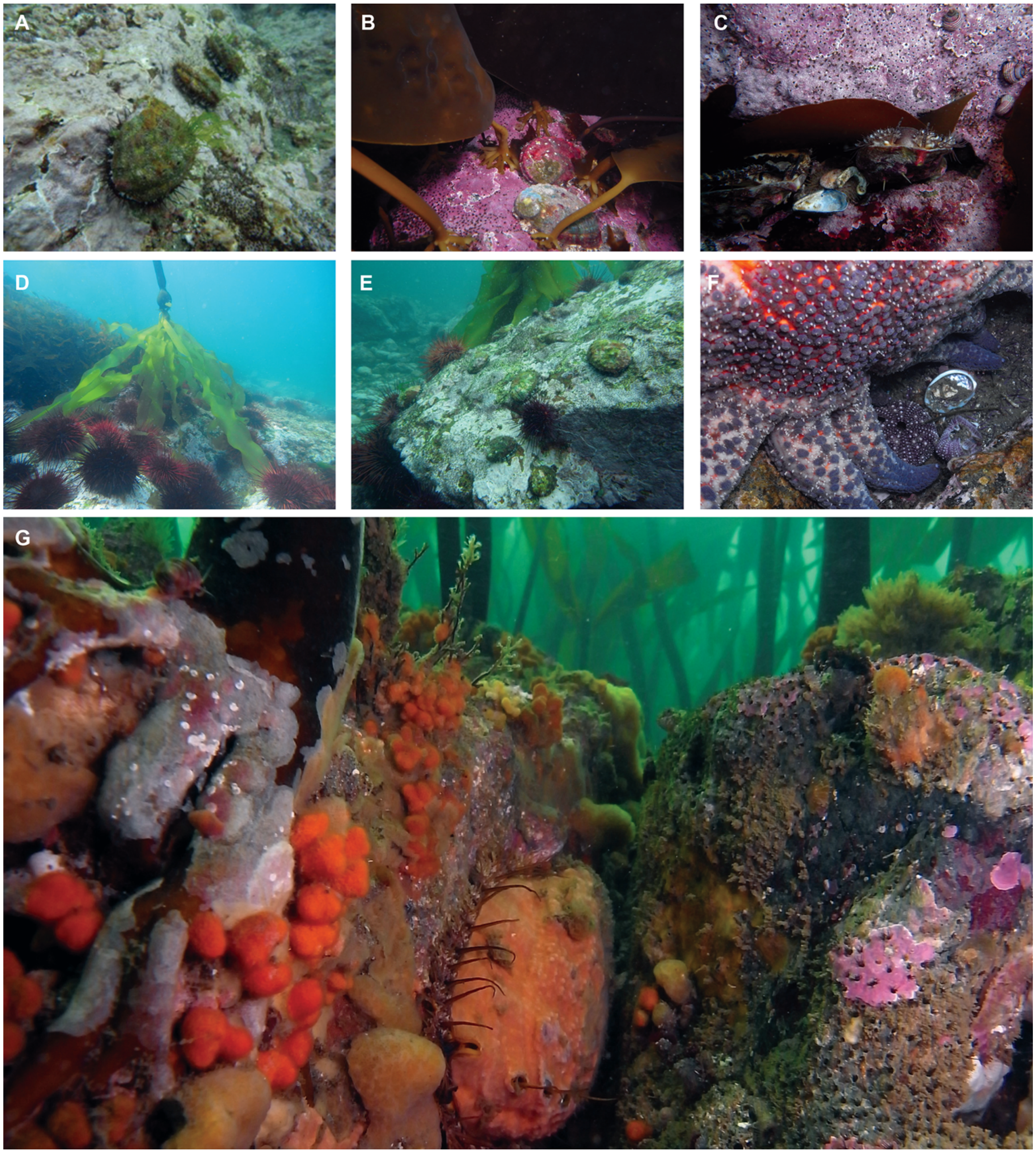

Plate 2.1 **Abalone in different behavioral classes: (A) three exposed abalone in urchin barrens habitat, (B) two covered abalone under Laminarian kelp in an area occupied by sea otters for three years, and (C) two cryptic abalone capturing drift kelp in an area occupied by sea otters for six years. Natural history observations: (D) red urchins capturing bull kelp in an urchin barrens, (E) nine abalone moving in to feed on kelp captured by red urchins, (F) abalone shell and urchin test expelled following digestion by a sunflower star in habitat with high complexity substrate, and (G) cryptic abalone in a kelp forest occupied by sea otters. Images by Lynn Lee.**

Lab predation experimental design

We tested the extent to which crevice habitat and alternate prey affect sunflower star predation rates on abalone. We placed hatchery-raised second-generation northern abalone in 1.24 x 0.90 x 0.30 m fiberglass tanks under three treatments: + crevice (addition of crevice habitat using four 9-cm high concrete blocks 20 x 19 cm in area, with 6-cm high x 13-cm long archways); + urchins (addition of three 65–70 mm diameter red sea urchins); and control (no crevice habitat or alternate prey). We conducted 3-hour long experimental trials randomly replicated in four separate tanks over three days. At the start of each trial, we placed one wild-caught sunflower star (45–70 cm diameter) held without food for 5–7 days into a trial tank with six abalone (55–75 mm length; mimicking aggregative behavior and high abalone transect densities up to 7.5 abalone/m^2) acclimatized in tanks overnight. Sunflower star and abalone behavior were continuously observed over the entire trial. Sunflower star behavior was noted as stationary, cruising (moving at slow speed without tracking abalone), hunting (tracking abalone), attacking (contact with abalone being hunted), and consuming (ingesting captured abalone). Each attack was classified as successful (abalone consumed) or unsuccessful (abalone escaped). Two trials could not be used because the sunflower stars did not move over the entire trial and these were not considered representative of hunting behavior (+ crevice, n = 3; + urchins, n = 3; control, n = 4).

We calculated capture efficiency (α; number of prey eaten as a function of search time and number of prey; Eq.1), handling time per abalone (h; Eq. 2), and feeding rate assuming a Type II prey-dependent functional response where the rate at which a predator captures and consumes prey is constrained by search and handling time (Eq. 3; Holling 1959; Gotelli 2008):

$$\alpha = \frac{n}{t_s V} \text{ (Eq.1)}$$

where $n =$ number of prey items captured in total trial time t, t_s = search time, and V = abundance of prey;

$$h = \frac{t_h}{n} \text{ (Eq. 2)}$$

where t_h = handling time, and n = number of prey items captured in total trial time t; and

$$\frac{n}{t} = \frac{\alpha V}{1+\alpha V h} \text{ (Eq. 3)}$$

where α, h and V are defined in Eq. 1 and Eq. 2, and t = total trial time (180 min). Search time, t_s, was defined as the sum of cruising, hunting and unsuccessful attack times. Handling time, t_h, was defined as the sum of successful attack and consumption time. All attacks were unsuccessful in one + urchins trial, resulting in n = 2 for feeding rate and handling time for this treatment. The number of trials was constrained due to limited access to captive-bred endangered abalone and lab facilities. Lastly, we measured the speed of abalone fleeing from sunflower stars in the lab and field, and the speed of hunting sunflower stars and fleeing urchins in the lab.

Statistical analysis

Field surveys. To test which biotic and abiotic factors drove abalone density and biomass, we fit generalized linear mixed effects models (GLMMs) of total abalone and three behavioral classes: exposed, covered and cryptic. In these models, the three-level categorical variable of region, seven continuous predictor variables – sea otter occupation time, depth, substrate complexity, wave exposure, kelp stipe density, urchin biomass, and sunflower star biomass – and an interaction between depth and sea otter occupation time were treated as fixed effects while site was treated as a random effect (see Appendix B: Table B1 for saturated models). We checked for multi-collinearity among all response variables using correlation coefficients and variance inflation factors (VIF; Zuur et al. 2010, Zuur et al. 2013). Correlation coefficients >0.6 and VIF scores >3.5 indicate variables considered to have a high degree of collinearity that may be problematic if collinear variables are included in the same model (Zuur et al. 2009). Correlation coefficients in this analysis ranged from 0.01–0.41 and all VIF scores were <3, indicating that multi-collinearity is unlikely to be a problem in this analysis (Appendix B: Fig. B1). To facilitate direct comparison of parameter coefficients among continuous variables on different scales and between continuous and categorical variables, we standardized all continuous variables by subtracting their mean and dividing by two standard deviations (Gelman 2008). Models of abalone density were fit with a negative binomial likelihood and exponential link function, accounting for zero-inflation as needed.

Abalone biomass was modeled as a two-stage Hurdle model. First, we determined factors that best predicted abalone presence/absence, then we modeled factors that best predict abalone biomass with the non-zero subset of these data (Barry and Welsh 2002). Models of abalone presence/absence were analyzed with a binomial likelihood and logit link function, while models of abalone biomass were analyzed with a gamma likelihood and exponential link function. All models were run in R version 3.1.0 using the glmmADMB package (R Development Core Team 2008, Fournier et al. 2012, Skaug et al. 2013).

To test for the effect of these biotic and abiotic predictor variables on abalone length, we fit linear mixed-effects models with Gaussian likelihoods and identity link functions (see Appendix B: Table B1 for saturated models) using the lme4 package in R (Bates et al. 2014). Abalone lengths from all transects within a site were pooled and individual lengths were centered about zero by subtracting the global mean length within each dataset (i.e., grouped for total, exposed, covered and cryptic abalone lengths separately) prior to model fitting to facilitate use of Gaussian likelihoods. To evaluate whether transect-level or abalone-level substrate was a better predictor of abalone length, we fit abalone length models to substrate complexity at both spatial scales. Model results were similar in explaining variation in the length of total, exposed and covered abalone, but abalone-level substrate explained more of the variation for cryptic abalone, therefore we used abalone-level substrate for length models.

We fit GLMMs to test the effect of sea otters and other biotic and abiotic factors on sunflower star presence and biomass, urchin presence and biomass, and kelp stipe density. In all models, standardized continuous factors of sea otter occupation time, depth, substrate, wave exposure, and an interaction between depth and sea otter occupation time were treated as fixed effects while site was treated as a random effect. In addition, urchin biomass was treated as a fixed effect in the kelp and sunflower star models, and both kelp stipe density and sunflower star biomass were treated as fixed effects in the urchin models (Appendix B: Table B2). Models of sunflower star and urchin presence were fit with a binomial likelihood and logit link function, while those for biomass were fit with a gamma likelihood and exponential link function. Models of kelp stipe density were fit with a negative binomial likelihood and exponential link function. Kelp, sunflower star and urchin models were run in R version 3.1.0 using the glmmADMB package (R Development Core Team 2008, Fournier et al. 2012, Skaug et al. 2013).

We evaluated relative support for models with all possible combinations of fixed factors using Akaike information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2004). Models were standardized to the best-fit and most parsimonious model to determine ΔAIC_c values. Using the dredge function in the R package MuMIn (Bartoń 2013), we generated an initial set of candidate models based on their cumulative Akaike weights (W_i), indicating the relative strength of evidence in favor of a given model. The dredge function did not include the random effect of site in model evaluation using glmmADMB, and also did not determine the degrees of freedom in model sets that included both models with and without the categorical factor of region. We therefore ran each model within the 95% cumulative W_i model set individually using glmmADMB to determine AIC_c values for each model. The final model set included models within $\Delta AIC_c < 2$. We evaluated the effect of biotic and abiotic factors on abalone based on three attributes: (1) the magnitude and direction of parameter coefficients, (2) 95% confidence intervals (CIs) around coefficient estimates, and (3) relative variable importance (RVIs) of each parameter, calculated by summing the W_i of candidate models in which the parameter was found (Burnham and Anderson 2002). Effects were considered weak and imprecise if the parameter coefficients were close to zero and their confidence intervals were widely overlapping zero.

To examine the effect of sea otter occupation time on the proportion of abalone in different behavioral classes, we fit and compared three alternative models: (1) non-linear, (2) linear, and (3) null (intercept only). We fit a non-linear exponential decay curve for exposed and covered abalone, based on the premise that exposed abalone would be most susceptible to sea otter predation, followed by covered abalone, such that proportions of both should decline over time: $y = a \times (1 - b)^x$. Conversely, we fit a saturation curve for cryptic abalone, under the hypothesis that the proportion of cryptic abalone should increase with sea otter occupation time: $y = a \times x / (b + x)$. We compared model AIC_c values to determine the strength of evidence supporting each of the three alternative relationships for exposed, covered and cryptic abalone.

Predictive models for Haida Gwaii region. We generated model predictions for the effect of sea otter occupation on abalone density using coefficients, in their original units, from the model with the lowest AIC_c. To illustrate the interaction effect between depth and otter occupation time for HG, we predicted abalone density as a function of otter occupation time for two depths (0 m and the average surveyed depth of 4.3 m chart datum), with all other continuous factors set to their average values, the categorical HG region coefficient set to 1, and the CC and WCVI coefficients set to 0.

Lab experiments. We used linear models to compare capture efficiency, feeding rate and handling time of sunflower stars between treatments, where each response variable was modeled as a function of treatment and compared to a null model (intercept only). We also constructed GLMMs of the probability of each of six abalone being consumed per trial with treatment as a fixed effect and trial as a random effect, using a binomial likelihood and logit link function (Appendix B: Table B3). Abalone seemed to tire, moving more slowly as each trial progressed, particularly in tanks where sunflower stars were very active. To test for the effect of abalone fatigue, we constructed GLMMs of sunflower star attack success with treatment and trial run time as fixed effects and trial as a random effect, using a binomial likelihood and logit link function (Appendix B: Table B3).

Results

Biotic and abiotic factors influence abalone distribution and abundance

The magnitude, direction and identity of key factors affecting abalone abundance, size and distribution differed for each behavioral class (Figs. 2.2-2.4; Appendix C: Figs. C1-C4; Appendix D: Tables D1-D4). Consequently, we report the relative strength of evidence for each factor on abalone density, length and biomass; factor by factor, and by behavioral class (Fig. 2.4). We also show the best model for each abalone population metric by behavioral class (Table 2.1).

Sea otter occupation time. Sea otter occupation time had a strong negative effect on exposed abalone density, length, and thus overall biomass (RVI = 1, 1, 1, respectively; Figs. 2.2B, 2.4B), with an effect on density that was three times greater than the magnitude of any other local-scale biotic or abiotic factor. In contrast, sea otter occupation time had a weakly positive but imprecise effect on covered and cryptic abalone density (RVI = 0.85, 0.66, respectively; Figs. 2.2CD, 2.4CD). Specifically, the strong negative effect of sea otter occupation time on exposed abalone density was 18 times greater than its weakly positive effect on cryptic and covered abalone densities, for which other local-scale biotic and abiotic factors had greater relative importance and magnitudes of effect (Fig. 2.4BCD). Consequently, the effect of sea otter occupation time on total abalone density was negative (RVI = 1; Fig. 2.4A). Abalone biomass declined with increasing sea otter occupation time due to decreasing size across all behavioral classes, with the largest effect on exposed abalone and the smallest effect on cryptic abalone (Fig. 2.4BCD).

Substrate complexity. Increasing substrate complexity was positively associated with abalone density across all behavioral classes (Fig. 2.4). Substrate complexity had the strongest effect on density of cryptic abalone (RVI = 1; Fig. 2.4D), a moderately important and certain effect on exposed abalone (RVI = 0.80; Fig. 2.4B), and an imprecise effect of low importance on covered abalone (RVI = 0.18; Fig. 2.4C). Substrate complexity was also an important positive driver for cryptic abalone biomass and length (RVIs = 1; Fig. 2.4D), yet had low to no importance for exposed and covered abalone length (RVIs <0.25; Fig. 2.4BC).

Wave exposure. Increasing wave exposure to prevailing NW-SE winds was associated with lower exposed and cryptic abalone densities, but was not important for covered abalone (Fig. 2.4BCD). Wave exposure was the strongest local-scale driver for cryptic abalone density (RVI = 1; 2.Fig. 2.4D), less important for exposed abalone (RVI = 0.82; Fig. 2.4B), and of no importance to covered abalone density (RVI = 0; Fig. 2.4C). Wave exposure had a strong negative effect on covered abalone length (RVI = 1; Fig. 2.4C), but an imprecise and less important effect on exposed abalone (RVI = 0.39; Fig. 2.4B), and was of no importance to cryptic abalone length (RVI = 0; Fig. 2.4D).

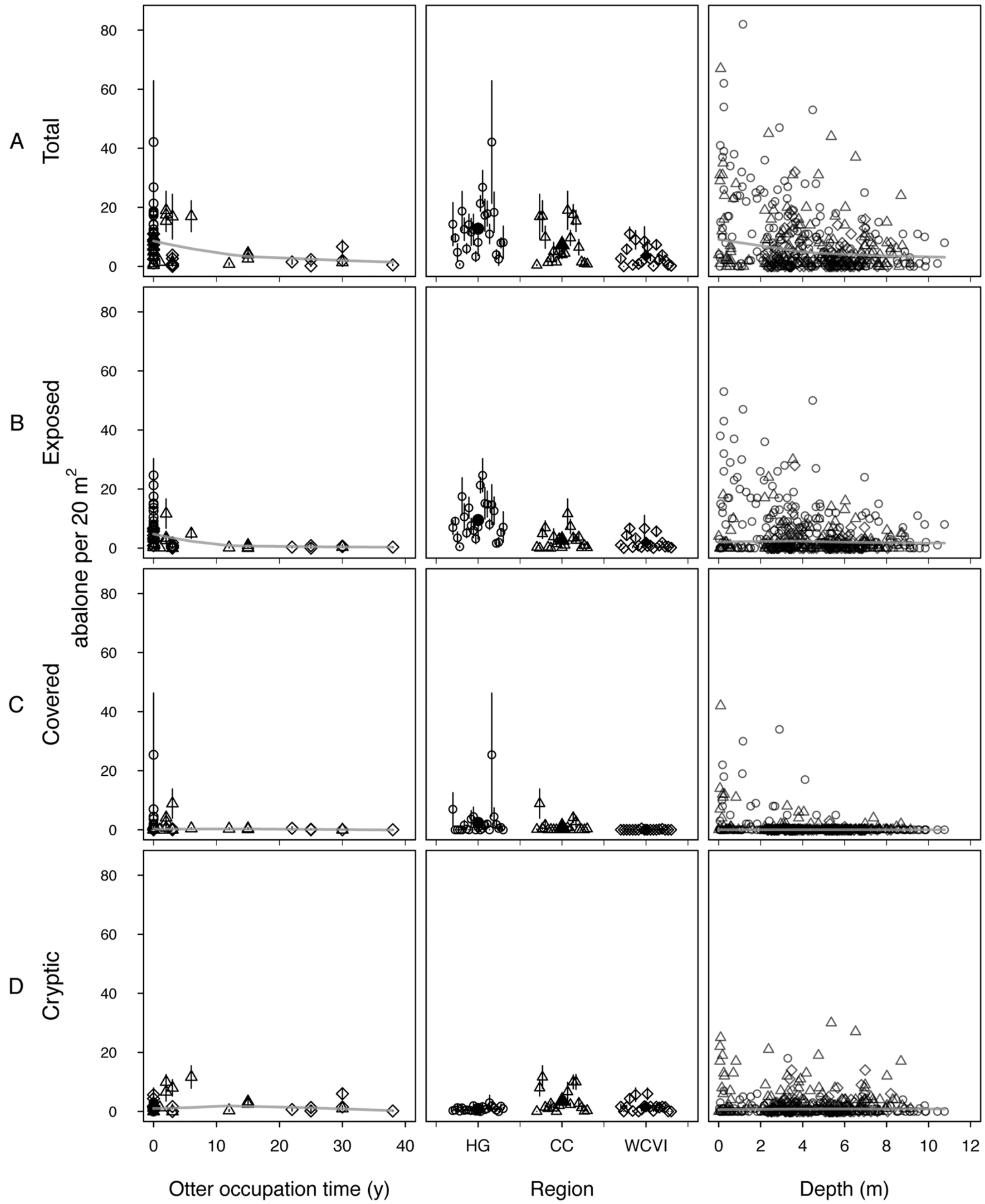

Figure 2.2 Bivariate relationships between density of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone and three factors: sea otter occupation time, region and depth. Symbols represent regions: Haida Gwaii (HG; open circles), Central Coast (CC; open triangles) and West Coast Vancouver Island (WCVI; open diamonds). Error bars are site means ± SE. Closed symbols (region panel) are the mean of site means by region. Lines are LOWESS smoothers (otter occupation time and depth panels).

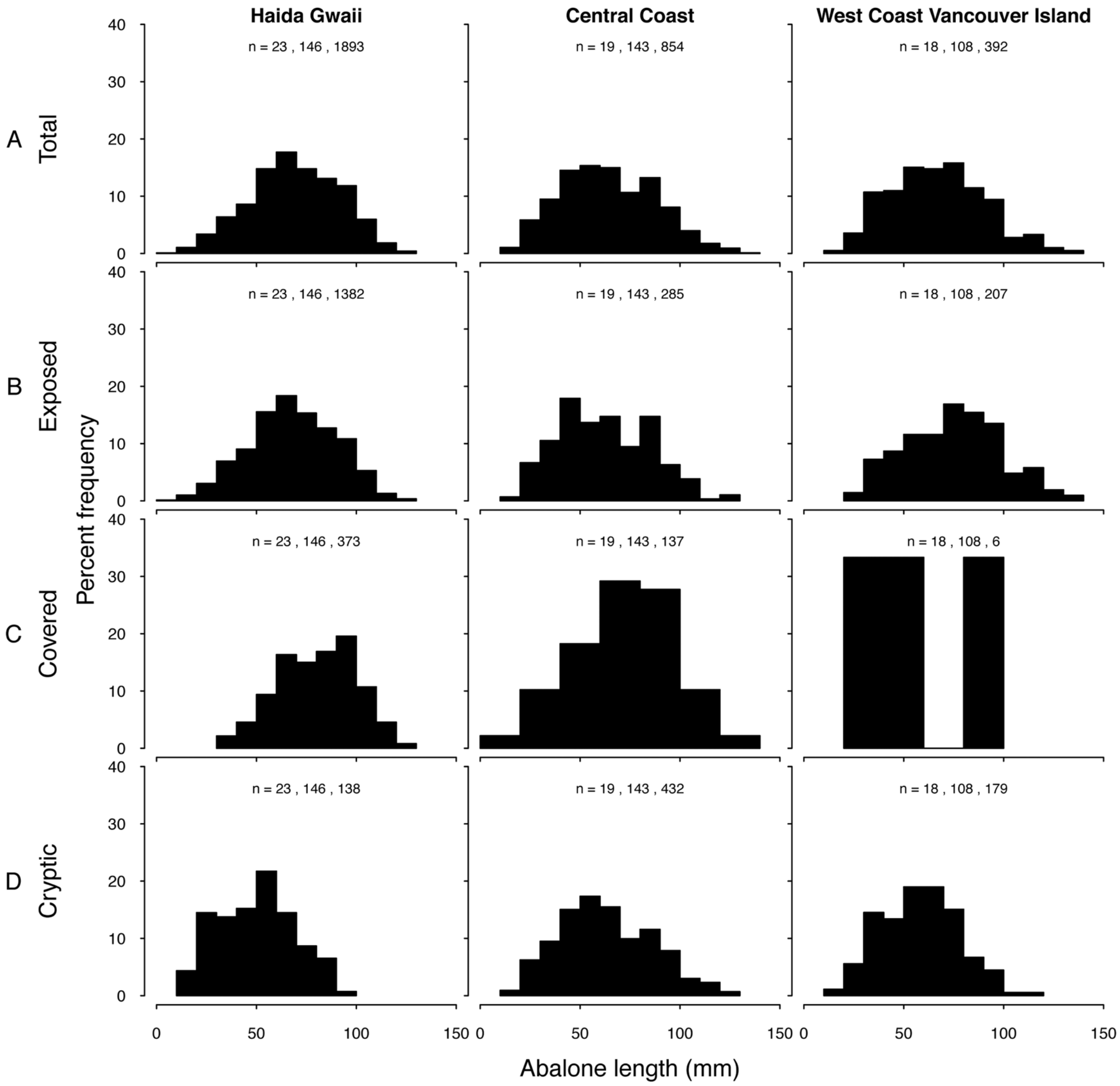

Figure 2.3 Size frequency histograms of shell length for (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone for each of three surveyed regions of BC. Sample sizes (n) are given in sequence: sites, transects, abalone. Number of sample sites and transects are the same within regions, but differ across regions. Bin sizes are 10 mm except for covered abalone in CC and WCVI that are 20 mm.

Table 2.1 Best models of the effects of biotic and abiotic factors on density, presence, length, and biomass of total, exposed, covered, and cryptic, abalone from field surveys.

Response	**Model**
Abalone density	
Total	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time + (1|Site)
Exposed	Region + Depth + Wave exposure + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time + (1|Site)
Covered	Region + Depth + Kelp stipe density + Otter occupation time + Depth x Otter occupation time + (1|Site)
Cryptic	Region + Depth + Wave exposure + Otter occupation time + Substrate complexity + Depth x Otter occupation time + (1|Site)
Abalone presence	
Total	Region + Wave exposure + Substrate complexity + (1|Site)
Exposed	Region + Depth + Wave exposure + Urchin biomass + (1|Site)
Covered	Region + Depth + Kelp stipe density + Otter occupation time + Depth x Otter occupation time + (1|Site)
Cryptic	Wave exposure + Otter occupation time + (1|Site)
Abalone length	
Total	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time + (1|Site)
Exposed	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + (1|Site)
Covered	Region + Depth + Kelp stipe density + Otter occupation time + (1|Site)
Cryptic	Region + Depth + Wave exposure + Sunflower star biomass + (1|Site)
Abalone biomass	
Total	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time + (1|Site)
Exposed	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time + (1|Site)
Covered	Depth + Kelp stipe density + Otter occupation time + Depth x Otter occupation time + (1|Site)
Cryptic	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Substrate complexity + Depth x Otter occupation time + (1|Site)

Notes: See Appendix D: Tables D1-D4 for strength of evidence for alternative candidate models.

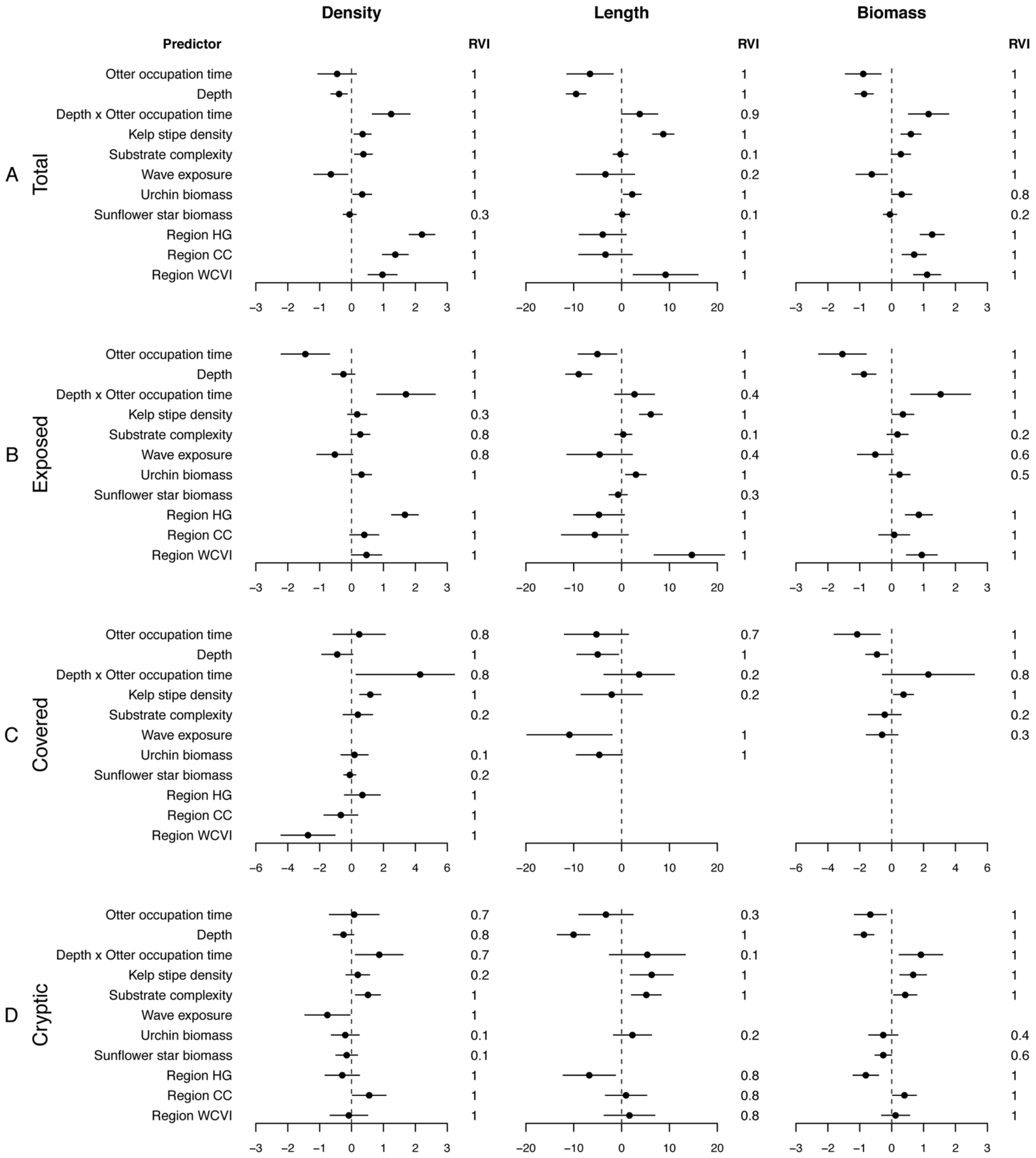

Figure 2.4 Standardized coefficients and 95% confidence intervals for relationships of biotic and abiotic factors with the density, length and biomass of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone from averaged models within $\Delta AIC_c < 2$. Factors without coefficient and relative variable importance (RVI) values were absent from final model sets.

Depth. We detected a strong negative effect of depth on the density, length, and thus biomass of abalone across all behavioral classes (RVI = 1 for all except cryptic abalone density where RVI = 0.78; Figs. 2.2, 2.4). Depth was the strongest driver of exposed and cryptic abalone length compared to all other factors. We found that the negative effect of depth on abalone density and biomass was mediated by sea otter occupation time where increasing otter time strongly reduced the negative effect of depth. This mediating effect was strongest for exposed abalone density (RVI = 1; Fig. 2.4B), greatest but most imprecise for covered abalone density (RVI = 0.85; Fig. 2.4C), and least important to cryptic abalone density (RVI = 0.66; Fig. 2.4D). Comparing predictive models of abalone density on Haida Gwaii as a function of sea otter occupation time at two depths illustrated this mediating effect (Fig. 2.5). As sea otter occupation time increased, a predicted distributional change occurred where abalone densities at 4.3 m exceeded those at 0 m after approximately 10 years.

Kelp stipe density. Kelp stipe density had a positive effect on total and covered abalone densities (RVI = 1, 1, respectively; Fig. 2.4AC), yet a weak and imprecise effect on exposed and cryptic abalone densities (RVI = 0.25, 0.24, respectively; Fig. 2.4BD). More kelp was strongly associated with larger abalone and thus higher abalone biomass across all behavioral classes (RVI = 1 for all except for covered abalone length where RVI = 0.16; Fig. 2.4).

Urchin biomass. Higher urchin biomass was associated with higher exposed abalone density, length and biomass (RVIs = 1, 1, 0.49, respectively; Fig. 2.4B); this was also the case for total abalone (RVIs = 1, 1, 0.79, respectively; Fig. 2.4A). In contrast, increasing urchin biomass was associated with decreasing covered abalone length (RVI = 1; Fig. 2.4C). Urchin biomass was otherwise unimportant to covered abalone density or biomass (RVIs <0.15; Fig. 2.4C) and of little importance to cryptic abalone density, length or biomass (RVIs <0.40; Fig. 2.4D).

Of the 3814 abalone surveyed where behavior was recorded, 46 (1.2%) were found under the spine canopy of sea urchins (majority under red urchins). Abalone under urchin spine canopies ranged from 18–107 mm, averaging 60.9 ± 3.0 mm. Of the 634 juvenile abalone ≤45 mm surveyed, 9 (1.4%) were sheltered under urchin spine canopies (mean length = 31.3 ± 2.6 mm).

Sunflower star biomass. Sunflower star biomass was not an important driver of abalone density, length or biomass across all behavioral classes (RVIs <0.30; Fig. 2.4). The exception was a potential negative association with cryptic abalone biomass (RVI = 0.63; Fig. 2.4D).

Region. We found strong regional differences in total abalone density with HG (sea otters absent) having higher densities than the CC and WCVI (0 – 38 years of otter occupation; Figs. 2.2A, 2.4A). The effect of region on total abalone density was primarily driven by variation in the number of exposed abalone (Figs. 2.2B, 2.4B). Specifically, total abalone densities on HG were 1.6 and 2.3 times greater than on the CC and WCVI (Fig. 2.4A), respectively; exposed abalone densities on HG were 4.2 and 3.6 times greater, respectively (Fig. 2.4B). Covered abalone density was slightly higher on HG than the CC, which was slightly higher than the WCVI (Figs. 2.2C, 2.4C). Cryptic abalone density was less variable between regions, slightly higher on the CC (~800 sea otters) than on the WCVI (~5000 sea otters), and lowest for HG (no sea otters; Figs. 2.2D, 2.4D).

Regional differences in length of exposed and cryptic abalone resulted in different trends in abalone biomass compared to density: total abalone length patterns were driven by variation in exposed abalone length. The average length of exposed abalone was larger on the WCVI than on HG and the CC (Figs. 2.3B, 2.4B), whereas the average length of cryptic abalone was lower for HG compared to the CC and WCVI (Figs. 2.3D, 2.4D). Thus we detected similar total and exposed abalone biomass on HG and the WCVI in spite of lower densities on the WCVI. The effect of region was not important to covered abalone biomass or length, which were more strongly influenced by local-scale biotic and abiotic factors (Figs. 2.3C, 2.4C).

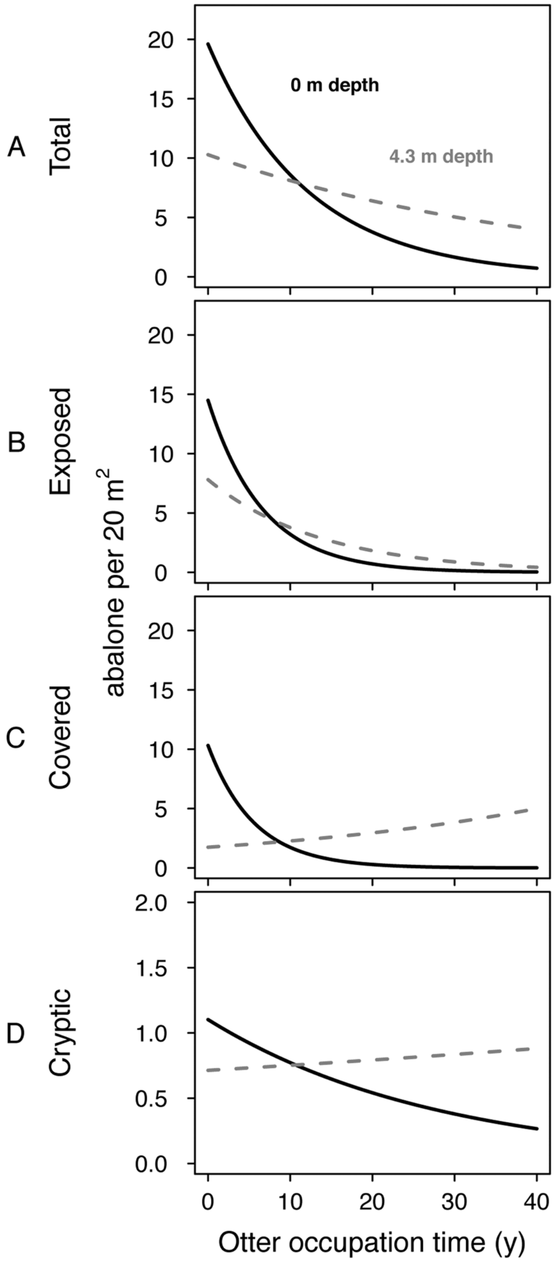

Figure 2.5 Predicted abalone densities from best model parameters for (A) total, (B) exposed, (C) covered, and (D) cryptic (note different scale bar), abalone on Haida Gwaii as a function of sea otter occupation time at two depths, 0 m and the average survey depth of 4.3 m, when other biotic and abiotic factors are held at their mean surveyed values.

Abalone behavioral class shifts with sea otter occupation

The proportion of abalone in each behavioral class shifted as a function of sea otter occupation time (Fig. 2.6). Increasing sea otter occupation time was associated with decreased proportions of exposed abalone and increased proportions of cryptic abalone (Fig. 2.6AC). By six years of sea otter occupation, the majority of abalone were cryptic (Fig. 2.6C). The relatively flat trend line for covered abalone proportion suggested little relationship with sea otter occupation time (Fig. 2.6B). We found strong evidence that the non-linear decay curve best-fit the effect of sea otter occupation time on proportion of exposed abalone, while the linear model best described the proportion of cryptic abalone; for covered abalone, all models were within ΔAIC_c <2 indicating no best model (Table 2.2).

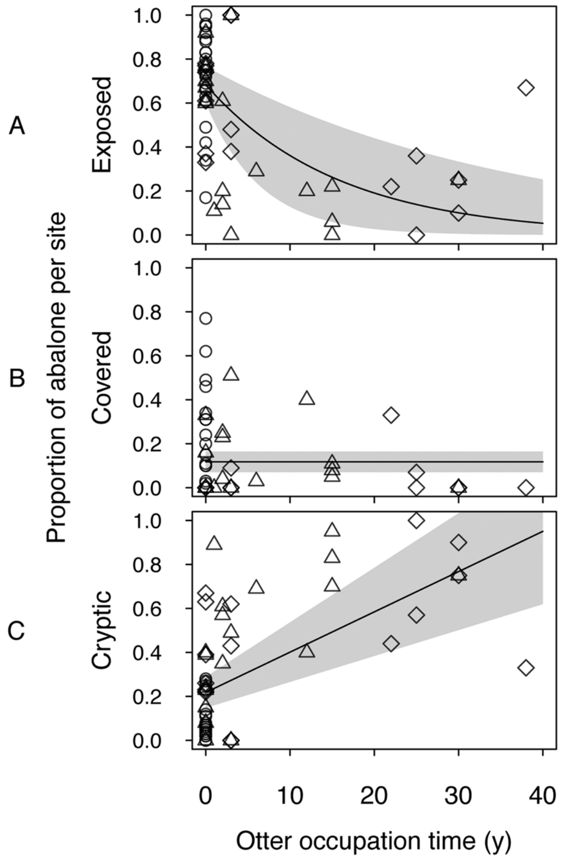

Figure 2.6 Proportion of (A) exposed, (B) covered, and (C) cryptic, abalone in each behavioral class by site. Symbols are as in Fig. 2.2. Shaded areas represent confidence intervals about best-fit relationships: (A) non-linear exponential decay, (B) intercept, and (C) linear.

Table 2.2 Strength of evidence for alternative candidate models of the effects of sea otter occupation time on the proportion of exposed, covered, and cryptic, abalone by site.

Response and Model	**df**	**log(*L*)**	**AIC_c**	**ΔAIC_c**	**W_i**
Exposed abalone proportion					
Non-linear decay	**3**	**-2.726**	**11.889**	**0.000**	**0.937**
Linear	3	-5.434	17.305	5.417	0.062
Intercept	2	-13.695	31.604	19.715	0.000
Covered abalone proportion					
Intercept	2	17.764	-31.314	0.000	0.475
Linear	3	18.318	-30.200	1.114	0.272
Non-linear decay	3	18.247	-30.057	1.257	0.253
Cryptic abalone proportion					
Linear	**3**	**1.803**	**2.830**	**0.000**	**0.993**
Non-linear saturation	3	-3.124	12.684	9.854	0.007
Intercept	2	-11.213	26.641	23.811	0.000

Notes: Models with varying degrees of freedom (df) were compared using likelihood of the model given the data (log(*L*)), differences in Akaike's information criterion corrected for small sample size (ΔAIC_c), and normalized Akaike weights (W_i). Models in bold typeface indicates that they had substantial empirical support relative to alternate candidate models (ΔAIC_c>2 from the next best model).

Biotic and abiotic factors may mediate predation outcomes

In lab experiments, we detected higher capture efficiency (α) and feeding rate of sunflower stars on abalone in trials with higher substrate complexity (+ crevice; Fig. 2.7CE), along with lower handling time in trials with alternate urchin prey (+ urchins; Fig. 2.7D). Sunflower stars used their tube feet to chase and capture fleeing abalone. When chased by sunflower stars, abalone could initially move at least twice the speed of the sea star both in the lab and in the wild (Fig. 2.7B; Appendix F: Video F1); however, we observed that the speed of each fleeing abalone decreased over time. If held by a sunflower star, abalone would attempt to escape by wildly twisting their shells to break the suction of the star's tubefeet, then flee away. Some abalone moved out of the water onto the tank edge to escape. Successfully captured abalone were engulfed whole into the sunflower star's stomach (Appendix F: Video F2). Most stars ingested only one abalone, but some ingested up to three during a trial. Handling time per abalone varied (range = 4–65 min), as a function of time needed to capture and ingest the abalone. Ingested abalone were digested over the following 24 hours, after which clean abalone shells were expelled. Although model summaries indicated that treatment effects explained much of the variation in the data ($R^2 = 0.86$ for α; $R^2 = 0.93$ for feeding rate), strength of evidence for a treatment effect was weak, in part due to low sample size. Specifically, null models (intercept only) of capture efficiency, handling time, feeding rate and abalone survival were ΔAIC_c >2 from models including treatment effects (Appendix G: Table G1). Irrespective of treatment, trial run time best explained variation in sunflower star attack success (Fig. 2.7A; Appendix G: Table G1).

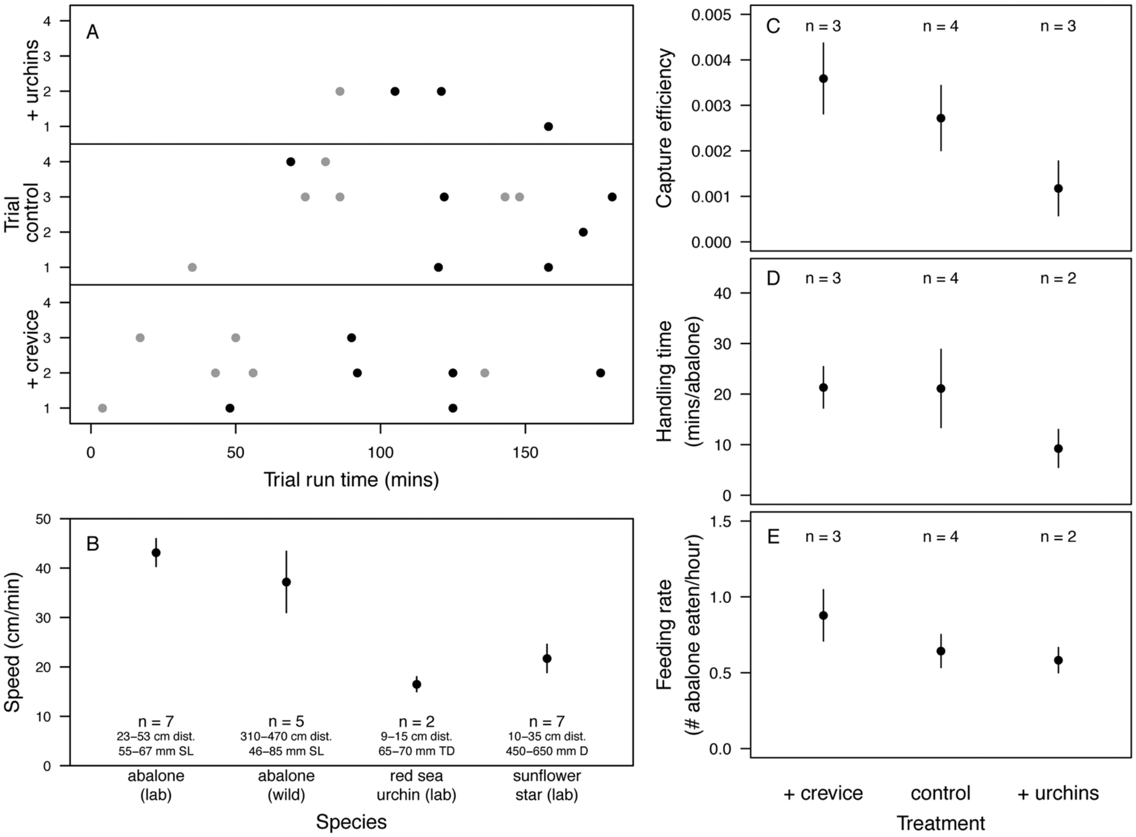

Figure 2.7 **(A) Successful (black) and unsuccessful (gray) attacks by sunflower stars on hatchery-raised abalone in lab predation trials (n = 4 per treatment). Trials with no circles indicate no attacks. (B) Escape speeds of abalone and red urchins, and attack speed of sunflower stars, measured in the lab and field. (C) Capture efficiency, (D) handling time and (E) feeding rate of sunflower stars by treatment (mean ± SE).**

Indirect benefits of sea otters for abalone

We found strong evidence that sea otter recovery was associated with an increase in kelp stipe density and decrease in the biomass of predatory sunflower stars and sea urchin competitors (Fig. 2.8; Appendix E: Tables E1-E3; also see Figs. E1-E2 for effects on presence of sunflower stars and urchins). Compared to other biotic and abiotic factors, sea otter occupation time had the greatest magnitude of effect on sunflower star biomass, urchin biomass, and kelp stipe density, and it was one of the most important factors along with depth. We also found a strong positive interaction between depth and sea otter occupation time, where increasing otter occupation time strongly reduced the negative effect of depth on urchin biomass and kelp stipe density (Fig. 2.8BC). At sites increasing in sea otter occupation time, these interactive effects were observed as an increase in the depth and areal extent of kelp forests, and a dramatic reduction in the high density of urchins concentrated along the sublittoral fringe.

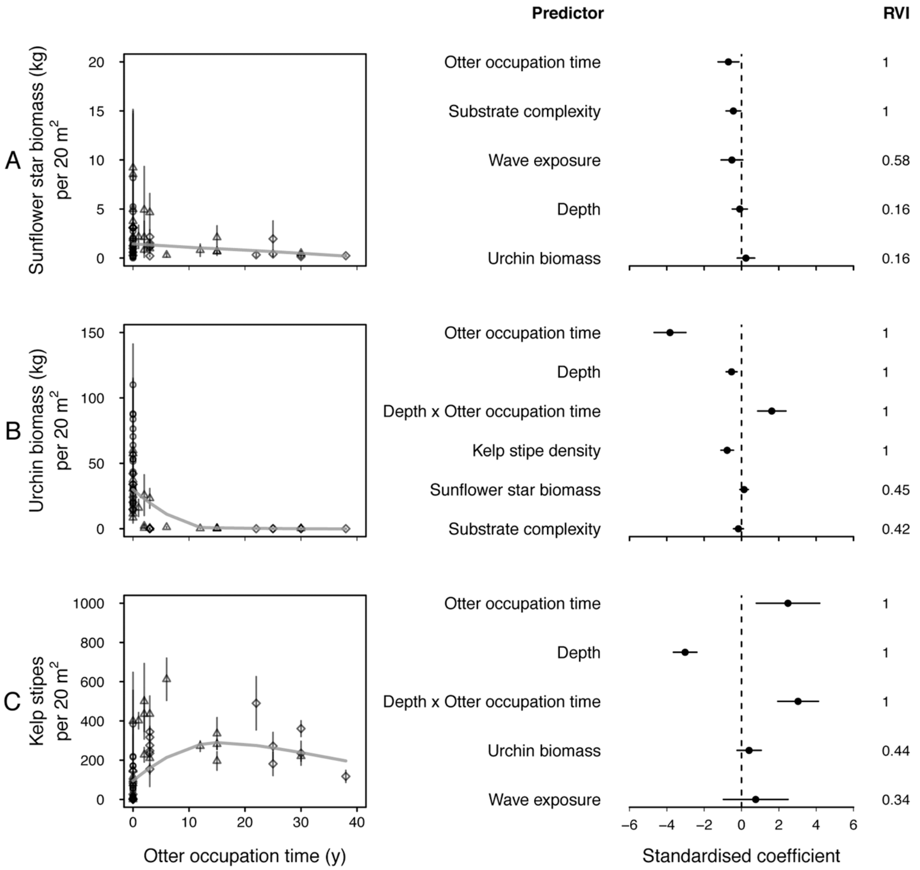

Figure 2.8 **Bivariate relationships (left) and standardized coefficients and 95% confidence intervals from averaged models within ΔAIC_c <2 (right) for relationships between (A) sunflower star biomass, (B) urchin biomass, and (C) kelp stipe density, and sea otter occupation time. For bivariate plots, symbols represent regions: Haida Gwaii (HG; open circles), Central Coast (CC; open triangles) and West Coast Vancouver Island (WCVI; open diamonds). Error bars are site means ± SE. Lines are LOWESS smoothers.**

Discussion

Here we show how the complex interplay between direct negative effects, indirect positive effects, and prey behavior, promotes the coexistence of a keystone predator and its endangered prey. Sea otter recovery had direct negative effects on abalone via predation, but positive indirect effects via food and habitat provisioning, and reduced abundance of mesopredators and competitive herbivores (Figs. 2.2, 2.4, 2.8; also see Plate 2.1DE for natural history observations of positive interactions between abalone and urchins). As has been observed elsewhere, sea otter recovery reduced average abalone size and abundance to low densities (Fig. 2.4) and likely triggered a change in behavior from exposed to cryptic (Fig. 2.6; Watson 2000, Micheli et al. 2008, Raimondi et al. 2015). Changes in abalone behavior may then dampen negative predation effects, suggested by sea otter recovery having a strong negative effect on the density of exposed abalone compared to a weak positive effect on covered and cryptic abalone (Figs. 2.4BCD, 2.5). At the same time, by dramatically reducing the abundance and size of one of the most important temperate reef grazers, sea urchins (Fig. 2.8B; Stevenson et al. 2016), sea otters also transformed two-dimensional urchin barrens into structurally complex three-dimensional kelp forest habitat (Fig. 2.8C; Estes and Palmisano 1974, Watson and Estes 2011, Markel and Shurin 2015). This indirect magnification of kelp forest habitat and associated drift kelp increases the availability of food and shelter for abalone, promoting the persistence of abalone as sea otters recovery.

Abalone behavior may reduce predation effects

We propose alternative yet not mutually exclusive mechanisms that may have led to the exponential decline in the proportion of exposed abalone (Plate 2.1A) with sea otter recovery. Our data suggest that the majority of abalone were cryptic (Plate 2.1CG) by six years of sea otter occupation (Fig. 2.6AC). This observation could be due to a change in abalone behavior from exposed to cryptic triggered by the presence of sea otters and/or increasing extent and depth of kelp forests, higher sea otter-induced mortality rates on exposed versus cryptic abalone, or some combination of these.

We expect that abalone mortality caused by sea otters would be highest for exposed individuals. Exposed abalone are likely easiest to detect and capture, resulting in a more rapid decline in their density compared to covered or cryptic abalone which are harder to detect and/or in refugia inaccessible to sea otters. Our finding that sea otter occupation time had a strong negative effect on exposed abalone density versus a weak positive effect on covered and cryptic abalone density (Fig. 2.4BCD) supports this hypothesis. Sites with sea otters had lower densities of exposed abalone than those without otters ($1.38 \pm 0.51/20m^{-2}$ versus $7.56 \pm 0.98/20m^{-2}$), but higher densities of cryptic abalone ($2.96 \pm 0.75/20m^{-2}$ versus $1.31 \pm 0.20/20m^{-2}$). In the initial years of sea otter occupation, site-specific predation rates on abalone may also be lower due to high availability of easily accessible alternate prey such as urchins, crustaceans and other molluscs (Honka 2014). This situation would afford the opportunity for surviving exposed and covered abalone to change behavior and move into cryptic habitats.

Alternatively, abalone behavioral changes may be triggered by sea otter predation pressure and/or increased extent of kelp habitat and food. Once exposed abalone experience the threat of sea otter predation, they may restrict their foraging behavior to spend more time in crevices and become increasingly cryptic. Increased extent of kelp forests with sea otter recovery may also assist abalone with obtaining food while they remain in crevices. The latter two hypotheses are suggested by the weak positive effect of sea otters on cryptic abalone (Fig. 2.4D), and predicted increase in densities of cryptic abalone with increasing sea otter occupation time (Fig. 2.5D). The positive effect of sea otters on cryptic abalone may in fact be greater than our estimate because some cryptic abalone would have gone undetected given our non-intrusive field survey protocol (Campbell and Cripps 1998, Cripps and Campbell 1998).

Foraging theory predicts that animals will alter their behavior to maximize energetic gain and minimize predation risk (Lima and Dill 1990, Brown and Kotler 2004), and diverse empirical evidence exists to support this trade-off in marine ecosystems (Heithaus et al. 2008). Drift kelp is scarce in deforested urchin barrens. We expect this scarcity of food to result in abalone spending more time foraging in the open and less time in refugia, leading to a higher proportion of exposed abalone. In contrast, drift kelp is abundant in kelp forests and abalone can obtain food while remaining in refugia with reduced predation risk. Other grazers such as urchins make a similar shift from active grazing to passive detritivory as drift kelp supply increases (Harrold and Reed 1985, Day and Branch 2002). In barrens habitat in areas without sea otters, urchins appear to react to predation risk by maintaining minimum distances from sunflower stars, creating a ‘halo’ effect, while staying close to the edge of shallow fringing kelp forests that provide food (Appendix F: Plates F1 & F2; also see Duggins 1981, Schultz et al. 2016).

While data from our study cannot tease apart the relative contribution of these alternative mechanisms, future field studies and experiments may help elucidate causal mechanisms. For example, experimental arenas in areas with similar crevice habitat availability and varying in levels of mock sea otter predation pressure (divers disturbing abalone by trying to pry them off the substrate) and kelp stipe density would provide evidence for whether exposed abalone will actively change their behavior in response to predation risk and/or food availability. Field studies observing a cohort of tagged abalone through time with sea otter recovery would help distinguish between abalone behavioral changes versus higher sea otter predation rates on exposed abalone compared to cryptic ones.

The importance of habitat characteristics

Habitat features important for abalone include substrate complexity, kelp abundance, wave exposure, depth, and sea urchin spine canopy cover (Sloan and Breen 1988, Campbell and Cripps 1998, Cripps and Campbell 1998, Tomascik and Holmes 2003, Lessard and Campbell 2007, Rogers-Bennett et al. 2011). Although evidence from temperate reefs elsewhere suggests that urchin spine canopies are important to the survival of juvenile abalone of other species (Rogers-Bennett and Pearse 2001, Day and Branch 2002), we did not detect such an effect for northern abalone in BC. The importance of habitat features can also vary depending on abalone life history stage (Griffiths and Gosselin 2008, Aguirre and McNaught 2012). For example, complex substrate is important to juvenile abalone because it provides refuge from large, mobile predators including sea stars, larger crabs and piscivorous fish (Aguirre and McNaught 2013, Read et al. 2013).

Predator recovery can cause dramatic changes in habitat conditions (Ripple et al. 2014), which can indirectly benefit prey species. Longer sea otter occupation time was associated with greater abalone densities at deeper depth (Figs. 2.4, 2.5), likely due to habitat change from urchin barrens to deeper and larger kelp forests created via the otter-urchin-kelp trophic cascade (Figs. 2.8BC, 2.9; Estes and Palmisano 1974, Breen et al. 1982, Estes and Duggins 1995, Watson and Estes 2011, Markel and Shurin 2015). In addition to providing food in the form of algal drift, kelp forests provide shelter for abalone by attenuating wave energy and reducing water flow through understory kelps (Duggins 1987, Eckman and Duggins 1991). Accordingly, higher wave exposure was associated with lower abalone densities within the semi to highly wave-exposed range of our study sites (Fig. 2.4).

Recovery of predators after a prolonged absence may also alter the habitat needs of their prey (e.g., Ripple and Beschta 2012). In otter-occupied areas, higher densities and larger abalone were associated with complex substrate, with the size of cryptic abalone likely dictated by refuge size. We generally found smaller abalone persisting as sea otters recovered (Fig. 2.4) potentially because larger abalone must emerge as they outgrow crevice refugia, placing them at risk of predation by sea otters. Although larger abalone have higher fecundity, many abalone mature at approximately 50 mm length (2–4 years of age; Sloan and Breen 1988), which allows reproductive individuals to persist in crevices within sea otter-occupied areas. Most abalone are cryptic in areas occupied by sea otter for over six years so we expect that semi wave-exposed kelp forests with complex substrate will become increasingly important habitat for northern abalone as sea otters expand their range.

Mesopredator effects

The loss of top predators can result in “mesopredator release”, a situation in which lower trophic-level predators become more abundant because higher trophic-level predators no longer control their abundance through predation and/or competition (Crooks and Soulé 1999, Roemer et al. 2009, Hughes et al. 2014, Ripple et al. 2014). Sea otters compete with and may also consume many invertebrate mesopredators including sunflower stars, giant Pacific octopus (*Enteroctopus dofleini*) and crabs (Garshelis and Garshelis 1984, Tinker et al. 2008, Honka 2014). Sea otter recovery is expected to result in smaller and fewer mesopredators including sunflower stars (Fig. 2.8A), which could have direct and indirect consequences for abalone. For example, fewer predatory crabs may reduce mortality particularly for juvenile abalone (Griffiths and Gosselin 2008), and fewer and smaller sunflower stars may also reduce predation rates on abalone.

Our laboratory investigation of mesopredator effects additionally highlights that predation rates can vary with habitat characteristics. Counter to simple expectations, we found that complex substrate actually increased the risk of abalone predation by sunflower stars (Fig. 2.7C; Plate 2.1F), similar to interactions between a molluscan prey and predatory sea star in Chile (Dayton et al. 1977). When sunflower stars moved to hunt, nearby abalone fled, often releasing a cloudy substance that appeared to trigger adjacent abalone to flee. Abalone can move at twice the speed of sunflower stars (Fig. 2.7B), and we observed three events in the field in which abalone escaped sea stars chasing them on low relief substrate (Appendix F: Video F1). However, our lab experiments showed that high complexity substrate can reduce the abalone's horizontal speed relative to that of the sunflower star (which can travel in the horizontal plane across high relief substrate) and compromise the abalone's ability to evade capture.

Ocean conditions and human influence

The three study regions differed in overall sea otter abundance, oceanographic conditions, abalone fishing history, and accessibility to poachers. These differences limit our ability to pinpoint a unique causal factor behind our detected effects of region. Nonetheless, the absence of sea otters likely best explains higher abalone density on Haida Gwaii, while the number and occupation time of sea otters likely explain lower abalone density on the west coast of Vancouver Island compared to the Central Coast (Fig. 2.4A). However, different oceanographic conditions over the latitudinal range of our study may also have an influence, with declining densities and failing recruitment of northern abalone at lower latitudes possibly due to warming sea water temperatures (Washington, USA; Rogers-Bennett 2007, Rogers-Bennett et al. 2011). Warmer water in southern BC may also foster larger average abalone size on the WCVI compared to CC and HG due to higher growth rates, larger maximum size and/or lower juvenile recruitment rates.

The history of abalone exploitation also varies between regions. Abalone catch per unit effort statistics show that HG and CC were more productive commercial abalone fishing areas than the WCVI (Farlinger 1990, Harbo and Hobbs 1997), reflecting our observed regional differences in total abalone density. However, the magnitude of abalone poaching within each region is not known (Fisheries and Oceans Canada 2012). For example, on southern Vancouver Island where the coastline is more accessible, abalone abundance was found to be highest only at well-enforced sites (Wallace 1999). Yet the remoteness of HG and the CC may enable more poaching given that the majority of poaching and suspected poaching reports come from northern BC (2002b, 2007, Lessard et al. 2007).

Implications for interacting species of conservation concern

The dynamic nature of interacting species over space and time challenge the efficacy of single-species based approaches to conservation. Recovery targets for endangered prey species based on their abundance and conservation status in an ecosystem bereft of their top predator can lead to conservation conundrums as their predators recover. For example, local-scale recovery of endangered wolves (*Canis lupus*) may be increasing the vulnerability of threatened European wild-forest reindeer (*Rangifer tarandus fennicus*) in Finland (Kojola et al. 2009). Here, northern abalone and sea otters co-evolved on the Northeast Pacific coast (Estes et al. 2005) and co-existed with people for thousands of years. Prior to the 18th century, traditional hunting of sea otters by coastal indigenous people (self-referred to as First Nations in Canada) likely maintained a mosaic of macroinvertebrate abundances along the BC coast (Corbett et al. 2008, McKechnie and Wigen 2011, Szpak et al. 2012, Salomon et al. 2015). In California, archaeological, historical and ecological evidence show persistence of red abalone over millennia, and suggest how both human hunting of sea otters and changing environmental conditions caused dramatic shifts in red abalone abundance over 8000 years (Tegner and Dayton 2000, Braje et al. 2009).

Sea otters are currently identified as a threat to northern abalone recovery where they co-occur (COSEWIC 2009, Fisheries and Oceans Canada 2012, Busch et al. 2014). Yet here, we found evidence that abalone persist in the face of sea otter recovery, albeit at reduced densities and sizes, and thus overall biomass (Figs. 4). Abalone densities from our study were consistent with low yet persistent densities of <0.05 northern abalone/m^2 on the west coast of Vancouver Island (Watson 1993) and 0.03 red abalone (*H. rufescens*)/m^2 in California (Micheli et al. 2008), at sites with decades of sea otter occupation. Although abalone recovery targets have not been established for areas with sea otters, abalone densities here were also consistent with predicted densities from simulation modeling for areas where sea otters have re-established (Chadès et al. 2012). Our data also support several mechanisms –

increased kelp abundance and depth, decreased sunflower star predators, and decreased urchin competitors – by which the indirect effects of sea otters could support the persistence of abalone (Figs. 2.8, 2.9). Similar cascading predator effects have been shown in other systems where reintroduction of a top predator controlled densities of a hyperabundant herbivore to indirectly benefit other competing herbivorous prey species. For example, gray wolf predation directly decreased elk density and indirectly increased the abundance of other prey including bison and beavers, likely by fostering growth and recruitment of woody browse tree species and reducing competition for herbaceous forage species (Ripple and Beschta 2012). In a perverse case of shifting baselines (Pauly 1995, Dayton et al. 1998), the extirpation of sea otters facilitated a hyperabundance of abalone and other macroinvertebrate prey in the mid-1900s (Tegner and Dayton 2000) that many fishers, resource managers, policy makers and scientists perceive as 'normal' today. Such perceptions can bias expectations of recovery and highlight the urgent need to move towards ecosystem-based approaches to management of interacting species of conservation concern, one that acknowledges linked social and ecological drivers of change from the present, the deep past, and into the future.

Holistic approaches could be used to address some of the complex and often conflicting social and ecological objectives that surround predator recovery (Brown and Trebilco 2014). For example in Canada, BC coastal First Nations, including the Haida on HG, Heiltsuk on the CC and Nuu-chah-nulth on the WCVI, hunted sea otters and fished abalone for millennia (McKechnie and Wigen 2011, Menzies 2015). The loss of abalone as a traditional food deeply affected coastal indigenous communities who now aim to restore abalone to self-sustaining levels that can support food fisheries (Sloan 2004, Menzies 2010, Menzies 2015). In this case, incorporating indigenous values into management plans (Plagányi et al. 2013) can help facilitate the constitutional rights of indigenous peoples to access and manage resources within their traditional territories (Sloan 2004, Trosper 2009, Menzies 2010, Salomon et al. 2015).

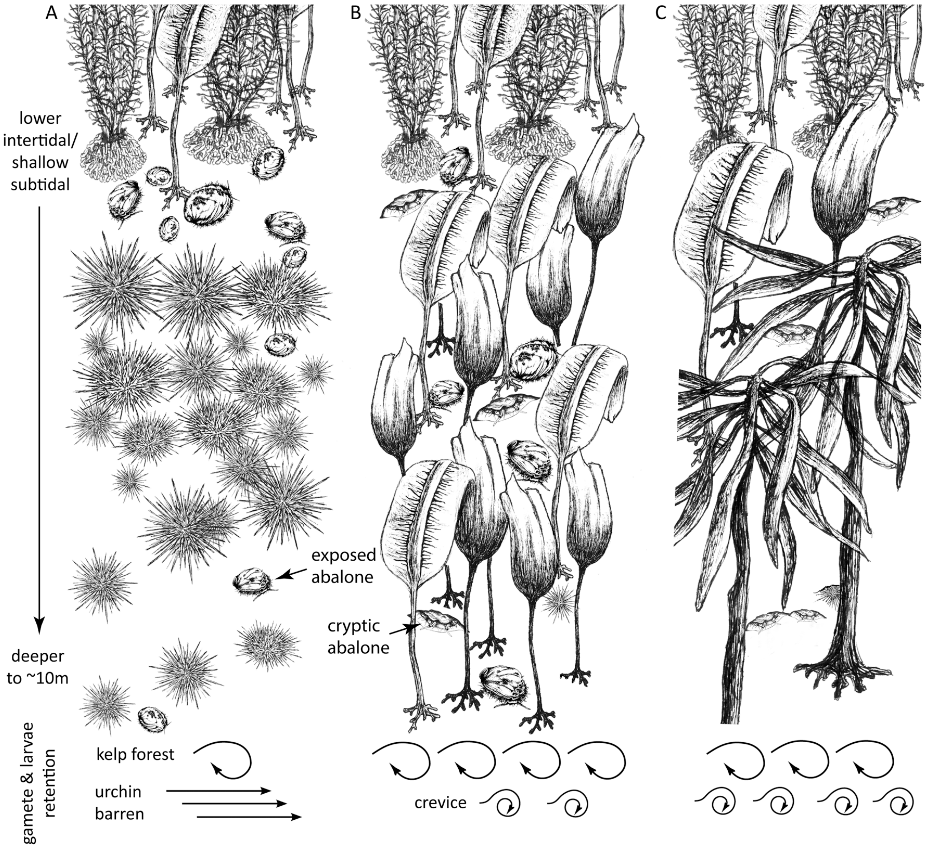

Figure 2.9 **Conceptual models of habitat and abalone conditions with (A) no sea otters, (B) short sea otter occupation time (≤6 yr), and (C) long sea otter occupation time (≥10 yr), illustrating multiple mechanisms by which sea otter recovery may facilitate abalone persistence at low densities. Moving from panel A to C demonstrates: (1) increased extent and depth of kelp cover, including growth of longer-lived kelp species, providing abalone with increased access to food and protection from predators that visually detect prey; (2) behavioral shift to higher proportions of cryptic abalone due to increased predation risk and/or drift kelp food supply; (3) distributional shift in abalone from concentration at the low intertidal/shallow subtidal kelp line to dispersion across deeper depths with increased depth of kelp forests; (4) increased abalone fertilization success due to gamete retention within kelp forests and crevices, potentially reducing Allee effects at low overall abalone densities; and (5) increased retention of short-lived abalone larva (3–12 d; Sloan and Breen 1988) to facilitate settlement within kelp forests (also see Watson 2000). Potential lower abundance and smaller size of mesopredators (e.g., sunflower stars, octopus, crabs) due to decreased prey availability and/or direct predation by sea otters, and higher abalone growth rates within kelp forests, may also indirectly benefit abalone. Arrows at the bottom of each panel illustrate expected retention of gametes and larva in urchins barrens, kelp forest and crevice habitats, with increasing spirals indicating higher retention. Drawings by Lynn Lee.**

Our results highlight the need to develop multispecies and ecosystem-based models and conservation plans that consider the direct and indirect effects of predator recovery on their recovering prey. Although the call for marine ecosystem-based management is by no means new (Norse 1993, Larkin 1996), implementation has been hampered by difficulty in finding a set of tools and approaches that can be broadly applied (Arkema et al. 2006, Thrush and Dayton 2010, Long et al. 2015). Our case study of northern abalone and sea otters in BC reveals how species interactions, environmental conditions, and historical change, are all critical considerations in developing conservation policy and ecosystem-based management strategies for interacting species. For sea otters and northern abalone, spatially and temporally explicit objectives could range from abalone enhancement areas where higher abalone densities are fostered, to sea otter protection areas where abalone will remain in cryptic habitats at lower densities. Such alternative strategies co-crafted with local communities and informed by ecosystem-based knowledge have the potential to deliver conservation plans that promote resilience in both ecological and human (social) communities.

Acknowledgements

This research was supported by an NSERC Discovery Grant, Parks Canada Contribution Agreement and Tula Foundation grant to A.K.S. and by graduate scholarships from NSERC, Hakai Institute and Simon Fraser University to L.C.L. R.T. was supported by an NSERC Vanier Graduate Scholarship, the J. Abbott/M. Fretwell Graduate Fellowship in Fisheries Biology, and a SFU Graduate Fellowship. Fieldwork was facilitated by in-kind contributions from DFO’s Pacific Biological Station, J.W., Hakai Institute, Marine Toad Enterprises Inc. and Stan Hutchings and Karen Hansen. For field assistance, we thank Leandre Vigneault, Taimen Lee Vigneault, Alejandro Frid, Eric White, Joel White, Hannah Stewart, Matt Drake, Stu Humchitt, Leah Saville, Erin Rechsteiner, Joanne Lessard, Seaton Taylor, Mike Atkins, Twylabella Frid, Gail Lotenberg, Rebecca Martone, Tammy Norgard, Mike Reid, Julie Carpenter, Harvey Humchitt and Mark Wunsch. Lab experiments at PBS were facilitated by Joanne Lessard, Seaton Taylor, Dominque Bureau, Juanita Rogers, Claudia Hand and Holly Hicklin, and conducted under DFO Species-at-Risk Act Permit Number SARA 233. Linda Nichol established sea otter occupation times for each site. Members of the CMEC lab and Stats Beerz, particularly Sean Anderson, provided valuable feedback on data analyses. We are grateful to Alejandro Frid, Paul Dayton, Norman Sloan, Rebecca Martone, Kyle Demes, and two anonymous reviewers who provided comments that improved previous versions of this manuscript. Thanks to the Gwaii Haanas Archipelago Management Board, Council of the Haida Nation Fisheries Committee, Heiltsuk Integrated Resource Management Department, and Pacific Rim National Park Reserve for supporting this research.

References

(2002) R. v. Sandover-Sly, BCCA 56 (CanLII) < http://canlii.ca/t/4z0x >. Provincial Court of British Columbia.

(2007) R. v. McNeill, BCSC 773 (CanLII) <http://canlii.ca/t/1rnpt>. Provincial Court of British Columbia.

Aguirre, J.D., McNaught, D.C. (2012) Ontogenetic variability in the habitat associations of *Haliotis iris* in central New Zealand. *Marine and Freshwater Research* **63**, 751-761.

Aguirre, J.D., McNaught, D.C. (2013) Habitat complexity mediates predation of juvenile abalone by starfish. *Marine Ecology Progress Series* **487**, 101-111.

Arkema, K.K., Abramson, S.C., Dewsbury, B.M. (2006) Marine ecosystem-based management: from characterization to implementation. *Frontiers in Ecology and the Environment* **4**, 525-532.

Barry, S.C., Welsh, A.H. (2002) Generalized additive modelling and zero inflated count data. *Ecological Modelling* **157**, 179-188.

Bartoń, K. (2013) MuMIn: Multi-model inference. R package version 1.9.13. http://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. http://CRAN.R-project.org/package=lme4.

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

Braje, T.J., Erlandson, J.M., Rick, T.C., Dayton, P.K., Hatch, M.B.A. (2009) Fishing from past to present: continuity and resilience of red abalone fisheries on the Channel Islands, California. *Ecological Applications* **19**, 906-919.

Breen, P.A., Carson, T.A., Foster, J.B., Stewart, E.A. (1982) Changes in subtidal community structure associated with British Columbia sea otter transplants. *Marine Ecology Progress Series* **7**, 13-20.

Brown, C.J., Trebilco, R. (2014) Unintended cultivation, shifting baselines, and conflict between objectives for fisheries and conservation. *Conservation Biology* **28**, 677-688.

Brown, J.S., Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**, 999-1014.

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

Burnham, K.P., Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**, 261-304.

Busch, S., Friedman, C., Gruenthal, K. *et al.* (2014) Status Review Report for Pinto Abalone (*Haliotis kamtschatkana*). National Marine Fisheries Service, Long Beach, California, USA.

Campbell, A., Cripps, K. (1998) Survey of abalone populations at Stryker Island, Tribal Group and Simonds Group, Central Coast of British Columbia, May, 1997. Canadian Manuscript Report of Fisheries and Aquatic Science 2451 (revised). Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada.

Chadès, I., Curtis, J.M.R., Martin, T.G. (2012) Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone. *Conservation Biology* **26**, 1016-1025.

Corbett, D.G., Causey, D., Clementz, M. *et al.* (2008) Aleut hunters, sea otters, and sea cows: three thousand years of interactions in the western Aleutian Islands, Alaska. pp. 43-75 in Rick, T.C., Erlandson, J.M. editors. *Human impacts on ancient marine ecosystems: a global perspective.* University of California Press, Berkeley and Los Angeles, California, USA.

COSEWIC. (2009) COSEWIC assessment and update status report on the Northern Abalone *Haliotis kamtschatkana* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.

Cripps, K., Campbell, A. (1998) Survey of abalone populations at Dallain Point and Higgins Pass, central coast of British Columbia, 1995-96. Canadian Manuscript Report of Fisheries and Aquatic Science 2445. *Canadian Manuscript Report of Fisheries and Aquatic Science.* Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada.

Crooks, K.R., Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented landscape. *Nature* **400**, 563-566.

Day, E., Branch, G.R. (2002) Effects of sea urchins (*Paraechinus angulosus*) on recruits and juveniles of abalone (*Haliotis midae*). *Ecological Monographs* **72**, 133-149.

Dayton, P.K., Rosenthal, R.J., Mahen, L.C., Antezana, T. (1977) Population-structure and foraging biology of predaceous chilean asteroid *Meyenaster gelatinosus* and escape biology of its prey. *Marine Biology* **39**, 361-370.

Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L. (1998) Sliding baselines, ghosts and reduced expectations in kelp forest communities. *Ecological Applications* **8**, 309-322.

Duggins, D.O. (1981) Interspecific facilitation in a guild of benthic marine herbivores. *Oecologia* **48**, 157-163.

Duggins, D.O. (1987) The effects of kelp forests on nearshore environments: biomass, detritus and altered flow. pp. 192-201 in VanBlaricom, G.R., Estes, J.A. editors. *The Community Ecology of the Sea Otters.* Springer-Verlag, New York, New York, USA.

Eckman, J.E., Duggins, D.O. (1991) Life and death beneath macrophyte canopies: effects of understory kelps on growth rates and survival of marine benthic suspension feeders. *Oecologia* **87**, 473-487.

Ekebom, J., Laihonen, P., Suominen, T. (2003) A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos. *Estuarine Coastal and Shelf Science* **57**, 887-898.

Estes, J.A. (1996) Predators and ecosystem management. *Wildlife Society Bulletin* **24**, 390-396.

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

Estes, J.A., Lindberg, D.R., Wray, C. (2005) Evolution of large body size in abalones (*Haliotis*): patterns and implications. *Paleobiology* **31**, 591-606.

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

Estes, J.A., Terborgh, J., Brashares, J.S. *et al.* (2011) Trophic downgrading of planet earth. *Science* **333**, 301-306.

Fanshawe, S., VanBlaricom, G.R., Shelly, A.A. (2003) Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. *Conservation Biology* **17**, 273-283.

Farlinger, S. (1990) Review of the biological basis for management of the British Columbia abalone fishery. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **2089**, 41-65.

Fisheries and Oceans Canada. (2007) Recovery Strategy for the Northern Abalone (*Haliotis kamtschatkana*) in Canada. *Species at Risk Act* Recovery Strategy Series. Fisheries and Oceans Canada, Vancouver, British Columbia, Canada.

Fisheries and Oceans Canada. (2012) Action Plan for the Northern Abalone (*Haliotis kamtschatkana*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Fisheries and Oceans Canada. (2014) Management Plan for the Sea Otter (*Enhydra lutris*) in Canada. *Species at Risk Act* Management Plan Series. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Fournier, D.A., Skaug, H.J., Ancheta, J. *et al.* (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods & Software* **27**, 233-249.

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

Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* **27**, 2865-2873.

Gotelli, N.J. (2008) Predation. pp. 125-153. *A Primer of Ecology.* Sinauer Associates Inc., Sunderland, Massachusetts, USA.

Griffiths, A.M., Gosselin, L.A. (2008) Ontogenetic shift in susceptibility to predators in juvenile northern abalone, *Haliotis kamtschatkana*. *Journal of Experimental Marine Biology and Ecology* **360**, 85-93.

Harbo, R., Hobbs, K. (1997) Pacific commercial fishery updates for invertebrate resources (1994). *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **2369**, 86-92.

Hargrove, W.W., Pickering, J. (1992) Pseudoreplication: a *sine qua non* for regional ecology. *Landscape Ecology* **6**, 251-258.

Harrold, C., Reed, D.C. (1985) Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* **66**, 1160-1169.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in ecology & evolution* **23**, 202-210.

Hobday, A.J., Tegner, M.J., Haaker, P.L. (2001) Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Reviews in Fish Biology and Fisheries* **10**, 493-514.

Holling, C.S. (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist* **91**, 293-320.

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

Hughes, B.B., Eby, R., Van Dyke, E. *et al.* (2014) Recovery of a top predator mediates negative eutrophic effects on seagrass. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 3644-3644.

Kojola, I., Tuomivaara, J., Heikkinen, S. *et al.* (2009) European wild forest reindeer and wolves: endangered prey and predators. *Annales Zoologici Fennici* **46**, 416-422.

Larkin, P.A. (1996) Concepts and issues in marine ecosystem management. *Reviews in Fish Biology and Fisheries* **6**, 139-164.

Lessard, J., Campbell, A. (2007) Describing northern abalone *Haliotis kamtschatkana* habitat: focusing rebuilding efforts in British Columbia Canada. *Journal of Shellfish Research* **26**, 677-686.

Lessard, J., Campbell, A., Zhang, Z., MacDougall, L., Hankewich, S. (2007) Recovery potential assessment for the northern abalone (*Haliotis kamtschatkana*) in Canada. Research Document 2007/061. Canadian Science Advisory Secretariat, Nanaimo, British Columbia, Canada.

Lima, S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions - What are the ecological effects of anti-predator decision-making? *Bioscience* **48**, 25-34.

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

Liu, J.G., Dietz, T., Carpenter, S.R. *et al.* (2007) Complexity of coupled human and natural systems. *Science* **317**, 1513-1516.

Long, R.D., Charles, A., Stephenson, R.L. (2015) Key principles of marine ecosystem-based management. *Marine Policy* **57**, 53-60.

Markel, R.W., Shurin, J.B. (2015) Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests. *Ecology* **96**, 2877-2890.

Marshall, K.N., Stier, A.C., Samhouri, J.F., Kelly, R.P., Ward, E.J. (2016) Conservation challenges of predator recovery. *Conservation Letters* **9**, 70-78.

McKechnie, I., Wigen, R.J. (2011) Toward a historical ecology of pinniped and sea otter hunting traditions on the coast of southern British Columbia. pp. 129-166 in Braje, T.J., Rick, T.C. editors. *Human impacts on seals, sea lions, and sea otters: Integrating archaeology and ecology in the Northeast Pacific.* University of California Press, Berkeley and Los Angeles, California, USA.

Menzies, C.R. (2010) Dm sibilhaa'nm da laxyuubm Gitxaała: picking abalone in Gitxaała territory. *Human Organization* **69**, 213-220.

Menzies, C.R. (2015) Revisiting “Dm sibilhaa’nm da laxyuubm Gitxaała (Picking abalone in Gitxaała territory)”: vindication, appropriation, and archaeology. *BC Studies*, 129-153.

Micheli, F., Shelton, A.O., Bushinsky, S.M. *et al.* (2008) Persistence of depleted abalones in marine reserves of central California. *Biological Conservation* **141**, 1078-1090.

Nichol, L.M., Boogaards, M.D., Abernethy, R. (2009) Recent trends in the abundance and distribution of sea otters (*Enhydra lutris*) in British Columbia. p. iv + 16 pp. *Research Document.* Canadian Science Advisory Secretariat, Nanaimo, British Columbia, Canada.

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

Norse, E.A. (1993) *Global marine biological diversity: a strategy for building conservation into decision making*. Island Press, Washington, D. C., USA.

Orrock, J.L., Preisser, E.L., Grabowski, J.H., Trussell, G.C. (2013) The cost of safety: refuges increase the impact of predation risk in aquatic systems. *Ecology* **94**, 573-579.

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

Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in ecology & evolution* **10**, 430.

Pickett, S.T.A. (1989) Space-for-time substitution as an alternative to long-term studies. pp. 110-135 in Likens, G.E. editor. *Long-term studies in ecology: approaches and alternatives.* Springer-Verlag, New York, New York, USA.

Plagányi, E.E., van Putten, I., Hutton, T. *et al.* (2013) Integrating indigenous livelihood and lifestyle objectives in managing a natural resource. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 3639-3644.

Polis, G.A., Strong, D.R. (1996) Food web complexity and community dynamics. *American Naturalist* **147**, 813-846.

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

Preisser, E.L., Bolnick, D.I., Benard, M.F. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* **86**, 501-509.

R Development Core Team. (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raimondi, P., Jurgens, L.J., Tinker, M.T. (2015) Evaluating potential conservation conflicts between two listed species: sea otters and black abalone. *Ecology* **96**, 3102-3108.

Read, K.D., Lessard, J., Boulding, E.G. (2013) Improving outplanting designs for northern abalone (*Haliotis kamtschatkana*): the addition of complex substrate increases survival. *Journal of Shellfish Research* **32**, 171-180.

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

Ripple, W.J., Estes, J.A., Beschta, R.L. *et al.* (2014) Status and ecological effects of the world's largest carnivores. *Science* **343**, 151-162.

Roemer, G.W., Gompper, M.E., Van Valkenburgh, B. (2009) The ecological role of the mammalian mesocarnivore. *Bioscience* **59**, 165-173.

Rogers-Bennett, L. (2007) Is climate change contributing to range reductions and localized extinctions in northern (*Haliotis kamtschatkana*) and flat (*Haliotis walallensis*) abalones? *Bulletin of Marine Science* **81**, 283-296.

Rogers-Bennett, L., Allen, B.L., Rothaus, D.P. (2011) Status and habitat associations of the threatened northern abalone: importance of kelp and coralline algae. *Aquatic Conservation: Marine and Freshwater Ecosystems* **21**, 573-581.

Rogers-Bennett, L., Pearse, J.S. (2001) Indirect benefits of marine protected areas for juvenile abalone. *Conservation Biology* **15**, 642-647.

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

Salomon, A.K., Wilson, B.J.K., White, E.X., Tanape, N.M., Happynook, T.M. (2015) First Nations perspectives on sea otter conservation in British Columbia and Alaska: insights into coupled human ocean systems. pp. 301-331 in Larson, S.E., Bodkin, J.L., VanBlaricom, G.R. editors. *Sea Otter Conservation.* Academic Press, Boston, Massachusetts, USA.

Schultz, J.A., Cloutier, R.N., Coté, I.M. (2016) Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ* **4**.

Sea Otter Recovery Team. (2007) Recovery Strategy for the Sea Otter (*Enhydra lutris*) in Canada. *Species at Risk Act* Recovery Strategy Series. Fisheries and Oceans Canada, Vancouver, British Columbia, Canada.

Sih, A. (1980) Optimal behavior: can foragers balance two conflicting demands? *Science* **210**, 1041-1043.

Sih, A. (1982) Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* **63**, 786-796.

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

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., Bolker, B.M. (2013) Generalized Linear Mixed Models using AD Model Builder. R package version 0.7.7.

Sloan, N.A. (2004) Northern abalone: using an invertebrate to focus marine conservation ideas and values. *Coastal Management* **32**, 129-143.

Sloan, N.A., Breen, P.A. (1988) Northern abalone, *Haliotis kamtschatkana* in British Columbia: fisheries and synopsis of life history information. *Canadian Special Publication of Fisheries and Aquatic Sciences* **103**, 46 pp.

Sloan, N.A., Dick, L. (2012) *Sea Otters of Haida Gwaii: Icons in Human - Ocean Relations*. Gwaii Haanas Archipelago Management Board & Haida Gwaii Museum, Skidegate, British Columbia, Canada.

Soulé, M., Estes, J.A., Berger, J., Martinez Del Rio, C. (2003) Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* **17**, 1238-1250.

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

Stevenson, C.F., Demes, K.W., Salomon, A.K. (2016) Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. *Ecology and Evolution* **6**, 1041-1053.

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

Tegner, M.J., Dayton, P.K. (2000) Ecosystem effects of fishing in kelp forest communities. *ICES Journal of Marine Science* **57**, 579-589.

Thomson, R.E. (1981) Oceanography of the British Columbia Coast. *Canadian Special Publication of Fisheries and Aquatic Sciences* **56**, 291 pp.

Thrush, S.F., Dayton, P.K. (2010) What can ecology contribute to ecosystem-based management? *Annual Review of Marine Science* **2**, 419-441.

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

Tomascik, T., Holmes, H. (2003) Distribution and abundance of *Haliotis kamtschatkana* in relation to habitat, competitors and predators in the Broken Group Islands, Pacific Rim National Park Reserve of Canada. *Journal of Shellfish Research* **22**, 831-838.

Trosper, R.L. (2009) *Resilience, Reciprocity and Ecological Economics: Northwest Coast Sustainability*. Routledge, New York, New York, USA.

Wallace, S. (1999) Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. *Conservation Biology* **13**, 882-887.

Watson, J.C. (1993) The effects of sea otter (*Enhydra lutris*) foraging on shallow communities off northwestern Vancouver Island, British Columbia. p. 169. *Biology.* University of California, Santa Cruz, California, USA.

Watson, J.C. (2000) The effects of sea otters (*Enhydra lutris*) on abalone (*Haliotis* spp.) populations. *Canadian Special Publication of Fisheries and Aquatic Sciences* **130**, 123-132.

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

Zhang, Z., Campbell, A., Lessard, J. (2007) Modeling northern abalone, *Haliotis kamtschatkana*, population stock and recruitment in British Columbia. *Journal of Shellfish Research* **26**, 1099-1107.

Zuur, A.F., Ieno, E.N., Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**, 3-14.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, New York, USA.

Zuur, A.F., M., H.J., N., I.E. (2013) *A beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists*. Highland Statistics Ltd., Newburgh, Lancashire, UK.

Chapter 3. Shifting baselines driven by social-ecological transformations alter perceptions of species status and trends[2]

Abstract

Mounting evidence suggests that knowledge of social-ecological system change over long historical time periods is essential to gauge the true conservation status of species. Modern ecological data spans only years to decades, often concealing the magnitudes of change that have already occurred due to human use of marine and terrestrial ecosystems. Fortunately, disparate knowledge sources are increasingly being bridged to reconstruct broader understanding of complex social-ecological system change. Here, we synthesized data from zooarchaeological, historical, traditional and western knowledge to illuminate trends in northern abalone abundance and size on temperate rocky reefs in British Columbia, Canada. We detected three social-ecological system regimes through the Holocene to present, each with unique trajectories for people and key species' relative abundance, size and distribution. Integrated models fit to traditional knowledge (TK) and western scientific knowledge (WSK) data revealed that both datasets supported a similar rate of annual decline at 3.7% from the 1940s-2010s for large abalone. However, abalone density estimates from TK data were 9.5-times higher than those from WSK. Currently listed as endangered, abalone are scarce compared to the mid-1900s yet likely more abundant than before the early-1800s, calling their true conservation status into question. Particularly for culturally important species like abalone, respectfully bridging multiple knowledge sources, and specifically engaging with traditional knowledge systems, allows us to collectively build SES understanding in a way that facilitates power-sharing and supports ecologically-sustainable and socially-just conservation decision-making.

---

[2] A version of this chapter is currently in review: Lee, L., J. Thorley, J. Watson, M. Reid, and A. K. Salomon. *In review*. Diverse knowledge systems reveal historical social-ecological and species abundance changes for gauging conservation status. Conservation Letters.

Introduction

Conservation science is increasingly acknowledging the need to understand social-ecological system (SES) change over long historical timescales in order to gauge the true conservation status of species. This long view is required to fully appreciate the magnitude of change that has occurred prior to the availability of modern ecological data that often spans only a few short years or decades. This limited snapshot in time can lead to erroneous conclusions about species status and trends because of shifting baselines where each successive generation of observers believes what they grew up with to be normal without knowledge of species abundances in the past (Pauly 1995, Soga and Gaston 2018).

To help counteract the shifting baselines syndrome, multiple unconventional data sources are increasingly being synthesized to help fill this knowledge gap, with acknowledgment of each source's uncertainties, spatial and temporal scales, and biases (e.g., Dayton et al. 1998, Jackson et al. 2001, Pandolfi et al. 2003, Baum and Myers 2004, Lotze and Milewski 2004, Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2006, Saenz-Arroyo and Roberts 2008, Costanza et al. 2012, Thurstan et al. 2015, Early-Capistran et al. 2018). For example, archaeological analyses can reveal important patterns of human use and relative species abundance and size over millennia at coarse temporal resolution (e.g., Simenstad et al. 1978, Braje et al. 2009, McKechnie et al. 2014, Braje et al. 2017b). Historical records impart snapshots of cultural and social-ecological conditions over hundreds of years, and fisheries records can span decades to centuries (e.g., Saenz-Arroyo et al. 2006). Traditional knowledge offers place-based observations building on generations of knowledge, practices and laws regulating interactions between people and their environment (e.g., Berkes et al. 2000). Finally, innovative multidisciplinary work is being applied to reconstruct historical baselines, such as integrating ethnographic knowledge with modeling of human consumption rates of a species to estimate its annual historic harvest over time (Early-Capistran et al. 2018).

Case studies using multiple lines of evidence have illuminated patterns of SES change over broad spatial and long temporal scales. For example, along California's coast, zooarchaeological and isotopic evidence showed how fishing pressure reduced size and abundance, and changed diets, of California sheephead over 10,000 years (Braje et al. 2017b). Throughout BC, zooarchaeological and ethnographic data suggested Pacific herring persisted in abundance over millennia, declining only within the last century (McKechnie et al. 2014). In south-central Alaska, combined evidence from historical records, traditional knowledge and ecological surveys demonstrated serial decline of multiple shellfish likely led to declines in a herbivorous mollusk (Salomon et al. 2007). Multiple data sources can broaden perceptions of species status and trends, altering perspectives on conservation issues to reveal previously overlooked SES transformations in coupled human-environment systems (Moore et al. 2014).

The northern abalone (*Haliotis kamtschatkana*) SES is one such complex, adaptive system (Folke et al. 2010). Northern abalone, a nearshore marine mollusk, is a culturally-important food for coastal Indigenous peoples in BC, Canada, (self-referred to as First Nations) with traditional use extending back millennia (Sloan 2004, Menzies 2010, 2015). Abalone also supported important commercial and recreational fisheries from 1950s until 1990 when all abalone fisheries were closed due to conservation concerns (Fisheries and Oceans Canada 2012). In Canada, northern abalone were designated as threatened in 1999, then uplisted to endangered status under the *Species At Risk Act* (SARA; 2002) in 2009 (Fisheries and Oceans Canada 2012). Recent observations of increasing abalone abundance in some areas have renewed First Nations interests in re-opening sustainable traditional food fisheries for abalone.

Concurrently, sea otters (*Enhydra lutris*), a once-extirpated and now-recovering abalone predator, are expanding their range and abundance since re-introduction from 1969-72 (Bigg and MacAskie 1978). Listed as endangered in 1978 due to low abundance and limited geographic distribution, sea otters were first downlisted to threatened in 1996, then to a species of special concern under SARA (2002) in 2007 (Sea Otter Recovery Team 2007). Sea otters are well-documented drivers of rocky reef ecosystem structure and function, transforming urchin barrens (devoid of kelp) to kelp-forested reefs by reducing abundance and size of kelp-grazing urchins (Estes and Palmisano 1974, Watson and Estes 2011, Markel and Shurin 2015, Lee et al. 2016, Stevenson et al. 2016).

Here, we use multiple knowledge sources to expand and refine trends in northern abalone abundance and size, and to reveal drivers of SES change. We asked, how does understanding social-ecological system change alter our perception of northern abalone status and trends? We developed a collaborative respectful approach for researchers and Indigenous communities to bring together traditional knowledge, ecological field surveys, archaeological data, historical records and fisheries landings, to build deeper, evidence-based understanding of SES transformations.

Methods

Study area

We reconstructed a historical timeline of major changes in key components of the northern abalone SES across BC, Canada, from the start of the Holocene to present. To assess more recent, finer-scale change in abalone abundance and size, we focused quantitative analyses within Heiltsuk First Nation traditional territory on BC's central coast (CC) near Bella Bella (Fig. 3.2A).

Zooarchaeological, historical and fisheries data

To estimate relative abundances of sea otter, urchins, abalone and kelp (via kelp-associated fish bones) over time, we drew on published archaeological shell midden analyses and historical maritime fur trade accounts (Table S1). We used number of sea otter pelts traded as an index of abundance before and during the fur trade, recognizing many early trade pelts were likely older pelts passed through generations of First Nations (Sloan and Dick 2012; Table S2). Lastly, we compiled commercial abalone catch data from Canada's federal fisheries agency (Fisheries and Oceans Canada; 1957-1990; Fig. S1).

Traditional knowledge

In 2012, we conducted ten semi-directive interviews (Huntington 1998) to document Heiltsuk First Nation traditional knowledge about (a) ecology, use and stewardship of abalone, (b) general changes in the abundance and distribution of sea otters, urchins, abalone and kelp, and in abalone size, and (c) traditional abalone management (see *Semi-directive interview questions* in Supplementary Materials). Respondents included 14 abalone experts – one woman and 13 men – from 39-90 years of age.

To assess decadal variation in intertidal abalone density and size through time, we asked experts to represent the number, size, location and configuration of abalone within a specified area of shoreline over each decade that they remembered, using color-coded, length-classified abalone shells: extra large (XL>120 mm), large (L=100-120 mm), medium (M=70-99 mm), small (S=50-69 mm), extra small (XS=30-49 mm), and juvenile (J<30 mm). We also documented how experts learned to harvest abalone, harvest locations and experiential timeframes. We conducted community-based verification sessions of verbatim transcripts and maps in 2013.

Western knowledge

To reconstruct a historical timeline, we estimated change in abalone densities following sea otter extirpation from a published stock-recruitment relationship at an assumed natural mortality rate of 10% (Table S2). Additionally, we estimated relative abundance changes for abalone, urchins and kelp using a space-for-time substitution with subtidal sites varying in sea otter occupation time (Lee *et al.* 2016; Table S2). Finally, sea otter population estimates were derived from federal field survey records (Nichol et al. 2015).

To compare proportional trends for abalone, urchins and kelp with increasing sea otter occupation time by decade and region, we used subtidal random transect data uncorrected for local site conditions for the CC (Lee et al. 2016) and permanent subtidal transect data for the west coast of Vancouver Island (WCVI; J. Watson, unpublished data). We calculated abalone density site means from transects within sites, and then means of site means by decades of sea otter occupation: 0, 1-10, 11-20, 21-30, and 31-40 years. For abalone population modelling, we used federal fisheries population index site survey data (1980-2016; methods in Fisheries and Oceans Canada 2016).

Population model of abalone abundance

For the CC, we estimated trends in density of abalone classified as large ≥70 mm (TK length-classes M, L & XL) and small <70 mm (TK length-classes J, XS & S) using data derived from TK and western scientific knowledge (WSK) with density-independent exponential population growth models fitted with Bayesian methods (Boxes S1-S3). Each TK observation represented the average abalone density over a harvest area for an entire decade. Each WSK observation was the total number of abalone at one survey site in one year. Accordingly, the residual error for TK densities was modeled using a lognormal distribution while WSK counts had a negative binomial error distribution (see *Statistical models summary* in Supplementary Materials for details of analyses and descriptions of full and alternate models for densities of large and small abalone).

Results

Drivers of the abalone social-ecological system

Key drivers of BC's northern abalone SES over millennia were: (1) dramatically reduced coastal First Nations populations from epidemics, erosion of traditional governance systems and lifestyles, and increasing influence of colonization, following European contact, (2) sea otter ecological extirpation by maritime fur trade hunting, (3) legal and illegal abalone fishing during and after the commercial abalone fishery, (4) sea otter recovery, and (5) revitalization of First Nations traditional lifestyles and increasing co-management (Fig. 3.1; Table S1, S2). Based on differences in state of human and ecological communities, we parsed the abalone SES into three regimes: sea otters present, absent, and recovering (Fig. 3.1).

Over the past 250 years, the rate, magnitude and spatial distribution of SES changes along the coast varied due to differences in timing and geographic range of sea otter extirpation and recovery. In areas re-occupied by sea otters, abalone and urchin densities declined by >75% within 1-5 years, and stabilized at low but persistent densities by 10 years (Fig. 3.2BC; Watson and Estes 2011, Lee et al. 2016). Kelp stipe densities increased for up to six years following sea otter arrival, declined, and then persisted at higher densities compared to reefs without otters (Figs. 3.2BC; Watson and Estes 2011, Lee et al. 2016; J. Watson, unpublished data). We assumed sites occupied by sea otters for over a decade represented potential abalone, urchin and kelp abundances at high sea otter densities.

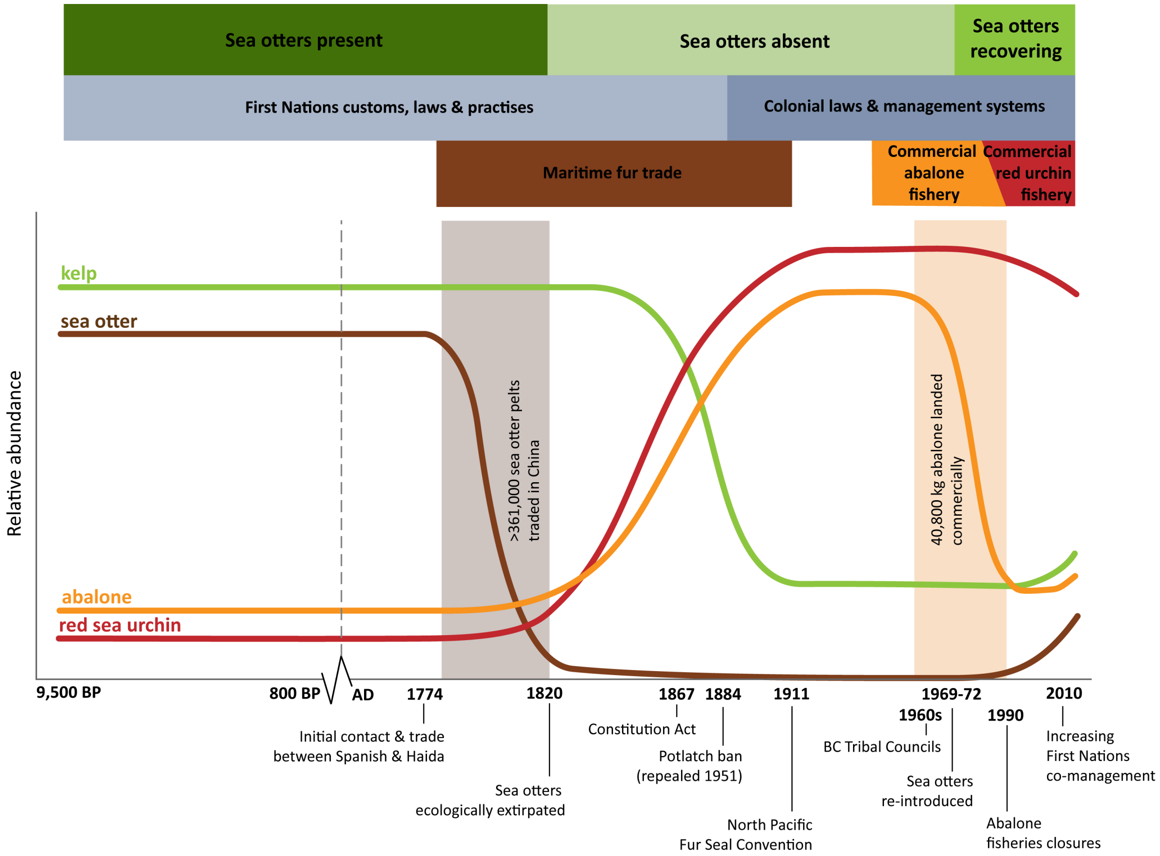

Figure 3.1 **Historical social-ecological timeline for northern abalone in British Columbia, Canada, highlighting key governance and management systems, events, and resource uses driving system change within three social-ecological system regimes – sea otters present, absent, and recovering – from start of the Holocene to present.**

Table 3.1 Representative observations of abalone use and ecology by decade from Heiltsuk traditional knowledge interviews.

Decade	Representative observations by Heiltsuk abalone experts
1940s	"They were just three, four on top, on top of each other." (GEH; abalone XL & L size) "...well, these guys are still eating. I went and picked two sacks [of abalone]." (GEH; abalone often picked for meals while out fishing for other seafood)
1950s	"Yah, we just row around the island and pick enough to eat and all these reefs outside here…" (FCR; picked abalone while working his trapline)
1960s	"… we're usually happy with one [100 lb] sack of it for our winter supply." (ARR; used to row out to pick abalone in the seine skiff)
Early 1970s	"...my older brother took me out there. He knew the area and he knew there was lots of them out there and we didn't spend much time gathering there so we did other things as well. ...We, there's seaweed out there, we would grab a little bit of seaweed and do a little bit of jigging… but in a short period of time we had a couple of sacks [of abalone] each." (MKR)
Late 1970s	"This [XL] was the size and it didn't take me very long to, at that particular trip, double back and just pluck them off of the kelp."; In the late 1980s, "I think around three different rocks now to get the same volume or… the amount of abalone from 1975 when I, in that same area." (MKR)
Early 1980s	"...you have to pick... start picking before you got off your boat… the whole rock was just right plugged." (DNW)
Late 1980s	"You know, you'd have to spend a lot of time walking the rocks the same areas where we used to just go to our little spots and you know you're going to get a bucket there to dump into your sack. If you go out to the same areas now, you're going to have to pick kelp up, leaves, and you're hoping to find one. I think it was probably late eighties when I started to see that change." (GGH)
1990s	"If I found one, the double red [XL], I'd get a hero's welcome." (HH)
2000s	"I said, 'look at all these baby ones; it's going to be good for later on.'" (DNW)
2010s	"Not very big. There's lots out there, but they're small." (Anonymous)

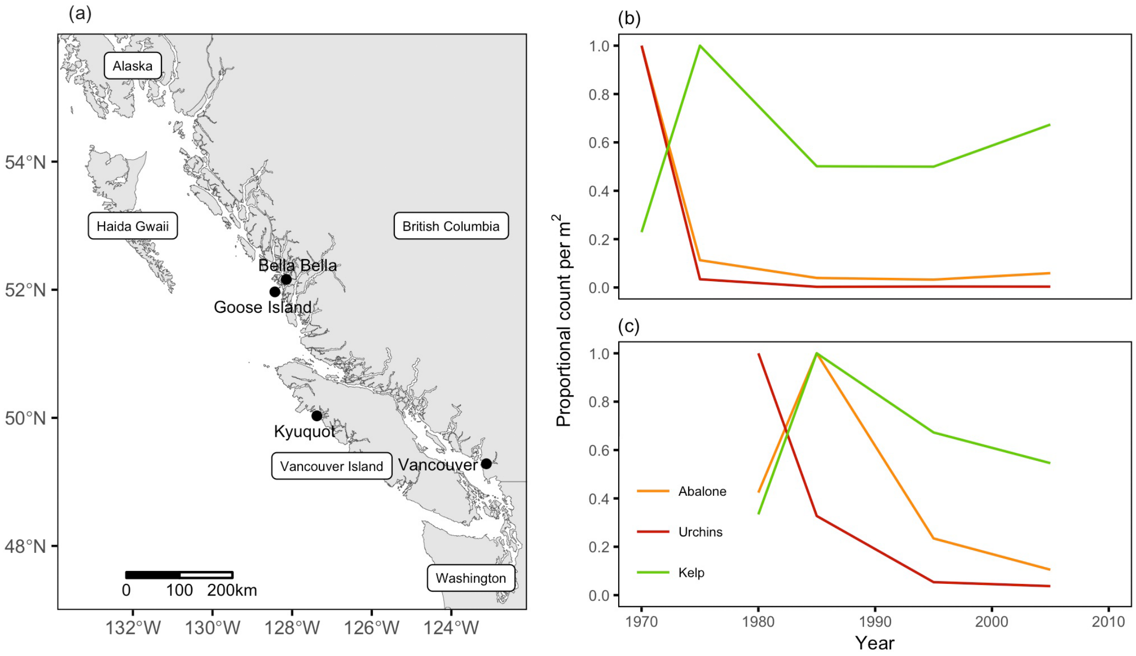

Figure 3.2 **(a) Map of the British Columbia coast, including the communities of Kyuquot in Nuu-chah-nulth traditional territory and Bella Bella in Heiltsuk traditional territory. Sea otters were re-introduced near Kyuquot from 1969-72. A sea otter raft was first documented in the Goose Islands in the 1980s. Proportional change in densities of abalone, urchins and kelp by region: (b) Nuu-chah-nulth traditional territory on the west coast of Vancouver Island and (C) Heiltsuk traditional territory on the central coast. Means of site means from transects within sites are plotted by decade of sea otter occupation.**

Causes of recent abalone decline in Heiltsuk territory

The subtidal commercial SCUBA dive fishery for abalone was intense and short-lived, leaving a profoundly reduced abalone population coastwide, and loss of First Nations traditional abalone food fisheries (Fig. 3.1). The CC fishery occurred mainly from 1970s-80s (Fig. S1), corresponding with abalone declines observed by Heiltsuk experts (Figs. 3.3, S2; Table 3.1). As the fishery was declining, the newly established sea otter population in this area was increasing (Figs. S1). From most to least mentioned, Heiltsuk experts attributed abalone declines to: (1) past and on-going illegal fishing, (2) sea otter predation, (3) commercial overfishing, and (4) increased predation by river otters and minks that were no longer being harvested (by trapping; Table S3).

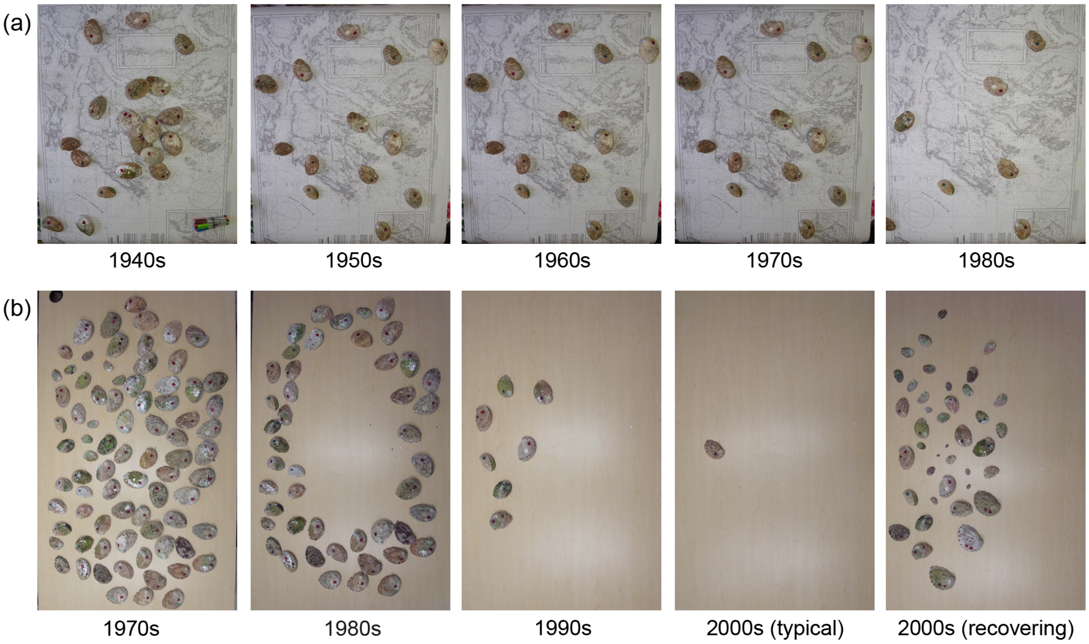

Figure 3.3 **Examples of abalone abundance and size reconstructions by decade from Heiltsuk traditional knowledge interviews with: (a) George and Gary Housty from 1940s-1980s, and (b) Davie Wilson from 1970s-2000s.**

Abalone population trends estimated from traditional and western knowledge

For large abalone ≥70 mm shell length, the population model with the most support ($w_i = 0.55$) included different initial densities and a shared annual population growth rate for TK and WSK data (Figs. 3.4AB; Table S10). The full model, including different initial densities and different annual population growth rates, also had substantial support ($w_i = 0.43$; Table S10). The most-supported model estimated that large abalone declined at an annual rate of 3.7% (CRI 2.2-5.2%) and that densities estimated from TK were 9.5-times (CRI 5.2-16.5) higher than those from WSK. The TK estimate for 1945 was 29.2 abalone/m^2 (CRI 15.1-56.5) and for 2016 was 2.2 abalone/m^2 (CRI 1.2-3.9); respectively, WSK estimates were 2.8 abalone/m^2 (CRI 1.2-6.5) and 0.2 abalone/m^2 (CRI 0.1-0.3).

For small abalone <70 mm shell length, the full model with a fixed step change in annual population growth rate in 2004 received all the support ($w_i = 1.00$; Table S10; WSK data only). Small abalone declined at an annual rate of 13.3% (CRI 9.9-16.9%) from 1980-2003, then increased at 24.5% (CRI 18.3-31.0%) from 2004-2016, mostly driven by increasing densities of J and XS abalone (Fig. 3.4D; Table S9). Estimated small abalone densities were 2.2 abalone/m^2 (CRI 1.2-4.1) for 1980, declining to 0.1 abalone/m^2 (CRI 0.1-0.2) by 2004, then increasing to 2.5 abalone/m^2 (CRI 1.8-3.7) in 2016 (Fig. 3.4D). TK data for small abalone density was insufficient to include in the model (Fig. 3.4C).

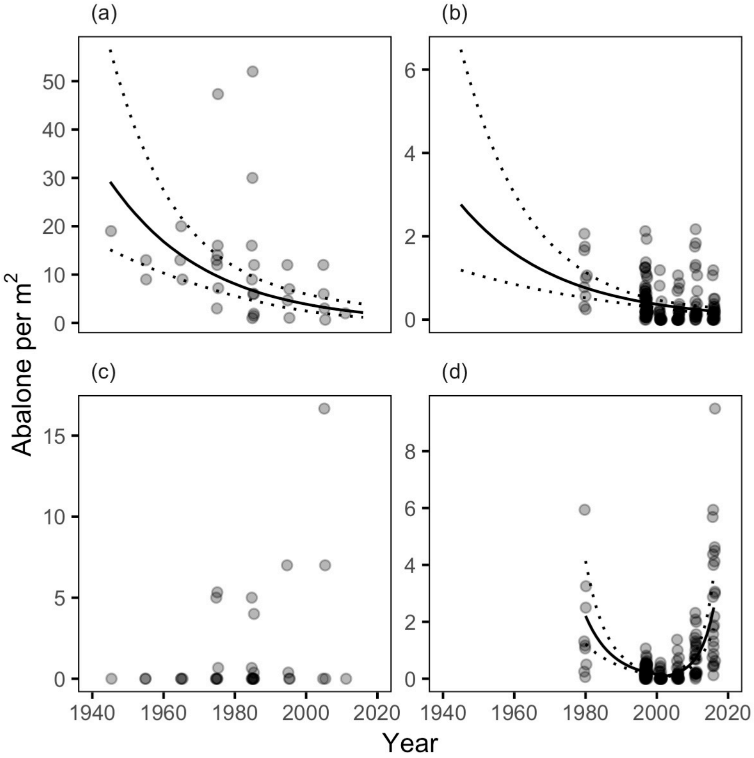

Figure 3.4 **Density of large ≥70 mm and small <70 mm abalone: (a, c) by decade from Heiltsuk traditional knowledge interviews, and (b, d) by year of federal fisheries agency population index site monitoring surveys. Black lines represent abalone density estimates from the most-supported population growth model for: (a, b) large abalone using data from traditional and western knowledge (WSK), and (d) small abalone using data from WSK only. Dotted lines indicate 95% credible intervals.**

Changes in abalone size structure

Traditional knowledge data suggested marked declines in proportions of L and XL abalone from 1940s-early 2000s, while proportion of M abalone increased (Fig. 3.5A). S and XS abalone were not recorded in TK reconstructions until 1970s, after which they increased in proportion, and J abalone were not noted until 2000s (Fig. 3.5A).

In contrast, WSK data showed proportions of L and XL increased from 1990s-early 2000s then declined while proportions of XS and J abalone increased by approximately six-times from mid-2000s to mid-2010s (Fig. 3.5B). Proportions of M and S abalone remained relatively high and consistent from 1980-2016 (Fig. 3.5B).

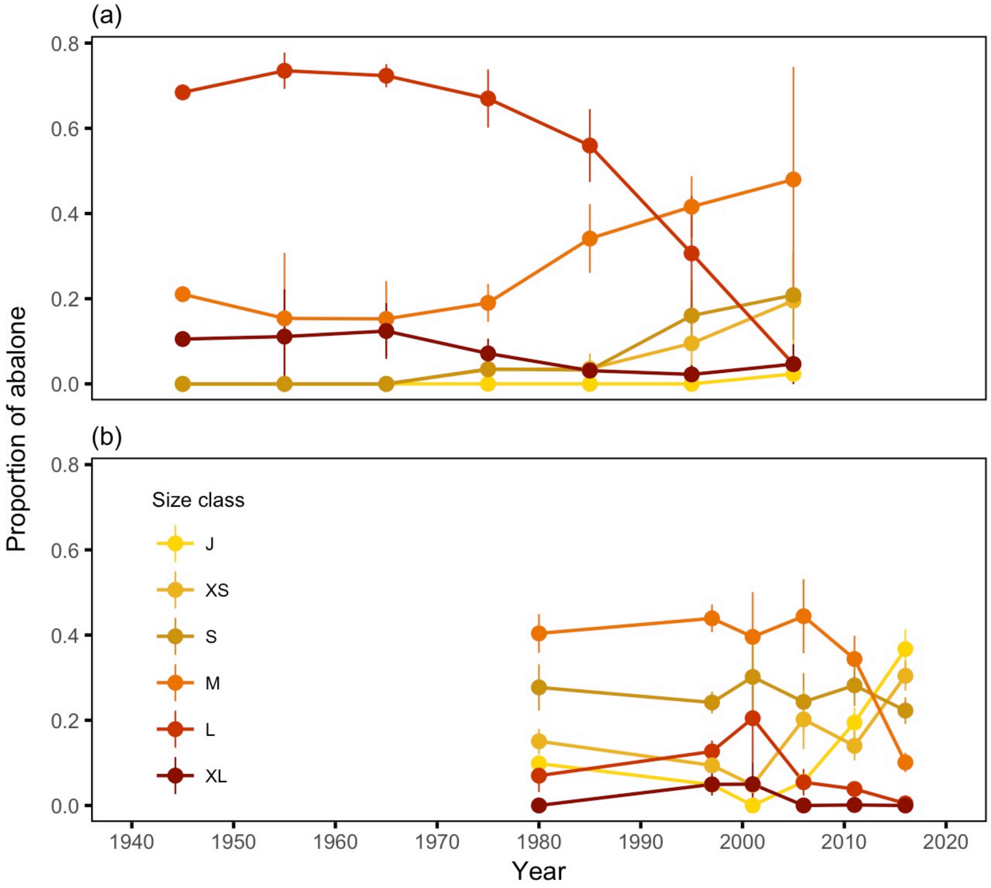

Figure 3.5 **Proportion of abalone in each length-class in Heiltsuk territory: (a) by decade from traditional knowledge interviews, and (b) by year from federal fisheries population index site monitoring surveys.**

Discussion

Multiple lines of evidence illuminate abalone social-ecological system transformations

Using multiple evidence-based (Saenz-Arroyo and Roberts 2008, Tengo et al. 2014) and historical ecology (Costanza et al. 2012, Thurstan et al. 2015) approaches, we reconstructed the BC abalone social-ecological system, allowing each knowledge source to contribute its unique frame of space and time. Human activities influenced abalone populations over at least 10,000 years of dramatic environmental change indirectly through hunting, extirpation and re-introduction of a keystone predator, the sea otter, and directly through fishing (Fig. 3.1; Table S1). While long-term oceanographic shifts likely affected abalone population dynamics over this timescale (Saenz-Arroyo & Roberts 2008; Micheli *et al.* 2012), we lacked the evidence to evaluate their potential effects. Together, these lines of evidence suggest magnitudes of change in abundance, size and social-ecological context of northern abalone that could not be revealed through any single source (sensu Jackson 2001, Saenz-Arroyo et al. 2005a, Braje et al. 2017b).

Zooarchaeological evidence showed relatively high abundance of sea otter bone consistently at many suitable outer-coast sites, and very few abalone shell fragments at few sites during the *sea otters present* regime (Orchard 2007; McKechnie and Wigen 2011, Menzies 2015). Although sea otters reduced abundance and size of abalone and urchins, they indirectly benefitted abalone by facilitating more extensive, structurally complex kelp forests that provide food and shelter (Fig. 3.1; Tables S1, S2; Watson 1993, Watson and Estes 2011, Markel and Shurin 2015, Lee et al. 2016). Hunting from hundreds of coastal First Nations villages likely affected sea otter abundance and spatial distribution, directly and indirectly, creating a patchwork of ecological conditions (Corbett et al. 2008; Salomon et al. 2015).

Over the short, intense maritime fur trade, sea otters were locally-extirpated, leading to the *sea otters absent* regime (Fig. 3.1; Sloan and Dick 2012). Concurrently, introduced diseases and deadly trade-related conflict reduced coastal First Nations populations by >90% (Tables S1, S2; Orchard 2007). Cultural customs, laws, practices, and traditional economies were disrupted, and survivors amalgamated into fewer village sites (Table S1). Absence of sea otter predation for over a century facilitated macroinvertebrate population growth beyond previous abundances, flipping ecosystem conditions to more large herbivores and less kelp (Fig. 3.1; Tables S1, S2). Hyperabundant macroinvertebrates fuelled development of the contemporary, now socio-economically important commercial and recreational shellfisheries. This more recent ecosystem condition is what we now perceive as normal.

In the current *sea otters recovering* regime, their recovery near Kyuquot in the 1970s and on the CC in the 1980s initiated local and regional ecosystem shifts from urchin to kelp-dominated (Fig. 3.2). Although abalone abundance declines in the face of sea otter predation, abalone can persist at relatively high densities under suitable local conditions especially during initial years of sea otter occupation (Fig. 3.2C; Lee et al. 2016). Small increases in abalone density, albeit still low, are also possible following decades of sea otter occupation (Fig. 3.2B; J. Watson, unpublished data). Factors such as sea otter occupation time, substrate complexity and wave exposure interact to create the spatial and temporal patchwork that defines the self-sustaining abalone population, which coevolved with sea otters.

Traditional and western knowledge broaden views of abalone trends

While the multiple evidence-based approach enabled deep-time SES understanding, integrated modeling (e.g., Maunder and Punt 2013) and consideration of TK and WSK data broadened understanding of local-scale trends and extended WSK inference by four decades (Figs. 3.4AB). Density estimates from TK for large abalone were nearly 10 times higher than from WSK likely reflecting higher abalone abundances in low intertidal/shallow subtidal areas where Heiltsuk harvested, while field surveys extended deeper where abalone densities are lower and sizes are smaller (Lee et al. 2016). Both sources agreed on annual population decline rates for large abalone, yet where few data points were available, such as at the beginning (few elder experts) and end (few people looking since fishery closure) of the TK time series, qualitative narratives provide critical context for interpreting model results. For example, models indicated declining densities of large abalone from 1940s-present, whereas elder Heiltsuk remembered stable abalone densities from 1940s-60s (Figs. 3.3, 3.4A, S2). Such information could inform future Bayesian analyses through informative prior distributions.

Differences in abalone size structure from TK and WSK may result from observational biases. Harvesters focusing on larger abalone recalled their abundances more readily than smaller abalone, reflected in the paucity of TK data about smaller abalone. Harvesters were consistently taught to take only larger abalone (XL, L or larger M-sized): “We were told, ‘Let it grow up to this size [L] before you take it home.’" (Howard Humchitt). Similar bias may apply to earlier WSK surveys focused on larger commercial fishery sizes. Despite biases, both data sources reflected marked increases in J abalone recruitment through the 2000s, albeit at different magnitudes (Figs. 3.4CD, 3.5AB).

Cultural resilience underpins governance transformations

Traditional abalone practices persisted through generations, despite escalating imposition of colonial religion, policies and laws throughout the *sea otters absent* regime, demonstrating high cultural resilience (Folke et al. 2010). Disruptions to the First Nations' societies and governance systems that had evolved over millennia included residential schools, banning of the potlatch that was central to coastal First Nations governance, Canada's *Indian Act*, and reservation system (Table S1; Fisher 1992, Gauvreau et al. 2017). Concurrent with sea otter recovery, First Nations cultural practices and resource use are strengthening, including harvesting of traditional foods, potlatching, language programs, cultural activities, and reaffirming alliances between Nations. This on-going reclamation of First Nations culture indicates emerging pre-conditions for governance transformation that are being facilitated by successful court cases and co-management agreements (Table S1).

Furthermore, First Nations communities and academic researchers are collaborating to develop research projects with outcomes that benefit society and conservation broadly. Such collegial relationships will shift management and decision-making legitimacy and power towards true co-management (Nadasdy 1999, Agrawal 2002). In this study, acknowledging Heiltsuk research protocols, retaining proprietary rights to TK within the community, and co-conducting interviews were key to project success (also Gauvreau et al. 2017).

Shifting baselines alter perceptions of abalone status: implications for conservation

Understanding shifting baselines is crucial to conservation as reference conditions are key to determining species status. Under Canada's *Species At Risk Act* (2002) and the International Union for Conservation of Nature (IUCN), decline is gauged against abundances and distributions within the last 10 years or three generations of the species, whichever is longer (Mace et al. 2008). For many species, lack of information about past abundances results in biased and/or underestimated baselines, which allow for lower species abundances to be acceptable because historically higher abundances and greater range distributions are not accounted for (e.g., Pauly 1995, Dayton et al. 1998, Jackson 2001, Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2006, Buckley et al.

2017, Silliman et al. 2018). In the northern abalone SES, the inverse occurs where current abundances are gauged against a recent baseline much higher than the expected historical baseline, leading to an inflated view of extinction risk. This arbitrary baseline led to abalone’s initial assessment as threatened and subsequent uplisting to endangered.

Should abalone be listed as endangered? Yes, according to the SARA and IUCN evaluation frameworks gauging abundance from 30 years ago. But the answer would change if a different point in time were chosen as the baseline. Mounting evidence from case studies worldwide demonstrate that baselines are dynamic and often driven by human activities (Hicks et al. 2016), limiting the value of using static baselines to judge conservation status. Further, these static baselines are often based on limited timescales of ecological data that conceal the true magnitudes of change, as show in case studies throughout the world (e.g., Pauly 1995, Saenz-Arroyo et al. 2005b, Saenz-Arroyo et al. 2006, Saenz-Arroyo and Roberts 2008, Ferretti et al. 2018). For conservation policies and legislation to be effective, concomitant change is needed that keeps pace with current understanding in conservation science.

What if the northern abalone is not really in imminent danger of extinction? How then should cultural considerations alter decisions about their status or use? Since its loss as a traditional food in 1990, a second First Nations generation now lacks opportunities to connect with abalone (sensu Turner et al. 2008). In 2000s, “I took my granddaughter out… showed her abalone and she said, ‘What do you do with these?’” (Davie Wilson). Elders have been deprived of abalone for decades: “I got that much [abalone] and that old lady was so happy. She damn near hugged me to death…” (Anonymous). Perhaps reconstructing changes in this complex, adaptive SES can help society weigh the risks of cultural and ecological losses to make management decisions that are ecologically-sustainable and socially-just.

Building understanding of how SESs have changed over historic time allows us to envision alternative futures. For example, in a similar system with sea otters and red abalone in California, zooarchaeological analyses of shell middens showed widely varying abundance yet persistence in abalone shell remains over 8000 years (Braje et al. 2009). Although large-scale oceanographic regimes can have significant effects on abalone productivity, abalone shell abundance was not found to correlate with cold and warm ocean periods through this time. In this case, it appeared that top-down sea otter predation, indigenous hunting of sea otters, and harvesting of abalone were likely stronger drivers of variation in abalone abundance over millennia. This case study suggests that BC's coastal rocky reef ecosystems may also be able to support some level of First Nations traditional abalone harvest while maintaining the persistence of abalone. This scenario has potential to balance and achieve both social justice for indigenous peoples and ecological justice for abalone. Reconstructing broader understanding of SES change using many knowledge sources should be broadly applied to many conservation issues to explore similar questions, help resolve conflicts, build common understanding, share power and legitimacy, and highlight leverage points for effective ecosystem-based conservation actions.

Acknowledgements

NSERC, Hakai Institute, SFU graduate scholarship and DFO Species At Risk grants supported LL under SFU Ethics permit 2011s0805. NSERC Discovery, Canadian Foundation for Innovation, Hakai Institute and Pew Fellowship grants to AKS funded this research. Walas Giaxsixa (thanks) to collaborators Jennifer Carpenter, Harvey Humchitt, and Gary Wilson of the Heiltsuk Nation, and *Gitla* (Elroy White) who co-interviewed Gus Brown, Bill Gladstone Sr, George and Gary Housty, Howard Humchitt, Sonny Hunt, Mike Reid, Tony and Emma Reid, Fred Reid, Davie Wilson, and three anonymous experts who generously shared their time and knowledge. We thank colleagues for thoughtful reviews.

References

Agrawal, A. (2002) Indigenous knowledge and the politics of classification. *International Social Science Journal* **54**, 287-297.

Baum, J.K., Myers, R.A. (2004) Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* **7**, 135-145.

Berkes, F., Colding, J., Folke, C. (2000) Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications* **10**, 1251-1262.

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

Braje, T.J., Erlandson, J.M., Rick, T.C., Dayton, P.K., Hatch, M.B.A. (2009) Fishing from past to present: continuity and resilience of red abalone fisheries on the Channel Islands, California. *Ecological Applications* **19**, 906-919.

Braje, T.J., Rick, T.C., Szpak, P. *et al.* (2017) Historical ecology and the conservation of large, hermaphroditic fishes in Pacific Coast kelp forest ecosystems. *Science Advances* **3**.

Buckley, S.M., Thurstan, R.H., Tobin, A., Pandolfi, J.M. (2017) Historical spatial reconstruction of a spawning-aggregation fishery. *Conservation Biology* **31**, 1322-1332.

Corbett, D.G., Causey, D., Clementz, M. *et al.* (2008) Aleut hunters, sea otters, and sea cows: three thousand years of interactions in the western Aleutian Islands, Alaska. pp. 43-75 in Rick, T.C., Erlandson, J.M. editors. *Human impacts on ancient marine ecosystems: a global perspective.* University of California Press, Berkeley and Los Angeles, California, USA.

Costanza, R., van der Leeuw, S., Hibbard, K. *et al.* (2012) Developing an Integrated History and future of People on Earth (IHOPE). *Current Opinion in Environmental Sustainability* **4**, 106-114.

Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L. (1998) Sliding baselines, ghosts and reduced expectations in kelp forest communities. *Ecological Applications* **8**, 309-322.

Early-Capistran, M.M., Saenz-Arroyo, A., Cardoso-Mohedano, J.G., Garibay-Melo, G., Peckham, S.H., Koch, V. (2018) Reconstructing 290 years of a data-poor fishery through ethnographic and archival research: The East Pacific green turtle (Chelonia mydas) in Baja California, Mexico. *Fish and Fisheries* **19**, 57-77.

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

Ferretti, F., Curnick, D., Liu, K.L., Romanov, E.V., Block, B.A. (2018) Shark baselines and the conservation role of remote coral reef ecosystems. *Science Advances* **4**.

Fisher, R. (1992) *Contact and Conflict*, 2nd ed. UBC Press, Vancouver, BC.

Fisheries and Oceans Canada. (2012) Action Plan for the Northern Abalone (*Haliotis kamtschatkana*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Fisheries and Oceans Canada. (2016) Review of Dive Survey Methods for Northern Abalone in British Columbia. *Canadian Science Advisory Secretariat Science Response* **2016/044**.

Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Chapin, T., Rockstrom, J. (2010) Resilience Thinking: Integrating Resilience, Adaptability and Transformability. *Ecology and Society* **15**.

Gauvreau, A.M., Lepofsky, D., Rutherford, M., Reid, M. (2017) "Everything revolves around the herring": the Heiltsuk-herring relationship through time. *Ecology and Society* **22**.

Hicks, C.C., Crowder, L.B., Graham, N.A.J., Kittinger, J.N., Le Cornu, E. (2016) Social drivers forewarn of marine regime shifts. *Frontiers in Ecology and the Environment* **14**, 253-261.

Huntington, H.P. (1998) Observations on the utility of the semi-directive interview for documenting traditional ecological knowledge. *Arctic* **51**, 237-242.

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

Jackson, C.A., Kirby, M.X., Berger, W.H. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629-637.

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

Lotze, H.K., Milewski, I. (2004) Two centuries of multiple human impacts and successive changes in a North Atlantic food web. *Ecological Applications* **14**, 1428-1447.

Mace, G.M., Collar, N.J., Gaston, K.J. *et al.* (2008) Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species. *Conservation Biology* **22**, 1424-1442.

Markel, R.W., Shurin, J.B. (2015) Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests. *Ecology* **96**, 2877-2890.

Maunder, M.N., Punt, A.E. (2013) A review of integrated analysis in fisheries stock assessment. *Fisheries Research* **142**, 61-74.

McKechnie, I., Lepofsky, D., Moss, M.L. *et al.* (2014) Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. *Proceedings of the National Academy of Sciences of the United States of America* **111**, E807-E816.

McKechnie, I., Wigen, R.J. (2011) Toward a historical ecology of pinniped and sea otter hunting traditions on the coast of southern British Columbia. pp. 129-166 in Braje, T.J., Rick, T.C. editors. *Human impacts on seals, sea lions, and sea otters: Integrating archaeology and ecology in the Northeast Pacific.* University of California Press, Berkeley and Los Angeles, California, USA.

Menzies, C.R. (2010) Dm sibilhaa'nm da laxyuubm Gitxaała: picking abalone in Gitxaała territory. *Human Organization* **69**, 213-220.

Menzies, C.R. (2015) Revisiting "Dm sibilhaa'nm da laxyuubm Gitxaała (Picking abalone in Gitxaała territory)": vindication, appropriation, and archaeology. *BC Studies*, 129-153.

Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L. *et al.* (2012) Evidence that marine reserves enhance resilience to climatic impacts. *Plos One* **7**.

Moore, M.L., Tjornbo, O., Enfors, E. *et al.* (2014) Studying the complexity of change: toward an analytical framework for understanding deliberate social-ecological transformations. *Ecology and Society* **19**.

Nadasdy, P. (1999) The politics of TEK: Power and the "integration" of knowledge. *Arctic Anthropology* **36**, 1-18.

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

Orchard, T.J. (2007) Otters and urchins: Continuity and change in Haida economy during the Late Holocene and maritime fur trade periods. p. 408 pp. + appendices. *Department of Anthropology.* University of Toronto, Toronto.

Pandolfi, J.M., Bradbury, R.H., Sala, E. *et al.* (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**, 955-958.

Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in ecology & evolution* **10**, 430.

Saenz-Arroyo, A., Roberts, C.M. (2008) Consilience in fisheries science. *Fish and Fisheries* **9**, 316-327.

Saenz-Arroyo, A., Roberts, C.M., Torre, J., Carino-Olvera, M. (2005a) Using fishers' anecdotes, naturalists' observations and grey literature to reassess marine species at risk: the case of the Gulf grouper in the Gulf of California, Mexico. *Fish and Fisheries* **6**, 121-133.

Saenz-Arroyo, A., Roberts, C.M., Torre, J., Carino-Olvera, M., Enriquez-Andrade, R.R. (2005b) Rapidly shifting environmental baselines among fishers of the Gulf of California. *Proceedings of the Royal Society B-Biological Sciences* **272**, 1957-1962.

Saenz-Arroyo, A., Roberts, C.M., Torre, J., Carino-Olvera, M., Hawkins, J.P. (2006) The value of evidence about past abundance: marine fauna of the Gulf of California through the eyes of 16th to 19th century travellers. *Fish and Fisheries* **7**, 128-146.

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

Salomon, A.K., Wilson, B.J.K., White, E.X., Tanape, N.M., Happynook, T.M. (2015) First Nations perspectives on sea otter conservation in British Columbia and Alaska: insights into coupled human ocean systems. pp. 301-331 in Larson, S.E., Bodkin, J.L., VanBlaricom, G.R. editors. *Sea Otter Conservation.* Academic Press, Boston, Massachusetts, USA.

Sea Otter Recovery Team. (2007) Recovery Strategy for the Sea Otter (*Enhydra lutris*) in Canada. *Species at Risk Act* Recovery Strategy Series. Fisheries and Oceans Canada, Vancouver, British Columbia, Canada.

Silliman, B.R., Hughes, B.B., Gaskins, L.C. *et al.* (2018) Are the ghosts of nature's past haunting ecology today? *Current Biology* **28**, R532-R537.

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

Sloan, N.A. (2004) Northern abalone: using an invertebrate to focus marine conservation ideas and values. *Coastal Management* **32**, 129-143.

Sloan, N.A., Dick, L. (2012) *Sea Otters of Haida Gwaii: Icons in Human - Ocean Relations*. Gwaii Haanas Archipelago Management Board & Haida Gwaii Museum, Skidegate, British Columbia, Canada.

Soga, M., Gaston, K.J. (2018) Shifting baseline syndrome: Causes, consequences, and implications. *Frontiers in Ecology and the Environment* **16**, 222-230.

Stevenson, C.F., Demes, K.W., Salomon, A.K. (2016) Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. *Ecology and Evolution* **6**, 1041-1053.

Tengo, M., Brondizio, E.S., Elmqvist, T., Malmer, P., Spierenburg, M. (2014) Connecting diverse knowledge systems for enhanced ecosystem governance: The multiple evidence base approach. *Ambio* **43**, 579-591.

Thurstan, R.H., McClenachan, L., Crowder, L.B. *et al.* (2015) Filling historical data gaps to foster solutions in marine conservation. *Ocean & Coastal Management* **115**, 31-40.

Turner, N.J., Gregory, R., Brooks, C., Failing, L., Satterfield, T. (2008) From Invisibility to Transparency: Identifying the Implications. *Ecology and Society* **13**.

Watson, J.C. (1993) The effects of sea otter (*Enhydra lutris*) foraging on shallow communities off northwestern Vancouver Island, British Columbia. p. 169. *Biology.* University of California, Santa Cruz, California, USA.

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

Chapter 4. Designing adaptive co-management to foster resilient and socially just coastal fisheries

Abstract

Building resilient coastal fisheries that provide persistent local benefits is an ongoing challenge given the high proportion of poorly performing fisheries worldwide. In less than half a century on Canada's west coast, centralized federal fisheries management led to closure of all abalone fisheries in 1990, including a traditional indigenous fishery that had previously persisted for millennia. Here, in collaboration with two coastal First Nations, we documented and applied traditional knowledge of abalone harvesting practices and stewardship protocols. We then assessed the degree to which both traditional and modern centralized fisheries governance and management systems aligned with seven theoretically grounded principles of social-ecological resilience. We found that historical First Nations environmental governance and management of abalone aligned well with these principles. Their rules of use included protocols of reciprocity and contingent proprietorship, and practices of family-based fishing areas and spatial-temporal limits to access. In contrast, centralized governance of abalone fisheries under Canadian federal management aligned poorly. The modern commercial fishery was initiated with almost no fisheries controls and monitoring, had largely unrestricted spatial-temporal limits, and when finally implemented, fisheries management regulations applied coast-wide. Fortunately, contemporary institutions associated with the current period of abalone recovery hold promise for transformation into future indigenous-state governance. Yet current issues of power asymmetries and trust remain to be addressed through collaborative processes such as adaptive co-management. Acknowledging the integral role of place-based indigenous knowledge systems in contemporary fisheries management would support innovative and respectful approaches to governance. Indigenous resource use and governance protocols generated from millennia of social learning and experimentation, offer insights into sustainable management practices from which we can learn today.

Introduction

Building resilient and persistent coastal fisheries with local benefits is central to the well-being of coastal communities and ecosystems (Davis and Wagner 2006, Pinkerton and Davis 2015, Bennett et al. 2018). This is particularly important for coastal indigenous communities who have relied on, and managed coastal resources for millennia (Caldwell et al. 2012, Lepofsky et al. 2017). Increasingly, indigenous communities throughout the world are successfully re-asserting their rights to access and responsibilities to manage ocean resources (Turner et al. 2013). However, state-led governance and fisheries management institutions have often failed to accept and accommodate the changing roles and legal authority of indigenous communities, as well as new insights into the factors that confer resilience in socio-ecological systems (SESs) (Pinkerton 1992, 1994, Folke 2006, Folke et al. 2010, Biggs et al. 2012, Folke et al. 2016).

The concept of social-ecological resilience offers a theoretical basis for assessing the capacity of management systems to achieve both social and ecological sustainability. Resilient SESs have the capacity to adapt or transform in the face of often-unexpected changes in ways that continue to support human well-being (Chapin et al. 2009, Biggs et al. 2015, Folke et al. 2016). Over several decades, the principles of SES resilience theory (e.g., Berkes and Folke 1998, Folke 2006, Walker and Salt 2006) have been advanced, and there are now comprehensive syntheses of SES resilience principles based on accumulated theoretical and empirical evidence (Biggs et al. 2012). Resilience principles have been applied to analyze complex adaptive systems including a wide variety of natural resource systems (e.g., Folke 2006, Chaffin et al. 2016, Sarkki et al. 2016, Sarkki et al. 2017, Salomon et al. 2018) and indigenous environmental governance along Canada’s northwest coast specifically (e.g. Trosper 2002, 2003, 2009).

Applying resilience principles to resource management in collaboration with indigenous peoples requires approaches and institutional characteristics that can meet diverse social and ecological goals, including positive livelihood and compliance outcomes (Cinner et al. 2012, Pinkerton et al. 2014). Adaptive co-management (ACM) is one such approach that embraces change and uncertainty, thereby fostering SES resilience (Folke et al. 2002, Olsson et al. 2004, Armitage et al. 2009, Plummer et al.

2012, Plummer et al. 2013). It is a context-specific community-based holistic approach that incorporates the adaptive aspect of learning-by-doing (Holling 1978) with cross-scale collaboration and co-management between governing authorities and resource users (Pinkerton 1989).

Evidence from case studies worldwide shows that many indigenous peoples have evolved natural resource management and stewardship practises that foster sustainable livelihoods and ecological well-being within their traditional lands and seas (Armitage 2005, Capistrano and Charles 2012, Brondizio and Le Tourneau 2016). For example, indigenous management of arapaima in Brazil was key to the recovery of this overexploited Amazonian fish (Castello et al. 2009). In the Canadian Arctic, indigenous co-management was critical to positive outcomes for communities and conservation of beluga whales and Dolly Varden char fisheries (Armitage et al. 2011, Kocho-Schellenberg and Berkes 2015). These management successes highlight the fundamental role of place-based indigenous knowledge and traditional stewardship practices in fostering resilient social-ecological systems. In many cases, indigenous harvesting practises and management systems have sustained local and regional resource use over centuries and millennia (Lepofsky and Lertzman 2008, Braje et al. 2009, Caldwell et al. 2012, McKechnie et al. 2014, Lepofsky et al. 2015, Mistry and Berardi 2016, Braje et al. 2017a, Lepofsky et al. 2017), attesting to their ability to support and enhance the resilience of coupled social-ecological systems.

Here, we use principles drawn from SES resilience theory to assess and compare historical indigenous and state (Canadian federal) governance systems that have controlled the conservation and harvest of northern abalone (*Haliotis kamtschatkana*) in western Canada. Northern abalone (hereafter abalone) is a culturally important and economically valued marine snail that is now federally listed as an endangered species. Profound shifts in natural resource governance over the past 250 years have triggered fisheries and conservation conflicts involving abalone and its major predators, sea otters (*Enhydra lutris*) and people (Sloan and Dick 2012, Salomon et al. 2015, Lee et al. *in review*). We assess the extent to which abalone fisheries management systems of coastal indigenous peoples in British Columbia (self-referred to as First Nations) and those of Canada's federal fisheries agency align with foundational resilience principles. We then apply an adaptive co-management approach to chart a course towards more socially just and ecologically sustainable indigenous-state co-management for abalone and other similar species, and broadly for small-scale coastal fisheries.

Social-ecological system description

> ...every spring time… Ah, that rock... the tide would come down that far and that rock would be there. Then my dad would say, 'Okay, it's time to go get abalone.' (Stephen Hunt, Heiltsuk Nation, Jan. 2012)

Study area, components and interactions

Northern abalone range from California to Alaska in the northeast Pacific, and are highly valued by multiple indigenous people who occupy the coast of British Columbia (BC), Canada (Sloan and Breen 1988, Turner et al. 2013). In this study, we draw primarily on knowledge from the Heilsuk Nation, which holds traditional territory on the central coast of BC, and the Haida Nation, which holds traditional territory on Haida Gwaii, an archipelago of islands off BC's north coast (Fig. 4.1). Archaeological and ethnographic evidence reveal that Heiltsuk and Haida are maritime cultures with persistent and strong ties to coastal resources, including abalone, (e.g., Orchard 2007, White 2011, McKechnie et al. 2014, Jackley et al. 2016, McKechnie and Moss 2016), that stretch back at least 13,500 years (Fedje et al. 2005, Wilson and Harris 2005, Braje et al. 2017a). Intercultural relationships that formed part of past governance institutions, specifically Peace Treaties between the Heiltsuk and Haida Nations, persist today (Salomon et al. 2018).

Across the northeastern Pacific, abalone populations are strongly controlled by the top-down forces of sea otter predation and human harvest. Sea otter predation directly reduces exposed abalone densities by up to 16x after 30 years of sea otter occupation, yet doubles the densities of cryptic abalone (Lee et al. 2016). By causing a well-known trophic cascade, sea otters increase the spatial extent and depth of kelp forests (Estes and Palmisano 1974, Duggins 1980, Watson and Estes 2011, Markel and Shurin 2015, Stevenson et al. 2016) thereby increasing the depth range and spatial extent of abalone (Lee et al. 2016).

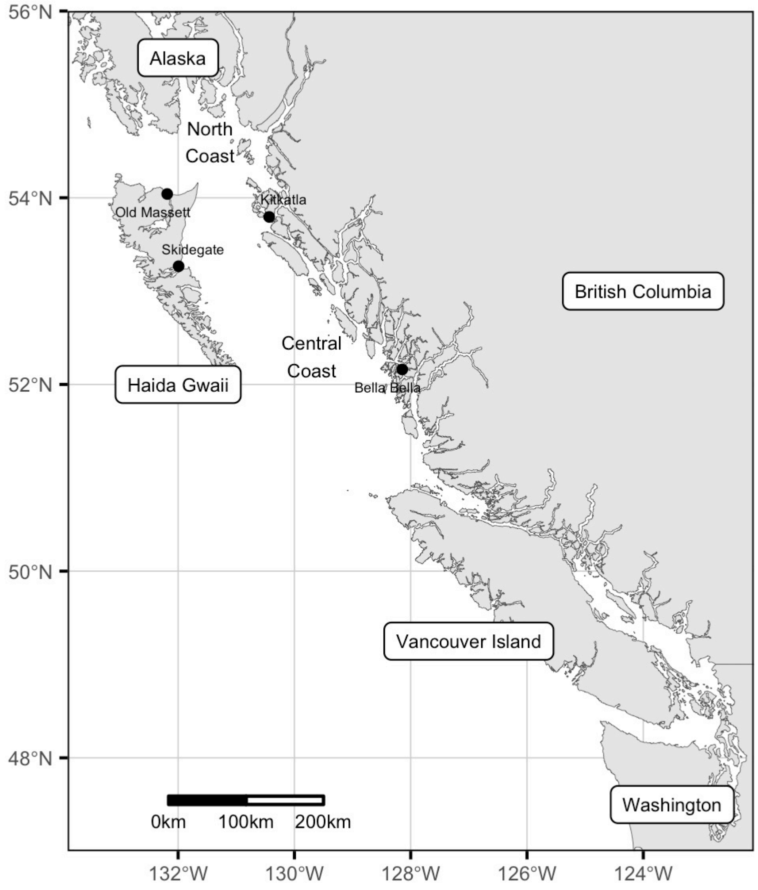

Figure 4.1 **Study area showing locations of communities where abalone harvesting practices and stewardship protocols were drawn from: Bella Bella where we conducted our primary research of collaborative interviews with Heiltsuk Nation abalone experts; Old Massett and Skidegate where the Haida Nation conducted interviews for the Haida Marine Traditional Knowledge Study (Haida Marine Traditional Knowledge Study participants et al. 2011a); and Kitkatla and surrounding territory where published Gitxaala Nation knowledge was documented (Menzies 2010, 2015).**

The other dominant predator of abalone, humans, has a long history of harvesting this marine mollusc (Fig. 4.2). For millennia, First Nations traditionally harvested abalone in the intertidal and shallow subtidal by hand-picking or using hand tools (Menzies 2010, Haida Marine Traditional Knowledge Study participants et al. 2011b, Fisheries and Oceans Canada 2012, Menzies 2015). As a cultural keystone species (Garibaldi and Turner 2004) for many coastal BC First Nations including Haida and Heiltsuk, abalone are important as food, for trade, and for ceremonial regalia (Sloan and Breen 1988, Sloan 2004, Menzies 2010, Haida Marine Traditional Knowledge Study participants et al. 2011b, Menzies 2015). Following colonization, abalone were recreationally harvested by people not of indigenous descent by intertidal hand-picking, and subsequently also by SCUBA diving in modern fisheries from the mid to late 1900s. Commercial fisheries in the early 1900s were very small in scale using intertidal hand-picking, however modern commercial fisheries were conducted by SCUBA diving (Sloan and Breen 1988). First Nations traditional (Aboriginal Food, Social and Ceremonial) fisheries have priority over commercial and recreational fisheries under Canada's Constitution (1867 [1982]).

Abalone fisheries are shaped by interacting forces that have changed dramatically through time including indigenous and colonial management systems, economic markets, Canadian federal policies, and local to global scale environmental conditions (Fig. 4.2). For example, trade during pre-contact times was largely limited to smaller-scale local and regional economies versus larger-scale modern national and international markets. Modern illegal fishing driven by black markets at regional to global scales was estimated at 2-4x the legal catch quota in later years of the commercial fishery (Farlinger 1990), and small- to large-scale illegal abalone fishing is considered the primary threat to abalone recovery today (Fisheries and Oceans Canada 2012). The decline in abalone abundances driven by formerly legal and continuing illegal commercial trade has perpetuated the loss of First Nations cultural use and connections with abalone (Haida Marine Traditional Knowledge Study participants et al. 2011b, Lee et al. 2016): "… they [commercial abalone fishery] just annihilated the biomass… after that my people were told that they couldn't eat that stuff [abalone] anymore." (William Gladstone Sr., Heiltsuk Nation, Jan. 2012).

Governance regimes

We identified two major historical abalone fisheries governance regimes and a current abalone recovery governance period, punctuated by profound cultural and social change (Fig. 4.3). The First Nations governance regime maintained sustainable abalone harvesting under traditional management systems, and persisted for at least 2000 years prior to European contact in 1774 (Trosper 2002, 2009, Menzies 2010). A transitional period of First Nations-colonial governance followed, characterized by rapid unsustainable exploitation of natural resources and decimation of First Nations populations by up to 80-90% through disease and conflicts (Fisher 1992, Robinson

1996, Harris 1997, Acheson 2005, Orchard 2007), and ending when BC joined the Canadian Confederation in 1871.

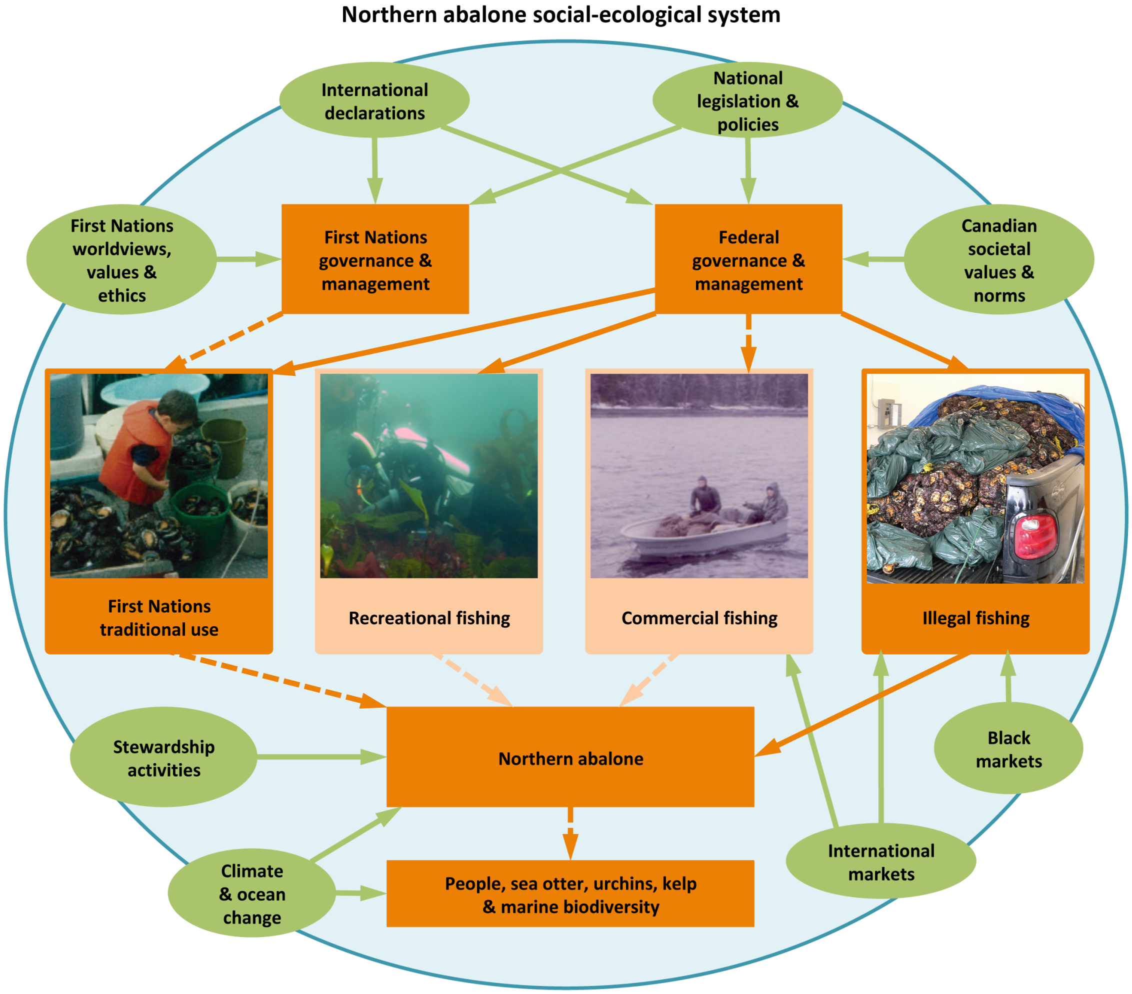

Figure 4.2 **Key components (orange rectangles), drivers (green ovals), direct linkages (solid arrows) and feedbacks (dashed arrows) in the northern abalone social-ecological system, including currently active (dark orange) and formerly active (light orange) components. Illegal fishing during and after the commercial fishery also affected the three legal fisheries, and commercial overfishing led to closure of the recreational and First Nations traditional fisheries. Photo credit left to right: The McNeill family of Skidegate, Haida Gwaii; Lynn Lee; Guy White, former commercial abalone fisher; and Fisheries and Oceans Canada.**

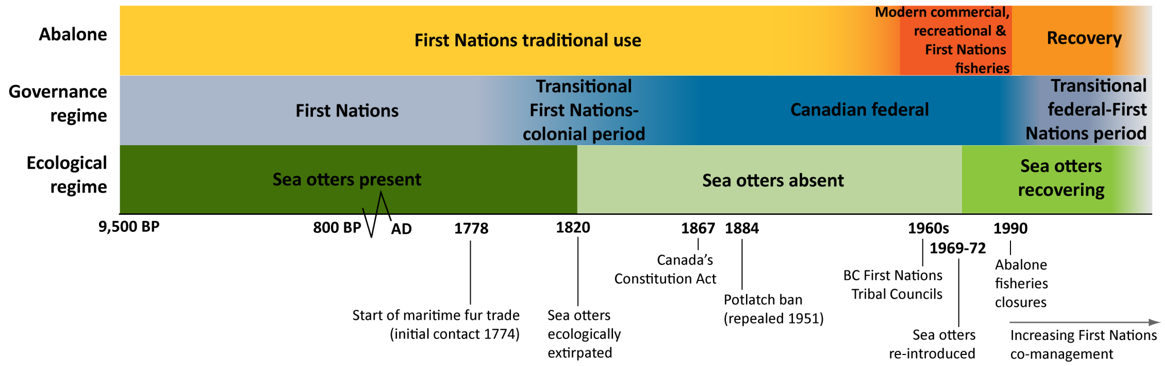

Figure 4.3 **Timeline of key events and changes in the northern abalone social-ecological system, including abalone use, major fisheries governance regimes and interim periods, and ecological regimes (also see Lee *et al.* 2016).**

The second regime, Canadian federal governance, occurred from 1871 to 1990 and was characterized by continuing colonial policies and laws intended to acculturate First Nations to “Canadian” society (e.g., foreign worldviews, residential schools, potlatch ban), while industrial-scale natural resource extraction rapidly expanded (Fisher 1992, Harris 2002). Under this regime, management of traditional, recreational and commercial abalone fisheries was federally prescribed under Canada’s Fisheries Act (1868 [1985]) and managed by the federal Department of Fisheries and Oceans Canada (DFO) in an agency command-and-control management system (Holling and Meffe 1996). The modern commercial abalone fishery by SCUBA dive was initiated in the 1950s under this regime, and had almost no fisheries regulations (minimum size limit only), lack of assessment and local-scale management, and low fisheries catch for its first two decades. A greater than 10-fold increase in catch starting in 1976 led to depletion of abalone populations, implementation of fisheries management measures, and finally the closure of all three legal abalone fisheries in 1990 (Farlinger 1990).

The current transitional Canadian federal-First Nations governance period began after closure of the modern abalone fisheries. Abalone decline was observed throughout the coast: “… you’d have to spend a lot of time walking the rocks the same areas where we used to… know you’re going to get a bucket there… If you go out to the same areas now… you’re hoping to find one” (Gary Housty, Heiltsuk Nation, Jan. 2012). Abalone was subsequently the first marine invertebrate to be listed as *threatened* under Canada’s Species at Risk Act (SARA; 2002c) in 2003 and then uplisted to *endangered* in 2009 due to continued decline and lack of recovery since the fisheries closures (COSEWIC 2009). This current governance period (examined further in adaptive co-management section) is characterized by a focus on restoring abalone populations, and broadening First Nations assertions of their title and rights, including demands for collaborative management, and litigation related to management of the land and sea (e.g., von der Porten et al. 2016, Gauvreau et al. 2017, Jones et al. 2017).

Methods

Evaluating the resilience of indigenous and federal fisheries governance regimes

To evaluate the degree to which the historical First Nations and Canadian federal abalone fisheries governance regimes align with the seven theoretical resilience principles identified by Biggs et al (2012), we drew on traditional knowledge interviews with Heiltsuk abalone experts, published reports, federal technical reports, grey literature and peer-reviewed literature about Pacific Northwest coastal First Nations resource management systems. Specifically, in collaboration with the Heiltsuk Nation, we conducted ten semi-directed interviews (Huntington 1998, Bernard 2013) with indigenous abalone experts identified by the Heiltsuk resource management department to document traditional management, use and stewardship of abalone (see Lee et al. *in review* for details). Participants included 14 abalone experts – one woman and 13 men – from 39-90 years of age, encompassing three generations of knowledge holders. For similar Haida knowledge of traditional abalone management practices, we drew on a summary from the Haida Marine Traditional Knowledge Study (HMTK) where 47 men and seven women between 29 and 95 years of age were interviewed (Haida Marine Traditional Knowledge Study participants et al. 2011a, Winbourne and Haida Oceans Technical Team 2014). We use the term governance when referring to broad environmental decision-making institutions and processes (Lemos and Agrawal 2006), and management systems when describing specific actions including practices and protocols for resource use and stewardship to achieve desired goals and objectives that are shaped by social norms and worldviews (Lertzman 2009).

Improving conservation using an adaptive co-management approach

To foster resilience in abalone use and conservation, including potential restoration of traditional fisheries, we generated recommendations for future co-management building on the new relationships and approaches that are developing under contemporary governance of abalone recovery. We framed our recommendations under the 10 key conditions that foster successful adaptive co-management (Section 5.1), as identified in a comprehensive review of accumulated knowledge from global case studies (Armitage et al. 2009). Our recommendations are based on the information sources listed above and federal and community-based species at risk recovery strategies and action plans for abalone.

Resilience assessment of abalone fisheries governance regimes

Here, we describe how characteristics of historical indigenous and Canadian federal abalone fisheries management systems under the first two major fisheries governance regimes described above align, or fail to align, with seven foundational principles of SES resilience (Biggs et al. 2012; Table 4.1). To be concise, examples are included under the principle where we felt they best fit, recognizing that elements of the resilience principles are not mutually exclusive.

Principle 1. Maintain diversity and redundancy

Options for responding to change are fostered by maintaining both diversity and redundancy in SES elements, interactions, and responses to disturbance (Elmqvist et al. 2003, Biggs et al. 2012). In the historical First Nations SES, a diverse harvest portfolio, in terms of species and their habitats, likely conferred resilience (Jackley et al. 2016, Mathews and Turner 2017). In Heiltsuk territory, families had designated fishing areas where they were responsible for ensuring the local-scale persistence of coastal resources and abalone was traditionally harvested and managed as one of a diversity of coastal resources: “I think it was… our way of keeping it at a stable. We didn’t just run all over an area, harvesting wherever we could. We went to one area and we harvested there and then we didn’t bother with any other particular areas, so that other families could harvest there. A lot of different families go to different areas to harvest seaweed, to harvest everything else" (Howard Humchitt, Heiltsuk Nation, Jan. 2012). Heiltsuk predominantly harvested abalone and black seaweed together in spring and also harvested abalone for fresh eating while fishing for other coastal species, including salmon, herring, halibut, seagull eggs, crabs, urchins, gumboot chitons and black katy chitons (Table 4.2). Haida harvested abalone with seaweed, clams, cockles, mussels, halibut and rockfish, among other species (Haida Marine Traditional Knowledge Study participants et al. 2011b). This diversity allowed harvest of alternative species: "… the old people called them *hamúlis*… when they can't find abalone, they pick all the *hamúlis*… it's like same taste as abalone" (Fred Reid, Heiltsuk Nation, Jan. 2012).

More broadly, diversity and redundancy was also evident in 'houses', the fundamental unit of northwest coastal indigenous management systems that encompassed family and clan relationships with kinship connections to other houses (Trosper 2003, Acheson 2005, Trosper 2009, Menzies 2010). The head titleholder of each house held contingent proprietorship over specific fishing sites and reciprocity among houses by way of potlatch ceremonies and feasts fostered response diversity to local disturbances for many resources including herring spawn areas (Powell 2012, Gauvreau et al. 2017), clam beds (Jackley et al. 2016) and salmon streams (Trosper 2003, Brown and Brown 2009, Trosper 2009). Local-scale house or family-based management matched the spatial scale of abalone population dynamics and likely fostered spatial heterogeneity and genetic diversity due to short larval duration and limited spatial dispersal (Table 4.3).

In contrast, low diversity of resource use and redundancy was evident in Canadian federal fisheries management where one governing authority managed for maximum commercial yield of one species, abalone, along the entire BC coast without considering other species in the ecosystem when making decisions about abalone (Sloan and Breen 1988). Without different commercial licenses, abalone fishers could not shift their efforts to harvest other species should abalone abundances and sizes be respectively low or small. Moreover, the commercial fishery was geared towards the demands of volatile regional, national and international markets (Farlinger 1990).

Table 4.1 **Summary of key characteristics of historical First Nations traditional and Canadian federal fisheries governance regimes for abalone in relation to seven foundational principles identified to enhance the resilience of coupled social-ecological systems (Biggs *et al.* 2012).**

Resilience principle	First Nations traditional governance	Canadian federal governance
Maintain diversity and redundancy	• System of houses (families and kinship relationships) and reciprocity within traditional territories maintains multiple management nodes • Harvest and management of multiple species occurs together	• Maximum yield-oriented outcome occurs for a single species • One federal decision-making body issues species-specific licenses with coast-wide regulations
Manage connectivity	• Worldview of *Everything depends on everything else* strongly connects people, place and a diversity of interacting species • Trade connects interactions locally and regionally • Family-based areas and traditional harvesting practices maintain ecological connectivity between abalone populations and habitat patches	• No fisheries regulations and only catch recording create few feedbacks for over two decades • Regulations and some population monitoring develop feedbacks in last 12 years of fisheries • Little to no meaningful communications with indigenous or local non-native coastal communities minimizes social feedbacks
Manage slow variables and feedbacks	• Intergenerational ethics and teachings of *Stewardship*, *Respect*, *Responsibility* and *Reciprocity* guide continuity of use over millennia of dynamic environmental change	• Intensive commercial fishing of high abalone abundance from ecological regime without sea otters causes rapid abalone decline leading to fisheries closures in less than two decades
Foster complex adaptive thinking	• Worldviews of *Adapting to change* and *Balance* inherently acknowledge uncertainty, disturbance and surprise as part of social-ecological systems • Regular physical connection between people and place create tight internal feedbacks	• Primary goal of maintaining relatively constant abalone catch ignores system complexity • Centralized decision-making unable to respond to local-scale changes in a timely manner
Encourage learning and experimentation	• Ethics of *Seeking wise counsel* and *Knowledge* reflect intergenerational learning by youth practicing stewardship and harvesting protocols with elders and experienced knowledge holders • Experimentation with diverse resource management tools facilitates social learning	• Coast-wide implementation of management measures limits experimentation and learning opportunities • No effectiveness monitoring of local-scale fisheries closure areas limits learning from management actions
Broaden participation	• Ethics of *Sharing* and *Seeking wise counsel* encourage participation through sharing knowledge and resources • Learning-by-doing fosters participation of whole community in fishing and processing • Public exchanges at potlatches promote transparency and public accountability	• Little to no participation of resource users in management process for over two decades • Participation of commercial fishing association in last decade of the fishery • Some limited participation by First Nations and recreational interests inform local-scale fisheries closures in last decade of the fishery

Resilience principle **First Nations traditional governance**	**Canadian federal governance**
Promote polycentric governance	
- System of houses creates multiple governance authorities with protocols for exchange among houses; no centralized regional governance	- Centralized, top-down federal decision-making limits polycentric management, except for limited local-scale fisheries closures
- Local spatial scale of proprietorship rights well-matches scale of ecological processes	- Coast-wide regulations create scale mismatch between governance and ecological processes

Table 4.2 Traditional indigenous abalone harvesting practices and stewardship protocols specified by Heiltsuk First Nation experts. Equivalent modern fishing regulations in [*italics*].

Management practice and representative quotes	**Experts**
Harvest during daytime low low tides in spring by hand-picking [*Season and gear restrictions*] "… we go out is May… in seaweed picking time." (William Gladstone Sr.) "… we used to go there for seaweed, and if we see abalone we used to take it." (Gary Housty) Hand-pick in several ways: grab fast by hand with no tools, pop off or prying with butter knife, pick those sitting on kelp, knock off rocks with yew wood club into a basket in the old days - only pick abalone that are out in the open or on kelp Also harvest with a gaff or spear at low tide, by free-diving, or more recently by SCUBA diving, but much less common than hand-picking	MR, DW, WGSr, GB, HH, FR, AR, HER, SH, GEH, GGH, 3 anonymous
Take only the larger abalone (between 70-100 mm) [*Size restrictions*] "Gran would get mad, Grandpa would get mad... they wouldn't just let it go. Like, when I was a little boy, it was okay, but first time – it was okay. Tried it again? They were mad, because it's too small." (Howard Humchitt) Minimum acceptable size for harvest ~80 mm shell length (larger medium-sized shells)	MR, DW, HH, FR, HER, SH, 2 anonymous
Take only what you need [*Total allowable catch restrictions*] and share what you have "But you know my grandfather always said, 'Don't take more than what you need.' You know, that's what, that's all I ever heard." (William Gladstone Sr.) "I don't think there was ever really a set amount, because when he got in, he shared… And the people that didn't have the boats, they were able to share with the guys that had boats." (Hazel Emma Reid)	DW, WGSr, GB, HER, GGH, 1 anonymous
Designated family fishing areas [*Designated access privileges*] "I went to this one particular place, another family went to another place and another family to another place." (Mike Reid) "You know... each family… had their own, real own places to go to." (Gary Housty)	MR, DW, HH, AR, GGH
Take only a portion of what is there [*Minimum density restrictions*] "...if this whole rock was filled right up, I'd only take a portion of that rock… Then I look for another rock to get on. Make sure there's enough, so they'll recover again." (Davie Wilson)	MR, DW, SH
Picking associated with harvesting other species [*Diverse harvest portfolio*] Most pick abalone and seaweed together on low low tides in spring Elders often put a gumboot chiton in their sack of abalone for flavour Many pick abalone to eat while out harvesting other species including black katy chiton, red urchin, herring, halibut, salmon, crabs and seagull eggs, and while trapping "Yah, we just row around the island and pick enough to eat and all these reefs outside here…" (while trapping river otter in the 1940s and 50s; Fred Reid) "Well it was like what the old people say 'Once the tide goes out, the table's set!'" (Fred Reid)	MR, DW, WGSr, GB, HH, FR, HER, SH, 2 anonymous
Transplanting abalone [*Enhancement strategies*] "...they'd just take the small ones and transplant them into the area where they'd be able to go – once they're big enough – they could go out and harvest it." (Davie Wilson)	MR, DW, WGSr, 1 anonymous

Principle 2. Manage connectivity

Connectivity between nodes (e.g., species, habitats, actors, institutions) through linkages (e.g., species interactions, communication channels) facilitates exchange of goods and information that alter (increase or decrease) the spread of disturbance outcomes and facilitate recovery afterwards (Biggs et al. 2012). Traditional abalone harvesting practices likely maintained ecological connectivity of abalone populations between habitat patches (Table 4.3). Harvesting only took place in the low intertidal during the spring and summer by hand-picking and occasionally with a gaff or spear, leaving an extensive depth refuge for abalone: "… we were told by the elders that you can't go and pick abalone when it's underwater..." (Stephen Hunt, Heiltsuk Nation, Jan. 2012) and "We used to just go pick what was above… the water line, because they'd be crawling around in the kelp" (Martin Williams, Haida Nation, HMTK, Feb. 2009). Both Heiltsuk and Haida were also taught: "...we weren't allowed to take the small ones. We had to just take the big ones and you had to do it fast" (Fred Reid, Heiltsuk Nation, Jan. 2012). Heiltsuk experts confirmed that 'big' abalone were at least 80 mm in shell length and often bigger. Abalone are often mature by 50 mm in shell length and 70 mm is the size at which all abalone are mature, therefore this practice ensured opportunities for abalone to spawn before being harvested.

The interconnectedness of people and place are acknowledged in the Heiltsuk truths of *Connection to nature*, *Creation*, and *Balance* (Brown and Brown 2009) and the Haida worldview that *Everything depends on everything else* (Jones et al. 2010): "We're probably responsible for both the sea otter population and the abalone population as people, so we need to recognize the need to bring a balance to them" (Mike Reid, Heiltsuk Nation, Jan. 2012). Trade between houses and villages within and among First Nations would have fostered strong horizontal linkages with regional connectivity supported by trade networks between coastal and interior First Nations (Robinson 1996, Trosper 2009): "… we give [abalone] to the people inland for… moose and all the other stuff. Trade and barter" (Gus Brown, Heiltsuk Nation, Jan. 2012). However, vertical linkages were limited to levels of house-based social hierarchy due to a lack of broader central governance (Trosper 2003, 2009). Markets for trade in historical times were also limited compared to national and global markets in the modern commercial fishery.

Table 4.3 Scale of ecological features for abalone compared with scale of management practices (Sloan and Breen 1988; Farlinger 1990; Lee *et al*. 2016).

Ecological feature and description	First Nations traditional management practices	Canadian federal management practices
Depth distribution • Majority distributed from lower intertidal down to 10 m chart datum depth on rocky habitats • Densities decrease with depth down to >20 m without sea otters • Densities increase with depth with increasing sea otter occupation time	• Harvested only at lower low tides I spring and summer by hand or with hand tools, sometimes including a spear or gaff that could reach up to 2 m into the water • Only harvested within a portion of the total depth range for abalone	• Commercially harvested by SCUBA diving at any time • Later fisheries management measures restricted the annual fishing season • Harvested throughout total depth range for abalone
Spawning and larval dispersal • Broadcast spawning with short ~1 week larval period, limiting larval dispersal to short distances especially within kelp forest habitat	• Designated house and family-based localized harvesting areas, allowing stewardship and sustainable management at a local-scale • Take only what you need • Only take some of the large abalone in an area, leaving some to reproduce • Transplanting abalone from one place to another	• Coast-wide open access fishery for over two decades • Coast-wide management measures implemented in last 12 years of fishery including maximum annual catch quota • Coast-wide quota with intense fishing in localized area (except local area closures) • Illegal fishing at unknown levels, estimated up to 2-4 times the legal annual quota
Spatial distribution • Highly variable densities over small spatial scales dependent on local site conditions • Adult movement generally limited to <100 m	• As above	• As above
Fecundity • Larger mature abalone have exponentially higher number of eggs	• Take only the larger mature abalone >80 mm and let the smaller abalone grow	• Minimum size limit of 90 mm, then 100 mm • Illegal fishing taking all sizes of abalone

In Canadian federal management, institutional connectivity between decision-making authorities, resource users, and resource conditions, was limited. Regional fisheries offices that implemented federal decisions had little communications with indigenous or other local communities. For over two decades from the 1950s to late 1970s, the modern commercial fishery occurred with almost no fishing regulations

(Farlinger 1990). During the last 12 years of the commercial fishery, further regulations were implemented based on information from monitoring of declining abalone populations and fisheries landings (Sloan and Breen 1988), forming some vertical linkages between local-scale conditions and federal decision-making. These regulations, including a minimum size limit of 90 mm and then 100 mm, fishing license limitations, seasonal restrictions and an annual coast-wide catch quota, likely maintained a degree of population connectivity and persistence, but were instituted too late to sustain the fishery that was subsequently closed in 1990.

Principle 3. Manage slow variables and feedbacks

Variables in SESs change and interact at different timescales with slow variables capable of creating regime shifts when they reach certain thresholds (Biggs et al. 2012). Although we have no direct evidence of whether or not traditional systems accounted for slow variables and feedbacks such as climate change, the temporal continuity of abalone use over millennia provides indirect evidence of this. The overarching Heiltsuk truth of *Stewardship* (Brown and Brown 2009) and Haida ethics of *Respect*, *Responsibility*, and *Reciprocity* (Council of the Haida Nation 2007, Jones et al. 2010) helped foster the sustainable resource use protocol of ‘Take only what you need’ and maintained stewardship practices: “One of the things I remember when we were picking abalone is when either one of them would say, ‘That’s enough now’... that’s a real important, important thing to say, because that’s how we conserve.” (Gary Housty, Heiltsuk Nation, Jan. 2012) and “… grandmother used to say, ‘Only take enough for what you need. You don’t need to take any more than that’… ‘If you look after it, it will always be there’” (Herb Jones, Haida Nation, HMTK Mar. 2007). Heiltsuk were also taught to take only a proportion of what was available in any location (Table 2). Importantly, pre-contact abalone economies were limited to local and regional scales of use and trade, and were not influenced by strong external and often volatile national and international markets that drive modern commercial fisheries (Crona et al. 2015, Eriksson et al. 2015).

Ecological regime shifts triggered by the presence and absence of sea otters dramatically changed the ecosystem’s ability to produce and sustain abalone, likely affecting the amount of abalone harvested through time (Fig. 4.3; Watson 2000, Lee et al. *in review*). For example, modern traditional abalone harvest may have been greater than in pre-contact times when abundant sea otters reduced abalone abundance and size (Watson 2000, Lee et al. 2016). However, even in pre-contact times with sea otters, alternative hypotheses suggest that First Nations hunting pressure and human presence created areas with low to no sea otters near villages (Corbett et al. 2008, Salomon et al. 2015), potentially facilitating higher localized abalone abundances (Szpak et al. 2012, Salomon et al. 2015). More extensive kelp forests during this time (Watson and Estes 2011, Markel and Shurin 2015, Stevenson et al. 2016) would also have improved overall habitat conditions and productivity for abalone (Lee et al. 2016), further enabling sustainable fishing. Underlying these ecological interactions, large-scale oceanographic regimes also influenced annual kelp production (Dayton et al. 1999, Parnell et al. 2010), in turn affecting abalone productivity.

We also have no direct evidence as to whether or not slow variables and feedbacks were considered in Canadian federal abalone management. However, we do know that the high abundance of abalone being fished had accumulated over a century without sea otter predation or significant levels of fishing (Tegner and Dayton 1999, Lee et al. *in review*) and was removed in less than two decades of intensive ‘mining’ by the commercial fishery (Farlinger 1990). Less intensive First Nations traditional and recreational fisheries with much lower harvest rates and spatially-restricted fishing practices may have remained sustainable in the absence of the modern commercial fishery.

Principle 4. Foster complex adaptive thinking

Understanding SESs as complex adaptive systems (CASs) that are unpredictable due to being highly connected, rife with feedbacks and yet modular, can foster resilience (Biggs et al. 2012). Haida and Heiltsuk worldviews recognize the need for *Adapting to change* and *Balance*, fundamentally understanding coupled human-ocean ecosystems as CASs prone to uncertainty and change (Council of the Haida Nation 2007, Brown and Brown 2009, Jones et al. 2010). A degree of ecological variability was expected: “One of the things he [father] mentioned... which keeps triggering to me how important it is... you go out, you don’t expect to get seaweed in that same place every time. And the reason for that is seaweed are so delicate, they don’t grow in certain ocean conditions” (Gary Housty, Heiltsuk Nation, Jan. 2012). For abalone, “You knew that when you were going there in that particular area, there would be populations of abalone there and you would be going home with some… Some years some of the rocks had lots of populations on them and other years they didn't" (Mike Reid, Heiltsuk Nation, Jan. 2012).

Close and regular physical connection between the well-being of people and places they lived created tight internal feedbacks within the SES. For example, if salmon abundance in one titleholder's rivers declined, the negative effects would be immediate (e.g., hunger and/or starvation, loss of respect and titleholder status), although the potlatch system provided some insurance against localized declines through kinship, gifts, trade and reciprocity (Trosper 2003, 2009). For Heiltsuk today, "I know our community is in… dire need of sustenance from the sea. Our economy is crashed; we don't have a base economy anymore. Our base economy used to be the sea… And when more of the food source disappears, it's harder to stay healthy" (Mike Reid, Heiltsuk Nation, Jan. 2012).

Canadian federal abalone management tended to be reductionist in its primary goal of maintaining a relatively constant commercial production of abalone (Bates 1984). Moreover, the ability to respond quickly to changing circumstances and alter actions was limited. For example, Heiltsuk experts noted that despite local observations and reports of abalone decline, changes in commercial quota and fisheries management were late and were not sufficient to halt the decline. Failure of federal management to recognize the properties of CASs is evident in the short duration (1950s-1990) of modern abalone fisheries.

Principle 5. Encourage learning and experimentation

Social learning, the modification of existing or acquisition of new and improved perspectives through social interactions, is a key process that enhances SES resilience (Biggs et al. 2012). Experimentation is an active form of management that can specifically enhance learning (Walters and Holling 1990, Turner and Berkes 2006, Gelcich et al. 2010). The Heiltsuk fundamental truth of *Knowledge* and Haida ethic of *Seeking wise counsel* reflect the importance of learning by experience and through intergenerational knowledge transmission (Brown and Brown 2009, Jones et al. 2010). In practice, Heiltsuk abalone experts learned abalone harvesting and stewardship protocols by going out to pick abalone with their grandparents, parents, aunt, uncles, siblings, elders and/or other community members: “Yeah, we have the punt, so… we load the kids up and away we go” (H. Emma Reid, Heiltsuk Nation, Jan. 2012) and “… the whole family can work there [jarring abalone and processing other seafood]. And they all know what to do too, if we get lots of fish” (George Housty, Heiltsuk Nation, Jan. 2012). Regular observations of the land and sea while engaging in harvesting activities facilitated learning about ecological structures and processes (Table 4.4) that could then inform management practices. Heiltsuk experts were also taught to experimentally translocate abalone from one area to another to enhance access (Table 4.2) and potentially to restore locally depleted areas.

Learning and experimentation appeared to be limited under Canadian federal abalone management. When abalone monitoring and fisheries regulations were implemented in the last 12 years of the fishery (Sloan and Breen 1988), they occurred without explicit learning opportunities. For example, fisheries closures for First Nations and recreational harvest, and for localized areas of low abalone abundance, were implemented but not monitored for effectiveness and such information did not feed back to inform future management actions (Bates 1984).

Principle 6. Broaden participation

Active engagement of relevant actors in governance processes can range from information exchange to the co-production of knowledge to the devolution of power to non-state actors (Biggs et al. 2012). The Heiltsuk fundamental truth of *Sharing* (Brown and Brown 2009) and Haida ethic of *Seeking wise counsel* encourage participation by sharing knowledge and resources in everyday life: “… depending on how many sacks of abalone we got, once it was taken in, a lot of it was given out to the people that couldn’t make it out or especially with the elders – a lot of the abalone was given to the elders” (Davie Wilson, Heiltsuk Nation, Jan 2012). Heiltsuk experts learned to harvest abalone as youth by picking abalone with more experienced family and community members. Many talked about working together to process seafood including abalone: “… it was an annual thing – abalone time, when you go out deer hunting – just about anything... halibut... beach line in Bella Bella, smokehouses were going, and everybody was down doing their fish. After school, that’s where every, everybody would go.” (Stephen Hunt, Heiltsuk Nation, Jan. 2012). Specifically for abalone processing, “… it was the whole family. Go in and you clean them and then you used to go and get the old wooden fingernail brush... And you grab the meat there and scrub… It was all black on the abalone but when you were finished scrubbing it you'd get down, and you'd clean it, it looked like that [tan-coloured]. And then they used to jar them..." (Stephen Hunt, Heiltsuk Nation, Jan. 2012).

Table 4.4 Examples of traditional ecological knowledge about abalone shared by Heiltsuk experts.

Ecological knowledge	Experts
Distribution and behaviour	
Most abalone are found at or below the kelp line at very low tides on the rocks, sometimes under kelp and sometimes on the kelp itself: "I don't why they'd know, but most of them were just under... there's very few that you'd get above tide, and if they were in and above tide, they'd be in gullies." (Stephen Hunt)	WG, Sr; GB; HH; AR; SGH; FCR; HER; DNW; 3 anonymous
Abalone used to be commonly found on the kelp at low tide: "Well, we used to get them on kelps. It was so hot up there they lay on the kelps and you could just pick them. Don't have to pull them out." (Anthony Reid)	
Abalone move up into shallower water when the temperature is warmer in spring and summer: "In the summer time they come quite a ways up." (Heiltsuk expert)	
Larger abalone tend to be at the very low tide line	
Abalone tend to be found in patches and clumped: "...some areas where they're real close together… other areas would be a little bit farther apart…" (Heiltsuk expert)	
Abalone used to be abundant in inside waters during grandparents' time	
Juvenile abalone are mostly noted under kelp or in crevices in the intertidal	
Interactions with other species	
Abalone are expected to be found with sea urchins: "...you can tell how close the abalone are to the surface by the urchin because the urchin are just below them all the time... if you watch, if you look, the urchins are always just below the abalone." (Mike Reid)	DNW; WG, Sr; HH; HER; FCR; MR; 2 anonymous
Kelp forest recovery provides more shelter for fish and food for shellfish that grow faster when there is more kelp: "And they're finding that the animals that hang around… the kelp forests are creating a lot of nutrients for the shellfish." (William Gladstone Sr.)	
Sea otters eat urchins, abalone, clams and Dungeness crab; Larger kelp forests are noted where urchin abundance is low	
River otters and eagles also eat abalone, with river otters leaving shells in the shoreline forest: "We used to walk inside the bushes a bit and we used to find a whole bunch of abalone shells in there." (Davie Wilson)	

Participation from diverse interests can increase legitimacy and transparency, leading to greater cooperation, compliance, stability and resilience (Pinkerton and John 2008, Biggs et al. 2012), such as through the potlatch system, albeit with power asymmetries inherent in traditional hierarchical First Nations societies (Acheson 2005, Trosper 2009). All official exchanges were announced at potlatches, providing an avenue for transparency and public accountability (Trosper 2003, 2009). Lesser titleholders could express their support or opposition for the head titleholder, and commoners could to some extent choose which house they belonged to through kinship ties (Trosper 2003). How much voice commoners or lesser titleholders were granted in making specific decisions about resource rules and use is less known.

Outside of the federal agency, participation in Canadian federal fisheries management occurred in the last decade of the fishery, when commercial fishers formed the Abalone Harvesters Association to communicate with and lobby the federal fisheries agency, and when local area closures were discussed with coastal communities, including First Nations (Sloan and Breen 1988, Farlinger 1990). This relationship created power asymmetries in that commercial interests could influence management decisions, while First Nations and recreational interests were marginalized (Bates 1984).

Principle 7. Promote polycentric governance

Polycentric governance systems, in which nested governing authorities have some degree of independence within specific geographic areas, create a level of functional redundancy that can buffer against management mistakes in any one setting and enhance opportunities for participatory learning and experimentation across scales (Biggs et al. 2012). Indigenous governance systems based on multiple governing houses within each Nation were inherently polycentric. Local place-based contingent proprietorship rights distributed governance authority among head titleholders, providing insurance against broad-scale effects of local-scale disturbances or management errors (see Principle 1). This polycentric governance system matched well with the scale of ecological processes driving abalone population persistence (Table 4.3; see Principle 1) and had potential to promote learning from local-scale experimentation with different management strategies such as translocations (see Principle 4). Sharing of knowledge and lessons from different management practices within and among houses and First Nations would have promoted social learning (see Principles 4 & 6).

In contrast, under centralized federal decision-making, coast-wide fishing regulations were mainly developed and instituted far from abalone fishing areas and coastal communities, creating scale mismatches with the smaller scale of dominant social and ecological processes (Table 4.3; *sensu* Cumming et al. 2006). In the later years of the fishery, local federal representatives were given authority to implement local area fisheries closures (Bates 1984), which represents limited devolution of power within the federal fisheries agency, but not to external institutions or individuals.

Building an adaptive co-management approach for abalone governance

Given the high degree of alignment between characteristics of historical First Nations fisheries management systems and foundational resilience principles (Table 4.1), incorporating First Nations stewardship practices and protocols into modern fisheries governance could facilitate greater sustainability and resilience (also see Jones and Williams-Davidson 2000, Turner et al. 2013, Pinkerton et al. 2014, Kittinger et al. 2016). Of course, the socio-economic context has changed substantially since pre-contact times when interactions were largely linked horizontally at local and regional scales. For example, the maritime fur trade introduced the dramatic influence of global markets that remain relevant today, imposing new vertical linkages and strong external drivers. But in the contemporary abalone recovery period, a variety of governance changes already underway suggest that transformation into a future hybrid First Nations-Canadian federal governance regime that incorporates the proven resilience of indigenous management offers hope for positive change that could be feasible and effective for abalone management specifically, and Canadian small-scale fisheries more broadly.

We believe that this new hybrid governance system would benefit from taking an adaptive co-management (ACM) approach to address the need to share power and responsibility between state governments and First Nations people who have constitutional rights to natural resources in their traditional territories (c.f., Carlsson and Berkes 2005, Armitage et al. 2009, Berkes 2009). Our recommended approach is founded on collaborative joint decision-making between First Nations and the Canadian federal government. It facilitates multi-scale management using multiple knowledge sources including indigenous knowledge, and addresses the complex adaptive nature of SESs that is recognized in indigenous governance. Since the listing of abalone as a federally endangered species, innovative management institutions for recovery are developing that could form the basis for future adaptive co-management. These include First Nations, regional and federal institutions that operate within the current transitional period of Canadian federal-First Nations governance (Fig. 4.4). We therefore draw on the conditions for successful adaptive co-management identified by Armitage et al (2009) to highlight critical considerations for building future environmental governance with First Nations in western Canada that is socially just and ecologically sustainable.

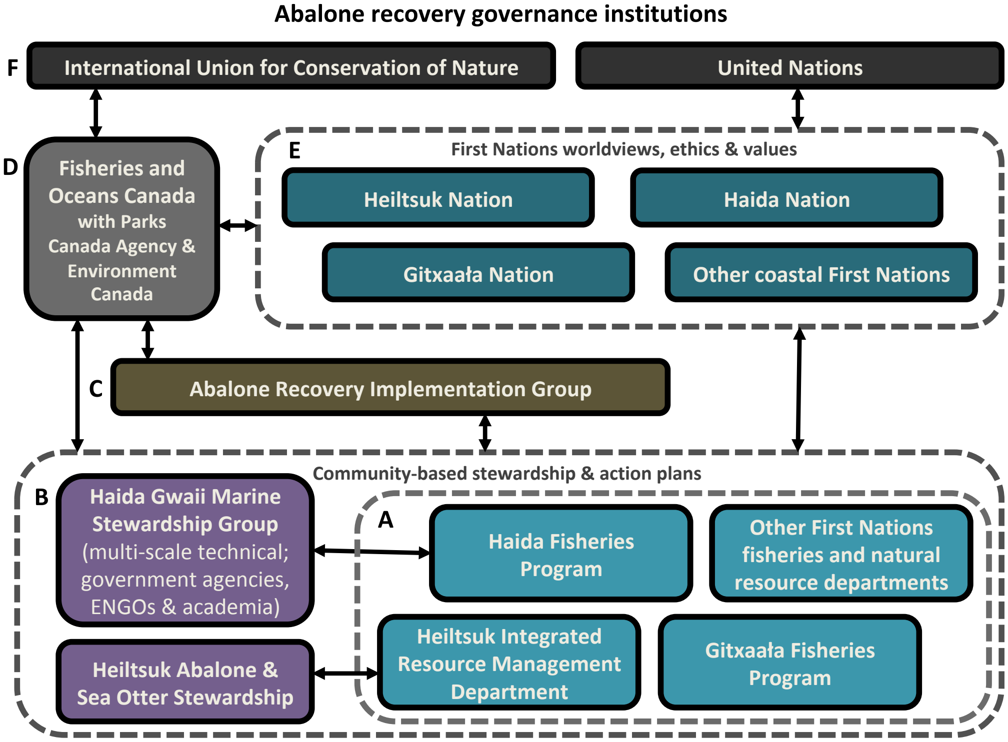

Figure 4.4 **Actors, institutions and multi-scale linkages governing abalone recovery in coastal BC: (A) Locally, First Nations Constitutions and governance oversee abalone recovery initiatives and First Nations natural resource organizations communicate and learn within and among each other; (B) Local-scale multi-interest and/or multi-species working groups led by First Nations organizations develop and implement community-based action plans; (C) Regionally, the technical advisory Abalone Recovery Implementation Group, initiated by Canada's federal fisheries agency, engages in regional learning by sharing knowledge and information related to abalone recovery; (D) Nationally, the Department of Fisheries and Oceans Canada, along with Parks Canada Agency and Environment Canada, are mandated to protect and conserve abalone under federal legislation; (E) First Nations governments that often communicate and learn between and among nations and are guided by their respective worldviews and ethics and values; and (F) Internationally, Canada's endorsement of the Convention on Biological Diversity, Convention on the International Trade of Endangered Species and United Nations Declaration on the Rights of Indigenous Peoples, establish overarching expectations for Canada's decision-making related to species conservation and First Nations.**

Current conditions that can foster successful adaptive co-management

Eight of the ten conditions for successful ACM (Armitage et al. 2009) have largely been met or can be readily addressed in the contemporary abalone SES, particularly in relation to restoring small-scale traditional fisheries. The abalone SES is a *well-defined resource system* [1] centered on a relatively sedentary marine snail with limited larval dispersal (Sloan and Breen 1988; Table 4.3), and traditional abalone fisheries are *small-scale* [2] in nature. Within this well-defined small-scale system, First Nations have *reasonably clear property rights* [3] to abalone and other coastal resources that are being leveraged in court cases (e.g., Takeda and Røpke 2010, von der Porten et al. 2016, Gauvreau et al. 2017, Jones et al. 2017) and policy arenas. Examples of existing co-management include the Gwaii Haanas Agreement (1993) and subsequent Marine Agreement (2010), intertidal clam fishery co-management with the Heiltsuk Nation for a new fishery (1993) and that for razor clam with the Haida Nation over an existing fishery (1994), Great Bear Rainforest Agreement (2016), and Marine Planning Partnership (2011) and its Implementation Agreements (2016).

Increasing co-management arrangements have led to increased *provision of training, capacity building, and resources* [4] particularly for coastal First Nations and also at provincial and federal scales to engage in meaningful co-management. Many cross-scale relationships continue to support abalone recovery, including local partnerships and collaborative research projects. To foster resilience, First Nations traditional management can draw on an *adaptable portfolio of management measures* [5], including identified Heiltsuk harvesting protocols and stewardship practices (Table 4.2) that were also consistent with Haida and other coastal First Nations practices (e.g., Gitxaala in Kitkatla) for sustaining traditional abalone fisheries (Fig. 4.1; Menzies 2010, Haida Marine Traditional Knowledge Study participants et al. 2011b, Winbourne and Haida Oceans Technical Team 2014).

Within the current abalone SES, *clearly-defined social entities with shared interests* [6] in promoting abalone recovery are working together (Fig. 4.4; e.g. HGMSG, Heiltsuk Sea otter–Abalone Stewardship (Fisheries and Oceans Canada 2015)), although specific definitions of recovery and local-scale livelihood objectives may differ. For example, many First Nations have objectives to restore abalone populations to self-sustaining levels that can support a traditional fishery (Haida Gwaii Abalone Stewards 2008), whereas federal recovery objectives are mainly ecological and currently defined only for areas not re-occupied by sea otters (Fisheries and Oceans Canada 2012). Furthermore, recovery is federally judged based on trends over a relatively short timeframe that is pre-defined as either 10 years or the timespan of three generations for the species, whichever is greater (SARA 2002c). For abalone, a generation time is 10 years therefore species status is gauged over the previous three decades, thus discounting profound effects of the ecological regime shifts that have occurred over the last two centuries (Fig. 4.3).

Actors within abalone recovery institutions *share and draw upon a plurality of knowledge systems and sources* [7] recognizing that complementarities between indigenous and western science knowledge can contribute to system understanding, trust-building and learning. Heiltsuk and Haida, among other First Nations, have documented traditional knowledge and conducted research in ecology, archaeology, and social sciences focused on abalone and other species (Sloan 2004, Orchard 2007, Haida Marine Traditional Knowledge Study participants et al. 2011b, Lee et al. 2016, Lee et al. *in review*). Federal legislation requires inclusion of Aboriginal Traditional Knowledge (ATK) in species at risk processes (SARA 2002c) and the Haida Nation contributed ATK to abalone recovery planning (Fisheries and Oceans Canada 2012), however overall implementation to include ATK has been slow. A few *key leaders prepared to champion the process* [8] have emerged in some Nations, including Haida Nation representatives who have championed continuous engagement in the abalone recovery process since 2000. For the most part, however, representatives of governing institutions at all scales are frequently changing, requiring continual relationship building (c.f. Westley et al. 2013).

The final two conditions for a national and regional policy environment explicitly supportive of collaborative management efforts [9] and commitment to support a long-term institution-building process [10] are currently two key barriers to overcome because they require short- and long-term devolution of abalone management authority, and explicit transformation of what remains a centralized federal governance system, to one that is polycentric. In our remaining discussion, we highlight considerations that address power-sharing and restoration of traditional abalone fisheries in relation to the current governance institutions for abalone recovery.

Addressing underlying power dynamics and trust

Coastal First Nations in BC are re-asserting authority to make management decisions and conservation decisions in their traditional territories and resources, including abalone (e.g., von der Porten et al. 2016, Gauvreau et al. 2017, Jones et al. 2017): “The big thing, like we say all over on First Nations within BC, we have to be able to manage it” (Stephen Hunt, Heiltsuk Nation, Jan. 2012). Thus, underlying power dynamics and biases may be the most critical challenge facing development of effective adaptive co-management for abalone in BC. In spite of its promising structure, decision-making authority in governance of contemporary abalone recovery still remains with federal institutions, thus limiting the ability of First Nations to enact ‘legal’ change. Devolution of management authority to appropriate spatial scales (e.g., First Nations traditional territories), potentially enabled through Canadian legislation (i.e., Fisheries Act (1868 [1985], Oceans Act (1996), SARA (2002b), and NMCA Act (2002a); c.f. Ayles et al. 2016), will be required to move beyond the *status quo*.

In Canada, incremental movement towards power sharing and co-management with indigenous peoples by provincial and federal agencies has been evident since the 1980s in the Arctic (Armitage et al. 2011, Kocho-Schellenberg and Berkes 2015) and since the 1990s in BC (see examples section above). In spite of co-management in decision-making, however, the natural resource institutions within which decisions are implemented remain largely operationalized under state policies, regulations and bureaucracies. Further, consensus-based decisions by representatives on joint management boards channel up through state (federal or provincial) and First Nations governance authorities to be separately approved by each party, rather than within true hybrid governance institutions between First Nations and the state. Further, federal agencies continue to resist coastal First Nations’ constitutional rights to decision-making authority over all marine resources within their traditional territories, spurring multiple and repetitive legal challenges (see section above). Decision-making for larger scale projects that the federal government deems to be in the ‘national interest’ (e.g., federal announcement of ban on tanker traffic through the Great Bear Rainforest and approval of Kinder Morgan transnational pipeline development and Enbridge pipeline replacement on 29 Nov 2016) also continues to be federally retained, creating local-scale conflicts when opinions differ about projects and rights.

Participation and trust building towards true hybrid governance must overcome a long history of deep mistrust between actors and institutions (c.f., Pretty and Ward 2001). Despite best intentions, differing perceptions about the validity of traditional, local and western scientific knowledge by different actors have often led to mistrust that limits the effective use and synthesis of knowledge sources to inform conservation actions. For example, these undercurrents limited progress for Dall's sheep conservation by co-management boards in the Yukon territory in northwestern Canada (Nadasdy 2003) and herring co-management in northern BC (Powell 2012, von der Porten et al. 2016, Gauvreau et al. 2017, Jones et al. 2017). Trust-building and a commitment to overcome power asymmetries is required at all scales of management, even locally where dominant voices and power relations in a community can marginalize others (Carlsson and Berkes 2005, Cinner et al. 2012, Finkbeiner and Basurto 2015). In academia, research projects like our collaborative abalone SES interviews with the Heiltsuk Nation can build trust by co-designing and co-implementing research projects that are based on free, prior and informed consent of participants and retain community control of the co-produced knowledge (Fernández-Llamazares and Cabeza 2018, Salomon et al. 2018, Lee et al. *in review*).

Finally, lack of long-term funding committed to institution and capacity building within and across all governance scales will be an on-going challenge. For current abalone recovery, institutions at all scales are primarily supported by short-term federal funding sources. Not only does this reinforce underlying power asymmetries that undermine power-sharing and trust-building, it also creates funding instability at the whim of changing federal government priorities. For example, reduced federal priority for marine conservation resulted in capacity and funding loss that led to a hiatus of the regional abalone recovery technical group from 2011-15, with recent re-establishment under a new government. Financially, sustaining long-term institution building, particularly to support on-going monitoring, assessment, experimentation and social learning, is needed for adaptive co-management, but has potentially high costs that may or may not be balanced by long-term SES benefits (Armitage et al. 2009, Plummer et al. 2012).

Future scenarios for polycentric governance of abalone with multiple centers of decision-making authority are possible (c.f., Pinkerton 1989, Ostrom 1998, Olsson et al. 2004). A key challenge is to determine what management decision-making authority will be devolved to coastal First Nations and how this will be legislated. For example, all scales of governance could collaboratively establish abalone population thresholds for harvest or conservation concern within which First Nations would have decision-making authority in their traditional territories. Reaching or crossing these thresholds could trigger management actions at different scales to minimize the risks of scale mismatch (Cumming et al. 2006, Olsson et al 2007). Strong horizontal linkages and feedbacks between coastal First Nations similar to pre-contact traditional governance systems and/or supporting regional and national institutions that bridge knowledge between scales could help mitigate these risks. Innovative governance solutions that allow for devolution of power to First Nations can promote management experimentation and social learning to foster resilience and sustainability of traditional abalone fisheries as the coastal seascape is altered by sea otter recovery, climate change and other disturbances. Lessons learned from this abalone fisheries 'management experiment' could inform development of future First Nations-Canadian federal governance and management of other coastal fisheries.

Restoring traditional abalone fisheries

Adaptive management is needed to support restoration of traditional abalone fisheries: "It's got to be managed so that it'll be there… if there's plentiful enough for every homeowner to have a feed… maybe once or twice a year... Do a feed at a time. Yeah. And don't go overboard when you... go out and get them" (Stephen Hunt, Heiltsuk Nation, Jan, 2012). Heiltsuk experts emphasized that enforcement of harvest protocols and monitoring of both abalone populations and fishing activities were critical management measures: "We've got to let it come back first. How much is out there now? And when was the last poacher out there? We don't know that yet" (Stephen Hunt, Heiltsuk Nation, Jan. 2012). If a traditional fishery were opened, "…they would have to make sure that the fisheries guardians are out… [while people are] harvesting… And they've got to report in how much they took in altogether" (Davie Wilson, Heiltsuk Nation, Jan. 2012). In spite of the local nature of future traditional abalone fisheries, Heiltsuk experts forewarned about the need to mitigate against external pressures from high-value black markets: "Some people will go nuts out there on it. And then they will sell it, because they know it's valuable" (Heiltsuk expert, Jan. 2012).

Some Heiltsuk experts also recommended the need for abalone stewardship areas to support more intensive monitoring, research and management (e.g., similar recommendations from Haida Gwaii Abalone Stewards 2008) and potential establishment of areas where no abalone harvesting would be allowed as insurance for continuing recovery. However, implementation would be challenging in the modern context where most people live in one village (Bella Bella) versus throughout many villages spread throughout the territory in the past: "… it'd be really hard to try and pick an area to close because families went to certain areas. If we chose one area to close, it might be one whole family's area of normal harvest. I don't think I'd want to pick something that impacted a family because in today's day and age, the fuel costs are so high and forcing the family to go elsewhere looking would be very difficult" (Mike Reid, Heiltsuk Nation, Jan. 2012). Other management considerations identified were to retire the existing commercial abalone fishing licenses to exclude any potential for re-opening unsustainable commercial fisheries, and predator control in their territory specifically via restoration of sea otter hunting and river otter trapping.

Abalone stewardship and recovery strategies have already created new opportunities for adaptive co-management including experimentation and learning between First Nations and federal agencies. For example, abalone rebuilding strategies have been collaboratively tested, including aggregating mature abalone to enhance fertilization success, outplanting hatchery-raised juvenile abalone to enhance recruitment, and establishing stewardship areas that are closed to sea urchin commercial fishing to reduce potential for poaching (Jones et al. 2003, Sloan 2004): "...when they're broadcasting their spawn… that spawn has a chance to connect somehow – maybe that means intervening a little bit and bringing the abalone into a safe structure of some type that their spawn at least connects…" (Mike Reid, Heiltsuk Nation, Jan. 2012). Current management experimentation in a collaborative Haida-federal pilot kelp forest restoration project (Parks Canada 2018) was inspired by recent ecological insights into abalone-sea otter interactions (Lee et al. 2016), and traditional management practices (Table 4.2) present alternative management strategies that can be experimentally tested for future fisheries.

Conclusion

> I took my granddaughter out with me one day and… showed her abalone and she said, 'What do you do with these?' (Davie Wilson, Heiltsuk Nation, Jan 2011)

Canadian federal abalone fisheries governance led to an ecological and cultural conservation crisis for abalone and people in less than two decade of intensive fishing. Generations of coastal First Nations youth now have no cultural connection to abalone because they have not been able to learn how to care for, harvest and use abalone from their elders. The damage due to loss of access to this cultural keystone species is immeasurable: "… everyone looked forward to the first abalone of the year. Ah, I have children now who haven't even had abalone and now I have grandchildren…" (Mike Reid, Heiltsuk Nation, Jan. 2012). For elders: "… when older people were getting ready to move on to the next journey, they always wished for abalone… I would've liked to…say, 'Oh, no problem. I'll send somebody out and get one for you,' but you can't" (Diane Brown, Haida Nation, HMTK, May 2007). And disruption of intergenerational knowledge transmission is not limited to abalone: "How many kids do you think go out on the land today? Not very many" (Heiltsuk expert, Jan. 2012).

For abalone governance and management, issues of social justice require re-thinking their true conservation status. Abalone is currently listed as *endangered* due to high baseline abundances caused by ecological extirpation of sea otters and continued lack of recovery since the fisheries closures. However, abalone today may actually be at similar or higher abundances than in pre-contact times (Tegner and Dayton 2000, Watson 2000, Lee et al. *in review*). If we accept the latter interpretation to be true, we can and should work together to restore traditional abalone fisheries that strive to be resilient and sustainable for abalone and people into the future. This social-ecological condition motivates deliberate transformation towards a collaborative First Nations-Canadian federal governance regime for abalone specifically, and nearshore fisheries more broadly (see Klain et al. 2014).

In indigenous societies throughout the world, close connections between people and place facilitated social learning and experimentation that developed sustainable resource use practices (Turner and Berkes 2006, Berkes 2009, Brondizio and Le Tourneau 2016). The return to indigenous stewardship of the land and sea is gaining traction in Canada and worldwide, yet challenges in hybrid governance remain to be addressed. For example, in Canada's western Arctic, indigenous Inuvialuit people, the federal fisheries agency and multiple other interests recently developed an integrated fisheries management framework to allow joint review, assessment and decision-making related to any new proposed commercial fisheries within the Canadian Beaufort Sea (Ayles et al. 2016). However, similar to existing co-management arrangements with First Nations in BC, new fisheries in the Beaufort Sea would follow established federal policies and frameworks, falling short of developing true hybrid governance institutions. Indigenous co-management of commercial fisheries in other parts of the world, including New Zealand and Australia, face similar issues with lack of power-sharing by state agencies (Memon and Kirk 2011, Turner et al. 2013).

> 'Why are you letting the white man control you?' (Stephen Hunt, Heiltsuk Nation, Jan. 2012)

In some cases, indigenous laws have been enacted to implement management actions where state policies have failed to conserve or monitor species at the local-scale. For example, First Nations on the BC central coast, including the Heiltsuk Nation, designed and implemented Dungeness crab fishery closures and surveys, and rockfish surveys inside and outside of existing closed area, to monitor effectiveness of these closures in deliberative experimentation and learning (Frid et al. 2016a, Frid et al. 2016b). Creative solutions that circumvented centralized governance institutions via direct negotiations between First Nations and commercial fisheries resource users have also enabled stronger conservation action, such as for sea cucumbers on the central coast of BC (Klain et al. 2014) and herring on Haida Gwaii and the BC central coast (Gauvreau et al. 2017, Jones et al. 2017).

Finding ways to navigate beyond centralized state problem-solving and decision-making is needed for successful adaptive co-management of coastal fisheries with indigenous peoples in BC and beyond. Concurrent with this re-assertion of indigenous rights and responsibilities is the need for innovative approaches to evaluate success at meeting ecological, cultural, social, economic, and governance goals and objectives, and to account for tradeoffs in alternative management decisions (e.g., Plagányi et al. 2013, Kittinger et al. 2014). Re-establishment of indigenous authority to use, manage and conserve coastal and marine resources and their coupled human-ocean systems could help navigate towards a socially just and ecologically sustainable operating space for the world's oceans and humanity.

Acknowledgements

NSERC, Hakai Institute, SFU graduate scholarship and DFO Species At Risk grants supported LL under SFU Ethics permit 2011s0805. NSERC Discovery, Canadian Foundation for Innovation, Hakai Institute and Pew Fellowship grants to AKS funded this research. Walas Giaxsixa (thanks) to collaborators Jennifer Carpenter, Harvey Humchitt, and Gary Wilson of the Heiltsuk Nation, and *Gitla* (Elroy White) who co-interviewed Gus Brown, Bill Gladstone Sr, George and Gary Housty, Howard Humchitt, Sonny Hunt, Mike Reid, Tony and Emma Reid, Fred Reid, Davie Wilson, and three anonymous experts who generously shared their time and knowledge. We thank colleagues for thoughtful reviews.

References

1867. Constitution Act. 30 & 31 Victoria, c. 3 (U.K.), Canada.

1868. Fisheries Act. Canada.

1982. Constitution Act. c. 11 (U.K.), Schedule B, Canada.

1985. Fisheries Act. c. F-14, s. 1., Canada.

1996. Oceans Act. c. 31, Canada.

2002a. Canada National Marine Conservation Areas Act. c. 18, Canada.

2002b. Species at Risk Act. c. 29, Canada.

Acheson, S. 2005. Gwaii Haanas settlement archaeology. Pages 303-336 *in* D. W. Fedje and R. W. Mathewes, editors. Haida Gwaii: Human History and Environment from the Time of the Loon to the Time of the Iron People UBC Press, Vancouver, British Columbia, Canada.

Armitage, D. 2005. Adaptive capacity and community-based natural resource management. Environmental Management **35**:703-715.

Armitage, D., F. Berkes, A. Dale, E. Kocho-Schellenberg, and E. Patton. 2011. Co-management and the co-production of knowledge: Learning to adapt in Canada's Arctic. Global Environmental Change-Human and Policy Dimensions **21**:995-1004.

Armitage, D. R., R. Plummer, F. Berkes, R. I. Arthur, A. T. Charles, I. J. Davidson-Hunt, A. P. Diduck, N. C. Doubleday, D. S. Johnson, M. Marschke, P. McConney, E. W. Pinkerton, and E. K. Wollenberg. 2009. Adaptive co-management for social-ecological complexity. Frontiers in Ecology and the Environment **7**:95-102.

Ayles, B., L. Porta, and R. M. Clarke. 2016. Development of an integrated fisheries co-management framework for new and emerging commercial fisheries in the Canadian Beaufort Sea. Marine Policy **72**:246-254.

Bates, K. T. 1984. Review of the 1982 commercial abalone fishery in British Columbia. Canadian Manuscript Report of Fisheries and Aquatic Sciences **1749**:22 p.

Bennett, N. J., M. Kaplan-Hallam, G. Augustine, N. Ban, D. Belhabib, I. Brueckner-Irwin, A. Charles, J. Couture, S. Eger, L. Fanning, P. Foley, A. M. Goodfellow, L. Greba, E. Gregr, D. Hall, S. Harper, B. Maloney, J. McIsaac, W. L. Ou, E. Pinkerton, D. Porter, R. Sparrow, R. Stephenson, A. Stocks, U. R. Sumaila, T. Sutcliffe, and M. Baileyk. 2018. Coastal and Indigenous community access to marine resources and the ocean: A policy imperative for Canada. Marine Policy **87**:186-193.

Berkes, F. 2009. Evolution of co-management: Role of knowledge generation, bridging organizations and social learning. Journal of Environmental Management:1692–1702.

Berkes, F., and C. e. Folke. 1998. Linking social and ecological systems: management practices and social mechanisms for building resilience. Cambridge University Press, Cambridge, UK.

Bernard, H. R. 2013. Social research methods: qualitative and quantitative approaches (2nd ed.). SAGE Publishing, Inc., USA.

Biggs, R., C. Rhode, S. Archibald, L. M. Kunene, S. S. Mutanga, N. Nkuna, P. O. Ocholla, and L. J. Phadima. 2015. Strategies for managing complex social-ecological systems in the face of uncertainty: examples from South Africa and beyond. Ecology and Society **20**.

Biggs, R., M. Schluter, D. Biggs, E. L. Bohensky, S. BurnSilver, G. Cundill, V. Dakos, T. M. Daw, L. S. Evans, K. Kotschy, A. M. Leitch, C. Meek, A. Quinlan, C. Raudsepp-Hearne, M. D. Robards, M. L. Schoon, L. Schultz, and P. C. West. 2012. Toward Principles for Enhancing the Resilience of Ecosystem Services. Pages 421-+ *in* A. Gadgil and D. M. Liverman, editors. Annual Review of Environment and Resources, Vol 37.

Braje, T. J., T. D. Dillehay, J. M. Erlandson, R. G. Klein, and T. C. Rick. 2017. Finding the first Americans. Science **358**:592-594.

Braje, T. J., J. M. Erlandson, T. C. Rick, P. K. Dayton, and M. B. A. Hatch. 2009. Fishing from past to present: continuity and resilience of red abalone fisheries on the Channel Islands, California. Ecological Applications **19**:906-919.

Brondizio, E. S., and F. M. Le Tourneau. 2016. Environmental governance for all. Science **352**:1272-1273.

Brown, F., and Y. K. Brown. 2009. Staying the Course, Staying Alive - Coastal First Nations fundamental truths: biodiversity, stewardship and sustainability. Biodiversity BC, Victoria, British Columbia, Canada.

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

Capistrano, R. C. G., and A. T. Charles. 2012. Indigenous rights and coastal fisheries: A framework of livelihoods, rights and equity. Ocean & Coastal Management **69**:200-209.

Carlsson, L., and F. Berkes. 2005. Co-management: concepts and methodological implications. Journal of Environmental Management **75**:65-76.

Castello, L., J. P. Viana, G. Watkins, M. Pinedo-Vasquez, and V. A. Luzadis. 2009. Lessons from Integrating Fishers of Arapaima in Small-Scale Fisheries Management at the Mamiraua Reserve, Amazon. Environmental Management **43**:197-209.

Chaffin, B. C., A. S. Garmestani, D. G. Angeler, D. L. Herrmann, C. A. Stow, M. Nystrom, J. Sendzimir, M. E. Hopton, J. Kolasa, and C. R. Allen. 2016. Biological invasions, ecological resilience and adaptive governance. Journal of Environmental Management **183**:399-407.

Chapin, F. S. I., S. R. Carpenter, G. P. Kofinas, C. Folke, N. Abel, W. C. Clark, P. Olsson, D. M. S. Smith, B. Walker, O. R. Young, F. Berkes, R. Biggs, J. M. Grove, R. L. Naylor, E. Pinkerton, W. Steffen, and F. J. Swanson. 2009. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. Trends in Ecology and Evolution **25**:241-249.

Cinner, J. E., T. R. McClanahan, M. A. MacNeil, N. A. J. Graham, T. M. Daw, A. Mukminin, D. A. Feary, A. L. Rabearisoa, A. Wamukota, N. Jiddawi, S. J. Campbell, A. H. Baird, F. A. Januchowski-Hartley, S. Hamed, R. Lahari, T. Morove, and J. Kuange. 2012. Comanagement of coral reef social-ecological systems. Proceedings of the National Academy of Sciences of the United States of America **109**:5219-5222.

Corbett, D. G., D. Causey, M. Clementz, P. L. Koch, A. Doroff, C. Lefevre, and D. West. 2008. Aleut hunters, sea otters, and sea cows: three thousand years of interactions in the western Aleutian Islands, Alaska. Pages 43-75 *in* T. C. Rick and J. M. Erlandson, editors. Human impacts on ancient marine ecosystems: a global perspective. University of California Press, Berkeley and Los Angeles, California, USA.

COSEWIC. 2009. COSEWIC assessment and update status report on the Northern Abalone *Haliotis kamtschatkana* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada.

Council of the Haida Nation. 2007. Towards a marine use plan for Haida Gwaii: A discussion paper. Pages 1-8 *in* H. O. T. Team, editor. Council of the Haida Nation, Haida Gwaii, British Columbia, Canada.

Crona, B. I., T. Van Holt, M. Petersson, T. M. Daw, and E. Buchary. 2015. Using social-ecological syndromes to understand impacts of international seafood trade on small-scale fisheries. Global Environmental Change-Human and Policy Dimensions **35**:162-175.

Cumming, G. S., D. H. M. Cumming, and C. L. Redman. 2006. Scale mismatches in social-ecological systems: Causes, consequences, and solutions. Ecology and Society **11**.

Davis, A., and J. Wagner. 2006. A right to fish for a living? The case for coastal fishing people's determination of access and participation. Ocean & Coastal Management **49**:476-497.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecological Monographs **69**:219-250.

Duggins, D. 1980. Kelp beds and sea otters: An experimental approach. Ecology **61**:447-453.

Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment **1**:488-494.

Eriksson, H., H. Osterblom, B. Crona, M. Troell, N. Andrew, J. Wilen, and C. Folke. 2015. Contagious exploitation of marine resources. Frontiers in Ecology and the Environment **13**:435-440.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. Science **185**:1058-1060.

Farlinger, S. 1990. Review of the biological basis for management of the British Columbia abalone fishery. Pages 41-65 *in* G. Thomas, editor. Shellfish Stock Assessments for the West Coast of Canada in 1990 as Reviewed by the Pacific Stock Assessment Review Committee (PSARC). Department of Fisheries and Oceans, Prince Rupert, British Columbia, Canada.

Fedje, D. W., A. P. Mackie, R. J. Wigen, Q. Mackie, and C. Lake. 2005. Kilgii Gwaay: An early maritime site in the south of Haida Gwaii. Pages 187-203 *in* D. W. Fedje and R. W. Mathewes, editors. Haida Gwaii: Human History and Environment from the Time of the Loon to the Time of the Iron People UBC Press, Vancouver, British Columbia, Canada.

Fernández ‐ Llamazares, Á., and M. Cabeza. 2018. Rediscovering the potential of indigenous storytelling for conservation practice. Conservation Letters **11**:e12398.

Finkbeiner, E. M., and X. Basurto. 2015. Re-defining co-management to facilitate small-scale fisheries reform: An illustration from northwest Mexico. Marine Policy **51**:433-441.

Fisher, R. 1992. Contact and Conflict. 2nd edition. UBC Press, Vancouver, BC.

Fisheries and Oceans Canada. 2012. Action Plan for the Northern Abalone (*Haliotis kamtschatkana*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Fisheries and Oceans Canada. 2015. Report on the progress of Recovery Strategy implementation for Northern Abalone (*Haliotis kamtschatkana*) in Pacific Canadian waters for the period 2007-2012. Fisheries and Oceans Canada, Ottawa, Canada.

Folke, C. 2006. Resilience: The emergence of a perspective for social-ecological systems analyses. Global Environmental Change-Human and Policy Dimensions **16**:253-267.

Folke, C., R. Biggs, A. V. Norstrom, B. Reyers, and J. Rockstrom. 2016. Social-ecological resilience and biosphere-based sustainability science. Ecology and Society **21**.

Folke, C., S. Carpenter, T. Elmqvist, L. Gunderson, C. S. Holling, and B. Walker. 2002. Resilience and sustainable development: Building adaptive capacity in a world of transformations. Ambio **31**:437-440.

Folke, C., S. R. Carpenter, B. Walker, M. Scheffer, T. Chapin, and J. Rockstrom. 2010. Resilience Thinking: Integrating Resilience, Adaptability and Transformability. Ecology and Society **15**.

Frid, A., M. McGreer, D. R. Haggarty, J. Beaumont, and E. J. Gregr. 2016a. Rockfish size and age: The crossroads of spatial protection, central place fisheries and indigenous rights. Global Ecology and Conservation **8**:170-182.

Frid, A., M. McGreer, and A. Stevenson. 2016b. Rapid recovery of Dungeness crab within spatial fishery closures declared under indigenous law in British Columbia. Global Ecology and Conservation **6**:48-57.

Garibaldi, A., and N. Turner. 2004. Cultural keystone species: Implications for ecological conservation and restoration. Ecology and Society **9**.

Gauvreau, A. M., D. Lepofsky, M. Rutherford, and M. Reid. 2017. "Everything revolves around the herring": the Heiltsuk-herring relationship through time. Ecology and Society **22**.

Gelcich, S., T. P. Hughes, P. Olsson, C. Folke, O. Defeo, M. Fernandez, S. Foale, L. H. Gunderson, C. Rodriguez-Sickert, M. Scheffer, R. S. Steneck, and J. C. Castilla. 2010. Navigating transformations in governance of Chilean marine coastal resources. Proceedings of the National Academy of Sciences of the United States of America **107**:16794-16799.

Haida Gwaii Abalone Stewards. 2008. Haida Gwaii Northern Abalone Community Action Plan. Council of the Haida Nation, Haida Gwaii, British Columbia, Canada.

Haida Marine Traditional Knowledge Study participants, J. Winbourne, Haida Oceans Technical Team, and Haida Fisheries Program. 2011a. Haida Marine Traditional Knowledge Study Volume 1: Methods and Results Summary. Council of the Haida Nation, Haida Gwaii, British Columbia, Canada.

Haida Marine Traditional Knowledge Study participants, J. Winbourne, Haida Oceans Technical Team, and Haida Fisheries Program. 2011b. Haida Marine Traditional Knowledge Study Volume 3: Focal Species Summary. Council of the Haida Nation, Haida Gwaii, British Columbia, Canada.

Harris, C. 1997. The Resettlement of British Columbia. Essays on Colonialism and Geographical Change. UBC Press, Vancouver, British Columbia, Canada.

Harris, D. C. 2002. Fish, Law, and Colonialism: The Legal Capture of Salmon in British Columbia. University of Toronto Press, Toronto, Ontario, Canada.

Holling, C. S., and G. K. Meffe. 1996. Command and control and the pathology of natural resource management. Conservation Biology **10**:328-337.

Holling, C. S. e. 1978. Adaptive environmental assessment and management. Wiley, New York, NY, USA.

Huntington, H. P. 1998. Observations on the utility of the semi-directive interview for documenting traditional ecological knowledge. Arctic **51**:237-242.

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

Jones, R., B. DeFreitas, N. Sloan, L. Lee, K. von Boetticher, and G. Martin. 2003. Abalone stewardship in Haida Gwaii: Forging a long-tenn commitment. Canadian Technical Report of Fisheries and Aquatic Sciences **2482**:5-19.

Jones, R., C. Rigg, and L. Lee. 2010. Haida Marine Planning: First Nations as a Partner in Marine Conservation. Ecology and Society **15**.

Jones, R., C. Rigg, and E. Pinkerton. 2017. Strategies for assertion of conservation and local management rights: A Haida Gwaii herring story. Marine Policy **80**:154-167.

Jones, R., and T.-L. Williams-Davidson. 2000. Applying Haida ethics in today's fishery. Pages 100-115 *in* H. Coward, R. Ommer, and T. Pitcher, editors. Just Fish: Ethics and Canadian Marine Fisheries. Institute of Social and Economic Research, St. John's, Newfoundland.

Kittinger, J. N., T. M. Bambico, D. Minton, A. Miller, M. Mejia, N. Kalei, B. Wong, and E. W. Glazier. 2016. Restoring ecosystems, restoring community: socioeconomic and cultural dimensions of a community-based coral reef restoration project. Regional Environmental Change **16**:301-313.

Kittinger, J. N., J. Z. Koehn, E. Le Cornu, N. C. Ban, M. Gopnik, M. Armsby, C. Brooks, M. H. Carr, J. E. Cinner, A. Cravens, M. D'Iorio, A. Erickson, E. M. Finkbeiner, M. M. Foley, R. Fujita, S. Gelcich, K. St Martin, E. Prahler, D. R. Reineman, J. Shackeroff, C. White, M. R. Caldwell, and L. B. Crowder. 2014. A practical approach for putting people in ecosystem-based ocean planning. Frontiers in Ecology and the Environment **12**:448-456.

Klain, S. C., R. Beveridge, and N. J. Bennett. 2014. Ecologically sustainable but unjust? Negotiating equity and authority in common-pool marine resource management. Ecology and Society **19**.

Kocho-Schellenberg, J. E., and F. Berkes. 2015. Tracking the development of co-management: using network analysis in a case from the Canadian Arctic. Polar Record **51**:422-431.

Lee, L., J. Thorley, J. Watson, M. Reid, and A. K. Salomon. *in review*. Diverse knowledge systems reveal historical social-ecological and species abundance changes for gauging conservation status. Conservation Letters.

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

Lemos, M. C., and A. Agrawal. 2006. Environmental governance. Pages 297-325 Annual Review of Environment and Resources.

Lepofsky, D., C. G. Armstrong, S. Greening, J. Jackley, J. Carpenter, B. Guernsey, D. Mathews, and N. J. Turner. 2017. Historical ecology of cultural keystone places of the Northwest Coast. American Anthropologist **119**:448-463.

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

Lepofsky, D., N. F. Smith, N. Cardinal, J. Harper, M. Morris, Gitla, R. Bouchard, D. I. D. Kennedy, A. K. Salomon, M. Puckett, and K. Rowell. 2015. Ancient shellfish mariculture on the northwest coast of North America. American Antiquity **80**:236-259.

Lertzman, K. 2009. The paradigm of management, management systems, and resource stewardship. Journal of Ethnobiology **29**:339-358.

Markel, R. W., and J. B. Shurin. 2015. Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests. Ecology **96**:2877-2890.

Mathews, D. L., and N. J. Turner. 2017. Ocean Cultures: Northwest Coast Ecosystems and Indigenous Management Systems. Pages 169-206 *in* P. S. Levin and M. R. Poe, editors. Conservation for the Anthropocene Ocean: Interdisciplinary Science in Support of Nature and People. Academic Press, USA.

McKechnie, I., D. Lepofsky, M. L. Moss, V. L. Butler, T. J. Orchard, G. Coupland, F. Foster, M. Caldwell, and K. Lertzman. 2014. Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. Proceedings of the National Academy of Sciences of the United States of America **111**:E807-E816.

McKechnie, I., and M. L. Moss. 2016. Meta-analysis in zooarchaeology expands perspectives on Indigenous fisheries of the Northwest Coast of North America. Journal of Archaeological Science-Reports **8**:470-485.

Memon, P. A., and N. A. Kirk. 2011. Maori commercial fisheries governance in Aotearoa/New Zealand within the bounds of a neoliberal fisheries management regime. Asia Pacific Viewpoint **52**:106-118.

Menzies, C. R. 2010. Dm sibilhaa'nm da laxyuubm Gitxaała: picking abalone in Gitxaała territory. Human Organization **69**:213-220.

Menzies, C. R. 2015. Revisiting “Dm sibilhaa’nm da laxyuubm Gitxaała (Picking abalone in Gitxaała territory)”: vindication, appropriation, and archaeology. BC Studies:129-153.

Mistry, J., and A. Berardi. 2016. Bridging indigenous and scientific knowledge. Science **352**:1274-1275.

Nadasdy, P. 2003. Reevaluating the co-management success story. Arctic **56**:367-380.

Olsson, P., C. Folke, and F. Berkes. 2004. Adaptive comanagement for building resilience in social-ecological systems. Environmental Management **34**:75-90.

Orchard, T. J. 2007. Otters and urchins: Continuity and change in Haida economy during the Late Holocene and maritime fur trade periods. University of Toronto, Toronto.

Ostrom, E. 1998. Scales, polycentricity, and incentives: designing complexity to govern complexity. Pages 149-167 *in* L. D. Guruswamy and J. A. McNeely, editors. Protection of global biodiversity: Converging strategies. Duke University Press, Burham, North Carolina, USA.

Parks Canada. 2018. Parks Canada's Conservation and Restoration Program: Chiixuu Tll iinasdll – Nurturing seafood to grow. https://www.pc.gc.ca/en/agence-agency/bib-lib/rapports-reports/core-2018/ouest-west/ouest-west14. Accessed on 24 Jun 2018.

Parnell, P. E., E. F. Miller, C. E. Lennert-Cody, P. K. Dayton, M. L. Carter, and T. D. Stebbins. 2010. The response of giant kelp (Macrocystis pyrifera) in southern California to low-frequency climate forcing. Limnology and Oceanography **55**:2686-2702.

Pinkerton, E., E. Angel, N. Ladell, P. Williams, M. Nicolson, J. Thorkelson, and H. Clifton. 2014. Local and regional strategies for rebuilding fisheries management institutions in coastal British Columbia: what components of comanagement are most critical? Ecology and Society **19**.

Pinkerton, E., and R. Davis. 2015. Neoliberalism and the politics of enclosure in North American small-scale fisheries. Marine Policy **61**:303-312.

Pinkerton, E., and L. John. 2008. Creating local management legitimacy. Marine Policy **32**:680-691.

Pinkerton, E. e. 1989. Co-operative management of local fisheries: New directions for improved management and community development. University of British Columbia Press, Vancouver, Canada.

Pinkerton, E. W. 1992. Translating legal-rights into management practice - overcoming barriers to the exercise of comanagement. Human Organization **51**:330-341.

Pinkerton, E. W. 1994. Local fisheries comanagement - a review of international experiences and their implications for salmon management in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **51**:2363-2378.

Plagányi, E. E., I. van Putten, T. Hutton, R. A. Deng, D. Dennis, S. Pascoe, T. Skewes, and R. A. Campbell. 2013. Integrating indigenous livelihood and lifestyle objectives in managing a natural resource. Proceedings of the National Academy of Sciences of the United States of America **110**:3639-3644.

Plummer, R., D. R. Armitage, and R. C. de Loe. 2013. Adaptive Comanagement and Its Relationship to Environmental Governance. Ecology and Society **18**.

Plummer, R., B. Crona, D. R. Armitage, P. Olsson, M. Tengo, and O. Yudina. 2012. Adaptive Comanagement: a Systematic Review and Analysis. Ecology and Society **17**.

Powell, M. 2012. Divided waters: Heiltsuk spatial management of herring fisheries and the politics of native sovereignty. Western Historical Quarterly **43**:463-484.

Pretty, J., and H. Ward. 2001. Social capital and the environment. World Development **29**:209-227.

Robinson, M. P. 1996. Sea Otter Chiefs. Bayeux Arts Incorporated, Calgary, AB.

Salomon, A. K., K. Lertzman, K. Brown, K. B. Wilson, D. Secord, and I. McKechnie. 2018. Democratizing conservation science and practice. Ecology and Society **23**.

Salomon, A. K., B. J. K. Wilson, E. X. White, N. M. Tanape, and T. M. Happynook. 2015. First Nations perspectives on sea otter conservation in British Columbia and Alaska: insights into coupled human ocean systems. Pages 301-331 *in* S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom, editors. Sea Otter Conservation. Academic Press, Boston, Massachusetts, USA.

Sarkki, S., A. Ficko, F. E. Wielgolaski, E. M. Abraham, S. Bratanova-Doncheva, K. Grunewald, A. Hofgaard, F. K. Holtmeier, A. P. Kyriazopoulos, G. Broll, M. Nijnik, and M. L. Sutinen. 2017. Assessing the resilient provision of ecosystem services by social-ecological systems: introduction and theory. Climate Research **73**:7-15.

Sarkki, S., T. Komu, H. I. Heikkinen, N. A. Garcia, E. Lepy, and V. P. Herva. 2016. Applying a synthetic approach to the resilience of Finnish reindeer herding as a changing livelihood. Ecology and Society **21**.

Sloan, N. A. 2004. Northern abalone: using an invertebrate to focus marine conservation ideas and values. Coastal Management **32**:129-143.

Sloan, N. A., and P. A. Breen. 1988. Northern abalone, *Haliotis kamtschatkana* in British Columbia: fisheries and synopsis of life history information. Canadian Special Publication of Fisheries and Aquatic Sciences **103**:46 pp.

Sloan, N. A., and L. Dick. 2012. Sea Otters of Haida Gwaii: Icons in Human - Ocean Relations. Gwaii Haanas Archipelago Management Board & Haida Gwaii Museum, Skidegate, British Columbia, Canada.

Stevenson, C. F., K. W. Demes, and A. K. Salomon. 2016. Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. Ecology and Evolution **6**:1041-1053.

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

Takeda, L., and I. Røpke. 2010. Power and contestation in collaborative ecosystem-based management: The case of Haida Gwaii. Ecological Economics **70**:178-188.

Tegner, M. J., and P. K. Dayton. 1999. Ecosystem effects of fishing. Trends in Ecology and Evolution **14**:260-261.

Tegner, M. J., and P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. ICES Journal of Marine Science **57**:579-589.

Trosper, R. L. 2002. Northwest coast indigenous institutions that supported resilience and sustainability. Ecological Economics **41**:329-344.

Trosper, R. L. 2003. Resilience in pre-contact Pacific Northwest social ecological systems. Conservation Ecology **7**.

Trosper, R. L. 2009. Resilience, Reciprocity and Ecological Economics: Northwest Coast Sustainability. Routledge, New York, New York, USA.

Turner, N. J., and F. Berkes. 2006. Coming to understanding: Developing conservation through incremental learning in the Pacific Northwest. Human Ecology **34**:495-513.

Turner, N. J., F. Berkes, J. Stephenson, and J. Dick. 2013. Blundering Intruders: Extraneous Impacts on Two Indigenous Food Systems. Human Ecology **41**:563-574.

von der Porten, S., D. Lepofsky, D. McGregor, and J. Silver. 2016. Recommendations for marine herring policy change in Canada: Aligning with Indigenous legal and inherent rights. Marine Policy **74**:68-76.

Walker, B., and D. Salt. 2006. Resilience thinking: sustaining ecosystems and people in a changing world. Island Press, Washington DC, USA.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

Watson, J. C. 2000. The effects of sea otters (*Enhydra lutris*) on abalone (*Haliotis* spp.) populations. Canadian Special Publication of Fisheries and Aquatic Sciences **130**:123-132.

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

Westley, F. R., O. Tjornbo, L. Schultz, P. Olsson, C. Folke, B. Crona, and O. Bodin. 2013. A Theory of Transformative Agency in Linked Social-Ecological Systems. Ecology and Society **18**.

White, E. 2011. Heiltsuk stone fish traps on the central coast of British Columbia. Pages 75-90 *in* M. L. Moss and A. Cannon, editors. The archaeology of North Pacific fisheries. University of Alaska Press, Fairbanks, Alaska, USA.

Wilson, B. J. K. i., and H. Harris. 2005. Tllsda X̲aaydas K̲'aaygang.nga: Long, Long Ago Haida Ancient Stories.*in* D. W. Fedje and R. W. Mathewes, editors. Human History and Environment from the Time of the Loon to the Time of the Iron People. UBC Press, Vancouver, BC.

Winbourne, J., and Haida Oceans Technical Team. 2014. Haida Marine Traditional Knowledge Summary: Kelp Forests, Abalone, Sea Urchins, Sea Otters & Coastal People. Council of the Haida Nation, Haida Gwaii, British Columbia, Canada.

Chapter 5. Conclusions

> The boat moves on, forever anchored in the same place. (Bill Reid, The Spirit of Haida Gwaii, 1991)

As impacts of people on the earth's biological and cultural diversity are exponentially increasing in this age of the Anthropocene (Vitousek et al. 1997, Waters et al. 2016), fewer and fewer places remain with potential to restore and sustain biodiversity and cultural continuity (Brondizio and Le Tourneau 2016). I am fortunate to live in such a place and work with Haidas who are maintaining cultural connections with, and stewardship of, the land and sea. In turn the land and sea are integral to their cultural continuity. Haida Gwaii, forever perched on the edge of the Pacific northeast continental shelf, remains rooted in place while the environmental and social context of the land, sea and people that Haida Gwaii supports, forever changes through time.

In this thesis, I use a social-ecological systems (SESs) approach and draw on a detailed empirical study of interacting species at risk: a keystone predator and one of its prey, and people. I document their trophic interactions on temperate rocky reefs, I reconstruct historical baselines using multiple knowledge sources, and I analyze current governance and management policies to advance future approaches that are ecologically sustainable and socially just. This work has important implications for understanding the direct and indirect effects of predator-prey interactions, ecological baselines as dynamic in nature, and the importance of people as integral interacting components and drivers of ecological systems. In this chapter, I synthesize these implications and discuss key directions for future research and policy action.

Trophic cascades and trait-mediated interactions can reduce predation effects on weakly-interacting alternative prey

Despite increasing knowledge that ecosystem interactions can yield conservation surprises (Mangel and Levin 2005), conservation for species at risk in Canada and around the world remains largely driven by single-species approaches, even for strongly interacting species (Soulé et al. 2003, Soulé et al. 2005, Chadès et al. 2012). By investigating a food web comprised of one keystone predator (sea otter), two herbivorous consumer prey (northern abalone and sea urchins), and one primary resource group (kelps) in Chapter 2, I contribute to current understanding of processes underlying the benthic community structure of temperate rocky reefs. Specifically, I quantify the direct and indirect effects of sea otter recovery and their role in a well-documented trophic cascade (sea otters-urchins-kelp; Estes and Palmisano 1974, Watson and Estes 2011, Markel and Shurin 2015, Stevenson et al. 2016), on their weakly interacting abalone prey. Consistent with other predator-prey interactions, sea otters predation has direct density-mediated interactions (DMIs) and indirect behavioural trait-mediated interactions (TMIs) with their prey, the magnitude of which can vary by prey species. We found that direct predation effects on urchins were strong and immediate, with <5% of urchin biomass remaining within five years of sea otter occupation. This radical urchin reduction led to trophic cascades that increased the depth and extent of kelp forests. Moreover, densities of exposed abalone were up to 16x lower in areas where sea otters had recovered for over three decades (Lee et al. 2016). Surprisingly however, densities of cryptic abalone were up to twice as high at long occupation sites (Lee et al. 2016). Sea otter predation effects on abalone were more variable in the first few years of sea otter occupation and mediated by habitat characteristics. In fact, some sites with sea otters had higher densities of abalone than sites without sea otters.

For weakly interacting prey such abalone, this thesis shows how increased kelp forest habitat in concert with TMIs can increase the density of cryptic abalone, mediating the negative direct effects of sea otter predation. Although sea otter recovery reduced overall abalone density and size, I detected a clear and positive effect of depth on abalone such that abalone densities increased with depth as sea otters recovered. Deeper and more extensive kelp forests increased the spatial extent of optimal habitat for abalone providing both food and protective cover. Similar to other studies across many ecosystems (Preisser et al. 2005), we found that abalone TMIs were likely driven by shifts in habitat use, spatial distribution and potentially reduced feeding opportunities due to the need to seek refuge from predation. By five years of sea otter occupation, most of the abalone were cryptic in refuge habitats. In comparison <10-30% of abalone were cryptic at most sites in the absence of sea otters. In areas where sea otters had recovered, abundant drift kelp was available for abalone that were now primarily using cryptic habitats, additionally minimizing predation risk by reducing the need to forage out in open habitat. The presence and amount of cryptic abalone habitat will become more critical for abalone persistence as sea otters recover and expand in geographic range. These detectable positive indirect effects of habitat alteration and TMIs are critical considerations for conservation planning because they may alter long-term population viability of recovering endangered northern abalone.

Key future conservation research should investigate further empirical evidence of co-existence between predator and prey. For example, intertidal black abalone densities increased at some sites after decades of sea otter occupation in California (Raimondi et al. 2015) and the trophic cascade increasing kelp forests and cryptic abalone behavior driven by intense predation by sea otters may increase food and habitat to promote abalone growth and reproduction (Estes et al. 2005). Abalone productivity may be higher due to increased gonadal development resulting from more readily available kelp resources in larger kelp forests, as has been shown for sea urchins (Larson et al. 1980). Moreover, fertilization success might be higher for abalone hiding in crevices together in a kelp forest compared to abalone out in an open urchin barren. Ironically, fertilization success might be higher at lower overall abalone densities where sea otters and kelp forests have locally recovered. Larval survival may also be higher due to entrainment by localized currents in more extensive kelp forests. Given that the indirect effects of sea otter occupation are predicted to expand kelp forests with consequences for abalone population dynamics at different life stages, understanding the nature and magnitude of these effects will have implications for multi-species conservation of protected predator and prey.

Assessing changes in abalone recruitment with increasing sea otter occupation time will help elucidate how indirect effects of sea otters affect abalone population dynamics. For example, a long time series showing stable or increasing abalone recruitment would indicate persistence and population viability. However, external factors can also dramatically affect abalone recruitment, including known oceanographic cycles such as the Pacific Decadal Oscillation, El Nino and La Nina, the negative effects of which were mitigated by the presence of enforced marine reserves (Micheli et al. 2012). Some unexpected, more abrupt disturbances have also affected abalone recruitment, including the recent ‘warm blob’ (Cavole et al. 2016) and likely positive effects of sea star wasting disease particularly on juvenile abalone survival (sensu

Schultz et al. 2016; Burt *et al. In review*). Simulation modeling of abalone population dynamics can be conducted to ask: (1) To what degree does indirect benefits of sea otter predation contribute to abalone population viability? (2) What are the minimum densities and/or area needed to maintain abalone population viability, taking into consideration the effects of sea otter presence/absence and occupation time? The varying hypothesized consequences of kelp forest expansion on abalone population dynamics could be incorporated into different model scenarios to explore potential outcomes for abalone population viability.

Shifting baselines affect perceptions of species status and trends

Since Pauly (1995) first diagnosed the ‘shifting baselines syndrome’ in fisheries science, the idea that each generation believes the ecological conditions they grew up with to be normal without knowledge of past conditions from which to gauge change, has been widely applied to many environmental issues (Dayton et al. 1998, Jackson et al. 2001, Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2005b, Beaudreau and Levin 2014). Where they exist, historical case studies in conservation typically reveal much higher historical species abundances and greater magnitudes of decline than previously thought. Recognition and concern that shifting baselines are therefore leading to increased societal acceptance of biodiversity loss and declining species abundances is spurring multidisciplinary efforts to reconstruct historical conditions and counter shifting baselines syndrome (Bonebrake et al. 2010, Soga and Gaston 2018). Fortunately, many unconventional sources of data are available to augment the limited years to decades timescale of modern ecological data. Combined, these multiple knowledge sources can elucidate historical changes in social and ecological conditions over decades, centuries and millennia, and are increasingly being used to broaden our timescale of SES understanding (e.g., Saenz-Arroyo et al. 2005a, Saenz-Arroyo et al. 2006, Saenz-Arroyo and Roberts 2008, Braje et al. 2009, Costanza et al. 2012, Beaudreau and Levin 2014, Thurstan et al. 2015, Saenz-Arroyo and Revollo-Fernandez 2016, Early-Capistran et al. 2018, Ferretti et al. 2018, Silliman et al. 2018).

Building on the identified imperative for effective conservation to draw on multiple sources of knowledge and synthesize them in appropriate ways (Saenz-Arroyo et al. 2006, Tengo et al. 2014, Thurstan et al. 2015), I drew on zooarchaeological data, historical records, fisheries landings, traditional knowledge, and ecological surveys, to construct a broader understanding of change over time in the abalone SES. In doing so, I advanced efforts to work collaboratively with coastal First Nations communities to document and use traditional knowledge (TK) in a way that respects community protocols, including free, prior and informed consent of participants, and where communities retain control of their knowledge (Fernández-Llamazares and Cabeza 2018, Salomon et al. 2018). Specifically, I contributed to the diversity of techniques available to quantify traditional knowledge by using an innovative method of elicitation for ecological variables by decade (sensu Sala et al. 2004). I asked Heiltsuk abalone experts to reconstruct remembered abundance and size structure of intertidal abalone by decade of harvest from their typical harvesting area, by placing real abalone shells (collected from shorelines and colour-coded by size class) of the appropriate size and in the remembered configuration on the interview table, which represented a specified area of shoreline. I could then use these reconstructions to generate quantitative density data from qualitative observations that operationally matched size and count data from contemporary ecological field surveys. This allowed me to fit population dynamics models to both TK data and survey data from western scientific knowledge (WSK) together. This novel integrated Bayesian model revealed similarities and differences in abalone abundance and trends between TK and WSK that enabled clearer evaluation of benefits, biases and cautions to be considered in knowledge integration.

The extended historical perspective of BC's abalone SES reveals how shifting baselines from over a century ago can alter our perceptions of abalone status and trends today (Chapter 3). Departing from the declining trends shown in most case studies, I show how ecological regime shifts triggered by human hunting of sea otters and fishing of abalone caused both increase and decrease in abalone abundances over centuries and millennia. In fact, contemporary abalone abundances are likely similar or perhaps higher than those from the deep past in pre-contact times, yet are exponentially lower than abundances from the mid-20th century, following ecological extirpation of sea otters. In California's Channel Islands, midden site analyses showed persistence of red abalone with oscillating periods of high and low abundance over 8000 years that were attributed to sea otter hunting by coastal indigenous people rather than linked to large-scale oceanographic conditions that can also affect abalone recruitment and kelp productivity (Braje et al. 2009). By using an uncommon case study involving a 'natural experiment' in which a once-extirpated keystone predator was re-introduced and is now recovering, I contribute to a growing body of literature that acknowledges the dynamic nature of social and ecological baselines (Hicks et al. 2016). This challenges the idea of a single static baseline for conservation similar to the pre-determined and arbitrary baseline set in Canada's Species At Risk Act (2002c) where species status is gauged against abundance within the past decade or three generations of the species, whichever time period is greater.

Contributing to an increasing number of publications from different systems and places, this thesis highlights that historical perspectives stretching back before modern fisheries records and ecological monitoring are essential to inform appropriate targets for conservation, restoration and management (e.g., Pauly 1995, Jackson et al. 2001, Saenz-Arroyo et al. 2005a, Saenz-Arroyo and Revollo-Fernandez 2016, Early-Capistran et al. 2018, Soga and Gaston 2018). The arbitrary baseline set by the SARA to gauge species status could not account for past SES regime shifts, thus resulting in abalone being listed as a threatened and then endangered species and perpetuating the loss of traditional First Nations abalone fisheries. Recognizing that people have been embedded in the land- and sea-scape of coastal BC for over 13,000 years and actively modifying the coast for at least centuries and millennia, people must clearly be considered in determining conservation targets and baselines. In this case, I believe broader consideration of historical abalone SES changes would allow for different conclusions to be drawn about species status where abalone would not be at risk, traditional fisheries would be restored, and innovative, socially just conservation solutions could be pursued.

The future of marine conservation and management for coastal British Columbia

Collaborative or cooperative management, often referred to as co-management, involves the sharing of power and responsibility between state governments and local resource users (Pinkerton 1989, McCay and Jentoft 1996, Berkes 2009). In BC fisheries, de facto sharing of power with industry and private actors has occurred over time due to strong lobbying power of commercial and recreational fisheries interests influencing federal fisheries decisions. In contrast, First Nations and other coastal community interests have historically been marginalized (Pinkerton 1994). Increasing implementation of Individual Transferable Quotas (ITQs) and license buy-back programs in BC commercial fisheries within the current neoliberal political context has only further reduced small boat operators, many of which were indigenous (Pinkerton and Davis 2015, Pinkerton 2017). This has further marginalized and increased barriers to participation of First Nations (Pinkerton et al. 2014, Bennett et al. 2018). More recently, co-management is being used to engage indigenous peoples in place-based governance of natural resources globally and in Canada, including northern BC (Jones et al. 2010, Pinkerton et al. 2014). However, equitable power sharing or devolution of power from state to non-state institutions to address conventional power asymmetries and institutional biases is not a prescribed condition for co-management (Carlsson and Berkes 2005) and remains limited in BC.

Co-management arrangements with the Haida and Heiltsuk Nations, in conjunction with the polycentric governance institutions for abalone recovery that I explore in Chapter 4, provide a strong foundation for development of future hybrid indigenous-state governance for abalone management. In particularly, future restoration of traditional abalone fisheries can build on traditional abalone harvesting practices and protocols as described in Chapter 4. I contribute to the growing call for co-management with indigenous peoples and increasing recognition of the need to learn from indigenous knowledge systems worldwide (e.g. Berkes 2009, Huntington 2010, Armitage et al. 2011, Turner and Spalding 2013, Turner et al. 2013, Stephenson et al. 2014, Gavin et al. 2015, Lepofsky et al. 2017, Mathews and Turner 2017) by demonstrating strong alignment between the seven principles that promote social-ecological resilience (Biggs et al. 2012) and traditional governance and management of abalone. Governance of abalone recovery has successfully engaged coastal First Nations and state institutions in cooperative experimentation, research and monitoring that fit well with an adaptive co-management approach. This process promotes continual social learning and improvement that is central to traditional First Nations worldviews and governance systems (Chapter 4).

Challenges to achieving hybrid governance highlighted in Chapter 4 include existing power asymmetries, the need to build trust and the need for diverse and sufficient sources of funding. To address these challenges, I think a fundamental change in how First Nations and the state view and relate to one another is needed. Devolution of some decision-making authority to the Council of the Haida Nation and the Heiltsuk

Tribal Council within their traditional territories will be required to begin equalizing power asymmetries, while working together to ensure sustainable resource use at all scales. Both Nations have a proven strong history of working with state agencies and stakeholders, including the federal fisheries department, industry, non-government organizations and academia, although not without conflict at times (e.g., Gauvreau et al. 2017, Jones et al. 2017). In spite of setbacks, I believe incremental successes in working together to achieve those goals and objectives that are commonly held will foster relationship and trust building over time. These stronger relationships will promote the social learning required to strengthen foundations for future collaborative management arrangements. The issue of funding may be the most difficult to address over the short-term for northern BC given the current Canadian context where First Nations have constitutional rights but not necessarily legal rights of access to natural resources in their traditional territories. Until some form of income base is generated, such as impact benefit agreements, taxations or rents from industrial and commercial developments on traditional territories, generating operational funds to support self-governance will remain a challenge.

Finally, although governance relationships between coastal First Nations and federal and provincial governments are moving in a positive direction, the reality is that most co-management institutions still operate within federal governance institutions and bureaucracy rather than within true hybrid governance institutions. For example, on Haida Gwaii, joint decision-making for Gwaii Haanas occurs through the co-managed Archipelago Management Board and the same for aspects of land use occur through the co-managed Haida Gwaii Management Council. However, operation of Gwaii Haanas occurs within rules of the federal Parks Canada Agency bureaucracy and that for land use occurs largely within bureaucracies of the BC Ministry of Forests, Lands, and Natural Resources Operations. I believe that there remains much room for progress towards more equitable co-management, in line with that defined by The World Bank (1999, p.11) as “a decentralized approach to decision-making that involves the local users [First Nations] in the decision-making process as equals with the nation-state.”

In over two decades of terrestrial and marine conservation work on Haida Gwaii, I have witnessed and participated in some truly significant progress in advancing indigenous rights, title and responsibilities in natural resource management by the Haida Nation. When I moved here in 1993, one co-management arrangement existed for Gwaii

Haanas National Park Reserve and Haida Heritage Site. Since then, the Council of the Haida Nation has successfully negotiated a multitude of additional co-management arrangements over land and sea resources with the Province of BC and/or federal agencies, punctuated and advanced by litigation and multiple successful court cases. These include co-management of the razor clam fishery, Haida Gwaii land and marine use planning and implementation processes, integrated land-sea-people management planning for Gwaii Haanas, and integrated planning for protected areas in northern BC along with other coastal First Nations. The Heiltsuk Nation has made equivalent progress in land and marine use co-management arrangements within their traditional territory.

In western Canada, recent political announcements and agreements offer hope for transformative change to a new First Nations-Canadian federal governance regime for the coast:

> The First Nations of the Pacific north and central coasts have been protecting Canada's waters for millennia. Working together, we will protect and preserve the Pacific north coast, and we will advance reconciliation along the way. (Prime Minister Justin Trudeau, 21 Jun. 2018)
>
> It is clear that to be successful oceans management and protection must be indigenous-led… Our elders tell us that if we take care of the ocean, the ocean will take care of us. (Marilyn Slett, Chief Councilor of Heiltsuk Tribal Council and President of Coastal First Nations, 21 Jun. 2018)

A willingness to transform fisheries management policies in order to facilitate the legal rights of First Nations to access their traditional resources, including abalone, will ultimately be required for social and ecological sustainability. In fact, social-ecological sustainability may require even broader community-based access rights to all marine resources and industries within their traditional territory to facilitate the diversity and redundancy required for social-ecological system resilience.

References

2002. Species at Risk Act. c. 29, Canada.

Armitage, D., F. Berkes, A. Dale, E. Kocho-Schellenberg, and E. Patton. 2011. Co-management and the co-production of knowledge: Learning to adapt in Canada's Arctic. Global Environmental Change-Human and Policy Dimensions **21**:995-1004.

Beaudreau, A. H., and P. S. Levin. 2014. Advancing the use of local ecological knowledge for assessing data-poor species in coastal ecosystems. Ecological Applications **24**:244-256.

Bennett, N. J., M. Kaplan-Hallam, G. Augustine, N. Ban, D. Belhabib, I. Brueckner-Irwin, A. Charles, J. Couture, S. Eger, L. Fanning, P. Foley, A. M. Goodfellow, L. Greba, E. Gregr, D. Hall, S. Harper, B. Maloney, J. McIsaac, W. L. Ou, E. Pinkerton, D. Porter, R. Sparrow, R. Stephenson, A. Stocks, U. R. Sumaila, T. Sutcliffe, and M. Baileyk. 2018. Coastal and Indigenous community access to marine resources and the ocean: A policy imperative for Canada. Marine Policy **87**:186-193.

Berkes, F. 2009. Evolution of co-management: Role of knowledge generation, bridging organizations and social learning. Journal of Environmental Management:1692–1702.

Biggs, R., M. Schluter, D. Biggs, E. L. Bohensky, S. BurnSilver, G. Cundill, V. Dakos, T. M. Daw, L. S. Evans, K. Kotschy, A. M. Leitch, C. Meek, A. Quinlan, C. Raudsepp-Hearne, M. D. Robards, M. L. Schoon, L. Schultz, and P. C. West. 2012. Toward Principles for Enhancing the Resilience of Ecosystem Services. Pages 421-+ *in* A. Gadgil and D. M. Liverman, editors. Annual Review of Environment and Resources, Vol 37.

Bonebrake, T. C., J. Christensen, C. L. Boggs, and P. R. Ehrlich. 2010. Population decline assessment, historical baselines, and conservation. Conservation Letters **3**:371-378.

Braje, T. J., J. M. Erlandson, T. C. Rick, P. K. Dayton, and M. B. A. Hatch. 2009. Fishing from past to present: continuity and resilience of red abalone fisheries on the Channel Islands, California. Ecological Applications **19**:906-919.

Brondizio, E. S., and F. M. Le Tourneau. 2016. Environmental governance for all. Science **352**:1272-1273.

Burt, J.M., T. M. Tinker, D. K. Okamoto, K. W. Demes, K. Holmes, Salomon, A.K. (*In review*) Sudden depletion of a mesopredator reveals its complementary role in mediating rocky reef regime shifts.

Carlsson, L., and F. Berkes. 2005. Co-management: concepts and methodological implications. Journal of Environmental Management **75**:65-76.

Cavole, L. M., A. M. Demko, R. E. Diner, A. Giddings, I. Koester, C. Pagniello, M. L. Paulsen, A. Ramirez-Valdez, S. M. Schwenck, N. K. Yen, M. E. Zill, and P. J. S. Franks. 2016. Biological impacts of the 2013-2015 warm-water anomaly in the Northeast Pacific. Oceanography **29**:273-285.

Chadès, I., J. M. R. Curtis, and T. G. Martin. 2012. Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone. Conservation Biology **26**:1016-1025.

Costanza, R., S. van der Leeuw, K. Hibbard, S. Aulenbach, S. Brewer, M. Burek, S. Cornell, C. Crumley, J. Dearing, C. Folke, L. Graumlich, M. Hegmon, S. Heckbert, S. T. Jackson, I. Kubiszewski, V. Scarborough, P. Sinclair, S. Sorlin, and W. Steffen. 2012. Developing an Integrated History and future of People on Earth (IHOPE). Current Opinion in Environmental Sustainability **4**:106-114.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts and reduced expectations in kelp forest communities. Ecological Applications **8**:309-322.

Early-Capistran, M. M., A. Saenz-Arroyo, J. G. Cardoso-Mohedano, G. Garibay-Melo, S. H. Peckham, and V. Koch. 2018. Reconstructing 290 years of a data-poor fishery through ethnographic and archival research: The East Pacific green turtle (Chelonia mydas) in Baja California, Mexico. Fish and Fisheries **19**:57-77.

Estes, J. A., D. R. Lindberg, and C. Wray. 2005. Evolution of large body size in abalones (*Haliotis*): patterns and implications. Paleobiology **31**:591-606.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. Science **185**:1058-1060.

Fernández ‐ Llamazares, Á., and M. Cabeza. 2018. Rediscovering the potential of indigenous storytelling for conservation practice. Conservation Letters **11**:e12398.

Ferretti, F., D. Curnick, K. L. Liu, E. V. Romanov, and B. A. Block. 2018. Shark baselines and the conservation role of remote coral reef ecosystems. Science Advances **4**.

Gauvreau, A. M., D. Lepofsky, M. Rutherford, and M. Reid. 2017. "Everything revolves around the herring": the Heiltsuk-herring relationship through time. Ecology and Society **22**.

Gavin, M. C., J. McCarter, A. Mead, F. Berkes, J. R. Stepp, D. Peterson, and R. F. Tang. 2015. Defining biocultural approaches to conservation. Trends Ecol Evol **30**:140-145.

Hicks, C. C., L. B. Crowder, N. A. J. Graham, J. N. Kittinger, and E. Le Cornu. 2016. Social drivers forewarn of marine regime shifts. Frontiers in Ecology and the Environment **14**:253-261.

Huntington, H. P. 2010. The local perspective. Nature **478**:182-183.

Jackson, C. A., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**:629-637.

Jones, R., C. Rigg, and L. Lee. 2010. Haida Marine Planning: First Nations as a Partner in Marine Conservation. Ecology and Society **15**.

Jones, R., C. Rigg, and E. Pinkerton. 2017. Strategies for assertion of conservation and local management rights: A Haida Gwaii herring story. Marine Policy **80**:154-167.

Larson, B. R., R. L. Vadas, and M. Keser. 1980. Feeding and nutritional ecology of the sea urchin *Strongylocentrotus drobachiensis* in Maine, USA. Marine Biology **59**:49-62.

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

Lepofsky, D., C. G. Armstrong, S. Greening, J. Jackley, J. Carpenter, B. Guernsey, D. Mathews, and N. J. Turner. 2017. Historical ecology of cultural keystone places of the Northwest Coast. American Anthropologist **119**:448-463.

Mangel, M., and P. S. Levin. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. Philosophical Transactions of the Royal Society B-Biological Sciences **360**:95-105.

Markel, R. W., and J. B. Shurin. 2015. Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests. Ecology **96**:2877-2890.

Mathews, D. L., and N. J. Turner. 2017. Ocean Cultures: Northwest Coast ecosystems and indigenous management systems. Pages 169-206 *in* P. S. Levin and M. R. Poe, editors. Conservation for the Anthropocene Ocean: Interdisciplinary Science in Support of Nature and People. Academic Press, USA.

McCay, B. J., and S. Jentoft. 1996. From the bottom up: Participatory issues in fisheries management. Society & Natural Resources **9**:237-250.

Micheli, F., A. Saenz-Arroyo, A. Greenley, L. Vazquez, J. A. Espinoza Montes, M. Rossetto, and G. A. De Leo. 2012. Evidence that marine reserves enhance resilience to climatic impacts. Plos One **7**.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol Evol **10**:430.

Pinkerton, E. 2017. Hegemony and resistance: Disturbing patterns and hopeful signs in the impact of neoliberal policies on small-scale fisheries around the world. Marine Policy **80**:1-9.

Pinkerton, E., E. Angel, N. Ladell, P. Williams, M. Nicolson, J. Thorkelson, and H. Clifton. 2014. Local and regional strategies for rebuilding fisheries management institutions in coastal British Columbia: what components of comanagement are most critical? Ecology and Society **19**.

Pinkerton, E., and R. Davis. 2015. Neoliberalism and the politics of enclosure in North American small-scale fisheries. Marine Policy **61**:303-312.

Pinkerton, E. ed. 1989. Co-operative management of local fisheries: New directions for improved management and community development. University of British Columbia Press, Vancouver, Canada.

Pinkerton, E. W. 1994. Local fisheries comanagement - a review of international experiences and their implications for salmon management in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **51**:2363-2378.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology **86**:501-509.

Raimondi, P., L. J. Jurgens, and M. T. Tinker. 2015. Evaluating potential conservation conflicts between two listed species: sea otters and black abalone. Ecology **96**:3102-3108.

Saenz-Arroyo, A., and D. Revollo-Fernandez. 2016. Local ecological knowledge concurs with fishing statistics: An example from the abalone fishery in Baja California, Mexico. Marine Policy **71**:217-221.

Saenz-Arroyo, A., and C. M. Roberts. 2008. Consilience in fisheries science. Fish and Fisheries **9**:316-327.

Saenz-Arroyo, A., C. M. Roberts, J. Torre, and M. Carino-Olvera. 2005a. Using fishers' anecdotes, naturalists' observations and grey literature to reassess marine species at risk: the case of the Gulf grouper in the Gulf of California, Mexico. Fish and Fisheries **6**:121-133.

Saenz-Arroyo, A., C. M. Roberts, J. Torre, M. Carino-Olvera, and R. R. Enriquez-Andrade. 2005b. Rapidly shifting environmental baselines among fishers of the Gulf of California. Proceedings of the Royal Society B-Biological Sciences **272**:1957-1962.

Saenz-Arroyo, A., C. M. Roberts, J. Torre, M. Carino-Olvera, and J. P. Hawkins. 2006. The value of evidence about past abundance: marine fauna of the Gulf of California through the eyes of 16th to 19th century travellers. Fish and Fisheries **7**:128-146.

Sala, E., O. Aburto-Oropeza, M. Reza, G. Paredes, and L. G. Lopez-Lemus. 2004. Fishing down coastal food webs in the Gulf of California. Fisheries **29**:19-25.

Salomon, A. K., K. Lertzman, K. Brown, K. B. Wilson, D. Secord, and I. McKechnie. 2018. Democratizing conservation science and practice. Ecology and Society **23**.

Schultz, J. A., R. N. Cloutier, and I. M. Coté. 2016. Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. Peerj **4**.

Silliman, B. R., B. B. Hughes, L. C. Gaskins, Q. He, M. T. Tinker, A. Read, J. Nifong, and R. Stepp. 2018. Are the ghosts of nature's past haunting ecology today? Current Biology **28**:R532-R537.

Soga, M., and K. J. Gaston. 2018. Shifting baseline syndrome: Causes, consequences, and implications. Frontiers in Ecology and the Environment **16**:222-230.

Soulé, M., J. A. Estes, J. Berger, and C. Martinez Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology **17**:1238-1250.

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

Stephenson, J., F. Berkes, N. J. Turner, and J. Dick. 2014. Biocultural conservation of marine ecosystems: Examples from New Zealand and Canada. Indian Journal of Traditional Knowledge **13**:257-265.

Stevenson, C. F., K. W. Demes, and A. K. Salomon. 2016. Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. Ecology and Evolution **6**:1041-1053.

Tengo, M., E. S. Brondizio, T. Elmqvist, P. Malmer, and M. Spierenburg. 2014. Connecting diverse knowledge systems for enhanced ecosystem governance: The multiple evidence base approach. Ambio **43**:579-591.

The World Bank. 1999. Report from the International Workshop on Community-Based Natural Resource Management (CBNRM), 10-14 May 1998. Washington, DC, USA.

Thurstan, R. H., L. McClenachan, L. B. Crowder, J. A. Drew, J. N. Kittinger, P. S. Levin, C. M. Roberts, and J. M. Pandolfi. 2015. Filling historical data gaps to foster solutions in marine conservation. Ocean & Coastal Management **115**:31-40.

Turner, N., and P. R. Spalding. 2013. "We Might Go Back to This"; Drawing on the past to meet the future in Northwestern North American Indigenous communities. Ecology and Society **18**.

Turner, N. J., F. Berkes, J. Stephenson, and J. Dick. 2013. Blundering Intruders: Extraneous Impacts on Two Indigenous Food Systems. Human Ecology **41**:563-574.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Mellilo. 1997. Human domination of the earth's ecosystems. Science **277**:494-499.

Waters, C. N., J. Zalasiewicz, C. Summerhayes, A. D. Barnosky, C. Poirier, A. Galuszka, A. Cearreta, M. Edgeworth, E. C. Ellis, M. Ellis, C. Jeandel, R. Leinfelder, J. R. McNeill, D. D. Richter, W. Steffen, J. Syvitski, D. Vidas, M. Wagreich, M. Williams, Z. S. An, J. Grinevald, E. Odada, N. Oreskes, and A. P. Wolfe. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. Science **351**:137-+.

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

Appendix A.

Length-mass relationships, substrate complexity scoring, and list of kelp species included in field survey data analyses

Table A1. Length–mass relationships for converting individual lengths to biomass for northern abalone, sea urchin species, and sunflower stars.

Species	Length-mass relationship	Reference
Northern abalone	0.0000578*(length.mm^3.2)	Zhang et al. 2007
Red urchin	0.0009689*(length.mm^2.7913)	Fisheries and Oceans Canada database 2015*
Purple urchin	0.00051*(length.mm^2.9035)	Oftedal et al. 2007
Green urchin	0.6137*(length.cm^2.5624)	R. Martone, *unpublished data*
Sunflower star	exp(-3.9989)*(length.cm^3.133)	A. Salomon, *unpublished data*

* Relationship established using approximately 10,000 red urchins measured from Tofino, Price Island, and Haida Gwaii, BC.

References

Oftedal, O. T., K. Ralls, M. T. Tinker, and A. Green. 2007. Nutritional constraints on the southern sea otter in the Monterey Bay National Marine Sanctuary and a comparison to sea otter populations at San Nicolas Island, California and Glacier Bay, Alaska. Monterey Bay National Marine Sanctuary and Marine Mammal Commission, Monteray, CA.

Zhang, Z., A. Campbell, and J. Lessard. 2007. Modeling northern abalone, *Haliotis kamtschatkana*, population stock and recruitment in British Columbia. Journal of Shellfish Research **26**:1099-1107.

Table A2. Kelp species surveyed in quadrats.

Species
Agarum sp.
Alaria marginata
Costaria costata
Cymathaere triplicata
Desmarestia sp.
Dictyoneurum californicum
Ecklonia arborea
Egregia menziesii
Laminaria ephemera
Laminaria setchellii
Laminaria yezoensis
Laminarian sp.
Lessionopsis littoralis
Macrocystis pyrifera
Nereocystis leutkeana
Pleurophycus gardneri
Pterygophora californica
Saccharina groenlandica
Saccharina sessilis

Table A3. Criteria defining a substrate complexity score for each substrate type. Substrate complexity is the sum of scores for three criteria: stability, cryptic habitat presence, and cryptic habitat amount. Specific bedrock and boulder types were occasionally not specified in the field data, requiring a proxy score.

Substrate type	Code	Stability (0-3)	Cryptic habitat presence (0/1)	Cryptic habitat amount (0-3)	Complexity score
Creviced bedrock	BRc	3	1	3	7
Lumpy bedrock	BRl	3	1	2	6
Bedrock	BR	3	1	2	6
Smooth bedrock	BRs	3	0	0	3
Large boulder	LB	3	1	3	7
Medium boulder	MB	2	1	3	6
Boulder	BO	2	1	3	6
Small boulder	SB	1	1	2	4
Cobble	CO	1	0	1	2
Gravel	GR	0	0	0	0
Pea gravel	PG	0	0	0	0
Sand	SD	0	0	0	0
Shell	SH	0	0	0	0
Mud	MD	0	0	0	0

Appendix B.

Saturated models for field and lab experimental analyses

Table B1. Saturated models for density, presence, biomass and length, of total, exposed, covered, and cryptic abalone from field surveys. The notation (1|Site) indicates that the intercept varies randomly with site.

Abalone response	Model specifications	Data set	Family (link)
Density (Total, Exposed, Covered)	Abalone count per transect ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	All transects	Negative binomial, zero inflation (exponential)
Density (Cryptic)	Abalone count per transect ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	All transects	Negative binomial (exponential)
Presence (Total, Exposed, Covered, Cryptic)	Abalone presence (1) or absence (0) ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	All transects	Binomial (logit)
Biomass (Total, Exposed, Covered, Cryptic)	Abalone biomass per transect (100g) ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	Transects with abalone	Gamma (exponential)
Length (Total)	Centered length of abalone (mm) ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	Sites with abalone	Gaussian (identity)
Length (Exposed)	Centered length of exposed abalone (mm) ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	Sites with exposed abalone	Gaussian (identity)
Length (Covered)	Centered length of covered abalone (mm) ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	Sites with covered abalone	Gaussian (identity)
Length (Cryptic)	Centered length of cryptic abalone (mm) ~ Region - 1 + Exposure + Substrate + Sunflower star biomass + Urchin biomass + Kelp stipe density + Depth x Otter occupation time + (1|Site)	Sites with cryptic abalone	Gaussian (identity)

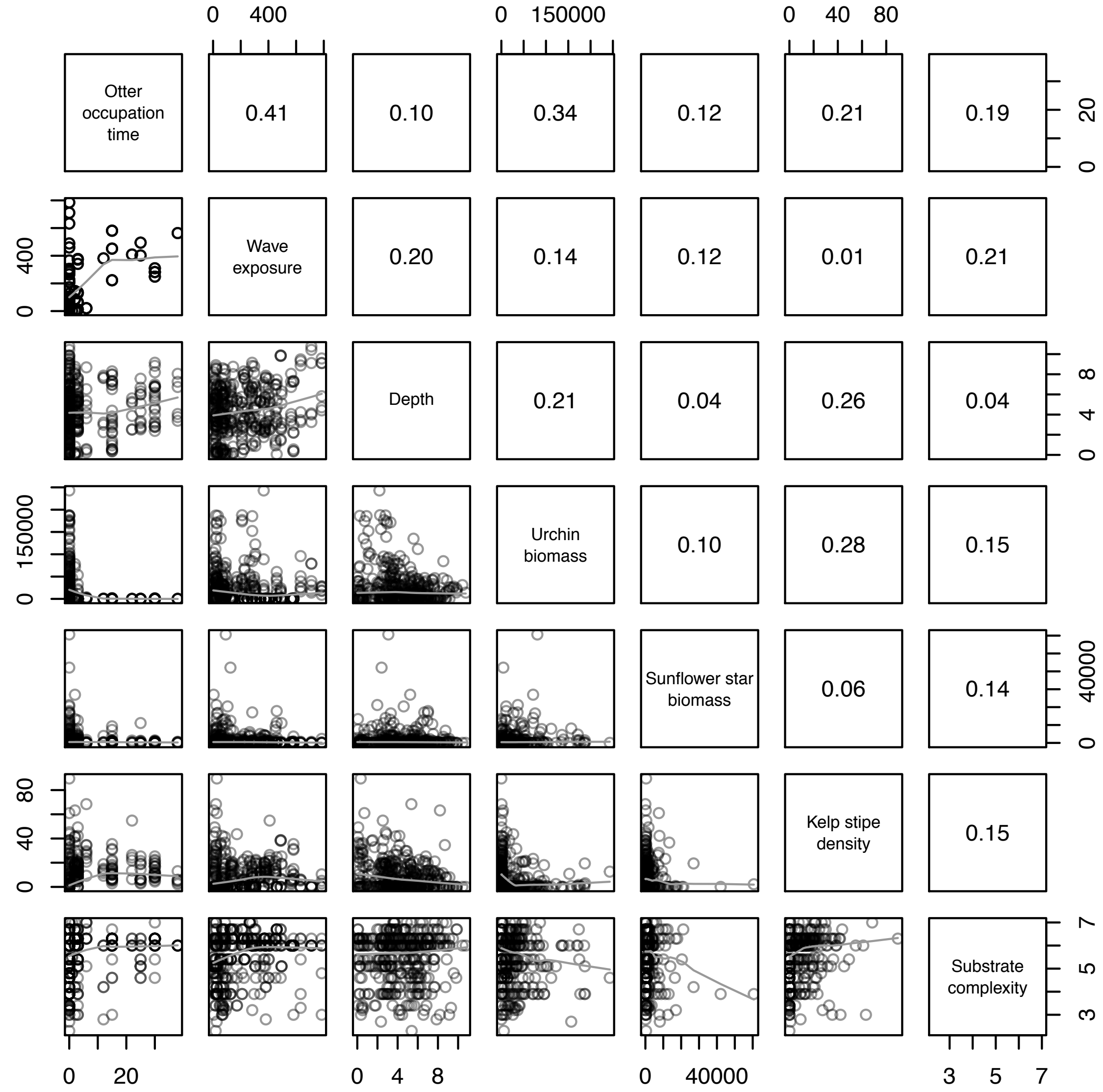

Fig. B1. **Correlation coefficients between biotic and abiotic factors included in models.**

Table B2. **Saturated models for kelp stipe density, and sunflower star presence and biomass from field surveys. The notation (1|Site) indicates that the intercept varies randomly with site.**

Response	Model Specifications	Data set	Family (link)
Kelp stipe density	Kelp stipe count per transect ~ Wave exposure + Urchin biomass + Substrate complexity + Depth x Otter occupation time + (1|Site)	All transects	Negative binomial (exponential)
Sunflower star presence	Sunflower star presence (1) or absence (0) ~ Wave exposure + Urchin biomass + Substrate complexity + Depth x Otter occupation time + (1|Site)	All transects	Binomial (logit)
Sunflower star biomass	Sunflower star biomass (kg) per transect ~ Wave exposure + Urchin biomass + Substrate complexity + Depth x Otter occupation time + (1|Site)	Transects with sunflower stars	Gamma (exponential)
Urchin presence	Urchin presence (1) or absence (0) ~ Wave exposure + Kelp stipe density + Substrate complexity + Sunflower star biomass + Substrate complexity + Depth x Otter occupation time + (1|Site)	All transects	Binomial (logit)
Urchin biomass	Sunflower star biomass (kg) per transect ~ Wave exposure + Kelp stipe density + Substrate complexity + Sunflower star biomass + Substrate complexity + Depth x Otter occupation time + (1|Site)	Transects with urchins	Gamma (exponential)

Table B3. **Saturated models for sunflower star predation on abalone in lab experiments. The notation (1|Trial) indicates that the intercept varies randomly with trial.**

Response	Model Specifications	Family (link)
Capture efficiency, alpha	alpha ~ Treatment	Gaussian (identity)
Handling time, h	h ~ Treatment	Gaussian (identity)
Feeding rate	Feeding rate ~ Treatment	Gaussian (identity)
Sunflower star attack success	Attack success (1) or failure (0) ~ Treatment + Trial time + (1|Trial)	Binomial (logit)
Abalone survival	Abalone eaten (1) or not (0) ~ Treatment + (1|Trial)	Binomial (logit)

Appendix C.

Field survey data: Region, site- and transect-level bivariate relationships between abalone density and biomass, and biotic and abiotic environmental factor

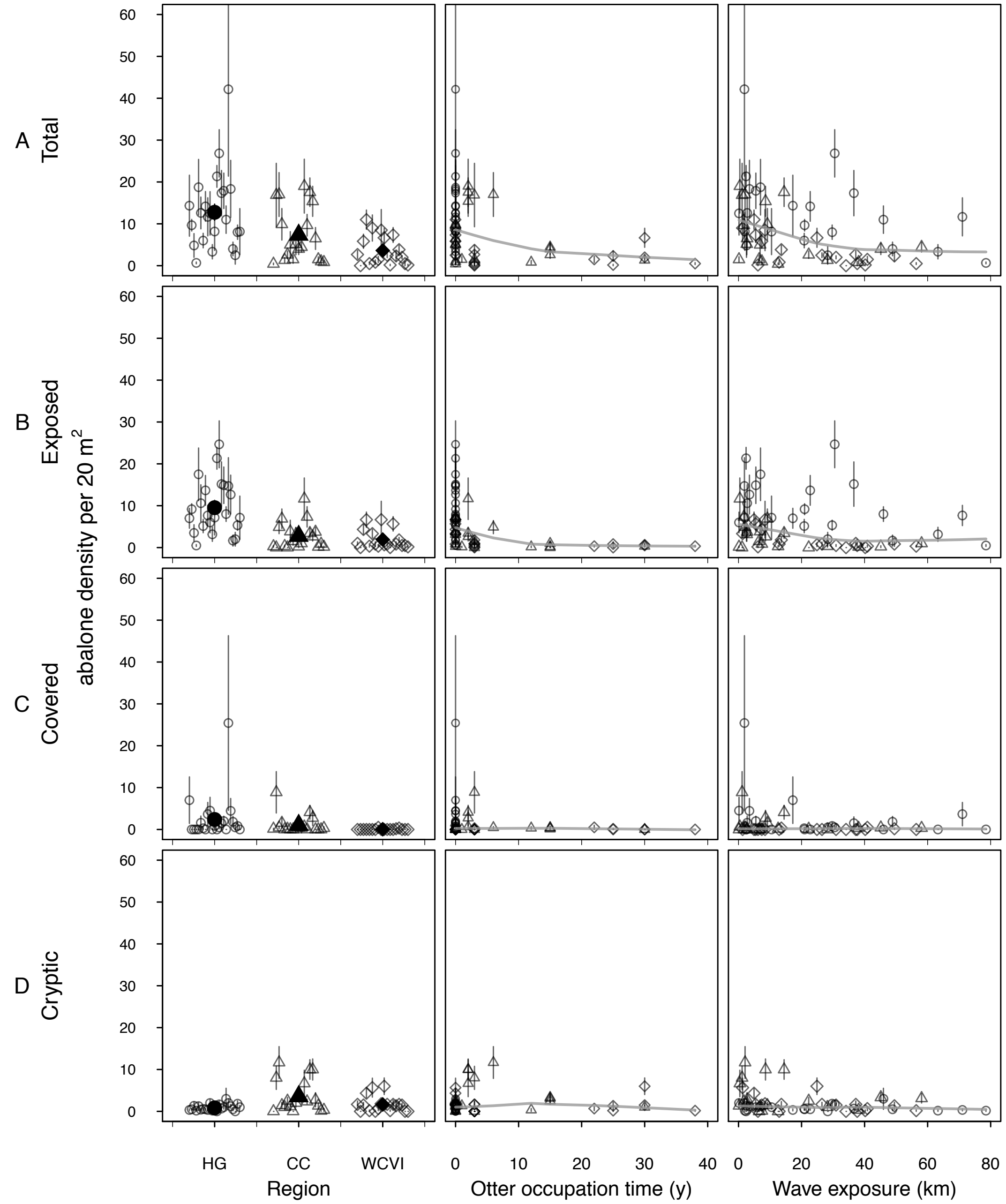

Fig C1. **Bivariate relationships between density of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone and region and site-level environmental factors of sea otter occupation time and wave exposure. Open symbols are site means ± SE. Closed symbols (region panel) are the mean of site means. Symbols represent regions: Haida Gwaii (HG; open circles), Central Coast (CC; open triangles) and West Coast Vancouver Island (WCVI; open diamonds). Lines are LOWESS smoothers (sea otter and wave exposure panels).**

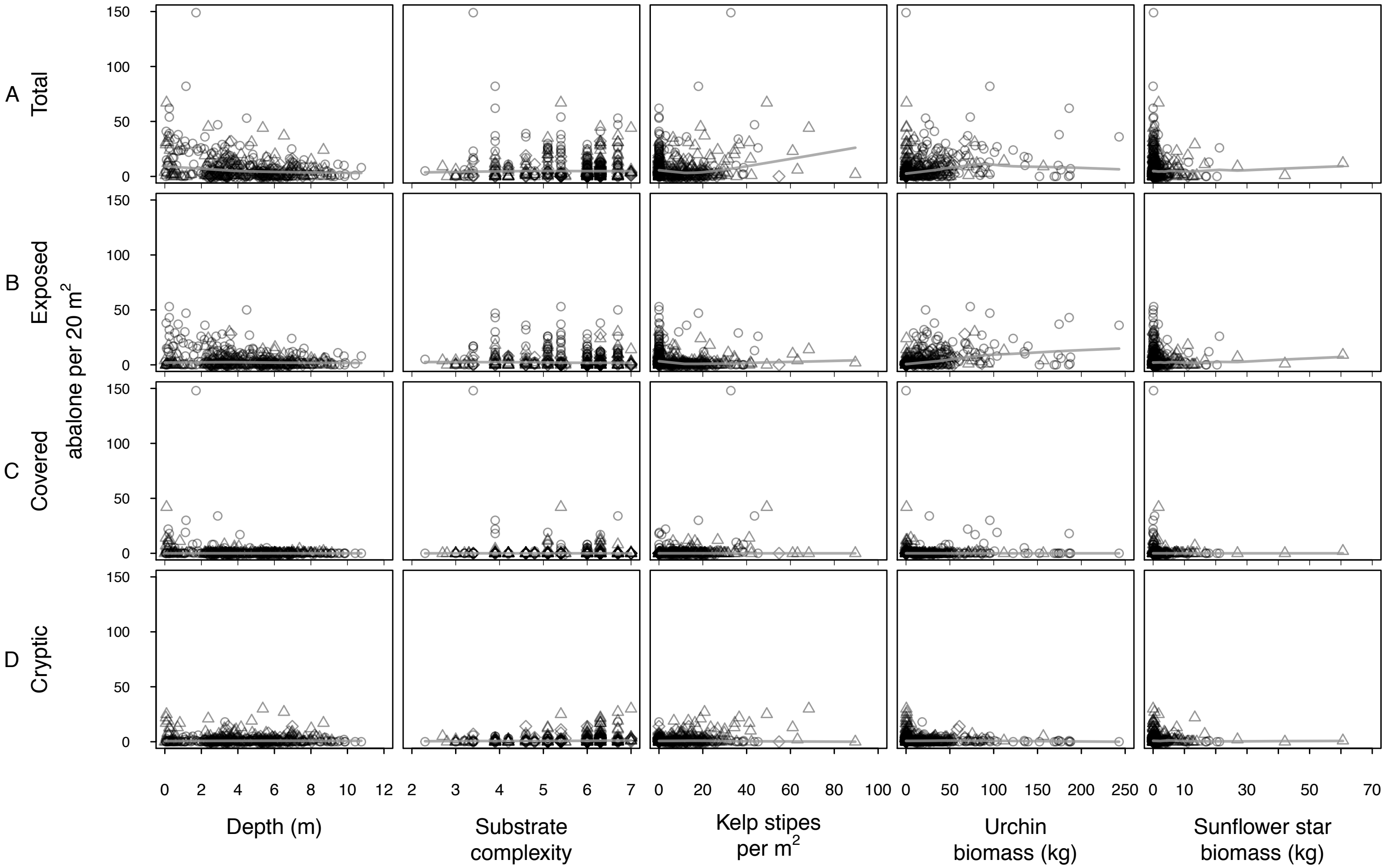

Fig. C2. **Bivariate relationships between density of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone and transect-level environmental factors of depth, substrate complexity, kelp stipe density, urchin biomass, and sunflower star biomass. Open symbols represent transects. Symbols represent regions as in Fig. C1. Lines are LOWESS smoothers.**

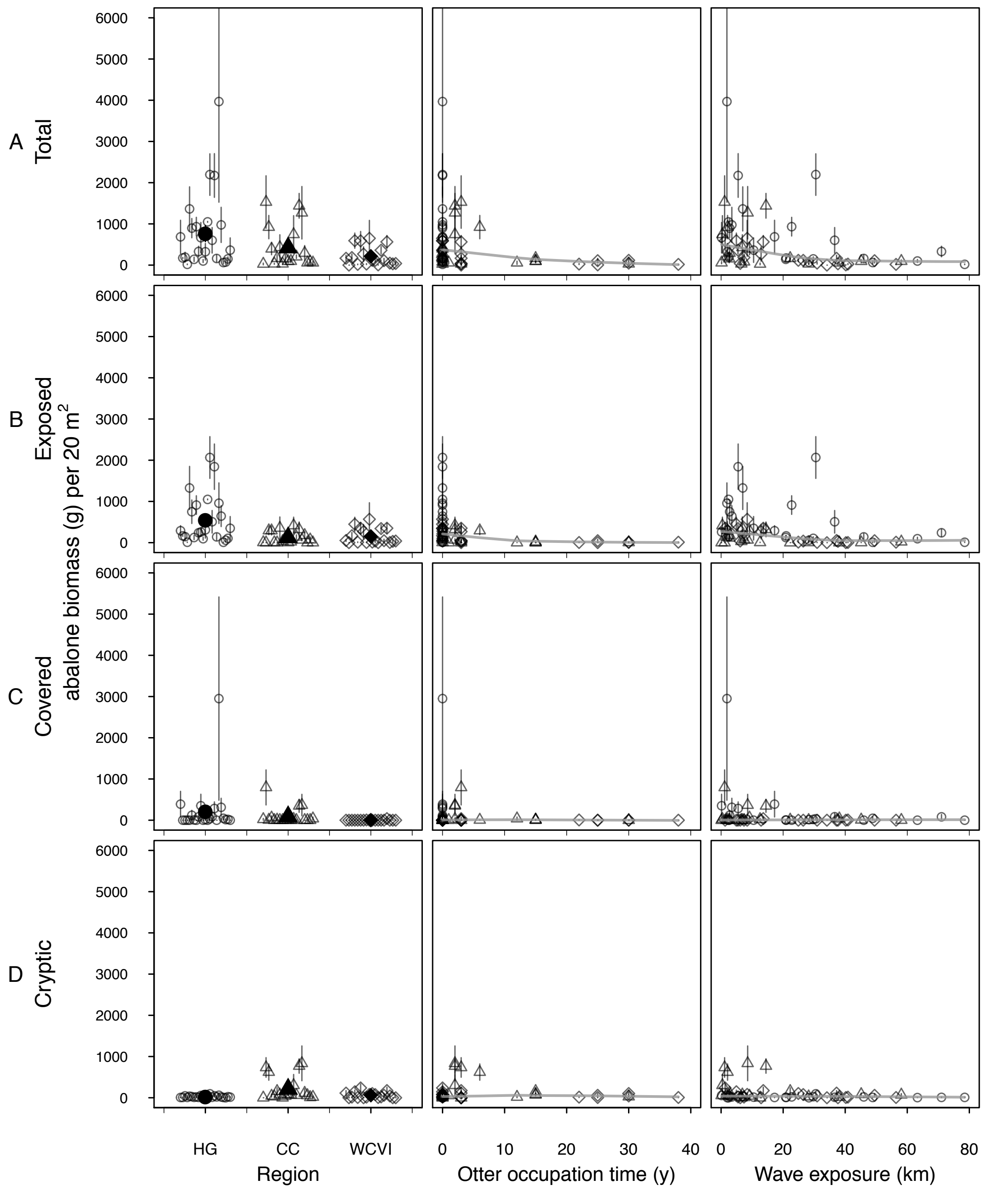

Fig. C3. Bivariate relationships between biomass of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone and region and site-level environmental factors of sea otter occupation time and wave exposure. Symbols and lines are as in Fig. C1.

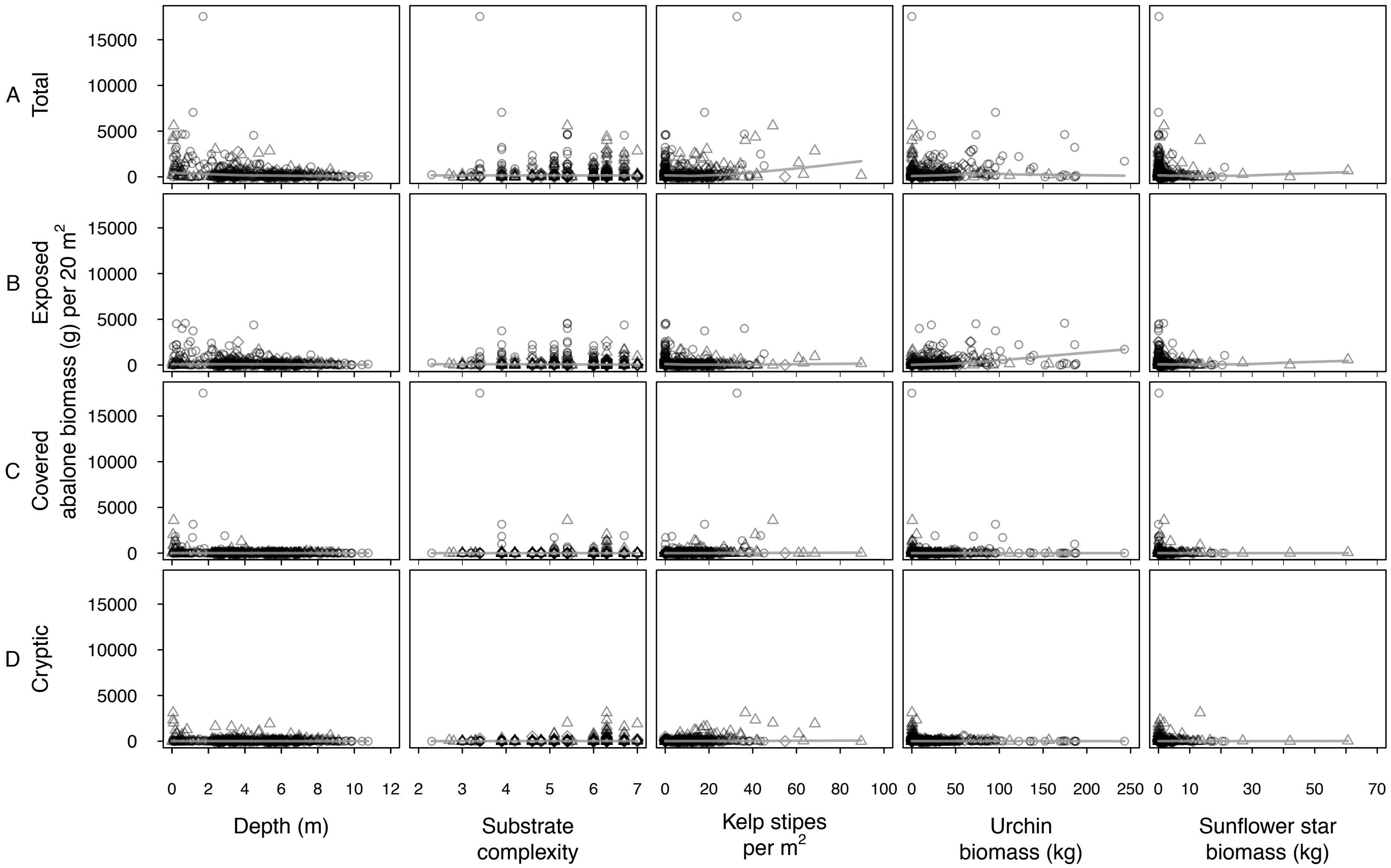

Fig. C4. **Bivariate relationships between biomass of (A) total, (B) exposed, (C) covered, and (D) cryptic, abalone and transect-level environmental factors of depth, substrate complexity, kelp stipe density, urchin biomass, and sunflower star biomass. Symbols and lines are as in Fig. C2.**

Appendix D.

Field survey analyses: Strength of evidence for alternative candidate models of abalone density, presence, length and biomass

Table D1. **Strength of evidence for alternative candidate models in the set $\Delta AIC_c < 2$ of the effects of biotic and abiotic factors on density of total, exposed, covered, and cryptic abalone. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i.**

Response	Model	df	logLik	AIC$_c$	ΔAIC$_c$	w$_i$
Total abalone density	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	13	-1131.29	2289.53	0.00	0.71
	Region + Depth + Wave exposure + Kelp stipe density + Sunflower star biomass + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	14	-1131.13	2291.36	1.83	0.29
Exposed abalone density	Region + Depth + Wave exposure + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	12	-891.51	1807.83	0.00	0.37
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	13	-890.82	1808.59	0.77	0.25
	Region + Depth + Wave exposure + Otter occupation time + Urchin biomass + Depth x Otter occupation time	11	-893.18	1809.05	1.22	0.20
	Region + Depth + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	11	-893.28	1809.25	1.42	0.18
Covered abalone density	Region + Depth + Kelp stipe density + Otter occupation time + Depth x Otter occupation time	10	-288.63	597.82	0.00	0.37
	Region + Depth + Kelp stipe density + Otter occupation time + Substrate complexity + Depth x Otter occupation time	11	-288.26	599.22	1.39	0.18
	Region + Depth + Kelp stipe density	8	-291.60	599.58	1.76	0.15
	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Depth x Otter occupation time	11	-288.46	599.60	1.78	0.15
	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	11	-288.53	599.74	1.92	0.14
Cryptic abalone density	Region + Depth + Wave exposure + Otter occupation time + Substrate complexity + Depth x Otter occupation time	10	-674.11	1368.78	0.00	0.26
	Region + Depth + Wave exposure + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	11	-673.71	1370.11	1.33	0.14
	Region + Depth + Wave exposure + Sunflower star biomass + Otter occupation time + Substrate complexity + Depth x Otter occupation time	11	-673.72	1370.12	1.33	0.13
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Depth x Otter occupation time	11	-673.77	1370.24	1.45	0.13
	Region + Depth + Wave exposure + Substrate complexity	8	-676.99	1370.34	1.56	0.12
	Region + Wave exposure + Substrate complexity	7	-678.12	1370.53	1.75	0.11
	Region + Wave exposure + Kelp stipe density + Substrate complexity	8	-677.09	1370.54	1.76	0.11

Table D2. Strength of evidence for alternative candidate models in the set ΔAIC_c <2 of the effects of biotic and abiotic factors on presence of total, exposed, covered, and cryptic abalone. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i.

Response	Model	df	logLik	AIC_c	ΔAIC_c	w_i
Total abalone presence	Region + Wave exposure + Substrate complexity	6	-170.76	353.73	0.00	0.30
	Region + Wave exposure	5	-172.07	354.30	0.57	0.22
	Region + Wave exposure + Substrate complexity + Urchin biomass	7	-170.59	355.46	1.73	0.13
	Region + Wave exposure + Sunflower star biomass + Substrate complexity	7	-170.62	355.52	1.79	0.12
	Region + Depth + Wave exposure + Substrate complexity	7	-170.62	355.53	1.80	0.12
	Region + Wave exposure + Kelp stipe density + Substrate complexity	7	-170.70	355.69	1.96	0.11
Exposed abalone presence	Region + Depth + Wave exposure + Urchin biomass	7	-205.94	426.17	0.00	0.24
	Region + Depth + Wave exposure + Otter occupation time + Urchin biomass	8	-205.18	426.73	0.56	0.18
	Region + Depth + Wave exposure + Otter occupation time + Urchin biomass + Depth x Otter occupation time	9	-204.35	427.16	0.99	0.15
	Region + Depth + Wave exposure + Kelp stipe density + Urchin biomass	8	-205.53	427.43	1.26	0.13
	Region + Depth + Wave exposure + Sunflower star biomass + Urchin biomass	8	-205.67	427.72	1.55	0.11
	Region + Depth + Wave exposure + Substrate complexity + Urchin biomass	8	-205.81	428.00	1.83	0.10
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Urchin biomass	9	-204.81	428.09	1.92	0.09
Covered abalone presence	Region + Depth + Kelp stipe density + Otter occupation time + Depth x Otter occupation time	8	-126.56	269.50	0.00	0.16
	Region + Depth + Kelp stipe density	6	-128.71	269.63	0.14	0.15
	Region + Depth + Kelp stipe density + Otter occupation time + Substrate complexity + Depth x Otter occupation time	9	-125.70	269.87	0.37	0.13
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Depth x Otter occupation time	9	-125.70	269.88	0.38	0.13
	Region + Depth + Kelp stipe density + Substrate complexity	7	-127.84	269.96	0.46	0.13
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Depth x Otter occupation time	10	-125.08	270.72	1.23	0.09
	Region + Depth + Wave exposure + Kelp stipe density	7	-128.34	270.98	1.48	0.08
	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	9	-126.41	271.29	1.79	0.07
	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Depth x Otter occupation time	9	-126.44	271.34	1.84	0.06
Cryptic abalone presence	Wave exposure + Otter occupation time	4	-251.10	510.30	0.00	0.21
	Wave exposure + Otter occupation time + Substrate complexity	5	-250.28	510.72	0.42	0.17
	Wave exposure + Substrate complexity	4	-251.35	510.79	0.49	0.17
	Region + Wave exposure	5	-250.79	511.74	1.44	0.10
	Depth + Wave exposure + Otter occupation time	5	-250.92	511.99	1.69	0.09
	Region + Wave exposure + Substrate complexity	6	-249.92	512.05	1.75	0.09
	Wave exposure + Sunflower star biomass + Otter occupation time	5	-251.00	512.15	1.85	0.08
	Wave exposure + Otter occupation time + Urchin biomass	5	-251.02	512.19	1.89	0.08

Table D3. **Strength of evidence for alternative candidate models in the set ΔAIC_c <2 of the effects of biotic and abiotic factors on length of total, exposed, covered, and cryptic abalone. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i.**

Response	Model	df	logLik	AIC_c	ΔAIC_c	w_i
Total abalone length	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	10	-13708.20	27436.47	0.00	0.36
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	11	-13707.62	27437.31	0.84	0.24
	Region + Depth + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	11	-13708.16	27438.40	1.93	0.14
	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Urchin biomass + Depth x Otter occupation time	11	-13708.18	27438.45	1.98	0.13
	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass	9	-13710.20	27438.46	1.99	0.13
Exposed abalone length	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass	9	-8093.65	16205.39	0.00	0.19
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Urchin biomass	10	-8092.72	16205.56	0.17	0.18
	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	10	-8092.76	16205.64	0.25	0.17
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	11	-8092.03	16206.20	0.81	0.13
	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Urchin biomass	10	-8093.37	16206.87	1.48	0.09
	Region + Depth + Wave exposure + Kelp stipe density + Sunflower star biomass + Otter occupation time + Urchin biomass	11	-8092.42	16206.99	1.60	0.09
	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Urchin biomass + Depth x Otter occupation time	11	-8092.50	16207.14	1.75	0.08
	Region + Depth + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass	10	-8093.57	16207.27	1.88	0.08
Covered abalone length	Region + Depth + Kelp stipe density + Otter occupation time	7	-2223.26	4460.74	0.00	0.36
	Region + Depth + Otter occupation time	6	-2224.60	4461.36	0.61	0.27
	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass	8	-2222.78	4461.85	1.10	0.21
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time	8	-2223.06	4462.40	1.66	0.16
Cryptic abalone length	Region + Depth + Wave exposure + Sunflower star biomass	8	-3299.80	6615.80	0.00	0.30
	Region + Depth + Wave exposure + Sunflower star biomass + Otter occupation time	9	-3299.17	6616.58	0.79	0.20
	Depth + Wave exposure + Sunflower star biomass	6	-3302.36	6616.84	1.04	0.18
	Region + Depth + Wave exposure + Kelp stipe density + Sunflower star biomass	9	-3299.33	6616.89	1.10	0.17
	Region + Depth + Wave exposure + Kelp stipe density + Sunflower star biomass + Substrate complexity	10	-3298.44	6617.18	1.39	0.15

Table D4. **Strength of evidence for alternative candidate models in the set $\Delta \mathrm{AIC}_c$ <2 of the effects of biotic and abiotic factors on biomass of total, exposed, covered, and cryptic abalone. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i.**

Response	Model	df	logLik	AIC_c	$\Delta \mathrm{AIC}_c$	w_i
Total abalone biomass	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	12	-724.08	1473.20	0.00	0.57
	Region + Depth + Wave exposure + Kelp stipe density + Sunflower star biomass + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	13	-723.96	1475.14	1.94	0.22
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Depth x Otter occupation time	11	-726.15	1475.19	1.99	0.21
Exposed abalone biomass	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	11	-504.99	1033.10	0.00	0.24
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Depth x Otter occupation time	10	-506.15	1033.23	0.13	0.23
	Region + Depth + Kelp stipe density + Otter occupation time + Urchin biomass + Depth x Otter occupation time	10	-506.54	1034.02	0.92	0.15
	Region + Depth + Kelp stipe density + Otter occupation time + Depth x Otter occupation time	9	-507.65	1034.06	0.96	0.15
	Region + Depth + Wave exposure + Kelp stipe density + Otter occupation time + Substrate complexity + Depth x Otter occupation time	11	-505.60	1034.32	1.22	0.13
	Region + Depth + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	11	-505.88	1034.89	1.79	0.10
Covered abalone biomass	Depth + Kelp stipe density + Otter occupation time + Depth x Otter occupation time	7	-125.70	267.79	0.00	0.52
	Depth + Wave exposure + Kelp stipe density + Otter occupation time + Depth x Otter occupation time	8	-124.99	269.12	1.33	0.27
	Depth + Kelp stipe density + Otter occupation time + Substrate complexity	7	-126.64	269.66	1.88	0.21
Cryptic abalone biomass	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Substrate complexity + Depth x Otter occupation time	11	-236.01	495.41	0.00	0.41
	Region + Depth + Kelp stipe density + Sunflower star biomass + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	12	-235.51	496.68	1.27	0.22
	Region + Depth + Kelp stipe density + Otter occupation time + Substrate complexity + Depth x Otter occupation time	10	-237.80	496.75	1.34	0.21
	Region + Depth + Kelp stipe density + Otter occupation time + Substrate complexity + Urchin biomass + Depth x Otter occupation time	11	-236.93	497.26	1.85	0.16

Appendix E.

Field survey analyses: Strength of evidence for alternative candidate models of sunflower star presence and biomass, urchin presence and biomass, and kelp stipe density

Table E1. **Strength of evidence for alternative candidate models in the set ΔAIC_c <2 of the effects of biotic and abiotic factors on sunflower star presence and biomass. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i.**

Response	Model	df	logLik	AIC_c	ΔAIC_c	w_i
Sunflower star presence	Intercept only	2	-210.72	425.47	0.00	0.30
	Depth	3	-209.81	425.67	0.20	0.27
	Otter occupation time	3	-210.33	426.73	1.25	0.16
	Depth + Otter occupation time	4	-209.34	426.79	1.31	0.16
	Wave exposure	3	-210.68	427.43	1.95	0.11
Sunflower star biomass	Depth + Otter occupation time + Depth x Otter occupation time	6	-1895.94	3804.10	0.00	0.36
	Depth + Otter occupation time + Urchin biomass + Depth x Otter occupation time	7	-1895.11	3804.51	0.41	0.30
	Depth + Wave exposure + Otter occupation time + Depth x Otter occupation time	7	-1895.54	3805.37	1.27	0.19
	Depth + Wave exposure + Otter occupation time + Urchin biomass + Depth x Otter occupation time	8	-1894.76	3805.89	1.80	0.15

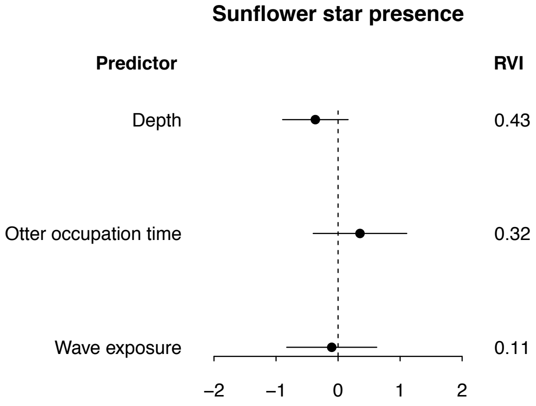

Fig. E1. **Standardized coefficients and 95% confidence intervals for relationships of biotic and abiotic factors with sunflower star presence from averaged models within ΔAIC_c <2.**

Table E2. **Strength of evidence for alternative candidate models in the set ΔAIC_c <2 of the effects of biotic and abiotic factors on urchin presence and biomass. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i.**

Response	Model	df	logLik	AIC_c	ΔAIC_c	w_i
Urchin presence	Depth + Otter occupation time + Depth x Otter occupation time	5	-94.70	199.56	0.00	0.17
	Depth + Otter occupation time	4	-95.81	199.72	0.16	0.16
	Depth + Kelp density + Otter occupation time + Depth x Otter occupation time	6	-93.92	200.05	0.48	0.13
	Depth + Kelp density + Otter occupation time	5	-95.17	200.50	0.93	0.11
	Depth + Wave exposure + Otter occupation time	5	-95.51	201.18	1.62	0.08
	Depth + Sunflower star biomass + Otter occupation time + Depth x Otter occupation time	6	-94.52	201.26	1.70	0.07
	Depth + Kelp density + Otter occupation time + Depth x Otter occupation time	6	-94.53	201.27	1.71	0.07
	Depth + Substrate complexity + Otter occupation time + Depth x Otter occupation time	6	-94.55	201.31	1.75	0.07
	Depth + Sunflower star biomass + Otter occupation time	5	-95.64	201.44	1.87	0.07
	Depth + Substrate complexity + Otter occupation time	5	-95.65	201.46	1.90	0.07
Urchin biomass	Depth + Kelp density + Otter occupation time + Depth x Otter occupation time	7	-1148.81	2311.94	0.00	0.31
	Depth + Kelp density + Sunflower star biomass + Otter occupation time + Depth x Otter occupation time	8	-1147.91	2312.23	0.29	0.27
	Depth + Kelp density + Substrate complexity + Otter occupation time + Depth x Otter occupation time	8	-1148.01	2312.43	0.49	0.24
	Depth + Kelp density + Sunflower star biomass + Substrate complexity + Otter occupation time + Depth x Otter occupation time	9	-1147.26	2313.03	1.10	0.18

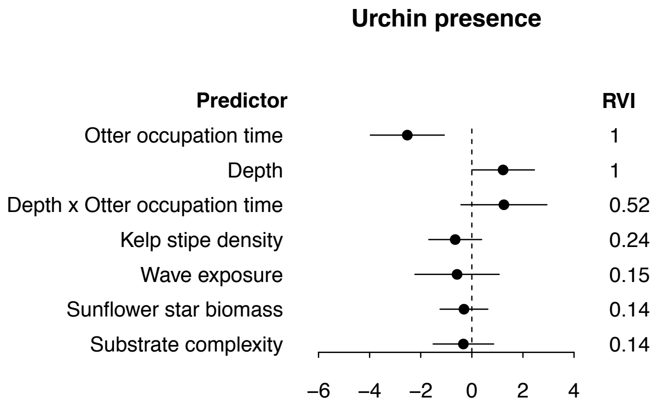
Urchin presence

Fig. E2. **Standardized coefficients and 95% confidence intervals for relationships of biotic and abiotic factors with urchin presence from averaged models within ΔAIC_c <2.**

Table E3. **Strength of evidence for alternative candidate models in the set ΔAIC_c <2 of the effects of biotic and abiotic factors on kelp stipe density. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i.**

Response	Model	df	logLik	AIC_c	ΔAIC_c	w_i
Kelp stipe density	Depth + Otter occupation time + Depth x Otter occupation time	6	-1895.94	3804.10	0.00	0.36
	Depth + Otter occupation time + Urchin biomass + Depth x Otter occupation time	7	-1895.11	3804.51	0.41	0.30
	Depth + Wave exposure + Otter occupation time + Depth x Otter occupation time	7	-1895.54	3805.37	1.27	0.19
	Depth + Wave exposure + Otter occupation time + Urchin biomass + Depth x Otter occupation time	8	-1894.76	3805.89	1.80	0.15

Appendix F.

Interactions between predatory sunflower stars and their prey, abalone and sea urchins, in the Haida Gwaii seascape and in laboratory tanks

Plate F1. **Wide aerial view of sunflower star 'halo effect' on purple and red sea urchins. Photo: Lynn Lee**

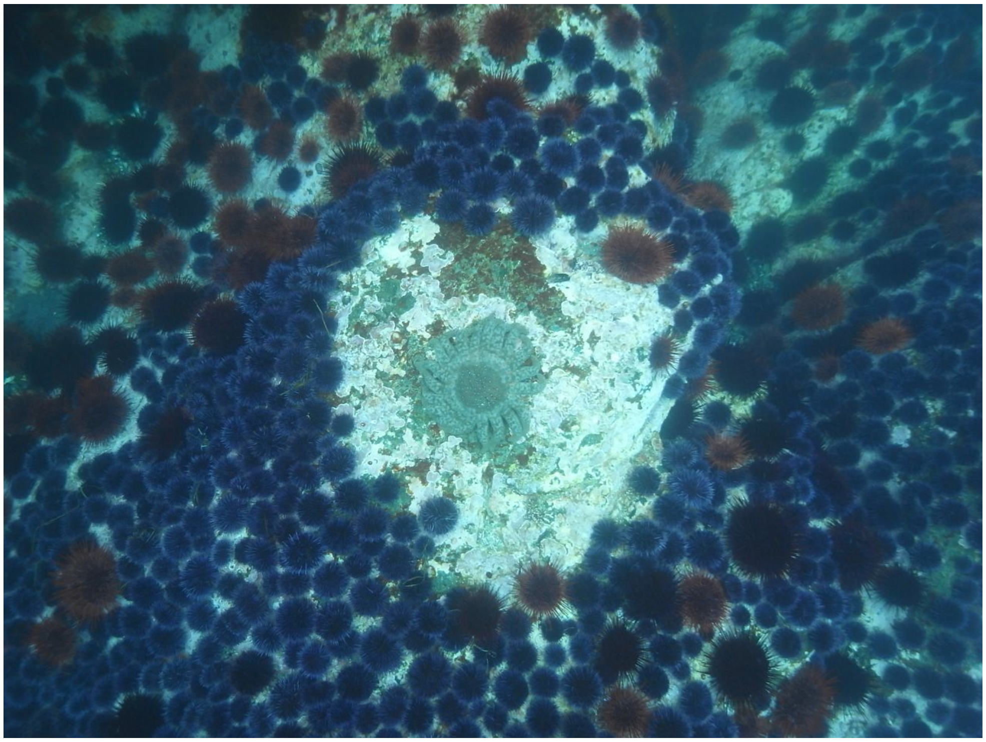

Plate F2. **Close-up aerial view of sunflower star 'halo effect' on purple and red sea urchins. Photo: Lynn Lee**

Video F1. **Predator-prey interactions on a temperate rocky reef in BC**

Creator:

Lynn Lee

Description:

This video shows a sunflower star hunting abalone and red sea urchins in urchin barren habitat on Haida Gwaii, shown at 4x real time.

Filename:

VideoF1_SunflowerStarHuntingAbaloneRedUrchins_Field.mp4

Publication URL:

https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.1604

Video F2. Predator-prey interaction in a laboratory tank

Creator:

Lynn Lee

Description:

This video shows a sunflower star engulfing an abalone captured during a predation experiment trial in a lab tank, shown at 8x real time.

Filename:

VideoF2_SunflowerStarEngulfingAbalone_Lab.mp4

Publication URL:

https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.1604

Appendix G.

Model results for lab experiment investigating the effects of substrate complexity and availability of alternate prey on predation of abalone by sunflower stars

Table G1. **Relative strength of support for models testing: (a) effects of treatment on capture efficiency, handling time, feeding rate and abalone survival, and (b) effects of treatment and trial run time on sunflower star attack success. Models are compared using differences in Akaike's Information Criterion corrected for small sample size (AIC_c), likelihood of the model given the data (loglik ($\mathcal{L}$)), and normalized Akaike's weight (W_i), indicating the weight of evidence in favor of model i. Bold typeface indicates a model that has substantial empirical support relative to alternate candidate models (ΔAIC_c >2 from the next best model).**

Response and Model	n	df	logLik	AIC_c	ΔAIC_c	w_i
Capture efficiency						
Intercept only	**10**	**2**	**51.19**	**-96.67**	**0.00**	**0.91**
Treatment	10	4	54.01	-92.02	4.66	0.09
Handling time						
Intercept only	**9**	**2**	**-34.27**	**74.54**	**0.00**	**0.99**
Treatment	9	4	-33.22	84.44	9.90	0.01
Feeding rate						
Intercept only	**9**	**2**	**0.58**	**4.83**	**0.00**	**0.99**
Treatment	9	4	2.13	13.73	8.90	0.01
Attack success						
Trial time	**28 abalone; 9 trials**	**3**	**-15.15**	**37.30**	**0.00**	**0.85**
Trial time + Treatment	28 abalone; 9 trials	5	-14.38	41.49	4.19	0.10
Intercept only	28 abalone; 9 trials	2	-19.34	43.15	5.85	0.05
Treatment	28 abalone; 9 trials	4	-18.88	47.51	10.21	0.01
Abalone survival						
Intercept only	**60 abalone; 10 trials**	**2**	**-33.74**	**71.69**	**0.00**	**0.83**
Treatment	60 abalone; 10 trials	4	-33.06	74.85	3.16	0.17

Appendix H.

Supplementary materials for Chapter 3

Table S1. **Qualitative data supporting the abalone historical social-ecological timeline.**

SES regime	Time period	Component	Details	FN territory	Source
Sea otters present	9450 BP - 2300 BP	Sea otters	(a) 9400s BP: "... assemblage... contains significant numbers of... harbour seals, and sea otters." (b) "Sea otters appear to be utilized by peoples on western Vancouver Island [over at least 5,000 years]."	Haida; Nuu-chah-nulth	(a) Fedje et al 2005c in Orchard 2007 (p. 342) (b) McKechnie and Wigen 2011 (p. 157)
		Kelp-associated fish	(a) 9400s BP: "... assemblage... is completely dominated by rockfish, and contains signfication numbers of dogfish, lingcod, cabezon..." (b) "... herring is the single-most ubiquitous fish taxon... and demonstrates a pervasive and previously underrecognized role for this species in indigenous economies spanning the Holocene."	Haida; Coastal FNs and tribes from Alaska to Washington	(a) Fedje et al 2005c in Orchard 2007 (p. 342) (b) McKechnie et al. 2014 (p. 3 of 10)
	2300 BP - 551 BP	Sea otters	"... k’oon (northern fur seal), t’iibn (northern sea lion), dziiw̓ (Pacific white-sided dolphin), płoon (sea otter), and wan (mule deer)" identified in midden site	Gitxaala	Menzies 2015 (p.149)
		Kelp-associated fish	"... assemblage shows stable, consistent presence of greenling, herring, and rockfish... showing no evidence of significant temporal variation."	Gitxaala	Menzies 2015 (p.149-50)
		Abalone	(a) "...intact bilhaa [abalone] shells ... in a shell-rich matrix that also included ts’maay (barnacle), ‘yaans (black katy chitons), ts’ak (gumboot chitons), ts’a’ax (clams), g̱aboox (cockle), hadza’üült (dog whelks and periwinkle), gyels (mussel), dzik’wits (red urchin), and aswit (green urchin)." (b) "... each [sample] contained bilhaa, although it was not abundant relative to other shellfish..."	Gitxaala	(a) Menzies 2015 (p. 149) (b) Menzies 2015 (p. 145 & 149)
	800 BP - contact	People	"... pre-contact population[of Haidas] that was likely greater than 10,000."	Haida	Acheson 1998 in Orchard 2007 (p.92)
		Sea otters	(a) "Birds and mammals are present in consistently low numbers compared to fish, although alcids, sea otters, harbour seals, and whales generally make substantial contributions..." (b) "... [otters] were likely consuming a diet of almost exclusively benthic invertebrates."	Haida	(a) Acheson 1998 in Orchard 2007 (p. 166-67) (b) Szpak et al. 2009 (p. 2739)
		Kelp-associated fish	"Other important fish taxa...include rockfish, halibut, and dogfish, with pricklebacks, sablefish, greenling, lingcod, sculpins, and other flatfish making small but relatively consistent contributions."	Haida	Acheson 1998 in Orchard 2007 (p. 166)
		Abalone	"... assemblages show... heavy use of California mussel and the minor use of other invertebrate taxa [including abalone]..."	Haida	Acheson 1998 and Wigen 1990 in Orchard 2007 (p. 166)

SES regime	Time period	Component	Details	FN territory	Source
Sea otters present	contact - 1830	People	(a) late 1770s: "… the first post-contact smallpox epidemic, and perhaps the most widespread..." (b) 1791: "...[the Kunghit Haida] in the summer of 1789, was large and powerful … but they were now dwindled to a few, as we did not see more than fifty different faces while here."	Haida	(a) Boyd 1994 in Orchard 2007 (p. 146) (b) Hoskins 1969 [1791] in Orchard 2007 (p. 123)
		Sea otters	(a) "Mammal assemblages are typically dominated by sea otter and harbour seal..." (b) "By about 1820 the fur trade was declining because of a scarcity of sea otters..."	BC coastal FNs & SE Alaska tribes	(a) Orchard 2007 (p. 240) (b) Duff 1965 in Orchard 2007 (p.145)
		Kelp-associated fish	"Kelp-derived carbon decreased in post-European contact rockfish relative to pre-European contact rockfish, likely as a result of the reduction of kelp forests associated with the local extirpation of sea otter."	Haida	Spzak et al. 2013 (p. 159)
		Abalone & Urchins	(a) "Generally, little change is seen [in shellfish use]..., with California mussel consistently dominant."* (b) "Patterns in abalone and urchin abundance are somewhat unclear... resulting primarily from the overall low abundances of these taxa."	Haida	(a) Orchard 2007 (p. 283) (b) Orchard 2007 (p. 288)
Sea otters absent	1830s - 1870s (post sea otter fur-trade)	People	(a) "… growth of the permanent European population on the coast..." (b) "Particularly devastating were introduced diseases (particularly smallpox and measles), which swept through the coastal [First Nations] population in the 1790s and later in the 1850s and 1860s."; (c) First Nations children taken away from communities to residential schools starting in the 1860s	Haida; Many BC coastal FNs	(a) Fisher in Orchard 2007 (p. 84) (b) McKechnie and Wigen 2011 (p.134) (c) British Columbia Teachers Federation 2015
		Sea otters	(a) "… a complete absence of sea otter and herring remains [in post-fur-trade deposits]…" (b) estimated <10 sea otter pelts traded from Haida Gwaii	Haida	(a) Orchard 2007 (p. 320) (b) Sloan and Dick 2012
		Urchins	"... [post-contact site] produced the greatest quantities of sea urchin..."; however, "Sea urchin remains... are generally scarce, with no apparent increase in contact-period deposits... impossible to assess this trend."	Haida	Orchard 2007 (pp. 320, 289)
	1870s - 1890	People	(a) "... characterised by the most dramatic changes in Haida culture... decline of traditional housing styles, a decline in the raising of totem poles, and the banning of the potlatch."; (b) 1867: *Constitution Act* grants Canadian government exclusive legislative authority over sea coast and inland fisheries; Anti-potlatch law enacted in 1884	Haida	(a) Blackman 1990 in Orchard 2007 (p. 93) (b) Newell 1993; Fisher 1992
		Sea otters	(a) estimated <100 sea otter pelts traded from Haida Gwaii; (b) estimated sea otter population <1000 animals in 12 populations along the west coast of North America	Haida; BC coastal FNs	(a) Sloan and Dick 2012 (b) Watson 2000
		Urchins	(a) 1877: “Below high water mark in some places the large urchins are very thickly strewn over the bottom.” (b) 1880: "sea-urchins... are often brought ashore in large quantities..."	Haida	(a) Dawson in Cole and Lockner 1989 (p. 451) (b) Dawson 1880 in Orchard 2007 (p. 81)

SES regime	Time period	Component	Details	FN territory	Source
Sea otters absent	1890 - early 1900s	People	(a) "By 1890, all the surviving Haida on Haida Gwaii, numbering less than 1,000..." (b) 1905: "... the last traditional house had disappeared from Masset."	Haida	(a) Duff 1965 in Orchard 2007 (p. 92) (b) Blackman 1990 in Orchard 2007 (p. 68)
		Sea otter	(a) "For many years now no sea-otter has been shot in the waters surrounding the Queen Charlotte Islands [now Haida Gwaii], they appear to have been well-nigh exterminated." (b) estimate 45 sea otter pelts traded by Tsimshian from hunting in Nuu-chah-nulth territory	Haida; Nuu-chah-nulth	(a) Harrison 1925 in Orchard 2007 (p. 82) (b) Sloan and Dick 2012
		Abalone	(a) "... [Haida] utilize the mollusc, known as *abalone* or *haliotus*, for food; they boil them or roast them on hot rocks at the camp fire." (b) "Bilhaa were first steamed in the shell in pit fires on the upper beach. Then the shells were removed and the bilhaa were threaded onto cedar dowels to be dried hanging over the cook stoves..."	Haida; Gitxaala	(a) Harrison 1925 in Orchard 2007 (p. 81) (b) Menzies 2015 (p. 141)
	early 1900s - 1970s	People	(a) 1951: Repeal of the anti-potlatch law (b) Reinterpret of Indian law as oral tradition without legal power in court cases, Calder v. Regina (1969) and Delgamuukw v. Regina (1987)		(a) & (b) Fiske 1998
		Sea otter	(a) 1911: International Fur Seal Treaty bans hunting of fur seals and sea otters; (b) 1929: Sea otters considered extirpated from the BC coast	BC coastal FNs	(a) & (b) Fisheries and Oceans Canada 2014
		Abalone	(a) First Nations intertidal abalone fishery continues, guided by practises passed from one generation to the next; (b) 1910s: Small-scale intertidal commercial abalone fisheries (e.g., Japanese abalone canning stations in Jedway Bay and Rose Harbour, Haida Gwaii); (c) 1940s: Commercial abalone fishing initiated, ramping up slowly through the 1950s and 60s, then rapidly peaking with subtidal SCUBA fishery in 1970s	Haida; Gitxaala; BC Coastal FNs	(a) Winbourne et al. 2011; Menzies 2015 (b) Dalzell 1993 (c) Sloan and Breen 1988
Sea otters recovering	1970s - 1990	People	(a) 1982: Section 35 of Canada's *Constitution Act* recognizes and affirms existing aboriginal and treaty rights of First Nations (b) 1984: The last residential school closed in BC	BC coastal FNs	(a) The Constitution Act, 1982 (b) British Columbia Teachers Federation 2015
		Sea otters	(a)1969-72: 89 sea otters reintroduced to Checleset Bay off the west coast of Vancouver Island from Alaska; (b)1978: Sea otters designated as endangered due to low population abundance and limited geographic range	Nuu-chah-nulth	(a) Bigg and MacAskie 1978 (b) Fisheries and Oceans Canada 2014
		Urchins	(a) Urchins continue to flourish in high densities along most of the coast in absence of sea otter predation, with lower densities in areas where sea otters have re-established (b) BC commercial red sea urchin fishery by SCUBA initiated in the early 1980s	BC coastal FNs	(a) Watson and Estes 2011 (b) Fisheries and Oceans Canada Shellfish Data Unit, commercial catch data, compiled 2013
		Abalone	1978-90: Abalone abundance declined by more than 75% due to overfishing, leading to closure of all abalone fisheries in 1990, including First Nations traditional fisheries	BC coastal FNs	Fisheries and Oceans Canada 2012
		Kelp	Less extensive and shallower kelp forests in areas of the coast not occupied by sea otters due to extensive urchin grazing; More extensive and deeper kelp forests in areas re-occupied by sea otters	Nuu-chah-nulth	Watson and Estes 2011

SES regime	Time period	Component	Details	FN territory	Source
Sea otters recovering	1990 - present	People	(a) Increasing co-management agreements between federal and provincial agencies and First Nations with contemporary examples in BC including: Gwaii Haanas Agreement (1993) and Marine Agreement (2010); Sgaan Kinghlas/Bowie Seamount Memorandum of Understanding (2007); Kunst'aa guu – Kunst'aayah Reconciliation Protocol (2009); Marine Planning Partnership (2011); Marine Protected Areas Technical Team (2012); Great Bear Rainforest Act (2016); and Pacific North Coast Integrated Management Area Plan (2017); (b) Increasing success in asserting Aboriginal Title and Rights to marine resources through direct action and court challenges (e.g., Ahousaht Indian Band and Nation v. Canada (2009); Ahousaht First Nation v. Canada (Fisheries and Oceans) (2014); Haida Nation v. Canada (Fisheries and Oceans) (2015))	BC coastal FNs	(a) Jones et al. 2010 (b) von der Porten et al. 2016; Gauvreau et al. 2017; Jones et al. 2017
		Sea otters	(a) 1996: Downlisted to threatened status due to increasing population size and range expansion; (b) 2007: Downlisted to a species of special concern, opening up the possibility of having localized sea otter hunting by First Nations where they have sufficiently recovered; (c) 2009: Nuu-chah-nulth and DFO draft a sea otter management plan including allowance for limited hunting (still in draft); (d) Sea otters continue to increase in abundance and expand their range on the WCVI and CC; At least one sea otter female-pup pair confirmed in 2017 in Gwaii Haanas National Marine Conservation Area Reserve and Haida Heritage Site, an area co-managed by Haida and federal agencies	BC coastal FNs	(a) & (b) Fisheries and Oceans Canada 2014 (c) Nuu-chah-nulth Tribal Council 2012 (d) Nichol et al. 2015; L. Lee, personal observations
		Urchins	Abundant sea urchin barrens throughout the BC outer coast where sea otters have not re-established	BC coastal FNs	Watson and Estes 2011; Lee et al. 2016
		Abalone	(a) 1999: Listed as threatened under Canada's Species At Risk Act due to continued decline and low abundances; (b) 2000s: Abalone stewardship partnership programs initiated between FIrst Nations, federal agencies and local organizations; (c) 2009: Uplisted to threatened due to continuing low densities; (d) 2010s: Evidence of increasing juvenile recruitment throughout northern BC; Sea star wasting disease causes dramatic decline of sunflower stars, reducing predation pressure on abalone	BC coastal FNs	(a) Fisheries and Oceans Canada 2012 (b) Sloan 2004 (c) Fisheries and Oceans Canada 2012 (d) Fisheries and Oceans Canada, unpublished data; J. Burt, unpublished data
		Kelp	Kelp forests at less than 25% of what would be expected with sea otters present due to extensive urchin grazing	Nuu-chah-nulth	Markel and Shurin 2015

* ubiquitous taxa included barnacles, California mussel, butter clam, general marine snail; giant barnacle, Pacific littleneck clam and sea urchin; other relatively widespread taxa include small mussels, rock scallops, cockles, horse clams, limpets, periwinkles, dogwinkles, red turban snails, black katy chitons, giant Pacific chiton; rarer taxa include a variety of small marine snails, Kennerly's venus and Arctic hiatella clams; very rare taxa include one large crab and tubeworm; California mussels make up most of proportion at exposed sites, while clams and small mussels (mostly blue mussels) make up most of proportion at protected sites (Orchard 2007; p. 271, 276)

Table S2. **Species-related quantitative data supporting magnitudes of change in the abalone historical social-ecological timeline.**

Decade	SES component	n	Estimated number/ density	Estimated relative magnitude of change	Source of estimated number/density	Calculation of estimated magnitude
1770s	Haida		10750	100.00	Acheson 1998 in Orchard 2007	% of estimated number of Haidas from 1770s; note that other sources have estimated the pre-contact population at over 30,000
1780s	Haida					
1790s	Haida					
1800s	Haida					
1810s	Haida					
1820s	Haida					
1830s	Haida		6700	62.33	Curtis 1916 in Orchard 2007	
1840s	Haida					
1850s	Haida					
1860s	Haida					
1870s	Haida					
1880s	Haida		800	7.44	Duff 1965 in Orchard 2007	
1890s	Haida					
1900s	Haida					
1910s	Haida					
1920s	Haida		650	6.05	Harrison 1925 in Orchard 2007	
1930s	Haida					
1940s	Haida					
1950s	Haida					
1960s	Haida		1200	11.16	Duff 1965 in Orchard 2007	
1770s	sea otter		52459	100.00	Gregr et al 2008; estimated pre-fur trade number of sea otters on BC coast	% of total estimated number of sea otters from 1770s
1780s	sea otter		4481	98.76	Sloan and Dick 2012; estimated number of sea otter pelts from BC coast	% of total number of sea otter pelts from 1770s-1910s
1790s	sea otter		140000	60.04		
1800s	sea otter		140000	21.31		
1810s	sea otter		54544	6.22		
1820s	sea otter		22359	0.04		
1830s	sea otter		1	0.04		
1840s	sea otter					
1850s	sea otter		8	0.03		
1860s	sea otter					
1870s	sea otter					
1880s	sea otter		44	0.02		
1890s	sea otter		80	0.00		
1900s	sea otter					
1910s	sea otter		2	0.00		
1920s	sea otter		0	0.00	Sloan and Dick 2012; last known sea otter in BC shot in 1929	% of total estimated number of sea otters from 1770s
1930s	sea otter					
1940s	sea otter					
1950s	sea otter					
1960s	sea otter					
1970s	sea otter		100	0.19	Nichol et al. 2015; estimated number of sea otters on the BC coast	% of total estimated number of sea otters from 1770s
1980s	sea otter		500	0.95		
1990s	sea otter		1400	2.67		
2000s	sea otter		3500	6.67		
2010s	sea otter		7200	13.73		

Decade	SES component	n	Estimated number/ density	Estimated relative magnitude of change	Source of estimated number/density	Calculation of estimated magnitude
1770s	abalone		0.12	2.70	data from Lee et al. 2016; est. density from sites with 10+ years of sea otter occupation	% of estimated high abalone density from 1940s based on magitudes of change from TK using the average density of abalone from DFO index site surveys in the 1980s on the CC
1780s	abalone					
1790s	abalone					
1800s	abalone					
1810s	abalone					
1820s	abalone					
1830s	abalone		0.12	2.70	assumed 1770s represents average abalone density until sea otters ecologically extirpated	
1840s	abalone		0.60	13.51	Zhang et al. 2007; estimated number of abalone at 10% mortality from Fig. 5B	
1850s	abalone		1.20	27.02		
1860s	abalone		2.00	45.04		
1870s	abalone		2.80	63.06		
1880s	abalone		3.60	81.07		
1890s	abalone		4.44	100.00	assumed 1940s represents high abundances following sea otter extirpation	
1900s	abalone					
1910s	abalone					
1920s	abalone					
1930s	abalone					
1940s	abalone	1	4.44	100.00	estimated number of abalone calculated using reference density from 1980s and estimated magnitude of change from TK interviews	% of mean proportional change by decade from TK interviews, assuming 1940s represents high densities following sea otter extirpation
1950s	abalone	1	3.04	68.28		
1960s	abalone	2	3.04	68.28		
1970s	abalone	3	2.06	46.28		
1980s	abalone	7	1.12	25.22	DFO index site surveys from CC; estimated average density for 1980s used as reference density	
1990s	abalone	4	0.78	17.51	estimated number of abalone calculated using reference density from 1980s and estimated magnitude of change from TK	
2000s	abalone	3	0.35	7.92		
2010s	abalone	1	0.12	2.64		
2020s	abalone	4	0.13	2.92	data from Lee et al. 2016; estimated density from sites with 30+ years of sea otter occupation	% of estimated high abalone density from 1940s

Decade	SES component	n	Estimated number/ density	Estimated relative magnitude of change	Source of estimated number/density	Calculation of estimated magnitude
1770s	urchin	11	0.15	2.27	density from sites with 10+ years of sea	% of estimated high urchin density from 1980s
1780s	urchin					
1790s	urchin					
1800s	urchin					
1810s	urchin					
1820s	urchin					
1830s	urchin	11	0.15	2.27	assumed average urchin density from 1770s until sea otters ecologically extirpated	
1840s	urchin					
1850s	urchin					
1860s	urchin					
1870s	urchin					
1880s	urchin					
1890s	urchin					
1900s	urchin					
1910s	urchin					
1920s	urchin					
1930s	urchin					
1940s	urchin					
1950s	urchin					
1960s	urchin					
1970s	urchin					
1980s	urchin	36	6.46	100.00	data from Lee et al. 2016; estimated density from sites with no sea otter occupation	
1990s	urchin	13	1.12	17.28	data from Lee et al. 2016; estimated density from sites with 1-9 years of sea otter occupation	
2000s	urchin	4	0.27	4.14	data from Lee et al. 2016; estimated density from sites with 10-19 years of sea otter occupation	
2010s	urchin	3	0.08	1.20	data from Lee et al. 2016; estimated density from sites with 20-29 years of sea otter occupation	
2020s	urchin	4	0.08	1.19	data from Lee et al. 2016; estimated density from sites with 30+ years of sea otter occupation	

Decade	SES component	n	Estimated number/ density	Estimated relative magnitude of change	Source of estimated number/density	Calculation of estimated magnitude
1770s	kelp	11	13.46	79.62	data from Lee et al. 2016; estimated density from sites with 10+ years of sea otter occupation	% of estimated high kelp density from 1990s
1780s	kelp					
1790s	kelp					
1800s	kelp					
1810s	kelp					
1820s	kelp					
1830s	kelp	11	13.46	79.62	assumed average kelp density from 1770s until sea otters ecologically extirpated	
1840s	kelp					
1850s	kelp					
1860s	kelp					
1870s	kelp					
1880s	kelp					
1890s	kelp					
1900s	kelp					
1910s	kelp					
1920s	kelp					
1930s	kelp					
1940s	kelp					
1950s	kelp					
1960s	kelp					
1970s	kelp					
1980s	kelp	36	3.79	22.40	data from Lee et al. 2016; estimated density from sites with no sea otter occupation	
1990s	kelp	13	16.91	100.00	data from Lee et al. 2016; estimated density from sites with 1-9 years of sea otter occupation	
2000s	kelp	4	13.56	80.19	data from Lee et al. 2016; estimated density from sites with 10-19 years of sea otter occupation	
2010s	kelp	3	15.72	92.99	data from Lee et al. 2016; estimated density from sites with 20-29 years of sea otter occupation	
2020s	kelp	4	11.67	69.01	data from Lee et al. 2016; estimated density from sites with 30+ years of sea otter occupation	

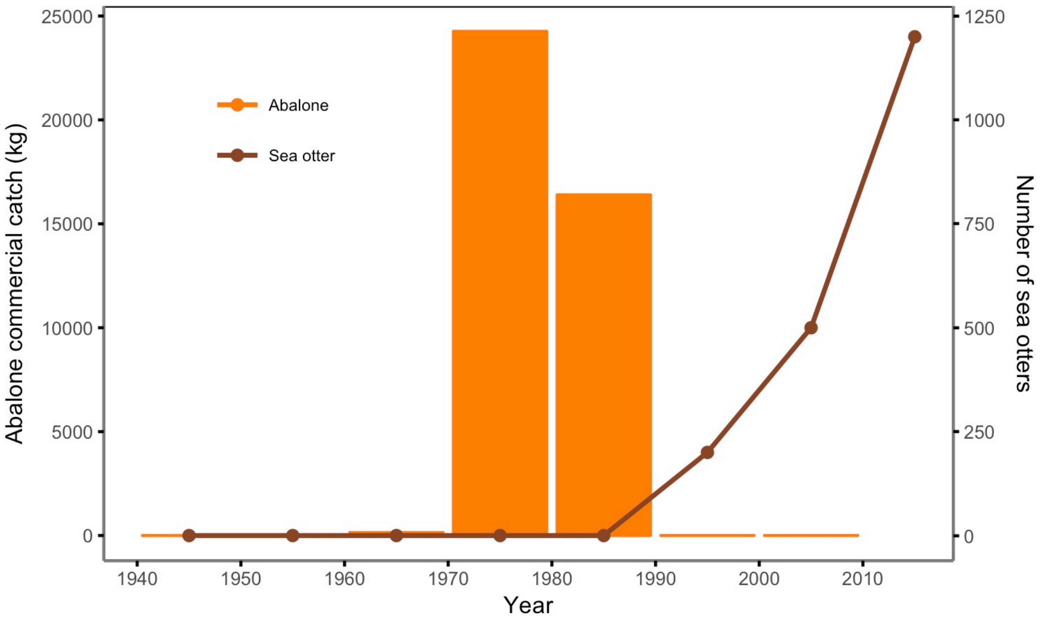

Figure S1. **Commercial catch of abalone by decade (DFO Statistical Areas 7-9; orange bars; Bates 1984, Thomas 1992) and estimated number of sea otters by decade (reproduced from Nichol et al. 2015; brown line) in Heiltsuk territory.**

Table S3. **Reasons attributed to abalone decline from Heiltsuk TK interviews from most to least mentioned.**

Topic no.	Causes of low abundance of abalone	Interview source (Jan 2012)
1	Illegal fishing (poaching) during and after the commercial abalone fishery; "...there's all those black marketers there… they should be monitored really. It's not monitored." (anonymous)	WG, Sr; FCR; HER; GGH; 2 anonymous
2	Sea otters eating abalone; "I think right now sea otters might be playing a role in some of the abalone not coming back." (DNW)	DNW; HH; FCR; 2 anonymous
3	Overfishing during commercial fishery; "And the planes would come right in, take their abalone, fly out from there [1960s and 70s]." (HER); "... they [commercial fishery] just annihilated the biomass…, after that my people were told that they couldn't eat that stuff [abalone] anymore." (WG, Sr)	DNW; WG, Sr; HER; GEH
4	Increased predation by river otters and mink; "You see lots of abalone [shells] in the [river] otter slides." (ARR)	HH; ARR; HER

Heiltsuk traditional knowledge interviews

Semi-structured interview questions

INTRODUCTORY QUESTIONS that establish the time and spatial scale of each person's observations:

1. Can you please tell me your full name?
2. What year were you born?
3. Where did you grow up? Where do you usually live? Do you live somewhere else at different times of the year?
4. Did you ever harvest abalone to feed your family? Who taught you? Did you go to harvest abalone only or would you go to harvest abalone along with other seafood?
5. Over what years did you harvest abalone and make observations about the rocky shore? How often would you go to harvest abalone each year and at what time of year?

PART 1. ECOLOGICAL QUESTIONS to add to our collective knowledge of kelp forest species, habitats and ecosystems, mapping some changes by timeframe (if possible):

Establish the area(s) on the map that the participant is familiar with in terms of describing changes over decades and be clear which areas are being talked about throughout the interview. Have copies of charts of Heiltsuk territory available for drawing on.

1. ***[establish area of expertise]*** What general abalone harvesting areas are you familiar with? Can you identify those general areas on the chart copies and tell me what years you harvested abalone in each of those areas? Why did you choose to harvest abalone in each of those areas? *If participants' experience is over several decades, ask the following questions by decade or specific time period.*
2. ***[habitat observations]*** I would like to understand what the places where you find abalone looked like in the past and how they have changed over time. Either by decade or by a specified time period that you remember, can you describe in detail what the places are like where you find abalone along the shore *(give descriptive example)*? What time of year did you see them? Can you describe any changes that you have noticed in those areas over time by each decade or specified time period?
3. ***[subtidal habitat observations]*** If you have been diving, can you describe what the places are like where you find abalone underwater? Can you describe any changes that you have noticed in those areas over time (by each decade or specified time period)?
4. ***[habitat explanations]*** What factors do you think caused those habitat changes?
5. ***[abalone, urchin and kelp observations]*** What changes have you observed in northern abalone, sea urchins, sea otters and kelp forests over time (by each decade or specified time period)? When and where did these changes occur? Were these areas always the same areas or did they change over time?

6. ***[abalone, urchin and kelp explanations]*** What factors do you think caused the changes you observed in abalone? Sea urchins? Kelp?
7. ***[abalone trends and explanations]*** Do you think abalone numbers have been going up or down since the fisheries closure in 1990 and in the past few years? Why do you think so and what factors do you think are most important in causing those changes?
8. ***[sea otter observations]*** When did you start observing sea otters? Can you show me on the map places where you first started seeing them? Where have you seen them since then by each decade? In the areas that you harvest abalone, what changes have you noticed in the sea otter population over time by each decade or specified time period?
9. ***[sea otter effects explanation]*** Do you think sea otters have an effect on abalone, sea urchins and kelp? If yes, what effect do you think sea otters have, and how long is the time period between when you first observe sea otters and when you first notice changes in habitat and species? How do you think sea otters will affect abalone, sea urchins, and kelp over time?

QUESTIONS TO QUANTIFY CHANGES in abalone and kelp forests over time:

Explain the purpose of this exercise in terms of trying to quantify participants' knowledge of changes in the ecology of abalone over time, so that we can compare this to contemporary survey data. Indicate throughout the interview which area or areas are being talked about in the following questions.

For each, or a combination of, the general abalone harvesting area(s) that you know, we have a set of questions to try and measure what you remember of changes in abalone, sea urchins, sea otters, and kelp over time.

1. ***[quantify density and size of abalone along shorelines]*** Can you imagine that the area marked out is the shoreline at low tide for the general areas that you are familiar with *(this will be an area of known size, likely 5, 10 or 20*m^2 *area depending on the space available)*? Using these abalone shells, can you place the abalone to show me what the sizes and distribution of abalone would have looked like for each decade in the 80s? 70s? 60s? 50s? 40s? or for specified time periods that you remember. *The interviewer will photograph and record the number of abalone shells of each size class placed for each decade or specified time period*.

   If you went out to this area in the 90s and 2000s, what did the size and distribution of abalone look like?

2. ***[quantify amount of abalone harvested for food]*** Using this bucket/gunny sack (use the standard collecting device that Heiltsuk would have used to harvest abalone for food) as a measure of the amount of abalone you picked for food, can you tell me the following for each decade or time period that you picked abalone: (a) How often would you go out each year to pick abalone and at what time of year? (b) How many buckets/gunny sacks full of abalone would you pick each time? (c) What range of sizes were the abalone that you picked and what do you think was the average size *(ask participants to show you with the shells available)*?

3. ***[quantify changes in sea urchins over time]*** Over the time that you were harvesting abalone, did you notice any sea urchins at the sites that you regularly visited? If yes, what species of sea urchins did you see and which type was most common? What year or time period did you first notice the different sea urchins? What changes in the size or abundance of the different sea urchins have you noticed over each decade or time period since you first saw them?
4. ***[quantify changes in sea otter abundance over time]*** Over the time that you were harvesting abalone, did you notice any sea otters at the sites that you regularly visited? If yes, what year or time period did you first notice the sea otters? What changes in abundance and behaviour of sea otters have you noticed over each decade or time period since you first saw them?
5. ***[quantify changes in kelp over time]*** Over the time that you were harvesting abalone, did you notice any changes in the kelp in front of the sites that you regularly visited? If yes, what changes did you notice in the type of kelp – for example, bull kelp or giant kelp – and extent of kelp over each decade or time period?

COMMUNITY BASED MANAGEMENT QUESTIONS to inform Heiltsuk management plan for abalone:

1. What traditional practices do you know of, or were you told about, to manage abalone in the past? When were these practices used? How have these management and stewardship practices changed from past to present?
2. Do you know of any abalone enhancement practices that were traditionally used? If yes, why was the practice used?
3. What are the signs that you would use to tell if abalone in an area were healthy or if they were in trouble? What do you think we need to monitor to make sure that abalone are being picked in a sustainable way?
4. If a food fishery for abalone could be allowed in future, what do you think are the most important factors to consider before that can happen?
5. What do you think are the concerns (risks) and benefits of a food fishery for abalone? How do you think we can minimize the concerns (risks) that come with a food fishery?
6. How do you think a food fishery for abalone should be managed? What do you think are key characteristics of a well-managed Heiltsuk abalone food fishery?
7. Are there particular areas that you feel should be considered as abalone stewardship and food fishing areas? Why do you think these areas would be good stewardship and food fishing areas?
8. Are there particular areas that you feel should be protected from abalone harvest even if a food fishery were to be opened in future? Why do you think these areas are important to protect from any harvest?
9. Can you also tell me about any traditional management and stewardship practices that you know of for sea urchins, sea otters, and kelp?
10. How do you envision people, abalone and sea otters co-existing today and into the future?
11. Is there anything else you would like to tell us?

Abalone density reconstructions

Figure S2. **All abalone reconstructions by decade from Heiltsuk traditional knowledge interviews. Each row represents a unique knowledge holder-area combination.**

Statistical analyses of abalone traditional & western scientific knowledge data

Statistical models summary

For density of large abalone, four alternative models were fitted to the data that all assumed constant annual population growth rates over the time period (models with a step change in rate did not converge) and a random effect of site. The full model estimated separate annual population growth rates (slopes) and initial densities (intercepts) for the traditional knowledge (TK) and western scientific knowledge (WK) data (Table S4, Box S4). The three reduced models had (1) shared growth rate; (2) shared initial density; and (3) shared growth rate and shared initial density.

For density of small abalone, only WSK data was analysed due to limited information from TK data. Two annual population growth rate models, both with random effect of site, were fitted to the data. The full model included a step change in the annual population growth rate (Table S8, Box S6) and the reduced model did not. Timing of the step change was fixed at 2004 based on a preliminary model with no random effect of site (Table S6; Box S5).

Support for each model was determined by its Akaike weight (w_i; Burnham and Anderson 2002) based on the Wanatabe-Akaike Information Criterion (WAIC; Watanabe 2010). Posterior distributions were estimated from 4,000 Markov Chain Monte Carlo (MCMC) samples thinned from the second halves of four chains (Kery and Schaub 2011). Model convergence was confirmed by ensuring the potential scale reduction factor, $\hat{R}$, ≤ 1.05 for each parameter (Kery and Schaub 2011). Model performance was confirmed by examination of residual plots. Models were fitted using STAN (Carpenter et al. 2017) and analyses implemented using R version 3.4.2 (R Core Team 2015) and the smbr package (Muir and Thorley 2018).

Model equations for density of large ($\geq$70 mm) and small (<70 mm) abalone

Box S1. Equations describing the full model for large abalone density using TK and WK data.

The full model for large abalone is described by the following equations:

$$\text{(Eq. 1)}\ \ \mathrm{O}_{h,t} \sim \mathrm{LN}(\log(\mathrm{D}_t^{TK}), \sigma_O)$$

where $\mathrm{O}_{h,t}$ is the density of abalone recalled by TK holders where *h* indexes knowledge holder and *t* indexes time; D_t^{TK} is the expected density from TK observations at time *t*; σ_E is the standard deviation for the residual variation in recalled densities.

$$\text{(Eq. 2)}\ \ \mathrm{C}_{s,t} \sim \mathrm{NB}\left(\mathrm{D}_{s,t}^{WK} \cdot \mathrm{AREA}_{s,t}, \phi_C\right)$$

where $\mathrm{C}_{s,t}$ is the count of large abalone observed by scientific divers at site *s* in time *t*; $\mathrm{D}_{s,t}^{WK}$ is the expected density for WK surveys at site *s* in time *t*; $\mathrm{AREA}_{s,t}$ is the area surveyed in m^2; and ϕ_C is the overdispersion parameter for the negative binomial distribution.

$$\text{(Eq. 3)}\ \ \log\left(\mathrm{D}_{s,t}^{WK}\right) = \log(\mathrm{D}_t^{WK}) + \alpha_s$$

where D_t^{WK} is the expected density of abalone from WK at a typical site at time *t*; and α_s is the random effect of site *s*.

$$\text{(Eq. 4)}\ \ \alpha_s \sim \mathrm{N}(0, \sigma_S)$$

where σ_S is the standard deviation of the random effect of site.

$$\text{(Eq. 5)}\ \ \mathrm{D}_t^{TK} = \mathrm{D}_{t-1}^{TK} \cdot \mathrm{R}^{TK}$$

where R^{TK} is the annual population growth rate estimated from TK.

$$\text{(Eq. 6)}\ \ \mathrm{D}_t^{SK} = \mathrm{D}_{t-1}^{SK} \cdot \mathrm{R}^{SK}$$

where R^{SK} is the annual population growth rate estimated from WK.

$$\text{(Eq. 7)}\ \ \mathrm{D}_0^{TK} = \mathrm{D}_0^{WK} + \mathrm{D}_\Delta$$

where D_0^{TK} is the expected density from TK knowledge holders for the initial year; D_0^{WK} is the expected density from federal index site surveys for the initial year; and D_Δ is the difference in density between TK and WK.

$$\text{(Eq. 8)}\ \ \mathrm{R}^{TK} = \mathrm{R}^{WK} + \mathrm{R}_\Delta$$

where R_{Δ} is the difference in annual population growth rate between TK and WK.

Box S2. Equations describing the full model for small abalone density using WK data.

The full model for small abalone is described by Eqs. 2-4 in Box S1 and:

$$\text{(Eq. 9)}\ \ \mathrm{D}_t^{WK} = \mathrm{D}_{t-1}^{WK} \cdot \mathrm{R}_t^{WK}$$

where R_t^{WK} is the annual population growth rate estimated from WK at time *t*.

$$\text{(Eq. 10)}\ \ \mathrm{R}_t^{WK} = \mathrm{R}_0 \text{ if } t < t_{\Delta}\text{; and}$$

$$\text{(Eq. 11)}\ \ \mathrm{R}_t^{WK} = \mathrm{R}_0 + \mathrm{R}_{\Delta} \text{ if } t \geq t_{\Delta}$$

where R_0 is the annual population growth rate for the initial time period; R_{Δ} is the difference in annual population growth rate between the initial period and subsequent period after the growth rate change; and t_{Δ} is the year of the growth rate change.

Box S3. Prior distributions for large and small abalone density models.

All models adopted low information prior distributions that included all biologically plausible values (Kery and Schaub 2011):

$$\log\left(\mathrm{D}_0^{WK}\right) \sim \mathrm{N}(0,5)$$

$$\log(\mathrm{D}_{\Delta}) \sim \mathrm{N}(0,5)$$

$$\log(\mathrm{R}^{WK}) \sim \mathrm{N}(0,5)$$

$$\log(\mathrm{R}_{\Delta}) \sim \mathrm{N}(0,5)$$

$$\sigma_O \sim \mathrm{U}(0,5)$$

$$\phi_C \sim \mathrm{U}(0,5)$$

$$\sigma_S \sim \mathrm{U}(0,5)$$

Large abalone model description and coefficient estimates

Table S4. Description of parameters in the full model for large abalone.

Parameter	Description
`Area`	The surface area surveyed (m2)
`bDensity`	The intercept for the `log(eDensity) or log(eCount)` in the first year
`bDensityTraditional`	The effect of `Traditional` on `bDensity`
`bRate`	The `log` inter-annual population growth rate
`bRateTraditional`	The effect of `Traditional` on `bRate`
`bSite`	The effect of `Site` on `bDensity`
`Count`	The number of abalone recorded
`Density`	The density of abalone (individual/m2) recalled by a Traditional Knowledge holder
`eCount`	The expected `Count`
`eDensity`	The expected `Density`
`sDensity`	The SD of the residual variation in `log(Density)`
`Site`	The site surveyed
`sPhi`	The overdispersion term
`sSite`	The SD of `bSite`
`Traditional`	Whether the information is from a Traditional Knowledge holder (not from federal index site surveys)
`Year`	The year as a integer starting at 0 (for 1945)

Box S4. Definition of full model integrating TK and WK data for large abalone.

```
data {
  int nObs;
  int nCount;
  int nDensity;

  int Traditional[nObs];

  int Count[nCount];
  real Area[nCount];
  int YearScientific[nCount];

  real Density[nDensity];
  int YearTraditional[nDensity];

  int nSite;
  int Site[nCount];

parameters {
  real bDensity;
  real bDensityTraditional;
```

```
  real bRate;
  real bRateTraditional;

  real<lower=0> sDensity;
  real<lower=0> sPhi;

  real<lower=0> sDensitySite;
  vector[nSite] bDensitySite;

model {
  vector[nCount] eCount;
  vector[nDensity] eDensity;

  bDensity ~ normal(0, 5);
  bDensityTraditional ~ normal(0, 5);

  bRate ~ normal(0, 5);
  bRateTraditional ~ normal(0, 5);

  sDensity ~ uniform(0, 5);
  sPhi ~ uniform(0, 5);
  sDensitySite ~ uniform(0, 5);
  bDensitySite ~ normal(0, sDensitySite);

  for(i in 1:nCount) {
    log_eCount[i] = bDensity + bRate * YearScientific[i] + log(Area[i]) + bDensitySite[Site[i]
];
    Count[i] ~ neg_binomial_2_log(log_eCount[i], sPhi);
  }
  for(i in 1:nDensity) {
    log_eDensity[i] = bDensity + bDensityTraditional + (bRate          + bRateTraditional) *
YearTraditional[i];
    Density[i] ~ lognormal(log_eDensity[i], sDensity);
  }
```

Table S5. **Coefficient estimates for model of large abalone density with the most support: WK density + TK density difference + WK rate.**

term	estimate	sd	lower	upper
bDensity	1.0165296	0.4320979	0.1714062	1.8687329
bDensityTraditional	2.3535098	0.2598386	1.8303487	2.8648341
bRate	-0.0368291	0.0075271	-0.0515837	-0.0221064
sDensity	1.0057187	0.1387790	0.7866032	1.3242407
sDensitySite	0.6876882	0.1335658	0.4367499	0.9666666
sPhi	1.2636513	0.2511300	0.8716062	1.8489434

Small abalone model descriptions and coefficient estimates

Table S6. Description of parameters in the full model for small abalone with change point and without site as a random factor.

Parameter	Description
`Annual`	The year as an integer starting at 1 (for 1980)
`Area`	The surface area surveyed (m2)
`bChangePoint`	The year of the change in the population growth rate
`bDensity`	The intercept for the `log(eCount)` in the first year
`bRate`	The `log` inter-annual population growth rate in the first year
`bRateChange`	The change in bRate after `bChangePoint`
`Count`	The number of abalone recorded
`eCount`	The expected `Count`
`sPhi`	The overdispersion term

Box S5. Definition of full model for small abalone with change point and without site as a random factor.

```
data {
   int nObs;

   int Count[nObs];
   real Area[nObs];

   int nAnnual;
   int Annual[nObs];
 }

 parameters {
   real bDensity;

   real bRate;
   real bRateChange;
   real<lower=2,upper=(nAnnual-1)> bChangePoint;
   real<lower=0> sPhi;
 }

 model {
   vector[nObs] eCount;
   vector[nAnnual] eDensityAnnual;

   bDensity ~ normal(0, 5);
   bRate ~ normal(0, 5);
   bRateChange ~ normal(0, 5);

   sPhi ~ uniform(0, 5);

   eDensityAnnual[1] = bDensity;
```

```
   for(i in 2:nAnnual) {
     eDensityAnnual[i] = eDensityAnnual[i-1] + bRate + bRateChange * (i >= bChangePoi
nt);
   }

   for(i in 1:nObs) {
     log_eCount[i]) = eDensityAnnual[Annual[i]] + log(Area[i]);
     Count[i] ~ neg_binomial_2_log(log_eCount[i], sPhi);
   }
 }
```

Table S7. **Coefficient estimates for full model of small abalone density with change point and without site as a random factor.**

term	estimate	sd	lower	upper
bChangePoint	24.5406905	1.0022350	22.3837194	26.4206440
bDensity	0.6375103	0.3225124	0.0572249	1.3442427
bRate	-0.1155630	0.0192674	-0.1562583	-0.0803662
bRateChange	0.3512888	0.0355136	0.2824154	0.4215246
sPhi	1.1693837	0.1718615	0.8643585	1.5368862

Table S8. **Description of parameters in the full model for small abalone with change point fixed at the year 2004 and site as a random factor.**

Parameter	Description
`Annual`	The year as an integer starting at 1 (for 1980)
`Area`	The surface area surveyed (m2)
`bChangePoint`	The year of the change in the population growth rate
`bDensity`	The intercept for the `log(eCount)` in the first year
`bRate`	The `log` inter-annual population growth rate in the first year
`bRateChange`	The change in bRate after `bChangePoint`
`bSite`	The effect of `Site` on `bDensity`
`Count`	The number of abalone recorded
`eCount`	The expected `Count`
`Site`	The site surveyed
`sPhi`	The overdispersion term
`sSite`	The SD of `bSite`

Box S6. **Definition of full model for WK data for small abalone with change point fixed at the year 2004 and with site as a random factor.**

```
   data {
 int nObs;

 int Count[nObs];
 real Area[nObs];
```

```
int nAnnual;
int Annual[nObs];
int nSite;
int Site[nObs];
}

parameters {
real bDensity;

real bRate;
real bRateChange;
real<lower=0> sPhi;
real<lower=0> sDensitySite;
vector[nSite] bDensitySite;
}

model {
vector[nObs] eCount;
vector[nAnnual] eDensityAnnual;

bDensity ~ normal(0, 5);
bRate ~ normal(0, 5);
bRateChange ~ normal(0, 5);

sPhi ~ uniform(0, 5);

sDensitySite ~ uniform(0, 5);
bDensitySite ~ normal(0, sDensitySite);

eDensityAnnual[1] = bDensity;
for(i in 2:nAnnual) {
eDensityAnnual[i] = eDensityAnnual[i-1] + bRate + bRateChange * (i >= 24.5);
}

for(i in 1:nObs) {
log_eCount[i] = eDensityAnnual[Annual[i]] + log(Area[i]) + bDensitySite[Site[i]];
Count[i] ~ neg_binomial_2_log(log_eCount[i], sPhi);
}
}
```

Table S9. Coefficient estimates for full model of small abalone density with change point fixed at the year 2004 and site as a random factor.

term	estimate	sd	lower	upper
bDensity	0.7924864	0.3134164	0.1970642	1.4205304
bRate	-0.1329305	0.0181116	-0.1694477	-0.0994421
bRateChange	0.3783671	0.0328337	0.3158391	0.4426320
sDensitySite	0.5331327	0.1466747	0.2388530	0.8278616
sPhi	1.6729109	0.3553670	1.1347001	2.5346164

Comparison of statistical models for densities of large ≥70 mm and small <70 mm abalone

Table S10. Strength of evidence for alternative candidate models of density and annual population growth rates for large abalone (≥70 mm) based on data from traditional knowledge (TK) and western knowledge (WK), and for small abalone (<70 mm) based on WK data. Full models are described in Boxes S4-S8. Best models within <2 ΔWAIC are highlighted in bold.

Response	Model	WAIC	ΔWAIC	w_i
Density of large abalone (with random effect of site and no step change and)	**WK density + TK density difference + WK rate**	**1078.420**	**0.0**	**0.55**
	WK density + TK density difference + WK rate + TK rate difference	**1078.882**	**0.5**	**0.43**
	WK density + WK rate + TK rate difference	1085.081	6.7	0.02
	WK density + WK rate	1131.091	52.7	0.00
Density of small abalone (with step rate change and no random effect if site)	**WK density + WK rate + WK rate step change**	**955.246**	**0.0**	**1.00**
	WK density + WK rate	1056.255	101.0	0.00
Density of small abalone (with fixed step rate change and random site effect)	**WK density + WK rate + WK rate step change**	**934.527**	**0.0**	**1.00**
	WK density + WK rate	1053.014	118.5	0.00

References

Ahousaht First Nation v. Canada (Fisheries and Oceans). (2014) Federal Court 197.

Ahousaht Indian Band and Nation v. Canada. (2009) British Columbia Supreme Court 1494.

Bates, K.T. (1984) Review of the 1982 commercial abalone fishery in British Columbia. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **1749**, 22 p.

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

British Columbia Teachers' Federation. (2015) Project of Heart: Illuminating the hidden history of Indian Residential Schools in BC. p. 37. British Columbia Teachers' Federation, Vancouver, BC.

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

Carpenter, B., Gelman, A., Hoffman, M.D. *et al.* (2017) Stan: A probabilistic programming language. *Journal of Statistical Software* **76 (1)**.

Cole, D., Lockner, B. (1989) *Journals of George M. Dawson, Volume 1: British Columbia 1875-1876*. UBC Press, Vancouver, BC.

Fisher, R. (1992) *Contact and Conflict*, 2nd ed. UBC Press, Vancouver, BC.

Fisheries and Oceans Canada. (2012) Action Plan for the Northern Abalone (*Haliotis kamtschatkana*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Fisheries and Oceans Canada. (2014) Management Plan for the Sea Otter (*Enhydra lutris*) in Canada. *Species at Risk Act* Management Plan Series. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Fiske, J.-A. (1998) From Customary Law to Oral Traditions: Discursive Formation of Plural Legalisms in Northern British Columbia, 1857-1993. *BC Studies* **115/116**, 267-288.

Gauvreau, A.M., Lepofsky, D., Rutherford, M., Reid, M. (2017) "Everything revolves around the herring": the Heiltsuk-herring relationship through time. *Ecology and Society* **22**.

Gregr, E., Nichol, L., Watson, J.C., Ford, J.K.B., Ellis, G.M. (2008) Estimating Carrying Capacity for Sea Otters in British Columbia. *Journal of Wildlife Management* **72**, 382-388.

Haida Nation v. Canada (Fisheries and Oceans). (2015) Federal Court 290.

Jones, R., Rigg, C., Lee, L. (2010) Haida Marine Planning: First Nations as a Partner in Marine Conservation. *Ecology and Society* **15**.

Jones, R., Rigg, C., Pinkerton, E. (2017) Strategies for assertion of conservation and local management rights: A Haida Gwaii herring story. *Marine Policy* **80**, 154-167.

Kery, M., Schaub, M. (2011) *Bayesian Population Analysis using WinBUGS: A Hierarchical Perspective*. Academic Press, UK.

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

Markel, R.W., Shurin, J.B. (2015) Indirect effects of sea otters on rockfish (*Sebastes* spp.) in giant kelp forests. *Ecology* **96**, 2877-2890.

McKechnie, I., Lepofsky, D., Moss, M.L. *et al.* (2014) Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. *Proceedings of the National Academy of Sciences of the United States of America* **111**, E807-E816.

McKechnie, I., Wigen, R.J. (2011) Toward a historical ecology of pinniped and sea otter hunting traditions on the coast of southern British Columbia. pp. 129-166 in Braje, T.J., Rick, T.C. editors. *Human impacts on seals, sea lions, and sea otters: Integrating archaeology and ecology in the Northeast Pacific.* University of California Press, Berkeley and Los Angeles, California, USA.

Menzies, C.R. (2015) Revisiting "Dm sibilhaa'nm da laxyuubm Gitxaała (Picking abalone in Gitxaała territory)": vindication, appropriation, and archaeology. *BC Studies*, 129-153.

Muir, C., Thorley, J. (2018) smbr: Analyses Using STAN. doi: https://doi.org/10.5281/zenodo.1162382.

Newell, D. (1993) *Tangled Webs of History: Indians and the Law in Canada's Pacific Coast Fisheries*. University of Toronto Press, Toronto, ON.

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

Orchard, T.J. (2007) Otters and urchins: Continuity and change in Haida economy during the Late Holocene and maritime fur trade periods. p. 408 pp. + appendices. *Department of Anthropology.* University of Toronto, Toronto.

R Core Team. (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sloan, N.A. (2004) Northern abalone: using an invertebrate to focus marine conservation ideas and values. *Coastal Management* **32**, 129-143.

Sloan, N.A., Breen, P.A. (1988) Northern abalone, *Haliotis kamtschatkana* in British Columbia: fisheries and synopsis of life history information. *Canadian Special Publication of Fisheries and Aquatic Sciences* **103**, 46 pp.

Sloan, N.A., Dick, L. (2012) *Sea Otters of Haida Gwaii: Icons in Human - Ocean Relations*. Gwaii Haanas Archipelago Management Board & Haida Gwaii Museum, Skidegate, British Columbia, Canada.

Szpak, P., Orchard, T.J., Grocke, D.R. (2009) A Late Holocene vertebrate food web from southern Haida Gwaii (Queen Charlotte Islands, British Columbia). *Journal of Archaeological Science* **36**, 2734-2741.

Szpak, P., Orchard, T.J., Salomon, A.K., Grocke, D.R. (2013) Regional ecological variability and impact of the maritime fur trade on nearshore ecosystems in southern Haida Gwaii (British Columbia, Canada): evidence from stable isotope analysis of rockfish (*Sebastes* spp.) bone collagen. *Archaeological and Anthropological Sciences* **5**, 159-182.

Thomas, G.A. (1992) Shellfish stock assessments for the west coast of Canada in 1991 as reviewed by the Pacific Stock Assessment Review Committee (PSARC). *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **No. 2169**, 287 p.

Watanabe, S. (2010) Asymptotic Equivalence of Bayes Cross Validation and Widely Applicable Information Criterion in Singular Learning Theory. *Journal of Machine Learning Research* **11**, 3571-3594.

Watson, J.C. (2000) The effects of sea otters (*Enhydra lutris*) on abalone (*Haliotis* spp.) populations. *Canadian Special Publication of Fisheries and Aquatic Sciences* **130**, 123-132.

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

Zhang, Z., Campbell, A., Lessard, J. (2007) Modeling northern abalone, *Haliotis kamtschatkana*, population stock and recruitment in British Columbia. *Journal of Shellfish Research* **26**, 1099-1107.