

**A MARINE MEGAFANAL EXTINCTION AND ITS CONSEQUENCES FOR KELP
FORESTS OF THE NORTH PACIFIC**

by

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Abstract

Restoration of lost ecosystem functions and species interactions is increasingly seen as central to addressing the extensive degradation of ecosystems and associated losses of biodiversity and ecosystem services. To be effective, such restoration efforts require an understanding of how ecosystems functioned prior to human-caused extinctions and ecological transformations. Global declines of megafauna, such as the extinction of the Steller's sea cow, are largely a consequence of human action and likely had significant and widespread ecological impacts.

Drawing on historical evidence, kelp forest ecology, and extant mammalian herbivore ecology, I first propose six discrete hypotheses about the effects Steller's sea cows may have had on North Pacific kelp forest dynamics. The natural history observations, historic accounts, and ecological evidence I review offer partial support for these hypotheses. Accordingly, I argue that Steller's sea cows exerted a significant top-down influence in kelp forests, likely affecting physical ecosystem structure, productivity, nutrient cycling, species interactions, and the export of nutrients to surrounding ecosystems.

Next, I build upon these hypotheses to develop an ecosystem model which re-introduces this extinct megaherbivore and highlights its former role in ecosystem dynamics and species interactions in kelp forests. I find that, while not a keystone species, Steller's sea cows likely had a significant effect on ecosystem dynamics, influencing community composition and increasing the productivity and resilience of kelp forests. The model indicates the presence of Steller's sea cows may also have enabled the coexistence of sea otters and some large invertebrates,

suggesting that the often-seen decline of invertebrate populations caused by sea otters may be a phenomenon exacerbated by lost ecosystem functions and species interactions associated with the extinction of the Steller's sea cow.

My findings suggest that kelp forest dynamics and resilience were significantly altered prior to the influence of more recent and well-known stressors, and demonstrate the important ecological roles that can be lost with megafaunal extinction. This work also illustrates the degree to which the loss of species interactions has likely affected North Pacific ecosystems, and how using ecosystem models to consider past ecosystem dynamics can inform management and restoration of current social-ecological systems.

Lay Summary

Understanding how the long history of human influence has changed ecosystems is critical for effectively addressing the widespread declines seen in nature. My research focused on one specific change, the extinction of the Steller's sea cow (a large coastal grazer), and its consequences for the North Pacific Ocean. I found that Steller's sea cows were more important than is often thought, in that their extinction may have had a large impact on kelp forest ecosystems. I also found that considering the missing role of the Steller's sea cow may help us understand current challenges in the management of kelp forests. This research shows that it is important to understand the many ways human actions have changed ecosystems, even if those changes happened hundreds or thousands of years ago. Studying these changes helps us better understand the history of these ecosystems, and hopefully improve their future management and restoration.

Preface

The two research chapters presented in this thesis (Chapter 2 and Chapter 3) are intended to be individual manuscripts submitted for publication in academic journals. Each of these chapters is deliberately self-contained, and therefore includes some repetition, primarily in the introductory and concluding remarks.

Chapter 2 has been prepared for submission to a peer-reviewed journal. I am the lead author of this manuscript, responsible for concept formation and writing. I was assisted in this research by several coauthors. Alberto Campos contributed to both concept formation and writing for subsection 2.4.6, as well as provided feedback on the manuscript. As members of the supervisory committee, Dr. Edward Gregr and Dr. Iain McKechnie assisted with concept design and provided feedback on the manuscript. As the supervisor and principle investigator of this research, Dr. Kai Chan provided initial project and concept design, assisted in the formation of the supervising committee, and provided substantial feedback on the manuscript.

Chapter 3 has also been prepared for submission in a peer-reviewed journal. I am the lead author of this manuscript, responsible for concept formation, research design, data analysis, data visualization, and writing. I was assisted in this research by several coauthors. As members of the supervisory committee, Dr. Edward Gregr and Dr. Villy Christensen assisted with concept formation, research design, data analysis, data visualization, and provided substantial feedback on the manuscript. As the supervisor and principle investigator of this research, Dr. Kai Chan provided initial project and concept design, assisted in the formation of the supervising

committee, assisted in the analysis and visualization of data, and provided substantial feedback on the manuscript.

The Appendix supports the modelling approach employed in Chapter 3, and provides additional detail on specific methods and model parameters. This appendix is intended to be published as supporting material alongside Chapter 3. I am the lead author of the Appendix, responsible for data analysis and writing. However, Table A2 has been adapted from the doctoral dissertation of Dr. Edward Gregr (2016).

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Considering the number of people who have contributed to this work – intellectually, emotionally, and literally – it almost feels wrong to have mine be the only name on the cover. I hope you are content with my immense gratitude.

Chapter 1: Introduction

Humanity is increasingly recognizing the prevalence and magnitude of the ecological degradation our actions have caused. Natural habitats have been lost (Brooks et al. 2002, Beck and Airoldi 2007), species and populations driven to extinction (Dulvy et al. 2009, Barnosky et al. 2011, Ceballos et al. 2017), and animal abundance reduced (Dirzo et al. 2014, McCauley et al. 2015), with human impacts continuing at unprecedented rates (Ceballos et al. 2015, IPBES 2019a, 2019b, Halpern et al. 2019). The pervasiveness of these human impacts means that no ecosystem can be considered untouched by human activity (Jackson 2001, Donlan et al. 2006), and some have argued that we have now entered into a new geological epoch defined by human influence; the Anthropocene (Steffen et al. 2011).

These anthropogenic changes have had significant implications for species interactions and ecological processes (Estes et al. 2011, Malhi et al. 2016), with consequences for the health and functioning of ecosystems, as well as the services people derive from these ecosystems (MEA 2005, Worm et al. 2006, IPBES 2019a). These consequences have been diverse and extensive, including changing wildfire and disease regimes (Ostfeld and Holt 2004, Lafferty 2004, Gill et al. 2009), altering the distribution of nutrients on land and in the ocean (Roman and McCarthy 2010, Doughty et al. 2013, Doughty 2017), and disrupting atmospheric carbon cycles (Schindler et al. 1997, Smith et al. 2010, Wilmers et al. 2012) to name just a few. In many cases, these changes have resulted in a loss of resilience and set the stage for current and future ecological declines (Jackson et al. 2001, Folke et al. 2004, Smith et al. 2016). Ecological degradation and

the loss of biodiversity are ultimately undermining the ability of ecosystems to sustain both themselves and the people who depend on them (IPBES 2019a, Díaz et al. 2019a).

Thus far, efforts to address biodiversity loss have largely centered on mitigating human impacts and conserving remaining biodiversity (Butchart et al. 2010, Tittensor et al. 2014). While critically important, there is a growing recognition that slowing the decline alone is not enough, and it is necessary to restore degraded ecosystems and ‘bend the curve’ of biodiversity loss (Mace et al. 2018, Díaz et al. 2019a). In many systems, restoration may help return ecosystems to more productive and resilient system states (e.g., Watson and Estes 2011, Ripple and Beschta 2012, Valdez et al. 2020, Guyton et al. 2020). Accordingly, the 2020-2030 period has been designated the decade for ecosystem restoration by the United Nations (UNEP and FAO 2020), and there are increasing calls for novel restoration and rewilding approaches (Donlan 2005, Seddon et al. 2014a, Svenning et al. 2016). Combined with ongoing efforts to minimize human impacts and conserve biodiversity, it is hoped that restoration may have the potential to help reverse widespread ecological degradation.

It is well known that individual species can play vital roles in structuring ecosystems. For instance, past research has identified apex consumers (Hairston et al. 1960, Estes et al. 2011), foundation species (Dayton 1975, Angelini et al. 2011), and keystone species (Paine 1969, Mills et al. 1993, Power et al. 1996) as types of species with particularly important functions in ecosystems. Recent loss or gain of these critical species has also been shown to have significant and widespread implications for ecological processes (Estes and Palmisano 1974, Ellison et al. 2005, Ripple and Beschta 2007). In many cases, species that were driven extinct or were reduced

in abundance may also have played more important roles in structuring ecosystems than is often recognized (e.g., Domning 2001, Roman et al. 2014, Bakker et al. 2016). Identifying these key missing species, and understanding the role once played by these ecological “ghosts” (Janzen and Martin 1982, Dayton et al. 1998, Silliman et al. 2018), is pivotal to recognizing the true magnitude of change in these systems.

However, a major challenge in addressing the loss of biodiversity is the insidiousness with which it has progressed. Many ecosystems have been gradually degraded over centuries or millennia (Dayton et al. 1998, Lotze et al. 2006, Estes et al. 2011, Stephens et al. 2019), inhibiting our ability to understand the true magnitude of change and resulting in what has been called the shifting baseline syndrome (Pauly 1995, Soga and Gaston 2018). These shifting baselines mean that historical abundances and sizes of species are often unimaginable by today’s standard (Jackson et al. 2001, Lotze et al. 2006), but more importantly, it may also mean that the underlying structure and function of the ecosystem was different. In several cases, we have reason to believe that historical anthropogenic change resulted in substantial change to fundamental ecological processes (e.g., Janzen and Martin 1982, Estes et al. 2011, Doughty et al. 2013). Thus, shifting baselines often result in the historical system state, and the potential target for ecological restoration, being unknown. Considering these historical baselines is critical to understand how ecosystems have changed over historical timescales and inform restoration and conservation efforts in these degraded ecosystems.

1.1 Approaches for studying historical system states

While important, the study of historical baselines and their ecological functioning may be challenging. There is an obvious mismatch between anthropogenic change, which has occurred over centuries or millennia (Martin 1966, Dirzo et al. 2014, Stephens et al. 2019), and ecological data, which is usually on the order of decades or less (Dayton et al. 1998, Jackson 2001, Hobbie et al. 2003). Therefore, research on historical baselines often relies upon paleoecological, archaeological, and historical evidence to elucidate early anthropogenic change (Jackson 2001, Lotze et al. 2006). Often, such research is by necessity exploratory, drawing on these diverse bodies of literature and lines of evidence to generate hypotheses about past ecosystem conditions and dynamics that cannot be studied directly (Janzen and Martin 1982, Dayton et al. 1998, Jackson 2001). Despite being exploratory in nature, this research can be invaluable for illustrating what ecosystems may have looked like prior to alteration.

Ecological modelling may complement these approaches, allowing past and future system states to be examined more quantitatively, even in the absence of direct data (e.g., Christensen and Walters 2004, Harfoot et al. 2014), and may result in a plausible (if not “correct”) understanding of ecological change (Box 1976, Fulton et al. 2003) due to physiological and ecological constraints. Ecosystem models have proven useful in several such cases, shedding light on both historical (e.g., Pitcher 2005, Ainsworth et al. 2008, Doughty 2017) and future (e.g., Lotze et al. 2019, Gregr et al. 2020) system states. Modelling approaches therefore provide quantitative estimates of how anthropogenic change has affected ecosystems over larger timescales than is possible using ecological data alone.

However, for ecosystem models to be useful in characterizing uncertain historic baselines it is important that they are able to capture underlying changes in species interactions and ecosystem structure that may have occurred. The majority of ecosystem models have not been designed to address these structural changes, often assuming static relationships and processes (GREGG and Chan 2015). Considering these structural relationships, to which models may be very sensitive (Wood and Thomas 1999), is key to accurately portraying the effects of anthropogenic change. To the extent that models are able to capture changes in species interactions and ecological dynamics, they may increase our understanding of historical baselines, and in so doing illustrate what might be possible through conservation and restoration.

Here, I use both approaches – synthesis of available evidence to generate hypotheses and ecological modelling – to examine historical anthropogenic change in an ecologically and socioeconomically important marine ecosystem, kelp forests.

1.2 Case study

Coastal rocky reefs of the Northeast Pacific are often held up as a system that was significantly altered by human influence but has benefited from restoration. Sea otters were extirpated from much of the Northeast Pacific by hunting (Kenyon 1969, Ravalli 2018), but the recovery (and active reintroduction; Jameson et al. 1982) of this keystone species has resulted in the return of highly productive kelp forest ecosystems (Estes and Palmisano 1974, Steneck et al. 2002, Gregg et al. 2020). In the absence of sea otters or other predators (e.g., Burt et al. 2018), invertebrate

herbivores such as sea urchins may consume all available kelp, resulting in an alternate stable state referred to as an urchin barren (Steneck et al. 2002, Filbee-Dexter and Scheibling 2014). Thus, the return of sea otters and kelp forests in the Northeast Pacific is often portrayed as a reversal of past degradation and a conservation success story (Sea Otter Recovery Team 2007, Nichol 2015).

However, the recovery of sea otters and associated ecological transitions have resulted in tension and conflict. Abundances of some species, primarily large invertebrates (Watson 2000, Fisheries and Oceans Canada 2012), have suffered in the presence of sea otters, along with the livelihoods and traditions of coastal communities who depend on these species (Salomon et al. 2015, Pinkerton et al. 2019, Burt et al. 2020). There is also reason to believe that the state being restored by sea otter recovery is substantially different to the historical system state maintained by Indigenous peoples across the Northeast Pacific (Simenstad et al. 1978, Corbett et al. 2008, Szpak et al. 2012, 2013). Therefore, this restoration of top-down ecosystem control by sea otters represents the reversal of one recent ecological shift but may neglect to consider the history of the system and other ways in which the ecosystem has been altered by human influence.

Missing from many discussions of kelp forest dynamics and restoration is a consideration of the now extinct Steller's sea cow (*Hydrodamalis gigas*). The sea cow was a large, cold-adapted sirenian once found around the North Pacific Rim from Japan to Northern Mexico (Domning 1978). Available evidence suggests that this megaherbivore was an obligate algivore, subsisting on the large, productive macroalgae of North Pacific kelp forests (Domning 1978, Estes et al. 2016a). It is believed that sea cows were extirpated from much of this range thousands of years

ago by the expansion of humans around the North Pacific Rim, although in some locations it would appear sea cows and indigenous peoples coexisted for hundreds or thousands of years (Domning et al. 2007). Sea cows persisted until recent times only in remote and infrequently habited areas of the North Pacific (Steller 1751, Domning 1978). It was here, at the Commander Islands, that the final remnant population of this megaherbivore was driven extinct in 1768 (Domning 1978), making it one of only a few known marine extinctions (Dulvy et al. 2009, McCauley et al. 2015).

As a megaherbivore in an ecosystem now conspicuously lacking large herbivores, the extinction of the sea cow may have significantly changed kelp forest dynamics. It has previously been suggested that the sea cow played an important ecological role in kelp forests (Domning 1989, Estes et al. 1989) and that they may even have been a keystone species (Pitcher 1998). Thus, their extinction represents a substantial change in North Pacific kelp forests, yet very little research has examined what the effects of this change may have been. Improving our understanding of these changes may help inform the conservation and restoration of this important ecosystem.

1.3 Research objectives

While kelp forests have been the focus of substantial study, Steller's sea cows were likely an important component of this system yet have received little attention. The objective of this research is therefore to consider the role of this megaherbivore in kelp forests of the North Pacific. In so doing, this project aims to provide insight into the historical baseline of this system

and inform its future management and restoration. Further, North Pacific kelp forests are one of many ecosystems where important species or functions have been lost, and this case study may expand our understanding of the numerous ways in which ecosystems have been altered by human activity. The main questions addressed by this research are:

1. *What functional role did the Steller's sea cow play in North Pacific kelp forests?*

To approach this question, I reviewed multiple lines of evidence to generate several hypotheses as to the effects Steller's sea cows may have had on kelp forest dynamics (Chapter 2). Drawing on historical descriptions of sea cows, kelp forest ecology, and the study of analogous large herbivores more generally, Chapter 2 argues that sea cows likely exerted an important top-down influence in North Pacific kelp forests. By proposing an answer to this research question, Chapter 2 also provides insight into the ways kelp forest dynamics have been altered by human actions over millennia.

2. *How might the presence of Steller's sea cows alter kelp forest community composition and ecosystem dynamics?*

This question was addressed, for a portion of the presumed original sea cow range, by adapting an existing ecosystem model to examine the hypothetical reintroduction of sea cows on the West Coast of Vancouver Island (Chapter 3). Chapter 3 uses the understanding of sea cow ecology developed in the previous chapter to examine the consequences of sea cow presence for the community composition, productivity, and resilience of Northeast Pacific kelp forests. Chapter 3

illustrates the degree to which sea cow extinction may have altered Northeast Pacific kelp forests, and provides insight into how considering these past ecosystem dynamics may inform future management and restoration of this social-ecological system.

3. *Are ecosystem models able to appropriately represent hypothesized species interactions and their consequences for ecosystem function?*

This final research question was examined using the same ecosystem model in Chapter 3. The modelling approach I employed was able to represent many, but not all, of the relevant species interactions associated with the sea cow. Chapter 3 demonstrates that ecosystem models can be a valuable tool for addressing questions of past and future ecological function, but certain complex species interactions and structural uncertainties remain hard to address.

Chapter 2: The Ghost of a Giant - Six Hypotheses for How an Extinct Megaherbivore Structured Kelp Forests Across the North Pacific Rim

2.1 Introduction

“no matter how well one understands kelp populations, any current program will fail to discern the ghosts of missing animals.” – Dayton et al. (1998)

Humanity has played a role in the decline of countless species, resulting in a rapidly accelerated extinction rate and leading many to argue that we are currently experiencing the Earth’s sixth mass extinction (Barnosky et al. 2011). Amongst those groups that have been most susceptible to extinction are the megafauna (Ripple et al. 2015, 2019), many of which disappeared thousands of years ago during the Late Pleistocene (Barnosky 2008, Malhi et al. 2016). While climatic changes contributed to some of these extinctions, current evidence suggests that humans contributed to the lost megafauna diversity and abundance around the globe (Martin 1966, Barnosky et al. 2004, Koch and Barnosky 2006, Broughton and Weitzel 2018).

While considerable effort has been devoted to understanding why these large animals went extinct (reviewed in Burney and Flannery 2005, Koch and Barnosky 2006), scientists have only recently begun to explore the ecological consequences of these extinctions (Malhi et al. 2016, Tóth et al. 2019). There is increasing evidence that the decline of megafauna in ecosystems around the world markedly altered ecosystem dynamics and functions, including nutrient cycling

(Roman and McCarthy 2010, Berzaghi et al. 2018), community composition and diversity (Janzen and Martin 1982, Wigley et al. 2014, Faurby and Svenning 2015), trophic interactions (Janzen and Martin 1982, Estes et al. 2011), climate (Smith et al. 2010), and the physical structure of ecosystems (Bakker et al. 2016a). Much of this research has focused on the loss of particularly important species, such as apex predators, keystone species, or ecosystem engineers (e.g., Ripple and Beschta 2007, Estes et al. 2011, Roman et al. 2014), however given their role in influencing flows of energy and system dynamics (Ehrlich and Mooney 1983, Smith et al. 2016), the loss of any megafauna species is likely to have ecological consequences. These consequences may be particularly pronounced when the species in question is the only representative of an entire functional group (Folke et al. 2004, Saint-Béat et al. 2015).

Marine environments have largely been spared megafaunal extinctions on the scale of terrestrial systems (Dulvy et al. 2009, McCauley et al. 2015), but centuries of human influence and declining large animal abundances means that very few, if any, marine ecosystems can be considered pristine (Jackson et al. 2001, Jackson 2001, Lotze et al. 2006). Even if extinctions have been rare, the consequences of reduced marine megafauna abundance is increasingly being recognized (Roman et al. 2014, McCauley et al. 2015, Estes et al. 2016b). In both marine and terrestrial communities we are left with simplified ecosystems and lost ecological functions, the “ghosts” of the megafauna (Dayton et al. 1998).

One such marine ecosystem that has been altered by anthropogenic change, including extinctions, are kelp forests (Dayton et al. 1998, Jackson et al. 2001, Krumhansl et al. 2016). These highly productive ecosystems are common along rocky temperate coastlines around the

world (Mann 1973, Steneck et al. 2002), and provide numerous important ecosystem services today (Smale et al. 2013, Gregr et al. 2020) and throughout the Holocene (Erlandson et al. 2007, Corbett et al. 2008, Braje et al. 2017). Kelp forests of the North Pacific are also notable for being the scene of one of the only known marine megafaunal extinctions, the 18th century extinction of the Steller's sea cow (*Hydrodamalis gigas*) (Domning 1978, Estes et al. 1989). Like many coastal ecosystems, kelp forests and their associated services are also threatened by contemporary anthropogenic stressors such as overgrazing (Steneck et al. 2002), climate change (Harley et al. 2012), fishing (Steneck et al. 2013), and invasive species (Levin et al. 2002). Indeed, the global decline of kelp forests has been identified as an emerging conservation issue (Sutherland et al. 2019). While much has been written on these more recent changes in kelp forests (Steneck et al. 2002, Smale et al. 2013, Ling et al. 2015, Krumhansl et al. 2016, Wernberg et al. 2019), very little is known about the role of the sea cow, and how its loss may have transformed kelp forests of the North Pacific.

Understanding the role once played by missing species, such as the sea cow, and the consequences of their extinction is essential for assessing how humans have altered kelp forest ecosystems (Dayton et al. 1998). This, in turn, is increasingly seen as central to informing the conservation and restoration of these systems (Jackson 2001, Estes et al. 2016b). In this paper we ask how sea cows may have structured kelp forests of the North Pacific, and how their extinction altered kelp forest dynamics. By synthesizing historical and present ecological lines of evidence, we identify six mechanisms through which sea cows may have fundamentally controlled kelp forest dynamics.

2.2 Steller's sea cows and kelp forests

The Steller's sea cow was a large, herbivorous sirenian, so named because it was first described by naturalist Georg Steller (Steller 1751). Steller encountered the sea cows in 1741 while shipwrecked at the remote and uninhabited Commander Islands of the North Pacific. It is now thought that by this time, the Commander Islands, perhaps along with other remote areas of the North Pacific (Domning et al. 2007, Crerar et al. 2014b), were the final refuge of a species already in decline (Domning 1978).

Sea cows were the last surviving species of hydrodamalid sirenians, which are thought to have adapted to cold-waters during Mio-Pliocene cooling, and spread across the North Pacific (Domning 1978). Fossil evidence suggests that at their peak, sea cows were distributed throughout the coastal waters of the North Pacific from Japan to Baja California (Domning 1978, Domning et al. 2007). As recently as 20,000 years ago, sea cows were present along much of the North American Pacific Coast (Domning 1978), however the peopling of the Americas and subsequent aboriginal hunting is presumed to have extirpated the sea cow from much of this range (Domning 1978, Estes et al. 2016a). Though the timing of this extirpation is uncertain, it likely occurred sometime between the Pleistocene and the arrival of European explorers in the North Pacific, and it has been suggested that in some cases Indigenous peoples and sea cows likely coexisted for hundreds or thousands of years (Domning et al. 2007).

The remnant population encountered and described by Steller in 1741 was lost when commercial fur hunters (primarily targeting sea otters) began visiting the Commander Islands and used sea

cows as their main source of food (Stejneger 1887). The impact of these hunting expeditions was so intense that direct overharvest of sea cows (Domning 1978, Turvey and Risley 2006), perhaps in combination with habitat alteration associated with loss of sea otters (Anderson 1995, Estes et al. 2016a), drove the sea cow to extinction by 1768 (Stejneger 1887), less than 30 years after their description.

The sea cow was incredibly large, with Commander Island individuals estimated to reach more than 5000 kg in weight and 7 meters in length (Domning 1978). However, based on Steller's observations, Domning (1978) argues the Commander Islands were marginal habitat for the sea cow, and consequently the species may have been even larger elsewhere in their range where oceanographic conditions would have been more favourable. In addition to being so large, the sea cow appears to have been largely restricted to the surface, and was perhaps completely unable to dive or submerge (Steller 1751, Stejneger 1887). Both observational (Steller 1751) and morphological (Domning 1978) evidence suggests that these giant sirenians were obligate algivores, grazing especially upon the large, canopy forming kelps that make up the kelp forests of the North Pacific (Steller 1751, Stejneger 1887, Estes et al. 2016a). The North Pacific contains the greatest diversity of kelps on earth (Bolton 2010, Starko et al. 2020), and sea cows almost certainly consumed a wide variety of macroalgae (Domning 1978). Sea cow diets likely included larger understory and intertidal macroalgae, but would have mainly consisted of the dominant canopy forming kelp genera of the North Pacific, including *Nereocystis*, *Laminaria*, *Eualaria*, and *Macrocystis* (depending on location; Wernberg et al. 2019), some of which (e.g. *Nereocystis* and *Eualaria*) may be annuals and thus available only at certain times of year (Dayton 1985).

As part of this evolutionary specialization on macroalgae, the sea cow completely lost its dentition, retaining only a set of boney pads for grinding algae (Steller 1751, Domning 1978). Given their aversion or inability to submerge, sea cow grazing on kelps is likely to have been restricted to approximately the upper meter of the kelp canopy or intertidal macroalgae (Domning 1989, Anderson 1995). It was additionally noted that sea cow movement was “sluggish” (Stejneger 1887), with animals rarely observed far from shore, and they exhibited an apparent preferences for shallow, sheltered areas and the mouths of rivers and creeks (Steller 1751), potentially concentrating their influence in kelp beds in bays, estuaries, and other protected locations (Domning 1989). Within this restricted foraging range, limited by both depth and wave exposure, the sea cow is said to have grazed “incessantly” (Steller 1751) and were likely dependent on kelp as abundant sources of food (Anderson 1995, Estes et al. 2016a).

As with other marine megafauna that are thought to have a large influence on marine ecosystems (Estes et al. 2016b), it is likely that the sea cow’s large size and appetite would have translated into a significant impact on the kelp forests in which they lived (Estes et al. 1989, Pitcher 1998). To fully understand kelp forests and how they have been altered by human action, one must therefore consider the ecological role of this extinct megaherbivore.

2.3 Lines of evidence

It is challenging to assess the role globally extinct megafauna would have played in ecosystems. It is much simpler to address this question for locally extinct species, or where the ecological data includes the pre- extinction period. In the absence of such contemporary observations, other

potential sources of knowledge allow us to imagine how such extinct species might have interacted with and altered the ecosystem in which they lived: historic description of live animals, the fossil record, and extrapolation from present analogues. Here, we synthesize knowledge from all three approaches to explore the role once played by Steller's sea cows.

Historic data from ships logs, naturalist notes, and oral histories provide insight into the ecology of sea cows, which are described extensively by Steller and other scientists (Stejneger 1887), and in the histories and archaeological records of at least some peoples of the Aleutian Islands (Domning et al. 2007, Corbett et al. 2008). Steller's detailed notes on sea cow behaviour, and his description of a dissection of an adult female sea cow (Steller 1751), are an invaluable and rare source of knowledge for this extinct megafauna. However, the interpretation of these historical records is not always straightforward (Pooley 2018), and requires a recognition of the limitations and context of these historical records (Taylor 2013). For instance, 'sea cows' have been mentioned in the journals and ships logs of several explorers and sailors south of the Aleutian Island on the coast of what is now British Columbia (Meares 1790, Jewitt 1807) since their apparent extinction in the late 18th century, but it is unclear if these descriptions are specific to sea cows and these records have not been substantiated with archival or archaeological research (McKechnie and Wigen 2011).

Additional insight into the biology of extinct species may be gained through the study of fossil remains. This approach is increasingly seen as a valuable source of knowledge for many globally extinct species and degraded ecosystems (Dietl and Flessa 2011, Rick and Lockwood 2013). In the case of sea cows, Domning (1978) conducted an extensive review of sirenian evolution in the

North Pacific, paying special attention to the distribution, biology, and ecology of the sea cow (also see Stejneger 1887, Anderson 1995, Domning et al. 2007, Crerar et al. 2014a). The understanding gained from the direct study of remains and fossils is likely to be the most robust but is limited in scope. Our understanding of sea cows from direct study is primarily restricted to the evolutionary history and biology of this species, and is largely unable to shed light on species interactions.

To examine ecosystem processes and species interactions that may have been lost through species extinctions, it is helpful to examine present day system dynamics and the role of extant, potentially analogous species. Fortunately for this examination of sea cows, North Pacific kelp forest dynamics – particularly in relation to herbivory – have received extensive attention and provide a robust framework within which to examine the role of sea cows (e.g., Dayton 1985, Steneck et al. 2002).

Analogous processes from other systems can also shed light on the ecology of the sea cow. Systems where large grazers still exist or have been lost more recently, as well as ecological theories derived from the study of such systems (e.g., McNaughton 1985), provide insights into the consequences of lost sea cow grazing in kelp forests. The primary analogue examined here is the dugong (*Dugong dugon*), the closest living species to the sea cow and an important grazer in seagrass ecosystems (Preen 1995, Valentine and Duffy 2006).

2.4 Hypothesized effects on community structure and ecosystem function

Large herbivores play important structural and functional roles in many ecosystems (McNaughton et al. 1997, Ripple et al. 2015, Bakker et al. 2016b), and their loss can have significant effects on ecosystem processes (Ripple et al. 2015, Doughty 2017). We have every reason to believe that the sea cow would have been similar, especially as sea cows co-evolved with kelp forests for at least 8-10 million years (Domning 1978, 1989, Estes and Steinberg 1988). Given the large size of the sea cow, their “incessant” grazing, and their tendency to live in small family herds (Steller 1751, Anderson 2002) – as well as their cold environment and reliance on relatively indigestible kelp forage (Domning 1978, 1989, Best 1981) – it is likely that where sea cows were found, they would have been a significant source of herbivory for shallow and canopy kelps (Domning 1989). The strength of this herbivory and its subsequent effects would almost certainly have been density dependent, and varied geographically in response to sea cow distribution and habitat preferences (Lubchenco and Gaines 1981, Domning 1989). Sea cow herbivory on kelp canopies would also have differed from extant herbivores, such as sea urchins which consume kelp holdfasts (Mann 1988, Filbee-Dexter and Scheibling 2014, Stevenson et al. 2016), and therefore have had very different ecological impacts. Here, we outline six hypothesized impacts of sea cow herbivory in kelp forests (Table 2.1 and Figure 2.1).

Table 2.1 Summary of hypothesized effects of Steller’s sea cow herbivory on the structure and dynamics of kelp forests of the North Pacific.

Ecosystem Effects	Description	Potential Consequences
1. Physical ecosystem structure	Sea cow herbivory of intertidal and canopy kelp likely altered the physical structure and community dynamics of kelp forests. Spatially restricted sea cow grazing would have decreased littoral and surface macroalgae biomass, but likely increased understory macroalgae biomass and diversity.	Decreased littoral seaweed and canopy kelp biomass near the surface Increased understory kelp biomass and diversity Altered biogenic habitat complexity, hydrodynamic flows, and patterns of larval settlement
2. Primary productivity	Through the consumption of fronds (not stipes), sea cow herbivory may have encouraged compensatory growth in grazed canopy kelps, and reduced light limitation resulting in increased productivity in understory kelp and phytoplankton.	Compensatory growth in grazed kelps Increased productivity of phytoplankton and understory seaweeds Constant (or increased) overall system productivity
3. Nutrient cycling & availability	Through physical grazing as well as the digestion of kelp biomass sea cows may have accelerated nutrient cycling and increased nutrient availability.	Increased nutrient cycling and availability of kelp-derived nutrients Increased secondary productivity throughout ecosystem, particularly in suspension feeders
4. Mediation of predator-prey interactions	Sea cows may have increased the availability of kelp particles and associated nutrients (hypothesis 3) and abundance of understory macroalgae (hypothesis 2), altering the vulnerability of prey and mediating predator-prey interactions such as the vulnerability of large mobile invertebrates to sea otter predation.	Reduced prey foraging times and vulnerabilities Increased invertebrate biomass and diversity due to expanded refuge from sea otter predation
5. Kelp export	Grazing by sea cows may have altered the amount of kelp exported from kelp forests, and changed the timing (i.e. seasonality) of this export.	Altered magnitude and lateral transport of kelp export Reduced seasonality of kelp export Changes in secondary productivity of receiving habitats
6. Biotic dispersal	Sea cows may have enhanced kelp recruitment and dispersal through physical grazing and/or the ingestion and transportation of spores. Kelp spores associated with sea cow feces may have experienced altered survival rates.	Increased spore dispersal distance Changes in spore dispersal dynamics Facilitate colonization of new areas and kelp genetic exchange

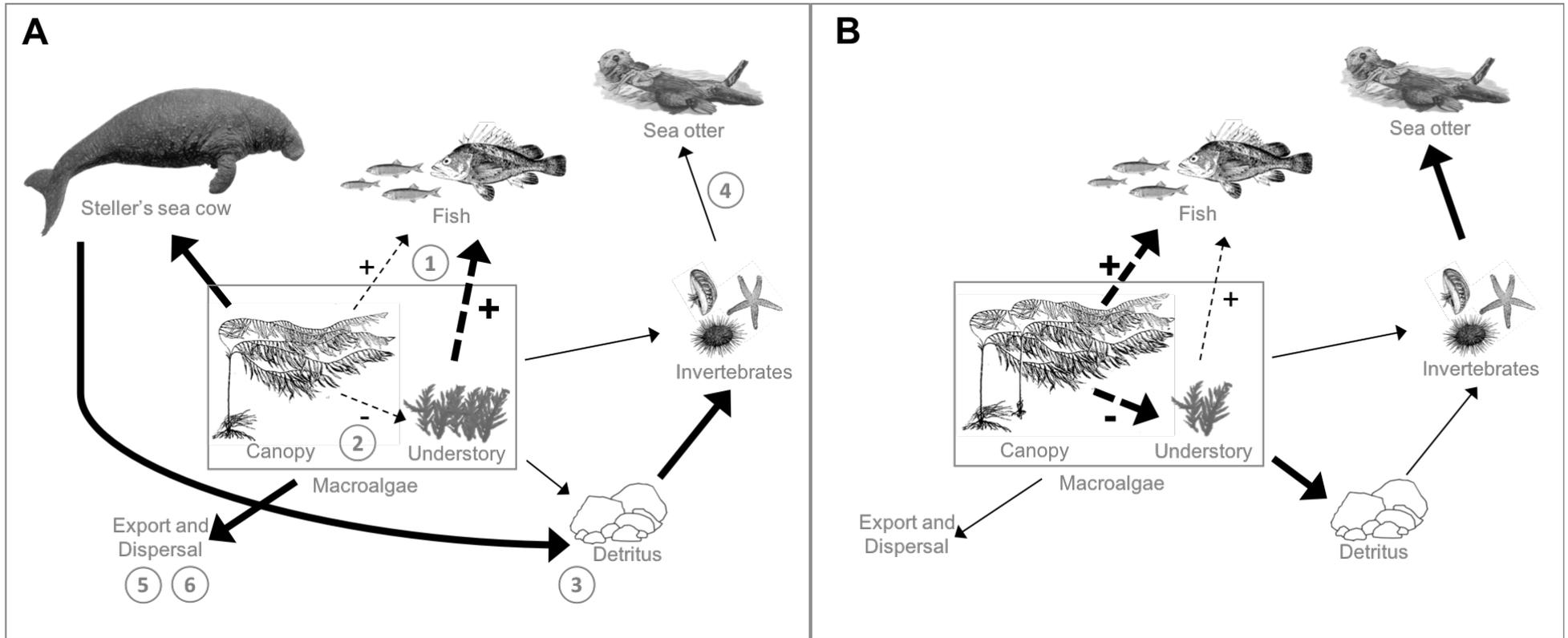


Figure 2.1 Kelp forest interaction web in the presence and absence of Steller's sea cows.

Simplified interaction web illustrating material flows (e.g., trophic, solid arrows) and indirect interactions (dashed arrows, positive or negative effects shown with '+' and '-') in the presence (A) and absence (B) of Steller's sea cows. The weight of the line corresponds to the relative strength of the interaction in the two system states. Numbers in (A) correspond to the six hypothesized effects of Steller's sea cow herbivory: 1) physical ecosystem structure, 2) primary productivity, 3) nutrient cycling, 4) predator-prey interactions, 5) kelp export, and 6) biotic dispersal. See the list of reproduced images for image citations.

2.4.1 Modified physical ecosystem structure

The primary direct effect of sea cow herbivory would have been on the biomass and distribution of its kelp forage. Given their intense grazing (Steller 1751), sea cows likely reduced canopy and littoral kelp biomass significantly in zones of heavy sea cow herbivory (Table 2.1). However, in subtidal areas where sea cows would have grazed on canopy kelps at the surface, a reduction in kelp canopy may have been associated with an increase in understory macroalgae biomass due to increased light availability (see following section; Reed and Foster 1984, Estes et al. 1989, Miller et al. 2011). Both canopy and understory kelps are known to play important structural roles in rocky reef ecosystems, providing complex three-dimensional habitat relied upon by numerous species (Duggins 1988, Markel 2011, Markel and Shurin 2015, Teagle et al. 2017), altering hydrodynamic flow rates (Eckman et al. 1989), and increasing larval retention and survival (Duggins et al. 1990, Eckman and Duggins 1991). Reduction in kelp biomass by other herbivores, predominately sea urchins, has been demonstrated to effect many of these ecosystem functions (Dayton 1985, Wilmers et al. 2012, Filbee-Dexter and Scheibling 2014, Ling et al. 2015). It is therefore likely that by grazing on surface and littoral kelp and in some cases mediating an increase in understory kelp biomass, sea cows would have altered the physical structure of the ecosystem and many of these important processes (Figure 2.1). It has even been suggested that by increasing abundance of understory macroalgae, sea cows may have decreased the abundance of benthic suspension feeders (e.g., bivalves, tunicates, bryozoans, etc.) that compete for space with understory macroalgae (Estes et al. 1989, Arkema et al. 2009).

Sea cow herbivory would therefore seem to constitute a top-down influence on kelp biomass and habitat structure now absent from North Pacific kelp forests. The spatial limits of sea cow grazing (i.e. only shallow and surface kelp) differs markedly from other herbivores such as sea urchins (Estes et al. 1989), and it is unlikely sea cows could have locally extirpated kelp forests as sea urchins do. Additionally, wave action likely would have affected the geographical extent of sea cow herbivory, restricting grazing to less exposed kelp forests (Domning 1989).

Therefore, while likely significant, the magnitude of the impact on kelp biomass by sea cows and the subsequent consequences for ecosystem functions such as habitat structure and larval retention are largely uncertain. Whatever influence they would have had was likely spatially heterogeneous, and would have worked in concert with other forms of disturbance, such as invertebrate herbivory and wave stress.

2.4.2 Altered primary productivity

Kelp forests are one of the most productive ecosystems in the world (Mann 1973), providing much of the production in many temperate coastal systems (Steneck et al. 2002, Krumhansl and Scheibling 2012). While grazing by sea cows would have reduced standing kelp biomass, it does not necessarily follow that algal primary productivity would similarly be reduced (Table 2.1).

Both compensatory growth and increased light availability may compensate for the effect of sea cow herbivory on kelp biomass to maintain the primary productivity of kelp forests.

Compensatory plant growth as a tolerance mechanism in response to herbivory is well described in a variety of terrestrial systems (reviewed in McNaughton 1983, Stowe et al. 2000), and to a

lesser extent in marine systems such as seagrasses (Valentine and Duffy 2006) and some kelps (Cerda et al. 2009, Gao et al. 2013, Franco et al. 2017). Most notably, *Macrocystis* (a dominant kelp of the Northeast Pacific) has been found to exhibit a large capacity for regrowth in response to commercial harvest (Krumhansl et al. 2017) [but see Geange (2014) for a counter example], a process that removes only the floating canopy in a manner remarkably similar to how sea cows may have grazed on canopy kelps. Krumhansl et al. (2017) found that individual *Macrocystis* canopies recovered from harvest at a rate of 4-30 cm/day, resulting in the recovery of 35-150% of pre-harvest canopy biomass after 4 weeks. This suggests that grazing by sea cows on *Macrocystis*, and perhaps other kelps of the North Pacific, may have encouraged rapid regrowth at a similar pace in grazed kelps. However, other kelps of the North Pacific (e.g., *Nereocystis*) may have a lower capacity for regrowth, and thus be more effected by canopy removal (Roland 1985, Springer et al. 2007). As in other grazing systems (Dyer 1982, McNaughton 1983), the importance of compensatory growth in sea cow forage was likely density and condition dependent, and would have varied with grazing intensity and environmental conditions (e.g., Oshurkov and Ivanjushina 1993). Therefore, while sea cow herbivory may have reduced kelp biomass, high productivity and compensatory growth may have quickly compensated for, or even have exceeded, lost biomass under some grazing regimes.

Sea cow grazing may also have increased light availability, an important determinant of kelp forest productivity and composition, as autotrophs such as phytoplankton, kelps, and other macroalgae compete for light as well as other nutrients (Dayton et al. 1984, Steneck et al. 2002, Desmond et al. 2015). Canopy forming kelps in particular can limit light availability in rocky reefs (Reed and Foster 1984). This shading has been shown to limit productivity and recruitment

(Reed and Foster 1984, Borchers and Field 2009), with removal of canopy kelps resulting in significant increases in productivity of phytoplankton and understory macroalgae (Miller et al. 2011), as well as juvenile macroalgae recruitment (Reed and Foster 1984, Santelices and Ojeda 1984). Miller et al. (2011) found that the increased productivity from understory algae can completely compensate for lost canopy kelps, resulting in total productivity remaining relatively constant. The increased light availability in combination with compensatory growth in grazed kelps may have counteracted any kelp biomass reduction to maintain, or even increase, overall productivity of the system (Figure 2.1). Given the importance of macroalgal productivity to coastal ecosystems (Steneck et al. 2002, Gregr et al. 2020), any increase in productivity caused by sea cows would have had significant implications for nutrient availability throughout coastal ecosystems.

2.4.3 Increased nutrient cycling and availability

Large herbivores are thought to play a critical role in accelerating nutrient cycling in a variety of terrestrial ecosystems, accelerating turnover and liberating nutrients stored in standing plant biomass (Zimov et al. 1995, Hobbs 1996, Tanentzap et al. 2013, Malhi et al. 2016). Herbivores likely play a similarly important role in marine systems, and sea turtles and sirenians have been shown to alter nutrient availability and accelerate decomposition in seagrass ecosystems (Thayer et al. 1982, 1984, Domning 2001). Sea cows may have played a similar role and increased the cycling and availability of nutrients through digestion of kelp biomass as well as the physical grazing process (Table 2.1).

Like large herbivores in other systems, the digestive process of sea cows may have increased rates of decomposition and therefore accelerated nutrient cycling in kelp forests. Available evidence suggests that the sea cow used hindgut fermentation to assist in the digestion of its kelp forage. The primary evidence for hindgut fermentation in sea cows is the presence of hindgut fermentation in sirenians globally (Murray et al. 1977, Best 1981, Thayer et al. 1984), but is also suggested by Steller's observation that the structure of sea cows' digestive tract and the feces itself were similar to that of a horse (Steller 1751). It is therefore probable that the digestive tract of sea cows would have accelerated kelp decomposition, returning nutrient rich kelp biomass to the system through fecal production. This nutrient rich feces would have been an important source of nutrients for detritivores and suspension feeders of kelp forests (Figure 2.1), many of which are greatly influenced by organic detritus (Duggins et al. 1989). The important role of marine mammal waste in nutrient cycles has previously been recognized, for example whale feces has been shown to be an important source of iron acting as a fertilizer in much of the world's oceans (Nicol et al. 2010, Roman and McCarthy 2010, Doughty et al. 2015).

The sea cow would have also increased the bioavailability of particulate kelp simply through mastication. The grazing of the toothless sea cows (Steller 1751, Domning 1978) seems likely to have left a trail of kelp fragments in their wake. Indeed, Steller observed that where sea cows grazed large amounts of discarded kelp was seen washed up on the shore (Steller 1751). Much like drift kelp and kelp detritus in present day kelp forests (Duggins et al. 1989, Feehan et al. 2018), this discarded kelp and feces from sea cows would have been an important source of nutrients to numerous coastal species. By accelerating nutrient cycling and increasing the

availability of kelp derived nutrients, sea cows would likely have magnified secondary productivity (Duggins et al. 1989).

This historic role of sea cows in nutrient cycling may be particularly significant given the lack of herbivory in many kelp forest systems today. Despite their high productivity (Mann 1973), relatively few organisms feed directly on kelp (Duggins 1988). In present-day kelp forests, the majority of kelp biomass is not directly consumed, but enters the food web indirectly, as particulate or dissolved organic matter (Gerard 1976, Harrold and Pearse 1987, Duggins et al. 1989). Krumhansl and Scheibling (2012) estimated that as much as 82% of global kelp productivity enters the detrital pathway. In the presence of sea cows, a much larger percentage of kelp biomass would have entered the food web as sea cow biomass or feces, representing a potentially significant change in the flow of kelp derived nutrients. Similar arguments for the historic importance of herbivory has been made in other ecosystems, most notably for seagrass meadows (Domning 2001, Valentine and Duffy 2006). Domning (2001) argued that

“the long-established tenet that seagrass ecosystems are largely detritus-based... must be revised to recognize that the modern situation is anomalous, and that the ‘normal’ pattern throughout most of tropical seagrass history has been that much (probably most) of the primary productivity has been channeled through the guts of herbivores, particularly sirenians”.

Our present understanding of kelp forests as being largely detritus and particulate-based (e.g., Duggins et al. 1989) may similarly be a relatively recent dynamic caused in part by the extinction of the sea cow.

2.4.4 Mediation of predator-prey interactions

Mediating relationships – the indirect effect of a third species on the trophic relationship between two species – are a common and important aspect of marine communities (Dill et al. 2003), including kelp forests (Espinosa-Romero et al. 2011, Markel and Shurin 2015, Lee et al. 2016). This indicates that the presence of sea cows in kelp forests of the North Pacific likely indirectly affected kelp forest communities by mediating interactions between other ecosystem components. The tightly linked trophic relationship between kelp, sea urchins, and urchin predators such as sea otters has been well studied throughout the North Pacific (e.g., Estes and Palmisano 1974, Watson and Estes 2011, Gregr et al. 2020), and this keystone predation is one such relationship that sea cows may have mediated (Table 2.1).

The increase in kelp bioavailability and nutrient cycling within kelp forests facilitated by sea cows (as discussed above) would have had significant implications for the kelp, sea urchin, sea otter relationship. When sea urchins or other mobile invertebrates in protected crevices and other habitats receive an adequate supply of drift algae and detritus, they do not emerge to forage on kelp (Dayton et al. 1998, Krumhansl and Scheibling 2012, Lee et al. 2016). Similarly, urchins located in relative safety below the foraging depth limit of sea otters may not enter shallow waters to forage if they receive an adequate flow of nutrients. By increasing the availability of kelp-derived particulate matter, sea cows would have increased food supplied to sea urchins in these protected habitats, allowing them to remain sheltered from sea otter predation. Thus, this indirect mediating effect of sea cows would have had significant implications for the dynamics between sea otters and their invertebrate prey (Figure 2.1).

2.4.5 Altered kelp export

The increased primary production released by sea cows would have partially been exported out of coastal systems, providing an important source of nutrients for surrounding ecosystems (Vetter 1995, Polis and Hurd 1996). Export of kelp biomass to shorelines, subtidal habitats, and the deep sea can represent significant nutrient subsidies and spatial linkages between these ecosystems (Harrold et al. 1998, Steneck et al. 2002, Gregr et al. 2020). Kelp export is primarily driven by wave action and currents (Cavanaugh et al. 2011, Filbee-Dexter and Scheibling 2012, Krumhansl and Scheibling 2012, Saunders 2014), but other factors such as temperature, encrusting invertebrates, herbivory, and trophic dynamics also contribute to detrital production and export (Duggins et al. 2001, Krumhansl and Scheibling 2011, 2012, Gregr et al. 2020).

As a significant source of herbivory, particularly on kelp canopies, sea cows may have had an important effect on kelp export (Figure 2.1). Some portion of the feces and kelp detritus released into the water column by sea cows would have been exported to nearby habitats (Steller 1751), potentially increasing the nutrient subsidies kelp forests provide to surrounding habitats, as well as the creation of floating seaweed rafts and associated communities (Rothäusler et al. 2012, Saunders 2014). In addition, removal of kelp canopies by sea cows would have reduced the drag of kelp canopies, potentially reducing the influence of wave stress in creating kelp export. The effect of sea cows on overall kelp export may have therefore been density dependent, and in combination with oceanographic and bathymetric heterogeneity (e.g., Wickham et al. 2020) contributed to variation in the export of kelp biomass. In any case, the influence of sea cows on

kelp export would have had significant and far-reaching consequences for surrounding habitats, many of which are significantly influenced by kelp derived nutrients (Vetter 1995, Polis and Hurd 1996, Saunders 2014).

Sea cow herbivory may also have affected the timing of kelp export. In present day kelp forests of the North Pacific, kelp export is strongly influenced by wave action and varies throughout the year in response to seasonal (winter) storms and currents (Sousa 1985, Tegner et al. 1997, Saunders 2014). The year-round grazing of sea cows may have significantly altered this yearly cycle (Estes et al. 1989), leading to a more constant export of kelp to surrounding habitats. The consequence of such a change in the timing of export are largely unpredictable, but would likely significantly influence how these nutrients are used. For instance, growth rates of *Mytilus californianus* are strongly influenced by both food abundance and temperature (Menge et al. 2008), and might therefore be expected to benefit from greater availability of kelp-derived nutrients in warmer months. By encouraging a more constant export of kelp biomass, sea cow herbivory may have supported increased growth rates in habitats that receive kelp biomass subsidies.

2.4.6 Biotic dispersal

Although terrestrial plants are known to use animals as vectors for seed dispersal, little is known about biotic dispersal of marine angiosperms such as seagrasses (Tol et al. 2017), and even less about seaweeds. Spores of marine algae have been found on the legs of amphipods and, together with vegetative fragments, have been reported to survive digestion by fish and molluscs

(Santelices and Paya 1989, Buschmann and Bravo 1990) but not echinoderms (Skern et al. 2003). Although the potential role of extant sirenians (i.e., manatees and dugongs) in seagrass seed dispersal has been widely discussed (Marsh et al. 2011, McMahon et al. 2014) only recently has it been demonstrated that biotic dispersal of tropical seagrass seeds by dugongs (and green sea turtles) provides a mechanism that enhances connectivity among seagrass meadows across large spatial extents (Tol et al. 2017).

Dispersal dynamics of kelp spores has long been thought to depend almost entirely on oceanographic factors, like currents and tides (Norton 1992, Gaylord et al. 2006, Bernardes Batista et al. 2018), although transport distances and mechanisms are still not well understood, especially for bull kelp (*Nereocystis*) (Dobkowski et al. 2019). It seems intuitive to speculate that kelp species would have developed complex co-evolutionary relationships with sea cows to allow for long-term co-existence, especially regarding their reproductive tissues. Such adaptations could take the form of chemical deterrents (phenolic compounds are produced in different concentrations by several brown algae; Estes and Steinberg 1988); producing an increased amount of spores to compensate for grazing; inducing kelps to allocate their reproductive tissues nearer the bottom [as in *Eualaria fistulosa* (Estes et al. 1989), a canopy-forming kelp dominant in colder waters, and described by Steller as a preferred focus for sea cow foraging around Bering Island (Steller 1751)]; or developing mutualistic strategies to benefit from grazing, such as ‘seed’ dispersal.

Bull kelp would be especially sensitive to canopy grazing, due to the location of the fertile *sori* with reproductive tissue at the margins of the fronds (Roland 1985, Druehl and Clarkston 2016). The physical grazing of sea cows may have detached sori, releasing them into the water column and facilitating the dispersal of bull kelp spores. Furthermore, the digestion of reproductive tissue by sea cows may have resulted in the dispersal of macroalgae spores in sea cow feces. Although the zoospores of brown algae lack a cell wall and seem to be sensitive to high temperatures (Hoffmann and Santelices 1991, Lind and Konar 2017), it has been reported that the gametophytes of some kelp species may remain dormant for months in a state of suspended growth, withstanding environmental factors that would be inadequate for normal development and survival (Dobkowski et al. 2019). This suggests the spores of some kelp species may have been able to withstand digestion by sea cows and be dispersed in their feces, however spore tolerance to digestion and associated high temperatures (Cabral de Oliveira 1991, Skern et al. 2003, Lind and Konar 2017) remains uncertain. As with biotic dispersal in other systems (e.g., Kendrick et al. 2012), these potential mechanisms of biotic dispersal may have promoted recruitment and colonization of new areas, enhancement of physical and nutritional conditions for spore survival and settlement, and reduced inbreeding by facilitating genetic exchange.

2.4.7 Other processes

Like other large herbivores (Ripple et al. 2014, 2015), it is likely that sea cows would also have served as prey for a variety of species. Steller observed that while foraging, sea cows with calves were careful to always keep their calf between themselves and the shore (Steller 1751), suggesting that sea cows may have feared predation from the open ocean. The most likely source

of this predation would seem to be transient killer whales (*Orcinus orca*) or sharks (Domning 1978). Transient killer whales in particular are known to prey upon a variety of marine mammals (Jefferson et al. 1991), and while no direct evidence exists for killer whale predation on sea cows, their ability to prey upon both large baleen whales and other sirenians such as dugongs (Jefferson et al. 1991) strongly suggests that sea cows experienced killer whale predation.

Not least amongst the predators of sea cows were humans. Buoyant, stationary, and dependent on coastal kelp forests as they were, sea cows were likely easy hunting, and an important food source for early people of the North Pacific (Stejneger 1887, Domning 1978). Human predation on sea cows is thought to have been so intense – and sea cows so vulnerable (Stejneger 1887) - that it contributed to their extirpation from habited areas of the North Pacific Rim (Domning 1978, Turvey and Risley 2006), and their final extinction at the Commander Islands (Domning 1978, Pitcher 1998) [but see (Anderson 1995, Estes et al. 2016a)].

Finally, Steller also observed that birds were often seen perching on the backs of sea cows, feeding on a marine parasite that infested their skin (Steller 1751, Domning 1978), much like the oxpecker (Buphagidae) on large mammals of southern Africa (e.g., Plantan et al. 2013). Diverse linkages between kelp forests and bird communities have been previously described (e.g., Irons et al. 1986, Anthony et al. 2008, Rechsteiner et al. 2018), however the mutualistic (or perhaps parasitic) relationship between seabirds and sea cows is another intriguing relationship that would have disappeared along with the sea cow.

2.5 Discussion

It would appear quite clear that sea cows played an important structural role in North Pacific kelp forests, and that the historical ecosystem dominated by this megaherbivore would have been very different from the kelp forests of today. The six processes examined here outline several ways sea cows may have helped structure ecosystems of the North Pacific, and illustrates the degree to which humanity may alter ecosystems over historical time scales.

In the language of Ehrlich and Mooney (1983), sea cows may have been “controllers” of the ecosystem, as their extinction would have significantly changed ecosystem function. A controller is broadly defined as a species that determines the structure and flow of energy within an ecosystem (Ehrlich and Mooney 1983). Although an herbivore, it appears sea cows exerted a significant top-down influence on kelp forests. As detailed here, it’s likely a sea cow-dominated system would have had a fundamentally different structure, with important consequences for species diversity and abundance, primary and secondary productivity, and the flow of biomass between habitats.

Furthermore, the extinction of the sea cow constituted the loss of an entire functional group that influenced ecosystem dynamics across numerous scales, and would almost certainly have had significant implications for resilience (Peterson et al. 1998, Folke et al. 2004). The loss of the numerous direct and indirect interactions associated with sea cow extinction in particular, such as those described here, is likely to have reduced ecosystem resilience (Saint-Béat et al. 2015, Smith et al. 2016). In some cases, perhaps including that of the sea cow, the historical decline of

megafauna and associated decreases in resilience that occurred centuries or millennia ago may have set the stage for more recent and ongoing ecological collapse (Jackson et al. 2001, Estes et al. 2011).

The diverse lines of evidence reviewed here provide at least partial support for all six hypotheses, and suggest several likely consequences of these hypothesized effects (Table 2.1). Several of these hypotheses (e.g., changes in ecosystem structure and primary productivity) can draw upon known kelp forest dynamics, allowing greater insight into the consequences of sea cow extinction. Others, however, have limited direct analogs and require extrapolating from other systems (e.g., biotic dispersal), or may build upon kelp dynamics which are less well understood (e.g., kelp export). In such cases, the implications of these hypotheses for ecosystem dynamics, and their importance compared to other drivers such as waves and currents, may be less clear. Nonetheless, the available evidence suggests that all six hypotheses would have had important consequences for the ecological dynamics of kelp forests, and in some cases the wider North Pacific.

This enhanced understanding of sea cows as top-down controllers of kelp forest structure and energy flows is consistent with our understanding of the role of many other megafauna. As we have argued for sea cows, work on other extinct or drastically reduced megafauna has highlighted their important influence on ecosystem structure (Bakker et al. 2016a), biogeochemical cycles (Roman and McCarthy 2010, Doughty et al. 2015), and trophic interactions (Estes et al. 2011). In aquatic and marine ecosystems, large herbivores in particular are thought to have played critical roles as ecosystem engineers or by modifying functional

pathways (Bakker et al. 2016b). Large herbivores may also have functional roles for which the remaining smaller herbivores are unable to compensate (Ripple et al. 2015), as appears to be the case here. Failing to consider the important roles played by these extinct species would therefore be to neglect the history that has shaped the present system and succumb to the syndrome of shifting baselines (Pauly 1995, Dayton et al. 1998, Soga and Gaston 2018).

Understanding changes in coastal ecosystem dynamics associated with the extinction of the sea cow is critical given the role of kelp forests in supporting economically and culturally valuable species. Kelp forests play an important role in a variety of ecosystem services such as food provision (Markel 2011) and carbon sequestration (Wilmers et al. 2012) amongst several others (Smale et al. 2013, Filbee-Dexter and Wernberg 2018, Gregr et al. 2020, Martone et al. 2020). The loss of sea cows and their numerous direct and indirect influences would almost certainly have altered the production of these ecosystem services. For instance, the changes in primary productivity, kelp export dynamics, and spore dispersal would have influenced carbon sequestration, while sea cow-mediated predator-prey dynamics and nutrient availability would have altered the abundance of important fish and invertebrate species, with many potentially positive effects.

Overall, it's clear that North Pacific coastal ecosystems under the influence of sea cows would have been different from the present. By extirpating the sea cow from much of the North Pacific thousands of years ago, and finally driving them extinct in the 18th century, humans substantially altered ecosystems of the North Pacific. These changes would have occurred long before the more recent and well described impacts of fur hunting (Kenyon 1969, Estes et al. 1989),

industrial fishing (Jackson et al. 2001, Steneck et al. 2013), and climate change (Harley et al. 2012, Arafeh-Dalmau et al. 2019) amongst others (Steneck et al. 2002, Krumhansl et al. 2016, Wernberg et al. 2019). These more recent stressors have therefore been applied to a system that was already considerably altered from its historical, more resilient state.

The sea cow is one of countless examples in which a valuable ecosystem component has been lost, and where the restoration of trophic interactions and ecosystem function may be important for maintaining and improving desired ecosystem states (Donlan et al. 2006, Svenning et al. 2016, Corlett 2016, Lundgren et al. 2018). Various approaches have been attempted in such cases, including rewilding and substitutions (Zimov et al. 1995, Griffiths et al. 2013, Guyton et al. 2020), often – but not always – with positive results (Ehrlich and Mooney 1983, Seddon et al. 2014a). In the case of the globally extinct sea cow, no analogous taxa exist in the North Pacific, so restoration would likely depend on active ecosystem management, or possibly the emerging and controversial concept of de-extinction (Seddon et al. 2014b, McCauley et al. 2017). Given the scale and significance of the potential sea cow effects we have explored here, any restoration of sea cow influence to the North Pacific would likely have a substantial impact on ecosystem dynamics, resilience, and the provision of ecosystem services.

2.5.1 Future directions

By drawing on diverse lines of evidence, we have illustrated several likely ways in which sea cows may have influenced the structure of North Pacific ecosystems, however this exploration has been entirely qualitative, and largely speculative. Exploring the historical role of extinct

organisms often requires such speculation (Jackson et al. 2001, Pringle 2020), as studying present kelp forest dynamics can offer only limited insight into the ghosts of missing species (Dayton et al. 1998, Jackson 2001). Due to this speculative approach, we are unable to predict the relative influence of the processes discussed here or the magnitude of their effect, important missing components in our understanding of ecosystem dynamics in the presence of the sea cow.

This is not to suggest that the hypothesized effects cannot be interrogated by further research. Efforts to model the consequences of extinctions have been fruitful in several contexts (Doughty 2017, Berzaghi et al. 2018), and could be constructively applied to this system. Future modelling efforts would also be helpful to examine both the direction and magnitude of sea cow's effects on ecosystem dynamics. Valuable insight into the influence of these extinct species may also be gained by experiments that examine the influence of missing species (Zimov et al. 1995, Bakker et al. 2016a). In the case of sea cows, the similarity between their grazing and some types of strictly regulated commercial kelp harvesting (e.g., Krumhansl et al. 2017, Kobluk 2018) may provide a convenient avenue of inquiry.

2.5.2 Conclusion

By drawing on sea cow biology, kelp forest ecology, and analogous herbivores, this study provides insight into the important role of Steller's sea cows in historical kelp forests, and the broader North Pacific Ocean. While it is challenging to predict the complex effects sea cows may have had in kelp forests, it is even harder to imagine that these large grazers would have had no effect on their surrounding ecosystem. Considering the disproportionate role that megabiota had

globally (Enquist et al. 2020), understanding these potential interactions is vital for assessing the historic baseline for these ecosystems.

We live on a planet denuded of its megafauna. Where large animals were once numerous, we are left at best with diminished populations, or at worst with only the archaeological and ecological legacies of their existence. Careful examination of these ecological ghosts can shed light on what ecosystems may have looked like in their presence, and how millennia of human influence have shaped life on our planet. Understanding these historical changes - not just over decades or centuries, but millennia - is vital for effective conservation and restoration of marine ecosystems and their associated ecosystem services.

Chapter 3: Modelling the Restoration of Ecological Interactions Associated with the Steller's Sea Cow in Northeast Pacific Kelp Forests

3.1 Introduction

Human activity on land and in the ocean has resulted in widespread ecological degradation, with extensive negative effects for biodiversity and ecosystem services (Jackson et al. 2001, Worm et al. 2006, Ceballos et al. 2017, Díaz et al. 2019b). In addition to redoubled efforts to prevent further destruction of natural systems, there is an increasing appreciation for the importance of restoring degraded ecosystems to bend the curve on biodiversity loss (Mace et al. 2018, Díaz et al. 2019b, UNEP and FAO 2020, Duarte et al. 2020). Central to this approach is the restoration of lost ecosystem functions and species interactions, critical components of ecosystems which have been lost through global and local extinctions and population declines (Donlan et al. 2006, Estes et al. 2011, Svenning et al. 2016, Valdez et al. 2020, Enquist et al. 2020). Such restoration efforts, often termed rewilding (Svenning et al. 2016, Perino et al. 2019), have the potential not only to slow the degradation of ecosystems, but in some cases reverse it. Where implemented, the restoration of ecological functions and species interactions has been largely encouraging, with significant and far reaching implications for biodiversity and ecosystem services [e.g., sea otters (Watson and Estes 2011, Wilmers et al. 2012, Gregr 2016); ungulate herbivores (Johnson and Cushman 2007, Guyton et al. 2020); wolves (Ripple and Beschta 2007, 2012, Kuijper et al. 2013); and others (Zimov 2005, Griffiths et al. 2013, Zamboni et al. 2017)].

A fundamental component in the restoration of ecological processes is an accurate understanding of how ecosystems functioned prior to extensive degradation by human actions, which may have been occurring for centuries or even millennia (Jackson et al. 2001, Lotze et al. 2006, Malhi et al. 2016). For example, current evidence suggests that global declines in megafauna, much of which occurred in the late Pleistocene, significantly altered ecosystem dynamics and trophic interactions (Janzen and Martin 1982, Estes et al. 2011, Malhi et al. 2016, Smith et al. 2016). Thus the historic baseline for many ecosystems – and the potential target for conservation and restoration efforts – may be unrecognizable for those of us familiar only with the present day ecosystem (Pauly 1995, Silliman et al. 2018, Soga and Gaston 2018).

In such cases, ecosystem models may be a valuable tool in developing an understanding of how baselines and species interactions have changed. The study of current systems can offer only limited insight into lost ecosystem functions and species interactions (Dayton et al. 1998, Jackson 2001), but modelling approaches can provide insights into altered dynamics due to species declines or extinctions (e.g., Eddy et al. 2017, Doughty 2017), as well as species introductions (e.g., Espinosa-Romero et al. 2011, Arias-González et al. 2011, Corrales et al. 2017). By increasing our understanding of past and future ecological dynamics, such models might play an important role in guiding ecosystem management and restoration (Fulton et al. 2011, Purves et al. 2013, Villasante et al. 2016). However, for ecosystem models to credibly capture the effects of changing species interactions, it is necessary for the structural relationships within the model to be malleable, as to allow the various possible relationships to be represented with uncertainty (Fulton et al. 2003, Link et al. 2012, Harvey 2014).

In any ecosystem, it is critical for ecological restoration and management efforts to consider how extinctions and population declines have altered species interactions and ecosystem dynamics. Often such discussions have centered on terrestrial systems (e.g. Malhi et al. 2016, Svenning et al. 2016), as extinctions and population declines have been more prevalent and noticeable on land (Dulvy et al. 2009, Dirzo et al. 2014, McCauley et al. 2015). However, despite experiencing few extinctions, many marine ecosystems have been substantially altered by human influence (Jackson et al. 2001, Jackson 2001, Estes et al. 2011) and it is thus important to consider how anthropogenic change has altered the full range of species interactions in all ecosystems. What role did extinct or substantially reduced species play in structuring or facilitating ecosystem dynamics? And how may a greater understanding of these absent interactions inform restoration, conservation, and management efforts? Here, we begin to address these questions for North Pacific kelp forests, the location of one of the only known marine megafauna extinctions, that of the Steller's sea cow.

Kelp forests are amongst the most productive systems on Earth (Mann 1973, Krumhansl and Scheibling 2012), and are important both ecologically (Steneck et al. 2002, Teagle et al. 2017) and socioeconomically (Smale et al. 2013, Filbee-Dexter and Wernberg 2018, Gregr et al. 2020, Martone et al. 2020). However like many ecosystems, kelp forests around the world are threatened by climate change (Harley et al. 2012, Starko et al. 2019), direct exploitation (Estes et al. 1989, Steneck et al. 2013), overgrazing by herbivores (Filbee-Dexter and Scheibling 2014, Ling et al. 2015), and numerous other, often interacting, stressors (Steneck et al. 2002, Wernberg et al. 2019, Rogers-Bennett and Catton 2019). On the West Coast of Vancouver Island (WCVI) on Canada's Pacific Coast, kelp forests have been undergoing drastic changes over the last 50

years in response to the reintroduction of sea otters (Watson and Estes 2011, Singh et al. 2013, Markel and Shurin 2015). This rewilding effort is often portrayed as successfully restoring historical conditions (Nichol 2015, Wernberg et al. 2019), but it has been controversial due to the consequences the rapid ecological transitions have had on invertebrate fisheries and coastal communities (Sea Otter Recovery Team 2007, Gregr 2016, Pinkerton et al. 2019).

The Steller's sea cow (*Hydrodamalis gigas*) was a large (4500 – 8500 kg, at least three times larger than the largest known manatee, and perhaps more than 9 meters in length as adults; Domning 1978, Anderson 2002) herbivorous grazer of macroalgae. Sea cow remains have been found at only a handful of locations in the North Pacific, but it is thought that at their peak distribution they were found across the North Pacific rim from Japan to Baja California (Domning 1978). These large manatee-like mammals are thought to have been extirpated from much of their range by human expansion around the Pacific Rim thousands of years ago (Domning 1978, Pitcher 1998, Erlandson et al. 2007), but persisted around the remote Commander Islands until they were finally driven to extinction in 1768 (Steller 1751, Domning 1978). While much research has examined ecological dynamics of kelp forests, particularly the trophic interactions between sea otters, sea urchins, and kelp (e.g., Estes and Palmisano 1974, Estes and Duggins 1995, Filbee-Dexter and Scheibling 2014) sea cows have received very little attention despite being conspicuously present in these ecosystems for much of the history of this system. Through several direct and indirect mechanisms, sea cows may have played a significant role in controlling the structure and function of North Pacific kelp forests (Chapter 2). Here, we use an ecosystem model to examine the theoretical reintroduction of sea cows on the WCVI, to gain insight into both the historical baseline for this ecosystem, and the potential for future

restoration and management of this social-ecological system. Specifically, we examine how sea cow presence may have influenced 1) the biomasses of trophic groups and 2) ecosystem productivity, flows, and trophic interactions. At the same time, we attempted to characterize 3) the uncertainty associated with modelling these uncertain dynamics.

3.2 Methods

We examined the ecological role of sea cows, and their potential effect on ecosystem dynamics, using Ecopath with Ecosim (EwE) version 6.6 (Christensen and Walters 2004, Christensen et al. 2008). A recent model for kelp forests on the WCVI (Gregr et al. 2020) was adapted and expanded to address these novel questions. Here, we 1) briefly describe the EwE modelling approach; 2) detail the static, mass-balanced Ecopath model; 3) describe the time-dynamic Ecosim model and model fitting procedure; 4) summarize the parameterization of hypothesized sea cow dynamics and uncertainty characterization; and 5) describe the analysis of model outputs. Each of these five steps is discussed in turn below, with additional detail provided in the Appendix.

3.2.1 EwE

EwE has been widely used to represent aquatic ecosystems around the world (Colléter et al. 2015), including ecosystems of the eastern North Pacific relevant to the research presented here (e.g., Ainsworth et al. 2002, Harvey et al. 2010, Gregr 2016, Kumar et al. 2016). EwE explicitly models both trophic and non-trophic interactions, and has commonly been used to model species

introductions similar to that presented here (e.g., Espinosa-Romero et al. 2011, Arias-González et al. 2011, Gregr 2016). The Ecopath component of EwE builds a static, mass-balanced snapshot of the ecosystem, depicting functional or taxonomic groups and their biomass, linked to other groups through trophic interactions (Christensen and Walters 2004, Christensen et al. 2008). Ecosim is the temporal model component and extends Ecopath to depict changes in biomass and trophic interactions through time (Christensen and Walters 2004, Christensen et al. 2008). We used both Ecopath and Ecosim to represent the hypothetical reintroduction of sea cows on the WCVI.

3.2.2 Ecopath: mass-balanced trophic model

The initial Ecopath model we developed was for an invertebrate dominated rocky reef system, as would have occurred prior to sea otter reintroduction to the WCVI (Figure 3.1). This model consists of 25 functional groups and two fishing fleets, and is based primarily off the WCVI kelp forest model developed by Gregr et al. (2020). The model is non-spatial, but has been scaled to represent 3043 km² along the WCVI from the low water line to the 50m depth contour (Figure 3.1), approximately 10% of which is considered potential kelp habitat (Gregr 2016). All model groups were initially parameterized following Gregr et al. (2020), with the exception of the Steller's sea cow which we parameterized here for the first time. The parameters selected by Gregr et al. (2020) were obtained from empirical evidence and previous models for the region, and were therefore left unchanged, except where changes were required to improve model performance (i.e. enabling the export of kelp biomass and improving diet compositions; Appendix).

The sea cow was parameterized using estimates found in the literature or values from previous population modelling efforts for the sea cow (e.g., Best 1981, Turvey and Risley 2006, Estes et al. 2016a). Initial sea cow biomass (B) was set at a near-zero value (0.01 tons/km²) to represent a system state without sea cows (as Ecopath is unable to represent an initial biomass of zero). Production rate (P/B; tons per ton biomass per year) was set at 0.037/year, based on an estimated median lifespan of 27 years calculated following the sea cow life history traits proposed by Turvey and Risley (2006). Consumption rate (Q/B; tons per ton biomass per year) was initially set at 3.65 /year, equivalent to a consumption of 1% bodyweight per day, in accordance with the upper value estimated by Best (1981). Also following Best (1981), unassimilated consumption (U) was set to 0.5. Diet composition was based on previous discussions of the ecology of sea cows, where all available evidence suggests the sea cow was an obligate algivore specialized for surface grazing (Steller 1751, Domning 1978, Estes et al. 2016a), and thus diet was split between all macroalgae groups with an emphasis on canopy forming kelps. Diet was partitioned primarily to *Macrocystis* (50%) and *Nereocystis* (30%) representing the approximate relative prevalence of these macroalgae in the model area (e.g., Watson and Estes 2011), with the remainder (20%) assigned to the diverse “other macroalgae” group. The addition of sea cows to the model required no additional model balancing.

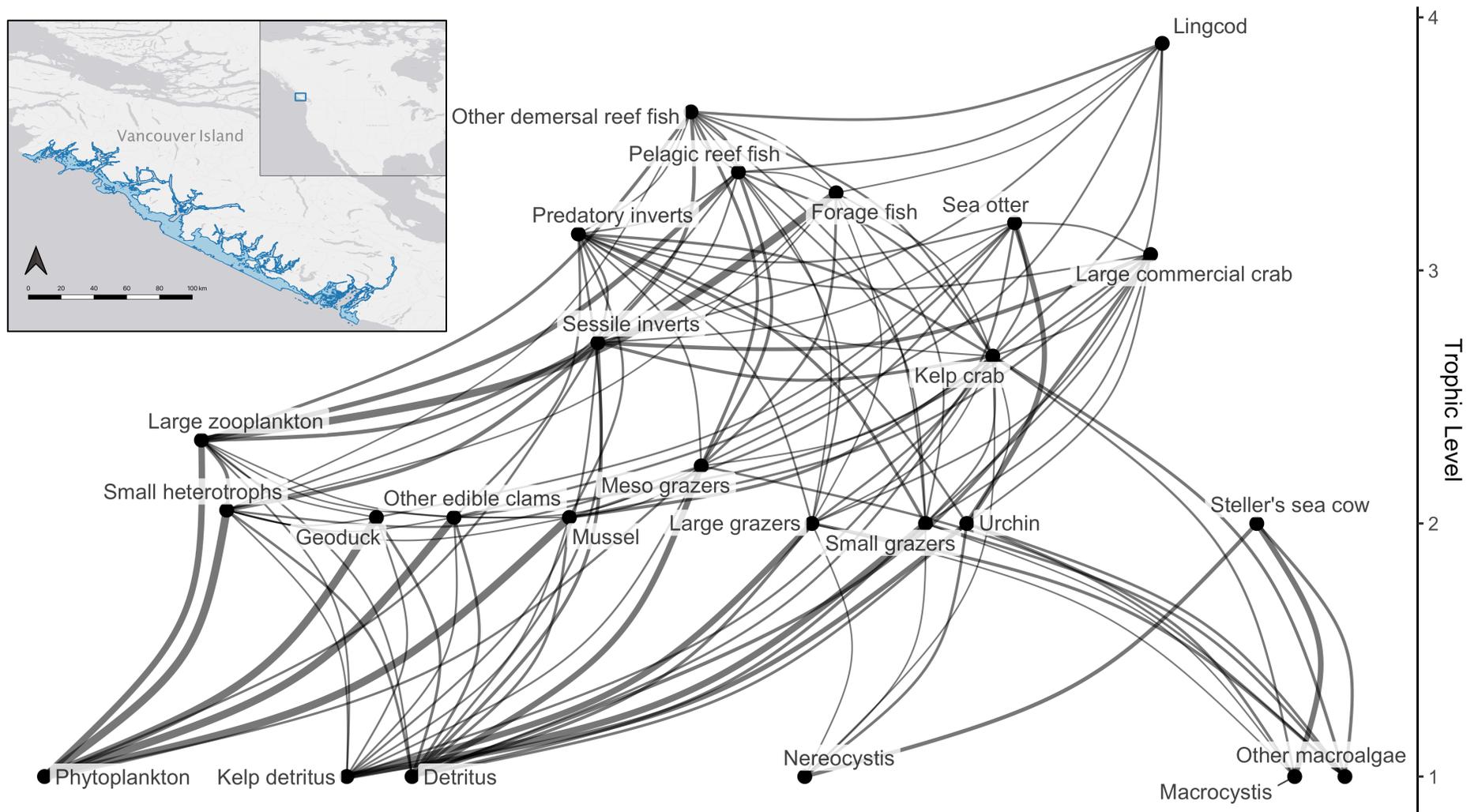


Figure 3.1 Model area and Ecopath trophic network structure

Map of model area (0 - 50m in depth) on the West Coast of Vancouver Island (WCVI) and Ecopath trophic network diagram depicting model groups arranged by trophic level. Line widths are proportional to the strength of trophic interactions (i.e. proportion of diet) between model groups.

3.2.3 Ecosim: temporal dynamics

We used Ecosim to represent changes to the mass-balanced Ecopath model over 280 years from 1970 to 2250 in response to first sea otter, and then sea cow reintroduction. Ecosim was run using monthly timesteps, but following Gregr et al. (2020) no seasonal dynamics were included. The initial Ecopath parameterization corresponds to 1970, the year prior to sea otter reintroduction on the WCVI (Jameson et al. 1982b). In the first time step, Steller's sea cows are removed from the model using hunting (i.e. fishing effort, as in Arias-González et al. 2011) and sea otters are allowed back into the system by removing hunting pressure (as in Gregr et al. 2020). After providing time for the system to reach equilibrium in a kelp forest state (around 2050), Steller's sea cows were then introduced into the model in the following year (at a B of 0.1 t/km²). We then ran the model until a new equilibrium was reached around 2250.

A time series fitting routine (Christensen et al. 2005) was used to set group vulnerabilities and improve the match between model predictions and available ecological data. Vulnerability is a key Ecosim parameter which controls how much a change in predator biomass will affect predation mortality for a given prey (Christensen et al. 2008). It is therefore an important parameter for accurately representing ecological dynamics (Ainsworth and Walters 2015). Nine biomass time series (Gregr et al. 2020) corresponding to the transition from an invertebrate dominated to a sea otter dominated system were used to fit the model. The majority of the time series were for invertebrate model groups and were based on a space-for-time substitution (e.g., Pickett 1989) of biomass changes in the presence of sea otters. The final time series was a logistic growth curve for sea otters (see the Appendix for more detail). No time series data were available to fit to the modelled recovery of sea cows. Eight vulnerability values were estimated

using the fit to timeseries procedure, and sea cow and sea otter vulnerabilities were set manually at high values to represent that both groups are far from carrying capacity in the initial model parameterization (Appendix). Model fit to time series data was evaluated using the sum of squares of the difference between predicted and observed (i.e., time series) biomass.

3.2.4 Steller's sea cow dynamics & uncertainty characterization

Drawing on multiple bodies of literature, several potential mechanisms by which Steller's sea cows may have altered kelp forest dynamics were presented in Chapter 2. Four of these indirect and mediating effects were explicitly included in the model: the hypothesized influence of sea cows on 1) physical ecosystem structure, 2) predator-prey interactions, 3) primary production, and 4) nutrient cycling (Chapter 2). We implemented the first three mechanisms using mediation functions in Ecosim (Christensen et al. 2008, Espinosa-Romero et al. 2011), and the nutrient cycling mechanism by varying Ecopath parameters for the Steller's sea cow (consumption [Q/B] and unassimilated consumption [U], Appendix). The final two mechanisms discussed in Chapter 2 (kelp export and spore dispersal) are explicitly spatial and beyond the scope of the present model.

Considerable uncertainty exists around the magnitude and relative importance of these hypothesized mechanisms. Structural considerations such as these can also have significant implications for model outcomes (Fulton et al. 2011, Harvey 2014). Consequently, we characterized the sensitivity of the model to these different structures by creating five alternate parameterizations of varying magnitudes for each hypothesis (see the Appendix for details). We ran the model using each of the five parameterizations, as well as with no function, for each of the four hypothesized mechanisms (i.e. 6 model runs per

mechanism, 24 runs total). The function corresponding to a hypothesized mechanism of intermediate strength (parameterization three in Figure A.1) was selected for each hypothesis and used for the primary model run.

Parameter uncertainty with respect to the diets and other parameters of the model groups can also be significant (Link et al. 2012). This is particularly true for the sea cow as, unlike the other model groups, no empirical values are available for this globally extinct species. The uncertainty related to the initial Ecopath sea cow parameters was characterized by examining the results of 1000 Monte Carlo simulations (see the Appendix for details).

3.2.5 Analysis of model results

The influence of Steller's sea cows on ecosystem dynamics was evaluated by comparing results for the three periods of equilibrium depicted in the model (represented by the years 1972, 2050, and 2250). Biomass estimates with uncertainty were obtained from Ecosim with Monte Carlo simulations, and the biomass of model groups in each period of equilibrium was compared using notched boxplots. Notches represent an approximate 95% confidence interval around the median (McGill et al. 1978, Chambers 1983) – calculated as $1.58 \times IQR/\sqrt{n}$, where IQR is the inter-quartile range and n is the sample size – and were used to assess significance. Ecosim biomass estimates were also used to calculate Pielou's evenness index (Pielou 1966, Smith and Wilson 1996) to examine the distribution of biomass in the three periods of equilibrium. Resilience is often considered to be associated with diversity (Stachowicz et al. 2002, Worm et al. 2006, Hillebrand et al. 2008, O'Gorman and Emmerson 2009, Harvey et al. 2010), and

here evenness is the relevant dimension of diversity (Smith and Wilson 1996, Jost 2010) as richness is constrained by the model parameterization and group selection.

To further compare ecosystem dynamics and trophic interactions between these periods, we extracted Ecopath models representing each of the three equilibrium periods from Ecosim, and calculated a suite of indicators. We calculated total ecosystem trophic flows (total system throughput, as well as flows through consumption, export, detritus, and respiration; Coll et al. 2007, Christensen et al. 2008), and changes in total system production and primary production between the three states. To specifically examine the influence of sea cows on detrital flows and understand the relative importance of these flows in the ecosystem, we calculated flow from detritus to each model group, as a proportion of the group's total consumption (Christensen et al. 2008). We assessed the relative importance of each model group using a mixed trophic impact network, an indicator derived from economic theory (Ulanowicz and Puccia 1990) that describes the direct and indirect trophic impact of each model group on the biomass of each other model group (Coll et al. 2007, Christensen et al. 2008). Mixed trophic impact, scaled by biomass, is also the basis for the identification of keystone species in EwE (Libralato et al. 2006, Valls et al. 2015), which was also examined here. Both mixed trophic impact and keystone species identification is ultimately derived from diet compositions, and consequently does not consider non-trophic interactions (Valls et al. 2015).

Finally, to assess the sensitivity of model results to alternate parameterizations of the four hypothesized indirect and mediating effects of sea cows, we extracted Ecopath models representing the final sea cow dominated system state (2250) for each alternate parameterization. This allowed a comparison between model iterations with and without the inclusion of these mechanisms, as well as with mechanisms of

different magnitudes. Variation in the biomass of model groups between these iterations was then quantified for each relationship. For the contribution of sea cows to nutrient cycling and detrital production (i.e., the fourth relationship), detrital flow rather than biomass was evaluated as it is more strongly influenced by the alternate parameterizations, and more accurately reflects the influence of the hypothesis on model results.

3.3 Results

3.3.1 Group biomass

The three equilibrium periods captured in the model – invertebrate dominated, sea otter dominated, and Steller’s sea cow dominated – show substantial differences in the predicted biomass of several groups (Figure 3.2). The first transition from an invertebrate dominated system to a sea otter dominated system accurately recreates the known ecological dynamics associated with sea otter recovery on the WCVI and elsewhere (Estes and Palmisano 1974, Gregr et al. 2008, Watson and Estes 2011, Singh et al. 2013, Markel and Shurin 2015, Gregr 2016). This transition was captured in the first 80 years (1970-2050) of the model, during which sea otter, macroalgae, finfish, and some invertebrate biomasses increase, while sea urchin and other sea otter prey groups decrease (Figure 3.2). The final fitted model fit the time series for this period relatively well ($SS = 48.4$), a marked improvement over using default vulnerabilities ($SS = 1090.2$). The only model groups for which the model was unable to replicate the time series were sessile invertebrates, where the model could not recreate the magnitude of change observed on the WCVI, and meso grazers, where the model predicts a slight increase but data shows a substantial decrease on the WCVI (Gregr 2016). Despite these discrepancies, the model appears to accurately capture the state shift

of rocky reefs driven by sea otters (Estes and Palmisano 1974, Estes and Duggins 1995, Watson and Estes 2011), particularly in regard to important groups such as macroalgae, sea otters, fish, sea urchins, and other large invertebrates.

The second transition, to a Steller's sea cow dominated state, also resulted in significant changes in biomass for several model groups, though Monte Carlo simulations often resulted in substantial variability (Figure 3.2). Sea cow biomass increased rapidly once introduced to the model, and when equilibrium was reached Steller's sea cow biomass was predicted to be 1.44 t/km² (median, 95% CI 1.35 – 1.54). Assuming a conservative weight of 5000 kg per individual (Domning 1978), this is equivalent to 876 adult sea cows in the model area. The presence of Steller's sea cows in the model significantly affects the biomass of their forage, with decreases in *Macrocystis* and the other macroalgae group, but an increase in *Nereocystis* as compared to the sea otter dominated state (Figure 3.2E). For all three macroalgae groups, biomass in the sea cow state is significantly greater than in the invertebrate dominated state. Given the important structural role played by macroalgae in the model (and in kelp forests; e.g., Espinosa-Romero et al. 2011, Teagle et al. 2017), these changes likely contributed to observed changes in the biomass of several of the other kelp-associated model groups, such as fish and some invertebrates (Figure 3.2). The sea cow dominated state also had increased biomass for plankton and detritus groups compared to both invertebrate and sea otter dominated states, which likely contributed to accompanying increases in consumer groups such as forage fish, mussels, sessile invertebrates, and other clams (Figure 3.2).

In addition, biomasses for sea otters and many of the large invertebrate groups they consume were significantly different in the sea cow dominated state (Figure 3.2). Sea otter biomass was increased in the

sea cow state as compared to the sea otter state, as were sea urchin, large grazer, mussel, and other edible clam biomasses. While higher in the sea cow dominated state compared to the sea otter dominated state, the biomass of these invertebrate groups was not as high as in the invertebrate dominated state. In contrast, geoducks appear to be negatively influenced by the indirect effects of sea cows, with geoduck biomass significantly lower in the sea cow dominated state than either of the other two states (Figure 3.2B).

Total model biomass and group evenness also changed significantly between the three periods of equilibrium (Figure 3.3). Total biomass was highest in the sea otter dominated state (median = 380.7 t/km², 95% CI 378.9 - 382.6 t/km²), followed by the sea cow dominated state (median = 336.2 t/km², 95% CI 332.4 – 340.0 t/km²) and the invertebrate dominated state (median = 326.4 t/km², 95% CI 326.0 – 326.7 t/km²). In contrast, group evenness was highest in the sea cow dominated state (median = 0.761, 95% CI 0.759 – 0.763) and lower, but similar, in the sea otter (median = 0.693, 95% CI 0.691 – 0.694) and invertebrate (median = 0.692, 95% CI 0.691 – 0.692) dominated states.

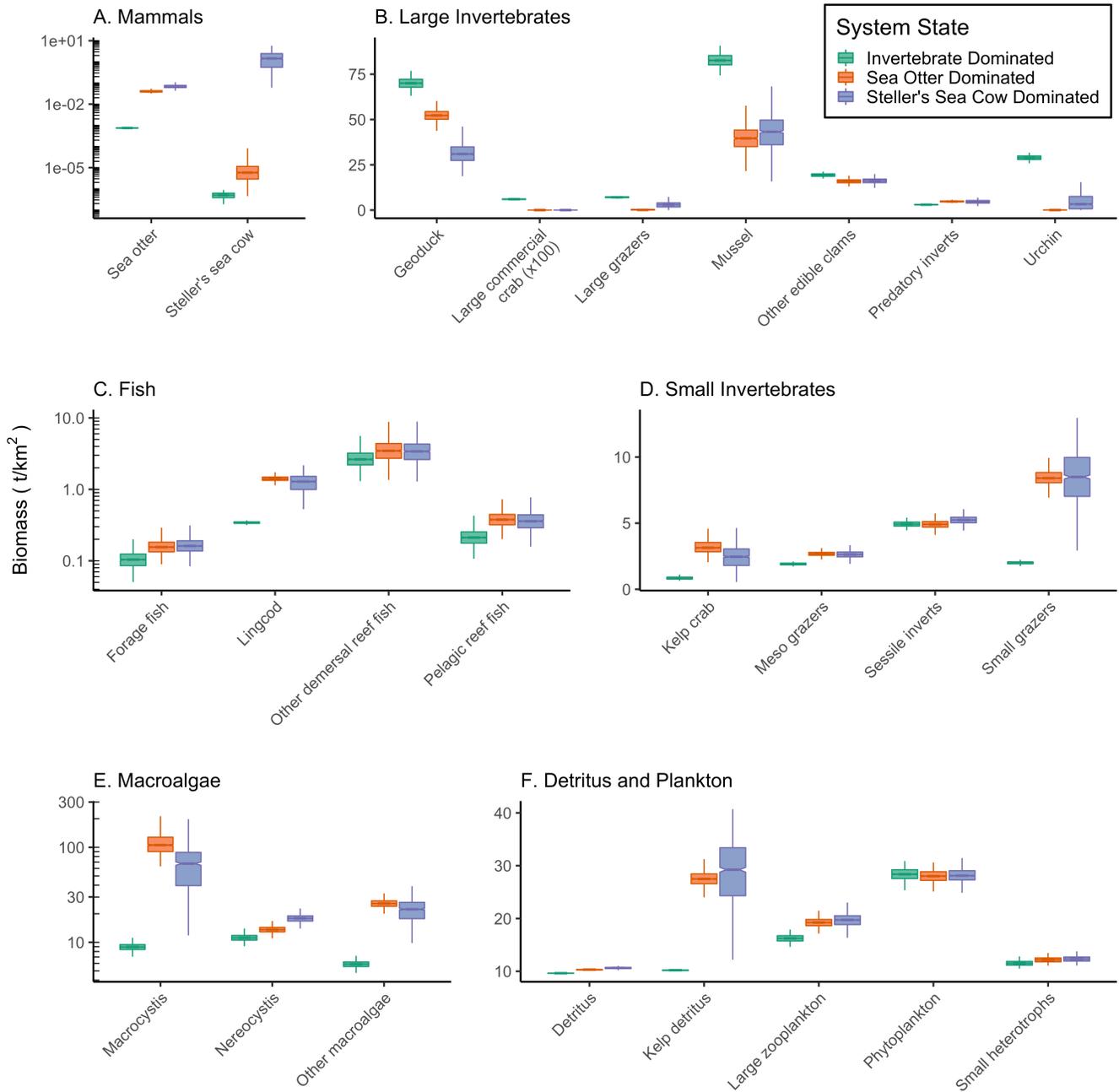


Figure 3.2 Modelled group biomasses.

Biomasses (t/km^2) for model groups in invertebrate (1972), sea otter (2050), and Steller's sea cow (2250) dominated modelled system states. Model groups are shown on differently scaled axes to accommodate variation in biomass, and are categorized into (A) Mammals, (B) Large Invertebrates, (C) Fish, (D) Small Invertebrates, (E) Macroalgae, and (F) Detritus and Plankton. Large commercial crab biomass was multiplied by 100 for visibility. Notched boxplots show the outcomes of 1000 Monte Carlo simulations (see the Appendix for details), with notches depicting the 95% CI calculated as $median \pm 1.58 \times IQR/\sqrt{n}$.

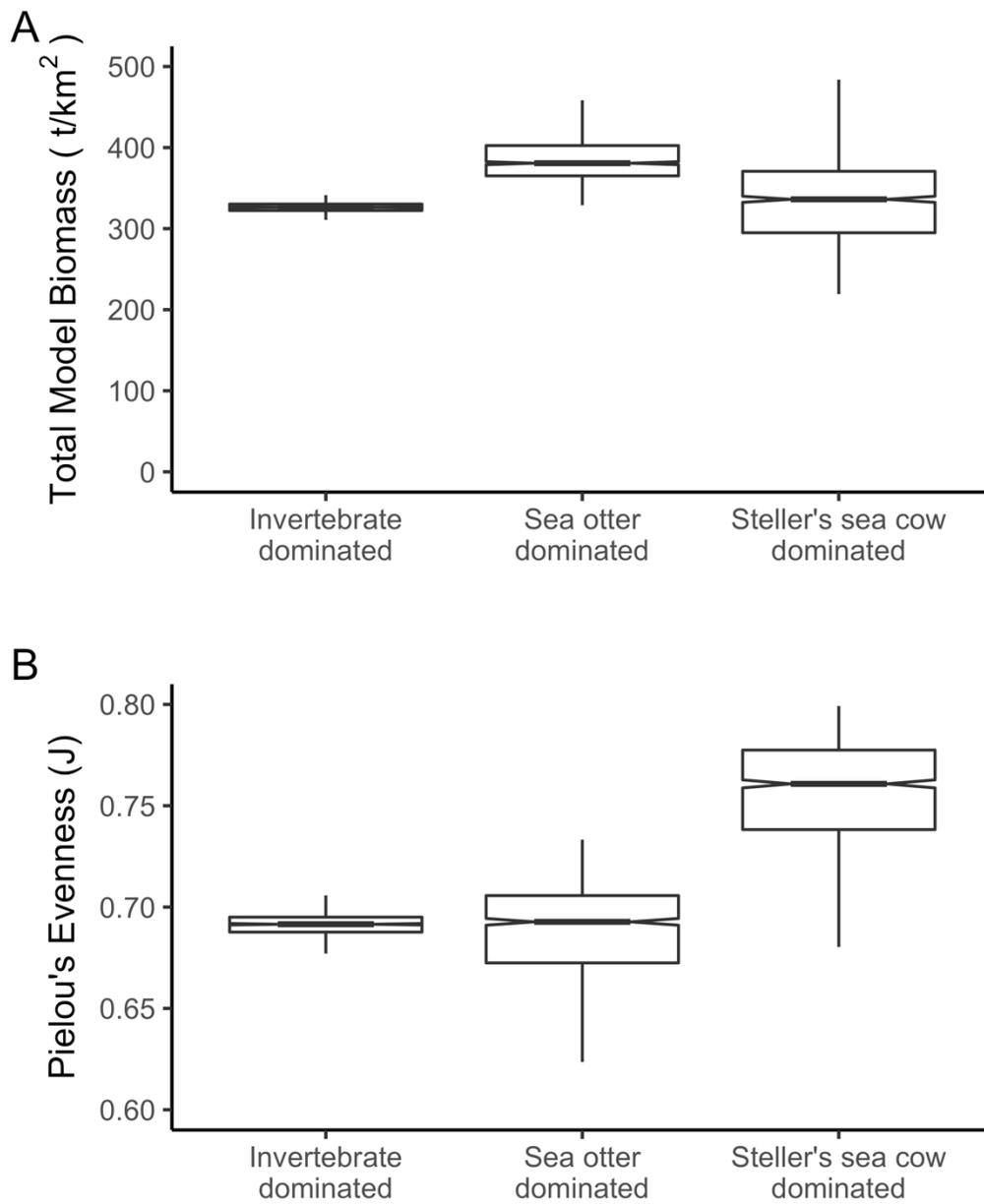


Figure 3.3 Total model biomass and Pielou's evenness

(A) Total model biomass (t/km²) and (B) Pielou's Evenness (J) in invertebrate (1972), sea otter (2050), and Steller's sea cow (2250) dominated modelled system states. Notched boxplots show the outcomes of 1000 Monte Carlo simulations (see the Appendix for details), with notches depicting the 95% CI calculated as $\text{median} \pm 1.58 \times IQR/\sqrt{n}$.

3.3.2 Ecosystem productivity, flows, and trophic interactions

In the sea cow dominated state total system throughput was 13,905 t/km²/year, while in the sea otter and invertebrate dominated states, total system throughput was 13,209 and 12,648 t/km²/year respectively (Table 3.1). Decomposing total system throughput into its various trophic flow components (consumption, export, flow to detritus, and respiration) shows a similar pattern for most types of trophic flow (Table 3.1). As with total system throughput, total system production and primary production were greatest in the sea cow dominated state, intermediate in the sea otter dominated state, and lowest in the invertebrate dominated state (Table 3.1).

The role of detrital pathways in the modelled systems was assessed by examining the proportion of trophic flow for each model group that originates in detritus (Table 3.2). Averaged across consumer groups, flows from detritus make up 41% of trophic flows in the invertebrate dominated state, 39% in the sea otter dominated state, and 42% in the sea cow dominated state. Differences across these states is much more variable for individual groups, but is generally lowest in the sea otter dominated state, and higher in the other two states. Bivalve, fish, and plankton groups have an increased proportion of trophic flows originating from detritus in the sea cow dominated state in particular (Table 3.2).

Finally, the relative strengths of direct and indirect trophic interactions between model groups in the sea cow dominated state were examined using a mixed trophic impact network (Figure 3.4A). As would be expected by their known role in structuring near shore ecosystems (e.g., Estes and Palmisano 1974, Watson and Estes 2011), the model predicts that sea otters have strong negative effects on their invertebrate prey, and positive effects on macroalgae groups as well as groups which benefit from the

presence of macroalgae (i.e. lingcod and Steller's sea cow). Sea otters also score highly on all four keystone indices implemented in EwE (Figure 3.4B). Phytoplankton, kelp detritus, kelp crabs, and small heterotrophs also stand out as having strong trophic impacts on a variety of model groups (Figure 3.4A), but do not score as highly as sea otters on the four keystone indices (Figure 3.4B). In contrast, the model predicts that sea cows have very little trophic impact, negatively impacting only themselves and the canopy forming kelp groups they consume, and sea cows do not score highly on the four measures of keystone indices (Figure 3.4). It is important to note, however, that mixed trophic impact and the associated keystone indices are model outputs derived from diet compositions, and do not consider non-trophic effects (Valls et al. 2015).

Table 3.1 Trophic flows and production

Trophic flows and production (t/km²/year) in invertebrate (1972), sea otter (2050), and Steller's sea cow (2250) dominated modelled system states.

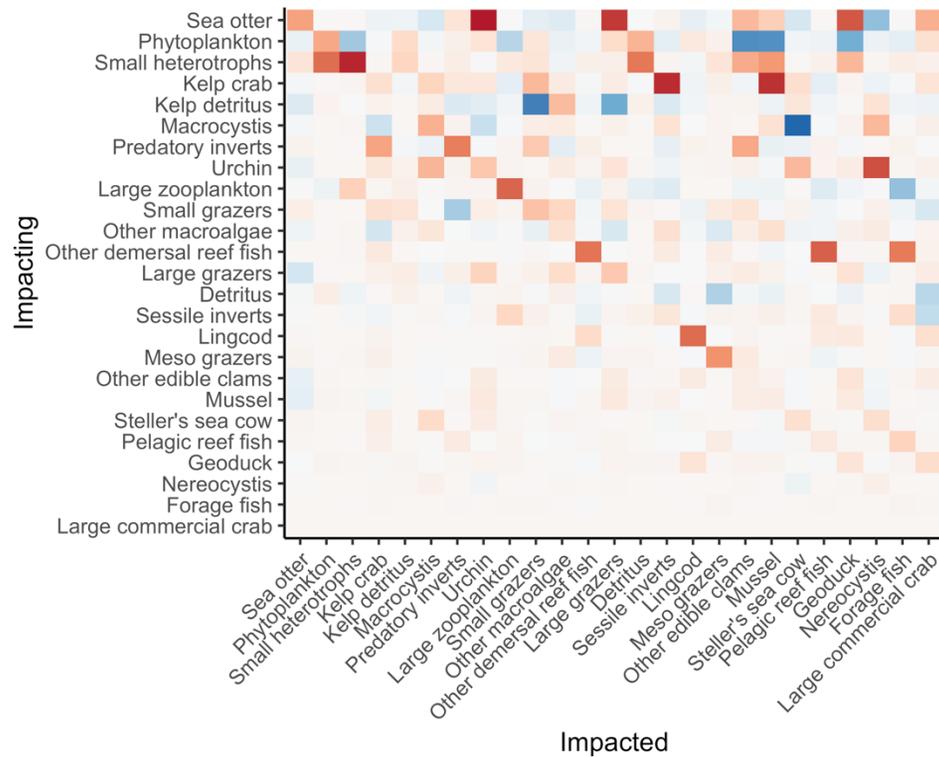
		Invertebrate dominated	Sea otter dominated	Steller's sea cow dominated
Trophic Flows				
Consumption	(t/km ² /year)	4739.6	4869.8	5113.1
Export	(t/km ² /year)	2769.6	2928.3	3029.4
Flow to detritus	(t/km ² /year)	3688.5	4002.8	4260.5
Respiration	(t/km ² /year)	1239.5	1167.5	1254.9
Total system throughput (TST)	(t/km ² /year)	12648	13209	13905
Production				
Total production	(t/km ² /year)	9,626	10,273	10,810
Total primary production	(t/km ² /year)	4115.4	4238.1	4466.3

Table 3.2 Modelled detrital flows

Proportion of consumption originating in detrital groups for each consumer group in the model, for invertebrate (1972), sea otter (2050), and Steller's sea cow (2250) dominated modelled system states. The proportion represents both direct consumption of detritus, and indirect consumption (i.e. consumption of groups which consumed detritus). A value of 1.0 therefore represents that all consumption originates in detritus, while a value of 0.5 would indicate that half of consumption originates in detritus while the other half originates in primary production. The average for all consumer groups in each system state is also reported.

Model group	Invertebrate dominated	Sea otter dominated	Steller's sea cow dominated
Steller's sea cow	0.00	0.00	0.00
Sea otter	0.53	0.31	0.45
Urchin	0.56	0.34	0.41
Large commercial crab	0.56	0.59	0.62
Geoduck	0.20	0.28	0.29
Mussel	0.20	0.28	0.29
Other edible clams	0.20	0.28	0.29
Lingcod	0.49	0.45	0.50
Other demersal reef fish	0.42	0.43	0.47
Pelagic reef fish	0.38	0.39	0.43
Forage fish	0.27	0.36	0.38
Kelp crab	0.39	0.24	0.30
Predatory inverts	0.56	0.55	0.61
Large grazers	0.79	0.66	0.70
Small grazers	0.84	0.73	0.76
Meso grazers	0.68	0.55	0.58
Sessile inverts	0.39	0.49	0.50
Large zooplankton	0.15	0.24	0.25
Small heterotrophs	0.15	0.20	0.21
Average	0.41	0.39	0.42

A



B

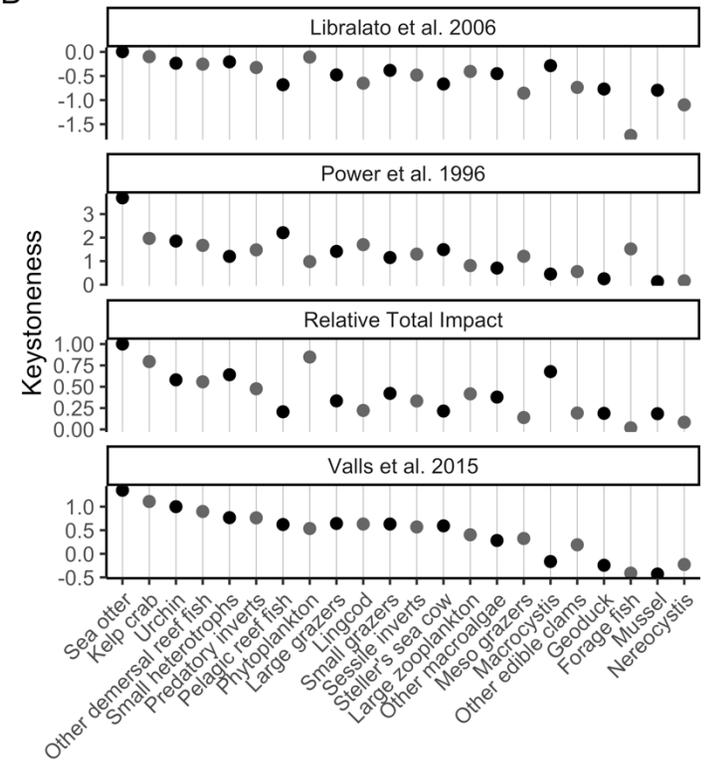


Figure 3.4 Mixed trophic impact and keystone indices

Mixed trophic impact plot (A) with model groups ordered by total impact, and keystone indices (B) with model groups ordered by average score across the four indices. Results are shown for the Steller’s sea cow dominated system state (2250). In the mixed trophic impact plot, the colour indicates that a small change in the impacting group has a negative (red) or positive (blue) impact on the impacted group, with colour intensity corresponding to degree of impact. Keystone indices (B) were calculated in EwE using the four methods available in the software (Power et al. 1996, Libralato et al. 2006, Valls et al. 2015).

3.3.3 Uncertainty characterizations

The alternate parameterizations of hypothesized non-trophic sea cow relationships led to variation in biomass for many model groups, with several groups showing substantial (>10%) variation between parameterization (Figure 3.5). The alternate parameterizations of these relationships affected model groups differently, and in some cases different parameterizations resulted in variation across orders of magnitude for some groups and very little variation in others. Compared to model iterations not including the mechanism (i.e. zero in Figure 3.5), the inclusion of habitat effects of kelp generally resulted in greater fish biomass (except for other demersal reef fish; Figure 3.5A). Similarly, the inclusion in the model of sea cow mediated changes in macroalgae productivity generally resulted in greater biomasses for model groups with the exception of sea urchins (Figure 3.5C). In contrast, the inclusion of sea cow mediation of predator-prey interactions in the model resulted in generally lower group biomasses (except for sea otters, sea urchins, crabs, and large grazers; Figure 3.5B). The large percent change in biomasses for some groups under the alternate parameterizations for this hypothesis reflect the small absolute biomasses involved. The final non-trophic relationship, the contribution of sea cows to detrital flows, resulted in no substantial (>10%) changes in biomass, but an increase in the flow of biomass from sea cows to detritus (Figure 3.5D).

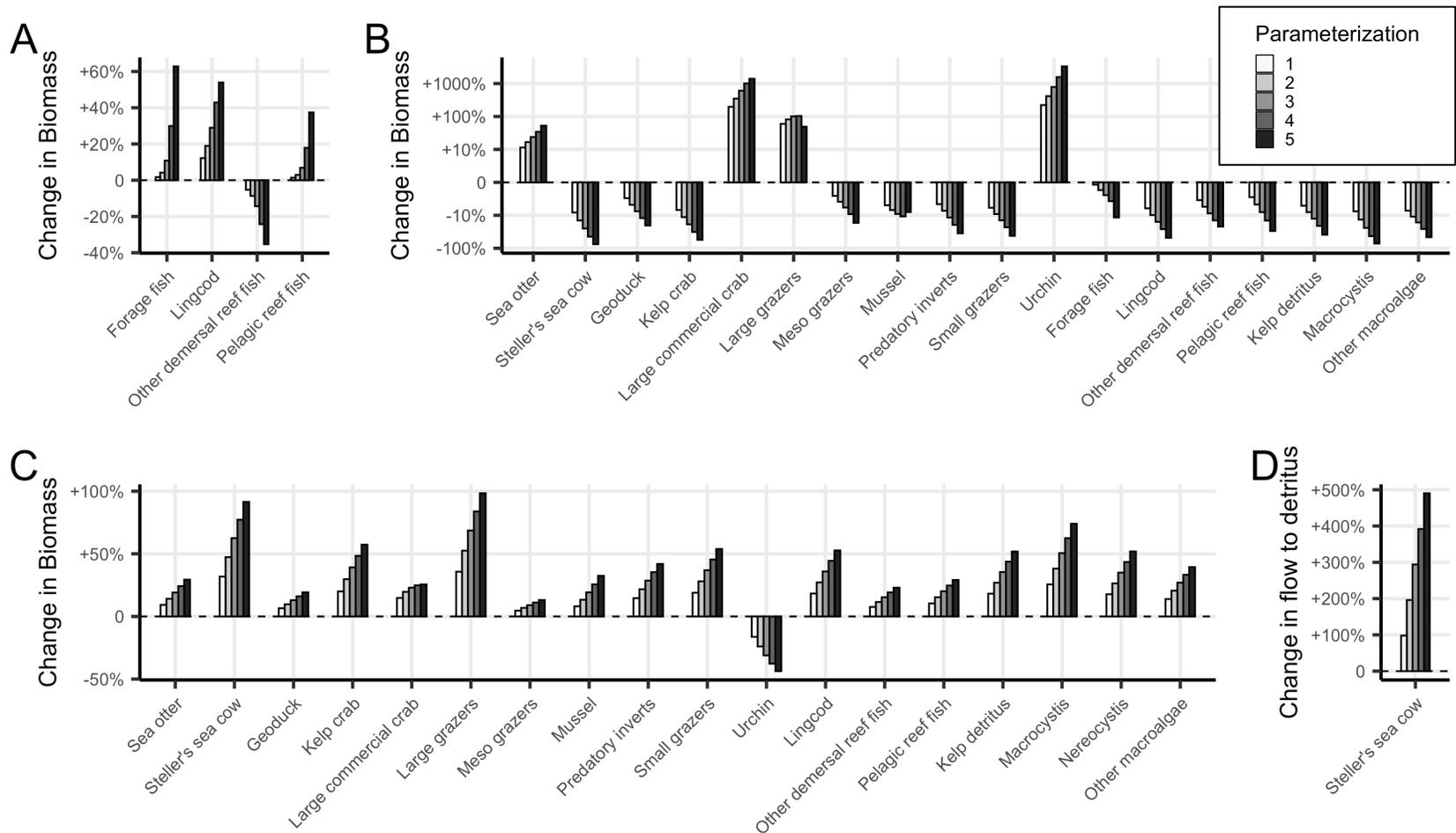


Figure 3.5 Model results from alternate hypothesis parameterizations

Model outputs from alternate (1-5) parameterizations of each hypothesized mechanism by which Steller's sea cows may have altered kelp forest dynamics (Chapter 2) relative to the null parameterization (i.e. the model not include the hypothesized mechanism). Percent change in model group biomass (t/km^2) are shown for groups which saw substantial variation ($>10\%$ for at least one parameterization) between alternate parameterization of (A) physical ecosystem structure, (B) predator-prey interactions, and (C) primary production hypotheses. (D) Shows percent change in flow to detritus ($t/km^2/yr$) for alternate parameterizations of the nutrient cycling hypothesis. Parameterization three was selected for primary model runs. See the Appendix for details on hypothesized mechanisms and their parameterization.

3.4 Discussion

These results suggest that Steller's sea cows, while not acting as keystone species, likely had a significant facilitating influence on community composition and structure of North Pacific kelp forests, with implications for the productivity and stability of temperate and subarctic systems. Further, our findings may complicate the traditionally dichotomous view of North Pacific rocky reefs as existing in either an invertebrate dominated, low productivity 'urchin barren' state, or a predator dominated, high productivity kelp forest state (Estes and Palmisano 1974, Watson and Estes 2011, Filbee-Dexter and Scheibling 2014), and the associated impacts of this transition on communities and fisheries (Salomon et al. 2015, Markel and Shurin 2015, Gregr 2016). It has previously been suggested that sea cows played an important role in kelp forest ecosystems of the North Pacific, and that their extinction may have led to major structural changes (Estes et al. 1989, Pitcher 1998) (Chapter 2). This model supports these assertions and provides insight into what these historical changes may have been, and how restoring sea cow function may support the management of kelp forests on the WCVI.

The model predicts several major structural differences in kelp forests with sea cows in comparison with either the invertebrate dominated or sea otter dominated system states. One of the most important structural differences is the increased primary productivity in the sea cow dominated model (Table 3.1), despite an overall decrease in macroalgae biomass (Figure 3.2E). Macroalgae productivity is the foundation of many coastal ecosystems (Mann 1973, Steneck et al. 2002, Krumhansl and Scheibling 2012), and this increase in productivity influences numerous model groups, overall system productivity, trophic flow rates, and would also be expected to

influence ecosystems beyond the model boundaries (Krumhansl and Scheibling 2012, Wernberg et al. 2019, Gregr et al. 2020). The question of kelp export was not explicitly addressed here. However, overall rates of macroalgae and detritus export (the only groups allowed to be exported in the current model) were increased in the sea cow dominated state, suggesting sea cows increased kelp export rates (Table 3.1).

While increased productivity may have broader implications, the predicted decrease in standing macroalgae biomass, driven by sea cow herbivory and increased invertebrate herbivory, has implications for habitat complexity, hydrodynamic flows, and larval survival (Duggins 1988, Eckman et al. 1989, Duggins et al. 1990, Teagle et al. 2017). The model partially captures this dynamic using mediation (Espinosa-Romero et al. 2011, Appendix), and predicts how the reduction in macroalgae biomass may reduce the biomass of some model groups, such as lingcod and kelp crabs (Figures 2C and 2D). However, the model is unable to represent the vertical limitations of sea cow grazing, and the consequence of this limitation for macroalgae biomass loss. Sea cow herbivory and subsequent reduction in biomass was likely restricted to the top meters of kelp canopy (Chapter 2) where it may have had a limited impact on biogenic habitat provision (Teagle et al. 2017), especially if larval and juvenile finfish and shellfish primarily use the lower parts of the water column and understory macroalgae. Furthermore, the model may overestimate invertebrate herbivory (particularly sea urchin herbivory) in the sea cow dominated state, as we expect the increase in invertebrate biomass in the sea cow dominated state is driven by an increased consumption of detritus, rather than live macroalgae. Thus, the model may predict a greater decrease in macroalgae biomass, and greater consequences of this decrease, than would be expected.

Another significant change, likely related to increased macroalgae productivity, is an increase in detrital biomass (Figure 3.2F) and an increased flow of energy through detrital pathways (Table 3.2). Within the model this increased detrital flow appears to have widespread implications, contributing to increased biomass for plankton and several invertebrate groups, and ultimately an increase in sea otter biomass (Figure 3.2). This increased biomass is most pronounced in sea urchins and the diverse large grazers group (e.g., abalone, chitons, sea cucumbers), which benefit from both the increased detritus and the explicitly modelled reduction in vulnerability to sea otter predation associated with reduced invertebrate foraging times in the presence of sea cows (Appendix). For many groups that do not see an increase in biomass, the proportion of consumption originating in detritus is still increased (Table 3.2). Detritus has been shown to be a critical component of kelp forest ecosystems (Duggins et al. 1989, Krumhansl and Scheibling 2012, Feehan et al. 2018), and thus increasing detrital flows within kelp forests may represent an important influence of sea cows in North Pacific kelp forests. Importantly, however, the model is unable to capture the different fates of kelp biomass and how this influences the nutritional value of kelp detritus (i.e. sea cow feces may be of different nutritional value to particulate kelp detritus created by sea cow foraging or other physical processes), which may influence model results and biomass estimates.

Furthermore, these findings also suggest that kelp forests with sea cows may have been more resilient than either the invertebrate dominated or sea otter dominated system states. In the sea cow dominated state, biomass was more evenly distributed across all model groups than in either of the other two states, indicating greater diversity and suggesting a more stable, resilient system

state (Stachowicz et al. 2002, Worm et al. 2006, Hillebrand et al. 2008, Lamy et al. 2020). Increased evenness facilitated by sea cows may also contribute to the portfolio effect, increasing resilience by dampening variance (Figue 2004, Schindler et al. 2010). These suggestions are further supported by the finding that sea cows have weak direct interactions (Figure 3.4), which may dampen the effects of strong interactors and trophic cascades to promote community stability (O’Gorman and Emmerson 2009). Sea cows represent an entire functional group with numerous trophic and non-trophic interactions (Chapter 2), and it is therefore unsurprising the model suggests that their presence should contribute to increased resilience (Peterson et al. 1998, Folke et al. 2004, Saint-Béat et al. 2015, Smith et al. 2016).

Our results demonstrate both the value of using ecosystem models to address questions of past and future ecological function, and also the challenges and remaining barriers to representing complex species interactions within model frameworks. The model’s ability to faithfully recreate known ecological dynamics associated with sea otter recovery, and identify sea otters as a keystone species, suggests a certain robustness to model results. Furthermore, non-trophic effects of sea cows (Chapter 2) were included in the primary model using moderate, and likely conservative parameterizations, and sensitivity analysis revealed a range of possible results under alternate parameterizations (Figure 3.5). However, some of these interactions could only be partially represented within the model, such as the numerous ecological effects of kelp biomass (Duggins 1988, Teagle et al. 2017), possible differences in the response of *Nereocystis* and *Macrosystis* to sea cow grazing (as suggested by harvesting; e.g., Roland 1985, Krumhansl et al. 2017), or structural differences in the mechanism and vertical distribution of sea cow and sea urchin grazing (Chapter 2). The non-spatial modelling approach used here also assumes a

uniform distribution of sea cows and their influence, when in reality sea cow herbivory would likely have been heterogeneous, concentrated in certain areas of the model (Chapter 2). These limitations suggest that the present model, while accurately characterizing kelp forest dynamics and providing insight into the historical system state, may still fail to capture the full influence of sea cows. It is important for future modelling efforts to continue to improve the ability of ecosystem models to accurately depict complex species interactions and their uncertainty (Fulton et al. 2011, Harvey 2014). The modelling approach employed here – grounding the model in known ecological dynamics while including, with uncertainty, hypothesized dynamics – may be applicable to a variety of applications where data is limited or species interactions uncertain such as species introductions, extinctions, and rewilding.

Several additional ecological dynamics were not included in the present model but are worthy of consideration as they may influence model outcomes. In the Northeast Pacific, availability of macroalgae changes throughout the year, particularly for annual species such as *Nereocystis*, but the model does not capture this seasonality. This seasonal availability of macroalgae would have influenced sea cow herbivory, and may have led to decreased consumption or even periods of starvation in the winter months (as observed by Steller; Steller 1751), with potentially important implications for the influence of sea cows. Similarly, predation (i.e. by killer whales, Chapter 2) or possible habitat requirements (i.e. for calving) were not included in the model and may have limited sea cow populations, with knock on effects for the ecosystem dynamics explored here. Including these dynamics in future modelling efforts might be expected to alter the magnitude, but likely not the direction of the results presented here.

In combination, the findings of this model provide a glimpse into how human influence has altered kelp forests on the WCVI, discussions of which often neglect to consider the role of sea cows. These results also have implications for the management and restoration of this social-ecological system. Recent transitions of rocky reef ecosystems on the WCVI, driven by the reintroduction of sea otters, have resulted in tension as some elements of this system benefit but to the detriment of others (Sea Otter Recovery Team 2007, Nichol 2015, Markel and Shurin 2015, Pinkerton et al. 2019). Hardest hit have been large invertebrates, such as the endangered Northern Abalone (Watson 2000, Fisheries and Oceans Canada 2012), crabs, sea urchins, and geoducks, as well as the people and communities who depend on these species for economic, social, and cultural uses (Salomon et al. 2015, Pinkerton et al. 2019, Gregr et al. 2020). This model suggests, however, that sea otters may not always have reduced invertebrate populations to the level currently seen. Where sea cow influence was present along the coast, sea cows may have created a more productive system and facilitated coexistence, enabling invertebrate biomasses at intermediate levels to co-occur with sea otters in the historic system state. Therefore, the inability for sea otters and abundant invertebrate populations to coexist may not be an innate characteristic of the system, but rather a property that has emerged due to lost ecosystem functions and species interactions associated with the extinction of the sea cow. These findings suggest that management or restoration efforts to restore these dynamics might move the system towards a more productive and resilient state where coexistence of sea otters and invertebrates is possible, with significant implications for coastal communities and fisheries.

The notable exception to this pattern of coexistence appears to be geoducks, for which the model predicts a decline in the presence of sea cows (Figure 3.2). This reduction in geoduck biomass is

driven by an increase in sea otter biomass in the presence of sea cows, and consequently increased geoduck predation. However, the model does not capture the depth refugia that exists for geoducks below the foraging limit of sea otters, and geoducks below this foraging limit would be expected to be unaffected by increasing sea otter biomass. Also of relevance to predicted geoduck biomass, as well as that of other benthic invertebrates, is the model's inability to represent competition for space in the model area. Competition for space is an important limitation in intertidal and subtidal coastal systems (e.g., Paine 1966, Arkema et al. 2009), and thus the changes in biomass predicted in the model might be expected to result in compensatory changes in productivity as space becomes more or less available. Given these limitations, the model may overpredict the effect of increasing sea otter biomass on geoduck biomass.

Conversations around the restoration of kelp forests in the eastern North Pacific have generally emphasized the role of sea otters as keystone species that increases productivity and structures nearshore communities (Nichol 2015, Pinkerton et al. 2019, Gregr et al. 2020). However, the model presented here adds perspective on the role of sea cows in maintaining ecosystem states in the past, and what might be missing from current dynamics in North Pacific kelp forests. As efforts to restore degraded ecosystems continue, and perhaps increase (e.g., UNEP and FAO 2020), a recognition of lost ecosystem functions and species interactions is critical. As demonstrated here for kelp forests of the eastern North Pacific, a broader effort to understand the ecosystem dynamics that occurred prior to historical baseline shifts may reveal new possibilities for management and restoration. This research illustrates the importance of considering recent and historic anthropogenic baseline shifts, thereby illuminating the broader history of human influence on marine ecosystems globally (Erlandson and Rick 2008, McCauley et al. 2015). In

most ecosystems it may not be possible, or desirable (Coleman et al. 2020), to fully restore these historic baselines. However, an accurate understanding of historical ecosystem function can provide an important benchmark for restoration efforts (Jackson 2001, Lotze et al. 2006). This suggests that a wider framing of ecological restoration, considering a broader suite of species interactions, might provide greater insight into historical system states and increase the potential for ecosystem management and restoration (Jackson 2001, Donlan et al. 2006).

Chapter 4: Conclusion

Overall, this thesis demonstrates that Steller's sea cows likely played an important role in rocky reef ecosystems of the North Pacific, a role that has generally been overlooked in the study of these systems. The first half of this research synthesized multiple lines of evidence to develop hypotheses as to the ecological role played by Steller's sea cows, and how their extinction may have altered kelp forest dynamics. I then built upon these hypotheses using an ecosystem model to examine the consequences of sea cow presence for the community composition and productivity of kelp forest. This model also demonstrated the ability of ecosystem models to address complex and uncertain species interactions. In combination, this work provides insight into the historical baseline for North Pacific kelp forests and provides context for current management and restoration. In this concluding chapter I synthesize these findings, discuss their significance, and acknowledge their limitations and possible next steps.

4.1 Findings

In reviewing relevant historical and ecological literature, I proposed six hypotheses through which sea cow herbivory likely influenced kelp forest dynamics (Chapter 2). I argued that grazing by this megaherbivore likely affected physical ecosystem structure, primary productivity, nutrient cycling, predator-prey interactions, kelp export, and the biotic dispersal of kelp spores. These hypothesized mechanisms were partially supported by the literature I reviewed, and suggest sea cows were important controllers of kelp forest dynamics and exerted a substantial top-down influence. This literature review also indicated that the influence of sea cows likely

extended beyond the bounds of kelp forests, affecting the flow of kelp biomass and nutrients to surrounding habitats. In demonstrating that the sea cow likely played these important roles in kelp forests prior to their extinction, I illustrate how kelp forest dynamics were altered prior to the onset of more recent and well-studied stressors such as climate change or sea otter extirpation.

Next, I examined how the restoration of species interactions associated with sea cows might affect kelp forest dynamics by modelling the hypothetical reintroduction of sea cows on the WCVI (Chapter 3). The results of the ecosystem model suggest that the presence of sea cows would enhance primary productivity, overall ecosystem productivity, and total system throughput (the sum of all flows in the system). Additionally, the sea cow dominated system state predicted by the model had a more even distribution of biomass between model groups, an indicator that this state may have been more resilient than system states without sea cows.

Finally, the sea cow dominated state in the model had a significantly altered community composition, with changes in the biomass of most model groups. The most notable change was an increase in the biomass of both sea otters and their large invertebrate prey, suggesting that the presence of Steller's sea cows enables the stable coexistence of this keystone predator and its prey. These model results build upon the hypotheses generated in Chapter 2 and indicate that while the sea cow was not a keystone species, it played an important role in kelp forests and altered fundamental system properties such as productivity and resilience.

In modelling the reintroduction of an extinct species and its interactions, I also demonstrated the ability of ecosystem models to represent some of these complex dynamics (Chapter 3).

Ecosystem models, such as EwE, excel at illustrating energy flows between groups, group biomasses, and indicators of ecological networks, as well as how these attributes change in response to different anthropogenic stressors (e.g., fishing or climate change; Eddy et al. 2017, Lotze et al. 2019). What is more challenging to represent in an ecosystem model, however, are changes in species interactions and the underlying structure of ecosystems (e.g., changing diet preferences, changing rates of production, or the fact that urchin grazing may result in the loss of whole kelp plants while consuming only a small amount of biomass). Many parameters relevant to these complex processes are typically assumed to be static (Gregn and Chan 2015). This may be particularly problematic for the accurate modelling of past and future ecosystem states. In this model, I was able to represent some, but not all, of the hypothesized effects of sea cows in kelp forests. For instance, I was unable to model structural differences in the herbivory of sea cows and sea urchins, and the compensatory growth likely driven by sea cow herbivory, and instead approximated this relationship using a mediation function. Several such compromises were required to model the role of sea cows and suggests that the results presented here are a conservative and incomplete estimate of the influence sea cows had in kelp forests.

4.2 Significance

I believe these findings make a modest yet valuable contribution to the literature on North Pacific ecosystem dynamics and have important implications for discussions around extinction and rewilding, kelp forest dynamics, ocean restoration, and ecosystem modelling.

In recent years, our understanding of the consequences of extinctions (particularly megafauna extinctions) has greatly increased (e.g., Malhi et al. 2016, Smith et al. 2016). In conjunction, the concepts of rewilding and de-extinction have gained momentum as strategies to reverse these consequences and restore lost ecosystem function (Seddon et al. 2014b, Svenning et al. 2016). This thesis contributes to this growing body of literature by examining the consequences of extinction and demonstrating the potential for restoration in an ecosystem often regarded as already in the process of being restored. Further, research on megafauna decline and rewilding has largely focused on terrestrial systems (with some notable exceptions; e.g., Roman and McCarthy 2010, McCauley et al. 2015, Valdez et al. 2020), and this work helps to extend these conversations into the marine realm. It is my hope this examination of the role of the Steller's sea cow may inspire those working on other systems (marine or otherwise) to consider the roles previously played by missing species and their consequences for current system dynamics. Such work may play a critical role in generating novel approaches to addressing the loss of biodiversity and ecosystem services.

This research also contributes to our understanding of the effect of past species declines on current ecosystem resilience. Previous research has demonstrated that historical extinctions and population declines may contribute to current declines and reduced ecological integrity (e.g., Jackson et al. 2001). My findings suggest a similar conclusion, with sea cow extinction appearing to have reduced resilience and contributed to trade-offs in present ecosystem dynamics. By extending this understanding to a new context, this work helps show that rather than applying in only a handful of cases, the role of historical declines in reducing present ecosystem resilience is likely a widespread phenomenon, deserving of more consideration.

Specific to the case study used here, a large body of research has focused on kelp forests of the North Pacific (e.g., Estes and Palmisano 1974, Dayton 1985, Steneck et al. 2002, Burt et al. 2018), however relatively little attention has been paid to the role of the Steller's sea cow in this system. By examining the role of this megaherbivore and developing a better understanding of what the historical baseline may have looked like, this thesis provides novel insights into kelp forest dynamics. These results suggest that kelp forests were once (and have the potential to be) more productive and resilient than they are currently, and also suggests that the conflict seen between sea otters and invertebrate fisheries may not be an innate characteristic of the system, but is at least partially a consequence of the sea cow's extinction. Present concerns such as the decline of invertebrate populations may have their origin in the extinction of the sea cow, rather than the more recent changes to which they are often attributed. This work may, therefore, help inform the future management and restoration of North Pacific kelp forests, with particular relevance for tensions between sea otters and invertebrate fisheries, as well as the harvesting of kelp, which shares some similarities with sea cow grazing.

Finally, this thesis contributes to the use of ecosystem models in addressing complex ecological dynamics. The modelling approach used here demonstrates the value in using ecosystem models such as EwE to address, with uncertainty, hypothesized and variable species interactions. These methods apply not only to questions of extinction and rewilding, but also species introductions and invasions, and therefore these methods may apply to a wide range of ecosystems and contexts. Furthermore, by attempting to represent several complex ecological dynamics and not always succeeding, this work shines light on the limitations in representing and parameterizing

these dynamics in current ecosystem models. Ecosystem modelling has developed rapidly in recent years, and continuing to address limitations such as these may allow such models to better address questions pertaining to uncertain and complex species interactions.

4.3 Limitations & next steps

While the contributions of this work are hopefully of value to a diverse audience, this research has a variety of limitations that place caveats on these results. These limitations primarily pertain to the modelling approach and our imperfect knowledge of ecological dynamics and suggest several avenues of future research.

The ecosystem models developed here were largely theoretical and as such entailed substantial uncertainties. I attempted to characterize this uncertainty, as it related to certain parameters and structures of the model, but uncertainties remain. One major source of unaddressed uncertainty is what is *not* in the model. As has previously been mentioned, the model presented in Chapter 3 is a conservative, and incomplete representation of ecological dynamics, and leaves out many potential interactions. The ecological states predicted in the models here are thus likely to be indicative of changes in system states, but are almost certainly not a “true” characterization of these system states. This is an issue commonly faced by modellers of all kinds, and past work has demonstrated that more is not always better, with increased complexity often resulting in worse model predictions (e.g., Fulton et al. 2003, Gregr et al. 2018). Continued efforts to characterize structural uncertainties and represent complex ecological interactions may help

answer questions such as those addressed by this thesis but should be cognizant of the potential dangers of additional complexity.

More fundamentally, incomplete ecological knowledge limits the confidence in both hypothesis generation (Chapter 2) and the parameterization of model groups and relationships (Chapter 3). This incomplete knowledge is most obvious in regards to the Steller's sea cow, where our biological and ecological understanding are informed estimates at best. Much is still unknown about the diet, distribution, abundance, and behaviours of this extinct species. However, our lack of knowledge also includes many other species and processes relevant to this work. Examples include rates of kelp export, diet compositions for benthic invertebrates, species abundance/occurrence within the model area, and the shapes and magnitudes of many mediation functions. The hypotheses proposed in Chapter 2 were therefore made within the context of this uncertainty, and will ideally be tested by future research. The modelling portion of this thesis partially accounted for this uncertainty using Monte Carlo simulations and mediation sensitivity analysis, but considerable uncertainty still remains. Additional research to ground-truth the model on the WCVI, and increase our understanding of sea cow ecology are warranted. Field experiments mimicking the role of sea cows, perhaps aligned with kelp harvesting, may be of particular value.

A further limitation relates to the use of the present approach – and other historical approaches – to inform management and restoration in the face of highly uncertain future conditions.

Pervasive stressors such as climate change may put past conditions out of reach, raising doubts for some about the feasibility of restoration (e.g., Coleman et al. 2020). In some contexts,

however, rewilding and restoration may be useful strategies in combating climate change (e.g., Sandom et al. 2019). Considering the interacting effects of sea cow rewilding and stressors such as ocean acidification or increasing sea surface temperatures is beyond the scope of this thesis, but might be valuable in informing management and restoration of kelp forests under future conditions.

This thesis considered many – but by no means all – of the potential effects Steller’s sea cows may have had on coastal ecosystem dynamics. Even considering this subset of processes, these results suggest that sea cows played an important role in kelp forests, and their extinction likely had a large impact on several ecosystem dynamics. Considering additional processes – some of which were touched upon here – will almost certainly bring to light additional consequences of the extinction of this megaherbivore. This research has made an important step in beginning to identify the historical baseline and the potential for restoration in kelp forests of the North Pacific, but future research is needed to confirm, and expand this understanding.

The broadest future directions for this work may be in extending the approaches used here, for kelp forests and sea cows, to a range of other ecosystems. As this work suggest for kelp forests, many systems which are considered ecologically healthy may in fact be substantially less productive and resilient than they once were. Thus, many marine, freshwater, and terrestrial ecosystems may benefit from a consideration of how historical extinctions or population declines altered ecological processes and shaped present system states. Such work has been occurring for many years, and this research is by no means the first, but the present research demonstrates the value in applying these approaches to ecosystems or species which may not have been

considered previously. Broader consideration of lost ecological function in a variety of ecosystems may help unearth the possibilities of ecosystem restoration and management, and contribute to halting or reversing biodiversity loss.

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Appendix

A.1 Ecopath

Group Parameters

All groups were initially parameterized (including diet compositions) following Gregr et al. 2020, with the exception of the Steller's sea cow, which was parameterized and added to the model here. The parameters used by Gregr et al. (2020) were obtained from empirical evidence and previous models for the region, and were left unchanged where possible. The addition of Steller's sea cows to the model required no additional model balancing, however some parameters were altered so as to improve ecological realism, particularly as related to the export of kelp biomass.

The export of kelp biomass is an important spatial subsidy to several marine and terrestrial habitats, and while the exact proportion of biomass that is exported is unknown it is likely to be a significant amount. To approximate this dynamic in the models, 25% of unconsumed *Macrocystis* and *Nereocystis* biomass production was allowed to be exported from the model system. This change resulted in an unbalanced model ($EE > 1$ for kelp detritus), and several changes were made to reduce consumption of kelp detritus. The proportion of kelp detritus in the diet was decreased for geoducks (10% to 5%), mussels (10% to 5%), other edible clams (10% to 5%), large grazers (68% to 58%), small grazers (83% to 63%), mesograzers (10% to 5%), sessile invertebrates (15% to 7.5%), large zooplankton (10% to 5%), and small heterotrophs (10% to

2.5%) with the balance in all cases made up for by increasing the proportion of regular detritus in the diet. In addition to balancing the model, these changes appear to better distribute consumption across detritus and kelp detritus, resulting in a reasonable EE for both kelp detritus (0.58) and the more abundant detritus group (0.17).

Finally, sea urchin diet was redistributed so as to increase the proportion of kelp detritus in the diet. This change was originally suggested by Gregr (2016) to better represent sea urchin foraging dynamics in urchin barren system states (Konar and Estes 2003). This modification also better represents the tendency for sea urchins to reduce active grazing and consume kelp detritus in the presence of predators (e.g., Filbee-Dexter and Scheibling 2014). After modification, sea urchin diet composition was 15% *Nereocystis*, 15% *Macrocystis*, 15% other macroalgae, 15% detritus, and 40% kelp detritus (whereas Gregr et al. (2020) split consumption evenly across all five model groups).

Final Ecopath parameters are presented in Table A.1. For a discussion of the selection process for these parameters (excluding sea cows), see Gregr (2016).

Table A.1 Ecopath parameters

Ecopath parameters and estimates for initial model year (1970), corresponding to an invertebrate dominated system state. Values estimated by Ecopath are shown highlighted in grey.

Group name	Trophic level	Biomass (t/km ²)	Production / biomass (year ⁻¹)	Consumption / biomass (year ⁻¹)	Unassimilated Consumption	Ecotrophic Efficiency	Production / consumption (year ⁻¹)
Steller's sea cow	2	0.010	0.037	3.65	0.5	0.000	0.004
Sea otter	3.19	0.000	0.186	140.000	0.2	0.931	0.001
Urchin	2	29.000	0.244	10.880	0.4	0.210	0.022
Large commercial crab	3.06	0.065	1.500	4.250	0.2	0.900	0.353
Geoduck	2.02	70.000	0.048	2.000	0.2	0.080	0.024
Mussel	2.02	82.600	0.428	1.420	0.2	0.142	0.301
Other edible clams	2.02	19.390	0.410	1.370	0.2	0.204	0.299
Lingcod	3.9	0.330	0.500	3.550	0.2	0.318	0.141
Other demersal reef fish	3.63	2.836	0.300	2.000	0.2	0.900	0.15
Pelagic reef fish	3.39	0.228	2.000	10.000	0.2	0.800	0.2
Forage fish	3.31	0.110	1.500	4.750	0.2	0.900	0.316
Kelp crab	2.66	0.872	3.500	20.000	0.2	0.900	0.175
Predatory inverts	3.14	3.000	0.760	4.000	0.2	0.422	0.19
Large grazers	2	7.100	0.500	10.100	0.4	0.273	0.05
Small grazers	2	2.000	3.000	14.000	0.4	0.659	0.214
Meso grazers	2.23	1.953	3.410	15.000	0.2	0.817	0.227
Sessile inverts	2.71	4.944	2.000	13.000	0.4	0.645	0.154
Large zooplankton	2.33	16.300	15.800	45.600	0.4	0.240	0.346
Small heterotrophs	2.05	11.700	125.000	290.000	0.4	0.260	0.431
Phytoplankton	1	28.000	125.000			0.969	
Nereocystis	1	11.285	43.000			0.100	
Macrocystis	1	9.158	6.080			0.900	
Other macroalgae	1	6.011	15.000			0.800	
Detritus	1	10.000				0.179	
Kelp detritus	1	10.000				0.942	

Fisheries

While fisheries and associated catches are not of interest in the present model, the fisheries included in the model in Gregr et al. (2020) for sea urchins, commercial crabs, geoduck, other edible clams, and lingcod were retained here. This decision was made taking into account the important role these fisheries play in the mortality rates of some groups and ecosystem dynamics more generally. The parameters for many model groups are calculated based on their current, exploited population dynamics, and thus fisheries are an important component of the model. Indeed, it was observed that the removal of these fisheries led to unrealistic and unstable model outcomes. A fishery for sea otters was also included in the model (as in Gregr et al. 2020) so as to suppress otter populations in the first timestep, but was then removed for all subsequent years (fishing effort set to zero). Fishery parameters used here are therefore identical to those in Gregr et al. (2020).

A.2 Ecosim

Group Parameters

Ecosim allows the user to set several additional group parameters which control various aspects of feeding, growth, and mortality rates, and the ability for these rates to change between timesteps in Ecosim (Christensen et al. 2008). Generally, these parameters were left at their default or recommended values (Christensen et al. 2008), with a few exceptions.

The maximum relative feeding time was left at the default value of 2 for all groups except sea otters, which was set at 25. This allows sea otters to increase the amount of time spent feeding to compensate for increasing sea otter biomass and decreasing prey availability, and Gregr et al. (2020) found this to be necessary for sea otters to reach estimated population levels and limit invertebrate populations to the levels expected.

Feeding time adjustment rate (FTAR) was set to zero for all groups (implying the amount of time they spend feeding is fixed) except marine mammal groups, as recommended by Christensen et al. (2008). FTAR was set to 0.75 for sea otters (as in Gregr et al. 2020), and 0.5 for Steller's sea cows.

Switching power controls the ability for model groups to switch between prey groups as their relative abundance changes. This parameter was left at the default value of 0 for all groups except sea otters, where it was set to 0.3. Gregr et al. (2020) showed that a non-zero switching power is necessary to allow sea otters to switch between the various prey groups.

Vulnerabilities and Fit to Time Series

Vulnerability is a key Ecosim parameter which controls how much a change in predator biomass will affect predation mortality for a given prey (Christensen et al. 2008). Furthermore, vulnerability is one of the main parameters which is modified to fit models to time series data and ensure the model is capturing ecological dynamics (Ainsworth and Walters 2015). Given the

exploratory nature of this research, it was important to ground the model in as much ecological data as possible.

Nine timeseries for group biomasses, corresponding to the transition from an invertebrate dominated to a kelp and sea otter dominated system were used to evaluate model fit. Eight of these timeseries were for the biomass of invertebrate model groups, while the final timeseries was a logistic growth curve for sea otter biomass (Table A2). Timeseries were obtained from Gregr et al. (2020), but were modified to fit the timespan of the present model. Table A2 shows the time series used in the model, but see Gregr (2016) for a detailed description of time series development.

To improve model performance, vulnerabilities were set manually for Steller's sea cows and sea otters, and set using the Ecosim time series fitting procedure for remaining model groups with time series data (8 groups). Steller's sea cow vulnerability was set to 50, to represent that in the initial parameterization sea cows are absent from the model and thus very far from carrying capacity. Similarly, sea otter vulnerabilities were set to large values to represent that initially sea otters are far from carrying capacity. Following Gregr et al. 2020, sea otter vulnerabilities were set at varying levels depending on prey value and accessibility: 100 for low-quality prey (sessile invertebrates, predatory invertebrates, and kelp crabs), 200 for medium-quality prey (geoduck and other edible clams), 400 for high-quality prey (mussels), and 1000 for very high-quality prey (sea urchins, large commercial crabs, and large grazers). The Ecosim timeseries fitting procedure was then used to estimate the vulnerabilities for the eight remaining model groups with time series. For all other groups, in the absence of time series data or empirical evidence,

vulnerabilities were left at the default value of 2. After these adjustments to the vulnerability values, the model had a greatly improved fit to the time series (Sum of Squares = 48.4) compared to default vulnerabilities (Sum of Squares = 1090.2).

Mediation

Mediation functions are the primary mechanism through which non-trophic interactions between species can be represented in EwE. Mediation allows the user to define a functional relationship by which one model group may indirectly influence the trophic interactions between two or more other model groups (e.g., facilitation or protection), or influence the production rates of primary producers (Christensen and Walters 2004, Christensen et al. 2008, Espinosa-Romero et al. 2011). Three mediation functions were incorporated into this model to represent potential non-trophic effects of Steller's sea cows. These mediation functions, as well as sensitivity analysis associated with them, are described in detail in the hypothesis parameterization section below.

Table A.2 Timeseries data used in model fitting

Timeseries data used in Ecosim's fit to time series procedure. Timeseries were developed by Gregr (2016) based on a space-for-time substitution of biomass change in response to sea otter recovery.

Year	Sea otter Biomass (t / km²)	Urchin Biomass (t / km²)	Geoduck Biomass (t / km²)	Mussel Biomass (t / km²)	Predatory Invert Biomass (t / km²)	Large Grazer Biomass (t / km²)	Small Grazer Biomass (t / km²)	Meso Grazer Biomass (t / km²)	Sessile Invert Biomass (t / km²)
1970	0.00051	29	70	82.6	3	7.1	2	1.95	4.94
1971	0.0006	-	-	-	-	-	-	-	-
1972	0.00071	-	-	-	-	-	-	-	-
...	...	-	-	-	-	-	-	-	-
2050	0.04678	0.25	56	57.1	5.1	0.2	6.6	0.8	56.5
...	...	-	-	-	-	-	-	-	-
2060	0.04703	0.25	56	57.1	5.1	0.2	6.6	0.8	56.5

A.3 Hypothesis parameterization

Four potential mechanisms through which Steller's sea cows may have indirectly altered kelp forest ecosystems were explicitly parameterized within the model. These indirect effects relate to physical ecosystem structure, primary production, nutrient cycling, and predator-prey mediation. Given the uncertainty associated with these hypothesized mechanisms, a range of values was used to represent each mechanism, and the sensitivity of the results to these parameterizations was explored.

Physical Ecosystem Structure

The role of kelp biomass in contributing to ecosystem structure, and the subsequent influence of sea cow herbivory on this physical structure (Chapter 2) was represented using mediation functions. An increasing hyperbolic function was selected as this is thought to be the most conservative (Harvey 2014), and defined the relationship between macroalgae biomass (Macrocystis, Nereocystis, and the other macroalgae group) and the vulnerability of prey to fish model groups, as well as the foraging area available to fish groups (Figure A.1A). In effect, this function represents that as macroalgae biomass increases, prey and habitat are increasingly available to fish groups and is similar to mediation functions used previously (Espinosa-Romero et al. 2011, Gregr 2016).

To explore the sensitivity of model results to this mediation function, various initial parameterizations were used (Harvey 2014), representing five relationships of varying strengths

(Figure A.1A). Because the mediation function is scaled to the initial Ecopath baseline (always at 1), changing the initial parameterization results in substantial changes to the shape of the function. The impact of these five initial parameterizations (plus the absence of a relationship, for a total of 6 models) on model results was then explored (see results). The central value, corresponding to a moderate strength relationship (parameterization 3), was selected for the primary model runs.

Predator-Prey Mediation

The potential role of the Steller's sea cow in mediating the trophic interactions between sea otters and their large invertebrate prey (Chapter 2) was also represented using a hyperbolic mediation function (Figure A.1B). In this case, these functions were used to define the relationship between Steller's sea cow biomass and the effective search rate of sea otters on their mobile invertebrate prey (sea urchins, large commercial crabs, kelp crabs, predatory invertebrates and large grazer model groups). This function therefore represents that in the presence of Steller's sea cows, mobile invertebrate prey may be less available to sea otters.

As for the physical ecosystem structure hypothesis, sensitivity of model results to this mediation function was explored using five initial parameterizations and a null parameterization (Figure A.1B). The central value, corresponding to a moderate strength relationship (parameterization 3), was selected for the primary model runs.

Primary Production

The potential impact of Steller's sea cow herbivory on primary production within kelp forests (Chapter 2) was also represented using mediation functions. In this case simple linear functions were selected as they allow for a gradual rate of change across the functional space (Figure A.1C). These mediation functions defined the relationship between sea cow biomass and the productivity of macroalgae groups. This approach was selected in place of alternatives (e.g., modelling light competition between primary producers and the subsequent influence of sea cows on this competition) as sea cow grazing on the top meter of canopy kelp would be expected to have a disproportionate impact on light availability, that would not be captured through changes to biomass alone.

To explore the sensitivity of model results to this mediation function, five separate linear functions were defined with different slopes (Figure A.1C). These alternate functions may be interpreted as representing various possible strengths of the interaction between sea cows and primary production. The impact of these five functions (plus the absence of a relationship, for a total of six parameterizations) on model results was then explored. The central value, corresponding to a moderate strength relationship (parameterization 3), was selected for the key model runs.

Nutrient Cycling

The potential role of the Steller's sea cow in the production of kelp detritus and nutrient cycling (Chapter 2) was represented by varying the amount of detritus produced by sea cows. This was

achieved by keeping the amount of assimilated consumption [assimilated consumption = $Q/B - (Q/B * U)$] constant at the levels estimated by Best (1981), and changing the amount of unassimilated consumption (i.e. detritus) produced by sea cows by simultaneously varying the Q/B and U parameters for Steller's sea cows in Ecopath (Figure A.1D; Table A3).

As for the other hypotheses, the sensitivity of model results to this hypothesis was examined by creating five alternate parameterizations of varying strength (plus a null parameterization, for a total of six). The impact of these six parameterizations on model results was then explored, and the central value (parameterization 3) was selected for the key model runs.

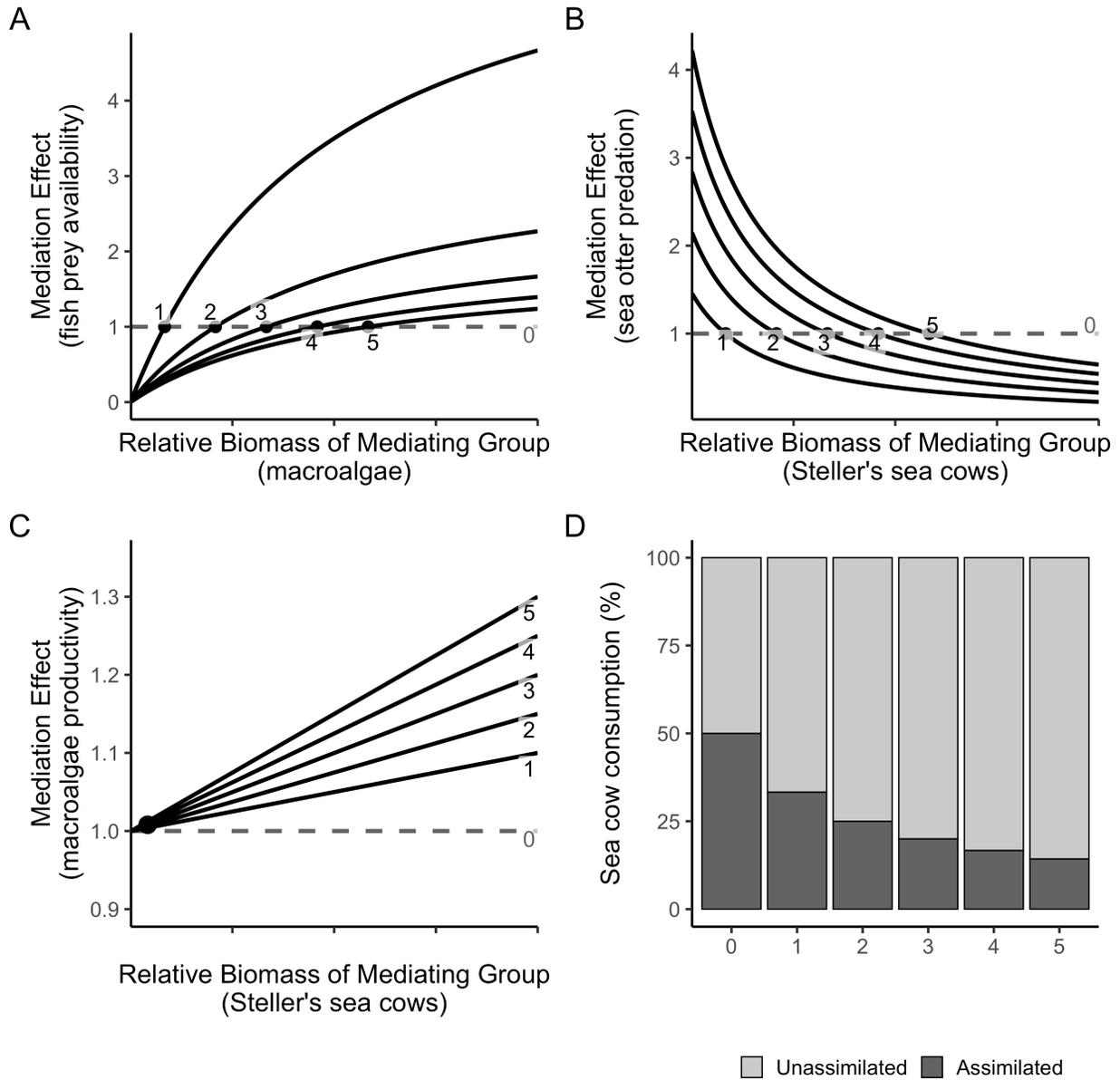


Figure A.1 Alternate hypothesis parameterizations

Parameterized functions for the hypothesized mechanisms by which sea cows may have altered kelp forests: (A) physical ecosystem structure, (B) predator-prey mediation, (C) primary productivity, and (D) nutrient cycling.

Table A.3 Parameters for the six parameterizations of the nutrient cycling hypothesis.

Parameterization	Q/B (year ⁻¹)	U (%)	Q/B - unassimilated (year ⁻¹)
0 No additional detritus (Q/B x 1)	3.650	50.0	1.825
1 Low additional detritus (Q/B x 1.5)	5.475	66.7	3.650
2 Low-Moderate additional detritus (Q/B x 2)	7.300	75.0	5.475
3 Moderate additional detritus (Q/B x 2.5)	9.125	80.0	7.300
4 Moderate-High additional detritus (Q/B x 3)	10.950	83.3	9.125
5 High additional detritus (Q/B x 3.5)	12.775	85.7	10.950

A.4 Parameter uncertainty

Model parameter uncertainty (Link et al. 2012), particularly as relating to the parameterization of the Steller's sea cow, was explored using Monte Carlo simulations. Ecosim's Monte Carlo procedure allows the user to randomly vary input parameters proportionally to the level of confidence in the value (termed "pedigree" in EwE), determines whether the resulting model is balanced, and if balanced runs the model (Christensen et al. 2008).

The primary focus of this model are the ecological impacts of the Steller's sea cow, and consequently the Monte Carlo simulations were designed to primarily explore the sensitivity of the model to the Steller's sea cow parameterization. All relevant Ecopath parameters were included in the sensitivity analysis (B, P/B, Q/B, EE, and diets). For the simulations, Steller's sea cow parameters were randomly selected within a +/- 80% range from the original parameterization, corresponding to the lowest pedigree setting (Christensen et al. 2005). Parameters for all other model groups were also allowed to vary, but to a lesser degree (+/- 10%), so as to ensure a full range of balanced models could be explored. The Monte Carlo procedure required an average of 2.6 runs to obtain a balanced parameterization.