Foraging Ecology and Population Dynamics of Northern Sea Otters (*Enhydra lutris kenyoni*) in Washington State

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A dissertation

submitted in partial fulfillment of the

requirements for the degree of

Doctor of Philosophy

University of Washington

2022

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Program Authorized to Offer Degree:

School of Aquatic and Fishery Sciences

University of Washington

Abstract

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Many marine mammal populations are currently recovering from population depletion after overharvest. As marine mammals are often important predators in shaping marine ecosystems, there is a need to understand the impacts of recovering populations on other species and the marine ecosystem as a whole. The depletion and subsequent recovery of these species presents biologists with natural experiments to study their ecology, including drivers of their population dynamics and the function of the species in the ecosystem. This dissertation focuses on the recovery of a translocated population of sea otters (*Enhydra lutris kenyoni*) in Washington State. The presence or absence of sea otters, a keystone species, can dramatically influence marine community structure. The overall aim of this dissertation was to utilize the natural experiment of sea otter translocation to Washington State to understand drivers of sea otter population dynamics as well as the ecological role that sea otters play in Washington State. In Chapter 2, my coauthors and I found that the

sea otter population in Washington has grown from an estimated 21 adult sea otters in 1977 to 2,336 adult sea otters in 2019, and the population is predicted to continue to grow and expand primarily to the south of the current range over the next 25 years. We also estimated that Washington State can support twice as many sea otters than previously estimated (equilibrium abundance of 6,080 vs. 2,734 sea otters), and that estimates of mean equilibrium density in currently occupied areas had the largest impact on predictions of population growth and range expansion. In Chapter 3, we quantified how sea otter population status (i.e., sea otter cumulative density) and habitat type (i.e., sea otter foraging in open water, kelp canopy, emergent rock, or intertidal) influence sea otter diet, and found that habitat was 1.77 times more important than sea otter population status in determining sea otter diet composition. We also found that sea otter long-term average rate of energy intake and diet diversity were negatively and positively correlated with sea otter cumulative density, respectively. In Chapter 4, we demonstrated the ecological role of sea otters in the nearshore marine ecosystem in Washington as a keystone species. We found that temporal transitions in the amount of kelp canopy were related to the duration of sea otter occupation, and that this relationship was more complex than a simple linear function. We also found that sea urchins were present at higher densities at sites more recently occupied by sea otters compared to long-occupied sites. In Chapter 5, we demonstrated the impact of sea otters as a recovering predator on the Pacific razor clam (*Siliqua patula*). We found that the magnitude of sea otter predation effects varied over time and space, with sea otter-caused razor clam mortality surpassing natural mortality in 2018 at Kalaloch Beach, occupied by sea otters since 2005. We also found that sea otters selectively consume the larger “recruit” size razor clams, the size that is also targeted in the

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Acknowledgements

This dissertation relies on decades of data collected on the Washington coast by Federal, State, and Tribal organizations on sea otter abundance, sea otter foraging, kelp canopy cover, oceanographic conditions, subtidal invertebrate community composition, razor clam size and density, and razor clam harvest. I am grateful to my collaborators for openly sharing their expertise, thoughts on knowledge gaps and science needs, and entrusting me with this data, including Ron Jameson, Deanna Lynch, Steve Jeffries, Shawn Larson, Jim Bodkin, Jon Scordino, Scott Mazzone, Daniel Ravenel, Joe Schumacker, Scott Pearson, Dan Ayres, Helen Berry, Rikk Kvitek, Jameal Samhouri, Ole Shelton, Steve Fradkin, Liam Antrim, and Ed Bowlby.

I am grateful to the co-authors of the manuscripts that have or will result from this work. I am especially grateful to Ron Jameson for his confidence in me, demonstrated as access to the 1990s sea otter foraging data and early sea otter survey data. Steve Jeffries was an incredible resource on all things sea otters in Washington, and gave me the opportunity to see the Washington coast and sea otters from the air, an experience I will not soon forget. I would like to acknowledge Tim Tinker for his patience, generosity, and uncritical approach to teaching me about Bayesian modeling. Thank you to my advisor Kristin Laidre, who trusted me to pursue my research and connected me to the right people, and whose expert direction kept me on the right path. Both Kristin and Tim provided invaluable input on early drafts of dissertation chapters and manuscripts, and helped me grow as a writer. Jon Scordino was a superb collaborator, and contributed essential data on sea otter use of the Strait of Juan de Fuca used in Chapter 2.

In addition to data previously collected, this work involved extensive field work collecting sea otter foraging data throughout the Washington coast. The Makah Ocean Policy Workgroup (MOA Nos. 2015-17 & 2016-12), Quinault Indian Nation Business Committee (Res. No. 15-199-94), and Olympic National Park (Study Number OLYM-00048) provided permissions to collect sea otter foraging observations from their lands. I would like to thank Dan Monson, Ben Weitzman, Shawn Larson, Jim Bodkin, and Caroline Hempstead for teaching me to make sea otter foraging observations, giving me the skills and confidence to pursue much of the research below. This work could not have been completed without the assistance and support of intrepid field technicians Carter Johnson, Allison Northey, Amanda Witt, Abby Van Hemmen, and Christine Phelan, who helped collect and record sea otter foraging data on the remote Washington coast, rain or shine. I will look back on our time together in the “otter office” fondly. I would also like to thank everyone involved in the annual sea otter survey for welcoming me with open arms and teaching me to count sea otters. I count my lucky stars that I got to join the ranks of this passionate group of individuals studying sea otters in Washington State. During my dissertation work, I was supported by the NOAA Dr. Nancy Foster Scholarship, Cooperative Institute for Climate, Ocean, and Ecosystem Studies Graduate Research Fellowship, and the School of Aquatic and Fishery Sciences. I also received funding support for field work from the Dr. Holly Reed Conservation Fund from Point Defiance Zoo and Aquarium and the School of Aquatic and Fishery Sciences.

Thank you to my committee members Kristin Laidre, Aaron Wirsing, Sarah Converse, Steve Jeffries, and Tim Tinker for expanding my thinking and guiding me throughout this process, from writing my proposal to writing this dissertation, and everything in between.

Collectively they have substantially improved the quality and scope of my research. Thanks also to Glenn VanBlaricom who served on my Master's committee before I bypassed to the PhD track. Thank you, Glenn, for treating me as a colleague, for the impromptu science chats that shaped my dissertation work, and for the opportunity to join you on San Nicolas Island.

Thank you to my current and past lab mates Erica Escajeda, Jenny Stern, Marie Zahn, Jessica Lindsay, Ben Cohen, Casey Clark, Richard McGovern, and Donna Hauser for your camaraderie and thoughtful input on my research over the years. Special thanks to Jenny for being my accountability buddy, especially during the pandemic. I am immensely grateful for your support. Thank you to SAFS alumnae Jessica Randall, Jenna Keeton, and Shannon Hennessey, whose friendship and support has buoyed me, especially during the pandemic. Thank you to my friend and colleague Erin Foster, who was a source of scientific inspiration, encouragement, and advice. I couldn't have asked for a more supportive and collaborative friend to study sea otters with. A special thank you to my partner Brent Grossman, whose unwavering support and affirmation allowed me to persevere, and who chipped in as a field technician on more than one occasion. Brent took me on my first backpacking trip, setting the stage for many, many more backpacking trips in pursuit of sea otter foraging data. Lastly, I would like to thank my family for supporting my aspirations. To my parents for instilling me with an appreciation for nature through camping trips and hikes during my childhood, and to my brother whose ability to make me feel truly understood was a source of comfort throughout this process.

Dedication

For Cadbury.

Chapter 1. Introduction

1.1 MARINE MAMMAL RECOVERY

Many marine mammal populations are currently recovering from population depletion after overharvest in portions of their historic range (Kent et al. 2012; Magera et al. 2013; Lowry et al. 2014; Thomas et al. 2016, 2019). Resource managers, who typically manage species in decline, are now tasked with managing recovering populations of marine mammals (Roman et al. 2015). As marine mammals are often important predators in shaping marine ecosystems (Bowen 1997), there is an urgent need to understand the impacts of these recovering populations on other species and the marine ecosystem as a whole. Increasing abundance of predators can have cascading impacts on ecosystems, in some cases including increased competition with human fisheries for the same prey (Marshall et al. 2015, Smith et al. 2015). Roman et al. (2015) lay out recommendations for coexisting with formerly depleted species as they recover, stating that part of this shift in management approach is to anticipate range expansion and ecological roles of recovering species. Predictions of range expansion allow for predictions of ecological impacts of recovery, including competition with fisheries, and in anticipating the ecological roles of recovering populations, it is important to recognize the top-down effects of marine mammals that can have far reaching effects on food webs. Sea otters (*Enhydra lutris spp.*) are a particularly salient example of a recovering marine mammal that shapes ecosystems, as their recovery may introduce significant new conservation challenges in areas where sea otters overlap with fisheries (Carswell et al. 2015), and their presence or absence can dramatically influence community structure (e.g., Estes and Palmisano 1974, Estes and Duggins 1995, Watson and Estes 2011, Hughes et al. 2013). There is a need to understand both sea otter population growth and recolonization, and ecological consequences of this population growth and recolonization in order to shift management approaches as sea otter populations recover.

1.2 POPULATION DYNAMICS

Sea otters were heavily targeted throughout their range during the Pacific maritime fur trade in the 18th and 19th centuries, resulting in extirpation of sea otters from portions of their range, including northern sea otters (*Enhydra lutris kenyoni*) from Washington State (Kenyon 1969, Scheffer 1940). Little information exists on the distribution and abundance of sea otters in Washington before extirpation, but the last sea otter in Washington was reported to have been shot in 1911 (Scheffer 1940). Sea otters were absent from Washington State until 1969/1970, when 59 sea otters were translocated from Amchitka Island, Alaska to the outer coast of Washington (Kenyon 1970, Vanblaricom 2015). Since this translocation, the Washington sea otter population has grown to over 2,785 individuals and has expanded its range to contain a large portion of the Washington coast (Jeffries et al. 2019). This population growth and range expansion has created a spatial gradient in sea otter occupation time and density along the coast of Washington, where the core of the sea otter's range has been occupied for up to 53 years, and areas at the periphery of the range have been occupied more recently. This population growth and range expansion following translocation has been monitored annually during summer surveys conducted by the U.S. Fish and Wildlife Service/U.S. Geological Survey and Washington Department of Fish and Wildlife.

Using this annual survey data, population modelling of sea otters in Washington State has been done at the range-wide scale (Gerber et al. 2004, Laidre et al. 2009). For example, Gerber et al. (2004) modeled sea otter population growth in Washington using total counts in each survey year with a Beverton-Holt model, and Laidre et al. (2009) modeled growth with an exponential growth model. In recent years, there has been a growing recognition that sea otter populations are structured and regulated at the scale of tens of kilometers rather than hundreds or thousands of kilometers, the scale at which a stock is defined and at which management has typically taken place (Bodkin et al. 1999, Bodkin 2015, Tinker 2015, Gagne et al. 2018, Tinker et al. 2019). Although the importance of local-scale processes in regulating sea otter populations is now generally recognized, population modelling has not been conducted for sea otters in Washington State at demographically relevant spatial scales, as has been done for in California (Tinker et al. 2021*a*, 2021*b*). Similarly, neither of the previous modeling efforts for sea otters in Washington include a spatial component to account for range expansion as has been conducted in California (Krkošek et al. 2007; Tinker et al. 2008*b*, 2021*a*; Smith et al. 2009). Addressing both of these research needs will be important for answering emerging questions for conservation and management.

One key management need for regulatory purposes (Marine Mammal Commission 2019) is an estimate of the total equilibrium abundance (also referred to as carrying capacity, or "*K*") for sea otters state-wide. Laidre et al. (2002) used annual survey data to estimate equilibrium abundance for sea otters in Washington based on the density of sea otters in an area believed to be at equilibrium and the total available habitat in the Strait of Juan de Fuca and outer coast of Washington. These efforts resulted in an estimated equilibrium abundance of 2,734 sea otters (Laidre et al. 2002), an estimate that was used to set recovery goals for sea otters in Washington (Lance et al. 2004). In 2015-2017, the average sea otter population estimate in Washington was 1,752, exceeding the previously estimated threshold for downlisting. As a result, sea otters in Washington State were downlisted from State endangered to State threatened in 2018 (Sato 2018). However, since then the number of sea otters in the area previously believed to be at equilibrium (and from which the equilibrium density was estimated) grew to be 1.6 times higher and a new estimate of equilibrium abundance is warranted. In order to robustly predict sea otter range expansion in Washington State to shift management approaches as sea otter populations recover, spatially explicit modelling at small spatial scales is needed, as well as updated estimates of equilibrium abundance in order to set recovery targets.

1.3 ECOLOGICAL ROLE OF SEA OTTERS AS PREDATORS

As sea otters recover, they assume their ecological role as predators in nearshore marine ecosystems. The sea otter's nearshore distribution and foraging behavior that includes bringing captured prey to the surface to consume, allow for direct observation and estimation of sea otter prey size, number, and type. Sea otters consume an estimated 30% of their body weight per day (Riedman and Estes 1990), and commonly prey on benthic invertebrates, such as sea urchins, clams, and crabs. Sea otters can alter the size distribution, abundance, and spatial distribution of their prey species by preferentially removing large, calorically rich, and easily captured prey (Estes 1978, Ostfeld 1982, Kvitek et al. 1992, Fanshawe et al. 2003, Laidre and Jameson 2006). Sea otters are considered diet generalists at the population level, and their diet can vary with habitat type, season, and sea otter occupation time in a given habitat in response to changes in prey availability. In the temporary absence of sea otters from portions of their range following extirpation, high-value invertebrate fisheries developed that target many of the same calorically rich prey preferred by sea otters. It is likely that some of these commercial and recreational shellfisheries could not have existed without the extirpation of sea otters (Bodkin et al. 2004). The recolonization and reintroduction of sea otters to areas of historical sea otter occupation, where sea otters now co-occur spatially with fisheries, have led to perceived conflicts between sea otters and fisheries along the North American Pacific Coast, (e.g., Estes and Vanblaricom 1985, Reidy 2011, Larson et al. 2013, Honka 2014, Hoyt 2015) and in some cases have had measurable impacts on fisheries species (Fanshawe et al. 2003, Larson et al. 2013, Hoyt 2015).

While sea otters and invertebrates have coexisted for millennia in Washington State and elsewhere, Federal, State, and Tribal resource managers are now faced with managing a translocated sea otter population that overlaps spatially with treaty and non-treaty recreational and commercial fisheries for the first time. During the nearly 60 years that sea otters were absent from the coast of Washington, recreational and commercial fisheries developed that target many of the same species that sea otters consume, including butter clam (*Saxidomus gigantea*), horse clam (*Tresus spp.*), razor clam (*Siliqua patula*), Dungeness crab (*Cancer magister*), red rock crab (*Cancer productus*), sea urchin (*Strongylocentrotus spp.*), and California sea cucumber (*Parastichopus californicus*) (Laidre and Jameson 2006; M. Ulrich, Washington Department of Fish and Wildlife, Personal communication, 2013). In 1996, the Makah tribal fishery for red sea urchin (*Strongylocentrotus franciscanus*) in Neah Bay closed, concurrent with sea otter range expansion into the area and increased proportions of red sea urchins in sea otter diets (Lance et al. 2004, Laidre and Jameson

2006). While concern over sea otter impacts on shellfisheries in Washington State is not new (Gerber and VanBlaricom 1999, VanBlaricom et al. 2001), limited empirical evidence has been provided to quantify the impact of sea otters on shellfisheries. Sea otter impacts on fisheries species likely vary spatially and temporally with sea otter population status. In addition, as sea otters are diet generalists at the population level but diet specialists at the individual level (Estes et al. 2003; Tinker et al. 2007, 2008*a*, 2009; Newsome et al. 2009, 2015), and individuals are known to make adaptive changes in diet in response to depletion of preferred prey, measuring the impacts of sea otters on their prey populations is challenging. There is a need for a quantitative assessment of the impacts of sea otter predation on shellfisheries in Washington State.

1.4 ECOLOGICAL ROLE OF SEA OTTERS AS KEYSTONE SPECIES

In addition to reprising their ecological role as predator species, recovering populations of sea otters resume their ecological role as keystone species. Sea otters are a well-known example of a keystone species that exerts top-down control on community structure (e.g., Estes and Palmisano 1974, Estes and Duggins 1995). Observations of nearshore marine communities in the western Aleutian Islands, Alaska with and without sea otters by Estes and Palmisano (1974) were the first to suggest that sea otters can dramatically influence the nearshore marine environment through predation on herbivorous invertebrates. The paradigm posits that an urchin-dominated community state occurs in areas where otters are absent, and a kelp-dominated community state occurs in areas where otter are present.

The relative frequency of urchin-dominated vs. kelp-dominated community states in Washington between sea otter extirpation in 1911 and translocation in 1969 and 1970 is unknown; nonetheless, more recent studies of benthic community composition have taken advantage of the "natural experiment" of sea otter translocation and subsequent recovery to compare benthic community composition in otter-free vs. otter-occupied areas, as well as community changes at various time points post-translocation (Kvitek et al. 1989, 1998, 2000; Shelton et al. 2018). This research has demonstrated that ecosystem changes observed in Washington after sea otter translocation appear to be consistent with the sea otter-sea urchin-kelp paradigm, as sea urchin abundance was inversely correlated with sea otter abundance, and coverage of foliose and canopy-forming kelps was positively correlated with sea otter abundance (Kvitek et al. 1989, 1998, 2000). There are, however, several studies that do not support the generality of the paradigm to Washington and other areas, and offer alternative hypotheses for observed ecosystem changes (Foster and Schiel 1988, Foster 1990, Dean et al. 2000, Carter et al. 2007) including physical disturbance and substratum type, suggesting contextual and geographic dependence of the generality of the sea otter-sea urchin-kelp paradigm. Subsequent subtidal surveys by Shelton et al. (2018) of the same sites used by Kvitek et al. (1989, 1998, 2000) in 2015 demonstrated additional declines in the abundance of urchins and that sea otter and canopy-forming kelp population growth rates were positively correlated up until 2002. Shelton et al. (2018) suggest that while the initial nearshore community responses to sea otter population expansion followed from the sea otter-sea urchin-kelp paradigm, that other factors were more important in influencing kelp forest community dynamics post 2002, as was suggested by Carter et al. (2007). The natural experiment of sea otter extirpation and recovery in Washington State presents a unique opportunity to explore the ecological role of sea otters as keystone species following extirpation.

1.5 RESEARCH GOALS

The overarching goal of my dissertation is to understand population growth and recolonization of sea otters in Washington State, as well as the ecological consequences of this population growth and recolonization in order to contribute to the information needed to make appropriate management decisions for sea otters and other species in the nearshore marine environment, including those species utilized as part of commercial, recreational, or tribal (including subsistence and ceremonial use) fisheries. Questions about sea otter population growth and recolonization are addressed in Chapter 2, while the ecological consequences of sea otter population growth and recolonization in Washington are addressed in Chapters 3–5. Throughout my dissertation, I make use of a spatio-temporal gradient in sea otter occupation time and density along the outer coast of Washington to determine the impact of sea otters on the nearshore marine community, and also make use of longitudinal data when available.

In Chapter 2, published in the Journal of Wildlife Management (Hale et al. 2022), my coauthors and I compiled available survey data for sea otters in Washington State since their translocation (1977–2019) and fit a Bayesian state-space model to estimate past and current abundance, and equilibrium abundance at multiple spatial scales. Our results help determine sea otter population status in Washington in relation to population recovery targets and predict future ecological impacts of sea otter recovery. We found that the regional population size in our model increased from an average of 21 adult (independent) sea otters in 1977 to 2,336 independent sea otters in 2019 as a result of an average estimated annual growth rate of 12.42%. We estimate that the regional equilibrium abundance (for all of Washington State) is 6,080 sea otters, over 2 times higher than the previous estimate of 2,734 by Laidre et al. (2002). Importantly, our model shows that growth trajectories and equilibrium density estimates vary at a sub-regional scale, with the average estimated annual growth rate varying from 6.42–14.92% and equilibrium densities varying from 0.68–3.44 independent otters/km^2. Estimated densities within the current range corresponded on average to 87% of mean sub-regional equilibrium values (range = 66–111%); therefore, the majority of sea otter population growth over the next 25 years is predicted to occur through range expansion into currently unoccupied areas. The predicted range expansion and increase in sea otter numbers highlights the potential for increased competition between sea otters and valuable State and Tribal shellfisheries, and inspired the questions I asked in Chapter 5.

In Chapter 3, published in Marine Mammal Science (Hale et al. 2019), my coauthors and I collected data on sea otter diet composition between 2010 and 2017 across a spatio-temporal gradient of sea otter occupation time and density and in various habitat types. Our results reveal how sea otter diet in Washington State varies with occupation history and habitat type, with the goal of better understanding the ecological role of sea otters in Washington State. We found that site, habitat type, and sea otter cumulative density were all significant in explaining variation in sea otter diet composition, and that habitat type was 1.77 times more important than sea otter cumulative density in explaining variation in sea otter diet composition. While sea otter diet composition was primarily dependent on site and habitat type, rates of energy intake and diet diversity were strongly related to sea otter cumulative density. We found that sea otter diet diversity was positively correlated with cumulative sea otter density, while rate of energy gain was negatively correlated with cumulative density. Our results set the groundwork for informed predictions of sea otter foraging patterns in a variety of habitats with a variety of occupation histories, and provide an additional metric of sea otter population status (in addition to the work done in Chapter 2). Our results also suggested that sea otters at Beach 4 (Kalaloch Area) were preferentially consuming razor clams, an important fishery species, in this recently occupied area, thus informing the questions to be addressed in Chapter 5.

In Chapter 4 (*manuscript in preparation*), my coauthors and I combined long-term data sets on regional kelp canopy cover, local subtidal invertebrate densities, local sea otter diet, and regional sea otter population counts to examine the influence of sea otters on kelp canopy transition dynamics. Our results reveal that kelp cover in Washington State varies as a function of several biotic and abiotic factors, including sea otter occupation history. However, we also show that the relationship between sea otters and kelp canopy cover is not a simple positive correlation, but rather involves non-linear effects on the frequency of transitions between kelp states. We found that sea otters in recently occupied areas consume sea urchins of a larger average size than sea otters in longer occupied areas, and that sea urchins were present at higher densities at more recently occupied sites, consistent with sea otter-urchin-kelp trophic cascade. These results highlight the ecological consequences of sea otter reintroduction to Washington State, including decreased urchin abundances and sizes, and impacts on the spatiotemporal dynamics of kelp canopy cover.

In Chapter 5 (*manuscript in preparation*), my coauthors and I evaluated the relative magnitude of human harvest, natural mortality, oceanographic factors, and sea otter predation effects on razor clam populations at 6 beaches using sea otter foraging observations, sea otter survey data, razor clam density and size data, razor clam harvest data, and data on a suite of environmental variables. Our research addresses an emerging resource management conflict between sea otters, a Washington State threatened species, and razor clams, an important recreational, commercial, and tribal fishery species in an area that has recently been reoccupied by sea otters. Our model estimated that sea otters selectively consumed recruit size clams (the size class targeted during harvest) at a rate over 25 times higher than smaller pre-recruit size clams. We found that the magnitude of sea otter predation effects varied over time, with estimated sea otter-caused mortality surpassing natural mortality at a beach 13 years after it was first occupied. We also found that the magnitude of sea otter predation effects varied over space, with sea otters in a more recently occupied beach consuming fewer razor clams than at a longer occupied beach, and the highest relative sea otter-caused mortality occurring between 350–600 feet beach elevation. Our results set the groundwork for informed predictions of future impacts of sea otters at other razor clam beaches that have not yet been reoccupied, and add to our understanding of the ecological role of sea otters post-reintroduction.

Overall, the results presented in Chapters 2–5 provide new and important insights into the spatial dynamics of sea otter recovery, and demonstrate the consequences of sea otters reprising their ecological role as both predator and keystone species in Washington State. We demonstrated that Washington State may be able to support more sea otters than previously estimated, and that sea otter reintroduction has influenced kelp canopy dynamics and invertebrate community composition, including razor clam populations. The predictions of sea otter range expansion and population growth presented in Chapter 2 combined with the investigations of the sea otters' ecological roles in Chapters 3–5 set the groundwork for informed predictions of the long-term ecological impacts of sea otter recovery in Washington State to aid in the management of sea otters and other species in the nearshore marine environment.

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Chapter 2. Status, trends, and equilibrium abundance estimates of the translocated sea otter population in Washington State

(Hale, J. R., K. L. Laidre, S. J. Jeffries, J. J. Scordino, D. Lynch, R. J. Jameson, and M. Tim Tinker. 2022. Status, trends, and equilibrium abundance estimates of the translocated sea otter population in Washington State. Journal of Wildlife Management e22215. https://doi.org/10.1002/jwmg.22215)

2.1 ABSTRACT

Sea otters (*Enhydra lutris kenyoni*) historically occurred in Washington State, USA, until their local extinction in the early 1900s as a result of the maritime fur trade. Following their extirpation, 59 sea otters were translocated from Amchitka Island, Alaska, USA, to the coast of Washington, with 29 released at Point Grenville in 1969 and 30 released at La Push in 1970. The Washington Department of Fish and Wildlife has outlined 2 main objectives for sea otter recovery: a target population level and a target geographic distribution. Recovery criteria are based on estimates of population abundance, equilibrium abundance (K), and geographic distribution; therefore, estimates of these parameters have important management implications. We compiled available survey data for sea otters in Washington State since their translocation (1977–2019) and fit a Bayesian state-space model to estimate past and current abundance, and equilibrium abundance at multiple spatial scales. We then used forward projections of population dynamics to explore potential scenarios of range recolonization and as the basis of a sensitivity analysis to evaluate the relative influence of movement behavior, frontal wave speed, intrinsic growth, and equilibrium density on future population recovery potential. Our model improves upon previous

analyses of sea otter population dynamics in Washington by partitioning and quantifying sources of estimation error to estimate population dynamics, by providing robust estimates of *K*, and by simulating long-term population growth and range expansion under a range of realistic parameter values. Our model resulted in predictions of population abundance that closely matched observed counts. At the range-wide scale, the population size in our model increased from an average of 21 independent sea otters (95% CI = 13–29) in 1977 to 2,336 independent sea otters (95% CI = 1,467–3,359) in 2019. The average estimated annual growth rate was 12.42% and varied at a sub-regional scale from 6.42–14.92%. The overall estimated mean *K* density of sea otters in Washington was 1.71 ± 0.90 (SD) independent sea otters/km^2 of habitat (1.96 ± 1.04 sea otters/km^2, including pups), and estimated densities within the current range correspond on average to 87% of mean sub-regional equilibrium values (range = 66–111%). The projected value of *K* for all of Washington was 5,287 independent sea otters (95% CI = 2,488–8,086) and 6,080 sea otters including pups (95% CI = 2,861–9,300), assuming a similar range of equilibrium densities in currently unoccupied habitats. Sensitivity analysis of simulations of sea otter population growth and range expansion suggested that mean *K* density estimates in currently occupied sub-regions had the largest impact on predicted future population growth (r^2 = 0.52), followed by the rate of southward range expansion (r^2 = 0.26) and the mean *K* density estimate of currently unoccupied sub-regions to the south of the current range (r^2 = 0.04). Our estimates of abundance and sensitivity analysis of simulations of future population abundance and geographic range help determine population status in relation to population recovery targets and identify the most influential parameters affecting future population growth and range expansion for sea otters in Washington State.

2.2 INTRODUCTION

Many marine mammal populations are currently recovering from population depletion after overharvest in portions of their historical range (Magera et al. 2013), including sea otters (*Enhydra lutris*; Bodkin 2015). Sea otters were heavily exploited during the Pacific maritime fur trade in the eighteenth and nineteenth centuries, resulting in a loss of approximately 99% of their original numbers (Kenyon 1969) and the extirpation of sea otters from portions of their historical range, including northern sea otters (*Enhydra lutris kenyoni*) from Washington State , USA (Scheffer 1940, Kenyon 1969). In some areas, sea otter populations have recovered from extant populations (CA, southwestern AK, USA), while in other areas sea otters have been translocated to reestablish local sea otter populations (WA, southeast AK; BC, Canada; Bodkin 2015).

In 1969 and 1970, sea otters were translocated from Amchitka Island, Alaska to sites within their former range on the outer Washington coast, with the first release of 29 sea otters at Point Grenville in 1969 and the second release of 30 sea otters at La Push in 1970 (Figure 2-1; Kenyon 1970, Jameson et al. 1982). Following their translocation, Washington's sea otter population grew from a founding population estimated to be as few as 10 individuals (10–21%/yr; Jameson et al. 1982, 1986; Bodkin et al. 1999). Between the late 1970s and early 1990s, the sea otter population range was limited to the outer coast of Washington between Makah Bay and Destruction Island (Figure 2-1), apparently reaching equilibrium levels between Petroleum Creek and La Push around the mid-1990s (Laidre et al. 2002). Sea otters expanded their range north and eastward into the Strait of Juan de Fuca in the mid-1990s, with small numbers of animals sighted in the area in winter 1995, and sighting frequency and group sizes increasing until 2000, when >100 animals were noted in the Strait of Juan de Fuca, east to Pillar Point (Laidre and Jameson 2006). Sighting frequency and group sizes in the Strait decreased after 2000 and have remained low (<25 otters; Laidre and Jameson 2006, Laidre et al. 2009). Beginning in the mid-2000s, sea otters began to expand their range southward from their established range (Figure 2-1). The most recent estimate of sea otter population abundance in Washington was 2,785 individuals (2,632 independents, 153 pups; Jeffries et al. 2019) and as of 2019 the population's range covers approximately 187 km of the Washington coast (Figure 2-1).

Sea otters in Washington are protected under the Marine Mammal Protection Act of 1972, as amended. Under the Marine Mammal Protection Act, a marine mammal population is considered depleted when the population level is below the lower limit of its optimum sustainable population level, defined as the maximum net productivity level. The current operational definition of maximum net productivity level is 60% of equilibrium abundance (K), the maximum number of sea otters that can be supported in the available suitable habitat (DeMaster et al. 1996). The Washington sea otter stock is not considered to be depleted (U.S. Fish and Wildlife Service 2018).

Sea otters in Washington were classified by the Washington Department of Fish and Wildlife (WDFW) as an endangered species in 1981 because of their small population size, limited geographic range, and vulnerability (Lance et al. 2004). The WDFW produced a species recovery plan for sea otters (i.e., Washington Sea Otter Recovery Plan) outlining recovery objectives, where sea otters in Washington will be considered for downlisting from state endangered to state threatened status when the average population estimate over a 3-year period is ≥1,640 sea otters (60% of previously estimated maximum K of 2,734 sea otters [Laidre et al. 2002]), and Washington's sea otter population is distributed in areas outside their geographic range (as measured in 2004), such that a single catastrophic event (e.g., major oil spill) would be unlikely to cause severe decline or extirpation of the population (Lance et al. 2004). Where the recovery of an extirpated marine mammal is the goal, the translocation of sea otters to Washington could be seen as largely successful based on the steady and considerable increase in sea otter numbers and status in relation to the previously estimated K of 1,372–2,734 otters (Laidre et al. 2002). Because the average population estimate from 2015–2017 equals 1,752, exceeding 60% of the previously estimated K threshold for downlisting (1,640), WDFW recently reclassified sea otters in Washington as state threatened (Sato 2018, WDFW 2018).

Sea otters are a non-migratory species that primarily occupy nearshore waters <40-m in depth (Riedman and Estes 1990, Bodkin et al. 2004, Laidre et al. 2009). Previous researchers suggest that density-dependent population regulation, and therefore equilibrium abundance (K), of sea otters is driven primarily by resource limitation at the scale of tens of kilometers (Estes 1979; Estes et al. 1996; Tinker et al. 2008*a*, 2012, 2019*a*). The small spatial scale at which sea otter populations are structured is a result of the limited mobility and high site fidelity of female sea otters (Tarjan and Tinker 2016, Breed et al. 2017) and because most sea otter prey species vary in abundance at small spatial scales (Burt et al. 2018). As a result, sea otter population growth following recovery from near extirpation or translocation is well described by density-dependent logistic (or theta-logistic) growth at biologically relevant scales (Tinker 2015, Tinker et al. 2019*a*). Because sea otter population regulation is thought to be driven by local resource limitation, their effective density at equilibrium abundance is also expected to vary spatially as a function of a suite of physical, biotic, and oceanographic habitat variables (including local bathymetry, benthic substrate composition, presence of kelp canopy, and net primary productivity) as well as prey productivity at the scale of tens of kilometers (Tinker et al. 2021*b*). In the absence of data measuring the limiting resource (prey availability), previous researchers have leveraged the relationship between substrate type (DeMaster et al. 1996; Laidre et al. 2001, 2002, 2011) and resource abundance to estimate habitat-based sea otter equilibrium abundance.

Previously, habitat-based equilibrium abundance estimates for sea otters in Washington (Laidre et al. 2002, 2011), British Columbia (Gregr et al. 2008), California (DeMaster et al. 1996, Laidre et al. 2001), and Alaska (Burn et al. 2003) were calculated as a product of the estimated density of sea otters in an area (or several areas) believed to already have reached equilibrium and the area of available habitat. This method relies on 2 key assumptions: the representative area on which *K* density is calculated has reached equilibrium abundance and *K* density is generalizable to all other areas with similar habitat. The upper limit of the habitat-based estimate of *K* by Laidre et al. (2002) for sea otters in Washington was 2,734 individuals and was used in the Washington Sea Otter Recovery Plan (Lance et al. 2004) to set sea otter population recovery objectives. Laidre et al. (2002) calculated the habitat-based estimate of *K* as the product of the density of sea otters assumed to be at equilibrium between Petroleum Creek and La Push (rocky equilibrium area; Figure 2-1), the amount of available habitat in Washington, and substrate type (rocky, mixed, sandy). Based on more recent survey data, however, it now seems likely that the rocky equilibrium area was not actually at *K* from 1996–1999, as the average number of adult sea otters (i.e., independent sea otters) has since increased from 275 to 446 in 2016–2019. Because sea otter counts in the rocky equilibrium area are now 1.6

times higher than in 1996–1999, this calls into question the reliability of regional estimates of K based on the earlier methods and equilibrium density estimates. Thus, an updated estimate of K for sea otters in Washington is warranted.

The recovery of a species depends on increasing abundance and on recolonization of the species' former range (Lubina and Levin 1988, Swenson 1999, Moro 2003, Lance et al. 2004, Tinker et al. 2008*b*). But traditional models used to estimate and predict population sizes of recovering species typically do not include a spatial component to account for range expansion. For example, Gerber et al. (2004) modeled growth of the sea otter population in Washington with a Beverton-Holt model, and Laidre et al. (2009) and Estes (1990) modeled growth with an exponential growth model, but these models cannot predict recolonization of the species' former range and did not include parameters for movement, immigration, or emigration. Previous researchers have reported the utility and feasibility of modeling and projecting sea otter range expansion and recolonization (Lubina and Levin 1988; Tinker et al. 2008*b*; Williams et al. 2017, 2019; Lu et al. 2019), and spatio-temporal state-space models have been developed to model sea otter population dynamics in California (Lubina and Levin 1988; Tinker et al. 2008*b*, 2021*b*) and Alaska (Williams et al. 2017, 2019; Tinker et al. 2019*a*; Lu et al. 2019; Raymond et al. 2019). Predictions of sea otter range expansion have implications for their management, including for evaluation of sea otter population status, for predicting spatial co-occurrence of sea otters with threats such as oil spills, or to predict future ecological impacts of sea otter recovery, including competition with fisheries (Carswell et al. 2015). Spatially explicit population models can provide powerful tools for modeling population growth and range expansions of remnant and translocated populations like sea otters in Washington, especially when they include species-habitat relationships and their variation in time and space (Williams et al. 2017, Lu et al. 2019, Tinker et al. 2021*b*).

Previous researchers have reported the utility of state-space models in modeling population abundance and trends (Royle and Dorazio 2008, Cressie et al. 2009), and have used Bayesian state-space models to analyze marine mammal survey data and make inference about abundance, trends, and population parameters (Gerrodette et al. 2011, Moore and Barlow 2011). Recently, state-space models have been used to estimate equilibrium abundance for sea otters in southeast Alaska (Lu et al. 2019, Tinker et al. 2019*a*, Eisaguirre et al. 2021) and California (Tinker et al. 2021*b*), and Lu et al. (2019), Eisaguirre et al. (2021), and Tinker et al. (2021*b*) estimate equilibrium abundance as a function of a suite of habitat variables. Unlike the earlier habitat-based K estimates, state-space models avoid the problematic assumption that certain areas have already reached K (and that these densities are generalizable), and instead infer the statistically most likely value of equilibrium abundance by fitting a density-dependent process model to the full time series. State-space models of sea otter population dynamics have employed 2 main approaches: a discrete space-time approach (Tinker et al. 2006, 2008*b*, 2019*a*, 2021*a*, 2021*b*; Monson et al. 2011) and a continuous space-time approach (Williams et al. 2017, 2019; Lu et al. 2019). In models using a discrete space-time approach, the available habitat is divided into discrete sub-regions that are large enough to capture a meaningful subset of the population, such that intrinsic demographic processes are more impactful on local trends than movements of animals between sub-regions, but small enough so that otters within a sub-region can be viewed as a well-mixed, inter-breeding population experiencing similar environmental conditions. Typically, this corresponds to 20–50 km of coastline, or 1 to 3 times the length of a typical adult female home range (Tarjan and Tinker 2016). Similarly, time is divided into discrete, equally spaced time steps (typically 1 year; Tinker et al. 2019*a*, 2021*b*), and dynamics within sub-regions are calculated as the summation of births and deaths within sub-regions and movements of animals between sub-regions. In the continuous space-time approach, an ecological diffusion model (Turchin 1998) describes sea otter abundance that is continuously changing across time and space, calculated using reaction-diffusion equations. Continuous space-time models allow for inferences about sea otter abundance at any point in space or time, in contrast to discrete space-time models where inferences are limited to the pre-defined sub-regions (although depending on model structure it may be possible to describe variation in relative density within sub-regions; Tinker et al. 2021*a*). With the inclusion of fine-scale habitat data and a time series of spatially explicit survey data, the continuous space-time approach can provide insights into how fine-scale habitat variation influences sea otter dispersal (diffusion) and equilibrium density (Williams et al. 2017, 2019; Lu et al. 2019). The ability to make inferences about small-scale processes is more limited with discrete space-time models; however, these models are computationally more tractable over large areas, are simpler to fit if habitat layers or survey data are not spatially resolved at smaller scales, and simplify inclusion of complexities such as environmental stochasticity, age or sex structure, and hierarchical random effects (e.g., unexplained spatial differences in equilibrium density). Both modeling approaches are useful for exploring different aspects of population dynamics and, encouragingly, both approaches have produced similar results for sea otters in Glacier Bay (Williams et al. 2017, 2019; Lu et al. 2019; Tinker et al. 2019*a*) and southeast

Alaska (Tinker et al. 2019*a*, Eisaguirre et al. 2021), including overall population trends and rates of range expansion.

We developed a discrete space-time model of population growth and range expansion for sea otters in Washington State. Our process model incorporated theta-logistic population growth, local density dependence, environmental stochasticity, and inter-area movements, and we fit this model to multiple survey time series using Bayesian state-space methods. Our objectives were to obtain updated estimates of potential equilibrium abundance (K) at the regional and sub-regional scale and use the parameterized model to conduct forward projections of population dynamics as the basis of a sensitivity analysis to evaluate the relative effects of model parameters on the future rate of population increase and range expansion for the sea otter population in Washington. We predicted that our estimates of regional K would be higher than previous estimates made by Laidre et al. (2002) because sea otter counts in the rocky equilibrium area are now 1.6 times higher than in 1996–1999, despite the area previously being assumed to be at equilibrium. We also predicted that forward projections of the model would predict range expansion primarily occurring at the southern range extent, with slower range expansion at the eastern range extent in the Strait of Juan de Fuca, based on previously observed patterns of range expansion.

2.3 METHODS

2.3.1 Study Area

The study area is 3,096 km^2 of habitat located in the Strait of Juan de Fuca and on the outer coast of Washington State, USA. The area is characterized by a temperate oceanic climate with relatively dry, warm summers (Jun–Aug) and wet, cool winters (Dec–Feb). There is a south to north spatial gradient of benthic substrate type, with generally sandy substrate in the south and rockier substrate in the north (Table 2-1; Laidre et al. 2002). The northern portion of the outer coast of Washington State (north of Point Grenville) is characterized by rocky headlands and cliffs, high wave energy, high productivity, and high species diversity, while the southern portion (south of Point Grenville) is characterized by long stretches of sandy beaches and lower species diversity and productivity (Strickland and Chasan 1989). The nearshore marine environment on the north coast is dominated by giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis luetkeana*) beds and associated species (invertebrates, fishes, sea otters), while nearshore marine environments on the southern coast often have extensive phytoplankton blooms and support invertebrates, fishes, and sea birds (Skewgar and Pearson, 2011). A large portion of the study area is located within Olympic Coast National Marine Sanctuary (designated 1994; northern boundary = approximately 7.11 km east of western edge of sub-region B, southern boundary = approximately 20.66 km south of Point Grenville; Figure 2-1), and is bounded on the east by Olympic National Park (southern boundary = approximately 17.05 km north of Split and Willoughby Rocks; northern boundary = approximately 2.19 km north of Petroleum Creek). Because of this, the northern portion of the outer coast of Washington State (north of Point Grenville, excluding the northern half of sub-region F; Figure 2-1) is largely characterized by a remote wilderness coastline with limited highway access that is primarily accessed for recreational activities like hiking, camping, and backpacking. The southern portion of the outer coast of Washington State (south of Point Grenville; Figure 2-1) is more populous and more easily accessed for recreational activities, including fishing and razor clamming.

We defined the study area as the sub-tidal benthos between the coast and the 40-m depth contour from Dungeness Spit in the Strait of Juan de Fuca to the Washington-Oregon border at the mouth of the Columbia River on the outer coast, following Laidre et al. (2002; Figure 2-1). This definition of sea otter habitat in Washington was based on observed foraging depths and distance from shore that were obtained from radio-telemetry data (Laidre et al. 2002, 2009). While sea otters in Washington are occasionally observed in waters deeper than 40-m (Laidre et al. 2009, Pearson 2019), average depth of sea otter locations (regardless of age or sex) is 10-m (Laidre et al. 2002). In addition, the reproductive portion of the population (adult females) spends the majority of their resting time (76%) and foraging time (60%) in shallow water (0–10-m; Laidre et al. 2009). While sea otters likely historically occupied estuaries and bays on the Washington coast (Scheffer 1940, Moss and Losey 2011), we did not include estuaries or bays in our study area (Figure 2-1). If sea otters were to reoccupy areas like Willapa Bay, Grays Harbor, or the Columbia River mouth at the Washington-Oregon border (Figure 2-1), the Washington coast may be able to support a higher number of sea otters than we estimate here. Previous research (Laidre et al. 2002) suggests that variation in the equilibrium density of sea otters in Washington occurs at small spatial scales, as with other sea otter populations (Tinker et al. 2021*b*). To allow for spatially varying demographic rates and following previous spatially structured models for sea otters (Tinker et al. 2008*b*, 2019*a*, 2021*b*), we divided the regional study area into distinct geographic sub-regions—contiguous spatial polygons that encompass the area currently known to be occupied by sea otters during the summer (occupied study area: Figure 2-1, sub-regions B–F) and additional suitable habitat in Washington <40-m deep that could be occupied in future (Figure 2-1, sub-regions A and G).

As in Tinker et al. (2019*b*), we defined sub-regions at the scale of tens of kilometers (Table 2-1) with boundaries between sub-regions defined so as to delineate areas of generally similar habitat and to be consistent with existing survey data sets (Tinker et al. 2019*a*, 2021*b*).

Although adult sea otters, particularly adult females, exhibit a strong degree of site fidelity and limited individual movements (Tarjan and Tinker 2016), a small number of animals (primarily non-territorial males and juvenile females) will occasionally make longer exploratory movements, including outside of the established range (Jameson 1989, Ralls et al. 1996, Tinker et al 2008*b*, Lafferty and Tinker 2014). For example, in Washington, scattered individual sea otters have been observed in the San Juan Islands and in Puget Sound, and as far south as Cape Arago, Oregon (Jeffries et al. 2019). Accordingly, we defined the eastern range boundary of the occupied study area (eastern edge of sub-region B) as the easternmost point that contained 99.97% of sea otters ever recorded (1977–2019) north of La Push during sea otter surveys and opportunistic skiff surveys in Washington (Sekiu Point). Similarly, we defined the southern range boundary of the occupied study area (southern edge of sub-region F) as the southernmost point that contained 99.97% of sea otters ever recorded (1977–2019) south of La Push during sea otter surveys in Washington (Split and Willoughby Rocks). We added sea otters counted outside of the occupied study area boundaries (either east or south of boundaries, in sub-regions A or G; Figure 2-1) to the counts in the closest occupied sub-region (sub-region B or F; Figure 2-1). In this way, we included all counted sea otters in the count data, but the spatially extralimital sea otters did not define the geographic extent of the occupied study area.

Each sub-region within the occupied study area (sub-regions B–F) ranged in length from 23.4–45.7 km of coastline (Table 2-1; $\bar{x}$ = 38.1 km), and in area from 48.6–552.8 km^2 of suitable sea otter habitat (assuming suitable habitat extends from shore to areas 40 m in depth; Table 2-1, $\bar{x}$ = 268.5 km^2). On the outer coast of Washington, there is a general south to north gradient in increasing coastline complexity and decreasing distance from shore of the 40-m depth contour (Figure 2-1).

2.3.2 Population data collection

Because of their benthic foraging, sea otter distribution is largely limited to nearshore areas where they can dive to the sea floor (Kenyon 1969, Bodkin et al. 2004), allowing for enumeration and observation from shore and sea with spotting scopes and binoculars, and from the air using a camera and visual detection. The first post-translocation surveys of sea otters in Washington occurred in 1977–1987 (excluding 1979–1980, 1982, 1984, 1986) and incorporated a combination of boat and shore-based counts, with data from aerial surveys supplementing counts in 1985 (Jameson et al. 1982, 1986; R. J. Jameson, USGS, unpublished data). These surveys attempted to survey all potential sea otter habitat and occurred over a period of several consecutive days each year primarily during summer months (Jul–Sep; Jameson et al. 1986, Bowlby et al. 1988). The United States Fish and Wildlife Service, United States Geological Survey, and WDFW conducted standardized ground and aerial surveys of sea otters in 1989–2019 in late June or early July (excluding 1997, 2009, 2018) and these data are summarized in annual reports (e.g., Jeffries et al. 2019). These surveys incorporate aerial and shore-based surveys that the agencies conducted concurrently, and the final estimate of sea otter abundance was a combination of aerial, photo, and shore-based counts (where available; Jeffries et al. 2019). These surveys attempted to survey all potential sea otter habitat in sub-regions B–F and portions of sub-regions A and G (Figure 2-1), dependent on the distribution of sea otters during a reconnaissance flight conducted prior to official surveys. We refer to surveys completed by Jameson et al. (1982, 1986), R. J. Jameson (unpublished data), and standardized surveys described above collectively as range-wide surveys. Range-wide surveys provide the estimated number and positions of sea otters. From 2016 onwards, the agencies recorded a single position for sea otters occupying the same general area, even if they were not rafted together. This method results in coarser scale position data, in which rafts and any individuals in an area are given a single position near the center of the area. Counts represent the minimum population count because no correction factor is applied to account for animals off of the flight path or missed because they are underwater (Jameson et al. 1986, Jeffries et al. 2019). The survey data sets, and the corresponding model estimates of abundance and equilibrium densities, are therefore understood to represent an index rather than an unbiased estimate of true abundance. Similar data from a combination of shore-based counts and aerial surveys have been used for extensive population modeling of southern sea otters in California (Tinker et al. 2006, 2008*b,* 2021*a*, 2021*b*).

Scordino et al. (2017) collected additional sea otter counts and positions during surveys conducted between March 2005 to November 2018 on a platform of opportunity (e.g., observers collected data on sea otter sightings opportunistically from a research vessel that was dedicated to gray whale [*Eschrichtius robustus*] surveys) in the Strait of Juan de Fuca (sub-region B; J. J. Scordino, Makah Fisheries Management, unpublished data); we refer to these surveys as opportunistic skiff surveys. Because opportunistic skiff surveys occurred year-round, and the range-wide surveys occurred during summer (Jun–Sep), we scaled the opportunistic skiff survey counts to the mean expected July count to account for seasonality in sea otter counts in sub-region B. We did this by fitting a generalized linear model to the counts with year and month as categorical covariates. The model resulted in the mean expected count in each month, and we used these predictions to calculate a correction factor for each month to appropriately scale counts to correspond to the mean expected July value. In this way, we were able to use all sea otter count data in sub-region B in the model despite seasonality in sea otter counts in this area. Similar data from a combination of skiff-based surveys and aerial surveys have been used for population modeling of northern sea otters in southeast Alaska (Tinker et al. 2019*a*). As with other published sea otter models (Tinker et al. 2021*b*), we excluded dependent pups from the population model because pups are not functionally independent from their mothers and because pup counts are subject to higher degrees of observer error and stochasticity.

Previous radio-telemetry studies of sea otters in Washington and California provided data on sea otter movements (Laidre et al. 2009, Tinker et al. 2019*c*) that we used to estimate average movement probabilities to and from each sub-region. Laidre et al. (2009) conducted a previous radio-telemetry study of sea otters in Washington in 1992–1999, but this data set alone was not of sufficient size to robustly estimate movement probabilities, so we used data from California (Tinker et al. 2019*c*) to supplement the data set. We assumed sea otter movement in the established California population along the 1-dimensional California coastline was representative of sea otter movement along the outer coast of Washington. We then used these probabilities to generate stochastic dispersal outcomes for each year (Table 2-2).

2.3.3 Mapping

We mapped counts and positions of independent sea otters from range-wide surveys (1977–2019) in ArcGIS 10.5 (Esri, Redlands, CA, USA) and assigned them to a geographic sub-region (Figure 2-1; B–F). We mapped counts and positions of independent sea otters from the opportunistic skiff surveys of sub-region B in ArcGIS 10.5. We removed potential double counts of sea otters from opportunistic skiff surveys because the opportunistic survey method allowed for potential double counting of individuals or rafts of sea otters within the same survey day. We defined a double count as a count made <1 km away from another sea otter count on the same day and counted >30 minutes after the first. We estimated the area surveyed each day for the opportunistic skiff surveys by creating and then buffering estimated survey tracklines. We created estimated tracklines by connecting all position data collected on each survey day chronologically in ArcGIS 10.5 using the following rules: tracklines must be representative of the survey path followed (i.e., the trackline cannot cut directly across the coastline to connect 2 points) and the estimated trackline must connect all positions on that day chronologically. Finally, we created a 200-m buffer on each side of the estimated trackline to estimate a minimum area surveyed. We calculated the proportion of rocky substrate in each sub-region in ArcGIS 10.5 using coarse-scale surficial geologic substrate data, compiled by the Oregon State University Active Tectonics and Seafloor Mapping Lab (Romsos et al. 2015; Table 2-1).

2.3.4 Population model overview

While some genetic exchange between the sea otter populations in Washington and British Columbia (translocated between 1969 and 1972 from Amchitka and Prince William Sound, AK) has been demonstrated (Larson et al. 2015), these longer-distance movements are likely rare (Laidre et al. 2009), so we chose to model the sea otter population in Washington as a distinct stock. Similar to Tinker et al. (2008*b*, 2019*b*, 2021*b*), we estimated the abundance of sea otters (N) across years (t) within each sub-region (i), using a process model that incorporates density-dependent population dynamics (where density-dependence operates at the local, sub-regional scale), range expansion and dispersal between sub-regions, and environmental stochasticity (Table 2-2). We used a hierarchical approach to derive sub-regional and range-wide estimates of equilibrium abundance (K) to allow for spatial variation in K among sub-regions because K varies with substrate type and availability (Laidre et al. 2002). This approach treats area-based differences in equilibrium density as a random effect, although we recognize that differences are likely explained by variation in local prey abundance and productivity for which empirical data are currently unavailable. The process model is linked to a data model, consisting of the observed survey counts ($y_{i,t}$) for each sub-region and accounting for observation error. We did not account for observation bias in our model (i.e., the count data is not corrected for detectability) and accounted only for observation error (because sea otters are counted imperfectly even when they are detectable; Table 2-2). By convention, we used uncorrected indices of sea otter population size produced from surveys for consistency with other studies (Nichol et al. 2005, Tinker et al. 2008*b*). This results in an index estimate of K, comparable with Laidre et al. (2002). We used a Bayesian state-space modeling framework to fit the model to survey data using JAGS (Plummer 2003) and the *runjags* package in *R* (Denwood 2016, R Core Team 2020) because this approach allows for ease of estimation in both process error (reflecting environmental stochasticity) and uncertainty arising from observation error and allows for characterization of spatial variation in sea otter trends and equilibrium densities at the sub-regional scale.

2.3.5 Process model

We modeled sub-regional dynamics using a stochastic discrete theta logistic growth model because previous researchers reported that logistic growth typically describes sea otter population growth well (Tinker 2015) and the theta logistic provides additional flexibility:

$$log\ (\lambda_{exp\ i,t}) = r_{max}\left(1 - \frac{N_{i,t}}{K_i}\right)^{\theta} \qquad (1)$$

We used a hierarchical approach for estimating K_i. Specifically, the expected value of K for each sub-region i is assumed to be drawn from a random normal distribution with a mean of K_{exp} and standard deviation σ_K, itself an estimated parameter representing spatial variation in K (Table 2-2). We integrated the estimated value of K for each sub-region into the stochastic theta-logistic equation that comprises the process model (Eq 1), where r_{max} is the maximum intrinsic growth rate. The realized finite annual growth rate $\lambda_{i,t}$ combines discrete theta logistic population growth with environmental stochasticity. Specifically, the expected finite annual growth rate ($\lambda_{exp\ i,t}$) for sub-region i at year t is calculated from the theta logistic model, and the realized log-transformed growth rate in sub-region i at year t is assumed to be drawn from a random normal distribution with a mean of $\lambda_{exp\ i,t}$ and standard deviation σ_p, itself an estimated parameter representing process error (Table 2-2). We treated immigration and emigration into and out of each sub-region ($D_{j,i,t}$ and $D_{i,j,t}$, respectively) as a stochastic process with average per capita dispersal probabilities between sub-regions based on telemetry data reported by Laidre et al. (2009) and Tinker et al. (2019*c*), and incorporated them into the process model:

$$N_{i,t} = N_{i,t-1} \times \lambda_{i,t} + \sum_{j\neq i}^{J} D_{j,i,t} - \sum_{j\neq i}^{J} D_{i,j,t} \qquad (2)$$

To calculate dispersal probabilities, we followed methods described in Tinker et al. (2019*b*), using maximum likelihood methods to fit an exponential distribution to data on annual net linear displacement of radio-tagged otters. We used the fitted exponential distribution to calculate the cumulative density function (CDF) values at x = the average distance from the centroid to the boundary of each sub-region. These CDF values represent the mean probability that an otter does not disperse from its current sub-region ($\phi_{i,i}$), the inverse of which (δ_i) represents the mean probability of dispersing away from sub-region *i*. To determine where dispersing otters would go, we first calculated the swimmable distances between all pairwise combinations of sub-region centroids as in Tinker et al. (2019*b*). We then computed the values of the exponential probability density function (PDF) corresponding to the pairwise distances between sub-regions, and we used these PDF values to represent the probability that an otter would disperse from sub-region *i* to sub-region *j* ($\phi_{i,j}$, where $j\neq i$), after first re-scaling so that $\sum_{j\neq i}^{J} \phi_{i,j,t} = \delta_i$ (where *J* was defined as the set of sub-regions occupied at time *t*). To account for stochastic dispersal outcomes, we used a Dirichlet distribution to draw random dispersal probability values for each year:

$$\pi_{i,j,t} \sim Dirichlet\left(\alpha = \phi_{i,j,t} \times N_{i,t} + 1\right), \qquad (3)$$

where we calculated the α parameters of the Dirichlet distribution as 1 plus the product of the mean expected probabilities and the number of otters in sub-region *i*. Finally, we calculated the actual number of animals emigrating from sub-region *i* to *j* as $D_{i,j,t} = \pi_{i,j,t} \times N_{i,t}$.

We used an informed prior for r_{max} based on previously documented values of this parameter (Table 2-2; $\overline{x}$ = 0.18; Estes 1990), and vague priors for all other demographic parameters, with prior distributions based on previous analyses of sea otter population dynamics in California and Alaska (Tinker et al. 2008*b*), to place reasonable biological constraints on the parameters of our model and to allow for geographic differences in sea otter population dynamics that may arise from the current data (Table 2-2). Estimated parameters for the process model include r_{max}, sub-regional K_i, overall K, and variance terms for process error, observation error, and variation in K (Table 2-3).

2.3.6 Data model and model validation

The observed data we used to fit the model were the number of sea otters counted on each survey in each sub-region ($y_{i,t}$), assumed to be drawn from a negative binomial distribution. Sea otter survey count data are described by the negative binomial distribution (Lu et al. 2019; Tinker et al. 2019*a*, 2021*b*; Williams et al. 2019) because the patchy distribution of sea otters leads to overdispersion of counts relative to a Poisson distribution and the negative binomial includes a dispersion parameter that allows the variance to exceed the mean. We modeled observed data from the range-wide surveys on the outer coast (sub-regions C–F, assumed to be un-biased), range-wide surveys in the Strait of Juan de Fuca (sub-region B, assumed to be biased low; Hale et al. 2019), and opportunistic skiff surveys of the Strait (sub-region B, assumed to be un-biased after accounting for area surveyed and seasonal variation) separately to allow for different dispersion parameters because survey methods differed between range-wide and opportunistic skiff surveys. We adjusted the range-wide survey data for the Strait of Juan de Fuca (sub-region B) by a correction factor (estimated as part of model fitting; Table 2-2), and adjusted the opportunistic skiff survey data of the Strait (sub-region B) for the area within sub-region B that was surveyed and for seasonal variation in counts for comparison with model predictions (Table 2-2). We used vague prior distributions (half-Cauchy priors) for dispersion parameters (Table 2-2; Gelman et al. 2008).

We accomplished model fitting using standard Markov chain Monte Carlo (MCMC) methods. We completed model validation using standard methods for Bayesian models: we assessed model convergence by visual inspection of trace plots of the Markov chains to ensure that they were well mixed, not autocorrelated, and were stationary, and by formally evaluating convergence by applying the Gelman-Rubin diagnostic test to the MCMC output (Hobbs and Hooten 2015). We assessed model goodness of fit using posterior predictive checks (Gelman et al. 2004, Hobbs and Hooten 2015, Conn et al. 2018), where data are simulated under the fitted model by sampling from the posterior distribution and then compared to the observed data. We used the sum of squared Pearson residuals of survey counts versus expected abundance as the discrepancy function. A well-fit model would have an associated Bayesian P-value within the range of 0.3–0.7.

2.3.7 Future range expansion and population growth as basis for sensitivity analysis

We expanded the model to project future population dynamics while allowing for range expansion into unoccupied habitat using a discretized approximation to a diffusion model (Lubina and Levin 1988, Okubo and Levin 2001), modified from Tinker et al. (2008*b*, 2019*b*). We simulated range expansion using published values of a population front wave speed parameter (v; the rate at which the population front moves along the coast as new habitats become occupied). We projected population growth, range expansion, and movements between occupied sub-regions for 25 years into the future, and iterated this process 5,000 times to produce a distribution of results. We explored the sensitivity of forward projections of population dynamics to variation in model parameters (Caswell and Gassen 2015) by evaluating the relative influence of different model parameters on the future rate of population increase (λ).

To model range expansion, we defined new blocks of potential habitat in addition to currently occupied sub-regions (Figure 2-1) by sub-dividing unoccupied sub-regions A and G every 10 km along the Washington coast as the otter swims (WATOS) line, where WATOS points occurred every 0.5 km along the 5-fathom contour (Figure 2-1; Laidre et al. 2002, Tinker et al. 2008*b*) between Dungeness Spit and the Washington-Oregon border. We determined the rate of occupation of new blocks by animals from neighboring occupied blocks using v (asymptotic wave speed, km/year) as in Tinker et al. (2008*b*). We parametrized v separately for southward and eastward range expansion, thereby allowing for differing rates of range expansion at either end of the range, consistent with previously observed patterns of range expansion (Figure 2-1). We set maximum v values to 5 km/year, comparable with previous studies (3–6 km/year; Lubina and Levin 1988, Tinker et al. 2008*b*, Williams et al. 2019, Eisaguirre et al. 2021). To allow for the possibility of range expansion stopping, we set the minimum v values to zero. We drew wave speed (v, rate of range expansion in km/year) for each simulation for each range edge from a random uniform distribution with these minimum and maximum values.

We randomly assigned equilibrium densities from a range of ± 2 standard deviations of the mean estimated value for each sub-region (Table 2-3). We then determined the abundance at *K* as the product of this randomly drawn equilibrium density and area of the sub-region for each simulation. We drew the initial population size in each sub-region from a lognormal distribution, with parameters μ and σ set to produce a mean and variance corresponding to the mean and variance of the posterior distribution of the survey count in that sub-region in 2019 (estimated during model fitting; Jeffries et al. 2019). We drew the values for r_{max}, theta logistic shape parameter (Θ), and environmental stochasticity (process error, σ_P) for each simulation from their respective posterior distributions that were estimated during model fitting (Table 2-3). We generated stochastic movement rates for each simulation between a low movement scenario and a high movement scenario. The exponential dispersal kernel (used in model fitting and described above) varied between a low value (equivalent to 6% probability of dispersing >25 km) and a high value (equivalent to 16% probability of dispersing >25 km) to encompass the full range of measured dispersal distances for sea otters (Laidre et al. 2009, Tinker et al. 2019*a*).

We estimated the relative contribution of variation in each parameter (frontal wave speed, equilibrium density, intrinsic growth rates, dispersal probabilities) to variation in the future rate of population increase (λ), using a multiple linear regression model:

$$\lambda = \alpha + \beta_1(x_1) + \beta_2(x_2) + \beta_3(x_3) \ldots + \beta_n(x_n) + \mathcal{E}, \qquad (4)$$

where $\mathcal{E} \sim \text{Normal}(0, \sigma^2)$. As in Gerber et al. (2004), we calculated the partial coefficients of determination ($r^2_{y1\cdot 2 \ldots n}$) for each explanatory variable (x_n), where the partial coefficient of determination is the relative amount of variance in λ that is explained by each independent variable after controlling for variance due to all other independent variables. We considered covariates to be significant in explaining the variation in future growth potential if $P < 0.05$.

2.4 RESULTS

The model converged well, with well-mixed chains providing robust posterior estimates for all model parameters. The maximum Gelman Rubin convergence diagnostic (psrf) for any fitted model parameter was 1.04 (for σ_P, SD of process error), and all other psrf statistics were <1.04 (Table 2-3). The posterior predictive check indicated a good fit of the model to the data with an associated Bayesian P value of 0.6492 (Figure 2-A1).

2.4.1 Trends, abundance, and equilibrium abundance estimates

Model results indicated that the number of independent sea otters increased from an average of 21 independent sea otters in 1977 (95% CI = 13–29) to 2,336 independent sea otters in 2019 (95% CI = 1,467–3,359; Figure 2-2A). This modeled population increase was the result of an average annual growth rate of 12.42% over 42 years. Model results suggested a smooth, decelerating exponential growth curve at the range-wide scale (Figure 2-2A), but growth trajectories varied at the sub-regional scale (Figure 2-2B–F) from between 6.42% and 14.92% growth/yr on average. The modeled region-wide 3-year average growth rate from 2017–2019 was 5.74%, varying between sub-regions from 2.09–10.64%. Opportunistic skiff survey data in conjunction with range-wide survey data in sub-region B suggests that sea otters have established occupancy in the Strait of Juan de Fuca (Figure 2-2B).

Estimates of equilibrium density and abundance converged well for all sub-regions. Mean K_i density estimates varied among sub-regions: equilibrium density estimates in sub-regions B–F were 2.02, 0.68, 1.55, 3.44, and 2.60 independent sea otters/km^2, respectively. Estimates of current independent sea otter densities within the currently occupied range correspond on average to 87% of mean sub-regional equilibrium density values. Sub-regions B–F were at 88%, 98%, 111%, 72%, and 66% of estimated sub-regional equilibrium density, respectively. The overall estimated mean K density of independent sea otters derived from currently occupied sub-regions in Washington was 1.71 ± 0.90 sea otters/km^2 of habitat (1.96 ± 1.04 sea otters/km^2 including pups). We estimated that 3,096 km^2 of habitat is available to sea otters in Washington to the 40-m depth contour from Dungeness Spit to the Washington-Oregon border (not including bays or estuaries). The projected value of K for all of Washington (within our study area) is 5,287 independent sea otters (95% CI = 2,488–8,086), assuming a similar range of equilibrium densities for currently unoccupied habitats and not including bays or estuaries in the total available habitat. After correcting for the presence of pups ($1.15 \times K$), the projected value of K is 6,080 sea otters (95% CI = 2,861–9,300).

2.4.2 Projected range expansion and population growth as basis of sensitivity analysis

The simulations of sea otter population growth and range expansion over the next 25 years showed that sea otters are generally expected to increase in numbers (Figure 2-3) and expand their range eastward and southward from their current geographic range (Figure 2-4). Forward projections of the model resulted in a mean forecasted abundance after 25 years of 4,960 independent sea otters; however, the range of outcomes varied widely (95% CI = 2,422–8,491 independent sea otters). Including pups, the mean forecasted number of otters in 2044 is 5,705 (95% CI = 2,786–9,765), approximately 93% of the predicted range-wide mean K of 6,080 sea otters, on average.

Multiple regression analysis indicated that all covariates were significant in explaining the variation in future growth potential, including rate of eastward range expansion ($P \leq 0.001$), rate of southward range expansion ($P \leq 0.001$), maximum intrinsic growth rate ($P = 0.0001$), theta logistic growth parameter ($P = 0.0395$), dispersal ($P = 0.0497$), equilibrium density in the sub-region east of the currently occupied range (sub-region A; $P \leq 0.001$), equilibrium density in the currently occupied range (sub-regions B–F; $P \leq 0.001$), and equilibrium density in the sub-region south of the currently occupied range (sub-region G; $P \leq 0.001$). Of the variance explained by the model (71.0%), equilibrium density in currently occupied sub-regions (B–F) explained 63% of the variation in future growth potential ($r^2 = 0.52$) and the rate of southward range expansion (v_{south}; km/yr) accounted for 31% of variation in λ ($r^2 = 0.26$). The equilibrium density in currently unoccupied habitat south of the currently occupied range (sub-region G) accounted for 5% of variation in λ ($r^2 = 0.04$). All other variables included in the model (rate of eastward range expansion, maximum intrinsic growth rate, theta, probability of dispersing >25 km, and equilibrium density in currently unoccupied habitat to the east of the current range [sub-region A]) together explained <1% (all $r^2 \leq 0.002$).

2.5 DISCUSSION

The model we have developed for analyzing population growth and range expansion of sea otters in Washington adds to the growing body of literature applying spatio-temporal state-space models to sea otter populations and provides the first comprehensive estimates of population dynamics, robust estimates of *K*, and simulations (with associated uncertainty) of long-term growth and range expansion of the sea otter population in Washington. While our model did not account for observation bias, it nonetheless results in the first estimates of trends for sea otters in Washington that separate observation and process error. Unlike previous estimates of *K* for Washington, the estimates of *K* reported here do not rely on *a priori* assumptions about which areas have already reached *K*; instead, the model infers a value of *K* for each sub-region based on the entire survey time series. In addition to *K* estimates, our model also produced sub-region and range-wide estimates of other population parameters such as environmental stochasticity and maximum intrinsic growth rate, which are the first estimates of population parameters at biologically relevant scales for sea otters in Washington. In addition, the population model for sea otters in Washington simulates long-term growth and range expansion.

2.5.1 Equilibrium density

As predicted, the equilibrium density of sea otters in Washington that we estimated, and therefore the overall index estimate of *K*, was higher than previously predicted by Laidre et al. (2002). Laidre et al. (2002) calculated the best index estimate of *K* based on linear densities to be 2,734 sea otters (95% CI = 2,082–3,452) and Lance et al. (2004) used this estimate of *K* in the Washington Sea Otter Recovery Plan (1,836 sea otters [CI = 1,597–2,074] not including estuaries and bays). Laidre et al. (2002) also estimated *K* based on densities within the 40-m depth contour to be 1,372 sea otters (95% CI = 1,031–1,713; encompassing 3,696 km^2 of habitat) and 1,214 sea otters (CI = 1,056–1,371) not including estuaries and bays in the available habitat (totaling 2,914 km^2 of habitat; Laidre et al. 2002). In contrast, we estimated an index value of *K* of 6,080 sea otters (95% CI = 2,861–

9,300) in a similar area (sub-regions A–G: encompassing habitat <40 m depth between Dungeness Spit and the Washington-Oregon border at the mouth of the Columbia River, not including bays and estuaries; totaling 3,096 km^2 of habitat). This higher estimated index of *K* stems primarily from a higher overall average *K* density (1.96 vs. 0.40 otters/km^2 by Laidre et al. [2002], adjusted for Laidre et al. [2002] to match our study area).

This difference in average estimated *K* density likely stems from 2 factors. The index estimates of *K* in Laidre et al. (2002) were based on the assumption that the rocky equilibrium area (Petroleum Creek to La Push) had already reached *K*, but it is now clear that this area was actually below *K* at the time because the numbers of sea otters in this area have increased beyond assumed equilibrium in the mid-1990s (Laidre et al. 2002). Unlike the earlier estimates, our current estimates do not make limiting assumptions about which areas have already reached *K.* As a result, we estimated a higher *K* density in the area roughly corresponding to the rocky equilibrium area (average of 1.25 otters/km^2 in sub-regions C and D versus 0.97 otters/km^2 estimated by Laidre et al [2002] between Petroleum Creek and La Push). Second, estimates by Laidre et al. (2002) of *K* densities for mixed and sandy substrates were comparatively low (mixed = 0.15 otters/km^2, sandy = 0.20 otters/km^2). As sea otters in Washington had not been established in mixed and sandy substrates long enough to reliably estimate density, Laidre et al. (2002) calculated equilibrium densities of sea otters in mixed and sandy substrates from sea otters in California (Laidre et al. 2001). Based on aerial substrate classifications by Laidre et al. (2002), sub-regions C, D, and E are rocky, sub-region B is primarily mixed (40.72% rocky, 59.28% mixed), and sub-region F is primarily sandy (20.36% rocky, 10.76% mixed, 68.88% sandy). Based on the estimated *K* density of sea otters in sub-regions C and D (area roughly corresponding to the rocky equilibrium area; weighted average = 1.25 otters/km^2), the ratios for mixed and sandy substrates (sandy:rocky = 0.21, mixed:rocky = 0.15; Laidre et al. 2001) and the proportion of each substrate type in each sub-region (according to Laidre et al. [2002] classification), the predicted *K* densities in sub-regions B–F are 0.62, 1.25, 1.25, 1.25, and 0.42 otters/km^2, respectively. In contrast, we estimated *K* densities of 2.02, 0.68, 1.55, 3.44, and 2.60 otters/ km^2, respectively (Table 2-3). These results suggest that higher densities in the rocky equilibrium area alone do not account for the increased *K* densities we estimated, and that densities within mixed and sandy substrates may be higher than were previously estimated for sea otters in California by Laidre et al. (2001). The inclusion of finer scale habitat data in future population models for sea otters in Washington, such as substrate data compiled by the Oregon State University Active Tectonics and Seafloor Mapping Lab (Romsos et al. 2015), will improve our understanding of the relationship between sea otter equilibrium density and substrate type.

One of the recovery objectives outlined in the Washington Sea Otter Recovery Plan (Lance et al. 2004) is for average sea otter population abundance over a 3-year period to be ≥60% of estimated *K*. Because we estimated a higher index of *K* than Laidre et al. (2002), our target population estimate was also higher: we estimated an index value of *K* of 6,080 sea otters (95% CI = 2,861–9,300) and a target population level (60% of this estimate) of 3,648 sea otters (95% CI = 1,716–5,580). The average number of sea otters counted during range-wide surveys in Washington (2016–2019, no survey in 2018) was 2,216 (36% of *K*), demonstrating that based on our results the sea otter population in Washington has not yet met this recovery objective outlined in Lance et al. (2004). Our model estimates *K* as the maximum number of sea otters that could be supported within the available habitat in

Washington. Because the coastal tribes of Washington historically hunted sea otters, the realized equilibrium abundance historically may have been lower than K we estimate here (Slade et al. 2021).

2.5.2 Range recolonization

Another objective outlined in the Washington Sea Otter Recovery Plan (Lance et al. 2004:50) is that the population be distributed in areas outside their geographic range circa 2004, such that "a single catastrophic event, such as a major oil spill, would be unlikely to cause severe decline or extirpation of the population." Based on our definition of the occupied range (the 2 points that contained 99.5% of sea otter positions), opportunistic skiff survey data in conjunction with range-wide survey data suggest that the eastern range edge boundary has moved approximately 45.5 km east from Cape Flattery to Sekiu Point in the Strait of Juan de Fuca since 2004 (Figure 2-1). Based on this definition of the occupied range since 2004, the southern range edge boundary has moved approximately 40 km south from Destruction Island to Split and Willoughby Rocks (Figure 2-1). While the range boundaries have expanded since 2004, the majority of the population is currently concentrated on the outer coast: in 2019, 80% of the population was observed within a 75-km segment of coastline between La Push and Point Grenville (Jeffries et al. 2019). This centrally biased distribution was particularly apparent in 2016, when a single raft of approximately 652 sea otters was observed near North Rock, off the mouth of the Hoh River (Jeffries et al. 2016), representing 36% of the population based on the population index at the time (1,806 individuals). Based on the 2019 census, if a catastrophic event such as a major oil spill was to occur on the outer coast, a large portion of the Washington sea otter population would be at risk.

Because range expansion is an objective of the Washington Sea Otter Recovery Plan (Lance et al. 2004), a standardized way to define sea otter geographic range extent is needed for sea otters in Washington. Several methods for defining range extent have been used for sea otter populations (Bowlby et al. 1988, Lubina and Levin 1988, Hatfield et al. 2019), and we estimated sea otter range extent in Washington and observed rates of range expansion using a variety of methods (Table 2-A1, available in Supporting Information; −0.8 km/year to 2.24 km/year). All of these methods resulted in lower estimated rates of range expansion for sea otters in Washington than typical rates from other studies (2–6 km/year; Lubina and Levin 1988, Tinker et al. 2008*b*, Williams et al. 2019, Eisaguirre et al. 2021), and each method produced very different estimates for the same range expansion front (north or east front and south front). We lacked reliable estimates of rates of range expansion for sea otters in Washington, so we used a diffusion approximation to simulate future population growth and range expansion under a range of biologically realistic population parameters (including rate of range expansion) and used these forward projections as the basis of a sensitivity analysis to explore how variation in population parameters would influence predictions of future population growth.

2.5.3 Sensitivity analysis of future population projections

The forward simulations of sea otter population growth and range expansion over the next 25 years using a diffusion approximation showed that sea otters are generally expected to increase in numbers and expand their range both eastward and southward from their current geographic range (Figures 2-3 and 2-4). Despite this predicted range expansion, the majority of sea otters are still predicted to occur within a small area of the outer Washington coast in the year 2044 (Figure 2-4), highlighting their continued vulnerability to catastrophic events. We made simulations under a wide range of biologically realistic population parameters as the basis of the sensitivity analysis, and the wide credible intervals around the projected future trends reflect this large degree of uncertainty. As such, these projections should not be interpreted as robust predictions of sea otter population growth and range expansion. Further research is needed to elucidate the factors determining rates of range expansion for sea otters in Washington to robustly predict future range recolonization and population growth, especially given the rate of southward range expansion explained a large proportion (31%) of the variability in future λ. Further research is also needed to determine if sea otters will expand their range into Willapa Bay, Grays Harbor, or Puget Sound and how they will use this habitat compared to the outer coast of Washington and the Strait of Juan de Fuca, as these habitats may have the potential to support high densities of sea otters based on other areas where sea otters occur in estuaries and protected inland waters (Bodkin et al. 2000, Hughes et al. 2019, Williams et al. 2019).

Previous researchers have demonstrated the utility of sensitivity analyses in conservation to explore how variation in model parameters influences the future rate of λ, including for sea otter populations (Wisdom et al. 2000, Gerber et al. 2004, Gerber and Heppell 2004, Tinker et al. 2006). Our sensitivity analysis results highlight the importance of equilibrium density estimates in understanding future population growth, and therefore the importance of continued monitoring of sea otter abundance in Washington, as estimates of equilibrium abundance rely on long-term data sets to estimate the most statistically likely index estimate of *K*. Because equilibrium abundance can vary through time, continued monitoring of sea otter population abundance may be particularly important in the context of future changes in productivity stemming from climate change. The sensitivity analysis also highlights the importance of the southern portion of the range in determining future population growth, as evidenced by the rate of southward range expansion and equilibrium abundance in sub-region G being identified as impactful parameters on λ. These results are consistent with our expectations of range recolonization for sea otters in Washington and with previously observed patterns of population growth, as the majority of the available habitat for range expansion exists on the outer coast in the southern portion of the range (Figure 2-1) and the majority of the population has occurred south of La Push since 2003 (Jeffries et al. 2019).

Independent sea otter densities within the current range correspond on average to 87% of mean sub-regional equilibrium densities; therefore, the majority of sea otter population growth over the next 25 years is predicted to occur through range expansion into currently unoccupied areas (Figure 2-4). However, potential for population growth within the currently occupied range (sub-regions B–F) varies at a sub-regional scale. Little management action could be taken to increase the abundance of sea otters within sub-regions C and D if the population is indeed approaching equilibrium abundance in these areas, where our model estimates that current densities are 98% and 111% of subregional equilibrium densities, respectively. In contrast, sub-regions B, E, and F are not yet approaching equilibrium abundance (88%, 72%, and 66% of subregional equilibrium, respectively); thus, population growth is likely to continue in these areas (Figure 2-4). The currently occupied range is predicted to continue to support the majority of sea otters in Washington (Figure 2-4), and sea otters in this area are likely a source population for the range edges. As such, the continued population growth of sea otters in Washington likely depends on both the continued protection of sea otters within their currently occupied habitat and continued expansion into unoccupied habitat.

2.5.4 Management implications

Our population model can provide a template for studying the recovery of other small, fragmented populations of endangered or recently translocated species. The estimates produced by our model are useful for sea otter management in Washington because they are produced from and directly relate to the abundance index based on un-corrected counts collected during the range-wide surveys used to monitor the sea otter population in Washington since 1989 and set recovery goals. Our updated estimate of K and use of forward projections of population dynamics as the basis of a sensitivity analysis on the future rate of population increase have the potential to aid in decision-making by entrusted co-management agencies regarding the population status of sea otters in Washington. The WDFW downlisted the sea otter from state endangered to state threatened in 2018 partly because of the population achieving a 3-year average of 1,752 sea otters, exceeding 60% of the previously estimated index of K threshold for downlisting (1,640); however, this previously estimated index estimate of K is considerably lower than the estimate derived from our model, and, if achieving a population size that is 60% of the index of K is an important threshold for downlisting, the population has not yet reached that threshold according to our model results. For future sea otter status reviews, we recommend that WDFW consider our new estimates in their decision-making process. Our forward projections of population dynamics also highlight the potential for increased competition between sea otters and valuable state and tribal shellfisheries, as sea otters are in general predicted to continue to increase in number and expand their geographic range in

Washington. The sensitivity analysis identifies the most influential parameters affecting future population growth and thus where additional studies should focus to robustly predict future population growth and range expansion, including new areas of competition between sea otters and fisheries.

2.6 ACKNOWLEDGMENTS

The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service or the WDFW. We gratefully acknowledge everyone involved with the Washington State sea otter surveys. This long-running survey is a collaborative effort between many agencies, organizations, and individuals. K. W. Kenyon and A. M. Johnson were instrumental with support and field work in the early surveys and without their help and support it is likely that none of this would have happened. Thanks to pilots J. Well, R. Mowbray, J. Hodgson, and M. Kimbrel. Survey participants included S. Ament, A. McMillan, M. Cope, B. L. Troutman, D. T. Noviello, S. Thomas, M. Merola-Zwartjes, K. M. Reagan, B. B. Hatfield, L. Triggs, S. Rager, C. Carter, K. Heffron, S. E. Larson, A. Olsen, C. Hempstead, P. McMahon, C. J. Casson, A. Theiss, J. Van Brocklin, T. Belting, J. Carpenter, K. Kegel, A. Annine, D. Hayward, F. Pope Jr., U. Willis, V. Molenaar, K. Allston, C. Kelly, H. May, D. Ravenel, R. T. Carnevali, D. D. Carnevali, A. M. Akmajian, L. D. Antrim, J. Waddell, J. Borman, M. S. Brancato, C. E. Bowlby, B. A. Blackie, J. Wengler, H. Claussenius-Kalman, E. Gurarie, G. Jameson, T. Zorman, J. Joyce, M. Langley, M. Long, M. Stafford, and additional survey participants. J. S. Oliver and B. Diehl assisted with image counting and data entry. Washington Department of Fish and Wildlife WILDCOM dispatch provided Aircraft Flight Following services. Funding for aerial and ground surveys was provided by the United States Fish and Wildlife Service, United States Geological

Survey, WDFW, and Point Defiance Zoo and Aquarium (2010 Conservation Committee grant). Funding for opportunistic skiff surveys was provided by Makah Fisheries Management, and surveys were conducted by E. M. Allyn, J. J. Scordino, and A. M. Akmajian. This publication is partially funded by the Joint Institute for the Study of the Atmosphere and Ocean under National Oceanic and Atmospheric Administration Cooperative Agreement NA15OAR4320063, Contribution number 2021-1154. Additional funding support to J. R. Hale was provided by the School of Aquatic and Fishery Sciences (University of Washington) and the National Oceanic and Atmospheric Administration Dr. Nancy Foster Scholarship.

2.7 ETHICS STATEMENT

All sea otter surveys (range-wide and opportunistic skiff surveys) were conducted in accordance with the United States Marine Mammal Protection Act. Overflights of Olympic Coast National Marine Sanctuary below 609.6-m Above Ground Level were conducted under National Oceanic and Atmospheric Administration permits issued to WDFW. Research activities in Olympic National Park were conducted under Scientific Research Permits (such as OLYM-2019-SCI-0026) for access to Olympic National Park locations used by ground observers. The Makah Tribe provided permits for access to Makah Tribe lands used by ground observers.

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Table 2-1. Attributes of existing and potential sea otter habitat in Washington State, USA, 2000–2014, from Dungeness Spit to the Washington-Oregon border. The regional study area was divided into distinct geographic sub-regions—contiguous spatial polygons that encompass the area currently known to be occupied by sea otters during summer (sub-regions B–F) and additional suitable habitat in Washington <40-m depth that could be occupied in the future (sub-regions A and G).

Sub-region (north to south)	Coastal length (km)	Area (km^2)	Percentage of sub-region composed of rocky substrate
A	122.45	238.70	33.45
B	44.21	48.60	42.58
C	38.09	219.19	15.96
D	23.35	192.23	13.13
E	45.73	329.73	9.37
F	39.06	552.83	2.99
G	144.05	1,514.59	1.76

Table 2-2. Summary of Bayesian state-space model used to estimate population dynamics for sea otters in Washington State, USA, 1977–2019. Equations are organized according to the hierarchical structure of the model: a data model (consisting of observed data sets and accounting for observation error), a process model (describing dynamics of the population, incorporating stochasticity in process model parameters), and the prior model (probability distributions representing our prior knowledge of the input parameters).

Model component	Description
Data model	
$y_{i,t} \sim \text{Negative Binomial}\ (\bar{x} = N_{i,t}\ , \text{SD} = N_{i,t} \times \text{CV}_o)$	Range-wide survey counts for sub-regions C to F (i) and time t ($y_{i,t}$) accounting for observation error (CV_o). Mean expected value ($\bar{x}$) depends on true population abundance (N).
$y_{i,t*} \sim \text{Negative Binomial}\ (\bar{x} = N_{i,t*} \times \mathit{crct}\ , \text{SD} = N_{i,t*} \times \mathit{crct} \times \text{CV}_{o*})$	Range-wide survey counts for sub-region B and time t ($y_{i,t*}$) accounting for observation error (CV_{o*}). Mean expected value ($\bar{x}$) depends on true population abundance (N) adjusted by fitted parameter (crct).
$y_{i,t**} \sim \text{Negative Binomial}\ \left(\bar{x} = \dfrac{N_{i,t**} \times \mathit{PropArea}}{\mathit{SeasonScalar}}, \text{SD} = \dfrac{N_{i,t**} \times \mathit{PropArea}}{\mathit{SeasonScalar}} \times \text{CV}_{o**}\right)$	Opportunistic skiff survey counts for sub-region B and time t ($y_{i,t**}$) accounting for observation error (CV_{o**}). Mean expected value ($\bar{x}$) depends on true population abundance (N) adjusted for area surveyed ($\mathit{PropArea}$)

	and scaled to the average July count ($SeasonScalar$).
Process model	
$N_{i,t} = N_{i,t-1} \times \lambda_{i,t} + \sum_{j \neq i}^{J} D_{j,i,t} - \sum_{j \neq i}^{J} D_{i,j,t}$	Population abundance dynamics in sub-region *i* at year *t*, including intrinsic demographic processes (λ , the finite annual growth rate) and emigration and immigration (D).
$log\ (\lambda_{i,t}) \sim \text{Normal}\left(\bar{x}\ = log(\lambda_{exp\ i,t}), \text{SD} =\ \sigma_p\right)$	Realized finite annual growth rate (λ) for sub-region *i* at year *t*, accounting for density dependence and environmental stochasticity.
$log(K_i) \sim \text{Normal}\left(\bar{x}\ = log(K_{exp\ i}), \text{SD} =\ \sigma_K\right)$	Realized density at equilibrium (*K*) for sub-region *i*.
$D_{i,j,t} = \pi_{i,j,t}\ \times N_{i,t},$ $\pi_{i,j,t} \sim \text{Dirichlet}\left(\alpha =\ \phi_{i,j} \times N_{i,t} + 1\ \right)$	Number of animals moving from sub-region *i* to *j* in year *t* ($D_{i,j,t}$) calculated from random dispersal probability values of moving from *i* to *j* in year *t* (π) and true abundance ($N_{i,t}$). Stochastic movement rate (π) depends on the mean expected probability that an otter would disperse from sub-region *i* to sub-region *j* ($\phi_{i,j}$).

$log\ (\lambda_{exp\ i,t}) = r_{max}\left(1 - \frac{N_{i,t}}{K_i}\right)^{\theta}$	Expected finite annual growth rate (λ) for sub-region *i* at year *t* (theta logistic model) calculated based on maximum intrinsic growth rate (r_{max}), true abundance (N), and density at equilibrium (K).

Prior model

$\sigma_K \sim$ Half Cauchy (location $= 0$, scale $= 2.5$)	Unexplained variation in equilibrium density (K) across sub-regions.
$\sigma_P \sim$ Half Cauchy (location $= 0$, scale $= 1.5$)	Standard deviation of process error.
$\mathrm{CV}_o \sim$ Half Cauchy (location $= 0$, scale $= 1.5$)	Coefficient of variation of observed range-wide survey counts for sub-regions C–F.
$\mathrm{CV}_{o*} \sim$ Half Cauchy (location $= 0$, scale $= 1.5$)	Coefficient of variation of observed range-wide survey counts for sub-region B.
$\mathrm{CV}_{o**} \sim$ Half Cauchy (location $= 0$, scale $= 0.2$)	Coefficient of variation of observed opportunistic skiff survey counts for sub-region B.
$crct \sim$ Beta (shape1 $= 1$, shape2 $= 1$)	Correction factor for range-wide survey counts in sub-region B.
$r_{max} \sim$ Normal ($\bar{x} = 0.18$, SD $= 1{,}000$)	Maximum intrinsic growth rate.

$log(\theta) \sim \text{Normal}(\bar{x} = -0.05, \text{SD} = 10)$	Theta parameter for theta logistic growth (distribution mean = 1).
$nn0_i \sim \text{Normal}\ (\bar{x} = n_{o_i}, \text{SD} = n_{o_i} \times \text{CV}_o)$	Initial population size, accounting for observer error.
$K_{exp\ i} \sim \text{Half Cauchy}\ (\text{location} = 2.5, \text{scale} = 2.5)$	Overall mean *K* density.

Table 2-3. Summary of parameter estimates for a model fit in a Bayesian state-space framework and used to estimate population dynamics for sea otters, Washington State, USA, 1977–2019. For each parameter we show the mean, standard deviation (SD) and 95% credible intervals (CI) of the posterior distributions, and the Gelman-Rubin statistic (psrf; providing indication of model convergence; values near 1 indicate well-mixed chains).

Parameter or variable[a]	$\overline{x}$	SD	$CI_{95\text{-low}}$	$CI_{95\text{-high}}$	psrf
CV_o	0.325	0.027	0.276	0.379	1.004
CV_{o*}	2.242	1.438	0.005	4.868	1.031
CV_{o**}	1.409	0.121	1.183	1.637	1.005
σ_P	0.126	0.027	0.074	0.182	1.041
r_{max}	0.221	0.022	0.178	0.263	1.004
θ	1.040	0.269	0.568	1.568	1.001
$K_{exp\ i}$	1.708	0.904	0.500	3.363	1.004
$K_{exp\ B}$	2.022	2.027	0.300	5.196	1.037
$K_{exp\ C}$	0.684	0.177	0.442	0.963	1.006
$K_{exp\ D}$	1.547	0.509	0.915	2.460	1.006
$K_{exp\ E}$	3.439	2.153	1.165	7.071	1.009
$K_{exp\ F}$	2.599	1.602	0.902	5.582	1.009
K_B	98.273	98.506	14.583	252.545	1.037
K_C	149.991	38.701	96.873	211.135	1.006
K_D	297.374	97.922	175.934	472.901	1.006
K_E	1,133.988	709.915	384.030	2,331.550	1.009
K_F	1,436.549	885.576	498.499	3,086.030	1.009

[a] Parameters and variables include coefficient of variation of observed range-wide survey counts for sub-regions C–F (CV_o) and for sub-region B (CV_{o*}); coefficient of variation of observed opportunistic skiff survey counts for sub-region B (CV_{o**}); standard deviation of process error (σ_P); maximum intrinsic growth rate (r_{max}); theta parameter for theta logistic growth (Θ); overall mean equilibrium density in all sub-regions ($K_{exp\ i}$), in sub-region B ($K_{exp\ B}$), in sub-region C ($K_{exp\ C}$), in sub-region D ($K_{exp\ D}$), in sub-region E ($K_{exp\ E}$), and in sub-region F ($K_{exp\ F}$); and mean equilibrium abundance in sub-region B (K_B), in subregion C (K_C), in sub-region D (K_D), in sub-region E (K_E), and in sub-region F (K_F).

Table 2-A1. Estimated range expansion rates (frontal wave speed [*v*], km/year) for sea otters in Washington State, USA, 1970–2018 calculated using a variety of methods. Each year, we estimated range extents (north [or east when otters are in the Strait of Juan de Fuca] and south) using the stated method, expressing extents as positions along the Washington as the otter swims (WATOS) line, where WATOS points occurred every 0.5 km along the 5-fathom contour. We fit a linear model to these positions (separately for north or east and south range extents) and estimated the frontal wave speed (km/year) as the slope of this linear model divided by 2 (to convert from WATOS to km).

Method	North or East wave speed (km/yr)	South wave speed (km/yr)	Data source
Farthest N or E and S sea otter (1970–2018)	2.24	0.87	Bowlby et al. (1988), range-wide survey data (e.g., Jameson et al. 1982, 1986; Jeffries et al. 2017), opportunistic skiff survey data (J. J. Scordino, Makah Fisheries Management, unpublished data).
Farthest N or E and S sea otter pup (1977–2014)	0.9	0.6	Range-wide survey data (e.g., Jameson et al. 1982, 1986; Jeffries and Jameson 2015).
98% quantile (1977–2017)	−0.78	−0.8	Range-wide survey data (e.g., Jameson et al. 1982, 1986; Jeffries et al. 2017).

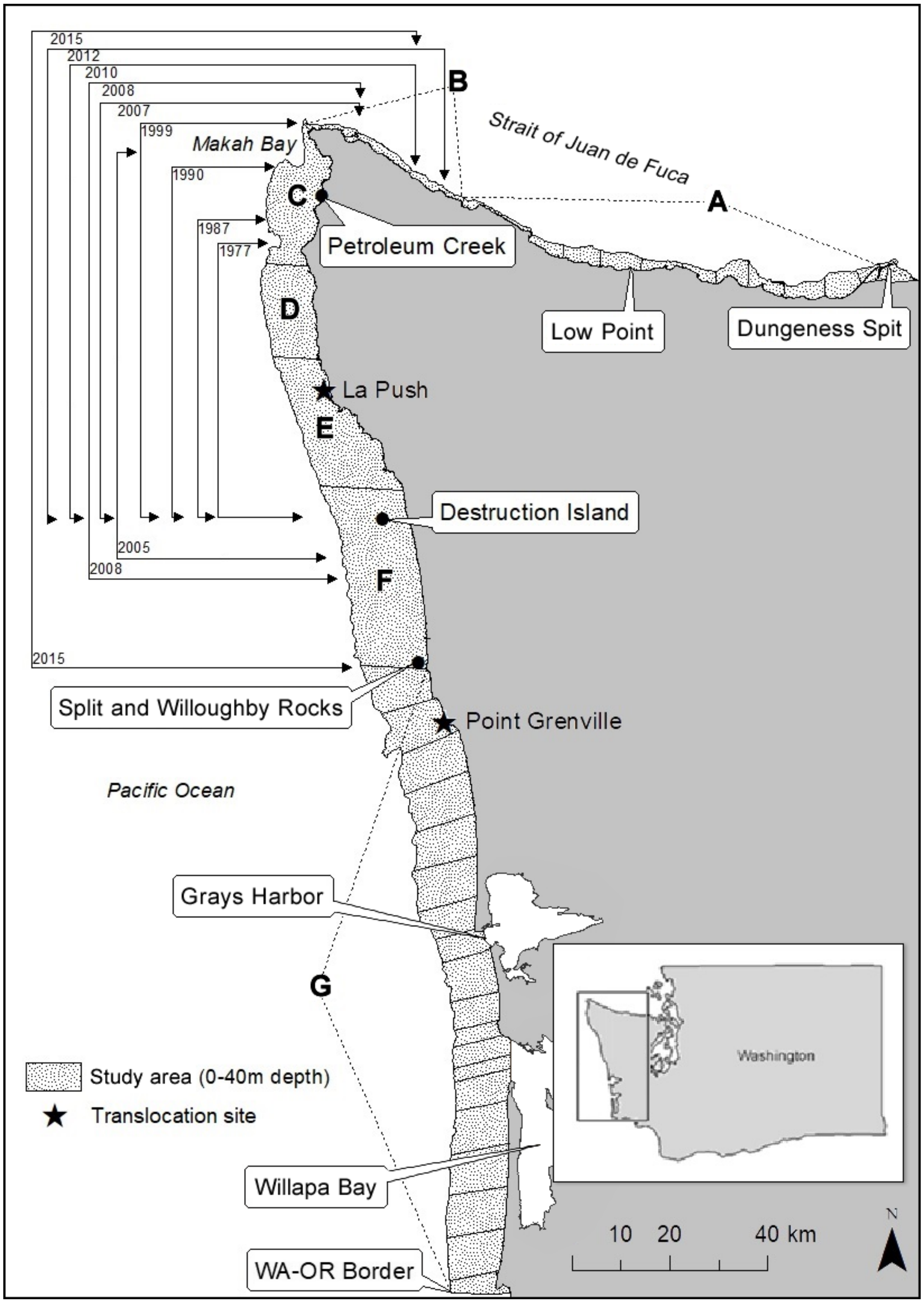

Figure 2-1. The Olympic Peninsula of Washington State, USA, showing changes in distribution of sea otters, 1977–2019, defined as the 2 points that contained 99.5% of sea otter positions. Stippled area shows the study area (available sea otter habitat from the coast to 40-m depth contour) between Dungeness Spit and the Washington-Oregon border. Each sub-region within the study area is labeled (A–G). Stars indicate sea otter translocation sites. Other locations mentioned in the text and other figures are labeled with call out bubbles.

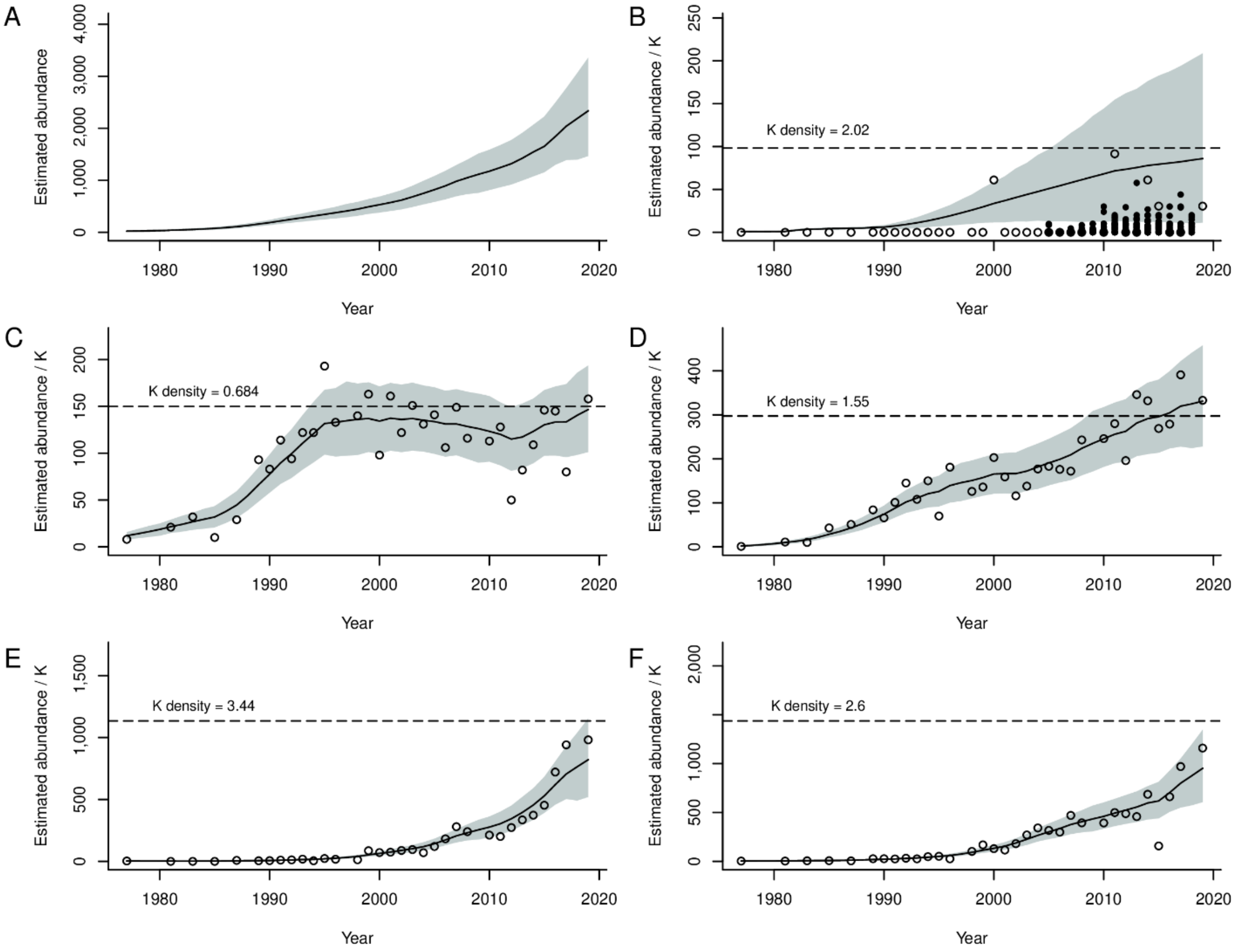

Figure 2-2. Estimated sea otter abundance trends (1977–2019) for all of Washington State, USA (A) and for sub-region B (B), sub-region C (C), sub-region D (D), sub-region E (E), and sub-region F (F). In each panel the solid trend line shows the mean estimated value and the grey-shaded areas show the 95% credible intervals. In panels B–F, the dashed line indicates the mean density at equilibrium abundance (*K*), open points indicate observed counts from range-wide surveys, and solid circles indicate opportunistic skiff counts in sub-region B.

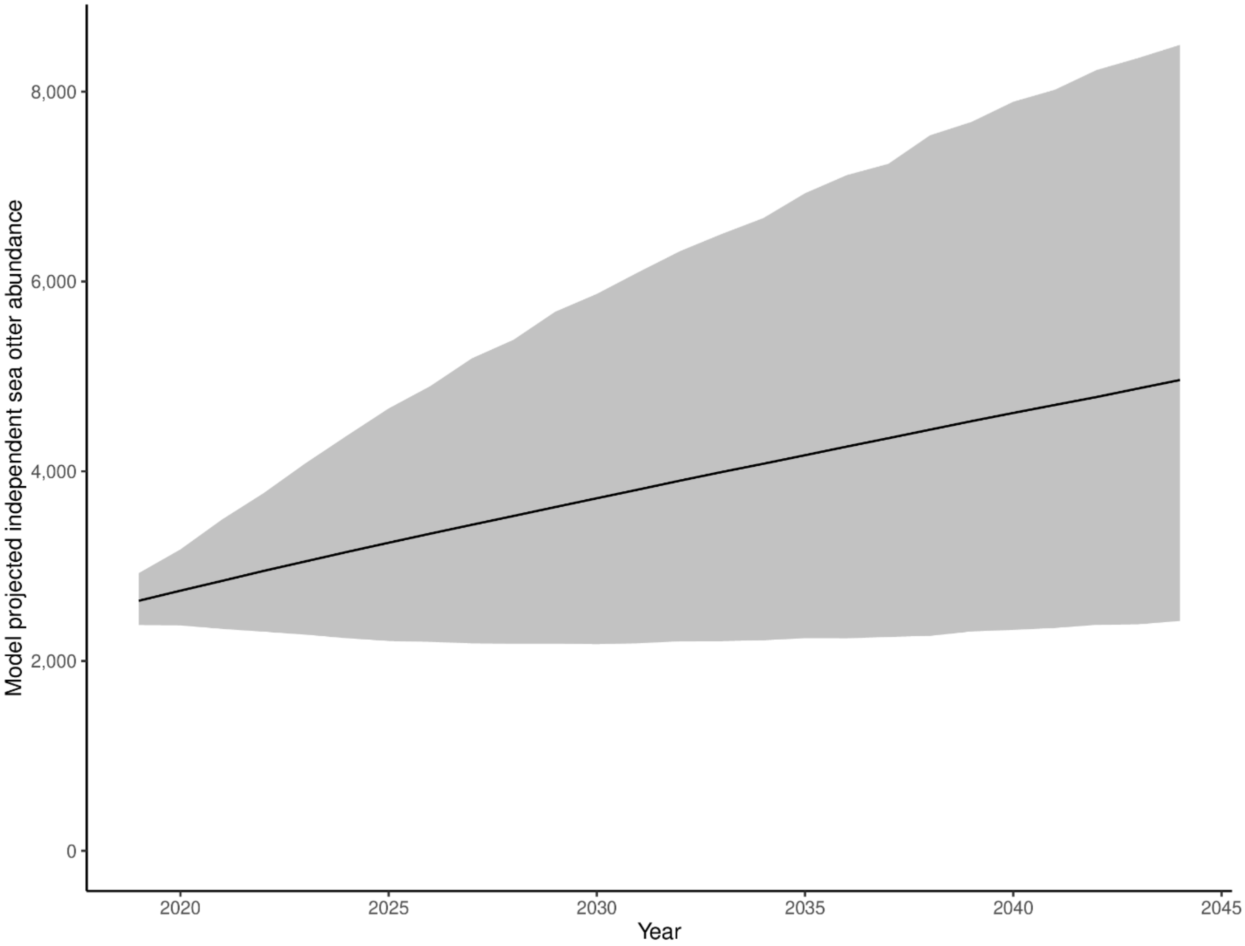

Figure 2-3. Diffusion approximation simulation results of sea otter population dynamics, 2019–2043, Washington State, USA. Solid trend line shows the mean estimated value. Light gray band shows 95% confidence intervals for simulations.

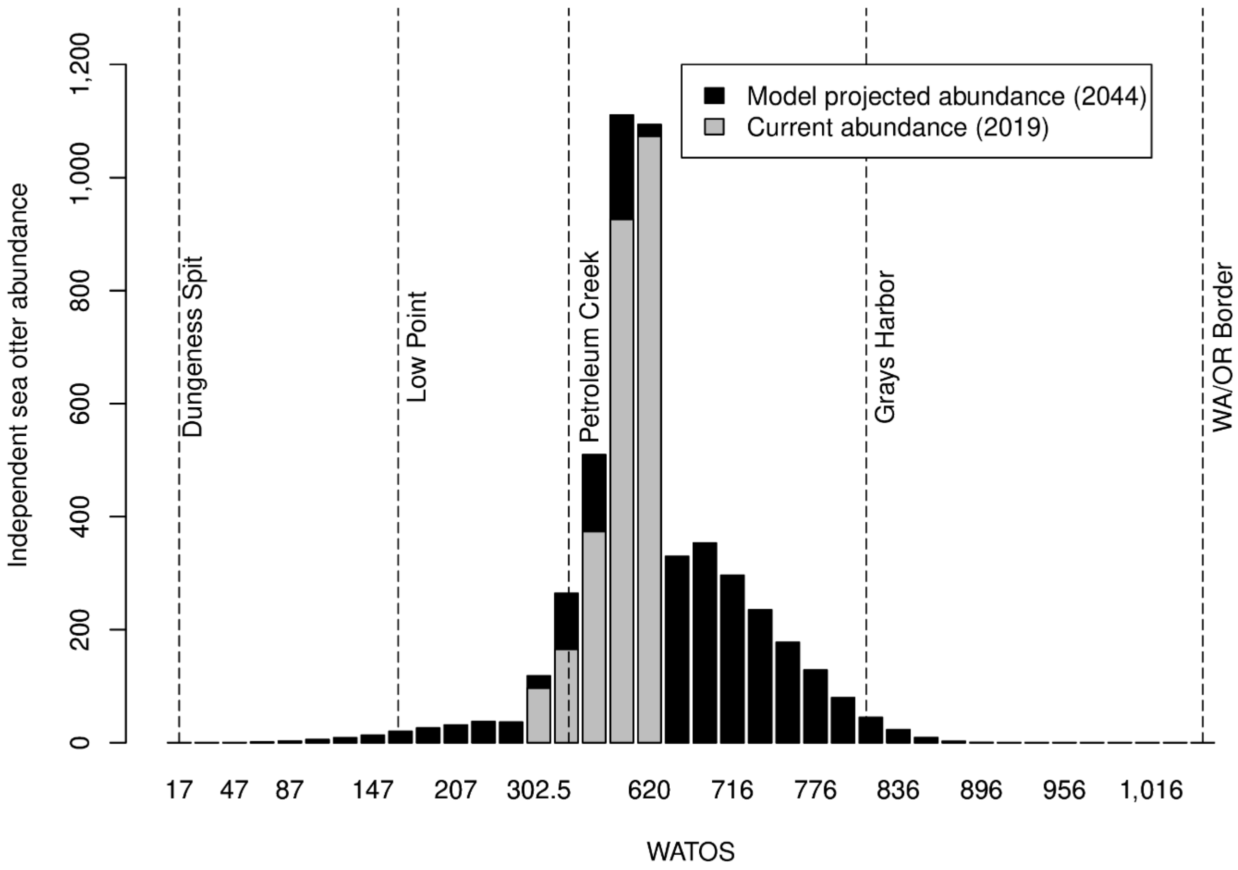

Figure 2-4. Adult sea otter abundance and geographic range in 2019 (grey) and after 25 years from diffusion approximation (black), Washington State, USA. Positions along the coast are expressed as 500-m intervals along the Washington as the otter swims (WATOS) line, where WATOS points occurred every 0.5 km along the 5-fathom contour. The WATOS numbering begins in the Strait of Juan de Fuca (Dungeness Spit = WATOS 17) and ends at the Washington-Oregon (WA-OR) border (WATOS = 1,046).

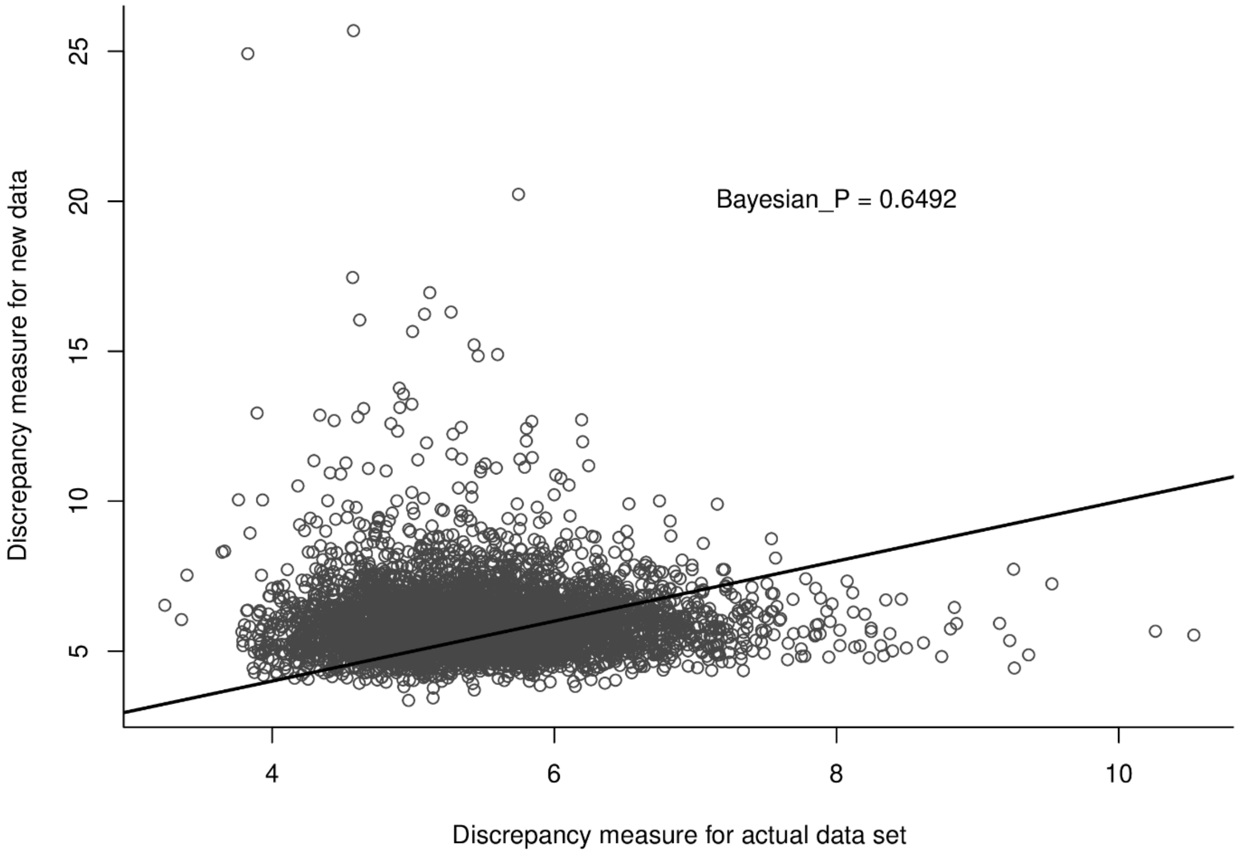

Figure 2-A1. Scatter plot of the posterior distribution of summed deviance scores for new data plotted against observed data, used in assessing goodness of fit for a model fit to survey data in a Bayesian state-space framework for sea otters, Washington State, USA, 1977–2019. The points show samples for a discrepancy measure generated from observed data versus posterior predictive samples of data simulated by the model, with the sum of squared Pearson residuals of survey counts versus expected abundance as the test statistic. A well-fit model would have points distributed around a line from the origin (0,0) with a slope of 1 and an associated Bayesian *P*-value within the range 0.3–0.7.

Chapter 3. Influence of occupation history and habitat on Washington sea otter diet

(Hale, J. R., K. L. Laidre, M. T. Tinker, R. J. Jameson, S. J. Jeffries, S. E. Larson, J. L. Bodkin. 2019. Influence of occupation history and habitat on Washington sea otter diet. Marine Mammal Science. https://doi.org/10.1111/mms.12598)

3.1 ABSTRACT

Habitat characteristics are primary determinants of nearshore marine communities. However, biological drivers like predation can also be important for community composition. Sea otters (*Enhydra lutris ssp.)* are a salient example of a keystone species exerting top-down control on ecosystem community structure. The translocation and subsequent population growth and range expansion of the northern sea otter (*Enhydra lutris kenyoni*) in Washington State over the last 5 decades has created a spatio-temporal gradient in sea otter occupation time and density, and acts as a natural experiment to quantify how sea otter population status and habitat type influence sea otter diet. We collected focal observations of sea otters foraging at sites across the gradient in varying habitat types between 2010 and 2017. We quantified sea otter diet composition and diversity, and long-term rates of energy gain across the gradient. We found that sea otter diet diversity was positively correlated with cumulative sea otter density, while rate of energy gain was negatively correlated with cumulative density. Additionally, we found that habitat type explained 1.77 times more variance in sea otter diet composition than sea otter cumulative density. Long-term diet studies can provide a broader picture of sea otter population status in Washington State.

3.2 INTRODUCTION

Understanding how organisms interact with the biotic and abiotic environment is among the fundamental goals of ecology (Sutherland et al*.* 2013). Habitat characteristics are often primary determinants of nearshore marine communities (e.g., Sebens 1991), while biological drivers like predation can also be important determinants of community composition (e.g., Paine 1966). In some cases habitat characteristics can also mediate the effects of predation on community structure (e.g., Menge 1978). Marine mammals are often important predators in shaping marine ecosystems (Bowen 1997) and sea otters (*Enhydra lutris ssp.)* are a salient example of a keystone species exerting top-down control on ecosystem community structure (e.g., Estes and Palmisano 1974, Garshelis et al*.* 1986, Riedman and Estes 1990, Estes and Duggins 1995). Sea otters are top predators with small home ranges and differ from most marine mammals in that they forage in shallow nearshore coastal waters and bring captured prey to the surface to handle and consume, allowing for direct observation (Riedman and Estes 1990). Within the nearshore marine environment, sea otters forage in a variety of habitat types, including rocky- and soft-bottom habitat, with and without surface kelp canopy (Riedman and Estes 1990). Therefore, sea otters are ideally suited for ecological studies investigating the interplay of biotic and abiotic drivers of organisms, setting the groundwork for understanding the drivers of marine mammals more broadly, especially those that may not lend themselves to comparative foraging studies.

Sea otters (*Enhydra lutris sspp.*) were heavily exploited during the maritime fur trade from the mid-1700s until the early 1900s, resulting in their extirpation from extensive portions of their range, including the northern sea otter (*E. l. kenyoni*) from Washington State (Scheffer 1940, Kenyon 1969). Following the translocation of 59 sea otters from

Amchitka Island, Alaska in 1969 and 1970 to the central portion of the Olympic Coast of Washington State (Jameson et al*.* 1982), Washington's sea otter population grew rapidly from a founding population estimated to be as few as 10 individuals (10%–21% per year, Jameson et al*.* 1982, 1986; Bodkin et al*.* 1999). Between the late 1970s and early 1990s, the sea otter population range was limited to the outer coast of Washington between Makah Bay and Destruction Island (Figure 3-1), apparently reaching equilibrium levels in core parts of the range (between Petroleum Creek and Little James Island) around the mid-1990s (Laidre et al*.* 2002). Sea otters temporarily expanded their range north and eastward into the Strait of Juan de Fuca, with small numbers of animals sighted in the area in the winter of 1995, and sighting frequency and group sizes increasing until 2000, when more than 100 animals were noted in the Strait of Juan de Fuca (Laidre and Jameson 2006). Sighting frequency and group sizes in the Strait decreased after 2000, and have remained low. Beginning in the mid-2000s, sea otters began to expand their range southward from their established range (Jameson and Jeffries 2005), and since 2002 the majority of the population has occurred in the southern portion of the range, south of La Push (Figure 3-1). The estimated number of sea otters in Washington State is now over 2,058 individuals (Jeffries et al*.* 2017).

The sea otter diet spans a diverse array of prey (Kenyon 1969, Riedman and Estes 1990, Estes 2015), primarily consisting of benthic marine invertebrates including mollusks, crustaceans, and echinoderms. Previous research has shown that sea otter diet selection, including prey type and size, depends on location, habitat type, season, and relative abundance of preferred prey types (e.g., Estes and Dug gins 1995, Watt et al*.* 2000, Tinker et al*.* 2012). Previous research also suggests that sea otter foraging site selection is based on habitat complexity (Stewart 2011), and that shoreline complexity (used to approximate sea otter proximity to diverse habitat types) likely mediates how sea otter foraging affects coastal communities (Hessing-Lewis et al. 2018).

The sea otter's nearshore distribution and foraging behavior allows a land-based observer with a high-powered telescope to estimate sea otter prey size, number, and type through direct observation, as well as to estimate energy intake rates (Dean et al. 2002, Tinker et al. 2008*a*). As a result, sea otter diets have been more closely studied than almost any other carnivore species (Tinker 2015). The relationship between population status and foraging behavior has been studied in various taxa, including birds (e.g., Lewis et al. 2001, Ballance et al. 2009, Newsome et al. 2015), insects (e.g., Kelly et al. 1996), and mammals, such as sea otters (*Enhydra lutris*; see review in Monson and Bowen 2015), Galapagos sea lions (*Zalophus wollebaeki*; Páez-Rosas and Aurioles-Gamboa 2010), white tailed deer (*Odocoileus virginianus*; Taillon et al. 2006), and reindeer (*Rangifer tarandus platyrhynchus*; Skogland 1985). Generally as populations approach environmental carrying capacity, competition for food increases and/or food becomes harder to find, leading to increased individual foraging effort, decreased energy intake rates, increased diet diversity and/or individual diet specialization (e.g., Kelly et al. 1996, Lewis et al. 2001, Bolnick et al. 2002, Svanbäck and Bolnick 2005, Ballance et al. 2009, Páez-Rosas and Aurioles-Gamboa 2010, Tinker et al. 2012, Visser and Fiksen 2013). These individual effects eventually result in changes to population level demographic rates (e.g., Skogland 1985) and declines in the intrinsic rate of population growth (Monson and Bowen 2015). Sea otter population growth and range expansion and associated dietary changes have been well documented. For example, sea otters exhibit different feeding habits depending on their occupation time in a given habitat; in many cases these predictable changes are a response to reduced abundance of preferred prey types, which are depleted by sea otter predation (Estes et al. 1981, Garshelis et al. 1986, Watt et al. 2000, Laidre and Jameson 2006, Tinker et al. 2008*a*). Optimal foraging theory predicts that animals forage to optimize their net energy intake per unit time (Macarthur and Pianka 1966). Thus, sea otters in newly occupied, food-rich areas, often target large, energy-rich, and abundant prey items (Estes et al. 1982, Ostfeld 1982, Garshelis et al. 1986, Laidre and Jameson 2006). In contrast, sea otters in longer occupied, food-poor areas focus on a wider variety of smaller, less abundant prey items (Estes et al. 1981; Kvitek et al. 1993; Laidre and Jameson 2006; Tinker et al. 2008*a*, 2012).

Northern sea otters in Washington State are listed as State Endangered, and both state and federal agencies have endeavored to monitor the population status through annual population counts to produce population indices since 1977 (Jeffries et al. 2017). In addition, studies of Washington sea otter foraging have been undertaken to understand their food habits and activity-time budgets as an indication of habitat quality, resource use, and population status (e.g., Bowlby et al. 1988, Laidre and Jameson 2006, Walker et al. 2008). The continued growth and range expansion of the Washington State sea otter population provides an opportunity to explore the interplay between habitat type and sea otter occupation history as drivers of sea otter diet, and to expand upon previous sea otter foraging studies in Washington State (e.g., Bowlby et al. 1988, Laidre and Jameson 2006, Walker et al. 2008) to estimate metrics of population status, including calorie intake rate and diet diversity. The population growth and range expansion of sea otters in Washington has created a spatial gradient in sea otter occupation time and density, with regions of the outer coast of Washington differing in their recent history of sea otter predation levels. In this study, we utilize this gradient to assess how sea otter diet composition and diversity, and energy intake rate change as a function of sea otter occupation history and quantify the effects of sea otter cumulative density and habitat type on sea otter diet.

3.3 METHODS

3.3.1 Sea otter population indices

Range-wide population surveys have been conducted annually in Washington State since 1977, in late June or early July (excluding 1978–1980, 1982, 1984, 1986, 1988, 1997, 2009). Aerial and ground-based surveys were conducted concurrently, following Jeffries et al. (2017). Each annual survey ideally resulted in 3 d of surveys, with up to 2 flight passes per day, and included aerial, photo, and ground estimates. The final index of sea otter abundance was a combination of aerial, photo, and ground counts, following Jeffries et al. (2017).

3.3.2 Sea otter distribution and density

We used the digitized annual indices of sea otter abundance and positions from 1977–2017 population surveys to create a continuous smoothed 2-D raster surface representing cumulative sea otter density using the Kernel Density Estimate (KDE) tool in ArcGIS 10.1, following Weitzman (2013). Kernel Density calculates the density of point features (in this case otter positions and associated number of otters) around each output raster cell by fitting a kernel surface over each point. The surface value is highest at the point, and decreases with increasing radial distance from the point, reaching zero at the search radius. The volume under the surface equals the number of otters counted at that point. The density at each output raster cell is calculated by summing the values of all the kernel surfaces that overlay that raster cell center. Annual kernel densities were calculated and summed to create cumulative density surfaces for 1977–2017. We used a raster cell size of 25 m^2, and a search radius of 5 km, as this distance has been found to produce an appropriate level of smoothing in previous analyses (e.g., Weitzman 2013, Tinker et al. 2008*b*). The year of occupation was calculated as the first year in which sea otters were counted during the annual summer survey within 5 km of a site, and rate of population change was calculated by fitting a linear model to the last 3 yr of counts (2015–2017) and determining the slope (Table 3-1). This method generates three important metrics of sea otter occupation, including: i) the cumulative number of sea otters that were at a site, ii) the length of time that sea otters have been at a site and, iii) the current trend in counts of sea otters at the site.

Sea otter cumulative densities were extracted from raster cells corresponding to general foraging areas observable from previously established land-based observation sites (n=29) to identify sea otter foraging observation sites used for this study. Sea otter foraging observation sites were then chosen across a gradient of sea otter cumulative density (0–233 cumulative sea otters/km^2) from the 29 previously established land-based observation sites.

3.3.3 Sea otter foraging observations

Foraging data collected prior to 2014 were collected as a part of the USGS Pacific Nearshore Project[1] and other studies[2] and were used in addition to data collected in 2014–2017. We identified 8 land-based sea otter foraging observation sites across the gradient of sea otter cumulative density (Figure 3-1). Other criteria for site selection, in addition to sea otter cumulative density, included ease of access and permitting restrictions. Sea otter cumulative densities at the sites ranged from 0 to 51.50 cumulative sea otters/km^2 in 2010 and 0.03 to 64.16 cumulative sea otters/km^2 in 2017 (Table 3-1). At these 8 sites, sea otters foraged in a range of habitats, from rocky, sand-bottom, to mixed habitats, with and without kelp canopies.

Foraging data were collected opportunistically from unmarked foraging sea otters from October 2010 to October 2017 with spotting scopes (Questar Corp., New Hope, PA, Field Model, 53–80X magnification; Carl Zeiss Inc., Chesterfield, VA, Victory Diascope 65 T* FL, 15–56X magnification) at each of the sites following standard protocols established and used in studies of sea otters throughout their range in North America (Dean et al*.* 2002, Tinker et al*.* 2008*a*, Esslinger et al*.* 2014, Tinker 2015). By the nature of observing unmarked individuals on subsequent days, data from some individuals may be overrepresented. After locating a foraging sea otter, observers initiated focal observations for a continuous sequence of foraging dives, referred to as a foraging bout. For each foraging dive, observers recorded key variables: dive duration (time underwater searching for prey), surface duration (time on surface between dives, usually spent consuming prey),

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[1] Unpublished data from J. L. Bodkin, U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA. June 2013.

[2] Unpublished data from S. E. Larson, Seattle Aquarium, 1483 Alaskan Way, Seattle, WA 98101, USA. November 2016 and January 2018.

and dive outcome (whether prey was successfully captured). For each successful foraging dive, observers identified prey type to the lowest possible taxonomic level, number of prey items, and prey size. Prey size was estimated in relation to average sea otter forepaw width (5 cm — Kvitek et al. 1993), where size 1 prey were <5 cm (smaller than sea otter forepaw width), size 2 prey were >5 cm <10 cm (larger than 1 sea otter forepaw width, but smaller than 2), size 3 prey were >10 cm <15 cm (larger than 2 sea otter forepaw widths, but smaller than 3), and size 4 prey were >15 cm (larger than 3 sea otter forepaw widths) (VanBlaricom 1987). Prey size categories (1, 2, 3, and 4) were further split into size category qualifiers *a*, *b*, and *c*, where *a* was the smallest 1/3 of the size class, *b* was the middle 1/3 of the size class, and *c* was the largest 1/3 of the size class.

3.3.4 Sea otter foraging data analysis

As with previous studies of sea otter foraging, the raw data contained missing or unobserved variables for many dives, and these missing values were often biased towards small prey or short surface durations. To account for these biases and associated uncertainty in parameter estimates, we used a Monte Carlo re-sampling algorithm (Dean et al. 2002; Tinker et al. 2008*a*, 2012) to estimate sea otter rate of energy intake and diet diversity. This algorithm, as described in detail by Tinker et al. (2015), consisted of 1,000 iterations of simulated foraging bouts, with dive variables drawn from appropriate density functions fit to our raw data. To parameterize distributions of prey biomass and energy density, we used previously assembled information on diameter-biomass relationships and calorific densities for each prey type (Oftedal et al. 2007), following Tinker et al. (2008*a*).

Multivariate statistics were used to determine correlations between habitat type, sea otter cumulative density, and sea otter diet composition. We summarized diet composition using the raw data in terms of the average proportion of dives on which 5 general prey classes occurred (clam, cancer crab, other crab, snail, and other) per site for each year and habitat type. Habitat type for each foraging bout was determined by observers in the field concurrent with foraging observations and was determined based on surface features and location of the area proximate to the foraging sea otter (e.g., floating kelp canopy, protruding rocks). Habitat types were defined as intertidal, open water, emergent rock, and kelp canopy, depending on the habitat in which the focal sea otter had begun its foraging bout. For foraging bouts that did not have habitat data recorded, but did have sea otter position recorded, we assigned the habitat type *post hoc* based on the location of the foraging sea otter in relation to environmental layers, including annual kelp layers from Washington State DNR (Van Wagenen 2015) and a digital bathymetry model (Weatherall et al*.* 2015) in ArcGIS 10.1. Foraging bouts that did not have habitat data or sea otter position data recorded were not included in the multivariate diet composition analysis. We calculated assemblage dissimilarity using Bray-Curtis distance and applied nonmetric multidimensional scaling (NMDS) to visualize relationships among diet composition, habitat type, and sea otter cumulative density in ordination space. Multivariate analyses were performed using *R* version 3.2.4 (R Core Team 2016) with the 'vegan' package, version 2.4-6 (Oksanen et al*.* 2018). We used the adonis2() function from the vegan library to fit a linear model to the distance matrix and conducted a permutation test with Pseudo *F*-ratios to determine the influence of habitat type and sea otter cumulative density on diet composition. As we could not include site as a random effect in the model due to the nature of a permutation test, we defined the model to respond similarly with site as a fixed effect.

3.4 RESULTS

3.4.1 Foraging data

Foraging records consisted of 5,573 individual foraging dives from 461 sea otter foraging bouts collected between 18 October 2010 and 16 October 2017 (Table 3-1). Of the data collected, 64% of dives (3,730 dives) were collected from females, 8% (490 dives) from males, and 28% (1,636 dives) from individuals of unknown sex. Approximately 77% of dives resulted in successful prey capture. The average dive duration was 50.40 ± 30.71 s, and the average surface duration was 38.90 ± 51.72 s. Aggregated prey diversity, as calculated by the Shannon Wiener diversity index (Shannon and Weaver 1949), for all observed foraging bouts was 1.38, and long term average rate of energy gain was 13.86 kcal/min.

Sea otters were observed to consume a total of 43 prey taxa. When prey selection was examined irrespective of habitat type or site, the dominant prey taxa in the diet of sea otters (prey taxa making up more than 5% of diet) were kelp crabs (*Pugettia spp*., percent of diet: 14.69%, mass intake: 2.43 g/min), followed by unidentified crabs (percent of diet: 13.71%, mass intake: 2.27 g/min), razor clams (*Siliqua patula*, percent of diet: 10.56%, mass intake: 1.75 g/min), Dungeness crabs (*Cancer magister*, percent of diet: 9.20%, mass intake: 1.52 g/min), red rock crabs (*Cancer productus*, percent of diet: 8.19%, mass intake: 1.35 g/min), unidentified snails (percent of diet: 7.09%, mass intake: 1.17 g/min), unidentified clams (percent of diet: 6.61%, mass intake: 1.09 g/min), butter clams

(*Saxidomus gigantea,* percent of diet: 6.18%, mass intake: 1.02 g/min), and graceful kelp crabs (*Pugettia gracilis,* percent of diet: 5.51%, mass intake: 0.91 g/min).

3.4.2 Geographic differences

The primary prey taxa in the diet of sea otters at each site were as follows: Koitlah Point, butter clam (*Saxidomus gigantea*, 4.82 g/min); Beach 4, Pacific razor clam (*Siliqua patula*, 19.26 g/min); Giants Graveyard, red rock crab (*Cancer productus*, 6.88 g/min); Norwegian Memorial, Dungeness crab (*Cancer magister*, 4.55 g/min); Sand Point, unidentified snail (4.48 g/min); Yellow Banks, kelp crab (*Pugettia spp.*, 3.46 g/min); Duk Point, unidentified clam (8.18 g/min); and Cannonball, unidentified crab (rate of mass gain = 5.74 g/min). The relative abundance of sea otter prey classes (urchin, bivalve, cancer crab, other crab, snail, and other) are reported in Table 3-2.

In general, sea otter rate of energy gain was negatively correlated with sea otter cumulative density (Figure 3-2A, residual SE: 7.392 on 5 degrees of freedom), and sea otter prey diversity was positively correlated with sea otter cumulative density (Figure 3-2B, residual SE: 0.3582 on 5 degrees of freedom). Energy recovery rates decreased with increasing sea otter cumulative density from approximately 27.71 ± 2.66 kcal/min at 5.63 otters/km^2 to approximately 15.51 ± 1.79 kcal/min at 64.16 otters/km^2 (Figure 3-2A). An analysis of the frequency of size classes consumed by sea otters across the gradient of sea otter occupation demonstrated that sea otter prey size generally decreased with increasing sea otter cumulative density (Figure 3-3). Sea otters at sites with sea otter cumulative densities ranging from 0.03–27.14 otters/km^2 primarily consumed larger prey items (mode: size 1C, 33.3–50 mm), while sea otters at sites with sea otter cumulative densities ranging from 41.26–64.16 otters/km^2 consumed smaller prey items (mode: size 1B, 16.7–33 mm).

3.4.3 Multivariate analyses

NMDS ordination of sea otter diet composition converged on a stable, 2-D solution (stress = 0.16) and indicated moderate separation of diet composition at high cumulative density sites from low cumulative density sites along NMDS1 (Figure 3-4A, 3-4C). We observed no differentiation of diet composition by habitat type (Figure 3-4B) or site. Sea otter prey categorized as "other" were negatively correlated with NMDS1, while "other crabs" were positively correlated with NMDS1 (Figure 3-4C). Cancer crabs were positively correlated with NMDS2, while clams and snails were negatively correlated with NMDS2 (Figure 3-4C). The NMDS also suggested that higher sea otter cumulative density was correlated with a higher proportion of "other crabs" in sea otter diet, while the proportion of clams was negatively correlated with cumulative density (Figure 3-4C). The NMDS also suggested that snail prey was mostly associated with intertidal habitat, clams and cancer crabs mostly associated with open water habitat, and prey categorized as "other crabs" and "other" mostly associated with kelp canopy habitat (Figure 3-4D). A test of multivariate homogeneity of group dispersions indicated homogeneity of dispersion ($P = 0.129$). perMANOVA analysis indicated that all three covariates were significant in explaining the dissimilarity in sea otter diet composition, including site ($P = 0.001$), cumulative density ($P = 0.017$), and habitat type ($P = 0.03$). Of the variance explained by the model (50%), site explained 75.1% of the variance in sea otter diet composition ($r^2 = 0.376$), while habitat type explained 16.02% ($r^2 = 0.08$) and sea otter cumulative density explained 9.04% ($r^2 = 0.045$).

3.5 DISCUSSION

3.5.1 Sea otter diving

Our study demonstrated that current sea otter foraging dive parameters, including dive success, dive duration, and surface duration were similar to those reported previously for Washington State in 1993–1999 (Laidre and Jameson 2006) and 2003–2004 (Walker et al*.* 2008). Approximately 77% of dives resulted in successful prey capture in our study, compared to a 77% success rate reported in 1993–1999 and 81.4% in 2003–2004. Average dive duration (irrespective of dive success) in Washington in the 1990s was 55 ± 1 s and 36.5 ± 19.9 s in 2003–2004, compared to 50.40 ± 30.71 s in our study. Average surface duration in the 1990s was 45 ± 2 s compared to the 38.90 ± 51.72 s in our study. The similarities between dive parameters in our study and those reported in Laidre and Jameson (2006) and Walker et al*.* (2008), as well as those reported in other areas (Ralls et al*.* 1995, Bodkin et al*.* 2004), suggest that Washington sea otters have similar foraging habits to other sea otter populations, at least at shallow depths.

Previous research of sea otter foraging depths in Southeast Alaska has shown that for deep foraging dives (38.5 – 49 m), sea otters exhibit almost double the dive and surface duration when compared to shallow foraging dives (7.1–8.1 m), and exhibit similar dive durations to those observed in this study (59–64 s for shallow dives in SE Alaska, versus 50.40 s in this study) (Bodkin et al*.* 2004). The similarity between observed dive durations and shallow dive durations in southeast Alaska, in combination with subsequent work by Laidre et al*.* (2009) that found time spent foraging was minimal beyond 40 m depth in Washington, suggests that the majority of foraging observations in this study occurred at shallow depths, well below 40 m offshore depth. While previous radiotelemetry studies have shown that foraging sea otters in Washington average 717–1163 m from shore depending on sex and age class (Laidre et al. 2009), offshore foraging may be particularly important for sea otters south of Cape Flattery on the outer coast of Washington, as the continental shelf provides usable foraging habitat to 40 m offshore depth and extends as much as 15 km offshore, compared to the Strait of Juan de Fuca where the 40 m depth contour extends as much as 1 km offshore. However, we are limited in our ability to observe sea otters foraging at deeper depths offshore by the viewing distance of spotting scopes (our maximum viewing distances averaged approximately 1 km). As such, our foraging observations are limited to a small proportion of available forage habitat and should not be considered representative of all sea otter diet in Washington. If sea otters in Washington are foraging throughout the total available habitat to 40 m offshore depth, their energy recovery rates may be lower than what we observed in this study. However, this also depends on their prey items, as there would be energy tradeoffs between diving to deeper depths and the energy intake from the prey recovered.

Previous studies of foraging sea otters have also shown that males typically dive to deeper depths farther offshore (Bodkin et al. 2004, Laidre et al. 2009), with adult females foraging 60% of the time between 0–10 m offshore depth and negligible time spent foraging beyond 30 m, and adult males foraging between 0–10 m 22% of the time, and 32%–34% of the time between 10–30 m, indicating that our foraging data may be biased towards females who forage closer to shore. Our findings suggest this may be the case as well: 64% of dives (3,730 dives) were collected from females, 8% (490 dives) from males, and 28% (1,636 dives) from individuals of unknown sex. This is likely due in part to the fact that sea otters sex segregate; male areas generally occur at the geographic range edges while female and pup areas occur in the core of the geographic range (Riedman and Estes 1990). Six of our 8 sites were located in female/pup areas. Additionally, as foraging observations were collected from unmarked individuals on subsequent days, our data may overrepresent the diet of some individuals. Thirty sea otters were flipper tagged in 2011 as a part of the USGS Pacific Nearshore Project[3]; however, we were unable to collect foraging data from these individuals during the course of our study. Although this is a potential bias of our study, previous foraging studies of unmarked sea otters have been used to assess the population status of various sea otter populations (see review of approaches to evaluating the status of individuals and populations in Monson and Bowen 2015). Additionally, the potential overrepresentation of some individuals was likely partially ameliorated, as we collected foraging data throughout the year, and in multiple years.

3.5.2 Sea otter diet

It has previously been established that sea otter diet diversity in Washington State is lower in recently occupied areas than in areas within the established sea otter population range (Laidre and Jameson 2006), and our study further demonstrated that at a finer geographic scale and across a gradient of occupation time and density. We also found that sea otter rate of energy gain is generally negatively correlated with sea otter cumulative density, and sea otters foraging at sites with low sea otter cumulative density consumed larger prey than sea otters foraging in areas with medium and high sea otter occupation time and density. Although these results are not surprising and suggest that Washington State sea

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[3] Unpublished data from J. L. Bodkin, U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA. March 2016.

otters are consistent with patterns established in other areas, they allow us to make informed predictions of future foraging patterns.

In the temporary absence of sea otters after their extirpation from portions of their range, high-value invertebrate fisheries developed that target many of the same calorically rich prey preferred by sea otters. The recolonization and reintroduction of sea otters to areas of historical sea otter occupation, that now co-occur spatially with fisheries, has led to conflicts between sea otters and fisheries along the North American Pacific Coast (e.g., Estes and VanBlaricom 1985, Reidy 2011, USFWS 2012, Larson et al. 2013, Honka 2014, Hoyt 2015), and in some cases has had measurable impacts on fisheries species (Fanshawe et al. 2003, Larson et al. 2013, Hoyt 2015). As the Washington State sea otter population continues to grow and expand its range, managers are faced with managing sea otters and fisheries that have never coexisted, similar to other areas of sea otter recolonization. Further research is needed to elucidate the potential interactions between sea otters and fisheries in Washington to set the ground work for predictive modeling necessary to inform management strategies. Sea otters in Washington have been observed consuming fishery species, including Dungeness crab, sea cucumbers, razor clams, and urchins (JH, personal observation). Despite this, there is a need for a formal evaluation of the potential impact of sea otters on these fished invertebrate populations and for a quantitative assessment of whether sea otter predation impacts are of sufficient magnitude to threaten the harvests of these species.

Interestingly, our observations of sea otters foraging primarily on Pacific razor clams (65% of diet in 2010–2017) near the southern extent of the current population range draws a parallel with past sea otter range expansion into the Strait of Juan de Fuca in 1995.

When sea otters temporarily expanded their range into the Strait, they began occupying urchin-rich habitat that they historically had not occupied since the beginning of the 20th century (Laidre and Jameson 2006). When sea otters first expanded their range into the Strait, their diet consisted almost exclusively (85–90%) of red urchins, an important commercial and tribal fishery until 1997. After 1995, urchin monitoring surveys reported a 71% decline in sea urchins over one year, and subsequent to this decrease in biomass, the fishery district was closed to commercial harvest by Tribal–State harvest agreement (Laidre and Jameson 2006). The percent of red urchins in sea otter diet decreased subsequent to their initial expansion into the Strait, from 85–90% in 1995 and 1996, to 60% in 1997, and 40% in 1998 and 1999 (Laidre and Jameson 2006). Sea otter predation was never formally implicated in the decline and subsequent fishery closure (Laidre and Jameson 2006). Sighting frequency and group sizes of sea otters in the Strait have remained low after 2000 and urchins now (2010–2017) comprise 15% of sea otter diet at Koitlah Point in the Strait of Juan de Fuca. In Southeast Alaska, sea otters have been found to consume the highest proportion of commercially important species in recently colonized, low density areas (Hoyt 2015), likely as a result of sea otters preferentially consuming large, energy-rich, and abundant prey items. In Washington, we observed sea otters primarily consuming razor clams near the southern range extent at Beach 4, as well as at other areas near Kalaloch Beach. While the diet of sea otters immediately following their occupation (2005–2009) of this area is unknown, our results suggest that sea otters in this area are preferentially consuming a fishery species in recently occupied habitat as they did previously when they temporarily expanded their range into the Strait. While the impact of sea otters on razor clam populations and fisheries is currently unknown in

Washington, and it is possible that sea otter consumption of razor clams may not conflict with the success of razor clam fisheries, there is a need for additional research given the majority of the sea otter population growth has occurred in the southern portion of the range (south of La Push) since 2002, the area where sea otters are spatially co-occurring with razor clam fisheries. As such, the potential for conflict between sea otters and razor clam fisheries, an important recreational and tribal fishery, should be evaluated.

3.5.3 Drivers of sea otter diet composition

As sea otter diet spans a diverse array of prey, a variety of factors can influence their specific prey choice, including sea otter occupation history and density, habitat type, prey size and density, and prey recruitment patterns and growth. Our analysis indicated that site, habitat type, and sea otter cumulative density explained approximately 50% of the variation in sea otter diet composition, and that of the covariates included in the model, site was the most important in explaining variation in sea otter diet composition. This may be reflective of the fact that sea otter diet composition is influenced by other environmental variables in the area surrounding a site, such as exposure or coastline complexity. In Southeast Alaska, exposure has been identified as an important variable describing sea otter diet (Hoyt 2015), and in British Columbia recent research has shown that coastline complexity, used to approximate sea otter proximity to shelter and diverse habitat types, is a driver of sea otter foraging (Hessing-Lewis et al*.* 2018). As sea otters in Washington experience a spatial gradient in shoreline complexity and exposure, with more complex shorelines to the north, and less complex, more exposed shorelines to the south, future research should investigate the relationship between shoreline complexity and exposure and sea otter diet composition in Washington. The availability of greater habitat diversity in other areas may also reduce the importance of habitat type on sea otter diet composition. We found that habitat type explained 1.77 times more variation in sea otter diet composition in Washington than sea otter cumulative density. Current research on drivers of sea otter diet in British Columbia has shown that sea otter occupation time is an important driver of diet, with the niches occupied by sea otters expanding at long occupation times to include more diverse prey items and habitats.[4] Occupation time may be a particularly important driver of sea otter diet in British Columbia because the coastline is more complex than Washington, and as a result sea otters can forage in diverse habitats in close proximity to each other (Hessing-Lewis et al*.* 2018), whereas habitats in Washington may be more spatially segregated.

Our determination of habitat type based on surface features where sea otters begin their foraging bouts may not necessarily reflect the diversity of habitat beneath the surface. The presence of a kelp canopy is reasonable evidence of consolidated substrate, however, the absence of surface canopy kelp says little about the underlying substrate or biogenic habitat like kelp and seagrass. Additionally, some species of kelp are seasonal and have reduced algal cover in the winter, adding to our inability to determine underlying substrate from surface features. As our study found that of the variance explained by the model (50%), habitat type explained 16.02% of variation in sea otter diet composition, accurate habitat classification when collecting sea otter foraging data will be important in future research. Prey recovered by sea otters may be an alternative to subjective habitat

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[4] Personal communication from E. U. Rechsteiner, Hakai Insitute, End of Kwakshua Channel, Calvert Island, BC, Canada. May 2018.

classification.[5] For example, clams and Dungeness crab (*Cancer magister)* are typically associated with unconsolidated, sandy substrate, and could be used as indicators of unconsolidated substrate, while kelp crabs (*Pugettia spp.)*, urchins, and chitons may be used to predict rocky substrate. However, in this case, classifying habitat type by prey would lead to circular logic when investigating habitat as a driver of sea otter diet.

3.5.4 Energy intake rate as metric of population status

Evaluating population status is a fundamental aspect of the management and recovery of species. Population status can be defined based on the trend in abundance of the population or the population's probability of persistence (Morris and Doak 2002). Population status can also be defined ecologically, such as the population status relative to environmental carrying capacity (Monson and Bowen 2015). When population size is small relative to carrying capacity, individuals are expected to more easily acquire the resources they need to survive, often manifested as little time and/or effort spent foraging, which can lead to a cascade of individual and population level effects. Individuals are predicted to be able to acquire excess onboard energy stores (stored as blubber or lipid), which is then reflected in individual body condition which can translate to improved reproductive and survival rates (Monson and Bowen 2015). Life history and demographic metrics can thus be used as indicators of population status (Eberhardt 1977*a*, *b*; Fowler 1987), as individual status is intrinsically linked to population status.

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[5] Personal communication from J. Bodkin, U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA. May 2018.

Various life history and demographic metrics have been used to infer the status of marine mammal populations, including: 1) individual body condition (e.g., fin whale [*Balaenoptera physalus*]; Williams et al. 2013), 2) time spent foraging (e.g., sea otter [*Enhydra lutris*]; Estes et al. 1982), 3) age at maturity (e.g., crabeater seal [*Lobodon carcinophagus*]; Bengtson and Laws 1985), 4) reproductive rate (e.g., hooded seal [*Cystophora cristata*]; Frie et al. 2012) and 5) survival rate (e.g., northern fur seal [*Callorhinus ursinus*]; Fowler 1990). While these metrics can be more labor intensive and expensive to estimate than population abundance, they reflect population status at different temporal scales, providing managers with additional evidence and potentially advanced warning of changes in population status that are not yet reflected as changes in abundance (Monson and Bowen 2015). These indices can also shed light onto the mechanisms behind potential changes in population abundance, rather than just identifying the current trend in abundance or probability of persistence (Monson and Bowen 2015). Population status metrics are especially useful in the absence of frequent population monitoring. In the case of Washington sea otters, no population survey was conducted in 2018, and in the absence of an updated population abundance index, metrics of population status like energy intake rate and diet diversity can provide another line of evidence for sea otter population status.

Previous research has demonstrated generalizable trends in sea otter rate of energy intake and diet diversity across a gradient of sea otter population growth rate and density (Tinker 2015, Coletti et al. 2016). While our results indicated that, in general, sea otter foraging patterns in Washington follow traditional patterns established from well-studied areas, our study also highlights the importance of replicated studies of sea otter foraging in similar systems across a variety of geographic areas. Our study demonstrated two important deviations from traditional patterns. While we observed decreasing energy intake rates with increasing sea otter cumulative density, we also observed much higher energy intake rates than we would have expected based on population status. Typical energy intake rates range from 12 – 21 kcal/min in recently-established and rapidly growing populations throughout the sea otter's North Pacific range, compared to energy intake rates ranging from 7 – 11 kcal/min in long-established, stable or slowly increasing populations where resource abundance is thought to be limiting further growth (Tinker et al. 2013, Tinker 2015, Coletti et al. 2016). As reported in Laidre et al. (2002), sea otters in Washington were apparently reaching equilibrium levels in core part of the range (between Petroleum Creek and Little James Island) around the mid-1990s. Therefore, we would expect the energy recovery rates of sea otters in that core area to reflect this equilibrium. Instead we observed energy intake rates ranging from 10.79 – 15.76 kcal/min, compared to the typical 7 – 11 kcal/min. Similarly, we observed higher than expected energy intake rates ranging from 21.20 – 27.71 kcal/min for sea otters foraging south of the core area, compared to the typical 12 – 21 kcal/min.

Sea otter populations have been shown to exhibit fairly uniform patterns of density-dependent growth (Estes 1990, Estes et al. 1996), best described by a logistic growth model when it is fit to populations at biologically meaningful spatial scales (Bodkin 2015, Tinker 2015, Tinker et al. 2017). As equilibrium density has been defined as the number of otters that can be supported by the habitat (Estes 1990), it logically follows that the density at which sea otter populations reach equilibrium varies with habitat characteristics and prey productivity (Laidre et al. 2001, 2002; Burn et al. 2003; Gregr et al., 2008). Laidre et al.

(2002) estimated the carrying capacity of Washington State sea otters by using sea otter densities in rocky habitat believed to be at equilibrium and calculating proportional densities for sandy and mixed areas based on current counts in the rocky equilibrium region and from previous calculations done in California (Laidre et al. 2001). The carrying capacity of Washington sea otters ranged from 1,372 (CV 0.13) to 2,734 (CV 0.13) (Laidre et al. 2002), compared to the current population index of 2,058 (Jeffries et al. 2017). These calculations were based on the assumptions that, 1) sea otters in the rocky equilibrium area (Petroleum Creek to Little James Island) were at equilibrium, and 2) that when sea otters reached carrying capacity in sandy and mixed habitats that they would use those habitats similarly to sea otters in California. The high energy intake rates estimated in our study may be indicative of the Washington coast's ability to support a higher number of sea otters than previously thought, largely as a consequence of abundant prey in relatively close proximity offshore, especially on the outer coast where the 40 m depth contour lies as far as 15 km offshore. In addition, previous radiotelemetry work in Washington demonstrates movements of animals throughout the occupied range (Laidre et al. 2009), compared to the small home ranges reported in long established sea otter populations at equilibrium densities (Bodkin 2015), suggesting that sea otters in Washington may not have been at environmental carrying capacity in the rocky equilibrium area at the time of the study. As these data were collected from 1992–1999, and there is no recent radiotelemetry data available for Washington sea otters, further research is needed to determine if sea otters in Washington State are at equilibrium in portions of their range as previously suggested, or are still below equilibrium densities as our energy intake rates suggest.

We found that the higher than expected energy intake rates were due in part to the estimated input of calories from kelp crabs (*Pugettia spp.*). Washington sea otters appear to be eating a kelp crab of a given size class almost twice as fast as in California[6] and British Columbia[7]. As kelp crabs are the primary prey item of sea otters in Washington State (14.69% of the diet), the net outcome of these faster kelp crab handling times is higher energy intake rate estimates. This faster kelp crab handling time in Washington was consistent across multiple independent observers during our study period (2010–2017), and across previous studies in the 1990s (Laidre and Jameson 2006). We explored this phenomenon by repeating our analysis after adjusting kelp crab edible biomass recovered per unit handling time to what we would expect for sea otters in British Columbia and California. We used a proportional reduction to adjust the edible biomass for kelp crab species and found the rate of energy gain across the gradient of sea otter occupation was more similar to those reported for California and British Columbia (Figure 3-A1). This exercise demonstrated that the higher than expected energy intake rates were in part a result of kelp crab consumption. Further research into the faster kelp crab handling time phenomenon will be important to understanding Washington sea otter foraging ecology, as previous research has assumed uniformity in sea otter prey, foraging behavior, and data collection methods.

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[6] Unpublished data from M. T. Tinker, Department of Ecology and Evolutionary Biology, University of California, Center for Ocean Health, 100 Scheffer Road, Santa Cruz, CA 95060, USA. August 2017.

[7] Unpublished data from E. U. Rechsteiner, Hakai Institute, End of Kwakshua Channel, Calvert Island, BC, Canada. July 2018.

The second deviation from previously established patterns in our study was at Koitlah Point, located near Neah Bay in the Strait of Juan de Fuca. Koitlah Point had the lowest cumulative sea otter density (0.03 sea otters/km^2) of any of our sites, and as such we expected it to have the highest energy intake rate and lowest prey diversity. However, Koitlah Point had the lowest energy intake rate (6.99 kcal/min) and a higher diet diversity (1.25) than expected based on Koitlah's sea otter occupation history that is reflected in the annual sea otter survey data. When we removed Koitlah Point from our models of energy intake rate and diet diversity, the model fits were more similar to the relationships that have been found in other areas (Figure 3-A2A and 3-A2B). Sea otters at Koitlah Point had the longest dive and surface durations of any site, with a mean dive duration of 83.49 ± 36.69 s (1.76 times the average dive duration of all other sites of 47.55 s), and an average surface duration of 48.59 ± 49.03 s (1.27 times the average surface duration of all other sites of 38.23 s). As male sea otters are known to dive deeper than females (Bodkin et al. 2004, Laidre et al. 2009) and congregate at range edges (Riedman and Estes 1990), and Koitlah Point is near the Northeastern most edge of the Washington sea otter range, we explored the possibility that this longer observed average dive duration could be a result of sex bias in our data. When we compared the average percent of dives across all sites made by females (62%), males (10%) and by individuals of unknown sex (28%) with dives made at Koitlah Point by females (58%), males (3%), and individuals of unknown sex (38%), we did observe a smaller proportion of dives by females and a larger proportion of dives by individuals of unknown sex. It is possible that those individuals of unknown sex could be males foraging farther from shore, where it is difficult to observe morphological indications of sex. As sea otters at Koitlah Point were primarily consuming clams equal or less than one sea otter paw width in size (≤ size 1C), we hypothesize that the energetic demand of making deep dives for small clams resulted in a lower kilocalorie intake rate than expected based on the sea otter cumulative density data at this site. In addition, Koitlah Point was the only site located in the Strait of Juan de Fuca (all other sites were on the outer coast of the Olympic Peninsula), thus the difference in kilocalorie intake rate and diet diversity may also be indicative of spatial variation in the sustainable carrying capacity of sea otters. Other explanations for this include the possibility that the cumulative density, calculated from the annual sea otter survey data, is not accurately reflecting the use of this site by sea otters. As the annual sea otter survey is conducted in late June or early July each year, the surveys may not be reflective of seasonal changes in occupancy. In contrast to the outer coast, sea otters appear to seasonally occupy Koitlah Point, with anecdotally more individuals in early spring when compared to summer and fall (JH, personal observation). As a result, the survey may be underestimating the actual densities of sea otters in this area in non-summer months. Future research is needed to investigate the intra-annual variation in sea otter occupation of Koitlah Point.

Many previous studies of sea otter diet have taken advantage of spatial and temporal gradients in sea otter recolonization and have used space-for-time substitutions to infer a temporal trend in sea otter diet with varying sea otter occupation dates (Kvitek 1989; Kvitek et al*.* 1992, 1998; Singh et al*.* 2013; Honka 2014). However, space-for-time substitutions fail to take into account varying degrees of occupation (*i.e.,* population density) and the fact that areas can become unoccupied (*i.e.,* the persistence of occupation). Cumulative density analyses, however, account for both potential changes in occupation status and abundance (Larson et al*.* 2013, Weitzman 2013), providing a more accurate measure of sea otter occupation history over time. An alternative metric of sea otter impact that accounts not only for sea otter persistence and degree of occupation, but also for the availability of potential foraging habitat, will be important as sea otter equilibrium densities have been shown to be spatially variable and will influence how the sea otter use metric is interpreted.

Our study highlights the importance of replicated studies of sea otter foraging in similar systems across a variety of geographic areas, and suggests that drivers of sea otter diet vary between geographic regions. Understanding the drivers of sea otter diet, in combination with predictive population modeling, could provide valuable insight into potential interactions between sea otters and fishery species and assist management decisions. Northern sea otters play a critically important ecological and cultural role on the Olympic Coast of Washington State, and this research contributes to a better understanding of the effect of sea otters on the nearshore marine system, as well as provides another measure of population status of a reintroduced sea otter population.

3.6 ACKNOWLEDGMENTS

We gratefully acknowledge everyone involved with the annual Washington State sea otter survey. We acknowledge Abigail Van Hemmen, Amanda Witt, Allison Northey, Carter Johnson, Christine Phelan, Amy Olsen, and Caroline Hempstead for their assistance in the field collecting sea otter foraging data. Sea otter foraging observations by JRH were made under a Memorandum of Agreement with the Makah Tribe (permit numbers 2015-17 and 2016-12) and under National Park Service Scientific Research Study number OLYM-00048. Sea otter foraging observations by SEL and JLB were made under a Memorandum of

Agreement with the Makah Tribe (permit numbers 2013-01, 2014-01, 2015-07 and 2016-02), and under National Park Service Scientific Research Study number OLYM-00161 and OLYM-00328. Funding support to JRH was provided by the School of Aquatic and Fishery Sciences (University of Washington), Point Defiance Zoo & Aquarium and the Point Defiance Zoo Society through the Dr. Holly Reed Conservation Fund, and the NOAA Dr. Nancy Foster Scholarship. The Seattle Aquarium supported costs associated with foraging data collected by SEL, Caroline Hempstead and Amy Olsen. Funding for JLB was provided by U.S. Geological Survey, Alaska Science Center. Funding for aerial and ground surveys was provided by U.S. Fish and Wildlife Service and Washington Department of Fish and Wildlife. We thank two anonymous reviewers for providing comments that improved the final manuscript.

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Table 3-1. Cumulative (1977–2017) density of sea otters (*Enhydra lutris kenyoni*) at foraging observation sites along the Washington Coast, year of occupation, rate of change in sea otter numbers, number of sea otter foraging dives and foraging bouts observed at each site, long-term rate of energy gain (kcal/min), and sea otter diet diversity as measured by the Shannon Weiner Index.

Site	Cumulative Density (otters/km^2)	Year of Occupation	Rate of Change, 2015–2017	Number of dives	Number of foraging bouts	Rate of Energy Gain (kcal/ min)	Diet Diversity
Koitlah Point	0.03	2011	0	506	69	6.99	1.25
Beach 4	5.63	2005	239	636	47	27.71	0.84
Giants Graveyard	27.14	1977	92.5	721	51	21.2	0.47
Norwegian Memorial	41.26	1977	25.5	530	52	12.8	0.89
Sand Point	47.13	1981	14.5	1059	80	15.76	1.23
Yellow Banks	52.30	1981	24	1067	79	10.79	0.78
Duk Point	52.82	1977	-25	617	51	13.34	1.34
Cannonball	64.16	1977	-34	437	32	15.51	1.28

Table 3-2. The relative abundance of sea otter prey classes output from the Monte Carlo resampling algorithm.

Site	Urchin	Bivalve	Cancer Crab	Other Crab	Snail	Other
Koitlah Point	0.16	0.66	0.02	0.08	0.00	0.08
Beach 4	0.00	0.65	0.04	0.24	0.00	0.06
Giants Graveyard	0.00	0.10	0.52	0.36	0.01	0.00
Norwegian Memorial	0.00	0.00	0.33	0.36	0.04	0.27
Sand Point	0.01	0.12	0.04	0.48	0.31	0.03
Yellow Banks	0.00	0.04	0.24	0.53	0.14	0.04
Duk Point	0.02	0.52	0.12	0.25	0.02	0.07
Cannonball	0.06	0.12	0.07	0.58	0.07	0.10

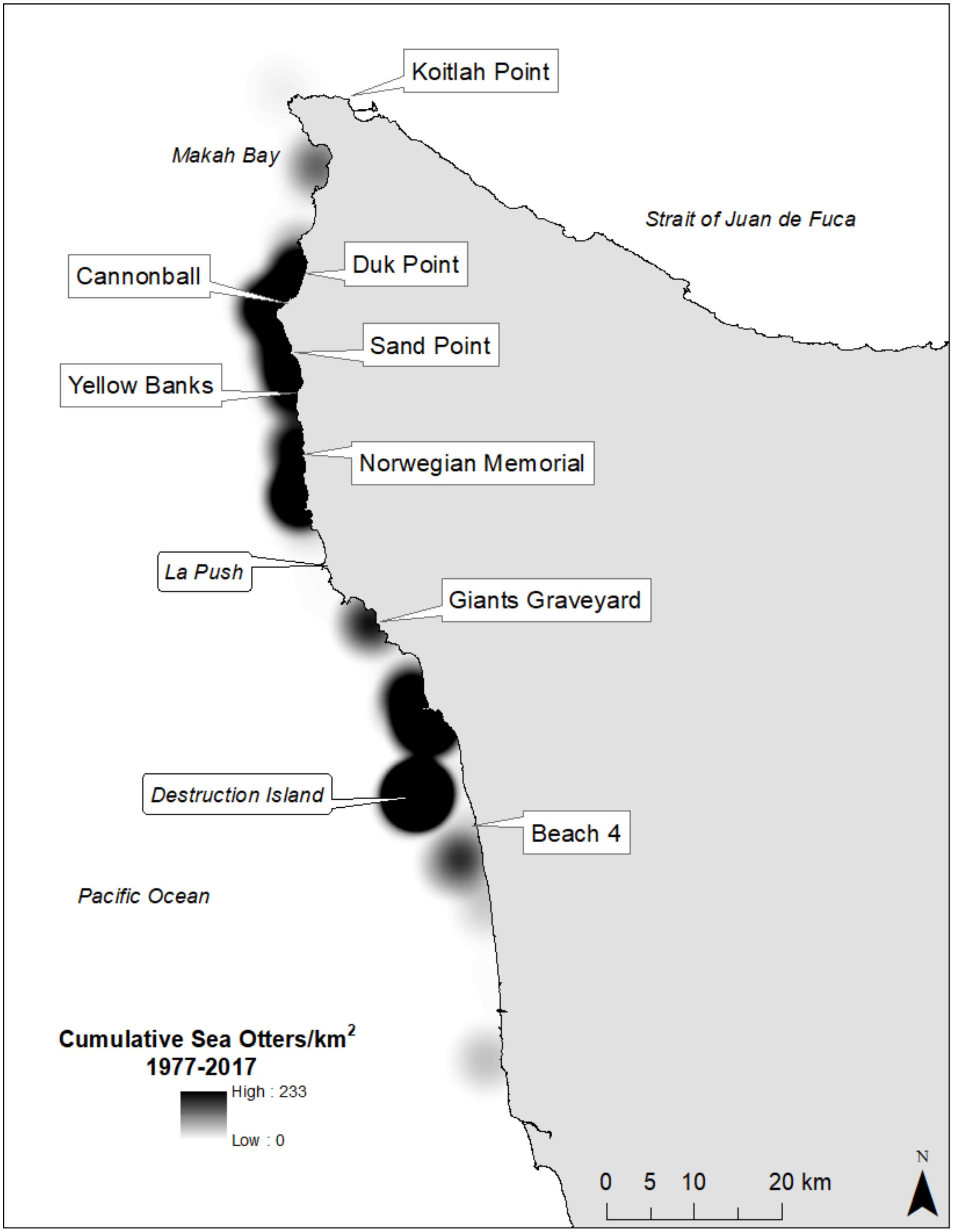

Figure 3-1. The Olympic Peninsula of Washington State with cumulative density of sea otters (*Enhydra lutris kenyoni*), 1977–2017. Darker shades indicate high sea otter cumulative density; lighter shades indicate low sea otter cumulative density. White callout bubbles indicate sea otter foraging observation sites, including Koitlah Point, Beach 4, Giant's Graveyard, Norwegian Memorial, Yellow Banks, Sand Point, Duk Point, and Cannonball (cumulative densities in Table 3-1).

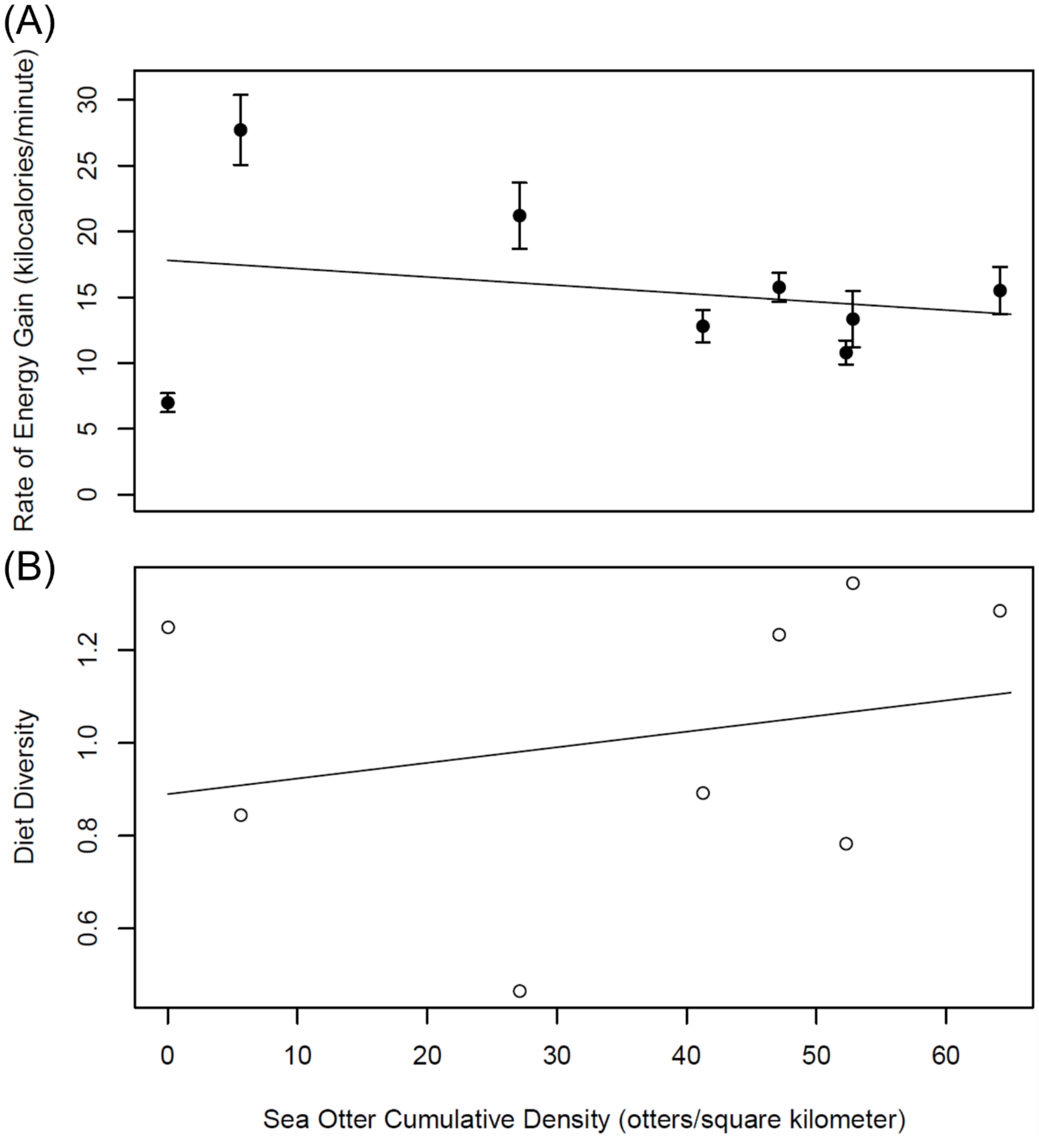

Figure 3-2. **A.** Rate of sea otter energy gain (kcal/min) versus sea otter (*Enhydra lutris kenyoni*) cumulative density (otters/km^2) fit with a 3-term exponential model. Error bars indicate standard deviations (residual SE: 7.392 on 5 degrees of freedom). **B.** Sea otter diet diversity versus sea otter cumulative density fit with a 3-term exponential model (residual SE: 0.3582 on 5 degrees of freedom).

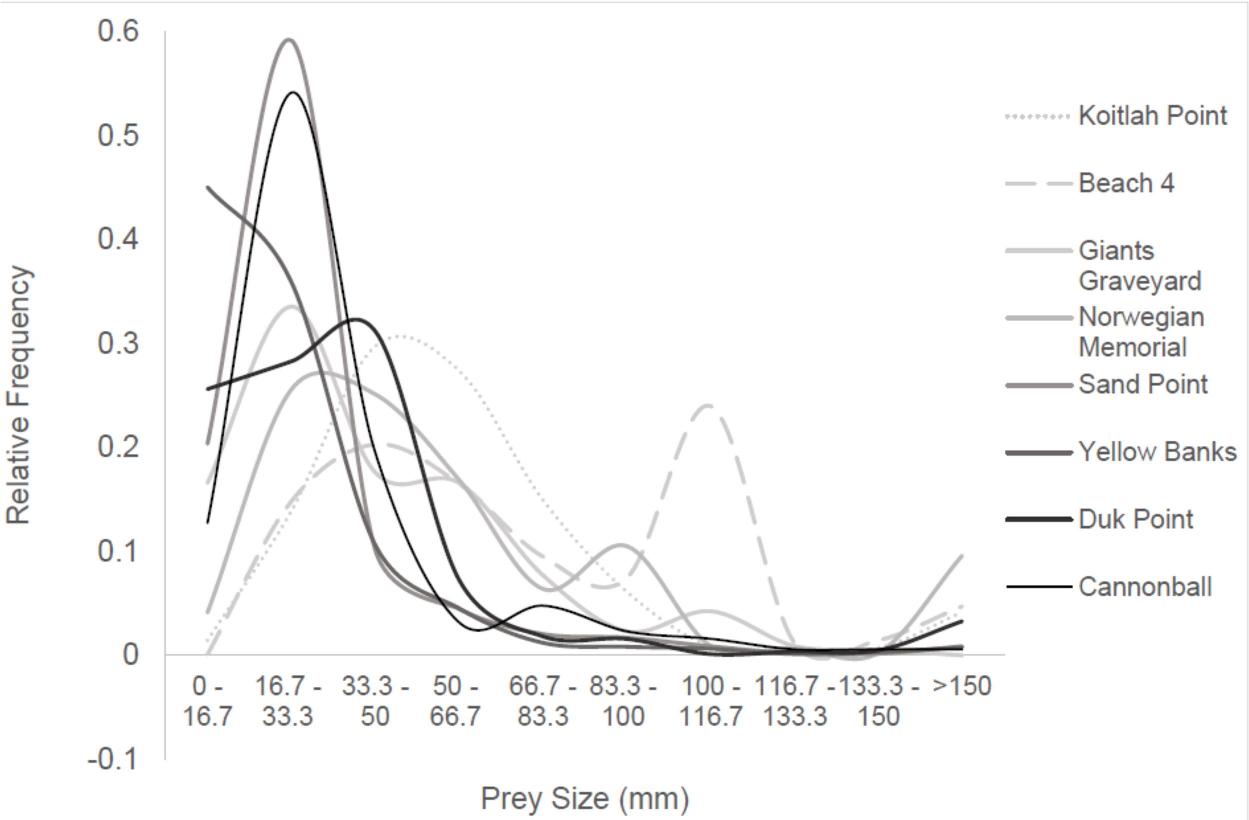

Figure 3-3. The frequency of prey size classes recovered by sea otters (*Enhydra lutris kenyoni*) in Washington State during foraging dives at sites with varying sea otter cumulative densities. Darker shades indicate high sea otter cumulative density, lighter shades indicate low sea otter cumulative density (cumulative densities in Table 3-1).

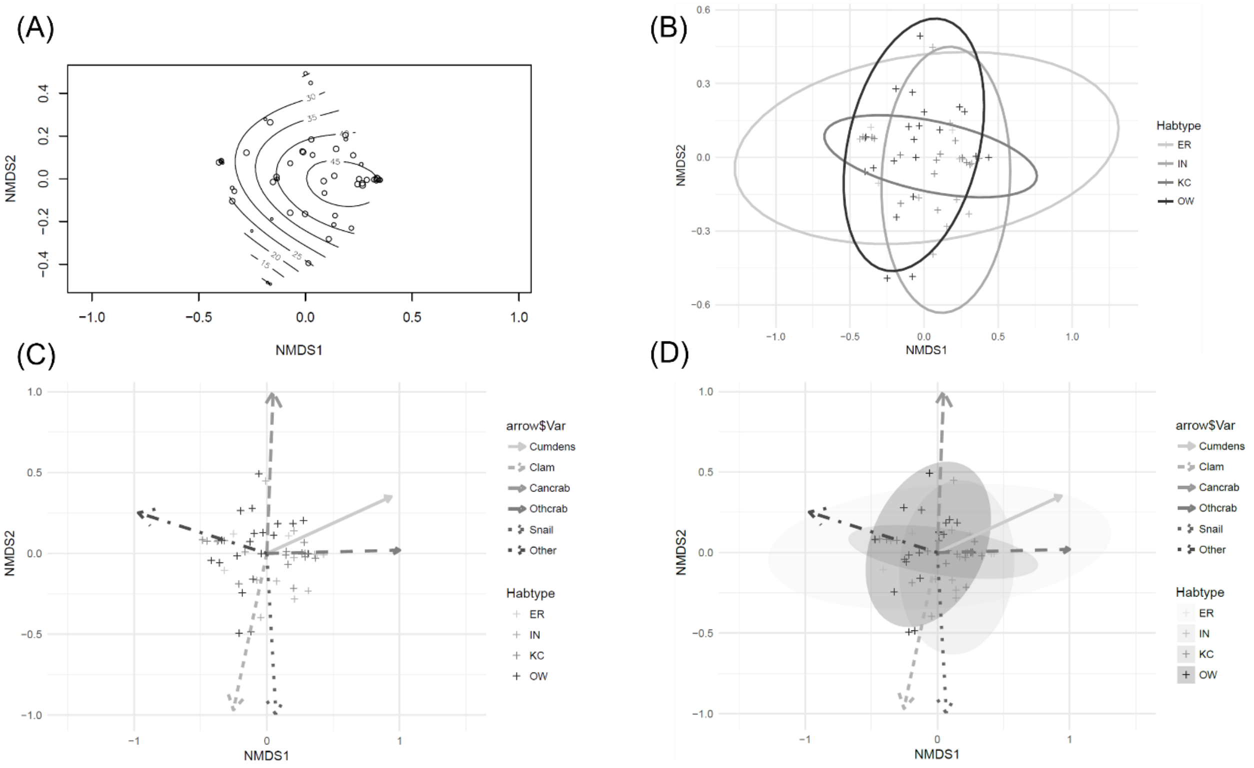

Figure 3-4. **A.** NMDS ordination of sea otter (*Enhydra lutris kenyoni*) diet composition based on the average proportion of dives that prey classes occur on from eight observation sites in Washington State, with the gradient of sea otter cumulative density shown. Bubble size corresponds to sea otter cumulative density. **B.** Ordination with 98% probability ellipses for each habitat type (ER= emergent rock, IN= intertidal, KC= kelp canopy, OW= open water) shown. **C.** Vectors are shown, scaled by their r^2 value, for each variable (sea otter cumulative density, clam, cancer crab, other crab, snail, other). **D.** Both habitat ellipses and variable vectors are shown.

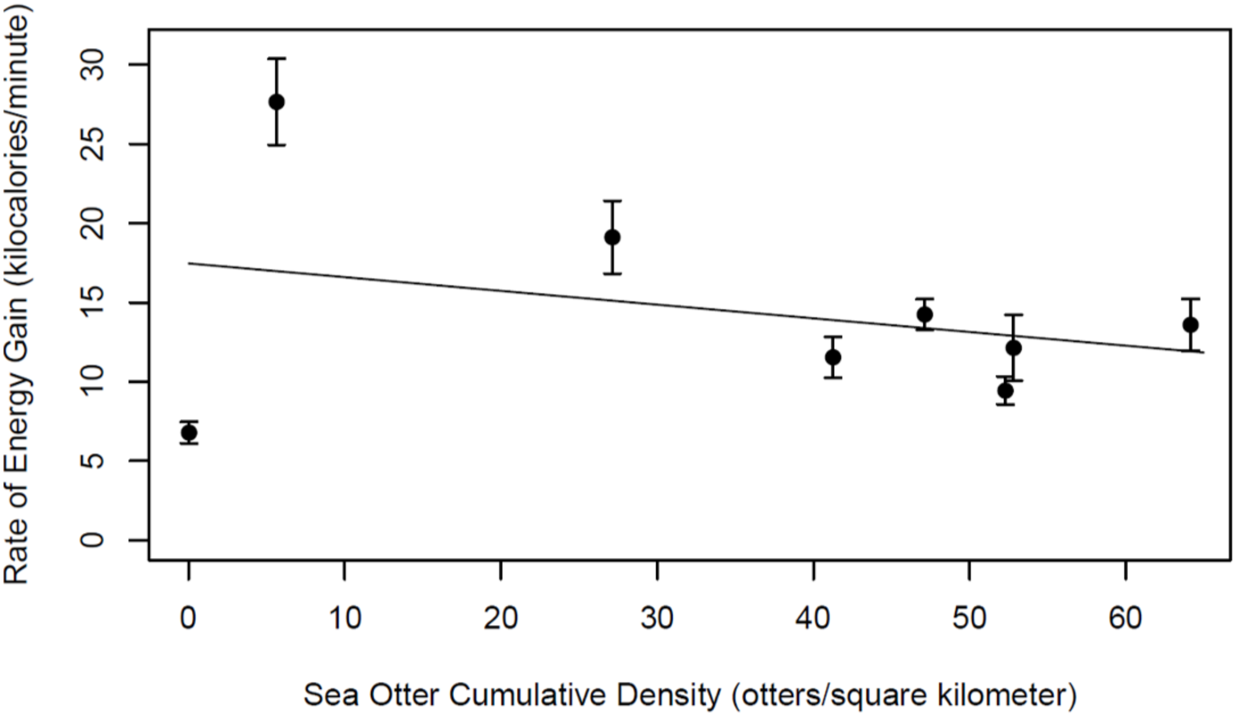

Figure 3-A1. Rate of sea otter energy gain (kcal/min) versus sea otter (*Enhydra lutris kenyoni*) cumulative density (otters/km^2) after being adjusted for percent edible biomass of kelp crabs. Error bars indicated standard deviation (Residual SE: 7.292 on 5 degrees of freedom).

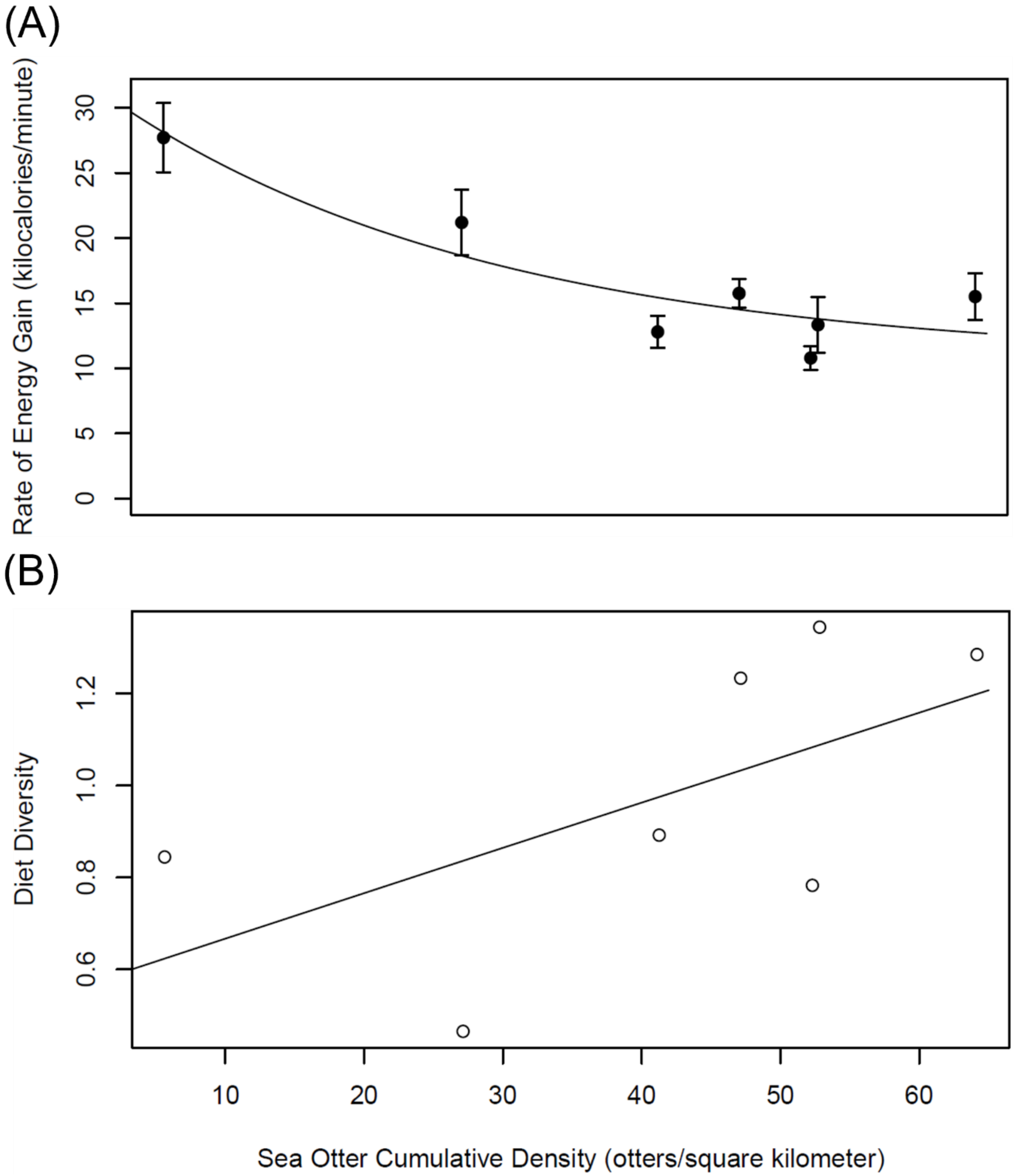

Figure 3-A2. **A**. Rate of sea otter energy gain (kcal/min) versus sea otter (*Enhydra lutris kenyoni*) cumulative density (otters/km^2) fit with a 3-term exponential model, not including Koitlah Point. Error bars indicate standard deviations (residual SE: 2.849 on 4 degrees of freedom). **B.** Sea otter diet diversity versus sea otter cumulative density fit with a 3-term exponential model, not including Koitlah Point (residual SE: 0.315 on 4 degrees of freedom).

Chapter 4. Longitudinal studies in Washington State reveal sea otter mediated kelp canopy transition dynamics

4.1 ABSTRACT

Nearshore marine ecosystems in rocky subtidal habitats of temperate regions are often classified into one of two alternative stable states: kelp-dominated or sea urchin-dominated. Transitions between these states can be caused by environmental perturbations and changes to herbivore populations. Sea otters (*Enhydra lutris spp.*) have been found to have a large impact on kelp forest community states in several regions because their predation on sea urchins releases kelp from herbivory pressure. We combine long-term data sets on kelp canopy cover, subtidal invertebrate densities, and sea otter (*Enhydra lutris kenyoni*) diet and population abundance to examine kelp canopy transition dynamics on the Pacific coast of Washington State, USA. We use a Markov transition matrix model to examine how sea otters and environmental covariates influence the probability of transitioning between kelp canopy states, where states were defined based on proportion of bedrock habitat with kelp canopy cover, and categorized as low kelp canopy state ($\bar{x} = 0.11\%$), medium kelp canopy state ($\bar{x} = 1.58\%$), and high kelp canopy state ($\bar{x} = 12.6\%$). q_{rs} represents the instantaneous risk that a strata transitions from state *r* to state *s*, and where (L)ow, (M)edium, and (H)igh. We also estimate sea otter diet composition using a Monte Carlo re-sampling algorithm and analyze subtidal invertebrate densities using nonmetric multidimensional scaling (NMDS) to determine if kelp canopy states are a consequence of sea otter predation on sea urchins. We found that kelp canopy transition dynamics were related to length of sea otter occupation. Specifically, we found that short-term sea otter occupation (0–2 years) increased the probability of transitioning from the low to medium kelp canopy state ($q_{LM} = 4.11$) compared to unoccupied areas. Long-term sea otter occupation (10–42 years) decreased the probability of transitioning out of the medium kelp canopy state ($q_{ML} = 0.30$; $q_{MH} = 0.47$) and increased the probability of transitioning into the medium kelp canopy state ($q_{HM} = 4.23$; $q_{LM} = 2.85$) compared to unoccupied areas. We found complementary shifts in sea otter diet and subtidal invertebrate community composition with increasing length of sea otter occupation: sea urchins were present at higher densities (unoccupied and 0–2 years: 8.32/m^2; 3–9 years: 0.01/m^2; 10–42 years: 0.60/m^2) and in higher proportions of sea otter diet (0–2 years: 87%; 3–9 years: 71%; 10–42 years: 0.7%) at sites more recently occupied by sea otters compared to long-occupied sites. We also found that the average size of sea urchins consumed by sea otters decreased with increasing sea otter occupation time (0–2 years: 193.0 mm [SD = 13.0 mm]; 3–9 years: 157.0 mm [SD = 15.2 mm]; 10–42 years: 36.8 mm [SD = 3.2 mm]). Long-term sea otter diet studies in combination with longitudinal kelp cover and subtidal invertebrate surveys provide insight into the relationship between sea otters and the nearshore marine community.

4.2 INTRODUCTION

Lewontin (1969) was the first to propose that natural communities can be found in one of several possible alternative stable states, where each state is characterized by a specific species assemblage and the states can be described as basins of attraction. Perturbations applied directly to the state variables (e.g., population densities) can push communities from one basin of attraction to another. The alternative stable state hypothesis suggests that nearshore marine ecosystems in rocky subtidal habitats of temperate regions can generally be classified into one of two states, either kelp- or sea urchin- dominated

(Steneck et al. 2002), and that both of these states are relatively stable until a large enough perturbation causes a shift in community state. Transitions from the kelp- to urchin-dominated state can result from storms, disease, herbivory, or physiological stress (Leighton et al. 1966, Lawrence 1975, Duggins 1980, Steneck et al. 2002), while transitions from the urchin- to kelp- dominated state can be aided by sea urchin disease, beneficial environmental conditions, or sea urchin predator recovery (Behrens and Lafferty 2004, Estes and Palmisano 1974, Steneck et al. 2002). The resilience of kelp beds has also been shown to vary with their size, with larger kelp patches being more stable than small patches (Layton et al. 2019). Observations of nearshore marine communities in the western Aleutian Islands, Alaska with and without sea otters (*Enhydra lutris*) by Estes and Palmisano (1974) were the first to suggest that sea otters can dramatically influence the nearshore marine environment through predation on herbivorous invertebrates, leading to a preponderance of urchin-dominated community states in areas without sea otters.

Following this foundational work, many studies have supported the generality of the otter-urchin-kelp paradigm (Estes and Duggins 1995, Konar and Estes 2003, Watson and Estes 2011, Steneck et al. 2013, Filbee-Dexter and Scheibling 2014, Rasher et al. 2020, Gorra et al. 2022), while other studies have highlighted this paradigm as a narrow view of kelp forest community dynamics (Foster and Schiel 1988, 2010; Foster 1990; Dean et al. 2000; Carter et al. 2007; Reed et al. 2014). Sea otters were extirpated from Washington State by 1911 (by the North Pacific Maritime fur trade), and then re-introduced by translocations from Alaska in 1969 and 1970, and the population has been increasing in abundance and distribution since then (Jameson et al. 1982, Hale et al. 2022). The relative frequency of urchin-dominated vs. kelp-dominated community states in Washington during the time period without sea otters is unknown; nonetheless, more recent studies of benthic community composition have taken advantage of the “natural experiment” of sea otter translocation and recovery to compare benthic community composition in otter-free vs. otter-occupied areas, as well as community changes at various time points post-translocation (Kvitek et al. 1989, 1998, 2000; Shelton et al. 2018). Kvitek et al. (1989) found that sea otter prey (including sea urchin) abundance, size, and biomass were negatively correlated with sea otter abundance, and a subsequent resampling of sites demonstrated significantly lower prey abundance and biomass in 1995 (Kvitek et al. 1998) and 1999 (Kvitek et al. 2000). Kvitek et al. (1989, 1998, 2000) also found that sea otter abundance was positively correlated with coverage of foliose and canopy-forming kelps. Subsequent surveys by Shelton et al. (2018) in 2015 demonstrated additional declines in the abundance of five major taxonomic groups (urchins, bivalves, sea cucumbers, crabs, and sea stars) and that sea otter and canopy-forming kelp population growth rates were positively correlated up until 2002. Shelton et al. (2018) suggested that while the initial nearshore community responses to sea otter population expansion followed the alternative stable state hypothesis, that other factors were more important in influencing kelp forest community dynamics post 2002, as was suggested by Carter et al. (2007).

The existing literature thus appears somewhat divided on the relative strength and ubiquity of the otter-urchin-kelp trophic cascade in Washington State. Some of this debate hinges on the consistency of the functional relationship between sea otter abundance and kelp canopy cover. However, in considering this relationship, it is worth noting that we would not expect sea otter population growth to lead to unbounded kelp canopy cover increases under the alternative stable state hypothesis. The transition between community states is expected to be non-linear and bi-phasic, resulting in relatively stable systems once sea otters have surpassed some critical density (Estes et al. 2010), after which we would expect the relationship between continued sea otter population growth and kelp canopy cover to weaken or even disappear. Previous studies have demonstrated that after initial sea otter reoccupation there is a dramatic reduction in urchin abundance and a rapid increase in abundance and diversity of annual algal species, followed by more complex successional dynamics after continued low herbivory. In these latter stages, other food web interactions besides herbivory become relevant in influencing kelp community dynamics, leading to a decline in diversity as one or a few perennial algal species become dominant (Paine and Vadas 1969, Duggins 1980, Watson 1993, Watson and Estes 2011). In some cases understory kelps may outcompete canopy-forming kelps after initial sea otter reoccupation, leading to an increase in understory algal cover and decrease in kelp canopy cover (Watson and Estes 2011, Burt et al. 2018, Kenner and Tinker 2018). These findings from other areas suggest that the apparent decoupling of otters and canopy-forming kelp in Washington post 2002 suggested by Shelton et al. (2018) may be reflective of a shift in dynamics and species interactions within kelp-dominated communities, rather than an inconsistency with the alternative stable state hypothesis.

Spatial patterns in sea otter population growth in Washington may also help explain the apparent decoupling between otter population growth and kelp canopy cover. In the early 2000s, the majority of sea otter population growth occurred along the southern Washington coast (south of La Push; Jeffries et al. 2019, Hale et al. 2022), an area dominated by unconsolidated sand substrate and thus unlikely to support canopy-forming kelps except in the few patches of rocky reefs (Mumford 2007). Increases in otter numbers in this area would not be expected to lead to continued increases in kelp canopy cover, which may account for the apparent decoupling of sea otter and kelp canopy cover growth rates post 2002. Thus, examinations of the relationship between sea otter recovery and kelp forest community dynamics must factor in spatial variation in habitat type.

In this study, we combine time series of sea otter, kelp canopy cover, and benthic invertebrate data to better understand how sea otters affect kelp canopy dynamics at regional and local scales. For the regional-scale analysis, we use long-term monitoring surveys of the abundance of kelp canopy cover (1989–2019 [Washington Department of Natural Resources, 2020]) and sea otter population abundance (1977–2019; e.g., Jeffries et al. 2019). For local-scale analysis, we use long-term monitoring surveys of benthic invertebrates (1987, 1995, 1999 [Kvitek et al. 1989, 1998, 2000] and 2015–2021 [Shelton et al. 2018]) and sea otter diet composition (1993–1998 [Laidre and Jameson 2006] and 2014–2019 [Hale et al. 2019]) for a subset of areas. Sea otter diet composition has been shown to reflect the composition of the benthic invertebrate community (Estes et al. 1982, Ostfeld 1982, Tinker et al. 2008), and shifts in sea otter diet have been shown to be indicative of shifts in community state in other areas (Estes et al. 1978).

4.3 METHODS

4.3.1 Study area & kelp cover data

The Washington Department of Natural Resources (WADNR) Nearshore Habitat Program has conducted long-term monitoring of floating kelp canopy extent along the Strait of Juan de Fuca and outer coast of Washington from 1989–2019 (excluding 1993), and these data are available online (Washington Department of Natural Resources 2020). Two species of surface canopy-forming kelp are monitored: the annual bull kelp (*Nereocystis luetkeana)* and the perennial giant kelp (*Macrocystis integrifolia*), and mixed canopies containing both species are present along much of the Washington coast (west of Low Point in Strait of Juan de Fuca; Van Wagenen 2015). Mature surface canopy reaches its maximum extent in July through October for bull kelp, and May through October for giant kelp (Van Wagenen 2015), and kelp surveys are conducted by air during low tide in July or August to estimate the seasonal maximum extent by species. Data on kelp canopy extent is collected using aerial color photography, which is then projected onto base maps, and kelp canopy extent is measured using computer image processing techniques (Van Wagenen 2015). Kelp canopy extent is recorded within spatially distinct kelp index map regions (strata; Figure 4-1), which are the smallest spatial unit for which it is appropriate to generate kelp area estimates given available data (Washington Department of Natural Resources 2020).

These strata along the Washington coast represent a gradient in substrate type, with rockier substrate occurring in the north and sandier substrate in the south. For our analyses, we excluded strata without any substrate data available, as well as strata without any bedrock habitat (as determined by coarse-scale surficial geologic substrate data, compiled by the Oregon State University Active Tectonics and Seafloor Mapping Lab; Romsos et al. 2015), as strata without bedrock habitat would not be expected to support canopy-forming kelps. This resulted in 65 spatially distinct strata with bedrock habitat for which both substrate and kelp canopy cover data were available (Figure 4-1). As we were interested in total canopy cover, we used data on both bull kelp and giant kelp canopy extent. As kelp canopy data were not available in 1993, we interpolated kelp canopy extent in each strata by averaging kelp cover in 1992 and 1994 in each strata, as the best predictor of kelp area in one year is kelp area in the adjacent year, and kelp canopy cover was not believed to be anomalous in 1993 (Pfister et al. 2018; H. D. Berry, Washington Department of Natural Resources, Personal communication, 2020). The Washington coast also represents a spatio-temporal gradient in sea otter occupation time and density (Hale et al. 2022), and therefore sea otter foraging pressure, as a result of variable sea otter population growth and range expansion following reintroduction.

4.3.2 Kelp canopy states

"Community state" can be described by one or many variables, including relative abundances of species (Beisner et al. 2003). Similar to other studies that use sea urchin density and canopy-forming kelp density as metrics of community composition (Estes and Duggins 1995, Watson and Estes 2011, Kenner and Tinker 2018, Gorra et al. 2022), we used kelp canopy cover as a metric to describe community composition in each stratum. We classified strata (Figure 4-1) into three states based on the log proportion of bedrock habitat with kelp canopy cover in each year using *k*-means cluster analysis (Jain and Dubes 1988) in *R*. For each stratum, we calculated the total area of bedrock habitat (fixed) and the total kelp canopy area (variable by year) in GIS, and then calculated the proportion of bedrock habitat with kelp canopy cover in each year (total kelp canopy area in stratum/total bedrock habitat in stratum). The *k*-means cluster analysis with 3 centers resulted in strata being categorized in either a low, medium, or high kelp canopy state in each year. Strata categorized into the same state were 94.7% similar to each other, indicating high compactness of clustering. The low kelp canopy state was defined as having 0.1–0.4% kelp cover ($\bar{x} = 0.11\%$), the medium kelp canopy state was defined as having 0.42–4.42% kelp cover ($\bar{x} = 1.58\%$), and the high kelp canopy state was defined as having 4.5–105% kelp cover ($\bar{x}$ = 12.6%; where > 100% cover indicates that kelp canopy extent exceeded bedrock habitat extent). We analyzed state transitions between consecutive years in each stratum.

4.3.3 Abiotic & biotic variables

Sea otter population surveys have been conducted annually in Washington State (1977–2019) in the summer (June–September; excluding 1979–1980, 1982, 1984, 1986, 1988, 1997, 2009, 2018; Jameson et al. 1986, Jeffries et al. 2019). These surveys result in estimated positions (latitude, longitude) and associated counts of sea otters in each year. The first post-translocation surveys (1977–1987) by U.S. Geological Survey incorporated a combination of boat and shore-based counts, with data from aerial surveys supplementing counts in 1985 (Jameson et al. 1982; 1986). The U.S. Fish and Wildlife Service, U.S. Geological Survey, and Washington Department of Fish and Wildlife conducted standardized surveys (1989–2019) that incorporated aerial and shore-based surveys conducted concurrently, and the final index of sea otter abundance is a combination of aerial, photo, and shore-based counts (where available; Jeffries et al. 2019). We digitized annual positions and associated indices of Washington sea otter abundance from 1977–2019 in GIS. We defined the year of sea otter occupation for each stratum as the first year that sea otters were counted in each stratum during an annual survey (e.g., the first year that a sea otter position fell within each stratum), except for strata 16.2 and 16.3 (Figure 4-1) where we assumed that sea otters first occupied this area in 1995 based on sightings reported in Laidre and Jameson (2006). We then categorized strata based on the number of years occupied by sea otters (current year – year occupied = number of years occupied), where strata categorized as otter metric 1 were not occupied, strata categorized as otter metric 2 had been occupied for 0–2 years (where year 0 is the year of occupation), strata categorized as otter metric 3 had been occupied for 3–9 years, and strata categorized as otter metric 4 had been occupied for 10–42 years. We also calculated the average kelp bed size within each stratum in each year in GIS.

In addition to the sea otter occupation metric and average kelp bed size, we also calculated abiotic covariates. We calculated the average depth within each stratum using the GEBCO 2019 grid in GIS (GEBCO Group 2019). We calculated the average Bakun upwelling index (measured at 48N) and Biologically Effective Upwelling Transport Index (BEUTI; measured at 47N) in each year during the upwelling season (April–September) from NOAA Pacific Fisheries Environmental Laboratory (https://www.pfeg.noaa.gov/). Positive values of the Bakun upwelling index indicate upwelling and negative values indicate downwelling. The BEUTI is an estimate of the total quantity of nitrate upwelled or downwelled in a given time period (Jacox et al. 2018). We also calculated the average Pacific Decadal Oscillation (PDO) April–September in each year from the National Centers for Environmental Information (https://www.ncei.noaa.gov/pub/data/cmb/ersst/v5/index/ersst.v5.pdo.dat). Finally, we calculated the average winter (October–March) significant wave height (in meters) using data from National Data Buoy Center Buoy #46041 (47.353, -124.742; approximately 31.81 km west of Cape Elizabeth) in each year. Significant wave height is calculated as the average of the highest one-third of all of the wave heights during the 20-minute sampling period each hour.

4.3.4 Markov transition matrix model

We used an alternative stable states framework to investigate how sea otters affect kelp canopy state transitions; specifically, whether the presence and duration of occupation of sea otters affects the probability of transitioning between states. We examined kelp canopy state within 65 strata (Figure 4-1) from 1989–2019 using a multi-state Markov Transition Matrix model in which state transitions during the interval t and $t+\Delta t$ are assumed to depend on the current state, as well as a suite of abiotic and biotic covariates (Jackson 2011, Van Den Hout 2016). We evaluated models including time-varying covariates for sea otter occupation status, upwelling indices (Bakun and BEUTI), significant wave height, and PDO, while average depth was considered as a static variable. All quantitative covariates were centered and scaled prior to analysis.

In our three-state transition model, the Markov process is governed by a 3 x 3 transition intensity matrix, Q, in which rows are the current states (r) and columns are the future states (s). The transition intensity (q_{rs}) is the instantaneous risk that a stratum transitions from state r to state s. As transitions from low to high kelp state (q_{LH}) and high to low kelp state (q_{HL}) were rarely observed in the data (0.24% and 0.12% of observed transitions, respectively), we fixed q_{LH} and q_{HL} at 0.

The intensities q_{rs} can be modelled as:

$$q_{rs}(t|x(t)) = q_{rs.0}(t) \exp(\beta'_{rs} x(t)),$$

where $x(t)$ is the matrix of explanatory variables, β_{rs} are coefficients to be estimated, and $q_{rs.0}(t)$ is a baseline hazard that describes the risk when environment $x(t) = 0$ (i.e., the means of standardized covariates and otter metric 1 [unoccupied]). Therefore, $\exp(\beta'_{rs} x(t))$ can be interpreted as the relative increase or decrease in transition risk associated with a set of explanatory variables $x(t)$. Estimation of model parameters was obtained by maximizing the log-likelihoods using the *R* function *optim*. We evaluated a null model that only included the baseline hazard $q_{rs.0}$ (no covariates), and univariate models for each of the individual covariates.

4.3.5 Model evaluation

We evaluated the goodness of fit of each model containing covariates against the null model using likelihood ratio tests to evaluate if the addition of a parameter significantly increased the likelihood of the model. After determining the significant covariates, we built a final model including those covariates. We then compared this final model to the null model using Akaike information criterion (AIC). The model with the lowest AIC was considered the best fit and was used for further analysis.

4.3.6 Model baseline and hazard ratios

We used the baseline hazards ($q_{rs.0}$) estimated by our best fit model as indicators of the underlying kelp canopy response. The baseline hazard for each pair of states describes the risk of transitioning for a mean stratum when all covariates are set to their mean. We then investigated the influence of abiotic and biotic covariates on kelp canopy transition dynamics by comparing the estimated hazard ratios (HRs) derived from our best fit model ($exp(\beta_{rs})$). Hazard ratios of covariates are interpretable as the multiplicative effects on hazard, where values above 1 indicate that the covariate is associated with a greater probability of transition and a value below 1 indicates the covariate is associated with a lower probability of transition.

4.3.7 Sea otter foraging observations

We examined sea otter diet in a subset of strata (*n*=6) from seven land-based observation sites on the Washington coast. Sea otter foraging data were previously collected from these observation sites (Figure 4-1; Cape Alava, Duk Point, Giants Graveyard, Koitlah Point, Norwegian Memorial, Sand Point, Yellow Banks) in 1993–1998 (Laidre and Jameson 2006). Additional foraging observations were made at these sites 2014–2019 (Hale et al. 2019). Foraging observations were made following standard protocols established and used in studies of sea otters throughout their range in North America (e.g., Dean et al. 2002, Tinker et al. 2008, Esslinger et al. 2014, Tinker 2015, Hale et al. 2019). We estimated diet composition at each level of the sea otter occupation metric (where sites categorized as otter metric 2 were occupied 0–2 years, sites categorized as otter metric 3 were occupied 3–9 years, and sites categorized as otter metric 4 were occupied for 10–42 years) on the basis of consumed wet edible biomass using a Monte Carlo re-sampling algorithm designed to account for uncertainty and biases inherent in sea otter foraging data ("Sea Otter Foraging Analysis"; Tinker et al. 2022). The algorithm consisted of 10,000 iterations of simulated foraging bouts for each otter occupation metric, with dive variables drawn from appropriate density functions fit to our raw data. Algorithm output includes rate of energy gain (kilocalories/minute), rate of mass gain (grams/minute), estimates of diet composition, and uncertainty estimates for each. We compared these diet metrics between the three non-zero otter occupation metrics (0–2 years, 3–9 years, 10–42 years), where foraging observation sites were considered first occupied by sea otters when a sea otter was first counted within 5 km during an annual sea otter survey, except for Koitlah Point which was assumed to be occupied in 1995 based on observations reported in Laidre and Jameson (2006).

4.3.8 Subtidal dive surveys

We examined subtidal invertebrate community composition in a subset of strata (*n*=9) at 10 subtidal dive sites (Figure 4-1; Anderson Point, Cape Alava, Cape Johnson, Chibadehl

Rocks, Destruction Island, Neah Bay, Point of the Arches, Dohodaaluh Rock [Rock 305], Tatoosh Island, and Teahwhit Head). All sites featured rocky subtidal habitat with canopy-forming kelp (*Macrocystis pyrifera* and *Nereocystis luetkeana*) and understory algae (Shelton et al. 2018). Fishery-independent subtidal SCUBA surveys were previously conducted by the Northwest Fisheries Science Center at these sites 2015–2021 (excluding 2020; Shelton et al. 2018). Divers counted large invertebrates (>5cm in diameter; anemones, bivalves, chitons, crabs, sea cucumbers etc.) along visual transects in kelp beds at each site (see Shelton et al. 2018 for detailed methods). Summary statistics on benthic invertebrate densities were also extracted by Shelton et al. (2018) from reports by Rikk Kvitek and colleagues on subtidal dive surveys conducted at the same sites in 1987, 1995, and 1999 (Kvitek et al. 1989, 1998, 2000) at the species group level for 7 invertebrate groups (bivalve, chiton, crab, sea cucumber, gastropod, sea star, urchin). Not all sites were sampled in each year (Table 4-1).

Using these two data sets, we calculated invertebrate species group densities in units of m^{-2} for all subtidal surveys. For comparison purposes between the two survey periods, invertebrate community composition was analyzed at the species group level, as the lowest possible resolution of earlier survey summaries was at the species group level. In addition, prey species groups were limited to those found in both time periods (i.e., species groups like anemone that were only recorded in the later survey effort were excluded from analysis). Prey species groups used in analysis included bivalves (primarily *Crassadoma gigantea*), chitons (primarily *Cryptochiton stelleri*), crabs (primarily genera *Pugettia* and *Cancer*), sea cucumbers (genera *Cucumaria* and *Parastichopus*), gastropods (limpets and snails, including whelks and *Tegula spp.*), sea stars (genera *Pisaster,* *Orthasterias, Dermasterias, Henricia*, and *Pycnopodia*), and urchins (genera *Mesocentrotus* and *Strongylocentrotus*). We summarized subtidal invertebrate community composition in terms of the average density of these 7 species groups per site for each year and used nonmetric multidimensional scaling (NMDS) to visualize subtidal invertebrate community composition between otter occupation metrics (0–2 years occupied [where unoccupied sites were included in this group], 3–9 years occupied, 10–42 years occupied). Sites were considered first occupied by sea otters when a sea otter was first counted within 5 km of a site during an annual sea otter survey, except for Neah Bay, Chibadehl Rocks and Tatoosh Island (Figure 4-1) which were assumed to be occupied in 1995 based on observations reported in Laidre and Jameson (2006). We calculated assemblage dissimilarity using Bray-Curtis distance. Multivariate analyses were performed using *R* version 4.1.0 (R Core Team 2021) with the *vegan* package, version 2.5-7 (Oksanen et al. 2019). We used the *adonis2()* function from the *vegan* library to fit a linear model to the distance matrix and conducted a permutation test with pseudo *F*-ratios to determine the influence of site and otter occupation metric on subtidal invertebrate community composition. As we could not include site as a random effect in the model due to the nature of a permutation test, we defined the model to respond similarly with site as a fixed effect.

4.4 RESULTS

4.4.1 Markov transition matrix model

The majority of observed transitions were of strata categorized in the medium kelp canopy state transitioning to the high kelp canopy state (17.3%; Figure 4-2). The low and high kelp canopy cover states were generally persistent (93.6% and 93.8%, respectively, did not transition during the study period), while the medium state was less persistent (75.7%;

Figure 4-2). Likelihood ratio tests for average patch size, average depth, significant wave height, and otter occupation metric were all significant ($P < 0.05$), and these covariates were all included in the final model. Bakun upwelling index, BEUTI upwelling index, and Pacific Decadal Oscillation were not significant ($P > 0.05$). The model that included sea otter occupation metric, average patch size, average depth, and significant wave height was the best fit model when compared to the null model. Therefore, we made inferences about transition probabilities from the best fit model.

The baseline transition intensities ($q_{rs.0}$) from the best fit model (where all covariates are set to 0, i.e., the means of standardized covariates and otter metric 1) provide information on underlying kelp canopy response. Kelp canopy dynamics were largely dominated by transitions from medium – high kelp canopy cover ($q_{MH} = 0.267$) and low – medium kelp canopy cover ($q_{LM} = 0.158$; Figure 4-3). Strata categorized as medium canopy cover were 3.4 times (q_{MH}/q_{HM}) more likely to transition to the high kelp canopy state than the reverse. Strata categorized as low kelp canopy cover were 1.6 times (q_{LM}/q_{ML}) more likely to transition to medium kelp canopy than the reverse.

Otter metric 2 (0–2 years occupied) was associated with an increased probability of low – medium kelp canopy transitions (Figure 4-4, Table 4-2). Otter metric 4 (10–42 years occupied) was associated with an increased probability of transitioning to the medium kelp canopy cover state, and a decreased probability of transitioning from the medium kelp canopy cover state (Figure 4-4, Table 4-2). Otter metric 3 (3–9 years occupied) did not have a significant influence on the probability of any state transitions (Figure 4-4, Table 4-2). However, both otter metric 2 and 3 were generally associated with an increased probability of transitioning to the medium kelp canopy state and a decreased probability of transitioning from the medium kelp canopy state (except for otter metric 2 for medium – low transition; Figure 4-4, Table 4-2).

Larger average kelp patch size was associated with an increased probability of transitioning to a higher kelp state (Figure 4-4, Table 4-2; although not significant for medium – high). Patch size did not significantly influence the probability of transition to a lower kelp state (Figure 4-4, Table 4-2). Deeper average depth was associated with an increased probability of transitioning to a lower kelp state (Figure 4-4, Table 4-2; although not significant for medium – low transition). Deeper average depth was also associated with a decreased probability of low – medium transitions, but did not have a significant influence on medium – high transitions (Figure 4-4, Table 4-2). Higher significant wave height significantly decreased the probability of medium – high transitions, and was also associated with a decreased probability of low – medium transition and an increased probability of transition to a lower kelp state (although was not significant; Figure 4-4, Table 4-2).

4.4.2 Foraging data

Foraging records consisted of 11,642 individual foraging dives from 20 bouts at sites occupied by sea otters for 0–2 years (otter metric 2), 5 bouts from sites occupied by sea otters for 3–9 years (otter metric 3), and 610 bouts from sites occupied by sea otters for 10–42 years (otter metric 4). Of the data collected, 83% of dives were from females, 9% from males, and 8% from individuals of unknown sex. Rate of energy intake decreased with increasing sea otter occupation time (0–2 years: 91.18 kilocalories/min [SD = 20.85 kcal/min]; 3–9 years: 51.37 kcal/min [16.17 kcal/min]; 10–42 years: 28.20 kcal/min [SD = 2.48 kcal/min]). Sea otters had a similar dive success rate regardless of the length of sea otter occupation (0–2 years: 92%; 3–9 years: 90%; 10–42 years: 89%). The average size of sea urchins consumed by sea otters decreased with increasing sea otter occupation time (0–2 years: 193.0 mm [SD = 13.0 mm]; 3–9 years: 157.0 mm [SD = 15.2 mm]; 10–42 years: 36.8 mm [SD = 3.2 mm]).

Sea otters foraging at sites occupied for 0–2 years consumed primarily urchins (87% of consumed biomass; Table 4-3). Sea otters foraging at sites occupied for 3–9 years consumed primarily urchins (71% of consumed biomass), followed by large clams (11%). Sea otters foraging at sites occupied for 10–42 years consumed a greater diversity of prey types, and primarily consumed large clams (37% of consumed biomass), followed by kelp crabs (17%), prey categorized as “other” (sea stars, worms, chitons, sea cucumbers, octopuses, rock scallops, fish eggs, moon snails; 17%), unidentified crabs (15%) and cancer crabs (11%). The largest diet shifts between otter occupation levels (proportional changes of over 15%) were for sea urchins (decrease of 16.4% between 0–2 years and 3–9 years occupied; decrease of 70.4% between 3–9 years and 10–42 years occupied) and large clams (increase of 26.4% between 3–9 years and 10–42 years occupied; Table 4-3).

4.4.3 Subtidal dive surveys

When invertebrate densities were examined by otter occupation level, invertebrate community composition was dominated by urchins at sites unoccupied by sea otters and at sites 0–2 years after otter occupation, with an average density of 8.32 urchins/m^2. Invertebrate community composition was dominated by sea stars at sites occupied by sea otters 3–9 years, with a density of 0.34/m^2. Invertebrate community composition was dominated by urchins at sites occupied by sea otters for 10–42 years with an average density of 0.60 urchins/m^2, followed by gastropods (0.38/m^2), sea stars (0.21/m^2) and sea cucumbers (0.18/m^2).

NMDS ordination of subtidal macroinvertebrate community composition converged on a stable 2-D solution (stress = 0.17) and indicated moderate separation between otter occupation levels along NMDS1 and NMDS2 (Figure 4-5). Of the variables included in the NMDS, the density of bivalves (P = 0.002), chitons (P = 0.001), crabs (P = 0.018), sea cucumbers (P = 0.001), gastropods (P = 0.003), and urchins (P = 0.001) were significant in the ordination. Sea stars were not significant in the ordination (P = 0.332). The NMDS suggested that sea urchins were present at higher densities at sites unoccupied by sea otters and at sites occupied by sea otters for 0–2 years than at sites occupied by sea otters for 3–9 years and 10–42 years (Figure 4-5). per-MANOVA analysis of subtidal invertebrate community composition indicated that both site (P = 0.001) and otter occupation level (P = 0.001) were significant in explaining the dissimilarity in subtidal invertebrate community composition.

4.5 DISCUSSION

Our results demonstrate that dynamics of kelp canopy cover on the Pacific coast of Washington State are related to length of sea otter occupation, although the nature of this relationship is more complex than a simple positive correlation between sea otter density and kelp canopy abundance. We found that short-term sea otter occupation (0–2 years, otter metric 2) was associated with a > 4X increase in the probability of transitioning from the low to medium kelp canopy state when compared to unoccupied strata (otter metric 1). These results are consistent with the otter-urchin-kelp paradigm, and reflect an initial increase in kelp canopy cover after sea otter reoccupation that has been observed elsewhere (Estes and Duggins 1995, Watson and Estes 2011). We found that areas that had been long-occupied by sea otters (10–42 years, otter metric 4) were associated with an increased probability of transitioning *to* the medium kelp canopy state (high – medium, low – medium) and a decreased probability of transitioning *from* the medium kelp canopy state (medium – high, medium – low). We also found this same pattern with otter occupation metric 3 (3–9 years occupation), although otter occupation metric 3 did not significantly influence the probability of any state transitions. These results may reflect successional kelp dynamics after initial sea otter occupation, whereby understory kelp in the absence of intense urchin herbivory out competes canopy-forming kelps, leading to a decrease in kelp canopy cover (i.e., from high to medium), but also to an overall increase in the stability of medium-cover kelp forests. This pattern has been observed in other areas 1–5 years after sea otter occupation, experimental urchin removal, or an urchin population crash caused by disease (Paine and Vadas 1969, Duggins 1980, Watson 1993, Watson and Estes 2011, Kenner and Tinker 2018). Understory kelp density has been monitored by NWFSC at Neah Bay, Tatoosh Island, Cape Alava, Cape Johnson, and Destruction Island since 2015; however, understory kelp density data were only available in earlier subtidal surveys in 1987 at Cape Johnson and Cape Alava, and this paucity of data precluded an analysis of understory kelp patterns in our study. Continued monitoring of kelp canopy cover by WADNR and subtidal monitoring by NWFSC, including of understory kelp, may help elucidate the mechanism of the observed decrease in kelp canopy cover at long-occupied sites. The fact that longer otter occupation times (3–9 years, 10–42 years) were associated with an increased probability of transitioning to the medium kelp canopy state may also explain the apparent statistical decoupling of sea otter and kelp canopy growth rates post

2002 suggested by Shelton et al. (2018), as kelp canopy growth rates have lagged behind sea otter population growth rates.

Results from our analyses of sea otter foraging and subtidal invertebrate community composition were also consistent with the otter-urchin-kelp paradigm. Sea otters appeared to reduce the mean size and density of sea urchins, as mean urchin size and proportion of sea urchins decreased in sea otter diet, and sea urchin density in subtidal surveys decreased with increasing sea otter occupation time. While we observed an overall decrease in sea urchin density with increasing sea otter occupation time (average of 8.32/m^2 to 0.6/m^2), we did observe a slight increase in sea urchin density between otter metrics 3 and 4 (3–9 years and 10–42 years occupied; from an average of 0.01/m^2 to 0.60/m^2). This observation is consistent with findings elsewhere, that demonstrate that small sea urchins can persist in the presence of sea otters, as sea otters are size-selective predators and foraging efforts for urchin prey are not linked to prey density but rather to energetically profitable prey (Burt et al. 2018, Smith et al. 2021). As we did not investigate urchin size distributions in our study, additional research will be needed to confirm this hypothesis and investigate the size frequency distribution of sea urchins in each otter occupation level.

Sea otter diet also showed a complementary shift with subtidal invertebrate community composition, as both sea otter diet and invertebrate community composition diversified with increasing sea otter occupation time. Sea urchins dominated both sea otter diet and the subtidal invertebrate community at sites occupied by sea otters for 0–2 years. The proportion of all other prey classes (small clam, large clam, kelp crab, cancer crab, unidentified crab, snails, mussels, other) in sea otter diets increased with length of otter occupation, consistent with findings elsewhere of sea otters diversifying their diets with increasing occupation time (Estes et al. 1981, 2003; Tinker et al. 2008). The invertebrate community similarly diversified to include increased densities of gastropods, sea stars, sea cucumbers, bivalves, and crabs with increasing sea otter occupation time. This result may be suggestive of an increase of kelp associated macroinvertebrates such as kelp crabs, limpets, and snails with increasing sea otter occupation time. These complementary shifts in sea otter diet and subtidal invertebrate community composition are consistent with previous research demonstrating that sea otter diet composition reflects the composition of the benthic invertebrate community (Estes et al. 1982, Ostfeld 1982, Tinker et al. 2008).

During our study period (1989–2019), the baseline hazards from the best fit Markov transition matrix model suggested that strata were more likely to transition to a higher kelp cover state than a lower one. This finding is consistent with previous research that has shown that kelp canopy cover on the outer coast is generally persistent (Pfister et al. 2018). Pfister et al. (2018) also suggested that kelp abundance on the outer coast and in the Strait of Juan de Fuca was correlated inversely with the Pacific Decadal Oscillation, however we did not find that the PDO was a significant covariate in explaining transitions between kelp canopy states (as defined by the proportion of rocky habitat with kelp canopy cover). As predicted, our analyses showed that strata with larger average kelp patches were more likely to transition to a higher kelp canopy state than strata with smaller average kelp patches, and strata with deeper water were more likely to transition to a lower kelp canopy state than strata in shallower water. We also found that increased winter storm activity, as measured by significant wave height, decreased the probability of strata transitioning to a higher kelp canopy cover state and increased the probability of strata transitioning to a lower kelp canopy state. These results demonstrate that abiotic as well as biotic factors influence kelp canopy transition dynamics, and have implications for predictions of kelp canopy state.

Our results provide new insights into expectations for kelp canopy dynamics and macroinvertebrate community composition following sea otter reintroduction to Washington State. While our results show marked effects of sea otters on sea urchins and kelp canopy dynamics, our results also suggest that continued sea otter population growth is unlikely to result in increased kelp canopy cover, perhaps because of successional processes. Spatial patterns in sea otter population growth in Washington may also contribute to this, as recent population growth has occurred primarily in habitat largely unsuitable for canopy-forming kelps. Mumford (2007) identified Copalis Rock (Figure 4-1; kelp map strata 31.1) as the southern-most extent of suitable substrate for *Nereocystis*, and kelp canopy has been recorded on aerial kelp surveys only as far south as Destruction Island (Figure 4-1; kelp map strata 25.2) (Washington Department of Natural Resources 2020). As the majority of sea otter population growth is predicted to occur through range expansion into currently unoccupied areas to the south of the current range in the next 25 years (Hale et al. 2022), an area with primarily sandy substrate, increased sea otter population numbers are unlikely to lead to increased kelp canopy cover.

4.6 ACKNOWLEDGEMENTS

We would like to thank R. Kvitek for providing access to the original 1987, 1995, and 1999 subtidal survey data, and S. Hamilton for assisting with digitization of these data. We would like to thank J. Samhouri and A.O. Shelton for sharing their subtidal survey data, as well as extracts from R. Kvitek’s reports. We gratefully acknowledge everyone involved with the annual Washington State sea otter survey, including S. Jeffries (WDFW), M. Kimbrel (WDFW), S. Ament (WDFW), J. Waddell (OCNMS), D. Lynch (USFWS), J. Well and K. Meek with Rite Bros. Aviation in Port Angeles, and WDFW WILDCOM dispatch for providing Aircraft Flight Following (AFF) services. We also acknowledge R. Jameson for collecting early post-translocation sea otter survey data and sharing sea otter foraging data from the 1990s. We acknowledge those who assisted in the field collecting sea otter foraging data, especially M. Stafford, B. Krause, A. Van Hemmen, A. Witt, A. Northey, C. Johnson, and C. Phelan. We would like to thank H. D. Berry of Washington State Department of Natural Resources for providing access to the most recent kelp canopy cover data and insight into kelp ecology. M.T. Tinker provided analytical expertise. Overflights of the Olympic Coast National Marine Sanctuary below 2000' above ground level were conducted under NOAA permit number OCNMS-2018-003 issued to WDFW and USFWS. Research activities in Olympic National Park were conducted under Scientific Research and Collecting Permit (OLYM-2019-SCI-0026) for access to ONP locations used by ground observers. Sea otter foraging observations by J. Hale were made under a Memorandum of Agreement with the Makah Tribe (permit numbers 2015-17 and 2016-12) and under National Park Service Scientific Research Study number OLYM-00048. Funding for aerial and ground surveys was provided by U.S. Fish and Wildlife Service and Washington Department of Fish and Wildlife. Funding support to J. Hale was provided by the School of Aquatic and Fishery Sciences (University of Washington), Point Defiance Zoo & Aquarium and the Point Defiance Zoo Society through the Dr. Holly Reed Conservation Fund, and the NOAA Dr. Nancy Foster Scholarship. This publication is [partially] funded by the Joint Institute for the Study of the

Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA15OAR4320063, Contribution No. 2022-1194.

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Table 4-1. Years surveyed at subtidal rocky reef dive sites surveyed by SCUBA for invertebrates on the Olympic Peninsula of Washington State.

Site	1987	1995	1999	2015	2016	2017	2018	2019	2021
Anderson Point	x	x	x	x					
Cape Alava	x	x	x	x	x	x	x	x	x
Cape Johnson	x		x	x	x	x	x	x	x
Chibadehl Rocks			x	x					
Destruction Island			x	x	x	x	x	x	x
Neah Bay	x	x		x	x	x	x	x	x
Point of the Arches	x		x	x					
Dohodaaluh Rock/Rock 305	x		x	x					
Tatoosh Island		x	x	x	x	x	x	x	x
Teahwhit Head	x		x	x					

Table 4-2. Table of baseline transition intensities (q_{rs0} in first column) and covariate hazard ratios (HR) and their 90% confidence intervals as estimated from the best multi-state transition model. The HR of covariates are interpretable as multiplicative effects on the baseline hazard, where values above 1 indicate that the predictor is associated with a greater probability of state transition, and values below 1 indicate a lower probability of transition. Covariates statistically different from 1 (90% confidence interval does not overlap 1) are colored in grey, and covariates with 95% confidence intervals that do not overlap 1 are preceded by an asterisk. Covariates include average kelp patch size (Patch size), average depth (Depth), Significant Wave Height (SWH), and three otter occupation metrics (0–2 years = Otter Metric 2; 3–9 years = Otter Metric 3; 10–42 years = Otter Metric 4).

Transitions	Baseline	Patch Size	Depth	SWH	Otter Metric 2	Otter Metric 3	Otter Metric 4
Low – Low	-0.1577 (-0.23079, -0.10775)						
Low – Medium	0.1577 (0.10775, 0.23079)	*5.1948 (2.7889, 9.676)	*0.3446 (0.2138, 0.5553)	0.7679 (0.5840, 1.0098)	4.108 (1.1485, 14.694)	2.1005 (0.7273, 6.067)	*2.8473 (1.5009, 5.4014)
Medium – Low	0.09878 (0.06331, 0.15413)	1.0971 (0.3302, 3.645)	1.4723 (0.9740, 2.2257)	1.252 (0.8695, 1.8027)	1.0631 (0.2880, 3.924)	0.9184 (0.3014, 2.798)	*0.3037 (0.1490, 0.6190)
Medium – Medium	-0.36578 (-0.45841, -0.29186)						
Medium – High	0.267 (0.20564, 0.34666)	1.8358 (0.9582, 3.517)	1.1401 (0.9265, 1.4030)	0.7842 (0.6274, 0.9801)	0.4541 (0.1654, 1.247)	0.4677 (0.2071, 1.057)	*0.4657 (0.2995, 0.7242)
High – Medium	0.07859 (0.05891, 0.10484)	0.6526 (0.3702, 1.151)	*1.4729 (1.1158, 1.9443)	1.1274 (0.8658, 1.4681)	2.6896 (0.7603, 9.515)	1.3226 (0.3738, 4.679)	*4.2346 (2.4599, 7.2894)
High – High	-0.07859 (-0.10484, -0.05891)						

Table 4-3. Proportion of sea otter (*Enhydra lutris kenyoni*) diet (calculated based on consumed biomass) for prey classes output from the Monte Carlo resampling algorithm by length of otter occupation (0–2 years; 3–9 years; 10–42 years). Small clams are <1 sea otter paw width, large clams are >1 sea otter paw width. “Other” prey class includes sea stars, worms, chitons, sea cucumbers, octopus, rock scallop, fish eggs and moon snails.

Otter Metric	urchin	small clam	large clam	kelp crab	cancer crab	unid crab	snails	mussels	other
0–2 yrs	0.874	0.001	0.071	0.011	0.011	0.011	0.001	0.000	0.018
3–9 yrs	0.711	0.004	0.106	0.059	0.041	0.024	0.004	0.001	0.051
10–42 yrs	0.007	0.018	0.369	0.174	0.112	0.149	0.004	0.001	0.166

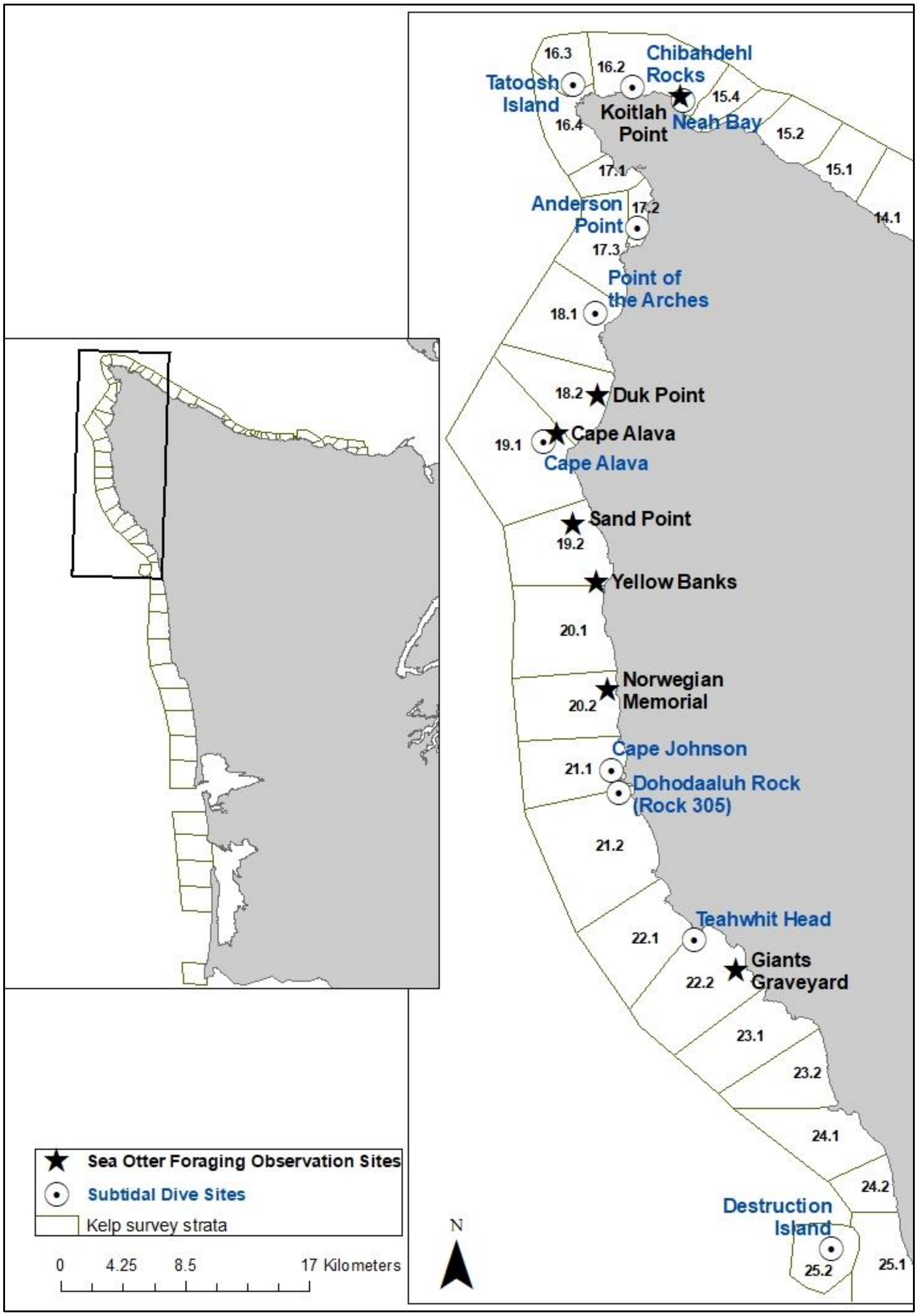

Figure 4-1. The Olympic Peninsula of Washington State showing sea otter (*Enhydra lutris kenyoni*) foraging observation sites (black labelled stars) and subtidal invertebrate survey sites (blue labelled circles). Numbered areas along the coast indicate kelp survey strata within which Washington Department of Natural Resources calculates kelp canopy area.

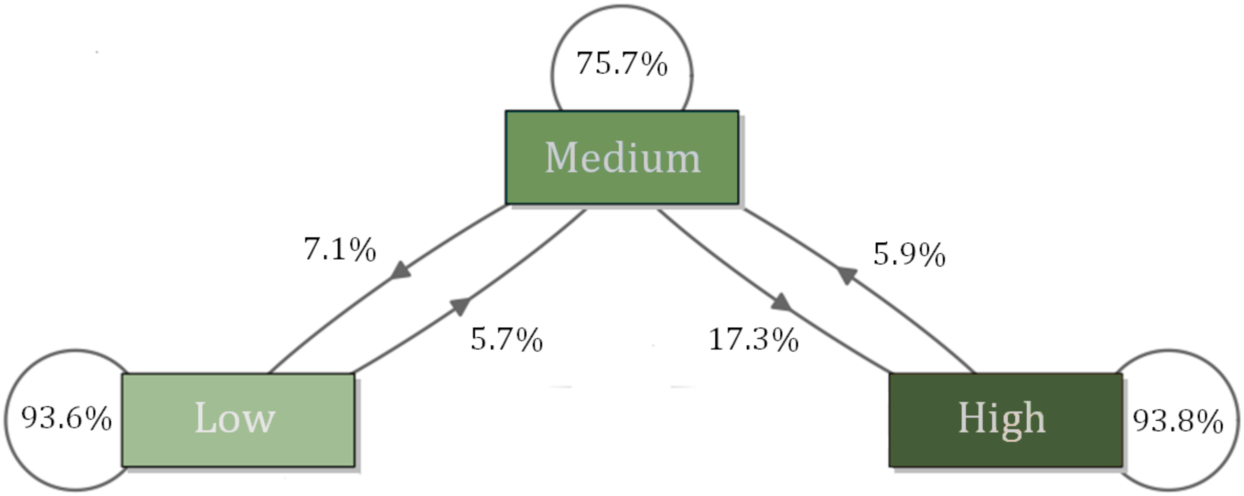

Figure 4-2. Multi-state transition diagram. Directional arrows depict the allowed transitions between states. The numbers represent the percentage of observed transitions between states (nb_{rs}/ nb_r × 100). Instantaneous transition from low to high kelp canopy state and vice versa are considered impossible in the model (hence the absence of arrows in the diagram); however, rare transitions from low to high and from high to low were observed in the data (<0.4%).

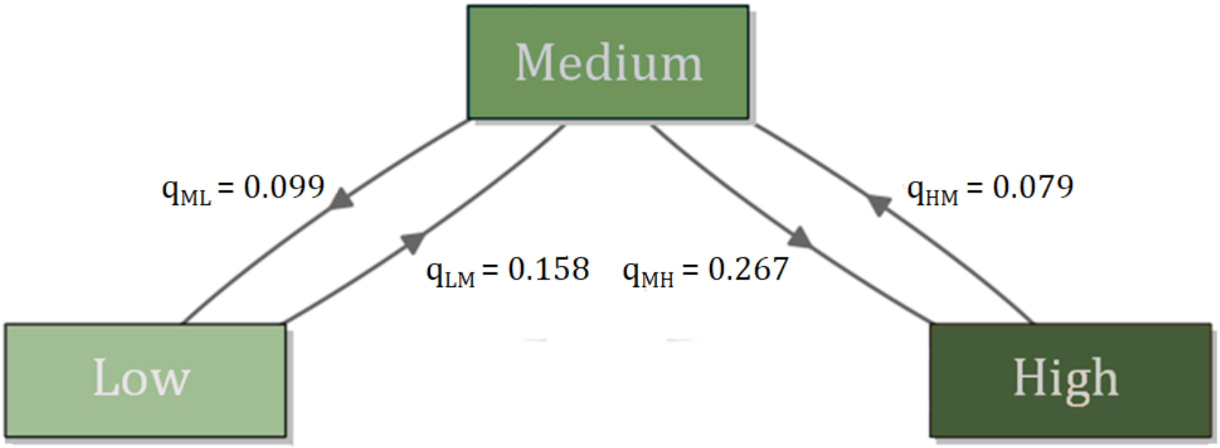

Figure 4-3. Baseline transition intensities estimated from the best fit multi-state transition model. Arrows depict transitions between kelp canopy states. The numbers also represent the estimated baseline hazards ($q_{rs.0}$), interpretable as the instantaneous risk of moving from one state to another when all covariates are set to 0 (i.e., the means of standardized covariates and otter occupation metric 1 [unoccupied by sea otters]).

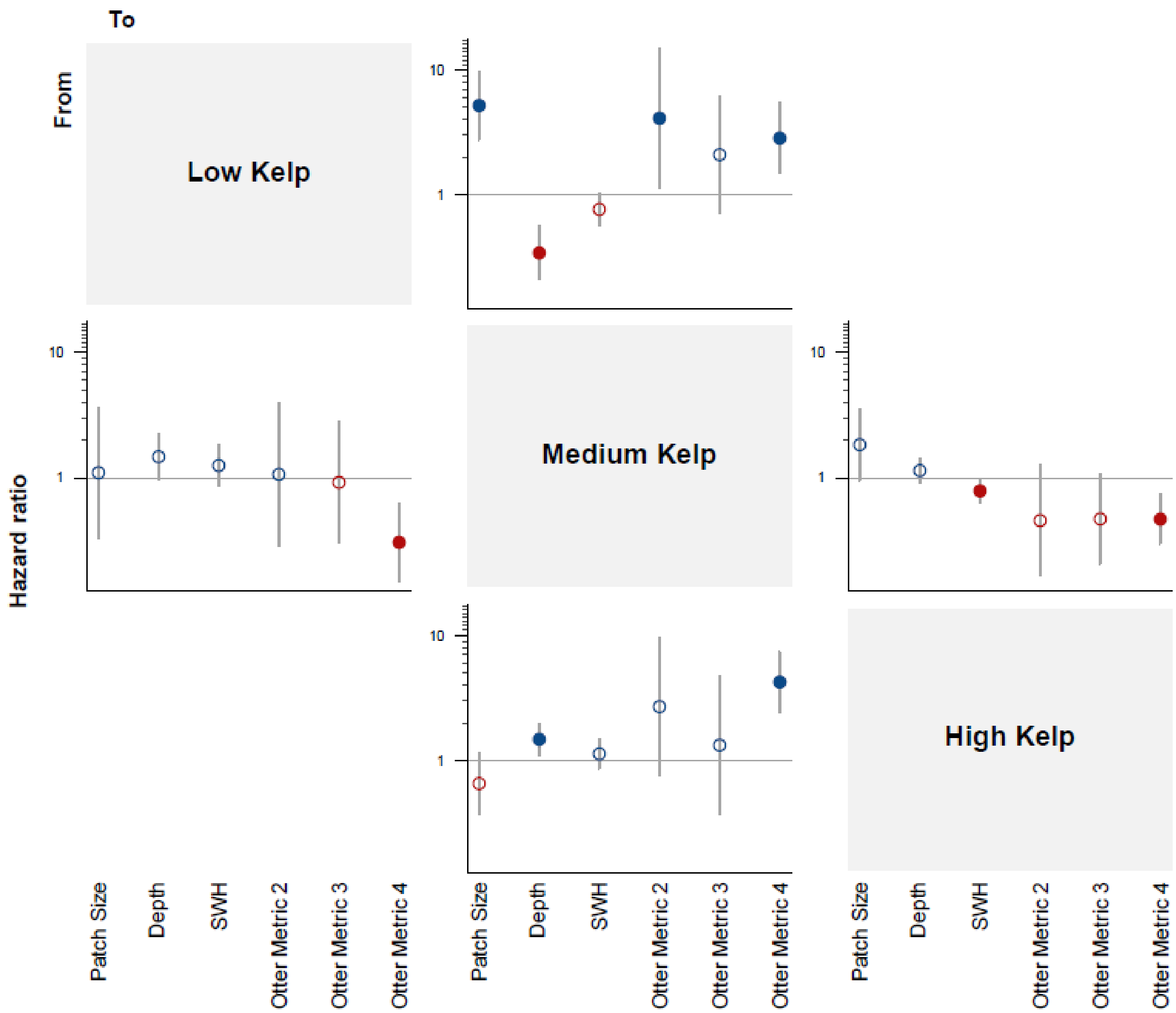

Figure 4-4. Hazard ratios (HR) and 90% confidence intervals as estimated by the best fit multi-state transition model. Each plot shows the estimated HR for transitions from the current state (rows) to a future state (columns). The HR of covariates can be interpreted as the multiplicative effect on the hazard, where values above 1 (in blue) indicate that the covariate is associated with an increased probability of state transition, and values below 1 (in red) indicate that the covariate is associated with a decreased probability of state transition. Predictors that are significantly different from 1 (90% CI does not cross overlap 1) are represented with solid points; predictors that are not significantly different from 1 are represented by open points. Numbers following Otter Metric indicate the level of sea otter occupation, where level 2: 0–2 years occupied, level 3: 3–9 years occupied, and level 4: 10–42 years occupied.

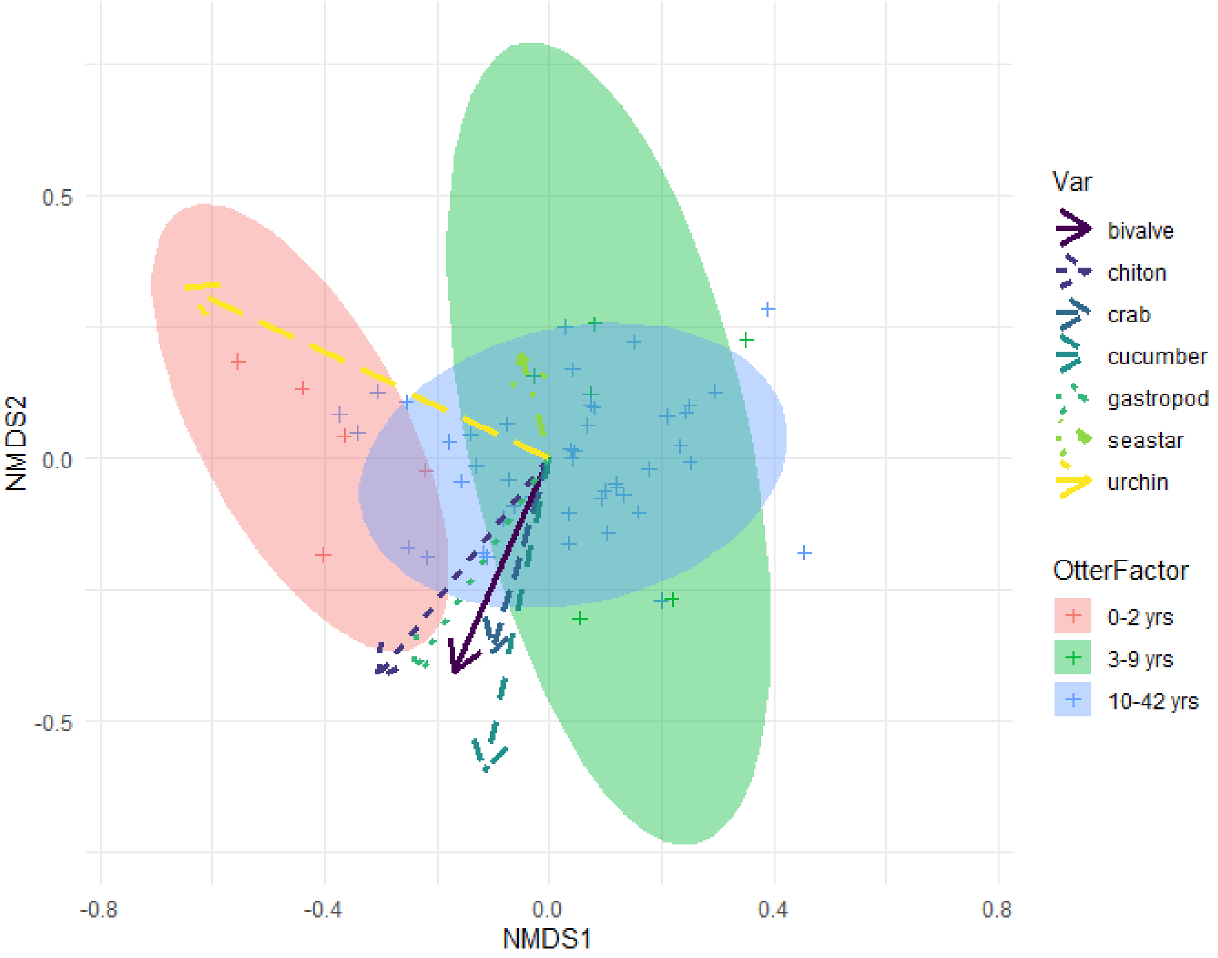

Figure 4-5. NMDS ordination of subtidal macroinvertebrate community composition based on the density of 7 invertebrate classes from 10 subtidal survey sites in Washington State. Both 98% probability ellipses for each otter occupation level (pink: unoccupied and 0–2 years occupied; green: 3–9 years occupied; blue: 10–42 years occupied) and vectors scaled by their r^2 value for each invertebrate class (bivalves, chitons, crabs, sea cucumbers, gastropods, sea stars, and urchins) are shown.

Chapter 5. Impacts of sea otter (*Enhydra lutris*) predation and abiotic processes on razor clams (*Siliqua patula*) in Washington State

5.1 ABSTRACT

Sea otters historically occurred in Washington State and were harvested during the maritime fur trade until their extirpation in 1911. Sea otters were translocated from Amchitka Island, Alaska to the Washington coast in 1969 and 1970, and the population has since grown and expanded its range to contain a large portion of the Washington coast, including the southern Washington coast where sea otters now co-occur with Pacific razor clams (*Siliqua patula*). Razor clams have been an important subsistence resource for Washington's coastal tribes for millennia, and became an important commercial and recreational resource in the temporary absence of sea otters. We evaluated the relative magnitude of human harvest, natural mortality, oceanographic factors, and sea otter predation effects on razor clam populations at 6 management beaches using sea otter foraging observations, sea otter survey data, razor clam density and size data, razor clam harvest data, and data on a suite of environmental variables. Foraging results indicated that sea otters consumed razor clams, and that allocation of foraging effort to razor clams varied by study area (Kalaloch area = 87%, Audubon Beach = 24%). The magnitude of sea otter predation effects also varied over time at Kalaloch Beach: sea otter-caused mortality surpassed natural mortality in 2018 when average sea otter density was 17.81 otters/km^2. Our model also estimated that sea otters selectively consumed recruit size clams at a rate over 25 times higher than pre-recruit size clams at Kalaloch Beach, despite the fact that pre-recruit clams were far more abundant. While we do not discount the importance of drivers of Pacific razor clam population dynamics outside of sea otter predation, our study

shows that sea otters play a key role in the dynamics of razor clam populations when present. This research aims to contribute to the information needed to make management decisions for both sea otters and razor clams in Washington State.

5.2 INTRODUCTION

Many marine mammal populations are currently recovering from population depletion following overharvest (Magera et al. 2013). Many marine mammals are high trophic level predators that exert strong top-down effects on marine ecosystems (Bowen 1997), thus there is an urgent need to understand both species- and ecosystem-level impacts of recovering populations. Increasing abundance of predators can have cascading impacts on marine food webs, and in some cases increased competition with human fisheries for the same prey (e.g., Beverton 1985, Treves and Karanth 2003, Marshall et al. 2015, Smith et al. 2015). Sea otters (*Enhydra lutris ssp.*) are a particularly salient example of this potential competition, in that they are a keystone species (Paine 1969) whose presence or absence can dramatically influence marine community structure (e.g., Estes and Palmisano 1974, Estes and Duggins 1995). Sea otter recovery may introduce significant new conservation challenges for Federal, State, and Tribal resource managers in areas where sea otters overlap with fisheries or other protected species (e.g., Estes and Vanblaricom 1985, Carswell et al. 2015, Raimondi et al. 2015, Estes and Carswell 2020), although sea otter recovery can also result in multiple social, economic, and ecological benefits (Duggins 1980, Estes and Duggins 1995, Estes et al. 2004, Reisewitz et al. 2006, Wilmers and Estes 2012, Hughes et al. 2013, Markel and Shurin 2015, Gregr et al. 2020).

Sea otters were heavily exploited throughout their range during the Pacific maritime fur trade in the 18th and 19th centuries, resulting in a loss of 99% of their historical numbers (Kenyon 1969, Larson and Bodkin 2015). As a result, sea otters were extirpated from portions of their range, including northern sea otters (*Enhydra lutris kenyoni*) from Washington State (Scheffer 1940, Kenyon 1969). Little information exists on the distribution and abundance of sea otters in Washington before extirpation, but it is believed that the last sea otter in Washington was shot in 1911 (Scheffer 1940). During the nearly 60 years that sea otters were absent from the coast of Washington following the maritime fur trade, recreational and commercial shellfisheries developed that target many of the same species that sea otters consume, including butter clam (*Saxidomus gigantea*), horse clam (*Tresus spp.*), razor clam (*Siliqua patula*), Dungeness crab (*Metacarcinus magister*), red rock crab (*Cancer productus*), sea urchin (*Strongylocentrotus spp.*), and California sea cucumber (*Parastichopus californicus*) (M. Ulrich, Washington Department of Fish and Wildlife, Personal communication, 2013; Hale et al. 2019). While four coastal treaty tribes (Hoh, Makah, Quileute, and Quinault Tribes) on the Washington coast have used marine mammals including sea otters and shellfish resources for millennia for ceremonial and subsistence purposes (Scheffer 1940, 1999; Singh 1956; Wessen 1982; Sepez 2008; Wessen et al. 2019), development of commercial and recreational shellfisheries in Washington is more recent, and it is likely that some of these shellfisheries could not have existed without the extirpation of sea otters (Bodkin et al. 2004).

In 1969 and 1970, 59 sea otters were translocated from Amchitka Island, Alaska to Washington as part of an effort to enhance sea otter recovery along the west coast of North America (Kenyon 1970, VanBlaricom 2015). Since this translocation, the Washington sea otter population has grown to over 2,785 individuals (Jeffries et al. 2019) and has expanded its range to contain a large portion of the Washington coast (Hale et al. 2022). While sea otter translocations throughout their range have been to the benefit of sea otter conservation (Bodkin 2015, Larson et al. 2021), their recovery in areas of historical occupation can introduce significant new conservation challenges, and in some cases conflicts with established fisheries. Sea otters can alter the size distribution, abundance, and spatial distribution of their invertebrate prey species by preferentially removing large, calorically rich, and easily captured prey (Estes et al. 1978, Ostfeld 1982, Kvitek et al. 1992, Fanshawe et al. 2003, Laidre and Jameson 2006). These changes in the invertebrate community may affect treaty and non-treaty recreational and commercial fisheries in WA, and could make current harvest levels unsustainable by decreasing the size, abundance, or density of some invertebrate species targeted in fisheries (VanBlaricom et al. 2001). For example, in 1996, the Makah Tribe's red sea urchin (*Strongylocentrotus franciscanus*) fishery in Neah Bay closed, concurrent with sea otter range expansion into the area and increased proportions of red sea urchins in sea otter diets (Lance et al. 2004, Laidre and Jameson 2006). Sea otter fisheries impacts are likely to vary spatially in WA, as the population growth and range expansion of sea otters since their translocation has created a spatial gradient in sea otter occupation time and density along the coast of Washington (Figure 5-1; Hale et al. 2022). As the majority of sea otter population growth in Washington has occurred in the southern portion of the sea otters' range since 2003 (south of La Push; Jeffries et al. 2019, Hale et al. 2022), and the majority of available habitat for range expansion exists on the outer coast in the southern portion of their range (Hale et al. 2022), there is potential for increased conflict between sea otters and fisheries in this area. This area is also home to the majority of WA's Pacific razor clam (*Siliqua patula*) populations, and treaty and non-treaty recreational and commercial razor clam fisheries.

The Pacific razor clam is a species of large marine bivalve mollusk characterized by its long narrow shell with olive to brown periostracum (Harbo 1997). Razor clam populations are found buried in the intertidal zone of open coast sandy beaches along the Washington coast (Crosman et al. 2019), with much less dense populations in the subtidal zone (D. Ayres, Washington Department of Fish and Wildlife, Personal communication, 2017) in water depths up to 55 m (Harbo 1997). The Quinault Indian Nation has long used razor clams (Crosman et al. 2019), and Washington State has actively managed a coastal commercial razor clam fishery since 1905 and a recreational razor clam fishery since 1929. Razor clam harvest is managed on a beach-by-beach basis based on season – razor clams are typically harvested September to June and spawn in late spring and early summer (Crosman et al. 2019). In addition to humans, razor clams are consumed by a variety of other predators, including sea otters (Kvitek and Oliver 1988, Laidre and Jameson 2006, Hale et al. 2019), Dungeness crabs (*Metacarcinus magister*; O'Clair and O'Clair 1998), some species of flatfish (including Pacific halibut, *Hippoglossus stenolepis*), birds (Tegelberg and Magoon 1969, Lassuy and Simons 1989), and perhaps Pacific gray whales (*Eschrichtius robustus*; S. Mazzone, Quinault Division of Natural Resources, Personal communication, 2017). Razor clam populations are also influenced by oceanographic and other regional and local scale abiotic processes. Razor clams broadcast spawn and their larval duration is 5–16 weeks (Lassuy and Simons 1989). As a result, the recruitment of larvae is largely dependent on oceanographic conditions and currents. Thus, razor clam abundance along the Washington coast is affected by human harvest, natural mortality, oceanographic factors that determine larval settlement, and (in a few areas in recent years) sea otter predation. The relative magnitude of these various effects has yet to be determined.

Sea otter consumption of razor clams has been observed in Washington (Laidre and Jameson 2006, Hale et al. 2019), although at present the distribution of sea otters limits their impacts to just a few of the major beaches where razor clam harvest occurs (Figure 5-1). However, as the sea otter population grows and expands, they will potentially affect razor clam populations on other beaches. There is therefore a need for a quantitative assessment to determine whether sea otter predation impacts are of sufficient magnitude to threaten the harvest of razor clams. Using stage-based Bayesian population models of the Pacific razor clam, we evaluated the potential impact of sea otters and a suite of environmental variables on razor clam populations between Kalaloch Beach and Long Beach Peninsula and characterize sea otter diet in a subset of these areas. Using these models, we examined how clam abundances and mortality rates from natural, harvest, and otter-caused mortality vary by beach. As scientific uncertainty about ecological interactions between recovering predators and prey species hinders progress towards resolving conflicts (Marshall et al. 2015), this research aims to contribute to the information needed to make management decisions for both sea otters and razor clams in WA.

5.3 METHODS

5.3.1 Study area

The Washington Department of Fish and Wildlife (WDFW) divides the recreational razor clam harvest area into five management beaches (Figure 5-1), including Long Beach (from the Columbia River north to the mouth of Willapa Bay), Twin Harbors (from Willapa Bay north to the south jetty at the mouth of Grays Harbor), Copalis Beach (from the north jetty at the mouth of Grays Harbor to the Copalis River), Mocrocks (from the Copalis River to the south boundary of the Quinault Indian Reservation), and Kalaloch (from the South Beach campground north to the Olympic National Park Beach Trail 3) (Figure 5-1). Razor clams are also found on a series of sand spits in the mouth of Willapa Bay (where the State's commercial razor clam fishery is conducted), on the Quinault Indian Reservation (including Point Grenville Beach; Figure 5-1), and other small beaches north of the Kalaloch area. On the three management beaches north of the mouth of Grays Harbor (Figure 5-1; Copalis, Mocrocks, and Kalaloch beaches), WDFW co-manages the razor clam resource with coastal tribes that have fishing rights in their usual and accustomed areas. The Quinault Indian Nation has fishing rights in the area that includes Copalis, Mocrocks, and Kalaloch management beaches. The Hoh Tribe and Quileute Nation also have fishing rights in the area that includes Kalaloch Beach and beaches to the north. Management of the recreational clam fishery at Kalaloch Beach is also conducted cooperatively by WDFW and Olympic National Park.

Based on aerial and ground surveys (Jeffries et al. 2019), sea otters first colonized the Kalaloch Beach area in 2005 and Audubon Beach in 2015 (Figure 5-1; Hale et al. 2022). At the time of the July 2019 Washington sea otter population survey, sea otters were counted for the first time at Point Grenville Beach (2 adults and 1 pup) and the southernmost sea otter (a single animal) was observed just north of Copalis Beach (Jeffries et al. 2019). Sea otters have yet to colonize areas or be observed during annual surveys in areas near Twin Harbors or Long Beach. The beaches along the southern part of the Washington coast are fairly uniform in their physical characteristics (Lewin et al. 1989).

5.3.2 Sea otter foraging data collection and analysis

Sea otter foraging data were collected from two areas near razor clam management beaches (Kalaloch Area [including Beach 6, Beach 4, Kalaloch Campground, Beach 1, and South Beach Campground] and Audubon Beach; Figure 5-1). As described in Tinker et al. (2022), sea otter diet composition was estimated on the basis of consumed wet edible biomass using a Monte Carlo re-sampling algorithm to calculate rate of energy gain (kilocalories/minute), rate of mass gain (grams/minute), estimates of diet composition, and uncertainty estimates for each. We also quantified the total number of razor clams consumed, both overall (NC_{tot}) and for each of two size classes, pre-recruits (NC_P = consumed clams <76 mm) and recruits (NC_R = consumed clams ≥76 mm) in the Kalaloch Area, for use as data input for the razor clam population model for Kalaloch Beach.

5.3.3 Razor clam population data

Fishery independent razor clam density and size data have been collected during annual surveys by coastal tribes (Hoh Tribe, Quileute Nation, and Quinault Indian Nation) and WDFW from 2001 to present on Copalis and Mocrocks beaches, and by coastal tribes, Olympic National Park, and WDFW from 2000 to present on Kalaloch Beach. The Quinault Indian Nation has conducted annual biomass assessments of razor clams on Point Grenville Beach since 2001. WDFW has also conducted annual biomass assessments on Twin Harbors and Long Beach since 2000. Surveys are typically conducted in June or July each year. At each beach, razor clam resource surveys are conducted along randomly selected transects perpendicular to the shore (Washington Department of Fish and Wildlife 2019). Transects start from a fixed point about 600 feet above the low tide line, and samples are taken at 50-foot intervals from this point towards the ocean (e.g., 50, 100, etc.), up to 600 feet. Each interval location is termed an elevation, with up to 12 possible elevations per transect. Six plots are usually sampled at each elevation within each transect, randomly selected on either the north or south side of the transect. Each plot is an aluminum ring that is ½ square meter in area with a depth of 48 inches, and is sampled using the Pumped Area Method. The Pumped Area Method uses water pumped from the surf or nearby lagoon to liquefy sand within the plot (Washington Department of Fish and Wildlife 2019). This sampling method assumed that all clams within each plot float to the surface upon liquefication, allowing for collection and measurement. After measurement, each clam is returned to the sand. These surveys result in razor clam density and size estimates for each management beach. Clam densities can be extrapolated into total abundances for each beach based on the total area of the beach and the density of randomly sampled clams in plots. Clams measuring less than 3 inches (< 76 mm) are termed "pre-recruits" and clams measuring at least 3 inches (≥ 76 mm) are termed "recruits", as this is the typical size at which razor clams begin to "show" in the sand (e.g., leave a hole or dimple in the sand by withdrawing their neck or starting to dig) and therefore recruit into the harvestable population as clammers search for clam "shows" to determine where to dig.

5.3.4 Razor clam harvest data

Data are collected by the State to estimate seasonal recreational harvest removal (including wastage) at Kalaloch, Copalis, Mocrocks, Twin Harbors, and Long Beach. On co-managed beaches (Kalaloch, Copalis, Mocrocks), the Quinault Indian Nation also estimates seasonal harvest removal. Finally, the Quinault Indian Nation tracks seasonal harvest removal from Point Grenville Beach. The Hoh Tribe does not currently maintain records on razor clam harvest at Kalaloch Beach, and the Quileute Nation did not provide harvest estimates for Kalaloch Beach. For our models, State and tribal harvest (including commercial, subsistence, and ceremonial use) data were summed for each harvest season (September–June) for the 2000–2001 to 2019–2020 seasons at Kalaloch, and 2001–2002 to 2019–2020 seasons at Mocrocks and Copalis Beach. Only State harvest data were used for Twin Harbors and Long Beach (2000–2001 to 2019–2020 seasons) as no tribal harvest occurs on those beaches, and only Quinault Indian Nation harvest data (2001–2002 to 2019–2020 seasons) were used for Point Grenville Beach as no recreational harvest occurs there. Harvest data are reported as the total number of clams removed, and are not divided into pre-recruit and recruit size clams. However, the vast majority of clams harvested are recruit size animals (D. Ayres, Washington Department of Fish and Wildlife, Personal communication, 2021), and thus we assumed that all harvest removal was of recruit size clams. We assumed that the majority of harvest came from 300 – 500 ft beach elevations (D. Ayres, Washington Department of Fish and Wildlife Personal communication, 2021).

5.3.5 Sea otter occupation time and density

As described in Hale et al. (2022), the first post-translocation surveys of sea otters in Washington occurred in 1977–1987 (excluding 1979–1980, 1982, 1984, 1986; Jameson et al. 1982, 1986). Standardized ground and aerial surveys of sea otters were conducted by USGS/USFWS and WDFW in 1989–2019 (excluding 1997, 2009, 2018) and these data were summarized in annual reports (e.g., Jeffries et al. 2019). Using data from these summer sea otter surveys (1977–2019), we calculated sea otter density in each year. As in Hale et al. (2019), we used the kernel density estimate (KDE) tool in ArcGIS 10.8 to create a continuous smoothed 2-D raster surface representing sea otter density in each year. Sea otter densities were then extracted from raster cells at each razor clam survey transect on Kalaloch Beach in each year as a metric of sea otter impact. As sea otters were only recently counted at Point Grenville (July 2019), we were unable to include sea otter density as a covariate in the model of razor clam population dynamics at Point Grenville Beach. There have been no sea otters recorded at Mocrocks Beach, Copalis Beach, Twin Harbors Beach, and Long Beach during annual summer surveys.

5.3.6 Environmental data

We focused our analyses on environmental measures directly related to mechanisms driving larval transport and habitability of the nearshore environment for razor clams, including the North Pacific Gyre Oscillation (NPGO), Bakun Upwelling Index (UI), salinity, temperature, significant wave height (SWH), and chlorophyll-*a* concentration. Monthly average North Pacific Gyre Oscillation (NPGO) indices were downloaded from [http://www.o3d.org/npgo/npgo.php]. These indices use the NPGO spatial pattern outlined in Di Lorenzo et al. (2008) and are calculated at the gyre-scale. Using the monthly average index, we calculated the average annual NPGO from July–June prior to razor clam surveys that are conducted in June or July each year.

We used monthly Bakun upwelling index values at latitudes that bracket our study region (45N and 48N) from NOAA Pacific Fisheries Environmental Laboratory (https://www.pfeg.noaa.gov/). Indices were averaged between the two latitudes from July–June prior to razor clam surveys in each year. Positive values of the Bakun upwelling index indicate upwelling and negative values indicate downwelling. Salinity (PSU) and temperature (ºC) were recorded in the surf zone at each beach by the Olympic Region

Harmful Algal Bloom Partnership. Measurements were taken at each beach every few days (average days between samples = 5) throughout the year. Using these measurements, we calculated the maximum salinity and temperature from July–June prior to the razor clam surveys each year at each beach when data were available.

Average winter (October–March) significant wave height measurements (in meters) were determined from National Data Buoy Center Buoy #46041 (approximately 31.81 km west of Cape Elizabeth; 47 N) in each year prior to razor clam surveys. Significant wave height is calculated as the average of the highest one-third of all of the wave heights during the 20-minute sampling period each hour. We quantified the concentration of chlorophyll-a (hereafter termed chl *a*), a proxy for phytoplankton abundance, using data collected by the Olympic Coast Region Harmful Algal Bloom Partnership. Bottle samples were taken in the surf zone at each beach approximately weekly (average number of days between samples = 6) throughout the year. Using these measurements, we calculated the average chlorophyll concentration from July–June prior to each razor clam survey when data were available.

5.3.7 Model design

We used size-structured population models to analyze razor clam population dynamics, with the goals of 1) elucidating the relative importance of various sources of mortality, and 2) assessing the degree to which mortality rates and larval settlement are affected by a suite of environmental variables. We note that settlement and mortality rates were not directly observed during razor clam population surveys, but rather were latent unobserved parameters estimated during model fitting. We analyzed razor clam mortality rates using a competing hazards model, where instantaneous mortality is treated as the sum of several cause-specific hazards. Specifically, at any instant we assume that razor clams are subject to possible mortality from human harvest, sea otter predation, or other factors (collectively referred to as natural mortality), and the overall frequency of mortality events from each cause depends on the relative magnitude of the hazards (Ergon et al. 2018). Annual survival is then estimated as an aggregate function of cumulative hazard rates within given time intervals (Ergon et al. 2018). This approach allowed us to compare the relative importance of natural, sea otter-caused, and harvest mortality, and establish a link between annual population dynamics and environmental and climate drivers. We assume that all vital rates vary as a function of size class (pre-recruits <76 mm, and recruits ≥76 mm), year, beach elevation, and several environmental variables.

For clams of recruit size class (R) in a given year (t) and beach elevation (i), we estimated hazard rates associated with natural mortality ($M^{N}_{R,t,i}$), otter mortality ($M^{O}_{R,t,i}$) and harvest mortality ($M^{H}_{R,t,i}$) as log-linear functions:

$$M^{N}_{R,t,i} = \exp\left(\gamma_R + \left[\sum_j \mathbf{X}_{S,j,t} \cdot \beta_{S,j}\right] + f_i^{N} + \varepsilon_{R,t}\right) \tag{1}$$

$$M^{O}_{R,t,i} = \exp\left(\alpha_1 + \alpha_2 \cdot Ott_t + f_i^{O}\right) \tag{2}$$

$$M^{H}_{R,t,i} = \exp\left(\zeta_0 + \zeta_t + f_i^{H}\right) \tag{3}$$

In equation (1), γ_R represents the mean log hazards rate from natural causes (an estimated parameter), $\mathbf{X}_{S,j,t}$ is a covariate effects matrix specifying the values of environmental variables (j = 1,2…J) at time t, $\beta_{S,j}$ is a vector of estimated parameters that determine the effects of the J environmental variables on clam mortality (recruits and pre-recruits), f_i^N is a non-linear function specifying the effect of beach elevation on natural mortality (estimated as an autoregressive AR(1) effect to allow for autocorrelation of adjacent elevation values, and re-scaled such that the maximum value = 0) and $\varepsilon_{R,t}$ is a random effects term specifying unexplained variation in natural mortality across years (drawn from a normal distribution with mean of 0 and standard deviation σ_R). In equation (2), α_1 and α_2 are estimated parameters describing (respectively) the mean log hazards for recruits from otter predation and the effect of sea otter density (Ott) on recruit mortality, while f_i^O is a non-linear function specifying the effect of beach elevation on sea otter predation mortality (estimated as an autoregressive AR(1) effect and re-scaled such that the maximum value = 0). In equation (3), ζ_0 and ζ_t are estimated parameters describing (respectively) the mean log hazards for recruits from harvest and the log ratio of harvest hazards in year t relative to this mean value (ζ_t is drawn from a normal distribution with mean of 0 and standard deviation σ_H), while f_i^H is a non-linear function specifying the effect of beach elevation on harvest mortality (we set the values of f_i^H, based on expert judgement [D. Ayres, Washington Department of Fish and Wildlife Personal communication, 2021], as the log of the ratio of harvest rates at elevation i relative to the elevation that experienced maximum harvest rates).

For clams of pre-recruit size class (*P*) in a given year (*t*) and beach elevation (*i*), we assume that harvest mortality was effectively 0 (despite small amounts of wastage) and we estimated hazards associated with natural mortality ($M_{P,t,i}^{N}$) and otter mortality ($M_{P,t,i}^{O}$) as log-linear functions:

$$M_{P,t,i}^{N} = \exp\left(\gamma_P + \left[\sum_j \mathbf{X}_{S,j,t} \cdot \beta_{S,j}\right] + f_i^N\right) \tag{4}$$

$$M_{P,t,i}^{O} = M_{R,t,i}^{O} \cdot \exp(\psi) \tag{5}$$

In equation **Error! Reference source not found.**, γ_P represents the mean log hazards from natural causes for pre-recruits, which we fixed at a value of 1.57 (corresponding to the previously published survival rate value of 0.09; Nickerson 1975, Crosman et al. 2019), $\mathbf{X}_{S,j,t}$ is a covariate effects matrix specifying the values of environmental variables (j = 1,2…J) at time t, $\beta_{S,j}$ is a vector of estimated parameters that determine the effects of the *J* habitat variables on clam mortality (pre-recruit and recruit), and f_i^N specifies the effect of beach elevation (as described above for recruits). In equation (5), the hazard rate from otter predation for pre-recruits is calculated as the product of the hazard rate for recruits and exp(ψ), where estimated parameter ψ is the log ratio of pre-recruit hazards relative to recruit hazards from sea otter predation.

We calculated annual changes in abundance based on three vital rates: survival (*S*), larval settlement (*LS*), and growth transition probability (*G*). We computed annual survival rates for recruits and pre-recruit size classes as derived parameters, varying by year and beach elevation, based on the summation of cause-specific hazard rates:

$$S_{R,t,i} = \exp\left(-[M_{R,t,i}^{N} + M_{R,t,i}^{O} + M_{R,t,i}^{H}]\right) \tag{6}$$

$$S_{P,t,i} = \exp\left(-[M_{P,t,i}^{N} + M_{P,t,i}^{O}]\right) \tag{7}$$

Larval settlement was assumed to vary stochastically across years but to be constant across beach elevations (and thus variation in abundance of razor clams across elevations is assumed to result from differential survival rather than differential settlement):

$$LS_t = \exp\left(\nu + \left[\sum_j \mathbf{X}_{LS,j,t} \cdot \beta_{LS,j}\right] + \varepsilon_{LS,t}\right) \tag{8}$$

In equation (8), ν represents the overall mean log settlement rate (an estimated parameter), $\mathbf{X}_{LS,j,t}$ is a covariate effects matrix specifying the values of environmental variables (j = 1,2…J) at time t, $\beta_{LS,j}$ is a vector of estimated parameters that determine the effects of the J habitat variables on larval settlement rates, and $\varepsilon_{LS,t}$ is a random effects term specifying unexplained variation in settlement rates across years (drawn from a normal distribution with mean of 0 and standard deviation σ_{LS}). The growth transition probability from pre-recruits to recruits (G) was set to a value of 0.95 based on available literature (Nickerson 1975, Crosman et al. 2019). Combining vital rates, we calculated annual expected abundance for pre-recruits and recruits at each beach elevation (i) as:

$$N_{P,t,i} = \left(LS_t + N_{P,t-1,i} \cdot (1-G)\right) \cdot S_{P,t,i} \tag{9}$$

$$N_{R,t,i} = \left[\left(N_{P,t-1,i} \cdot G\right) \cdot \sqrt{S_{P,t,i}} \cdot \sqrt{S_{R,t,i}}\right] + \left[N_{R,t-1,i} \cdot S_{R,t,i}\right] \tag{10}$$

We also needed to track the total number of razor clams dying each year, as this allowed us to compute expected harvest numbers and proportional number of otter predation events for pre-recruits vs. recruits. Re-arranging equations (9) and (10), we calculated total deaths (D) each year for pre-recruits and recruits:

$$D_{P,t,i} = \left(LS_t + N_{P,t-1,i} \cdot (1-G)\right) \cdot \left(1 - S_{P,t,i}\right) \tag{11}$$

$$D_{R,t,i} = \left[\left(N_{P,t-1,i} \cdot G\right) \cdot \left(1 - \sqrt{S_{P,t,i}} \cdot \sqrt{S_{R,t,i}}\right)\right] + \left[N_{R,t-1,i} \cdot \left(1 - S_{R,t,i}\right)\right] \tag{12}$$

The expected number of harvested clams at each beach elevation was then calculated as:

$$Hexp_{t,i} = Area_i \cdot D_{R,t,i} \cdot \left(M^{H}_{R,t,i} \middle/ M^{N}_{R,t,i} + M^{O}_{R,t,i} + M^{H}_{R,t,i} \right) \tag{13}$$

where $Area_i$ is the total square meters of beach at elevation i, and the right-hand term in equation (13) represents the expected proportional allocation of total deaths to harvest mortality. Similarly, the expected number of clams of each size class consumed by sea otters at each beach elevation was calculated as:

$$NCexp_{P,t,i} = Area_i \cdot D_{P,t,i} \cdot \left(M^{O}_{P,t,i} \middle/ M^{N}_{P,t,i} + M^{O}_{P,t,i} \right) \tag{14}$$

$$NCexp_{R,t,i} = Area_i \cdot D_{R,t,i} \cdot \left(M^{O}_{R,t,i} \middle/ M^{N}_{R,t,i} + M^{O}_{R,t,i} + M^{H}_{R,t,i} \right) \tag{15}$$

Combining the results of equations **Error! Reference source not found.** and (15) we can then estimate the total expected proportion of consumed clams that were pre-recruits vs. recruits ($PCPexp$) as:

$$PCPexp = \sum_t \sum_i NCexp_{P,t,i} \middle/ \sum_t \sum_i NCexp_{R,t,i} \tag{16}$$

The calculations and dynamics summarized in equations (1) to (16) represent the process model. To estimate the most likely values of the parameters in these equations (summarized in Table 5-1), we compared expected values of key latent parameters with observed data sets (the "data model") while explicitly accounting for uncertainty in the observation process. Specifically, we assumed that observed annual survey counts (*Cobs*) of pre-recruits and recruits, for each beach elevation, were described by negative binomial distributions:

$$Cobs_{P,t,i} \sim Negative\_binomial\left(mean = Area_i \cdot N_{P,t,i}, invscale = \phi_P\right) \tag{17}$$

$$Cobs_{R,t,i} \sim Negative\_binomial\left(mean = Area_i \cdot N_{R,t,i}, invscale = \phi_R\right) \tag{18}$$

Where the degree of over-dispersion of counts relative to a Poisson distribution (for pre-recruits and recruits, respectively) is determined by the estimated inverse scale parameters ϕ_P and ϕ_R. We assumed that observed harvest counts (*Hobs*) for each year were described by a Poisson distribution:

$$Hobs_t \sim Poisson\left(mean = \sum_i Hexp_{t,i}\right) \tag{19}$$

Finally, we assumed that the observed number of sea otter predation events of pre-recruit clams (NC_P), relative to the total observed predation events for all size classes (NC_{tot}), was described by a binomial distribution:

$$NC_P \sim binomial\left(n = NC_{tot},\ prob = PCPexp\right) \tag{20}$$

We analyzed data from each beach separately to allow for the inclusion of different environmental covariates (based on data coverage and hypothesized effects of environmental covariates). Table 5-2 includes the environmental covariates included in the model for each beach. We recognize that some environmental covariates (like chl *a*) likely affect both larval settlement and clam survival, but due to the nature of the data (e.g., larval settlement was not directly observed) we were unable to include the same environmental covariate as a predictor for larval settlement and clam survival as this would result in an identifiability issue. Similarly, due to identifiability issues, we were not able to estimate the effects of environmental covariates separately for pre-recruit and recruit size clams.

5.3.7 Model evaluation

Model fitting was accomplished using standard Markov Chain Monte Carlo (MCMC) methods. The models were coded and fit using STAN programming language (Stan Development Team 2022) implemented using the package CmdStanR (v0.4.0; Gabry and Cešnovar 2021) in *R* version 4.1.0 (R Core Team 2021). Model convergence was assessed by visual inspection of trace plots of the Markov Chains to ensure that they were well mixed, not autocorrelated, and were stationary, and by formally evaluating convergence by applying the Gelman-Rubin diagnostic test to the MCMC output (Hobbs and Hooten 2015). Potential scale reduction factor (psrf) of the Gelman-Rubin statistic < 1.1 indicates convergence was reached (Brooks and Gelman 1997). Model goodness of fit was assessed using posterior predictive checks (Gelman et al. 2004, Hobbs and Hooten 2015, Conn et al. 2018), where data are simulated under the fitted model by sampling from the posterior distribution and then compared to the observed data. We used the sum of Pearson's chi-squared residuals of observed recruit clam abundance vs. expected abundance as the discrepancy function. A well-fit model would have an associated Bayesian *P*-value within the range 0.3–0.7. Oceanographic and environmental covariates were considered significant if ≥ 80% of the coefficient posterior distribution was either above or below zero.

5.4 RESULTS

5.4.1 Sea otter foraging

Foraging records consisted of 63 foraging bouts from the Kalaloch area (Beach 1, Beach 4, Beach 6, Kalaloch Campground, and South Beach) and 43 bouts from Audubon Beach, collected between 21 February 2015 and 19 January 2019. Long term average rate of energy gain was 5.69 kcal/min for the Kalaloch area and 17.43 kcal/min for Audubon Beach. Approximately 91% of dives in the Kalaloch area resulted in successful prey capture, compared to 84% of dives at Audubon Beach. The dominant prey taxa (prey taxa making up more than 15% of consumed biomass) in the Kalaloch area were razor clams (*Siliqua patula*, percent of diet: 61.35%, mass intake: 5.74 g/min). The dominant prey taxa at Audubon Beach were Dungeness crabs (*Metacarcinus magister*, percent of diet: 43.16%, mass intake: 23.91 g/min), followed by gaper clams (*Tresus capax*, percent of diet: 29.90%, mass intake: 76.25 g/min). Sea otters in the Kalaloch area consumed razor clams with a mean size of 56.67 mm and handled them in an average of 12.58 seconds, compared to 58.41 mm and 12.62 seconds at Audubon Beach. Sea otters allocated most of their foraging effort to razor clams (*Siliqua patula*) in the Kalaloch area (87%), while sea otters at Audubon Beach allocated most of their foraging effort (40%) to Dungeness crabs (*Metacarcinus magister*).

5.4.2 Model diagnostics

All models converged well, with well mixed-chains providing posterior estimates for all parameters (Table 5-A1). The maximum Gelman-Rubin convergence diagnostic (psrf) for any fitted model parameter in any model was 1.38 (Table 5-A1) and all other psrf statistics were <1.33. Posterior predictive checks indicated moderate to good fit of the model to the data with associated Bayesian *P* values of 0.41–0.83 (Table 5-A1).

5.4.3 Razor clam population model: Kalaloch Beach

Model results indicated that the hazard rate for sea otter-caused mortality was approximately 25 times higher for recruit size clams than pre-recruit size clams (ψ = -3.23). No environmental covariates were significant in explaining variation in larval settlement (Table 5-3), but several covariates affected clam survival. Higher values of significant wave height (SWH) were associated with decreased clam survival (β_{S1} 80% CI = 0.07, 0.20) and higher temperature was associated with increased clam survival (β_{S2} 80% CI = -0.36, -0.22). Relative natural mortality was highest at the 50-ft beach elevation (farthest from the surf; Figure 5-2). Relative otter mortality was lowest at the 50- and 100-ft beach elevations and highest between 350- and 600-ft elevation (Figure 5-2). Contributions to recruit clam mortality varied over time (Figure 5-3): natural mortality exceeded both harvest mortality and otter mortality through most of the time series, until sea otter-caused mortality surpassed natural mortality in 2018. This pattern in sea otter mortality over time was consistent across 200 – 600 ft beach elevations.

5.4.4 Razor clam population model: Point Grenville Beach

North Pacific Gyre Oscillation indices were significant in the model, and higher NPGO indices were associated with increased larval settlement (β_{L1} 80% CI = 0.10, 0.74). Both significant wave height and salinity were significant in the model and higher SWH and salinity were associated with decreased clam survival (β_{S1} 80% CI = 0.08, 0.18; β_{S3} 80% CI = 0.13, 0.24). Temperature was also significant in the model, and higher temperature was associated with increased clam survival (β_{S2} 80% CI = -0.20, -0.07). Natural mortality was highest at 50 ft beach elevation, and lowest between 300 and 500 ft beach elevation.

5.4.5 Razor clam population model: Mocrocks Beach

Upwelling indices were significant in the model, and higher UI were associated with decreased larval settlement (β_{L2} 80% CI = -0.60, -0.004). Significant wave height was significant in the model, and higher SWH was associated with decreased clam survival (β_{S1} 80% CI = 0.09, 0.19). Temperature was also significant in the model, and higher temperatures were associated with increased clam survival (β_{S2} 80% CI = -0.11, -0.005). Natural mortality was highest at 50 ft beach elevation, and lowest between 300 and 450 ft beach elevation.

5.4.6 Razor clam population model: Copalis Beach

Upwelling indices were significant in the model and were associated with decreased larval settlement (β_{L2} 80% CI = -0.69, -0.17). Salinity was significant in the model, and higher salinity was associated with increased clam survival (β_{S3} 80% CI = -0.21, -0.07). Natural mortality was highest at 50 ft beach elevation, and lowest between 300 and 450 ft beach elevation.

5.4.7 Razor clam population model: Twin Harbors

North Pacific Gyre Oscillation indices were significant in the model, and higher NPGO indices were associated with increased larval settlement (β_{L1} 80% CI = 0.23, 0.75). Upwelling indices were also significant in the model, and higher UI were associated with decreased larval settlement (β_{L2} 80% CI = -0.89, -0.34). Significant wave height, temperature, and salinity were significant in the model, and were associated with decreased clam survival (β_{S1} 80% CI = 0.15, 0.27; β_{S2} 80% CI = 0.004, 0.12; β_{S3} 80% CI = 0.06, 0.15). Chlorophyll was significant in the model, and higher chlorophyll was associated with increased clam survival (β_{S4} 80% CI = -0.23, -0.12). Natural mortality was highest at 50 ft beach elevation, and lowest between 300 and 450 ft beach elevation.

5.4.8 Razor clam population model: Long Beach

No environmental covariates were significant in explaining variation in larval settlement (Table 5-3). Significant wave height, temperature, salinity, and chlorophyll were all significant in the model, and higher SWH, temperature, salinity, and chlorophyll were associated with decreased clam survival (β_{S1} 80% CI = 0.09, 0.17; β_{S2} 80% CI = 0.02, 0.10; β_{S3} 80% CI = 0.28, 0.37; β_{S4} 80% CI = 0.07, 0.16). Natural mortality was highest at 50 ft beach elevation, and lowest between 300 and 450 ft beach elevation.

5.5 DISCUSSION

5.5.1 Sea otter foraging

We found that sea otters in a longer occupied area had a lower energy intake rate compared to otters in a more recently occupied area (5.69 kcal/min for the Kalaloch area, occupied since 2005 vs. 17.43 kcal/min for Audubon Beach, occupied since 2015). This is consistent with patterns outlined in other studies (e.g., Estes et al. 1981, Ostfeld 1982, Kvitek and Oliver 1992, Tinker et al. 2012, Weitzman 2013, Hale et al. 2019, Foster 2021). This observed decrease in energy intake rate with increased sea otter occupation time may be larger than observed in other areas, as energy intake rates drop quickly for sea otters foraging in soft sediment habitats (e.g., Weitzman 2013). The dominant prey taxa in sea otter diet in the Kalaloch area were razor clams (*Siliqua patula*), and the dominant prey taxa at Audubon Beach were Dungeness crabs (*Metacarcinus magister*), followed by gaper clams (*Tresus capax*). This finding is consistent with previous studies that suggest that Dungeness crab are the preferred prey in soft-sediment habitat, but that as they are depleted, clams appear to be the next most important prey and that bivalve productivity is sufficient to sustain a sea otter population long-term (Garshelis et al. 1986, Kvitek and Oliver 1992, Estes and Bodkin 2002, Wolt et al. 2012, Foster 2021). This was also reflected in how sea otters allocated their foraging effort between prey types: sea otters in the Kalaloch area allocated the majority (87%) of their foraging effort to razor clams (*Siliqua patula*), while sea otters at Audubon Beach allocated most of their foraging effort (40%) to Dungeness crabs (*Metacarcinus magister*). Presumably prey species associated with soft-bottom communities, such as clams and crabs, were the resources that allowed historic population levels of sea otters to thrive from Point Grenville to the mouth of the Columbia River (Bowlby et al. 1988).

5.5.2 Razor clam population dynamics

Our model estimated that sea otters selectively consume recruit size razor clams at a rate over 25 times higher than pre-recruit size clams at Kalaloch Beach, despite the fact that pre-recruit clams were far more abundant. This finding is consistent with optimal foraging theory. While we do not discount the importance of drivers of Pacific razor clam population dynamics outside of sea otter predation, our study shows that sea otters play a key role when present. Our model results illustrate that contributions to recruit clam mortality varied with beach elevation: otter-caused recruit clam mortality was lowest at the 50 and 100 ft beach elevations (farthest from the surf) and highest between 350 and 600 ft elevation at Kalaloch Beach (Figure 5-2). This result is consistent with observations of sea otters foraging very near shore at high tide at times and is consistent with the fact that sea otters typically do not forage in water <5 m deep (Bodkin et al. 2004, Laidre et al. 2009) which precludes them from foraging higher up on the beach. This result also highlights the spatial overlap of razor clam harvest and sea otter predation on razor clams, as the majority of razor clam harvest is assumed to occur between from 300 – 500 ft beach elevations (D. Ayres, Washington Department of Fish and Wildlife, Personal communication, 2021), where otter-caused mortality was also estimated to be at its highest (Figure 5-2). Contributions to recruit clam mortality also varied over time as the sea otter population became more dense at Kalaloch Beach: sea otter-caused mortality surpassed natural mortality in 2018 when average sea otter density was 17.81 otters/km^2. Our results demonstrate the initial impacts of sea otters on razor clam populations over a period of recolonization, and do not necessarily reflect the long term effects as sea otters reach equilibrium. For example, in Pismo Beach, California, the initial recolonization of that area by sea otters in the 1970s to 1980s precluded a pismo clam (*Tivella stultorum*) recreational fishery (Wendell et al. 1986). However, decades later there is evidence of incredibly high pismo clam recruitment and abundance (e.g., 2017, 2020, and 2021; California Department of Fish and Wildlife 2020), illustrating continued changes in food web dynamics once sea otters reach equilibrium abundance.

North Pacific Gyre Oscillation (NPGO) was significant in models for Point Grenville and Twin Harbors, and an increased NPGO index was associated with increased larval settlement. This result is consistent with the pattern observed with mussels on the Oregon coast (Menge et al. 2009). Upwelling indices were significant in models for Mocrocks, Copalis and Twin Harbors Beaches, and increased upwelling indices were associated with decreased larval settlement. This finding is consistent with previous research on larval transport that has found that larvae can be transported away from shore in surface currents during strong upwelling events, limiting larval recruitment (e.g., Morgan 2014). We also found that Significant Wave Height was significant for the majority of beaches (Kalaloch, Point Grenville, Mocrocks, Twin Harbors and Long Beach), and was associated with decreased clam survival, suggesting that winter storms may result in significant razor clam mortality.

Temperature, salinity, and chl *a* had varying associations with clam survival depending on the beach. Increased temperature was significantly associated with increased clam survival for three northern beaches (Kalaloch, Point Grenville, and Mocrocks) and associated with decreased survival at the two southernmost beaches (Twin Harbors and Long Beach). Given that strong year classes in the razor clam population coincided with reduced maximum temperatures off the coast of Washington in a previous study (Schlechte 1996), it is unclear what might be driving this varying relationship between temperature and clam survival. Similarly, increased salinity was significantly associated with decreased clam survival at Point Grenville, Twin Harbors, and Long Beach, but increased clam survival at Copalis, and increased chl *a* was significantly associated with increased clam survival at Twin Harbors and decreased clam survival at Long Beach. Further research is needed to elucidate the varying relationships between temperature, salinity, and chl *a* and Pacific razor clam survival.

Gray whales feeding in the surf zone in the Kalaloch area were first observed in summer 2017, when 11–21 different individual whales were observed each day (J. Calambokidis, Cascadia Research Collective, Personal communication, 2022). Between July–December 2017, 37 individual gray whales were photo identified using this area, 33 of which are part of the Pacific Coast Feeding Aggregation (J. Calambokidis, Cascadia Research Collective, Personal communication, 2022). 10–15 gray whales were again observed in summer 2021 exhibiting the same behavior (S. Jeffries, Washington Department of Fish and Wildlife, Personal communication, 2021). While gray whale consumption of razor clams has not been definitively confirmed via scat analysis or through stomach contents, the presence of gray whales feeding so close to shore in two years with exceptionally high pre-recruit razor clam abundances suggests this may be the case. We did not attempt to estimate this potential predation as a separate source of razor clam mortality, and if occurring, this mortality is subsumed by the natural mortality estimate in our current model. While our results indicate that sea otters are preferentially consuming recruit size clams, gray whales are unlikely to be foraging selectively if they are consuming razor clams. Due to their suction feeding strategy where they take mouthfuls of sediment from the seafloor and filter it through their baleen, if gray whales are feeding on razor clams, they are likely feeding on them in proportion to what is available in the environment (e.g., consuming more pre-recruit than recruit size clams).

Washington State's recreational clam fishery is estimated to generate as much as $40M in income to small coastal communities within a single razor clam season (Dyson and Huppert 2010). Our results suggest that in recent years sea otters have become an important source of mortality for recruit size razor clams at Kalaloch Beach, and that otter-caused mortality for recruit size razor clams targeted by the recreational fishery has surpassed both harvest and natural mortality rates at Kalaloch Beach. In addition to the recreational razor clam fishery, previous studies have identified razor clams as a critical food resource for the Quinault people historically (Olson 1936), and razor clams continue to be a staple food source for the Quinault people (Crosman et al. 2019). The Quinault Indian Nation allocates their proportion of the Total Allowable Catch (50%) from usual and accustomed areas (Copalis, Mocrocks, and Kalaloch beaches) between their commercial fishery, harvest for home use (subsistence harvest), and other purposes, with most of the Quinault Indian Nation commercial razor clam harvest occurring in their usual and accustomed areas, and ceremonial and subsistence razor clam harvest occurring on reservation beaches (including Point Grenville; Wyer 2013). The Quinault Indian Nation is also responsible for the majority of commercial razor clam harvest and sales in Washington (Crosman et al. 2019). While previous studies have found that the overall monetary benefits of sea otters can outweigh the costs (Gregr et al. 2020), it is important to note that sea otters can still have large negative impacts on local fisheries. This is especially important to note in relation to tribal use of these shellfish resources, as recreational fishers in general have more latitude in selecting areas to fish but tribal fishers are limited by their tribes federally adjudicated Usual and Accustomed Fishing Areas (Silvern 1999, Berkes and Jolly 2002, Gregr et al. 2020).

5.6 ACKNOWLEDGEMENTS

We would like to acknowledge Dan Ayres (WDFW), Scott Mazzone (QIN), Joe Schumacker (QIN), and Steve Fradkin (ONP) for sharing their razor clam expertise and guiding the development of this research. We gratefully acknowledge the Olympic Region Harmful Algal Partnership for sharing salinity, temperature, and chlorophyll *a* data. We would like to thank the Quinault Business Committee for providing access to razor clam harvest data as well as access to their lands for sea otter foraging observations (Res. No. 15-199-94). We acknowledge the Washington Department of Fish and Wildlife, Olympic National Park, and tribal comanagers for sharing razor clam survey results, and Washington Department of Fish and Wildlife for sharing recreational razor clam harvest estimates. Olympic National Park also provided access to park lands for sea otter foraging observations (National Park Service Scientific Research Study number OLYM-00048). We would also like to acknowledge everyone involved in the annual sea otter survey, including S. Jeffries (WDFW), M. Kimbrel (WDFW), S. Ament (WDFW), J. Waddell (OCNMS), D. Lynch (USFWS), J. Well and K. Meek with Rite Bros. Aviation in Port Angeles, and WDFW WILDCOM dispatch for providing Aircraft Flight Following (AFF) services. This long-running survey is a collaborative effort between many agencies, organizations, and individuals. Funding for the annual sea otter survey is provided by U.S. Fish and Willdife Service and Washington Department of Fish and Wildlife. We also acknowledge Ron Jameson for collecting early post-translocation sea otter survey data. We acknowledge Abigail Van Hemmen, Amanda Witt, Allison Northey, Carter Johnson, Christine Phelan, Erin Foster, and Elizabeth Weinberg for their assistance in the field collecting sea otter foraging data. M.T. Tinker provided analytical expertise. Funding support to J. Hale was provided by the School of

Aquatic and Fishery Sciences (University of Washington), the NOAA Dr. Nancy Foster Scholarship, and Point Defiance Zoo & Aquarium and the Point Defiance Zoo Society through the Dr. Holly Reed Conservation Fund. This publication is partially funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA15OAR4320063, Contribution No. 2022-1193.

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Table 5-1. Summary of Bayesian state-space model used to estimate population dynamics of Pacific razor clams (*Siliqua patula*) in Washington State, USA at 6 beaches. Equations are organized according to the hierarchical structure of the model: a data model (consisting of observed data sets and accounting for observation error), a process model (describing dynamics of the population, incorporating stochasticity in process model parameters), and the prior model (probability distributions representing our prior knowledge of the input parameters). Model was applied to each beach, and sea otter related parameters were only included for Kalaloch Beach.

Model component	Description
Data model	
$Cobs_{P,t,i} \sim Negative\_binomial\left(mean = Area_i \cdot N_{P,t,i}, invscale = \phi_P\right)$ $Cobs_{R,t,i} \sim Negative\_binomial\left(mean = Area_i \cdot N_{R,t,i}, invscale = \phi_R\right)$	Observed annual survey counts (*Cobs*) of pre-recruits (*P*) and recruits (*R*), for each beach elevation *i* and time *t*. Mean expected value depends on true population abundance in sampled plots (*N*) and Area sampled at each elevation *i*.
$Hobs_t \sim Poisson\left(mean = \sum_i Hexp_{t,i}\right)$	Observed harvest counts (*Hobs*) for each year *t*. Assumed to be all recruit size clams.
$NC_P \sim binomial\left(n = NC_{tot}, prob = PCPexp\right)$	Observed sea otter predation events of pre-recruit clams (NC_P), relative to the total observed predation events for all size classes (NC_{tot}).
Process model	
$M^N_{R,t,i} = \exp\left(\gamma_R + \left[\sum_j \mathbf{X}_{S,j,t} \cdot \beta_{S,j}\right] + f_i^N + \varepsilon_{R,t}\right)$	Estimated hazard rate associated with natural mortality ($M^N_{R,t,i}$) for recruit size class (*R*) in a given year (*t*) and beach elevation (*i*). γ_R represents the mean log hazards rate from natural causes (an estimated parameter), $\mathbf{X}_{S,j,t}$ is a covariate effects matrix specifying the values of environmental variables (*j* = 1,2…*J*) at time *t*, $\beta_{S,j}$ is a vector of estimated parameters that determine the effects of the *J* environmental variables on clam mortality, f_i^N is a non-linear function specifying the effect of beach elevation on

	natural mortality (re-scaled such that the maximum value = 0) and $\varepsilon_{R,t}$ is a random effects term specifying unexplained variation in natural mortality across years (drawn from a normal distribution with mean of 0 and standard deviation σ_R).
$M^{O}_{R,t,i} = \exp\left(\alpha_1 + \alpha_2 \cdot Ott_t + f_i^{O}\right)$	Estimated hazard rate associated with otter-caused mortality ($M^{O}_{R,t,i}$) for recruit size class (*R*) in a given year (*t*) and beach elevation (*i*). α_1 and α_2 are estimated parameters describing (respectively) the mean log hazards for recruits from otter predation and the effect of sea otter density (*Ott*) on recruit mortality, while f_i^{O} is a non-linear function specifying the effect of beach elevation on sea otter predation mortality (re-scaled such that the maximum value = 0).
$M^{H}_{R,t,i} = \exp\left(\zeta_0 + \zeta_t + f_i^{H}\right)$	Estimated hazard rate associated with harvest mortality ($M^{H}_{R,t,i}$) for recruit size class (*R*) in a given year (*t*) and beach elevation (*i*). ζ_0 and ζ_t are estimated parameters describing (respectively) the mean log hazards for recruits from harvest and the log ratio of harvest hazards in year *t* relative to this mean value (ζ_t is drawn from a normal distribution with mean of 0 and standard deviation σ_R), while f_i^{H} is a non-linear function specifying the effect of beach elevation on harvest mortality (we set the values of f_i^{H}, based on expert judgement, as the log of the ratio of harvest rates at elevation *i* relative to the elevation that experienced maximum harvest rates).

$M^{N}_{P,t,i} = \exp\left(\gamma_P + \left[\sum_j \mathbf{X}_{S,j,t} \cdot \beta_{S,j}\right] + f_i^{N}\right)$	Estimated hazard associated with natural mortality ($M^{N}_{P,t,i}$) for pre-recruit size class (*P*) in a given year (*t*) and beach elevation (*i*). γ_P represents the mean log hazards from natural causes for pre-recruits (fixed at a value of 1.57, corresponding to the previously published survival rate value of 0.09; Crosman et al. 2019, Nickerson 1975), $\mathbf{X}_{S,j,t}$ is a covariate effects matrix specifying the values of environmental variables (j = 1,2…J) at time t, $\beta_{S,j}$ is a vector of estimated parameters that determine the effects of the J habitat variables on clam mortality, and f_i^{N} specifies the effect of beach elevation.
$M^{O}_{P,t,i} = M^{O}_{R,t,i} \cdot \exp(\psi)$	Estimated hazards associated with otter mortality ($M^{O}_{P,t,i}$) for pre-recruit size class (*P*) in a given year (*t*) and beach elevation (*i*) calculated as the product of the hazard rate for recruits and exp(ψ), where estimated parameter ψ is the log ratio of pre-recruit hazards relative to recruit hazards from sea otter predation.
$S_{R,t,i} = \exp\left(-[M^{N}_{R,t,i} + M^{O}_{R,t,i} + M^{H}_{R,t,i}]\right)$ $S_{P,t,i} = \exp\left(-[M^{N}_{P,t,i} + M^{O}_{P,t,i}]\right)$	Annual survival rates (*S*) for recruit (*R*) and pre-recruit (*P*) size classes as derived parameters, varying by year (*t*) and beach elevation (*i*), based on the summation of cause-specific hazard rates (natural mortality [$M^{N}_{R,t,i}$], otter mortality [$M^{O}_{R,t,i}$], and harvest mortality [$M^{H}_{R,t,i}$] for recruit size clams; natural mortality [$M^{N}_{P,t,i}$] and otter mortality [$M^{O}_{P,t,i}$] for pre-recruit size clams).

$$LS_t = \exp\left(\nu + \left[\sum_j \mathbf{X}_{LS,j,t} \cdot \beta_{LS,j}\right] + \varepsilon_{LS,t}\right)$$

Larval settlement at time t based on overall mean log settlement rate (ν, an estimated parameter), $\mathbf{X}_{LS,j,t}$ (covariate effects matrix for environmental variables [$j = 1,2 \ldots J$] at time t), $\beta_{LS,j}$ (vector of estimated parameters that determine the effects of the J habitat variables on settlement rates), and $\varepsilon_{LS,t}$ (a random effects term specifying unexplained variation in settlement rates across years; drawn from a normal distribution with mean of 0 and standard deviation σ_{LS}).

$$N_{P,t,i} = \left(LS_t + N_{P,t-1,i} \cdot (1-G)\right) \cdot S_{P,t,i}$$

$$N_{R,t,i} = \left[\left(N_{P,t-1,i} \cdot G\right) \cdot \sqrt{S_{P,t,i}} \cdot \sqrt{S_{R,t,i}}\right] + \left[N_{R,t-1,i} \cdot S_{R,t,i}\right]$$

Annual expected abundance for pre-recruits (P) and recruits (R) at each beach elevation (i) as a product of larval settlement (LS), abundance in previous year ($N_{t-1,i}$), growth transition probability from pre-recruit to recruit size class (G, set to 0.95), and survival rate (S).

$$D_{P,t,i} = \left(LS_t + N_{P,t-1,i} \cdot (1-G)\right) \cdot \left(1 - S_{P,t,i}\right)$$

$$D_{R,t,i} = \left[\left(N_{P,t-1,i} \cdot G\right) \cdot \left(1 - \sqrt{S_{P,t,i}} \cdot \sqrt{S_{R,t,i}}\right)\right] + \left[N_{R,t-1,i} \cdot \left(1 - S_{R,t,i}\right)\right]$$

Total deaths (D) each year for pre-recruits (P) and recruits (R) as a product of larval settlement (LS), abundance in previous year ($N_{t-1,i}$), growth transition probability from pre-recruit to recruit size class (G, set to 0.95), and survival rate (S).

$$Hexp_{t,i} = Area_i \cdot D_{R,t,i} \cdot \left(M^{H}_{R,t,i} \middle/ M^{N}_{R,t,i} + M^{O}_{R,t,i} + M^{H}_{R,t,i} \right)$$

Expected number of harvested clams at each beach elevation as a function of $Area_i$ (total square meters of beach at elevation i) and the expected proportional allocation of total deaths to harvest mortality.

$$NCexp_{P,t,i} = Area_i \cdot D_{P,t,i} \cdot \left(M^{O}_{P,t,i} \middle/ M^{N}_{P,t,i} + M^{O}_{P,t,i} \right)$$

$$NCexp_{R,t,i} = Area_i \cdot D_{R,t,i} \cdot \left(M^{O}_{R,t,i} \middle/ M^{N}_{R,t,i} + M^{O}_{R,t,i} + M^{H}_{R,t,i} \right)$$

The expected number of clams of each size class (pre-recruits [P] and recruits [R]) consumed by sea otters at each beach elevation as a function of $Area_i$ (total square meters of beach at elevation i), total deaths (D) each year and the expected proportional allocation of total deaths to otter mortality.

$PCPexp = \sum_t \sum_i NCexp_{P,t,i} \Big/ \sum_t \sum_i NCexp_{R,t,i}$	Total expected proportion of consumed clams that were pre-recruits vs. recruits (*PCPexp*) as a function of the expected number of clams of each size class (pre-recruits [*P*] and recruits [*R*]) consumed by sea otters at each beach elevation.

Prior model

Φ_P ~ *Cauchy (location = 0, scale = 2.5)*	Inverse scale parameter for pre-recruit clams determining the degree of overdispersion of counts relative to a Poisson distribution.
Φ_R ~ *Cauchy (location = 0, scale = 2.5)*	Inverse scale parameter for recruit clams determining the degree of overdispersion of counts relative to a Poisson distribution.
σ_L ~ *Cauchy (location = 0, scale = 2.5)*	Variance in annual log larval settlement.
σ_H ~ *Cauchy (location = 0, scale = 1)*	Variance in annual log harvest hazard rate.
σ_R ~ *Cauchy (location = 0, scale = 1)*	Variance in recruit annual log natural mortality hazard rate.
σ_{En} ~ *Normal (mean = 0, sd = 1)*	Autoregressive parameter for variance in natural mortality by elevation.
σ_{Eo} ~ *Normal (mean = 10, sd = 1)*	Autoregressive parameter for variance in otter mortality by elevation.
ν ~ *Normal (mean = 0, sd = 1)*	Log mean larval settlement rate.
Z_{mn} ~ *Normal (mean = 0, sd = 2)*	Mean log hazard rate for harvest mortality.
γ_R ~ *Normal (mean = 0, sd = 1)*	Mean log hazard rate from natural causes for recruit clams.
γ_P ~ *Normal (mean = 0, sd = 1)*	Mean log hazard rate from natural causes for pre-recruit clams.
α ~ *Normal (mean = 0, sd = 1)*	Effect of sea otter density on recruit mortality.

$N_{R0} \sim Normal\ (mean = 0, sd = 10)$	Initial density of recruit size clams.
$N_{P0} \sim Normal\ (mean = 0, sd = 10)$	Initial density of pre-recruit size clams.
$\Psi \sim Normal\ (mean = 0, sd = 1)$	Log ratio of pre-recruit hazards relative to recruit hazards from sea otter predation.
$\rho_n \sim Beta\ (shape\ 1 = 1, shape2 = 1)$	Autoregressive parameter for variance in natural mortality by elevation.
$\rho_o \sim Beta\ (shape\ 1 = 1, shape2 = 1)$	Autoregressive parameter for variance in otter mortality by elevation.
$\beta_L \sim Normal\ (mean = 0, sd = 1)$	Covariate effects on larval settlement.
$\beta_S \sim Normal\ (mean = 0, sd = 1)$	Covariate effects on clam mortality.

Table 5-2. Summary of environmental covariates included in models fit in a Bayesian state-space framework and used to estimate population dynamics of Pacific razor clams (*Siliqua patula*) in Washington State, USA. "Population parameter" indicates the age class the environmental covariate was included as a predictor for, where LS = larval settlement and S = pre-recruit (<76 mm) and recruit (≥76 mm) mortality. Environmental covariates include North Pacific Gyre Oscillation (NPGO), Bakun Upwelling Index (UI), Significant Wave Height (SWH), temperature (Temp), Salinity, and Chlorophyll-*a* concentration (Chl).

Beach	Population Parameter	NPGO	UI	SWH	Temp	Salinity	Chl
Kalaloch	LS	X	X				
	S			X	X	X	X
Point Grenville	LS	X	X				
	S			X	X	X	
Mocrocks	LS	X	X				
	S			X	X	X	
Copalis	LS	X	X				
	S			X	X	X	X
Twin Harbors	LS	X	X				
	S			X	X	X	X
Long Beach	LS	X	X				
	S			X	X	X	X

Table 5-3. Summary of parameter estimates for models fit in a Bayesian state-space framework and used to estimate population dynamics of Pacific razor clams (*Siliqua patula)* in Washington State, USA. For each parameter we show the mean, standard deviation (SD) and 95% credible intervals (CI) of the posterior distributions, and the Gelman-Rubin statistic (psrf; providing indication of model convergence; values near 1 indicate well-mixed chains). Results are reported for each beach, as each was modeled separately.

Beach	Parameter/Variable[a]	Mean	SD	CI$_{95\text{-low}}$	CI$_{95\text{-high}}$	psrf
Kalaloch	Φ_P	3.006	0.387	2.409	3.674	1.002
	Φ_R	2.938	0.428	2.273	3.700	1.001
	σ_L	1.652	0.242	1.328	2.083	1.004
	σ_H	5.754	0.964	4.471	7.525	1.010
	σ_R	2.229	0.656	1.420	3.488	1.004
	γ_R	-0.267	0.579	-1.292	0.585	1.005
	ν	4.639	0.308	4.114	5.136	1.015
	α_1	-0.638	0.221	-1.010	-0.281	1.010
	α_2	0.355	0.074	0.239	0.484	1.004
	ψ	-3.234	0.206	-3.565	-2.887	1.009
	σ_{En}	0.430	0.151	0.226	0.696	1.008
	ρ_n	0.328	0.1006	0.165	0.496	1.004
	σ_{Eo}	9.928	1.014	8.230	11.617	1.000
	ρ_o	0.778	0.185	0.409	0.982	1.002
	LS_{mn}	296.841	65.845	200.771	411.956	1.010
	Z_{mn}	-1.511	0.948	-3.061	0.071	1.023
	β_{L1}	-0.331	0.322	-0.841	0.213	1.007
	β_{L2}	-0.335	0.291	-0.806	0.144	1.008
	β_{S1}	0.132	0.053	0.048	0.221	1.003
	β_{S2}	-0.289	0.056	-0.385	-0.197	1.003
	β_{S3}	-0.051	0.058	-0.153	0.040	1.003
	β_{S4}	0.045	0.036	-0.017	0.102	1.001
Point Grenville	Φ_P	6.035	0.798	4.814	7.435	1.001
	Φ_R	5.430	0.837	4.180	6.903	1.004
	σ_L	1.208	0.208	0.936	1.584	1.013
	σ_H	0.736	0.121	0.580	0.958	1.007
	σ_R	2.493	0.632	1.684	3.659	1.024
	γ_R	0.086	0.555	-0.916	0.929	1.010
	ν	4.654	0.251	4.253	5.072	1.030
	σ_{En}	0.538	0.150	0.345	0.812	1.005
	ρ_n	0.358	0.094	0.203	0.511	1.007
	LS_{mn}	171.751	20.337	144.035	207.877	1.018
	Z_{mn}	3.187	0.165	2.919	3.452	1.029

	β_{L1}	0.427	0.253	-0.003	0.819	1.010
	β_{L2}	0.158	0.234	-0.227	0.528	1.011
	β_{S1}	0.133	0.040	0.070	0.201	1.006
	β_{S2}	-0.134	0.051	-0.218	-0.057	1.011
	β_{S3}	0.183	0.044	0.108	0.255	1.009
Mocrocks	Φ_P	4.330	0.470	3.570	5.114	1.014
	Φ_R	6.596	0.890	5.224	8.129	1.021
	σ_L	1.066	0.211	0.756	1.454	1.063
	σ_H	2.331	0.240	1.967	2.748	1.251
	σ_R	2.675	0.734	1.746	4.050	1.021
	γ_R	-1.356	0.591	-2.421	-0.480	1.038
	ν	4.212	0.207	3.854	4.529	1.060
	σ_{En}	0.484	0.133	0.304	0.729	1.070
	ρ_n	0.338	0.109	0.143	0.515	1.084
	LS_{mn}	107.900	15.386	87.643	137.337	1.022
	Z_{mn}	3.309	0.400	2.658	3.978	1.328
	β_{L1}	0.087	0.224	-0.273	0.428	1.228
	β_{L2}	-0.306	0.243	-0.679	0.121	1.112
	β_{S1}	0.137	0.039	0.075	0.202	1.034
	β_{S2}	-0.055	0.039	-0.119	0.010	1.091
	β_{S3}	0.041	0.053	-0.051	0.122	1.059
Copalis	Φ_P	2.404	0.258	2.002	2.863	1.013
	Φ_R	9.830	1.467	7.595	12.435	1.009
	σ_L	1.104	0.185	0.856	1.446	1.024
	σ_H	0.955	0.114	0.780	1.156	1.137
	σ_R	2.653	0.664	1.834	3.828	1.057
	γ_R	-0.785	0.594	-1.797	0.108	1.066
	ν	3.814	0.241	3.416	4.184	1.165
	σ_{En}	0.451	0.182	0.276	0.705	1.049
	ρ_n	0.326	0.087	0.189	0.466	1.046
	LS_{mn}	64.877	7.824	53.541	78.909	1.051
	Z_{mn}	4.007	0.177	3.685	4.272	1.289
	β_{L1}	-0.284	0.258	-0.703	0.136	1.174
	β_{L2}	-0.425	0.205	-0.756	-0.095	1.075
	β_{S1}	0.052	0.045	-0.022	0.128	1.068
	β_{S2}	-0.024	0.036	-0.087	0.030	1.076
	β_{S3}	-0.138	0.054	-0.228	-0.052	1.058
	β_{S4}	0.021	0.054	-0.068	0.112	1.008
Twin Harbors	Φ_P	1.916	0.201	1.604	2.266	1.007
	Φ_R	12.630	2.067	9.554	16.269	1.004
	σ_L	0.881	0.195	0.608	1.231	1.045
	σ_H	6.817	0.993	5.409	8.688	1.180
	σ_R	3.064	0.832	2.036	4.754	1.058

	γ_R	-1.406	0.637	-2.524	-0.406	1.021
	ν	4.036	0.193	3.723	4.348	1.047
	σ_{En}	0.497	0.137	0.325	0.752	1.006
	ρ_n	0.266	0.086	0.127	0.407	1.005
	LS_{mn}	102.560	21.003	73.963	141.171	1.031
	Z_{mn}	1.285	1.110	-0.474	3.233	1.381
	β_{L1}	0.490	0.203	0.153	0.825	1.039
	β_{L2}	-0.620	0.213	-0.960	-0.264	1.056
	β_{S1}	0.212	0.048	0.132	0.290	1.015
	β_{S2}	0.062	0.045	-0.013	0.136	1.031
	β_{S3}	0.106	0.035	0.049	0.164	1.020
	β_{S4}	-0.173	0.041	-0.241	-0.106	1.011
Long Beach	Φ_P	4.941	0.656	3.957	6.074	1.008
	Φ_R	3.151	0.386	2.546	3.808	1.005
	σ_L	1.868	0.293	1.475	2.407	1.034
	σ_H	6.454	0.785	5.322	7.848	1.077
	σ_R	2.759	0.705	1.831	4.124	1.012
	γ_R	-0.901	0.602	-1.953	0.037	1.006
	ν	3.394	0.353	2.833	3.986	1.030
	σ_{En}	0.392	0.116	0.245	0.606	1.003
	ρ_n	0.303	0.077	0.170	0.425	1.008
	LS_{mn}	78.159	52.129	49.677	140.303	1.005
	Z_{mn}	1.311	0.980	-0.292	2.957	1.197
	β_{L1}	0.050	0.361	-0.549	0.634	1.045
	β_{L2}	0.264	0.333	-0.307	0.802	1.012
	β_{S1}	0.130	0.034	0.075	0.186	1.005
	β_{S2}	0.065	0.031	0.011	0.114	1.010
	β_{S3}	0.325	0.035	0.266	0.380	1.005
	β_{S4}	0.114	0.037	0.051	0.173	1.001

[a] Parameters include inverse scale parameter for pre-recruit clams determining the degree of overdispersion of counts relative to a Poisson distribution (Φ_P); inverse scale parameter for pre-recruit clams determining the degree of overdispersion of counts relative to a Poisson distribution (Φ_R); variance in annual log larval settlement (σ_L); variance in annual log harvest hazard rate (σ_H); variance in recruit annual log natural mortality hazard rate (σ_R); mean log hazards rate from natural causes for recruit clams (γ_R); log mean settlement rate (ν); mean log hazards for recruits from otter predation (α_1); effect of sea otter density on recruit mortality (α_2); log ratio of pre-recruit hazards relative to recruit hazards from sea otter predation (ψ); autoregressive parameter for variance in natural mortality by elevation (σ_{En}); autoregressive parameter for variance in natural mortality by elevation (ρ_n); autoregressive parameter for variance in otter mortality by elevation (σ_{Eo}); autoregressive parameter for variance in otter mortality by elevation (ρ_o); mean larval settlement (LS_{mn}); mean log hazard rate for harvest mortality (Z_{mn}); effect of North Pacific Gyre Oscillation on larval settlement (β_{L1}); effect of Bakun

Upwelling Index on larval settlement (β_{L2}); effect of significant wave height on clam mortality (β_{S1}); effect of temperature on clam mortality (β_{S2}); effect of salinity on clam mortality (β_{S3}); and effect of chlorophyll-*a* on clam mortality (β_{S4}).

Table 5-A1. Summary of diagnostics for models fit in a Bayesian state-space framework and used to estimate population dynamics of Pacific razor clams (*Siliqua patula*) in Washington State, USA at 6 beaches. For each model, we show the maximum Gelman-Rubin statistic for any fitted model parameter (psrf; providing indication of model convergence; values near 1 indicate well-mixed chains), the associated parameter, and the Bayesian *P*-value (a well-fit model would have a *P*-value within the range 0.3–0.7).

Beach	Max psrf	Parameter[a]	Bayesian *P*-value
Kalaloch	1.023	Z_{mn}	0.759
Point Grenville	1.030	ν	0.5094
Mocrocks	1.328	Z_{mn}	0.8304
Copalis	1.289	Z_{mn}	0.75
Twin Harbors	1.381	Z_{mn}	0.7012
Long Beach	1.197	Z_{mn}	0.4124

[a] Parameters include mean log hazard rate for harvest mortality (Z_{mn}); log mean larval settlement (ν); mean log hazard rate for harvest mortality (Z_{mn}); mean log hazard rate for harvest mortality (Z_{mn}); mean log hazard rate for harvest mortality (Z_{mn}); and mean log hazard rate for harvest mortality (Z_{mn}).

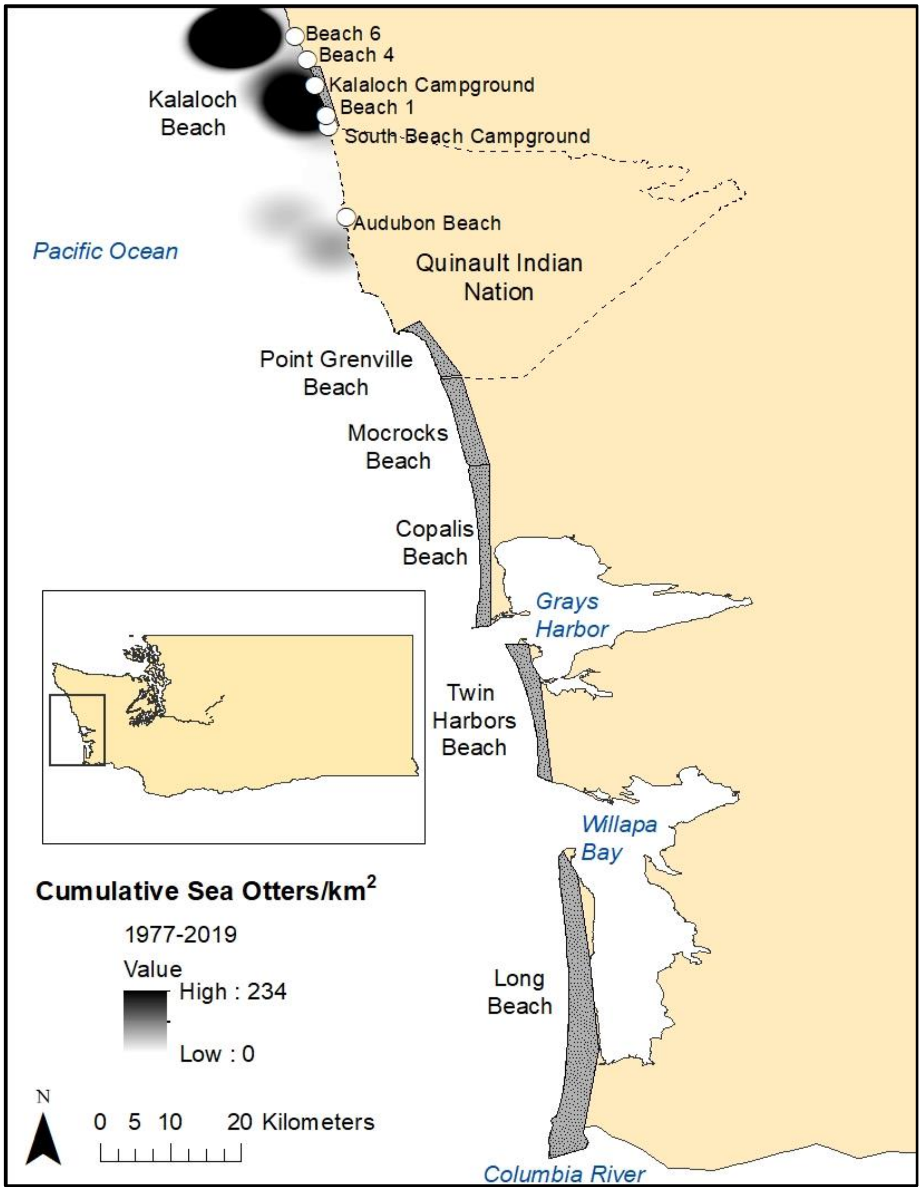

Figure 5-1. Map of the study region, the southern Olympic Peninsula of Washington State, showing the cumulative density of sea otters (*Enhydra lutris kenyoni*), 1977–2019. Darker shades indicate high sea otter cumulative density; lighter shades indicate low sea otter cumulative density. Open circles indicate sea otter foraging observation sites, including Beach 6, Beach 4, Kalaloch Campground, Beach 1, South Beach Campground, and Audubon Beach. Razor clam (*Siliqua patula*) beaches are indicated by grey stippled polygons, including Kalaloch Beach, Point Grenville Beach, Mocrocks Beach, Copalis Beach, Twin Harbors Beach, and Long Beach. The Quinault Indian Nation's reservation lands are outlined with a dashed line. The small inset map shows Washington State, USA; the study area is outlined in a rectangle.

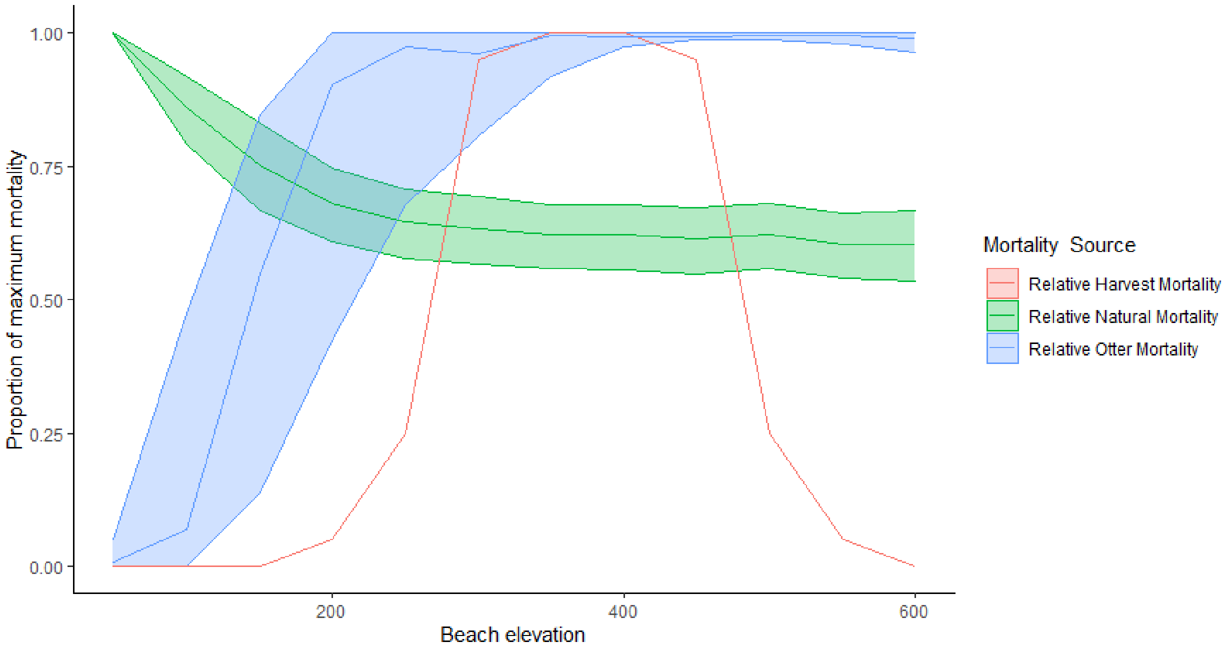

Figure 5-2. Relative magnitude of mortality impacts on Pacific razor clams (*Siliqua patula*) as a function of beach elevation at Kalaloch Beach, WA, for 3 categories of hazards: 1) harvest mortality, 2) natural mortality, and 3) sea otter-caused mortality. Harvest mortality was set to a fixed value dependent on beach elevation based on expert judgement (e.g., no confidence intervals), while the functional relationships between elevation and mortality from sea otters and natural causes were estimated in the model.

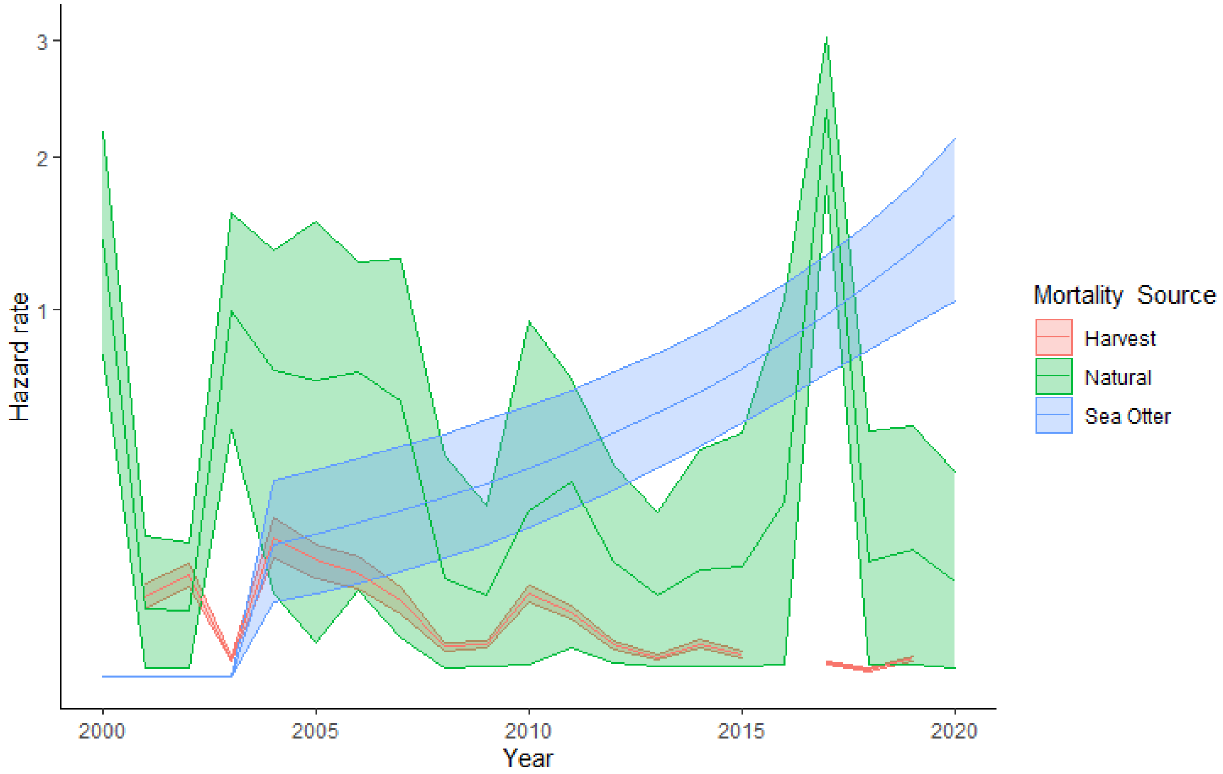

Figure 5-3. Temporal variation in the magnitude of 3 types of hazards - harvest mortality, natural mortality, and sea otter predation - for Pacific razor clams (*Siliqua patula*) at Kalaloch Beach, WA, between 2000–2020. Estimates correspond to 350 foot beach elevation (a representative beach elevation affected by sea otters), with center lines indicating mean posterior estimates and shaded bands indicating 95% CI.