AN ABSTRACT OF THE DISSERTATION OF

Elizabeth B. Cerny-Chipman for the degree of Doctor of Philosophy in Zoology presented on August 29, 2016.

Title: Changing Climate, Changing Contexts: Variation in Rocky Intertidal Predator-prey Interactions Seen Through an Environmental Stress Framework

Abstract approved:

Bruce A. Menge

The multifaceted role of the environment in regulating the structure and dynamics of biological communities has long fascinated ecologists and motivated much debate and research. Now, in a time of accelerated global changes due to human impacts, the need to understand how the environment shapes communities has gained new urgency. The environment acts directly on communities by causing direct mortality and changes to vital rates of individuals. However, the environment can also exert indirect effects on communities by changing the nature of biotic interactions. This occurs either through changes to the physiological performance of interacting species or through shifts in the abundance of other species in the community. Much of the effort to understand how global change will influence communities has focused on direct effects of environmental conditions. However, the essential influence of biotic interactions suggests that we will need to improve our conceptual understanding of indirect environmental effects to better predict outcomes of anthropogenic change.

Understanding how the interactions of predators and prey are vulnerable to environmental context may provide a useful pathway to link relatively well-resolved individual effects of climate change to a broader community context. Predators are often important in determining community structure and stability through their control of lower trophic levels. However, predators also tend to be particularly sensitive to environmental stress. As a result, environmental stress models predict that the impacts of predators will lessen as stress increases, which could weaken existing processes regulating communities. Top predators, which often have the strongest impacts, may be especially vulnerable to climate change because of their large body size, energy needs, range requirements, and dependence on prey populations. The effects of environmental change on top predators have been justifiably well-studied, yet changing contexts require a more comprehensive view of which species may be important in novel environmental contexts. Subordinate predators are often weak interactors in communities, but they may play increasingly critical roles if top predators decline. Similarly, because weak interactions are highly variable, shifting environmental contexts could lead to different outcomes with subordinate predator interactions.

Communities that experience high environmental variability across short spatial and temporal scales, such as rocky intertidal communities, are particularly useful for examining effects of environmental context on predator-prey interactions. The rocky shores along the US west coast have a rich history of study, enabling us to combine new insights and existing knowledge to build a greater context for predicting the impacts of environmental changes. Due to anthropogenic climate change, communities along rocky shores in the NE Pacific are predicted to experience warmer air temperatures, intensified upwelling, and greater exposure to low pH waters. These abiotic changes are likely to influence biotic changes, such as shifting species abundances and distributions, reductions in performance, and increases in disease and mortality.

This dissertation explores how three different environmental contexts – two abiotic and one biotic – influence the interactions between a predator and its prey species. My focal predators are two gastropod congeners, the whelks *Nucella canaliculata* and *N. ostrina* that feed on mussels and barnacles. Whelks are abundant predators in the mid-intertidal zone, and we know their interactions can be sensitive to environmental conditions. My aim in this dissertation is to expand our understanding of predation in the rocky intertidal and how it is affected by 1) ocean acidification, 2) existing variability in the environment, and 3) the disease-driven decline of the keystone sea star *Pisaster ochraceus*, which are all contexts relevant to climate change.

In Chapter 2, I explore how interactions between whelks and mussel prey are affected by ocean acidification (OA), an abiotic stressor that can influence species physiology and behavior. I use two separate mesocosm experiments designed to capture mechanistic changes in the two pairwise predator-prey interactions. Specifically, I test how the feeding rate and handling time of whelk predators is influenced by elevated CO_2, which has the effect of lowering the pH and reducing the saturation state of carbonate minerals used by both whelks and mussels for building shells. The results show that whelks consume fewer mussels in elevated CO_2, and that this may be caused in part by substantially longer handling times of prey. These results are consistent with the idea that predators are more vulnerable to the stresses associated with OA than prey, at least on shorter time scales.

In Chapter 3, I use a comparative experiment at eight sites in Oregon to assess how variability in the interaction between whelks and mussels is shaped by dynamic conditions in the field. Previous experiments have focused on local-scale gradients such as wave exposure and tidal elevation in testing environmental stress models. I expand on these studies to test how predation rate responds to larger-scale variability in upwelling and temperature, both of which are relevant to climate change in the intertidal. In three similar experiments that span 14 years, I observe patterns in mussel survival and assess whether the importance of environmental variables has changed through time. I find that predation by whelks is relatively consistent in the field context, but is explained in part by upwelling. In the final year of study (2013), there was evidence that variability in air temperatures decreased predation, which may point to shifting environmental influences on whelk predators.

In Chapter 4, I follow the population responses and community effects of whelks after the striking decline of the keystone sea star *Pisaster ochraceus* along rocky shores in Oregon. Sea star wasting disease has caused declines in *P. ochraceus* populations by up to 80%, greatly reducing the population impact of this keystone species. Past research has demonstrated that when *P. ochraceus* is removed, it often results in the formation of a near-monoculture of the mussel *M. californianus* in the low intertidal zone. I hypothesize that whelks will be able to minimize mussel invasion following declines in *P. ochraceus* because whelks will be able to control sessile prey species, like barnacles, that facilitate mussel establishment. However, my field experiment provides no evidence of compensation by whelks; instead, they weakly facilitate mussel establishment. To understand whelk population responses to keystone species loss, I also monitor whelk abundance, distribution with tidal elevation, and population size structure. My results indicate the potential for a lagged whelk population response suggested by a shift of the size structure towards smaller individuals.

Overall, my dissertation highlights the sensitivity of rocky intertidal predator-prey interactions to environmental contexts relevant to anthropogenic change. It also points to the need to continue studying predation in relevant environmental contexts in order to scale existing knowledge in species responses to the community level. Further, my results reveal that at both the per capita and population levels, weak interactors have variability in their interactions with other species that will likely influence their role in communities undergoing change. Even in a well-understood system, our results were often unexpected and did not necessarily match the predictions of environmental stress models and other existing frameworks. This suggests we need to build further conceptual and empirical frameworks to determine how sensitivity in species interactions will ultimately affect community structure, functioning, and the provision of ecosystem services.

Changing Climate, Changing Contexts: Variation in Rocky Intertidal Predator-prey Interactions Seen Through an Environmental Stress Framework

by
Elizabeth B. Cerny-Chipman

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented August 29, 2016
Commencement June 2017

Doctor of Philosophy dissertation of Elizabeth B. Cerny-Chipman presented on August 29, 2016.

APPROVED:

Major Professor, representing Zoology

Chair of the Department of Integrative Biology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Elizabeth B. Cerny-Chipman, Author

ACKNOWLEDGEMENTS

It takes a village to write a dissertation, and mine would not have been possible without the support, guidance and hard work of many other people. First and foremost, I want to acknowledge my advisor, Bruce Menge, who is unparalleled in his patience and kindness. Bruce showed his humor and humility in all moments but especially during my (thankfully few) blunders that made it to the wall of shame, which included forgetting him the field. Bruce taught me so much and inspired my lasting love of the rocky intertidal. I also want to thank Dr. Jane Lubchenco for the chance to work with her during my final year. I feel deeply fortunate for this opportunity, which taught me about everything from fisheries to grammar. My research with Jane solidified my desire to work at the science-policy interface and cleared the path to get there. I thank Bruce and Jane both for letting me join the Lubmenge family.

My committee has been hugely helpful during my graduate career. Sally Hacker has been a mentor in the truest sense of the word. I could always count on Sally when I needed to think through an issue, get advice, or find cleaning supplies. Mark Novak was a voice of reason and clarity, especially on the more technical aspects of predator-prey interactions. George Waldbusser was so knowledgeable, always let our meetings run long to work through the details, and his help definitely improved my OA research. My graduate representative Katie Dugger has been a great intellectual addition to my committee as an ecologist from a study system very different from my own.

My fellow Lubmenge grads were tireless in their role as my sounding board, field helpers, editors, and cheerleaders. Allie Barner was not only a great friend, but also such

a role model. I looked to her example at so many times, and I would never have made it through graduate school without her. Chenchen Shen, my trusty officemate, housemate and companion never failed to give me valuable perspective; I admire her composure in all things. Jenna Sullivan was a fantastic friend, collaborator, and editor whose good-natured spirit made even the longest field days feel worth laughing about. I don't know what I would have done without Sarah Close, Alison Iles, Kirsten Grorud-Colvert, Sarah Gravem, Alissa Rickborn, Barbara Spiecker, Jeremy Rose, Dafne Eerkes-Medrano, Margo Hessing-Lewis, Vanessa Constant, or Joe Tyburczy in my lab.

I want to thank the PISCO technicians and coordinators for their help during graduate school. Angela Johnson was a generous friend in all aspects of life, including helping me in the field extensively. Jonathan Robinson always had encouragement or an extra hand to lend. I am thankful for the chance to work with Brittany Poirson, who has breathed new life to our lab. Jerod Sapp makes things tick around our lab in million tiny and often-unrecognized ways, and I am grateful to him for all of them. Mike Frenock, Kristin Milligan, Cindy Kent and Kathleen Norris, Tully Rohrer, Lindy Hunter and Megan Poole also helped me clear many logistical hurdles over the years.

Francis Chan and Annaliese Hettinger were both instrumental in setting up the OA mesocosm and teaching me how to run it. Tarik Gouhier was a generous teacher of statistics and assisted with gathering all sorts of environmental data. There are too many volunteers and assistants who helped me to list here, but I want to acknowledge their contribution, particularly that of Celeste Moen, Courtney Jackson, Dani Smull, Kersten Schnurle, Melissa Britsch, and Silke Bachhuber, who is joining our lab this fall.

The students in the department made my time in graduate school richer, both intellectually and socially, including Casey Benkwitt, Tye Kindinger, Jessie Reimer, Sheila Kitchen, and Trang Nguyen, Reuben Biel, and Jeremy Henderson. My broader Corvallis community reminded me of the life going on beyond Cordley Hall including Hannah O'Leary, Hannah Satein, Ashley Edlund, Sarah Gishe Hagan and their partners. The IB office staff (Trudy Powell, Traci Durrell-Khalife, Torri Givigliano, Tara Bevandich and Jane Van Order) helped me navigate through reimbursements, courses, and assistantships with competence and warmth.

I am forever grateful for my family, who has kept me grounded through graduate school with constant love and support. My twin Kathryn is my other half, and our phone calls and visits kept me going and meant so much to me. My parents have always encouraged me to follow my interests and given me examples to live by. Finally, I want to thank Dustin Hollabaugh, who has given me the strength to do my dissertation. He was my steady comfort and support – cooking meals while I was worked, driving from Portland on his weekends so he would wake up at 3 am to join me in the field, cheering me up, and helping me envision our future goals. Part of this degree belongs to him.

I would be remiss not to mention my sources of financial support, which included teaching assistantships from the department and research assistantships from Bruce and Jane. The Mamie Markham Research Award from Hatfield allowed me to do my mesocosm work. A grant from the Pacific Northwest Shell Club, an NSF RAPID Grant on SSWD awarded to Bruce (OCE 14-48913), and several years of Zoology Research Funds and discretionary funds from Bruce and Jane were also indispensable.

CONTRIBUTION OF AUTHORS

Chapter 2: Francis Chan and Annaliese Hettinger are responsible for the creation of the mesocosm system that was used and provided guidance during the experiments.

Chapter 4: Jenna Sullivan was a full collaborator in the design of the project as well as the field work, particularly in the manipulative experiment. She was also an editor of the written work for the chapter.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

Page

LIST OF FIGURES

LIST OF TABLES

LIST OF TABLES (Continued)

Table Page

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

LIST OF APPENDIX TABLES (Continued)

Dedicated to my grandparents: the set I knew and loved, who would be proud of the first PhD in their family, and the set I never got to meet, whose footsteps into marine biology I unknowingly followed

CHANGING CLIMATE, CHANGING CONTEXTS: VARIATION IN ROCKY INTERTIDAL PREDATOR-PREY INTERACTIONS SEEN THROUGH AN ENVIRONMENTAL STRESS FRAMEWORK

1 – GENERAL INTRODUCTION

Understanding the many ways that the environment shapes the structure and functioning of ecological communities has long been one of the central goals of community ecology (Elton 1927, Whittaker 1956, Connell 1961b). Environmental stress can act on organisms directly by causing sub-lethal stress or mortality (Feder and Hofmann 1999), influencing vital rates like growth and reproduction (Petes et al. 2007), altering behavior and life history (Dugger et al. 2014) and setting range distributions for populations (Jones et al. 2009, 2010). Environmental conditions can also indirectly change the sign and strength of biotic interactions (Bertness et al. 1999) based on either differential physiological and behavioral responses or changes in the abundance of other species within the community (Adler et al. 2009). These environmental controls on species interactions are likely to be the rule rather than the exception, and thus are important to incorporate into conceptual models of community regulation.

We have come to acknowledge our own central role as a biotic component regulating many communities and ecosystems globally (Vitousek et al. 1997, Strong and Frank 2010, Estes et al. 2011). The human role has been both direct (e.g. harvest of individuals), and, increasingly, indirect as we modify the climate. Further, our influence on biodiversity on a global scale will ultimately alter the functioning and stability of ecosystems (McCann 2000, Duffy 2003). Studying this anthropogenic change has become a central focus of ecology, and ecologists are now tasked with both understanding the underlying dynamics of ecosystems and making predictions for outcomes. Such a task requires finding ways to reach generality and identifying important conceptual gaps in light of global environmental change. A critical gap in our knowledge is how anthropogenic changes will influence species interactions (Agrawal et al. 2007, Angert et al. 2013).

Many models of community regulation, along with theoretical and empirical research, have shown that predator-prey interactions can have large impacts on community structure (Hairston et al. 1960, Paine 1966, Menge 2000). Importantly, predator-prey interactions are also particularly malleable across environmental conditions (Sanford 1999, Chamberlain et al. 2014). It is hypothesized that predator-prey interactions act as a “biotic multipliers” of climate change because predators are particularly sensitive to environmental stress and predation is an important structuring agent in many communities. Thus, climate change effects on predation can influence the persistence and viability of species in a community (Zarnetske et al. 2012). However, the broader effects of predator loss and changing predator impacts can also be mediated by the interplay of other abiotic (Wootton et al. 1996, Pace et al. 1999, Borer et al. 2005) and biotic processes (Shurin and Seabloom 2005, Finke and Denno 2005).

Much of the focus of research on the effects of environmental variation on predation impacts has been justifiably on top predators because of their strong effects on community structure. However, other predators with lesser community impacts may also be important in the context of climate change and species loss. Through extinctions and species removal experiments with strong interactors, we have come to understand that in some places and contexts, weakly interacting species can be highly important for communities, for example by compensating for the loss of a keystone species or acting as a top predator and community driver in their own right (e.g., Dayton 1971, Berlow 1999). Weak interactors can often have highly context-dependent and variable interaction strengths, which may be important in dampening or mediating the impacts of perturbations within communities (Novak et al. 2011) and maintaining community stability (Berlow 1999, McCann 2000). For example, Berlow (1999) discovered that subdominant predator species can have variable effects on prey that are larger in magnitude than the direct effects of a keystone predator. Thus, exploring context-dependency in predators that are weak and variable interactors may help improve our understanding of the consequences of environmental change.

In marine systems, global environmental changes have many manifestations. Water temperatures have already warmed and continue to increase (IPCC 2014). As more carbon dioxide enters the atmosphere, it also enters the oceans, which both lowers oceanic pH and makes the oceans less favorable for the formation of calcified structures that a host of organisms from corals to mussels to phytoplankton to fish rely upon (Sabine et al. 2004, Orr et al. 2005, Doney et al. 2009). Hypoxia is becoming a more frequent occurrence in the oceans both from changing climate and as a result of eutrophication in many places; the formation of dead zones is a pressing concern (Vaquer-Sunyer and Duarte 2008). Sea level ice is melting, sea level is rising, and seas are getting stormier and wavier (IPCC 2014). We have sullied the ocean with pollutants, debris (Derraik 2002), and microplastics (Glaser 2015). We have also acted as a top super-predator (Darimont et al. 2015), changing the ocean in profound ways by overharvesting fish and other organisms, particularly top predators with critical ecosystem functions (Pauly et al. 1998).

In this dissertation, I apply existing conceptual frameworks that deal with environmental effects on community structure to better inform our understanding of climate change. My focus is on a single pathway through which the environment indirectly shapes communities: by influencing predator-prey interactions, which in turn influence communities. Relying on the conceptual links between physiological processes, organismal performance, and the strength of species interactions, my dissertation can provide insight into potential community responses to environmental changes. I study abundant subordinate predators that have variable but often weak interactions with several prey species because they may play increasingly important top-down roles as top predators are vulnerable to extinction and population decline (Duffy 2003, Borrvall and Ebenman 2006, Sanders et al. 2013). Environmental context can be broken down into two main components (Menge 2003): the abiotic context, which includes stress, disturbance, and productivity, and the biotic context, which includes characteristics of the community including species diversity, traits of individual species, recruitment, and species interactions. My dissertation includes anthropogenic changes from both these contexts: two of my chapters deal with factors causing physical and physiological stress, and the other chapter deals with the effects from the loss of a top predator, which is a biotic change in community structure.

To understand the responses of subordinate predators to environmental stressors relevant to climate change, I utilize the rocky intertidal ecosystem along the coast of Oregon. There is a rich legacy of experimentation in rocky intertidal ecosystems (Menge and Farrell 1989) that has led to valuable insights into community regulation (Connell 1961b, Paine 1969, Dayton 1971, Lubchenco 1978, Menge and Sutherland 1987, Wootton 1994, Harley 2011). Rocky intertidal systems in the NE Pacific have strong gradients of temperature, desiccation risk, and wave exposure that occur over short spatial scales. At larger scales, there is considerable variation among sites and capes in air and water temperatures, pH, nutrients, and the delivery of propagules driven largely by differences in bathymetry and upwelling (Menge et al. 2004, 2015). I use two gastropod predators, the whelks *Nucella canaliculata* and *N. ostrina*, and their prey (largely the mussel *Mytilus trossulus* and several barnacle species) as my study system. Whelks use their proboscis to drill into and consume prey, which leaves a clear sign of predation in many cases (though whelks can also pry open the shells of their prey). Whelks are vulnerable to environmental conditions while feeding (Sanford 2002b) because they are unable to behaviorally avoid environmental stress when consuming sessile prey, which often takes several days (Miller 2013).

In Chapter 2, I test the response of predator feeding rates to a relevant anthropogenic stressor, ocean acidification (OA). Globally, ocean acidification is a serious consequence of the addition of carbon dioxide to the atmosphere; CO_2 in the atmosphere enters the oceans and, through a series of chemical reactions, lowers the pH of the water and reduces the favorability of the formation of calcium carbonate (Orr et al. 2005, Feely et al. 2009), an important mineral that makes up shells, coral skeletons, and many other biological structures. OA is of concern in coastal systems (Waldbusser and Salisbury 2014), particularly in the NE Pacific where coastal waters are already acidified (Feely et al. 2008, Hauri et al. 2013). The direct effects of OA on organisms tend to be negative and are well-documented, at least in mesocosm experiments (Kroeker et al. 2010, 2013), but the impacts on species interactions remain a gap in our understanding (Kroeker et al. 2014b) despite their important predicted role in mediating ecosystem effects (Gaylord et al. 2014). I assessed how whelk feeding rates and handling times are influenced by decreased pH. I link these results to integrated measurements of organismal physiology to see how changes in predator performance influence in predation. Overall, results suggest that whelks decrease feeding rates in decreased pH, and that this reduction is related to longer handling times. Despite changes in predation, whelks demonstrated few changes in gross physiological metrics under OA conditions during the two-week experiment.

While the use of single-stressor laboratory studies has been instrumental in building comprehensive understanding of environmental effects like OA (Riebesell and Gattuso 2015), results are not necessarily applicable to broader contexts. In the field, many environmental conditions can cause stress, and the magnitude and duration of stressful events highly variable over small and large scales. Further, many stressors can interact in ways that can be synergistic. Environmental stress models predict that predation will weaken in stressful environments (Menge and Sutherland 1987, Hacker and Gaines 1997, Bruno et al. 2003). This prediction is based on the implicit assumption that predators are more vulnerable to stress than their prey (i.e., the “consumer stress model,” Menge and Olson 1990), and thus links predator performance to broader community effects. These models have been tested in the rocky intertidal in response to strong local gradients in tidal elevation and wave stress (Menge and Farrell 1989, Menge et al. 2002a). However, many environmental drivers in the rocky intertidal are multivariate (e.g., upwelling brings cold water to intertidal sites, which could be less stressful, but also lowers seawater pH and can induce hypoxia, both of which are likely stressful). I was interested in first establishing patterns of predation along the coast and then exploring them in relation to environmental variables

In Chapter 3, I compare three years of manipulative experiments at eight sites spanning fourteen years to examine existing variability in predation rates in the field. I focus on how site air and water temperatures and coastal upwelling, can influence predation beyond strong localized environmental gradients. My rationale was to understand the patterns of variability in predation that occurred as a way to provide context for future changes, asking whether the interaction was robust or sensitive to change. I found that predation was largely consistent across sites and years, yet there was an overall relationship between mussel survival and ocean upwelling in all years as well as differences in the responses of whelk predators in 2013 across sites and with variation in air temperature.

For Chapter 4, I shift my focus to a changing biotic context relevant to predicted impacts of climate change. In 2014, sea star wasting disease (SSWD), likely caused by a virus, spread along the coast of Oregon (Hewson et al. 2014, Menge et al. 2016). In the next several months, over 80% mortality occurred in populations of the keystone sea star *Pisaster ochraceus* at many sites (Menge et al. 2016). The disease essentially created a large-scale natural experiment that echoed the original small-scale removal of *P. ochraceus* on Mukkaw Bay, WA by Paine (1966). The evidence for relationships between SSWD and temperature and other climate-related factors is mixed (Eisenlord et al. 2016, Kohl et al. 2016, Menge et al. 2016). However, mass mortality events are increasing in marine invertebrates (Fey et al. 2015), and marine diseases are predicted to become more prevalent with climate change and warming waters (Burge et al. 2014). Thus, disease outbreaks are an expected biotic change in the environmental context of marine communities. Likewise, my focus on a disease in a top predator is relevant because top predator loss is a serious risk from climate change as top predators are more often vulnerable than other community members (Borrvall and Ebenman 2006). I ask whether subordinate whelk predators will be able to compensate for keystone species declines and document their population responses to the loss of both a predator and a competitor using a manipulative experiment and surveys. In this instance, I discovered that whelks had limited effects on the prey community, but this was dependent on an unanticipated biotic change – the recruitment failure of the main prey mussel *M. trossulus*. I also found that whelk predators did not modify their spatial distribution in response to keystone species declines, but that increases in abundance of individuals at the smallest size classes may portend lagged population effects.

Ecologists face the dual challenge of understanding the processes that structure communities and applying this knowledge to systems in a state of unprecedented change with the goal of providing better prediction and ultimately better management. Given the sheer diversity of communities that exist in many dynamic environmental contexts, ecologists have often searched for general principles and debated whether context dependency limits our ability to apply findings across systems (Lawton 1999, Simberloff 2004). With global environmental change, it has become necessary to embrace this context-dependence and further understand the factors that drive it. My dissertation explores three important contexts relevant to environmental change with the aim of translating single-species impacts of anthropogenic change to broader community levels.

2 – OCEAN ACIDIFICATION WEAKENS PREDATION AND INCREASES HANDLING TIMES IN A SNAIL PREDATOR FEEDING ON CALCIFIED MUSSEL PREY

Abstract

Our understanding of the sensitivity of species interactions to global environmental change remains a critical gap in predicting the broader effects of climate change. Predator-prey interactions are important drivers of community structure in many systems, and they may be particularly vulnerable to environmental changes. Here, we test the strength of predator-prey interactions under present and future scenarios of ocean acidification, a major consequence of anthropogenic carbon emissions. We studied the NE Pacific whelks *Nucella canaliculata* and *N. ostrina*, which are congeneric predators that both feed on the mussel *Mytilus trossulus*. In separate 14-day experiments, we measured feeding rates and handling times of predators and followed gross physiological metrics related to growth, such as length change and shell and body weights. We found that whelks were less likely to drill prey in high CO_2 treatments. Handling time measurements revealed that whelks also took longer to consume prey in acidified water, though results were dependent on whelk species, mussel size, and predation method. Our results demonstrate that ocean acidification can reduce predator-prey interaction strength through short-term behavioral changes even in predators adapted to the highly variable carbonate environment of the NE Pacific.

Introduction

Environmental stress can act on organisms directly by causing sub-lethal stress or mortality (Feder and Hofmann 1999), influencing growth and reproduction (Petes et al.

2007), and setting range distributions for populations (Jones et al. 2009, 2010). Further, the environment also has an indirect signature on organisms by influencing species interactions and the biotic context in which they live (Menge and Sutherland 1987, Menge and Olson 1990, Hacker and Gaines 1997, Adler et al. 2012). Because organisms may exhibit different physiological and behavioral responses to a given environment, changes in environmental conditions can change the sign and magnitude of species interactions (Bertness and Hacker 1994, Bertness et al. 1999) with potential impacts for entire ecosystems. In many ecosystems, predator-prey interactions can have large impacts on community structure (Hairston et al. 1960, Paine 1966, Menge 2000) and functioning (Duffy 2003). However, trophic interactions can change across environmental conditions, such as temperature (Sanford 1999) as interacting organisms respond to their environment. Predator-prey interactions may act as a "biotic multipliers" of climate change because 1) predators can be particularly sensitive to environmental stress and 2) predation is important for community structure. Thus, climate change effects on predation can critically impact the persistence and viability of species in a broader community (Zarnetske et al. 2012). Hence, better understanding how environmental effects on predators and prey manifest with regard to interactions will enable us to better gauge the full suite of impacts of climate change on communities.

In marine systems, ocean acidification (OA) is one of the most serious impacts of climate change (Harley et al. 2006, Hofmann et al. 2010). The oceans have absorbed approximately one third of the total carbon emitted as a result of human activities since the start of the industrial revolution (Sabine et al. 2004), and ocean surface waters have on average become 30% more acidic with the pH dropping 0.1 pH units (Caldeira and Wickett 2003, Hall-Spencer et al. 2008). The process of ocean acidification is driven by the addition of anthropogenic emissions of carbon dioxide (CO_2) into the ocean through mixing between the atmosphere and surface waters. In a broader sense, OA is caused by the decoupling of the rate of formation of an acid (H_2CO_3) in ocean waters (due to the addition of anthropogenic CO_2) that decreases pH and the rate at which the other buffering components of the seawater carbonate system can be introduced into the ocean via processes related to the chemical weathering of rock (Hönisch et al. 2012, Waldbusser and Salisbury 2014).

When atmospheric CO_2 enters the ocean, the gas dissolves and mixes with water to form carbonic acid (H_2CO_3). This weak acid is short-lived and quickly dissociates into protons that titrate CO_3^{2-} to form bicarbonate (HCO_3^-) (Waldbusser and Salisbury 2014). This process, which increases the concentration of HCO_3^- and lowers CO_3^{2-}, serves to lower the pH in seawater as the concentration of H^+ increases (Feely et al. 2009). Reducing the concentration of CO_3^{2-} lowers the saturation state of calcium carbonate ($CaCO_3$), an important biogenic (and abiotic) mineral. This affects the thermodynamics of the formation of $CaCO_3$ and increases the energetic cost for organisms to produce and maintain skeletons and other structures by lowering the saturation state of $CaCO_3$. While it is still possible for organisms to calcify in under-saturated seawater (when $\Omega < 1$), they must utilize costly adaptations or processes to do so (Waldbusser et al. 2016).

The consequences of OA on marine organisms are diverse and wide-ranging, and research efforts have revealed physiological effects in many taxa and systems (Kroeker et al. 2010, Wittmann and Pörtner 2013). There are two chief concerns among the physiological effects. The first is that OA may challenge acid-base regulation, or the ability to maintain internal pH, as a result of reduced seawater pH that can affect organismal function by impacting internal biochemical reactions (Fabry et al. 2008). The second is that the reduced saturation states of $CaCO_3$ minerals (such as aragonite and calcite) makes it more difficult for organisms to build and maintain calcified structures such as shells. Changes in acid-base regulation and calcification will both influence the tradeoffs organisms must make when they allocate their limited energy towards processes of growth, reproduction, and defense (Kroeker et al. 2014b).

If OA increases the energetic costs of acid-base regulation and/or calcification, it may reduce energy allocation towards processes of growth and reproduction with potential impacts at the population level (Waldbusser et al. 2015b). Indeed, a meta-analysis of the biological effects of OA reveals decreased calcification, growth, and reproduction, and survival (Kroeker et al. 2010), with the strongest effects of OA on calcification and survival. Other effects include reduced immune function and health (Beesley et al. 2008, Bibby et al. 2008), variable effects on photosynthesis (Mackey et al. 2015), and reduced tolerance to other abiotic stressors (O'Donnell et al. 2008). Organisms that form shells may calcify less (Gazeau et al. 2007, Fabry et al. 2008), or change the strength (Gaylord et al. 2011) or composition (Fitzer et al. 2014) of calcified structures. Ocean acidification can be a particularly critical bottleneck at the larval stage when energetic demands are high and the primary formation of calcified structures tends to occur (Kroeker et al. 2013, Waldbusser et al. 2015b).

How the effects of OA translate to shifts in species interactions and ultimately to community structure is less well understood. Consumers often must increase allocation of energy to acid-base regulation (Pörtner 2008, Gaylord et al. 2014), while some primary producers may perform better (or the same) under OA if they are able to utilize additional carbon (Gaylord et al. 2014). Even within species or functional guilds, competitive hierarchies may be shifted if one species is able to perform better than another (Kroeker et al. 2012, Connell et al. 2013, McCormick et al. 2013, McCoy et al. 2016). In areas where volcanic activity leads to naturally elevated CO_2 in marine waters, which can provide insights into future conditions under OA, community structure shifts towards reduced species diversity, fewer taxa, and the loss of some calcifying species such as scleractinian corals, coralline algae, and gastropods (Hall-Spencer et al. 2008, Kroeker et al. 2011).

How might predator-prey interactions be influenced by OA and the suite of physiological changes it causes? The strength of predator-prey interactions are determined by the relative performance of predator and prey; if the performance of either interactor is affected by environmental conditions, the interaction strength could change (Menge and Olson 1990, Menge et al. 2002a). With OA, it could be energetically costly for many organisms to maintain acid-base balance when pH is reduced (Wittmann and Pörtner 2013), and increased metabolic costs could reduce the growth and performance of both predators and prey. Further, calcifying predators and prey may face increased costs from shell dissolution and new shell production.

For predators, predation can be broken down in to the energetic costs associated with the search, attack, and digestion of prey versus the energetic gains from consumption. If predators are less tolerant of OA stress than prey, intake of energy through increased ingestion rates may not be able to match increased metabolic costs, as has been shown with temperature (Iles 2014), and could ultimately reduce predator performance (e.g., feeding rates, locomotion, growth, and reproduction, see Bennett and Huey 1990, Harley 2013). Further, predators may take longer to find prey items if their chemosensory abilities are limited, as has been demonstrated in some fish (Cripps et al. 2011). On the other hand, predators may be able to meet higher energetic demands by increasing their feeding rate if prey supply is not limiting, switching the types of prey they consume, or switching the method of consumption. Overall, predators are predicted to be more sensitive to OA and its potential energetic costs as compared to prey (Kroeker et al. 2014b).

For prey, energy is allocated towards defense against predators when there is a threat of predation. For prey reliant on calcified structures for defense, reductions in shell thickness or strength due to lower pH could increase vulnerability to predation and decrease the handling times of predators (Amaral et al. 2012). Prey might also be able to allocate increased energy to maintain calcification by reducing energy towards somatic growth and maintenance. This could make prey smaller or of lower nutritional quality, and may mean that gape (size limited) predators consume more prey in general (Kroeker et al. 2014b). Decreased pH may disrupt the chemosensory detection of prey in fish (Dixson et al. 2010, Ferrari et al. 2011), and marine invertebrates (Watson et al. 2014) such that they may ignore or become attracted to cues from predators (Dixson et al. 2010).

Using knowledge of these potential effects of OA on predators and prey, we can begin to test how OA can mechanistically change the feeding rates of a predator and ultimately interaction strength. Changes to predation can arise from changes to the functional response (e.g., reduced feeding rates of individual predators). Feeding rates, as the number of individuals consumed per predator per unit time, can be broken down into time spent searching for prey and the time spent handling prey. Mathematically, this is commonly represented by a type II functional response (Rall et al. 2010, Vucic-Pestic et al. 2011), whereby predator feeding rates saturate as the density of prey increases. The feeding rate, *F*, dependent on prey abundance *N*, is estimated as:

$$F = \frac{cN}{1 + chN} \quad (1)$$

where *c* is the per capita attack rate (i.e. the instantaneous rate of discovery or successful capture), and *h* is the handling time, which includes ingestion and digestion (Holling 1959).

For a given prey density, there are two main mechanisms by which the feeding rate could decrease with OA: through decreased attack rates (measured as the number of feeding events per predator per prey per unit time) driven by lower capture or discovery rates if predators were less adept at sensing or capturing prey, or through longer handling times. Conversely, feeding rates could increase if handling times decrease (e.g., if prey shells become thinner or if predators are able to digest prey faster), if attack rates increase as a result of reduced predator satiation (i.e., predators have met metabolic requirements), or if predators are better able to discover or capture prey during foraging.

Beyond OA, predators and prey face a dynamic mosaic of environmental conditions that can influence species interactions. Recent research has revealed that OA can act synergistically with other local environmental drivers, such as temperature, hypoxia, and changes to the vertical structure of the water column (Doney et al. 2012, Gruber et al. 2012). Along the west coast of the United States, upwelling during summer months in the California Current System (CCS) results in high variability in the carbonate chemistry of coastal waters due to seasonal upwelling. When equatorward winds move surface waters offshore, water from depth is that is cold, nutrient rich, high in dissolved inorganic carbon, and low in pH is upwelled to the surface. This upwelling fuels productivity, but it can also lead to the formation of natural hypoxic events and shoaling of low-saturation state waters (Grantham et al. 2004, Feely et al. 2008, Chan et al. 2008, Hauri et al. 2013, Harris et al. 2013). Coastal waters in the CCS already reach pH values that are as low as those predicted for the global ocean in the future under ocean acidification (Hauri et al. 2009, Kroeker et al. 2016), and can be under-saturated with respect to aragonite across increasingly large areas (Feely et al. 2008). As such, ecosystems within the CCS may be particularly relevant to study as they are likely to see effects of OA on pH and calcium carbonate saturation states in the near future.

To examine how ocean acidification conditions would influence the strength of predator-prey interactions within a coastal ecosystem along the CCS, we used a mesocosm to explore how reduced pH (increased partial pressure of CO_2, or $p\text{CO}_2$)

would influence the interaction between calcifying predators and prey. We looked at patterns in feeding rate and handling time to better understand what components of predation might be vulnerable to OA. Our focal predators were two species of muricid whelks, *Nucella canaliculata* and *N. ostrina*. These whelks are common along the U.S. West coast in the rocky intertidal zone and consume largely sessile prey including mussels (*Mytilus trossulus* and *M. californianus*) and barnacles (*Balanus glandula*, *Semibalanus cariosus*, *Pollicipes polymerus* and *Chthamalus dalli*). Predation by whelks is sensitive to temperature (Sanford 2002b, Yamane and Gilman 2009), wave exposure (Menge 1978), and tidal cycle (Hayford et al. 2015), indicating high potential for responses to the stress of lower pH that could impact predation.

Using two separate laboratory experiments in an OA mesocosm system, we tested *N. canaliculata and N. ostrina* 1) feeding rates (number of prey consumed during the experiment) and 2) handling times (length of time per predation event) for mussel prey (*Mytilus trossulus*) in relation to elevated CO_2. In our first experiment, we aimed to observe the pattern in feeding rates at different pH levels to test the hypothesis that predators would perform more poorly than prey and reduce feeding with elevated CO_2 and decreased pH. Results from this first experiment were used to identify possible mechanisms that would either increase feeding rates (e.g., reduced handling time, reduced search times, or decreased satiation) or decrease feeding rates (e.g., increased search times, increased handling times). In our second experiment, we sought to explain our observed patterns by testing one mechanism, changes to prey handling times, in relation to pH. We hypothesized that handling times would be longer if predator performance was reduced under lower pH (higher CO_2). In both experiments, we hypothesized changes to predation would be related to reductions in measures of performance related to growth because of the direct negative effects of OA predicted for predators. Our experimental set-up, which used adult animals from ambient conditions, limited the possibility for changes in prey defenses (e.g., shell thickness), or differences in the caloric content of prey, which allowed us to specifically isolate predator behavioral responses to OA.

Methods

Mesocosm design and carbonate measurements

We used an ocean acidification mesocosm system located at Oregon State University's Hatfield Marine Science Center in Newport, Oregon for experiment I (feeding rate determination) and experiment II (handling time measurement). Six mass flow controllers (Alicat Scientific, models MCP-50 SLPM-D/5M and MC-500 SCCM-D/5M) set the level of incoming CO_2 and air to each of three header reservoir tanks (similar to the design of Fangue et al. 2010). The incoming compressed air was filtered with 5.0 micron and 0.1 micron filters, scrubbed of CO_2 using a CO_2 adsorber (Twin Towers CAS2-11), and filtered again at 0.05 microns prior to entering the system. Incoming CO_2 was provided using tanks of compressed CO_2 (Airgas®), and was filtered using a 40 micron particulate filter and a 0.3 micron coalescing filter prior to entering the system. Once CO_2-free air had been mixed with CO_2, it was added to header tanks with seawater using a system of Venturi injectors (Mazzei®) and pumps. The CO_2 concentration of the mixed air into each treatment was analyzed using a CO_2 sensor

(CO2meter.com, K-30, 0-1%), and the pH of the water was measured using a Honeywell Durafet pH/temperature probe. Airflow into the Venturi injectors was controlled using three rotameters (OMEGA FL-2021-NV). Water from each treatment header tank was gravity-fed into the eight 10L experimental chambers separately at a rate of approximately 3.5-4 L/min using Tygon tubing. Mass flow controllers were run using the program ‘Flow Vision’, and the CO_2 Meter was run using the program ‘DAS’ from CO2Meter.com. Lights above experimental chambers were kept on a 12:12 light cycle. Organisms were unable to leave the water and were submerged for the experimental duration.

In both experiments, we had three target pCO_2 treatment levels to emulate present (400 ppm), near future (1000 ppm), and far future (1600 ppm) conditions globally. These levels are also within the range of variation that organisms experience along the coast of Oregon (Evans et al. 2015). We designated treatments based on their relative target pCO_2 levels as low, medium, and high. Because pCO_2 and pH are negatively related, this means that the lowest pH values were in the high treatment (see Table 2.1). Though we had the same target values for our pCO_2 treatments in both experiments, the actual treatment values were not identical between the two experiments. Despite this, the differences among the three treatment levels within an experiment were greater than the differences within a treatment level between the two experiments, and thus the experiments are comparable.

Water chemistry analyses

To confirm the pH treatments in both experiments, we monitored carbonate chemistry in a number of ways throughout the experiment. The pH of each chamber (n=24) and the three header tanks were checked daily using a Honeywell Durafet pH probe. Temperature and salinity were measured using a YSI meter. To obtain data on alkalinity and check the accuracy of probe measurements, water samples were obtained from reservoir tanks. Samples were placed in acid-washed brown glass bottles with 50 μL $HgCl_2$ to arrest any biological activity that could alter water chemistry measurements. Bottles were immediately capped after sampling and stored for later analysis. In experiment I, a single bottle sample was taken daily from a single reservoir for analysis (n=14), while in experiment II, a single bottle sample was taken daily from each reservoir for analysis (n=33).

We validated pH data from the Durafet probes and calculated the full suite of carbonate system parameters using water samples collected from the header tanks during each experiment. In the lab, pH was measured spectrophotometrically using a SAMI Ocean pH Sensor (Sunburst Sensors), by running samples from each bottle until three replicates were obtained within 0.0050 units. During pH measurements, temperature was recorded with a temperature probe (VWR) placed in a sample of room temperature seawater for later use in back-calculating *in situ* carbonate system parameters.

Alkalinity was determined using spectrophotometric titration (Yao and Byrne 1998). We used certified seawater reference material from the lab of Dr. Andrew Dickson (Scripps Institution of Oceanography, La Jolla, CA); our material was from Batch 145 (see *http://cdiac.ornl.gov/oceans/Dickson_CRM/batches.html*). We measured the alkalinity of the standard as 2215.26 ± 1.41 μmol kg^{-1}; batch reference value = 2226.16 ± 0.71 μmol kg^{-1} (means ± standard deviations). We corrected for variability in the molarity of the HCl used in titrations using the difference between the reference true and measured values for all samples.

With alkalinity, temperature and pH, we calculated the carbonate system parameters (including Ω_{arag}, DIC and $p\text{CO}_2$) using the ‘seacarb’ package in R (Gattuso et al. 2016). Prior to system parameter calculation, *in situ* pH values were calculated based on differences between temperatures during sample collection and later measurement. pH was measured on the total scale with constant salinity (34 ppt). As recommended as best practices by Dickson et al. (2007), we used the constants included in Lueker et al. (2000) for K_1 & K_2, Dickson (1990) for K_s, and Perez and Fraga (1987) for K_f. For the daily bottle samples from the reservoir in experiment I, some samples became contaminated after being capped, likely because they did not receive adequate $HgCl_2$. In these cases, the pH measured by the SAMI and the pH measured by the probe differed by more than 0.2 pH units. To address this discrepancy, we used a global correction from non-contaminated bottles between SAMI and probe values (corrected for *in situ* temperature) and applied this to the probe values from the original point of water sampling. These corrected values were used in the carbonate system calculations. There were no contaminated samples in experiment II.

Carbonate system parameters

Confirming our assignment of low, mid, and high CO2 treatment levels, in experiment I, pH differed among treatments (Kruskal-Wallis Test, $\chi^2 = 10.54$, df = 2, p =

0.0051, Table 2.1, Figure 2.1), as did *p*CO_2 (Kruskal-Wallis Test, $\chi^2 = 10.52$, df = 2, p = 0.0052, Table 2.1, Figure 2.1). Temperature did not differ among treatments (Kruskal-Wallis Test, $\chi^2 = 0.5457$, df = 2, p = 0.76). In experiment II, pH also differed among treatments (ANOVA: $F_{2,32} = 158.8$, $p < 2.2 \times 10^{-16}$, Tables 2.2, 2.3, Figure 2.2), and post-hoc tests revealed that all treatments differed from one another. Similarly, *p*CO_2 differed among treatments (ANOVA: $F_{2,32}$, = 125.5, $p = 2.66 \times 10^{-15}$, Tables 2.2, 2.3). Temperature marginally differed among the treatments (Kruskal-Wallis test, $\chi^2 = 5.33$, df = 2, p = 0.070), and varied with date (Kruskal-Wallis test, $\chi^2 = 26.19$, df = 10, p-value = 0.0035).

Though temperature was marginally lower in the high CO_2 (low pH) in experiment II, such conditions are biologically-realistic for organisms from an ocean upwelling system where low pH events correspond with low temperatures rather than low pH/high temperature. There are multiple lines of evidence that upwelling has intensified in recent decades (Iles et al. 2012), and will continue to do so with climate change (Wang et al. 2015), which make it likely that water that is cold and low in pH will remain common in the NE Pacific. Given the interplay between temperature and pH, it is more realistic to consider pH in conjunction with upwelling conditions for our study system.

Experiment I: feeding rate patterns

Whelks (n=96) and mussels (n=960) were collected from Strawberry Hill, Oregon (44.250 N, 124.115 W) on 9 September 2014. Previous research has shown that whelks can exhibit strong inter-individual variability in feeding preferences (West 1986, 1988). To minimize the effects of inter-individual variability in prey preference on our results, we only selected whelks that were either feeding on or in close contact with beds of *M. trossulus.* Animals were placed in ambient seawater tables at Hatfield Marine Science Center (HMSC) in Newport, OR for a seven-day acclimation period. During this time, the whelks were starved in order to begin the experiment with consistent satiation levels. Each whelk received a small plastic numbered bee marking tag (Bee Works, Canada) affixed with superglue to ensure consistent monitoring and sorting for later physiological measurements. Only mussels of length 18-24 mm were included in this experiment. At the experimental outset, we placed individual whelks in mesh-sided plastic containers with ten live mussels. These containers were placed within one of eight experimental chambers for each pH level. Within each chamber, there were two containers with *N. canaliculata* and two with *N. ostrina*.

We recorded the wet weights of all whelks to the nearest 0.1 g and measured length from the apex to the bottom of the siphonal canal to the nearest 0.1 mm with calipers. Buoyant weight, which represents the weight of the calcified shell, was measured to the nearest 0.1 g by suspending each whelk in water underneath a scale (Palmer 1983). At the end of the experiment, the measurements were repeated on the surviving whelks. We also measured the responsiveness of whelks using a behavioral test (see Appendix B).

Feeding rates were estimated by observing whelks in containers every other day to obtain a total count of the number of mussels consumed by each whelk over the course of the experiment. To measure feeding rate, we opened each container and recorded live, dead, and consumed mussels. Any dead or consumed mussel shells were removed unless it would have been disruptive for an actively feeding whelk, in which case the mussels were removed at the next time point. Consumed mussels were categorized into two categories: mussels with a drill hole from a whelk proboscis were considered drilled while mussels with no remaining tissue but no visible drill hole were considered to have been pried open, which is another predation mechanism utilized by other muricid species (Wells 1958, Vermeij 1978) and by nucellid whelks when prey are gaping (Ebling et al. 1964, Freeman 2007). We measured the length of each dead or consumed mussel and froze it. The experiment ran for 14 days (16-30 September 2014). Mussels were fed twice with 100 mL of algae obtained from a nearby algal culture laboratory.

Experiment II: handling time patterns

Whelks (n = 168) and mussels (n = 1,071) were collected from mid zone, wave-exposed areas at Strawberry Hill on 19 April 2015. We transported animals to HMSC and held them in separate ambient seawater tables for 4 days. After that time, we measured the length and wet weight of all whelks. The organisms were then placed in one of three separate CO_2 treatment levels and allowed to acclimate for 3 additional days. In each treatment, mussels were placed loose at the bottom of seven 10 L chambers. In order to prevent predation on mussels during acclimation, whelks were kept away from mussels in smaller mesh-sided 500 mL containers within the 10 L chambers.

At the end of three-day CO_2 acclimation period, we initiated the experiment by adding mussels to whelk containers. Each whelk was given either six large or six small mussels to capture variation in changes to handling time across a range of prey sizes. Small mussels ranged from 15-20 mm, and large mussels from 23-28 mm. We checked sizes for a subset of mussels we had previously assigned to ensure that our two size groups were distinct. In each CO_2 level, 14 whelks of each species were given mussel prey (as in experiment I, each chamber held 2 containers for each whelk species). In an eighth chamber within each treatment, 14 additional whelks of each species were placed in a single container without food for the duration of the experiment to use in later physiological measurements. We supplemented food for mussels using Shellfish Diet (Reed Mariculture) according to manufacturer instructions. We fed mussels once a week for 30 minutes, and tanks were cleaned after feeding to reduce the impact of feeding events on the carbonate chemistry in tanks. We ran the experiment for 14 days.

To measure handling times (length of time per predation event), whelks were observed frequently to determine whether or not they were feeding on provided mussels. For the first 6 days of the experiment, we checked tanks hourly, except overnight when the tanks were not checked for a period of approximately seven hours. We considered whelks to be feeding when they were in direct contact with a mussel. While this was not always the case (i.e., sometimes whelks were on a mussel without feeding), this metric of feeding was the only way to minimize disturbing whelks during potential feeding events. We also noted the location of the whelk on the mussel as well as the location of the whelk/mussel pair in the container to minimize the chance that two separate feeding events would be counted as a single event.

We checked containers thoroughly when the whelk switched from feeding to non-feeding, when the position of a feeding whelk changed across time periods, or when a whelk had been recorded as feeding over many successive time points. In these checks, we visually assessed whether any mussels had been consumed. We removed any consumed or dead mussels from containers, recorded their length to the nearest 0.01 mm. In this experiment, we kept prey density constant by replacing dead or consumed mussels with a similarly sized new individual that had been kept in the same treatment conditions. Sometimes, whelks were in contact with a mussel but did not complete a feeding event, which we designated as a “false start.” In other cases, whelks began drilling but did not complete drilling. Following these incomplete drilling events, mussels with partial drill holes were removed, frozen, and replaced. After six days of hourly checks (excepting the overnight hours), we continued to observe feeding but ended handling time measurements. Our measurements of the number of feeding events (per predator per unit time) correspond with measurements of predation rate in experiment I above.

At the end of the experiment, we measured the wet weights (± 0.001 g) and length (± 0.01 mm) of all whelks. We assessed the survival of reference mussels (n=21 per treatment level) and recorded the wet weight and length of survivors. We measured the dry weight of the tissue and shell of all whelks for comparison across treatments. Dry weights were determined using the procedure established in Palmer (1982), where whelk tissue was dried for 24h at 80°C. Shells were dried to constant weight for 5 days at 40°C.

Data Analysis

In all analyses, we checked for normality and homogeneity of variance prior to analysis and transformed data as appropriate (including log and square root transformations). In experiments I and II, the numbers of consumed mussels (drilled, pried, total) by each whelk were analyzed using either Poisson regression or ANOVAs with untransformed or square-root transformed data. Although the responses were counts, in many cases residuals from untransformed data were better than those from other models. We used Akaike's Information Criterion corrected for small samples sizes (AICc) to reduce models starting from a saturated model with all model terms and all interactions. When Poisson models were fit, we estimated standard errors using the 'sandwich' package in R. In experiment I, we found a significant positive relationship between initial length of whelks and treatment despite random assignment to treatments. To account for this, we included a treatment x length term as part of the saturated model assessing treatment effects. There was no such relationship in experiment II, so these terms were not included. In experiment II, we included a binary variable for mussel size to indicate whether the whelk was given large or small mussels.

To obtain handling times in experiment II, we found the midpoint between the first observation when a whelk was feeding and the previous observation, as well as the midpoint between the last observed feeding and the next observation time (Novak 2010). We summed these and took the inverse to obtain weights for analysis where estimates associated with wider windows (and greater uncertainty) would receive a lower weight. In some cases (n=5), at the end of a feeding bout we found multiple shells that had been drilled. If these could not be assigned to an earlier observation period, we split the existing observation frame using estimates of the time spent drilling and ingesting mussels. We based our estimates from Miller (2013) for *N. lapillus* feeding on *M. edulis*, assuming ~25% of time feeding was spent drilling, while the remaining ~75% was spent on ingestion. Handling times were analyzed using a similar process as described above that involved comparing residuals from AICc selected models for different transformed (log, square root) and untransformed variables. We did not analyze the handling times of incomplete drills or pried mussels because the sample size was too small to assess differences.

All analyses were conducted using R version 3.0.0 (R Core Team 2016) with RStudio version 0.99.896 (RStudio Team 2014) and including the packages ‘car’ (Fox and Weisberg 2011), ‘AICcmodavg’ (Mazerolle 2015), ‘sandwich’ (Zeileis 2004, 2006), ‘phia’ (De Rosario-Martinez 2015), ‘MASS’ (Venables and Ripley 2002), ‘seacarb’ (Gattuso et al. 2016), ‘PMCMR’ (Pohlert 2014), and ‘pscl’ (Zeileis et al. 2008).

Results

Experiment I: patterns of predation

The number of mussels drilled by whelks was affected by CO_2 treatment (ANOVA: $F_{2,95} = 5.8332$, p = 0.0041; Table 2.4, Figure 2.3A). Over the course of the two-week experiment, whelks in the highest CO_2 treatment drilled 33% less (0.73 mussels fewer, 95% CI: 0.303 to 1.15 mussels fewer) than those in the ambient CO_2 treatment (linear model: treatment: high vs. low, t-value = 3.411, p = 0.00097, Table 2.5). This pattern was consistent across both whelk species, although drilling was dependent on species (Type II SS ANOVA: $F_{1,95} = 21.10$ p = 1.4×10^{-5}). *N. ostrina* drilled 1.05 fewer mussels (95% CI: 0.599 to 1.51 fewer mussels) than *N. canaliculata* overall (linear model: species, t-value = 4.594, p = 1.4×10^{-5}, Table 2.5). For mussels that were pried open, rather than drilled, there was no overall effect of OA (Table A1, Figure 2.3B), but

N. ostrina pried, on average, 0.20 more mussels (95% CI: 0.050 - 0.460) than *N. canaliculata* (ANOVA, species, t-value =3.945, p =1.6 x 10^{-4}, Table A2).

Contrary to our hypothesis that exposure to elevated CO_2 would reduce growth, growth (measured as change in whelk length) was not different among CO_2 treatments (Type II SS ANOVA, $F_{2,95}$ = 1.104, p = 0.34; Table A3, A4, Figure 2.4A), but it differed between species (Type II SS ANOVA: $F_{1,95}$ = 19.16, p = 3.2 x 10^{-5}, Table A4, Figure 2.4A) with *N. ostrina* adding less length than *N. canaliculata*. The median length added by *N. ostrina* was 0.25 mm less (95% CI: 0.14 - 0.34 mm) than that added by *N. canaliculata*. The dry body weight of whelks, which is a measure of their tissue weight, depended on an interaction between treatment and species after accounting for initial whelk length (Type III SS ANOVA: $F_{2,95}$ = 4.760, p = 0.011, Table A5, A6, Figure 2.4C). Shell dry weight at the end of the experiment did not differ among CO_2 treatments (Type II SS ANOVA: $F_{2,95}$ = 0.6790, p = 0.51, Tables A5, A6, Figure 2.4B). Another metric of shell mass, change in buoyant weight, indicated that whelks were able to add more shell mass in the high CO2 treatment relative to the low (Tables A3, A4, Figure 2.4D), though the effect of treatment overall was not significant and the linear model had low explanatory power overall (R^2= 0.043).

Experiment II: handling time observations

When whelks were fed mussels *ad libitum* in experiment II, CO_2 treatment had no effect on drilling (Poisson Analysis of Deviance, χ^2 = 0.416, p = 0.81, Tables 2.6, 2.7, Figure 2.5), which was in contrast to experiment I, where whelks were given a limited number of mussels. Drilling was dependent on the species, with *N. ostrina* drilling less

(Poisson regression, species: $z = -5.469$, $p = 4.5 \times 10^{-8}$, Table 2.7). For the *N. ostrina* that drilled mussels, drilling was dependent on prey size, with smaller mussels drilled more readily than large (Poisson regression, mussel size: $z = -2.986$, $p = 0.0028$, Table 2.7, Figures A2, A3). Though there were no effects of treatment on the number of drilled mussels, handling time depended on treatment and whelk species (Table 2.8, Figure 2.6). On average, whelks in the highest CO_2 treatment took 9.4 hours (95% CI 2.9 - 16.0 hours) longer to drill than those in the low treatment (linear model, treatment; t-value = 2.860 $p = 0.0053$, Table 2.8, 2.9). Handling times for both species depended on mussel size, with smaller mussels greatly reducing handling times (Table A7, Figures A4, A5). In addition to whelk predation by drilling, there were times that whelks pried mussels open or incompletely drilled them, but these were not numerous enough to allow analysis across treatment levels and species (only 28 instances among 84 whelks). Seven whelks consumed no mussels during the experiment; of these, four were in the high, one in the mid, and two in the low CO_2 treatment.

Unlike in experiment I, we found an overall effect of treatment on growth (length change) in whelks in experiment II (Type III ANOVA $F_{2,83} = 3.313$, $p = 0.042$, Tables A8, A9, Figure 2.7), with whelks in high CO_2 treatment growing less than those in the low (Table A9). However, growth also depended on an interaction between species and the mussel size given to whelks (Type II ANOVA, $F_{1,83} = 7.760$, $p = 0.0067$, Tables A8, A9). *N. ostrina* given smaller mussels gained more length than those given larger mussels while mussel size was not important for *N. canaliculata* growth (Table A10). Final dry weight of both the shells and body tissue of whelks depended on species but not treatment or mussel size (Tables A11, A12, Figure 2.7).

Discussion

In our study, we aimed to understand how predator-prey interactions of whelks would be influenced by carbonate conditions that match those predicted for future ocean acidification. We also linked behavioral changes in whelk predators in low pH conditions to other integrated physiological metrics, such as growth, in order to more fully understand the outcomes of these changes for whelk predators. We found that predation on mussels by whelks displayed differing and often species-specific responses for a range of metrics when exposed to conditions of high pCO_2 associated with ocean acidification within the next century. In our first experiment, where whelks were given a limited number of mussels to consume, feeding rates (number of drilled mussels per predator per prey per time) were reduced in elevated pCO_2. In experiment II, whelks clearly demonstrated longer handling times in acidified water, which reveals a potential mechanism for reductions in drilling we observed in experiment I. Whelks in higher CO_2 waters (~1700 ppm CO_2) took almost 9.5 hours longer to consume their prey than those in waters more representative of ambient current conditions (400-500 ppm CO_2). In our second experiment, where whelks were given food *ad libitum* and allowed time to acclimate, we found no changes in feeding rate across CO_2 treatment levels, which contrasts with our first experiment and points to the potential impact of prey density and acclimation time on predator responses. Interestingly, although *N. ostrina* and *N.*

canaliculata are co-occurring congeners, they were affected differently by future OA conditions as predators. The behavioral changes we observed, however, were associated with few differences in the gross physiological parameters that we measured,

That predators reduced feeding in response to elevated CO_2 has been observed in other systems. For example the sea star *Asterias rubens* decreased its consumption rate by 50% in acidified conditions, growing less while its prey, *Mytilus edulis* grew at higher rates with acidification (Keppel et al. 2015). Yet, in other cases, predators consumed more prey in response to acidification (Amaral et al. 2012, Sanford et al. 2014). These responses can be related to behavioral and physiological changes in the predator, the prey, or both interactors. We address some of the potential mechanisms for these changes below in relation to our study and other relevant research.

Handling Time

Whelks in our study exhibited much longer handling times to consume prey in acidified water. Handling time is a function of prey and predator sizes, metabolic rate, and predator experience, and is sensitive to typical variation in environmental conditions (Rall et al. 2010). Longer handling times with exposure to acidification could result from behavioral changes, or from differences in prey defenses. Given the short duration of our experiment, as well as the fact that we used adult prey from a single site, it is likely that our results stem from behavioral changes in the predator rather than morphological prey changes. Longer handling times lead to lower feeding rates in a given time frame, and thus interaction strengths can weaken. Likewise, predators receive less energetic gain for the same amount of effort, which can ultimately affect growth rates, reproduction, and other measures of fitness.

There are relatively few studies with explicit measurements of handling time in response to OA. In a study of *N. lapillus*, Queirós et al. (2015) found that handling times increased with acidification, but measurements only included a few hours of observation rather than entire feeding events. Other studies with *N. lapillus* have found that warming temperatures reduce handling times because ingestion time is reduced (Miller 2013), and so warming temperatures may be able to offset what we observed with acidification. Green crabs *Carcinus maenas* kept in ambient waters were able to handle littorine snails from acidified water faster than snails from ambient water (Landes and Zimmer 2012). However, this effect disappeared when the predators themselves were exposed to elevated CO_2, which suggests both biomechanical changes in the acidified prey (which initially increased handling times), and the potential for behavioral impacts on the predator in acidified water.

Foraging times and attack rates

In order to survive, predators must be able to find prey and complete sufficient feeding events to gain enough energy for maintenance and growth. We did not directly examine foraging behavior in our study, but insights from similar systems suggest high potential for OA effects. In a congener species, the whelk *N. lapillus,* exposure to elevated CO_2 increased the distance that individuals traveled to find food, and took longer to consume food (Queirós et al. 2015). In our study, *N. canaliculata* in the high CO_2 treatments spent less time overall in direct contact with mussel prey, which could indicate the potential for increased foraging times (Figure A7A). Longer foraging times and decreased attack rates could be the result of reduced ability to detect prey. Increasingly, there has been growing recognition of the potential that decreased pH could disrupt of synaptic transmission in the system of GABA receptors in invertebrates (Watson et al. 2014, Clements and Hunt 2015). Despite this, other muricid species do not appear to lose olfactory ability to detect prey in acidified waters. For example, the snail *Concholepas concholepas* reared in elevated CO_2 conditions was able to detect prey normally, but had impaired predator avoidance behaviors (Manriquez et al. 2014).

Bringing prey into the picture

We have focused on how the behavior of predators is influenced by OA conditions. However, feeding rates are also highly dependent on attributes of prey. For example, predator feeding rates and handling times are prey size-dependent. Thus, if OA affects growth rates of either predator or prey differentially, it can change interaction strength (Kroeker et al. 2014b). We found complex relationships between whelk species and mussel size that affected whelk growth. Regardless of OA treatment, handling times depended on mussel size for both species, but only growth of *N. ostrina* depended on the size of mussels offered. This makes sense given that *N. canaliculata* is larger on average than *N. ostrina* and is able to handle larger mussels more readily. In addition, while both whelk species consume *M. trossulus*, it more commonly consumed by *N. canaliculata* (E. Cerny-Chipman, unpublished data). In another study, the oyster drill *Urosalpinx cinerea* was tolerant of elevated CO_2, but its oyster prey grew more slowly under acidified conditions, and thus were consumed preferentially over larger oysters raised in ambient conditions (Sanford et al. 2014).

Although our study focused on predator responses to OA, prey responses are also critical to understanding how interaction strength might change with OA. Several *Mytilus* species have demonstrated negative responses to OA (Bibby et al. 2008, Gaylord et al. 2011), but effects differ with temperature (Waldbusser et al. 2011, Gazeau et al. 2014, Kroeker et al. 2014a), variability in pH (Kroeker et al. 2016), and food availability (Waldbusser et al. 2010, Melzner et al. 2011, Thomsen et al. 2013). Mussels must invest heavily in calcified defenses against predators, and thus may be more vulnerable to crushing and drilling attacks of predators if calcifying is more costly under OA. Evidence points to shifts that are already underway; mussel shells (*M. californianus*) are thinner now than in past centuries and decades (Pfister et al. 2016). Among intertidal prey species more generally, prey may be less able to sense predators, leading to increased predation risks. For example, in the herbivorous snail *Tegula funebralis,* acidification within rocky intertidal tide pools led to disrupted anti-predator abilities against the keystone species predator *Pisaster ochraceus* (Jellison et al. 2016).

Physiological effects

Though longer-term effects of OA and other stressors are predicted to include a suite of physiological changes, physiological differences between treatments in our experiment were generally small and did not appear to underlie differences in predation. In our first experiment (with whelks fed a single supply of ten mussels) there were no differences in whelk length change between CO_2 treatments. Instead, we found slight differences in body (tissue) weight that appeared to be driven primarily by a difference between the whelk species in the low treatment rather than by treatment itself. In contrast, in experiment II (where whelks were fed *ad libitum*), we found that whelks added less length in the high CO_2 treatment, but there were no differences in body weights. It is difficult to say whether such differences would be biologically meaningful, and there were no differences in shell weights with treatment in either experiment. There are likely a few reasons for these equivocal effects. The first is that whelks were well fed during the experiment and prey were in close proximity. As a result, whelks may not have been constrained in acquiring enough energy to meet energetic demands. Sufficient food availability can offset negative costs of OA in primary consumers (Melzner et al. 2011, Thomsen et al. 2013), and it is likely that the same effect applies to higher-order consumers. The second reason is that the duration of our experiment was relatively short and could have precluded physiological changes that appear over longer time scales.

Finally, our failure to detect physiological effects on predators likely stems from our choice of measures at the whole-organism scale, which could mask effects at finer scales such as calcification, metabolism, or molecular changes that ultimately influence performance (Hofmann et al. 2010). With longer exposures, it is likely that both whelks and mussel prey would be affected by OA in terms of calcification and metabolism. Molluscs have relatively low metabolic rates in comparison to vertebrates, indicating relatively low ability to compensate for decreased pH (Pörtner 2008, Wittmann and Pörtner 2013). If extracellular or intracellular pH changes cannot be compensated, metabolic depression may occur and limit performance, though this may not be typical within the range of values expected with OA (Thomsen and Melzner 2010). In terms of calcification, mineralization often occurs internally (Gazeau et al. 2013) and thus may be protected from changes in seawater chemistry (Findlay et al. 2009). In the whelk *N. lamellosa*, increased shell dissolution was more of an issue than reduced shell deposition (calcification) in low pH water as the outer shell is exposed (Nienhuis et al. 2010). In our experiment, the lack of differences in shell mass between pCO_2 treatments could suggest that whelks either do not face reduced ability to deposit shell or that the time scale (two weeks) was too short to observe relevant changes.

Ecological and Community Effects

We found that the interaction strengths between two intertidal predators and their mussel prey were sensitive to elevated CO_2 conditions. This result points to the potential for OA impacts at the community levels for rocky intertidal habitats. Environmental stress models in general (Menge and Sutherland 1987, Bruno et al. 2003) predict that as stress increases, predation becomes less important, and eventually the stressors themselves become more dominant determinants of community structure than competition or predation. Our results are consistent with the idea that elevated CO_2 could reduce the strength of top-down effects. In addition, OA can benefit basal resources, and thus, OA might be able to influence communities simultaneously from the top down and bottom up by reducing performance of consumers and increasing algal growth (Gaylord et al. 2014).

For rocky intertidal habitats in Oregon, reductions in consumption of mussels similar to what was found in this study (on the order of 30%) could have considerable impacts on the interaction between whelks and *M. trossulus*. Whelks are highly abundant and important predators in the mid intertidal zone, and can reach high densities when in feeding aggregations. Typically, patches of *M. trossulus* are almost entirely consumed by whelks and by sea stars over the course of the summer months, and persistence of these mussel patches facilitates the recruitment of other sessile prey, such as barnacles and *M. californianus* (Paine 1974, Petersen 1984, Gouhier et al. 2011). In a manipulation of the intensity and temporal frequency of predation, Navarrete (1996) demonstrated that sessile prey community composition was influenced by temporal variability in whelk predation. Therefore, predation weakened by OA could have direct effects on the *M. trossulus* population, but also indirect effects on the population and interactions among a suite of other prey species.

OA may influence spatial variation in interaction strength, as with temperature, and ultimately drive selection for the strength of interactions (Kroeker et al. 2016). We studied whelks from a single site, but whelks have crawl-away larvae and are likely locally adapted, which means there is the potential for large variation in response to OA among isolated populations. The high inter-individual variability in our experiment could point to such capacity for adaptation in behaviors. It would be particularly informative to investigate drilling behavior across whelks from different populations given the variation in consumption of *M. californianus* by *N. canaliculata* (Sanford et al. 2003, Sanford and Worth 2009) that may arise in part due to morphological differences in prey species that exist across the dynamic environmental context of the U.S. West Coast (Kroeker et al. 2016).

Effects of CO_2 in the context of other environmental stressors

While our study altered pCO_2 in a manner realistic for future predations, we cannot identify which changes to the carbonate system (pH, pCO_2, Ω_{arag}) were most influential on our results. In larvae, saturation state is particularly critical determining growth and development (Waldbusser et al. 2015a). However, in adult predators and prey, with less restrictive growth demands, acid-base regulation, and thus pH, may be more important overall responses to OA (Wittmann and Pörtner 2013). On a broader level, OA is a multiple stress in and of itself because of impacts to both acid-based regulation and to calcification through changes to the carbonate system (Waldbusser et al. 2015b). Importantly, aside from OA, temperature is known to have pervasive effects on physiology and species interactions, and in this study was dependent on treatment in experiment II, though not in experiment I. Metabolic rate scales logarithmically with temperature (Somero et al. 2016), so even small differences in temperature can be meaningful.

Assessing multiple studies on the effect of temperature on the feeding rates in muricid gastropods (including *Nucella canaliculata*), Sanford (2002b), estimated that 3°C difference in temperature typically resulted in a 20-44% reductions in prey consumption. The reductions in prey consumption in our second experiment across the three pCO_2 treatments were within this range, yet our temperature differences were typically <1°C. This suggests that reductions in feeding were greater than would be expected from temperature effects alone, and that pCO_2 does indeed have effects on predation. In addition, temperature did not differ among treatments in experiment I, where the strongest and most consistent effects on whelk drilling were observed. Higher temperatures typically reduce handling time (Novak 2010, Vucic-Pestic et al. 2011), which is likely responsible for some of the observed differences in handling time between treatments.

Aside from the carbonate system variables we controlled, conditions in the lab are likely much less stressful for whelk predators than field conditions where prey abundances are uncertain, whelks face the threat of predation, and other environmental factors such as wave exposure and tidal elevation limit foraging time and increase the riskiness of increased handling times. In addition, feeding trials under any conditions in the lab may overestimate natural feeding rates for a variety of reasons (Ruesink 2000), thus our estimates are not directly comparable to estimates from field measurements.

As the number of studies testing the effects of OA on interactions grows, it is critical to consider how best to gain generality. With single-species experiments, the choice of treatment levels, exposure times, and response metrics are important for inference. However, when measuring pairwise interactions, many more experimental choices emerge. Thinking about species interactions from a more theoretical perspective can help drive experimental design and move us beyond species- and interaction-specific understanding. Our study is one of the first to consider how one mechanism for decreases in predation due to reductions in pH could result from a behavioral change in the predator that affects the functional response. We also link behavioral change with measurement of gross physiological change, integrating from individual organisms to species interactions. However, our experiment was short-term and the individuals were taken as adults from ambient conditions, both of which reduce our inference and rule out hypotheses about specific components of predation vulnerable to OA. Disentangling these sorts of experimental choices in existing OA studies can help structure information of individual species effects, resolve apparent contradictions among studies, and help identify knowledge gaps.

Conclusions

The looming question for understanding community level effects of OA is whether species-specific responses to OA can be used predict changes in species interactions, and whether it is possible to generalize the results of species interaction changes to the interactions between other predators or prey. At a broad scale, meta-analyses of OA impacts show that there are many negative effects on organisms that largely transcend taxonomic differences (Kroeker et al. 2010, 2013, Wittmann and Pörtner 2013). Yet, moving beyond species-specific responses yields new opportunities and challenges for understanding and prediction under OA. In our study, we looked at the responses of co-occurring congeneric predators feeding on a shared prey; we found that they both responded to OA, but there were important differences in the magnitude of the response (and the presence of high intra-individual variability). This points to the primacy of physiology and natural history of individual species to understand effects and move towards generality.

Understanding the responses of predators to ocean acidification, even under short-term temporal exposure, is essential for prediction at the community level. It is not solely the abiotic effects of climate change that will induce ecological extinctions; biotic interactions are critical proximate factors influencing the persistence of species and communities with change (Cahill et al. 2012). Predators are often disproportionately important to community structure (e.g. keystone species, apex predators) and are often the most vulnerable to a changing environment (Zarnetske et al. 2012). Our results show that changes consistent with ocean acidification lead to reductions in the impacts of predators on a primary prey species, likely mediated through changes in predator handling times. These effects emerged on relatively shorter scales, though much remains to be determined about the nature of predator-prey interactions in relation to longer-term exposure to OA and other synergistic environmental changes. At shorter-term scales, it is likely that behavioral impacts on the predator swamp the costs for prey of maintaining shell deposition and overcoming dissolution for heavily-calcified defensive structures like shells. On longer time scales, or at critical life stages with high energetic demands, the balance between predators and prey could shift with implications for interaction strengths, food web stability, and ultimately community structure and functioning.

Acknowledgements

Funding for this study was provided by a Mamie Markham Research Grant from Hatfield Marine Science Center at OSU (ECC), the Kingfisher Foundation (BAM), the Oregon State University Integrative Biology Research Fund (ECC), and the Partnership for Interdisciplinary Studies of Coastal Oceans. We would like to thank Francis Chan, Annaliese Hettinger, Allison Barner, Jenna Sullivan, Chenchen Shen, Silke Bachhuber, Alissa Rickborn, Tully Rohrer, Jerod Sapp, and Isaac Shepard for assistance in running the experiments. Mark Novak, George Waldbusser, Sally Hacker and Kyle Coblentz provided helpful input on analysis and conceptual design. Allison Barner and Jenna Sullivan provided feedback on earlier drafts. We are grateful to those at HMSC who made the experiment possible, including Jessica Miller, Melody Pfister, Jeff Wiseman, Jim Lewis, Chris Langdon and the HMSC facilities staff.

Figures

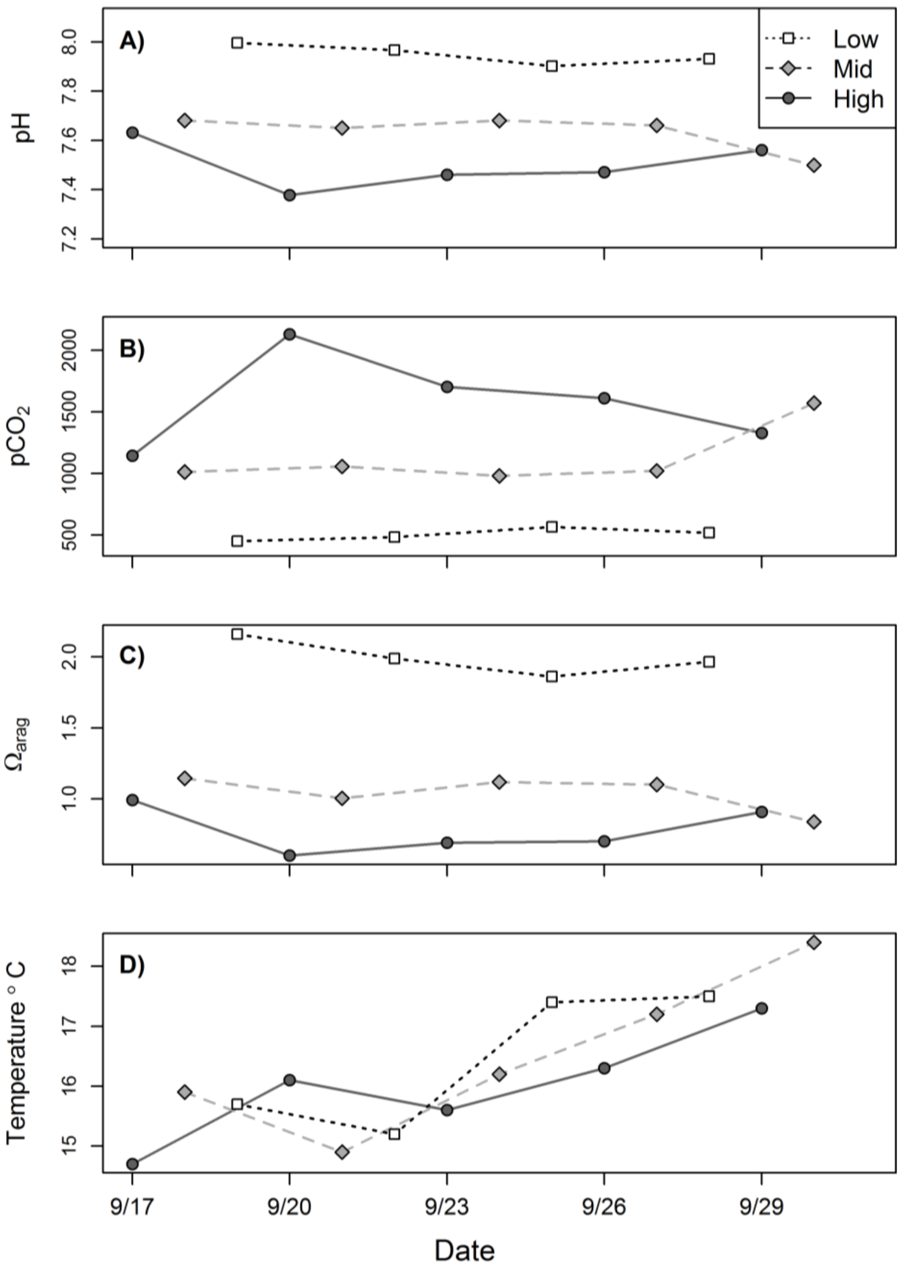

Figure 2.1. Carbonate system parameters over time for experiment I, with A) pH, B) pCO_2, C) Ω_{arag}, and D) temperature. Values for the mid treatment on 9/18, 9/21, 9/24, and 9/27 and high treatment 9/23 and 9/26 were calculated based on globally-corrected probe measurements due to contamination in the samples, in which probe and SAMI measurement were more than 0.20 pH units apart.

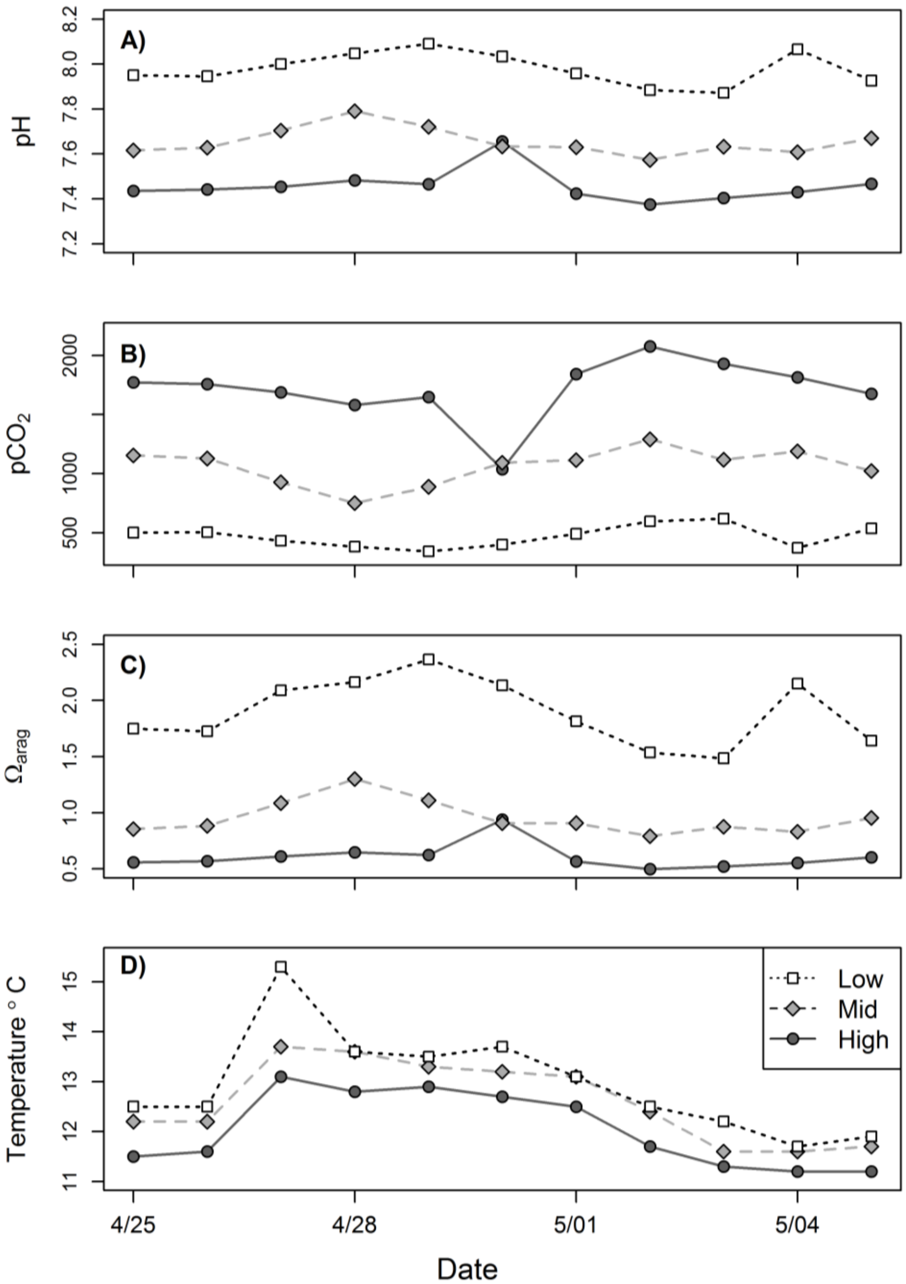

Figure 2.2. Carbonate system parameters over time for experiment II, with A) pH, B) pCO_2, C) Ω_{arag}, and D) temperature. In this case, a sample was taken from each header tank daily and there were no contaminated samples.

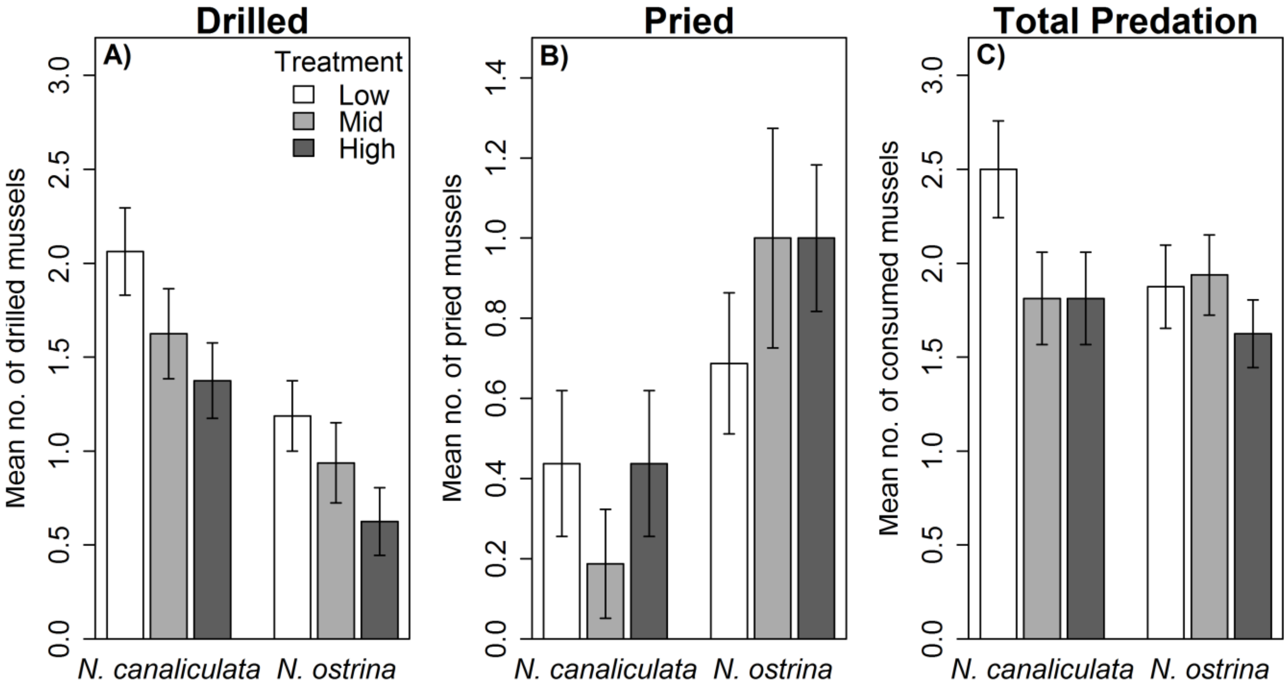

Figure 2.3. Mean mussels consumed by whelks in experiment I by predation method and species, with A) mussels that were successfully drilled, B) mussels that were pried open for consumption, and C) total predation on mussels, or the combination of drilled and pried mussels. Values represent the mean total number of mussels over the two week experimental period for each whelk. Note the differences in the scale of each plot. Error bars are +1 SE.

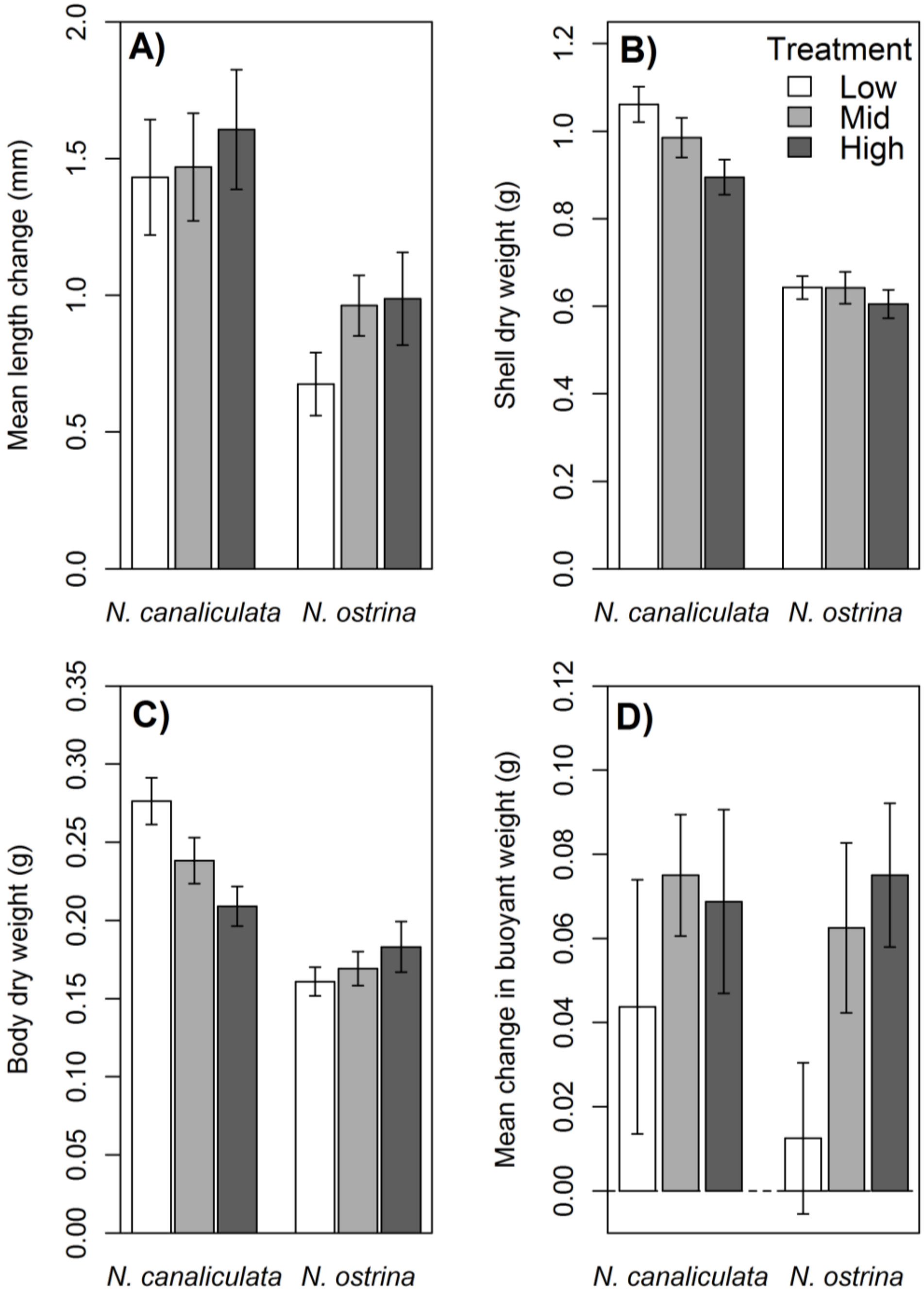

Figure 2.4. Mean changes in gross physiology of whelks in experiment I , including A) change in length, B) the dry weight of shells and C) body tissue measured at the termination of the experiment, and D) change in buoyant weight, which is a measure of the shell weight. Error bars are +1 SE.

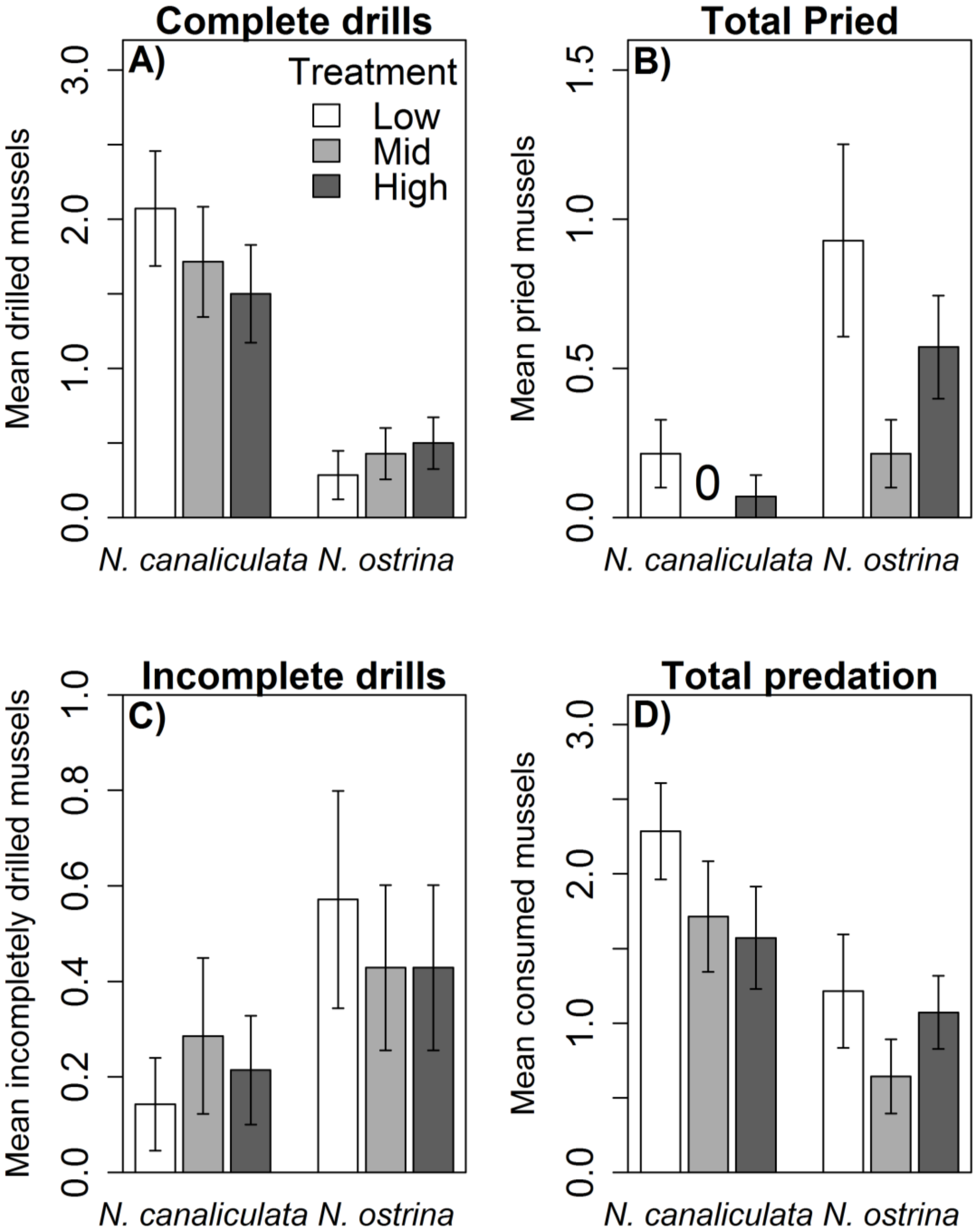

Figure 2.5. Mean mussels consumed by whelks in experiment II by predation method and species, including A) mean number of fully drilled mussels, B) mean number of pried mussels, C) mean number of incomplete or partial drills, and D) total mussel consumption across predation method. Values represent means for the two week experiment by treatment and species. The scale differs between the different plots. Error bars are +1 SE

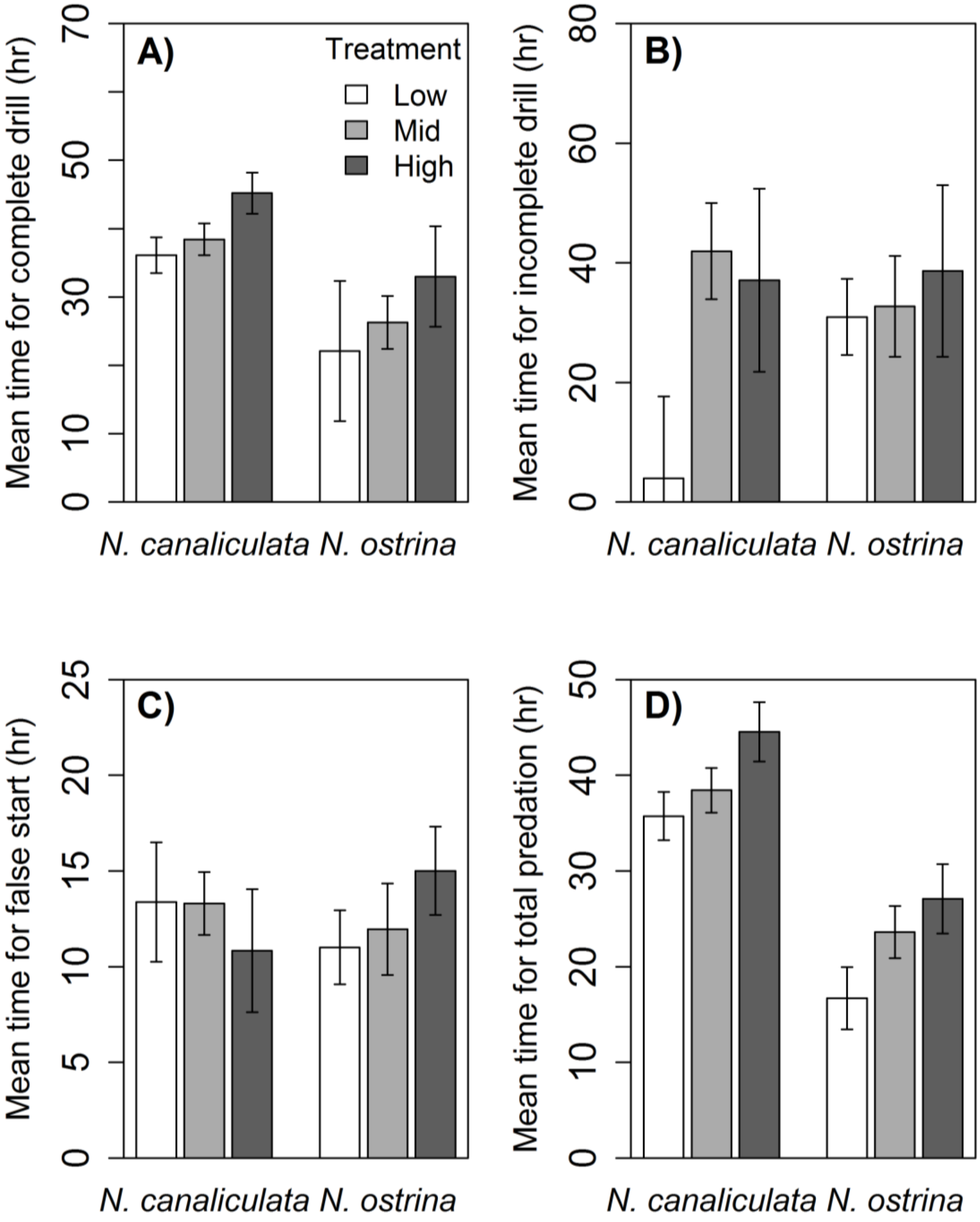

Figure 2.6. Mean handling times by treatment and species for A) drilling, B) incomplete drilling, C) false starts, and D) total predation. Means and standard deviations are weighted by the inverse of the length of the window over which the beginning and end of observations were measured. Error bars are +1 SE.

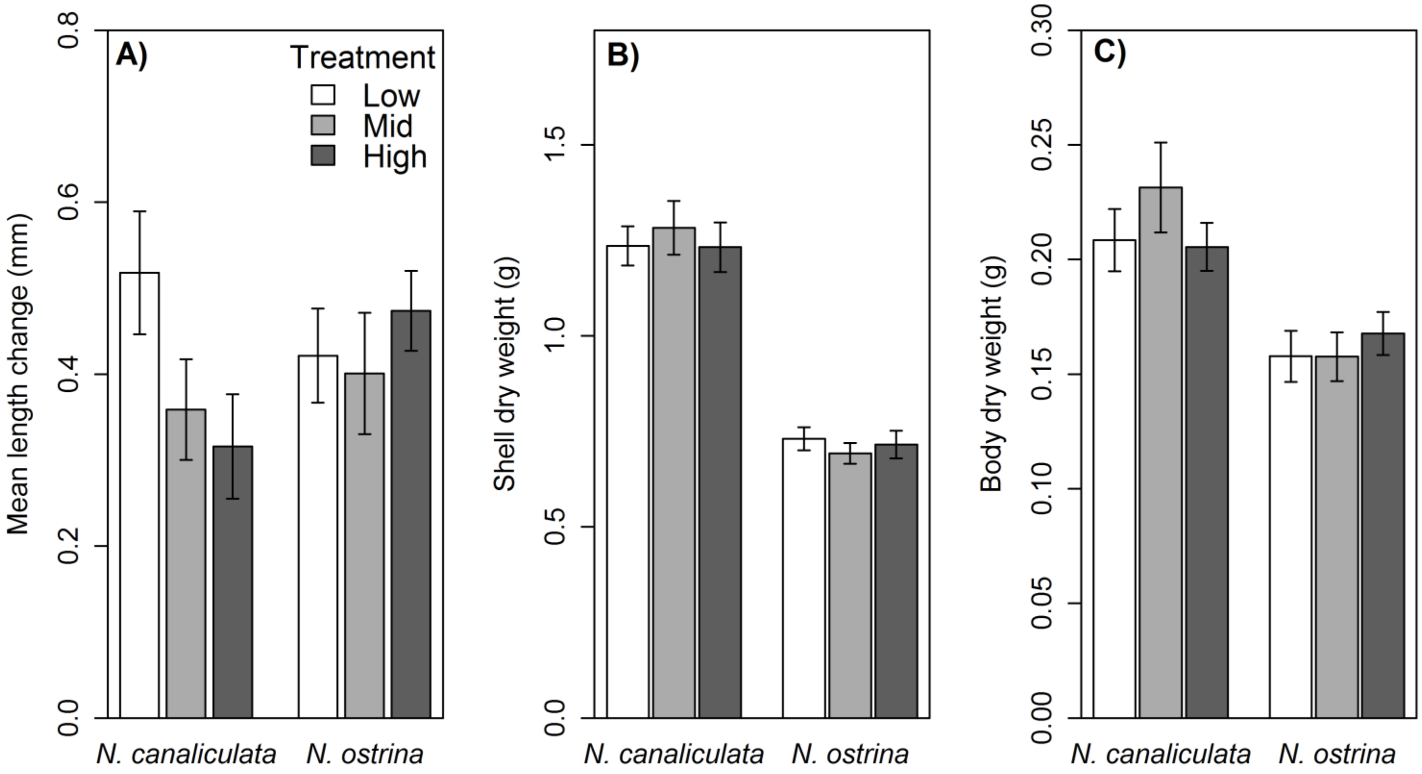

Figure 2.7. Mean changes in gross physiology of whelks in experiment II, including A) change in length, B) the dry weight of shells and C) body tissue measured at the termination of the experiment. Error bars are +1 SE.

Tables

Table 2.1. Carbonate parameters (means ± SE) by treatment for each experiment. Because of contamination to several water samples in the mid treatment in experiment I, the values for this treatment level were calculated using pH from probe measurements corrected using a global correction based on SAMI measurements.

Experiment	Treatment	pH	$p\mathrm{CO}_{2\mathrm{calc}}$	Ω_{arag}	Temp	Alkalinity	$f\mathrm{CO}_2$
Experiment I	Low	7.949 (± 0.041)	504.11 (± 49.64)	1.99 (± 0.12)	16.45 (± 1.17)	2210.32 (± 31.31)	502.32 (± 49.49)
	Mid	7.634 (± 0.077)	1128.04 (± 249.25)	1.04 (± 0.13)	16.52 (± 1.33)	2189.83 (± 37.35)	1124.05 (± 248.43)
	High	7.500 (± 0.10)	1582.73 (± 377.82)	0.78 (± 0.16)	16.00 (± 0.95)	2204.58 (± 53.28)	1577.08 (± 376.47)
Experiment II	Low	7.980 (± 0.073)	470.37 (± 92.13)	1.9 (± 0.29)	12.95 (± 1.03)	2222.26 (± 21.72)	468.62 (± 91.78)
	Mid	7.655 (± 0.062)	1061.42 (± 153.26)	0.96 (± 0.15)	12.60 (± 0.80)	2221.18 (± 21.16)	1057.46 (± 152.67)
	High	7.458 (± 0.072)	1710.54 (± 263.04)	0.61 (± 0.12)	12.05 (± 0.75)	2213.62 (± 23.83)	1704.11 (± 262.03)

Table 2.2. One-way ANOVA table (from Type II SS) for testing overall differences in pH and CO_2 among treatments in experiment II.

	Sum Sq	Df	F-value	p-value
pH				
Treatment	0.0256014	2	158.9	$< 2.2 \times 10^{-16}$
Residuals	0.0024168	30		
CO_2				
Treatment	8465242	2	125.5	2.7×10^{-15}
Residuals	1011693	30		

Table 2.3. Poisson regression coefficients and standard errors for pH and CO_2 differences by treatment in experiment II. pH response was log-transformed to meet assumptions of normality. pH model $R^2 = 0.91$; pCO_2 model $R^2 = 0.89$. The low treatment was the reference group in both cases.

	Estimate	Std. Error	t value	p-value
pH				
Intercept	2.077	0.0027	767.44	$< 2.0 \times 10^{-16}$
Treatment: Mid	-0.0415	0.0038	-10.84	6.8×10^{-12}
Treatment: High	-0.0677	0.0038	-17.68	$< 2.0 \times 10^{-16}$
CO_2				
Intercept	470.4	55.4	8.495	1.8×10^{-9}
Treatment: Mid	591.1	78.3	7.548	2.0×10^{-8}
Treatment: High	1240	78.3	15.84	4.1×10^{-16}

Table 2.4. 3-way ANOVA table (Type II SS) testing the effect of species and treatment on total drilling by whelks in experiment I.

	Sum Sq	Df	F value	p-value
Treatment	7.883	2	5.833	0.0041
Species	14.26	1	21.10	1.4×10^{-5}
Initial length	2.219	1	3.284	0.073
Residuals	61.49	91		

Table 2.5. Linear regression coefficients and standard errors for the effects of treatment and species on drilling in experiment I. The reference for treatment is low CO_2 and *N. canaliculata* for species. Model adjusted $R^2 = 0.24$.

Term	Estimate	Std. Error	t-value	p-value
Intercept	2.203	0.1987	11.09	$< 2.0 \times 10^{-16}$
Treatment: Mid	-0.3949	0.2074	-1.904	0.060
Treatment: High	-0.7266	0.2130	-3.411	0.00097
Species: *N. ostrina*	-1.055	0.2297	-4.594	1.4×10^{-5}
Initial Whelk Length	-0.1270	0.0701	-1.812	0.073

Table 2.6. Analysis of Deviance Table (Type II test) for the effect of treatment, mussel size, and whelk species on drilling by whelks in experiment II based on a Poisson regression model.

	LR χ^2	Df	p-value
Species	38.51	1	5.5×10^{-10}
Mussel Size	9.405	1	0.0022
Treatment	0.4160	2	0.81

Table 2.7. Poisson regression coefficients and standard errors results for a model including species, mussel size, and treatment on the number of mussels drilled in experiment II. The reference levels were *N. canaliculata* for species, small for mussel size, and low CO_2 for treatment. The model had a residual deviance of 79.75 on 79 df.

	Estimate	Std. Error	z-value	p-value
Intercept	0.9273	0.1962	4.726	2.3×10^{-6}
Species: N. ostrina	-1.471	0.2690	-5.469	4.5×10^{-8}
Size: Large	-0.6604	0.2212	-2.986	0.0028
Treatment: Mid	-0.0953	0.2523	-0.378	0.71
Treatment: High	-0.1643	0.2569	-0.639	0.52

Table 2.8. ANOVA table (Type III SS) testing the effect of species and treatment on handling time for completely drilled mussels in experiment II. The model included weights that were the inverse of the total window of time surrounding each observation.

	Sum Sq	Df	F value	p-value
Intercept	135719	1	186.1	$< 2.2 \times 10^{-16}$
Treatment	5963	2	4.090	0.020
Species	10120	1	13.88	0.00035
Mussel Size	4015	1	5.507	0.021
Species x Mussel Size	2307	1	3.165	0.079
Residuals	61972	85		

Table 2.9. Poisson regression model coefficients and standard errors for the effects of treatment and species on handling time for completely drilled mussels in experiment II. The reference for treatment is low CO_2 and *N. canaliculata* for species, and small for mussel size. Model adjusted $R^2 = 0.24$. The model included weights that were the inverse of the total window of time surrounding each observation.

	Estimate	Std. Error	t-value	p-value
Intercept	33.03	2.421	13.64	$< 2.0 \times 10^{-16}$
Treatment: Mid	4.051	3.180	1.274	0.21
Treatment: High	9.444	3.302	2.86	0.0053
Species: N. ostrina	-13.24	3.554	-3.726	0.00035
Mussel size: Large	7.629	3.251	2.347	0.021
Species: *N. ostrina* x Mussel size: large	15.92	8.951	1.779	0.079

3 – VARIATION IN WHELK PREDATION RATES AND PERFORMANCE ACROSS SITES AND YEARS AND IN RELATION TO TEMPERATURE AND UPWELLING

Abstract

Interaction strengths are important for determining pattern in biological communities, but they are highly variable across environmental contexts. Such variability is a challenge both for creating more generalizable models describing regulation of community structure across scales and for predicting the community-level outcomes of global environmental change. In particular, the nature of predator-prey interactions often changes along environmental gradients as the relative performance of predators and prey shift asymmetrically. The consumer stress model posits that predation is weakened with environmental stress because predators are more sensitive than prey. We were interested in understanding how predation was influenced by broad-scale environmental conditions in a rocky intertidal system with mobile predators, where previous research has largely considered local gradients such as tidal elevation and wave exposure. Our aim was to understand whether predation was variable over space and time, and whether this related to environmental gradients important for ecological processes in rocky intertidal.

Using a comparative experimental approach, we explored relationships between predation and broader-scale variables of upwelling and temperature, which are both important for community structure and are predicted to change in the NE Pacific with climate change. Contrary to previous studies, we found that predation was relatively consistent across years, sites, and environmental gradients. However, hierarchical partitioning revealed that upwelling was a driver of predation in some cases, indicating the potential importance of broader oceanographic factors in setting the strength of local biotic interactions. We also considered changes over time from 1999-2000 and 2013. We found that variability in air temperature was important in 2013 when it had not been in other years. Our findings suggest that relationships between predation and environmental context are not straightforward in a dynamic coastal system, which complicates our ability to predict outcomes related to climate change.

Introduction

How the environment shapes community structure and functioning has long been one of the central questions in community ecology (Elton 1927, Whittaker 1956, Connell 1961b). Likewise, given the sheer diversity of communities existing across wide-ranging environmental conditions, ecologists have often searched for general principles and laws and debated whether, instead, context dependency limits our ability to apply findings across systems (Lawton 1999, Simberloff 2004). The environment acts on organisms directly by affecting physiology, behavior, and ultimately survival. This means that environmental conditions can also critically influence the nature of biotic interactions when interacting organisms respond asymmetrically, with the potential for impacts on the broader interaction web (Gilbert et al. 2014). Because the links between the environment and community structure are many, quantifying the role of environmental conditions can prove particularly challenging. However, given global environmental change, it is increasingly critical to incorporate understanding of environmental effects on species interactions to better predict the responses of populations, communities and ecosystems (Agrawal et al. 2007, Angert et al. 2013). Communities that experience high environmental variation across short spatial and temporal scales, such as rocky intertidal communities, may be particularly useful for examining how environmental variation influences biotic interactions and community structure.

Certain environmental conditions act on organisms directly by causing physiological stress (Menge et al. 2002a) and altering vital rates. For any species, certain conditions promote growth, provide essential resources, and support fecundity and reproductive success (e.g., optimal conditions). Conversely, conditions that fall too far outside of what is required for optimal performance can cause mortality (Somero 2002, Kuo and Sanford 2009). Likewise, changes in abundance of interacting species due to environmental stress can indirectly shift interaction strengths and community structure (Menge and Sutherland 1987, Bertness and Callaway 1994, Adler et al. 2009).

However, even in the absence of mortality, the environment can change species interactions when less severe conditions induce sub-lethal effects on physiology that influence performance and fitness of individual organisms and increase the “cost of living” of organisms (Menge et al. 2002a, Somero 2002, Petes et al. 2007). At a per capita level, interaction strengths reflect the performance of the interacting species, and they can change if species responses are asymmetrical (Laska and Wootton 1998, Berlow 1999, Berlow et al. 2004, Burnaford 2004, Navarrete and Berlow 2006). For example, interacting species may have different performance optima for an environmental stressor, the shape of their performance curves may differ, or one species may have higher performance overall (Sanford 2002a, Harley 2013, Dell et al. 2014). These changes to interactions, taken in the context of dynamic natural environments, are likely to be the rule rather than the exception.

Predator-prey interactions may be particularly malleable in response to environmental stress. For example, a recent meta-analysis found that predator-prey interactions were more variable across spatial and abiotic contexts than competitive interactions (Chamberlain et al. 2014). This is critical for communities because the top-down effects of predators can exert strong influences on structure (e.g., Paine 1969, Estes and Palmisano 1974) and coexistence among prey (Chesson 2000). Predators and their prey often differ in size (Cohen et al. 1993) and physiological rates (Rall et al. 2012) in ways that can create asymmetries in performance across environmental gradients. Indeed, there are many examples where predation is highly context-dependent and interaction strengths can vary considerably across different environmental gradients (Moore and Townsend 1998, Sanford 1999, Kishi et al. 2005, Seifert et al. 2014) in ways that change impacts on the community more broadly (Power et al. 1996a). In marine benthic communities, predation can be susceptible to temperature (Sanford 1999, Miller 2013), pH (Keppel et al. 2015), salinity (Witman and Grange 1998), and wave stress (Menge 1978).

A number of different conceptual models predict the relative importance of different species interactions along gradients of environmental stress, disturbance and productivity (Connell 1975, 1978, Menge and Sutherland 1976, 1987, Oksanen et al. 1981, Bertness and Callaway 1994, Hacker and Gaines 1997, Bruno et al. 2003). Most of these models have roots in the model of Hairston, Smith and Slobodkin (1960), which promoted the idea of top-down community regulation. The environmental stress model (ESM) of Menge and Sutherland (1987) clarified the role of predation as a disturbance separate from physical stress, while later models added the important effects of facilitation (Louda and Collinge 1992, Hacker and Gaines 1997, Bruno et al. 2003). These models are a useful tool to structure understanding of the role of environmental factors operating at different scales to influence ecological processes with implications for diversity and community structure (Menge and Olson 1990). ESMs, while not quantitative, act as a conceptual link between performance of organisms, the strength of interactions, and their importance on community structure.

Under non-limiting recruitment, ESMs predict that predation is most important to community structure at low stress levels, while competition and physical disturbance become respectively more important as stress increases (Menge and Sutherland 1987). One implicit assumption of ESMs is that predators are more affected by stress than their prey, which limits predation at higher levels of environmental stress. This assumption forms the basis of the consumer stress model, or CSM (see Menge and Olson 1990, Menge et al. 2002a). Reductions in performance are riskier for prey than for predators for several potential reasons. The first is that the stakes are higher for prey to perform in all conditions (e.g., the life-dinner principle) because the cost of low performance is high (mortality), while for predators the costs are lower (i.e., a missed energetic gain) (Dawkins and Krebs 1979, Dell et al. 2014). Second, when prey are largely sessile, as is true in many hard-bottom benthic marine systems, they have limited capacity for behavioral avoidance mechanisms to environmental stress and thus have developed high tolerance. Mobile predators, however, can utilize behavioral avoidance with more limited need for tolerance (Petes et al. 2008).

ESMs can be applied in comparisons across systems (Menge and Olson 1990), but they can also be used to consider dynamics within the same ecosystem over time, for example within an estuary during hypoxic events (Altieri and Witman 2006) or across gradients of salinity and temperature (Cheng and Grosholz 2016). Within a single community, variability in predation rates will be set in part by the physiology and behavior of predators under given conditions and how the environment affects their foraging, feeding rates, and prey preferences. Spatio-temporal variation in predation rate is critical when considering the effects of global environmental change. Assessing variation in predation along environmental gradients using an ESM framework can build further generality for understanding effects of anthropogenic climate stressors.

We were interested in testing the performance of predators and prey and whether variation in predation rate supported the predictions of environmental stress models in a rocky intertidal ecosystem along environmental gradients. Organisms residing in the rocky intertidal experience many separate axes of environmental stress including large swings in temperature, desiccation at low tide exposures, wave stress and the need to remain attached to the substrate, and, increasingly, the stress of building and maintaining calcified structures in a highly dynamic coastal carbonate environment (Somero 2002, 2010, Harley et al. 2006). Previous work on environmental stress models in the system has focused on strong gradients of tidal elevation and wave exposure (Menge and Sutherland 1976, Menge and Farrell 1989, Menge et al. 2002a). We aimed to expand on this work to include broader-scale factors of temperature (at the site scale) and upwelling. Temperature varies as small spatial scales in intertidal systems (Helmuth et al. 2010); we minimized this within-site variation by placing plots at similar tidal elevations and wave exposures to focus on differences among sites.

To first understand pattern, we took the tack of measuring the same pairwise interactions along an environmentally dynamic coast and asked whether there was variation in species interactions over space and time. Given consumer stress models, we expected predation rates to decrease and predator mortality to increase at sites that were more stressful; thus, we expected to find variability in predation in a dynamic environment. Then, we asked how the relative performance of predators varied in relation to specific environmental conditions relevant to climate change by looking at relationships between predation and ocean upwelling and temperature. Because we had data for three one-year studies that spanned 14 years overall (with experiments in 1999, 2000, and 2013), we were also interested in whether the relative importance of different environmental variables in explaining variation in predation changed over time and whether changes were consistent with climate change predictions. We predicted that broader-scale environmental variables would be more important for explaining variation in predator-prey interactions if conditions were more stressful among years.

Temperature is one of the most pervasive drivers of pattern in the intertidal (Somero 2010). Temperature sets the rate of key biochemical and physiological interactions that affect vital rates. The impacts of temperature also have implications for interactions. For example, predators may be able to handle prey more rapidly in high temperatures (Miller 2013). Metabolic rates scale with temperature in ectotherms, with relatively small changes in temperature increasing rates meaningfully (Somero et al. 2016). We examined performance of predators and prey in relation to several metrics of air and water temperatures, which have different effects. Warmer water temperatures tend to speed up rates of biochemical and physiological reactions (Somero 2010), but higher air temperature may be more stressful, particularly as high temperature, insolation, and desiccation often co-occur. For intertidal organisms along the Oregon coast, air temperatures are often most physiologically challenging in the late spring and summer months during daytime low tides (Helmuth et al. 2002). For example, in an intertidal whelk species, elevated air temperatures in a lab experiment led to a decrease in predation while elevated water temperatures caused an increase in predation (Yamane and Gilman 2009).

Along the U.S. West Coast, the predictions for temperature with climate change are complicated by upwelling. Air temperatures will likely increase but seawater temperatures will decrease due to increased upwelling. For example, upwelling has strengthened and likely will continue to strengthen as the land-sea temperature difference increases (Iles et al. 2012, Wang et al. 2015). Upwelling, along with local bathymetry, controls subsidies, such as larvae and phytoplankton, that reach local intertidal sites, and thus on coastal scales upwelling is important for community structure (Menge et al. 2004, Menge and Menge 2013). Where upwelling is very high (e.g., California sites), materials are moved continually offshore, lowering productivity, while where upwelling is low and the system is characterized by downwelling, there is also low productivity without the influx of nutrients from upwelled waters. Sites with intermittent upwelling (Menge and Menge 2013) receive the high nutrients from upwelling, but alternating downwelling keeps nutrients near shore for utilization.

Other stressors are also likely to be important with changing climate. In rocky intertidal systems, a number of other changes are now occurring including increased air temperatures, greater storm intensity and wave heights (Ruggiero et al. 2010a), increasing exposure to hypoxic waters (Grantham et al. 2004, Chan et al. 2008, Somero et al. 2016), and ocean acidification (Harley et al. 2006, Feely et al. 2008, Hauri et al. 2013).

Disentangling the importance of indirect effects of environmental stressors on community structure mediated through predator-prey interactions is critical for improving understanding impacts of climate change on the community. A central goal of studying climate change is to predict whether species can persist in their existing ranges and how distributions will shift. Many models that predict species distribution shifts with climate change do not include species interactions (Araújo and Luoto 2007), which are critical for the persistence of species and maintenance of diversity. However, understanding the conditions under which interactions are important, and how the environment shapes the strength of interactions will also be required. If predators are more highly affected by environmental stress, as predicted by CSM models, climate change will weaken top down effects with implications for community stability in both cases (Paine 1992, Ruiter et al. 1995, McCann et al. 2005).

Methods

Study system

We conducted our experiment at eight rocky intertidal sites spanning approximately 240 km of coastline in Oregon, USA. Sites were located within four capes, (typically with multiple sites per cape, see Figure 3.1) that overlap in their species pools but differ in overall community structure and dynamics (Menge et al. 2015). Furthest north, the Boiler Bay (BB) and Fogarty Creek (FC) sites on Cape Foulweather are defined by a narrow continental shelf offshore that limits retention of propagules such as larvae and phytoplankton. In the low intertidal zone, this results in low abundances of sessile invertebrates, and high abundance of macrophytes (seaweeds and seagrasses). FC is also exposed to low pH waters (pH < 7.6) during upwelling periods more than other sites in Oregon and California (Hofmann et al. 2013, Kroeker et al. 2016).

Further south, Yachats Beach (YB), Strawberry Hill (SH), and Tokatee Klootchman (TK) sites are located on Cape Perpetua, which has a wide continental shelf and high retention of phytoplankton and invertebrate larvae. On Cape Perpetua, sessile invertebrates dominate the low intertidal zone and mobile invertebrate predators, such as whelks, are highly abundant. Some studies have indicated that water and air temperatures at Cape Perpetua sites are warmer than those on Cape Foulweather (Menge et al. 2008, but see Menge et al. 2015), which can be physiologically stressful, though the overall site means were similar to one another in our experimental years (see Figures C1, C2). At Cape Perpetua, pH values tend to be more moderate than at Cape Foulweather (Hofmann et al. 2013).

In southern Oregon, Rocky Point (RP) and Cape Blanco (CB) sites are on Cape Blanco, and the South Cove (SC) site is located on Cape Arago approximately 50 km north. Cape Blanco is a rocky headland and represents a geographic break where water in the North California Current is deflected offshore as it moves south (Castelao and Barth 2005, Krenz et al. 2011). At Cape Blanco, upwelling is stronger than at Cape Foulweather sites (see Figure C1, C2 for temperature and upwelling means). On Cape Blanco, macrophytes are abundant in the low intertidal zone, and mussel beds defining the mid-intertidal zone are higher up on the shore. *N. canaliculata* is sparse at Cape

Blanco and Rocky Point sites, likely due to the scarcity of its preferred prey *Mytilus trossulus*. Both species of whelks were abundant at all other sites. Cape Arago is unusual in experiencing very strong, nearly-continuous upwelling (Sanford et al. 2003, Sanford and Worth 2009, 2010). Experiments were conducted here only once, in 2000, at the South Cove site. Sessile invertebrates were sparse in the low zone at this site, which was dominated by macroalgae (primarily *Saccharina sessilis*).

2013 Experiments

We measured the spatial and temporal variation in interaction strength for two gastropod predators, the whelks *N. canaliculata* and *N. ostrina,* feeding on the abundant mussel *M. trossulus*, using a comparative experimental approach (Menge et al. 2002b). To do this, we transplanted predators and prey from a single site to six study sites (FC, BB, YB, SH, CB, RP). We collected *M. trossulus*, for experimental transplantation from Strawberry Hill in spring 2013. We were careful to select mussels from patches of *M. trossulus*, which limited the likelihood of selecting a small *M. californianus* and helped ensure that mussels were similarly sized (mussels were approximately 15-25 mm in size). After collection, we placed mussels and whelks in flow-through seawater tables at Hatfield Marine Science Center in Newport, Oregon, where they were kept for at least seven days to eliminate any acclimation differences prior to transplantation. For transport to southern sites, we kept mussels in a cooler packed with moist algae to keep the air inside humid until they could be placed in a seawater table at the Oregon Institute of Marine Biology in Charleston, Oregon. After being kept overnight in the seawater table, they were transplanted at RP or CB sites the next morning. There is no indication that this transport protocol influenced mussel mortality in our experiment based on survival following transplantation.

To transplant individual mussels at each site, we cleared plots in areas of moderate wave exposure within or adjacent to existing mussel beds (where *Nucella* and *M. trossulus* typically occur). In cleared plots, which were 10 x 10 cm in size, we placed clumps of 50 mussels under squares of Vexar plastic mesh held down with stainless steel lag screws and PVC washers. This method secures mussels to the rock, allowing them to form byssal thread attachments and withstand wave action once transplanted (Menge 1992, Menge et al. 1994, Wieters and Navarrete 1998). After allowing mussels to attach to the rock substrate for two weeks, we loosened the Vexar mesh slightly, which increased wave force and promoted stronger attachment. At this time, any dead mussels were removed and replaced with new mussels to keep total mussel numbers consistent. After an additional two weeks, mussels were securely attached, so we removed the Vexar mesh and installed the full experiment.

To determine how the effect of whelk predators on mussel prey varied across a large spatial scale, our study included four treatments (n = 5) at each site. Each replicate included a treatment for each whelk predator (one treatment with two *N. canaliculata* and the other with two *N. ostrina)* and one treatment with mussels only (predator exclosure). For these three treatments, animals were placed within 10 x 10 cm stainless steel cages. The final treatment was a marked plot open to all predators. Marked plots, indicated with 4 lag screws at the corners of a plot with previously transplanted mussels, measured ambient predation levels. We installed these treatments in May 2013 and maintained the experiment through October 2013. We monitored the experiment as frequently as possible, which was typically biweekly or monthly. At each monitoring, we counted the number of live mussels in each plot and recorded the number of dead mussels and their length (to the nearest 1 mm). We removed dead mussels and looked for the presence of drill holes, which was a clear sign of predation by whelks. Small mussels recruiting into cages were not counted and were removed when possible.

To maintain treatments, we removed any whelks or sea stars (*Leptasterias* spp. or *Pisaster ochraceus*) that had invaded the cages and recorded their size. For treatments that included whelks, we measured the size of the two whelk individuals in each cage at each monitoring. When whelks in a cage died, they were replaced with new whelks of similar size. We used replacement whelks from the original collection site, Strawberry Hill as much as possible. In all treatments except for the ambient predation plots, mussel densities remained above zero for the experimental duration (i.e., whelk predators did not consume all prey).

We measured ambient predator densities around our plots using surveys at each monitoring point. For each replicate, we counted the number of whelks in five 0.0625 m^2 quadrats. These quadrats were haphazardly placed and were located within 1 m of the focal replicate. Our quadrats were not large enough to reliably detect accurate numbers of the sea star *Pisaster ochraceus*, but we did note any individuals that we encountered in the quadrats, along with the smaller sea star *Leptasterias* spp.

Field predation experiments 1999 & 2000

To assess whether patterns were potentially consistent over time, we compared our results to an experiment conducted in 1999 at five sites along the Oregon coast (BB, FC, SH, TK, and CB) and in 2000 (with the same sites as in 1999 with the addition of the SC site). This experiment included four treatments: a marked plot to measure ambient predation, a plot with roof of stainless steel piece of mesh 5 cm above the substratum to measure the effects of cage lids, a predator exclusion plot with a stainless steel mesh cage containing only mussels, and a mesh predator enclosure cage with two *N. canaliculata* individuals added. Thus, three of the treatments (marked plot, + *N. canaliculata* enclosure, - predator exclosure) were analogous to treatments in our 2013 experiment. The roof plot was a single piece of stainless steel mesh that was bolted to the rock on two sides with two open sides to allow predator access, thereby controlling for mesh shading. Cages, roof and marked plots in these experiments also were 10 x 10 cm in size. Mussels were attached to the substrate using the same procedure as in 2013 experiments with Vexar mesh but with only 30 mussels initially transplanted. The experiments ran June 1999 – October 1999 and May 2000 – October 2000 and were monitored biweekly to monthly, including counts of surviving mussels and removal of invading whelks or other predators. As in 2013, ambient predator densities around each replicate were recorded in five 0.0625 m^2 quadrats monthly.

Environmental measurements

Environmental data were recorded using several methods. At each site, three replicate Hobo Pendant or TidBit (or both) data loggers (Onset Computer Corporation, Bourne, MA, USA) recorded temperature at 6-minute intervals for both the 1999-2000 and 2013 experiments in the low intertidal zone. This habitat level measurement of temperature is unlikely to match the body temperatures of adjacent organisms (Helmuth

2002, Broitman et al. 2009), but serves to provide data on the relative thermal environment experienced by organisms across sites and time points. Temperature data were separated into air and water temperatures using de-tiding scripts in Matlab. We obtained air and water means and standard deviations for the whole summer and for intervals of 1-day, 1-week, 2-weeks, and 1-month prior to each monitoring at each site.

We obtained values of the Bakun Upwelling Index, which is measured as the cubic meters of upwelled water per second per 100 m of coastline, from the Pacific Fisheries Environmental Laboratory at NOAA (http://www.pfeg.noaa.gov). We used average daily values at each site to obtain means and standard deviations for the summer months (May-October) for each experimental year.

Tide heights were recorded for each replicate for 2013 experiments using a laser level. Water levels were referenced using data from the nearest NOAA water level station, which were the South Beach and Port Orford, Oregon, stations. Although average tide heights tended to be higher at Boiler Bay, tide heights of our experiments did not differ between the six sites in 2013 (ANOVA, $F_{5,29} = 2.281$, $p = 0.079$). The mean tide height of plots was +1.3 m above mean low low water (MLLW) (SD = 0.24 m). Experiments in 2013 were placed in similar locations at overlapping sites in 1999-2000, so tide heights in the earlier experiment were similar to those measured in 2013.

Data analysis

To obtain survival numbers, we counted the number of surviving mussels at each time point. In some cases, the number of mussels did not always decrease over time, likely due to potential recruitment and failure to count obscured mussels in cages during previous counts. If numbers increased in plots over successive time points, we kept them at the pre-increased value until they decreased again. Because experiments were run for different lengths of time over years and sites, we standardized survival to a rate. We did this by taking the slope of the proportion surviving over time (with data arcsine-square root transformed for linearization) for each replicate cage. In cases where survival reached zero, the slope calculation was based only on the non-zero observation period. We analyzed data both as proportions surviving and as a function of slopes of predation (mortality) rates with qualitatively similar results.

We analyzed the effect of treatment and site on mussel survival rates using ANOVAs. We visually checked plots of residuals to ensure that assumptions of homogeneity of variance and normality were met. We ran models that included all years (on only the common +*N. canaliculata* and - predator treatments at common sites) to look at changes over time, and models within each year to assess treatment and site differences. To analyze differences in the marked plot treatments across sites and years we used a Kruskal-Wallis test and a Conover post-hoc test as the data were highly non-normal. For the remaining treatments (control, + *N. canaliculata*, + *N. ostrina*), we started with a saturated model that included terms for site, treatment and a site x treatment interaction, which would indicate that effects of predation differed among sites. Models terms were removed using the corrected Akaike’s Information Criterion (AICc); the exception was our comparisons of mussel survival rates between years, in which we kept a saturated model to facilitate comparison. We removed one outlier point at FC in 2000, in which the slope of survival rate was an order of magnitude larger than all other values (potentially because the cage started out with fewer mussels).

In 2013, we had a more comprehensive dataset that included the number of drilled mussels in each treatment as well as whelk survival and growth. We analyzed drilling by converting it to a rate (by dividing the total number drilled by the length of the experiment at each site days). We also included a continuous variable of the total number of whelks that invaded the cage in our models to account for whelk invasion into plots. Whelk survival and growth were also analyzed using ANOVA, and were log-transformed prior to analysis.

We wanted to test the mechanistic relationships between environmental factors and mussel survival and our other response variables to better understand any observed differences among sites. Given our numerous variables representing environmental stress, we hoped to determine which were the most important in explaining variance in our responses while addressing the fact that the data were likely to be multi-collinear. We used hierarchical partitioning (Chevan and Sutherland 1991, Mac Nally 2002) to identify which environmental variables were able to independently contribute to the total explained variation in mussel survival rates (and drilling rates). This technique partitions the variance explained by each predictor into a portion that is independent of all other predictors and a joint effect by calculating the R^2 in all possible model combinations. Our predictor variables included site, treatment, year (if applicable), mean air temperature, standard deviation of air temperature, mean water temperature, standard deviation of water temperature, mean upwelling, and the standard error of upwelling. While there were other components of temperature and upwelling that may be relevant, the technique does not produce reliable results when more than nine predictors are used (Olea et al. 2010). We used the package ‘hier.part’ in R (Walsh et al. 2013) to run hierarchical partitioning models with R^2 as the goodness-of-fit metric. To test the significance of the independent contribution of each predictor, we used randomization tests to obtain z-scores based on a 0.95 confidence limit.

All analyses were run in R version 3.3.1 (R Core Team 2016) with R Studio (R Studio Team 2014) with the following packages: ‘plyr’ (Wickham 2011), ‘AICcmodavg’ (Mazerolle 2015), ‘lubridate’ (Grolemund et al. 2011), ‘car’ (Fox and Weisberg 2011) , ‘PMCMR’ (Pohlert 2014), ‘multcomp’ (Hothorn et al. 2013).

Results

Mussel survival in experiments across years

In the 1999 and 2000 experiments, we found that the rate of mussel survival was affected by the presence of whelk predators but not site; in 2013 both site and treatment had effects (Table 3.1). In all years, the effect of whelk predators on mussel survival rates was consistent across sites (no site x predator treatment interaction in selected models, see Table 3.1, Figures 3.2, 3.3, 3.4). The final model explaining mussel survival rates for all years together included only a term for predator treatment (ANOVA, $F_{1,113} = 36$, $p = 2.5 \times 10^{-8}$, Table 3.2). When all three years are included, mussel survival decreased at rates 2.04 times faster when predators were present than when they were excluded (95% CI: 1.70 to 2.38 times faster, Table C1).

Hierarchical partitioning revealed that some environmental variables were important for explaining mussel survival, but they tended to be much less important than treatment, year, and site. The mean and standard deviation of upwelling were the only environmental variables that had a significant independent contribution to the total explained variance in a model with all sites, years and treatments, yet each explained only 1% of the total variance (Table 3.3). When only the control (- predator) and + *N. canaliculata* treatments were included, treatment was the only variable that explained a significant portion of the variance (Table 3.4, Figures 3.5, 3.6). In all years, the presence of whelk predators was the most important factor explaining mussel survival rates (between control and +*N. canaliculata* treatments). In 1999 and 2000, no environmental factors were important in explaining in mussel survival (Table C2). However, in 2013, the standard deviation in air temperatures was also important in explaining the variance in mussel survival rates. A regression testing the effects of predator presence and air variation on mussel survival rates revealed that for each degree of variation in air temperatures, mussel survival rate was increased by 0.00036 mussels day^{-1} (linear regression, $t = 4.646$, $p = 2.0 \times 10^{-5}$, $R^2 = 0.41$).

In marked plots open to all ambient predators, survival rates differed by site in 1999 and 2013, but not in 2000 (Table 3.5). In both 1999 and 2013, differences among sites in plots open to all predators were driven by survival at Cape Foulweather sites (FC and BB, Table C3), which tended to have higher survival of mussels than other sites (Figures 3.2, 3.4). In the marked plots open to all predators, site (20% of the total variance) and the standard deviation of upwelling (5% of the variance) were the primary independent contributors to the total explained variance in mussel survival (Table 3.6).

Drilling behavior and whelk performance: 2013

The rate at which whelks drilled mussels in the 2013 experiment depended on several factors. After accounting for invasion by whelks into cages, the rate of drilling depended on site and whelk species (*N. canaliculata* or *N. ostrina*) (Table 3.7, Figure 3.7), where *N. ostrina* drilled 0.05 mussels day^{-1} fewer than *N. canaliculata* on average (95% CI: 0.032 to 0.071 mussels day^{-1} fewer, Table 3.8). Among sites, drilling rates by whelks were greater at FC than at RP (Tukey HSD, z-value = -3.209, p = 0.029). Drilling rates did not vary with any environmental factors (Table 3.9). Instead, the rate at which whelks drilled mussels was related to species, which explained 28% of the total variance independent of site or any environmental variables.

In other metrics of predator performance, there was an effect of site on whelk mortality, however pairwise comparisons did not reveal any significant site differences when p-values were adjusted for multiple comparisons (ANOVA, site: $F_{5,59} = 2.905$, p = 0.022, Table C4, Figure C3). Whelk species was not included in the best model for mortality. Growth rates of neither *N. canaliculata* nor *N. ostrina* varied among sites (Figure C4), though sample sizes were small (n = 19, n=20, respectively) because we were only able to use cages where no whelks died during the experiment. Overall, whelks grew very little, though *N. canaliculata* grew more than *N. ostrina* (ANOVA, species, $F_{1,38} = 15.899$, $p < 0.001$).

Discussion

We were interested in the spatio-temporal variation in an important rocky intertidal predator-prey interaction, and whether changes in the interaction could be explained by broad scale environmental gradients. The two primary goals of our study were to understand how the predictions of a consumer stress model performed with stressors beyond wave exposure and tidal elevation, which are relatively well-tested, and to determine whether inter-annual variability in the interaction suggested changing environmental stress regimes. We tested the effects of whelk predators on mussel prey at eight sites differing in environmental conditions and in three different experimental studies separated by a total of 14 years.

We found that whelk predation exerted significant impacts on mussel survival, but these effects were largely consistent across sites and years. Further, environmental variables (upwelling and temperature) were only weakly associated with mussel survival rates between treatments. However, not all our results match this general pattern. Most notably, our 2013 experiment differed from the experiments in 1999 and 2000. In 2013, we tested drilling rates by whelks (in addition to mussel survival rates) and found that variation in air temperatures was an important predictor of mussel survival but drilling was not associated with any environmental variables. We also observed differences between the two species of whelk predators in their how much they drilled prey and their growth: *N. canaliculata* drilled more mussels and grew faster.

Environmental effects on predation: the role of upwelling and year

Previous tests of environmental stress models in intertidal systems have focused on wave exposure and tidal elevation (Menge and Sutherland 1976, Menge and Farrell 1989, Menge et al. 2002a), both of which we have minimized in our study. Within rocky intertidal ecosystems, wave and elevation gradients are strong and relatively well characterized (see, for example Menge et al. 1996), as are their biological impacts. The paradigm is that predation is more important at lower tidal elevations, with abiotic stress setting the upper limit of intertidal species (Menge and Branch 2001). Higher tidal elevation does generally reduce predation because the foraging capabilities of predators are limited (Connell 1961a, Paine 1966, Menge 1978, Yamada and Boulding 1996, Petes et al. 2008). Likewise, wave exposure can limit predators (Menge and Sutherland 1976), as has been shown for whelk foraging in New England (Menge 1978). However, wave exposure often co-varies with temperature and desiccation, where exposed areas are cooler, have reduced effective emersion time and lower desiccation risk due to wave splash (Harley and Helmuth 2003). In addition, wave-exposure increases the abundance of sessile filter-feeding species, which provide more food for predators (McQuaid and Branch 1985). By reducing variation in tidal height and wave exposure, we focus on environmental differences among sites.

There is evidence to suggest predation by whelks can be influenced by other environmental stressors beyond those due to wave exposure and tidal elevation along the rocky shores of Oregon in the summer months. For example, Dahlhoff et al. (2001) found consistent differences in the heat shock responses of *N. ostrina* between Boiler Bay and Strawberry Hill sites, but this was mediated by the availability of shaded habitat that could reduce physiological stress. Thermal and desiccation stress can result in change to predation by whelks. In lab studies, feeding by whelks was dependent on temperature, where whelks consumed more prey in warmer water (Sanford 2002b) and fewer prey in higher air temperatures (Yamane and Gilman 2009). We also found reduced feeding rates of whelks in response to elevated CO_2 in our lab study (see chapter 2).

Of the environmental factors we included in our analysis, upwelling more frequently explained variation in mussel survival than air and water temperatures. We found an overall positive relationship between mussel survival and upwelling, where stronger upwelling led to higher survival rates across all sites, years, and treatments. Upwelling may be important because it acts as a key driver variable controlling water temperatures, nutrients, and the importance of bottom-up factors in the summer months in Oregon (Menge et al. 1997a, 2003, Barth et al. 2007). Because upwelling brings nutrient-rich waters low in dissolved oxygen and pH from depth to the surface (Grantham et al. 2004, Barth et al. 2007, Feely et al. 2008), it could influence organismal physiology and increase the food available for mussel prey (Dahlhoff et al. 2001, Barth et al. 2007).

Upwelling is critical to community structure in nearshore communities along eastern boundary systems because it impacts recruitment (Connolly and Roughgarden 1999) and the strength of predation in other species in the low zone (Menge et al. 2004). In a previous study, upwelling strength explained almost 40% of the variance in the total effect of predators along an upwelling gradient that included coastal sites in the NE Pacific and in New Zealand (Menge and Menge 2013). Many ecological processes show a unimodal relationship with upwelling, where intermittent upwelling (like that observed along the Oregon coast) is associated with the highest rates (Menge and Menge 2013), Similarly, upwelling variables were the best predictors of rocky intertidal biogeography along the US west coast (Fenberg et al. 2015). While the effects of upwelling on predation rates are primarily from setting prey inputs, lower temperatures can also change predator behavior (Sanford 1999) and lower metabolic and feeding rates (Iles 2014). In a recent study, this combination of alternating upwelling (and pH) created the highest growth and lowest predation vulnerabilities at sites along the west coast in the mussel *M. californianus* (Kroeker et al. 2016).

Another goal of the study was to compare experiments conducted in 1999 and 2000 to one done 14 years later with the question of whether or not patterns of predation might have changed as climatic changes occurred. We know that, in the last century with climate change in Oregon, coastal air and water temperatures have increased (Mote et al. 2010), corrosive waters low in pH have shoaled in coastal areas (Hales et al. 2005, Feely et al. 2008, Hauri et al. 2013, Harris et al. 2013) upwelling has intensified (Iles et al. 2012, Bakun et al. 2015), and the coast has experienced greater wave heights (Ruggiero et al. 2010b), with some of these changes occurring in the last two decades. We expected to find inter-annual variability because of the dynamic coastal environment at our sites, and perhaps see relationships to climatic trends (Menge et al. 2009). Instead, we found consistent results across study years when we compared the sites common across all years, and we found few relationships to larger scale environmental variables. Such temporal consistency in community dynamics is not unusual. For example, predation by sea star predators of mussels at SH and BB sites was consistent across years in the 1990s and 2000s (Menge et al. 2011a).

In 2013, however, we found that variation in air temperatures was important for explaining predation, with the underlying pattern suggesting that mussel survival rates in 2013 were higher at sites with more variation in air temperatures. This could indicate that temperature variation inhibited whelk predators, as has been shown in sea stars (Pincebourde et al. 2008), or that variable air temperatures were better for mussels overall. It does appear that temperature variability can, in some cases, increase population growth rates (Lawson et al. 2015), indicating that effects of variability are not always negative. However, mussels exhibit behavioral changes in elevated air temperatures, such as gaping and reduced valve closure times, that may make them more susceptible to predation (Dowd and Somero 2013), so if variation increases the likelihood of high temperatures it is unlikely to help mussel survival. Variability, along with frequency, may be more important for biological effects of abiotic stressors than means alone (Miller et al. 2014, Dillon et al. 2016). Likewise, air temperatures can driver greater deviations in animal body temperatures than water temperatures, in which animal body temperature approximates the surrounding water (Helmuth 1998).

Interestingly, site was also an important predictor of mussel survival rates in our 2013 experiment (but not in other years), with low survival at YB and high survival at RP driving effects. At YB, ambient whelk densities are very high (see Figure C5), and the number of whelks invading cages was higher than any other site, which is the likely reason for lower survival across treatments there. Previous work by Menge et al. (2015) has demonstrated that the environment at RP was more similar to sites in northern California than other sites in Oregon based on a cluster analysis. In addition, the mean upwelling at the two Cape Blanco sites (CB and RP) was much higher in 2013 than in all other years and sites, which could drive site differences and the account for the importance of upwelling over other environmental drivers in hierarchical partitioning.

Potential explanations for observed patterns

Overall, our results do not show clear patterns in predation along the coast that relate to known differences among sites in environmental conditions. Further still, when we minimized differences due to wave exposure and tidal elevation, we found that predation rate was largely invariant across the environmental gradients we studied. Some of the main potential explanations for these results include: 1) the range of conditions we used were relatively benign as far as whelks and mussels were concerned, so their responses to the environment were minimal, 2) sites were not variable enough to distinguish differences in performance, 3) there was a mismatch between the time, scale, or environmental metrics we chose and those which affect organismal performance, or 4) our results were obscured by variation in other factors, such as intraspecific variation. We address these different reasons briefly below, and discuss the potential consequences of each.

It is possible that the conditions encompassed in our field studies were relatively benign for whelk predators and mussel prey. Whelks tend to have robust body condition, in wave-exposed conditions (Dahlhoff et al. 2001). *N. canaliculata* in Oregon are less stressed (lower induced Hsp 70 response) than populations of whelks at the southern edge of their range, where temperatures are higher (Sorte and Hofmann 2004), and whelks from Oregon appeared to have higher thermotolerance in lab studies (Kuo and Sanford 2009) than whelks from California. Similarly, *M. trossulus* is able to maintain a similar growth rate in aerial temperatures up to ~30°C (Schneider 2008), though the species is less warm-adapted than other Mytilid species (Zippay and Helmuth 2012). *M. trossulus* has mechanisms to respond to acute temperature stress, for example, by synthesizing heat shock proteins (Hsps) and other molecular chaperones, changing cytoskeletal proteins, and altering energy metabolism (Tomanek and Zuzow 2010, Fields et al. 2012). Thus, differences in environmental stress may not necessarily translate to noticeable differences in performance if environments are relatively benign.

In other rocky intertidal locations, environmental stress may have already shifted communities to those that are too stressful for predators or important prey. ESMs were developed in part based upon comparisons between the rocky intertidal coastlines on the east and west coasts of North America (Sorte et al. 2011). Menge & Sutherland (1976) demonstrated that predation was important only at protected sites in Massachusetts, and that physical stress limited the top-down effects of the whelk *Nucella lapillus* in exposed areas (Menge 1978). Since that time, there have been dramatic declines in mussel cover on the east coast, and even sharper declines in whelk predators (Sorte et al. 2016). In Oregon, while organisms experience thermal stress (Dahlhoff et al. 2001, Helmuth et al. 2002, Gilman et al. 2006), changes in climate thus far are not as extreme as those in the Gulf of Maine on the east coast, which is one of the most rapidly warming areas of the global ocean (Pershing et al. 2015, Sorte et al. 2016).

Another factor that may have limited environmental stress was our use of cages to contain predators and prey. Cages do have known artifacts, such as reducing water velocities (Miller and Gaylord 2007), which can lower the energy organisms require to remain attached to the substrate and encourage more movement for predators. In our case, there were no differences between the experimental marked plots with and without a roof in the 1999 and 2000 experiments, which suggests that the presence of shading was not critical for our results. Further, previous experiments that observed differences in *Nucella* predation across sites have used cages, suggesting our results do not stem from cage artifacts alone (Menge et al. 1994, Navarrete and Menge 1996).

It is also possible that we saw few differences in mussel survival with site, year or environmental variables because environmental conditions were not meaningfully different across sites. This is difficult to assess because of the many aspects of environmental factors to consider (e.g. means, variability, frequency of extreme values). However, rocky intertidal sites in the NE Pacific have a long history of study and environmental differences among sites have been well characterized. Our study sites in Oregon, which span ~240 km of coastline, tend to vary predictably as a result of oceanic factors such as bathymetry and upwelling (see Menge et al. 2015). These persisting oceanic drivers may explain the consistency we observed across years.

Differences between sites and years could be minimized if there were mismatches in our metrics and those that are physiologically meaningful to the organisms themselves. For example, air temperature does not necessarily reflect true animal body temperatures during emersion (Helmuth et al. 2010), and body temperatures of predators and prey can vary considerably in the same conditions (Broitman et al. 2009). For the purpose of simplicity across years and sites, we used means and standard deviations as our metrics, but future exploration using metrics such as temperature thresholds could prove fruitful for further understanding patterns. Variability in environmental conditions may be more critical than mean values because performance curves are typically nonlinear across gradients (Vasseur et al. 2014). Alternation between harsh and more moderate environmental conditions could also allow organisms to make up for poor performance in stressful periods. We have also measured survival rates of mussels over time with the effects of predators essentially summed over the course of a summer, but it may be that variations in performance occur on shorter time scales. However, it is important to note that previous studies have found effects of environmental stress in our system using these simplified metrics (e.g., with mean temperatures and predation in Sanford 1999).

Our experiments focused on differences across sites and years in the per capita consumption rates of predators, but there are numerous mechanisms by which environmental changes could affect predation. Environmental stress can alter foraging behavior, which can shift per capita species interactions. In *N. ostrina*, peak foraging corresponds with the tidal cycle in ways that minimize temperature and allows whelks to forage with the least risk on cool days (Hayford et al. 2015). With climate change, these other impacts on predation could be severe. For example, local extinctions of prey or predator populations, or differences in shifts of predator and prey ranges could change community dynamics (Gilman et al. 2010). Changes to the abundance of other species in the food web (e.g., the loss of the top predator or of other basal species) could also indirectly change interaction strengths (Adler et al. 2009). Predictions for climate-change effects on communities based on species distribution shifts that do not account for changes to species interactions will be inadequate if species interactions are highly variable across environmental context (e.g. Suttle et al. 2007, Araújo and Luoto 2007).

Variation among individual predators and prey may mask patterns among sites and with environmental gradients. Intraspecific variation in traits such as predator handling times and diet preferences can have meaningful consequences for overall species interaction and ecological dynamics (Bolnick et al. 2011). For example, phenotypic variation in marsh grasses was more important in determining competitive interaction strengths than a precipitation gradient (Noto and Shurin 2015). *Nucella* individuals do exhibit prey specialization and differences in foraging (West 1986, Burrows and Hughes 1991), as well as variation in handling times. Further, as stress increases, the differences between individuals within a species may become more pronounced and raise intraspecific variation (Killen et al. 2013), thus stress and variation would be confounded. However, our results do not suggest that variation differed among sites. It is interesting that in 2013, when site effects were significant, we had used animals from a single site in order to minimize intraspecific variation due to factors like adaptation or acclimation from populations at different sites.

In addition to intraspecific differences, we were also interested in the responses of the two whelk congeners in 2013. Based on previous research indicating that *N. ostrina* has a higher temperature tolerance than *N. canaliculata* (Sorte and Hofmann 2005), we predicted that performance would be more strongly reduced in *N. canaliculata*. There were differences between the species, with *N. canaliculata* generally performing better (i.e., drilling more mussels and growing faster), but neither the effects of whelks on mussel survival nor whelk mortality were different between the two species. The higher relative performance of *N. canaliculata* is likely not in response to stress, but instead to a general preference of *N. ostrina* for barnacles.

Conclusion

The effects of many different environmental stressors are continually integrated by organisms and reflected in changes to behavior, physiology, and fitness. In the lab, these changes in response to a single stressor, such as temperature, and their subsequent effects on interaction strength are often clear, but field conditions can muddy the conceptual waters. Yet without understanding how environmental variability in the field will affect interactions, it will be difficult to make useful predictions for future climate changes. The limited environmental effects on predation in our study point to the complex relationships between environmental drivers and biotic interactions. They also highlight the need for refining empirical understanding even in ecosystems where environmental and community dynamics are well-characterized. We found that whelk predators exerted relatively strong impacts on their prey regardless of context, but that some environmental drivers, like upwelling, were important for understanding their interactions with mussel prey.

Acknowledgements

We wish to thank Angela Johnson, Jonathan Robinson, Shawn Gerrity, Allison Barner, Chenchen Shen, Danielle Smull, Kersten Schnurle, Jonathan Robertson, Courtney Jackson, and Dustin Hollabaugh for their assistance in the field in 2013, and Greg Hudson, Melissa Foley, and Jacqueline Nichols in 1999-2000. Funding for this project was provided in part with a grant from the Pacific Northwest Shell Club. Jerod Sapp and Michael Frenock provided the temperature logger data, and Tarik Gouhier prepared the upwelling indices.

Figures

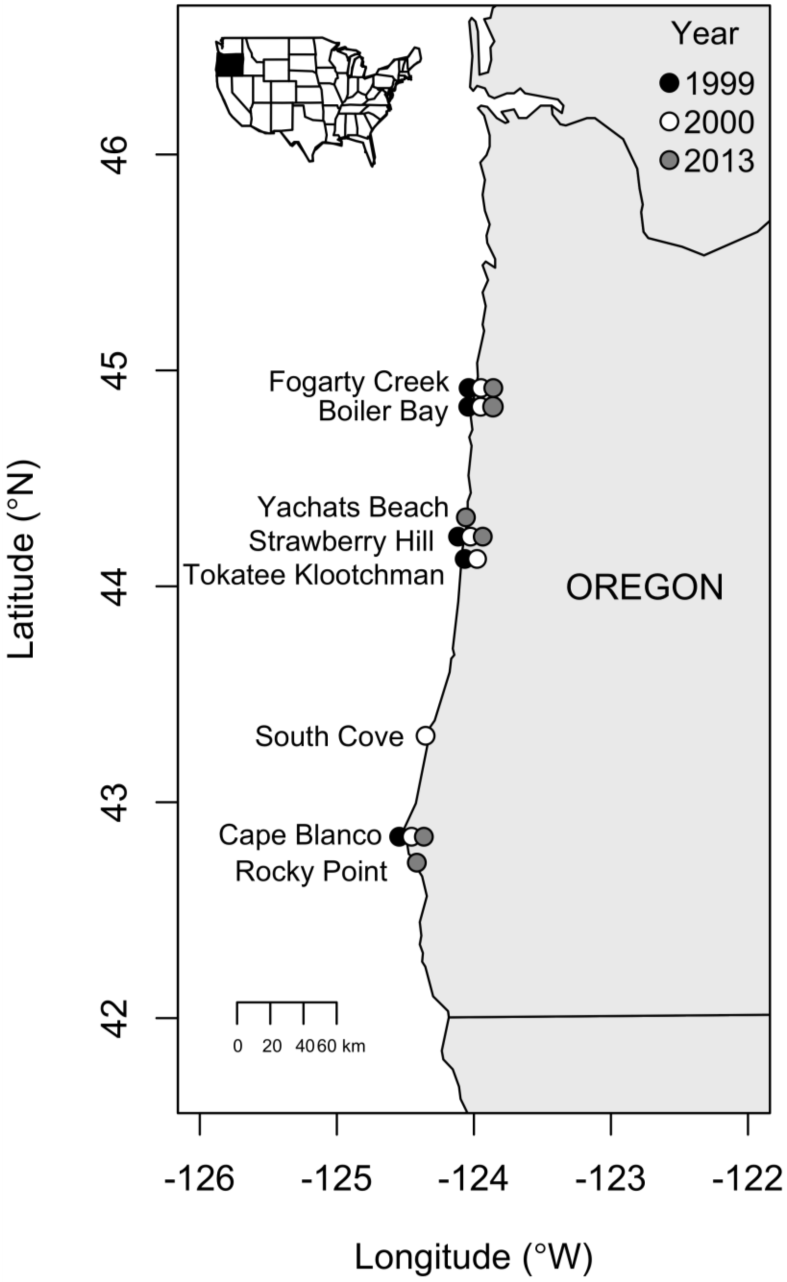

Figure 3.1. Map of experimental study sites. Black circles indicate sites used in the 1999 experiments, white circles those in 2000, and dark grey circles those in 2013 experiments.

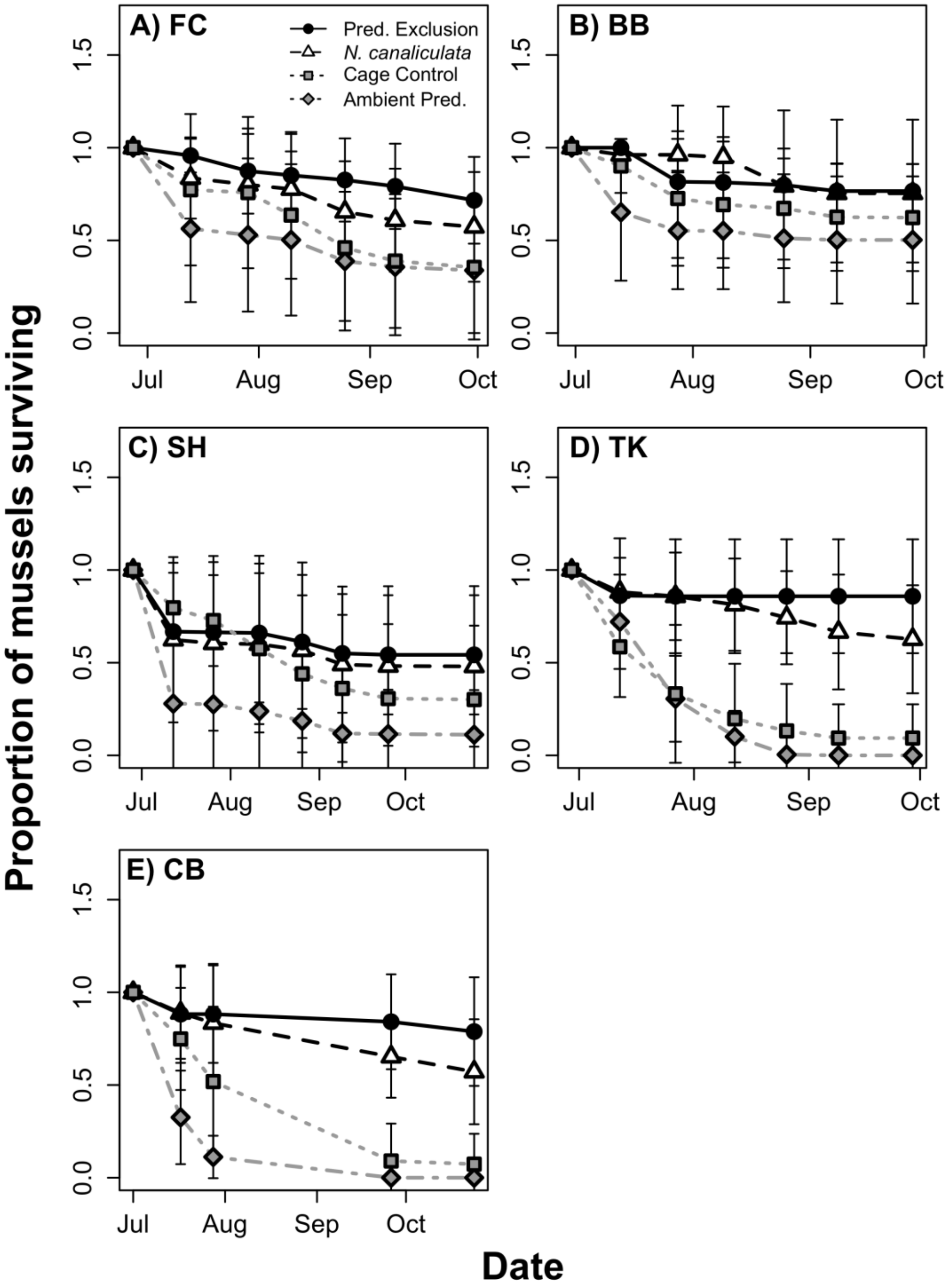

Figure 3.2. Proportion of mussels surviving over time in 1999 in each of four treatments. Data are means and 1SE.

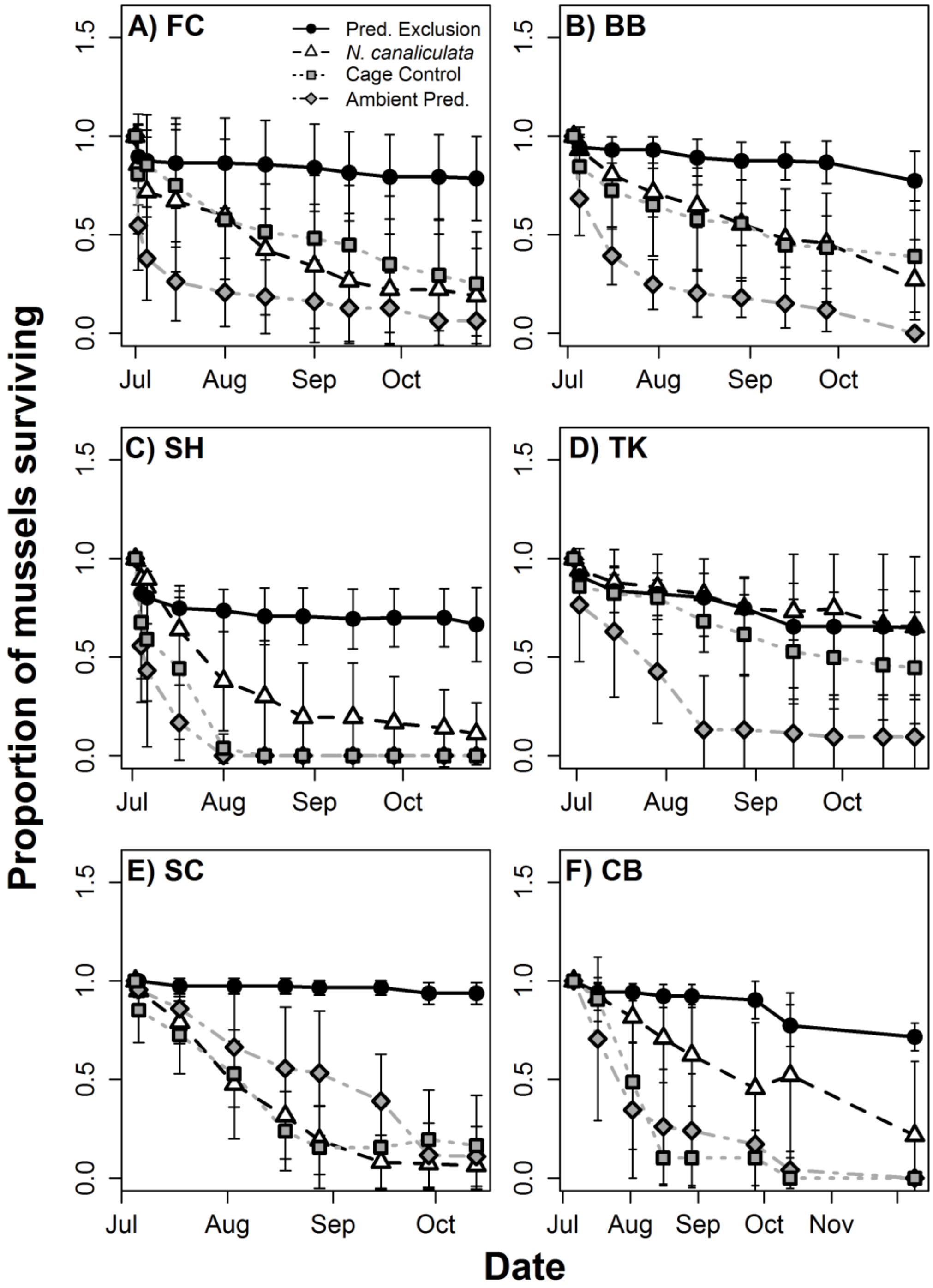

Figure 3.3. Proportion of mussels surviving over time in 2000 in each of four treatments. Data are means + 1SE.

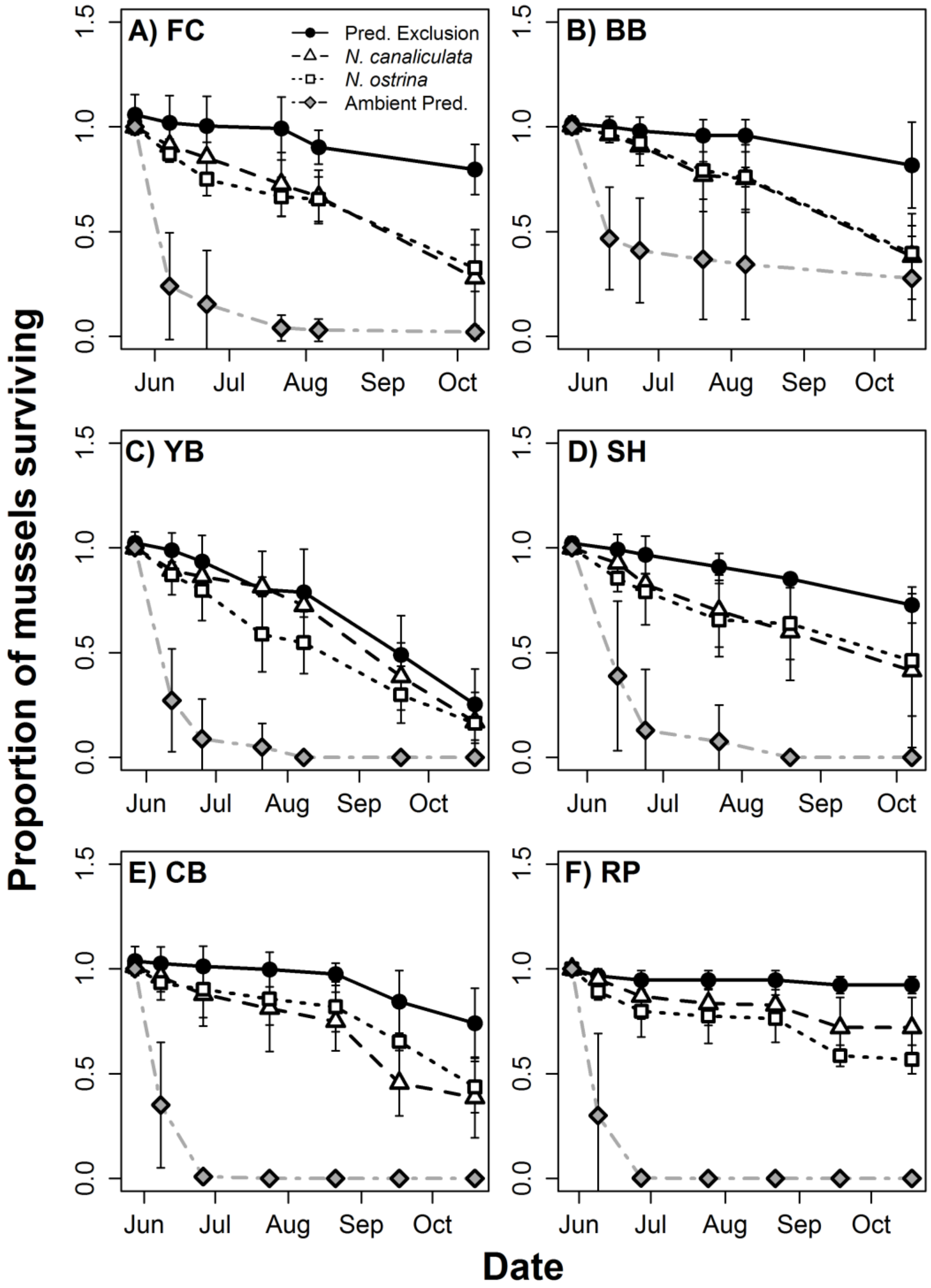

Figure 3.4. Proportion of mussels surviving over time in 2013 in each of four treatments. Note that the treatments are different than in 1999 or 2000. Data are means + 1SE.

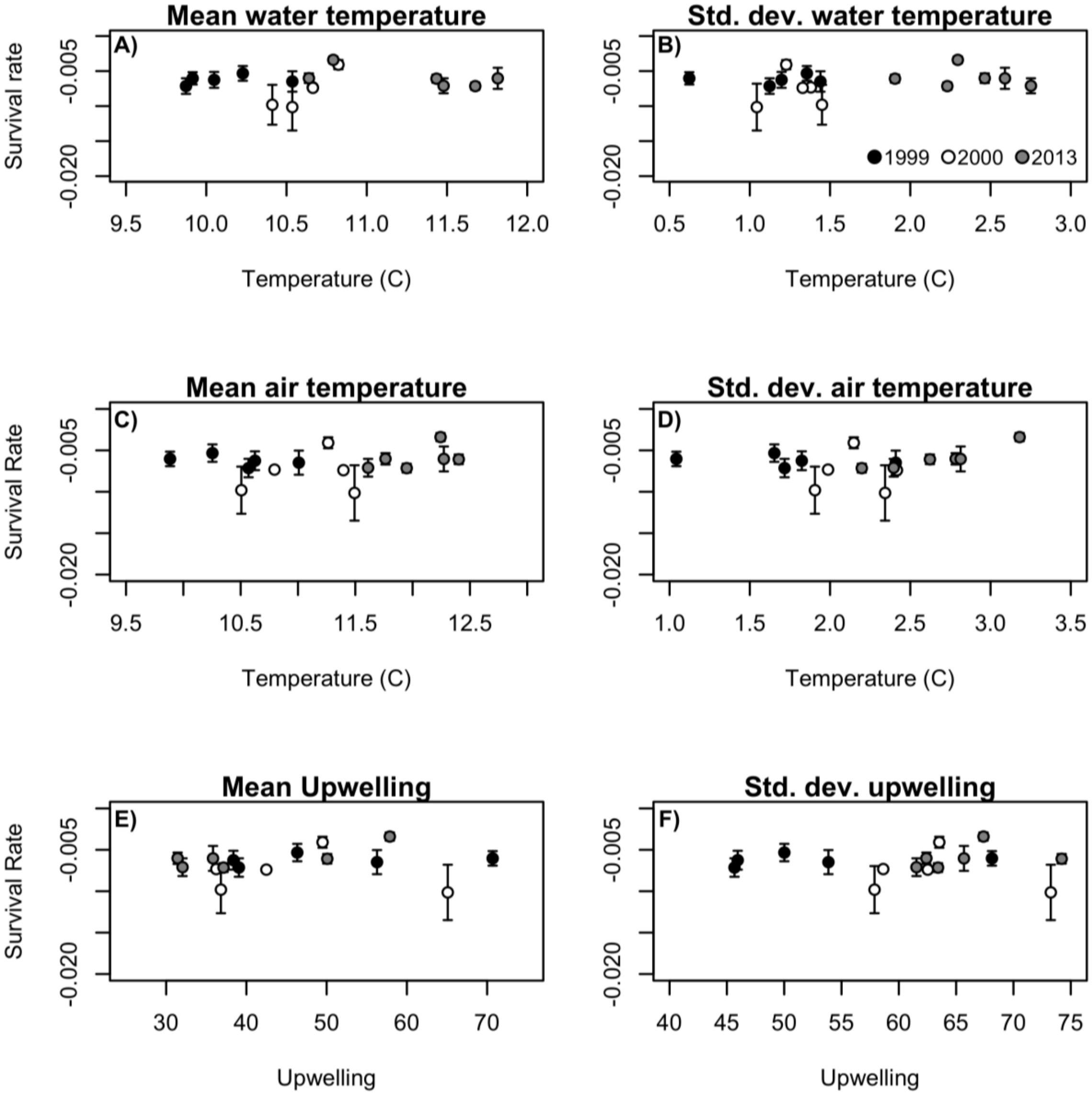

Figure 3.5. Survival rate in relation to environmental variables in cages with predators across all years. Data are means + 1SE.

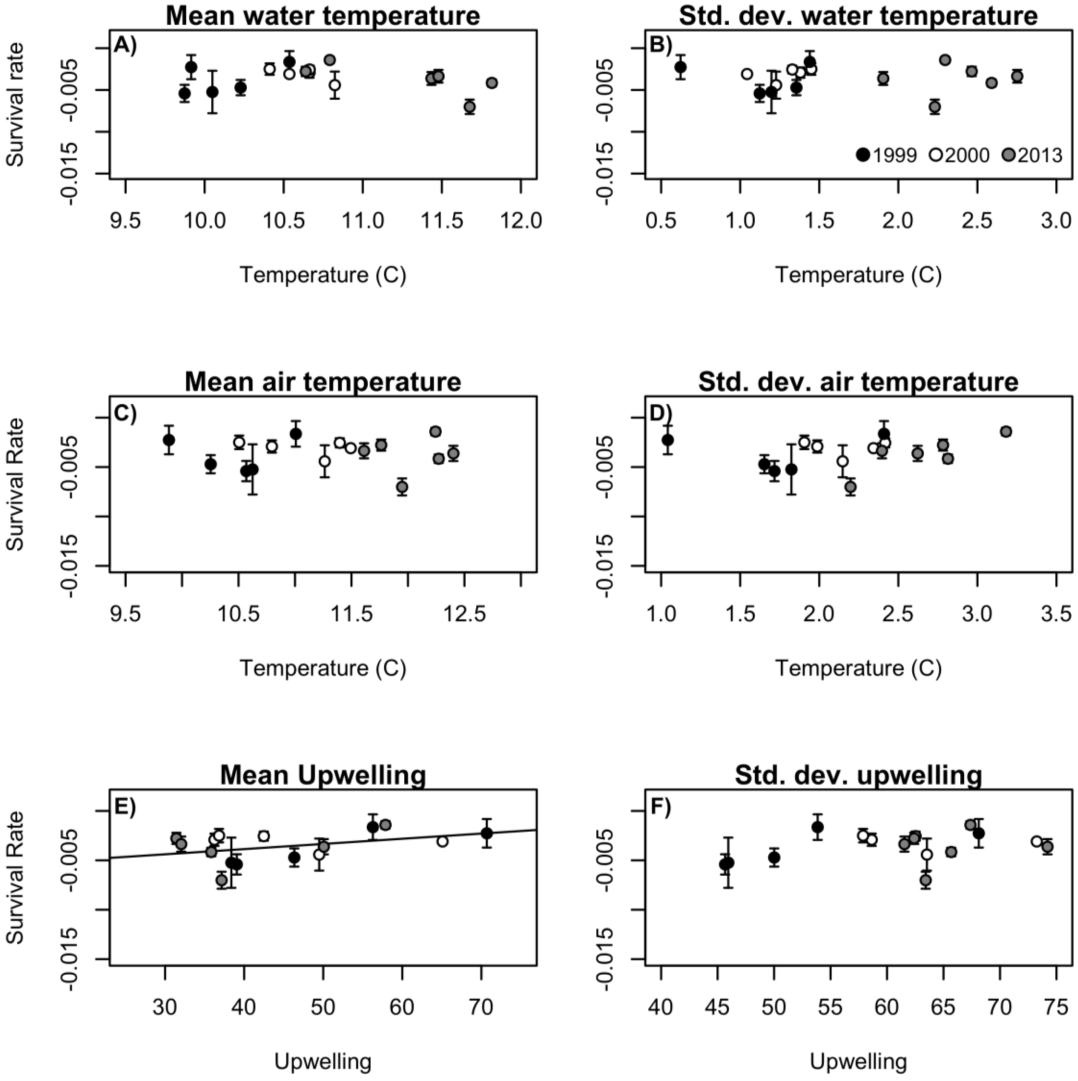

Figure 3.6. Survival rate in relation to environmental variables in control treatments across all years. Data are means + 1SE. When regression lines are present, there was a significant effect of the environmental variable on mussel survival rates using a simple linear regression model.

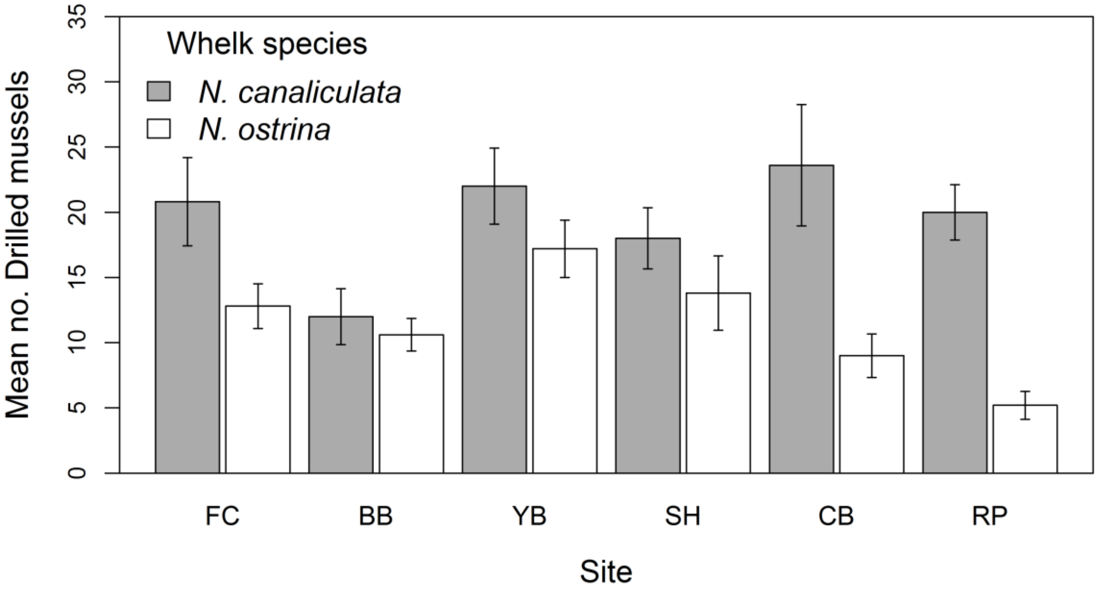

Figure 3.7. Drilling by each whelk species at the study sites in 2013 experiment. Numbers are for the total number of mussels drilled over the course of the experiment. Bars indicate means + 1 SE.

Tables

Table 3.1. ANOVA tables for model testing the effects of site and predator treatment (i.e. +/- *N. canaliculata*) on mussel survival rates in 1999, 2000, and 2013 experiments. Because no interactions were significant, we used Type II SS. One plot was removed from analysis at FC in 2000 because its rate of decrease of mussel survival was an order of magnitude larger than other sites and years, and it appeared to be anomalous.

	Sum Sq	Df	F value	p-value
1999 Experiment				
Treatment	0.00007167	1	7.7447	0.0077
Residuals	0.00044417	48		
2000 Experiment				
Treatment	0.0010158	1	18.021	9.2×10^{-5}
Residuals	0.0028747	51		
2013 Experiment				
Site	1.14×10^{-4}	5	7.2326	3.2×10^{-5}
Treatment	7.53×10^{-5}	1	23.9618	9.6×10^{-6}
Residuals	1.66×10^{-4}	53		

Table 3.2. Type II SS ANOVA table testing difference between predator treatments and controls (i.e. +/- *N. canaliculata*) for all years and all common sites. The model was selected using AICc, with year and site not included in the model with the lowest AICc. One plot was removed from analysis at FC in 2000 because its rate of decrease of mussel survival was an order of magnitude larger than other sites and years, and it appeared to be anomalous.

	Sum Sq	Df	F value	p-value
Treatment	0.0003923	1	36	2.5×10^{-8}
Residuals	0.001221	112		

Table 3.3. The independent contribution (I) of each environmental and treatment variable towards the overall variance explained from hierarchical partitioning for data including all sites, years, and treatments. All variables combined explained 34.9% of the total variance.

	I	Z-score	p <0.05
Site	0.05	3.36	*
Year	0.01	0.91	
Treatment	0.23	23.96	*
Mean water temperature	0.01	0.72	
Std. dev of water temperature	0.01	0.62	
Mean air temperature	0.01	1.06	
Std. dev of air temperature	0.01	1.09	
Upwelling	0.01	2.3	*
Std. dev of Upwelling	0.01	2.08	*

Table 3.4. The independent contribution (I) of each environmental and treatment variable towards the overall variance explained in mussel survival rates from hierarchical partitioning. Data are for predator and control treatments (i.e. +/- *N. canaliculata*). All the variables combined only explained 17.9% of the total variance.

	I	Z-score	p <0.05
Site	0.04	0.15	
Year	0.02	0.55	
Treatment	0.09	14.72	*
Mean water temperature	0	-0.55	
Std. dev of water temperature	0	-0.29	
Mean air temperature	0.01	-0.14	
Std. dev of air temperature	0.01	-0.04	
Upwelling	0.01	0.48	
Std. dev of Upwelling	0	-0.38	

Table 3.5. Results of Kruskal-Wallis tests on the effect of site on mussel survival in marked plots open to ambient predation. Comparisons are within each year.

	χ^2	df	p-value
1999 site effect	15.714	4	0.0034
2000 site effect	8.47	5	0.13
2013 site effect	15.743	5	0.0076

Table 3.6. The independent contribution (I) of each environmental and treatment variable towards the overall variance explained in mussel survival rates from hierarchical partitioning. Data are for marked plots open to all ambient predators at all sites across all years. All the variables combined explained 47.6% of the total variance.

	I	Z.score	p < 0.05
Site	0.2	3.25	*
Year	0.04	0.89	
Mean water temperature	0.03	1.13	
Std. dev of water temperature	0.03	0.58	
Mean air temperature	0.04	1.54	
Std. dev of air temperature	0.03	1.54	
Upwelling	0.04	1.58	
Std. error of Upwelling	0.05	2.18	*

Table 3.7. ANOVA table (type II SS) for selected model testing effect of site, whelk species, and total number of invading whelks on the drilling rate on mussels in whelk treatment cages in the 2013 experiment.

	Sum Sq	Df	F value	p-value
Site	0.018118	5	2.6505	0.033
Treatment	0.039631	1	28.9885	1.8×10^{-6}
Total number of invading whelks	0.026047	1	19.0525	6.1×10^{-5}
Residuals	0.071091	52		

Table 3.8. Selected linear model testing effect of site, whelk species, and total number of invading whelks on the mussel drilling rates in the two whelk treatment cages in the 2013 experiment. $R^2 = 0.52$. The reference site was SH, and the whelk species was *N. canaliculata*.

	Estimate	Std. Error	t value	p-value
Intercept	0.123957	0.01367	9.068	2.7×10^{-12}
Site: BB	-0.030448	0.016702	-1.823	0.074
Site: CB	-0.003994	0.016539	-0.241	0.81
Site: FC	0.02061	0.016969	1.215	0.23
Site: RP	-0.027967	0.016542	-1.691	0.097
Site: YB	-0.018602	0.018209	-1.022	0.31
Treatment: N. ostrina	-0.051709	0.009604	-5.384	1.8×10^{-6}
Total number of invading whelks	0.004894	0.001121	4.365	6.1×10^{-5}

Table 3.9. The independent contribution (I) of each environmental and treatment variable towards the overall variance explained in the rates at which mussels were drilled from hierarchical partitioning. Data are for the two whelk treatments in 2013. All variables combined explained 41.9% of the total variance.

	I	Z.score	$p < 0.05$
Site	0.05	-0.67	
Treatment	0.28	14.45	*
Mean Water Temperature	0.04	1.08	
Std. dev of Water Temperature	0	-0.75	
Mean Air temperature	0	-0.61	
Std. dev of Air Temperature	0.03	0.75	
Upwelling	0	-0.57	
Std. dev of Upwelling	0	-0.87	

4 – WHELK PREDATORS EXHIBIT LIMITED POPULATION RESPONSES AND COMMUNITY EFFECTS FOLLOWING DISEASE-DRIVEN DECLINES OF THE KEYSTONE SEA STAR *PISASTER OCHRACEUS*

Abstract

The recent outbreak of sea star wasting disease (SSWD) along the U.S. West Coast, which has decimated the intertidal keystone predator *Pisaster ochraceus*, is predicted to change community structure by reducing sea star predatory control of the competitively dominant mussel *Mytilus californianus*. However, keystone species effects can be variable, and the role of other predators without the keystone is not well understood. We were interested in the 1) effects of subordinate whelk predators (*Nucella ostrina, N. canaliculata*) on prey communities following SSWD, and 2) whelk population responses to declines of their predator and competitor *P.ochraceus*. We hypothesized whelks would limit *M. californianus* establishment by reducing prey species facilitating its recruitment. We also predicted that whelk populations would increase and shift downshore without *P. ochraceus*. We addressed our questions using a whelk removal experiment started immediately before the SSWD outbreak peak and with surveys of whelk distribution, abundance, and size structure. In the absence of *P. ochraceus,* whelks weakly facilitated, rather than limited, the establishment of the competitively dominant mussel but had few effects on other prey. One year after SSWD onset, surveys indicated no change in whelk elevational distributions but diverging patterns in abundance between the two whelk species. Whelk size structure shifted towards smaller individuals, indicating a potential lagged population response. Our results suggest that, in the short-term, subordinate

predators do not have strong impacts on prey communities after keystone species decline. However, poor prey recruitment may have limited potential whelk effects and population changes. Our study provides important context for understanding community changes following one of the largest marine disease outbreaks recorded.

Introduction

Top predators often exert strong effects on prey that can cascade to lower trophic levels. As a result, the loss of top predators has coincided with changes to community structure with implications for conservation (Sergio et al. 2006, Ritchie and Johnson 2009), community stability (Rooney et al. 2006), ecosystem processes (Estes et al. 2011) and the delivery of ecosystem services (Estes et al. 2011, Karp and Daily 2013, Atwood et al. 2015). Large community shifts have been observed in many ecosystems when top predators are removed, for example, following otter extirpation in Alaska (Estes and Palmisano 1974), after the removal of wolves in Yellowstone (Ripple et al. 2001), and in lakes with the removal of largemouth bass (Carpenter et al. 2001). However, the broader effects of top predator loss and trophic cascades can also be mediated by the interplay of other abiotic (Wootton et al. 1996, Pace et al. 1999, Borer et al. 2005) and biotic processes (Shurin and Seabloom 2005, Finke and Denno 2005), and top predator loss does not always lead to large community effects (Polis et al. 2000). Given that top predators may be more vulnerable to extinction and population decline than lower trophic levels (Duffy 2003, Borrvall and Ebenman 2006, Sanders et al. 2013), it is particularly important to understand what factors and ecosystem characteristics alter the outcomes of top predator loss.

Top predators that preferentially consume the competitively dominant prey species are often keystone species with community impact disproportionate to their abundance (Paine 1969, Power et al. 1996b, Menge and Sanford 2013). When keystone predators are lost, it leads to the rapid expansion of the dominant prey species and result in strong effects on community structure. Effects of keystone species removal can include competitive exclusion of other subdominant prey, but this can be highly variable and dependent on other factors such as resource supply and the number of basal species (Brose et al. 2005). In systems with three trophic levels, subordinate predators may be able to compensate and maintain community structure following keystone species loss, particularly if they consume the same prey species.

In the presence of a top predator, subordinate predators typically have low relative impact on community structure (Navarrete and Menge 1996). These subordinate predators often consume similar prey species as the top predator, but have weak effects on dominant prey species and limited ability to control community structure (Robles and Robb 1993, Menge et al. 1994). However, following the loss of a top predator, subordinate predators can increase in abundance (as in mesopredator release, see Crooks and Soulé 1999, Prugh et al. 2009), body size (Menge et al. 1994), and effect (Navarrete and Menge 1996, Navarrete et al. 2000) in ways that are compensatory. In the context of intraguild predation (IGP), subordinate (or intermediate) predators can be especially responsive to the loss of the top predator because they are released not only from competition for the shared prey resource but also from the threat of consumption. Subordinate predators are often more effective than the top predator at suppressing prey (though not when a keystone species is an IGP predator). In such cases, presence of a top predator reduces prey suppression as intraguild predation lowers the ability of the more effective subordinate predator (Kolesar 2006, Vance-Chalcraft et al. 2007). In marsh systems, for example, increasing the diversity of intraguild omnivorous predators present dampened the strength of the trophic cascade as they consumed the intermediate predators, and thus increased plant biomass (Finke and Denno 2005). As a result, subordinate predators may be able to limit top predator impacts and minimize the effects of top predator loss.

Here, we test the response of subordinate predators following disease-driven declines in a rocky intertidal keystone predator, the sea star *Pisaster ochraceus*. Since 2013, sea stars along the U.S. West Coast have experienced drastic declines as the result of Sea Star Wasting Disease (SSWD) (www.seastarwasting.org). The disease appeared at Oregon sites in April 2014 (prevalence was <1%), with peak disease prevalence of 60-80% observed by mid-summer 2014. By the start of 2015, disease prevalence at Oregon sites had declined to 25% or less (Menge et al. 2016), but by then the density of *P. ochraceus* adults has declined by 2-9 fold (Menge et al. 2016). The disease, which appears to involve a viral pathogen (Hewson et al. 2014), causes sea stars to undergo a progression of symptoms that include abnormally twisted arms, lesions, inability to maintain body turgor, loss of arms, and death. SSWD is unprecedented in its spatial and temporal extent, and has affected at least 20 sea star species in the northeast Pacific (Hewson et al. 2014).

P. ochraceus was the first identified keystone species, and it can exert strong effects on community structure by preferentially consuming the competitively dominant mussel, *Mytilus californianus* (Paine 1969, 1974). Rocky intertidal communities display strong patterns of biological zonation across a short tidal elevational range due in part to strong environmental gradients. On the US west coast, the high zone is dominated by fucoid algae and barnacles, the mid zone is dominated by mussels, and the low zone is dominated by macrophyte algae. While the upper limit of the mussel bed is determined largely by environmental stress (Menge and Branch 2001), Paine's experiments indicate that the lower extent of the mussel bed can be set by *P. ochraceus*, which consumes all *M. californianus* within its foraging range. By excluding mussels from the low zone, *P. ochraceus* can promote the establishment of a diverse low zone community dominated by macrophyte and invertebrate species.

Since Paine's studies (1966, 1969), several studies have experimentally supported this keystone species effect in other intertidal locations (e.g. Vancouver Island: Robles et al. 1995, Oregon wave-exposed shores: Menge et al. 1994, and California: see Menge and Sanford 2013), but exceptions exist (Menge and Sanford 2013). Several other factors can influence the strength of predation by *P. ochraceus* on *M. californianus*. For example, the feeding of *P. ochraceus* can be regulated by temperature (Sanford 1999, Pincebourde et al. 2008) and wave exposure (Menge et al. 1994). Additionally, if mussel recruitment is consistently limiting, predation by *P. ochraceus* is minimized and recruitment itself drives community structure (Menge et al. 1994). In these contexts, the effects of *P. ochraceus* loss would be less acute. In other cases, the presence of other predators in the intertidal food web may be able to limit the impacts of *P. ochraceus* declines.

P. ochraceus co-occurs with several subordinate predator species that could exhibit compensatory responses in its relative absence, including the gastropod whelks *Nucella canaliculata* and *N. ostrina* and the smaller sea star *Leptasterias* spp. Both whelk species are consumed by *P. ochraceus* (Navarrete et al. 2000) and share multiple prey species in an intraguild predation interaction. However, whelks do not generally feed on the dominant *M. californianus* along Oregon rocky intertidal shores (Sanford et al. 2003), and thus would not be able to exert compensatory effects via the mechanism of direct consumption of the competitive dominant prey. Instead, whelks could limit *M. californianus* establishment in the low zone through consumption of early- and mid-successional species. *M. californianus* is not able to recruit substantially to bare rock substrate, and prefers to recruit to areas with adult *M. californianus* (Paine 1974), the mid-successional mussel, *Mytilus trossulus* (Petersen 1984), to filamentous algae such as *Endocladia muricata* (Paine 1974) and to acorn barnacles such as *Balanus glandula* and *Chthamalus dalli* (Berlow 1997, Menge et al. 2011b, Gouhier et al. 2011). If subordinate predators influence the low zone abundance of these species, it is possible that they may prevent *M. californianus* recruitment and eventual mussel bed establishment.

Following the 2-9x decline in density of the keystone predator *P. ochraceus* from SSWD, we explored: 1) the impact of subordinate whelk predators on prey community structure, and, 2) their population-level responses to presumed reductions in competition and consumptive pressure. We used a combination of surveys and an experimental manipulation to assess changes in whelk populations and their potential impacts on prey community structure in the context of SSWD (before and after peak disease prevalence). We hypothesized that whelks would exert negative effects on *M. californianus* in the absence of the *P. ochraceus* by limiting recruitment-facilitating species. We also hypothesized that subordinate predators would increase in population abundance and increase mean body size when presumably released from the consumptive and nonconsumptive effects of *P. ochraceus*; alternately we predicted a possible shift towards smaller individuals if whelks experienced high reproductive success. Finally, we predicted that whelk predators would shift their spatial distribution lower on the shore in order to utilize resources in an area previously dominated by *P. ochraceus*.

Methods

Study system

Our study included 4 sites along the Oregon coast: Strawberry Hill (44.250°N-124.115°W) and Yachats Beach (44.319°N-124.109°W), located on Cape Perpetua, and Fogarty Creek (44.837°N-124.0587°W) and Boiler Bay (44.832°N-124.061°W) located on Cape Foulweather (Figure 4.1). Cape Perpetua is a rocky headland adjacent to a wide continental shelf offshore that promotes retention of propagules such as larvae and phytoplankton (Menge et al. 2015). As a result, Cape Perpetua intertidal sites are characterized by high phytoplankton productivity and high recruitment of invertebrates

(Menge et al. 1997b, 2004, 2015). Cape Foulweather, in contrast, is characterized by a narrower offshore continental shelf, which leads to reduced larval retention, lower invertebrate abundance, and high macrophyte abundance. Prior to the onset of SSWD, the mean densities of *P. ochraceus* at the site scale could be as high as 8 individuals m^{-2} at Cape Perpetua and 4 individuals m^{-2} at Cape Foulweather (Menge et al. 2016).

Subordinate predator removal experiment

To assess the effects of subordinate predators in the absence of the keystone species, we conducted a factorial removal experiment at two intertidal sites located on Cape Perpetua, Oregon (Strawberry Hill and Yachats Beach, see Figure 4.1). We predicted that whelk predators would affect establishment of the dominant mussel, *Mytilus californianus,* by consuming the mid-successional prey species that facilitate its recruitment. As such, we chose to follow prey dynamics from a mid-successional stage by placing plots where there was abundant cover of the mussel *Mytilus trossulus* and several barnacle species. This mid-successional community is where we expected to see the greatest effects of subordinate predators and the largest changes in community structure following SSWD. We originally examined the effects of two groups of subordinate predators, gastropod whelks *Nucella canaliculata* and *N. ostrina* (W) and the smaller sea star *Leptasterias* spp. (L), in a factorial design including four treatments: +W +L, -W+L, +W -L, and -W-L. However, *Leptasterias* spp. were rare in our plots, and treatments were combined to include control (+W) and whelk removal (–W) treatments only (see data analysis section below). It is important to note that our experiment tested the effects of subordinate predators at reduced *P. ochraceus* densities, rather than comparing their effects in the presence or absence of *P. ochraceus*.

We followed prey community structure over time at 10 replicate plots within each site at the upper edge of the low zone. The main treatment plots were 0.25 m^2 in size and corners were marked with stainless steel lag screws. Each main plot was surrounded by four additional subplots adjacent to each plot side that were meant to act as a buffer against predator reinvasion into the main plot. We monitored plots either bi-weekly or monthly as tides permitted from experimental initiation in June 2014 through May 2015. At each monitoring, we counted the total number of each subordinate predator species (*N. canaliculata*, *N. ostrina*, and *Leptasterias* spp.), as well as any less common predators, such as the whelk *Nucella lamellosa*, in all plots. When possible, we conducted a full monitoring with counts and removals of predators in the main plot, the four adjacent subplots, and in the corners between subplots. On some occasions, particularly during winter months with limited site access, we only monitored the main plots. All removal of whelks and *Leptasterias* spp. was conducted using forceps, and removed predators were relocated away from the plot area. In plots without removals, we mimicked the use of forceps in the plot (by scraping the substrate lightly) while counting subordinate predators to limit the possibility that the physical action of predator removal would influence our results. Although SSWD caused declines in *Pisaster ochraceus* densities, it did not extirpate the species entirely from our sites. We recorded and removed any *P. ochraceus* within each plot and any adult and juvenile *P. ochraceus* from a 3m radius around each plot.

Photo analysis of prey communities

We used photo analysis to follow changes in prey community structure across experimental treatments over time. At each monitoring point, we took a photograph of each plot including a quadrat to provide a grid for estimating cover of prey species. Photo analysis was conducted for four time points: June 2014, September 2014, February 2015, and May 2015. Percent cover of *M. californianus* and several groups of mid-successional prey species including *M. trossulus* and the barnacles *Balanus glandula*, *Semibalanus cariosus*, *Chthamalus dalli*, *Pollicipes polymerus*, and *B. nubilus* were visually estimated from the photographs as a metric of abundance (e.g. Dethier et al. 1993). Barnacle recruits were too small to be identified to species and were put into a single separate category. We also separately estimated the percent cover of *Mytilus* recruits, which were less than roughly 5 mm in length and were not identifiable to species. It is difficult to differentiate *M. californianus* and *M. trossulus* when individuals are small or in very high densities. As such, it is possible that some mussel individuals identified as adult *M. trossulus* were later identified as *M. californianus* if they developed clear morphological traits of *M. californianus*, though misidentification would be consistent across treatment.

Because other low zone organisms were likely to respond to variation in abundance of mussels and barnacles, we quantified the abundance of macrophyte algae, anemones (*Anthopleura elegantissma* and *Anthopleura xanthogrammica*) and sponges. Macrophytes were sorted into functional groups including crusts, turfy algae, and canopy-forming algae. Overall, the cover of macrophytes was low in our plots throughout the experiment. We also quantified the abundance of non-focal mobile invertebrates including sea urchins (*Strongylocentrotus purpuratus*), chitons (e.g., *Katharina tunicata, Tonicella lineata, Mopalia* spp.), and limpets *(Lottia* spp.).

Surveys of subordinate predator distribution

In the absence of the keystone predator, we predicted that whelk predators would shift toward foraging lower down on the shore in response to reduced consumptive pressure and increased resource density. We tested for changes in the vertical distribution of whelks from April-September of 2014 (before and after peak SSWD incidence in *P. ochraceus*) and in January-July of 2015 (when incidence was low and adult densities had been fully reduced) using vertical transect surveys. In our surveys, we measured the density of whelks, *Leptasterias* spp., and any *P. ochraceus* within five intertidal zones at four sites. These zones were defined by ecological community type rather than by absolute tide height, and included (from low to high on the shore): the upper algal zone dominated by algae and barnacles, the lower edge of the mussel bed, the middle section of mussel bed, the upper edge of the mussel bed, and the high zone dominated by barnacles and fucoid algae. In some cases where *M. trossulus* was abundant within the upper algal zone, we conducted additional quadrats to target this zone specifically.

At each of four sites (Boiler Bay, Fogarty Creek, Strawberry Hill, and Yachats Beach, Figure 4.1) we conducted surveys using five replicate transect lines that ran vertically along the shore. These transect lines were marked at both ends with stainless steel lag screw. Within each transect, we measured density in one 0.25 m^2 quadrat within each of the five ecological zones, recording the distance of each quadrat along the transect line for consistency over temporally repeated sampling. Because we expected to see the greatest changes due to SSWD in the lower ecological zones where *P. ochraceus* had previously been abundant, we measured predator density in additional quadrats in the upper algal zone and the lower edge of the mussel bed. This was done using a horizontal transect line that ran perpendicular from the low point of each vertical transect line described above forming an inverted “T” shape. Along each of the five replicate horizontal transect lines, we included four quadrats in the upper algal zone and four in the lower edge of the mussel bed.

We conducted these surveys to track changes in the vertical distribution of subordinate predators and changes in their overall abundance. We also took a photograph of every quadrat monitored in order to have a record of prey availability for each set of predators counted. Surveys were mostly conducted during morning low tides and, when possible, we attempted to finish all four sites within a single tide series. We recorded the tidal height of each quadrat in July 2015 relative to Mean Low Low Water (MLLW) using a laser level and stadia rod to measure the height of each plot above reference measurements at the water line in centimeters (Pincebourde et al. 2008).

Whelk size distributions

With *P. ochraceus* at low densities, whelks presumably were relieved from both competitive and consumptive pressure. Thus, we predicted that whelks would become both more abundant and larger in size as a result of greater food resources and less predation. We measured whelk size distributions at the same four sites used in our vertical abundance surveys. We placed 0.0625 m^2 quadrats in the intertidal and extracted all whelks in the quadrat taking care to include small individuals. Whelks were sorted by species and measured with calipers to the nearest millimeter. This sampling was done in a semi-stratified pattern vertically along the shore within areas of intermediate wave exposure until we had at least 200 individuals of each species at each site. Size distribution surveys were conducted in July in 2014 and 2015. When possible, all counts were conducted in a single day at each site in order to minimize the chance of repeatedly counting the same individuals.

Statistical Analyses

Percent-cover data were arcsine-square root transformed prior to analysis. In all tests, we examined plots of residuals for assumptions of normality, homogeneity of variance, and independence of error terms. In our experimental subordinate predator removals, *Leptasterias* spp. predators were very low in all treatment plots (zero in most plots). We used ANOVAs and Tukey's HSD post-hoc tests to see if a) removals of only *Leptasterias* spp. (-L+W) were different from the no-removal treatment (+L+W), and b) removals of only whelks (-W+L) were different from removals of both predators (-W-L) to ensure that there was no underlying *Leptasterias* treatment effect. Because *Leptasterias* spp. were so uncommon and had no effects, so we combined treatments (at the replicate level) to make a +Whelks (i.e. +W+L and +W-L) and -Whelks (-W+L and –W-L) comparison.

To test the effects of whelks on prey species, we used linear mixed effects models to analyze percent cover of prey species separately using the 'nlme' package in R (Pinheiro et al. 2014). Models included a random effect for plot to account for repeated measurements over time. The final model for each prey species was determined by removing terms from a full model based on the Akaike Information Criterion corrected for small sample size (AICc) from in the package ‘AICcmodavg’ (Mazerolle 2015). We used AICc to determine if adding a weighted variance structure was necessary in cases where plots of residuals revealed heterogeneity of variance. Time was treated as a categorical variable because of non-linear relationships with percent cover. Because plots started with different prey communities, we analyzed both percent cover and change in percent cover from initial cover with qualitatively similar results. We made post-hoc comparisons using the ‘phia’ package in R (De Rosario-Martinez 2015) using p-values obtained from a Holm-Bonferroni sequential correction..

To determine whether population abundances of each whelk species had changed from 2014 to 2015, we used negative binomial regression for survey count data, which were overdispersed, in the ‘MASS’ package (Venables and Ripley 2002) in R. In this case, a full model included a site x year interaction, which was dropped if non-significant. Because 2014 had many surveys, whereas 2015 had fewer, we tried analyzing data from all surveys and also from only surveys conducted in July 2014 and July 2015. We used all survey data as results were similar in both cases. To assess spatial changes in subordinate predator distributions, we ordered quadrats by measured tide height and analyzed differences in the cumulative distributions of whelk counts between the two years using two-sample Kolmogorov-Smirnov Tests with p-values bootstrapped using the package ‘Matching’ (Sekhon 2011). For these tests, we used only matched surveys in July in order to minimize distributional changes due to season.

Whelk size distributions were normally distributed and were analyzed using ANOVAs, which included terms for site, year and site x year. For *N. ostrina*, the site x year interaction was not significant, so we used a Type II Sums of Squares ANOVA as data were unbalanced. Pairwise contrasts of interest were examined using the 'phia' package. Analysis was performed using R version 3.3.1 (R Core Team 2014) and RStudio version 0.98.1085 (RStudio Team 2014).

Results

Whelk removal experiment

The whelk removal treatments reduced the cumulative presence of whelks relative to controls once the experiment was initiated (Figure 4.2, Table D1). Including the 0.5 m buffer surrounding each plot, we recorded and removed 31,929 whelks from removal plots and recorded 41,050 whelks in control plots over 11-months.

We predicted that the cover of the dominant mussel species, *Mytilus californianus* would be negatively influenced by whelks, which don't eat the mussel but instead can limit the other prey species that facilitate its recruitment. By the final monitoring time point, *M. californianus* cover was higher (2.11x higher), not lower, when whelks were present (contrasts: whelk removal vs. control in May 2015, $p = 0.036$; Table D2), but cover remained low in plots overall. The difference between treatments increased over time and the treatment x time interaction was marginally significant (Figures 4.3A, 4.3B, GLMM treatment x time point interaction, $p = 0.087$; Table D3). By the end of the experiment, cover in removal treatments was lower than in controls. *M. californianus* cover increased over time in both treatments, and the effect varied with site (GLMM site x time interaction: p = 0.016) with Strawberry Hill reaching higher cover than Yachats Beach in May 2015 (contrasts: SH vs YB May 2015, p = 0.0043).

We expected that whelk presence would reduce cover through consumption of the remaining subdominant prey species, but whelk presence had mixed effects on prey. The mid-successional mussel *Mytilus trossulus* had lower cover in the presence of whelks (Figures 4.3C, 4.3D, GLMM treatment, p = 0.021; Tables D3), but the treatments were only marginally different in September 2014 and May 2014 (Table D2). By the final monitoring, *M. trossulus* cover was 1.99 times higher in whelk removals, but cover was low overall relative to starting values. For *M. trossulus*, cover differed between sites depending on time point (Figure 4.3, GLMM site x time interaction, p = 0.0017). Cover of the small barnacle *Chthamalus dalli* was higher in the presence of whelks (Figure 4.4A, 4.4B, GLMM treatment, p = 0.019; Table D4), but treatments were only different in February 2015 (Table D2). For *C. dalli*, cover also decreased over time, but this effect depended on site (Figure 4.4A, 4.4B, GLMM site x time interaction, p = 0.0010).

For the remaining subdominant prey species, whelk presence had no effect on cover, and instead patterns were driven by site and time. For the barnacle *Pollicipes polymerus*, cover increased over time, but this effect depended on site (Figure 4.4C, 4.4D, GLMM site x time interaction, p < 0.0001; Table D4). The cover of *P. polymerus* was higher at Strawberry Hill than Yachats Beach for the final two time points (contrast: SH vs YB: February: p = 0.0002, May: p < 0.0001). For the barnacle *Balanus glandula*, cover peaked in September and then decreased, but the effect of time depended on site

(Figure 4.4E, 4.4F, GLMM site x time interaction, p = 0.028; Table D4). For the acorn barnacle *Semibalanus cariosus*, cover depended on both time point and site (Figure 4.4G, 4.4H, GLMM site x time interaction, p = 0.0014; Table D4). Cover at Yachats Beach was always higher than at Strawberry Hill, with the difference between the sites increasing over time.

Whelk density surveys 2014-2015

Nucella canaliculata abundance decreased over time with mean densities of 18.98 (se ± 2.42) individuals m^{-2} in 2014 and 11.32 (se ± 1.76) individuals m^{-2} in 2015, but the effect of time was only marginally significant (Figure 4.5A, GLM: date, p = 0.062; Table D5). When we excluded quadrats in the *M. trossulus* zone, which often led to aggregations of whelks in 2014 but not in 2015, there was no clear decrease in *N. canaliculata* over time (negative binomial regression, time, p = 0.30, Table D5). Within quadrats in the *M. trossulus* zone specifically, densities of *N. canaliculata* decreased in 2015 relative to 2014 (negative binomial regression year, p = 0.013). In contrast, *Nucella ostrina* abundance increased over time, with mean densities of 70.57 (se ± 5.04) individuals m^{-2} in 2014 versus 76.29 (se ± 6.93) individualsm^{-2} in 2015 (Figure 4.5B, time effect with all dates included, negative binomial regression, p = 0.0094; Table D6).

Whelk size structure

We hypothesized that, as in previous experiments (Navarrete and Menge 1996), mean whelk body lengths would increase in the absence of *Pisaster ochraceus*. However, mean length decreased in 2015 relative to 2014 for both species. The mean length of *N.*

canaliculata was 2 mm smaller in 2015 than 2014, but this effect depended on site (Figure 4.6, ANOVA site x year interaction, $F_{3,39} = 6.41$, $p = 0.003$; Table 4.1) with length decreasing at all sites except Boiler Bay (Tukey HSD, 2014-2015 = 0.933, df = 1, $p = 0.07$, Table 4.2). For *N. ostrina*, mean body length also decreased by 2 mm from 2014 to 2015, and this effect was consistent across site (Figure 4.6; ANOVA: year, $F_{1,39} = 230.85$, $p < 0.0001$; Tables 4.3, 4.4). These decreases appear to be driven by increased densities of smaller and midsize individuals and reduced densities of larger individuals in 2015 in both *N. canaliculata* and *N. ostrina* (Figure 4.6).

Whelk spatial patterns

We had hypothesized that whelk populations would shift lower on the shore in the absence of *P. ochraceus,* thus shifting the distribution of whelks across tide height between years. Our results suggest that there was no movement downshore because the cumulative distribution of whelks across tidal elevation did not differ (non-significant two-sample K-S tests, Table 4.5, Figures D1, D2) for either species at any site from 2014 to 2015. The exception was Strawberry Hill, where the distribution of *N. canaliculata* moved downshore in 2015 (K-S test, $d^{-} = 0.1574$ $p = 0.046$, Figure D1).

Discussion

Whelks had few direct effects on prey species in our study following declines in the keystone predator *Pisaster ochraceus* due to SSWD in Oregon. However, our results suggested that whelks facilitated establishment of the competitively dominant prey species *Mytilus californianus* although changes in abundance of this mussel were small and overall cover remained low. Thus, in the short-term at least, whelks in Oregon appeared to be unable to limit mussel establishment following keystone species loss. This result contrasts to our original hypothesis (and to prior results) that whelk predation may strengthen when the keystone *P. ochraceus* is removed (Menge et al. 1994, Navarrete and Menge 1996). We also found that whelk predators demonstrated distinct population-level differences during the emergence (2014) and persistence (2015) of SSWD. While there were almost no shifts in whelk distributions across tidal elevation, there were shifts towards smaller individuals in surveys of size structure, presumably reflecting increased recruitment success, consistent across sites and species. We also found that one species of whelk *Nucella ostrina* increased over time, while *Nucella canaliculata* abundance patterns were driven by patches of *Mytilus trossulus*.

In conjunction with broader community predictions for the loss of *P. ochraceus* (Paine 1969), cover of the competitive dominant *M. californianus* increased in plots over time, though it remained low overall. Our finding that whelks promoted establishment of the competitive dominant *M. californianus* (i.e. cover of the mussel was higher in +W treatments) has been previously observed (Navarrete and Menge 1996, Berlow 1997, Wootton 2002), and may depend on a few factors. First, Oregon whelks do not typically consume *M. californianus*, particularly at large mussel size classes (Sanford et al. 2003), so the direct effects of whelks are minimal, limiting their potential impact (as hypothesized for Oregon in Sanford et al. 2003). Whelks instead consume several species that are spatial competitors of *M. californianus*, including the mussel *M. trossulus*, which also acts as an important settlement substratum for *M. californianus* (Paine 1974, Petersen 1984).

For whelks to have a positive effect on *M. californianus* thus depends on the timing and patterns of whelk predation (Navarrete and Menge 1996): whelk predation must be weak enough so that whelks do not entirely eliminate mussel patches before late summer, allowing for *M. californianus* to recruit. Further, continued whelk predation on *M. trossulus* after the recruitment of *M. californianus* would reduce competition for *M. californianus* recruits as they grow. This effect would occur for new *M. californianus* recruits, but adults already established in 2014 would also likely benefit from reduced competition as whelks consumed *M. trossulus*. Our 2014 data were consistent with this overall pattern. Patches of adult *M. trossulus* were able to persist in the upper low zone through the winter regardless of whelk presence (probably due to low sea star densities), but whelk predation on those patches continued throughout that time period following recruitment of *M. californianus*.

We saw few effects on other species, in contrast to expectations that whelks are important predators of prey other than *M. californianus*. Dayton (1971) noted that whelks ate all *Balanus glandula* in experimental enclosures within 10 days in the San Juan Islands and consumed all *Mytilus* < 30 cm when allowed to feed in areas where *P. ochraceus* was experimentally excluded. In Oregon, whelks were able to limit increases in *M. trossulus* following *P. ochraceus* removal (Menge et al. 1994, Navarrete 1996). Why did we obtain different results? First, we observed relatively rapid reinvasion of our removal treatments by whelks, so treatments reduced but did not eliminate whelk predation. Thus, though we did reduce the cumulative impact of whelks over time, it is possible that our treatments were not effective enough to reveal actual differences between removals and controls. However, our methods were similar to previous studies using manual removals of whelks within a similarly sized plot area (Navarrete and Menge 1996). We also observed that as the experiment progressed, most whelks reinvading removal plots were very small (~5 mm in size), suggesting that treatments effectively excluded larger individuals with the greatest impacts. Second, it is possible that differences would have emerged on longer timeframes had we extended the experiment beyond 11 months. However, our experiment ran as long as previous studies showing whelk effects (Menge et al. 1994, Navarrete and Menge 1996), so this explanation is not convincing.

Third, and most likely, mussel recruitment (or survival over winter) was anomalously low in 2014-15, leading to near-absence of *M. trossulus* beds in 2015 (Figure 4.7). As an intraguild predator, the impacts of *P. ochraceus* on whelks are through both predation and competition. The effects of *P. ochraceus* on whelks are primarily competitive and are mediated through reduction of *M. trossulus* (Navarrete et al. 2000). In 2015, low *M. trossulus* abundances in the absence of *P. ochraceus* were unexpected and without precedent (B. Menge, pers. obs.). In over 30 years of research at these sites, *P. ochraceus* had typically consumed all *M. trossulus* within the low intertidal zone by summer’s end. We do not know why either the recruitment or survival of *M. trossulus* was poor, but it likely affected the strength of whelk predation and compensation because the absence of sea stars did not increase access to valuable prey.

Previous removals of *P. ochraceus* at the Strawberry Hill site led to high colonization by *M. trossulus*, which were eventually controlled by whelks (Menge et al. 1994). Low abundances of *M. trossulus* could limit the ability of the dominant mussel *M. californianus* to establish in the low zone by minimizing recruitment substrate (Paine 1974). This result suggests that the environmental drivers of prey recruitment may have modified the role of whelks following SSWD (Figure 4.8). *P. ochraceus* is only a keystone species when prey recruitment is high (Menge et al. 1994); likewise, low prey recruitment may limit the compensatory capacity of other predators without the keystone species.

Limited whelk effects on prey communities could have also been driven by trait-mediated indirect interactions by the remaining *P. ochraceus* at our sites. Whelks, though rarely consumed by *P. ochraceus* (Sanford 1999), can still exhibit marked responses to its presence. Research in southern California has shown that whelks grew less and changed their feeding preferences in the presence of cues from *P. ochraceus* in the laboratory setting (Gosnell and Gaines 2012); further, whelk responses to predators were non-linear across predator density, suggesting that predator presence may be more important than density (Gosnell and Gaines 2012). With approximately 20% of the *P. ochraceus* population remaining at each site, predator cues therefore may have been strong enough to retain a behaviorally-mediated cascade in whelk predators. However, long-term observations at our sites indicate that prior to the onset of SSWD, whelks were typically extremely abundant at SH and YB and preyed heavily on *M. trossulus*, even when sea stars were present in high abundance and close proximity (B. Menge, pers. obs.). While trait-mediated effects of sea stars on whelks cannot be ruled out in our study, prior observations are not consistent with such an effect.

Our study did not include factorial treatments to look at effects of whelks in the presence and absence of *P. ochraceus*. Previous studies using this factorial approach have found that whelks have negligible effects in the presence of *P. ochraceus*, but they are important in the absence of the keystone species (Navarrete and Menge 1996). Given the high disease incidence and the reduced density of adult *P. ochraceus*, we determined that such factorial manipulations were not advisable. This limits our ability to infer how SSWD changed whelk interactions with prey; instead, we assessed whelk effects in the context of a highly reduced density of *P. ochraceus*. Our results differ from previous work, but were consistent at both study sites, underscoring the need for further study of what factors determine the outcome of whelk interactions with the prey community both with and without *P. ochraceus* and in the context of variable prey production.

Community Dynamics Implications

Subordinate consumers in other systems have also shown mixed responses to the loss of a keystone species. In a long-term study tracking the removal of kangaroo rats from experimental enclosures in an aridland system, Brown et al. (2001) found that other granivores in the system were unable to consume as much energy as the keystone kangaroo rat. This lack of compensation persisted until a novel species of granivore colonized the exclosures from nearby areas and assumed the keystone species role. In other systems, however, subordinate predators can be important following top predator loss. In the California Channel Islands, removal of the spiny lobster *Panulirus interruptus* induced a transition from a red algal turf assemblage to one dominated by *M. californianus*, but a whelk species that consumed *M. californianus* increased its predation on mussels when lobsters were removed (Robles and Robb 1993). Further, the transition to mussel bed required both the loss of lobsters and whelks, indicating support for diffuse predation by whelks through compensatory foraging shifts, though whelks were not able to control mussel populations entirely (Robles and Robb 1993).

In our study, *N. ostrina* increased in abundance while *N. canaliculata* remained at similar densities following the decline of *P. ochraceus*. These surveys are observational, following the "natural experiment" of sea star wasting, so any patterns cannot be attributed directly to SSWD. In other studies, whelk densities have increased following *P. ochraceus* removal (Menge et al. 1994, Navarrete and Menge 1996). We also found few elevational distribution changes in whelks between years. It is well known that whelks alter their elevational distribution seasonally and in response to wave action (Menge 1978), temperature (Hayford et al. 2015), and the presence of predators (Trussell et al. 2003). In other systems, subordinate species have altered their spatial distribution in response to release from a top predator (Ritchie and Johnson 2009). In our study, poor recruitment of *M. trossulus* could have limited population increase and vertical elevation shifts as the mussels are a preferred food item. Without *M. trossulus*, whelks would have less impetus to move into the low zone to forage. In 2014, we found the highest numbers of whelks aggregating around patches of *M. trossulus* in the low zone, with little aggregation occurring in 2015. Low *M. trossulus* abundance could also reduce population abundance of whelks. We observed the converse of this trend at sites in southern Oregon, where unusually high recruitment of *M. trossulus* following SSWD in 2015, resulted in large increases in *N. canaliculata* densities (B. Menge, pers. obs.).

We found that the population size structure of both whelk species shifted towards smaller individuals. This could indicate several contrasting things about whelk populations. It could, for example, indicate that whelks experienced increased reproductive success in 2015, thus increasing the numbers of small individuals. Increased survival of whelk recruits seems possible given that small prey (e.g., recent barnacle recruits and adults) abundance was high during the study period. However, in winter and spring 2015, unusually high densities of *P. ochraceus* recruits and *Leptasterias* spp. individuals had appeared, both of which feed on small whelks as well as small mussels and barnacles. Secondly, with the recruitment failure of *M. trossulus*, it is possible that growth rates of juvenile whelks were poor, and as a result the juvenile cohort was smaller in July of 2015 than they were at the same time the previous year. In *N. ostrina*, smaller hatchlings growth more slowly than larger hatchlings; if food resources were limited, it could reduce maternal investment in egg organic content and lead to smaller juveniles in the next year (Moran and Emlet 2001). A shift towards smaller size classes could also indicate the loss of adults from the population, which could relate to food limitation or environmental stress. In any case, our findings contrast with previous research showing increases in individual sizes of *N. canaliculata* following removal of *P. ochraceus* (Menge et al. 1994, Navarrete and Menge 1996). Whelk populations can also experience high mortality rates in response to environmental stress (Connell 1972), which we did not measure. It is also possible that the low abundance of *M. trossulus* could have limited the abundance of larger adults, particularly in *N. canaliculata*, or caused them to retreat to deep within the mussel bed.

Conclusions

As the unprecedented outbreak of SSWD continues along the U.S. West Coast, there are opportunities for future research to inform our understanding of both the ecological consequences of the disease and our understanding of intertidal community dynamics more generally. Evidence from the current outbreak of SSWD (2014-2015) along the Oregon coast indicates that the predation by *P. ochraceus* on *M. californianus*, as determined from predation rate experiments involving mussel transplants, was dramatically lower in 2014 than the mean value for 1990-2013 at our sites (SH: -15.2x, YB: -6.4x) (Menge et al. 2016). The progression of the disease and the rate of *P. ochraceus* population recovery will be central determinants of the community outcomes of SSWD, but in addition, it is critical to understand what factors may dampen or magnify the effects of keystone species declines. Comparisons between intertidal community changes in California, where whelks feed on *M. californianus* readily, and Oregon, where they do not, would be particularly powerful at clarifying whelk compensatory roles.

Overall, we found that, in a one-year study, whelks exhibited a limited capacity to influence prey community structure when populations of the keystone predator were reduced by 80% in Oregon during a natural disease outbreak. This weak effect contrasted to prior experimental results, and seems likely to have resulted from unusual and unprecedented conditions, particularly the near absence of mussel recruitment at our sites. The extent to which this situation persists and its longer term consequences on intertidal community structure will be intriguing to investigate.

Acknowledgements

We thank Angela Johnson, Jonathan Robinson, Brittany Poirson, Jerod Sapp, Allison Barner, Chenchen Shen, Alissa Rickborn, Barbara Spiecker, Alexander Carsh, Dustin Hollabaugh, Joe Stack, Kathryn Cerny-Chipman, Lacey Schrock-Purkey, Silke Bachhuber, Lindsey Sadlou, Courtney Jackson, Melissa Linn, Melissa Britsch, Trevor Baley, Kaelie Sivihok, and Skylar Peven for field assistance. We also thank Celeste Moen, Kristi Knoll, and Raine Robison for their help with analysis of photographs. This work was funded with grants from the David and Lucile Packard Foundation, the Kingfisher Foundation, NSF (OCE14-48913), and endowments from the Wayne and Gladys Valley Foundation. This work was part of PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, funded in part by the David and Lucile Packard Foundation. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Figures

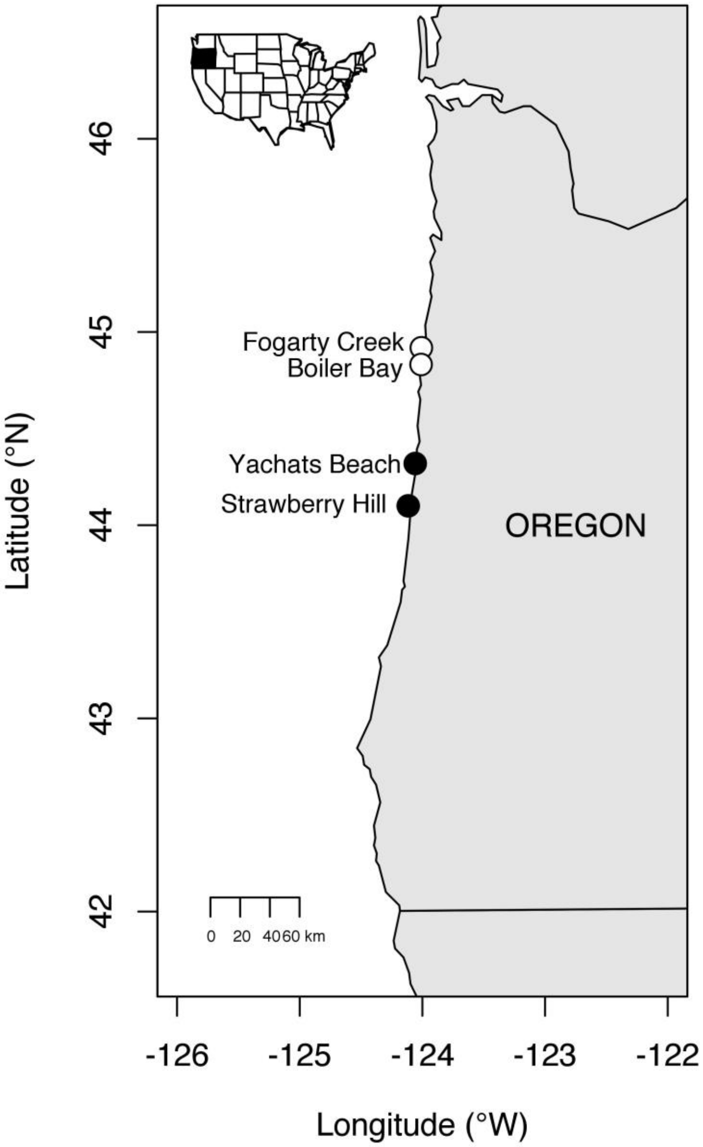

Figure 4.1. Map of study sites. Black symbols indicate sites where both surveys and experiments were conducted, while white symbols show sites with only surveys.

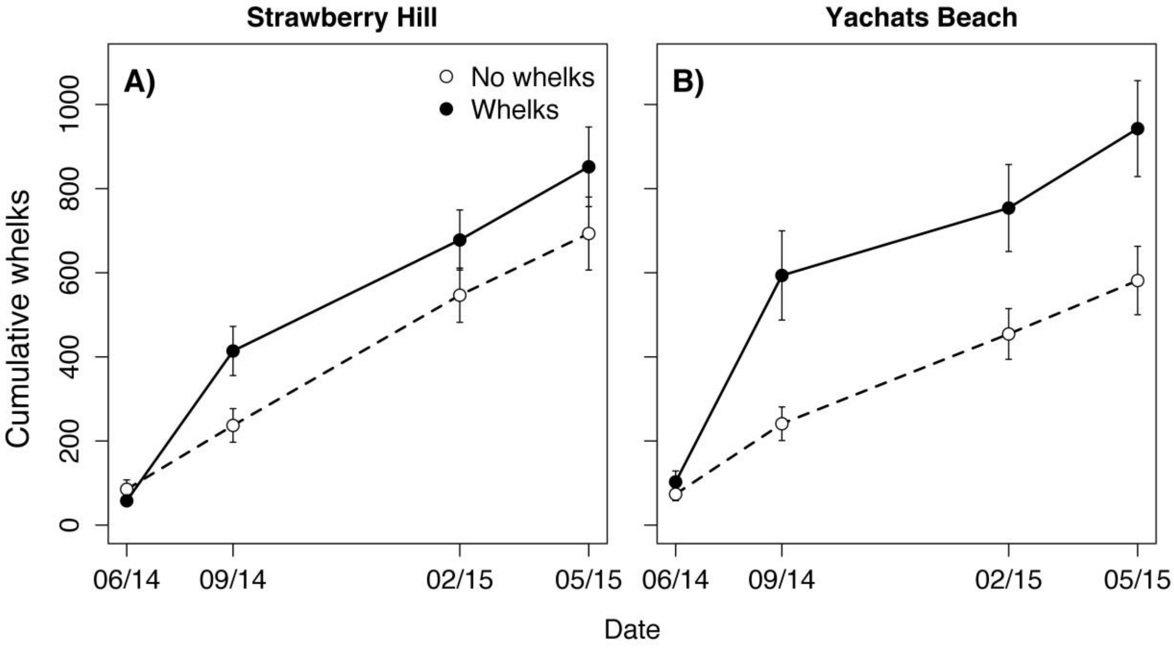

Figure 4.2. Cumulative whelk densities (individuals m^{-2}) over the course of the experiment for whelk removals (open circles) and controls (filled circles) at Strawberry Hill (SH, left panel) and Yachats Beach (YB, right panel). Cumulative densities are calculated from all monthly monitoring data, but only time points that match prey abundance data are displayed. Whelks were recorded by species and pooled for analysis. Error bars are +1 SE.

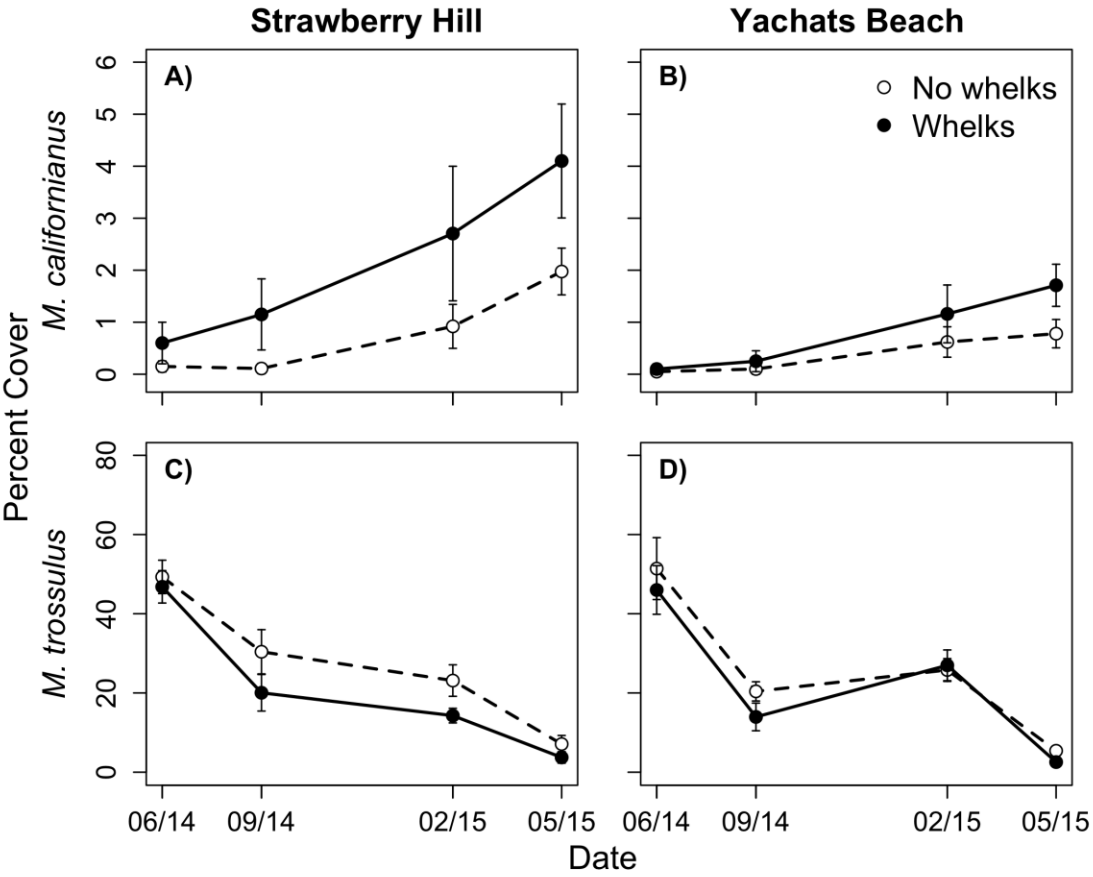

Figure 4.3. Percent cover of dominant mussel *M. californianus* (upper panel) and subdominant mussel *M. trossulus* (lower panel) over time for whelk removals (open circles) and controls (filled circles). Error bars are +1 SE.

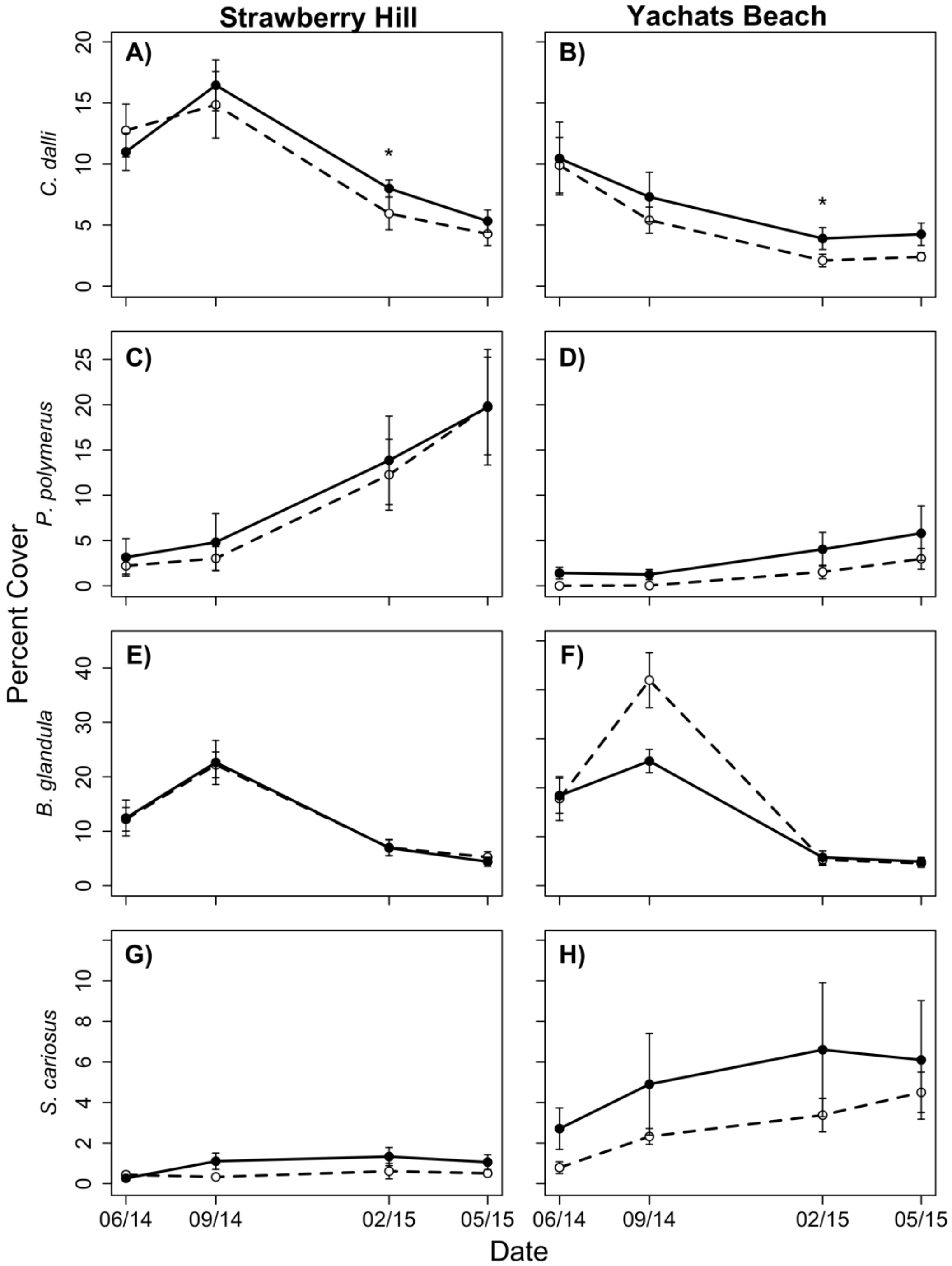

Figure 4.4. Percent cover of four subdominant barnacle species over time in whelk removals (open circles) and controls (filled circles). Error bars are +1 SE. Paired panels represent the two sites for each species. Stars represent significant comparisons when all pairwise contrasts are made.

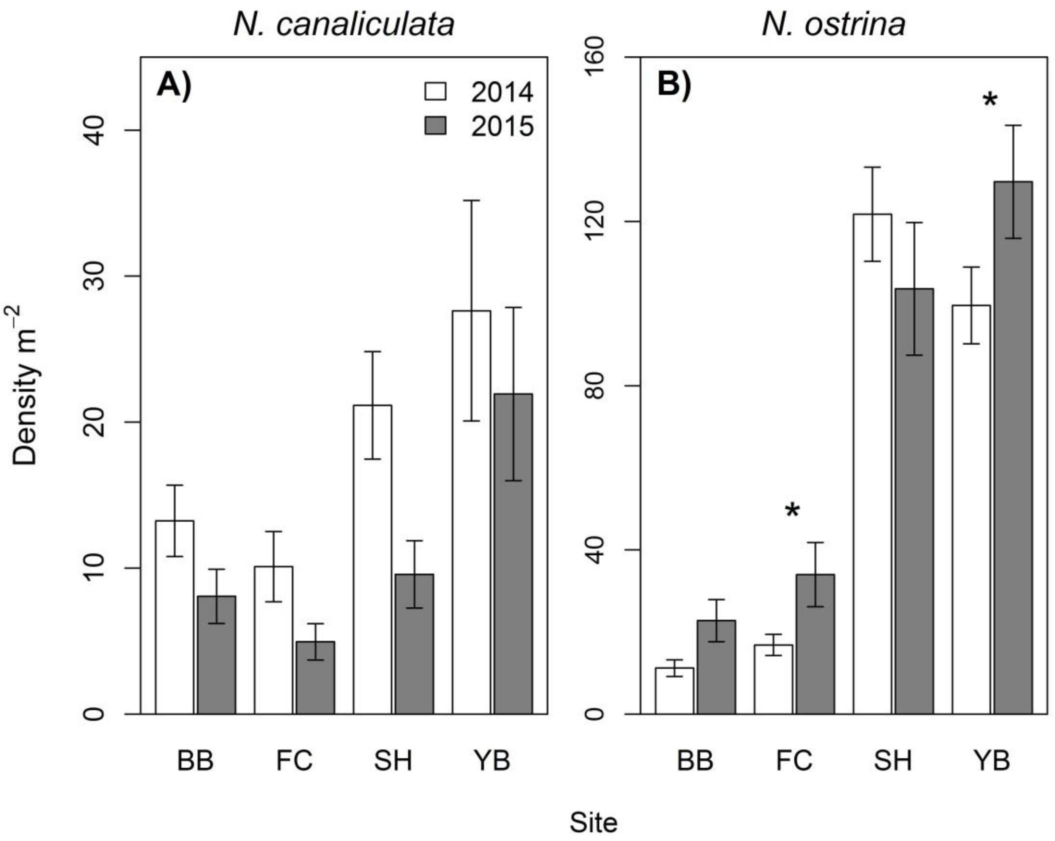

Figure 4.5. Abundance at four survey sites of *N. canaliculata* (left) and *N. ostrina* (right) in 2014 (white bars) and 2015 (grey bars). Error bars are +1 SE. Refer to text for site abbreviations. Data include quadrats from the *M. trossulus* zone.

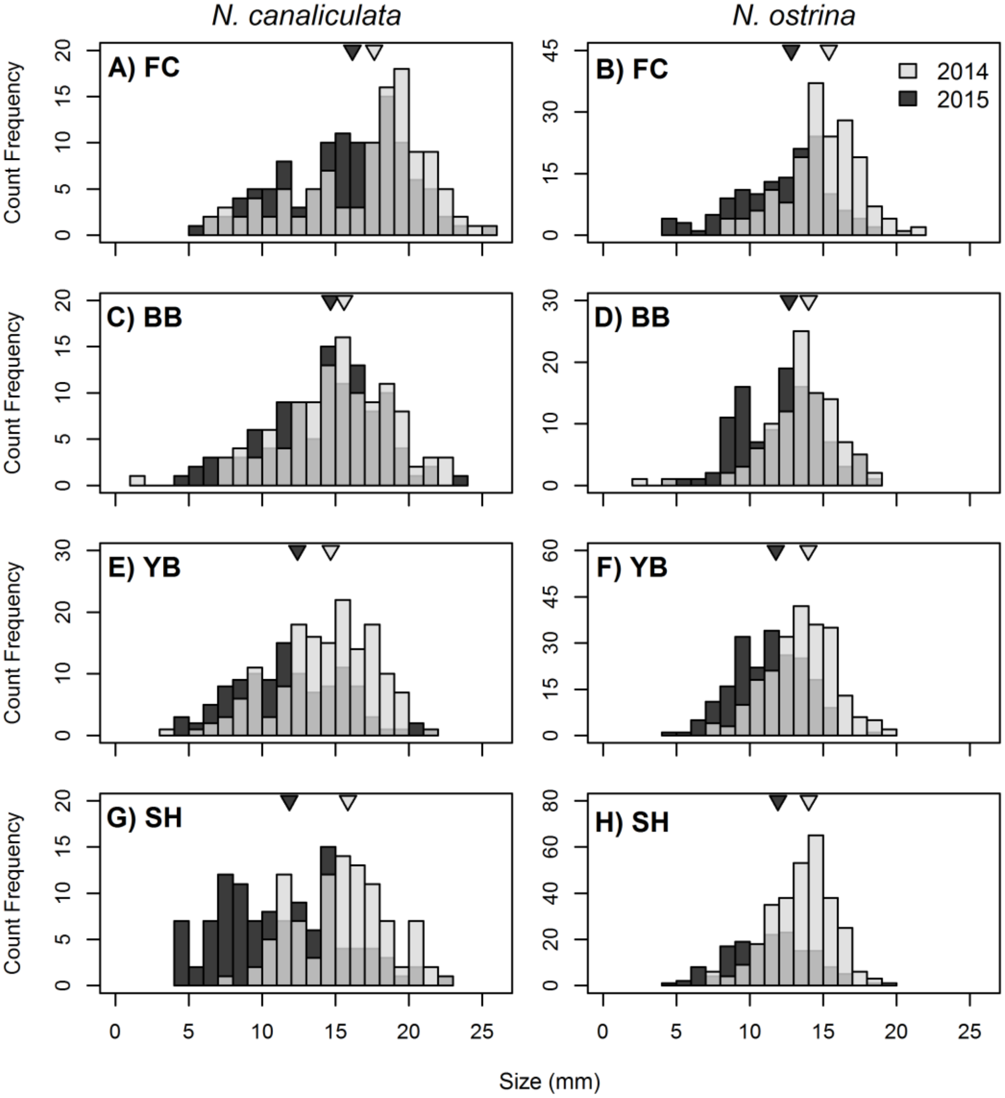

Figure 4.6. Whelk size distributions from 2014 and 2015 surveys for both species at Fogarty Creek (A, B), Boiler Bay (C, D), Yachats Beach (E, F), and Strawberry Hill (G, H). The two distributions are superimposed, with the region of overlap appearing as a medium grey color. Triangles at the top of each plot indicate the means for 2014 (light grey), and 2015 (dark grey).

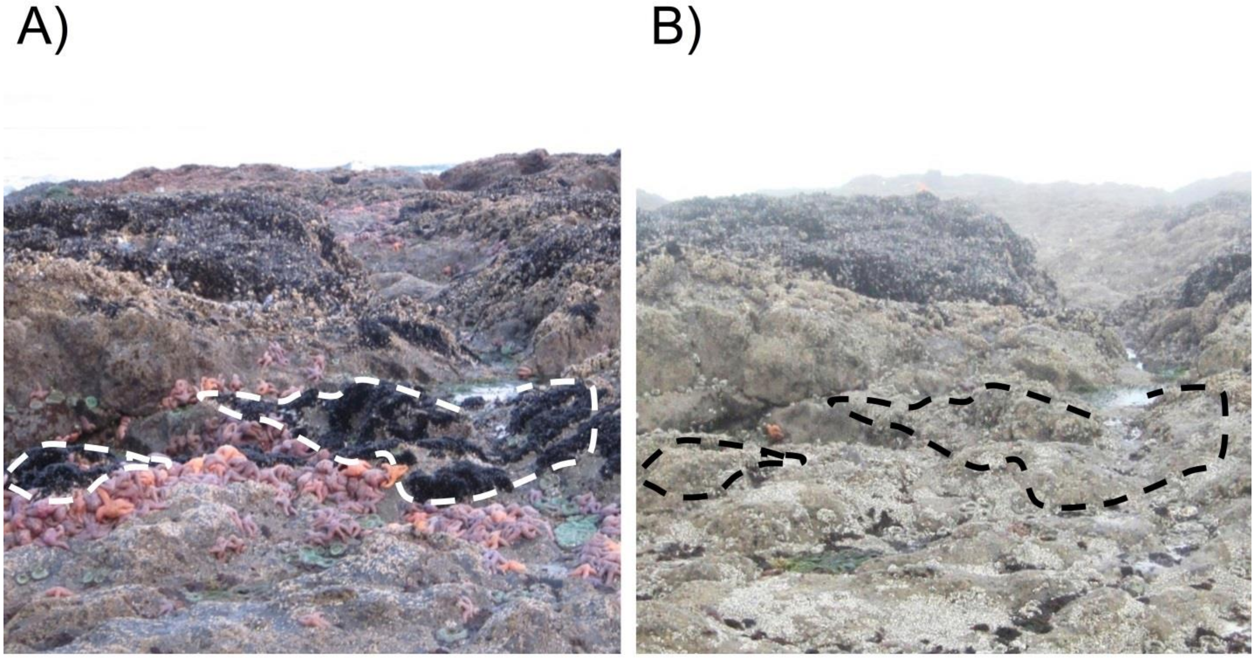

Figure 4.7. Photograph of Strawberry Hill site in a) 2013 and b) 2015. In 2013, there is a visible aggregation of *P. ochraceus* feeding on the mussel *M. trossulus*, which forms the black beds outlined with the dashed line. In 2015, there are few sea stars visible and no beds of *M. trossulus*. The space formerly occupied by the beds is indicated with the dashed area.

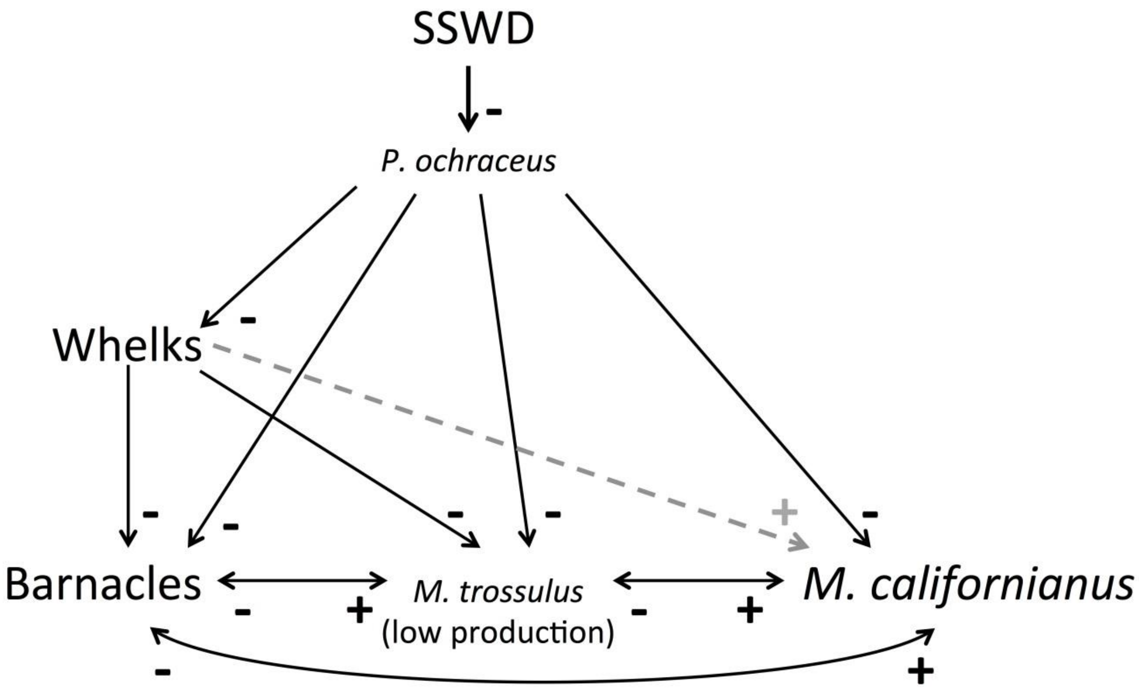

Figure 4.8. Food web indicating the hypothesized effects of SSWD and low *M. trossulus* production. The web shows little effect of whelks on barnacles and *M. trossulus* (at low abundances) as well as the presence of an indirect positive effect of whelks on *M. californianus* (grey dashed arrow). The mechanism of this indirect positive effect is unclear given the limited effects of whelks on the spatial competitors of *M. californianus* adults and recruits.

Tables

Table 4.1. Two-way ANOVA testing the effect of site and year on *N. canaliculata* body length. R^2=0.1736.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Site	3	1530	511.2	34.3639	<0.0001
Year	1	1050	1052.83	70.7738	<0.0001
Site x Year	3	286	95.43	6.4153	0.0003
Residuals	919	13671	14.88		

Table 4.2. Linear contrasts for differences in *N. canaliculata* size (in mm) by year. Tests of interaction contrasts from ‘phia’ package in R. p-values were adjusted using a Holm’s correction.

Site	Hypothesis	Estimate	df	Sum of Squares	F-value	p-value
BB	2014-2015 = 0	0.9332	1	48.8	3.2771	0.0706
FC	2014-2015 = 0	1.4779	1	122.7	8.2505	0.00834
YB	2014-2015 = 0	2.2660	1	336.5	22.6196	6.87×10^{-6}
SH	2014-2015 = 0	3.9939	1	831.2	55.8726	7.20×10^{-13}
	Residuals		919	13671.0		

Table 4.3. Two-way ANOVA test of the effect of site and year on *N. ostrina* body length. Type II sum of squares were used because data were unbalanced and there was no significant interaction. R^2=0.1651.

	df	Sum Sq	F value	p-value
Site	3	339	17.044	<0.0001
Year	1	1530	230.845	<0.0001
Residuals	1410	9350		

Table 4.4. Linear contrasts for differences in *N. ostrina* size (in mm) by year. Tests of interaction contrasts from ‘phia’ package in R. p-values were adjusted using a Holm’s correction.

Site	Hypothesis	Estimate	df	Sum of Squares	F-value	p-value
BB	2014-2015 = 0	1.3343	1	96.3	14.599	0.000139
FC	2014-2015 = 0	2.5590	1	504.0	76.377	2.2×10^{-16}
YB	2014-2015 = 0	2.2057	1	518.6	78.601	2.2×10^{-16}
SH	2014-2015 = 0	2.0984	1	458.1	69.427	3.72×10^{-16}
	Residuals		1409	9297.2		

Table 4.5. Results from two-sample Kolmogorov-Smirnov tests with bootstrapped p-values testing vertical distribution shifts in whelk abundance. The null hypothesis is that the whelk distributions (ordered over tidal elevation) from 2014 and 2015 are from same empirical distribution function (EDF). The test statistic, D, is the maximum difference in value between the two EDFs. The alternative hypothesis is that the 2014 EDF is stochastically larger than the EDF from 2015 (i.e. it would lie below and to the right of the 2015 EDF) if whelks had shifted distributions towards lower tide heights in 2015. Result are from July 2014 and 2015 surveys only because of uneven sampling across years when all dates are included.

Species	Site	D^- statistic	p-value
N. canaliculata	FC	0.0769	0.474
	BB	0.1538	0.103
	YB	0.1029	0.371
	SH	0.1574	0.046
N. ostrina	FC	0.0615	0.603
	BB	0.0000	1.0000
	YB	0.0882	0.527
	SH	0.0901	0.429

5 – CONCLUSION

Overall, my dissertation explores how predators, acting as key components of rocky intertidal communities, respond to environmental contexts relevant to global change. I focused on three contexts: pH and ocean acidification, temperature and upwelling, and the biotic context of disease-driven top predator loss. The motivation behind my work was to use subsets of environmental stress models (Menge and Sutherland 1987, Menge and Olson 1990) as a conceptual frame for predicting the broad consequences of environmental change on predator-prey interactions. In general, I found that predators may reduce their consumption in response to environmental stressors (e.g., OA, temperature), but that the resultant effects on prey were more much more complex and nuanced than expected.

In Chapter 2, I assessed how feeding rates of whelk predators responded to elevated CO_2 in two mesocosm experiments. I found that, consistent with consumer stress models, consumption decreased with increasing CO_2 and decreasing pH, and that this was mediated by longer handling times. The exact physiological mechanisms remain unclear, as do the short-term impacts to predators, who suffered few physiological consequences of acidification, at least in the context of my experiments. These results are in line with previous studies in similar predator-prey systems (Queirós et al. 2015, Keppel et al. 2015), but novel in their integration of feeding rate, handling time, and gross physiological metrics including growth. That I saw decreases in feeding rates with increased CO_2 is also interesting given previous results showing reduced feeding during upwelling by whelks and the sea star *P. ochraceus* (Sanford 1999, 2002b), and suggests that low pH conditions that occur during upwelling may be another possible driver of predation. My results also emphasize the need to ensure that the design of experiments testing species interactions with OA matches the precise questions of interest, where considerations such as whether both the predator and prey are exposed and for how long are essential for inference. Likewise, the diversity of experimental designs within the existing body of research represents an opportunity to glean a more synthetic perspective on changes to species interactions with OA

In Chapter 3, I broadened the scope of my research by placing whelk-mussel interactions in a dynamic field environment. I minimized two local-scale gradients of stress, tidal elevation and wave stress, in order to isolate stressors working at broader scales. Transplants of whelks and mussels to sites in three different years revealed little variation in predation rates or drilling behaviors in whelks. However, there were some potential links to mesoscale environmental drivers such as upwelling. The consistency I found among years is in line with previous studies documenting strong cape-scale drivers in interactions and community structure (Menge et al. 1994). In 2013, sites with increased variability in air temperature had higher mussel survival. This was not the case in 1999 or 2000 and may suggest that predators were negatively impacted by stress, as previous lab studies have shown for whelks (Yamane and Gilman 2009). Despite the relationship to temperature, drilling rates by whelks were not affected by any environmental variables in 2013 but differed between the two species. Overall, my work leaves open as well the possibility that multiple stressors can mask or offset one another, or can be integrated over time or spatial scales in ways that obscure potentially meaningful patterns.

In Chapter 4, I examined the consequences of the decline in abundance of a keystone predator *P. ochraceus* due to disease from the perspective of the subordinate predator. In other cases, subordinate predators, even whelks, have been able to compensate for the loss of a top predator (see examples in Menge 2003). However, in my case, effects of whelk predators on the prey community were generally weak and whelks even facilitated the establishment of the competitive dominant mussel *M. californianus.* I conclude that whelk effects were curtailed by unusually low mussel recruitment, and prey inputs also likely drove patterns in whelk abundances over time and in space. My results suggest that understanding interactions between prey input or recruitment and top predator loss may be important for understanding the ability of intermediate trophic levels to regulate prey. Further, my results match the prediction that when recruitment is low, species interactions are generally less important (Menge and Sutherland 1987). My study was also one of the first to compare subordinate predator effects and spatial distribution shifts following a natural top-predator decline.

Together, these chapters suggest that whelk predators play many different roles along rocky shores that will depend on changing context. Beyond those discussed above, there are two additional points that can be taken from this work. The first is that predictions of environmental stress models, which assume predators are more sensitive to stress than their prey, tended to hold in under OA conditions, but patterns were less clear in the dynamic field environment and with a biotic change of keystone species decline. Adding specificity to these models and linking them more closely with physiology would provide greater cross-scale prediction. My dissertation and the gaps it leaves unfilled point to the need for integration across levels of biological organization in order to fully understand and predict the impacts of climate change on communities (Harley 2013). It also suggests the potential primacy of key physiological variables in understanding how environmental context shapes communities. Several important conceptual frameworks are making strides in this area, including the use of metabolic rates, body size, and temperature to describe community structure and ecosystem dynamics (e.g., Brown et al. 2004, Rall et al. 2012). In addition, the expanding integration and links between traditional physiologists and ecologists and the utilization of new techniques holds much promise for improved prediction and insight.

Secondly, one consistent pattern in my dissertation was that the both species of whelk predators, which appear to occupy similar niches, often responded very differently to their environmental context. For example, *N. canaliculata* was more likely to drill mussels overall, but was also more sensitive to the recruitment failure of *M. trossulus* than *N. ostrina*. Slight differences in prey preference, size, and feeding mode are the likely reasons for these distinct responses to environmental contexts, and I think these areas are worth exploring further. This adds yet another wrinkle in our understanding of making predictions for predator-prey interactions with climate change and how much species identity might matter. To my knowledge, few other studies have compared congeners in the context of ocean acidification (but see (Couturier et al. 2013, Waldbusser et al. 2015b), though the study of congeners can provide unique insights in the physiological response to stressors (Somero 2010, 2012).

Overall, my dissertation explored the importance of environmental context by focusing on a single set of predator-prey interactions within contexts important in global change. By using the relatively well-characterized interaction of whelks and their mussel prey, my research leverages existing knowledge to move towards more generality with respect to environmental variables relevant to climate change. We know that species interactions, and predator-prey interactions in particular, are central determinants of community structure. Existing species distribution models and predictions for climate change largely ignore these biotic effects, which often means they may make poor predictions (Araújo and Luoto 2007, Urban et al. 2013). What my results show is that, at both the per capita and population levels, even weak interactors have variability in species interactions that will likely influence their role in communities undergoing change. This suggests we need to deepen our understanding and work to determine how sensitivity in species interactions will ultimately affect community structure, functioning, and provision of ecosystem services. Environmental stress models can provide a useful starting point for framing thinking and moving further conceptual development forward. My findings contribute to our understanding of the mechanisms by which environmental stress can affect predators and their prey, and of the links between physiological stress and broader community outcomes.

BIBLIOGRAPHY

Adler, P. B., H. J. Dalgleish, and S. P. Ellner. 2012. Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? Journal of Ecology 100:478–487.

Adler, P. B., J. Leiker, and J. M. Levine. 2009. Direct and Indirect Effects of Climate Change on a Prairie Plant Community. PLOS ONE 4:e6887.

Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. Maron, K. A. Mooney, and others. 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment 5:145–152.

Altieri, A. H., and J. D. Witman. 2006. Local extinction of a foundation species in a hypoxic estuary: integrating individuals to ecosystem. Ecology 87:717–730.

Amaral, V., H. N. Cabral, and M. J. Bishop. 2012. Effects of estuarine acidification on predator–prey interactions. Marine Ecology Progress Series 445:117–127.

Angert, A. L., S. L. LaDeau, and R. S. Ostfeld. 2013. Climate change and species interactions: ways forward. Annals of the New York Academy of Sciences 1297:1–7.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743–753.

Atwood, T. B., R. M. Connolly, E. G. Ritchie, C. E. Lovelock, M. R. Heithaus, G. C. Hays, J. W. Fourqurean, and P. I. Macreadie. 2015. Predators help protect carbon stocks in blue carbon ecosystems. Nature Climate Change 5:1038–1045.

Bakun, A., B. A. Black, S. J. Bograd, M. García-Reyes, A. J. Miller, R. R. Rykaczewski, and W. J. Sydeman. 2015. Anticipated Effects of Climate Change on Coastal Upwelling Ecosystems. Current Climate Change Reports 1:85–93.

Barth, J. A., B. A. Menge, J. Lubchenco, F. Chan, J. M. Bane, A. R. Kirincich, M. A. McManus, K. J. Nielsen, S. D. Pierce, and L. Washburn. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. Proceedings of the National Academy of Sciences 104:3719.

Beesley, A., D. Lowe, C. Pascoe, and S. Widdicombe. 2008. Effects of CO2-induced seawater acidification on the health of Mytilus edulis. Clim Res 37:215–225.

Bennett, A. F., and R. B. Huey. 1990. Studying the evolution of physiological performance. Oxford surveys in evolutionary biology 7:251–284.

Berlow, E. L. 1997. From Canalization to Contingency: Historical Effects in a Successional Rocky Intertidal Community. Ecological Monographs 67:435–460.

Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. Nature 398:330–334.

Berlow, E. L., A. Neutel, J. E. Cohen, P. C. De Ruiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. Iwan Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. M. Montoya, and O. Petchey. 2004. Interaction strengths in food webs: issues and opportunities. Journal of Animal Ecology 73:585–598.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology & Evolution 9:191–193.

Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. American Naturalist:363–372.

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the Relative Contribution of Positive and Negative Interactions in Rocky Intertidal Communities. Ecology 80:2711–2726.

Bibby, R., S. Widdicombe, H. Parry, J. Spicer, and R. Pipe. 2008. Effects of ocean acidification on the immune response of the blue mussel Mytilus edulis. Aquatic Biology 2:67–74.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What Determines the Strength of a Trophic Cascade? Ecology 86:528–537.

Borrvall, C., and B. Ebenman. 2006. Early onset of secondary extinctions in ecological communities following the loss of top predators. Ecology Letters 9:435–442.

Broitman, B. R., P. L. Szathmary, K. a. S. Mislan, C. A. Blanchette, and B. Helmuth. 2009. Predator–prey interactions under climate change: the importance of habitat vs body temperature. Oikos 118:219–224.

Brose, U., E. L. Berlow, and N. D. Martinez. 2005. Scaling up keystone effects from simple to complex ecological networks. Ecology Letters 8:1317–1325.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a Metabolic Theory of Ecology. Ecology 85:1771–1789.

Brown, J. H., T. G. Whitham, S. Morgan Ernest, and C. A. Gehring. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. Science 293:643.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18:119–125.

Burge, C. A., C. Mark Eakin, C. S. Friedman, B. Froelich, P. K. Hershberger, E. E. Hofmann, L. E. Petes, K. C. Prager, E. Weil, B. L. Willis, S. E. Ford, and C. D. Harvell. 2014. Climate Change Influences on Marine Infectious Diseases: Implications for Management and Society. Annual Review of Marine Science 6:249–277.

Burnaford, J. L. 2004. Habitat Modification and Refuge from Sublethal Stress Drive a Marine Plant–Herbivore Association. Ecology 85:2837–2849.

Burrows, M. T., and R. N. Hughes. 1991. Variation in Foraging Behaviour Among Individuals and Populations of Dogwhelks, Nucella lapillus: Natural Constraints on Energy Intake. Journal of Animal Ecology 60:497–514.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, O. Warsi, and J. J. Wiens. 2012. How does climate change cause extinction? Proc. R. Soc. B:rspb20121890.

Caldeira, K., and M. E. Wickett. 2003. Oceanography: Anthropogenic carbon and ocean pH. Nature 425:365–365.

Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecological Monographs 71:163–186.

Castelao, R. M., and J. A. Barth. 2005. Coastal ocean response to summer upwelling favorable winds in a region of alongshore bottom topography variations off Oregon. Journal of Geophysical Research: Oceans 110:C10S04.

Chamberlain, S. A., J. L. Bronstein, and J. A. Rudgers. 2014. How context dependent are species interactions? Ecology Letters 17:881–890.

Chan, F., J. A. Barth, J. Lubchenco, A. Kirincich, H. Weeks, W. T. Peterson, and B. A. Menge. 2008. Emergence of Anoxia in the California Current Large Marine Ecosystem. Science 319:920–920.

Cheng, B. S., and E. D. Grosholz. 2016. Environmental stress mediates trophic cascade strength and resistance to invasion. Ecosphere 7(4):e01247.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics:343–366.

Chevan, A., and M. Sutherland. 1991. Hierarchical Partitioning. The American Statistician 45:90–96.

Clements, J. C., and H. L. Hunt. 2015. REVIEW Marine animal behaviour in a high CO2 ocean. Marine Ecology Progress Series 536:259–279.

Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldaña. 1993. Body Sizes of Animal Predators and Animal Prey in Food Webs. Journal of Animal Ecology 62:67–78.

Connell, J. H. 1961a. Effects of Competition, Predation by Thais lapillus, and Other Factors on Natural Populations of the Barnacle Balanus balanoides. Ecological Monographs 31:61–104.

Connell, J. H. 1961b. The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle Chthamalus Stellatus. Ecology 42:710–723.

Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. Annual Review of Ecology and Systematics:169–192.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Ecology and evolution of communities 460:490.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Connell, S. D., K. J. Kroeker, K. E. Fabricius, D. I. Kline, and B. D. Russell. 2013. The other ocean acidification problem: CO2 as a resource among competitors for ecosystem dominance. Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120442.

Connolly, S. R., and J. Roughgarden. 1999. Theory of Marine Communities: Competition, Predation, and Recruitment-dependent Interaction Strength. Ecological Monographs 69:277–296.

Couturier, C. S., J. A. W. Stecyk, J. L. Rummer, P. L. Munday, and G. E. Nilsson. 2013. Species-specific effects of near-future CO2 on the respiratory performance of two tropical prey fish and their predator. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 166:482–489.

Cripps, I. L., P. L. Munday, and M. I. McCormick. 2011. Ocean Acidification Affects Prey Detection by a Predatory Reef Fish. PLoS ONE 6:e22736.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Dahlhoff, E. P., B. A. Buckley, and B. A. Menge. 2001. Physiology of the rocky intertidal predator Nucella ostrina along an environmental stress gradient. Ecology 82:2816–2829.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science 349:858–860.

Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. Proceedings of the Royal Society of London B: Biological Sciences 205:489–511.

Dayton, P. K. 1971. Competition, Disturbance, and Community Organization: The Provision and Subsequent Utilization of Space in a Rocky Intertidal Community. Ecological Monographs 41:351–389.

De Rosario-Martinez, H. 2015. Phia: post-hoc interaction analysis. R package version 0.2-1.

Dell, A. I., S. Pawar, and V. M. Savage. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70–84.

Derraik, J. G. B. 2002. The pollution of the marine environment by plastic debris: a review. Marine Pollution Bulletin 44:842–852.

Dethier, M. N., E. S. Graham, S. Cohen, and L. M. Tear. 1993. Visual versus random-point percent cover estimations: “objective” is not always better. Marine ecology progress series 96.

Dickson, A. G. 1990. Standard potential of the reaction: AgCl(s) + 12H2(g) = Ag(s) + HCl(aq), and and the standard acidity constant of the ion HSO4− in synthetic sea water from 273.15 to 318.15 K. The Journal of Chemical Thermodynamics 22:113–127.

Dickson, A. G., C. L. Sabine, and J. R. Christian. 2007. Guide to best practices for ocean CO2 measurements. PICES special publication 3.

Dillon, M. E., H. A. Woods, G. Wang, S. B. Fey, D. A. Vasseur, R. S. Telemeco, K. Marshall, and S. Pincebourde. 2016. Life in the Frequency Domain: the Biological Impacts of Changes in Climate Variability at Multiple Time Scales. Integrative and Comparative Biology:icw024.

Dixson, D. L., P. L. Munday, and G. P. Jones. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. Ecology Letters 13:68–75.

Doney, S. C., V. J. Fabry, R. A. Feely, and J. A. Kleypas. 2009. Ocean acidification: the other CO2 problem. Marine Science 1.

Doney, S. C., M. Ruckelshaus, J. Emmett Duffy, J. P. Barry, F. Chan, C. A. English, H. M. Galindo, J. M. Grebmeier, A. B. Hollowed, N. Knowlton, J. Polovina, N. N. Rabalais, W. J. Sydeman, and L. D. Talley. 2012. Climate Change Impacts on Marine Ecosystems. Annual Review of Marine Science 4:11–37.

Dowd, W. W., and G. N. Somero. 2013. Behavior and survival of Mytilus congeners following episodes of elevated body temperature in air and seawater. Journal of Experimental Biology 216:502–514.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Dugger, K. M., G. Ballard, D. G. Ainley, P. O. Lyver, and C. Schine. 2014. Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. Interdisciplinary Climate Studies 2:68.

Ebling, F. J., J. A. Kitching, L. Muntz, and C. M. Taylor. 1964. The Ecology of Lough Ine. Journal of Animal Ecology 33:73–82.

Eisenlord, M. E., M. L. Groner, R. M. Yoshioka, J. Elliott, J. Maynard, S. Fradkin, M. Turner, K. Pyne, N. Rivlin, R. van Hooidonk, and C. D. Harvell. 2016. Ochre star mortality during the 2014 wasting disease epizootic: role of population size structure and temperature. Phil. Trans. R. Soc. B 371:20150212.

Elton, C. S. 1927. Animal ecology. University of Chicago Press.

Estes, J. A., and J. F. Palmisano. 1974. Sea Otters: Their Role in Structuring Nearshore Communities. Science 185:1058–1060.

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

Evans, T. G., J. L. Padilla-Gamiño, M. W. Kelly, M. H. Pespeni, F. Chan, B. A. Menge, B. Gaylord, T. M. Hill, A. D. Russell, S. R. Palumbi, E. Sanford, and G. E. Hofmann. 2015. Ocean acidification research in the "post-genomic" era: Roadmaps from the purple sea urchin Strongylocentrotus purpuratus. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 185:33–42.

Fabry, V. J., B. A. Seibel, R. A. Feely, and J. C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science: Journal du Conseil 65:414–432.

Fangue, N. A., M. J. O'Donnell, M. A. Sewell, P. G. Matson, A. C. MacPherson, and G. E. Hofmann. 2010. A laboratory-based, experimental system for the study of ocean acidification effects on marine invertebrate larvae. Limnol. Oceanogr. Methods 8:441–452.

Feder, M. E., and G. E. Hofmann. 1999. Heat-shock proteins, molecular chaperones, and the stress response. Annual Review of Physiology 61:243–282.

Feely, R. A., C. L. Sabine, J. M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive" acidified" water onto the continental shelf. Science 320:1490.

Feely, R., S. Doney, and S. Cooley. 2009. Ocean Acidification: Present Conditions and Future Changes in a High-CO2 World. Oceanography 22:36–47.

Fenberg, P. B., B. A. Menge, P. T. Raimondi, and M. M. Rivadeneira. 2015. Biogeographic structure of the northeastern Pacific rocky intertidal: the role of upwelling and dispersal to drive patterns. Ecography 38:83–95.

Ferrari, M. C. O., M. I. McCormick, P. L. Munday, M. G. Meekan, D. L. Dixson, Ö. Lonnstedt, and D. P. Chivers. 2011. Putting prey and predator into the CO2 equation – qualitative and quantitative effects of ocean acidification on predator–prey interactions. Ecology Letters 14:1143–1148.

Fey, S. B., A. M. Siepielski, S. Nusslé, K. Cervantes-Yoshida, J. L. Hwan, E. R. Huber, M. J. Fey, A. Catenazzi, and S. M. Carlson. 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. Proceedings of the National Academy of Sciences 112:1083–1088.

Fields, P. A., M. J. Zuzow, and L. Tomanek. 2012. Proteomic responses of blue mussel (Mytilus) congeners to temperature acclimation. Journal of Experimental Biology 215:1106–1116.

Findlay, H., H. Wood, M. Kendall, J. Spicer, R. Twitchett, and S. Widdicombe. 2009. Calcification, a physiological process to be considered in the context of the whole organism. Biogeosciences Discussions 6:2267–2284.

Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecology Letters 8:1299–1306.

Fitzer, S. C., V. R. Phoenix, M. Cusack, and N. A. Kamenos. 2014. Ocean acidification impacts mussel control on biomineralisation. Scientific Reports 4:6218.

Fox, J., and S. Weisberg. 2011. An R Companion to Applied Regression. R package version 2.0-2. Second edition. Sage, Thousand Oaks, CA.

Freeman, A. S. 2007. Specificity of induced defenses in Mytilus edulis and asymmetrical predator deterrence. Marine Ecology Progress Series 334:145–153.

Gattuso, J.-P., J.-M. Epitalon, and H. Lavigne. 2016. seacarb: Seawater Carbonate Chemistry. R package version 3.0.14.

Gaylord, B., T. M. Hill, E. Sanford, E. A. Lenz, L. A. Jacobs, K. N. Sato, A. D. Russell, and A. Hettinger. 2011. Functional impacts of ocean acidification in an ecologically critical foundation species. The Journal of Experimental Biology 214:2586–2594.

Gaylord, B., K. J. Kroeker, J. M. Sunday, K. M. Anderson, J. P. Barry, N. E. Brown, S. D. Connell, S. Dupont, K. E. Fabricius, J. M. Hall-Spencer, T. Klinger, M. Milazzo, P. L. Munday, B. D. Russell, E. Sanford, S. J. Schreiber, V. Thiyagarajan, M. L. H. Vaughan, S. Widdicombe, and C. D. G. Harley. 2014. Ocean acidification through the lens of ecological theory. Ecology 96:3–15.

Gazeau, F., S. Alliouane, C. Bock, L. Bramanti, M. López Correa, M. Gentile, T. Hirse, H.-O. Pörtner, and P. Ziveri. 2014. Impact of ocean acidification and warming on the Mediterranean mussel (Mytilus galloprovincialis). Global Change and the Future Ocean 1:62.

Gazeau, F., L. M. Parker, S. Comeau, J.-P. Gattuso, W. A. O’Connor, S. Martin, H.-O. Pörtner, and P. M. Ross. 2013. Impacts of ocean acidification on marine shelled molluscs. Marine Biology 160:2207–2245.

Gazeau, F., C. Quiblier, J. M. Jansen, J. P. Gattuso, J. J. Middelburg, C. H. R. Heip, and others. 2007. Impact of elevated CO2 on shellfish calcification. Geophysical Research Letters 34.

Gilbert, B., T. D. Tunney, K. S. McCann, J. P. DeLong, D. A. Vasseur, V. Savage, J. B. Shurin, A. I. Dell, B. T. Barton, C. D. G. Harley, H. M. Kharouba, P. Kratina, J. L. Blanchard, C. Clements, M. Winder, H. S. Greig, and M. I. O’Connor. 2014. A bioenergetic framework for the temperature dependence of trophic interactions. Ecology Letters 17:902–914.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution 25:325–331.

Gilman, S. E., D. S. Wethey, and B. Helmuth. 2006. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. Proceedings of the National Academy of Sciences 103:9560–9565.

Glaser, J. A. 2015. Microplastics in the environment. Clean Technologies and Environmental Policy 17:1383–1391.

Gosnell, J. S., and S. D. Gaines. 2012. Keystone intimidators in the intertidal: non-consumptive effects of a keystone sea star regulate feeding and growth in whelks. Marine Ecology Progress Series 450:107–114.

Gouhier, T. C., B. A. Menge, and S. D. Hacker. 2011. Recruitment facilitation can promote coexistence and buffer population growth in metacommunities. Ecology Letters 14:1201–1210.

Grantham, B. A., F. Chan, K. J. Nielsen, D. S. Fox, J. A. Barth, A. Huyer, J. Lubchenco, and B. A. Menge. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429:749–754.

Grolemund, G., H. Wickham, and others. 2011. Dates and times made easy with lubridate. Journal of Statistical Software 40:1–25.

Gruber, N., C. Hauri, Z. Lachkar, D. Loher, T. L. Frölicher, and G.-K. Plattner. 2012. Rapid Progression of Ocean Acidification in the California Current System. Science 337:220–223.

Hacker, S. D., and S. D. Gaines. 1997. Some Implications of Direct Positive Interactions for Community Species Diversity. Ecology 78:1990–2003.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community Structure, Population Control, and Competition. The American Naturalist 94:421–425.

Hales, B., T. Takahashi, and L. Bandstra. 2005. Atmospheric CO2 uptake by a coastal upwelling system. Global Biogeochemical Cycles 19:GB1009.

Hall-Spencer, J. M., R. Rodolfo-Metalpa, S. Martin, E. Ransome, M. Fine, S. M. Turner, S. J. Rowley, D. Tedesco, and M.-C. Buia. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454:96–99.

Harley, C. D. G. 2011. Climate Change, Keystone Predation, and Biodiversity Loss. Science 334:1124–1127.

Harley, C. D. G. 2013. Linking ecomechanics and ecophysiology to interspecific interactions and community dynamics. Annals of the New York Academy of Sciences 1297:73–82.

Harley, C. D. G., A. Randall Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9:228–241.

Harley, C. D., and B. S. Helmuth. 2003. Local-and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. Limnology and Oceanography 48:1498–1508.

Harris, K. E., M. D. DeGrandpre, and B. Hales. 2013. Aragonite saturation state dynamics in a coastal upwelling zone. Geophysical Research Letters 40:2720–2725.

Hauri, C., N. Gruber, G.-K. Plattner, S. Alin, R. Feely, B. Hales, and P. Wheeler. 2009. Ocean Acidification in the California Current System. Oceanography 22:60–71.

Hauri, C., N. Gruber, M. Vogt, S. C. Doney, R. A. Feely, Z. Lachkar, A. Leinweber, A. M. McDonnell, M. Munnich, and G.-K. Plattner. 2013. Spatiotemporal variability and long-term trends of ocean acidification in the California Current System. Biogeosciences 10:193–216.

Hayford, H. A., S. E. Gilman, and E. Carrington. 2015. Foraging behavior minimizes heat exposure in a complex thermal landscape. Marine Ecology Progress Series 518:165–175.

Helmuth, B. 2002. How do we Measure the Environment? Linking Intertidal Thermal Physiology and Ecology Through Biophysics. Integrative and Comparative Biology 42:837–845.

Helmuth, B., B. R. Broitman, L. Yamane, S. E. Gilman, K. Mach, K. a. S. Mislan, and M. W. Denny. 2010. Organismal climatology: analyzing environmental variability at scales relevant to physiological stress. Journal of Experimental Biology 213:995–1003.

Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O’Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate Change and Latitudinal Patterns of Intertidal Thermal Stress. Science 298:1015–1017.

Helmuth, B. S. T. 1998. Intertidal Mussel Microclimates: Predicting the Body Temperature of a Sessile Invertebrate. Ecological Monographs 68:51–74.

Hewson, I., J. B. Button, B. M. Gudenkauf, B. Miner, A. L. Newton, J. K. Gaydos, J. Wynne, C. L. Groves, G. Hendler, M. Murray, S. Fradkin, M. Breitbart, E. Fahsbender, K. D. Lafferty, A. M. Kilpatrick, C. M. Miner, P. Raimondi, L. Lahner, C. S. Friedman, S. Daniels, M. Haulena, J. Marliave, C. A. Burge, M. E. Eisenlord, and C. D. Harvell. 2014. Densovirus associated with sea-star wasting disease and mass mortality. Proceedings of the National Academy of Sciences 111(48):17278–17283.

Hofmann, G. E., J. P. Barry, P. J. Edmunds, R. D. Gates, D. A. Hutchins, T. Klinger, and M. A. Sewell. 2010. The Effect of Ocean Acidification on Calcifying Organisms in Marine Ecosystems: An Organism-to-Ecosystem Perspective. Annual Review of Ecology, Evolution, and Systematics 41:127–147.

Hofmann, G. E., T. G. Evans, M. W. Kelly, J. L. Padilla-Gamiño, C. A. Blanchette, L. Washburn, F. Chan, M. A. McManus, B. A. Menge, B. Gaylord, and others. 2013. Exploring local adaptation and the ocean acidification seascape—studies in the California Current Large Marine Ecosystem. Biogeosci. Discuss 10:11825–11856.

Holling, C. S. 1959. Some Characteristics of Simple Types of Predation and Parasitism. The Canadian Entomologist 91:385–398.

Hönisch, B., A. Ridgwell, D. N. Schmidt, E. Thomas, S. J. Gibbs, A. Sluijs, R. Zeebe, L. Kump, R. C. Martindale, S. E. Greene, W. Kiessling, J. Ries, J. C. Zachos, D. L. Royer, S. Barker, T. M. Marchitto, R. Moyer, C. Pelejero, P. Ziveri, G. L. Foster, and B. Williams. 2012. The Geological Record of Ocean Acidification. Science 335:1058–1063.

Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S. Scheibe. 2013. multcomp: Simultaneous inference in general parametric models. Version 1.3-0.

Iles, A. C. 2014. Toward predicting community-level effects of climate: relative temperature scaling of metabolic and ingestion rates. Ecology 95:2657–2668.

Iles, A. C., T. C. Gouhier, B. A. Menge, J. S. Stewart, A. J. Haupt, and M. C. Lynch. 2012. Climate-driven trends and ecological implications of event-scale upwelling in the California Current System. Global Change Biology 18:783–796.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Page (R.K. Pachauri, L.A. Meyer, and Core Writing Team, Eds.). IPCC, Geneva, Switzerland.

Jellison, B. M., A. T. Ninokawa, T. M. Hill, E. Sanford, and B. Gaylord. 2016. Ocean acidification alters the response of intertidal snails to a key sea star predator. Proc. R. Soc. B 283:20160890.

Jones, S. J., F. P. Lima, and D. S. Wethey. 2010. Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, Mytilus edulis L., in the western Atlantic. Journal of Biogeography 37:2243–2259.

Jones, S. J., N. Mieszkowska, and D. S. Wethey. 2009. Linking thermal tolerances and biogeography: Mytilus edulis (L.) at its southern limit on the east coast of the United States. The Biological Bulletin 217:73–85.

Karp, D. S., and G. C. Daily. 2013. Cascading effects of insectivorous birds and bats in tropical coffee plantations. Ecology 95:1065–1074.

Keppel, E. A., R. A. Scrosati, and S. C. Courtenay. 2015. Interactive effects of ocean acidification and warming on subtidal mussels and sea stars from Atlantic Canada. Marine Biology Research 11:337–348.

Killen, S. S., S. Marras, N. B. Metcalfe, D. J. McKenzie, and P. Domenici. 2013. Environmental stressors alter relationships between physiology and behaviour. Trends in Ecology & Evolution 28:651–658.

Kishi, D., M. Murakami, S. Nakano, and K. Maekawa. 2005. Water temperature determines strength of top-down control in a stream food web. Freshwater Biology 50:1315–1322.

Kohl, W. T., T. I. McClure, and B. G. Miner. 2016. Decreased Temperature Facilitates Short-Term Sea Star Wasting Disease Survival in the Keystone Intertidal Sea Star Pisaster ochraceus. PLOS ONE 11:e0153670.

Kolesar, S. E. 2006. The effects of low dissolved oxygen on predation interactions between Mnemiopsis leidyi ctenophores and larval fish in the Chesapeake Bay ecosystem. Dissertation, University of Maryland, Baltimore, Maryland, USA.

Krenz, C., B. A. Menge, T. L. Freidenburg, J. Lubchenco, F. Chan, M. M. Foley, and K. J. Nielsen. 2011. Ecological subsidies to rocky intertidal communities: Linear or non-linear changes along a consistent geographic upwelling transition? Journal of Experimental Marine Biology and Ecology 409:361–370.

Kroeker, K. J., B. Gaylord, T. M. Hill, J. D. Hosfelt, S. H. Miller, and E. Sanford. 2014a. The Role of Temperature in Determining Species’ Vulnerability to Ocean Acidification: A Case Study Using Mytilus galloprovincialis. PLoS ONE 9:e100353.

Kroeker, K. J., R. L. Kordas, R. Crim, I. E. Hendriks, L. Ramajo, G. S. Singh, C. M. Duarte, and J.-P. Gattuso. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Global Change Biology 19:1884–1896.

Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology letters 13:1419–1434.

Kroeker, K. J., F. Micheli, and M. C. Gambi. 2012. Ocean acidification causes ecosystem shifts via altered competitive interactions. Nature Climate Change 3:156–159.

Kroeker, K. J., F. Micheli, M. C. Gambi, and T. R. Martz. 2011. Divergent ecosystem responses within a benthic marine community to ocean acidification. Proceedings of the National Academy of Sciences 108:14515–14520.

Kroeker, K. J., E. Sanford, B. M. Jellison, and B. Gaylord. 2014b. Predicting the Effects of Ocean Acidification on Predator-Prey Interactions: A Conceptual Framework Based on Coastal Molluscs. The Biological Bulletin 226:211–222.

Kroeker, K. J., E. Sanford, J. M. Rose, C. A. Blanchette, F. Chan, F. P. Chavez, B. Gaylord, B. Helmuth, T. M. Hill, G. E. Hofmann, M. A. McManus, B. A. Menge, K. J. Nielsen, P. T. Raimondi, A. D. Russell, and L. Washburn. 2016. Interacting environmental mosaics drive geographic variation in mussel performance and predation vulnerability. Ecology Letters 19:771–779.

Kuo, E. S. L., and E. Sanford. 2009. Geographic variation in the upper thermal limits of an intertidal snail: implications for climate envelope models. Marine Ecology Progress Series 388:137–146.

Landes, A., and M. Zimmer. 2012. FEATURE ARTICLE Acidification and warming affect both a calcifying predator and prey, but not their interaction. Marine Ecology Progress Series 450:1–10.

Laska, M. S., and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79:461–476.

Lawson, C. R., Y. Vindenes, L. Bailey, and M. van de Pol. 2015. Environmental variation and population responses to global change. Ecology Letters 18:724–736.

Lawton, J. H. 1999. Are There General Laws in Ecology? Oikos 84:177–192.

Louda, S. M., and S. K. Collinge. 1992. Plant Resistance to Insect Herbivores: A Field Test of the Environmental Stress Hypothesis. Ecology 73:153–169.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist:23–39.

Lueker, T. J., A. G. Dickson, and C. D. Keeling. 2000. Ocean pCO2 calculated from dissolved inorganic carbon, alkalinity, and equations for K1 and K2: validation based on laboratory measurements of CO2 in gas and seawater at equilibrium. Marine Chemistry 70:105–119.

Mac Nally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. Biodiversity and Conservation 11:1397–1401.

Mackey, K. R., J. J. Morris, F. M. Morel, and S. A. Kranz. 2015. Response of photosynthesis to ocean acidification. Oceanography 28(2):74-91.

Manriquez, P. H., M. E. Jara, M. L. Mardones, R. Torres, J. M. Navarro, M. A. Lardies, C. A. Vargas, C. Duarte, and N. A. Lagos. 2014. Ocean acidification affects predator avoidance behaviour but not prey detection in the early ontogeny of a keystone species. Marine Ecology Progress Series 502:157–167.

Mazerolle, M. J. 2015. AICcmodavg: model selection and multimodel inference based on (Q) AIC (C). R package Version 2.0-3.

McCann, K. S. 2000. The diversity–stability debate. Nature 405:228–233.

McCann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. Ecology Letters 8:513–523.

McCormick, M. I., S.-A. Watson, and P. L. Munday. 2013. Ocean acidification reverses competition for space as habitats degrade. Scientific Reports 3.

McCoy, S. J., S. Allesina, and C. A. Pfister. 2016. Ocean acidification affects competition for space: projections of community structure using cellular automata. Proc. R. Soc. B 283:20152561.

McQuaid, C. D., and G. M. Branch. 1985. Trophic structure of rocky intertidal communities: Response to wave action and implications for energy flow. Marine ecology progress series. Oldendorf 22:153–161.

Melzner, F., P. Stange, K. Trübenbach, J. Thomsen, I. Casties, U. Panknin, S. N. Gorb, and M. A. Gutowska. 2011. Food Supply and Seawater pCO2 Impact Calcification and Internal Shell Dissolution in the Blue Mussel Mytilus edulis. PLoS ONE 6:e24223.

Menge, B. A. 1978. Predation Intensity in a Rocky Intertidal Community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. Oecologia:17–35.

Menge, B. A. 1992. Community Regulation: Under What Conditions Are Bottom-Up Factors Important on Rocky Shores? Ecology 73:755–765.

Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:257–289.

Menge, B. A. 2003. The Overriding Importance of Environmental Context in Determining the Outcome of Species-deletion Experiments. The Importance of Species: Perspectives on Expendability and Triage:16-43.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The Keystone Species Concept: Variation in Interaction Strength in a Rocky Intertidal Habitat. Ecological Monographs 64:249.

Menge, B. A., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. Ecological Monographs 74:663–684.

Menge, B. A., and G. M. Branch. 2001. Rocky intertidal communities. Marine community ecology:221–251.

Menge, B. A., E. B. Cerny-Chipman, A. Johnson, J. Sullivan, S. Gravem, and F. Chan. 2016. Sea Star Wasting Disease in the Keystone Predator Pisaster ochraceus in Oregon: Insights into Differential Population Impacts, Recovery, Predation Rate, and Temperature Effects from Long-Term Research. PLOS ONE 11:e0153994.

Menge, B. A., F. Chan, and J. Lubchenco. 2008. Response of a rocky intertidal ecosystem engineer and community dominant to climate change. Ecology Letters 11:151–162.

Menge, B. A., F. Chan, K. J. Nielsen, E. D. Lorenzo, and J. Lubchenco. 2009. Climatic variation alters supply-side ecology: impact of climate patterns on phytoplankton and mussel recruitment. Ecological Monographs 79:379–395.

Menge, B. A., B. A. Daley, and P. A. Wheeler. 1996. Control of interaction strength in marine benthic communities. pp. 258-274 in: Food Webs: Integration of Pattern and Dynamics, G. A. Polis and K. O. Winemiller, eds., Chapman and Hall, New York. Pages 258–274 *in* G. A. Polis and Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997a. Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences 94:14530–14535.

Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub. 1997b. Rocky Intertidal Oceanography: An Association Between Community Structure and Nearshore Phytoplankton Concentration. Limnology and Oceanography 42:57–66.

Menge, B. A., and T. M. Farrell. 1989. Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. Advances in Ecological Research 19:189–262.

Menge, B. A., T. C. Gouhier, T. Freidenburg, and J. Lubchenco. 2011a. Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: Toward explaining “unexplained” variation. Journal of Experimental Marine Biology and Ecology 400:236–249.

Menge, B. A., T. C. Gouhier, S. D. Hacker, F. Chan, and K. J. Nielsen. 2015. Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. Ecological Monographs 85:213–233.

Menge, B. A., S. D. Hacker, T. Freidenburg, J. Lubchenco, R. Craig, G. Rilov, M. Noble, and E. Richmond. 2011b. Potential impact of climate-related changes is buffered by differential responses to recruitment and interactions. Ecological Monographs 81:493–509.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences 100:12229–12234.

Menge, B. A., and D. N. L. Menge. 2013. Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. Ecological Monographs 83:283–310.

Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology & Evolution 5:52–57.

Menge, B. A., A. M. Olson, and E. P. Dahlhoff. 2002a. Environmental Stress, Bottom-up Effects, and Community Dynamics: Integrating Molecular-Physiological and Ecological Approaches. Integrative and Comparative Biology 42:892–908.

Menge, B. A., and E. Sanford. 2013. Ecological Role of Sea Stars from Populations to Meta-Ecosystems. Page 67Starfish: biology and ecology of the Asteroidea. Johns Hopkins Publisher, Oxford, UK.

Menge, B. A., E. Sanford, B. A. Daley, T. L. Freidenburg, G. Hudson, and J. Lubchenco. 2002b. Inter-hemispheric comparison of bottom-up effects on community structure: Insights revealed using the comparative-experimental approach. Ecological Research 17:1–16.

Menge, B. A., and J. P. Sutherland. 1976. Species Diversity Gradients: Synthesis of the Roles of Predation, Competition, and Temporal Heterogeneity. The American Naturalist 110:351–369.

Menge, B. A., and J. P. Sutherland. 1987. Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. The American Naturalist 130:730–757.

Miller, L. P. 2013. The effect of water temperature on drilling and ingestion rates of the dogwhelk Nucella lapillus feeding on Mytilus edulis mussels in the laboratory. Marine Biology 160:1489–1496.

Miller, L. P., and B. Gaylord. 2007. Barriers to flow: The effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. Journal of Experimental Marine Biology and Ecology 344:215–228.

Miller, L. P., C. M. Matassa, and G. C. Trussell. 2014. Climate change enhances the negative effects of predation risk on an intermediate consumer. Global Change Biology 20:3834–3844.

Moore, M. K., and V. R. Townsend. 1998. The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. Oikos 81:329–336.

Moran, A. L., and R. B. Emlet. 2001. Offspring Size and Performance in Variable Environments: Field Studies on a Marine Snail. Ecology 82:1597–1612.

Mote, P. W., D. Gavin, and A. Huyer. 2010. Climate change in Oregon's land and marine environments. Oregon Climate Assessment Report. Oregon Climate Change Research Institute. College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis:1–45.

Navarrete, S. A. 1996. Variable Predation: Effects of Whelks on a Mid-Intertidal Successional Community. Ecological Monographs 66:301.

Navarrete, S. A., and E. L. Berlow. 2006. Variable interaction strengths stabilize marine community pattern. Ecology Letters 9:526–536.

Navarrete, S. A., and B. A. Menge. 1996. Keystone Predation and Interaction Strength: Interactive Effects of Predators on Their Main Prey. Ecological Monographs 66:409.

Navarrete, S. A., B. A. Menge, and B. A. Daley. 2000. Species interactions in intertidal food webs: prey or predation regulation of intermediate predators? Ecology 81:2264–2277.

Nienhuis, S., A. R. Palmer, and C. D. G. Harley. 2010. Elevated CO2 affects shell dissolution rate but not calcification rate in a marine snail. Proceedings of the Royal Society B: Biological Sciences 277:2553–2558.

Noto, A. E., and J. B. Shurin. 2015. Population variation affects interactions between two California salt marsh plant species more than precipitation. Oecologia 180:499–506.

Novak, M. 2010. Estimating interaction strengths in nature: experimental support for an observational approach. Ecology 91:2394–2405.

Novak, M., J. T. Wootton, D. F. Doak, M. Emmerson, J. A. Estes, and M. T. Tinker. 2011. Predicting community responses to perturbations in the face of imperfect knowledge and network complexity. Ecology 92:836–846.

O'Donnell, M. J., L. M. Hammond, and G. E. Hofmann. 2008. Predicted impact of ocean acidification on a marine invertebrate: elevated CO2. Marine Biology 156:439–446.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation Ecosystems in Gradients of Primary Productivity. The American Naturalist 118:240–261.

Olea, P. P., P. Mateo-Tomás, and Á. de Frutos. 2010. Estimating and Modelling Bias of the Hierarchical Partitioning Public-Domain Software: Implications in Environmental Management and Conservation. PLoS ONE 5:e11698.

Orr, J. C., V. J. Fabry, O. Aumont, L. Bopp, S. C. Doney, R. A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, R. M. Key, K. Lindsay, E. Maier-Reimer, R. Matear, P. Monfray, A. Mouchet, R. G. Najjar, G.-K. Plattner, K. B. Rodgers, C. L. Sabine, J. L. Sarmiento, R. Schlitzer, R. D. Slater, I. J. Totterdell, M.-F. Weirig, Y. Yamanaka, and A. Yool. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437:681–686.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist:65–75.

Paine, R. T. 1969. A Note on Trophic Complexity and Community Stability. The American Naturalist 103:91–93.

Paine, R. T. 1974. Intertidal community structure. Oecologia 15:93–120.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. , Published online: 02 January 1992; | doi:10.1038/355073a0 355:73–75.

Palmer, A. R. 1983. Growth rate as a measure of food value in thaidid gastropods: Assumptions and implications for prey morphology and distribution. Journal of Experimental Marine Biology and Ecology 73:95–124.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. Science 279:860–863.

Perez, F. F., and F. Fraga. 1987. A precise and rapid analytical procedure for alkalinity determination. Marine Chemistry 21:169–182.

Pershing, A. J., M. A. Alexander, C. M. Hernandez, L. A. Kerr, A. L. Bris, K. E. Mills, J. A. Nye, N. R. Record, H. A. Scannell, J. D. Scott, G. D. Sherwood, and A. C. Thomas. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350:809–812.

Petersen, J. H. 1984. Larval settlement behavior in competing species: Mytilus californianus Conrad and M. edulis L. Journal of Experimental Marine Biology and Ecology 82:147–159.

Petes, L. E., B. A. Menge, and G. D. Murphy. 2007. Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. Journal of Experimental Marine Biology and Ecology 351:83–91.

Petes, L. E., M. E. Mouchka, R. H. Milston-Clements, T. S. Momoda, and B. A. Menge. 2008. Effects of environmental stress on intertidal mussels and their sea star predators. Oecologia 156:671–680.

Pfister, C. A., K. Roy, J. T. Wootton, S. J. McCoy, R. T. Paine, T. H. Suchanek, and E. Sanford. 2016. Historical baselines and the future of shell calcification for a foundation species in a changing ocean. Proc. R. Soc. B 283:20160392.

Pincebourde, S., E. Sanford, and B. Helmuth. 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. Limnology and Oceanography 53:1562–1573.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2014. R Core Team. nlme: linear and nonlinear mixed effects models. R Package Version 3.1-117.

Pohlert, T. 2014. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR).

Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? Trends in Ecology & Evolution 15:473–475.

Pörtner, H. O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: a physiologist’s view. Effects of ocean acidification on marine ecosystems 373:203–217.

Power, M. E., M. S. Parker, and J. T. Wootton. 1996a. Disturbance and food chain length in rivers. Pages 286–297Food Webs. Springer.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996b. Challenges in the quest for keystones. BioScience 46:609–620.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. BioScience 59:779–791.

Queirós, A. M., J. A. Fernandes, S. Faulwetter, J. Nunes, S. P. S. Rastrick, N. Mieszkowska, Y. Artioli, A. Yool, P. Calosi, C. Arvanitidis, H. S. Findlay, M. Barange, W. W. L. Cheung, and S. Widdicombe. 2015. Scaling up experimental ocean acidification and warming research: from individuals to the ecosystem. Global Change Biology 21:130–143.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013. ISBN 3-900051-07-0.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmüller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. Phil. Trans. R. Soc. B 367:2923–2934.

Rall, B. C., O. Vucic-pestic, R. B. Ehnes, M. Emmerson, and U. Brose. 2010. Temperature, predator–prey interaction strength and population stability. Global Change Biology 16:2145–2157.

Riebesell, U., and J.-P. Gattuso. 2015. Lessons learned from ocean acidification research. Nature Climate Change 5:12–14.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park’s northern range. Biological Conservation 102:227–234.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Robles, C., and J. Robb. 1993. Varied carnivore effects and the prevalence of intertidal algal turfs. Journal of Experimental Marine Biology and Ecology 166:65–91.

Robles, C., R. Sherwood-Stephens, and M. Alvarado. 1995. Responses of a Key Intertidal Predator to Varying Recruitment of Its Prey. Ecology 76:565–579.

Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442:265–269.

RStudio Team. 2014. RStudio: integrated development for R. RStudio, Inc., Boston, MA.

Ruesink, J. L. 2000. Intertidal mesograzers in field microcosms: linking laboratory feeding rates to community dynamics. Journal of Experimental Marine Biology and Ecology 248:163–176.

Ruggiero, P., P. D. Komar, and J. C. Allan. 2010a. Increasing wave heights and extreme value projections: The wave climate of the US Pacific Northwest. Coastal Engineering 57:539–552.

Ruggiero, P., P. D. Komar, and J. C. Allan. 2010b. Increasing wave heights and extreme value projections: The wave climate of the US Pacific Northwest. Coastal Engineering 57:539–552.

Ruiter, P. C. de, A.-M. Neutel, and J. C. Moore. 1995. Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems. Science 269:1257–1260.

Sabine, C. L., R. A. Feely, N. Gruber, R. M. Key, K. Lee, J. L. Bullister, R. Wanninkhof, C. Wong, D. W. R. Wallace, B. Tilbrook, and others. 2004. The oceanic sink for anthropogenic CO2. Science 305:367.

Sanders, D., L. Sutter, and F. J. F. van Veen. 2013. The loss of indirect interactions leads to cascading extinctions of carnivores. Ecology Letters 16:664–669.

Sanford, E. 1999. Regulation of Keystone Predation by Small Changes in Ocean Temperature. Science 283:2095–2097.

Sanford, E. 2002a. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. Integrative and Comparative Biology 42:881.

Sanford, E. 2002b. The feeding, growth, and energetics of two rocky intertidal predators (Pisaster ochraceus and Nucella canaliculata) under water temperatures simulating episodic upwelling. Journal of Experimental Marine Biology and Ecology 273:199–218.

Sanford, E., B. Gaylord, A. Hettinger, E. A. Lenz, K. Meyer, and T. M. Hill. 2014. Ocean acidification increases the vulnerability of native oysters to predation by invasive snails. Proceedings of the Royal Society B: Biological Sciences 281:20132681.

Sanford, E., M. S. Roth, G. C. Johns, J. P. Wares, and G. N. Somero. 2003. Local Selection and Latitudinal Variation in a Marine Predator-Prey Interaction. Science 300:1135–1137.

Sanford, E., and D. J. Worth. 2009. Genetic differences among populations of a marine snail drive geographic variation in predation. Ecology 90:3108–3118.

Sanford, E., and D. J. Worth. 2010. Local adaptation along a continuous coastline: prey recruitment drives differentiation in a predatory snail. Ecology 91:891–901.

Schneider, K. R. 2008. Heat Stress in the Intertidal: Comparing Survival and Growth of an Invasive and Native Mussel Under a Variety of Thermal Conditions. The Biological Bulletin 215:253–264.

Seifert, L. I., F. de Castro, A. Marquart, U. Gaedke, G. Weithoff, and M. Vos. 2014. Heated Relations: Temperature-Mediated Shifts in Consumption across Trophic Levels. PLoS ONE 9:e95046.

Sekhon, J. S. 2011. Multivariate and propensity score matching software with automated balance optimization: the matching package for R. Journal of Statistical Software 42:1–52.

Sergio, F., I. Newton, L. Marchesi, and P. Pedrini. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. Journal of Applied Ecology 43:1049–1055.

Shurin, J. B., and E. W. Seabloom. 2005. The strength of trophic cascades across ecosystems: predictions from allometry and energetics. Journal of Animal Ecology 74:1029–1038.

Simberloff, D. 2004. Community Ecology: Is It Time to Move On? (An American Society of Naturalists Presidential Address). The American Naturalist 163:787–799.

Somero, G. N. 2002. Thermal Physiology and Vertical Zonation of Intertidal Animals: Optima, Limits, and Costs of Living. Integrative and Comparative Biology 42:780–789.

Somero, G. N. 2010. The Physiology of Climate Change: How Potentials for Acclimatization and Genetic Adaptation Will Determine “winners” and “losers.” Journal of Experimental Biology 213:912–920.

Somero, G. N. 2012. The physiology of global change: linking patterns to mechanisms. Annual Review of Marine Science 4:39–61.

Somero, G. N., J. M. Beers, F. Chan, T. M. Hill, T. Klinger, and S. Y. Litvin. 2016. What Changes in the Carbonate System, Oxygen, and Temperature Portend for the Northeastern Pacific Ocean: A Physiological Perspective. BioScience 66:14–26
.

Sorte, C. J., and G. E. Hofmann. 2004. Changes in latitudes, changes in aptitudes: Nucella canaliculata (Mollusca: Gastropoda) is more stressed at its range edge. Marine Ecology Progress Series 274:263–268.

Sorte, C. J. B., V. E. Davidson, M. C. Franklin, K. M. Benes, M. M. Doellman, R. J. Etter, R. E. Hannigan, J. Lubchenco, and B. A. Menge. 2016. Long-term declines in an intertidal foundation species parallel shifts in community composition. Global Change Biology:n/a-n/a.

Sorte, C. J. B., and G. E. Hofmann. 2005. Thermotolerance and heat-shock protein expression in Northeastern Pacific Nucella species with different biogeographical ranges. Marine Biology 146:985–993.

Sorte, C. J. B., S. J. Jones, and L. P. Miller. 2011. Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. Journal of Experimental Marine Biology and Ecology 400:209–217.

Strong, D. R., and K. T. Frank. 2010. Human Involvement in Food Webs. Annual Review of Environment and Resources 35:1–23.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

Thomsen, J., I. Casties, C. Pansch, A. Körtzinger, and F. Melzner. 2013. Food availability outweighs ocean acidification effects in juvenile Mytilus edulis: laboratory and field experiments. Global Change Biology 19:1017–1027.

Thomsen, J., and F. Melzner. 2010. Moderate seawater acidification does not elicit long-term metabolic depression in the blue mussel Mytilus edulis. Marine Biology 157:2667–2676.

Tomanek, L., and M. J. Zuzow. 2010. The proteomic response of the mussel congeners Mytilus galloprovincialis and M. trossulus to acute heat stress: implications for thermal tolerance limits and metabolic costs of thermal stress. Journal of Experimental Biology 213:3559–3574.

Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2003. Trait-Mediated Effects in Rocky Intertidal Food Chains: Predator Risk Cues Alter Prey Feeding Rates. Ecology 84:629–640.

Urban, M. C., P. L. Zarnetske, and D. K. Skelly. 2013. Moving forward: dispersal and species interactions determine biotic responses to climate change. Annals of the New York Academy of Sciences 1297:44–60.

Vance-Chalcraft, H. D., J. A. Rosenheim, J. R. Vonesh, C. W. Osenberg, and A. Sih. 2007. The influence of intraguild predation on prey suppression and prey release: a meta-analysis. Ecology 88:2689–2696.

Vaquer-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences 105:15452–15457.

Vasseur, D. A., J. P. DeLong, B. Gilbert, H. S. Greig, C. D. G. Harley, K. S. McCann, V. Savage, T. D. Tunney, and M. I. O'Connor. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proceedings of the Royal Society B: Biological Sciences 281:20132612.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S 4 edition Springer. New York.

Vermeij, G. J. 1978. Biogeography and Adaptation: Patterns of Marine Life. Harvard University Press.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human Domination of Earth's Ecosystems. Science 277:494–499.

Vucic-Pestic, O., R. B. Ehnes, B. C. Rall, and U. Brose. 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biology 17:1301–1310.

Waldbusser, G. G., H. Bergschneider, and M. A. Green. 2010. Size-dependent pH effect on calcification in post-larval hard clam Mercenaria spp. Marine Ecology Progress Series 417:171–182.

Waldbusser, G. G., B. Hales, and B. A. Haley. 2016. Calcium carbonate saturation state: on myths and this or that stories. ICES Journal of Marine Science: Journal du Conseil 73:563–568.

Waldbusser, G. G., B. Hales, C. J. Langdon, B. A. Haley, P. Schrader, E. L. Brunner, M. W. Gray, C. A. Miller, and I. Gimenez. 2015a. Saturation-state sensitivity of marine bivalve larvae to ocean acidification. Nature Climate Change 5:273–280.

Waldbusser, G. G., B. Hales, C. J. Langdon, B. A. Haley, P. Schrader, E. L. Brunner, M. W. Gray, C. A. Miller, I. Gimenez, and G. Hutchinson. 2015b. Ocean Acidification Has Multiple Modes of Action on Bivalve Larvae. PLOS ONE 10:e0128376.

Waldbusser, G. G., and J. E. Salisbury. 2014. Ocean Acidification in the Coastal Zone from an Organism's Perspective: Multiple System Parameters, Frequency Domains, and Habitats. Annual Review of Marine Science 6:221–247.

Waldbusser, G. G., E. P. Voigt, H. Bergschneider, M. A. Green, and R. I. E. Newell. 2011. Biocalcification in the eastern oyster (Crassostrea virginica) in relation to long-term trends in Chesapeake Bay pH. Estuaries and coasts 34:221–231.

Walsh, C., R. Mac Nally, and M. C. Walsh. 2013. Package "hier. part."

Wang, D., T. C. Gouhier, B. A. Menge, and A. R. Ganguly. 2015. Intensification and spatial homogenization of coastal upwelling under climate change. Nature 518:390–394.

Watson, S.-A., S. Lefevre, M. I. McCormick, P. Domenici, G. E. Nilsson, and P. L. Munday. 2014. Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels. Proceedings of the Royal Society of London B: Biological Sciences 281:20132377.

Wells, H. W. 1958. Feeding Habits of Murex Fulvescens. Ecology 39:556–558.

West, L. 1986. Interindividual Variation in Prey Selection by the Snail Nucella (= Thais) Emarginata. Ecology 67:798–809.

West, L. 1988. Prey Selection by the Tropical Snail Thais Melones: A Study of Interindividual Variation. Ecology 69:1839–1854.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:2–80.

Wickham, H. 2011. The Split-Apply-Combine Strategy for Data Analysis. Journal of Statistical Software 40:1–29.

Wieters, E. A., and S. A. Navarrete. 1998. Spatial variability in prey preferences of the intertidal whelks Nucella canaliculata and Nucella emarginata. Journal of Experimental Marine Biology and Ecology 222:133–148.

Witman, J. D., and K. R. Grange. 1998. Links Between Rain, Salinity, and Predation in a Rocky Subtidal Community. Ecology 79:2429–2447.

Wittmann, A. C., and H.-O. Pörtner. 2013. Sensitivities of extant animal taxa to ocean acidification. Nature Climate Change 3:995–1001.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165.

Wootton, J. T. 2002. Mechanisms of successional dynamics: Consumers and the rise and fall of species dominance. Ecological Research 17:249–260.

Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of Disturbance on River Food Webs. Science 273:1558–1561.

Yamada, S. B., and E. G. Boulding. 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. Journal of Experimental Marine Biology and Ecology 204:59–83.

Yamane, L., and S. E. Gilman. 2009. Opposite responses by an intertidal predator to increasing aquatic and aerial temperatures. Marine Ecology Progress Series 393:27–36.

Yao, W., and R. H. Byrne. 1998. Simplified seawater alkalinity analysis: Use of linear array spectrometers. Deep Sea Research Part I: Oceanographic Research Papers 45:1383–1392.

Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. Biotic Multipliers of Climate Change. Science 336:1516–1518.

Zeileis, A. 2004. Econometric Computing with HC and HAC Covariance Matrix Estimators. Journal of Statistical Software 11:1–17.

Zeileis, A. 2006. Object-oriented Computation of Sandwich Estimators. Journal of Statistical Software 16:1–16.

Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression Models for Count Data in R. Journal of Statistical Software 27.

Zippay, M. L., and B. Helmuth. 2012. Effects of temperature change on mussel, Mytilus. Integrative zoology 7:312–327.

APPENDICES

Appendix A – Chapter 2 Supplementary Figures & Tables

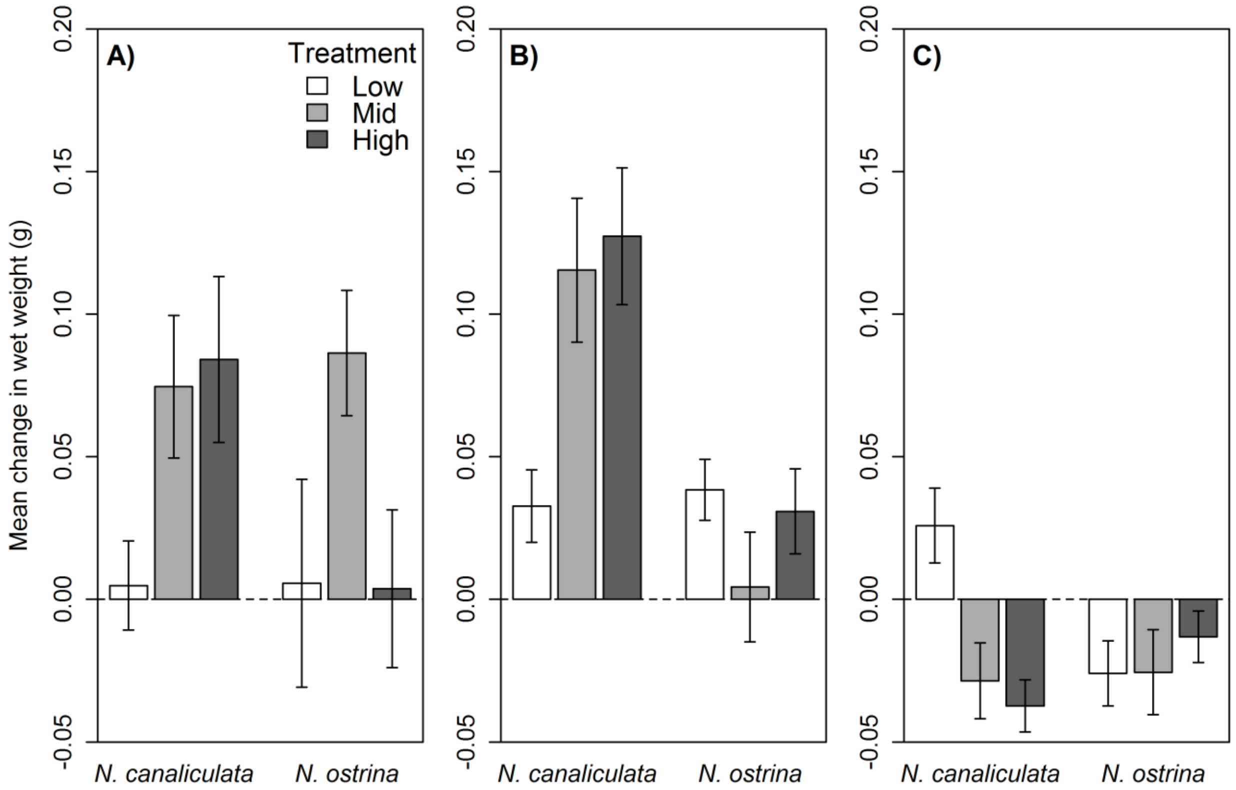

Figure A1. Mean changes in wet weights of whelks during A) experiment I and B) experiment II, by species and treatment, with C) mean wet weight change in starved whelks in experiment II for reference. Error bars are +1 SE.

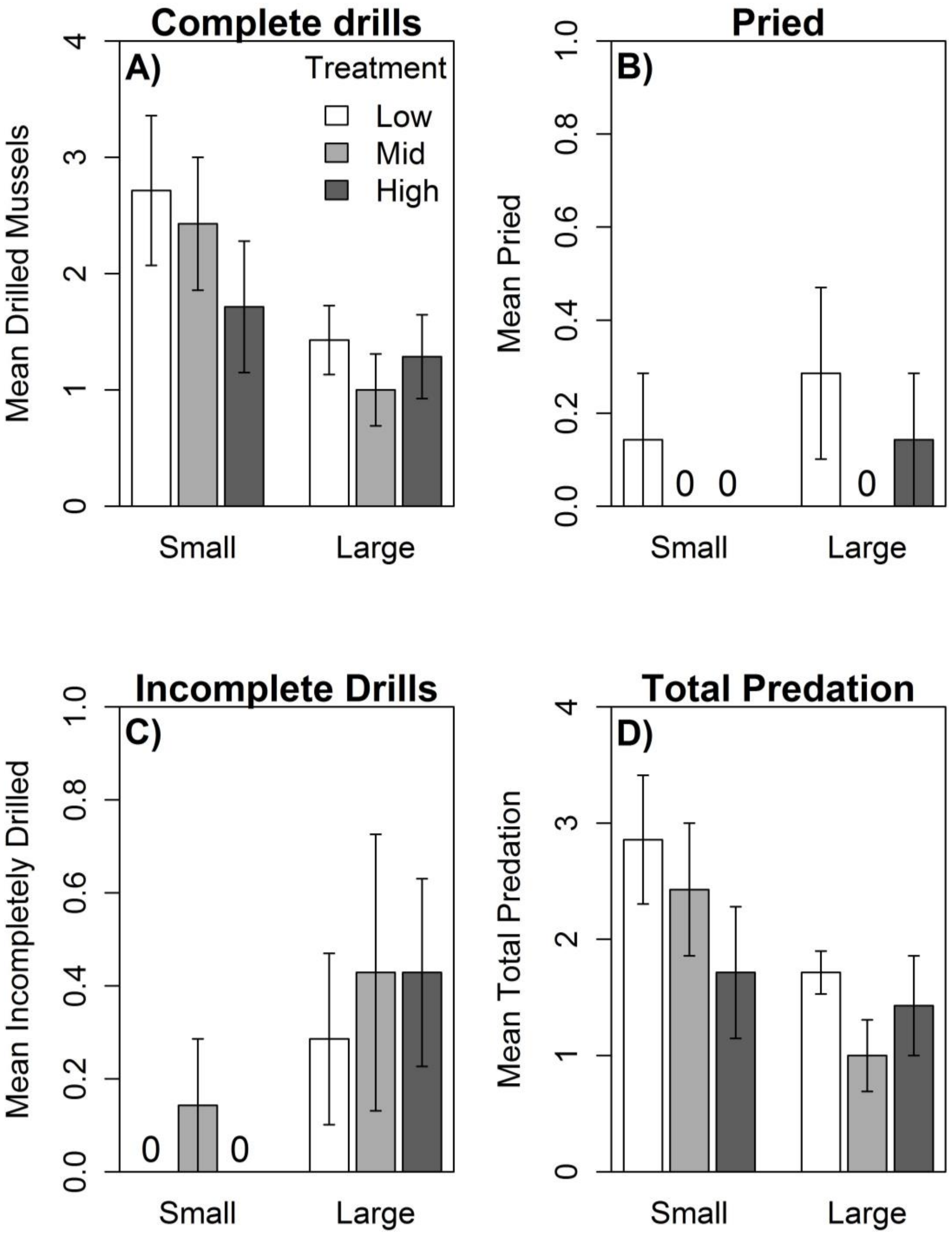

Figure A2. Predation by *N. canaliculata* by mussel size in experiment II with the mean number of A) complete drills, B) pried mussels, C) incomplete drills, and D) total predation. Numbers given are means and error bars are +1 SE.

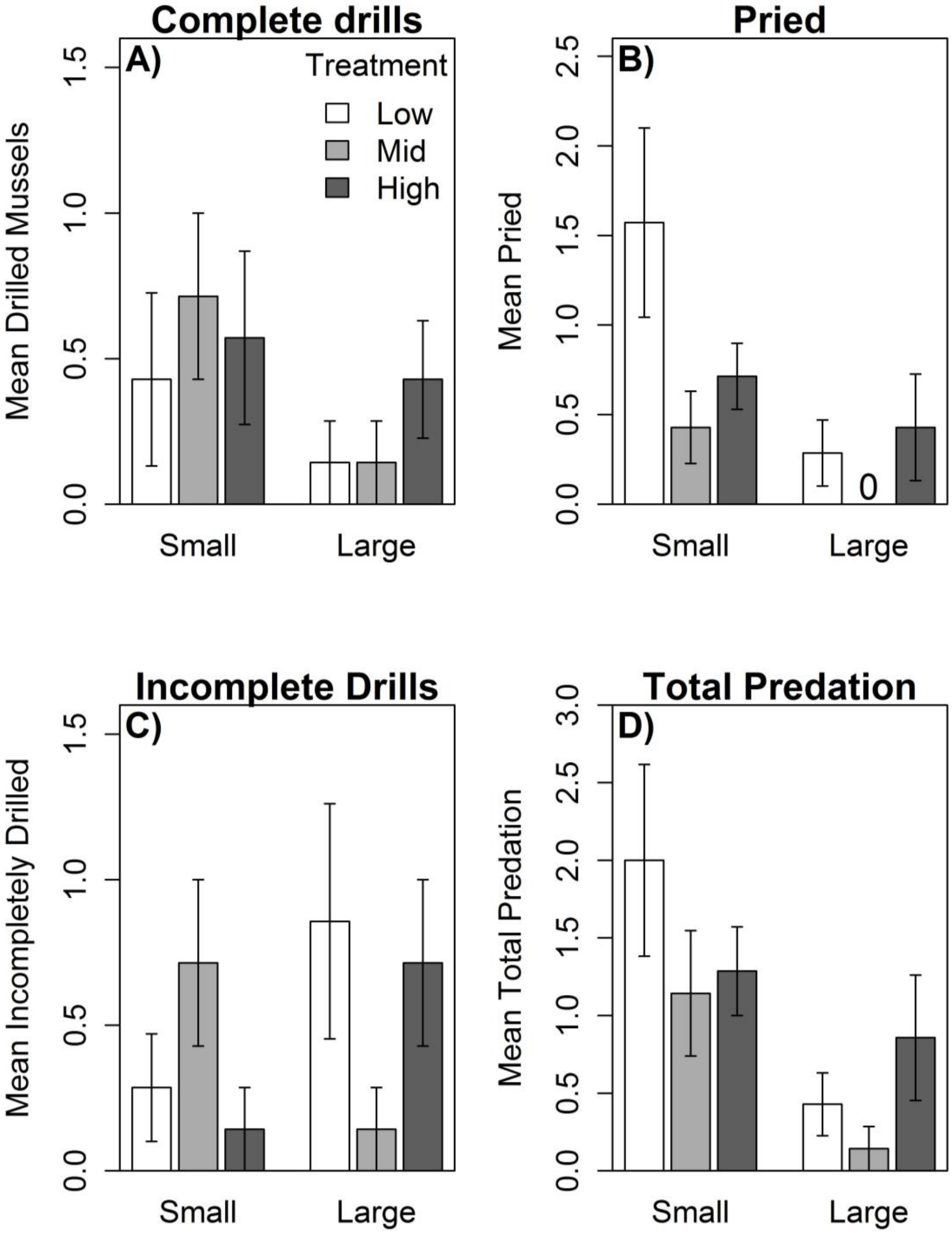

Figure A3. Predation by *N. ostrina* by mussel size in experiment II with the mean number of A) complete drills, B) pried mussels, C) incomplete drills, and D) total predation. Numbers given are means and error bars are +1 SE.

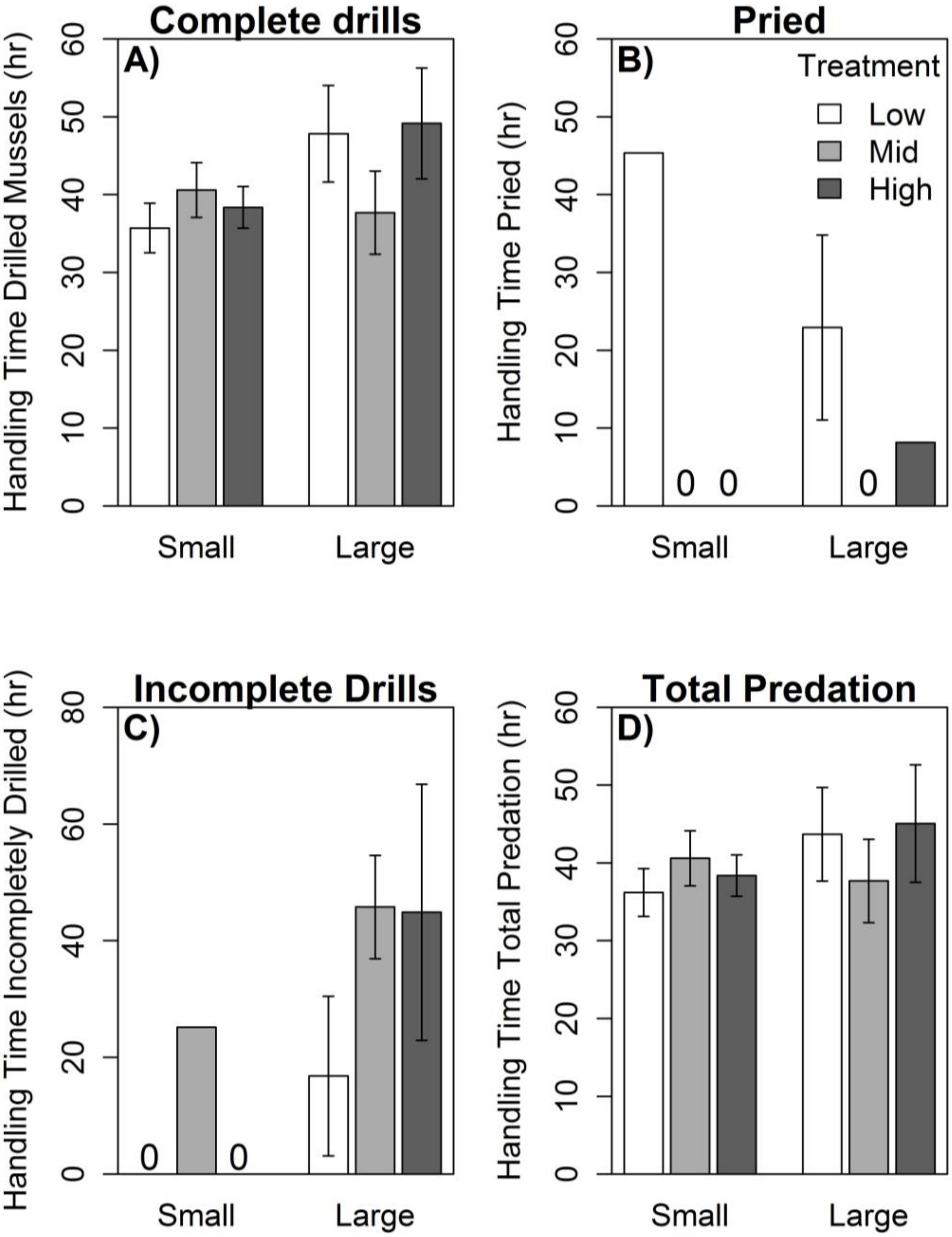

Figure A4. Mean handling time by *N. canaliculata* by mussel size in experiment II for A) complete drills, B) pried mussels, C) incomplete drills, and D) total predation. Numbers given are means and error bars are +1 SE. Means are not weighted.

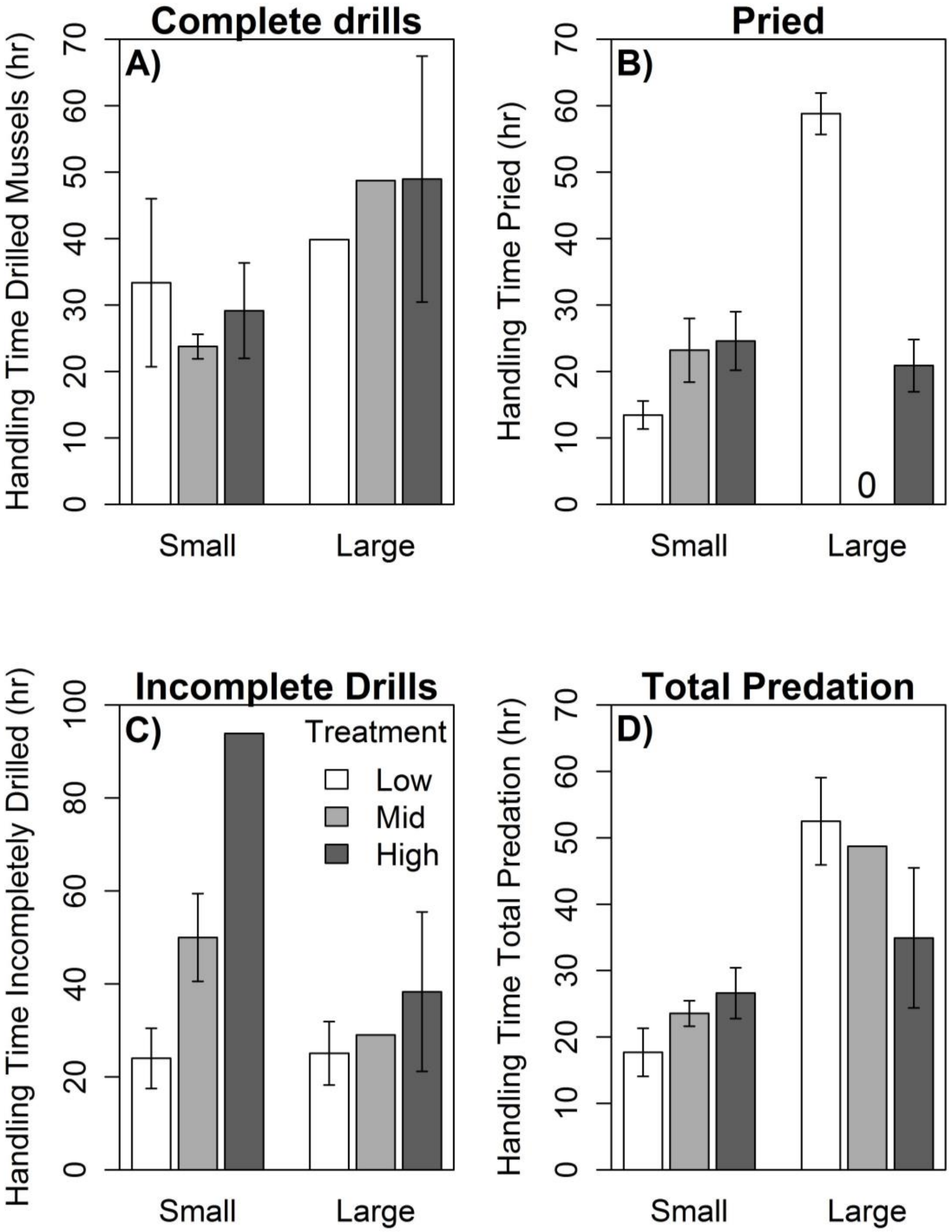

Figure A5. Mean handling time by *N. ostrina* by mussel size in experiment II for A) complete drills, B) pried mussels, C) incomplete drills, and D) total predation. Numbers given are means and error bars are +1 SE. Means are not weighted.

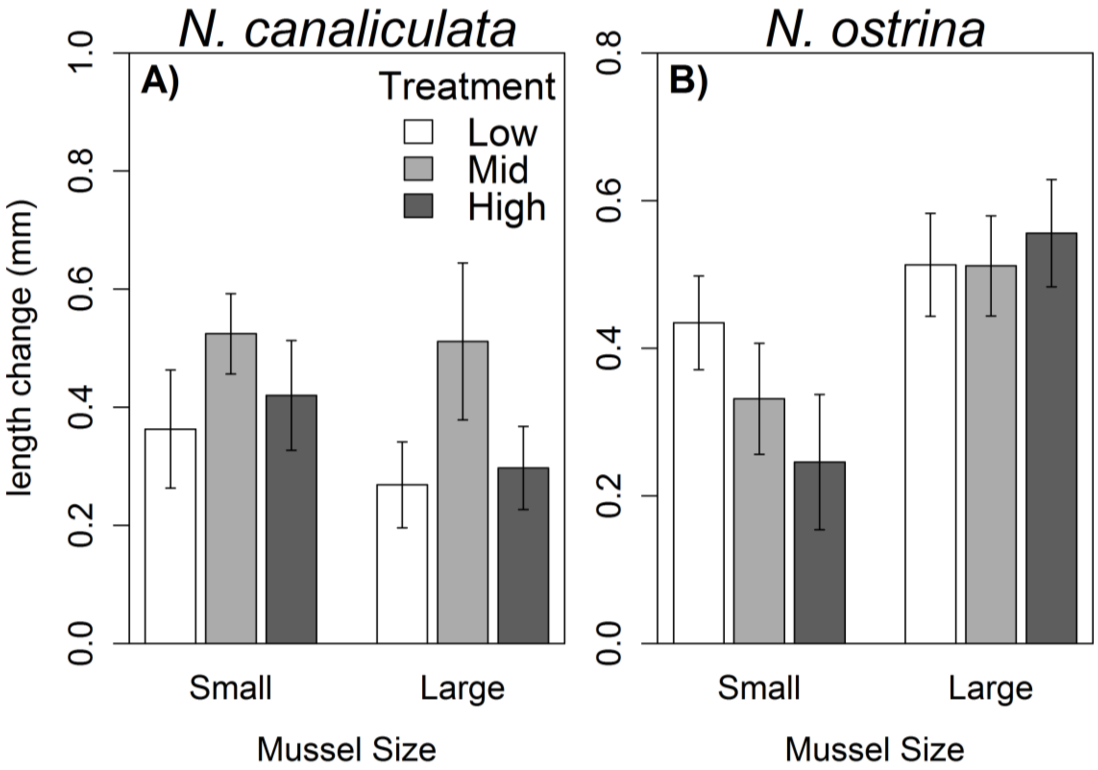

Figure A6. Mean length change in mm for A) *N. canaliculata* and B) *N. ostrina* by treatment and mussel size in experiment II. Error bars are +1 SE.

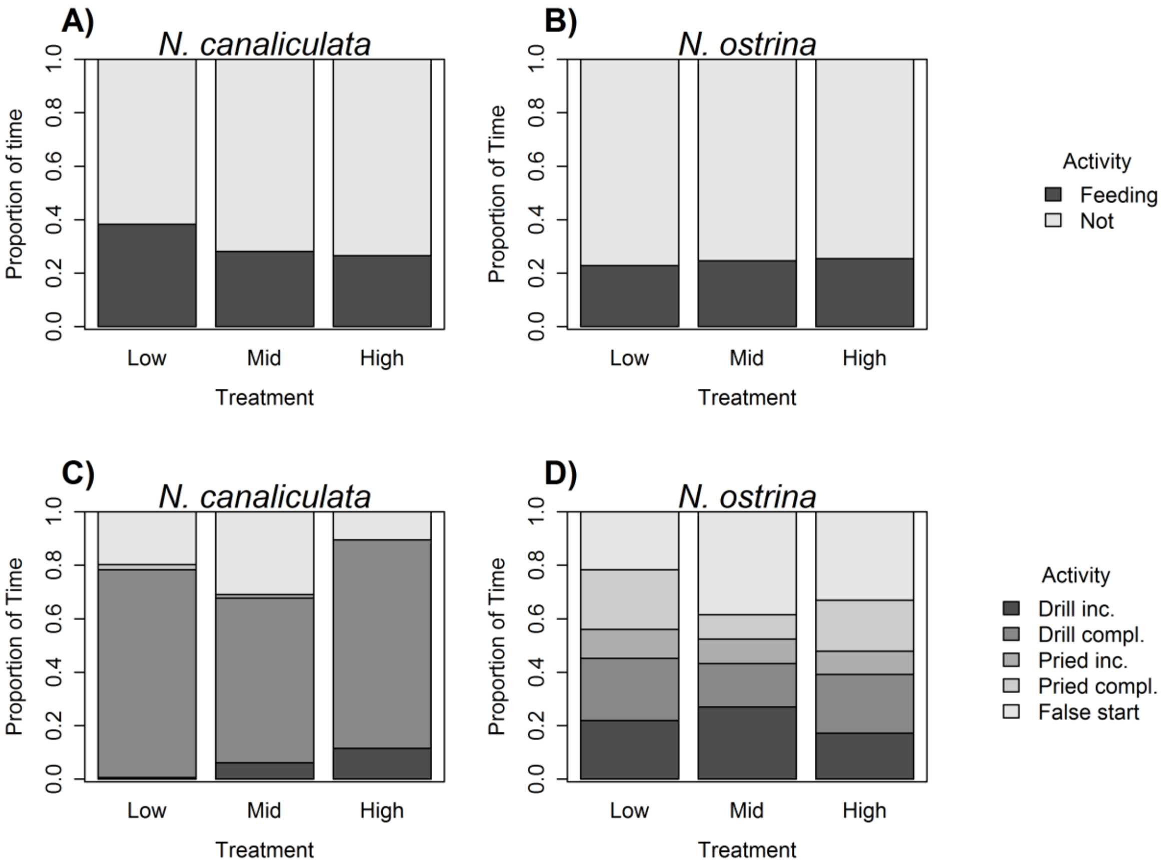

Figure A7. Proportional breakdown of whelk activity in experiment II by treatment. A) and B) show proportion of time whelks were in contact and / or feeding on a mussel (feeding) versus proportion of time spent out of contact with a mussel (not), while C) and D) show proportion of time spent on different feeding activities out of total time feeding including incomplete drilling, complete drilling, incomplete prying, complete prying, and false starts. Figure is for observations on 4/16-5/1.

Table A1. Type II SS ANOVA results testing the effect of species and treatment on the number of mussels pried open by whelks in experiment I. Response was square-root transformed to meet assumptions of normality.

	Sum Sq	Df	F-value	p-value
Treatment	0.4059	2	0.6467	0.53
Species	4.886	1	15.57	0.00016
Residuals	28.88	92		

Table A2. Linear model summary for effect of treatment and species on number of mussels pried in experiment I. The reference for treatment is low CO_2 and *N. canaliculata* for species. Model adjusted $R^2 = 0.13$. Response was square-root transformed to meet assumptions of normality.

	Estimate	Std. Error	t-value	p-value
Intercept	0.2637	0.1144	2.306	0.024
Treatment: Mid	-0.03125	0.1401	-0.2230	0.83
Treatment: High	0.1196	0.1401	0.8540	0.40
Species: N. ostrina	0.4512	0.1144	3.945	1.6×10^{-4}

Table A3. Type II SS ANOVA results testing the effect of species and treatment on length change and buoyant weight change by whelks in experiment I. Both responses were log(y+1) transformed to meet assumptions of normality.

	Sum Sq	Df	F-value	p-value
Length change				
Treatment	0.2219	2	1.104	0.34
Species	1.926	1	19.16	3.2×10^{-5}
Residuals	9.245	92		
Buoyant Weight				
Treatment	0.03862	2	3.125	0.049
Residuals	0.5746	9		

Table A4. Linear model summary for effects of treatment and species on length change and buoyant weight change in whelks in experiment I. The reference for treatment is low CO_2 and *N. canaliculata* for species. Responses were both log(y+1) transformed to meet assumptions of normality. Length change model adjusted $R^2 = 0.16$; buoyant weight change model adjusted $R^2 = 0.043$.

	Estimate	Std. Error	t-value	p-value
Length change				
Intercept	0.7994	0.06471	12.35	$< 2.0 \times 10^{-16}$
Treatment: mid	0.09711	0.07925	1.23	0.22
Treatment: high	0.1063	0.07925	1.341	0.18
Species: N. ostrina	-0.2833	0.06471	-4.378	3.2×10^{-5}
Buoyant Weight				
Intercept	0.02322	0.01389	1.671	0.098
Treatment: mid	0.04121	0.01965	2.097	0.039
Treatment: high	0.04377	0.01965	2.227	0.028

Table A5. ANOVA table for the effect of species, treatment, and initial length on final shell dry weight (Type II SS) and body dry weight (Type III SS) of whelks in experiment I. Responses were log(y+1) transformed to meet assumptions of normality.

	Sum Sq	Df	F-value	p-value
Shell Dry Weight				
Treatment	0.00264	2	0.679	0.51
Species	0.06376	1	32.74	1.3×10^{-7}
Initial Length	0.4232	1	217.3	$< 2.2 \times 10^{-16}$
Residuals	0.1772	91		
Body Dry Weight				
Intercept	0.01342	1	11.528	0.0010
Treatment	0.005517	2	2.370	0.099
Species	0.007423	1	6.376	0.013
Initial Length	0.06400	1	54.97	6.8×10^{-11}
Treatment x Species	0.01108	2	4.760	0.011
Residuals	0.1036	89		

Table A6. Linear model summary for effects of treatment, species, and initial length on final shell dry weight (g) and dry body weight of whelks in experiment I. The reference for treatment is low CO_2 and *N. canaliculata* for species. Shell dry weight model adjusted $R^2 = 0.88$; body dry weight model adjusted $R^2 = 0.60$. Responses were log(y+1) transformed to meet assumptions of normality.

	Estimate	Std. Error	t-value	p-value
Shell Dry Weight				
Intercept	-0.4330	0.07768	-5.574	2.5×10^{-7}
Treatment: mid	0.002101	0.01114	0.189	0.85
Treatment: high	-0.01017	0.01144	-0.89	0.38
Species: N. ostrina	-0.07036	0.01230	-5.722	1.3×10^{-7}
Initial Length	0.05548	0.003764	14.741	$< 2.0 \times 10^{-16}$
Body Dry Weight				
Intercept	-0.2089	0.06154	-3.395	0.0010
Treatment: mid	-0.01676	0.01220	-1.374	1.7
Treatment: high	-0.02715	0.01259	-2.156	0.034
Species: N. ostrina	-0.03629	0.01437	-2.525	0.013
Initial length	0.02181	0.002942	7.414	6.8×10^{-11}
Treatment: mid x Species: *N. ostrina*	0.02777	0.01711	1.623	0.11
Treatment: high x Species: *N. ostrina*	0.05320	0.01725	3.084	0.0027

Table A7. Test of linear contrasts for the hypothesis of no difference in handling times of mussels of different sizes for each whelk species in experiment II. p-values are Holm's corrected.

Contrast	Estimate	Df	Sum of Sq	F	p-value
N. canaliculata: small – large == 0	-7.629	1	4015	5.507	0.021
N. ostrina: small – large == 0	-23.55	1	5816	7.978	0.012
Residuals		85	61972		

Table A8. Type III SS ANOVA results testing the effect of species, treatment, and mussel size on length change of whelks in experiment II. Response was log(y+1) transformed to meet assumptions of normality.

	Sum Sq	Df	F value	p-value
Intercept	3.248	1	67.75	4.0×10^{-12}
Treatment	0.3177	2	3.313	0.042
Species	0.2766	1	5.769	0.019
Mussel Size	0.0617	1	1.287	0.26
Treatment x Species	0.2269	2	2.368	0.10
Species x Mussel Size	0.3720	1	7.760	0.0067
Residuals	3.644	76		

Table A9. Linear model summary for effects of treatment and species on final whelk length change in experiment II. The reference for treatment is low CO_2, N. *canaliculata* for species, and small for mussel size. Model adjusted $R^2 = 0.11$. Response was log(y+1) transformed to meet assumptions of normality.

	Estimate	Std. Error	t-value	p-value
Intercept	0.5562	0.06757	8.231	4.0×10^{-12}
Treatment: mid	-0.1593	0.08276	-1.925	0.058
Treatment: high	-0.2021	0.08276	-2.443	0.017
Species: N. ostrina	-0.2295	0.09556	-2.402	0.019
Mussel Size	-0.07667	0.06757	-1.135	0.26
Treatment: mid x Species: *N. ostrina*	0.1386	0.1170	1.184	0.24
Treatment: high x Species: *N. ostrina*	0.2543	0.1170	2.173	0.033
Mussel size x Species: *N. ostrina*	0.2662	0.09556	2.786	0.0067

Table A10. Tests of linear contrasts (Tukey's HSD) for interaction between mussel size and species on the length change of whelks in experiment II. Model is given in Table A9.

Hypothesis	Estimate	Std. Error	t value	p-value
N. canaliculata: large – small == 0	0.07667	0.06901	1.111	0.47
N. ostrina: large - small == 0	-0.1895	0.06901	-2.746	0.015

Table A11. Type II SS ANOVA table for effect of species and treatment on final shell dry weight and body dry weight of whelks in experiment II. Response was log(y+1) transformed to meet assumptions of normality.

	Sum Sq	Df	F value	Pr(>F)
Shell Dry Weight				
Treatment	0.0046	2	0.07370	0.93
Species	6.542	1	209.0	$< 2.0 \times 10^{-16}$
Residuals	2.504	80		
Body Dry Weight				
Treatment	0.03220	2	0.2523	0.78
Species	1.723	1	26.973	1.5×10^{-6}
Residuals	5.111	80		

Table A12. Linear model summary for effects of treatment and species on final whelk shell dry weight (g) in experiment II. The reference for treatment is low CO_2 and *N. canaliculata* for species. Shell dry weight model adjusted $R^2 = 0.71$. Body dry weight model adjusted $R^2 = 0.23$. Responses were log(y+1) transformed to meet assumptions of normality.

	Estimate	Std. Error	t value	p-value
Shell Dry Weight				
Intercept	0.2167	0.03861	5.612	2.8×10^{-7}
Treatment: Mid	-0.0119	0.04728	-0.252	0.80
Treatment: High	-0.01782	0.04728	-0.377	0.71
Species: N. ostrina	-0.5582	0.03861	-14.46	$< 2.0 \times 10^{-16}$
Body Dry Weight				
Intercept	-1.59565	0.05516	-28.93	$< 2.0 \times 10^{-16}$
Treatment: Low	0.04539	0.06755	0.672	0.50
Treatment: Mid	0.03618	0.06755	0.536	0.60
Species: N. ostrina	-0.2865	0.05516	-5.194	1.5×10^{-6}

Appendix B – Measuring Whelk Responsiveness in Chapter 2

In addition to the metrics included in the chapter, we also considered other metrics of whelk condition in our experiments. We recorded survival of whelks and at the end of experiment I, we tested whelk responsiveness to prodding the foot of each whelk with dissecting forceps, following the methods of Sorte & Hofmann (2005). For this assessment, whelks were rated on a scale of 0-3 where 0 = dead (with no response to probe), 1 = moribund (needed extensive probing to respond), 2 = alive (responded immediately to probe by withdrawing), and 3 = recovered (able to right body and reattach to substrate). This behavioral assessment at the end of experiment I indicated that 89 of the 96 whelks showed full responsiveness (of the remaining 7 whelks, 1 was dead, and the others received a score of 2, meaning they were responsive but did not right themselves). In both experiments, whelk mortality was very low (experiment I: 1 of 96 whelks, experiment II: 1 of 84 whelks).

Appendix C – Chapter 3 Supplementary Figures & Tables

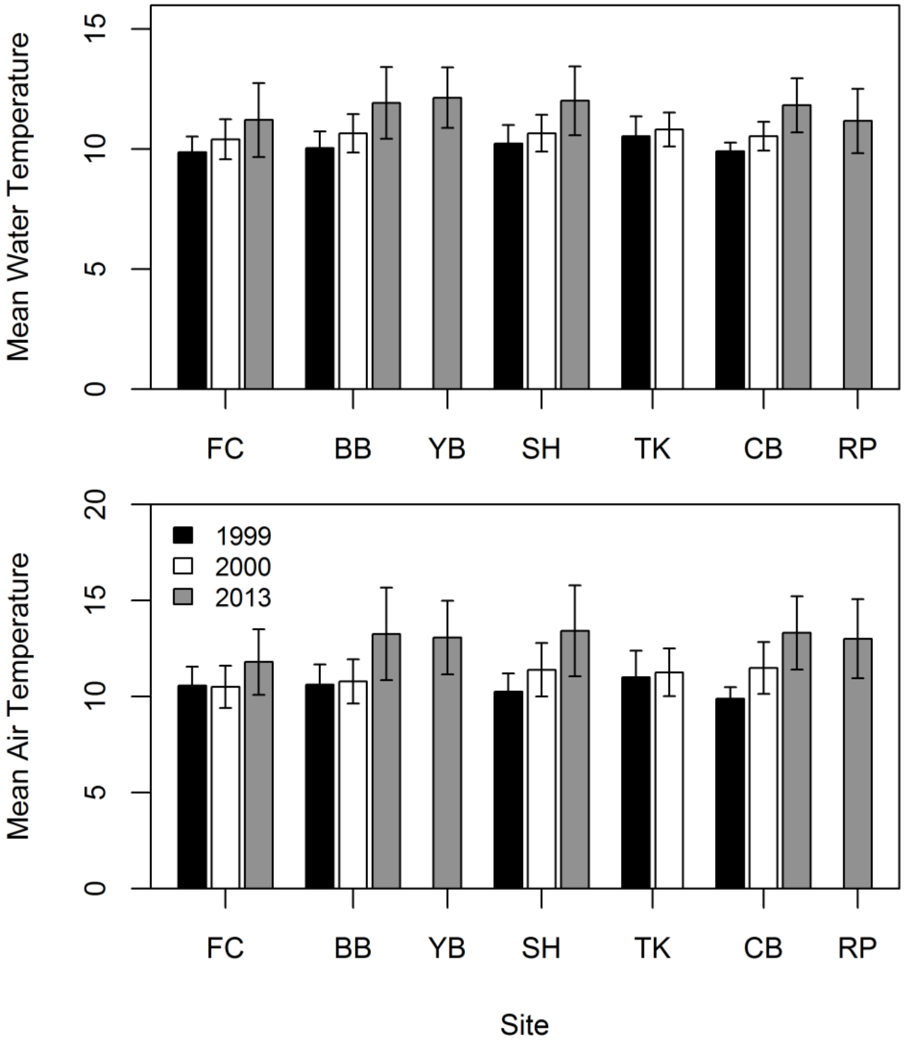

Figure C1. Mean water and air temperatures at each sites (from May through November) for the three different experimental years. Not all sites were used in all three years. Error bars are +1 SE.

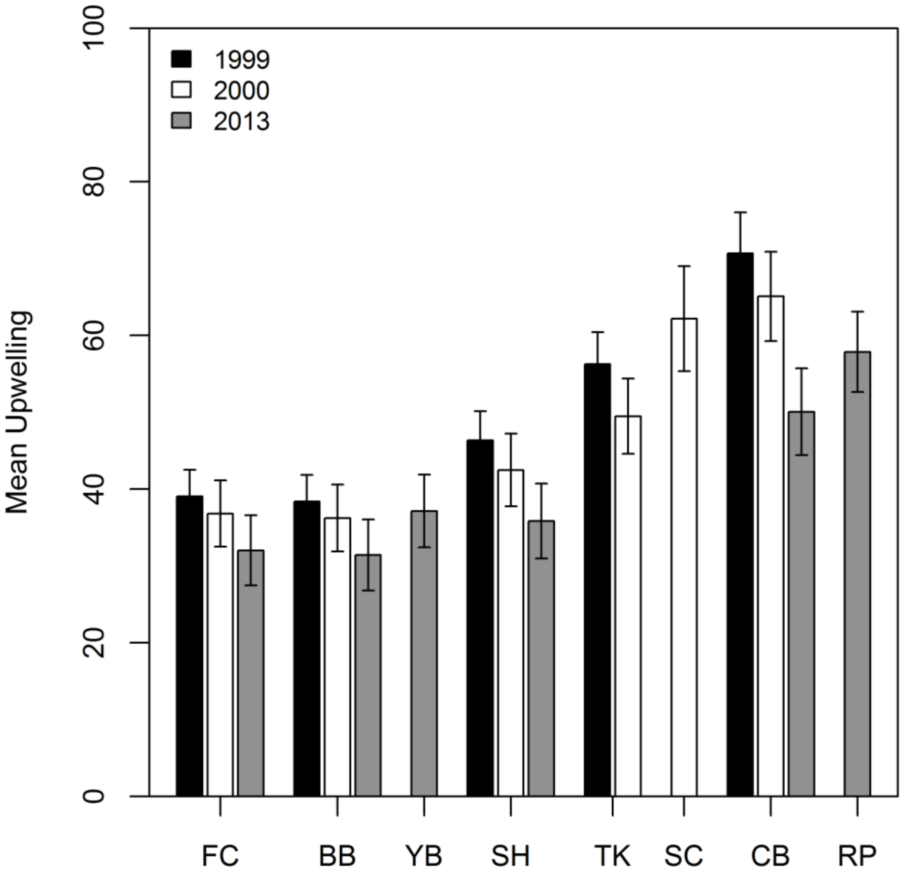

Figure C2. Mean upwelling values at experimental sites in each year (from May through November). Not all sites were used in all three years. Error bars are +1 SE.

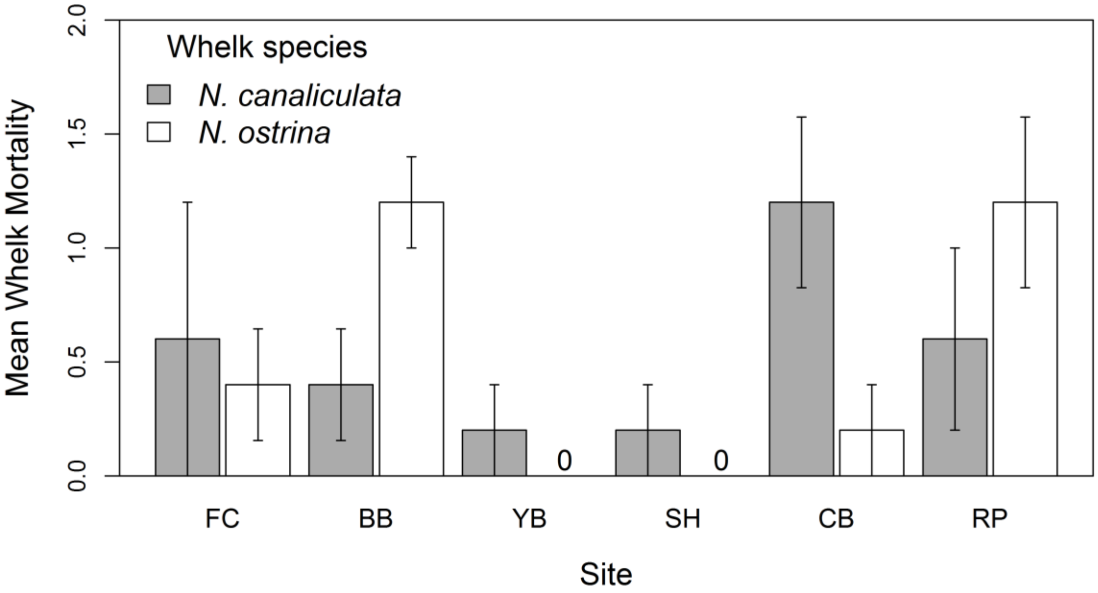

Figure C3. Mean mortality in experimental cages in the 2013 experiment for each whelk species. The means are calculated from the total mortality within each cage. Error bars are +1 SE.

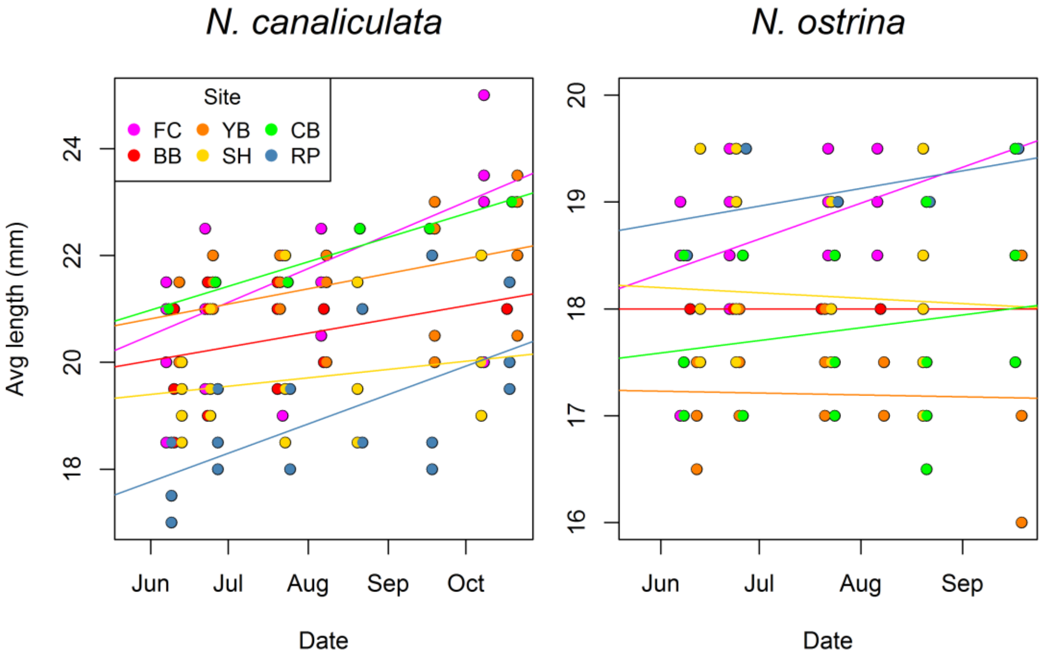

Figure C4. Mean length in mm of both whelk species in 2013 during the experiment. Data are only shown for cages where both whelks survived through the whole experiment, thus sample sizes are not equal at all sites. For *N. ostrina*, we took growth rates only until September because by October, there were sites where all replicates had lost at least one individual.

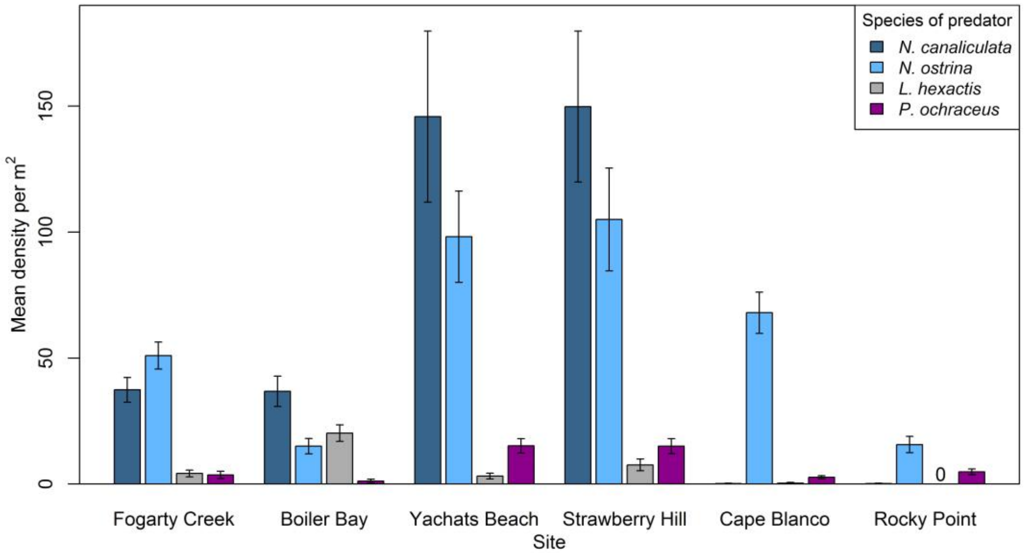

Figure C5. Mean densities of ambient predators m^{-2} at the six study sites in 2013. Data were obtained by surveying using five separate 0.25 x 0.25 m quadrats around each replicate at each monitoring point. Error bars are +1 SE.

Table C1. Linear model summary for one-way ANOVA testing difference in predator treatments and controls (i.e. +/- *N. canaliculata*) for all years and common sites (BB, CB, FC, SH). Model was selected using AICc. Model $R^2 = 0.24$. One plot was removed from analysis at FC in 2000 because its rate of decrease of mussel survival was an order of magnitude larger than other sites and years, and it appeared to be anomalous.

	Estimate	Std. Error	t value	p-value
Intercept	-0.003567	0.0004298	-8.3	2.6×10^{-13}
Treatment: +Predator	-0.003713	0.0006188	-6.0	2.5×10^{-8}

Table C2. The independent contribution (I) of each environmental and treatment variable towards the overall variance explained in mussel survival rates from hierarchical partitioning. Data are for predator and control treatments (i.e. +/- *N. canaliculata*) at all sites within each year. All variables combined explained 21.2%, 20.7%, and 53.1% of the total variance for 1999, 2000, and 2013 respectively.

	I	Z.score	p <0.05
1999			
Site	0.02	-1.14	
Treatment	0.14	4.87	*
Mean water temperature	0.01	-0.4	
Std. dev of water temperature	0	-0.56	
Mean air temperature	0	-0.64	
Std. dev of air temperature	0	-0.58	
Upwelling	0.02	-0.18	
Std. dev of Upwelling	0.01	-0.17	
2000			
Site	0.02	-1.84	
Treatment	0.13	4.47	*
Mean water temperature	0.02	-0.26	
Std. dev of water temperature	0.01	-0.42	
Mean air temperature	0.01	-0.55	
Std. dev of air temperature	0	-0.77	
Upwelling	0.01	-0.84	
Std. dev of Upwelling	0	-0.66	
2013			
Site	0.11	0.51	
Treatment	0.21	7.02	*
Mean water temperature	0.05	1.54	
Std. dev of water temperature	0.01	-0.34	
Mean air temperature	0.01	-0.25	
Std. dev of air temperature	0.09	3.08	*
Upwelling	0.04	0.9	
Std. dev of Upwelling	0.01	-0.43	

Table C3. Conover's test for multiple comparisons of independent samples for post-hoc on Kruskal-Wallis tests of effects of site on mussel survival in marked plots (ambient predation) in each year. Values are p-values for each pairwise comparison within a year.

1999					
	BB	CB	FC	TK	
CB	0.00043	-	-	-	
FC	0.60	0.0029	-	-	
TK	0.0041	0.60	0.027	-	
SH	0.066	0.13	0.27	0.59	
2000					
	BB	CB	FC	TK	SC
CB	1	-	-	-	-
FC	1	1	-	-	-
TK	1	1	1	-	-
SC	1	1	1	1	-
SH	0.19	0.43	0.23	1	0.16
2013					
	BB	CB	FC	RP	SH
CB	0.013	-	-	-	-
FC	0.075	1	-	-	-
RP	0.00051	1	0.44	-	-
SH	0.12	1	1	0.29	-
YB	0.022	1	1	1	1

Table C4. Type II SS ANOVA from model testing effect of site on whelk mortality in 2013. The model was selected based on AICc from a full model that included site, whelk species, and a site x species interaction.

	Sum Sq	Df	F value	p-value
Site	2.2873	5	2.905	0.021
Residuals	8.5035	54		

Appendix D – Chapter 4 Supplementary Figures & Tables

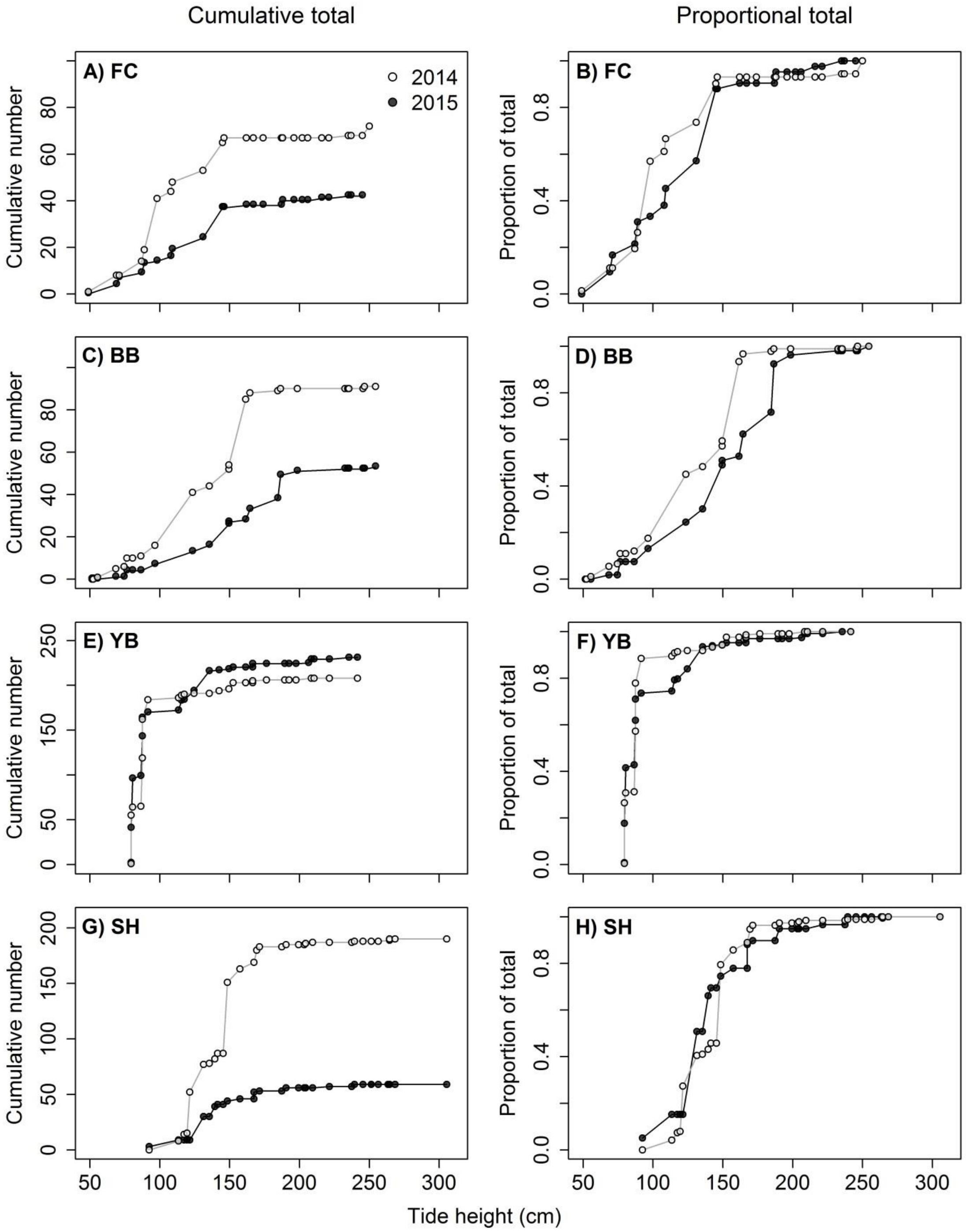

Figure D1. Abundance of *N. canaliculata* with tide height (cm above MLLW) for July 2014 (white) and July 2015 (black). Left panel shows cumulative whelk numbers with increasing tidal height. Right panel is cumulative proportion of whelks with tidal height.

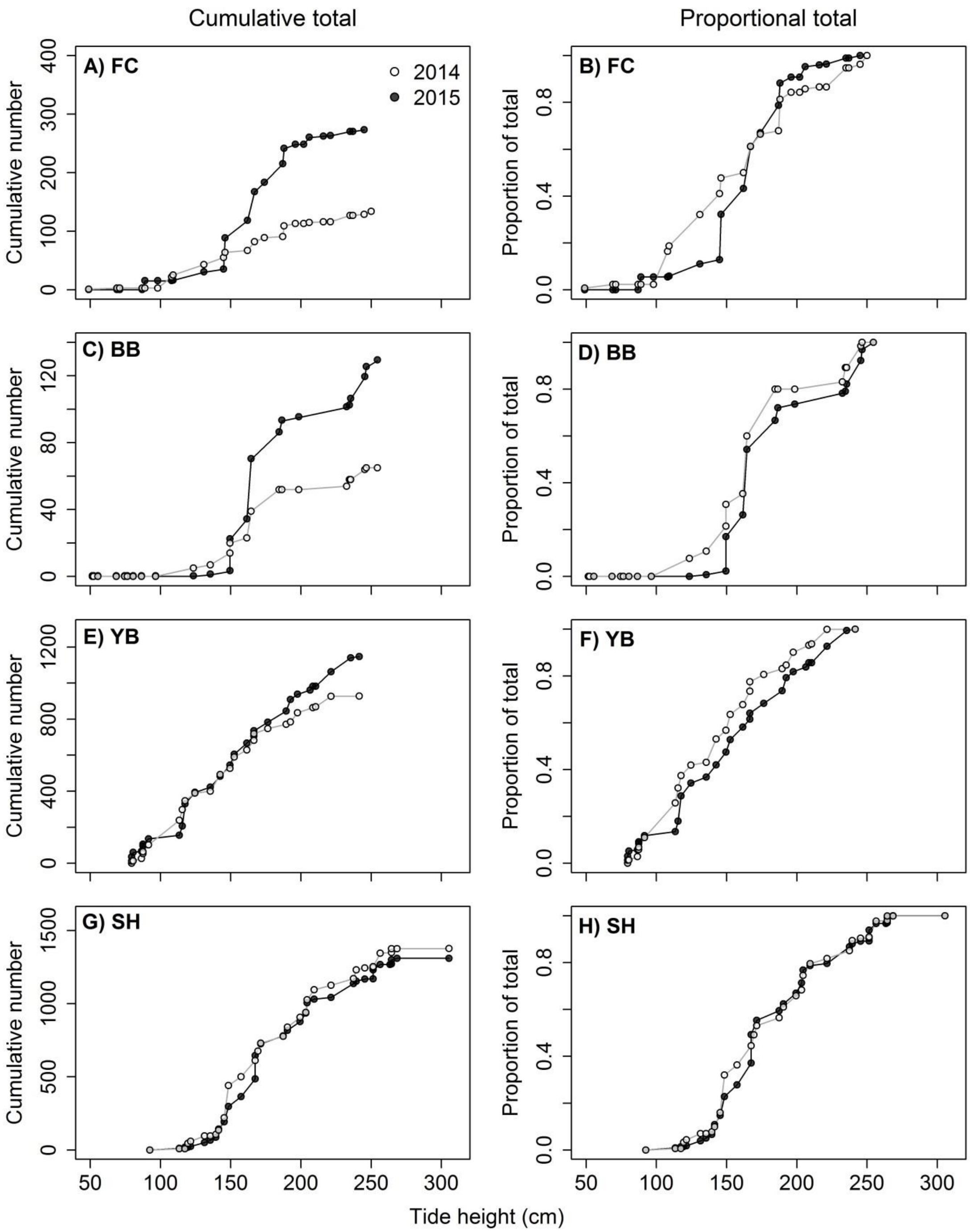

Figure D2. Abundance of *N. ostrina* with tide height (cm above MLLW) for July 2014 (white) and July 2015 (black). Left panel shows cumulative numbers of whelks with increasing tidal height. Right panel is cumulative proportion of total whelks with tidal height.

Table D1. Two-way ANOVA of the effect of whelk removal treatments and site on the number of cumulative whelks in plots. Because the cumulative numbers were non-independent over time, we modeled each time period separately. Non-significant interaction terms were dropped in models. Time 1 represents the first monitoring prior to removal in June 2014.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Time 1 (June 2014)					
Site	1	2756	2755.6	0.7203	0.4015
Treat	1	6	6.4	0.0017	0.9676
Residuals	37	141554	3825.8		
Time 2 (September 2014)					
Site	1	84272	84272	1.8516	0.1818
Treat	1	701190	701190	15.4063	0.0004
Residuals	37	1683987	45513		
Time 3 (February 2015)					
Site	1	2146	2146	0.0358	0.8510
Treat	1	463579	463579	7.726	0.0085
Residuals	37	2220104	60003		
Time 4 (May 2015)					
Site	1	1092	1092	0.0121	0.9132
Treat	1	675740	675740	7.4602	0.0096
Residuals	37	3351431	90579		

Table D2. Post-hoc results from experimental analysis using GLMMs for each species across the 4 experimental time points (0=June 2014, 1=September 2014, 2=February 2015, and 3=May 2015). To run post-hoc analyses on differences over time, we forced a time x treatment interaction in the GLMM model. Analyses were obtained using the 'phia' package in R.

Species	Time point	Hypothesis	Estimate	d.f.	χ^2	p-value
M. californianus	0	Control-removal= 0	0.0103	1	0.2749	0.6001
	1	Control-removal= 0	0.0277	1	1.1979	0.3189
	2	Control-removal= 0	0.0363	1	3.4074	0.1947
	3	Control-removal= 0	0.0515	1	6.8260	0.0359
M. trossulus	0	Control-removal= 0	-0.0465	1	0.5094	0.8914
	1	Control-removal= 0	-0.1260	1	5.1459	0.0757
	2	Control-removal= 0	-0.0292	1	0.5743	0.8914
	3	Control-removal= 0	-0.0711	1	5.5074	0.0757
B. glandula	0	Control-removal= 0	0.0104	1	0.0466	1.0000
	1	Control-removal= 0	-0.0788	1	2.8605	0.3631
	2	Control-removal= 0	0.0065	1	0.0738	1.0000
	3	Control-removal= 0	-0.0040	1	0.0297	1.0000
C.dalli	0	Control-removal= 0	-0.0079	1	0.0418	0.8379
	1	Control-removal= 0	0.0283	1	0.6977	0.8071
	2	Control-removal= 0	0.0511	1	7.4944	0.0248
	3	Control-removal= 0	0.0370	1	2.5770	0.3251
S. cariosus	0	Control-removal= 0	0.0194	1	0.6105	0.7506
	1	Control-removal= 0	0.0456	1	3.3875	0.2275
	2	Control-removal= 0	0.0472	1	3.6261	0.2275
	3	Control-removal= 0	0.0220	1	0.7861	0.7506
P. polymerus	0	Control-removal= 0	0.0492	1	1.0215	1.0000
	1	Control-removal= 0	0.0347	1	0.5081	1.0000
	2	Control-removal= 0	0.0365	1	0.5614	1.0000
	3	Control-removal= 0	0.0039	1	0.0066	1.0000

Table D3. Effect of treatment, time point, and site on the cover of the primary space-occupying mussel species for the best-performing models. Results are from mixed effects models (GLMM) with only fixed effects presented. The reference groups are: control for treatment, time 0 for time point (June 2014), and Strawberry Hill (SH) for site. YB=Yachats Beach site.

Species	Parameter	Estimate	Std. Error	d.f.	z-value	p-value
M. californianus	Intercept	0.0311	0.0171	111	1.8235	0.0709
	Time1	0.0180	0.0140	111	1.2830	0.2021
	Time2	0.0894	0.0140	111	6.3672	<0.0001
	Time3	0.1562	0.0140	111	11.1194	<0.0001
	SiteYB	-0.0174	0.0197	37	-0.8834	0.3827
	Whelk removal	-0.0103	0.0197	37	-0.5243	0.6032
	Time1:SiteYB	-0.0022	0.0162	111	-0.1374	0.8909
	Time2:SiteYB	-0.0191	0.0162	111	-1.1801	0.2405
	Time3:SiteYB	-0.0470	0.0162	111	-2.8967	0.0045
	Time1:Whelk removal	-0.0174	0.0162	111	-1.0725	0.2858
	Time2:Whelk removal	-0.0260	0.0162	111	-1.6060	0.1111
	Time3:Whelk removal	-0.0411	0.0162	111	-2.5377	0.0125
M. trossulus	Intercept	0.7330	0.0477	114	15.3739	<0.0001
	Time1	-0.2608	0.0553	114	-4.7152	<0.0001
	Time2	-0.3064	0.0474	114	-6.4693	<0.0001
	Time3	-0.5624	0.0442	114	-12.7344	<0.0001
	SiteYB	0.0131	0.0644	37	0.2034	0.8399
	Whelk removal	0.0646	0.0281	37	2.2989	0.0273
	Time1:SiteYB	-0.1149	0.0782	114	-1.4688	0.1446
	Time2:SiteYB	0.0687	0.0670	114	1.0261	0.3070
	Time3:SiteYB	-0.0273	0.0624	114	-0.4370	0.6629

Table D4. Effect of treatment, time point, and site on the cover of the primary space-occupying barnacle species for the best-performing models. Results are from mixed effects models (GLIMM) with only fixed effects presented. The reference groups are: control for treatment, time 0 for time point (June 2014), and Strawberry Hill (SH) for site. YB=Yachats Beach site.

Species	Parameter	Estimate	Std. Error	d.f.	z-value	p-value
B. glandula	Intercept	0.3398	0.0335	114	10.1270	<0.0001
	Time1	0.1451	0.0449	114	3.2331	0.0016
	Time2	-0.0846	0.0340	144	-2.4881	0.0143
	Time3	-0.1296	0.0335	114	-3.8646	0.0002
	SiteYB	0.0475	0.0474	38	1.0013	0.3230
	Time1:SiteYB	0.0408	0.0634	114	0.6424	0.5219
	Time2:SiteYB	-0.0888	0.0480	114	-1.8463	0.0674
	Time3:SiteYB	-0.0582	0.0474	114	-1.2286	0.2218
C. dalli	Intercept	0.3633	0.0291	114	12.5049	<0.001
	Whelk removal	-0.0424	0.0174	37	-2.4376	0.0187
	Time1	0.0532	0.0332	114	1.5979	0.1128
	Time2	-0.0823	0.0267	114	-3.0827	0.0026
	Time3	-0.1333	0.0282	114	-4.7185	<0.001
	SiteYB	-0.0421	0.0392	37	-1.0749	0.2894
	Time1:SiteYB	-0.1150	0.0470	114	-2.4441	0.0161
	Time2:SiteYB	-0.0558	0.0378	114	-1.4767	0.1425
	Time3:SiteYB	0.0075	0.0400	114	0.1883	0.8510
S. cariosus	Intercept	0.0679	0.0203	114	3.3491	0.0011
	Whelk removal	-0.336	0.0221	37	-1.520	0.1370
	Time1	0.0168	0.117	114	1.4358	0.1538
	Time2	0.0301	0.117	114	2.5740	0.0113
	Time3	0.0284	0.117	114	2.4333	0.0165
	SiteYB	0.0548	0.0251	37	2.1804	0.0357
	Time1:SiteYB	0.0459	0.0195	114	2.3489	0.0205
	Time2:SiteYB	0.0619	0.0195	114	3.1673	0.0020
	Time3:SiteYB	0.0741	0.0195	114	3.7920	0.0002
S. cariosus	Intercept	0.1120	0.0377	114	2.9741	0.0036
	Time1	0.0211	0.0328	114	0.6453	0.5200
	Time2	0.2028	0.0328	114	6.1925	0.0001
	Time3	0.2966	0.0328	114	9.0561	0.0001
	SiteYB	-0.0698	0.0498	38	-1.4022	0.1690
	Time1:SiteYB	-0.0220	0.0378	114	-0.5816	0.5620
	Time2:SiteYB	-0.1290	0.0378	114	-3.4119	0.0009
	Time3:SiteYB	-0.1813	0.0378	114	-4.7928	<0.0001

Table D5. Negative binomial regression results for *N. canaliculata* density over time when *M. trossulus* zone quadrats are included and excluded.

<table>
<tr><td colspan="5">With <i>M. trossulus</i> quadrats
*Residual deviance: 596.87 on 632 df, theta=0.1787</td></tr>
<tr><td>Parameter</td><td>Estimate</td><td>Std. Error</td><td>z value</td><td>p-value</td></tr>
<tr><td>Intercept</td><td>20.7942</td><td>9.6252</td><td>2.16</td><td>0.0307</td></tr>
<tr><td>SiteBB</td><td>-0.3875</td><td>0.2579</td><td>-1.502</td><td>0.1330</td></tr>
<tr><td>SiteFC</td><td>-0.7212</td><td>0.2735</td><td>-2.637</td><td>0.0084</td></tr>
<tr><td>SiteYB</td><td>0.4755</td><td>0.2505</td><td>1.898</td><td>0.0577</td></tr>
<tr><td>Time</td><td>-0.0011</td><td>0.0006</td><td>-1.869</td><td>0.0616</td></tr>
<tr><td colspan="5">Without <i>M. trossulus</i> quadrats
*Residual deviance: 548.33 on 596 df, theta=0.1768</td></tr>
<tr><td>Parameter</td><td>Estimate</td><td>Std. Error</td><td>z value</td><td>p-value</td></tr>
<tr><td>Intercept</td><td>13.1437684</td><td>9.968754</td><td>1.318</td><td>0.1873</td></tr>
<tr><td>SiteBB</td><td>-0.4298958</td><td>0.2779597</td><td>-1.547</td><td>0.1220</td></tr>
<tr><td>SiteFC</td><td>-0.7750118</td><td>0.2925467</td><td>-2.649</td><td>0.0081</td></tr>
<tr><td>SiteYB</td><td>-0.3922723</td><td>0.2660658</td><td>-1.474</td><td>0.1404</td></tr>
<tr><td>Time</td><td>-0.0006294</td><td>0.0006095</td><td>-1.033</td><td>0.3018</td></tr>
</table>

Table D6. Negative binomial regression results for *N. ostrina* density over time. In this analysis results were the same whether or not *M. trossulus* quadrats were included, so we have only shown regression with the full analysis.

With M. trossulus quadrats *Residual deviance: 733.81 on 632 df, theta=0.3431				
Parameter	Estimate	Std. Error	z value	p-value
Intercept	-13.2	6.93	-1.908	0.0564
SiteBB	-2.07	0.186	-11.128	<0.0001
SiteFC	-1.67	0.197	-8.497	<0.0001
SiteYB	-0.0819	0.180	-0.454	0.6496
Time	0.0011	0.0004	2.597	0.0094