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The shifting ecological impacts of dominant and invasive marine species under climate change

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The shifting ecological impacts of dominant and invasive marine species under climate change

DISSERTATION

submitted in partial satisfaction of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in Ecology and Evolutionary Biology

by

Samuel Alwood Mahanes

Dissertation Committee:
Associate Professor Cascade Sorte, Chair
Professor Matthew Bracken
Professor Jennifer Martiny

2022

DEDICATION

I dedicate this dissertation to my family and friends:

you know who you are,

how much you mean to me,

and that I could never have done this without you.

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Finally, I would like to thank everyone I’ve met, played soccer with, sang karaoke with, gone hiking with, played trivia with, seen concerts with, laughed with, cried with, celebrated with, failed with, and succeeded with in Irvine. I moved here in 2017 knowing next to no one and leave in 2022 with a veritable lifetime's-worth of memories.

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2. **Mahanes SA**, Sorte CJB (2019). Impacts of climate change on marine species invasions in northern hemisphere high-latitude ecosystems. *Frontiers of Biogeography 11*(1).
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Research Experience

University of California, Irvine, PhD Student, Sorte Lab 2017-Present

- Studied how seaweeds provide habitat through removal and mesocosm experiments, how the impact of invasive species varies by latitude and how climate change affects coastal ecosystems

Graduate Student Researcher on a Climate Change Research Project 2018-2019, 2021-2022

- Participated in a multi-year project manipulating temperature, CO_2 and species composition in tide pools to simulate global change and determine its impacts on coastal ecosystems
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- Managed a large, multifactor dataset
- Developed research and community impact summaries to distribute to stakeholders

Graduate Student Researcher on an Invasive Species Impact Project 2020-2021

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Presenter, UC Irvine Earth Day Fair, impacts of plastic on marine ecosystems	2019
Presenter, UC Irvine Homecoming, impacts of plastic on marine ecosystems	2019
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UC Irvine Graduate Division Mentoring Excellence Program	2018

ABSTRACT OF THE DISSERTATION

The shifting ecological impacts of dominant and invasive marine species under climate change

by

Samuel Alwood Mahanes

Doctor of Philosophy in Ecology and Evolutionary Biology

University of California, Irvine, 2022

Associate Professor Cascade Sorte, Chair

Global change is impacting ecosystems worldwide, driving widespread biodiversity loss and disrupting a broad spectrum of ecological processes. Ecosystems are organized by interactions among species, which dictate everything from species composition to how biomass and energy flow through the system. Only by studying the effects of global change in the context of existing ecological structures and species interactions can the impacts be fully understood. My dissertation research has focused on the ways in which climate change affects the ecological roles of species: whether by altering the relative importance of common species in ecosystems, directly impacting ecosystem function via species loss, or accelerating the proliferation of invasive species. In my first chapter, I consider the potential for an abundant marine producer to engineer habitat for other species and how that role may shift with climate change. I found that this dominant alga raised pH when in isolation but not in the context of a tide pool community, suggesting that the most abundant species do not necessarily affect the impacts of global change in coastal ecosystems. My second chapter focuses on the contributions of dominant species to ecosystem multifunctionality in coastal areas, as well as the potential effects of dominant species loss on ecosystem multifunctionality. I found that a dominant producer and a dominant consumer had largely opposite effects on ecosystem function and that the loss of the producer altered the functional impact of the consumer, suggesting that species loss may impact ecosystem multifunctionality beyond the functional footprint of the individual species. In my third chapter, I identified the ways that climate change is likely to influence factors that historically limited species invasion in high-latitude, marine ecosystems. Each of these invasion barriers is likely to become increasingly porous, potentially increasing invasions in high-latitude areas in decades to come. The results of this research could be incorporated into (1) conservation plans, sharpening the focus on species which have the greatest ecological impact, either by stabilizing environmental conditions or by driving ecosystem function, and (2) invasive species management strategies, by highlighting the increasing vulnerability of high-latitude ecosystems to species invasion under warming conditions and stressing the importance of international cooperation in monitoring programs.

INTRODUCTION

Global change comprises multiple shifting factors and affects nearly every organism on Earth. The drivers of global change, including climate change, ocean acidification, and the proliferation of invasive species both directly and interactively impact ecosystems (Hendriks *et al.*, 2010; Wernberg *et al.*, 2011; Diffenbaugh and Field, 2013; Simberloff *et al.*, 2013). The ecological effects of global change are complex and will differ in impact across ecosystems depending on the variation in rates of change across biomes, the resistance and resilience of the species in different communities, and the interactions among those species (Gilman *et al.*, 2010; Bulleri *et al.*, 2018). The ways in which species function and interact, either positively through ecosystem engineering and contributing to ecosystem function or negatively by becoming invasive, dictate how ecosystems are structured and how susceptible they may be to global change (Harley *et al.*, 2006; Mantyka-Pringle *et al.*, 2012; Miranda *et al.*, 2019). As the ecological roles of species transform in a changing world, it will be critical to understand how those changing roles manifest within ecosystems and whether such shifts will ameliorate or exacerbate the impacts of climate change.

Climate change, driven by the anthropogenic release of CO_2 into the atmosphere, is causing rising temperatures worldwide (IPCC, 2022). Elevated temperatures can affect organisms at the individual level, by way of metabolic or other physiological stress, or on a broader scale, extirpating populations of a species from certain areas where the rate of temperature change outpaced the species' capacity to adapt (Sorte *et al.*, 2011; Wernberg *et al.*, 2011; Bellard *et al.*, 2012). Climate change manifests in numerous different ways across ecosystems; from shifting the phenology of plant-pollinator relationships (Memmott *et al.*, 2007) to increasing tree mortality in forest communities (Ellison *et al.*, 2005; Allen *et al.*, 2010). Climate change is impacting marine ecosystems by driving biogeographic shifts, including shifts in the ranges of critical fishery species (Stenevik and Sundby, 2007; Cheung *et al*., 2010) and declines in foundation species populations (Wernberg *et al*., 2011; Doney *et al*., 2012; Sorte *et al*., 2017). In addition to altering climatic conditions, the anthropogenic release of CO_2 is driving ocean acidification: a process where increased atmospheric CO_2 infuses into seawater, causing a reduction in seawater pH (Calderia and Wickett, 2003; Kroeker *et al*., 2013). Broad-scale impacts of reduced seawater pH include increased physiological stress, sensory impairment, and reduction of calcification ability (Orr *et al*., 2005; Doney *et al*., 2009; Munday *et al*., 2009; Kroeker *et al*., 2021). The acidification-driven impact on calcification may be particularly detrimental to many species which serve foundational roles in marine ecosystems and provide habitat for other species, including mollusks, corals, and coralline algae (Orr *et al*., 2005; Doney *et al*., 2009; Bell *et al*., 2022). Climate change and acidification will impact species at different rates depending on their vulnerability and may drive rapid shifts in community composition across marine ecosystems (Sorte *et al*., 2011; Kroeker *et al*., 2013).

The effects of climate change and ocean acidification on ecosystems may be mediated by dominant species which, by virtue of their sheer abundance, can exert strong effects on the surrounding ecosystem (Tingley *et al*., 2002). Dominant species, which can include a wide variety of trees, seaweeds, sessile invertebrates, and marsh grasses (Ellison *et al*., 2005; Franz *et al*., 2019; Watson *et al*., 2016), can create habitat and alter local environmental conditions (Jones *et al*., 1997; Jurgens and Gaylord, 2018), potentially enabling other species to survive in areas which would otherwise be inhospitable under climate change (Bulleri *et al*., 2018; Ellison, 2019). Some abundant marine producers, including seaweeds and seagrasses, have shown the ability to raise pH through photosynthesis, which may help to mitigate the effects of ocean acidification in coastal ecosystems (Hendriks *et al*., 2010; Bracken *et al*., 2018; Silbiger and Sorte, 2018). However, dominant species are also susceptible to rapid environmental change, and the potential loss of dominant species threatens to curtail these positive interactions amid increasingly stressful environmental conditions, when such interactions may be most critical to ecological stability (Ellison *et al*., 2005; Fraser *et al*., 2014; Franz *et al*., 2019).

The impacts of dominant species loss may extend beyond shifts in local environmental conditions if the species fills additional roles in the ecosystem. Dominant species have been shown to contribute to primary productivity, decomposition, and nutrient cycling, all of which constitute ecosystem multifunctionality: the total of all biological processes occurring in an ecosystem (Smith and Knapp, 2003; Lohbeck *et al*., 2016; Manning *et al*., 2018). Accelerating species loss highlights the importance of assessing how individual species, particularly those which are highly abundant, affect ecological function (Cardinale *et al*., 2006). The role of dominant species in driving ecosystem multifunctionality will have significant implications for the wider impacts of biodiversity loss (Hillebrand *et al*., 2008; Wohlgemuth *et al*., 2016).

The loss of dominant species threatens to disrupt ecosystem function, but similar levels of disruption may be driven, conversely, by the additional of invasive species. Species invasion occurs when organisms are transported by humans to an area where they are non-native, either deliberately (e.g., for use as decorative plants) or inadvertently (e.g., fouling species being transported on the hulls of ships), and successfully establish expanding populations (Theoharides and Dukes, 2007). Invasive species can have severe negative impacts on native communities and represent one of the greatest threats to global biodiversity (Occhipinti-Ambrogi, 2007; Simberloff *et al*., 2013; Bellard *et al*., 2016). In addition to relying on human transportation, invasive species are often only able to successfully establish populations due to direct human disturbance, either through direct impacts on native species or through the creation of novel habitat, such as agricultural fields or dock pilings (Vitousek *et al*., 1997; Simberloff *et al*., 2013). Climate change and ocean acidification can exacerbate the effects of species invasion in marine ecosystems by enhancing the growth rates of invasive species while negatively impacting native species, potentially increasing the frequency and scope of marine species invasion (Dukes and Mooney, 1999; Anderson, 2005; Occhipinti-Ambrogi, 2007; Sorte *et al*., 2013; Roth-Schulze *et al*., 2018). Preventing the introduction of non-native species which may become invasive, as well as more effectively managing established invasive populations, is critical to maintaining biodiversity, particularly in areas which may be increasingly vulnerable to species invasion under ongoing climate change (Molnar *et al*., 2008; Verna *et al*., 2016).

This thesis focuses on the ways in which global change may alter the roles of species: assessing whether the importance of ecosystem engineers will change, examining potential consequences of dominant species loss for ecosystem multifunctionality, and evaluating whether changing conditions will influence species invasion in specific biomes. My first chapter focuses on the role of an abundant, basal species in an ecosystem and how that role may shift amid changing conditions. I found that the dominant alga, *Neorhodomela oregona*, is resilient to disturbance but did not impact pH or water temperature in tide pools, suggesting that dominant producers do not necessarily ameliorate changing conditions in coastal ecosystems. In my second chapter, I investigated the roles of two dominant species in driving ecosystem multifunctionality in coastal ecosystems as well as the potential impact if one of the dominant species is lost. I found that a dominant consumer (the mussel *Mytilus trossulus*) affected ecosystem multifunctionality while a dominant producer (*N. oregona*) affected individual ecosystem functions, almost uniformly in the opposite direction from the dominant consumer. However, when the dominant producer is removed from the system, the consumer's effect on multifunctionality shifts, suggesting that the dominant species have an interactive role in driving ecosystem function. My third chapter is a review and synthesis of the potential for climate change to increase species invasion in high-latitude, marine ecosystems. I outline the barriers which have historically limited species invasion in these areas and how those barriers are being eroded by climate change and shifting patterns of human activity. These results collectively highlight the ways in which climate change can affect the ecological roles that species play, which may in turn influence how climate change impacts ecosystems around the globe.

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CHAPTER 1

Climate change amelioration by marine producers: does dominance predict impact?

In press at Biological Bulletin

Abstract

Climate change threatens biodiversity worldwide, and assessing how those changes will impact communities will be critical for conservation. Dominant primary producers can alter local-scale environmental conditions, reducing temperature via shading and mitigating ocean acidification via photosynthesis, which could buffer communities from the impacts of climate change. We conducted two experiments on the coast of southeastern Alaska to assess the effects of a common seaweed species, *Neorhodomela oregona*, on temperature and pH in field tide pools and tide pool mesocosms. We found that *N. oregona* was numerically dominant in this system, covering >60% of habitable space in the pools and accounting for >40% of live cover. However, while *N. oregona* had a density-dependent effect on pH in isolated mesocosms, we did not find a consistent effect of *N. oregona* on either pH or water temperature in tide pools in the field. These results suggest that the amelioration of climate change impacts in immersed marine ecosystems by primary producers is not universal and likely depends on species' functional attributes, including photosynthetic rate and physical structure, in addition to abundance or dominance.

Introduction

Global change poses a threat to biodiversity worldwide, from forests (Sánchez-Salguero *et al.*, 2017) and arid plains (McKechnie *et al.*, 2012) to coastal seas (Doney *et al.*, 2012; Wernberg *et al.*, 2011). Climate change can increase physiological stress on organisms (McKechnie *et al.*, 2012; Jurgens and Gaylord, 2018), rendering entire habitats no longer viable for some species (Morelli *et al.*, 2017). In marine ecosystems, the ongoing effects of climate change are accompanied by ocean acidification, the process of declining seawater pH driven by rapid increases in atmospheric CO_2 (Delille *et al.*, 2000; Doney *et al.*, 2009; Kroeker *et al.*, 2013). The impacts of ocean acidification include increased physiological stress on certain taxa, particularly calcifying organisms, as reduced pH makes calcification more difficult (Fabry *et al.,* 2008; Milazzo *et al.,* 2019; Kroeker *et al.,* 2021). Recent research suggests that the effects of climate warming and ocean acidification may be mediated by dominant or "leverage" species (Hawkins *et al.*, 2009; Wahl *et al.*, 2018), which can alter local environmental conditions (Spurr, 1957; Jones *et al.*, 1997; Bracken *et al.*, 2018; Jurgens and Gaylord, 2018). It is critical to identify the importance of biological feedbacks for determining how changing conditions manifest in ecosystems (Davis *et al.*, 1998; Valiente-Banuet *et al.*, 2015; Bulleri *et al.*, 2018). Here, we evaluated the role of a numerically dominant species (defined as any species constituting >12% relative abundance in a community; Mariotte, 2014) in driving local environmental conditions in one of the fastest warming regions in the world.

Individual species can exert strong effects on the surrounding community by altering temperatures, which may moderate the impact of global change within ecosystems (Gilman *et al.*, 2010; Beerman *et al.*, 2013; Avolio *et al.*, 2019). Species can form biogenic habitats that maintain lower temperatures than the surrounding areas, enabling associated species that would otherwise be extirpated from the area to persist (Lloret *et al.*, 2012; Martin *et al.*, 2015; Jurgens and Gaylord, 2018; Avolio *et al.*, 2019). For example, dominant shrubs can facilitate the germination of herbaceous plant seedlings by reducing soil temperature (Holzapfel and Mahall, 1999), and tree species with the greatest canopy density, which provide superior shade, are preferentially occupied by birds in the Kalahari Desert during the hottest times of year (Martin *et al.*, 2015). Similar patterns have been observed in marine systems. Shading by surfgrass (*Phyllospadix* spp.), for example, has been shown to reduce water temperature in Washington State (Shelton, 2010), and temperature reduction via shading during low tide drives a close association between chitons (*Katharina tunicata*) and kelp (*Hedophyllum sessile*; Burnaford, 2004). However, other studies have shown some dominant species to have no effect on temperature, as is the case with American beachgrass in coastal dune ecosystems in Massachusetts (Rajaniemi and Allison, 2009). To predict how climate change will impact ecosystems, it is critical to determine whether dominant species are altering local temperatures and understand how these temperature-mediating effects may change in magnitude or importance under warming conditions (Hawkins *et al.*, 2009; Wernberg *et al.*, 2010; Valladares *et al.*, 2016; Jurgens and Gaylord, 2018).

Ocean acidification is another growing threat to marine biodiversity, and recent research suggests that marine producers can ameliorate the impact of acidification on coastal ecosystems (Bracken *et al.*, 2018). Macrophytes (seaweeds, seagrasses, and other marine primary producers) can strongly affect seawater pH, increasing mean pH (Camp *et al.,* 2016; Wahl *et al.,* 2018; Ricart *et al.*, 2021) and pH variation over the course of a diel cycle (Hendriks *et al.*, 2014; Silbiger and Sorte, 2018; Pacella *et al.,* 2018). Macrophytes can raise seawater pH in the presence of light via photosynthesis, which removes inorganic carbon from the water column, but they can also reduce pH via respiration (Murru and Sandgren, 2004; Krause-Jensen *et al.*, 2015; Bracken *et al.*, 2018), which is most prominent when photosynthetic rate declines in low light conditions (Zou *et al.,* 2011; Pacella *et al.,* 2018; Silbiger and Sorte, 2018). Past studies suggest that producer-driven shifts in temporal pH patterns can have community-wide consequences, such as for population sizes of shellfish and other calcifying species (Semesi *et al.*, 2009; Wahl *et al.,* 2018). Therefore, dominant marine producers that form dense aggregations, including *Fucus vesiculosus* in the Baltic Sea (Wahl *et al.,* 2018) and *Prionitis sternbergii* in tide pools in northern California (Bracken *et al.*, 2018), may influence the impacts of ocean acidification in coastal ecosystems.

Understanding the role of dominant producers in altering environmental conditions is critical to understanding how global change will impact ecosystems (Gilman *et al.*, 2010; Avolio *et al.*, 2019). Here, we studied the Oregon pine seaweed *Neorhodomela oregona*, a turf-forming alga which is the most abundant producer in tide pools in a high-latitude coastal ecosystem near Sitka, Alaska (Sorte and Bracken, 2015; Figure 1.1A). We studied *N. oregona* in three contexts: isolated in seawater-filled mesocosms, over a natural gradient of abundance in intact tide pools, and in a presence-absence comparison produced by a removal experiment. Based on previous studies with dominant algal species, we predicted that greater abundance of *N. oregona* would be associated with reduced water temperature, increased pH (i.e., reduced ocean acidification) during the day, and reduced pH during the night.

Materials and Methods

Study Site

To evaluate the role of the abundant alga *Neorhodomela oregona* (Doty) Masuda in driving local climate conditions, we conducted "removal" and "mesocosm" experiments at John Brown's Beach (57.05° N, 135.33° W) near Sitka, Alaska from 05 Jul 2019 to 27 Sep 2019. Southeast Alaska was an ideal location for this study as it has been subjected to relatively low levels of direct human disturbance yet is experiencing rapid environmental change (Stafford *et al.*, 2000). Air temperature in Southeast Alaska has increased by ~0.11°C per decade since 1830 (Wendler *et al.*, 2016; Jewett and Romanou, 2017), well above the global mean rate of 0.07°C per decade (since 1880; Blunden and Arndt, 2019). Sea surface ocean pH has declined by 0.03 units over a recent 15-year window (1991-2006) in the northeast Pacific waters off the Alaskan coast (Byrne *et al.*, 2010).

Removal Experiment

We selected 10 tide pools, which ranged 2.5 - 23.5 L in volume and 2.49 - 3.29 m in tide height (i.e., vertical position within the intertidal zone), which were separated by an average distance of 4 m, for the removal experiment. We began by assessing the physical characteristics of the experimental tide pools. We measured volume by pumping the water from a tide pool into a graduated bucket, and we assessed basal surface area of the pool, as well as *N. oregona* abundance, by placing a flexible mesh quadrat with 10 cm × 10 cm squares on the bottom of each tide pool (Bracken and Nielsen, 2004; Sorte and Bracken, 2015; Silbiger and Sorte, 2018). Tide heights (in meters above mean lower low water) for each pool were measured using a sight level, a surveying rod, and tidal predictions from the National Oceanic and Atmospheric Administration (2019). We assigned pools to treatment and control groups ($n = 5$, removal or control) by randomizing assignments until various physical and biological metrics did not vary between treatment and control (based on a generalized linear model with threshold of $p > 0.2$). Metrics included tide height, volume, basal surface area, percent cover of *N. oregona*, and species richness. We removed *N. oregona* from the treatment pools using scissors and by cutting as close to the substratum as possible without removing the holdfasts to avoid damaging surrounding organisms. We measured the wet biomass of *N. oregona* from each removal pool in the field before using that algal biomass in the mesocosm experiment (described below).

To assess the abundance of *N. oregona* and community composition in the tide pools, we conducted biodiversity surveys in the pools before and immediately after *N. oregona* removal (06 Jul – 19 Jul 2019), and then every two weeks until 27 Sep 2019 (for a total of seven surveys; Figures 1B & A1). During the surveys, we pumped water out of each tide pool, laid down a flexible mesh quadrat with 10 cm × 10 cm squares along the bottom, recorded the surface area covered by each sessile species (algae and invertebrates; 0.1 square or 10 cm^2 being the minimum measurement assigned for a species present in trace amounts) and counted all mobile invertebrates present (Bracken and Nielsen, 2004; Silbiger and Sorte, 2018). We identified organisms to the lowest possible taxonomic level: species when possible and genus when species were impossible to differentiate in the field (as with, e.g., *Littorina* *plena* and *Littorina scutulata*). In some cases, species were pooled and tallied together (e.g., "limpets" or "coralline algae").

To assess the impacts of *N. oregona* removal on tide pool pH, we conducted time-series samplings in the tide pools during the daytime and nighttime both before and after *N. oregona* removal (10 Jul – 16 Jul 2019; Figure A1). We measured temperature and salinity with a ProDSS Multiparameter Water Quality Meter (YSI, Yellow Springs, Ohio), and light intensity with a MQ-210 Underwater Quantum Meter (Apogee, Logan, Utah). Over the four sampling periods (day and night, both before and after removal), we took physical measurements at five time points over a ~2.5 h time series during low tide, sampling once every 30 min beginning immediately following isolation of the tide pools from the ocean. We also collected water samples on the first, third and fifth time points. The water samples were collected by hand-pumping 250 mL of water from the bottom of the tide pool into a vacuum flask, and then carefully siphoning the water into two 125 mL amber glass sample bottles to minimize gas exchange between the water sample and the atmosphere. All sample containers were rinsed three times with seawater prior to sample collection. We immediately preserved each water sample with 60 µL $HgCl_2$ and sealed them for later analyses to determine pH and total alkalinity.

We analyzed pH in the water samples from both experiments on a UV-1800 benchtop spectrophotometer (Shimadzu, Carlsbad, California), following best practices as described in Dickson *et al*. (2007). We divided each water sample into triplicate subsamples and analyzed them separately. We took an initial reading of each subsample at three wavelengths, added 50 µL of m-cresol dye, and mixed and re-analyzed the subsample at the same three wavelengths (Liu and Chan, 2011). We calculated the difference between the initial reading and the dye-added measurement, which we then used to calculate the pH value of each subsample. We took the mean of all subsamples with < 0.005 pH unit difference among them (subsamples outside that range were excluded) for each individual sample to produce a preliminary pH value. We then used CO2calc software (Robbins *et al*., 2010) to correct the preliminary pH value for total alkalinity (TA; analyzed as described below), salinity, temperature, and stoichiometric dissociation constants and calculate final pH on the total scale (Mehrbach *et al.*, 1973; Dickson and Millero, 1987; Kroeker *et al.*, 2021).

We analyzed the TA of the water samples with open-cell titrations (as in Silbiger and Sorte, 2018) on a T50 titrator with LabX software (Mettler-Toledo AG, Schwerzenbach, Switzerland). We measured a certified reference material (Marine Physical Laboratory, Scripps Institution of Oceanography, La Jolla, California) at the beginning of each session as a standard (acceptable range: ±1% error), following an established protocol for open-cell TA analysis (SOP 3b) (Dickson *et al.*, 2007; Silbiger and Sorte, 2018).

We conducted two additional samplings using a light-dark incubation method (Noël *et al.*, 2010; Bracken *et al.*, 2022) to assess how pH in the tide pools responded to differing light conditions. During these trials, we measured pH values across three time points using a HI9829 multiparameter meter with a 7609829 glass pH electrode (Hanna Instruments, Woonsocket, Rhode Island), which was calibrated using a Tris solution according to the best practices specified in SOP 6a by Dickson *et al.* (2007). We measured initial pH, remeasured following a ~30 min dark incubation period under an opaque, black plastic sheet, and collected a final measurement after a ~30 min light incubation period following the removal of the sheet.

Tide pool water temperatures were recorded every 5 min for the duration of the study by HOBO Pendant® Temperature/Light 64K Data Loggers (Onset Computer Corporation, Bourne, Massachusetts) anchored in the center of the pools. For comparison to our seawater temperature data, ambient air temperature data were sourced from the weather station at nearby Sitka Rocky Gutierrez Airport (Sitka, Alaska; < 1 km from the site) via CustomWeather, Inc. (2021).

We conducted all statistical analyses in R (R-version 4.0.4; R Core Team, 2013) using generalized linear mixed model (GLMM) repeated measures analyses and generalized linear models (GLM). We used a GLMM ('lmer' function; Bates *et al.*, 2015) to evaluate the effect of the removal treatment on *N. oregona* abundance (cover) in the experimental tide pools and track recovery over time. *N. oregona* cover was modeled as a function of the fixed factors of treatment, time (bi-weekly surveys), and treatment × time, with tide pool included as a random effect. We applied Kenward-Roger corrections to the GLMM to adjust the degrees of freedom to accurately reflect a repeated measures structure (Kenward and Roger, 1997; Kuznetsova *et al.*, 2017) and conducted post hoc pairwise comparisons on *N. oregona* cover using Tukey's HSD ('emmeans' function; Lenth, 2018).

To evaluate the effects of *N. oregona* on pH, we used the pH values at each of the three time points at which water was sampled to calculate the rate of pH change in tide pools (i.e., slope of the relationship between pH and time), and we compared abundances of *N. oregona* to the calculated rate of pH change during the daytime and nighttime sampling periods. Similarly, we used the field pH measurements from the light-dark trials (which were subsequently converted from mV to pH units) to calculate the rate of pH change between the initial measurement and the measurement taken at the end of the dark incubation period to represent the rates of pH change during the night (Bracken *et al.*, 2022), as well as the rate of pH change between the end of the dark incubation period and the final measurement (after a ~30 minute light incubation period) to correspond to the daytime water samplings. To assess the effects of *N. oregona* on water temperature in tide pools, we calculated the daily maximum water temperature for each tide pool over the full 11-week period following *N. oregona* removal.

We used GLMs ('glm' function in R) to assess the effects of *N. oregona* on pH. For intact pools prior to *N. oregona* removal, we evaluated the rate of pH change as a function of *N. oregona* area (in cm^2 of surface area per L of water volume), with the tide height of each pool, mean light in each pool (average of five time points; light was not included in night analyses as it was uniformly measured as 0 at night), and mean water temperature in each pool during the sampling (across the five time points) included as covariates. Identical analyses were conducted on the pH data from the light-dark trials, with light intervals substituted for daytime samplings and dark intervals replacing nighttime samplings, except that individual temperature measurements were used rather than a mean value. This analysis of intact tide pools (before the removal) was also run with assigned treatment group included as an additional factor, an analysis which confirmed that there was no initial difference in pH change between the treatment groups prior to removal ($p > 0.4$).

To test the effect of the *N. oregona* removal on pH, we evaluated the rate of pH change after removal as a function of treatment (removal vs. control), with tide height, mean water temperature, mean light, and pre-removal *N. oregona* area (in two-dimensional basal cover as measured in the biodiversity surveys) included as covariates, as well as an interaction between treatment and pre-removal *N. oregona* area. The interaction effect was included to assess whether the amount of *N. oregona* removed influenced the results, and we separately tested the effect of pre-removal *N. oregona* area in the removal and the control groups in the absence of other covariates to further investigate the role of initial *N. oregona* area as a potential driver of pH change. Finally, we conducted a combined analysis of the rates of pH change during day and night based on treatment, with pre-removal *N. oregona* area included as a covariate, as well as post-hoc tests comparing the treatment groups ('emmeans' function; Lenth, 2018). Assumptions of normality and homogeneity of variances were checked using the Shapiro-Wilk test and Levene's tests, respectively.

We evaluated the role of the total producer and consumer assemblage in driving pH by comparing the pH change in each pool to total consumer abundance and producer dominance. Total consumer abundance was calculated using the surface area of all basal invertebrate species and converting counts of mobile invertebrates to surface area (Table A1). We did this conversion using photographic image analysis (with ImageJ; Abràmoff *et al.*, 2004) of ~10 individuals per species of mobile invertebrate to find a mean surface area for an individual of each species and then multiplying that value by the number of individuals in each pool. For the few species we could not collect in the field, we substituted the measurements of species known to be of similar size (Table A1). We used 10 cm^2 as a minimum surface area for any mobile invertebrate species present, consistent with our methods used for the basal species in our community surveys. We then calculated consumer abundance as the total area per tide pool volume of non-photosynthetic species. Producer dominance, a metric used to represent the relative abundance of producers and consumers in an ecosystem, was calculated as the total abundance of all producer species (in two-dimensional basal cover from the biodiversity surveys) minus the total abundance of all consumers present. We modeled the rate of pH change as a function of total consumer abundance (cm^2 L^{-1}; 'glm' function) with tide height, mean water temperature, and mean light included as covariates, and ran similar analyses (with the same covariates included) on pH and producer dominance. Additionally, to account for the potential effects of the highly productive producer *Ulva* spp. (Sand-Jensen, 1988; Israel *et al.*, 1995), we also ran the pre-removal and post removal analyses of *N. oregona* abundance and pH with *Ulva* spp. abundance included as an additional covariate. The GLMs used in the removal experiment used a Gaussian distribution (identity link) except for the models of total consumer abundance and nighttime pH, which used a Gaussian distribution with an inverse link after the model failed to pass the Shapiro-Wilk test using an identity link.

To evaluate the effect of *N. oregona* removal on tide pool water temperature, we conducted a repeated measures analysis using a GLMM ('lmer' function, with Kenward-Roger corrections applied; Kenward and Roger, 1997; Bates *et al.*, 2015; Kuznetsova *et al.*, 2017) with data from the first month (prior to significant *N. oregona* recovery following the removal treatment; Figure 1.1) and, in a separate analysis, for the full 11-week duration of the study. Temperature was modeled as a function of the fixed factors of treatment, time (days), ambient air temperature, and an interaction between treatment and time, with tide pool included as a random effect.

Mesocosm Experiment

We set up mesocosms on the beach adjacent to the experimental pools at our John Brown's Beach study site on 13 Jul 2019. Mesocosms (12-L plastic tubs, n = 5 *N. oregona* addition and n = 3 control) were arrayed in two parallel lines of four, randomly arranged with regards to treatment. We added *N. oregona* biomass from one of the n = 5 removal tide pools to each of the n = 5 addition treatment mesocosms. Each mesocosm also contained the quantity of seawater equal to the volume of the pool from which the *N. oregona* was removed (except that 10 L of seawater was added to the two mesocosms corresponding to the removal pools with >10 L volume). We added 10 L of seawater but no *N. oregona* biomass to the control mesocosms.

We conducted water sampling using a time-series similar to the removal experiment (as described above), except that there was no "before" sample collection. We sampled the mesocosms after *N. oregona* addition during the daytime (4 h after algae were added to the mesocosms) and nighttime (10 h after addition; Figure A1). Prior to each time-series sampling, we simulated tidal inundation by flushing the mesocosms with seawater. We secured the algae in the mesocosms with wire mesh, poured the water out of the mesocosms, and used a graduated bucket to refill the mesocosms with the assigned volume of seawater. We took physical measurements at five time points over a ~2.5 h time series, sampling once every 30 min, and collected water samples on the first, third and fifth time points for later pH and TA analyses.

To test the effect of *N. oregona* on the rate of pH change in isolation, we applied GLMs (‘glm’ function) to the data from the mesocosms, for which we used two metrics of *N. oregona* abundance: source pool *N. oregona* surface area per mesocosm volume (cm^2 L^{-1}), which was the same metric we used for the algae in the field tide pools, and *N. oregona* biomass per mesocosm water volume (g L^{-1}), values that were only available for the mesocosms populated with the detached algae. We included mean water temperature as a covariate. We also used two GLMs (‘glm’ function) to analyze the combined day and night rates of pH change by treatment, with *N. oregona* biomass or source pool surface area of *N. oregona* included as a covariate, as well as post-hoc tests comparing the treatments in each model. Light measurements were not available for these analyses; however, the mesocosms were situated in an area of the beach with relatively homogenous light conditions (S. Mahanes, pers. obs.). Assumptions of normality and homogeneity of variances were checked using the Shapiro-Wilk test and Levene’s tests, respectively. All GLMs for the mesocosm pH analyses used a Gaussian distribution (identity link) except the analyses on the daytime sampling using biomass, which used a gamma distribution (inverse link) after the model failed to pass the Shapiro-Wilk test using a Gaussian distribution.

Results

Neorhodomela oregona was numerically dominant in the community in the experimental tide pools prior to the removal experiment (06 Jul – 09 Jul 2019; Figure A1), occupying 56% of tide pool surface area and accounting for 43% of total biotic cover on average (layering of multiple species allowed biotic cover to exceed 100%; Figure 1.1A). The removal treatment reduced *N. oregona* area in the manipulated tide pools relative to the unmanipulated controls ($F_{1,8}$ = 7.09, p = 0.029), particularly in the two surveys within 3 weeks following the removal treatment (pairwise comparisons; $p \leq 0.001$; Figure 1.1B). *N. oregona* recovered approx. 1 month after removal, regrowing in the treatment pools so that there was no significant effect of treatment on *N. oregona* abundance in the final four surveys of the study ($p \geq 0.075$).

When *N. oregona* was isolated in mesocosms, we found that greater *N. oregona* abundance led to more rapid acidification (i.e., reductions in pH) at night, a pattern that was significant using biomass as the abundance metric (t(5) = -2.946, p = 0.032; Figure 1.2A) but not when using area (t(5) = -2.154, p = 0.083; Figure 1.2B). Greater *N. oregona* abundance tended to be associated with increased pH when isolated during the day, a trend that was apparent when using biomass as the abundance metric (t(5) = -2.238, p = 0.075) but not area (t(5) = 0.186, p = 0.859) (Figure 1.2C, D). The addition of *N. oregona* amplified the difference in pH change between day and night, which was evident whether biomass ($F_{1,6}$ = 16.88, p = 0.0063) or area ($F_{1,6}$ = 16.81, p = 0.0064) was used (Table A2).

In field tide pools with a natural abundance gradient prior to the removal treatment, *N. oregona* abundance (using area as the abundance metric) was associated with the rate of pH change in the light-dark trial, leading pH change to be more negative during the light interval (t(5) = -2.63, p = 0.049; Table A3; Figure A2) and more positive during the dark phase (t(5) = 4.08, p = 0.006; Table A3; Figure A2). However, during our expanded time-series sampling, we did not detect a relationship between *N. oregona* abundance (using area as the abundance metric) and pH change either during the day (t(5) = -0.814, p = 0.453; Figure 1.3A) or night (t(5) = -1.497, p = 0.185; Figure 1.3C). Following removal, *N. oregona* abundance contributed to less negative rates of pH change during the dark phase of the light-dark trials (t(5) = 4.46, p = 0.021; Table A3; Figure A2), but there was no detectable relationship between *N. oregona* abundance and pH change in the water samplings during the day (t(5) = 0.262, p = 0.811; Figure 1.3B) or at night (t(5) = -0.538, p = 0.628; Figure 1.3D). However, interestingly, the amount of *N. oregona* removed (in area) was related to the rate of pH change in the removal pools during the day (t(5) = 3.475, p = 0.040; Figure 1.3B) but not at night (t(5) = 0.184, p = 0.866; Figure 1.3D). This effect was also apparent in the differences between treatments (control vs. removal) in the effect of pre-removal abundance (*N. oregona* area) on pH change during the day (initial *N. oregona* area × treatment interaction: t(5) = 4.740, p = 0.018; Figure 1.3B) but not at night (t(5) = -1.312, p = 0.260; Figure 1.3D). Pools with higher pre-removal *N. oregona* abundance acidified more quickly during the night, regardless of treatment (t(5) = -3.290, p = 0.030; Figure 1.3D). Overall, removing *N. oregona* did not impact pH change in tide pools, a pattern that was evident in both the separate (day: t(5) = -2.294, p = 0.106; night: t(5) = 1.901, p = 0.130; Figure 1.3B, D) and combined analyses ($F_{1,8}$ = 0.218, p = 0.653; Table A4).

pH dynamics in the pools were also not explained by the total and relative abundance of producers and consumers in the pools, nor were they explained by the abundance of a group of algal species, *Ulva* spp., which are known to be highly productive (p > 0.5; Table A5). We found no effect of consumer abundance (consumer area per pool water volume) on rates of pH change in intact tide pools or after removal, during the day or at night (p > 0.2). Producer dominance (producer % cover – consumer % cover; Silbiger and Sorte, 2018) also had no effect on the rate of pH change in the tide pools (p > 0.3; Figure A3).

pH in the tide pools was influenced by abiotic covariates. Temperature affected pH in the tide pools, with pH increasing faster in warmer pools during the day (p = 0.044) and warmer pools becoming more acidic at night (p = 0.053). Additionally, pH increased more rapidly in pools that received higher levels of light during the day (p = 0.033) and tide pools located higher in the intertidal zone acidified more slowly during the night (p = 0.030).

N. oregona presence was not associated with pool temperature: *N. oregona* removal did not affect maximum water temperature over the month following *N. oregona* removal ($F_{1,7} = 0.12$, $p = 0.741$; Figure A3), as well as the entire 11-week duration of the experiment ($F_{1,7} = 0.27$, $p = 0.620$; Figure A4). In fact, there was a tendency for pools with *N. oregona* present (control pools) to be ~0.8 °C warmer than those with *N. oregona* removed. Tide pool water temperature varied over time ($p < 0.001$), irrespective of treatment, and was strongly related to ambient air temperature ($p < 0.001$).

Discussion

The dominant seaweed *N. oregona* showed the capacity to alter the rate of pH change in isolation. However, we did not detect a consistent effect of *N. oregona* abundance or its removal on pH in intact tide pools within the context of the natural community, despite a similar experimental design to previous studies (e.g., Bracken *et al.*, 2018). Biotically-driven declines in seawater pH are generally associated with respiration (Krause-Jensen *et al.*, 2015; Bracken *et al.*, 2018), while a dominant producer would be expected to primarily raise pH via photosynthesis (Wahl *et al.,* 2018). Our findings suggest that dominant primary producers do not necessarily drive local pH conditions per se, but rather that the impact of a dominant producer on seawater pH likely depends on traits of the producer itself, the identity and abundance of the other species present, and environmental context.

Our finding that *N. oregona* increased the rate of acidification at night in isolation more than it increased pH during the day in mesocosms suggests that, to the degree that it influences tide pool pH conditions, *N. oregona* may be more strongly impacting these conditions via respiration than photosynthesis. This finding is supported by the results of the light-dark trials, with greater abundance of *N. oregona* corresponding to light and dark rates of pH change which were closer to zero than highly positive or negative, respectively. These observations run counter to expectations that the primary effect of a dominant producer on pH would be positive and photosynthesis-driven (Zou *et al.,* 2011; Pacella *et al.,* 2018). One possibility is that under conditions of low light and temperature, a producer-dominated tide pool could become heterotrophic during the day (Lowe *et al.*, 2019). We found that both light levels and temperatures were lower during the mesocosm measurements: light levels were ~524 µmol m^{-2} s^{-1} prior to removals vs. ~199 µmol m^{-2} s^{-1} during the mesocosm measurements, and temperature was 20.7 °C prior to removals vs. 18.9 °C during the mesocosm experiment. However, light levels were more than sufficient to maximize photosynthetic rates in this species (M. Bracken, *unpublished data*; Bracken *et al*., 2022), so the patterns we observed likely reflect low productivity of the dominant species in the pools.

Despite our finding that *N. oregona* impacts pH in isolation, we were surprised to discover that this role of *N. oregona* in driving pH dynamics did not generally extend to samplings in natural ecosystems. As the effects of photosynthesis and respiration on pH have been well-documented, the absence of the predicted effect of a dominant producer on pH is most likely attributable to lower-than-expected rates of these processes. As noted above, the absence of an effect may be related to the specific photosynthetic traits of *N. oregona*. Whereas *N. oregona* can substantially increase pH in the water column (to a maximum pH of 10.2, which was 0.7 units higher than the average maximum of comparable red algae species; Murru and Sandgren, 2004), this ability may be limited to springtime periods of high growth. The seasonal senescence of *N. oregona* may be contributing to the absence of an effect. Sampling was conducted after the summer solstice, and *N. oregona* steadily declined in abundance throughout the summer, suggesting that the *N. oregona* may have already begun to senesce at the time of the experiment, adversely impacting its metabolic rates. Any of these factors may have contributed to reduced photosynthesis and respiration, resulting in a minimal effect of *N. oregona* on tide pool pH, especially in the context of a diverse ecosystem, despite being the most abundant species present. Overall, our findings indicate that while certain dominant marine producers can raise local pH (Bracken *et al.*, 2018; Lowe *et al.*, 2019; Ricart *et al.*, 2021), the pattern is not universal, and marine producers should not be assumed to raise coastal pH amid ongoing ocean acidification.

We also found that *N. oregona* had no effect on water temperature, suggesting that it is not mitigating thermal stress for the rest of the tide pool community. This is in contrast to previous work showing that dominant terrestrial plants can affect temperature stress for surrounding organisms, leading to increases in associated species survival and biomass, especially during extreme climate events (Holzapfel and Mahall, 1999; Lloret *et al.*, 2012; Morelli *et al.*, 2017). In marine systems, dominant producers can reduce the impacts of thermal stress and desiccation on other species and increase biodiversity (Schiel, 2006; Lilley and Schiel, 2006; Ape *et al.*, 2018) by forming complex structures that shelter other species (Shelton, 2010; Wilson *et al.*, 2015). These examples, however, involve intertidal algae that prevent desiccation on emergent rock surfaces or, in the case of *Phyllospadix* spp., a bright-green seagrass which floats near the surface in tide pools and actively shades the water column (Shelton, 2010). In contrast, *N. oregona* inhabits a fully submerged habitat but often does not grow tall enough to reach the surface of the water, limiting its ability to provide shade. In fact, if anything, *N. oregona* tended to make the tide pools warmer, potentially due to its dark coloration absorbing solar radiation more readily than other surfaces.

There is an assumption, typified by the "mass ratio hypothesis" (Grime, 1998), that the abundance of a species will necessarily relate to ecological impact, and there is support for dominant species affecting small-scale environmental conditions across ecosystems, but there are also compelling arguments that the role of dominant species may be overstated. Arguments against this dominant species paradigm include the likelihood of publication bias against negative results (i.e., studies where dominant species have little to no effect). Mariotte

(2014) contends that non-dominant, or subordinate, species may also have substantial impacts in an ecosystem, but that these effects are less understood due to the preferential study of dominant species and a methodological focus on randomly assembled communities, or that the effects of subordinate species may only be apparent when multiple species are clustered into functional groups. There are fewer studies explicitly focusing on non-dominant (e.g., rare) species, but, where studied, non-dominant species can mitigate the effects of drought on soil communities (Mariotte *et al.*, 2015), strongly affect community composition (Garbin *et al.*, 2016), and stabilize food webs (Shao *et al.*, 2016). Bracken and Low (2012) found that the removal of rare basal species, comprising <10% of sessile biomass in total, lead to a ~45% decline in consumer biomass, while the removal of a similar amount of a dominant basal species had no effect on consumer biomass. This growing body of research suggests that dominant species do not always play dominant ecological roles and that a focus on dominant species can overshadow important roles of subdominant species.

For example, as shown here, dominant producers may not drive pH dynamics including mitigating climate change in marine ecosystems. While some dominant producers have been shown to increase pH via photosynthesis and facilitate calcification (Bracken *et al.*, 2018; Lowe *et al.*, 2019; Punchai *et al.*, 2020), recent studies complicate the picture, and more research is necessary to understand how increased pH variation affects associated species such as corals and other calcifying organisms (Rivest *et al.,* 2017; Ricart *et al.,* 2021). We found that neither consumer abundance nor producer dominance, reflective of the abundance of producers relative to consumers, affected pH, suggesting that at this coarse scale, the abundance of these functional groups was not a primary driver of pH change in these tide pools during our study. At the species level, Pacific blue mussels (*Mytilus trossulus*) were abundant in the tide pools (Figure 1.1A) and *Ulva* spp., the third most abundant producer present, can be highly productive (Sand-Jensen, 1988; Israel *et al.*, 1995);

however, our analysis suggested that *Ulva* spp. was not responsible for pH dynamics on its own. Mussel species can affect water chemistry via respiration and calcification, reducing seawater pH and total alkalinity (Ninokawa *et al.*, 2020). Other producers are likely altering water chemistry in the tide pools through photosynthesis, which may have accelerated during the experiment if the removal of *N. oregona* increased the available light (Sand-Jensen, 1988). Cycles of pH changes in coastal ecosystems have been related to changes in dissolved oxygen associated with photosynthesis and respiration (Bracken *et al.*, 2018; Lowe *et al.*, 2019; Punchai *et al.*, 2020; Ricart *et al.*, 2021), the balance of which may be driven by which species are present or abundant. Additionally, shifts within a single ecosystem between autotrophic (i.e., primarily photosynthesis) and heterotrophic (i.e., primarily respiration) states, as appear to have occurred in the experimental tide pools, have been observed in conjunction with shifts in pH (Lowe *et al.*, 2019). Further investigation of how community composition affects pH is crucial to understanding how coastal systems will be affected by ocean acidification, particularly as habitat-structuring coastal species (e.g., macroalgae beds or seagrass meadows) are declining in abundance (Duarte *et al.*, 2013). Furthermore, our findings on the impacts of a dominant species differed when they were based on studies in mesocosms versus intact ecosystems, highlighting the importance of corroborating mesocosm-based results with field studies (Stachowicz *et al.*, 2008; Doo *et al.*, 2020).

In conclusion, we found that there was not a consistent effect of a dominant marine producer on temperature or pH in a natural system across time, despite the presence of an effect on pH in isolation. These results provide a counterexample to studies which conclude that primary producers, particularly in dense aggregations, are able and poised to mitigate climate change and ocean acidification in some coastal ecosystems. To address the impacts of global change, we need to better understand the extent to which biological feedbacks can minimize the local effects of climate change, and this should expand beyond just species abundance and dominance to consider species- and community-level traits.

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Figures

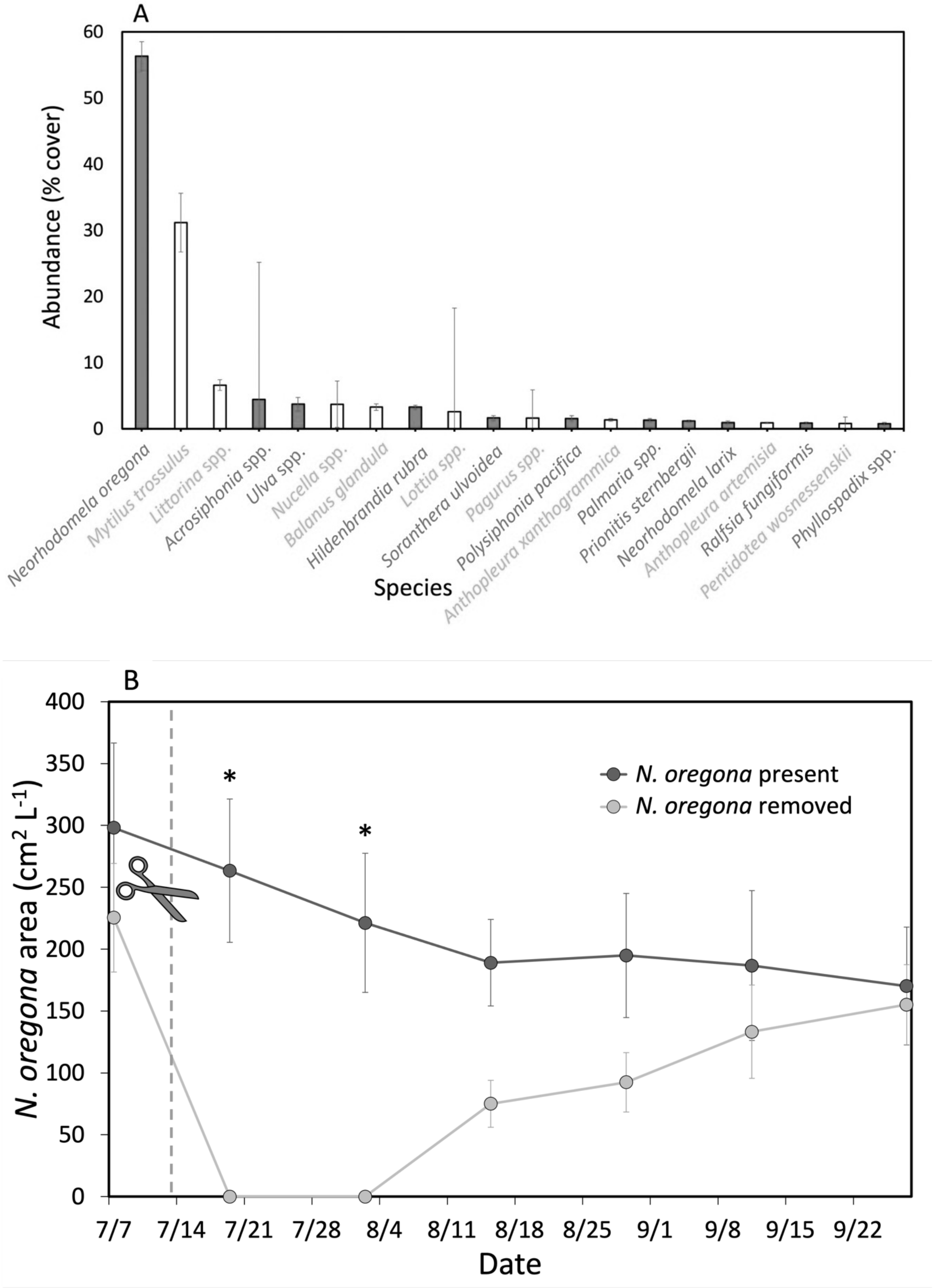

Figure 1.1. Abundance of *Neorhodomela oregona* and other tide pool species. (A) *N. oregona* was the most abundant species in the N = 10 tide pools, and 11 of the 20 most

abundant species were producers (gray), while 9 were consumers (white). (B) The removal (date indicated by a dashed line) of *N. oregona* reduced its area in the N = 5 removal treatment tide pools (light gray) relative to the N = 5 control pools (dark gray). *N. oregona* recovered within 1 month in the removal pools, and the two treatment groups had similar *N. oregona* densities for the final four surveys of the study. Each data point represents mean (±SE) abundance and * in (B) indicates significant differences between treatment groups.

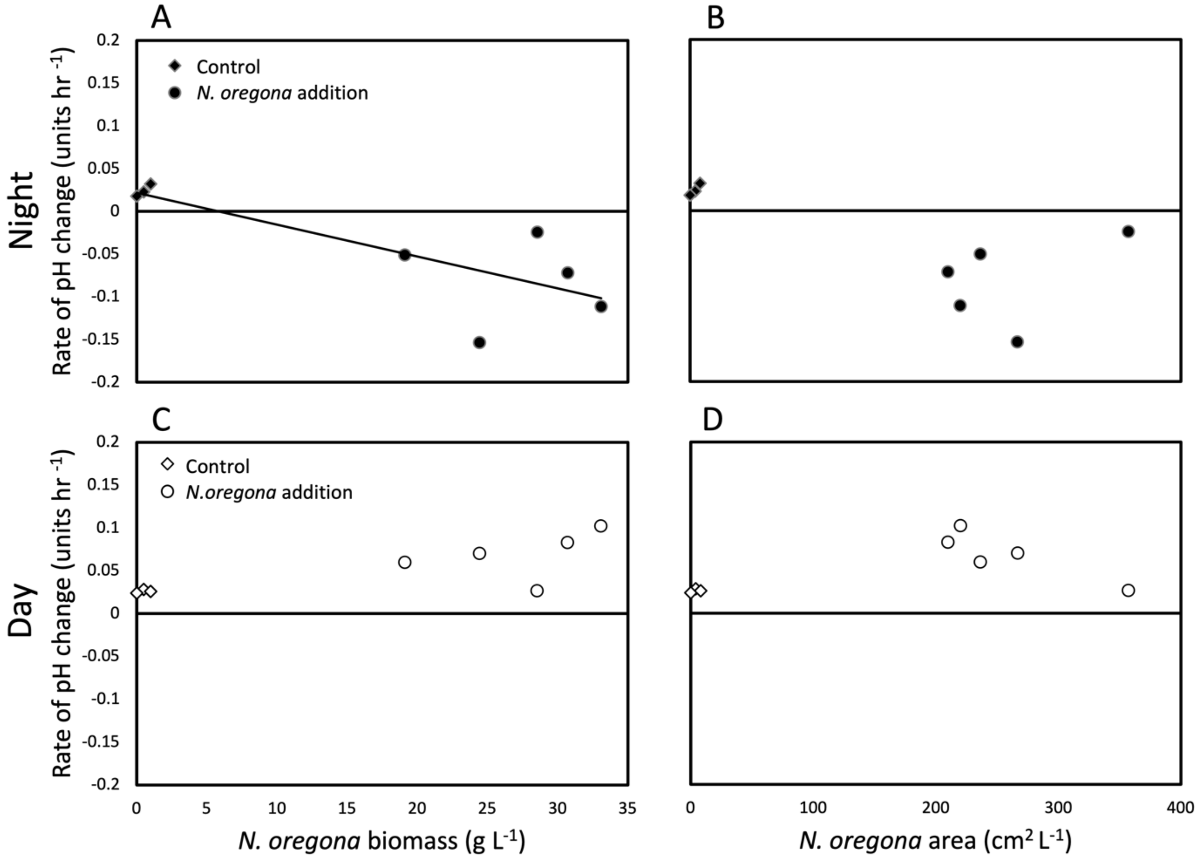

Figure 1.2. Relationships between *Neorhodomela oregona* abundance and the rate of pH change in experimental mesocosms. (A) Mesocosms with greater biomass (g L^{-1}) of *N. oregona* became more acidic at night, but (B) there was no detectable relationship between *N. oregona* area (cm^2 L^{-1}) and pH change during the night. Neither (C) biomass nor (D) area of *N. oregona* was significantly associated with pH change during the day. Each data point represents a single mesocosm, either with *N. oregona* added (N = 5, circles) or controls with no *N. oregona* (N = 3, diamonds).

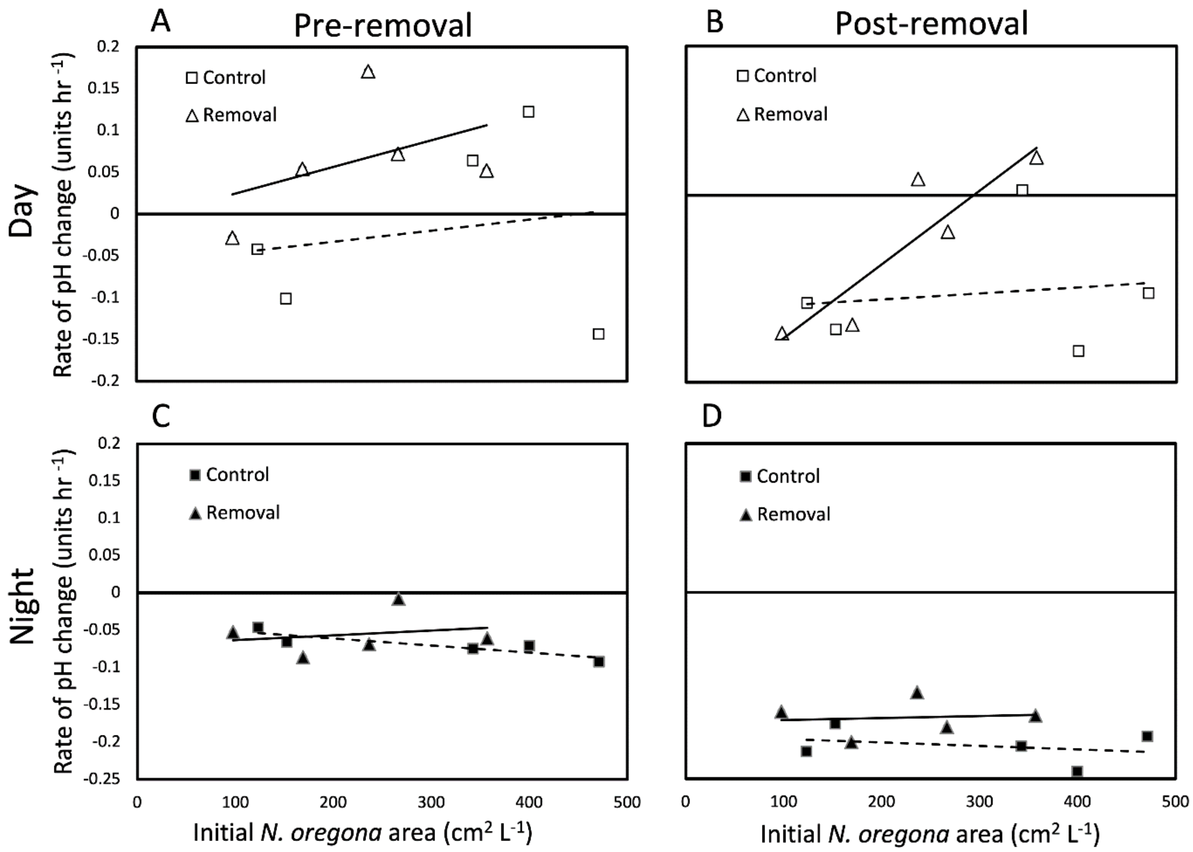

Figure 1.3. Relationships between pre-removal *Neorhodomela oregona* abundance and the rate of pH change in tide pools in the field, including (A) pre-removal and (B) post-removal changes in pH during the day and (C) pre-removal and (D) post-removal changes at night (with solid and dashed lines reflecting trends in the removal and control groups, respectively). There was no effect of *N. oregona* abundance on pH change in intact, pre-removal tide pools during the day or at night. *N. oregona* removal interacted with initial *N. oregona* abundance to increase pH more rapidly during the day, while tide pools with greater initial *N. oregona* abundance tended to acidify more quickly at night following removal, irrespective of treatment. Each data point represents a single tide pool during a single sampling.

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CHAPTER 2

The functional effects of a dominant consumer are altered following the loss of a dominant producer

Submitted to Functional Ecology

Abstract

Human impacts on ecosystems are resulting in unprecedented rates of biodiversity loss worldwide. The loss of species results in the loss of the multiple roles or functions (i.e., “ecosystem multifunctionality”) that each species plays. A more comprehensive understanding of the effects of species on ecosystem multifunctionality is necessary for assessing the ecological impacts of species loss. We studied the effects of two dominant intertidal species, a primary producer (the seaweed *Neorhodomela oregona*) and a consumer (the shellfish *Mytilus trossulus*), on twelve ecosystem functions in a coastal ecosystem, both in undisturbed tide pools and following the removal of the dominant producer. We modified analytical methods used in biodiversity-multifunctionality studies to investigate the potential direct and indirect effects of individual dominant species on ecosystem function. The effects of the two dominant species from different trophic levels tended to differ in directionality (+/-) consistently (92% of the time) across the twelve individual functions considered. Using averaging and multiple threshold approaches, we found that the dominant consumer – but not the dominant producer – was associated with ecosystem multifunctionality, and the relationship differed depending on whether the dominant producer was present. Our findings suggest that interactions among dominant species can drive overall ecosystem function. The results of this study highlight the utility of methods previously used in biodiversity-focused research for studying functional contributions of individual species, as well as the importance of species abundance and identity in driving ecosystem multifunctionality, in the context of species loss.

Keywords

algae – dominant species – ecosystem function – intertidal – multifunctionality – mussel

Introduction

Global change is driving biodiversity loss worldwide, making it more important than ever to understand the different roles that individual species play in ecosystems (Bellard et al., 2012; Mantyka-Pringle et al., 2012;Valiente-Banuet et al., 2015). Whereas most previous biodiversity research focused on the effects of species loss on one ecosystem function (e.g., productivity; Cardinale et al., 2007), it is important to recognize that species simultaneously mediate multiple functions (Hector and Bagchi, 2007; Gamfeldt et al., 2008). Quantifying the role of a species in an ecosystem – and understanding the functional consequences of loss – requires evaluating that species' simultaneous contributions to multiple ecosystem functions (e.g., net primary productivity, decomposition, nutrient cycling), also known as "ecosystem multifunctionality" (Manning et al., 2018).

Much of the multifunctionality research conducted to date has focused on the effect of community-level biodiversity on ecosystem functions (Tolkkinen et al., 2013). Community diversity has been shown to strongly influence ecological function, both at the scale of single functions and overall multifunctionality within an ecosystem (Hector and Bagchi, 2007; Zavaleta et al., 2010). Researchers have identified a combination of sampling and species identity effects, by which individual species, rather than the number of species per se, are the primary drivers of the biodiversity-multifunctionality relationship (Cardinale et al., 2006; Slade et al., 2017; Brun et al., 2022). Individual species, particularly those that are highly abundant in an ecosystem, have emerged as potential key drivers of ecosystem multifunctionality (Hillebrand et al., 2008; Lohbeck et al., 2016; Fields and Silbiger, 2022). Applying methodologies designed for biodiversity-multifunctionality studies (Byrnes et al., 2014) may allow us to further elucidate the functional effects of numerically dominant species.

Dominant species may serve as primary drivers of ecosystem function or, if they are weak functional contributors, potentially limit ecosystem multifunctionality (Hillebrand et al., 2008; Orwin et al., 2014; Wohlgemuth et al., 2016). Dominant species, defined based on their abundance (e.g., >12% relative abundance in community; Mariotte et al., 2015), display a wide variety of forms across ecosystems, from the northern red oak (*Quercus rubra*) in the forests of the northeastern United States (Ellison et al., 2019) to red oat grass (*Themeda triandra*) in the shrublands of South Africa (Cowling, 1983). The more abundant a species is in an ecosystem, the more likely it is to significantly influence local environmental conditions and overall ecosystem function (Tolkkinen et al., 2013; Lohbeck et al., 2016; Wohlgemuth et al., 2016; Ellison, 2019; Brun et al., 2022). This phenomenon is typified by the "mass ratio hypothesis", which states that the functional traits of dominant species in an ecosystem will strongly influence ecosystem processes (Grime, 1998; Orwin et al., 2014). Understanding how dominant species contribute to ecosystem function, as well as the possibility that they limit overall ecosystem function by crowding out other species (Tingley et al., 2002; Altieri et al., 2009), is critical for understanding how climate change and biodiversity loss will impact ecological function (Hillebrand et al., 2008; Tolkkinen et al., 2013; Giling et al., 2019).

Many ecosystems contain multiple dominant, foundation, and/or habitat-forming species, and the interactions between these species may affect ecosystem functioning (Angelini et al., 2011; Austin et al., 2021). Altieri et al. (2007) documented interactions between dominant species on cobble-beaches: where cordgrass aggregations and ribbed mussel beds overlap, they interact to produce a shaded, wave-sheltered habitat that supports higher species diversity than the surrounding area. The functional complementarity of some pairs of dominant species, as well as the potential facilitation of one dominant species by another (Angelini et al., 2011), raises the question of how an ecosystem would be affected by the loss of one of multiple dominant species present (Angelini and Silliman, 2014). If the dominant species compete (e.g., for space; Yakovis et al., 2008), have a facilitative relationship (e.g., through complementary nutrient cycling; Aquilino et al., 2009), or exert an interactive effect on the ecosystem (e.g., by forming complex habitat; Altieri et al., 2007), the loss of one species may affect the other dominant species and ultimately ecosystem function. In this study, we investigated the contributions of, and potential interactions between, a pair of dominant species – the algal producer *Neorhodomela oregona* and bivalve consumer *Mytilus trossulus* – to critical functions in coastal ecosystems.

Many of the key ecological processes in coastal ecosystems can be grouped into three sets of functions: productivity, nutrient cycling, and effects on water chemistry (Tolkkinen et al., 2013). Primary productivity is the fixation of carbon via photosynthesis and can be measured though oxygen production and related chemical fluxes (Bracken and Williams, 2013). Primary productivity has been strongly associated with the functional traits of dominant species (Bruno et al., 2006; Mouillot et al., 2011), raising the possibility that the association between biodiversity and productivity is predominantly an effect of these abundant, functionally unique species being included more frequently in more biodiverse samples (i.e., sampling effect; Aarssen, 1997; Huston, 1997).

Primary production, itself, can be limited by nutrient availability (Bruno et al., 2006), which positions the cycling of ammonium, nitrate, nitrite, and phosphate as critical to the overall functionality of coastal ecosystems (Vanni, 2002; Bracken and Williams, 2013). While nitrate and phosphate can reach high concentrations in coastal waters, ammonium – which is typically at low concentrations in seawater due to preferential uptake –often accumulates in tide pools, due to excretion by invertebrates (Bracken and Nielsen, 2004; Aquilino et al., 2009; Bracken and Williams, 2013). Local-scale accumulation of ammonium and phosphate in coastal ecosystems has been directly tied to the abundance of mussels

(Asmus et al., 1995; Bracken and Nielsen, 2004), which corroborates findings that nutrient-limited seaweeds are more abundant and grow more rapidly on mussel beds than on other intertidal surfaces (Bracken, 2004; Aquilino et al., 2009). The dominance of different species in otherwise similar communities can lead to divergence in nutrient cycling rates among communities (Bracken and Williams, 2013; Wohlgemuth et al., 2016). Because seaweeds can account for most of the primary productivity in temperate coastal ecosystems (Mann, 1973) and can strongly influence nutrient fluxes in these ecosystems (Bracken and Nielsen, 2004), understanding the contributions of dominant seaweeds to individual ecosystem functions and ecosystem multifunctionality is critical for anticipating impacts of ongoing species loss.

Dominant species in coastal ecosystems may drive changes in other characteristics of water chemistry, with implications for rates of ocean acidification (Kroeker et al., 2013; Aiuppa et al., 2021). Marine producers can raise seawater pH via photosynthesis (Bracken et al., 2018) as well as increase pH variation over diel cycles, which may help mitigate local-scale acidification in marine ecosystems (Camp et al., 2016; Wahl et al., 2018). However, producers may also reduce pH in the absence of light, when photosynthesis ceases but respiration continues, shifting the balance from a reduction of inorganic carbon in the water column to a net increase and contributing to further acidification (Krause-Jensen et al., 2015; Silbiger and Sorte, 2018; Mahanes et al., *in press*). Producer-driven changes in pH can affect other species in the ecosystem, particularly calcifying species (e.g., mussels and oysters; Semesi et al., 2009; Wahl et al., 2018), which are disproportionately impacted because calcification, the process in which organisms absorb calcium carbonate from the water column to build body structures, can be reduced at low pH (Kroeker et al., 2013). Acidification shifts the chemical equilibrium toward calcium carbonate dissolution, raising the metabolic cost of calcification for organisms or preventing calcification altogether

(Andersson and Gledhill, 2013); therefore, robustly photosynthetic species can serve an important function by raising seawater pH.

We assessed the effects of dominant species from different trophic levels on individual ecosystem functions, groups of functions, and overall multifunctionality in coastal systems, both when acting in concert and after simulated species loss. We conducted a removal experiment on the dominant algal producer *N. oregona* in tide pools where the mussel *M. trossulus* was also highly abundant and applied a methodology adapted from biodiversity-multifunctionality studies to measurements of twelve ecological functions. Based on the results of past studies on comparable seaweed and mussel species (e.g., Mahanes et al., *in press*), we predicted that the dominant producer species would contribute to ecosystem productivity, raise pH, increase calcification, and drive nutrient absorption, while the dominant consumer was expected to increase respiration, reduce pH, increase calcification, and drive nutrient accumulation.

Materials and Methods

Study site

We studied effects of the dominant Oregon pine seaweed (*Neorhodomela oregona* [Doty] Masuda) and Pacific blue mussel (*Mytilus trossulus* Gould) on ecosystem function in a coastal ecosystem. *N. oregona* is a turf-forming seaweed which is numerically dominant in tide pools at John Brown's Beach on Japonski Island, Sitka, Alaska, USA (57.06°N, 135.37°W), comprising >55% of total tide pool surface area (Mahanes et al., *in press*). *N. oregona* is common in tide pools throughout Southeast Alaska, and its range spans the North Pacific from California to parts of Japan and Russia (Lindeberg and Lindstrom, 2010). *M. trossulus* is a sessile mussel species, generally smaller than its relatives *M. californianus* and *M. galloprovincialis*, which can form dense aggregations and is commonly found along the coastline from California to Alaska, USA (Braby and Somero, 2006). *Mytilus trossulus* is a dominant species in tide pools at John Brown's Beach, accounting for >30% of tide pool surface area (Mahanes et al., *in press*). The coexistence of these two species provided an opportunity to investigate the effects of and interactions between two numerically dominant species across a set of tide pools which function as individual, largely self-contained ecosystems when isolated during low tide (Sorte and Bracken, 2015). To quantify the degree to which a dominant producer and a dominant consumer drive ecological function, we conducted a species-removal experiment at our study site from July 5 to July 19, 2019.

Tide pool physical characteristics

We selected 10 tide pools with similar dimensions and tide height (i.e., position within the intertidal zone) for this study. We measured the physical characteristics of the tide pools by: (1) pumping the water from a tide pool into a graduated bucket to assess volume, (2) placing a flexible mesh quadrat with 10 cm x 10 cm squares on the bottom of each tide pool to measure basal surface area (Bracken and Nielsen, 2004; Sorte and Bracken, 2015; Silbiger and Sorte, 2018), and (3) using a sight level and a surveying rod to gauge tide height in meters (above mean lower-low water). We assigned experimental treatments to the tide pools by repeatedly randomizing assignments until volume, surface area, tide height, *N. oregona* abundance (calculated as percent cover), and species richness (calculated from community survey data, see below) did not vary between treatments (N = 5, removal or control, based on a generalized linear model with threshold of $p > 0.2$). The abundance of *N. oregona*, *M. trossulus*, and all other species present were assessed via biodiversity surveys following methods used by Bracken and Nielsen (2004; Supplemental Appendix 1).

Ecosystem function data collection

We conducted light/dark productivity trials, as well as time series water samplings during the day and night, on the unmanipulated experimental tide pools between July 9-12, 2019 (for a timeline of the experiment and sampling, see Figure S1). On July 13, we initiated the manipulations and removed *N. oregona* from the removal treatment tide pools with scissors, cutting as close to the holdfast as possible without damaging any surrounding species. We then repeated the productivity trials and water samplings on the full set of tide pools between July 14-16, 2019 (Figure S1).

Light/dark productivity trials

To assess impacts of these dominant species on the productivity of the tide pools, we conducted light/dark incubation experiments before and after the removal of *N. oregona* (Noël et al., 2010; Sorte and Bracken, 2015; Bracken et al., 2022; Figure S1). We took initial dissolved oxygen measurements from each tide pool with a ProDSS Multiparameter Water Quality Meter (YSI, Yellow Springs, Ohio, USA). We then covered each pool with an opaque, black tarp for 30 min of dark incubation. We repeated the measurements and then removed the tarps for a 30 min light-incubation period, at the end of which we took a third and final set of measurements.

Water sample collection

To assess impacts of these dominant species on tide pool water chemistry and nutrient fluxes, we conducted paired time-series samplings (day and night) before and after *N. oregona* removal (Figure S1). We sampled across three time points over a ~2.5 h time series following isolation of the tide pools from the ocean, collecting water chemistry samples at each time point (Silbiger and Sorte, 2018) by hand-pumping 250 mL of water from the bottom of the tide pool into a vacuum flask, and then siphoning the water into two 125 mL amber glass sample bottles to minimize gas exchange. We added the remaining water to a 50 mL plastic tube for nutrient analysis. All containers were rinsed three times with seawater before use. We immediately added 60 µL $HgCl_2$ to preserve each 125 mL water chemistry sample and then sealed the sample bottles for later pH and total alkalinity analysis. Nutrient samples were stored on ice while in the field and then frozen at -20 °C prior to analysis.

At each time point, we also measured salinity and temperature with a ProDSS Multiparameter Water Quality Meter (YSI, Yellow Springs, Ohio, USA) and light intensity with a MQ-210 Underwater Quantum Meter (Apogee, Logan, Utah, USA) in each pool. Salinity and temperature data were collected for later use in calculating pH values, and light was recorded to document any changes in weather between sampling dates that might affect biological processes. Samples were processed for pH and total alkalinity according to protocols outlined by Dickson et al. (2007) and nutrient concentrations were analyzed using methods of Bracken et al. (2018; Supplemental Appendix 1).

Data analysis

Calculated metrics

We calculated rates of change (i.e., slopes) for all water chemistry metrics collected over the three-sample time series, which included pH, ammonium, phosphate, and nitrate + nitrite. We calculated calcification rate using the formula below (Silbiger and Sorte, 2018).

$$\mathrm{NEC} = (\Delta TA \cdot \rho \cdot V) / (2 \cdot SA \cdot t)$$

where ΔTA is the change in total alkalinity between the first and third time points in the sampling (mmol kg^{-1}), ρ is the density of seawater (1023 kg m^{-3}), V is the water volume of the tide pool (m^3), SA is the bottom surface area of the tide pool (m^2), and t is the time elapsed (h). The 2 is included because a single mole of $CaCO_3$ is formed for every two moles of TA.

We used the dissolved oxygen measurements from the light/dark experiments to calculate net community productivity (NCP) and respiration (R) in the tide pools according to the formulas below (Noël et al., 2010; Sorte and Bracken, 2015).

$$NCP = \Delta[O_2]_{light} / \Delta t_{light}$$

$$R = | \Delta[O_2]_{dark} / \Delta t_{dark} |$$

In the formulas, $\Delta[O_2]$ is the change in dissolved oxygen concentration (mg O_2 L^{-1}), Δt indicates change in time, and “dark” and “light” correspond to the covered and uncovered incubation periods, respectively.

Analyses

All statistical analyses were conducted in R (R-version 4.0.4; R Core Team, 2013) using linear models (lm), mixed-effects models (lmer), and the *multifunc* package (Byrnes et al. 2014). We adapted the *multifunc* R package by substituting *N. oregona* and *M. trossulus* abundance for species richness to gauge the effect of individual species rather than overall community diversity (Figures 1-4, S2-S6). We used liner models to compare the abundances of the dominant consumer to dominant producer abundance, the total abundance of non-dominant producers, and the most abundant individual non-dominant producer to ensure that any functional effects were not confounded by abundance correlations among the species.

We analyzed the effect of *N. oregona* (the dominant producer) and *M. trossulus* (the dominant consumer) abundance on 12 ecosystem functions in intact tide pools, as well as the impact of removing *N. oregona* on the functional effect of *M. trossulus*. For each analysis, we began by calculating the effect of the dominant species abundances on each individual functional response in the tide pools (Giling et al., 2019). Next, we standardized the data by dividing each functional response value by the greatest value observed for that function and then calculating the proportion of that maximum value for each functional response (Byrnes et al., 2014; Moi et al., 2021). This standardization method enabled the aggregation of multiple functional responses into values of average functionality (Mouillot et al., 2011) across the suite of ecosystem functions we studied, which we calculated by taking the mean value of all standardized functional values within a single tide pool during a phase of the experiment (pre-removal or post-removal). We used the averaging approach on all twelve functions combined as well as subsets of functions, including productivity (net primary productivity and respiration), water chemistry (the rate of pH change and net calcification; both during day and night for four total responses), and nutrient cycling (fluxes of nitrate and nitrite, ammonium, and phosphate; each during day and night for six total metrics).

We also used the standardized data to determine the number of functions in each pool which exceeded the set threshold (Zavaleta et al., 2010), as well as expanded that approach to include all possible thresholds from 5%-99% (Byrnes et al., 2014). In this multiple threshold approach, the output is the range of potential thresholds for which there is a significant effect of the driver - in this case either dominant producer or dominant consumer abundance - on the number functions exceeding the threshold. A strong dominant species effect is indicated when there is a wide range of thresholds at which its abundance is important in determining the degree of multifunctionality (i.e., the number of functions exceeding a threshold) while a narrow band of significance indicates a weak or negligible effect.

In the analyses on individual functions, averaged functions, and multiple thresholds, we assigned directionality to the response metrics to align with the predicted effects of a dominant producer during the day: higher NCP and respiration were indicated by more positive values, as were higher rates of ecosystem calcification, more positive rates of pH change, and greater nutrient uptake (Table S1). In a second analysis, we repeated the averaging and threshold calculations with all functions denoted as positive (i.e., factors which showed negative trends with dominant producer abundance were ‘reflected’ to become positive; Austin et al., 2021; Figure S2, Figures S4-S6, Table S1). This was done to remove the possibility that multiple functions would counteract each other based on differing directionality of impact, leading to an underestimate of the effect of the dominant producer on groups of related functions (Giling et al., 2019).

We evaluated the effect of removal of the dominant producer on the functional role of the dominant consumer as follows. Using the lme4 and lmerTest packages (Kuznetsova et al., 2017), we ran mixed effects models with each individual ecosystem function as the response and the following factors: dominant consumer abundance (continuous), dominant producer removal treatment (control vs. removal), and time (before vs. after the removal treatment), as well as the consumer abundance : treatment, treatment : time, and consumer abundance : treatment : time interactions; tide pool was included as a random effect. The three-way interaction (mussel abundance : treatment : time) is of particular interest, as it represents the potential shift in dominant consumer function when the dominant producer is present versus absent. The two-way interaction between consumer abundance and time was not significant across functions and was therefore removed from the analysis. Data were log- or inverse-transformed where necessary (daytime ammonium and phosphate data, respectively) to satisfy the normality assumptions of mixed models.

Results

Opposing functional effects of the dominant producer and dominant consumer

We found that increases in both dominant producer and dominant consumer abundance were associated with changes in individual ecosystem functions in almost uniformly opposite directions (Figure 2.1). Increases in dominant producer abundance were associated with changes in two of the twelve ecosystem functions, reducing the respiration rate ($F_{1,8} = 9.34$, $p = 0.016$) and increasing the rate of daytime net ecosystem calcification

($F_{1,8}$ = 10.01, p = 0.013). Increases in dominant consumer abundance were associated with changes in three of the twelve ecosystem functions studied, including increases in net community productivity ($F_{1,8}$ = 5.63, p = 0.045) and respiration ($F_{1,8}$ = 6.49, p = 0.034), as well as a reduction in the rate of daytime net ecosystem calcification ($F_{1,8}$ = 7.01, p = 0.029). Virtually all (11/12) of the relationships between functions and dominant producer abundance were in the opposite direction from the trends of the relationships between those same functions and dominant consumer abundance. The only exception was the rate of change in phosphate concentrations during the day, though it was not significantly related to the abundance of either species (p > 0.5 for *N. oregona* and p > 0.9 for *M. trossulus*). The slopes of the relationships between dominant producer abundance and individual ecosystem functions were negative (i.e., increases in abundance were associated with declines in functioning) for seven functions and positive for five functions, whereas the directionality of relationships between ecosystem function and dominant consumer abundance were generally positive (eight positive versus four negative).

Abundances of neither the dominant producer nor the dominant consumer were associated with average ecosystem multifunctionality ($F_{1,8}$ = 0.18, p = 0.686, and $F_{1,8}$ = 0.12, p = 0.741, respectively), though certain groups of functions were affected in opposing directions by the different species (Figure 2.2). We observed a negative trend in the relationships between dominant producer abundance and productivity ($F_{1,8}$ = 4.59, p = 0.065), while consumer abundance and productivity were positively associated ($F_{1,8}$ = 9.92, p = 0.013). Dominant producer abundance displayed a positive trend in its relationship with water chemistry during the day ($F_{1,8}$ = 3.64, p = 0.093; Table S2), compared to a negative relationship between dominant consumer abundance and daytime changes in water chemistry ($F_{1,8}$ = 5.79, p = 0.043; Table S3).

We found that ecosystem multifunctionality was associated with dominant consumer abundance, but not dominant producer abundance, in unmanipulated tide pools using the multiple threshold approach (Figure 2.3). The abundance of the dominant consumer was positively associated with ecosystem function by the multiple threshold approach over two distinct ranges of thresholds (threshold values 51%-56%, 64%-77%; $p < 0.05$). In those same tide pools, the dominant producer was not associated with ecosystem multifunctionality ($p > 0.1$), though the relationship between producer abundance and multifunctionality tended to be negative across thresholds. Results for identical analyses using the reflected data are shown in Figures S2, S4, and S5.

Impact of dominant producer removal on the functional effect of the dominant consumer

Following the removal of the dominant producer, the relationships between dominant consumer abundance and several individual functions, particularly nutrient fluxes, changed markedly. The associations between dominant consumer abundance and daytime fluxes of ammonium and nitrate + nitrite ($F_{2,6} = 25.15$, $p = 0.001$, and $F_{2,6} = 5.36$, $p = 0.049$, respectively; dominant consumer abundance : treatment : time) differed between pools where the dominant producer had been removed and control pools where it was still present. Changes in ammonium fluxes were also associated with the removal of the dominant producer, irrespective of dominant consumer abundance, ($F_{1,5} = 7.10$, $p = 0.041$; treatment : time). In addition, both ammonium ($F_{1,10} = 17.82$, $p = 0.002$) and nitrate + nitrite ($F_{1,12} = 8.09$, $p = 0.015$; dominant consumer abundance: treatment) fluxes were associated with an interaction between dominant consumer abundance and treatment group. Dominant consumer abundance was associated with increased NCP ($F_{1,12} = 6.92$, $p = 0.022$), as well as more rapid acidification (i.e., negative pH change) and greater ammonium accumulation during the day ($F_{1,9} = 8.16$, $p = 0.02$; $F_{1,10} = 38.30$, $p < 0.001$), regardless of time or removal treatment.

The dominant consumer tended to reduce overall averaged ecosystem function after dominant producer removal ($F_{1,6} = 4.88$, $p = 0.069$; Figure S3), driven by negative associations between consumer abundance and daytime water chemistry ($F_{1,6} = 23.06$, $p = 0.003$) and nutrient fluxes ($F_{1,6} = 12.25$, $p = 0.012$). However, we did not find evidence of an interaction between the removal of the dominant producer and the effect of dominant consumer abundance on averaged ecosystem function or any individual set of functions ($p > 0.1$; dominant consumer abundance : treatment; Table S4).

The relationship between dominant consumer abundance and ecosystem multifunctionality, as assessed using the multiple threshold approach, differed depending on whether the dominant producer was present (Figure 2.4). In the experimental tide pools, dominant consumer abundance was negatively related to ecosystem multifunctionality over a narrow band of thresholds where the dominant producer was present (threshold values 5%-23%; $p < 0.05$), while the relationships between consumer abundance and multifunctionality tended to be positive in the pools where the producer had been removed (NS; $p > 0.2$). Results for analyses on the reflected data are shown in Figure S6.

Discussion

We found that the relationships between the abundances of each dominant species and individual ecosystem functions, as well as groups of functions, were consistently in opposing directions. This pattern may reflect the differing roles of producers and consumers in supporting overall ecosystem function, in which different trophic levels tend to contribute to certain functions, or types of functions, in specific ways (e.g., producers raising pH during the day or absorbing nutrients; Aquilino et al., 2009; Bracken et al., 2018). However, dominant consumer abundance was related to many of the functions in the direction predicted to be associated with a producer. This producer-like effect of the dominant consumer may reflect an indirect effect in which the consumer is affecting ecosystem function through facilitation of non-dominant producers (Aquilino et al., 2009), the abundance of which was found to be positively related to dominant consumer abundance ($F_{1,8} = 6.12$, $p = 0.038$). The opposing effects of *N. oregona* and *M. trossulus* may be more specifically indicative of the well-documented interactions between tide pool algae and mussels, particularly in terms of nutrient cycling (Bracken and Nielsen, 2004; Pfister, 2007). Either way, the nearly uniform counter-directionality of effects between these two dominant species suggests an ecological equilibrium, maintained by the presence of both species, which may be disrupted if one species is lost.

Interestingly, we found that there was a directional change in the relationship between dominant consumer abundance and ecosystem multifunctionality, from positive during the pre-removal sampling to negative in the control pools in the post-removal sampling (i.e., with the dominant producer still present; Figure S1). This directional change might have been driven by shifts in temperature and light levels between samplings: mean temperature and light measurements of 20.7 °C and 524 μmol m^{-2} s^{-1} prior to removal dropped to 15.3 °C and 64 μmol m^{-2} s^{-1} during the post-removal sampling (S. Mahanes et al., *unpublished data*). This decline in temperature could have altered the functional effect of the dominant consumer by affecting metabolic rate (Tagliarolo et al., 2012; Bracken et al. 2022). Shifts in light availability could also have disrupted possible indirect effects of the consumer on function via non-dominant producers (Aquilino et al., 2009). The shift in effect direction highlights the potential for changes in the functional impacts of individual species under different environmental contexts and raises intriguing questions about how the ecological roles of abundant species may shift across timescales, driven by changes in weather patterns, seasonal cycles, or long-term environmental change.

We found that the direction of the effect of dominant consumer abundances on ecosystem multifunctionality differed between treatment groups, suggesting that the presence of the dominant producer affected the functional effect of the dominant consumer, and this finding is additionally supported by a negative correlation between abundances of the dominant producer and the dominant consumer species in these tide pools (S. Mahanes et al., *unpublished data*). The tide pools where the dominant producer had been removed tended to have more positive rates of pH change relative to pools with the dominant producer still present, suggesting that either (1) *N. oregona* is largely functioning as a consumer in low light conditions, reducing pH in the pools and restricting calcification, or that (2) non-dominant producers were released from photosynthetic limitation by the removal of the abundant alga. The removal-treatment pools tended to have positive relationships between dominant consumer abundance and calcification, which may be related to increased pH in those pools relative to the control group. The association between consumer abundance and daytime fluxes of nitrogen compounds (i.e., ammonium, nitrate, nitrite) also differed between the producer-removal pools and the control pools, suggesting that the disruption of reciprocal nutrient cycling could be driving the differences in the functional role of the dominant consumer following the loss of a dominant producer. These results were supported by our analysis of changes in relationships before *versus* after removal, which identified multiple individual functions where the effect of dominant consumer abundance differed following removal of the dominant producer.

We did not find a comparable effect using the averaging method, which may be due to methodological differences between the two approaches: the multiple threshold method is weighted toward consistent baseline levels across functions, rather than exceptionally high levels of individual functions which may elevate the overall average. If substantial contributions across a broad range of functions is indicative of high multifunctionality (Manning et al., 2018), then the multiple threshold approach may be the most appropriate metric for functional assessment. The multiple threshold approach also allows for relatively straightforward comparisons across studies, which may prove useful in future meta-analyses (Byrnes et al., 2014).

We found that certain patterns appeared only in the analyses on the reflected data while others were present in both the reflected and un-reflected data. The rationale for reflecting the data, where necessary, to produce a positive slope with dominant producer abundance in unmanipulated tide pools was to ensure that significant overall effects were not being obscured by opposing effects on similar functions. This was the case with dominant producer abundance and daytime nutrient fluxes in intact tide pools: both ammonium and phosphate accumulation tended to be more positive in pools with greater dominant producer abundance, while nitrate and nitrite tended to accumulate more slowly in those pools. The result was an association between dominant producer abundance and daytime nutrient function in unmanipulated tide pools with the reflected data but no corresponding effect in the un-reflected data analysis, as the counter-directional fluxes cancelled out when averaged across all these nutrient types. For this reason, although we focused on the un-reflected data, we included identical analyses on the reflected data in the supplement for additional context (Figures S2, S4-S6).

Our rationale for grouping certain functions together was the expectation that related functions may be similarly associated with species abundances. Studies have shown, for example, that calcification rates tend to be higher in relatively high-pH conditions (Semesi et al., 2009; Wahl et al., 2018), though we did not observe those two functions to be related in this study. However, there may be intergroup interactions occurring among ecosystem functions as well. Respiration can directly affect pH by modifying CO_2 levels (Krause-Jensen et al., 2015), and productivity and respiration may be intertwined with nutrient cycling due to potential oxygen limitation of nitrification (Joo et al., 2005; Pfister and Altabet, 2019). Such interactions among ecosystem functions should be considered in the interpretation of results to effectively disentangle the effects of interrelated functions on ecosystem multifunctionality.

This study focused explicitly on dominant species, but less abundant species can also play considerable roles in structuring the community and driving ecological function. Mariotte (2014) highlights the importance of non-dominant species in influencing an ecosystem and suggests grouping species into functional groups to effectively account for their impact. Recent studies of non-dominant species have shown their ability to reduce the effect of drought on soil communities (Mariotte et al., 2015), stabilize food webs (Shao et al., 2016), and impact community composition (Bracken and Low, 2012). However, this is not a clean dichotomy because dominant species can affect the abundances of non-dominant species, indirectly impacting ecosystem function (Fields and Silbiger, 2022). We found an intriguing pattern in which net community productivity was positively related to dominant consumer abundance, suggesting that the consumer may be indirectly driving ecosystem function through facilitation of non-dominant producers. In fact, abundance of non-dominant producers was positively correlated with *M. trossulus* abundance in our tide pools (S. Mahanes et al. *unpublished data*), highlighting the potential for an indirect effect of a dominant consumer on sub-dominant producers. Dominant species may play significant ecological roles, but the contributions of non-dominant species, whether independent of or related to the presence of dominant species, should be accounted for as well.

We adapted approaches designed for evaluating diversity-multifunctionality relationships to focus on the effects of dominant species on multifunctionality in tide pools, but the methods employed in this study could be applicable across a wide range of ecosystems. For example, the patterns we uncovered regarding the opposing effects of species from different trophic levels and potential interactive functional impacts of dominant species could be evaluated in other ecosystems with both dominant producers and consumers present (e.g., forests with a highly abundant variety of tree and a dominant fungal species) to determine whether those trends are widespread or unique to marine ecosystems such as tide pools where consumers are often dominant. Considerable effort has been devoted to identifying species which drive critical functions in ecosystems, including keystone species (Paine, 1966), foundation species (Ellison, 2019; Fields and Silbiger, 2022), and ecosystem engineers (Losapio et al., 2021). Dominant species may have similarly substantial impacts on the ecosystem by virtue of their abundance (Grime, 1998; Orwin et al., 2014). The approach applied here could advance our mechanistic understanding of the roles of individual species – and their interactions – in mediating multiple ecosystem functions. Understanding both the role of abundant species in ecosystems and their susceptibility to global change will be critical to forecasting future alterations in the functioning of these ecosystems.

Figures

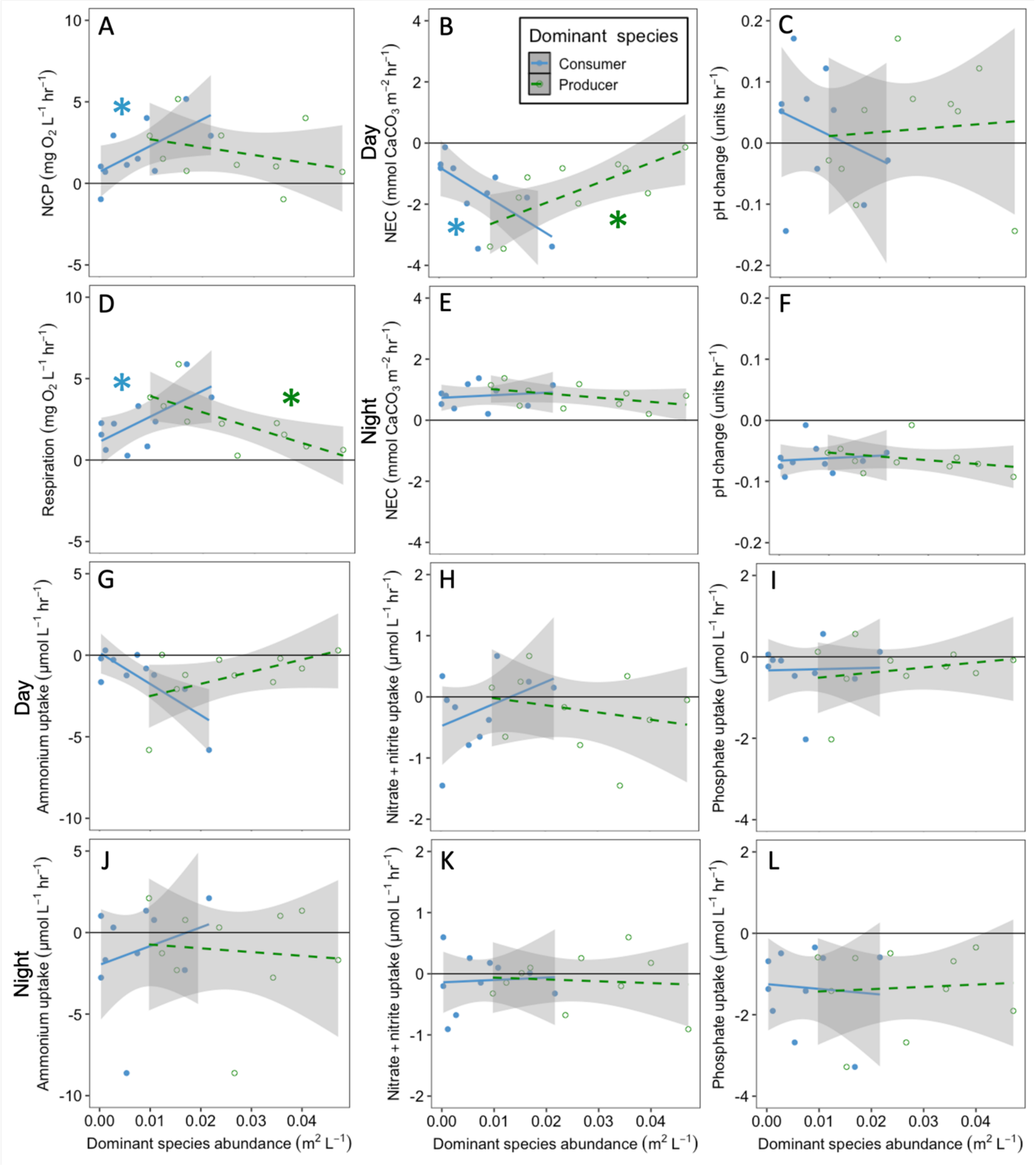

Figure 2.1: Relationships between the abundances of the dominant producer (the alga *Neorhodomela oregona*; green, open symbols and dashed regression lines) and consumer (the mussel *Mytilus trossulus*; blue, closed symbols and solid regression lines) on 12 individual ecosystem functions: (A) net community production; daytime (B) net ecosystem calcification and (C) pH change; (D) community respiration; nighttime (E) net ecosystem calcification and

(F) pH change; daytime (G) ammonium accumulation, (H) nitrate + nitrite uptake, and (I) phosphate uptake; and nighttime (J) ammonium accumulation, (K), nitrate + nitrite uptake, and (L) phosphate uptake. Producer abundance was related to two functions: daytime net ecosystem calcification and respiration. Consumer abundance was related to four functions: net community productivity, daytime net ecosystem calcification, respiration. Each data point represents the abundance of producer (green) or consumer (blue) in a single tide pool. Asterisks indicate significance, and shaded areas are 95% confidence intervals.

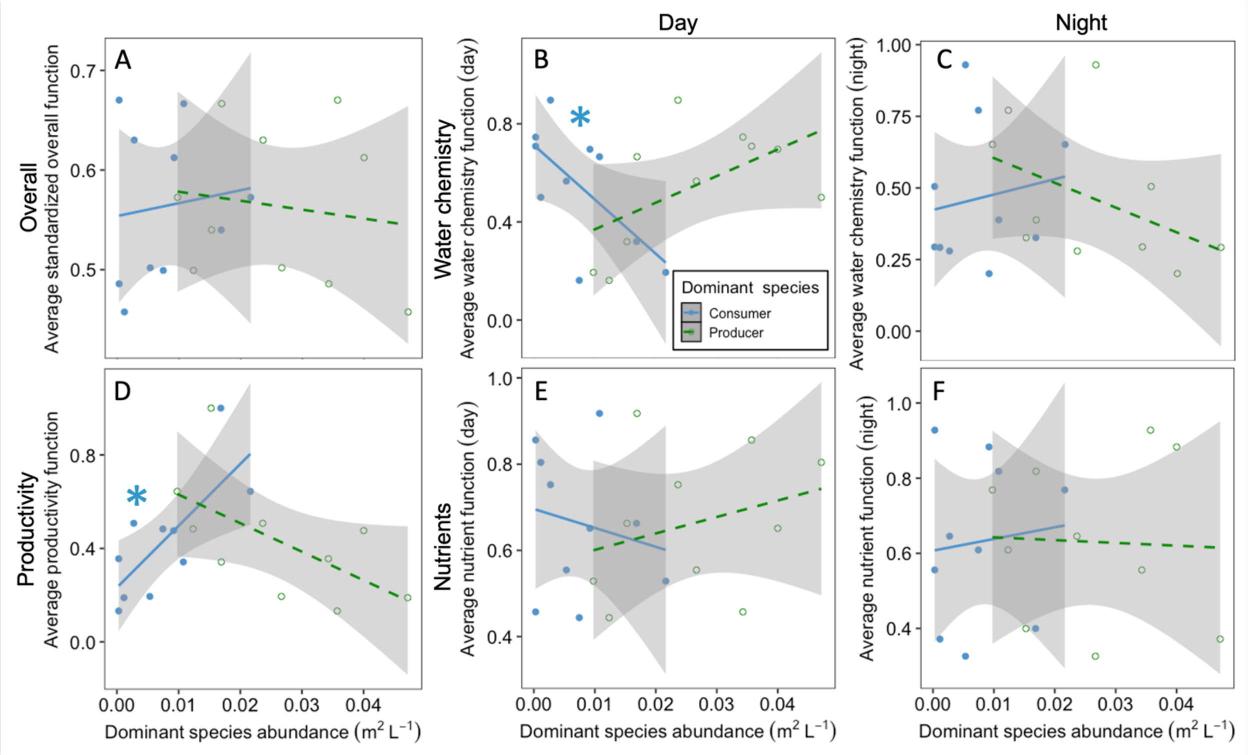

Figure 2.2: Relationships between the abundances of a dominant producer (green) and a dominant consumer (blue) on averaged rates of (A) overall ecosystem functions as well as groups of functions including change in water chemistry during the (B) day and (C) night, (D) productivity, and change in nutrient levels during the (E) day and (F) night. Abundances of neither the producer *N. oregona* nor the mussel *M. trossulus* were associated with averaged overall ecosystem multifunctionality (the mean of all twelve standardized function values). Dominant consumer abundance, however, showed a positive association with productivity and a negative correlation with daytime water chemistry. The average function of each pool (N=10) is represented in each plot by two points, corresponding to the abundance of the dominant consumer (in blue) and the dominant producer (in green). Asterisks indicate significance, and shaded areas are the 95% confidence interval.

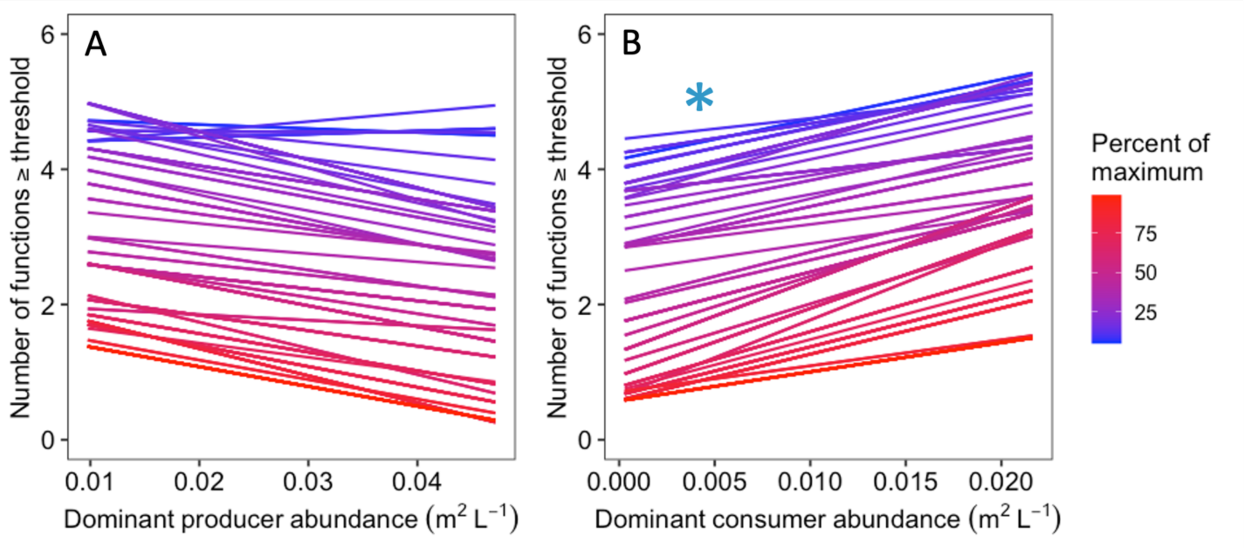

Figure 2.3: Number of functions exceeded by the (A) dominant producer and (B) dominant consumer based on multiple thresholds to evaluate effects on ecosystem multifunctionality in intact (unmanipulated) tide pools. The abundance of a dominant producer, the alga *Neorhodomela oregona*, was not related to ecosystem multifunctionality, whereas abundance of a dominant consumer, the mussel *Mytilus trossulus*, was positively associated with ecosystem multifunctionality across a wide range of thresholds. Each line indicates the relationship between species abundance and the number of ecosystem functions exceeding a threshold value (indicated by color based on the gradient to the right). Asterisks indicate significance.

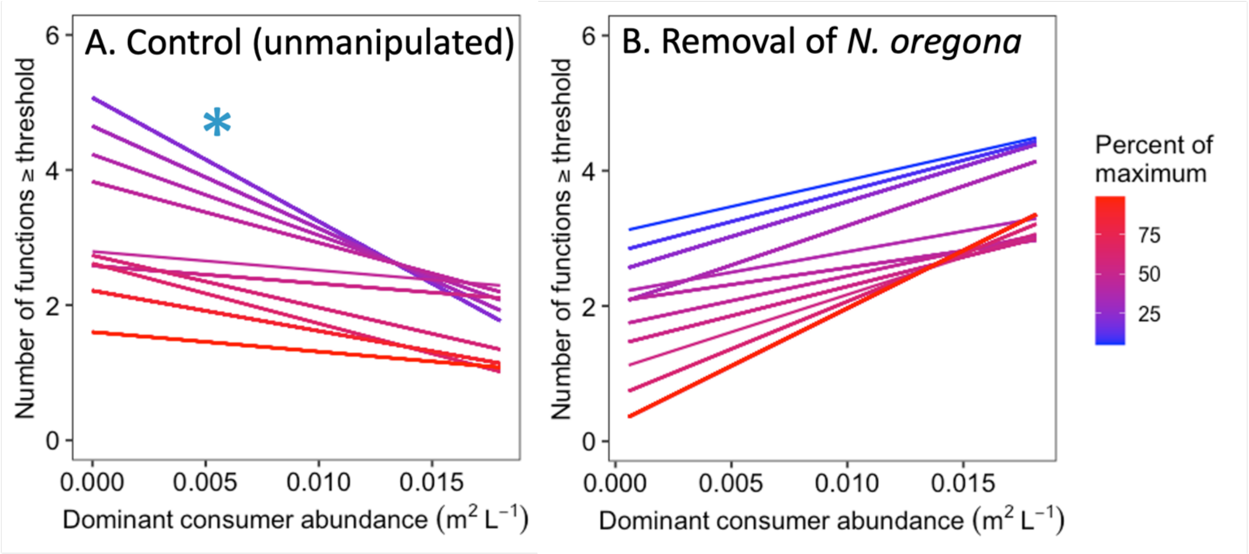

Figure 2.4: After the removal of the dominant producer, the abundance of the dominant consumer was negatively associated with multifunctionality across a narrow range of thresholds in the (A) control tide pools (with *N. oregona* still present) but (B) showed non-significant positive trends with ecosystem function in pools from which the dominant producer was removed. These analyses follow the multiple threshold approach, as in Figure 2.3.

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CHAPTER 3

Impacts of climate change on marine species invasions in northern hemisphere high-latitude ecosystems

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Abstract

High-latitude marine ecosystems have experienced fewer species invasions than temperate marine ecosystems, a discrepancy that may be attributed to barriers such as low propagule pressure, extreme and seasonal abiotic conditions, and biotic resistance of relatively intact communities. Each of these barriers is being affected by climate change and increasing human activity in high-latitude (>55° N) areas. We reviewed the evidence for each of these barriers limiting species invasion in high-latitude areas in the northern hemisphere. Based on records from government documents of high-latitude countries, non-native species appear to be increasing in number (in Denmark and the United States) although there remains a paucity of data on invasive species establishment for high-latitude regions. Future study is needed to identify the drivers and impacts of invasions at high latitudes so that managers looking to prevent invasions can focus their efforts on bolstering barriers to invasion in these unique ecosystems.

Introduction

Species invasions and climate change are two of the greatest threats to global biodiversity (Bellard *et al.*, 2016a; Occhipinti-Ambrogi, 2007; Simberloff *et al.*, 2013). Invasive species are defined, here, as species that have been introduced by humans to an area outside their native range and have successfully established and spread within their non-native range. Understanding the degree to which invasion and climate change interact, either synergistically or antagonistically, in different contexts is critical to anticipating and effectively mitigating impacts on biodiversity (Sorte *et al.*, 2013).

One way that these two aspects of global change could interact is that climate change could increase species invasions by breaking down existing barriers to invasion. Species invasion proceeds along a known pathway: propagules are *transported* to a new area, individuals that survive the novel conditions are able to *colonize*, a population is *established* when individuals successfully reproduce, and this established population may then *expand* its range to adjacent locations within the non-native region (Theoharides and Dukes, 2007). Invasion may be obstructed by barriers along this pathway (Figure 3.1), including a lack of transportation vectors, lethal abiotic conditions that prevent colonization, or interactions with native species that make establishment untenable (Hellmann *et al.*, 2008; Ruiz and Hewitt, 2009). These barriers have historically been strongly represented (Willig *et al.*, 2003) in northern high-latitude ecosystems (defined here as areas located at >55° N latitude), where far fewer introduced species have been documented than in temperate (30°-55° latitude) areas (Krug *et al.*, 2009; Ruiz and Hewitt, 2009; Ware *et al.*, 2014). However, climate change is acting on each of these barriers, reducing them to a degree that may allow an unprecedented wave of species invasions in these historically uninvaded high-latitude ecosystems (Figure 3.1) (Stachowicz *et al.*, 2002; Holland and Bitz, 2003; Ruiz and Hewitt, 2009; de Rivera *et al.*, 2011; Thyrring *et al.*, 2017).

Marine ecosystems may be vulnerable to the breakdown of invasion barriers due to rapid increases in human disturbance and propagule pressure, as well as a tendency for non-native marine species to outperform their native counterparts under climate change (Molnar *et al.*, 2008; Sorte *et al.*, 2013). We conducted a literature review to evaluate the factors limiting invasion in high-latitude marine ecosystems and the evidence that these barriers are changing. We focus on three types of barriers: low propagule pressure, harsh abiotic conditions, and biotic resistance, all of which we expect to be affected by climate change. To determine whether changes in these barriers were reflected in the number of species invasions, we compiled a database of invasive marine species in high-latitude countries (from national government documents) and in Alaska, USA (from the peer-reviewed literature). Where available, we used dates of first record (i.e., the date of first collection or documentation of an invasive species in an area) to analyze changes in the number of invasive species present over time.

Propagule Pressure

The most significant sources of invasive propagule pressure in marine systems are shipping, aquaculture and the aquarium trade (Rueness, 1989; Padilla and Williams, 2004; Keller *et al.*, 2011; Hughes and Ashton, 2017). Ship-mediated transport (e.g., hull biofouling or ballast water) accounts for much of the non-native marine species introduction in high-latitude ecosystems and globally (Ruiz *et al.*, 1997; Seebens *et al.*, 2013). Aquaculture has allowed the escape of cultivated organisms and the incidental introductions of hitchhiker species like the alga *Sargassum muticum* (Rueness, 1989; Josefsson and Jansson, 2011; Keller *et al.*, 2011; Piccolo and Orlikowska, 2012), and the aquarium trade has been responsible for the release of lionfish *Pterois volitans* (Padilla and Williams, 2004) and the toxic alga *Caulerpa taxifolia* (Jousson *et al.*, 1998).

High-latitude areas have historically experienced lower levels of human traffic and development than more temperate areas, limiting propagule pressure in these ecosystems; however, this longstanding barrier to invasion appears primed for change due to increases in shipping, accessible trade routes, and tourism (Miller *et al.*, 2007; Ruiz and Hewitt, 2009; Ware *et al.*, 2014). Over 50 million metric tons of ballast water were discharged along the coast of Alaska during a three-year period from 2009-2012, which is a higher per-year rate of discharge than was documented from 1999-2003 (McGee *et al.*, 2006; Verna *et al.*, 2016). Most of this water can be traced back to ports on the west coast of North America, many of which are populated by species already identified as potential invaders in Alaska based on their climate tolerances (de Rivera *et al.*, 2011). Arctic ice melt is also opening new trade routes and enabling oil extraction in previously inaccessible sites, increasing shipping traffic in these areas (Seebens *et al.*, 2013; Eguíluz *et al.*, 2016; Pizzolato *et al.*, 2016; Verna *et al.*, 2016). The possibility of introducing non-native species in ballast water is becoming increasingly recognized and regulated (Molnar *et al.*, 2008). International treaties on the handling of ballast water are supplemented by individual government mandates on the removal of hull-fouling organisms and ballast water exchange (Williams *et al.*, 2013). This wave of regulations, coupled with technological advances in ballast water treatment, has great potential to reduce species introduction through these vectors (Rivas-Hermann *et al.*, 2015). However, it is unclear whether these changes will offset increases in shipping to prevent an increase in propagule introduction in high-latitude areas (Verna *et al.*, 2016; Hughes and Ashton, 2017).

Propagule pressure is also likely to increase due to intentional and unintentional introductions associated with aquaculture and tourism. The increase in sea surface temperatures will lead to a poleward shift in the areas with optimal conditions for key aquaculture species, like the Atlantic salmon *Salmo salar* (Stenevik and Sundby, 2007). Commercially raised Atlantic salmon frequently escape into the wild and may compete with – and introduce pathogens to – populations of native salmon species (e.g., *Oncorhynchus* spp. in Alaska; Piccolo and Orlikowska, 2012). Tourism has also increased dramatically in high-latitude areas, and this trend is expected to continue (Lasserre and Têtu, 2015). High-latitude tourism provides opportunities to view glaciers, observe whales in their natural habitat and experience pristine ecosystems, but may be endangering the species that they are traveling to observe (Hall *et al.*, 2010). Cruise ship traffic in high-latitude areas of Canada has been increasing since 1984 (Stewart *et al.*, 2007). More recently, the number of cruise ships operating in Greenland waters tripled over a five-year period and similar trends were observed in Iceland, Alaska and other high-latitude areas (Hall *et al.*, 2010; Ware *et al.*, 2012).

Abiotic Resistance

Once non-native species are introduced to high-latitude ecosystems, their persistence is often precluded by abiotic conditions, including low seasonal temperatures and variable resource availability (Peck *et al.*, 2006; Aronson *et al.*, 2007; Krug *et al.*, 2009). Temperature limits invasion in high-latitude marine ecosystems by increasing physiological stress or exceeding physiological tolerances of potentially invasive species (Thatje, 2005; Thatje *et al.*, 2005; Aronson *et al.*, 2007). Temperature dissimilarity between locations is so widely accepted as a barrier to invasion that it is frequently used as the sole parameter when modeling invasion potential (Seebens *et al.*, 2013). For example, Thatje *et al.* (2005) argue that ocean temperature is the main factor limiting king crab (*Lithodes confundens*) incursion into Antarctic waters. Thyrring *et al.* (2017) identified air temperature as a factor limiting the abundance of high-latitude populations of *Mytilus* species along the coast of Greenland. With climate change, temperatures in polar areas will rise by 2-3 times the global average (Holland and Bitz, 2003), making non-native species from lower latitudes more likely to survive throughout the year (Holland and Bitz, 2003; de Rivera *et al.*, 2011; Ware *et al.*, 2014; Thyrring *et al.*, 2017). de Rivera *et al.* (2011) compared the physiological tolerances of four invasive marine species inhabiting the contiguous USA to present and future conditions along the coast of Alaska. They found that current conditions in parts of Alaska were suitable for each of the four species, and the potential ranges of these species expanded dramatically when climate change projections were incorporated. The rapid environmental shifts in high-latitude ecosystems are particularly notable when considered alongside the latitudinal diversity gradient: biodiversity generally increases with decreasing latitude, meaning that a modest shift in environmental conditions in a high-latitude ecosystem could enable invasion by a significantly larger set of species (Valentine *et al.*, 2008; Krug *et al.*, 2009).

Rising temperatures are also driving changes in latitudinal patterns of seasonal resource variability (Thatje *et al.*, 2005; IPCC, 2007). Resource availability across trophic levels exhibits extreme seasonal variation due to variation in temperature, light availability, and water mixing across the year (Clarke, 1982; Polovina *et al.*, 1995; Valentine *et al.*, 2008; Krug *et al.*, 2009). Species native to high-latitude areas are better adapted to cope with temporal variation in resource availability than those native to temperate areas, via mechanisms including highly variable growth rates and intensive direct, as opposed to planktotrophic, larval development (Clarke, 1982; Conover and Present, 1990; Kendall *et al.*, 1997; Valentine *et al.*, 2008; Krug *et al.*, 2009). Species native to temperate latitudes, conversely, are accustomed to less seasonal variation in primary producer growing season and shorter periods of relative resource scarcity, and they demonstrate increased resource specialization (Krug *et al.*, 2009). The role of a short growing season, limited by temperature and photoperiod, as a barrier to invasion in high-latitude ecosystems has been extensively studied in trees (Saikkonen *et al.* 2012). However, the same principle likely applies to invasive marine primary producers and consumers, when there is a large discrepancy between the growing season in the native range and the invasive range of a species (Saikkonen *et al.* 2012).

Climate change is affecting spatial and temporal patterns of resource availability, including extending the length of the growing season in terrestrial ecosystems (Barichivich *et al.*, 2013), and this extension may also occur in marine systems. Furthermore, rising CO_2 levels may have a fertilizing effect, increasing marine primary production by as much as 30% at the lower light intensities found in the winter at high-latitude areas (Hein and Sand-Jensen, 1997; Bopp *et al.*, 2001; Gao *et al.*, 2012). Climate change may also alter the competitive balance between invasive and native species (Cheung *et al.*, 2009; Sorte *et al.*, 2013). Studies in a temperate, epibenthic fouling community showed that higher temperatures increased the recruitment and establishment of invasive species whereas native species recruitment was reduced or unchanged under warmer conditions (Stachowicz *et al.*, 2002; Sorte *et al.*, 2010b). Given that space is the limiting resource in epibenthic systems, differential impacts of temperature on recruitment could significantly advantage invasive species if they are the first to colonize the substrata and priority effects perpetuate. Furthermore, results of a cross-ecosystem synthesis indicated that invasive species fared better than native species under changing climatic conditions, particularly when resources were increased and more so in aquatic than terrestrial systems (Sorte *et al.*, 2013). If invasive species are favored over native species by changes in abiotic conditions, this could subsequently influence the ability of native communities to resist invasion.

Biotic Resistance

Biotic resistance is defined as the inhibition of invader establishment via interactions with the native community (Elton, 1958; Stachowicz *et al.*, 1999; de Rivera *et al.*, 2005) and is directly related to community diversity at local scales (Levine, 2000; Melbourne *et al.*, 2007;). More diverse communities use resources more effectively (e.g., Byers and Noonburg, 2003), either due to complementarity (i.e., niche partitioning; Stachowicz *et al.*, 1999, Stachowicz and Byrnes, 2006) or a sampling effect (i.e., greater probability of including a highly competitive species or group; Arenas *et al.*, 2006). Establishment and spread of invasive species can also be limited by native consumers, including consumers to which invasive prey are currently relatively naïve and undefended (Levine *et al.*, 2004; de Rivera *et al.*, 2005; Parker and Hay, 2005). Diversity itself is negatively associated with disturbance, which drives mortality, potentially opening up resources for non-native species and reducing biotic resistance (Kennedy *et al.*, 2002; Britton-Simmons, 2006; Clark and Johnston, 2009).

Biotic resistance is the least studied barrier to invasion in high-latitude marine ecosystems (Ruiz and Hewitt, 2009; de Rivera *et al.*, 2011), and the ways in which it may be affected by climate change are largely unresolved. However, we might expect that biotic resistance will decrease under increased disturbance due to direct human actions and rapid abiotic shifts (Byers, 2002; Britton-Simmons and Abbott, 2008; Clark and Johnston, 2009; Sorte *et al.*, 2013). Increased human activity in high-latitude areas – such as through shipping and tourism as described above – will disturb native ecosystems by releasing pollutants (Cloern and Jassby, 2012) and clearing or altering substrate (Airoldi and Bulleri, 2011; Simkanin *et al.*, 2012). These activities will increase mortality for existing populations while also potentially freeing up resources for establishment of new species (Stachowicz *et al.*, 1999; Byers, 2002). Disturbance might also drive cascading extinctions when it leads to mortality of foundation species, who themselves increase diversity of associated native species (Reusch, 1998; Paulay *et al.*, 2002; Williams, 2007; Simkanin *et al.*, 2012).

Eutrophication, a frequent consequence of human activity, can reduce local species diversity (and, thus, biotic resistance) when one or a few species are best able to capitalize on pulses of increased resources (Smith *et al.*, 1999), leading to algal blooms and downstream effects such as hypoxia-driven mortality across the community (Diaz and Rosenberg, 2008). One particularly impactful algal bloom, dubbed the "Silent Spring in the Sea", occurred in high-latitude waters off the northern coast of Denmark in 1988 (Rosenberg *et al.*, 1988). The bloom occurred during an unseasonably warm period that coincided with high levels of nitrogen and phosphorous in the surface water from unusually high runoff. The bloom caused widespread mass mortality across taxonomic groups, including habitat-forming kelp species *Saccharina latissima* and the predatory sea-star *Asterias rubens* (Rosenberg *et al.*, 1988). The extirpation of habitat-forming and consumer species from high-latitude areas would likely reduce local biodiversity and, by extension, biotic resistance. Climate change may also increase the disturbance of native communities by increasing the frequency of extreme weather events, including severe storms and heat waves, which can cause widespread mortality and provide openings for invasive colonists (Valentine *et al.*, 2008; Krug *et al.*, 2009).

Although disturbance is a relatively non-selective force that could reduce biotic resistance by decreasing diversity, human activities might also reduce biotic resistance by selectively removing consumers from high-latitude ecosystems (de Rivera *et al.*, 2005; Simkanin *et al.*, 2013). Predation pressure has been historically altered by humans through fishing, which is globally skewed toward large predatory fish (Pauly *et al.*, 1998), and the fur trade, which extirpated sea otters in certain high-latitude areas (Doroff *et al.*, 2004). The active removal of predators may rise with increasing human presence, reducing predation pressure on invasive species and weakening biotic resistance (de Rivera *et al.*, 2005; Simkanin *et al.*, 2013). Conversely, increased regulation of fishing practices and otter reintroduction programs may increase predation pressure in high-latitude areas. We also note that the magnitude and direction of the effect of predation pressure on biotic resistance varies by taxon. A predator which selectively preys on non-native species might increase biotic resistance whereas a generalist predator or one which prefers native prey might have a negligible or negative effect on biotic resistance (de Rivera *et al.*, 2005).

Of the three barriers reviewed here (propagule pressure, abiotic conditions and biotic resistance), biotic resistance is the least well supported as driving the historically low level of invasion in high-latitude ecosystems. In fact, biotic resistance may generally be weak in these ecosystems given that it increases with diversity and that diversity of many groups decreases with increasing latitude (Kimbro *et al.*, 2013; Harper and Peck, 2016). There is even a possibility that biotic resistance in high-latitude ecosystems will increase with climate change as species from adjacent regions undergo poleward range shifts into high-latitude communities.

Baseline Data on High-Latitude Marine Invasions

A Global Perspective

There are currently no published studies reporting the changes in marine invasions over time in high-latitude ecosystems. Despite the limitations to empirical analysis, we used the following methods to compile a baseline data set of invasive marine species recorded in northern high-latitude ecosystems (>55° N) in documents published by or specifically for government agencies after an initial search yielded few peer-reviewed publications. We identified thirteen countries with high-latitude marine habitat in the northern hemisphere and searched their government websites or the sites of agencies responsible for natural resource management for lists of invasive species in these countries' waters. We supplemented this with Google Scholar searches using the country name with terms to specify invasive species and high-latitude, marine ecosystems. We found ten government documents that reported the number or names of invasive species present in six of the thirteen high-latitude countries: Denmark, Estonia, Finland, Norway, the United Kingdom and the United States (Table 1). These documents included 188 established invaders and 65 species that were predicted to invade in the near future. Where provided, we collected the date of first record (i.e., the year in which an invasive species was first observed or collected in a given area; Ruiz *et al.*, 2000). These dates represent when a species was detected, and therefore may lag behind the true date of establishment. When a period of time was given for the first record or detection, we used the midpoint of the time period (e.g., 1975 for a record of first detection that only specified the 1970s).

The cumulative number of invasive species recorded in Denmark and the United States (the only documents that provided dates of first record) has increased over time (Figure 3.2). Although these patterns suggest that Denmark was invaded earlier and by a greater number of species than the United States, which might make sense given the longer history of high-volume shipping around Denmark than in Alaskan waters, these data likely reflect significant biases in monitoring. These biases likely obscure patterns across space (as species in less accessible areas are less likely to be detected) and time (as sampling protocols change with interest and technology). More recent patterns are likely most reliable. Denmark instituted a standardized monitoring protocol in 1989, after which the cumulative number of invasive species continued to increase. Continuing increases are also apparent in the United States data set, which was compiled in all years using standardized collection protocols for sessile species and supplemental surveys for mobile species, allowing comparison across all time points.

The government document data set included 144 unique species documented across six high-latitude countries, with 40 of these species documented in more than one country. 30 species were documented in two countries, eight were observed in three countries and only two species (the Pacific oyster *Crassostrea gigas* and alga *Sargassum muticum*) were documented as invasive in four countries. The two marine invaders that have established in the most high-latitude countries are associated with transportation via aquaculture (Sjøtun *et al.*, 2008; Williams *et al.*, 2013). The Pacific oyster, *C. gigas*, was introduced in northern Europe for use in aquaculture, and individuals escaped (Nehring, 2011). *C. gigas* has planktonic larvae and is especially reproductive in years following warm winters, giving the species a potential advantage over native competitors amid warming temperatures (Stachowicz *et al.*, 2002; Nehring, 2011). *S. muticum* is believed to have been introduced incidentally with imported oysters (Josefsson and Jansson, 2011). *C. gigas* and *S. muticum* displace native competitors while also providing habitat and increasing water filtration (Josefsson and Jansson, 2011; Nehring, 2011).

Seven of the ten most prolific high-latitude invaders, those which have invaded three or four high-latitude countries, have native ranges primarily in temperate zones, mostly between 30° and 45° latitude. The trend of lower-latitude species invading high-latitude areas reflects poleward shifts in climate isoclines and may also be fueled by the larger pool of potential invaders in more biodiverse lower-latitude zones (Ware *et al.*, 2014). This trend (of movement of species from temperate to high-latitude areas) may be intensified by movement from highly invaded temperate ports that serve as stepping stones, so that ship traffic from even a single temperate port may lead to the secondary introduction of a wide variety of species to high-latitude areas (de Rivera *et al.*, 2011).

Alaska as a Case Study

To evaluate whether there is evidence that climate change is altering invasibility of Alaska, in particular, we searched all records in Web of Science through 29 May 2018 using “Alaska” as a search term along with search strings for marine invasive species published in Sorte *et al.* (2010a). After narrowing by categories, we reviewed 402 titles and 109 abstracts, finding a total of 15 relevant papers that reported eight established invasive species (four ascidians and one each of bryozoans, amphipods, bivalves and algae; Table 2) and seven species likely to invade under current or future conditions. Interestingly, our review of government documents, described above, provided a more complete listing of established invaders in Alaska (22 species) than our literature search (eight species).

The most striking pattern among the species from the Alaska literature review is the prevalence of species inhabiting the marine epibenthic “fouling” community, which account for five of the eight invasive species reported and are also well-represented (16 established invasive species and nine predicted invaders) in the government document data set. It is important to note than the economic impact and high visibility of fouling species may have garnered them more attention than less conspicuous or economically relevant species. In addition, many of the scientists who contributed to the government documents and scientific literature are tunicate specialists which likely leads to a sampling bias towards fouling community habitats. Fouling community species have many of the traits of successful invaders (Kolar and Lodge, 2001): they can be transported either attached to the hulls of ships or to debris in the ballast water, display rapid growth, quickly achieve sexual maturity, and require relatively few individuals to establish a breeding population (Lambert and Lambert, 1998; Sorte *et al.*, 2010b; Lord *et al.*, 2015). The native Alaskan fouling community has lower species diversity than temperate fouling communities and does not appear to be space-limited, suggesting that biotic resistance is comparatively low and invasive susceptibility may be high in these communities (Elton, 1958; Lord *et al.*, 2015).

Comparison with Temperate and Tropical Systems

The barriers to species invasion and the potential impacts of climate change on these barriers differ between high-latitude, temperate, and tropical systems. Temperate regions have historically been hotspots of invasion detection (Coles and Eldredge, 2002; Hewitt, 2002; Molnar *et al.*, 2008) and are also susceptible to shifts in invasion dynamics under climate change (Raitsos *et al.*, 2010; Bellard *et al.*, 2016b), although the relative impact given current high levels of invasion may be lower than that in high-latitude systems. An assessment of publicly available datasets by Molnar *et al.* (2008) identified the temperate northern Atlantic Ocean and the temperate northern Pacific Ocean as the most invaded open-water marine ecosystems globally. San Francisco Bay alone contains more invasive species than the 144 invasive species identified by our study across all high-latitude marine regions.

The 234 invasive species identified in San Francisco Bay collectively account for as much as 99% of biomass in some locations (Cohen and Carlton, 1998). The same changes increasing invasion in high-latitude ecosystems may be affecting invasion in temperate areas. Shipping is a primary driver of propagule pressure in temperate areas (Bellard *et al.*, 2016b), as 16 of the 20 of the ports most central to the global shipping network are located in temperate zones (Kaluza *et al.*, 2010). Many of these shipping routes connect ports with similar environmental conditions (Seebens *et al.*, 2013) which likely increases establishment success for species with propagules transported through ballast water or hull fouling. Increasingly, tropical species may be transported to temperate regions through widening of canals (Galil *et al.*, 2015; Muirhead *et al.*, 2015) and shipping, and rising water temperatures are making temperate areas more hospitable to tropical species (Raitsos *et al.*, 2010). Another key barrier to invasion, biotic resistance, is likely being affected by human disturbance through the reduction of abundance and diversity of native species (Early *et al.*, 2016). A land cover study of terrestrial human disturbance by Hannah *et al.* (1995) identified temperate areas to be the most impacted, followed by tropical areas, with high-latitude areas being least disturbed. The increases in propagule pressure, likelihood of tropical species establishment under warming conditions, and human disturbance effects on biotic resistance suggest that species invasion in temperate areas will increase in the coming years. On one hand, the relative effect of increasing invasion on temperate systems as a whole is likely to be lower than in high-latitude systems, given that many temperate systems are already highly invaded. However, it is also possible that temperate systems will see more local extinctions due to increasingly precipitous declines in native populations (Wilcove *et al.*, 1998; Streftaris and Zenetos, 2006; Maggi *et al.*, 2015).

Comparatively few invasive species have been detected in tropical marine areas (Hewitt, 2002; Havel *et al.*, 2015; Tricarico *et al.*, 2016), but barriers to invasion in these systems also appear poised for change. Ports in the tropics experience lower shipping intensity than ports in other parts of the world (Seebens *et al.*, 2013), suggesting that tropical marine ecosystems experience lower propagule pressure than other regions. Although abiotic conditions tend to be relatively benign with low temperature variability (Mahlstein *et al.*, 2011; Barlow *et al.*, 2018), biotic resistance to invasion in tropical ecosystems is high (Coles and Eldredge, 2002; Freestone *et al.*, 2013) as a result of unparalleled species diversity and low human disturbance relative to temperate areas (Hannah *et al.*, 1995; Fine, 2002). In the future, propagule pressure in tropical areas is likely to increase (Ducruet and Notteboom, 2012). In addition, climate change is expected to increase temperature variation and extremes in tropical ecosystems to globally unique levels (Barlow *et al.*, 2018). This shift might increase physiological stress on native species that are adapted to less variable thermal conditions (Tewksbury *et al.*, 2008), reducing biotic resistance, while also potentially favoring species adapted to more variable environmental conditions (including temperate species; Astudillo *et al.*, 2016). Direct human-mediated disturbance is also on the rise in many tropical systems worldwide (Laurance and Useche, 2009; Peh, 2010; MacNeil *et al.*, 2015). The impacts of increases in propagule pressure and decreases in biotic resistance could, therefore, lead to increases in the invasion of tropical ecosystems, many of which occur in countries that have lower capacity to detect and manage such increases (Early *et al.*, 2016). We note that invasions in tropical ecosystems – particularly tropical marine ecosystems – have been less well studied than those in temperate zones (Drake and Lodge, 2004) and existing tropical studies have often focused on islands (Coles and Eldredge, 2002; Hutchings *et al.*, 2002), which are more susceptible to invasion than mainland areas (Sax and Brown, 2000). Further studies are required to understand the implications of human disturbance and climate change on species invasion in tropical ecosystems.

Conclusions

High-latitude ecosystems have experienced few species invasions relative to many lower-latitude regions, likely due to limited propagule transport, low rates of human disturbance, low minimum annual temperatures, and high resource seasonality (Ruiz *et al.*, 2006; Ruiz and Hewitt, 2009). These factors are changing with shifting human activity and climate change, potentially precipitating a breakdown of these same invasion barriers which could be contributing to the increasing number of documented species invasions in high-latitude regions. There are still few data identifying these drivers and impacts in northern high-latitude ecosystems (Ruiz and Hewitt, 2009; de Rivera *et al.*, 2011), and future studies are needed to resolve the effect of shifting, interactive factors and expand our understanding of invasion resistance in high-latitude ecosystems. Data on the number and abundance of invasive species as a proportion of the total community, which would be integral to a more quantitative assessment of invasion, are particularly scarce. In addition, although our study focused on northern high-latitude systems (where propagule pressure is increasing rapidly unlike in the Antarctic; Ruiz and Hewitt, 2009), southern high-latitude ecosystems are also experiencing changes in abiotic conditions (Aronson *et al.*, 2007; Turner *et al.*, 2009), potentially increasing habitat suitability for non-native species while increasing physiological stress on – and therefore reducing biotic resistance from – native species. Insight from increased study of high-latitude ecosystems globally could then be applied to management, identifying mechanisms most important for conferring invasion resistance and most susceptible to decline with climate change or direct human disturbance.

National and international efforts to prevent the spread of non-native species are ongoing. International organizations like the European Network on Invasive Alien Species (NOBANIS) compile data and disseminate information to the public with the goal of reducing invasive species dispersal (https://www.nobanis.org). The Ballast Water

Management convention, an international agreement through the United Nations International Marine Organization which began enforcement in 2017, standardizes protocol for the dumping of ballast water to reduce the likelihood of species introduction (David *et al.*, 2015; Yang *et al.*, 2017). At the same time as regulations to prevent transport via ballast water and hull fouling are likely reducing propagule pressure, the effects of climate change on abiotic invasion resistance may make individual propagules more likely to establish. Furthermore, our study uncovered high variability by country in government documentation of invasive species, which may be biased across ecosystems and taxa by accessibility or the expertise of the surveyors. Improved, standardized monitoring programs will provide a more thorough picture of species invasion to inform further action.

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Figures

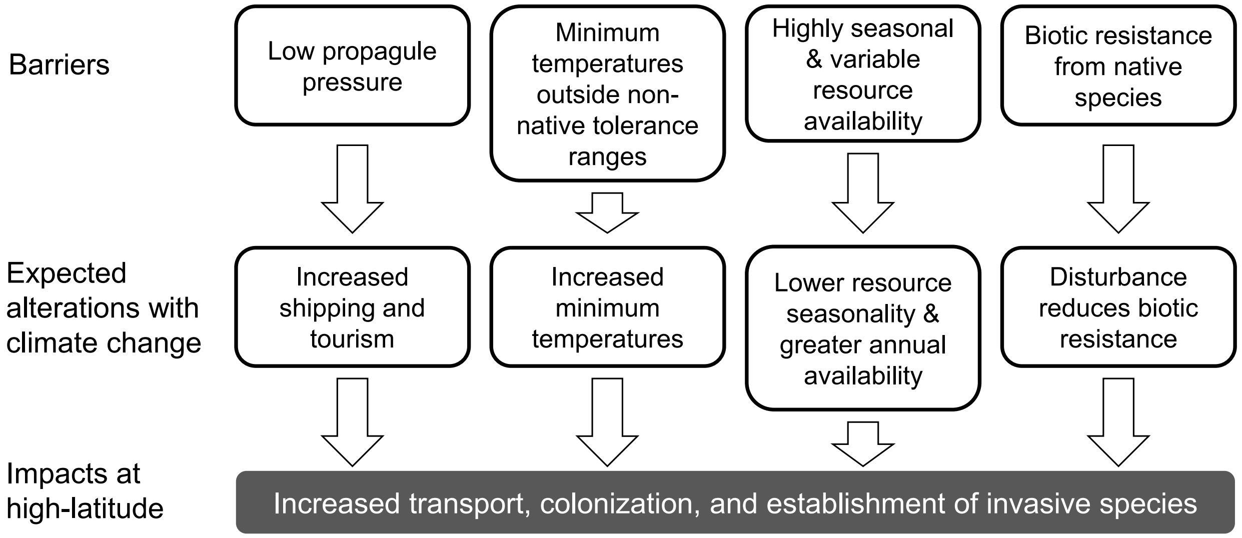

Figure 3.1. Climate change is likely to increase the invasion of high-latitude ecosystems by breaking down existing invasion barriers across the invasion pathway, from transport to colonization and establishment.

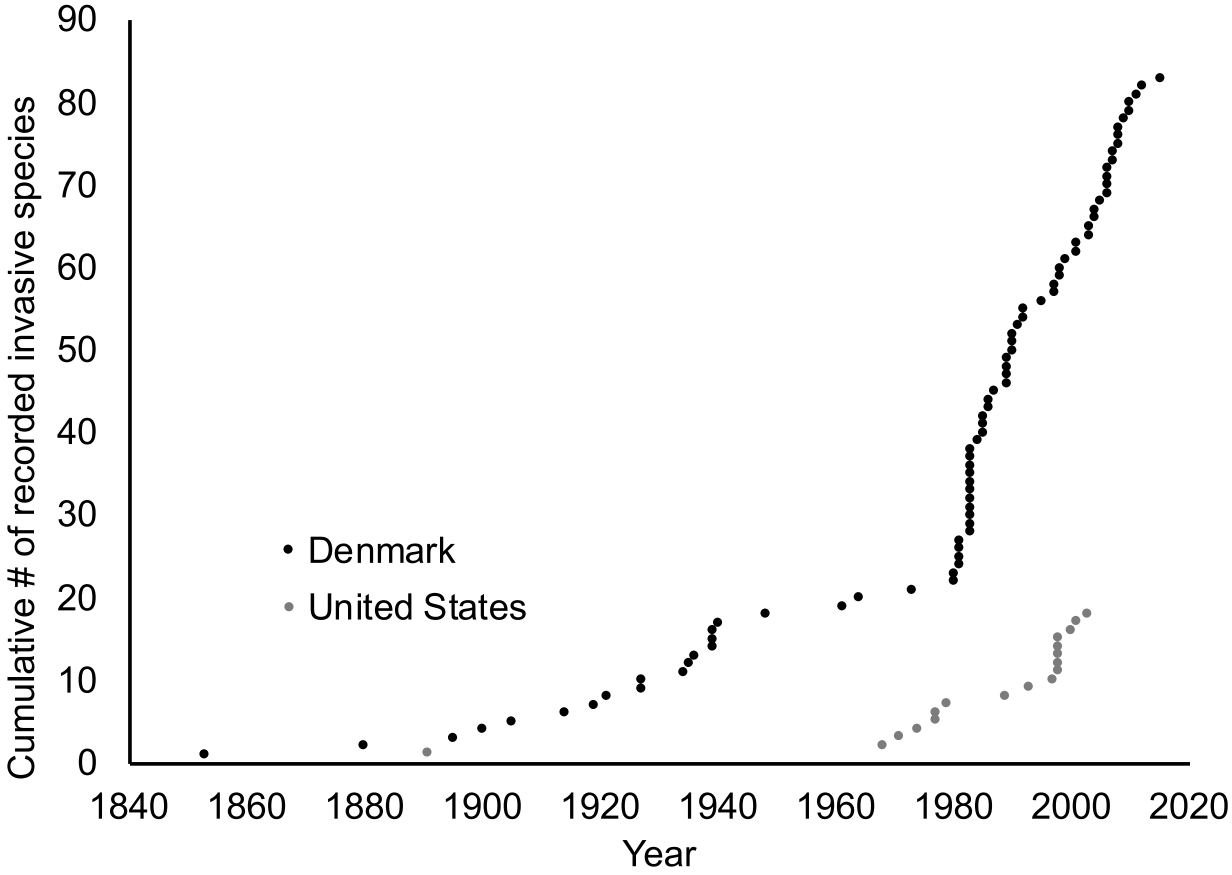

Figure 3.2. Cumulative number of invasive marine species reported in government documents in Denmark (blue) and the United States (Alaska; green). Standardized monitoring protocols were used in the United States (all years) and in Denmark after 1989.

Country	Agency	Title	Citation	# Invasive Species Present	# Invasive Species Predicted
Denmark	Danish Centre for Environment and Energy	Trends in records and contribution of non-indigenous species (NIS) to biotic communities in Danish marine waters	Stæhr *et al.,* 2016	83	
Estonia	Ministry of the Environment	CBD Thematic Report on Alien Species- Estonia	Eek, 2000	2	
Finland	Ministry of Agriculture and Forestry in Finland	Finland's National Strategy on Invasive Alien Species	Ministry of Agriculture and Forestry, 2012	14	5
Finland	Ministry of the Environment	Alien species in Finland	Nummi, 2001	2	
Norway	The Norwegian Biodiversity Information Centre	Ecological Risk Analysis of Alien Species	Gederaas *et al.,* 2007	42	
Norway	The Norwegian Biodiversity Information Centre	Alien Species in Norway	Gederaas *et al.,* 2012	13	55
United Kingdom	Department for Environment, Food and Rural Affairs	Invasive Identification Sheets	Sewell, 2011; Stebbing *et al.* , 2012; Wade *et al* . (undated)	3	
United Kingdom	Scottish Natural Heritage	Scottish Natural Heritage	Sweet, 2011; Sweet, 2012a; Sweet, 2012b; Sweet, 2012c; Bishop, 2012	7	
United States	Alaska Department of Fish and Game	Alaska Aquatic Nuisance Species Management Plan	Fay, 2002		5
United States	Prince William Sound Regional Citizens' Advisory Council & U.S. Fish & Wildlife Service	Biological Invasions in Alaska's Coastal Marine Ecosystems: Establishing a Baseline	Ruiz *et al.,* 2006	22	

Table 3.1. Summary of invasive species management documents prepared by 6 high-latitude countries.

Species	Taxon	Established	Predicted	Reference
Amphibalanus improvisus	Crustacean		x	De Rivera *et al.*, 2011
Botrylloides violaceus	Ascidian	x		Lambert and Sanamyan, 2001
Botryllus schlosseri	Ascidian	x		Simkanin *et al.*, 2016
Caprella mutica	Crustacean	x		Ashton *et al.*, 2008
Carcinus maenas	Crustacean		x	De Rivera *et al.*, 2011
Didemnum vexillum	Ascidian	x		Cohen *et al.*, 2011
Eriocheir sinensis	Crustacean		x	Hanson and Sytsma, 2008
Littorina saxatilis	Mollusc		x	De Rivera *et al.*, 2011
Molgula citrina	Ascidian	x		Lambert *et al.*, 2010
Mya arenaria	Bivalve	x		Powers *et al.*, 2006
Salmo salar	Fish	s	x	Piccolo and Orlikowska, 2012
Sargassum muticum	Alga	x		Kerrison and Le, 2016
Schizoporella japonica	Bryozoan	x		Dick *et al.*, 2005
Spartina spp.	Plant		x	Morgan and Sytsma, 2013
Styela clava	Ascidian		x	De Rivera *et al.*, 2011

Table 3.2. Invasive species established or predicted to colonize Alaska based on a structured literature review.

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CONCLUSIONS

Ecosystems are formed by webs of species interacting such that a disturbance can ripple through the network, amplified or dampened by interactions among the constituent species. Climate change will have a multitude of impacts across ecosystems depending which species are present, the abundance and ecological role of each species, and how those species interact. One type of species which may play a key role in determining the effects of climate change are ecosystem engineers, which can alter local environmental conditions. In marine ecosystems, abundant ecosystem engineers can reduce temperature and raise pH, which may reduce the local impacts of climate change and ocean acidification. Recent studies have cited these habitat-altering species as potential “climate rescuers”. However, as I highlight in my first chapter, it is important to recognize that not all dominant marine producers fill that role. I provide a counterexample: *Neorhodomela oregona*, a seaweed which, despite being overwhelmingly abundant in tide pools in southeastern Alaska, affected neither water temperature nor pH in tide pools, despite displaying an effect on pH when isolated in mesocosms. Dominant species can affect multiple ecosystem functions. In my second chapter, I found that a pair of dominant species, the producer *N. oregona* and the shellfish consumer *Mytilus trossulus*, had largely opposing effects on ecosystem functions, including productivity, calcification, and nutrient cycling (specifically, ammonium flux). Interestingly, the effect of the dominant consumer shifted markedly when the dominant producer was removed, suggesting that the loss of critical species has the potential to destabilize ecosystems. At the same time, species addition can also affect functioning by means of species invasion. Whether climate change will alter the rate of species invasion, and the extent to which it will drive biogeographic reorganization writ large, will be critical to assessing, forecasting, and potentially mitigating the impacts of species invasion in the 21st century. One of the most potentially concerning interactions between climate change and species invasion, as I highlight in high-latitude areas in my third chapter, is that changing conditions may present opportunities for invasion in ecosystems which have been historically insulated from its effects. Meanwhile, climate change may negatively affect native biota, further reducing resistance to non-native species establishment and triggering a surge of species invasion. These findings could inform conservation priorities by highlighting the importance of rigorously assessing which dominant species affect local environmental conditions and serve as key drivers of ecosystem function, as well as underscore the vulnerability of historically invasion-resistant ecosystems to increased species invasion amid ongoing climate change.

APPENDIX A

Supplementary figures for Chapter 1: Climate change amelioration by marine producers: Does dominance predict impact?

Species	Mean Surface Area of Individual (cm^2)	Sample Size	Substitute species
Hemigrapsus	4.66	1	NA
Pagurus	0.61	10	NA
Nucella	1.75	10	NA
Limpets	0.26	10	NA
Littorina sitkana	0.34	10	NA
Litt. plena/scutulata	0.15	10	NA
Idotea	1.75	NA	*Nucella*
Amphipod	0.34	NA	*Littorina sitkana*
Chitons	1.75	NA	*Nucella*

Appendix Table 1: Surface area for mobile invertebrate species identified in the tide pools was calculated based on collection of representative individuals (n = 1-10, as shown below) at the field site. Collected specimens were photographed and their surface area was calculated using ImageJ. For those relatively rare species not measured, similarly sized species were substituted.

A	*F*		*df*	*df res*	*p value*
Treatment	0.5726		1	5	0.4833
Day/Night	29.2480		1	6	**0.0016**
Biomass	0.0689		1	5	0.8034
Treatment*Day/Night	16.8799		1	6	**0.0063**
Treatment	0.1825		1	5	0.6870
Day/Night	29.1219		1	6	**0.0017**
Area	0.0212		1	5	0.8900
Treatment*Day/Night	16.8072		1	6	**0.0064**
B	*Estimate*	*SE*	*df*	*t ratio*	*p value*
Alga Addition (Biomass) – Control: Day	0.0262	0.0662	5.81	0.396	0.7065
Alga Addition (Biomass) – Control: Night	-0.1227	0.0662	5.81	-1.851	0.1152
Alga Addition (Area) – Control: Day	0.0501	0.0598	6.02	0.838	0.4340
Alga Addition (Area) – Control: Night	-0.0988	0.0598	6.02	-1.652	0.1495

Appendix Table 2: (A) Analysis of the rates of pH change in the mesocosm experiment that includes day and night samplings in a single model, using either *N. oregona* biomass added or the surface area of the *N. oregona* prior to removal. Results indicate differences in pH change between the day and night, as well as an interaction between the addition of *N. oregona* and the presence or absence of light. (B) Pairwise post-hoc comparisons showed no difference in the rate of pH change with respect to *N. oregona* abundance (either biomass or surface area) during day or night.

A: Pre-removal light	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^{2}L^{-1})	-0.0014	0.0005	-2.63	**0.0468**
Tide height	-0.0525	0.1443	-0.36	0.7307
Light	-0.0015	0.0012	-1.24	0.2710
Temperature	0.0228	0.0543	0.42	0.6923
B: Pre-removal dark	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	0.0018	0.0004	4.08	**0.0065**
Tide height	0.9357	0.4686	2.00	0.0928
Temperature	-0.5363	0.2425	-2.21	0.0690
C: Post-removal control light	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	-0.0008	0.0004	-1.86	0.1594
D: Post-removal control dark	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	0.0025	0.0005	4.46	**0.0210**
E: Post-removal removal light	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	-0.0019	0.0009	-2.09	0.1270
F: Post-removal removal dark	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	0.0015	0.0017	0.87	0.4470
G: Post-removal light	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	-0.0009	0.0004	-2.45	0.0913
Treatment	0.2141	0.1421	1.51	0.2290
Tide height	-0.1221	0.1965	-0.62	0.5785
Light	0.0002	0.0001	2.63	0.0785
Temperature	0.1646	0.0618	2.66	0.0762
N. oregona density (cm^2 L^{-1})*treatment	-0.0013	0.0005	-2.45	0.0920
H: Post-removal dark	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	0.0025	0.0011	2.25	0.0875
Treatment	0.7665	0.4448	1.72	0.1599
Tide height	0.6390	0.5394	1.18	0.3017
Temperature	-0.2427	0.1807	-1.34	0.2504
N. oregona density (cm^2 L^{-1})*treatment	-0.0019	0.0017	-1.12	0.3255

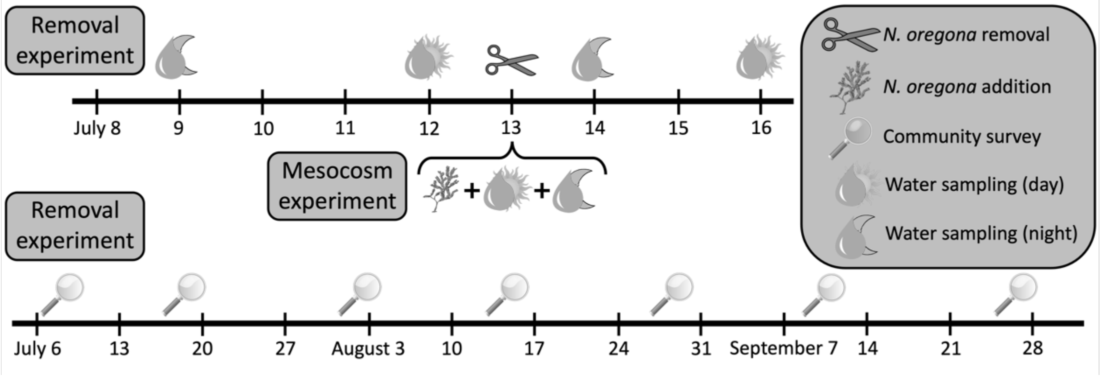
Appendix Table 3: (A) Analysis of the rates of pH change from the light-dark trials prior to (A, B) and following removal (C-H). *N. oregona* had a significant negative effect on the rate of pH change during the light phase of the pre-removal trial (A) as well as a positive effect during the dark phase of the pre-removal (B) and post-removal (D) trials. Treatment and an interaction effect of initial *N. oregona* biomass and treatment were included in the full post-removal analyses (G, H), and tide height, light, and temperature were included as covariates where relevant.

A	*F*		*df*	*df res*	*p value*
Treatment	3.1651		1	7	0.1185
Day/Night	9.5331		1	8	**0.0149**
Area	1.1939		1	7	0.3107
Treatment*Day/Night	0.2183		1	8	0.6528
B	*Estimate*	*SE*	*df*	*t ratio*	*p value*
Alga Present (Control) – Removal: Day	-0.0763	0.0455	13.9	-1.677	0.1159
Alga Present (Control) – Removal: Night	-0.0495	0.0455	13.9	-1.089	0.2947

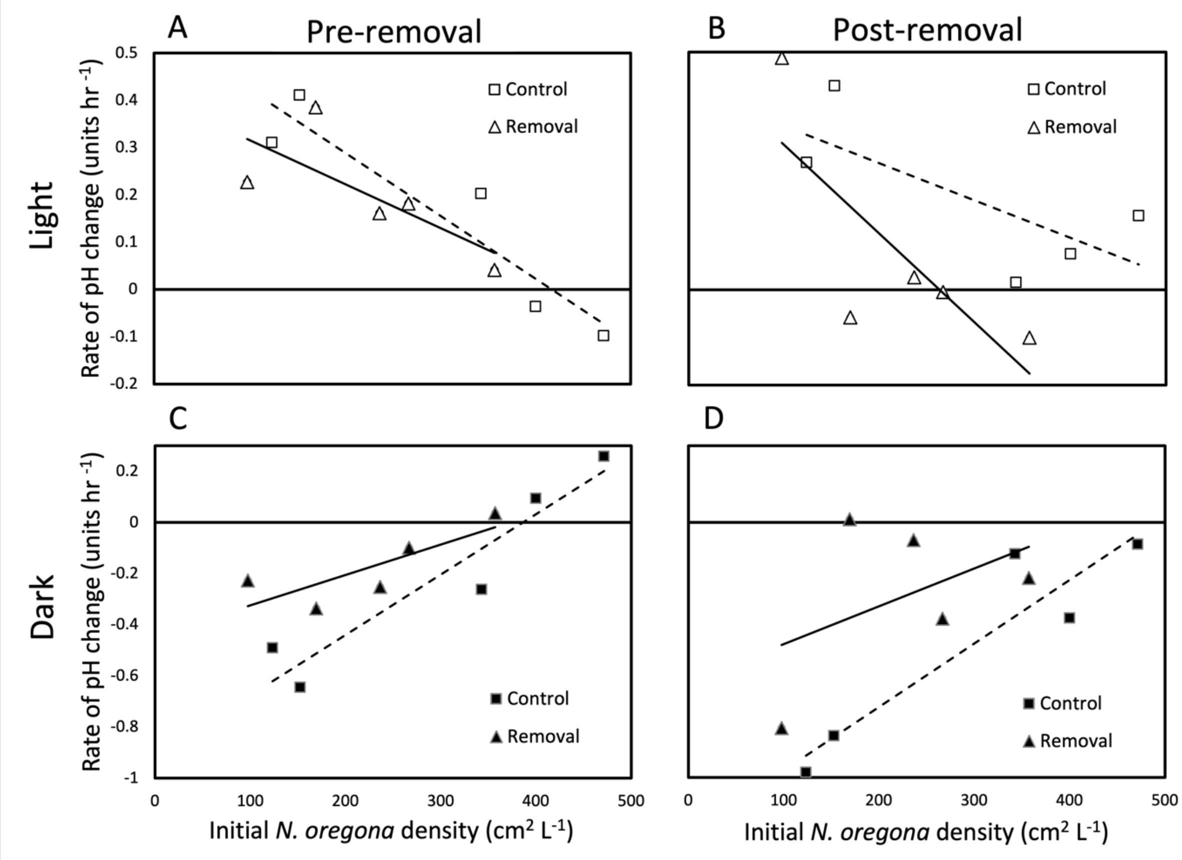
Appendix Table 4: (A) Analysis of the rates of pH change from the day and night samplings following removal, incorporating pre-removal *N. oregona* surface area as a covariate, show differences in pH change between the day and night but no effect of *N. oregona*. (B) Pairwise post-hoc comparisons showed no effect of *N. oregona* removal on the rate of pH change during day or night.

A: Pre-removal day	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	-1.9214	3.3533	-0.57	0.597
Tide Height	0.2660	0.1434	1.86	0.137
Light	-0.0004	0.0005	-0.79	0.474
Temperature	-0.0225	0.0408	-0.55	0.611
Ulva spp. density (cm^2 L^{-1})	15.6170	24.994	0.62	0.566
B: Pre-removal night	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	-1.4600	1.1379	-1.28	0.256
Tide Height	0.0713	0.0718	0.99	0.367
Temperature	-0.0174	0.0288	-0.60	0.572
Ulva spp. density (cm^2 L^{-1})	0.0165	7.0488	0.00	0.998
C: Post-removal day	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2 L^{-1})	-0.9082	1.7484	-0.52	0.655
Treatment	-0.1293	0.1752	-0.74	0.537
Tide Height	-0.1254	0.1960	-0.64	0.588
Light	0.0027	0.0019	1.42	0.293
Temperature	0.4630	0.2079	2.23	0.156
N. oregona density (cm^2 L^{-1})*Treatment	10.4546	6.6255	1.58	0.255
Ulva spp. density (cm^2 L^{-1})	2.6067	19.647	0.13	0.907
D: Post-removal night	*Estimate*	*SE*	*t ratio*	*p value*
N. oregona density (cm^2/L)	-3.0575	1.1337	-2.697	0.0740
Treatment	0.0581	0.0606	0.959	0.4084
Tide Height	0.2924	0.1180	2.478	0.0895
Temperature	-0.1068	0.0546	1.956	0.1454
N. oregona density (cm^2 L^{-1})*Treatment	-1.5705	2.2373	-0.702	0.5333
Ulva spp. density (cm^2 L^{-1})	0.1272	4.9446	0.026	0.9811

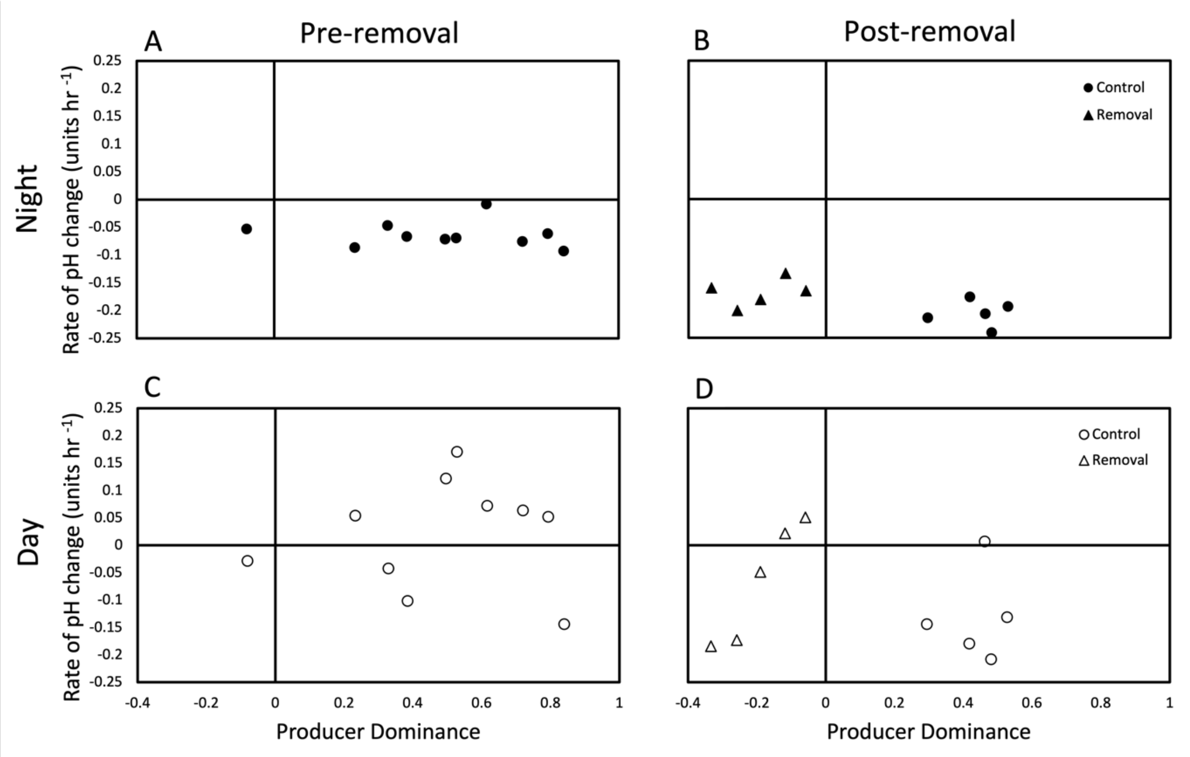
Appendix Table 5: Analysis of the potential effects of *N. oregona* and *Ulva* spp. on the rates of pH change prior to (A, B) and following removal (C, D), with tide height, light, and temperature were included as covariates where relevant. Neither *N. oregona* nor *Ulva* spp. affected the rate of pH change during the experiment.



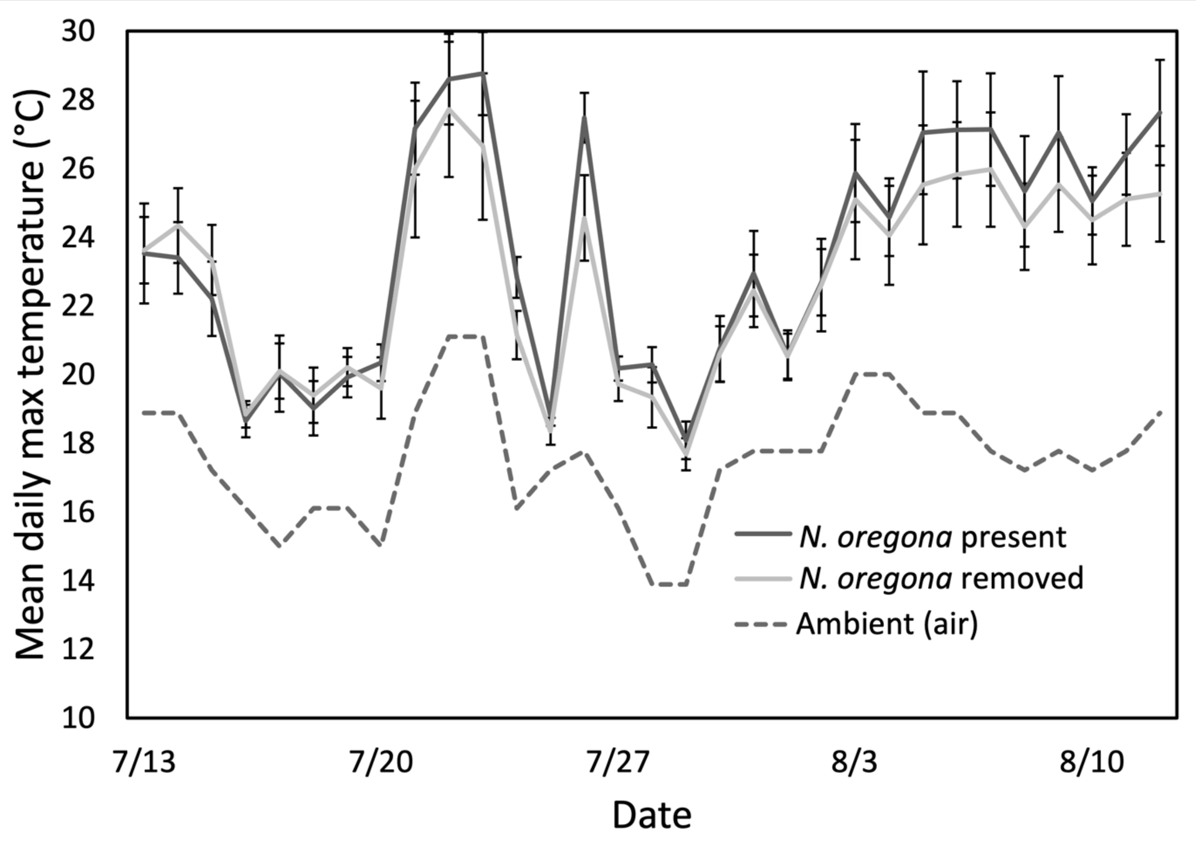
Appendix Figure 1: Timeline of the experiment. Primary data collection took place over seven days for the removal experiment and one day for the mesocosm experiment. Community surveys for the removal experiment started prior to *N. oregona* removal and continued for 11 weeks after removal.



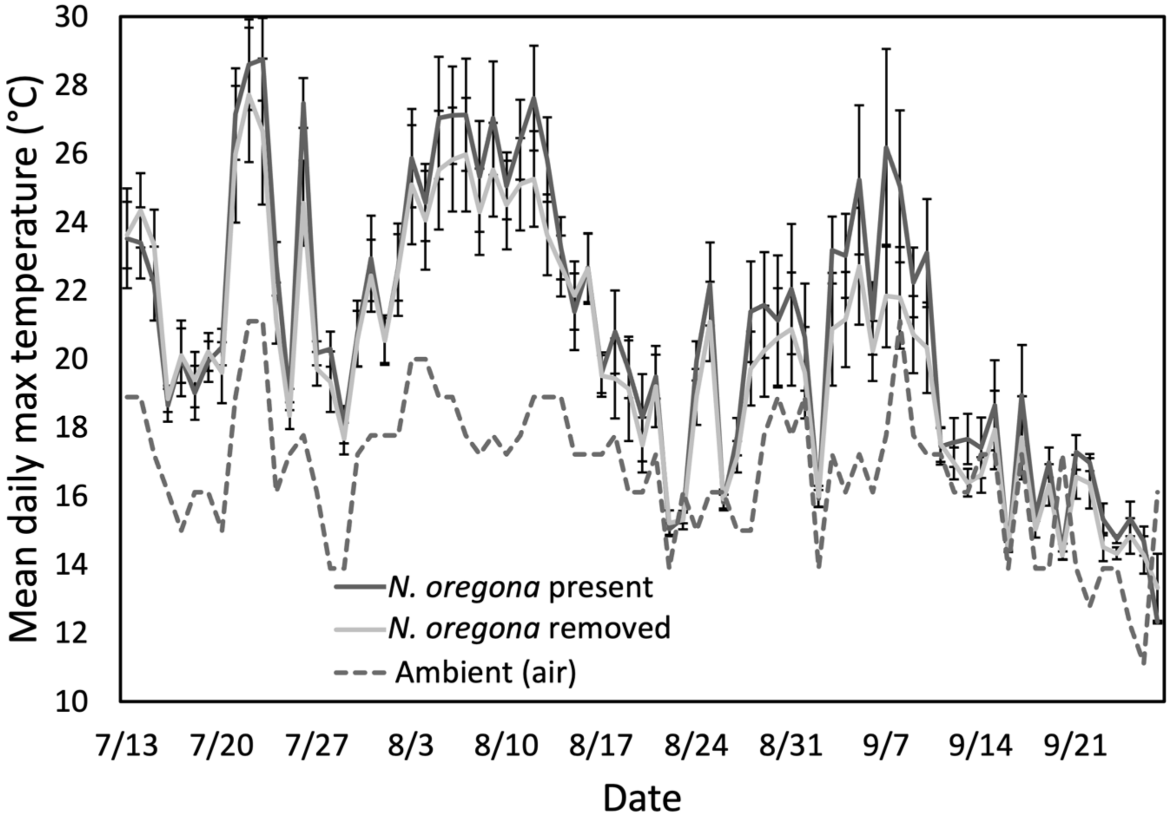
Appendix Figure 2: Relationships between pre-removal *Neorhodomela oregona* abundance and the rate of pH change in tide pools, as measured in the field during the light/dark incubation trials before and after removal. Prior to removal (A), the rates of pH change during the light incubation were generally positive and decreased with increasing *N. oregona* abundance, while a similar but non-significant trend occurred in the post-removal light sampling (B). The rates of pH change in dark conditions prior to removal (C) were largely negative but were more positive in pools with greater *N. oregona* abundance, an effect which remained significant in the post-removal (D) sampling in the control pools but not the removal group. Each data point represents a single tide pool during a single sampling.



Appendix Figure 3: Producer dominance did not affect the rate of pH change in tide pools, including before (A, B) or after (C, D) the manipulation nor during the night (A, C) or day (B, D). There was no effect of producer dominance (% cover of producers - % cover of consumers) on rates of pH change in the n = 10 tide pools prior to manipulation nor after the manipulation, when n = 5 pools contained *N. oregona* (circles) while n = 5 had *N. oregona* removed (triangles). Each point represents data from a single pool; (A, C) and (B, D) are from the same set of pools surveyed on two separate dates (immediately before and after the removal).



Appendix Figure 4: *Neorhodomela oregona* did not affect water temperature in tide pools. *N. oregona* removal did not affect maximum daily water temperatures in tide pools during the month following *N. oregona* removal. Each point represents the mean daily maximum temperature of N = 5 pools that were either unmanipulated (dark gray) or in which *N. oregona* was removed (light gray). Ambient air temperature values (gray dashed) reflect temperatures measured at Rocky Gutierrez Airport in Sitka, Alaska (CustomWeather, Inc., 2021). Error bars indicate standard error calculated using the pooled variance method.



Appendix Figure 5: ***N. oregona*** **did not affect tide pool water temperature over the full 11-week experiment.** Each point represents the mean daily maximum temperature of n = 5 pools that were either unmanipulated (dark gray) or in which *N. oregona* was removed (light gray). Ambient air temperature values (gray dashed) reflect temperatures measured at Rocky Gutierrez Airport in Sitka, Alaska (CustomWeather, Inc., 2021). Error bars indicate standard error calculated using the pooled variance method.

APPENDIX B

Supplementary figures for Chapter 2: The functional effects of a dominant consumer shift following dominant producer loss

Function	**Function group**	**Units**	**Positive direction assigned (un-reflected)**	**Rationale**	**Positive direction assigned (reflected)**
Net Community Productivity (NCP)	Productivity	$mgO_2\ L^{-1}\ hr^{-1}$	Increase in O_2	Dominant producers are expected to increase net primary productivity during the day	Decrease in O_2
Respiration	Productivity	$mgO_2\ L^{-1}\ hr^{-1}$	Decrease in O_2	Dominant producers are expected to increase resipration during the day	Increase in O_2
Rate of pH change (day)	Water chemistry (day)	units hr^{-1}	Increase in pH	Dominant producers are expected to raise pH through photosynthesis by extracting inorganic carbon from the water column during the day	Increase in pH
Rate of pH change (night)	Water chemistry (night)	units hr^{-1}	Increase in pH		Decrease in pH
Net Ecosystem Calcification (NEC, day)	Water chemistry (day)	mmol $CaCO_3\ m^{-2}\ hr^{-1}$	Positive NEC	Dominant producers are expected to increase NEC during the day by producing a higher pH environment that is more suitable to calcification	Positive NEC
Net Ecosystem Calcification (NEC, night)	Water chemistry (night)	mmol $CaCO_3\ m^{-2}\ hr^{-1}$	Positive NEC		Negative NEC
Ammonium flux (day)	Nutrients (day)	µmol $NH_4^+\ L^{-1}\ hr^{-1}$	Decrease in concentration	Dominant producers are expected to take up nutrients during the day, leading to reduced nutrient concentration in the water column	Decrease in concentration
Ammonium flux (night)	Nutrients (night)	µmol $NH_4^+\ L^{-1}\ hr^{-1}$	Decrease in concentration		Increase in concentration
Nitrate + nitrite flux (day)	Nutrients (day)	µmol $(NO_3^- + NO_2^-)\ L^{-1}\ hr^{-1}$	Decrease in concentration		Increase in concentration
Nitrate + nitrite flux (night)	Nutrients (night)	µmol $(NO_3^- + NO_2^-)\ L^{-1}\ hr^{-1}$	Decrease in concentration		Increase in concentration
Phosphate flux (day)	Nutrients (day)	µmol $PO_4^{3-}\ L^{-1}\ hr^{-1}$	Decrease in concentration		Decrease in concentration
Phosphate flux (night)	Nutrients (night)	µmol $PO_4^{3-}\ L^{-1}\ hr^{-1}$	Decrease in concentration		Decrease in concentration

Supplementary Table 1: We assigned directionality to each of the twelve ecological functions based on the predicted effects of a dominant producer during the day. We also reflected the data based on the associations between dominant producer abundance and each individual function in intact tide pools to avoid positive and negative values obscuring overall patterns (Figures S2, S4-6).

Function set	Factor	Sum of Squares	Df	F value	p value
Overall function	*N. oregona* abundance (m^2L^{-1})	0.00118	1,8	0.1764	0.6856
Productivity	*N. oregona* abundance (m^2L^{-1})	0.21754	1,8	4.5886	0.0646
Water chemistry (day)	*N. oregona* abundance (m^2L^{-1})	0.17233	1,8	3.6367	0.0929
Water chemistry (night)	*N. oregona* abundance (m^2L^{-1})	0.10967	1,8	2.0667	0.1885
Nutrients (day)	*N. oregona* abundance (m^2L^{-1})	0.021259	1,8	0.7426	0.4139
Nutrients (night)	*N. oregona* abundance (m^2L^{-1})	0.0008	1,8	0.015	0.9055

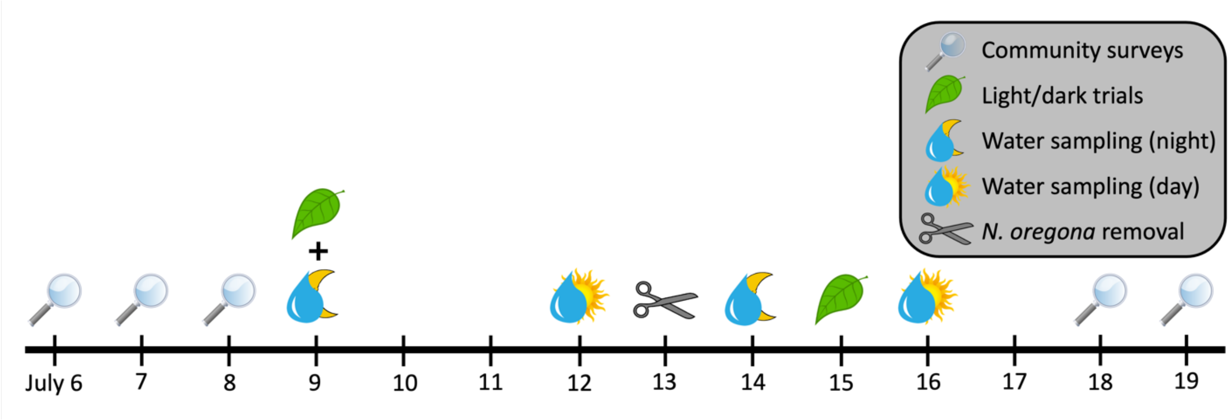
Supplementary Table 2: Analysis of the associations between the abundance of a dominant alga (*Neorhodomela oregona*) and averaged sets of ecosystem functions (all twelve functions, followed by subsets of related functions) in N=10 unmanipulated tide pools near Sitka, AK.

Function set	Factor	Sum of Sq	Df	F value	p value
Overall function	*M. trossulus* abundance (m^2L^{-1})	0.000791	1,8	0.1174	0.7407
Productivity	*M. trossulus* abundance (m^2L^{-1})	0.33013	1,8	9.9034	**0.0137**
Water chemistry (day)	*M. trossulus* abundance (m^2L^{-1})	0.23165	1,8	5.7951	**0.0427**
Water chemistry (night)	*M. trossulus* abundance (m^2L^{-1})	0.01374	1,8	0.2112	0.6581
Nutrients (day)	*M. trossulus* abundance (m^2L^{-1})	0.009095	1,8	0.3017	0.5978
Nutrients (night)	*M. trossulus* abundance (m^2L^{-1})	0.00457	1,8	0.0867	0.7759

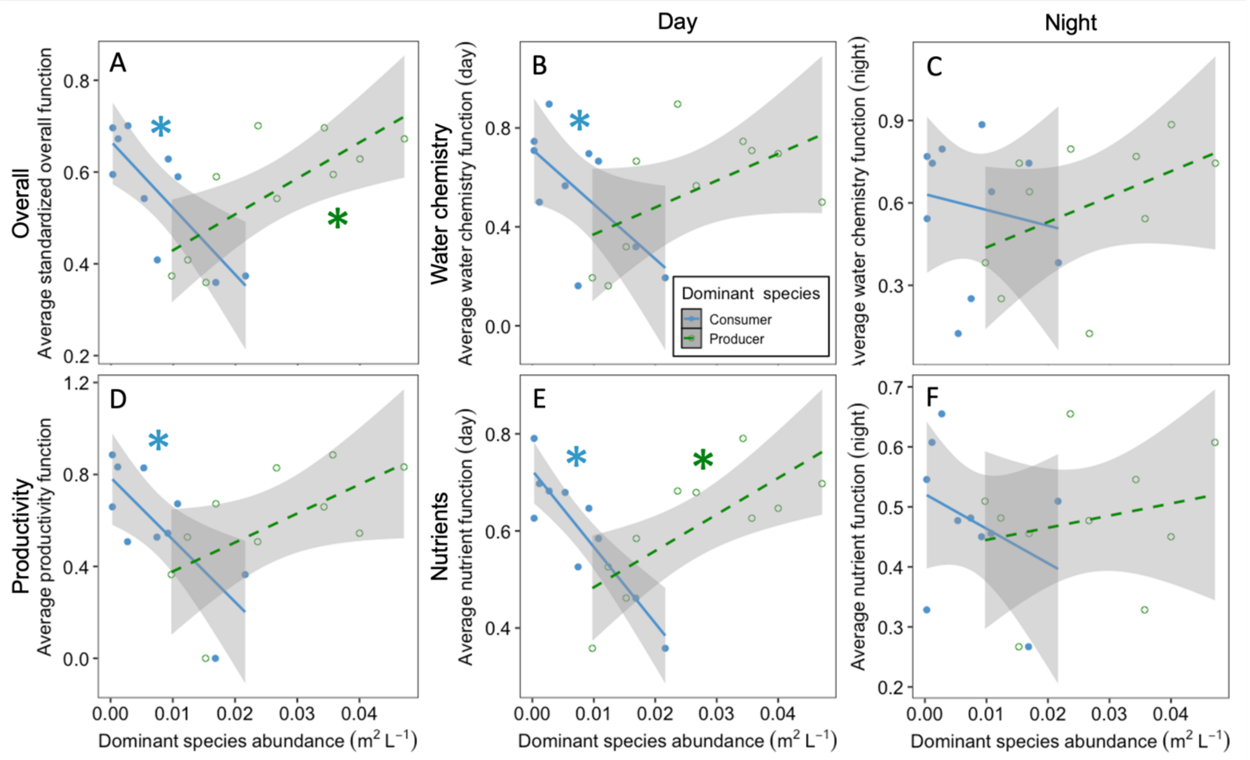
Supplementary Table 3: Analysis of the associations between the abundance of a dominant consumer (*Mytilus trossulus*) and averaged sets of ecosystem functions (all twelve functions, followed by subsets of related functions) in tide pools.

Overall function	*M. trossulus* abundance	0.046759	1,6	4.8849	0.06913
	Treatment	0.002673	1,6	0.2793	0.61615
	M. trossulus abundance*Treatment	0.028573	1,6	2.985	0.13478
Productivity	*M. trossulus* abundance	0.1249	1,6	1.7003	0.24
	Treatment	0.05275	1,6	0.7181	0.4293
	M. trossulus abundance*Treatment	0.13089	1,6	1.7818	0.2303
Water chemistry (day)	*M. trossulus* abundance	0.36551	1,6	23.057	**0.002995**
	Treatment	0.00692	1,6	0.4366	0.533312
	M. trossulus abundance*Treatment	0.02598	1,6	1.6387	0.247767
Water chemistry (night)	*M. trossulus* abundance	0.001436	1,6	0.0392	0.8496
	Treatment	0.011795	1,6	0.3221	0.5909
	M. trossulus abundance*Treatment	0.029854	1,6	0.8152	0.4014
Nutrients (day)	*M. trossulus* abundance	0.27876	1,6	12.249	**0.01283**
	Treatment	0.01515	1,6	0.6657	0.44573
	M. trossulus abundance*Treatment	0.012084	1,6	0.531	0.49364
Nutrients (night)	*M. trossulus* abundance	0.020816	1,6	1.2836	0.3005
	Treatment	0.00342	1,6	0.2109	0.6622
	M. trossulus abundance*Treatment	0.010482	1,6	0.6464	0.4521

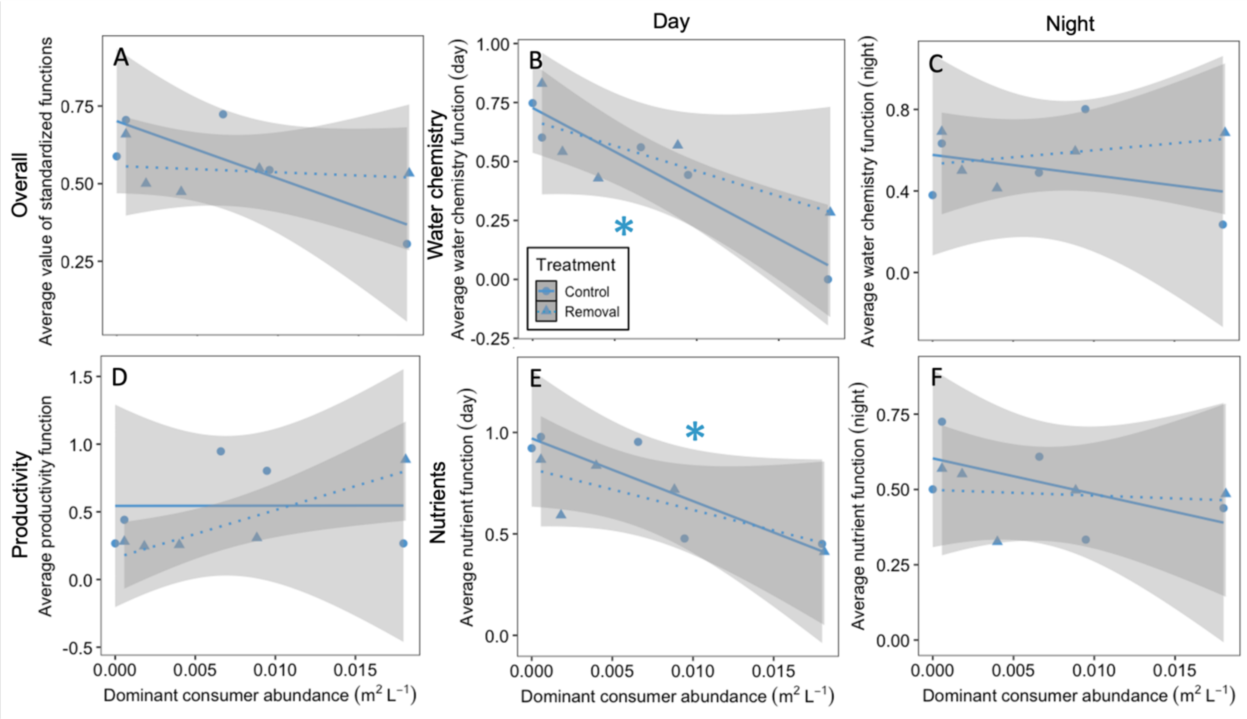
Supplementary Table 4: Analyses comparing the abundance of a dominant consumer (*Mytilus trossulus*) to averaged sets of ecosystem functions (all twelve functions, followed by subsets of related functions) in tide pools (N=5 controls with *Neorhodomela oregona* present and N=5 with the dominant alga removed). Dominant consumer abundance was negatively associated with daytime water chemistry and daytime nutrient function across both treatments and the effect did not differ between treatment groups.



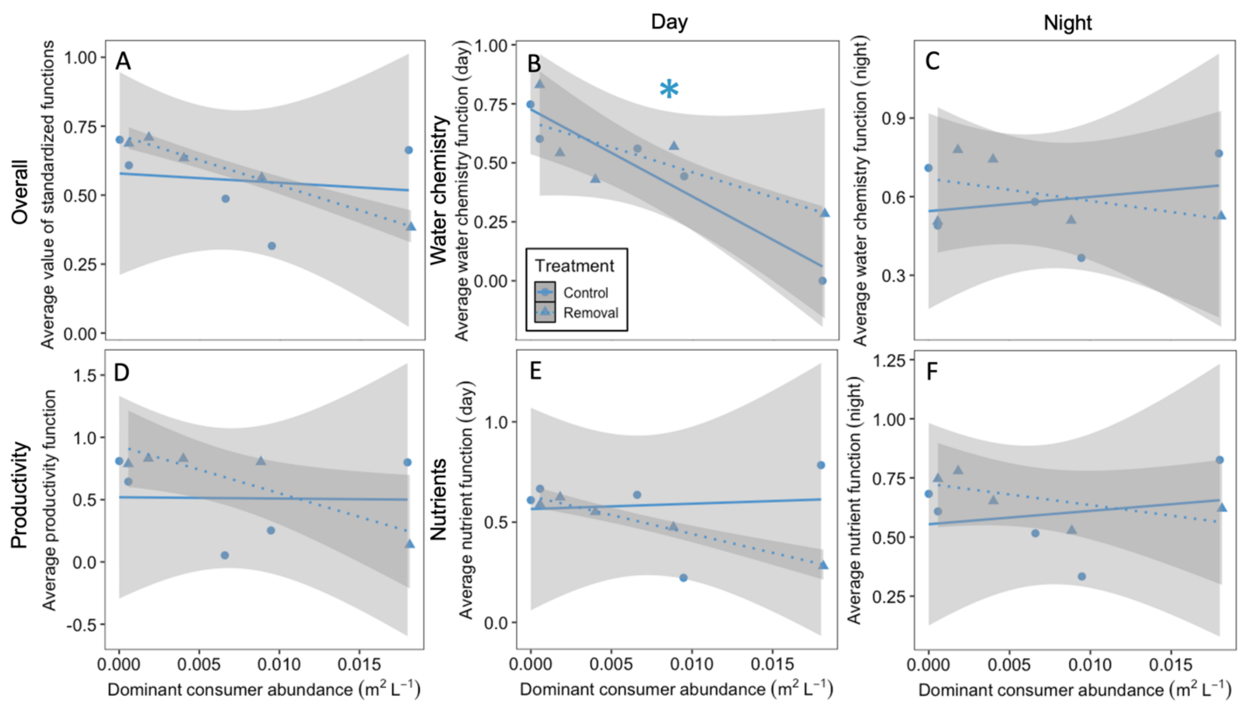
Supplementary Figure 1: The data used in this project were collected from N=10 tide pools at John Brown's Beach near Sitka, Alaska, USA during a 14-day time period in July 2019. Water sampling was conducted as close as possible prior to and immediately following the removal of a dominant producer, the alga *Neorhodomela oregona*, to minimize the possibility for uncontrolled factors (such as changing weather patterns) to influence measurements.



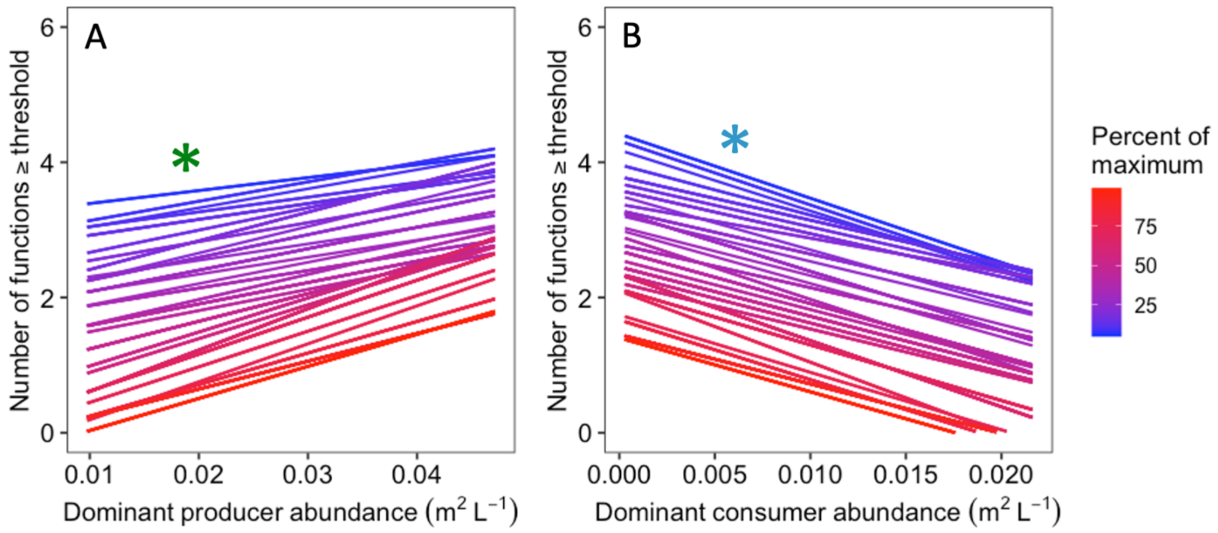
Supplementary Figure 2: Relationships between the abundances of a dominant consumer (blue) and a dominant producer (green) on averaged rates of (A) overall ecosystem functions, change in water chemistry during the (B) day and (C) night, (D) productivity, and change in nutrient levels during the (E) day and (F) night, using data that have been reflected to establish positive directionality for the relationship between each function and *N. oregona* abundance. The abundance of a dominant consumer, the mussel *M. trossulus*, was (A) negatively associated with averaged overall ecosystem multifunctionality, driven by negative relationships with (D) averaged productivity, (B) water chemistry, and (E) nutrient function during the day. The average function of each pool is represented in each plot by a pair of points, corresponding to the abundance of the dominant consumer (in blue) and the dominant producer (in green) in that tide pool. Algal (*N. oregona*) abundance was (A) associated with averaged overall ecosystem multifunctionality (the mean of all twelve standardized function values) in N=10 unmanipulated tide pools, driven most strongly by (E) averaged nutrient function during the day (the mean of the standardized daytime function values of the three nutrients responses. Asterisks indicate significance and shaded areas represent a 95% confidence interval.



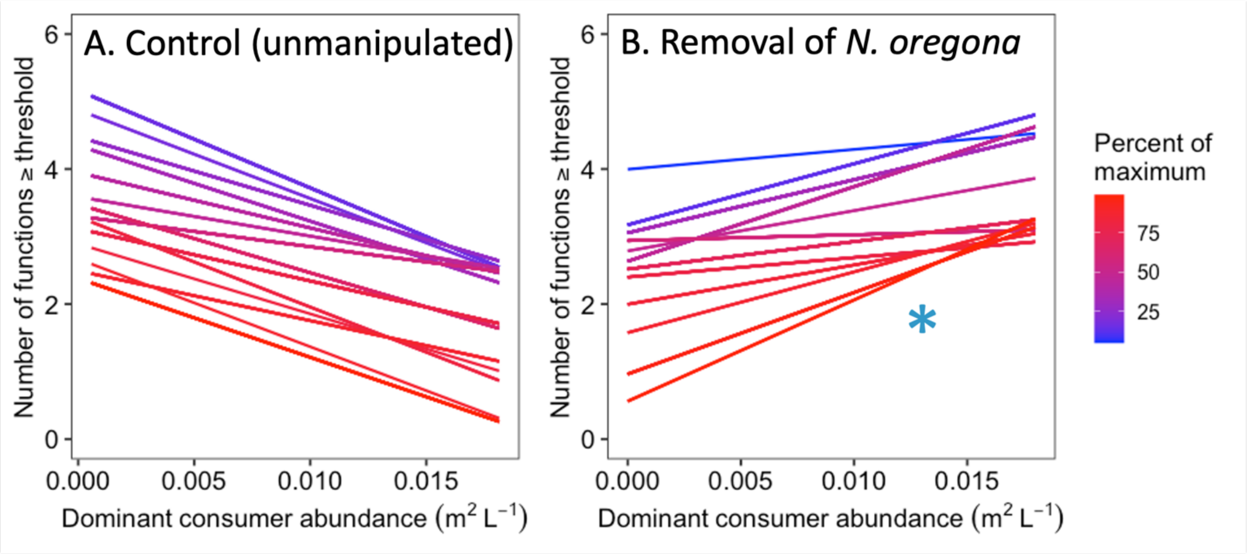
Supplementary Figure 3: Relationships between the abundances of a dominant consumer on averaged rates of ecosystem functions including (A) overall function, change in water chemistry during the (B) day and (C) night, (D) productivity, and change in nutrient levels during the (E) day and (F) night, separated by treatment group: control (dominant producer present; blue, circles and solid regression lines) and removal (dominant producer removed; blue, triangles and dotted regression lines). Following removal of a dominant alga (*N. oregona*), the abundance of mussels (*M. trossulus*) was negatively associated with (B) daytime water chemistry and (E) daytime nutrient function across both treatments. The effect of *M. trossulus* did not differ between tide pools where *N. oregona* was present and pools where *N. oregona* had been removed. Asterisks indicate significance and shaded areas correspond to a 95% confidence interval.



Supplementary Figure 4: Relationships between the abundances of a dominant consumer in two treatment groups, control (dominant producer present; blue, circles and solid regression lines) and removal (dominant producer removed; blue, triangles and dotted regression lines), on averaged rates of ecosystem functions including (A) overall function, change in water chemistry during the (B) day and (C) night, (D) productivity, and change in nutrient levels during the (E) day and (F) night, using data that have been reflected to ensure positive relationships between each function and dominant produer abundance. Following removal of a dominant alga (*N. oregona*), mussel (*M. trossulus*) abundance was (B) associated with daytime water chemistry, but the effect of *M. trossulus* did not differ between tide pools where the dominant producer was present and pools where it had been removed. Asterisks indicate significance, and the shaded areas represent a 95% confidence interval.



Supplementary Figure 5: The multiple threshold approach, using data that have been reflected to establish positive directionality between individual functions and *N. oregona* abundance, showed the abundance of a dominant producer to be (A) positively associated with ecosystem multifunctionality in tide pools. The abundance of a dominant consumer, the mussel *M. trossulus*, was (B) negatively associated with ecosystem multifunctionality using the same method. Each line indicates the relationship between target species abundance in each tide pool and the number of ecosystem functions in that pool which exceed a certain threshold value, with asterisks included to indicate significance.



Supplementary Figure 6: Following the elimination of a dominant alga (*Neorhodomela oregona*) from the removal tide pools, mussel (*Mytilus trossulus*) abundance tended to (A) increase multifunctionality in the control group pools (with *N. oregona* still present) but was (B) negatively associated with ecosystem function in the removal group across a small range of thresholds (using reflected data with positive directionality between individual ecosystem functions and *N. oregona* abundance). These analyses follow the multiple threshold approach, where each line indicates the relationship between *M. trossulus* abundance in each tide pool and the number of ecosystem functions in that pool which exceed a certain threshold value, with asterisks indicating significance.

Supplemental Appendix 1:

Supplemental methods

Community surveys

To measure the abundance of individual species and the overall diversity of the tide pool community, we conducted biodiversity surveys to measure the abundance of species in the pools before and shortly after *N. oregona* removal (Figure S1). During each survey, we pumped water out of each tide pool, set down a flexible mesh quadrat with 10 cm x 10 cm squares at the bottom, measured the surface area occupied by each sessile species (algae and invertebrates; with 10 cm^2 as the minimum measurement assigned for a species) and counted the mobile invertebrates present (Bracken and Nielsen, 2004; Silbiger and Sorte, 2018). We identified organisms to the lowest taxonomic level possible in the field, which was typically to the species level. Some taxa that could not be identified in the field were grouped together (e.g., "limpets" or "coralline algae").

Sample Analysis

We measured the total alkalinity (TA) of the water samples through open-cell titrations (as in Silbiger and Sorte, 2018) with a T50 titrator and LabX software (Mettler-Toledo AG, Schwerzenbach, Switzerland). We analyzed a certified reference material standard (Marine Physical Laboratory, Scripps Institution of Oceanography, La Jolla, California, USA) at the beginning of each sample analysis session (acceptable range: ±1% error) and adhered to an established protocol for TA analysis (SOP 3b in Dickson et al., 2007; Silbiger and Sorte, 2018).

We analyzed pH for all water samples with a UV-1800 benchtop spectrophotometer (Shimadzu, Carlsbad, California, USA) according to the best practices outlined in Dickson et al. (2007). We divided each water sample into three subsamples and analyzed each separately to maximize precision. We collected initial readings for each subsample at three wavelengths before adding 50 µL of m-cresol dye and re-analyzing each at the same three wavelengths (Liu and Chan, 2010). We used the difference between the initial and dye-added measurements to calculate the pH value of each subsample. We then took the mean of the subsamples with < 0.005 pH unit difference among them (excluding subsamples outside that range) for each water sample to produce a raw pH measurement. We then used CO2calc software (Robbins et al., 2010) to adjust the raw pH value for total alkalinity, temperature, salinity, and stoichiometric dissociation constants and calculate a final pH value on the total scale (Mehrbach et al., 1973; Dickson and Millero, 1987; Kroeker et al., 2021).

We analyzed the frozen 50 mL water samples for dissolved inorganic nutrient concentration (Bracken et al., 2018; Silbiger and Sorte, 2018). We measured NO_3^-, NO_2^-, and PO_4^{3-} concentrations (mmol L^{-1}) with a QuickChem 8500 Series Analyzer (Lachat Instruments, Loveland, Colorado, USA) and ammonia (NH_4^+) concentrations (µmol L^{-1}) with the phenolhypochlorite method (Solórzano, 1969) on a UV-1800 benchtop spectrophotometer (Shimadzu, Carlsbad, California, USA).