Climate Change Amelioration by Marine Producers: Does Dominance Predict Impact?

Samuel A. Mahanes*, Matthew E. S. Bracken, and Cascade J. B. Sorte

Department of Ecology and Evolutionary Biology, University of California, 321 Steinhaus Hall, Irvine, California 92697-2525

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 (Wernberg *et al.*, 2011; Doney *et al.*, 2012). 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, because 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; 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

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* Corresponding author: smahanes@uci.edu.

Abbreviations: GLM, generalized linear model; GLMM, generalized linear mixed model; TA, total alkalinity.

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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 (Hendriks *et al.*, 2014; Pacella *et al.*, 2018; Silbiger and Sorte, 2018) over the course of a diel cycle. 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 that is the most abundant producer in tide pools in a high-latitude coastal ecosystem near Sitka, Alaska (Sorte and Bracken, 2015; Fig. 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.

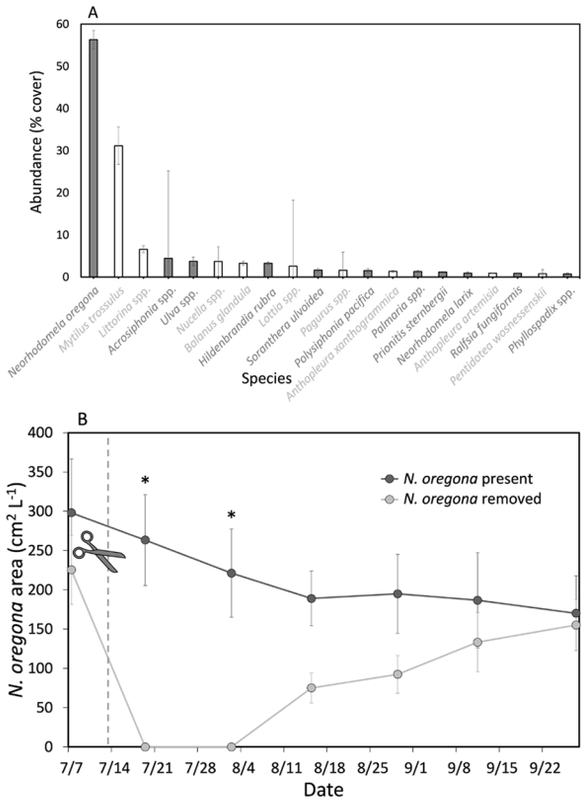

Figure 1. Abundance of *Neorhodomela oregona* and other tide pool species. (A) *Neorhodomela oregona* was the most abundant species in the $n = 10$ tide pools, and 11 of the 20 most abundant species were producers (gray bars), while 9 were consumers (white bars). (B) The removal (date indicated by a dashed line) of *N. oregona* reduced its area in the $n = 5$ removal treatment tide pools (light gray line) relative to the $n = 5$ control pools (dark gray line). *Neorhodomela oregona* recovered within 1 month in the removal pools, and the 2 treatment groups had similar *N. oregona* densities for the final 4 surveys of the study. Each data point represents mean (±SE) abundance, and the asterisks in (B) indicate significant differences between treatment groups.

Materials and Methods

Study site

To evaluate the role of the abundant alga *Neorhodomela oregona* (Doty) Masuda, 1982 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 July 5, 2019, to September 27, 2019. Southeast Alaska was an ideal location for this study because 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 of the Alaskan coast (Byrne *et al.*, 2010).

Removal experiment

We selected 10 tide pools, ranging from 2.5 to 23.5 L in volume and from 2.49 to 3.29 m in tide height (*i.e.*, vertical position within the intertidal zone) and 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 × 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 by 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 (see *Mesocosm experiment*, 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 (July 6–July 19, 2019) and then every two weeks until September 27, 2019 (for a total of seven surveys; Figs. 1B, A1). During the surveys, we pumped water out of each tide pool, laid down a flexible mesh quadrat with 10 × 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 (July 10–July 16, 2019; Fig. 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, UT). Over the 4 sampling periods (day and night, both before and after removal), we took physical measurements at 5 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 2 125-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 (TA).

We analyzed pH in the water samples from both experiments on a UV-1800 benchtop spectrophotometer (Shimadzu, Carlsbad, CA), following best practices as described by 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 3 wavelengths, added 50 μL of m-cresol dye, and mixed and reanalyzed the subsample at the same 3 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 between 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 TA (analyzed as described below), salinity, temperature, and stoichiometric dissociation constants and to 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, Schwerzenbach, Switzerland). We measured a certified reference material (Marine Physical Laboratory, Scripps Institution of Oceanography, La Jolla, CA) 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 by 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, RI), 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, Bourne, MA) 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 (2021).

We conducted all statistical analyses in R version 4.0.4 (R Core Team, 2013), using generalized linear mixed model (GLMM) repeated-measures analyses and generalized linear models (GLMs). 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. *Neorhodomela oregona* cover was modeled as a function of the fixed factors of treatment, time (biweekly 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 we conducted *post hoc* pairwise comparisons on *N. oregona* cover by using Tukey's honest significant difference (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 millivolt 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 rates of pH change between the end of the dark incubation period and the final measurement (after a ~30-min 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 square centimeters of surface area per liter 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 because 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 that 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 *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 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 Shapiro-Wilk 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 made this conversion by 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 (square centimeters per liter; 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; Fig. 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 July 13, 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 regard 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 2 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 by using a time series similar to the removal experiment (see *Removal experiment*, 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) (Fig. 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 5 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 (square centimeters per liter), which was the same metric we used for the algae in the field tide pools, and *N. oregona* biomass per mesocosm water volume (grams per liter), 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 (SAM, pers. obs.). Assumptions of normality and homogeneity of variances were checked using Shapiro-Wilk 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 (July 6–9, 2019; Fig. 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%; Fig. 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 2 surveys within 3 weeks following the removal treatment (pairwise comparisons; $P \leq 0.001$; Fig. 1B). *Neorhodomela oregona* recovered about 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 4 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 ($t_5 = -2.946$, $P = 0.032$; Fig. 2A) but not when using area ($t_5 = -2.154$, $P = 0.083$; Fig. 2B). Greater *N. oregona* abundance tended to be associated with increased pH when isolated during the day, a trend that was apparent when

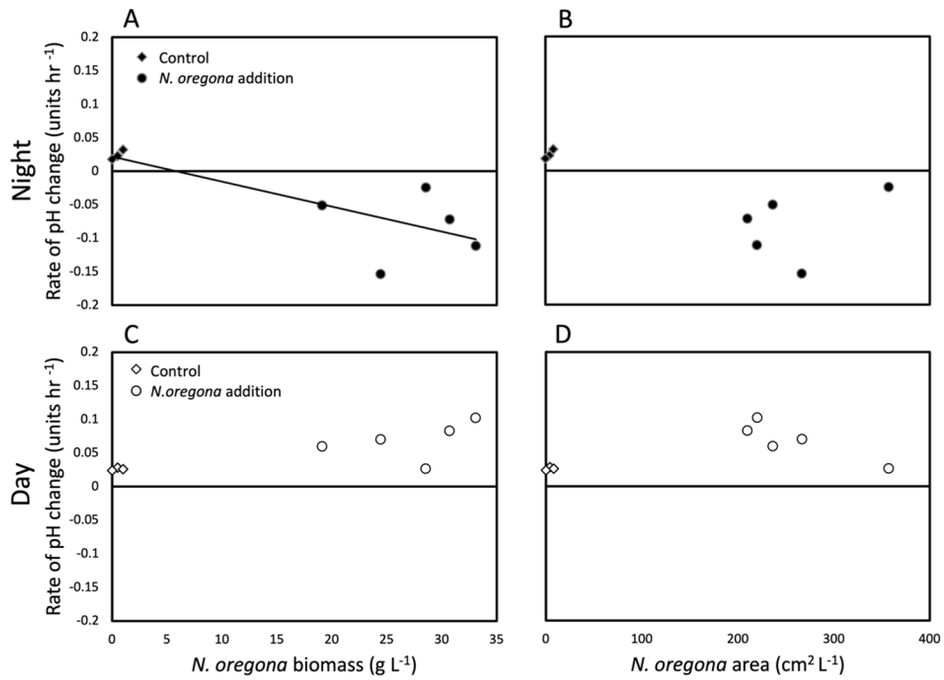

Figure 2. Relationships between *Neorhodomela oregona* abundance and the rate of pH change in experimental mesocosms. Mesocosms with greater biomass (g L^{-1}) of *N. oregona* became more acidic at night (A), but there was no detectable relationship between *N. oregona* area (cm^2 L^{-1}) and pH change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

using biomass as the abundance metric ($t_5 = -2.238$, $P = 0.075$) but not area ($t_5 = 0.186$, $P = 0.859$; Fig. 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; Fig. A2) and more positive during the dark phase ($t_5 = 4.08$, $P = 0.006$; Table A3; Fig. 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 ($t_5 = -0.814$, $P = 0.453$; Fig. 3A) or during the night ($t_5 = -1.497$, $P = 0.185$; Fig. 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; Fig. A2), but there was no detectable relationship between *N. oregona* abundance and pH change in the water samplings during the day ($t_5 = 0.262$, $P = 0.811$; Fig. 3B) or at night ($t_5 = -0.538$, $P = 0.628$; Fig. 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 ($t_5 = 3.475$, $P = 0.040$; Fig. 3B) but not at night ($t_5 = 0.184$, $P = 0.866$; Fig. 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: $t_5 = 4.740$, $P = 0.018$; Fig. 3B) but not at night ($t_5 = -1.312$, $P = 0.260$; Fig. 3D). Pools with higher pre-removal *N. oregona* abundance acidified more quickly during the night, regardless of treatment ($t_5 = -3.290$, $P = 0.030$; Fig. 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: $t_5 = 1.901$, $P = 0.130$; Fig. 3B, D) and combined ($F_{1,8} = 0.218$, $P = 0.653$; Table A4) analyses.

The 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 percentage cover minus consumer percentage cover; Silbiger and Sorte, 2018) also had no effect on the rate of pH change in the tide pools ($P > 0.3$; Fig. A3).

The 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

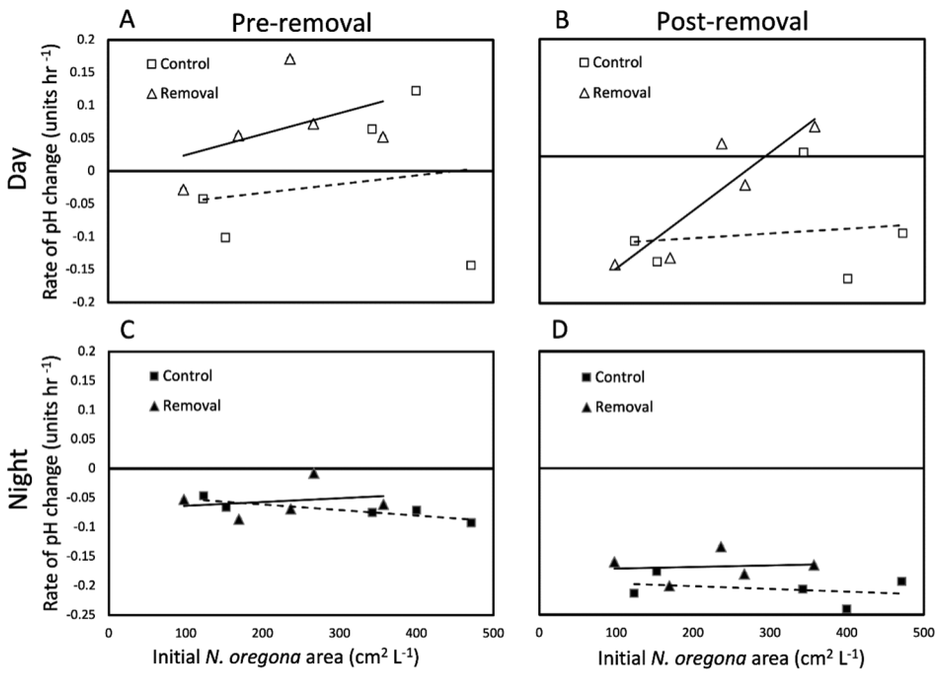

Figure 3. Relationships between pre-removal *Neorhodomela oregona* abundance and the rate of pH change in tide pools in the field, including pre-removal (A) and post-removal (B) changes in pH during the day and pre-removal (C) and post-removal (D) changes at night (with solid and dashed lines reflecting 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. *Neorhodomela 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.

($P = 0.033$), and tide pools located higher in the intertidal zone acidified more slowly during the night ($P = 0.030$).

Neorhodomela oregona presence was not associated with pool temperature: *N. oregona* removal did not affect maximum water temperature over the month following *N. oregona* removal ($F_{1,7} = 0.12$, $P = 0.741$; Fig. A4), as well as the entire 11-week duration of the experiment ($F_{1,7} = 0.27$, $P = 0.620$; Fig. A5). 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 *Neorhodomela 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 in 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 raise pH primarily *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 that were closer to 0 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 (MESB, unpubl. 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. Because 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 *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 (Lilley and Schiel, 2006; 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 that 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 as a result of 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 nondominant, or subordinate, species may also have substantial impacts in an ecosystem, but that these effects are less understood because of the preferential study of dominant species and a methodological focus on randomly assembled communities, or that the effects of subordinate species may be apparent only when multiple species are clustered into functional groups. There are fewer studies explicitly focusing on nondominant (*e.g.*, rare) species; but, where studied, nondominant 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, led 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 (Fig. 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 TA (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 counter-example to studies that 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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Data Availability

The data sets used in this study are available in the Dryad Digital Repository at https://datadryad.org/stash/share/F4suBJiVWxsasDPGeoBxFCLLXuicObJg9E655HW4wI0.

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Appendix

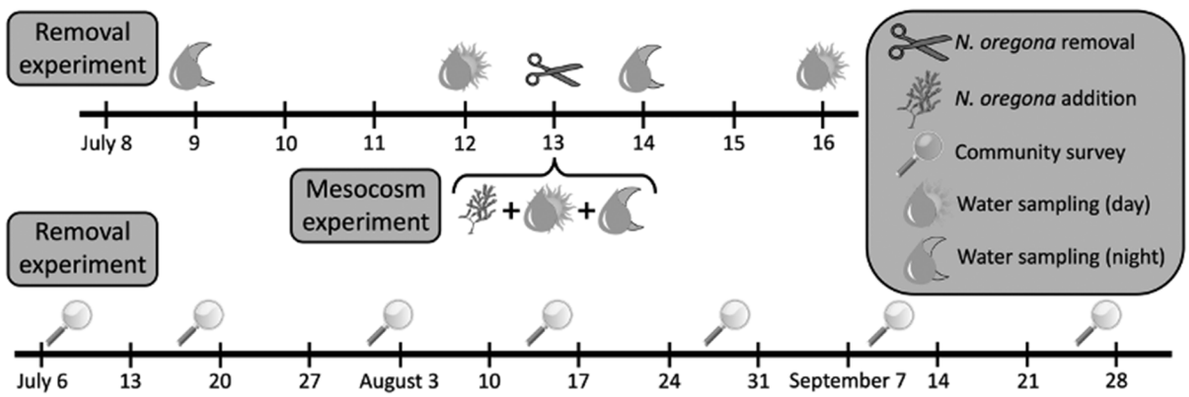

Figure A1. Time line of the experiment. Primary data collection took place over 7 days for the removal experiment and 1 day for the mesocosm experiment. Community surveys for the removal experiment started prior to *Neorhodomela oregona* removal and continued for 11 weeks after removal.

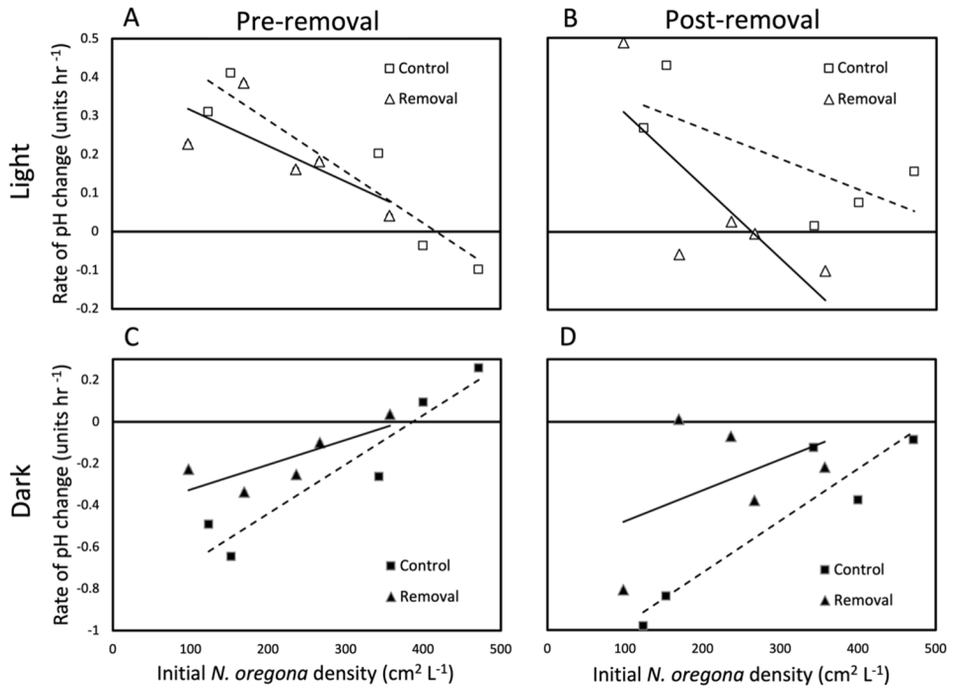

Figure A2. Relationships between pre-removal *Neorhodomela oregona* abundance and the rate of pH change in tide pools, as measured in the field during the light-dark incubation trials before and after removal. Prior to removal (A), the rates of pH change during light incubation were generally positive and decreased with increasing *N. oregona* abundance, while a similar but nonsignificant 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 that remained significant in 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.

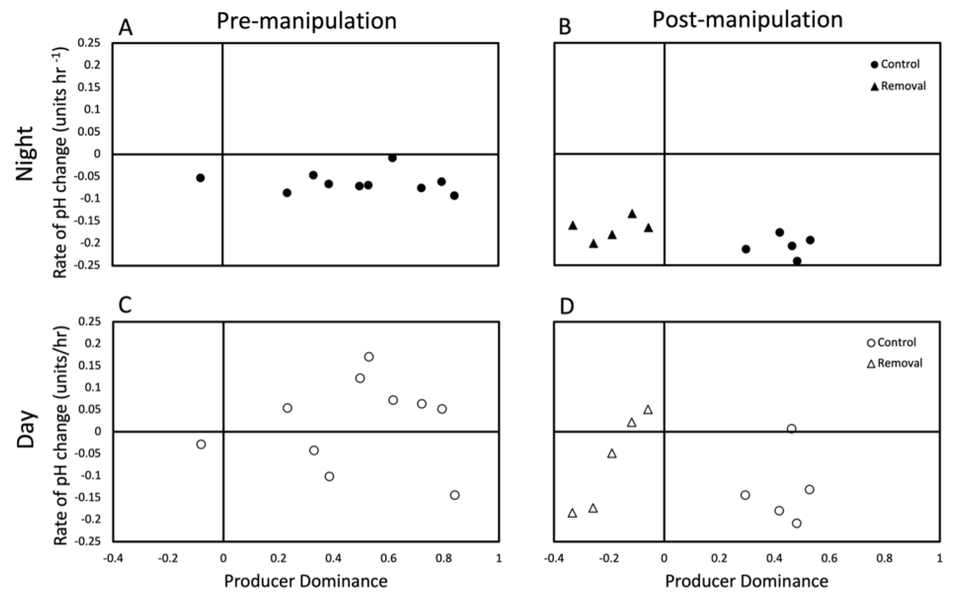

Figure A3. Producer dominance did not affect the rate of pH change in tide pools, including before (A, C) or after (B, D) the manipulation or during the night (A, B) or day (C, D). There was no effect of producer dominance (percentage cover of producers minus percentage cover of consumers) on rates of pH change in the $n = 10$ tide pools prior to manipulation or after the manipulation, when $n = 5$ pools contained *Neorhodomela 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).

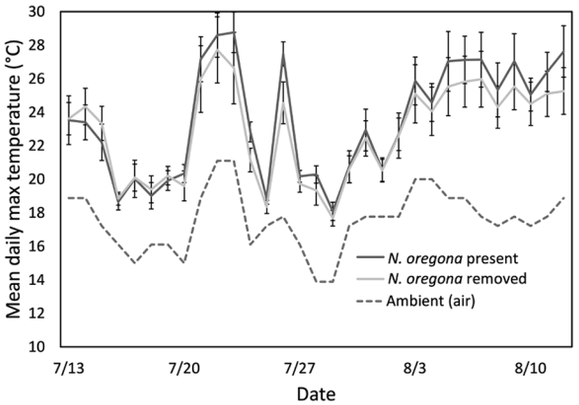

Figure A4. *Neorhodomela oregona* did not affect water temperature in tide pools. *Neorhodomela oregona* removal did not affect maximum daily water temperatures in tide pools during the month following *N. oregona* removal. Each point represents the mean daily maximum temperature of $n = 5$ pools that were either unmanipulated (dark gray line) or in which *N. oregona* was removed (light gray line). Ambient air temperature values (dashed line) reflect temperatures measured at Rocky Gutierrez Airport in Sitka, Alaska (CustomWeather, 2021). Error bars indicate standard error calculated using the pooled variance method.

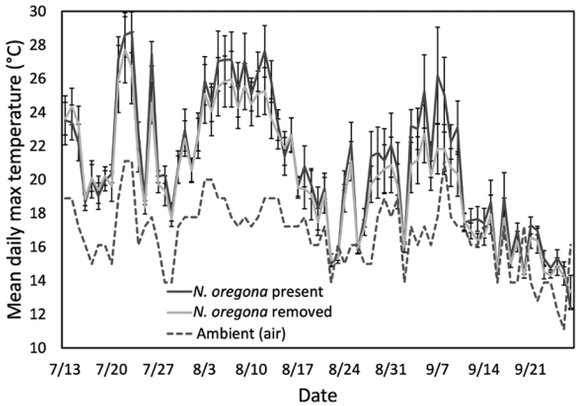

Figure A5. *Neorhodomela oregona* did not affect tide pool water temperature over the full 11-week experiment. Each point represents the mean daily maximum temperature of $n = 5$ pools that were either unmanipulated (dark gray line) or in which *N. oregona* was removed (light gray line). Ambient air temperature values (dashed line) reflect temperatures measured at Rocky Gutierrez Airport in Sitka, Alaska (CustomWeather, 2021). Error bars indicate standard error calculated using the pooled variance method.

Table A1

Surface area for mobile invertebrate species identified in the tide pools, calculated based on collection of representative individuals ($n = 1$–10) at the field site

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
Littorina plena/scutulata	0.15	10	NA
Idotea	1.75	NA	*Nucella*
Amphipod	0.34	NA	*L. sitkana*
Chitons	1.75	NA	*Nucella*

Collected specimens were photographed and their surface area was calculated using ImageJ (Abràmoff *et al.*, 2004). For those relatively rare species not measured, similarly sized species were substituted. NA, not applicable.

Table A2

Analysis of the rates of (A, B) day and night pH change in the mesocosm experiment and (C, D) pairwise *post hoc* comparisons between the rate of pH change and *Neorhodomela oregona* abundance

	F		df	df res	*P*
A: *N. oregona* biomass and pH change in the mesocosms					
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**
B: *N. oregona* biomass and pH change in the mesocosms					
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**
	Estimate	SE	df	*t*-ratio	*P*
C. Pairwise comparison of *N. oregona* biomass and pH change in the mesocosms					
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
D. Pairwise comparison of *N. oregona* surface area and pH change in the mesocosms					
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

(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 *N. oregona* prior to removal. Results indicate differences in pH change between 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.

Table A3

Analysis of the rates of pH change from the light-dark trials before (A, B) and following (C–H) *Neorhodomela oregona* removal

	Estimate	SE	*t*-ratio	*P*
A: Pre-removal light				
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				
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				
N. oregona density ($cm^2\ L^{-1}$)	−0.0008	0.0004	−1.86	0.1594
D: Post-removal control dark				
N. oregona density ($cm^2\ L^{-1}$)	0.0025	0.0005	4.46	**0.0210**
E: Post-removal removal light				
N. oregona density ($cm^2\ L^{-1}$)	−0.0019	0.0009	−2.09	0.1270
F: Post-removal removal dark				
N. oregona density ($cm^2\ L^{-1}$)	0.0015	0.0017	0.87	0.4470
G: Post-removal light				
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				
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

Table A3 (*Continued*)

	Estimate	SE	*t*-ratio	*P*
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

Analysis of the rates of pH change from the light-dark trials prior to (A, B) and following (C–H) removal. *Neorhodomela 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.

Table A4

Analysis of the rates of pH change in the removal experiment (A) during day and night and (B) using pairwise *post hoc* comparisons of the rate of pH change and *Neorhodomela oregona* abundance

	F		df	df res	*P*
A. Rates of post-removal pH change with pre-removal *N. oregona* surface area included as a covariate					
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
	Estimate	SE	df	*t*-ratio	*P*
B. Pairwise *post hoc* comparisons of pH change between control and *N. oregona* removal tide pools					
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

(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, shows differences in pH change between 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.

Table A5

Analysis of the potential effects of *Neorhodomela oregona* and *Ulva* spp. on the rates of pH change (A, B) prior to and (C, D) following removal

	Estimate	SE	*t*-ratio	*P*
A: Pre-removal day				
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				
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				
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				
N. oregona density ($cm^2\ L^{-1}$)	−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

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.