Journal of Experimental Marine Biology and Ecology 606 (2027) 152235



Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe



A factorial field manipulation reveals direct and indirect effects of ocean acidification and warming on community composition

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ARTICLE INFO

Keywords:
Climate change
Community
Diversity
Field experiment
Marine ecology
Ocean acidification
Warming

ABSTRACT

Ecosystems are experiencing changes in multiple environmental factors, and these changes have the potential to influence species both directly and indirectly via altered species interactions. We conducted a factorial field manipulation of CO_2 (reducing pH) and temperature in twenty tide pools over a six-month growing season on the coast of Alaska, USA. Our manipulations resulted in unexpected increases in community evenness due to reduced abundance of dominant mobile herbivores, which reflected relationships with basal species. The climate factor most strongly related to population changes differed by species, and we observed greater changes upon exposure to single rather than multiple environmental factors. Total taxon richness did not differ between treatments over the time scale and magnitude of our experimental manipulations. These findings highlight the importance of long-term experiments in natural, dynamic ecosystems to account for environmental variation, community interactions, and behavioral responses of mobile species.

1. Introduction

As the climate continues to change, ecosystems are faced with multiple environmental drivers changing simultaneously (Lee et al., 2021). Furthermore, the level of stress that individual organisms experience will depend on biological feedbacks in dynamic natural communities (Henson et al., 2022; Schofield et al., 2010). Climatic changes over the past century have been smaller than forecasts for the coming century (Lee et al., 2021). However, past changes have already led to major alterations in biological systems worldwide (IPCC, 2022), and climate change has been identified as a primary driver of decreased diversity across Earth's ecosystems (Jaureguiberry et al., 2022).

Marine community shifts have been most often linked to warming seawater temperatures (Fredston et al., 2021; Harley et al., 2006), but there is increasing concern that ocean acidification (i.e., increases in dissolved CO_2 and decreases in ocean pH) will cause similar changes in community composition in the future (Nagelkerken and Connell, 2022; Zunino et al., 2021). Whereas early work evaluating the impacts of climate change on marine organisms typically considered one climatic factor (e.g., temperature alone or CO_2 alone) and followed single species in isolation through laboratory or mesocosm experiments (Harley et al., 2006; Kroeker et al., 2013b; Wernberg et al., 2012), multi-factor studies are increasing (Edmunds et al., 2012; Göbeler et al., 2025; Kroeker et al., 2013a; Liu et al., 2020) and are key to encompassing the complexity of climate change and biological responses. However, our understanding of emergent effects at the community level is limited. There is a pressing need to experimentally address the impacts of multiple drivers within dynamic natural ecosystems (Carrier-Belleau et al., 2021). Importantly, species often respond differently when subjected to multiple climate drivers at the same time, and meta-analyses have shown that the interactive effects of ocean acidification and temperature can be highly variable in both magnitude and direction (Hu et al., 2024; Kroeker et al., 2013b).

To make future prediction even more complicated, it is also clear that without considering the community context, we are likely to make mistakes when predicting species responses to climate change (Davis et al., 1998). This is because species can be affected by climate change both directly (e.g., if mortality rates are elevated) and/or indirectly via changes in the community (Kroeker et al., 2013a; Miller et al., 2014; Sorte et al., 2017; Sunday et al., 2017). In fact, meta-analyses have shown that across a broad range of marine species, responses to ocean acidification differed when they were measured in studies with single

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https://doi.org/10.1016/j.jembe.2026.152235
Received 6 April 2026; Received in revised form 24 September 2026; Accepted 2 November 2026
Available online 12 November 2026
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versus multiple species (Kindinger et al., 2022; Kroeker et al., 2013b). Thus, to predict future impacts of climate change on biodiversity or ecosystem function, we need to consider responses to multiple, interacting aspects of climate change and how these responses manifest in the context of a natural community.

Field manipulations have the potential to provide some of the best predictions of climate change impacts, yet in situ experiments, particularly of multiple climate drivers, are notably lacking in marine systems as compared to the relative plethora of terrestrial climate manipulations (Castro et al., 2010; Chapin III et al., 1995; Hanson et al., 2005; Harte and Shaw, 1995; Van Sundert et al., 2023; Williams et al., 2007). Previous climate-change field studies in marine systems have typically used observational methods, examined a single environmental factor, and/or focused on a single species (Bass et al., 2021; Harley et al., 2006; Kordas et al., 2017; Kroeker et al., 2013a; Wernberg et al., 2012). Recent progress has been made in manipulating single global-change drivers in marine systems (Göbeler et al., 2025; Harris et al., 2025; Jellison et al., 2022; Montie and Thomsen, 2023). However, to our knowledge, our earlier short-term (< 3 week) experiment (Sorte and Bracken, 2015) is the only other study to factorially manipulate CO_2 and temperature in situ within a marine system.

We conducted a factorial environmental manipulation experiment to assess the impacts of ocean acidification and warming on a natural, coastal marine ecosystem in Sitka, Alaska, USA (Fig. 1). We manipulated pCO_2 (leading to acidification) and temperature in twenty tide pools during low tide. These pools acted as natural experimental replicates that contained a diverse set of algae and invertebrates representative of all abundant species groups in the broader coastal benthic system (Drumm et al., 2016; Lindstrom, 2009). Isolation of pools at low tide (~66% of the time) allowed us to manipulate both mean and variability of climate conditions (per future projections; (Lee et al., 2021)) during the time when the communities naturally experience the most impactful CO_2/pH levels due to biological processes (Kwiatkowski et al., 2016; Silbiger and Sorte, 2018) and highest temperatures due to solar heating during the daytime low tide (Helmuth et al., 2006). High tide provides a relative respite from the more stressful low tide period, and our results are likely to be conservative given that the broader ocean acidity and temperature – which are also increasing with climate change –were not manipulated during high tide. Tide pool climate manipulations were maintained continuously through a full ~6 month growing season

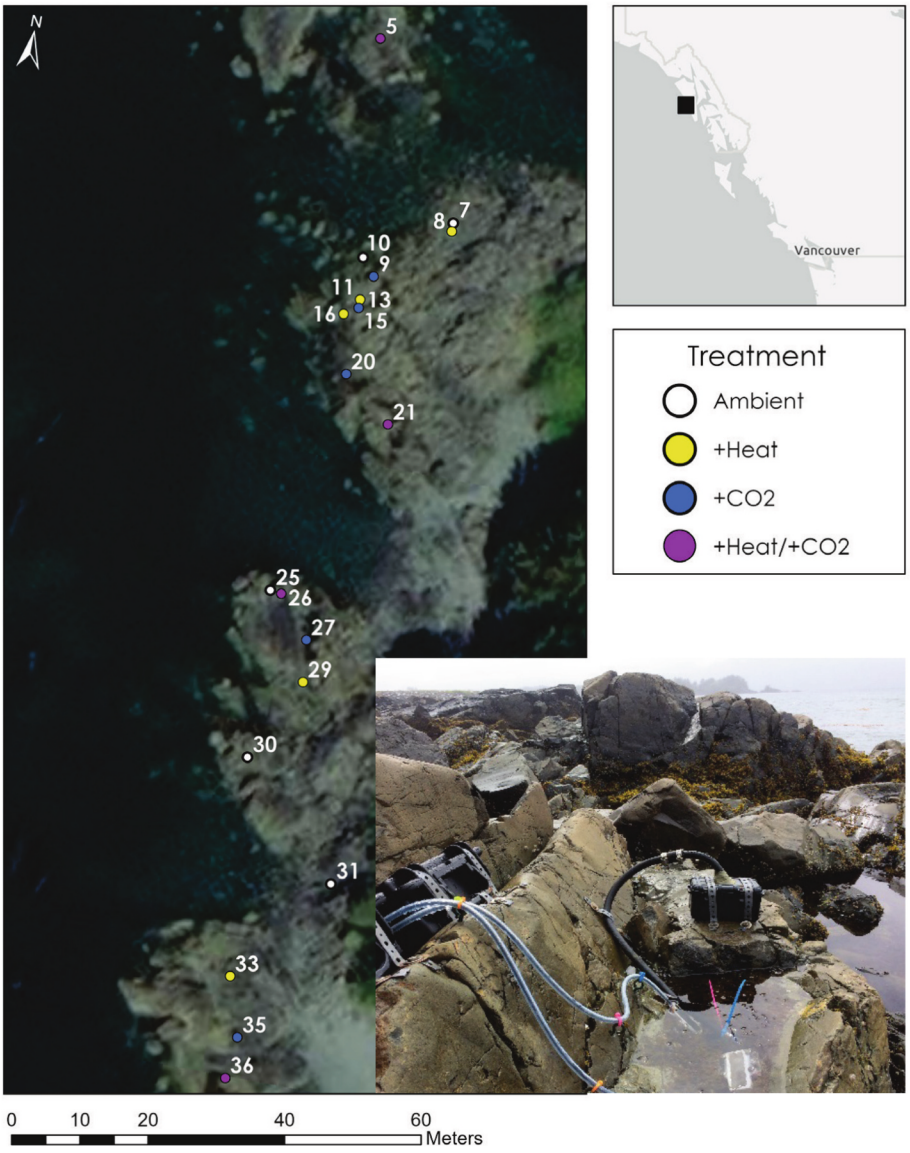

Fig. 1. The study was conducted in 20 tide pools ($N = 5$ pools per treatment) on Japonski Island near Sitka, Alaska, USA. Tide pool CO_2 levels were manipulated using yeast reactors (box in middle of inset photo), and warming was achieved by battery operated heaters connected to microcontrollers (in box to left) and a heating element in the pool (bottom) (Map: ESRI; Photo: M. Bracken).

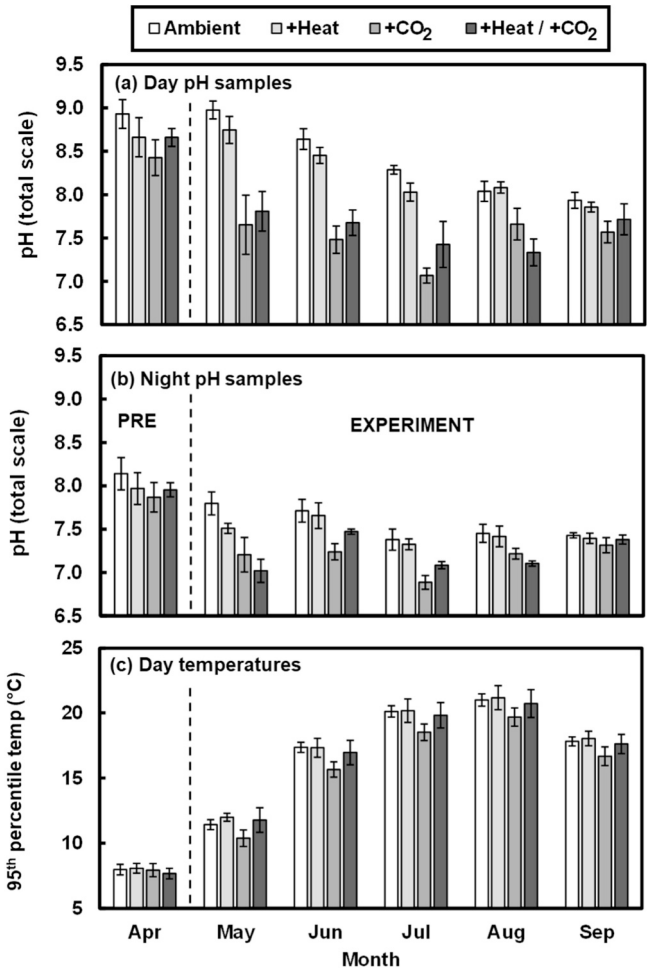

Fig. 2. Experimental manipulations altered tide pool pH and temperature. Adding CO_2 to pools resulted in a reduction in pH (a) during the day and (b) at night. (c) Daytime heating of pools resulted in an increase in temperature. Values are means ± SEs across the $N = 5$ pools per treatment based on the average of three daytime (a) or nighttime (b) measurements taken during a monthly sampling period for pH and based on daytime monthly 95th percentile from continuous monitoring for temperature (c).

(Fig. 2). We measured responses of both populations (i.e., individual taxa) and communities comprised of interacting seaweeds, sessile invertebrates, and mobile invertebrates. We hypothesized that ocean acidification and warming would each decrease community diversity and that, in combination, these two climate drivers would have impacts that could not be predicted by their individual effects.

2. Methods

2.1. Study site and treatment assignments

Our study was conducted on a rocky shore at John Brown's Beach on Japonski Island near Sitka, Alaska, USA (57.06°N, 135.37°W) on the ancestral and unceded territory of the Tlingit people. We had previously surveyed physical attributes and community diversity of 34 tide pools in June 2018 for an observational study of seasonality under ambient conditions (Sorte et al., 2023), and we used these data when assigning treatments. We included 20 pools in this study (Fig. 1) which were characterized by (mean ± 1 SE) shore height (2.56 ± 0.08 m above mean lower-low water), volume (13.5 ± 2.2 L), and bottom surface area (0.26 ± 0.03 m^2). The replication (number of pools per treatment) is modest given the high level of heterogeneity in physical and biological characteristics, so we randomized pools to treatments using a blocked design based on tide pool location along the shoreline so that treatments were spatially dispersed (Fig. 1). We re-randomized until treatments did not differ significantly with respect to shore height, pool volume, bottom surface area, sessile taxon richness, mobile taxon richness, and abundance of the most common alga in the pools, *Neorhodomela oregona*. We factorially manipulated CO_2 levels and temperature for ~6 months (02 April – 22 September 2019) in $n = 5$ pools per treatment: an unmanipulated control ("Ambient"), warmed ("+Heat"), CO_2 added ("+CO_2"), and both warmed and CO_2 added ("+Heat / +CO_2").

2.2. CO_2 and temperature manipulations

Tide pool CO_2 levels were elevated – leading to acidification – using yeast reactors (Sorte and Bracken, 2015). Each +CO_2 tide pool received CO_2 from a 1-L sealed plastic waterproof case containing 500 mL warm tap water, 60 g sugar, 0.7 g yeast, and 2 g $NaHCO_3$ to buffer the internal pH of the reactor. Reactors were bolted to the rock adjacent to the tide pools and delivered CO_2 to the pools via airline tubing ending in air stones (Fig. 1). This method made it possible to continuously deliver CO_2 to multiple tide pools for several months. The gas bubbled into the pool, while ~99% pure CO_2 (Xu et al., 2010), also contained trace amounts of water vapor and volatile metabolites (Aldridge et al., 2016). The solution in each reactor was replaced every three days to maintain reduced pH conditions in +CO_2 pools. We selected this quantity of yeast and timeline to refresh the reactors based on initial trials conducted in environmental chambers, previous field experiments (Bracken et al., 2018; Sorte and Bracken, 2015), and multiple daily pH measurements during the first week of the manipulations (Appendix S1). Because continuous monitoring (Kwiatkowski et al., 2016) was not feasible due to the size and number of replicate pools, we monitored pH conditions in the pools throughout the experiment via discrete monthly measurements over one daytime and one nighttime low tide event. Each sampling event took ~2.5 h per pool and started when pools were isolated by the receding tide. Pools not flushed by the previous high tide were flushed manually with buckets of seawater. We took initial readings of pH (HI9829 Meter with HI7609829 glass pH electrode calibrated with a TRIS buffer standard, Hanna Instruments, Woonsocket, RI, USA) and temperature (ProDSS optical DO meter, YSI, Inc., Yellow Springs, OH, USA) at a marked location in the center of each pool. After intervals of ~1.25 h, subsequent measurements (for a total of 3 measurements) were taken, and measurements were averaged by pool to characterize the pH during each daytime and nighttime sampling. This monthly sampling and initial monitoring over multiple days early in the experiment indicated that we successfully reduced pH in the pools with CO_2 added (Fig. 2; Appendix S1); however, we acknowledge that monthly sampling provides an incomplete record of the strong temporal variation in pH conditions (Sorte et al., 2023). Across the experiment, the addition of CO_2 to tide pools reduced daytime pH by 0.77 ± 0.06 units (mean ± SE of $n = 10$ pools per treatment averaged across 5 sampling events) and reduced nighttime pH by 0.31 ± 0.02 units (repeated-measures general linear model [GLM]; daytime: $F_{1,18} = 66.0$, $P < 0.001$; night: $F_{1,18} = 24.1$, $P < 0.001$) (Fig. 2). Effects of CO_2 on pH were most apparent during daytime in spring and early summer months, when high productivity resulted in high pH values in tide pools with ambient CO_2 levels. This asymmetry in acidification between day and night also reflects the seasonal pattern – seen here in ambient pools and in a seasonal study of all pools the year prior to our manipulations – in which high nighttime community respiration drives pH levels to be naturally so low in isolated pools that there is not as much scope for pH variation as during the daytime (Sorte et al., 2023). Expanded carbonate chemistry metrics are provided in and discussed by Rangel et al., in revision.

Tide pools were warmed using heating systems comprising a custom microcontroller powered by two rechargeable 14 A-h gel cell batteries, both housed in a waterproof case bolted to the rock, attached to a submerged silicone-coated heating element (30 W 2.5 × 15 cm) and

temperature sensor (Fig. 1). To conserve battery power for this energy intensive manipulation, the controllers were programmed to activate the heating elements only during daytime low tides (Miller and Long, 2015). Rechargeable batteries – weighing a total of >80 kg and transported in backpacks – were changed daily. Temperature was monitored continuously with Onset ® HOBO TidbiT data loggers submerged within the pools. After accounting for temperatures measured during the previous (unmanipulated) summer as a covariate ($F_{1,17} = 24.2$, $P < 0.001$), daytime heating of pools increased 95th percentile temperatures by 0.98 ± 0.49 °C (repeated-measures GLM: $F_{1,17} = 24.2$, $P < 0.001$) (Fig. 2, Appendix S1). The warming effect was consistent throughout the summer ('time × heat' interaction: $F_{4,68} = 0.3$, Greenhouse-Geisser-adjusted $P = 0.771$). The temperature manipulation was relatively modest given that similar thermal anomalies of mean ocean temperature have been recently recorded in this region (Weitzman et al., 2021) whereas our acidification treatment represents conditions expected well into the future (Currie, 2022; Lee et al., 2021). Our results should be interpreted in the context of these treatment magnitudes.

Treatment hardware was installed so as to minimize disturbance to the biota (e.g., tubing for the $+CO_2$ treatment was attached to the same bolt as the temperature logger in all 20 pools), and maintenance did not require any modification within the pools themselves. Heater bars were installed on the bottom of the heated pools only (no similar disturbance was applied to unheated pools) after the initial community surveys (described below) were completed allowing some recovery time before the next monthly survey.

2.3. Monitoring community responses

We measured the impacts of the experimental manipulations on tide pool communities monthly. To assess population sizes and community diversity, we surveyed relative abundances of all organisms in the pools identified to the lowest feasible taxonomic level. Non-mobile (algae and sessile invertebrates) and mobile taxa were enumerated as cover (m^2) and counts, respectively. We converted mobile taxon densities to cover (to be consistent with abundance estimates for non-mobiles) using standardized area measurements (Mahanes et al., 2022) to calculate diversity metrics.

2.4. Data analysis

We first focused our analyses on composite diversity metrics (Appendix S2) given the large number of taxa enumerated in the pools (89 unique taxa; Appendix S2, S3) and then used a multivariate approach to identify responsive taxa. We calculated richness, Shannon diversity, and Pielou's evenness for all taxa combined as well as three subsets: producers and sessile and mobile invertebrate consumers. Diversity analyses across months were conducted using linear mixed-effects models with the lmer function in the *lme4* package in R (Bates et al., 2015) and included the random effect (random intercept) of "pool" given our design of repeated monthly sampling (Appendix S2). We checked normality of raw residuals using visual assessment of quantile-quantile plots and Shapiro-Wilk tests and homogeneity of variances using Levene's test.

To identify taxa driving differences between treatments, we applied the Principal Response Curves (PRC) multivariate ordination method (Cabecinha et al., 2024; Hermann et al., 2023; Van den Brink and Braak, 1999) because this method is particularly useful for integrating treatment differences over multiple points in time. We compared communities under treatment conditions to those in the ambient, unmanipulated controls and generated PRC curves based on standardized (Hellinger transformed) taxon abundances using *prc* in the vegan package (Oksanen et al., 2022). We identified taxa with the highest PRC weights (Appendix S3), indicating that their responses to the treatments were key to the overall changes in community structure, and focused on these responding taxa in subsequent analyses of changes in population abundance. For illustration and subsequent analyses, we selected taxa whose mean abundance across the pools was >5%. When comparing PRC weights using a range of cutoff abundance values of 1–5%, the top six (3 in each direction) taxa at a 1% cutoff also met the 5% cutoff.

Using structural equation modeling (SEM), we evaluated hypothesized correlations that could signal direct (climate-driven) and indirect (interaction-driven) changes in the abundances of four taxa strongly associated with structural shifts. The abundances of these four taxa (across all pools and months of our broader three year study) accounted for an average of ~69% of live cover in the pools. The SEM analysis was conducted using the *piecewisesem* package (Lefcheck, 2016) and included the four focal taxa, as well as month (May through September, the 5 months after the initiation of the manipulations), pH (average pH across all 3 time points during the monthly daytime sampling), temperature (95th percentile of all temperatures logged in the month prior to community surveys), and pool as a random effect. Thus, our SEM analysis included 20 pools (i.e., pools were not separated by treatment; instead, continuous environmental conditions were used in this analysis) and 7 parameters (month, pH, temperature, and 4 taxa). We evaluated normality of our parameters and visually assessed quantile-quantile plots, square-root transforming parameters as needed. Model fit was assessed using Fisher's C with a cutoff of $P > 0.05$.

We specified hypothesized relationships in the SEM model based on previous studies and our own observations. The SEM model included the algae *Neorhodomela* (the sum of *N. oregona* and *N. larix*), algae in the genus *Polysiphonia*, the mussel *Mytilus trossulus*, and the periwinkle snails *Littorina plena/scutulata* (two species that cannot be differentiated by morphology). We hypothesized that the most abundant sessile taxa – the algae (*Neorhodomela* spp.) and mussels – would influence mobile species and lower density algae (i.e., *Polysiphonia* spp.) by providing habitat and/or food but that, due to their relative abundances, there would not be a measurable effect of consumers on the algae (a recursive effect that also could not be estimated). We also hypothesized that there would be competition for space and/or light between *Neorhodomela* and *Polysiphonia* species. All analyses were conducted in R v. 4.1.2 (R Core Team, 2021).

3. Results

Diversity did not vary prior to our manipulations between the four treatments: (1) Ambient (control), (2) + Heat (warmed/heated), (3) + CO_2 (CO_2 added/acidification), and (4) + Heat / +CO_2 (both CO_2 added and warmed/heated). However, diversity was altered during the nearly six months of exposure to elevated CO_2 and warming, mainly due to impacts on the invertebrate assemblage (Fig. 3, Appendix S2). The number of sessile invertebrate taxa (richness) tended to increase in the presence of warming but was unaffected under concurrent acidification (Heat × CO_2 interaction: $F_{1,16} = 4.273$, $P = 0.055$; Appendix S2). Irrespective of temperature, acidification led to greater evenness of mobile invertebrates ($F_{1,16} = 4.809$, $P = 0.043$; Fig. 3, Appendix S2), a pattern that was especially apparent in May (after one month of exposure) and August (the time of peak summer temperatures). Abundance of herbivorous snails increased dramatically through time in pools with ambient CO_2 levels but not in acidified pools, and these changes in the relative abundance of consumers resulted in corresponding changes in evenness (Fig. 3).

In comparison to the ambient pools, community structure was altered in pools exposed to acidification alone or warming alone, whereas there was less structural change in pools exposed to both acidification and warming (Principal Response Curves ordination; Appendix S3). Overall shifts in community structure were most apparent in the first two months of the experiment, with acidified and warmed tide pool communities responding similarly. Structural shifts were most strongly associated with numerically abundant algae (*Neorhodomela oregona, N. larix,* and *Polysiphonia* species) and sessile (mussels *Mytilus trossulus*) and mobile shellfish (periwinkle snails in the genus *Littorina*)

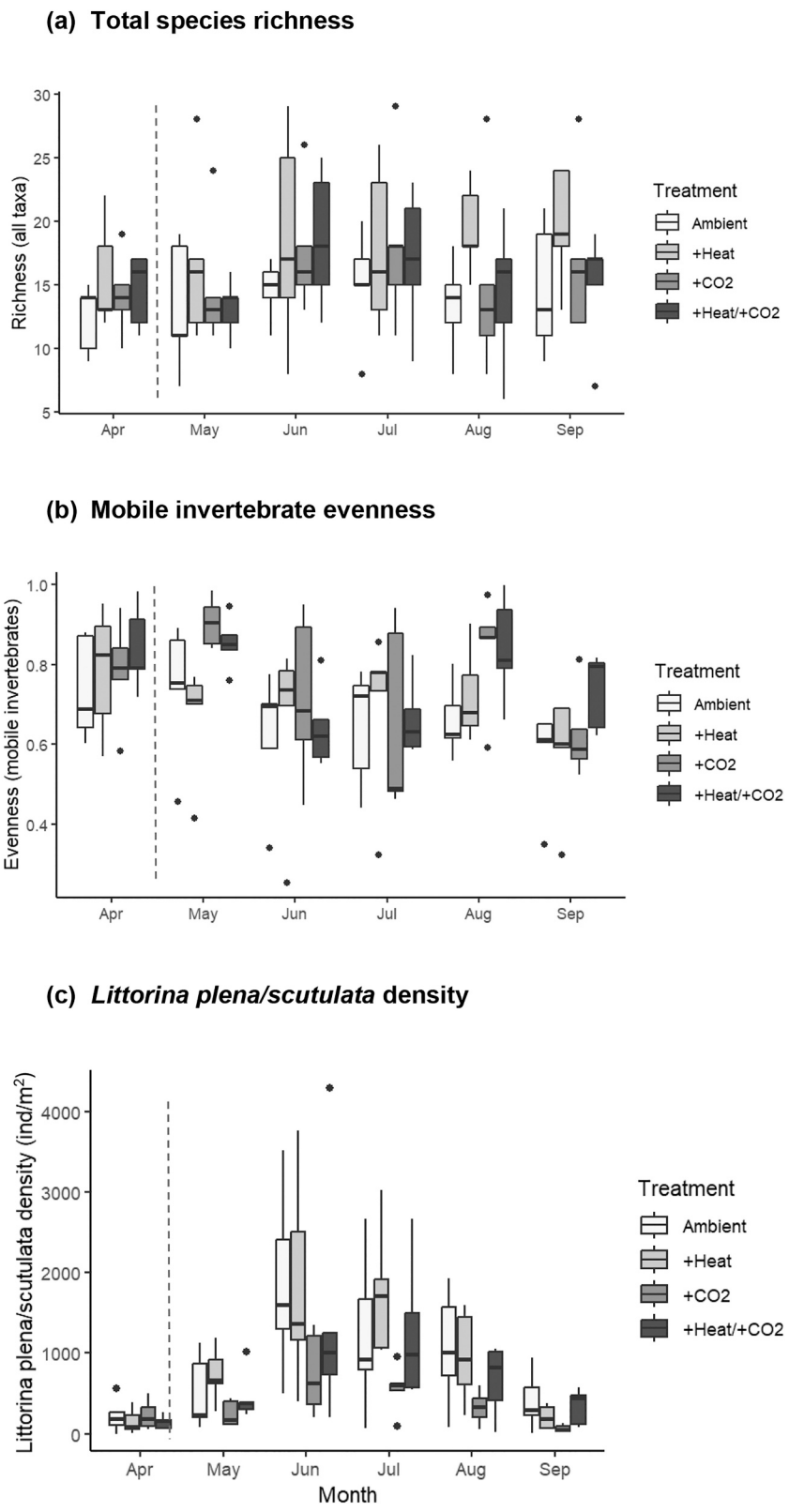

Fig. 3. (a) Total taxon richness did not differ between treatments. (b) However, acidification via CO_2 addition was associated with increased evenness of mobile invertebrates, and (c) lower numbers of the most abundant mobile invertebrates, periwinkle snails (*L. plena* and *L. scutulata*). Boxes show median and interquartile range (25–75%ile) of values for $N = 5$ pools per treatment. April values indicate initial conditions, with the start of the manipulation indicated by the dotted lines.

as well as some rarer algae (e.g., *Mastocarpus* and crustose corallines) and sea anemones (*Anthopleura xanthogrammica* and *A. artemisia*) (Appendix S3).

For these numerically dominant taxa, whose responses to the climate manipulations led to shifts in community structure, the structural equation model was a good fit to the data ($P = 0.541$; Fig. 4, Appendix S4). Taxa varied in whether their abundances were most strongly associated with direct effects of environmental conditions (CO_2/pH or temperature) or with other species, suggesting indirect, interaction-mediated effects (Fig. 4, Appendix S4). Among the basal species in the system, abundance of the seaweed *Neorhodomela* spp. were most negatively associated with acidity while the abundance of *Polysiphonia* spp. were most negatively associated with increased temperature. Abundances of the herbivorous snail *Littorina plena/scutulata* were primarily associated with acidity via changes in abundance of algae (i.e., habitat and food). In contrast, the seaweed *Polysiphonia* spp. appeared to respond both to changes in environmental conditions (temperature) as well as abundance of mussels, a habitat-forming species.

4. Discussion

Across pools, we detected no clear impacts of ocean acidification or warming on taxon richness. While these findings must be considered in the context of the replication (5 pools per treatment), duration (approx. 6 months) and magnitude of our manipulations, they also suggest that mortality thresholds were not reached for most species in most pools. Species that are exposed to a broader range of temperature and pH conditions can be more tolerant of environmental extremes (Rivest et al., 2017; Sorte et al., 2011), and there is high variability in this ecosystem's thermal (>20 °C) and pH (>2 pH units) conditions on both daily and seasonal timescales that is reflected in species' physiology (Rangel and Sorte, 2022; Sorte et al., 2023). Tolerance to climate change might also be assisted by adaptation if evolution can keep pace with climate shifts (Visser, 2008). Despite being adapted to high variability in abiotic stressors, as suggested from physiology (Somero, 2002) and biogeography studies (Sunday et al., 2012), coastal species have been experiencing mass die-offs and therefore can be living at the edge of their tolerance limits (Raymond et al., 2022; Weitzman et al., 2021). Furthermore, it is important to note that the community-level patterns presented here can obscure sublethal stresses which could translate into changes in population size over time. Studies of organismal and ecosystem-level responses in the same pools showed that acidification led to reduced shell thickness and strength for the mussel *Mytilus trossulus* (Rangel et al., 2025), impacts that are likely to become more widespread as the system shifts toward more frequent periods of dissolution (Rangel et al. in revision).

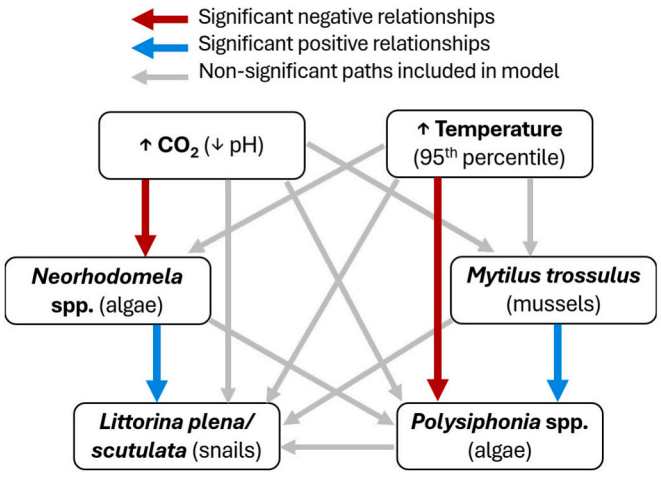

Fig. 4. Structural equation model results showing hypothesized direct and indirect (interaction-mediated) impacts of climate conditions on taxa in the tide pool communities that were identified as strongly responding to climate manipulations from the PRC analysis (see Appendix S3). Colored arrows indicate that there was a strong association ($P \leq 0.0507$) between factors, including elevated CO_2 (i.e. acidification) or elevated temperature (95th percentile). Red = decrease in abundance; blue = increase in abundance; grey = no significant change. *Neorhodomela* represents the abundances of *N. oregona* and *N. larix* combined. Coefficients and test statistics are provided in Appendix S4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The most responsive biodiversity metric to our environmental manipulations was mobile taxa evenness, which increased in acidified pools due to declines in littorine snails, the numerically dominant herbivores in the system. Declines in biodiversity in benthic communities exposed to acidification have been shown in mesocosms (Hale et al., 2011) and CO_2 vent studies (Kroeker et al., 2011), but overall, meta-analysis has revealed that impacts on biodiversity can be highly idiosyncratic, highlighting a need to pinpoint the responding species and underlying mechanisms (Nagelkerken and Connell, 2022). Whereas richness is most often equated with biodiversity (Gotelli and Colwell, 2001), evenness captures additional, often unrelated facets of biodiversity change that can underpin shifts in ecosystem functioning (Altieri et al., 2009; Hillebrand et al., 2008; Soininen et al., 2012). However, while higher evenness is often viewed as a "desired" response or conservation goal (Palumbi et al., 2009), this is not always the case, and interpreting shifts in evenness requires considering the baseline state of the study system (Robinson et al., 2014).

In many coastal ecosystems, mobile consumer assemblages are characterized by an uneven distribution of relative abundances across species. In our study, higher evenness resulted from a system negatively impacted by acidification, leading to declines in the most abundant herbivores, snails in the genus *Littorina*. These declines may reflect behavior (either lower immigration or higher emigration), mortality, or a combination of the two. In contrast to sessile invertebrates and seaweeds, which cannot move in the face of environmental stress, mobile organisms can respond behaviorally and rapidly to environmental changes via emigration (Bracken and Low, 2012) and may therefore be more responsive on timescales from days to seasons (Rangel and Sorte, 2022). Changes in movement patterns might help to explain the significantly reduced *Littorina* abundance in acidified pools in May, after one month of exposure which coincided with a typical seasonal increase of *Littorina*. While we cannot distinguish between mortality and behavioral changes through the full time series, we do know that mortality played a role during the summer because we directly observed mortality in August, following peak summer temperatures, which led to up to 97% declines in littorines.

Our observations of declines in calcifying herbivores exposed to acidification supported expectations from mesocosm and CO_2 vent studies; however, unlike previous studies, we detected no change in top consumers and a tendency toward declines in algal producers. There is strong evidence that calcifiers – including molluscs and especially gastropod herbivores – are likely to decline in the face of ocean acidification. Such declines of calcifiers have been seen in mesocosm studies, both in the presence (Hale et al., 2011; Hu et al., 2024) and absence of concurrent warming (Nagelkerken and Connell, 2022), as well as observations at naturally acidified CO_2 vents with extreme low pH (Hall-Spencer et al., 2008; Kroeker et al., 2011; Nagelkerken and Connell, 2022) and in our field experiment. We did not detect a significant change in top consumers (e.g., whelks) which occurred in relatively low abundance in the pools and were not identified as driving compositional shifts (Appendix S3). Furthermore, while non-calcified algae (both fleshy and turf-forming) have been shown to increase in abundance in acidified mesocosms (Hu et al., 2024) and at CO_2 vents (Hall-Spencer et al., 2008; Nagelkerken and Connell, 2022), in our manipulations, algal abundance tended to decline. While changes in abundance of species in the most common genus *Neorhodomela* contributed strongly to compositional shifts, *Neorhodomela* abundance was not significantly

lower in acidified than ambient CO_2 pools (post hoc GLMM: CO_2 treatment $P = 0.17$) although its abundance decreased with acidity in the SEM. *Neorhodomela* species are among the most effective local seaweeds at using bicarbonate as an alternative carbon source (Murru and Sandgren, 2004), so it is not surprising that they did not benefit from CO_2 addition. Duration of exposure does not fully explain this difference: mesocosm studies were shorter than our experiment on average (Hu et al., 2024) and after removal, algae have been shown to re-establish near CO_2 vents within a shorter period than the duration of our manipulations (Kroeker et al., 2013a).

Ocean acidification and warming appear to be more likely to act antagonistically than synergistically, reducing rather than amplifying their individual effects, with the possible exception of extreme events. In their recent meta-analysis of 162 factorial ocean acidification × warming mesocosm experiments, the impact of acidification tended to be stronger than that of warming, and there was no discernible impact of ocean acidification and warming together (Hu et al., 2024). We also found that compositional changes in our pools were similar between acidified and warmed pools, and compositional shifts were less apparent in pools exposed to both acidification and warming. Although warming did not have a main effect across pools for the most responsive species in our study, there was a clear indication of context-dependency at the community level in the impact of temperature. Specifically, we witnessed mass mortality during the peak of summer temperatures in communities exposed to our experimental manipulations and located highest on the shore, where they were likely to naturally experience the most extreme temperatures and pH levels. The combination of naturally extreme conditions due to location on shore, experimental manipulations, and maximum annual temperatures led to 80–100% declines in shellfish including mussels, barnacles, littorine snails, limpets, and whelks.

A key limitation of studies in simplified (e.g., lab-based) ecosystems is that they do not represent the full suite of potential feedbacks and interactions. Our factorial field manipulation revealed that acidification and warming can drive shifts in community structure directly, via changes in pH and temperature, and are also likely to influence the community indirectly through reduced abundance of basal taxa which support associated species. We uncovered associations in the SEM analysis that suggest high variability in underlying mechanisms responsible for shifts in abundance across four taxa that were most important in driving changes in community composition. For the most abundant and responsive mobile invertebrates, the littorine snails, indirect effects of habitat-forming algae were more strongly associated with their population sizes than the direct relationship with acidification or warming, highlighting the importance of species interactions in responses to altered climate conditions. While abundance of the dominant sessile invertebrate, the mussel *Mytilus trossulus*, was not significantly associated with acidification, we observed sublethal effects of acidification on the mussels in the pools (Rangel et al., 2025), and there was nearly 100% mussel mortality in the highest shore pools (which were also acidified pools) following peak summer temperatures. Thus, there were clear negative effects of acidification on this calcifying species which might also have affected the other calcifiers, including littorines, a possibility that begs further study.

Our results are, therefore, consistent with interactive, direct and indirect responses to altered climate conditions, highlighting the strength of multi-factor, multi-species, field-based studies over extended time periods which allow for emergent, community-level feedbacks (Bass et al., 2021; Hale et al., 2011). Our study revealed several expectations for future responses of the benthic coastal system to climate change. First, we might expect the initial species to respond to altered climate conditions to be mobile species, which may be able to move to avoid climate extremes (Beever et al., 2017; Woods et al., 2015). Second, while one might assume that numerically abundant species have populations that are flourishing and therefore relatively robust, such as the numerically abundant herbivores in coastal ecosystems, these populations also have the farthest to fall (Hung et al., 2014). Finally, the outcomes of changes in common taxa – and particularly those that support associated species in the community by creating habitat and providing food – could be far-reaching, affecting species in interaction webs that are not directly impacted by climate change (Gilman et al., 2010; Tylianakis et al., 2008). For the most responsive herbivores in this coastal ecosystem, indirect associations with interacting species were as strongly or more strongly related to declines under acidification than direct associations with climate alterations. Uncovering complex outcomes of climate change requires experimentation in natural communities in the field, where species' responses are the result of their interactions with both each other and altered climate conditions.

CRediT authorship contribution statement

Cascade J.B. Sorte: Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Luke P. Miller:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Racine E. Rangel:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Matthew E.S. Bracken:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We acknowledge that this study was conducted on the homeland of the Tlingit people. K. Kroeker gave essential assistance with the pH/carbonate chemistry measurements and manuscript feedback. We are exceedingly grateful for the many members of the Sitka NSF team that contributed their effort, expertise, and enthusiasm to the field surveys, data management, and analyses: S. Mastroni, L. Strope, G. Bernatchez, G. Gallaher, L. Samuels, S. Mahanes, G. Kalbach, K. Monuki, L. Pandori, E. O'Brien, L. Bell, Z. Danielson, K. Kroeker, U. Hoshijima. and J. C. Basile. We gratefully acknowledge partnerships with the Sitka Sound Science Center, U.S. Coast Guard Air Station Sitka, and the University of Alaska, Southeast – Sitka Campus which made this work possible. We thank C. Bracken-Sorte for sharing his GIS expertise to make Fig. 1, R. Beshai for suggesting and assisting with the PRC analysis, and the Sorte Lab for manuscript feedback. This work was supported by the National Science Foundation (OCE-1756173 to C.J.B.S. and M.E.S.B., OCE-1904185 to L.P.M., and OCE-1756208 to K. Kroeker).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2026.152235.

Data availability

Raw community survey data are available at BCO-DMO (https://www.bco-dmo.org/dataset/872957 and https://www.bco-dmo.org/dataset/872885). Additional files used for data analyses are available on Dryad (DOI: https://doi.org/10.5061/dryad.bzkh189qf).

References

Aldridge, R.L., Britch, S.C., Allan, S.A., Tsikolia, M., Calix, L.C., Bernier, U.R., Linthicum, K.J., 2016. Comparison of volatiles and mosquito capture efficacy for three carbohydrate sources in a yeast-fermentation CO2 generator. J. Am. Mosq. Control Assoc. 32, 282–291. https://doi.org/10.2987/16-6609.1.

Altieri, A.H., Trussell, G.C., Ewanchuk, P.J., Bernatchez, G., Bracken, M.E.S., 2009. Consumers control diversity and functioning of a natural marine ecosystem. PLoS One 4, e5291. https://doi.org/10.1371/journal.pone.0005291.

Bass, A., Wernberg, T., Thomsen, M., Smale, D., 2021. Another decade of marine climate change experiments: trends, Progress and knowledge gaps. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.714462.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Beever, E.A., Hall, L.E., Varner, J., Loosen, A.E., Dunham, J.B., Gahl, M.K., Smith, F.A., Lawler, J.J., 2017. Behavioral flexibility as a mechanism for coping with climate change. Front. Ecol. Environ. 15, 299–308. https://doi.org/10.1002/fee.1502.

Bracken, M.E.S., Low, N.H.N., 2012. Realistic losses of rare species disproportionately impact higher trophic levels. Ecol. Lett. 15, 461–467. https://doi.org/10.1111/j.1461-0248.2012.01758.x.

Bracken, M.E.S., Silbiger, N.J., Bernatchez, G., Sorte, C.J.B., 2018. Primary producers may ameliorate impacts of daytime CO_2 addition in a coastal marine ecosystem. PeerJ 6, e4739. https://doi.org/10.7717/peerj.4739.

Cabecinha, E., Pardal, M.Â., Cabral, J.A., Monteiro, S.M., Cortes, R., Saavedra, M.J., Varandas, S., Van den Brink, P., 2024. Assessing the ecological potential of reservoirs: a principal response curve (PRC) analysis approach. Hydrobiologia 851, 25–44. https://doi.org/10.1007/s10750-023-05310-7.

Carrier-Belleau, C., Drolet, D., McKindsey, C.W., Archambault, P., 2021. Environmental stressors, complex interactions and marine benthic communities' responses. Sci. Rep. 11, 4194. https://doi.org/10.1038/s41598-021-83533-1.

Castro, H.F., Classen, A.T., Austin, E.E., Norby, R.J., Schadt, C.W., 2010. Soil microbial community responses to multiple experimental climate change drivers. Appl. Environ. Microbiol. 76, 999–1007. https://doi.org/10.1128/AEM.02874-09.

Chapin III, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Laundre, J.A., 1995. Responses of Arctic tundra to experimental and observed changes in climate. Ecology 76, 694–711. https://doi.org/10.2307/1939337.

Currie, J., 2022. Assessing annual nearshore carbonate chemistry trends in Alaska's marginal seas. Thesis. University of Alaska, Fairbanks.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., Wood, S., 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391, 783–786. https://doi.org/10.1038/35842.

Drumm, D.T., Maslenikov, K.P., Van Syoc, R., Orr, J.W., Lauth, R.R., Stevenson, D.E., Pietsch, T.W., 2016. An Annotated Checklist of the Marine Macroinvertebrates of Alaska (NOAA Professional Paper NMFS), NOAA Professional Paper NMFS. US Department of Commerce, NOAA, NMFS Scientific Publications Office. https://doi.org/10.7755/PP.19.

Edmunds, P.J., Brown, D., Moriarty, V., 2012. Interactive effects of ocean acidification and temperature on two scleractinian corals from Moorea, French Polynesia. Glob. Chang. Biol. 18, 2173–2183. https://doi.org/10.1111/j.1365-2486.2012.02695.x.

Fredston, A., Pinsky, M., Selden, R.L., Szuwalski, C., Thorson, J.T., Gaines, S.D., Halpern, B.S., 2021. Range edges of north American marine species are tracking temperature over decades. Glob. Chang. Biol. 27, 3145–3156. https://doi.org/10.1111/gcb.15614.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends Ecol. Evol. 25, 325–331. https://doi.org/10.1016/j.tree.2010.03.002.

Göbeler, N., Kauppi, L., Norkko, A., Norkko, J., 2025. Marine heatwaves amplify benthic community metabolism and solute flux in a seafloor heating experiment. Funct. Ecol. 39, 1856–1868. https://doi.org/10.1111/1365-2435.70028.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x.

Hale, R., Calosi, P., McNeill, L., Mieszkowska, N., Widdicombe, S., 2011. Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. Oikos 120, 661–674. https://doi.org/10.1111/j.1600-0706.2010.19469.x.

Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D., Buia, M.-C., 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454, 96–99. https://doi.org/10.1038/nature07051.

Hanson, P.J., Wullschleger, S.D., Norby, R.J., Tschaplinski, T.J., Gunderson, C.A., 2005. Importance of changing CO2, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. Glob. Chang. Biol. 11, 1402–1423. https://doi.org/10.1111/j.1365-2486.2005.00991.x.

Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241. https://doi.org/10.1111/j.1461-0248.2005.00871.x.

Harris, O., King, N.G., Foggo, A., Smale, D.A., 2025. Intraspecific facilitation in an intertidal foundation species plays fundamental role in promoting resistance to extreme climatic events. Oikos 2025, e11079. https://doi.org/10.1111/oik.11079.

Harte, J., Shaw, R., 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. Science 267, 876–880. https://doi.org/10.1126/science.267.5199.876.

Helmuth, B., Mieszkowska, N., Moore, P., Hawkins, S.J., 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. Annu. Rev. Ecol. Evol. Syst. 37, 373–404. https://doi.org/10.1146/annurev.ecolsys.37.091305.110149.

Henson, S.A., Laufkötter, C., Leung, S., Giering, S.L.C., Palevsky, H.I., Cavan, E.L., 2022. Uncertain response of ocean biological carbon export in a changing world. Nat. Geosci. 15, 248–254. https://doi.org/10.1038/s41561-022-00927-0.

Hermann, M., Peeters, E.T.H.M., Van den Brink, P.J., 2023. Heatwaves, elevated temperatures, and a pesticide cause interactive effects on multi-trophic levels of a freshwater ecosystem. Environ. Pollut. 327, 121498. https://doi.org/10.1016/j.envpol.2023.121498.

Hillebrand, H., Bennett, D.M., Cadotte, M.W., 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89, 1510–1520. https://doi.org/10.1890/07-1053.1.

Hu, N., Bourdeau, P.E., Hollander, J., 2024. Responses of marine trophic levels to the combined effects of ocean acidification and warming. Nat. Commun. 15, 3400. https://doi.org/10.1038/s41467-024-47563-3.

Hung, C.-M., Shaner, P.-J.L., Zink, R.M., Liu, W.-C., Chu, T.-C., Huang, W.-S., Li, S.-H., 2014. Drastic population fluctuations explain the rapid extinction of the passenger pigeon. Proc. Natl. Acad. Sci. 111, 10636–10641. https://doi.org/10.1073/pnas.1401526111.

IPCC, 2022. Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA, p. 3056.

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., Purvis, A., 2022. The direct drivers of recent global anthropogenic biodiversity loss. Sci. Adv. 8, eabm9982. https://doi.org/10.1126/sciadv.abm9982.

Jellison, B.M., Elsmore, K.E., Miller, J.T., Ng, G., Ninokawa, A.T., Hill, T.M., Gaylord, B., 2022. Low-pH seawater alters indirect interactions in rocky-shore tidepools. Ecol. Evol. 12, e8607. https://doi.org/10.1002/ece3.8607.

Kindinger, T.L., Toy, J.A., Kroeker, K.J., 2022. Emergent effects of global change on consumption depend on consumers and their resources in marine systems. Proc. Natl. Acad. Sci. USA 119, e2108878119. https://doi.org/10.1073/pnas.2108878119.

Kordas, R.L., Donohue, I., Harley, C.D.G., 2017. Herbivory enables marine communities to resist warming. Sci. Adv. 3, e1701349. https://doi.org/10.1126/sciadv.1701349.

Kroeker, K.J., Gambi, M.C., Micheli, F., 2013a. Community dynamics and ecosystem simplification in a high-CO2 ocean. Proc. Natl. Acad. Sci. 110, 12721–12726. https://doi.org/10.1073/pnas.1216464110.

Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., Duarte, C.M., Gattuso, J.-P., 2013b. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Glob. Chang. Biol. 19, 1884–1896. https://doi.org/10.1111/gcb.12179.

Kroeker, K.J., Micheli, F., Gambi, M.C., Martz, T.R., 2011. Divergent ecosystem responses within a benthic marine community to ocean acidification. Proc. Natl. Acad. Sci. 108, 14515–14520. https://doi.org/10.1073/pnas.1107789108.

Kwiatkowski, L., Gaylord, B., Hill, T., Hosfelt, J., Kroeker, K.J., Nebuchina, Y., Ninokawa, A., Russell, A.D., Rivest, E.B., Sesboüé, M., Caldeira, K., 2016. Nighttime dissolution in a temperate coastal ocean ecosystem increases under acidification. Sci. Rep. 6, 22984. https://doi.org/10.1038/srep22984.

Lee, J.-Y., Marotzke, J., Bala, G., Cao, L., Corti, S., Dunne, J.P., Engelbrecht, F., Fischer, E., Fyfe, J.C., Jones, C., Maycock, A., Mutemi, J., Niaye, O., Panickal, S., Zhou, T., Christensen, H.M., 2021. Future Global Climate: Scenario-Based Projections and near-Term Information.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579. https://doi.org/10.1111/2041-210X.12512.

Lindstrom, S.C., 2009. The biogeography of seaweeds in Southeast Alaska. J. Biogeogr. 36, 401–409. https://doi.org/10.1111/j.1365-2699.2007.01855.x.

Liu, P.-J., Ang, S.-J., Mayfield, A.B., Lin, H.-J., 2020. Influence of the seagrass *Thalassia hemprichii* on coral reef mesocosms exposed to ocean acidification and experimentally elevated temperatures. Sci. Total Environ. 700, 134464. https://doi.org/10.1016/j.scitotenv.2019.134464.

Mahanes, S., Bracken, M., Sorte, C.J.B., 2022. Climate change amelioration by marine producers: does dominance predict impact? Biol. Bull. 243, 299–314.

Miller, L.P., Long, J.D., 2015. A tide prediction and tide height control system for laboratory mesocosms. PeerJ 3, e1442. https://doi.org/10.7717/peerj.1442.

Miller, L.P., Matassa, C.M., Trussell, G.C., 2014. Climate change enhances the negative effects of predation risk on an intermediate consumer. Glob. Chang. Biol. 20, 3834–3844. https://doi.org/10.1111/gcb.12639.

Montie, S., Thomsen, M.S., 2023. Facilitation of animals is stronger during summer marine heatwaves and around morphologically complex foundation species. Ecol. Evol. 13, e10512. https://doi.org/10.1002/ece3.10512.

Murru, M., Sandgren, C.D., 2004. Habitat matters for inorganic carbon acquisition in 38 species of red macroalgae (Rhodophyta) from Puget Sound, Washington, USA. J. Phycol. 40, 837–845. https://doi.org/10.1111/j.1529-8817.2004.03182.x.

Nagelkerken, I., Connell, S.D., 2022. Ocean acidification drives global reshuffling of ecological communities. Glob. Chang. Biol. 28, 7038–7048. https://doi.org/10.1111/gcb.16410.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H., Szoecs, E., Wagner, H., 2022. Vegan: Community Ecology Package. CRAN.

Palumbi, S.R., Sandifer, P.A., Allan, J.D., Beck, M.W., Fautin, D.G., Fogarty, M.J., Halpern, B.S., Incze, L.S., Leong, J.-A., Norse, E., Stachowicz, J.J., Wall, D.H., 2009.

Managing for ocean biodiversity to sustain marine ecosystem services. Front. Ecol. Environ. 7, 204–211. https://doi.org/10.1890/070135.
R Core Team, 2021. R-4.1.2 for Windows. The R-project for statistical computing [WWW Document]. https://cran.r-project.org/bin/windows/base/ (accessed 3.16.22).
Rangel, R.E., Bracken, M.E.S., Kroeker, K.J., Miller, L.P., Sorte, C.J.B., 2025. Factorial field manipulation reveals CO2 and temperature effects on a critical habitat-forming shellfish. J. Exp. Biol. 228. https://doi.org/10.1242/jeb.250787 jeb250787.
Rangel R.E., Kroeker K., Bracken M.E.S., Miller L.P., Sorte C.J.B., (in revision). Individual metabolism drives alterations in net ecosystem calcification under ocean acidification and warming. Ecology.
Rangel, R.E., Sorte, C.J.B., 2022. Local-scale thermal history influences metabolic response of marine invertebrates to warming. Mar. Biol. 169, 126. https://doi.org/10.1007/s00227-022-04110-2.
Raymond, W.W., Barber, J.S., Dethier, M.N., Hayford, H.A., Harley, C.D.G., King, T.L., Paul, B., Speck, C.A., Tobin, E.D., Raymond, A.E.T., McDonald, P.S., 2022. Assessment of the impacts of an unprecedented heatwave on intertidal shellfish of the Salish Sea. Ecology 103, e3798. https://doi.org/10.1002/ecy.3798.
Rivest, E.B., Comeau, S., Cornwall, C.E., 2017. The role of natural variability in shaping the response of coral reef organisms to climate change. Curr. Clim. Chang. Rep. 3, 271–281. https://doi.org/10.1007/s40641-017-0082-x.
Robinson, J.P.W., White, E.R., Wiwchar, L.D., Claar, D.C., Suraci, J.P., Baum, J.K., 2014. The limitations of diversity metrics in directing global marine conservation. Mar. Policy 48, 123–125. https://doi.org/10.1016/j.marpol.2014.03.012.
Schofield, O., Ducklow, H.W., Martinson, D.G., Meredith, M.P., Moline, M.A., Fraser, W. R., 2010. How do polar marine ecosystems respond to rapid climate change? Science 328, 1520–1523. https://doi.org/10.1126/science.1185779.
Silbiger, N.J., Sorte, C.J.B., 2018. Biophysical feedbacks mediate carbonate chemistry in coastal ecosystems across spatiotemporal gradients. Sci. Rep. 8, 796. https://doi.org/10.1038/s41598-017-18736-6.
Soininen, J., Passy, S., Hillebrand, H., 2012. The relationship between species richness and evenness: a meta-analysis of studies across aquatic ecosystems. Oecologia 169, 803–809. https://doi.org/10.1007/s00442-011-2236-1.
Somero, G.N., 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of Living1. Integr. Comp. Biol. 42, 780–789. https://doi.org/10.1093/icb/42.4.780.
Sorte, C.J.B., Bracken, M.E.S., 2015. Warming and elevated CO2 interact to drive rapid shifts in marine community production. PLoS One 10, e0145191. https://doi.org/10.1371/journal.pone.0145191.
Sorte, C.J.B., Davidson, V.E., Franklin, M.C., Benes, K.M., Doellman, M.M., Etter, R.J., Hannigan, R.E., Lubchenco, J., Menge, B.A., 2017. Long-term declines in an intertidal foundation species parallel shifts in community composition. Glob. Chang. Biol. 23, 341–352. https://doi.org/10.1111/gcb.13425.
Sorte, C.J.B., Jones, S.J., Miller, L.P., 2011. Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. J. Exp. Mar. Biol. Ecol. 400, 209–217. https://doi.org/10.1016/j.jembe.2011.02.009.
Sorte, C.J.B., Kroeker, K.J., Miller, L.P., Bracken, M.E.S., 2023. Biological modification of coastal pH depends on community composition and time. Ecology 104, e4113. https://doi.org/10.1002/ecy.4113.
Sunday, J.M., Bates, A.E., Dulvy, N.K., 2012. Thermal tolerance and the global redistribution of animals. Nat. Clim. Chang. 2, 686–690. https://doi.org/10.1038/nclimate1539.
Sunday, J.M., Fabricius, K.E., Kroeker, K.J., Anderson, K.M., Brown, N.E., Barry, J.P., Connell, S.D., Dupont, S., Gaylord, B., Hall-Spencer, J.M., Klinger, T., Milazzo, M., Munday, P.L., Russell, B.D., Sanford, E., Thiyagarajan, V., Vaughan, M.L.H., Widdicombe, S., Harley, C.D.G., 2017. Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. Nat. Clim. Chang. 7, 81–85. https://doi.org/10.1038/nclimate3161.
Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11. https://doi.org/10.1111/j.1461-0248.2008.01250.x.
Van den Brink, P.J., Braak, C.J.F.T., 1999. Principal response curves: analysis of time-dependent multivariate responses of biological community to stress. Environ. Toxicol. Chem. 18, 138–148. https://doi.org/10.1002/etc.5620180207.
Van Sundert, K., Leuzinger, S., Bader, M.K.-F., Chang, S.X., De Kauwe, M.G., Dukes, J.S., Langley, J.A., Ma, Z., Mariën, B., Reynaert, S., Ru, J., Song, J., Stocker, B., Terrer, C., Thoresen, J., Vanuytrecht, E., Wan, S., Yue, K., Vicca, S., 2023. When things get MESI: the manipulation experiments synthesis initiative—a coordinated effort to synthesize terrestrial global change experiments. Glob. Chang. Biol. 29, 1922–1938. https://doi.org/10.1111/gcb.16585.
Visser, M.E., 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proc. R. Soc. B Biol. Sci. 275, 649–659. https://doi.org/10.1098/rspb.2007.0997.
Weitzman, B., Konar, B., Iken, K., Coletti, H., Monson, D., Suryan, R., Dean, T., Hondolero, D., Lindeberg, M., 2021. Changes in rocky intertidal community structure during a marine heatwave in the northern Gulf of Alaska. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.556820.
Wernberg, T., Smale, D.A., Thomsen, M.S., 2012. A decade of climate change experiments on marine organisms: procedures, patterns and problems. Glob. Chang. Biol. 18, 1491–1498. https://doi.org/10.1111/j.1365-2486.2012.02656.x.
Williams, A.L., Wills, K.E., Janes, J.K., Vander Schoor, J.K., Newton, P.C.D., Hovenden, M.J., 2007. Warming and free-air CO2 enrichment alter demographics in four CO-occurring grassland species. New Phytol. 176, 365–374. https://doi.org/10.1111/j.1469-8137.2007.02170.x.
Woods, H.A., Dillon, M.E., Pincebourde, S., 2015. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. Journal of thermal biology, what sets the limit? How thermal limits, performance and preference in ectotherms are influenced by water or energy balance, 54, pp. 86–97. https://doi.org/10.1016/j.jtherbio.2014.10.002.
Xu, Y., Isom, L., Hanna, M.A., 2010. Adding value to carbon dioxide from ethanol fermentations. Bioresour. Technol. 101, 3311–3319. https://doi.org/10.1016/j.biortech.2010.01.006.
Zunino, S., Libralato, S., Melaku Canu, D., Prato, G., Solidoro, C., 2021. Impact of ocean acidification on ecosystem functioning and services in habitat-forming species and marine ecosystems. Ecosystems 24, 1561–1575. https://doi.org/10.1007/s10021-021-00601-3.