

Experimental reef communities persist under future ocean acidification and warming

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Abstract

Coral reefs are among the most sensitive ecosystems affected by ocean acidification and warming, and are predicted to shift from net accreting calcifier-dominated systems to net eroding algal-dominated systems over the coming decades. Here we present a long-term experimental study examining the responses of entire mesocosm coral reef communities to acidification (-0.2 pH units), warming (+ 2°C), and combined future ocean (-0.2 pH, + 2°C) treatments. We show that under future ocean conditions, net calcification rates declined yet remained positive, corals showed reduced abundance yet were not extirpated, and community composition shifted while species richness was maintained. Our results suggest that under Paris Climate Agreement targets, coral reefs could persist in an altered functional state rather than collapse.

Main Text

Many studies project that the combination of ocean acidification and warming will lead to the functional collapse of coral reef ecosystems at a global scale over the next few decades, driving major losses in biodiversity and ecosystem services¹⁻⁵. Reefs are expected to shift from net calcification to net carbonate dissolution sometime later this century when atmospheric CO₂ reaches 550-650 μatm, seawater pH declines by 0.1-0.15 units, and seawater temperature increases by 1-1.5 °C^{4,6}. Likewise, corals are expected to be essentially extirpated from reefs in the next few decades (>99% decline)^{7,8} once coral bleaching becomes an annual phenomenon. These projected future scenarios are typically based on either short-term laboratory perturbation experiments with few species that are then scaled up to long-term responses of complex communities in nature^{3,4,9,10} or *in situ* observations of coral reefs that span natural gradients in chemistry or thermal stress¹¹⁻¹⁴. Laboratory experiments, however, typically do not include natural ecological interactions among species which could affect community function, and some experiments may not have provided organisms with sufficient time to fully respond to the treatments. Likewise, natural gradient studies do not reflect the intensity of heat stress expected later this century and often do not incorporate acidification and warming simultaneously (but see¹⁵⁻¹⁷). An alternative approach to lab or natural gradient studies is the use of mesocosms which allow diverse communities to be exposed to future ocean levels of acidification and warming at the same time while preserving realistic ecological interactions and environmental conditions¹⁸⁻²³. While no study can incorporate every aspect of future reef ecosystem composition and function, mesocosms provide some of the most complete experimental systems to test the hypothesis that sustained future ocean acidification and warming will induce the functional collapse of experimental reef communities. With eight coral species representing three divergent families (Acroporidae, Pocilloporidae, and Poritidae), both major evolutionary lineages of scleractinians (Complexa and Robusta), and all four of their major life history strategies (see Supplementary Information), along with the literally thousands of other species surveyed in our study (ranging from bacteria and archaea to many of the major animal and algal phyla), we present a long-term experimental examination of coral reef organismal and community responses under future ocean

conditions. This dataset provides unprecedented insights into the likely responses of coral reef communities to ocean acidification and warming over coming years.

We conducted a two-year ecologically realistic outdoor flow-through mesocosm experiment at the Hawai'i Institute of Marine Biology to examine the long-term responses of biologically diverse coral reef communities to chronic acidification and warming similar to levels projected to occur toward the end of this century given current commitments under the Paris Climate Agreement (conditions between Representative Concentration Pathways RCP 6.0 and RCP 8.5)²⁴. Mesocosms were initially stocked with replicate communities of the regionally most common reef-building corals, each sourced from multiple locations around the island of O'ahu, as well as reef rubble, reef sand, algae, invertebrates, and fish (see Supplementary Information). We determined the multilocus genotype of each coral colony sampled to ensure results were not biased by inclusion of clones. Replicate clonal fragments (ramets) of each genetically unique coral colony (genet) were included in all four treatments. Over time, the mesocosms recruited a diverse assemblage of algae, invertebrates, and microbes (Fig. 1). These communities developed under one of four treatments with 10 mesocosms per treatment: control treatment (present-day pH and temperature), ocean acidification treatment (present-day temperature with acidification of -0.2 pH units relative to control), ocean warming treatment (present-day pH with elevated temperature of +2 °C relative to control), or combined future ocean treatment (both acidification of -0.2 pH units and elevated temperature of +2 °C relative to control). All mesocosms experienced natural diurnal and seasonal variation in temperature, chemistry, and irradiance (Table 1, Fig. 2, S1). After approximately two years of exposure, we assessed (i) coral bleaching, survivorship, recruitment, skeletal extension, metabolism, and energy reserves, (ii) net calcification by the mesocosm communities, coral communities, and rubble-associated communities, and (iii) community structure and species richness of the major functional groups, including benthic algae and invertebrates, coral-associated algal endosymbionts (Symbiodiniaceae), coral-associated microbes, and water column-associated microbes (Fig. S2).

Table 1. Carbonate chemistry and temperature from the experiment. Data are daily mean values derived from weekly sampling at 1200 hr as well as monthly sampling every 4 hr over the diel cycle (see Supplementary Information) and are shown as mean±SD. The uncertainties associated with these values reflect daily and seasonal variability, as well as variability among replicate mesocosms in each treatment. The mean uncertainties among mesocosms on a given sampling day are provided in parentheses. Note that the variation among mesocosms is relatively small and most of the variation is explained by daily and seasonal fluctuation of these parameters. See Fig. 2, S1 for additional environmental information.

Treatment	Salinity (psu)	Temperature (°C)	pH	Total alkalinity ($\mu\text{mol kg}^{-1}$)	pCO ₂ (μatm)	Ω_{arag}
Control	34.26±0.34 (0.02)	25.08±1.18 (0.09)	7.99±0.05 (0.01)	2177±51 (12)	448±60 (12)	2.88±0.32 (0.05)
Ocean acidification	34.26±0.34 (0.02)	25.09±1.18 (0.09)	7.78±0.07 (0.02)	2184±49 (12)	794±132 (44)	1.94±0.31 (0.08)
Ocean warming	34.29±0.34 (0.02)	26.99±1.18 (0.17)	7.98±0.05 (0.01)	2187±49 (12)	453±61 (16)	3.06±0.33 (0.07)
Future ocean	34.30±0.34 (0.02)	27.03±1.15 (0.16)	7.77±0.07 (0.02)	2196±48 (9)	811±134 (45)	2.07±0.32 (0.08)

Corals in the treatments with elevated temperature (ocean warming and combined future ocean treatments) were exposed to severe³ heat stress in successive years. These corals experienced temperatures at or above the nominal bleaching threshold for 3.5 months per year, during which they accumulated 24 Degree Heating Weeks (DHW) annually (Fig. 2). Many studies predict that this level of repeated annual bleaching stress should have been more than sufficient to extirpate corals in our elevated temperature mesocosms^{1,3,7,8} and that acidification should have exacerbated the heat stress³. As expected, many of the corals that bleached severely subsequently died during the trials, with up to 13% of the corals in the heated treatments remaining pale or bleached at the end of the experiment, compared to less than 2% under the control and ocean acidification treatments (Fig. S3, Table S1). Contrary to projections of near total mortality^{7,8}, coral survivorship was reduced by only 35% in the heated treatments compared to the present-day temperature treatments, with no evidence that acidification affected either survivorship or the incidence of bleaching (Fig. S3, Table S1). Among the survivors, the extent of paling, however, was 14-18% higher in the ocean acidification, ocean warming, and combined future ocean treatments relative to the control (Fig. S3, Table S2). Indeed, some individual corals in this study bleached and died, whereas others bleached annually yet survived to the end, and still others never bleached at all. These responses differed by coral genus. All individuals of both species of *Pocillopora* paled or bleached, though some survived, whereas responses within the other genera were more variable and some individuals within each of the three *Montipora* species and the three *Porites* species exhibited all of these response patterns. Coral species richness declined under warming, primarily due to the loss of one or both *Pocillopora* species from many of the heated mesocosms (Table S3). Some corals are capable of increasing zooplankton feeding rates to survive and recover from bleaching²⁵. Although we used unfiltered sea water and fishes in the mesocosms were fed to simulate natural zooplankton import to the communities (see Supplementary Information), live zooplankton densities in the mesocosms were at the

lower end of values typically reported for reefs (Fig. S4), making our results potentially conservative. Among the surviving corals, horizontal skeletal extension was reduced 22% in the heated mesocosms (ocean warming and combined future ocean treatments) relative to those under present-day temperatures (control and ocean acidification treatments), but was unaffected by acidification (Fig. S5, Table S3). In contrast, total organic carbon fluxes increased under warming (Table S3, Fig. S4). Coral photosynthesis, respiration, and energy reserves, however, did not differ significantly among those individuals that survived the treatments (Fig. S5, Table S3). While severe, this 35% reduction in survivorship and 22% decline in skeletal extension among the survivors is far less than the >99% loss of corals projected for reefs^{7,8}. The discrepancy between our data and these projections may reflect some of the challenges associated with scaling up prior results. In particular, few projections quantitatively account for the substantial variation in bleaching tolerance we observed within and among species or the biotic interactions which could modulate these outcomes²⁶.

Large numbers of one coral species (*Pocillopora acuta*) recruited into the mesocosms, undoubtedly due to spawning of the adult corals housed in them^{18,27}, but recruitment rate was unaffected by any of the treatments²⁷. Similarly, we observed widespread spawning of another coral species (*Montipora capitata*) across all four treatments (CPJ pers. obs. in June 2018), though it was infeasible to assess reproductive output or gamete quality at the time of release. Hence, many of the corals grew from the size of pre-reproductive juveniles to reproductive adults (and completed a substantial fraction of their life cycles) over the course of the experiment. If coral individuals that are resistant to bleaching or resilient to annual bleaching (like some of those in this study) proliferate in the future, then they could help to offset some of the negative effects of ocean warming on coral abundance predicted for coral reefs. Indeed, coral communities in Hawai'i already appear to be mounting adaptive responses to climate change with bleaching and mortality occurring at higher temperatures and after longer exposures than reported 50 years ago^{17,28}.

The calcification rates measured in the control mesocosm communities were very similar to those measured on the nearby reefs²⁹, indicating that the mesocosms adequately replicated the processes involved in community calcification. Net calcification of the mesocosm communities (sometimes referred to as net community calcification, NCC, or net ecosystem calcification, NEC, in other studies) declined in all treatments relative to the control, with the largest decline under the combined future ocean scenario (Fig. 3, Table S3). The 19-24% reduction in mesocosm calcification attributable to acidification is lower but roughly similar to the 30% reduction measured on an experimentally acidified reef flat³⁰, further illustrating the efficacy of our approach to simulate the natural system. Nevertheless, all communities continued calcifying. Even under the combined future ocean treatment, reef community calcification was positive, albeit at only 56% the rate of control reef communities. At present-day rates of calcification, however, few reefs are expected to accrete fast enough to be able to keep up with sea level change and many future reefs may become submerged as the oceans rise³¹. Acidification does not by itself kill corals but rather tends to inhibit their skeletal growth by an average of 15-20%¹⁰, which may compromise their competitive abilities in nature^{11,12,15}. Acidification, however, had no effect on net coral community

calcification or skeletal extension within this study (Fig. 3, Fig. S5, Table S3). While these results differ from many prior laboratory experiments, both *ex situ* and *in situ* studies have found that some corals can maintain normal calcification rates under lower pH^{12,13,17,32-34}. Further, irradiance and water flow are both known to affect coral responses to acidification¹⁹. We conducted this experiment using natural sunlight (attenuated by shade cloth to ambient levels at mean collection depth of 2 m), rapid unfiltered natural seawater turnover rate (1 hr), and additional water circulation provided by seawater pumps (10-15 cm s⁻¹) to replicate light and flow conditions on the natural reefs as closely as possible (Fig. 2), which may help to explain the observed insensitivity of coral calcification to low pH relative to many previous laboratory studies. In addition, corals may show threshold responses to acidification such that they are able to maintain calcification rates under a 0.2 pH unit reduction yet experience reduced calcification rates at higher levels of acidification^{17,18,35}. Unlike acidification, elevated temperature reduced coral community calcification and coral abundance by nearly half due to bleaching, mortality, and reduced skeletal extension among the survivors (Fig. 3, Table S3). In contrast, net calcification by rubble-associated communities declined under ocean acidification conditions yet was insensitive to warming (Fig. 3, Table S3). These results suggest that the measured reductions in calcification for mesocosm communities^{22,23,36} and natural communities^{6,30,37} due to acidification are driven largely by processes occurring within the reef framework and soft sediments rather than by the corals themselves. The calcification budget of the mesocosms exceeded that explained by the corals and rubble, and this additional carbonate production was likely from the growth of coralline algae, coral recruits, and other organisms which formed thick, calcified crusts on the mesocosm walls (Fig. 1). Future reefs will undoubtedly experience a major decline in growth due to the loss of corals from heat stress, and reduced calcification by the reef framework under acidification. Nonetheless, our findings indicate that under mitigated CO₂ emissions consistent with current commitments under the Paris Climate Agreement, reefs may be capable of maintaining positive carbonate balances and net calcification despite these climate change stressors.

Corals are ecosystem engineers, yet coral reef biodiversity is derived largely from the array of algae, invertebrates, and microbes which live within, among, and upon the reefs. Coral reefs occupy less than 0.2% of the seafloor but are home to an estimated 32-38% of all marine species³⁸. Yet almost nothing is known about how this biodiversity will respond to ocean acidification, warming, or the combination of both factors. To determine how algal, microbial, and non-coral invertebrate composition varied within each treatment, at the end of the experiment we 1) retrieved 3-tiered settlement tile arrays (modified Autonomous Reef Monitoring Structures³⁹) which had recruited diverse benthic assemblages while soaking in the mesocosms for the duration of the experiment; 2) sampled the coral-associated algal endosymbionts and coral-associated microbes, as well as the water column-associated microbes; and 3) sampled the mesocosms for benthic, fleshy algae. The settlement tile arrays mimicked the three-dimensional structure of the reef framework and provided a standardized tool with which to examine this often-overlooked cryptobenthic community. The settlement tiles provided four data sets: 1) benthic cover by functional group from tile image analysis; 2) sponge species richness from individual morphological identification with DNA barcoding confirmation; 3) coralline algal richness from individual morphological

identification; and 4) overall metazoan richness from DNA metabarcoding of the homogenized biomass scraped from each tile array³⁹⁻⁴¹. Given the relatively short reproductive cycles of many algae and invertebrate species (weeks to months), they experienced multiple generations over the course of the experiment, providing a time-integrated measure of the treatment effects on community composition and abundances. Throughout the course of the experiment the benthic community transitioned from early colonizing species to a mature and diverse community that underwent seasonal variation in abundance similar to adjacent reef communities (JV, KDB, MAT, CPJ, and RJT, pers. obs.)

Benthic cover analyses revealed that only a subset of the functional groups responded significantly to the treatments. Calcifying vermetid gastropods declined under acidification but increased under warming (Fig. 4, Table S3). Calcifying coralline algal cover increased with warming, non-calcifying turf algal cover decreased with warming, but neither group responded to acidification (Fig. 4, Table S3). Encrusting green algal cover increased in the combined future ocean scenario relative to the other treatments (Fig. 4, Table S2). Other calcifying taxa (including bivalves and serpulid worms) were unaffected by either low pH or elevated temperature (Fig. 4, Table S2, & S3). The lack of an acidification effect on the benthic cover of most calcifying taxa is unexpected considering that individual species are often particularly sensitive to reduced pH in other studies⁹. Overall benthic community structure, however, was unaffected by pH, indicating that it is not changes in the dominance of functional groups, but rather the relative sensitivity of species within functional groups that alter this structure. Benthic functional group community structure differed only by temperature, and this effect was driven largely by separation of the control and ocean warming treatments in a community ordination (Fig. 5, Table S4).

Species richness of coralline algae and most other heavily calcified taxa were not significantly different among treatments⁴¹, whereas the richness of some non-calcifiers declined under acidification (Table S3). Total metazoan richness on the settlement tiles was significantly reduced by acidification, significantly enhanced by warming, and these two factors offset each other in combination, resulting in species richness estimates that were not significantly different between the control and the combined future ocean scenarios⁴¹. The water column-associated microbial species composition and richness in the mesocosms did not differ significantly among treatments (Table S4). In contrast, the coral-associated microbial communities showed higher richness under warming and shifted structure depending on both temperature and pH (Table S3 & S4). Richness of coral-associated algal symbionts (Symbiodinaceae, resolved to the genera *Cladocopium* and *Durusdinium*) increased under warming (ocean warming and combined future ocean treatments) because a higher proportion of the *Montipora* corals that survived those treatments hosted both symbiont genera rather than *Cladocopium* alone (Table S1). The proportional contribution of each type to the overall symbiont community, however, was unchanged by any of the treatments (Table S1). Likewise, fleshy algal species richness did not respond to either warming or acidification (Table S3). Hence, taxonomic and functional groups showed variable responses to the experimental treatments (Fig. 4). However, when all taxonomic datasets (sponges, coralline algae, and metabarcoding of metazoans from settlement tiles, coral-associated microbes, water column-associated microbes, coral-associated algal endosymbionts, fleshy algae, and corals) were pooled to

examine the effects of low pH and elevated temperature on proportional changes in overall species richness, the number of species was not significantly affected by any of the treatments (Fig. 5, Table S1).

Our experiments support predictions that future reefs will have less coral and reduced calcification rates. Yet, when experimental mesocosms were exposed to future ocean levels of simultaneous acidification and warming, consistent with current commitments under the Paris Climate Agreement (but in the absence of local stressors), we did not observe coral extirpation, reef community collapse, or net community carbonate dissolution. Instead, responses to ocean acidification, warming, and the combined future ocean stressors varied greatly among taxa, and many showed no significant effect of the treatments. Despite repeated severe annual heat stress (24 DHW annually), overall species richness was unchanged in future ocean conditions relative to present-day. The species richness or benthic cover of calcifiers (such as coralline algae) that have been predicted to do poorly based on previous work instead showed unexpected persistence, while some non-calcifiers (such as turf algae) declined under low pH or elevated temperature. Our results highlight the challenges of scaling up single-species studies to predict the outcome in diverse reef communities. Higher levels of acidification and warming, either due to unmitigated CO₂ emissions or during periodic marine heatwaves, will undoubtedly result in more severe effects on reef ecosystems and reduced capacity to provide valuable ecosystem services.

The results of our long-term experimental study, which includes the most diverse spectrum of organismal and community responses examined to date, demonstrate that future ocean acidification and warming pose grave threats to coral reef ecosystems, and that unmitigated CO₂ emissions will undoubtedly result in severe damage to these iconic ecosystems. However, these results also suggest that future reefs are likely to maintain a degree of function and avoid global collapse under realistic levels of ocean acidification and warming so long as local stressors can be mitigated⁴². Our study predicts that the community structure of reefs under future ocean warming will shuffle significantly, undoubtedly altering ecosystem function, but the ultimate outcome of such changes depends on species interactions and the specific ecological functions affected. Previous studies have underscored the importance of also mitigating local stressors for maintaining reef resilience^{17,43,44}, especially because such local stressors increase the magnitude of coral loss from marine heatwaves⁴². The reef communities in these mesocosms were free from local anthropogenic stressors such as destructive fishing practices, sedimentation, and coastal pollution, which may have facilitated their persistence in the face of future ocean conditions. Overall, our results support projections that scleractinian corals will have lower abundance on future reefs, but also suggest that they will not be extirpated, that reef calcification will decline, yet will remain positive, and that a substantial fraction of reef biodiversity and ecosystem function could be preserved, even in the face of climate change, if serious action is taken to limit local human stressors on these iconic ecosystems.

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Competing interests: Authors declare that they have no competing interests.

Data and materials availability: These data will be submitted to an online repository to enable open access with a persistent link and DOI. For the purpose of review, the datasets generated and analyzed herein are available from the corresponding author upon request.

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Figures

a



b



c



d



Figure 1

Representative photos of the mesocosms after nearly two years of exposure under treatment conditions. Images are from the (a) control, (b) ocean acidification, (c) ocean warming, and (d) combined future ocean treatments.

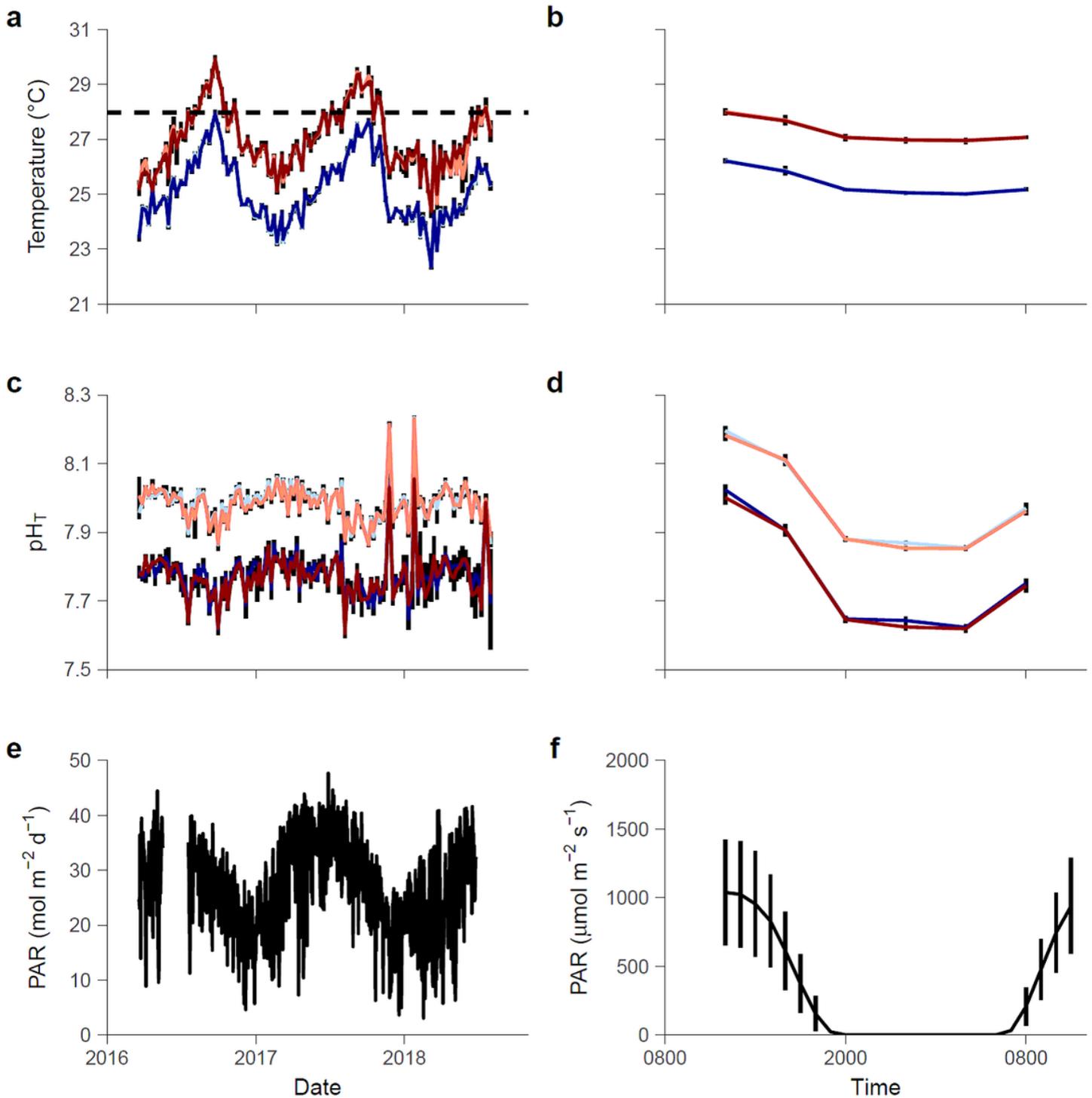


Figure 2

Environmental data from the mesocosm experiment. Panels show timeseries of temperature (a,b) and pH (reported on the Total hydrogen ion scale) (c,d), as well as photosynthetically active radiation (PAR) (e,f) as daily means over the course of the experiment (a,c) and hourly means over the diel cycle (b,d,f) for the control (light blue), ocean acidification (dark blue), ocean warming (light red), and combined future ocean (dark red) treatments (individual lines not visible where they overlap). Horizontal dashed line (a) shows the nominal coral bleaching threshold. Temperature and pH are derived from weekly samples collected at

1200 hr local time as well as the mean of samples collected every 4 hr over the diel cycle once per month. Irradiance data are daily integral values (e), or the mean of hourly values (f). All data (except e) shown as mean±SD. Error shown as vertical black bars (not visible where smaller than the line thickness). Mesocosms were covered in 30% shade cloth to replicate irradiance at mean collection depth (2 m). Maximum instantaneous irradiance was about 1730 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the mesocosms and 2470 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the air. Water circulation in the mesocosms was provided by seawater pumps (10-15 cm s^{-1}) and seawater turnover rate was 1 hr. See Table 1 and Fig. S1 for additional chemistry data, and see the Supplementary Information for additional details.

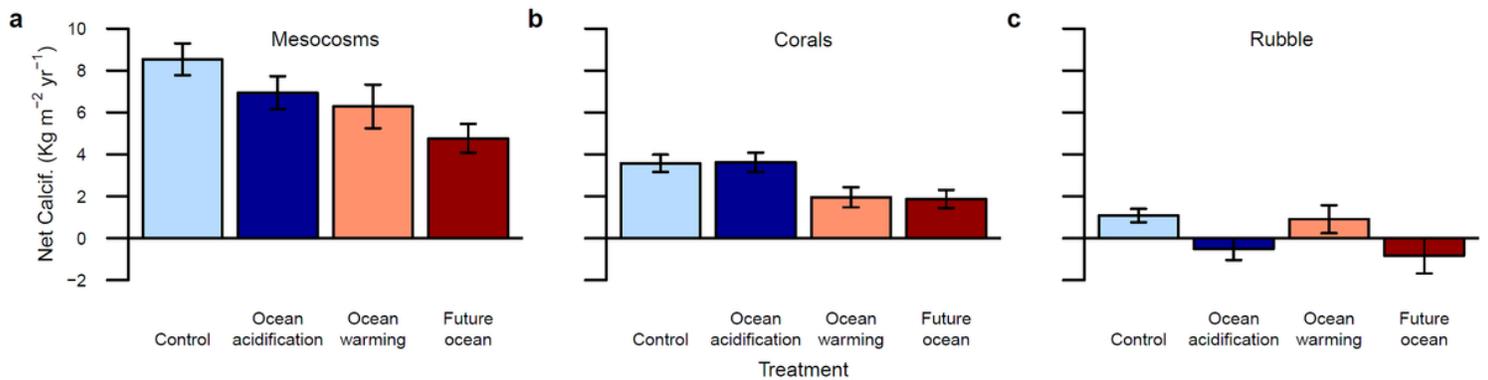


Figure 3

Effects of experimental acidification, warming, and combined future ocean conditions on net community calcification. (a) Entire mesocosm communities (sometimes referred to as net community calcification, NCC, or net ecosystem calcification, NEC, in other studies), (b) coral communities, and (c) rubble-associated communities. Net calcification was determined by the total alkalinity anomaly technique in (a) and by the buoyant weight technique in (b,c). Data bars show the mean±SD (n = 10 communities per treatment). Mesocosm calcification declined with acidification and warming, whereas coral calcification declined only with warming and rubble calcification declined only with acidification. See Table S3 for test results.

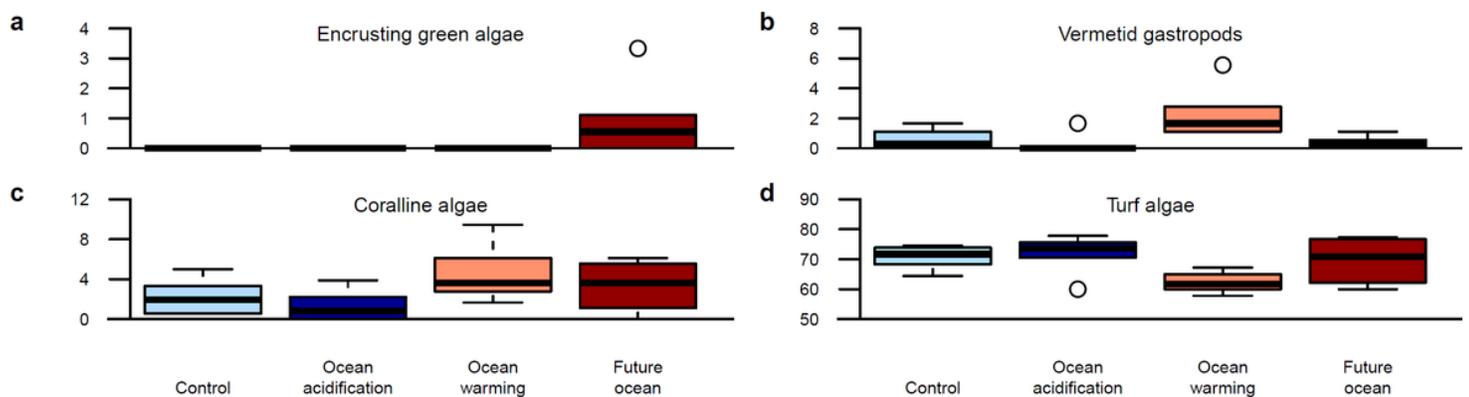


Figure 4

Benthic cover of functional groups on settlement tiles colonized in the mesocosms. (a), encrusting green algae, (b), vermetid gastropods, (c), coralline algae, (d), turf algae (n = 6 tile arrays per treatment).

Vermetid gastropods, coralline algae, and turf algae showed significant responses to warming, whereas only vermetid gastropods responded negatively to acidification. Encrusting green algae attained significantly higher abundance under the combined future ocean scenario as compared to the other treatments. None of the other 10 functional groups responded significantly to treatment conditions. Box-plots show the median as center line, box limits are upper and lower quartiles, whiskers are 1.5x interquartile range, and open circles as outliers. Boxes are not visible where values were below detection limits of 0.09%. See Table S2 & S3 for test results.

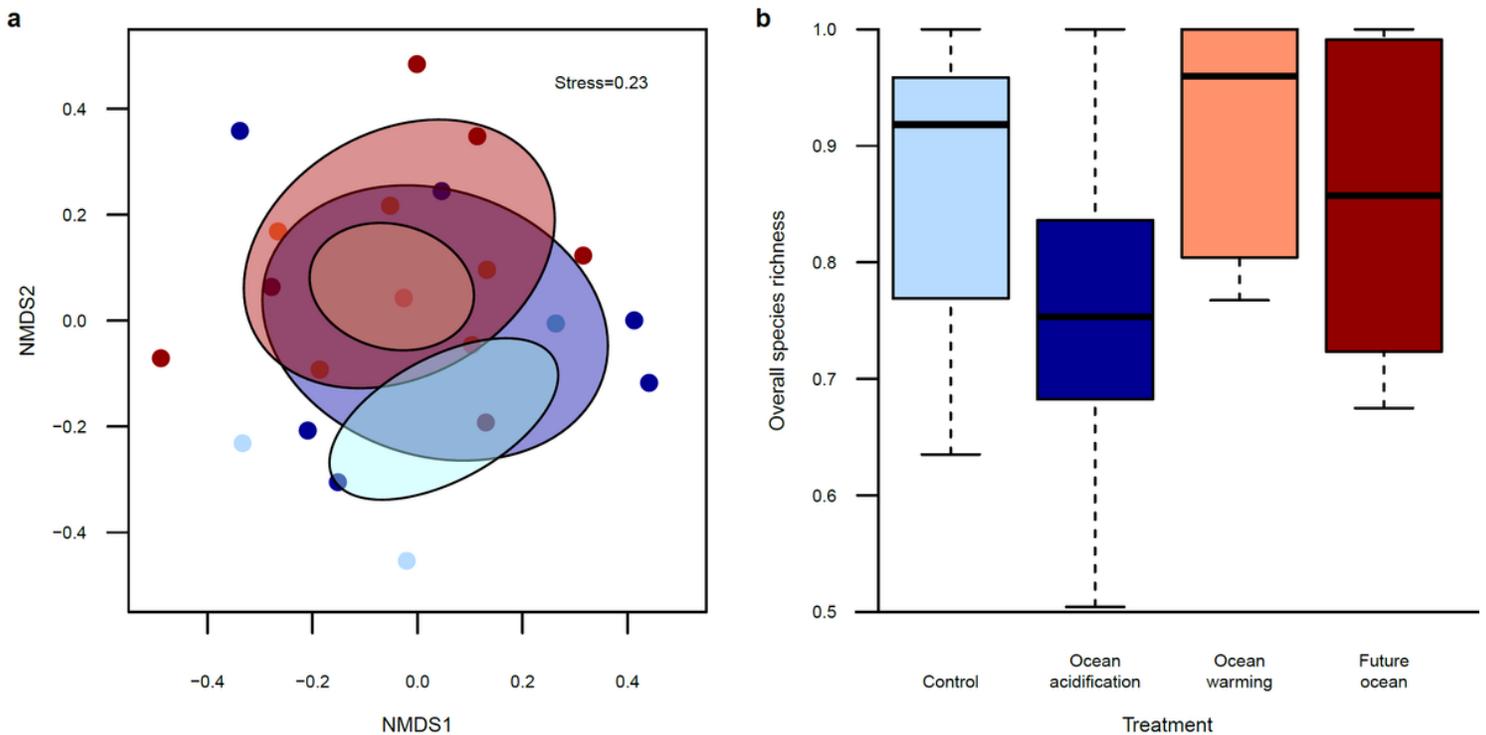


Figure 5

Benthic community structure and overall species richness in the mesocosms. (a) Non-metric multidimensional scaling ordination illustrating the effects of ocean acidification and warming on benthic community structure from settlement tiles colonized in the mesocosms for the control (light blue), ocean acidification (dark blue), ocean warming (light red), and combined future ocean treatments (dark red) ($n = 6$ tile arrays per treatment). Ellipses overlaid on scatterplots show the standard deviation around the centroid for each group. Community structure differed according to temperature but not pH, which was driven largely by separation of the control and ocean warming treatments. (b) Treatment effects on overall species richness in the mesocosms (data shown as proportional variation in species richness relative to the maximum observed richness among treatments) derived from samples of sponges, coralline algae, and metabarcoding of metazoans from settlement tiles, coral-associated microbes, water column-associated microbes, coral-associated algal endosymbionts, fleshy algae, and corals ($n = 8$ datasets representing thousands of species). Box-plots show the median as center line, box limits are upper and lower quartiles, whiskers are 1.5x interquartile range, and there were no outliers. Treatment effects were not significant. See Table S1, & S4 for test results.

Supplementary Files

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