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Understanding coralline algal responses to ocean acidification: meta-analysis and synthesis

Running title: Coralline algae and ocean acidification

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Abstract:

Ocean acidification (OA) is a major threat to the persistence of biogenic reefs throughout the world's oceans. Coralline algae are comprised of high magnesium calcite, and have long been considered one of the most susceptible taxa to the negative impacts of OA. We summarise these impacts and explore causes of variability in coralline algal responses using a review/qualitative assessment of all relevant literature, meta-analysis, quantitative assessment of critical responses, and a discussion of physiological mechanisms and directions for future research. We find that most coralline algae experienced reduced abundance, calcification rates, recruitment rates, and declines in pH within the site of calcification in laboratory experiments simulating ocean acidification or at naturally elevated CO_2 sites. There were no other consistent physiological responses of coralline algae to simulated OA (e.g. photo-physiology, mineralogy and survival). Calcification/growth were the most frequently measured parameters in coralline algal ocean acidification research, and our meta-analyses revealed greater declines in seawater pH were associated with significant decreases in calcification in adults and similar but non-significant trends for juveniles. Adults from the family Mesophyllumaceae also tended to be more robust to OA, though there was insufficient data to test similar trends for juveniles. OA was the dominant driver in the majority of laboratory experiments where other local or global drivers were assessed. The interaction between OA and any other single driver was often additive, though factors that changed pH at the surface of coralline algae (light, water motion, epiphytes) acted antagonistically or synergistically with OA more than any other drivers. With advances in experimental design and methodological techniques, we now understand that the physiology of coralline algal calcification largely dictates their responses to OA. However, significant challenges remain, including improving the geographic and life-history spread of research effort and a need for holistic assessments of physiology.

Keywords: Climate change, ocean acidification, coralline algae, CCA. Rhodoliths, maerl, calcification, meta-analysis

Introduction:

Ocean acidification (OA) is the absorption of anthropogenically-derived CO_2 by the surface seawaters of the world's oceans (Caldeira and Wickett 2003). OA alters seawater chemistry as follows: hydrogen ions (H^+) and carbon dioxide (CO_2) increase, dissolved inorganic carbon (DIC) and bicarbonate (HCO_3^-) increase slightly, and carbonate (CO_3^{2-}) concentrations and the calcium carbonate saturation states (**Ω**) decrease (Feely et al. 2004). These changes in seawater chemistry have physiological repercussions for many marine organisms, particularly those that calcify or photosynthesize (Harvey et al. 2013; Kroeker et al. 2013).

Coralline algae are important foundation species in shallow ecosystems from the tropics to the poles, both forming and cementing reefs, acting as settlement substrates and nurseries for marine invertebrates, and providing coastal sediments (Nelson 2009; Milazzo et al. 2014; Cornwall et al. 2021). However, as calcifying species, they are particularly sensitive to ocean acidification (McCoy and Kamenos 2015; Martin and Hall-Spencer 2017). Earlier laboratory experiments indicated that the complex changes in seawater carbonate chemistry occurring under ocean acidification would impact coralline algae through reduced calcification rates, sizes and/or numbers of recruits, and observations along natural gradients showed that coralline algae decline in abundance as CO_2 levels in seawater rise (Anthony et al. 2008; Hall-Spencer et al. 2008; Jokiel et al. 2008; Kuffner et al. 2008; Martin et al. 2008; Martin and Gattuso 2009). While coralline algae are one of the most sensitive taxa to ocean acidification (Kroeker et al. 2013), there is considerable variability between different species' responses (Peña et al. 2021a). This variability could be related to differences in mineralogy, the ability to regulate favourable carbonate chemistry at the site of calcification, and morphology (e.g. thallus thickness or geniculate versus non-geniculate) (Nash et al. 2013; McCoy and Pfister 2014; Cornwall et al. 2017; Barner et al. 2018). Earlier observations were that ocean acidification could increase mortality through bleaching that could be exacerbated by warming (Anthony et al. 2008; Martin and Gattuso 2009), as well as change the photo-physiology (Borowitzka 1981) or mineralogy of these important foundation species (Ries et al. 2009; Ries 2011).

To more accurately predict the future of reefs where coralline algae play essential ecological roles, the scientific community needs to better understand the drivers of variability in response to ocean acidification caused by phylogeny, geography and physiology. Earlier reviews on the topic (Hurd et al. 2009; Nelson 2009; Hofmann and Bischof 2014; McCoy and Kamenos 2015) provided good starting points for the field of research but were too premature to assess generalisable results properly, the mechanisms responsible, or get accurate estimates of the magnitude of the effects. Thirteen years from the initial burst of publications and 6 years from the last specialised review, we critically re-evaluate the literature. Here, we aim to both collate the knowledge of coralline algal responses to ocean acidification and provide numerical estimates of its effects using meta-analyses and predictive models. The manuscript is split into 1) qualitative review, 2) meta-analyses, 3) projected declines in cover, recruitment and calcification, and 4) coralline algal calcification physiology under ocean acidification and frontiers in future research.

Methods:

Qualitative analysis:

We searched Web of Science with different combinations of coralline algal terms and "ocean acidification". The different coralline algal terms were "coralline algae", "calcifying algae" and "CCA". The list of suitable publications was then cross-checked against the OAICC database on Pangaea and the list used in Kroeker et al. (2013). This search was completed on December 1st, 2020 and resulted in 298 papers (see Table S1). We then compiled the main effects of ocean acidification on the coralline algae from each suitable paper, the main effects of any other assessed driver (e.g. temperature or seasonality), the directionality of the interaction between OA and the other driver (antagonistic, synergistic, additive, or one or both and their interaction are unmeasurable Crain et al. 2008), and which driver was the putative "dominant" driver. We used an approach where four of our author team reviewed the findings of every study to reduce bias and misinterpretation. In some instances, we also assessed each study using an alpha = 0.05, rather than the reduced alpha used in some research as corrections for multiple analyses are not optimal. Concerning the main effects of OA, we classified responses as "net dissolution or complete mortality or lack of recruitment/cover", statistically significant negative, statistically significant parabolic (including both positive and negative parabolic), no measurable effect, statistically significant positive effect. Hereafter, we refer to these scores as dissolution or complete removal, negative, parabolic, no measurable effect, and positive. By dominant driver, we qualitatively refer to the one with the most considerable effect that can assist future decisions regarding experimental design in multi-driver experiments (sensu Boyd et al. 2015; Boyd et al. 2018). We refer to these (usually) environmental factors as "drivers" because their effects did not always manifest in a negative direction. We found 392 responses to OA that could be scored in this manner. Here, we refer to "responses" as all combined treatments in any one experiment per species.

Meta-analysis:

During this process, it became evident that adult calcification/linear extension/growth and juvenile growth/linear extension were the most commonly recorded parameters. Because of their importance as overall indicators of "success" under these OA experiments, we chose to conduct meta-analyses to further explore patterns in these responses. We used the same papers identified above. To obtain the calcification and growth data, we extracted means of calcification rates and their associated error whenever they were listed. When data were not deposited freely online those data were extracted from figures within publications using the software Datathief (http://www.datathief.org).

Seawater carbonate chemistry (pH_T, total alkalinity, dissolved inorganic carbon), salinities, and temperatures were extracted or calculated along with the calcification data in instances where they were not given. Seawater carbonate chemistry was recalculated in some studies where inconsistencies were found between pH scales. Studies using the NBS scale were converted to the total scale using the excel macro CO2Sys (Pierrot et al. 2006). Research examining the effects of ocean acidification were excluded if they did not present standardized measurements of seawater carbonate chemistry that could allow us to determine pHT values (Dickson et al. 2007) accurately. That rarely occurred (Smith and Roth 1979; Borowitzka 1981; Gao et al. 1993). We found a total of 538 calcification rates measured across different seawater pH treatments that we could include in our analysis.

We used the bias-corrected Hedge's g parameter in our assessment. Hedges g was calculated as treatment − control divided by the pooled standard deviation. The bias correction $\left(1-\frac{3}{4(df)-1}\right)$ (Hedges 1981) was used to control for the often-small samples sizes within studies. There were instances where the total alkalinity anomaly was used to measure calcification rates. Because some papers only published light calcification rates, while others also presented dark calcification rates, we excluded all dark calcification measurements in our analyses.

We conducted a meta-analysis in R with the *metafor* package that assessed the effects of decreasing pH relative to the control values designated by the authors of each study. This software used a multivariate mixed-effects linear model (function: *rma.mv*), with the unique observation ID nested within the study ID as random effects. This approach meant that the impacts of any one study with multiple pH levels were controlled for. For moderators, we used relative change in pH_T between the control and treatment within the experiment (ΔpH_T; continuous), the temperature of the experiment (°C; continuous), the duration (in days; continuous), the photosynthetically active radiation level (µmol·photons m^{-2} s^{-1}; continuous), and the taxonomic family of the study organism (categorical: Corallinaceae, Lithothamniaceae, Lithophyllaceae, Mesophyllumaceae, and Sporolithaceae). In terms of carbonate chemistry, we choose ΔpH_T because we considered it to be physiologically more robust than any other seawater carbonate chemistry parameter to test against (Comeau et al. 2018). We additionally tested the model using 'climate' (modified from Nybakken 2001 where we also consider the Mediterranean sea as "warm temperate") with tropical, warm-temperate, cold-temperate and polar, and 'ocean basin' (Atlantic, Pacific and Indian Oceans) as categorical moderators. However, these were subsequently dropped from the model due to their non-significant effects on the model. Our choice of the taxonomic families for the moderator followed the current systematics of coralline algae, with reference to Algaebase (Guiry and Guiry 2021).

Cook's distance (function: *cooks.distance.rma.mv*) was used to test for extreme outliers, using a conservative cut-off threshold of $2\sqrt{((k+1)/(n-k-1))}$. This resulted in a cut-off value of 0.31 for adult responses (removing 12 from 255 observations), and 0.69 for juvenile responses (removing 4 from 57 observations). Studies removed for the adult responses were from Bergstrom et al. 2020 (6), Fine et al. 2016 (1), Ragazzola et al. 2013 (3) and Sordo et al. 2018 (2)), and for the juvenile responses were recorded in Page & Diaz-Pulido 2020 (2), Russell et al. 2011 (1) and Padilla-Gamiño et al. 2016 (1).

Meta-analysis results are presented using bubble plots (function: *regplot.rma*). The results of the multivariate mixed-effects linear model were extrapolated for each of the RCP 2.6, RCP4.5 and RCP8.5 scenarios (function: *predict.rma*) using yearly global mean surface pH_T values from the CanESM2 climate model (Canadian Centre for Climate Modelling and Analysis; CMIP5, ensemble r1i1p1) along with mean values used for the other moderators (temperature, duration, irradiance and taxonomic family).

Proportional responses:

Our initial qualitative review revealed that natural cover of coralline algae along pH/pCO_2 gradients and the percent cover of juvenile coralline algae on recruitment tiles had been measured in consistent ways that could easily be compared between studies. We fitted non-linear models (negative exponential models) for each location individually and pooled the locations together for an overall model. For both the natural cover and juvenile recruitment, non-linear models were deemed to provide a better fit compared to linear models based on lower Akaike information criterion, Bayesian information criterion and estimated standard error of the residuals. We projected estimates of uncertainty (95 % confidence intervals) in coverage for the overall models by bootstrapping the model fits for 1,000 runs.

Qualitative analysis

Table S1 details the findings of all research we could find on coralline algal responses to OA. This table summarises what we consider are the main findings. While individual researchers may argue of the nuances of each study for such a subjective analysis, we used an approach where four of our author team ultimately reviewed the findings of every study to reduce bias and misinterpretation. In some instance, we also assessed each study using an alpha = 0.05, not reduced values used in some research. Arguments of why are beyond this paper, but corrections for multiple analyses are now considered non-optimal. Especially in this case, i.e. hundreds of analyses were conducted by the collective research papers, should these be counted up and corrected for in each study?

Results:

Qualitative analysis of main effects

There were 392 recorded responses of coralline algae to the effects of ocean acidification, within which 108 were responses of calcification/growth. The top 10 most frequently recorded were as follows with numbers of responses in parentheses: photosynthetic rates (40; including 26 with respiration rates), cover (24), Fv/Fm (20), mineralogy (20), chlorophyll *a* content (18), recruitment rates/sizes (16), bleaching/mortality (14), electron transport rates

(ETR; 14), phycobilin contents (11) and pH in the calcifying fluid (pH_{cf}; 9). We focus mostly on these parameters for the remainder of this review and in Figure 1. Five of these response types were negative more often than not (recruitment 94%, calcification rates 75%, cover 71% and pH_{cf} 67%). Bleaching/mortality was negative 50% of the time; however, this response is something visually obvious that was not noted in the majority of laboratory studies. Therefore, the proportion of times it truly would have been significantly negative is extremely low (< 5%). Negative effects of OA on Fv/Fm, mineralogy (classified as decrease in Mg content or increase in aragonite content), photosynthetic rates, chlorophyll *a* content, ETR and respiration occurred 30% or less in occasions where they were recorded. Positive responses of photosynthetic rates (15%) and ETR (14%) occurred more frequently for these top ten measured metrics than any others. Parabolic responses were noted in 21 responses from all measured 392 responses (i.e. 5% of times).

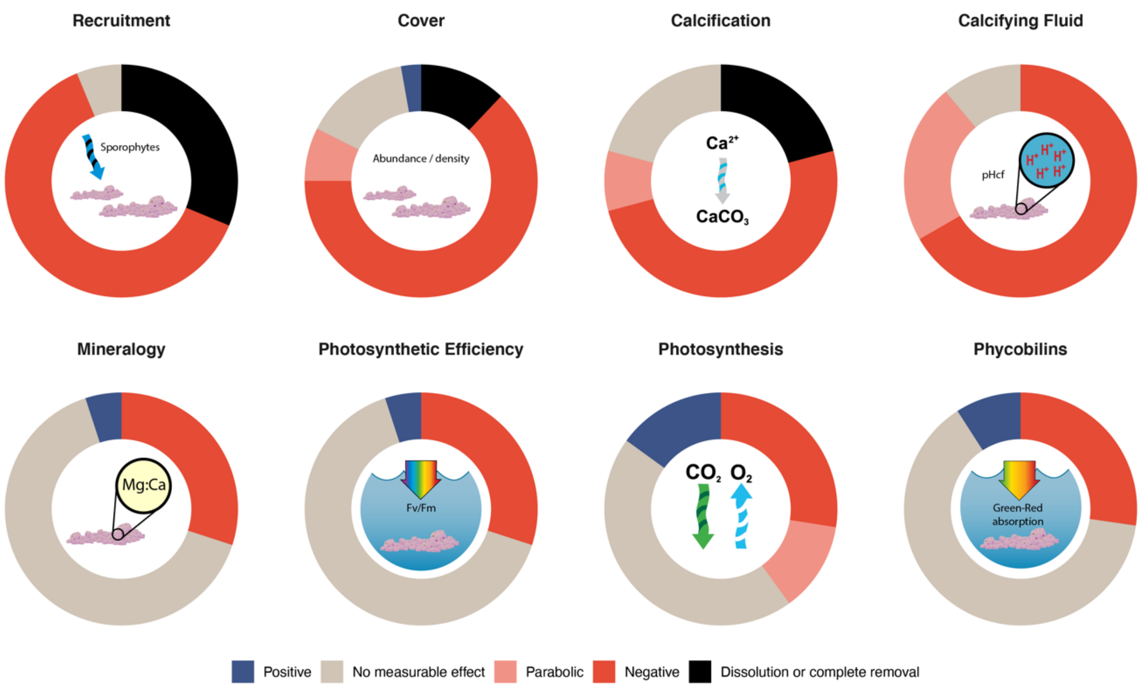

Figure 1: Effects of OA on coralline algae recorded in the literature, with the eight most negatively affected response parameters shown here for those parameters that were measured at least nine times. Responses are described as either ‘positive’, ‘no measurable effect’, ‘parabolic’, ‘negative’ or ‘dissolution or complete removal’, see methods for more details.

Dominant driver

Seasonality was the dominant driver more times than any other (67%: Figure 2). OA was the next, being the putative dominant driver 37% of occasions, then light quality/quantity (27%), temperature (23%), epiphyte/turf presence (22%), and past pH history of the coralline algae (17%). Water velocity, pH variability, herbivory/grazing and nutrients were never dominant.

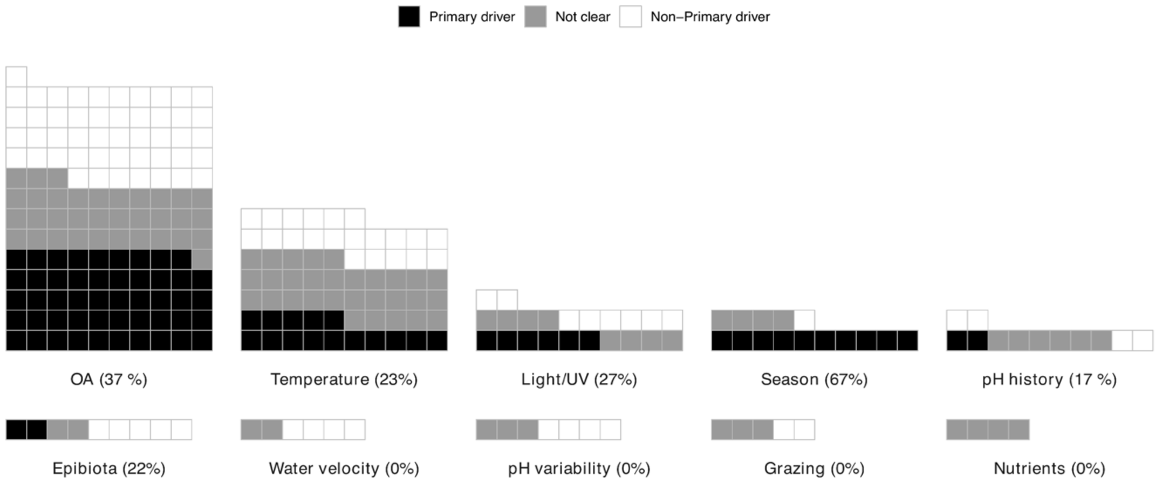

Figure 2: Number and proportion of times different drivers were assessed in combination with OA or another driver in 3+ factorial approaches. In parentheses are the percentage of times the driver was dominant. See methods for the definition of dominant.

Interaction types

Here we split the interactions by the measured response type (e.g. calcification rates, etc.) and the driver that was tested. We report response types that were measured in multi-driver experiments 10 or more times. Photosynthetic rates had the highest number of "non-surprising" interactions (additive or unmeasurable main effects and interactions; 87%), followed by Fv/Fm (83%), calcification rates (72%) and respiration rates (60%). There was a total of 21 antagonistic and 18 synergistic response from 153 recorded, 14% and 12% respectively.

There were clear patterns in the driver types that more often resulted in these antagonist and synergistic interactions. These were mostly drivers that can alter the pH at the surface of coralline algae or their photo-physiology: epiphyte/turf presence (50% of antagonistic + synergist interactions), light (45%) and water velocity (40%). Season (33%) and temperature (27%) also had some antagonistic or synergistic interactions. Interactions with pH variability, nutrients, herbivory and past pH history did not result in synergistic or antagonistic effects.

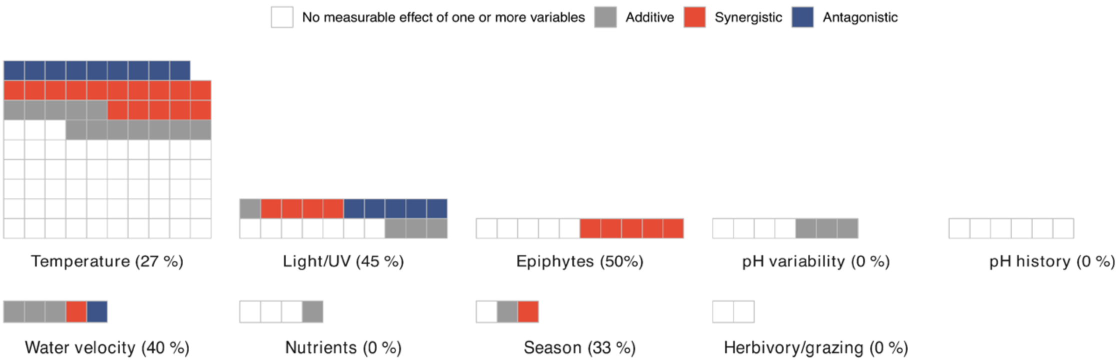

Figure 3: Number of different interaction types between OA and other drivers within coralline algal OA research. The proportion of synergistic and antagonistic interactions is indicated within parentheses. Note here we define "no measurable effect of one or more variables" as being separate from "additive", with the former being occasions where one or both drivers have no measurable effect in either direction, and the addition of the other driver does not change the effect of OA.

Proportional effects

Field cover and recruitment rates

There were large reductions in coralline algae cover as pH declined, with the non-linear model predicting that relative coverage may drop to ~ 15 % (2 – 27, 95 % CI) of their associated reference/control site(s) once pH_T declines below -0.4, and continue to approach towards zero covers (Figure 4a). Recruitment cover demonstrated a similar decline as pH is reduced, albeit less steeply, with ~ 21 % (11 – 32, 95 % CI) compared to the reference/control site(s) at a pH_T decline of -0.4 (Figure 4b).

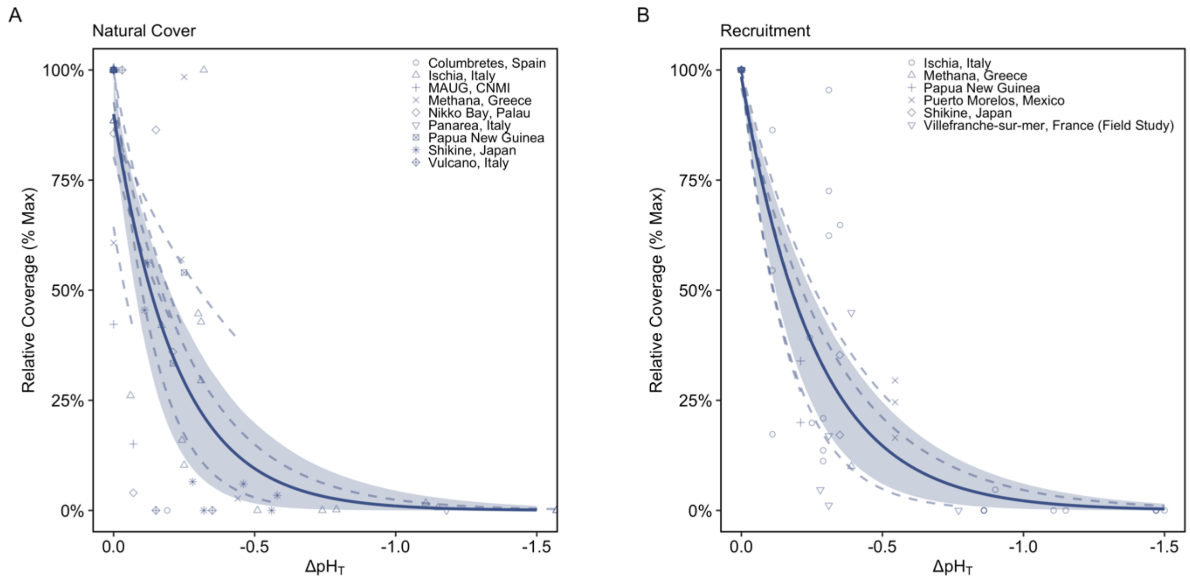

Figure 4: A) Relative cover change (%) of coralline algae at reduced pH sites in the field compared to nearby control sites. B) Relative coverage (%) of coralline algal recruits on settlement tiles at reduced pH locations compared to nearby controls.

Meta-analysis

ΔpH_T had a significant relationship with calcification in the multivariate meta-analysis model for adult coralline algae (Fig. 5), indicating that as pH_T is reduced, the negative impact on calcification may become greater. Based on the model, after a threshold of −0.062 ΔpH_T (at Hedge's g: −0.53 ± 0.53 95% CI), adult coralline algae had their calcification significantly reduced, reaching (for example) effect size of −1.68 ± 0.36 (95 % CI) at −0.4 ΔpH_T (where the effect size of Hedge's is deemed to be a 'large effect' at 0.8). Some phylogenetic differences were found within the adult coralline algae responses, where those coralline algae from the family Mesophyllumaceae had a significantly different slope than the other families (Table S2, S1).

There were fewer responses available in the literature for juvenile coralline algae, and those that were available assessed growth/calcification over a smaller range of ΔpH_T, which likely led to no significant effect of ΔpH_T on the model outcome (Table S3, Fig. S2). Although the calcification response did not significantly change with ΔpH_T, the observations themselves were still almost entirely negative; for example, at −0.4 ΔpH_T an effect size of

−1.79 ± 0.57 (95 % CI) was observed, indicating a significant and large negative effect on the calcification of juvenile coralline algae. In addition, there was a significant difference between the responses of juveniles from both families Lithophyllaceae and Corallinaceae compared to other families. This is likely simply because there is sufficient statistical power to assess differences between these two families but not enough data for the others.

When considering our analysis in the context of the RCP scenarios, we found the effects of altered seawater pH were highly dependent on the RCP scenario being considered. For the subtle effects of seawater pH under conditions representing RCP2.6, we predict non-significant declines in adult calcification by 2100 compared to the present-day (Figure 6). We also predict significant declines in calcification under RCP4.5 and 8.5 by 2100 compared to present-day, with calcification rates declining drastically in the RCP8.5 scenario as this scenario deviates from RCP4.5 around the year 2040 (Figure 6).

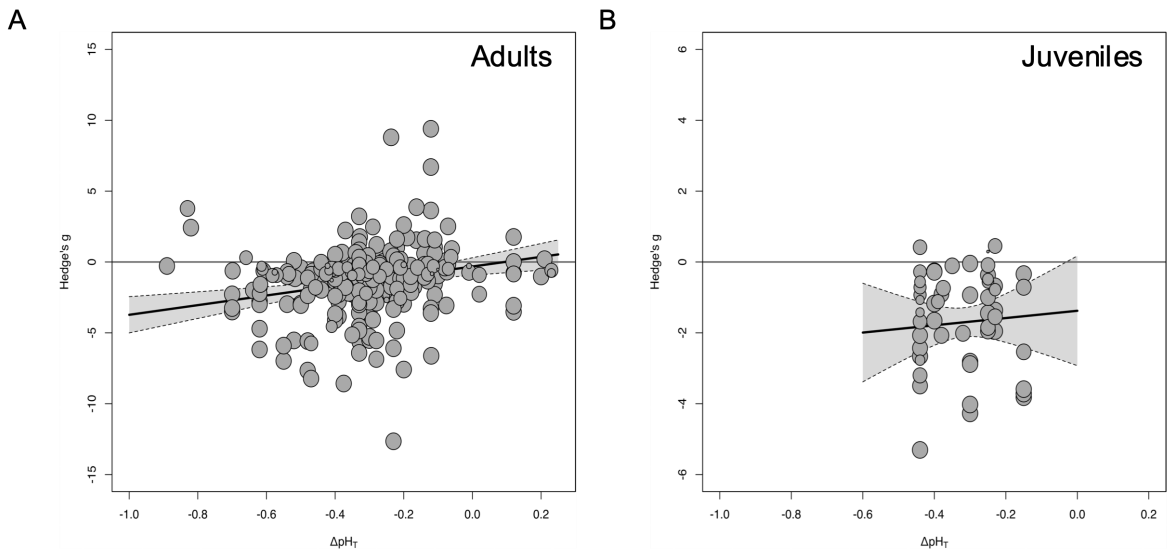

Figure 5: (A and B) – Bubble plots for adults and juveniles, respectively, showing how the effect size on calcification changes with ΔpHT (while still considering the other predictors). The size of the points indicates the weighting, and the dashed line indicates 95% CI.

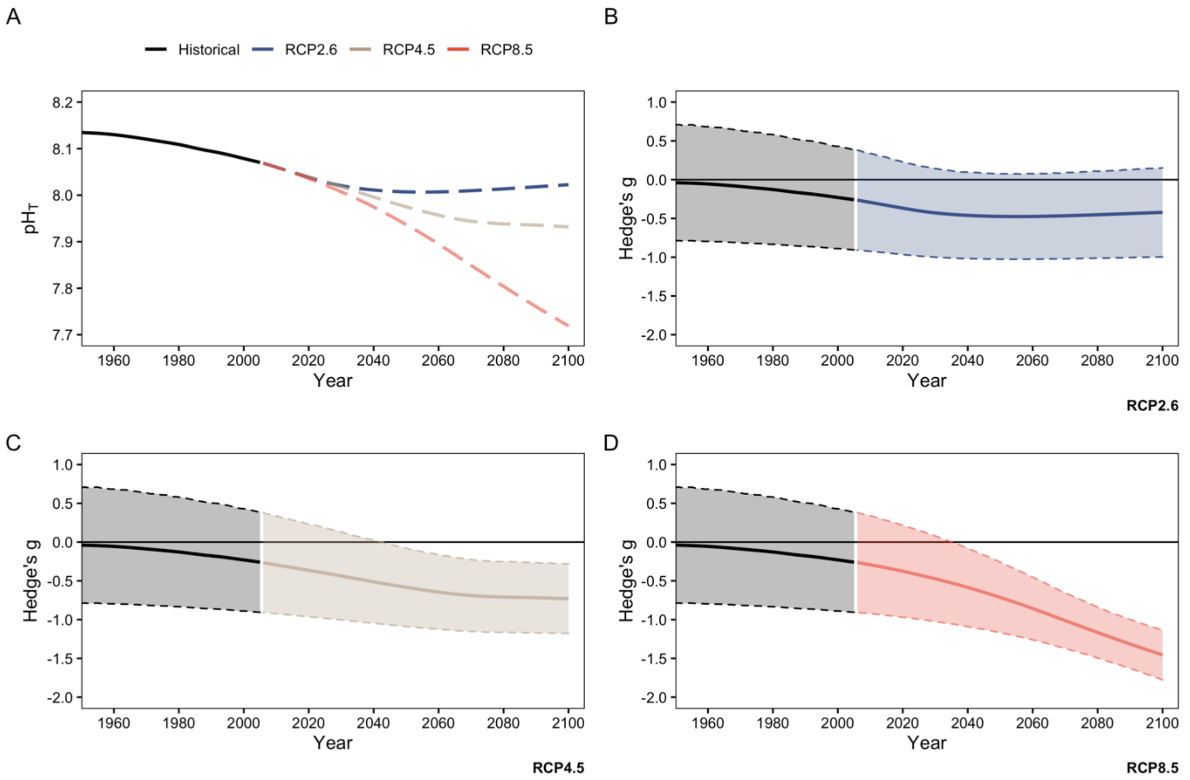

Figure 6: (A) Predicted global mean pH$_T$ level historically, and projected for RCP2.6, 4.5 and 8.5 scenarios up to the year 2100 using the CanESM2 climate model. (B – D) The mean effect size ± 95% CI for adults at the predicted global mean pH$_T$ level historically, and for RCP2.6 (B), 4.5 (C) and 8.5 (D) scenarios up to the year 2100.

Discussion:

We demonstrate here that OA is a major threat to the persistence of coralline algae in the future using multiple lines of evidence. Early studies that reported severe declines in coralline algal cover and recruitment at high CO_2 sites (Hall-Spencer et al. 2008; Martin et al. 2008; Fabricius et al. 2011), and declines in calcification and recruitment (Anthony et al. 2008; Jokiel et al. 2008; Kuffner et al. 2008; Martin and Gattuso 2009; Russell et al. 2009) have been fully corroborated by a host of research demonstrating that such effects are the norm, rather than the exception. Though not explicitly tested, no such "decline effect" (Clements et al. 2020), as has been purported in other taxa, was found here. Indeed, the studies that showed the larger effect sizes, were some of the most recent (Barner et al. 2018; Sordo et al. 2018; Qui-Minet et al. 2019; Bergstrom et al. 2020). Declines in calcification, recruitment, coralline cover at naturally high CO_2 analogues (and less commonly, pH within the calcification fluid (pH_{cf})) were the norm, rather than the exception across all published literature.

Despite consistent responses of many of these vital ecological and physiological processes, some other physiological processes had inconsistent responses to OA. By understanding such distinctions, we can better assess how coralline algal communities are likely to be altered by future climate change. For example, some Authors showed that OA would cause widespread coralline algal mortality due to bleaching and declines in pigment concentrations and decreases in photosynthetic rates or DIC uptake (Anthony et al. 2008; Martin and Gattuso 2009). These results led to speculation that OA could cause similarly catastrophic impacts for coralline algal dominated reefs as the increased temperature does for corals. Fortunately, we find little evidence for this. However, the declines in calcification observed here still threaten the ability of coralline algae to perform vital ecological services, such as providing settlement substrata or building and cementing biogenic reefs (Cornwall et al. 2021). Additionally, we find inconsistent evidence for other benefits to photosynthesis, photo-physiology or DIC uptake that earlier studies proposed (Cornwall et al. 2012), or changes in mineralogy that could either benefit or impair their physiology (Ries 2011; Diaz-Pulido et al. 2014). That highlights the importance of pooling studies for reanalysis to refine hypotheses. Conversely, it was clear that OA usually impacts pH_{cf} of the coralline algae (e.g. Cornwall et al. 2017; Donald et al. 2017), though other elemental or geochemical differences were unclear. Irrespective of their findings, these earlier studies collectively led and developed the field of coralline algal responses to OA, allowing the current synthesis of the results.

The relative importance of global and local drivers in determining ecological change is highly dependent on the taxa being assessed. For corallines, OA was the dominant driver more often than any other local or global stressor it was assessed against, with seasonality being the only driver that was dominant more often. Despite the sensitivity of many taxa to changes in seawater temperature, it was rarely the clear dominant driver of coralline algal responses. This observation supports recent work questioning the relative importance of temperature on coralline algal physiology, compared to more temperature-sensitive organisms such as corals or kelps (Cornwall et al. 2019; Anton et al. 2020). The combined effects of ocean warming and OA are better constrained in the literature than the role of other drivers. However, there is still very little known regarding its impacts (Cornwall et al. 2019), and it should be noted that multiple responses recorded here were from the same study (e.g. multiple species or multiple response metrics). While 15 "responses" were recorded where temperature played a dominant role, 6 of these were recorded from the same study (Vásquez-Elizondo and Enríquez 2016). Conversely, there is little understanding of how marine heatwaves will impact coralline algae, and these would be expected to have much greater impacts than slow ongoing ocean warming that was often simulated in most research we assessed here, for example that possessed treatments that were simply 2 or 3 degrees above a control seawater. Likewise, the role of light was often complex and only sometimes (6/22) played a dominant role in determining the physiological state of the coralline algae. It is more difficult to synthesise the effects of light quality and quantity into a single category to assess their role as dominant or not. Exposure to differing spectra or total PAR daily doses (either too low or too high) within the realms of that experienced at any one collection site could elicit stronger responses than changes in light. Multi-stressor experiments need to carefully choose stress levels and combinations to obtain the most informative results (Boyd et al. 2018).

Here we found that environmental/ecological factors that were most likely to elicit antagonistic or synergistic effects were those that impacted either photo-physiology or pH at the surface of coralline algae. A possible reason for that may be that the pH experienced by the organism is more important than that of the bulk seawater. At the surface of most photoautotrophs, pH is set by the thickness of the diffusion boundary layer (DBL: a region of seawater where the movement of dissolved substances is primarily by molecular diffusion). The theoretical maximum of the DBL is set by water velocity near the organism, and this near-surface velocity would be reduced by the presence of any epiphytes or canopy-forming species above the coralline algae, hence increasing pH gradients (Cornwall et al. 2015). The pH achieved within the DBL will be dependent on the rate of metabolic activity within it (e.g. photosynthesis or respiration) and the DBL thickness. Therefore, it is not surprising that drivers that modify pH within the DBL (light, epiphytes, and water velocity) often nullify the impacts of OA (Cornwall et al. 2014; Guy-Haim et al. 2020), although not always when nutrient concentrations are low (Comeau et al. 2014; Comeau et al. 2019b). However, the mechanisms responsible for the antagonistic roles of season and temperature are harder to disentangle. Indeed, interpreting many of the seasonal impacts on coralline algae were difficult during the process of constructing Table S1, especially when additional factors such as temperature and light were either modified at each season or tested interactively (e.g. Qui-Minet et al. 2018; Legrand et al. 2019; Qui-Minet et al. 2019).

Changes to the ecological role of coralline algae in a future low pH/high CO_2 ocean is uncertain; we demonstrate their ability to calcify, recruit and persist in abundances similar to those today are impacted by OA. We also demonstrate that their calcification rates will depart significantly from that of today's as OA intensifies. The effects noted in our qualitative analysis are mostly linear, with few parabolic or rapid "tipping point" type responses. Our meta-analyses indicate that under RCP8.5 they might be particularly severely impacted, highlighting the urgent need to reduce our CO_2 emissions to allow these critical species continuing their role as reef accrete and preferred settlement substrate for many invertebrate species (Fabricius et al. 2017). Surface seawater pH has been declining since the industrial revolution, meaning that the impacts of OA have likely already manifested in some way across global oceans (McCoy and Pfister 2014), and this is supported by comparing sites with naturally low, pre-industrial levels of seawater CO_2 (Agostini et al. 2018). Select coralline algae can acclimatise over multiple generations to completely resist the effects of OA (Cornwall et al. 2020; Moore et al. 2021). However, whether all species can respond similarly, if the presence of rapidly growing competitors reduces this ability, or whether there are trade-offs in genetic diversity that occur in these populations remains unknown.

The negative effects on calcification manifest across all major oceans and across the range from tropical to polar climates. Specific phylogenies appeared more robust than others, particularly the adult Mesophyllumaceae. A scientific effort in monitoring the abundance or ecology of coralline algae beyond simply acknowledging their collective presence or absence is lacking. That is hindered by the only recent understanding that coralline algae diversity is greater than previously believed (Gabrielson et al. 2018; Twist et al. 2019; Peña et al. 2021b), and extends far beyond the previous mostly morphological groupings and has important implications for much of the previous work in this field (Twist et al. 2020). Recent molecular work shows that some groups of coralline algae are more vulnerable to OA than others and that the projected adverse effects on coralline algal biodiversity have been greatly underestimated (Peña et al. 2021a). Likely changes in species abundances, competitive hierarchies, and physiologies (McCoy and Pfister 2014; McCoy and Ragazzola 2014) before the advent of molecular technology make it challenging to establish a baseline abundance for most coralline algae. Future research should focus on pairing physiological and molecular identifications wherever possible.

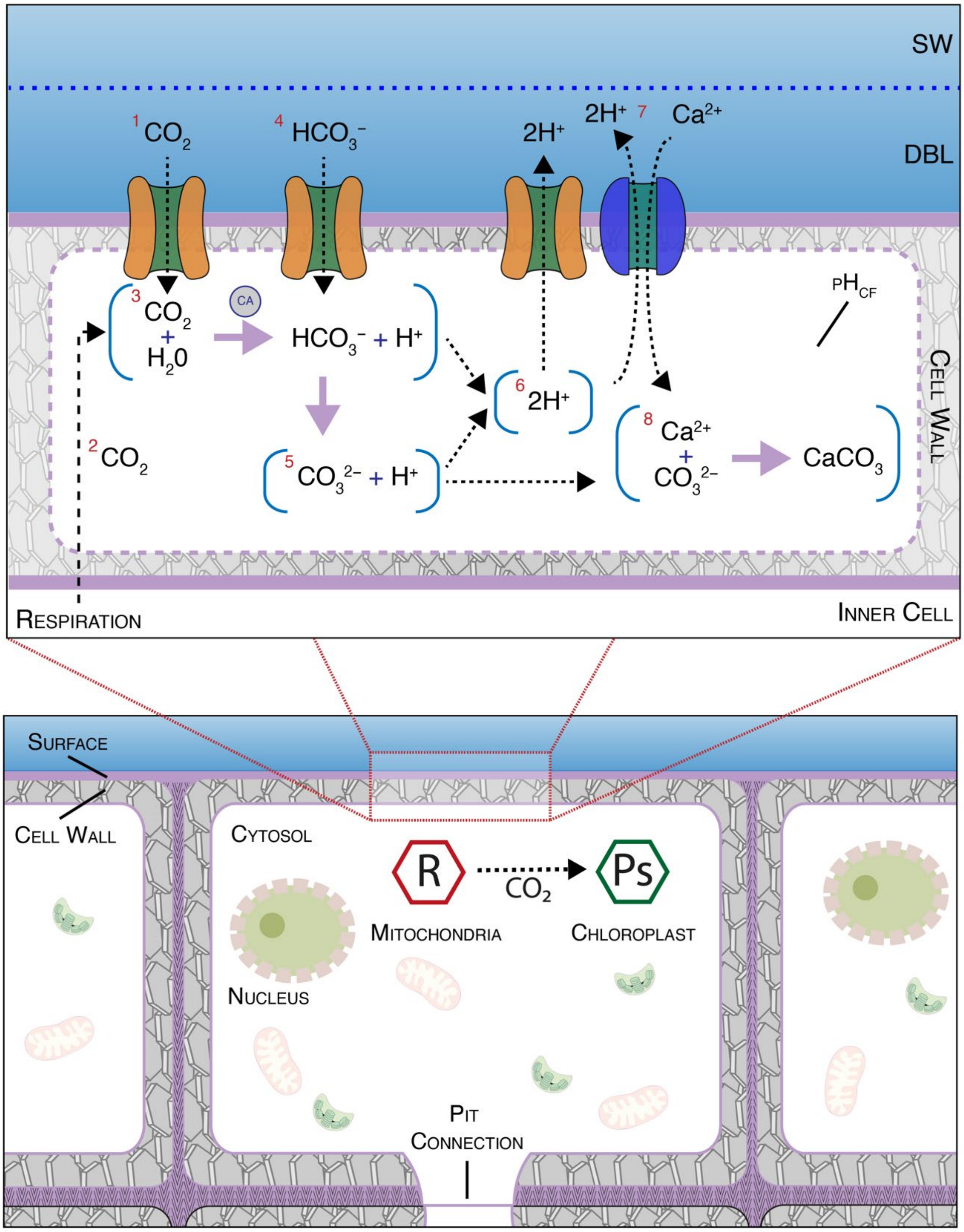

Figure 7: Schematic showing movement of dissolved substances in and out of coralline algal cells. This gives an overview of the processes that could be affected by ocean acidification, it is not intended to describe the full calcification process. In some taxa there can be multiple cells between seawater and the site of calcification hereafter "Calcifying fluid = CF". Provision of photosynthesis by 1) movement of CO_2 (or external carbonic anhydrase mediated conversion of HCO_3^- to CO_2) across aquaporins or through seawater entering the

cell wall and 2) produced during respiration. 3) The reaction from CO_2 to HCO_3^- will be catalysed by internal carbonic anhydrase to some extent within the cell, while 4) active transport of incoming HCO_3^- will occur via CO_2 concentrating mechanisms involving influx or efflux to balance the charge (not shown). 6) Increasing pH_{cf} will be due to proton pumps or 7) Ca^{2+} ATPases or other mechanisms of H^+ efflux. 8) Elevated saturation state of $CaCO_3$ will increase precipitation rates within the calcifying fluid pockets.

The physiology of coralline algae is poorly understood, hindering our ability to interpret many of the observed responses to seawater carbonate chemistry. Their calcification is impacted by declining seawater pH via both increased dissolution rates and an inhibition in the precipitation of calcium carbonate. The amount of dead exposed skeletal material within any experiment would therefore strongly influence the rate of dissolution, further impairing our ability to compare experimental results. After decades of models based on eco-physiology, scanning electron microscope images, and some carbon isotope work, new models and techniques have emerged. These have allowed us to determine that calcification in coralline algae is highly controlled by the organism, while at the same time is still dictated by environmental conditions. Recent models have demonstrated that control within the site of calcification, likely µm or smaller sized pockets of instantaneous fluid that we term the "calcifying fluid" (CF), is strongly influenced by ocean acidification. The $\delta^{11}B$ of calcium carbonate tracks the pH of the solution in which it is formed (Klochko et al. 2006). For coralline algal calcite, experimental work has demonstrated that this proxy tracks pH within the CF, finding that it is highly upregulated, beyond what is possible simply due to photosynthetic activity, in the majority (but not all) of the species measured to date (Cornwall et al. 2017; Donald et al. 2017; Cornwall et al. 2018; Anagnostou et al. 2019; Comeau et al. 2019a; Comeau et al. 2019b). Importantly, the species-specific magnitude of its decline under simulated ocean acidification is linked with a greater capacity for calcification to resist ocean acidification for some species (Cornwall et al. 2017). However, it is likely to be more complex than suggested by those initial observations

Both DIC and the saturation state of calcite within CF are likely important factors in the regulation of calcification in coralline algae, even if these have not been measured directly with existing technology. Raman spectroscopy (FWHM) and B/Ca ratios track Ω_{cf} and DIC_{cf} in coral aragonite (Holcomb et al. 2016; DeCarlo et al. 2017; McCulloch et al.

2017). However, similar calibrations do not exist for coralline algal high Mg calcite. In both corals and coralline algae these parameters are altered by the same environmental factors (pH, DIC, light and water flow) in the same direction (with some species-specific offsets), leading to the more likely scenario that they also represent Ω_{cf} and DIC_{cf} in coralline algal calcite. There have been some suggestions for corals that B/Ca may even represent a differential uptake of boron under changing DIC (Gagnon et al. 2021). However, this would not account for the remarkably similar DIC_{cf} estimated with electrodes (Cai et al. 2016). Overall, these proxies would indicate that coralline algal calcite saturation state and DIC is likely much higher than that of seawater. This would rule out photosynthetic control over carbonate chemistry within the CF, even if DIC was slightly higher than that of seawater, as DIC would be expected to decrease under higher photosynthetic rates. However, that is not to say that higher photosynthetic rates would not further elevate pH_{cf} or Ω_{cf} if this was in concert with increased pumping of H^+/Ca^{2+} due to increasing energy. This potential Ω_{cf} remains invariant under many conditions, though it is influenced by Mg content and should be adjusted accordingly (Perrin et al. 2016). There are, however, two conditions in which it is altered. Like in corals, it appears that very rapid calcification is associated with lower Ω_{cf} values for some fast growing juveniles (Cornwall et al. 2020); which could be associated with the drawdown of Ca^{2+} and would slow the precipitation of calcium carbonate when combined with lower pH_{cf} under OA. Conversely, this could also represent changes in Ω_{cf} driven by an inability to adequately regulate a combination of DIC_{cf} and pH_{cf}. Ω_{cf} declined in *Neogoniolithon* sp. (but not *Sporolithon durum*) when seawater DIC was reduced experimentally (Comeau et al. 2018). Interestingly, *S. durum* pH_{cf} increased and DIC_{cf} declined in response to the same conditions, with pH_{cf} declining and DIC_{cf} increasing under lower seawater pH, but with no effect on *Neogoniolithon* sp. Low light can reduce Ω_{cf} (Comeau et al. 2019b), likely due to a reduced ability to pump Ca^{2+}, as pH_{cf} and DIC_{cf} remain constant under low light. Further species-specific investigations are required, especially those that assess apparent phylogenetic differences in calcification modes (Auer and Piller 2020) with differential responses of CF chemistry. Though previously identified morphological differences in calcification modes (Auer and Piller 2020) did not match more resistant or suspectable taxa here, it could reveal important information if indeed crystal orientation does impact the CF chemistry or responses to OA and other abiotic factors.

There are still many fundamental questions left unanswered in understanding the responses of coralline algae to OA. Coralline algal CF chemistry is species-specific and has large uncertainties compared to that of aragonitic corals. While small windows of knowledge have been opened by using these proxies, there is still much work to be done in calibrating B/Ca and FWHM to understand the actual values of DIC_{cf} and Ω_{cf} in coralline algae and how they respond to different environmental drivers, particularly OA. Taxonomic variation in responses, and its influence on other factors that we explored here can only be guessed at currently with the existing issues of non-molecular identification in the majority of studies included here (Twist et al. 2020). Better integration of molecular work while assessing their response to OA is needed in the laboratory. How this can be implemented in field settings such as natural CO_2 vents is a more difficult consideration. If plans can be implemented to include molecular identification in CO_2 vent work, this will go a large way in disentangling which species are tolerant there, as has been recently completed at two CO_2 seep sites (Peña et al. 2021a). Additionally, the next steps are to combine "omics" tools with physiological and geochemical tools to better determine the mechanisms responsible for individual species tolerance to OA, and how and why these tolerances can change over multiple lifetimes in some coralline algae (Cornwall et al. 2020). Here, we do not attempt to fully discuss calcification mechanisms, but future inclusions of emerging techniques with morphological knowledge (e.g. Auer and Piller 2020) will also further our ability to understand taxa-specific responses. Only by not ignoring all available information will progress be made in better predicting the future of ecosystems in which coralline algae act as important foundation species.

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