ICES Journal of Marine Science, 2025, Vol. 82, Issue 4, fsaf050
https://doi.org/10.1093/icesjms/fsaf050
Received: 17 February 2025; **revised:** 26 March 2025; **accepted:** 27 March 2025
Food for Thought

ICES
CIEM
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

Corals in ocean acidification and the role of calcium ion homeostasis to maintain calcification

David A. Armstrong* and Keisha D. Bahr

Harte Research Institute, Texas A&M University-Corpus Christi, Corpus Christi, TX, 78412, USA

*Corresponding author. David A. Armstrong, Harte Research Institute, Texas A&M-Corpus Christi, 6300 Ocean Drive Unit 5869, Corpus Christi, TX, 78412, USA, E-mail: david.alexander.armstrong04@gmail.com

Abstract

Coral calcification is essential to provide the structural foundation for coral reefs and is integral in supporting marine biodiversity reliant on reef ecosystems. The drivers for calcification in corals are undoubtedly highly complex and require several perspectives to identify vulnerabilities in the context of environmental change. Specifically, ocean acidification (OA) resulting from the rise of anthropogenic carbon dioxide (CO_2) emissions poses a potential threat to the physiological mechanisms that drive calcification in corals. Therefore, this report goes beyond environmental seawater chemistry to examine the physiological mechanism of calcium ion homeostasis. Calcium's role in calcification physiology is well established, but how calcium homeostasis could shift under acidification has little been considered a significant driver in reduced calcification. Calcium is potentially the most actively transported substrate in coral calcification, though in high chemical abundance in seawater, corals are likely utilizing the most energy to concentrate calcium at the site of calcification. We argue for increased consideration of the calcium ion in the context of OA when identifying sensitivities. The concepts proposed here are justified through a combination of results from novel RAMAN spectroscopy and molecular work that provides insight into shifts in calcium homeostasis when exposed to acidification. We speculate that future work incorporating methodologies considering calcium dynamics in OA could benefit by narrowing in on what physiological mechanisms are potentially vulnerable. It is imperative that we identify what drives lower calcification in corals under OA to inform efficient directives in identifying species sensitivities to future climate change.

Keywords: coral reef; calcium carbonate; aragonite saturation state (Ω); pCO_2; climate change; organismal physiology

Environmental perspective on tropical coral calcification

Colonial corals are animals that provide the primary structural framework for coral reefs, which support some of the world's most productive and diverse communities (Smith 1978, Hoegh-Guldberg 2011, Al-Horani 2015). The biogenic growth process of synthesizing calcium carbonate ($CaCO_3$), termed calcification, is fundamental to this framework, and without it we could see rapid declines in reef building corals ability to support marine communities through their structures (Hoegh-Guldberg et al. 2007, Graham and Nash 2013, Bahr et al. 2016, Jokiel 2016). Corals and coral reefs will face global ocean change, including ocean warming and acidification, in the future as atmospheric carbon dioxide (CO_2) increases, threatening the existence of reefs worldwide (Kleypas et al. 1999, Caldeira and Wickett 2003, Sabine et al. 2004, Jokiel 2016). Predictions for the years 2081–2100 show that pH levels are *virtually certain* to decrease by 0.28–0.29 pH units (RCP8.5) and *very likely* to warm 2–4 times (low emission RCP2.6; IPCC 2022). There has been growing interest in understanding how lowered pH will impact biological functions, with 1500 documented publications in marine taxa between 2008 and 2023 (OA-ICC 2023). Specifically for coral growth, calcification responses broadly vary and currently range from +45% to −100% relative to ambient conditions in tropical corals (Reynaud et al. 2003, Langdon and Atkinson 2005, Andersson and Mackenzie 2012, Chan and Connolly 2013). Global net ecosystem calcification due to lowered pH was predicted to decline on average between 14% and 30% (Kleypas et al. 1999, Chan and Connolly 2013). Ocean acidification (OA) will not be the sole driver for coral reef declines in the future (Klein et al. 2024). However, experimental work in OA allows us to tease apart the physiological burden of maintaining calcification in chemically stressful but sublethal conditions. This is particularly valuable for understanding the mechanisms behind calcification and creating a baseline to apply toward future interactive stressors.

Coral calcification is a function of precipitating $CaCO_3$ and thus requires both calcium (Ca^{2+}) and dissolved inorganic carbon (DIC; i.e. CO_2, HCO_3^-, and CO_3^{2-}). Initially, the conventional theory used to connect the seawater environment's interactions with the drivers of calcification is the utilization of aragonite saturation state (Ω_{arag}) values (Kleypas et al. 1999, Marubini et al. 2001, Langdon and Atkinson 2005, Castillo Alvarez et al. 2024).

$$\Omega_{arag} = \left[Ca^{2+}\right]\left[CO_3{}^{2-}\right]/K_{sp}. \qquad (1)$$

Equation 1 shows concentrations of calcium and carbonate ($[Ca^{2+}]$ and $[CO_3{}^{2-}]$, respectively) and K_{sp} as the solubility constant of aragonite (Dickson et al. 2007). Aragonite is a polymorph of $CaCO_3$ primarily used by corals, which has distinct constants and chemical behaviors in seawater compared to other polymorphs found in calcifying organisms (Dickson et al. 2007). In the context of OA, the Ω_{arag} parameter decreases as a function of carbonate ion concentrations, resulting in a hypothesized substrate limitation of calcification

(Langdon and Atkinson 2005, Castillo Alvarez et al. 2024). However, in the present day, this theory has been confounded by reports identifying the Ω_{arag} parameter as dependent on processes such as calcification and production, not the inverse (Jokiel et al. 2014, DeCarlo et al. 2017a, Davis et al. 2021). Expanding on the influence of seawater chemistry, some studies suggest that bicarbonate ion concentrations ($[HCO_3^-]$) drive calcification sensitivity in corals (Jury et al. 2010, Bach 2015). However, molecular research indicates that corals possess only physiological pathways for HCO_3^- ion transporters (Zoccola et al. 2004), challenging the CO_3^{2-} based perspective. Furthermore, Bach et al. (2015) and Jokiel (2016) also present the seawater ratios of bicarbonate or dissolved inorganic carbon to protons ($[HCO_3^-]$ or [DIC]: $[H]^+$) as having greater explanatory power compared to Ω_{arag} under OA. Lastly, it has been discussed that net ecosystem marine heterotrophy and productivity could drive net ecosystem calcification independent of pH or Ω_{arag} and thus the ratios of inorganic carbon to protons (Kealoha et al. 2019). Therefore, this report goes beyond environmental seawater chemistry to examine the physiological mechanisms that drive calcification in corals (Chan and Connolly 2013).

To expand our perspective on calcification in a future acidified ocean, our objective is to propose the factor of calcium ion dynamics as a potential driver for reduced calcification in corals. Specifically, when exposed to low pH, little focus has been put on the calcium ion's role in calcification's response to acidification (DeCarlo et al. 2018). We acknowledge that OA does not chemically limit the calcium ion concentration in seawater. Therefore, our stance is derived purely from a physiological perspective. We are confident of calcium ion's direct importance to calcification through foundational studies manipulating seawater availability (Gattuso 1998) and within coral tissues (Marshall 1996, Tambutté et al. 1996). However, if the physiological burden of maintaining calcium homeostasis is too steep, then calcification in corals could suffer. Therefore, we argue that the physiological dynamics of calcium flux should be further examined under changing ocean chemistry and considered as a potential driver of lower calcification in corals.

What is physiologically driving calcification?

Calcification occurs when calcium combines with dissolved inorganic carbon (i.e. $CO_2(aq)$, HCO_3^-, or CO_3^{2-} as DIC), synthesizing $CaCO_3$ and two protons (H^+) in excess (Jokiel 2011a, 2011b, 2016).

$$Ca^{2+}+DIC \rightleftarrows CaCO_3+2H^+. \qquad (2)$$

Jokiel (2011a) proposed the boundary layer limitation—proton flux model, arguing for increased representation of calcification rates away from Ω_{arag} (i.e. ratios of DIC to H^+; Bach 2015). Ocean acidification causes the hydrogen ion concentration ($[H^+]$) to increase (decreasing pH) and thus could increase the diffusive gradient following Fick's First Law of diffusion on the flux of protons (Eq. 2; Jokiel et al. 2014, Jokiel 2016). Protons would act as calcification inhibitors. In support of proton flux, aspects in Comeau et al. (2019) and Venn et al. (2022) show that the boundary layer's pH correlates with the extracellular calcifying fluid's (ECF) pH and shows a reduction in interstitial pH under OA. It is worth noting, however, that the calcifying fluid's pH does not always explain reduced calcification under OA, resulting in a heterogeneity of responses across species (Comeau et al. 2019). However, other contributions to the variation of calcification responses have been shown i.e. life stages (Albright and Langdon 2011), growth rate (Comeau et al. 2014), methodology (Chan and Connolly 2013), and heterotrophy (Kealoha et al. 2019). Despite these influences, aragonite crystal nucleation in tropical corals occurs within the ECF, where the chemical environment facilitates coral skeleton precipitation (Allemand et al. 2011, Al-Horani 2015).

The ECF is mainly isolated from the external seawater and thus relies greatly on biological regulation to support calcification (Allemand et al. 2004, 2011). This biological regulation consists of ion transporters, such as those that concentrate calcium and bicarbonate (Marshall 1996, Allemand et al. 2011, Hohn and Merico 2015, Reymond and Hohn 2021) and/or export protons (Allemand et al. 2011). This regulation is usually energy-dependent, supported by metabolism from heterotrophy or photosynthesis (Allemand et al. 2011). Hohn and Merico (2015) modeled physiological ion-flux energy budgets for calcification in detail. However, briefly, the most likely pathway for all ion flux (transcellular and paracellular as "H4") requires a positive energy budget of 0.676 mol ATP (mol $CaCO_3$) to precipitate 1.11 mmol $CaCO_3$ m^{-2} d^{-1}. Where ions transcellularly concentrated are calcium at 1.30 mmol m^{-2} d^{-1} (active or passive), bicarbonate at 0.0001 mmol m^{-2} d^{-1} (active), and CO_2 at 1.26 mmol m^{-2} d^{-1} (passive) along with paracellularly concentrated/transported bicarbonate at 0.0163 mmol m^{-2} d^{-1} (passive). Conversely, transcellularly effluxed are protons at -2.59 mmol m^{-2} d^{-1} (active; Hohn and Merico 2015). Thus, in a substrate comparison, calcium is concentrated transcellularly (active or passive) in the ECF 195.02% greater than bicarbonate and one-to-one with CO_2 (passive; calculated from Hohn and Merico 2015). Leading calcium to be the highest transported substrate in coral calcification, though in high abundance in seawater, corals are likely utilizing the most energy to concentrate calcium at the ECF (Eq. 1). Protons are thus the leading active effluxed material from the ECF, and in concert with calcium regulation, we begin to define the dynamics of energetic maintenence of substrate to waste products in the physiology of coral calcification.

Transcellular active transport requires the hydrolysis of ATP to actively concentrate materials across the diffusion gradient, which is an energetically costly process (Allemand et al. 2011, Al-Horani 2015). Where high-energy budgets exist, disruptions in homeostasis caused by environmental change could impact the energy-dependent physiological pathways. Therefore, calcium (substrate) and proton (waste) regulation in calcification could be the most influential physiological mechanisms for regulating calcification in environmental change. There is growing evidence on the impact of ecological change regarding proton flux (Jokiel 2011a, Bach 2015, Bahr et al. 2018, Comeau et al. 2019, Venn et al. 2022), little work has focused on calcium flux as a function of environmental change, specifically under OA or ocean warming (DeCarlo et al. 2018).

The calcium ion and coral physiology

The quantification of energy budgets for transcellular calcium transport related to calcification by Hohn and Merico (2015) can be supported by studies addressing coral ion transport dynamics. Briefly, transcellular calcium transport occurs via

L-type voltage-gated channel proteins (Marshall 1996, Zoccola and Failla et al. 1999) and plasma membrane Ca^{2+}/H^+ ATPase (PMCA) proteins (Zoccola et al. 2004). The proteins here are essential for concentrating calcium in the ECF, promoting $CaCO_3$ nucleation. In Reymond and Hohn (2021), the ratios of calcium and carbonate (Ca^{2+}:$CO_3{}^{2-}$) were assessed in a mimicked ECF of corals and found a 3x increase in calcification in a high Ca^{2+}:$CO_3{}^{2-}$ (higher [Ca^{2+}]) compared to a low Ca^{2+}:$CO_3{}^{2-}$ (lower [Ca^{2+}]). Indicating greater nucleation of aragonite with a higher concentration of calcium in the ECF specifically (Reymond and Hohn 2021). Conversely, they suggest magnesium removal mechanisms play a significant role in mineralization, though mentioning overall the mechanism for calcium concentration and magnesium removal to explain taxon-specific responses to OA in low Ω_{arag} (Reymond and Hohn 2021). Using an Ussing chamber and studying electrophysical properties in coral ion transport, Taubner et al. (2017) showed tight regulation of the ECF through active ion transport. They concluded that active transport of calcium was required to maintain calcification rates in corals (Taubner et al. 2017). Therefore, the active biological regulation of calcium concentration and proton export at the ECF is essential for calcification in corals.

Focusing on PMCA, calcium concentration and proton export are simultaneous, and it has been shown that pH increases in the ECF along with calcium concentrations (Al-Horani et al. 2003). Though this correlation is not only a function of PMCA (i.e. several other active proteins used in the regulation of ions independently), based on energy conservation, PMCA would be the most efficient mechanism in regulating calcium and protons influencing substrate dynamics and waste products in coral calcification. From a stoichiometric perspective, PMCA consumes ATP at a ratio of 2:4:1 (Ca^{2+}:H^+:ATP, respectively) compared to singularly pumping protons at 4:1 (H^+: ATP respectively; Hohn and Merico 2015). Thus, potentially, being more energetically favorable to utilize PMCA by corals in regulating the ECF rather than separate ion transport mechanisms. Therefore, considering the impact, calcium concentrations in the ECF have on calcification (Reymond and Hohn 2021) and the need for active ion transport of calcium to sustain calcification (Taubner et al. 2017), PMCA is a valuable mechanism for corals to sustain calcification (Al-Horani et al. 2003, Hohn and Merico 2015). This concept is well understood. However, most of the attention PMCA has received as impacted by OA lies in the export of protons from the ECF, not its ability to supply calcium (Jury et al. 2010, Cyronak et al. 2016, Allison et al. 2018). Theoretically, both processes are vulnerable to acidification, as is the entire PMCA enzyme, and potentially shifting the focus to calcium may provide insight into coral sensitivity to calcification.

What we know: ocean acidification and calcium dynamics

OA has been shown to decrease the pH of the immediate environment (defined as the mesoglea) above the cells that carry out ion transport for the ECM, decreasing by 0.58–0.71 pH units relative to ambient conditions (Venn et al. 2022). Thus, essential transport mechanisms, i.e. PMCA and proton pumps responsible for the regulation of the ECF, are exposed to decreased pH from OA. There has been no work on the direct measures of kinetic reaction differences between pH environments in marine invertebrates concerning the two transport mechanisms. However, from a crude biochemical perspective, both transporters (similarly with all enzymes) have optimal pH ranges for reaction efficiency, recently addressed in Bisswanger (2014) and visually represented in Fig. 1 (Allison et al. 2018). All enzymes rely on similar tolerance thresholds, not limited to pH, where temperature also plays a significant role (Bisswanger 2014, Allison et al. 2018).

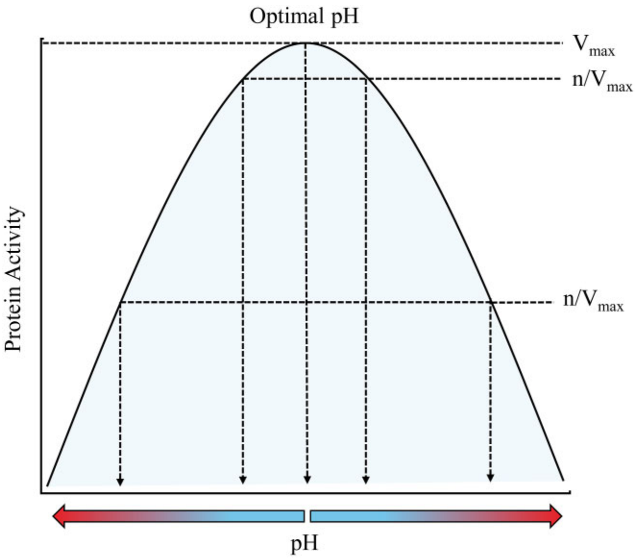

Figure 1. Theoretical schematic of protein function dependent on pH. Where the highest activity (V_{max}) is shown, as pH increases (right) or decreases (left), the resulting V_{max} is a fraction (n) of optimal values (Bisswanger 2014).

The V_{max} of PMCA in marine invertebrates involved in calcification has not been characterized, and we are unaware of the rate limitations (n/V_{max}) imposed by acidification. This assay has also not been done for any calcification supporting ion-transport mechanisms in marine invertebrates. A rate-limiting disequilibrium could disrupt calcium transport and, in concert, proton export from the ECF, potentially impacting calcification in corals. Molecular work that could be used to support this concept was shown recently by Radice et al. (2024), which utilized RNA-seq methodologies to highlight the phenotypic plasticity of corals in an acidified environment. We find results from Radice et al. (2024) extremely valuable as corals were exposed to low seawater pH for ∼2 years *in situ*, compensating for a significant source of variability in *ex-situ* examination. They found significant gene upregulation of P-type calcium ATPases (GO:0 005 388) and the downregulation of genes associated with V-type proton ATPases (GO:0 046 961, GO:0 008 553, GO:0 016 471)—the difference herein being a higher priority of transporting calcium and exporting protons over exporting protons alone (Fig. 2). As discussed, stochiometric energy conservation would favor PMCA over singular proton pumps. However, if proton concentrations were the sole driver for this stress response, we could assume the animal also upregulates or maintains normal expression of proton ATPases (potentially a more efficient/rapid mechanism). We speculate that instead, the observation of downregulation by Radice et al. (2024) could point toward prioritizing calcium, as the major difference between both transporters is the movement of calcium to the ECF. Not only was PMCA upregulated, but

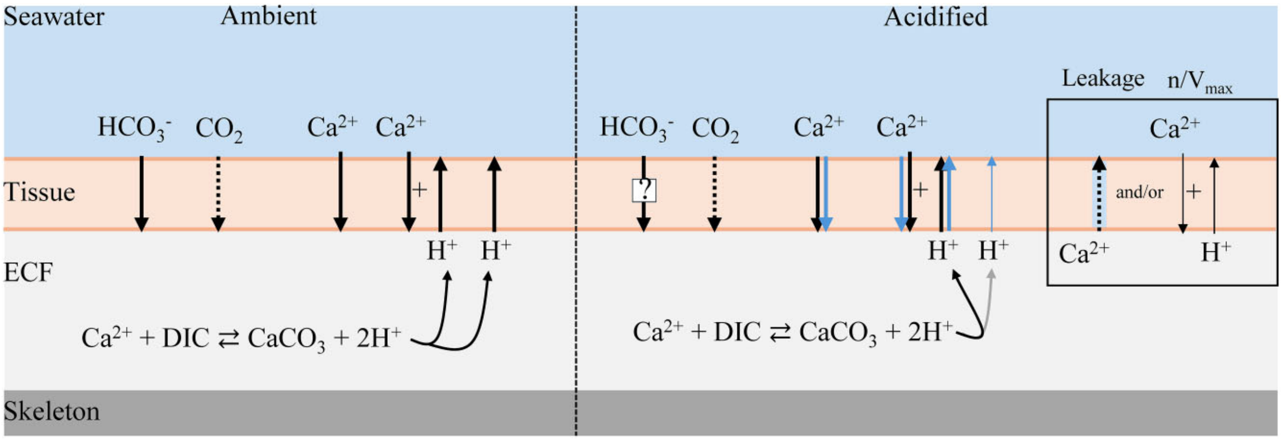

Figure 2. Calcification ion-transport mechanisms in ambient and acidified seawater conditions. Solid arrows are transcellular transport (active or passive), and dashed arrows are transcellular or paracellular passive transport. In ambient seawater, from left to right, HCO_3^- is transported actively across the membrane; however, we are unsure how this is impacted when acidified. CO_2 transport should not be impaired in ambient and acidified seawater. Plasma membrane Ca^{2+} ATPase and Ca^{2+} channel genes were upregulated in acidified conditions compared to ambient. Proton pumps were downregulated when exposed to acidification compared to ambient conditions. Proposed calcium dynamic shifts in acidification are shown in the far right box, with leakage in the ECF (Hohn and Merico 2015) and rate-limited decrease of calcium transport.

calcium channels and exchangers involved in calcium transport were also upregulated (Fig. 2). Responses discussed here were found in Radice et al. (2024), but similar responses to calcium transport were also shown in Yuan et al. (2019), Teixidó et al. (2020), and Scucchia et al. (2021). These data are some of the first high-throughput RNA-seq experiments assessing this level of phenotypic plasticity on corals exposed to OA, where the first was conducted by Moya et al. (2012), and we could learn a great deal more by continuing similar experiments.

Phenotypic plasticity is variable and highly dependent on the species in question, apparent in more comprehensive examinations of marine taxa in OA (Ries et al. 2009, Leung et al. 2022). From a physiological perspective, higher conservation of calcium ATPases by the coral animal could potentially point toward a chemical rate-limited decrease in the V_{max} of these proteins (n/V_{max}), necessary to compensate for and maintain calcification (Figs 1 and 2). Conversely, Radice et al. (2024) found that cell adhesion genes (calcium-dependent) were also disrupted by low pH, supporting the model in Hohn and Merico (2015), pointing toward a function of paracellular leakage from the ECF due to susceptibility to OA (Fig. 2). Calcium would be highly susceptible to paracellular leakage, thus compensated by a greater need for active transport in acidified seawater. Suggested by all groups (Hohn and Merico 2015, Yuan et al. 2019, Radice et al. 2024) and similar studies (Galli and Solidoro 2018) is that regulation of the ECF by active transporters contribute significantly to coral response to OA. Therefore, calcium transport could potentially be identified as contributing to the calcification of corals in OA, as well as several other underlying mechanisms, i.e. proton export, carbon concentration mechanisms, and cell adhesion. This is a species-specific property limited to the phenotypic plasticity of the individual to regulate calcification and potentially a function of calcium concentration at the ECF.

Quantifying the calcium concentration in the ECF when corals are exposed to acidified seawater would provide valuable insight into the end product of environmental change related to calcium specifically (regardless of all physiological mechanisms). Before DeCarlo et al. (2018), no such study exists. DeCarlo et al. (2018) conducted a novel RAMAN spectroscopy study, combining recent (at the time of publication) boron isotope schematics to quantify ECF chemistry (DeCarlo et al. 2017b, Comeau et al. 2019). DeCarlo et al. (2018) cultured two coral species (*Pocillopora damicornis* and *Acropora youngei*) in OA conditions to assess calcium concentration differences in the ECF. When exposed to OA (pH_{sw} 7.8), *P. damicornis* elevated the ratio of calcium in the ECF to seawater ($Ca^{2+}{}_{cf}/Ca^{2+}{}_{sw}$) from 1.06 to 1.25 (±0.06). However, *A. youngei* only increased from 0.89 to 0.97 (±0.03; DeCarlo et al. 2018). As a result, bulk calcification was maintained in *P. damicornis* under OA, whereas *A. youngei* showed decreased calcification. The major difference between the two species was control over calcium concentrations in the ECF (DeCarlo et al. 2018). Supporting arguments in DeCarlo et al. (2018), an interdisciplinary study using calcein fluorescence as a metric, Scucchia et al. (2021) showed that a lower amount of calcium was included in the skeleton in acidified seawater. This was coupled with increased gene expression related to calcium transport, which, interestingly, was found only in calcium-specific channels (Scucchia et al. 2021). Since then, this topic has not received much attention besides exploratory molecular studies and could potentially hold great value in explaining coral calcification in a future ocean. Therefore, we urge action to continue investigating calcium's role in calcification, as the complexities of coral calcification have yet to be fully unraveled.

The future for corals: a path forward

Coral reefs are essential for marine ecosystem's biodiversity, and calcification's biogenic process is fundamental to supporting reefs worldwide (Graham and Nash 2013, Jokiel 2016, Bahr et al. 2017). However, seawater chemistry changes resulting from increasing OA could threaten calcification in corals (IPCC 2022). If we can understand how OA drives lower calcification in corals, then species-specific adaptive capacities could be assessed in targeted directives. Therefore, we have aimed to expand on the driver of calcium dynamics for coral calcification under altered ocean chemistry, which may not have received significant attention in direct measures or manipulation studies (DeCarlo et al. 2018).

We feel that the arguments here provide sufficient justification to investigate calcium dynamics under OA and interacting stressors, combining methods in DeCarlo et al. (2018) utilizing RAMAN spectroscopy and Radice et al. (2024) as an omics approach. Proper quantification in concentrations of calcium and carbonate in the ECF, correlated with phenotypic plasticity as a function of gene expression, would provide valuable information on calcium's role in calcification under OA. If calcium is a significant driver in lower calcification in corals, then the animal's ability to maintain calcium homeostasis in the ECF would determine coral species-specific responses to OA (DeCarlo et al. 2018). We also suggest building from these data in transgenerational studies, with targeted directives in calcium dynamics and other physiological mechanisms that regulate the ECM. Assessing how gene expression for ion-regulatory mechanisms changes over generations could define potentially vulnerable species concerning the adaptive capacities of these individuals (Yuan et al. 2019, Radice et al. 2024). For example, if calcium dynamics drive lower calcification in corals under OA, assessments of the transgenerational ability to maintain calcium homeostasis would define a coral's adaptive capacity (Figs 1 and 2). However, we need to first identify the driver(s) for lower calcification in corals, and we argue that calcium dynamics should be included.

Concerning big picture climate change, OA is not occurring independently, and corals will face many stressors where interactive effects could add complexities to predicting their response in the future (Bahr et al. 2018, Leung et al. 2022, Klein et al. 2024). It is important to isolate the predicted stressors to understand baseline sensitivities, but these data provide a limited context to the state of future coral reefs (Klein et al. 2024). Utilizing the methodologies described above with interacting stressors could provide a valuable comparison for the calcification of corals in the future. The state of reefs will ultimately be determined by the ability of sessile calcifiers such as corals to overcome the effects of climate change. We would suggest that when the drivers for lower calcification can be confidently identified in an OA context, these studies should be furthered with predicted disease, local threats, temperature, sedimentation, and population shifts to understand the state of future coral reefs. As for the sessile benthic calcifier with limited physiological tolerance ranges, it is imperative to identify if adaptation is feasible in a future ocean.

In conclusion, expanding on calcium dynamics and coral calcification under OA could be crucial to identify what could be driving lower calcification in corals. By integrating novel geochemical methods (i.e. RAMAN spec) with molecular analyses of ion-transporter genes, we can isolate how corals allocate energy to maintain ECF homeostasis in our future ocean. As anthropogenic CO_2 emissions continue to drive climate change, knowledge of the drivers for calcification is essential for safeguarding the future of coral reefs and the ecosystems they support.

Acknowledgements

Along with our peer reviewers and editor for providing constructive and detailed feedback through the submission process, which has improved this manuscript significantly.

Author contributions

David A. Armstrong (Conceptualization [lead], Data curation [lead], Investigation [lead], Writing – original draft [lead], Writing – review & editing [lead]), and Keisha D. Bahr (Funding acquisition [lead], Investigation [supporting], Project administration [lead], Resources [lead], Supervision [lead], Writing – review & editing [equal]).

Conflict of interest: None declared.

Funding

We thank the National Science Foundation (NSF award # OCE-2049406) for funding and support.

Data availability

There are no new data associated with this article.

References

Albright R, Langdon C. Ocean acidification impacts multiple early life history processes of the Caribbean coral *Porites astreoides*: Ocean acidification impacts coral recruitment. *Global Change Biol* 2011;**17**:2478–87. https://doi.org/10.1111/j.1365-2486.2011.02404.x

Al-Horani FA. Physiology of skeletogenesis in scleractinian coral. In: C M Woodly, C A Downs, A W Bruckner, J W Portner, S B Galloway (eds.), *Diseases of Coral*, 1st edn, Hoboken, NJ: Wiley. 2015;192–205.

Al-Horani FA, Al-Moghrabi SM, de Beer D. Microsensor study of photosynthesis and calcification in the scleractinian coral, *Galaxea fascicularis*: active internal carbon cycle. *J Exp Mar Biol Ecol* 2003;**288**:1–15. https://doi.org/10.1016/S0022-0981(02)00578-6

Allemand D, Ferrier-Pagès C, Furla P *et al.* Biomineralisation in reef-building corals: from molecular mechanisms to environmental control. *CR Palevol* 2004;**3**:453–67. https://doi.org/10.1016/j.crpv.2004.07.011

Allemand D, Tambutté É, Zoccola D *et al.* Coral calcification, cells to reefs. In: Z Dubinsky, N Stambler (eds.), *Coral Reefs: An Ecosystem in Transition*. Dordrecht: Springer Netherlands, 2011;119–50.

Allison N, Cole C, Hintz C *et al.* The effect of ocean acidification on tropical coral calcification: insights from calcification fluid DIC chemistry. *Chem Geol* 2018;**497**:162–9. https://doi.org/10.1016/j.chemgeo.2018.09.004

Andersson AJ, Mackenzie FT. Revisiting four scientific debates in ocean acidification research. *Biogeosciences* 2012;**9**:893–905. https://doi.org/10.5194/bg-9-893-2012

Bach LT. Reconsidering the role of carbonate ion concentration in calcification by marine organisms. *Biogeosciences* 2015;**12**:4939–51. https://doi.org/10.5194/bg-12-4939-2015

Bahr KD, Jokiel PL, Rodgers KS. Relative sensitivity of five Hawaiian coral species to high temperature under high-pCO_2 conditions. *Coral Reefs* 2016;**35**:729–38. https://doi.org/10.1007/s00338-016-1405-4

Bahr KD, Jokiel PL, Rodgers KS. Seasonal and annual calcification rates of the Hawaiian reef coral, *Montipora capitata*, under present and future climate change scenarios. *ICES J Mar Sci* 2017;**74**:1083–91. https://doi.org/10.1093/icesjms/fsw078

Bahr KD, Rodgers KS, Jokiel PL. Ocean warming drives decline in coral metabolism while acidification highlights species-specific responses. *Mar Biol Res* 2018;**14**:924–35. https://doi.org/10.1080/17451000.2018.1551616

Bisswanger H. Enzyme assays. *Perspect Sci* 2014;**1**:41–55. https://doi.org/10.1016/j.pisc.2014.02.005

Caldeira K, Wickett ME. Anthropogenic carbon and ocean pH. *Nature* 2003;**425**:365–. https://doi.org/10.1038/425365a

Castillo Alvarez C, Penkman K, Kröger R *et al.* Insights into the response of coral biomineralisation to environmental change from aragonite precipitations in vitro. *Geochim Cosmochim Acta* 2024;**364**:184–94. https://doi.org/10.1016/j.gca.2023.10.032

Chan NCS, Connolly SR. Sensitivity of coral calcification to ocean acidification: a meta-analysis. *Global Change Biol* 2013;**19**:282–90. https://doi.org/10.1111/gcb.12011

Comeau S, Cornwall CE, Pupier CA *et al.* Flow-driven micro-scale pH variability affects the physiology of corals and coralline algae under ocean acidification. *Sci Rep* 2019;**9**:12829. https://doi.org/10.1038/s41598-019-49044-w

Comeau S, Edmunds PJ, Spindel NB *et al.* Fast coral reef calcifiers are more sensitive to ocean acidification in short-term laboratory incubations. *Limnol Oceanogr* 2014;**59**:1081–91. https://doi.org/10.4319/lo.2014.59.3.1081

Cyronak T, Schulz KG, Jokiel PL. The Omega myth: what really drives lower calcification rates in an acidifying ocean. *ICES J Mar Sci* 2016;**73**:558–62. https://doi.org/10.1093/icesjms/fsv075

Davis KL, Colefax AP, Tucker JP *et al.* Global coral reef ecosystems exhibit declining calcification and increasing primary productivity. *Commun Earth Environ* 2021;**2**:1–10. https://doi.org/10.1038/s43247-021-00168-w

DeCarlo TM, Cohen AL, Wong GTF *et al.* Community production modulates coral reef pH and the sensitivity of ecosystem calcification to ocean acidification. *J Geophys Res: Oceans* 2017;**122**:745–61. https://doi.org/10.1002/2016JC012326

DeCarlo TM, Comeau S, Cornwall CE *et al.* Coral resistance to ocean acidification linked to increased calcium at the site of calcification. *Proc R Soc B Biol Sci* 2018;**285**:20180564. https://doi.org/10.1098/rspb.2018.0564

DeCarlo TM, D'Olivo JP, Foster T *et al.* Coral calcifying fluid aragonite saturation states derived from Raman spectroscopy. *Biogeosciences* 2017b;**14**:5253–69. https://doi.org/10.5194/bg-14-5253-2017

A G Dickson, C L Sabine, J R Christian. (eds). *Guide to Best Practices for Ocean CO_2 Measurements*. Sidney, Australia: PICES special publication, 2007, 191.

Galli G, Solidoro C. ATP supply may contribute to light-enhanced calcification in corals more than abiotic mechanisms. *Front Mar Sci* 2018;**5**:68. https://doi.org/10.3389/fmars.2018.00068

Gattuso J. Effect of calcium carbonate saturation of seawater on coral calcification. *Global Planet Change* 1998;**18**:37–46. https://doi.org/10.1016/S0921-8181(98)00035-6

Graham NAJ, Nash KL. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 2013;**32**:315–26. https://doi.org/10.1007/s00338-012-0984-y

Hoegh-Guldberg O. Coral reef ecosystems and anthropogenic climate change. *Reg Environ Change* 2011;**11**:215–27. https://doi.org/10.1007/s10113-010-0189-2

Hoegh-Guldberg O, Mumby PJ, Hooten AJ *et al.* Coral reefs under rapid climate change and ocean acidification. *Science* 2007;**318**:1737–42. https://doi.org/10.1126/science.1152509

Hohn S, Merico A. Quantifying the relative importance of transcellular and paracellular ion transports to coral polyp calcification. *Front Earth Sci* 2015;**2**:37. https://doi.org/10.3389/feart.2014.00037

IPCC. Changing ocean, marine ecosystems, and dependent communities. In: *The Ocean and Cryosphere in a Changing Climate: Special Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 2022;447–588.

Jokiel PL. The reef coral two compartment proton flux model: A new approach relating tissue-level physiological processes to gross corallum morphology. *J Exp Mar Biol Ecol* 2011b;**409**:1–12. https://doi.org/10.1016/j.jembe.2011.10.008

Jokiel PL. Ocean acidification and control of reef coral calcification by boundary layer limitation of proton flux. *Bull Mar Sci* 2011a;**87**:639–57. https://doi.org/10.5343/bms.2010.1107

Jokiel PL. Predicting the impact of ocean acidification on coral reefs: evaluating the assumptions involved. *ICES J Mar Sci* 2016;**73**:550–7. https://doi.org/10.1093/icesjms/fsv091

Jokiel PL, Jury CP, Rodgers KS. Coral-algae metabolism and diurnal changes in the CO_2-carbonate system of bulk sea water. *PeerJ* 2014;**2**:e378. https://doi.org/10.1594/PANGAEA.839068

Jury CP, Whitehead RF, Szmant AM. Effects of variations in carbonate chemistry on the calcification rates of *Madracis auretenra (= Madracis mirabilis sensu* Wells, 1973): bicarbonate concentrations best predict calcification rates. *Global Change Biol* 2010;**16**:1632–44. https://doi.org/10.1111/j.1365-2486.2009.02057.x

Kealoha AK, Shamberger KEF, Reid EC *et al.* Heterotrophy of oceanic particulate organic matter elevates net ecosystem calcification. *Geophys Res Lett* 2019;**46**:9851–60. https://doi.org/10.1029/2019GL083726

Klein SG, Roch C, Duarte CM. Systematic review of the uncertainty of coral reef futures under climate change. *Nat Commun* 2024;**15**:2224. https://doi.org/10.1038/s41467-024-46255-2

Kleypas JA, Buddemeier RW, Archer D *et al.* Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 1999;**284**:118–20. https://doi.org/10.1126/science.284.5411.118

Langdon C, Atkinson MJ. Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *J Geophys Res: Oceans* 2005;**110**:C09S07. https://doi.org/10.1029/2004JC002576

Leung JYS, Zhang S, Connell SD. Is ocean acidification really a threat to marine calcifiers? A systematic review and meta-analysis of 980+ studies spanning two decades. *Small* 2022;**18**:2107407. https://doi.org/10.1002/smll.202107407

Marshall AT. Calcification in hermatypic and ahermatypic corals. *Science* 1996;**271**:637–9. https://doi.org/10.1126/science.271.5249.637

Marubini F, Barnett H, Langdon C *et al.* Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar Ecol Prog Ser* 2001;**220**:153–62. https://doi.org/10.3354/meps220153

Moya A, Huisman L, Ball EE *et al.* Whole transcriptome analysis of the coral acropora millepora reveals complex responses to CO_2-driven acidification during the initiation of calcification. *Mol Ecol* 2012;**21**:2440–54. https://doi.org/10.1111/j.1365-294X.2012.05554.x

OA-ICC. Data compilation on the biological response to ocean acidification: 2008-2023 [dataset]. *PANGAEA*, 2023. https://doi.pangaea.de/10.1594/PANGAEA.962556

Radice VZ, Martinez A, Paytan A *et al.* Complex dynamics of coral gene expression responses to low pH across species. *Mol Ecol* 2024;**33**:e17186. https://doi.org/10.1111/mec.17186

Reymond CE, Hohn S. An experimental approach to assessing the roles of magnesium, calcium, and carbonate ratios in marine carbonates. *Oceans* 2021;**2**:193–214. https://doi.org/10.3390/oceans2010012

Reynaud S, Leclercq N, Romaine-Lioud S *et al.* Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Global Change Biol* 2003;**9**:1660–8. https://doi.org/10.1046/j.1365-2486.2003.00678.x

Ries JB, Cohen AL, McCorkle DC. Marine calcifiers exhibit mixed responses to CO_2-induced ocean acidification. *Geology* 2009;**37**:1131–4. https://doi.org/10.1130/G30210A.1

Sabine CL, Feely RA, Gruber N *et al.* The oceanic sink for anthropogenic CO_2. *Science* 2004;**305**:367–71. https://doi.org/10.1126/science.1097403

Scucchia F, Malik A, Zaslansky P *et al.* Combined responses of primary coral polyps and their algal endosymbionts to decreasing seawater pH. *Proc R Soc B Biol Sci* 2021;**288**:20210328. https://doi.org/10.1098/rspb.2021.0328

Smith SV. Coral-reef area and the contributions of reefs to processes and resources of the world's oceans. *Nature* 1978;**273**:225–6. https://doi.org/10.1038/273225a0

Tambutté É, Allemand D, Mueller E *et al.* A compartmental approach to the mechanism of calcification in hermatypic corals. *J Exp Biol* 1996;**199**:1029–41. https://doi.org/10.1242/jeb.199.5.1029

Taubner I, Böhm F, Eisenhauer A *et al.* An improved approach investigating epithelial ion transport in scleractinian corals. *Limnol Oceanogr: Methods* 2017;**15**:753–65. https://doi.org/10.1002/lom3.10194

Teixidó N, Caroselli E, Alliouane S *et al.* Ocean acidification causes variable trait-shifts in a coral species. *Global Change Biol* 2020;**26**:6813–30. https://doi.org/10.1111/gcb.15372

Venn AA, Tambutté E, Comeau S *et al.* Proton gradients across the coral calcifying cell layer: Effects of light, ocean acidification and carbonate chemistry. *Front Mar Sci* 2022;**9**:973908. https://doi.org/10.3389/fmars.2022.973908

Yuan X, Huang H, Zhou W *et al.* Gene expression profiles of two coral species with varied resistance to ocean acidification. *Mar Biotechnol* 2019;**21**:151–60. https://doi.org/10.1007/s10126-018-9864-y

Zoccola D, Tambutté E, Kulhanek E *et al.* Molecular cloning and localization of a PMCA P-type calcium ATPase from the coral *Stylophora pistillata*. *Biochimica et Biophysica Acta (BBA)—Biomembranes* 2004;**1663**:117–26. https://doi.org/10.1016/j.bbamem.2004.02.010

Zoccola D, Tambutté E, Sénégas-Balas F *et al.* Cloning of a calcium channel $\alpha 1$ subunit from the reef-building coral, *Stylophora pistillata*. *Gene* 1999;**227**:157–67. https://doi.org/10.1016/S0378-1119(98)00602-7

Handling Editor: Howard Browman
