Responses of the temperate calcareous sponge *Grantia* sp. to ocean acidification

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Abstract

Sponges are important components of marine systems globally, and while sponges have generally been shown to tolerate ocean acidification (OA), most earlier studies have focused on demosponges with siliceous skeletons. In contrast, little is known of how calcareous sponges, with calcite or aragonite skeletons, may react to OA conditions. Here we measured tissue necrosis and respiration rate of the temperate New Zealand calcareous sponge *Grantia* sp. to simulated OA. Our treatment conditions were based on the IPCC RCP8.5 (pCO_2 $1131.9 \pm 113\,\mu$atm) scenario over a 28 day experiment, and responses were compared to current day control conditions (pCO_2 $512.59 \pm 23\,\mu$atm). Sponge respiration rate was not significantly different between the control and treatment sponges and there was no evidence of tissue necrosis over the course of the experiment. Overall, our study is consistent with earlier studies on demosponges, showing calcareous sponges to be resilient to OA.

Introduction

Atmospheric carbon dioxide concentrations ($CO_{2\,atm}$) are currently around 417 ppm, which is over 100 ppm more than prior to the industrial revolution (NOAA, 2021). $CO_{2\,atm}$ levels are predicted to rise beyond 1000 ppm by the year 2100 if no action is taken to reduce CO_2 emissions (IPCC, 2021). Due to its buffering abilities, the ocean has absorbed approximately a quarter of the CO_2 that has been released into the atmosphere from anthropogenic activities, resulting in decreased ocean pH (IPCC, 2021). Under the worst-case scenario, by 2100 ocean pH is predicted to decrease by a further 0.3–0.5 units (Orr *et al.*, 2005; The Representative Concentration Pathway [RCP] 8.5; IPCC, 2021). This changing ocean chemistry is leading to an increase in hydrogen ions (H^+) in a phenomenon known as ocean acidification (OA), which has the potential to impact a wide range of marine organisms (Caldeira and Wickett, 2003; Kroeker *et al.*, 2010;, 2013).

There are a number of ways that marine organisms can be impacted by OA, although most focus has been on calcifying organisms, particularly molluscs, echinoderms, corals and crustaceans (Medeiros and Souza, 2023). These impacts include changes to growth, metabolism, acid-base balance, calcification, survival rates, settlement, reproduction and cell signalling processes (Espinel-Velasco *et al.*, 2018; Melzner *et al.*, 2020; Medeiros and Souza, 2023). Of particular concern is the dissolution of calcium carbonate structures, particularly as a result of biominerals being prone to dissolution when seawater is undersaturated with respect to calcium carbonate (Melzner *et al.*, 2020). While much of the focus of such dissolution has focused on coral reefs (Cornwall *et al.*, 2021), many other organisms with calcium carbonate structures are at risk. Furthermore, disruption of acid-base regulation ability and cell signalling pathways may actually interfere with the process of calcification either directly or indirectly (see Melzner *et al.*, 2020 for review).

Sponges are abundant benthic organisms in temperate, polar, and tropical marine ecosystems (Bell *et al.*, 2020). As sedentary suspension feeders, sponges are integral in linking benthic and pelagic ecosystems, filtering large volumes of water per unit body mass, retaining small particles and nutrients, and providing a link to higher trophic levels (Turton *et al.*, 1997; Bell, 2002; Perea-Blázquez *et al.*, 2010; De Goeij *et al.*, 2013). Due to their sessile nature and the presence of an aquaferous system, sponges are continuously exposed to ambient seawater, potentially increasing their vulnerability to alterations in seawater chemistry (Bergquist, 1978; Aguilar-Camacho and McCormack, 2017). However, despite this, some sponges can tolerate changes in salinity (e.g. Leamon and Fell, 1990) and have been shown to both osmoregulate (Brauer, 1975) and control intracellular pH (e.g. Webb *et al.*, 2019). These abilities of sponges may enable them to cope with changes in the pH of the surrounding seawater, although this might come with increased metabolic demand.

A number of studies have shown tropical sponges to be resilient to climate change impacts (Fabricius *et al.*, 2011; Wissak *et al.*, 2012;, 2014; Fang *et al.*, 2013; Bennett *et al.*, 2016; Bell *et al.*, 2018; Agostini *et al.*, 2018), but far less known about temperate sponges (but see Goodwin *et al.*, 2013; Bates and Bell, 2018). Importantly, the majority of all previous sponge climate studies have focused on demosponges with siliceous skeletons, with much less know about climate impacts on calcareous sponges species that have spicules made of calcium carbonate (see Bell *et al.*, 2018). Class Calcarea make up approximately 5–8% of the phylum

Porifera, with many species still undescribed (Uriz, 2006; Smith *et al.*, 2013). Calcareous sponges are often abundant in caves and other dark environments where they can be more abundant than demosponges (e.g. Bell, 2002; Rapp, 2006; Fromont *et al.*, 2012). Calcareous sponges are the only sponge class with spicules formed of calcium carbonate (Jones, 1970). Therefore, these sponges may be more vulnerable to OA impacts compared to demosponges. However, earlier studies have found the spicules of calcareous sponges to be surrounded by an organic sheath (Jones, 1955), which has the potential to prevent dissolution of spicules once formed.

To date, only two experimental laboratory studies have considered the impact of OA on non-tropical calcareous sponges (Peck *et al.*, 2015; Ribeiro *et al.*, 2020). Peck *et al.* (2015) found that *Leucosolenia* sp. increased in abundance 2.5-fold in low pH (pH 7.7, pCO_2 not given) conditions compared to controls and suggested that sponge resilience may be a result of the organic sheath described above (see Jones, 1955). More recently, a 9-day laboratory study by Ribeiro *et al.* (2020) examined the effect of temperature, pH, and their combined effects on the skeleton and microbial community of the calcareous sponge *Sycettusa hastifera* (Ribeiro *et al.*, 2020; treatment conditions: control: 22 °C, pH 8.1, pCO_2 301 ± 30 μ atm; low pH: 22 °C, pH 7.6, pCO_2 1182 ± 119 μ atm; high temperature: 26 °C, pH 8.1, pCO_2 278 ± 319 μ atm; combined effects: 26 °C, pH 7.6, pCO_2 1156 ± 167 μ atm). These authors found that none of the treatments caused any significant sponge degeneration, but they did find that higher temperature affected spicule shape, and sponges in the reduced pH treatment had smaller spicules in their exterior layer (Ribeiro *et al.*, 2020).

These limited earlier studies show the potential resilience of calcareous sponges to OA, but longer experiments with more species are needed before any generalisations can be made. We hypothesise that calcareous sponge respiration rates will increase as a result of OA impacting cellular processes, particularly the maintenance of intracellular pH. To test this we conducted a 28-day experiment, to measure respiration rate (as a measure of metabolic demand) and tissue necrosis in the calcareous sponge *Grantia* sp. Sponges were exposed to pH 7.6 (treatment, pCO_2 1131.9 ± 113 μ atm) and pH 8 (control, pCO_2 512.59 ± 23 μ atm), consistent with the IPCC RCP8.5 scenario for 2100 (IPCC, 2013).

Materials and methods

Grantia sp. is a common New Zealand sponge that has an off-white colouration and a network of delicate erect singular tubes, with oscula that are slightly hispid (Dendy, 1924). This species is typically found in rocky caves and on vertical reef walls that experience high levels of turbulence and water flow. A 28-day laboratory experiment was undertaken to investigate how our study species is affected by the IPCC worst case scenario RCP8.5 conditions. We compared sponges kept in three replicate treatment tanks (pCO_2 1131.9 ± 113 μ atm) to three control tanks (pCO_2 512.59 ± 23 μ atm) (Bates and Bell, 2018; Figure S1). Eighty-one *Grantia* sp. were collected via SCUBA from Breaker Bay, Wellington, New Zealand (41° 19′ 58″ S, 174° 49′ 52″ E) (see Bates and Bell, 2018 for location).

Sponges were attached to ceramic tiles and haphazardly placed in tanks, with a total of 13 sponges in each tank (6 tanks in total) and acclimated for two weeks, after which a secondary acclimation period began where the pH was reduced in the treatment tanks by 0.1 units per day until the desired pH/pCO_2 was reached to simulate a gradual OA decline (e.g. Johnson *et al.*, 2019). A Neptune APEX controller (Neptune System LLC, USA) was used to keep the tanks within 0.1 unit of the target value via the slow-release

bubbling of CO_2 from a solenoid box connected to a 6.8 kg CO_2 cylinder. The sponges were kept at the average mean temperature (13 °C) for the Wellington South Coast (Greater Wellington Regional Council, 2021), which was also similar to the temperature at the time of collection. This temperature was maintained inside a 100L header tank (see Figure S1) using a heater and chiller that were controlled automatically using the APEX system. The water from a main tank was transferred into individual secondary header tanks (see supplemental information for more information), which then flowed into a corresponding tank where the 13 sponges per tank were housed ($n = 39$ per treatment). Temperature and pH were monitored weekly (Supplemental Table S1) throughout the experiment using the APEX probes and real-time measurements of pH(T) (mV) using a HQ40d portable pH multi-parameter (HACH, USA). To determine the carbonate chemistry of the system pHT [H +], total alkalinity (TA), temperature and salinity were measured throughout the experiment to complete the calculations using dissociation constant of water and Henry's law (Zeebe, 2012) (Tables 1 and S1).

At T0, baseline respiration measurements were made for three randomly selected sponges per tank (meaning a total $n = 9$ per treatment), thereafter respiration rates were measured on day T3, T6, T14, T17, T24, and T28 (Tend). Randomisation was achieved using the numbers on the tiles and random number tables. We used a similar method as Bates and Bell (2018), Cummings *et al.* (2020), and Micaroni *et al.* (2021). See supplemental information for further details.

All statistical analyses were performed in R version 3.1.3 (R Core Team, 2013). The effects of pCO_2 (ambient – control), RCP8.5 (treatment) and time (day of measurement throughout the 28 day trial, T0–T28) were tested using linear mixed-effects models (LMM) with normally distributed errors and random intercepts (*lmer*, lme4 package; Bates *et al.*, 2015). Treatment and time were considered fixed effects and experimental tank was considered a random effect. An experimental tank effect was included to address pseudoreplication and possible tank effects (Hurlbert, 1984). For all the models, fixed- and random-effect terms were tested using the function anova and ranova (R package lmerTest, Kuznetsova *et al.*, 2017). The goodness of fit, normality and homoscedasticity of the errors were checked for all models by inspecting plots of the normalised residuals and the quantile-quantile plots (see Figure S3). For mixed-effect models there were slight concerns about normality of residuals, so the analyses were supplemented with a more robust non-parametric model (univariate PERMANOVA, Anderson, 2001, 2014).

Results

There were no signs of tissue necrosis in any of the control or treatment sponges over the course of the experiment. Respiration rate of *Grantia* sp. (Figure 1) fluctuated over the course of the experiment for both the control and treatment sponges. The LMM analysis determined that treatment had no significant effect on the sponge respiration ($F_{1,102} = 2.18$, $p = 0.14$; Table S2). However, there was a significant effect of time on respiration rate ($F_{1,102} = 9.27$, $p = 0.003$; Table S2). Both treatment and controls experienced an approximate 50% reduction in mean respiration rate over the experiment based on a comparison between T0 and T28 (Figure 1). The PERMANOVA model confirmed the results of the mixed-effect model (Table S3).

Discussion

While there is a considerable amount of data available on the impacts of OA and warming on demosponges, we know

Table 1. Summary of measured (*) and calculated (**) seawater parameters represented as the mean (±SD) of measurements taken during the acclimation period and weekly during the experiment ($n = 4$ sampling periods)

|	Temperature (°C)*	pHT* (in tank)	Salinity (ppm)*	TA (μ mol/kg^{-1}) *	Ωca	Ωar	pCO$_2$ (μ atm)**
Acclimation							
(pH 8.0)	13.18 (±0.18)	7.93 (±0.12)	NA	NA	NA	NA	NA
Control							
(pH 8.0)	12.92 (±0.23)	7.95 (±0.02)	34.9	2294.83 (±8.98)	2.87	1.84	512.59 (±23)
Treatment							
(pH 7.6)	12.89 (±0.26)	7.63 (±0.02)	34.9	2297.28 (±7.81)	1.50	0.96	1131.9 (±113)

Measured values of temperature, salinity, pH (pHT), and total alkalinity (TA) were measured in all aquaria weekly. pCO$_2$ (μ atm) and seawater saturation states (Ωca and Ωar) were calculated by entering the recorded values of temperature, pHT, salinity and TA into the CO$_2$ calc software (Robbins et al., 2010).

comparatively little about calcareous sponges. *Grantia* sp. showed no signs of tissue necrosis over the course of the experiment. We also found no impact of our OA simulation on the respiration rate of sponges, although there was an effect of time. Our results are consistent with the emerging picture that calcareous sponges show tolerance to changes in the pH of the external environment.

Reduced ocean pH can cause serious physiological stress to marine organisms, resulting in alterations to respiration rates as they use their energy to activate detoxification and survival mechanisms (Sokolova et al., 2012). Several recent reviews have examined the impacts of OA on the physiology and ecology of marine invertebrates. Both Shi and Li (2023) and Medeiros and Souza (2023) identified a number of broader direct and indirect impacts on marine invertebrates including impacts on calcification, behaviour, immunity, energy budget, metabolism, growth, development, genetics, oxidative stress, and disruption of acid-base balance. These reviews highlight the wide range of invertebrates that are negatively impacted by OA. However, results for our study species, and the previous studies on OA impacts on calcareous sponges (see Peck et al., 2015; Ribeiro et al., 2020) contrast with reported impacts on other organisms with calcareous skeletons. For example, calcium carbonate accretion by reef building corals in tropical ecosystems is expected to be reduced 156% by 2100 under the worst case RCP 8.5 scenario (Cornwall et al.,

2021). However, no negative physiological impacts were found for our study species. A number of previous studies have suggested that sponges may be winners in future warmer and more acidic oceans (e.g. Bell et al., 2013), however, this hypothesis is based largely on tropical demosponges, with far less known about the climate change impacts on temperate species, and particularly calcareous sponges. Our results support this hypothesis for temperate calcareous sponges, albeit based on a single species, at least in responses to OA.

We found no significant differences in the respiration rate of *Grantia* sp. between the control and treatment sponges, however, we did find a significant effect of time in both treatments. Both control and treatment sponge respiration rates declined over the course of the 28 day experiment however, the sponges did not show any other signs of deterioration over this period, suggesting that they stayed healthy in experimental set up. We believe the decline in respiration rates over time was likely due to lower food in our experimental system compared to natural environments. Our respiration results contrast with those for a non-calcareous temperate sponge, *Tethya bergquistae*. For this sponge, respiration increased in response to low pH conditions compared to the controls (treatment pH 7.6; pCO$_2$ 1514 ± 13.6 μ atm). (Bates and Bell, 2018). Intracellular pH (pHi) directly impacts basic cell functions (Casey et al., 2010), therefore, the increase
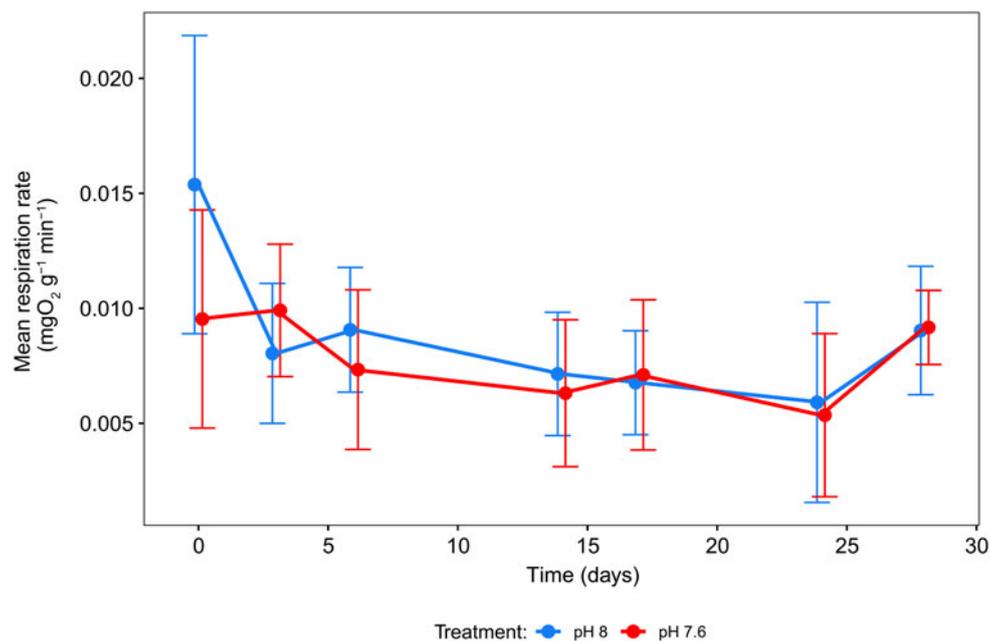
Figure 1. Change in mean respiration rate (mgO$_2$ g^{-1} min^{-1}) of *Grantia* sp. over a 28 day experiment exposed to pCO$_2$ 1131.9 ± 113 μ atm (pH 7.6) and pCO$_2$ 512.59 ± 23 μ atm (pH 8). Error bars indicate standard deviation.

in respiration rate of the *T. bergquistae* could be a result of cellular acidosis as seen with increased temperature in corals and their symbionts (Gibbin *et al.*, 2015), and with decreased pH in corals and other marine invertebrates (Orr *et al.*, 2005). However, consistent with our study, Bates and Bell (2018) did not find a significant change in the respiration rate of a second demosponge species, *Crella incrustans*, which was exposed to the same conditions. Species specific differences might occur due to differences in acid-base regulation abilities (Pörtner *et al.*, 2004), which may explain why *T. bergquistae* has a different response than either *C. incrustans* or our study species, although little is known about acid-base regulation specifically in sponges and needs further investigation.

Conclusion

We found no evidence for negative impacts of reducing ocean pH on the calcareous sponge *Grantia* sp., with our study providing evidence that despite calcareous sponges having calcareous spicules they are resilient to the short term impacts of changing pH. However, the exact mechanisms of tolerance still require further investigation, particularly around how sponges either regulate internal pH conditions or how they tolerate changes to pH without increasing energy expenditure.

References

Agostini S, Harvey B, Wada S, Kon K, Milazzo M, Inaba K and Hall-Spencer J (2018) Ocean acidification drives community shifts towards simplified non-calcified habitats in a subtropical-temperate transition zone. *Scientific Reports* **8**(1), 11354. https://doi.org/10.1038/s41598-018-29251-7

Aguilar-Camacho J and McCormack G (2017) Molecular responses of sponges to climate change, climate change. In Carballo JL and Bell JJ (eds), *Ocean Acidification and Sponges.* Cham: Springer, pp. 79–104. https://doi.org/10.1007/978-3-319-59008-0_4

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**, 32–46.

Anderson MJ (2014) Permutational multivariate analysis of variance (PERMANOVA). Wiley statsref: statistics reference online, 1–15. https://doi.org/10.1002/9781118445112.stat07841

Bates T and Bell J (2018) Responses of two temperate sponge species to ocean acidification. *New Zealand Journal of Marine and Freshwater Research* **52**, 247–263.

Bates D, Maechler M, Bolker B and Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48.

Bell J (2002) The sponge community in a semi-submerged temperate sea cave: density, diversity and richness. *Marine Ecology* **23**, 297–311.

Bell J, Bennett H, Rovellini A and Webster N (2018) Sponges to be winners under near-future climate scenarios. *BioScience* **68**, 955–968.

Bell JJ, Davy SK, Jones T, Taylor MW and Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology* **19**, 2613–2624.

Bell JJ, McGrath E, Kandler N, Marlow J, Beepat S, Bachtiar R, Shaffer M, Mortimer C, Macaroni V, Mobilia V, Rovellini A, Harris B, Farnham E, Strano F and Carballo J (2020) Interocean patterns in shallow water sponge assemblage structure and function. *Biological Reviews* **95**, 1720–1758.

Bennett H, Altenrath C, Woods L, Davy S, Webster N and Bell JJ (2016) Interactive effects of temperature and pCO2 on sponges: from the cradle to the grave. *Global Change Biology* **23**, 2031–2046.

Bergquist P (1978) *Sponges.* Berkeley: University of California Press.

Brauer EB (1975) Osmoregulation in the fresh water sponge, *Spongilla lacustris. Journal of Experimental Zoology* **192**, 181–192.

Caldeira K and Wickett A (2003) Anthropogenic carbon and ocean pH. *Nature* **425**, 365.

Casey J, Feinstein S and Orlowski J (2010) Sensors and regulators of intracellular pH. *Nature Review of Molecular and Cellular Biology* **11**, 50–61.

Cornwall CE, Comeau S, Kornder NA, Perry CT, van Hooidonk R, DeCarlo TM, Pratchett MS, Anderson KD, Browne N, Carpenter R and Diaz-Pulido G (2021) Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proceedings of the National Academy of Sciences* **118**, e2015265118.

Cummings V, Beaumont J, Bell JJ, Tracey D, Clark M and Barr N (2020) Responses of a common New Zealand coastal sponge to elevated suspended sediments: indications of resilience. *Marine Environmental Research* **155**, 104886.

De Goeij JM, Van Oevelen D, Vermeij MJ, Osinga R, Middelburg JJ, De Goeij AF and Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science (New York, N.Y.)* **342**, 108–110.

Dendy A (1924) Porifera, Part I. Non-Antarctic sponges. IN: Natural History Report, British Antarctic (Terra Nova) Expedition, 1910 (Zoology) 6, 269–392.

Espinel-Velasco N, Hoffmann L, Agüera A, Byrne M, Dupont S, Uthicke S, Webster NS and Lamare M (2018) Effects of ocean acidification on the settlement and metamorphosis of marine invertebrate and fish larvae: a review. *Marine Ecology Progress Series* **606**, 237–257.

Fabricius KE, Langdon C, Uthicke S, Humphrey C, Noonan S, De'ath G, Okazaki R, Muehllehner N, Glas MS and Lough JM (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change* **1**, 165–169.

Fang J, Mello-Athayde M, Schönberg C, Kline D, Hoegh-Guldberg O and Dove S (2013) Sponge biomass and bioerosion rates increase under ocean warming and ocean acidification. *Global Change Biology* **19**, 3581–3591.

Fromont J, Althaus F, McEnnulty FR, Williams A, Salotti M, Gomez O and Gowlett-Holmes K (2012) Living on the edge: the sponge fauna of Australia's southwestern and northwestern deep continental margin. In Maldonado M, X Turon, MA Becerro and Maria J Uriz (eds), *Ancient Animals, New Challenges: Developments in Sponge Research.* Springer, pp. 127–142. https://doi.org/10.1007/978-94-007-4688-6_12

Gibbin E, Putman H, Gates R, Nitschke M and Davy S (2015) Species-specific differences in thermal tolerance may define susceptibility to intracellular acidosis in reef corals. *Marine Biology* **162**, 717–723.

Goodwin C, Roldolfo-Metalpa R, Picton B and Hall-Spencer J (2013) Effects of ocean acidification on sponge communities. *Marine Ecology* **35**, 41–49.

Greater Wellington Regional Council (2021) Environmental Monitoring and Research Environmental Monitoring and Research (gw.govt.nz). Accessed 01 March 2021.

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187–211.

IPCC (2013) *Climate Change 2013: The Physical Science Basis.* Cambridge, UK: Cambridge University Press. 10.1017/9781009157896

IPCC (2021) Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V.,

P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge, UK: Cambridge University Press.

Johnson M, Rodriguez Bravo L, O'connor S, Varley N and Altieri A (2019) pH variability exacerbates effects of ocean acidification on the Caribbean crustose coralline algae. *Frontiers in Marine Science* **6**, 150. https://doi.org/10.3389/fmars.2019.00150

Jones W (1955) The sheath of spicules of *Leucosolenia complicate*. *Journal of Cell Science* **3**, 411–421.

Jones W (1970) The composition, development, form, and orientation of calcareous sponge spicules. *Symposium of the Zoological Society of London* **25**, 91–123.

Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, Singh GS, Duarte CM and Gattuso JP (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology* **19**, 1884–1896.

Kroeker KJ, Kordas RL, Crim RN and Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* **13**, 1419–1434.

Kuznetsova A, Brockhoff PB and Christensen RH (2017) lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* **82**, 1–26.

Leamon J and Fell PE (1990) Upper salinity tolerance of and salinity-induced tissue regression in the estuarine sponge *Microciona prolifera*. *Transactions of the American Microscopical Society* **109**, 265–272.

Medeiros IPM and Souza MM (2023) Acid times in physiology: a systematic review of the effects of ocean acidification on calcifying invertebrates. *Environmental Research* **231**, 116019.

Melzner F, Mark FC, Seibel BA and Tomanek L (2020) Ocean acidification and coastal marine invertebrates: tracking CO_2 effects from seawater to the cell. *Annual Review of Marine Science* **12**, 499–523.

Micaroni V, Strano F, McAllen R, Woods L, Turner J, Harman L and Bell J (2021) Adaptive strategies of sponges to deoxygenated oceans. *Global Change Biology* **28**, 1972–1989.

NOAA (2021) Mauna Loa CO_2 Monthly mean data. Available at https://gml.noaa.gov/webdata/ccgg/trends/co2/co2_mm_mlo.txt. Accessed 20 February 2021.

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F and Key RM (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organism. *Nature* **437**, 681–686.

Peck L, Clark M, Power D, Reis J, Batista F and Harper E (2015) Acidification effects on biofouling communities: winners and losers. *Global Change Biology* **21**, 1907–1913.

Perea-Blázquez A, Price K, Davy S and Bell JJ (2010) Diet composition of two temperate calcareous sponges: *Leucosolenia echinata* and *Leucetta* sp.

from the Wellington South Coast, New Zealand. *Open Marine Biology Journal* **4**, 65–73.

Pörtner H, Langenbuch M and Reipschläger A (2004) Biological impact of elevated ocean CO_2 concentrations: lessons from animal physiology and earth history. *Journal of Oceanography* **60**, 705–718.

Rapp HT (2006) Calcareous sponges of the genera *Clathrina* and *Guancha* (Calcinea, Calcarea, Porifera) of Norway (north-east Atlantic) with the description of five new species. *Zoological Journal of the Linnean Society* **147**, 331–365.

R Core Team (2013) R: A Language and Environment for Statistical Computing (2013).

Ribeiro B, Padua A, Barno A, Villela H, Duarte G, Rossi A, Fernandes F, Peixoto and Klautau R (2020) Assessing skeleton and microbiome responses of a calcareous sponge under thermal and pH stress. *ICES Journal of Marine Science* **78**, 855–866. https://doi.org/10.1093/icesjms/fsaa231

Robbins L, Hansen M, Kleypas J and Meylan S (2010) CO2 calc: A User-Friendly Seawater Carbon Calculator for Windows Mac OS X, AND iOS (iPhone). U.S. Geological Survey Open-File Report 2010–1280, 17.

Shi Y and Li Y (2023) Impacts of ocean acidification on physiology and ecology of marine invertebrates: a comprehensive review. *Aquatic Ecology* **58**, 207–226. https://doi.org/10.1007/s10452-023-10058-2

Smith A, Berman J, Key M and Winter J (2013) Not all sponges will thrive in a high-CO_2 ocean: review of the mineralogy of calcifying sponges. *Palaeogeography* **392**, 463–472.

Sokolova I, Frederich M, Bagwe R, Lanning G and Sukhotin A (2012) Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. *Marine Environmental Research* **79**, 1–15.

Turton X, Galera J and Uriz M (1997) Clearance rates and aquiferous systems in two sponges with contrasting life-history strategies. *Journal of Experimental Zoology* **278**, 22–36.

Uriz M (2006) Mineral skeletogenesis in sponges. *Canadian Journal of Zoology* **84**, 322–356.

Webb AE, Pomponi SA, van Duyl FC, Reichart GJ and de Nooijer LJ (2019) pH regulation and tissue coordination pathways promote calcium carbonate bioerosion by excavating sponges. *Scientific Reports* **9**, 758.

Wissak M, Schönberg C, Form A and Freiwald A (2012) Ocean acidification accelerates reef bioerosion. *PLoS One.* **7**: e45124.

Wissak K, Schönberg C, Form A and Freiwald A (2014) Sponge bioerosion accelerated by ocean acidification across species and latitudes? *Helgolander* **68**, 253–262.

Zeebe R (2012) History of seawater carbonate chemistry, atmospheric CO_2, and ocean acidification. *Annual Review of Earth, and Planetary Sciences* **40**, 141–165.