



Titelboim, D., Lord, O. T., & Schmidt, D. N. (2021). Thermal stress reduces carbonate production of benthic foraminifera and changes the material properties of their shells. *ICES Journal of Marine Science*, 78(9), 3202–3211. <https://doi.org/10.1093/icesjms/fsab186>

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Original Article

Thermal stress reduces carbonate production of benthic foraminifera and changes the material properties of their shells

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Titelboim, D., Lord, O. T., and Schmidt, D. N. Thermal stress reduces carbonate production of benthic foraminifera and changes the material properties of their shells. – ICES Journal of Marine Science, 78: 3202–3211.

Received 21 June 2021; revised 7 September 2021; accepted 7 September 2021; advance access publication 24 September 2021.

In shallow marine environments, benthic foraminifera are important foundation species and carbonate producers. Understanding their response to future climate is often drawn from their acclimation potential in short laboratory experiments, thereby limiting our understanding of migration, species replacement, and adaptive potential. To overcome this challenge, we examine two species of benthic foraminifera from a thermally polluted field site mimicking future warming. This site and a control station cover 13–36°C causing both warm and cold stress to the local species. Computer Tomography reveals that under heat stress, even with acclimation, *Lachlanella* significantly reduced its shell volume. In contrast, *Pararotalia calcariformata* did not reduce its shell volume but reduced the relative amount of calcite with respect to shell volume and changed its reproduction cycle from twice to once per year. Raman spectroscopy indicates that thermal conditions alter the chemical composition of the calcite shells of both species. Calcification during thermal stress creates alterations in the crystal structure that are unexpectedly more prominent under cold stress than warm stress indicating warming might positively affect the shell's protective function. Supported by previous laboratory experiments and observations from the geological record, our results provide new perspective to the effect of warming on benthic foraminifera.

Keywords: benthic foraminifera, calcification, dwarfism, field experiment, Raman spectroscopy, thermal stress, warming.

Introduction

Climate change is projected to impact organism in many ways, from physiological constraints on growth of individuals, impacts of reproduction on populations through to biogeographical range shifts, and ecosystem changes (Pörtner *et al.*, 2014). In the case of calcifying organisms, the predicted changes in the environmental conditions have been suggested to influence their ability to perform one of their primary functions: the regulation of the marine inorganic carbon cycle through carbonate production (Kroeker *et al.*, 2013).

Nearly half of the carbonate in the oceans is produced in shallow water environments (Milliman, 1993). To date, research on impacts of climate change in warm, shallow water ecosystems has focused predominantly on the biocalcification of corals (De'ath *et al.*, 2012; DeCarlo *et al.*, 2019). Yet, single-celled benthic foraminifera

are a prolific foundation species (i.e. have a strong role in structuring of communities) and significant calcifiers in many reef and other shallow marine systems (Langer, 2008; Hamylton *et al.*, 2013). Their shells contribute to carbonate production (Langer, 2008) and in places such as the low-lying islands in the south Pacific, foraminifera are the main source of beach sands and thus maintain the stability of shorelines (Collen, 1996).

Their calcification is often supported by symbiosis with eukaryotic microalgae, contributing also to primary production in the photic zone of tropical to subtropical areas (Lee, 2006). Specifically, photosymbiosis enhances the calcification rate, leading to the large shells of symbiont bearing species (Duguay, 1983; Hallock, 1985; Hallock and Seddighi,) though this process is suggested to be negatively impacted by long-term heat stress akin to coral bleaching (Schmidt *et al.*, 2011; Uthicke *et al.*, 2012; Prazeres and Pan-

dolfi, 2016; Titelboim *et al.*, 2016; Deldicq *et al.*, 2021; Kinoshita *et al.*, 2021). However, in some corals and large benthic foraminifera, functionally diverse symbionts create an ecological advantage because changes in the symbiont community (known as “symbiont shuffling”) can provide the holobiont (the combination of host and symbiont) with higher thermal tolerance (Lesser, 2006; Momigliano and Uthicke, 2013a; Schmidt *et al.*, 2018a).

Most of our understanding of the impacts of warming on foraminifera stem from laboratory experiments which demonstrated specific species responses with a general negative effect of thermal stress. However, some species demonstrate high resilience with no response to elevated temperatures (Doo *et al.*, 2014). The variation between species might be related to the diversity and flexibility of symbionts community, the ability for local acclimatization, and evolutionarily adaptation (Narayan *et al.*, 2021). Furthermore, laboratory experiments are usually short-term, mainly excluding transgenerational processes that might mitigate the effect of long-term environmental changes (i.e. over decades and longer), and usually performed on a limited number of species, precluding effects stemming from the complexity of ecosystem interactions, competition, and species replacement (Schmidt *et al.*, 2011, 2016; Momigliano and Uthicke, 2013b; Doo *et al.*, 2014; Prazeres *et al.*, 2016; Stuhr *et al.*, 2017, 2018, 2021; Pinko *et al.*, 2020; Narayan *et al.*, 2021). Thus, laboratory experiments are valuable for isolating the effects of specific environmental parameters and for investigation of species-specific responses. However, for more realistic predictions on the response of organisms to future changes, a more natural setting is required.

In situ environmental gradients can be used as ‘windows into the future’ to study the ability of organisms to acclimatize to predicted future climate changes. This was previously done using carbon dioxide seeps creating a natural gradient of pH mimicking ocean acidification (Hall-Spencer *et al.*, 2008; Martin *et al.*, 2008; Dias *et al.*, 2010; Fabricius *et al.*, 2011; Uthicke *et al.*, 2013). A unique situation representing the effect of future warming on benthic foraminifera is presented by a permanent local thermal anomaly along the Eastern Mediterranean coast of Israel, persisting since 1981. This anomaly is created by the release of cooling water from a power plant and follows the natural seasonal cycle but up to 9°C above the natural baseline (Titelboim *et al.*, 2016; Figures 1 and 2). Most species typical for the region are excluded from the warmest part of the anomaly. Only two species inhabit the site throughout the year: *Pararotalia calcariformata* and *Lachlanella* sp. 1 (Titelboim *et al.*, 2016). Both species continue calcifying in the high temperatures of the thermal anomaly (Titelboim *et al.*, 2017) providing an excellent opportunity to study changes in calcification under elevated temperature but otherwise natural conditions.

These two species differ from each other substantially: *P. calcariformata* is symbiont-bearing with a hyaline shell (multi-layered radial calcite creating a glassy appearance), and *Lachlanella* is symbiont barren with a miliolid shell (made from calcite needles arranged randomly in dense rows). These shell types are the result of different calcification mechanisms stemming from their evolutionary origins (Pawlowski *et al.*, 2013). The high thermal tolerance of *P. calcariformata* has been demonstrated in several laboratory experiments (Schmidt *et al.*, 2015, 2016) and was suggested to be linked to a diverse symbiont community including the diatom species *Minutocellus polymorphus*. This symbiont is different from those in other predominantly diatom-bearing foraminifera, possibly facilitating its ability to survive and calcify at 40°C (Schmidt *et al.*, 2018a). *Lachlanella* is a very common species in the shallow water hard bottom habitats along the Mediterranean coast of Israel

(Hyams-Kaphzan *et al.*, 2014). Its abundance within the thermal anomaly indicates a high thermal tolerance (Arieli *et al.*, 2011; Titelboim *et al.*, 2016).

Additionally to changes in physiology, warming is expected to influence other, less studied, responses of calcifiers such as changes in material properties of the calcite shell. The calcite is fundamentally important for the species survival as the shell provides protection for the organisms. Calcification under elevated temperatures increases the Mg/Ca ratio of calcite which in turn affects fundamental material properties such as hardness and elasticity as demonstrated in echinoderms (Wang *et al.*, 1997; Zhang and Reeder, 1999; Ma *et al.*, 2008; Xu *et al.*, 2009). The Mg/Ca ratio is furthermore positively correlated with the solubility of calcite in water (Chave *et al.*, 1962; Walter, 1984; Andersson *et al.*, 2008).

We use the thermal anomaly as a field laboratory to study the effect of heat stress on two thermally resilient species by comparing samples from the thermal anomaly and a control station and their seasonal variability. We applied Computed Tomographic (CT) imaging to specimens collected throughout a year to determine shell and calcite volume (following Schmidt *et al.*, 2013) in a warmer world scenario. To increase our understanding of changes to the crystallography of the shells we applied Raman spectroscopy. High-precision Raman spectroscopy is commonly used in fields such as materials science to detect very small changes to crystal lattices induced by external stimuli such as mechanical stress (Liu *et al.*, 2012). Here, we report such measurements to understand the magnitude of changes caused by warming to the crystal structure of calcite that could impact the resilience of these shells to external stressors such as predation, breakage and dissolution.

Methods

Study site and sample collection

The study site is located on the northern coast of Israel where, since the 1980s, a power plant has caused local thermal pollution creating an anomaly reaching up to 9°C above the natural baseline. There is no indication of chemical pollution in the area (Glazer, 2010, 2014). Specimens examined in this study were collected from two stations: Station H2, in the core of the heat plume, about 300m from the power plant (32.27° 41.0' N 34.52° 57.0' W) and, Station N, 18 km north of the powerplant (32.37° 23.2' N 34.55° 10.2' W) representative of the natural temperatures along the Eastern Mediterranean coast (Figure 1). These two stations represent a warmer world scenario and a control station.

Specimens were collected every month between March 2013 and January 2014 and provide a complete seasonal cycle with annual temperature ranges of 13–31°C in station N and 15–36°C in station H2 (Figure 2, daily averages (Titelboim *et al.*, 2016)). The environmental conditions and foraminiferal population at both stations, at a 0.5 m water depth, were monitored monthly during this period. The methods and results of this monitoring are described in detail in Titelboim *et al.* (2016). Briefly, the temperature was recorded every 15 min using *in situ* data loggers (Figure 2). Salinity (38–41psu), pH (8.1–8.3), and dissolved oxygen (5–9 mg/L) were measured monthly at the time of sample collection using an SI 6600 UPG sampler. Water samples were collected and analysed for their chemical composition and nutrient concentrations. The chemical composition of the water did not differ between the stations and was constant throughout the year. An increase in salinity, always lower than 1.5 psu was measured at the station H2 but is most likely not significant enough to affect the foraminiferal population

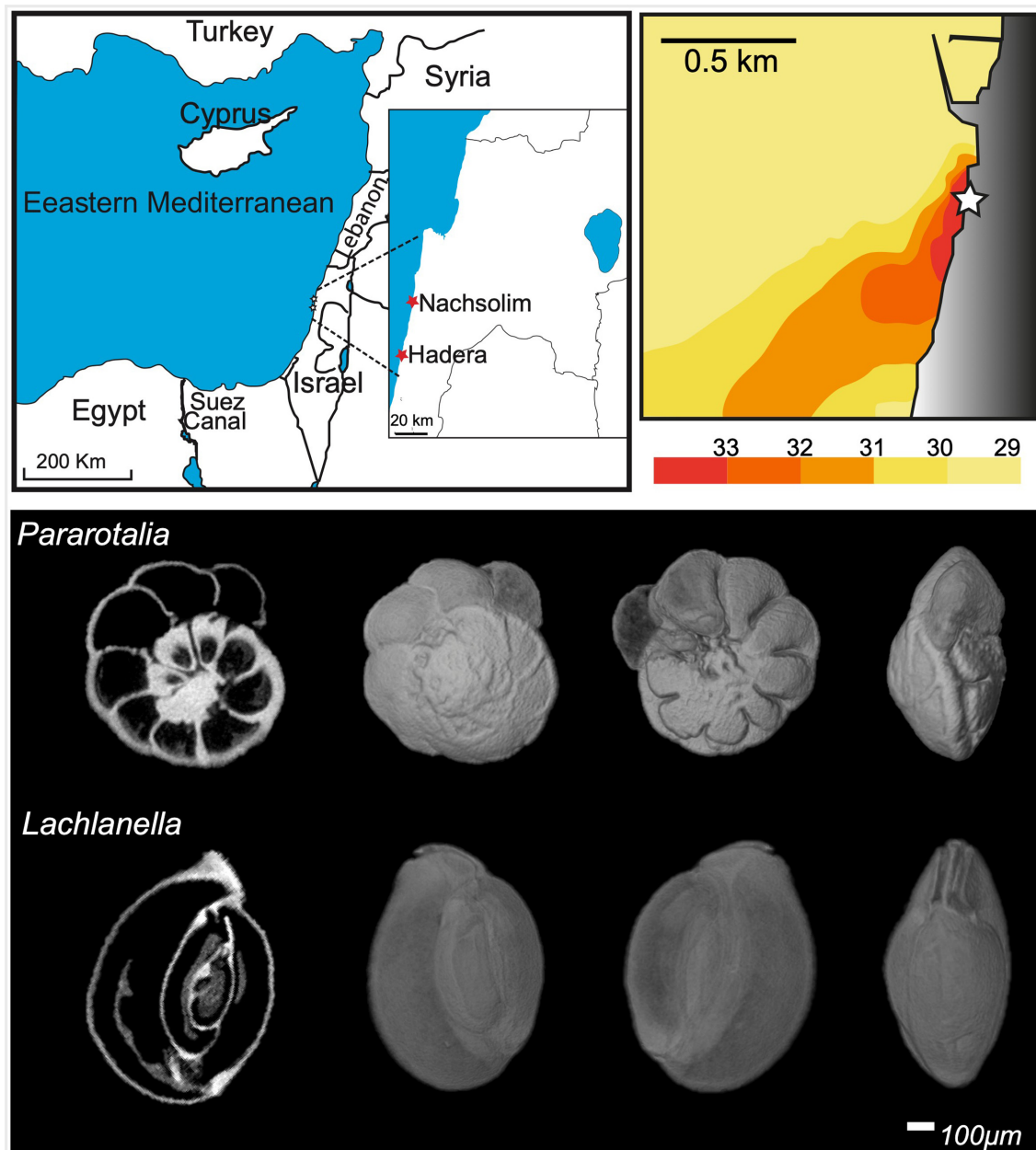


Figure 1. A graphical summary of the study's setup. Location map (top left) and illustration of the thermally polluted area in spring (top right) (modified from Glazer, 2014). The star is indicating the location of the warm station (H2). Bottom: Images of the CT scanned species: *P. calcariformata* and *Lachlanella*.

or their growth (Titelboim *et al.*, 2016). Samples of algal mats and the foraminifera within them were scrapped from the rocks surface with a flat knife and placed in Rose Bengal solution until further processing in the lab. Samples were collected from three sites within each station to include any spatial variation.

CT scanning and processing

To determine changes in shell morphology in response to environmental stress, 8–10 specimens of each species collected from each station during various months (for details see Supplementary Table S1 and Figure 2) were scanned using a Nikon XT H 225 ST CT scanner with an accelerating voltage of 80 kV, a beam current of 87–88 μ A and an exposure time of 0.7 s. Each scan consisted of 3141 projections resulting in images with a voxel size of 2.3–3.2 μ m. Images

were imported to the three-dimensional visualization software Avizo where pixels were manually assigned to the calcite shell according to their grey-scale value following methods established in Schmidt *et al.*, (2018b). The foraminiferal shell was reconstructed in 3D and surface area, shell volume, and calcite volume were measured for each specimen. Shell thickness is represented as the percentage of calcite volume to total volume of the shell calculated as $(\text{volume calcite}/\text{total volume}) * 100$ (= cc/volume ratios). For details on statistical analysis see Supplementary Tables S2 and S3.

Raman spectroscopy

To determine whether elevated temperatures affect the composition and/or crystal structure of the calcite, Raman spectroscopic analysis was performed on shells from stations H2 and N. This

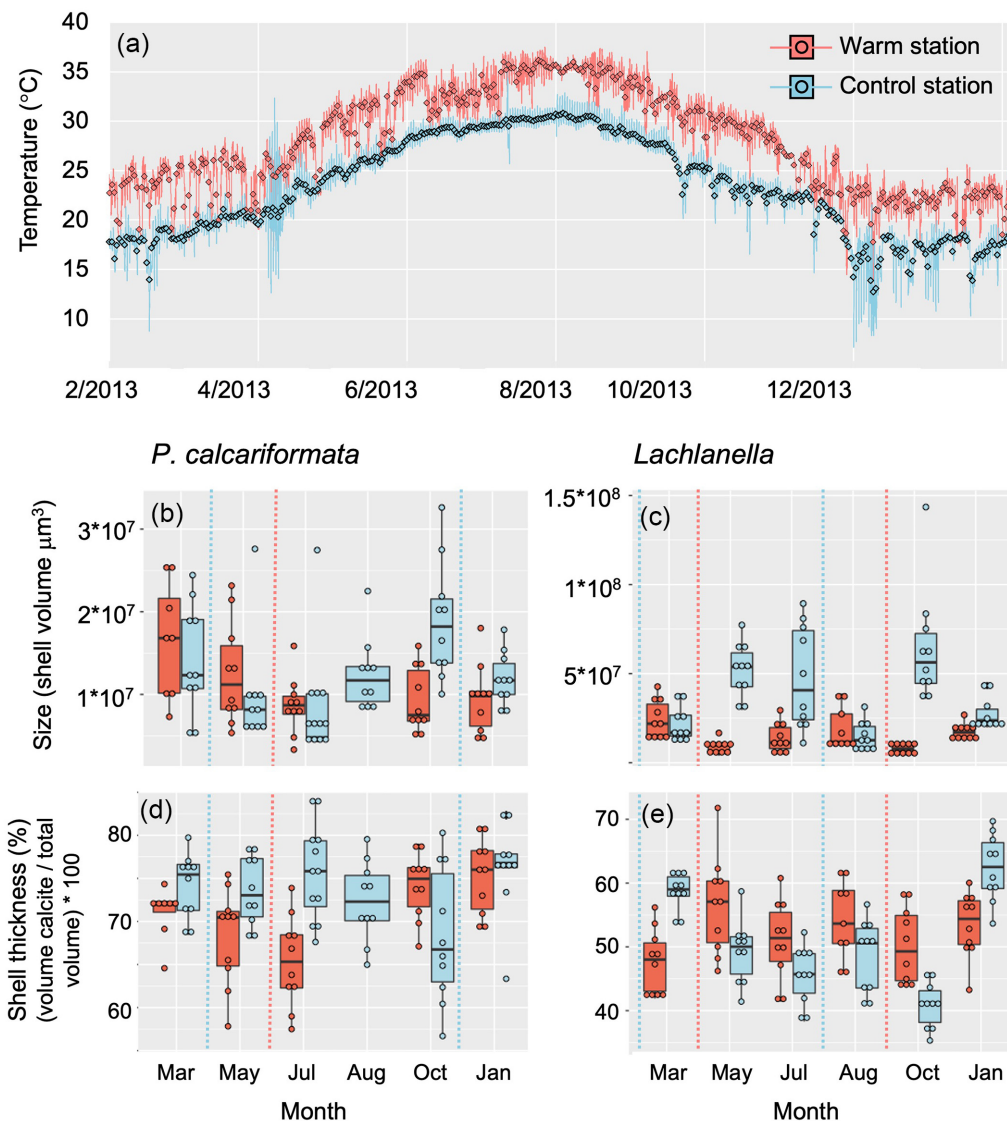


Figure 2. Temperatures throughout the sampling period (a) and differences in morphology between *P. calcariformata* (b and d) and *Lachlanella* (c and e) from station H2, (red) and N (blue). (a) Circles are daily average temperatures and lines represent the measurements taken by the data loggers. (b and c) Size is represented by the volume of the shell. (d and e) Shell thickness. Dotted vertical lines are estimated times of reproduction events in each station according to their colour.

technique is sensitive to subtle variations in the polarizability of bonds within the carbonate lattice which controls the position and shape of the Raman modes, as has been demonstrated for biogenic and synthetic carbonates (Bischoff *et al.*, 1985; Rividi *et al.*, 2010; Borromeo *et al.*, 2017). These previous studies have focused on establishing and calibrating the chemical composition of carbonates with changes in their Raman spectra, mostly focusing on Mg concentrations over a wide compositional range or across a broad range of different species. Since we are attempting to resolve very small differences within the same species, we provide a detailed description of our methodology.

We collected Raman spectra from shells of both species collected from both stations representing: minimum (January, station N), moderate (May, station N), and maximum (July, station H2) temperatures. For convenience throughout the paper, these examined groups will be referred to as “cold,” “moderate,” and “warm”

months. Since the winter in the Eastern Mediterranean is colder than the calcification threshold of both species, the specimens collected during the “cold” month do not represent the ambient temperature but a temperature near the minimum threshold of each species, 22°C for *P. calcariformata* and 15°C for *Lachlanella* (Titelboim *et al.*, 2017). As such, these specimens likely precipitated their shells under stress. To include the full temperature range over which both species calcify we also measured shells of *Lachlanella* collected in January from station H2 (this will be referred to as the “moderate cold” month). Average temperature in this month was just below 22°C, allowing *Lachlanella* to calcify during this time. This cold month was not sampled for *P. calcariformata* since its lower thermal calcification range is already captured by the moderate months in which the average ambient temperature was ~22°C.

We analysed between 6 and 15 *P. calcariformata* specimens and between 9 and 10 *Lachlanella* specimens from each group to

account for variability within each group, allowing us to identify statistically significant differences. In each shell we targeted the final chamber that would have formed most recently before collection. Differences in Raman spectra were analysed as a function of ambient temperature and Mg/Ca concentration of specimens from the same collection (see Titelboim *et al.*, 2017).

We examined three Raman modes of calcite: the two high-frequency external lattice modes relating to translational and librational motion between the cations and the oxygens to which they are bonded ($\sim 153\text{ cm}^{-1}$ and $\sim 282\text{ cm}^{-1}$, respectively) and the internal symmetric stretching mode of the $(\text{CO}_3)^{2-}$ anion group (ν_1 , $\sim 1088\text{ cm}^{-1}$, and Supplementary Figure S1). The internal in-plane bending mode (ν_4 , $\sim 712\text{ cm}^{-1}$) was too weak to be accurately fitted and thus was not considered in this study. All other vibrational modes were outside of the range that could be analysed without slewing the diffraction grating, which could reduce precision due to any non-kinematic behaviour of the driving motor. To determine whether differences between groups are significant we examined the measurements of each peak using the same approach described for the morphological data. Additionally, we applied a multivariate pairwise PERMANOVA test that considered all three peaks simultaneously.

Raman spectra were collected on a confocal Jobin Yvon Horiba T64000 instrument equipped with a 1200 l/cm diffraction grating yielding a spectral resolution of $\sim 1\text{ cm}^{-1}$, a Laser Quantum Torus 532 nm solid state laser source operating at 100% power ($\sim 500\text{ mW}$) and a 100x objective, yielding a diffraction limited focal volume with a diameter of $\sim 4\text{ }\mu\text{m}$. Each spectrum was generated from between 10 and 20 accumulations each with an exposure time of 10 s. The wavenumber-pixel relationship of the detector was calibrated using a weighted linear orthogonal distance regression to the following calibrants: the $321.0 \pm 0.5\text{ cm}^{-1}$ mode of CaF_2 , the $479.0 \pm 0.1\text{ cm}^{-1}$ mode produced by a Hg calibration lamp (Oriel instruments Model 6035), the $520.7 \pm 0.1\text{ cm}^{-1}$ mode of Si, and the $620.9 \pm 0.7\text{ cm}^{-1}$, $795.8 \pm 0.8\text{ cm}^{-1}$, $1001.2 \pm 0.5\text{ cm}^{-1}$, and $1031.8 \pm 0.4\text{ cm}^{-1}$ modes of polystyrene. In addition, the Hg calibration lamp was lit throughout the analysis session so that a constant wavenumber correction could be applied to every spectrum, accounting for minor spectral shifts caused by temperature fluctuations. The centre positions of Raman modes were determined to a precision of $< 0.4\text{ cm}^{-1}$ by fitting to Pseudo-Voigt functions in the software package fityk (Wojdyr, 2010). Repeatability based on multiple analysis of the Hg calibration lamp is estimated as 0.2 cm^{-1} .

Results

Shell morphology

Both species exhibited morphological differences between the stations, with a stronger response in *Lachlanella*. For each species, the surface area, shell volume, and calcite volume exhibited a similar trend and thus are here described together as size (Supplementary Figure S2). All measurements are presented in Supplementary Table S1 and the complete statistical analysis is available in Supplementary Tables S2 and S3.

The seasonal size trend of *Lachlanella* shells is similar in both stations and indicates two reproduction events in spring and in autumn, slightly shifted in time between the stations. However, their size is severely reduced at station H2 (Supplementary Tables S1 and S2; Figure 2c). The seasonal pattern in shell thickness (percentage of calcite from the shell) varies between the stations: at the control

station, N, shells are thinner from May to October with cc/volume ratios of 41–49% compared to 59–62%, (Supplementary Tables S1 and S3; Figure 2e) while at station H2 a the cc/volume ratios is in the range of 48–57% (Supplementary Tables S1 and S2, Figure 2e). This results in thicker shells in station H2 compared to station N through much of the year.

In contrast, shells of *P. calcariformata* exhibit a different response to the elevated temperatures. The seasonal size trend of *P. calcariformata* indicates that reproduction occurs once a year in station H2 (June) and twice in the station N (April and November). Shells in both stations reach the same maximum size during October in N and March in H2 (Figure 3b; Supplementary Tables S1 and S3). The cc/volume ratios in each station are different throughout the year but with no trend (Figure 3c; Supplementary Table S3). However, they are either of equal (October–January) or lower (March–August) cc/volume ratios in station H2 compared to station N. This indicates that shells are either equal or thinner, but never thicker as in the case of *Lachlanella*.

Shell crystallography

The ν_1 symmetric stretching mode exhibits a positive linear correlation with Mg/Ca. This is expected because the smaller radius of the Mg cation compared to the Ca cation, for which it substitutes, changes the strength of bonds within the calcite lattice (Chave *et al.*, 1962; Bischoff *et al.*, 1985). However, the centre position of this peak in shells of *Lachlanella* collected during the cold and warm months deviate from this simple linear relationship as evident in the higher residuals of these two groups (> 0.2 , Table 1, and Figure 3a). This deviation does not correlate to changes in Mg and thus plausibly represents changes in the crystal structure.

The centre position of the external lattice translational mode is significantly higher in *P. calcariformata* shells compared to those of *Lachlanella* (Figure 3b and e). It is similar between all *P. calcariformata* shells with a suggestion of a negative correlation to Mg (Figure 3b). In *Lachlanella* there is no dependence of this Raman mode on Mg content despite the differences in Mg between the moderate cold and the cold months (Figure 3b and e). In *P. calcariformata*, the position of the external lattice librational mode increases with Mg/Ca ($r^2 = 0.6$, Figure 3c) but does not create significant differences between shells collected under different thermal conditions (Kruskal–Wallis test: $p = 0.064$). In *Lachlanella*, there is no clear correlation with Mg; but specimens collected during the moderate and moderate cold months are similar to each other and different from those collected in the cold month. Shells collected during the warm month exhibit intermediate values. The lack of correlation between the external modes to Mg, indicates changes to the crystal structure rather than changes in chemical composition.

Multivariate statistical analysis (PERMANOVA) including all three Raman modes indicates a significant difference between shells of *Lachlanella* collected in the cold vs all other months. For *P. calcariformata*, significant differences were only identified between the cold and warm months although the p -value was very close to 0.05 indicating borderline significance (Supplementary Table S4).

Discussion

The morphological and crystallographic changes occurring in the unique field laboratory provides the opportunity to assess the calcification response of two species of benthic foraminifera to elevated temperatures. Both stations are similar in all physical parameters

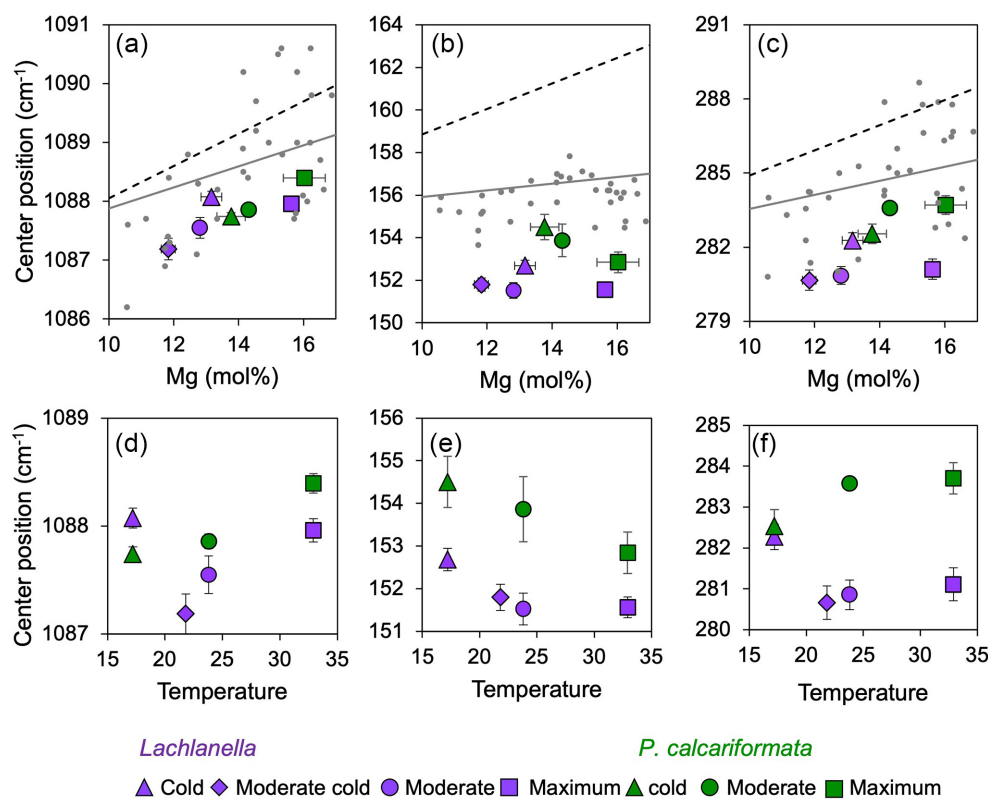


Figure 3. Correlation between Raman mode positions and Mg content in this study and in previously published data (a–c) and with ambient temperature before collection of the samples (d–f). Error bars are SE. In a–c, grey dots are data points from Borromeo *et al.*, 2017. The correlation by Rividi *et al.* (2010) marked with a black dashed line are of non-biological carbonates, Borromeo *et al.* (2017) marked with a grey continuous line is of biological carbonate of diverse organisms. The difference between them represents the impact of the biological control on the crystal structure. Note that data points from this study cluster together at the low end of Borromeo *et al.* (2017).

Table 1. Ambient and calcification temperatures for each thermal condition and their predicted ν_1 symmetric stretching mode, according to Mg concatenation including the residuals.

Species	Month, station	Group name	Average + SD ambient temperature	Average + SD calcification temperature	Predicted ν_1	Residuals
<i>Lachlanella</i>	May, control	Moderate	22.14 ± 2.1	21.6 ± 1.3	1087.6	−0.03
<i>Lachlanella</i>	July, warm	Warm	32.99 ± 1.7	30.1 ± 1.2	1088.2	−0.22
<i>Lachlanella</i>	January, warm	Moderate Cold	21.88 ± 1.9	18.6 ± 2.1	1087.4	−0.19
<i>Lachlanella</i>	January, control	Extreme cold	16.38 ± 2.5	22.6 ± 3.2	1087.7	0.41
<i>P. calcariformata</i>	May, control	Moderate	22.14 ± 2.1	29.6 ± 1.3	1087.9	−0.05
<i>P. calcariformata</i>	July, warm	Warm	32.99 ± 1.7	35.0 ± 3.1	1088.3	0.13
<i>P. calcariformata</i>	January, control	Extreme cold	16.38 ± 2.5	27.9 ± 3.1	1087.8	−0.05

other than the temperature. Thus, any other drivers of the observed changes, for example prey and predator abundance and their dynamics, would also be driven by temperature and thus provide a realistic response of foraminifera to a potential future warming. Our study examines species specific differences in species with a high thermal tolerance (Figure 1): *P. calcariformata* is more suited to the elevated temperatures in comparison to *Lachlanella*; while *Lachlanella* and the other species (*Rosalina globularis* and *Tretomphalus bulloides*) present in station H2 reduce their abundance when temperature reaches ~30°C, *P. calcariformata* retains high abundance up to ~33°C (Titelboim *et al.*, 2016). Additionally, *P. calcariformata*

calcify at higher temperatures compared to *Lachlanella* (Titelboim *et al.*, 2017) but do decrease growth rates above 35°C (Schmidt *et al.*, 2015, 2016). What has been little understood to date is the impact of heat stress on other traits such as calcification or reproduction of these two species with different thermal sensitivities.

Our results suggest that despite adaptation over generations, calcification of even highly tolerant benthic foraminifera species will be negatively affected by the warming projected to occur during this century. Even though *P. calcariformata* does not show a smaller shell size at station H2, calcification is reduced (Figure 2c). A similar response was observed in the shallow water species *Ammonia tepida*

(Dissard *et al.*, 2010), *Amphistegina lobifera* (Prazeres and Pandolfi, 2016), and *Sorites orbiculus* (Kinoshita *et al.*, 2021) under simulated warming in laboratory experiments. Among these are both symbiotic barren and symbiotic bearing species from different evolutionary groups (Pawlowski *et al.*, 2013) implying a consistent response across many benthic foraminifera species.

Lachlanella significantly reduced their shell size in station H2 but sustained similar shell thickness throughout the year (Figure 2b and d) suggesting a reduction in carbonate production but not a negative impact on the absolute ability of individual specimens to calcify. Differences in shell thickness in station N most likely result from different stages of ontogeny and thus do not exist in station H2 where growth is impaired due to thermal stress. Interestingly, the observed reduction of volume by around 50% in station H2 is similar to a record of calcification in deep-sea benthic foraminifera during a past record of abrupt warming, the Palaeocene–Eocene Thermal Maximum (PETM; Foster *et al.*, 2013). The PETM sediment, 56 Ma ago, recorded warming of 5°C (Honisch *et al.*, 2012), similar to the yearly average difference between station N and H2. The fact that both a deep sea and a shallow species show a similar response to warming might imply that a possible minimal size exists in benthic foraminifera, which is probably determined by the minimal space needed for the organism's cytoplasm. Further, the PETM species, exhibited thicker shells during the PETM compared to baseline conditions (Foster *et al.*, 2013). This observation can be possibly explained by evidence of acclimative mechanisms mitigating acidified conditions (without elevated temperature) for calcification (Stuhr *et al.*, 2021). However, results from our natural laboratory reveal thicker shells at station H2 compared to station N, and suggest that the thickening of the PETM species could be interpreted as a secondary effect of dwarfism and possible lower reproductive frequency.

The convergence of field, laboratory experiments, and observations from the geological record increases confidence in our ability to project impacts of rapid warming. Importantly, our findings highlight that while laboratory experiments report stress responses during short-term exposure such as shell thinning, they do not capture the more acute impact of chronic exposure such as dwarfism. Dwarfism strongly reduces the absolute amount of carbonate produced in response to stress (Abramovich and Keller, 2003; Garilli *et al.*, 2015; Schmidt *et al.*, 2018b). Under stress free conditions, calcification in planktic foraminifera has been suggested to equate to around 30% of the metabolic energy of an individual (Grigoratou *et al.*, 2019). Therefore, the reduction of the energy needed for carbonate precipitation allows a reallocation to other more basic physiological activities (e.g. metabolic processes) needed to survive in extreme conditions (DeSalvo *et al.*, 2010; Barshis *et al.*, 2013; Granados-Cifuentes *et al.*, 2013). Following the Q10-law (i.e. the doubling of the energy demands every 10°C, (Johnston, 1990; Tjoelker *et al.*, 2001), the food intake of the individuals would have to increase dramatically with warming in order to sustain all metabolic functions at the same rate.

Another important effect of future climate change on many organisms are changes to their reproductive cycle which affects body size as well as the number of individuals in a population (Lawrence and Soame, 2004; Grazer and Martin, 2012). Benthic foraminifera exhibit distinct thermal thresholds for reproduction (Murray, 1991), in this case resulting in changes in the life cycle of *P. calcariformata* at station H2. Changing the reproductive cycle has the potential to impact final body size due to delayed reproduction resulting in larger shell size (Poag, 1978), though the non-optimal

conditions may slow or limit growth resulting in smaller shells. Combined, these may result in “normal” shell size as seen in *P. calcariformata* that because of longer growth period did not reduce size even when its reproduction was impaired. The observed change in reproduction, combined with the observed change to their growth, implies that even before thermal thresholds for growth and calcification are exceeded, reproduction might be severely reduced by future warming. These changes might be related to the symbiont's sensitivity to heat-stress limiting the growth of *P. calcariformata* since if their photosynthesis is impaired, this might likely cause a decrease in growth and reproduction capacity (Hallock, 1981; 2021).

Annually, carbonate production by *P. calcariformata* at station H2 declined by ~10% and *Lachlanella* by ~60% compared with station N (Supplementary Table S1 and Figure 2). The numerical abundance of both species in station H2 declined by ~70%, compared to the control (Titelboim *et al.*, 2016). Based on this we estimate that under an average 5°C increase, although thermally tolerant, these benthic foraminifera could decrease their carbonate production by up ~73–90%. The geological record indicates an ecological shift from coral dominated to benthic foraminifera dominated ecosystems in response to warming thereby implying that the latter might be relatively more adaptable to compound drivers of ocean climate changes (Scheibner and Speijer, 2008; Kawahata *et al.*, 2019). Therefore, as coral calcification is already declining (Cantin *et al.*, 2010; De'ath *et al.*, 2012; Castillo *et al.*, 2014; DeCarlo *et al.*, 2019), this new evidence raises concerns about shelf inorganic carbonate production.

In addition to the decrease in carbonate production by calcifying organisms, it is also important to understand how warming causes changes to the material properties of the carbonate shells given their protective function. As Mg/Ca increases with temperature, warming is predicted to increase the susceptibility of shells to co-occurring acidification (Chave *et al.*, 1962; Andersson *et al.*, 2008). Material properties can also be affected by physiological adjustments in calcification as a response to changes in environmental conditions, previously referred to as crystallographic vital effect (Raja *et al.*, 2005; Coronado *et al.*, 2019; Singh *et al.*, 2021).

Previous studies indicate a positive linear correlation between Mg/Ca in the range of biogenic carbonates and the position of all Raman modes in both inorganic and biogenic carbonate (Bischoff *et al.*, 1985; Rividi *et al.*, 2010; Borromeo *et al.*, 2017). However, these are mainly driven by a wide range of Mg/Ca which in our much narrower range is only observed in the ν_1 peak (Figure 3). Moreover, our measurements cluster tightly toward the low end of the previously published Raman measurements of biogenic carbonate (Figure 3) which are scattered due to the variability in the crystallographic features of the shells of different organisms.

The two studied species both precipitate high Mg calcite shells but through different calcification mechanisms resulting in different shell type (de Nooijer *et al.*, 2009). Despite the differences in calcification, a positive and significant relationship is apparent between Mg/Ca, largely controlled by calcification temperature, and the ν_1 peak representing the symmetric stretching mode of the carbonate ion (Figure 3a). The deviation from the linear relationship is lowest in shells of both species collected in the moderate month and largest in *Lachlanella* shells collected during the extreme cold month (Table 1). This observation suggests that the biological control on calcite precipitation is impaired under cold stress. This interpretation is further supported by the significant changes in the external lattice modes in the same samples. Both the translational and librational motions (those of the CO_3^- anion relative to the Ca

or Mg cations) are different in *Lachlanella* collected during the cold month compared to the moderate months as indicated by a shift to a higher wavenumber of the corresponding modes. The same interpretation arises when all three modes are considered simultaneously (Supplementary Table S4). Such behaviour is clearest in *Lachlanella* and is probably related to its wider calcification temperature range compared to *P. calcariformata* (Titelboim *et al.*, 2017). Raman modes with higher wavenumbers are associated with higher Mg/Ca that affects the crystal structure and the correlated material properties such as hardness and elasticity (Wang *et al.*, 1997; Zhang and Reeder, 1999; Ma *et al.*, 2008; Xu *et al.*, 2009). However, our results show that under cold stress, *Lachlanella* precipitated calcite with higher wavenumber compared to its Mg content suggesting that its crystal structure is changed. We speculate that the impaired calcite precipitation in cold temperatures is creating a more defective crystal structure similar to that of higher Mg/Ca. These defects are impacting properties such as hardness and solubility which in turn affects the protection function of the shell against erosion, breakage, and ultimately dissolution. Thus, with warming, benthic foraminifera might produce less carbonate but their shells will have a less defective structure than shells created under cold stress, creating a more robust calcite with better performance against external stress. Further, our results show for the first time that Raman modes have the potential to be a highly sensitive proxy for the stress response in calcifying organisms. Combined with traditional proxies, they can provide new insight into physiological responses induced by past and present climate change.

Conclusions

Using a thermal anomaly as a field laboratory allows an understanding of the effect of future warming on reproduction and carbonate production of an important group of shelf calcifiers. Our results predict a reduction of calcite production through dwarfism. Combined with changes in reproduction, this projects a 73–90% decline in carbonate produced by these organisms. Our results further show that when calcified under cold stress, the calcite crystal structure is impaired. Thus, warming may improve the crystal structure produced allowing benthic foraminiferal shells, while fewer and smaller, to sustain the protective function of the shell against external stressors.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Data availability statement

The data underlying this article and the scanned data are available at the University of Bristol data repository, data.bris, at <https://doi.org/10.5523/bris.2dp6gppdz8krn278vks70p218m>

Conflict of interest statement

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

Acknowledgements

We acknowledge funding from the Royal Society: DT through a Royal Society–Kohn International Fellowship, OTL through a University Research Fellowship and DNS via Wolfson Merit Award.

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Handling Editor: Howard Browman