



Stress event alters skeletal structure but not geochemistry in a long-lived crustose coralline alga (*Clathromorphum compactum*)

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Received: 11 February 2026 / Accepted: 16 May 2026 / Published online: 9 June 2026
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Abstract

Crustose coralline algae (CCA) are foundational species in shallow-water marine ecosystems, playing a critical role in their structural and ecological integrity. Additionally, their calcium carbonate skeletons serve as high-resolution paleoclimate archives, offering valuable insights into historical oceanic variability. Here, the effects of bleaching under controlled culture conditions on skeletal structure and geochemistry were investigated in the long-lived subarctic CCA *Clathromorphum compactum*. Cell wall thickness, interfilament crystal thickness, and skeletal Mg/Ca ratios derived from weight% were quantified in material formed before and after bleaching. Skeleton deposited following bleaching exhibited a distinct transition characterized by irregular cellular organization and was significantly thinner than pre-bleaching growth. Reductions in thickness occurred in individuals that later recovered as well as in those that died, indicating that calcification continued during physiological stress. In contrast, no significant difference in Mg/Ca ratio was detected between pre- and post-bleaching skeleton. These results suggest that *C. compactum* exerts some control over the geochemistry at its calcification site, maintaining stability despite environmental stressors that impact calcification. Thus, bleaching can leave pronounced structural irregularities in CCA skeletons, potentially affecting skeletal integrity, even when geochemical proxies remain unchanged.

Keywords Marine carbonate · Crustose coralline algae · Bleaching · Environmental stressors · Scanning electron microscope · Geochemistry

Introduction

Crustose coralline algae (CCA) are key structural habitat formers in littoral and shallow sublittoral zones, producing substantial carbonate at rates comparable to coral reefs (Chenelot et al. 2011; Cornwall et al. 2023). CCA also contribute

to primary production, provide food for herbivores, and create critical settlement substrate for many invertebrates (Adey 1998; Chisholm 2003; Steneck 1983). In addition to their ecological importance, some CCA, particularly the genus *Clathromorphum*, serve as high-resolution paleoclimate archives. Their long lifespan (approaching a millennium) and annual banding provide a climate archive that can be geochemically sampled with a chronological precision of a few years (Adey et al. 2013). Their skeletal geochemistry documents ambient seawater properties during calcification: some trace element concentrations and stable isotopic values reflect that of the ambient seawater (e.g., Ba/Ca, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) while others reflect processes that determine their incorporation into the calcite lattice (e.g., Mg/Ca and $\delta^{18}\text{O}$ vary with seawater temperature) (Anagnostou et al. 2019; Doherty et al. 2021; Halfar et al. 2008; Hetzinger et al. 2013; Williams et al. 2011). Thus, measurements of these geochemical tracers over the lifespan of these CCA provide important insights into multi-centennial variability

Responsible Editor: A. Checa.

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in mid-to-high latitude ocean conditions (e.g., Chan et al. 2017a; Halfar et al. 2013; Williams et al. 2017).

Abiotic stressors can alter skeletal morphology and geochemistry in CCA, increasing vulnerability to external pressures (Nash and Adey 2017, 2018). One physiological response of CCA to stress is bleaching, the loss of surface pigmentation (Anthony et al. 2008; Calderon et al. 2024), which may be triggered by desiccation, freshwater input, low pH, thermal stress, or elevated light (Anthony et al. 2008; Latham 2008; Martone et al. 2010; Muth et al. 2020; Noisette et al. 2013). Under sustained high irradiance, CCA may bleach from rich pink to pale green or white, indicating photoinhibition (Irving et al. 2004, 2005; Littler 1973). Some CCA can recover, depending on damage severity and subsequent reductions in light levels (Figueiredo et al. 2000; Irving et al. 2004). Individuals can even retain reduced but measurable photosynthetic activity, indicating incomplete photoinhibition even while bleached (Irving et al. 2004). However, the effects and causes of bleaching are identified as areas requiring further research (McCoy and Kamenos 2015).

Here, we investigated how an unexpected bleaching event affected skeletal structure and geochemistry in *Clathromorphum compactum* during a culturing experiment in which some specimens recovered while others died. We quantified cell wall and interfilament crystal thickness as indicators of skeletal density, and thus integrity (Adey et al. 2013; Chan et al. 2017b; Rasher et al. 2020). Further, we measured Mg/Ca ratio to assess potential changes in calcification-site chemistry or diagenetic alteration. Understanding how bleaching alters these properties advances our understanding into CCA responses to acute environmental stress and informs the reliability of *Clathromorphum* skeletal geochemistry as a paleoclimate archive.

Materials and methods

Specimen collection and culturing experiment

Twenty-six living samples of *C. compactum* were collected from a single population located on the Schoodic Peninsula in the Gulf of Maine on November 6th, 2021, from between 9 and 12.2 m depth by divers using SCUBA. These samples were transported to the Schiller Coastal Studies Center (Bowdoin College, Maine), photographed the following day to document post-harvest pigmentation, and placed in a flow-through tank under ambient conditions to recover and acclimate to tank conditions.

On January 12, 2022, specimens were stained with calcein fluorescent dye as a time marker in the skeleton. A batch of calcein solution was prepared in a seawater tank

and an aliquot was transferred to an aquarium tank for staining the *C. compactum* specimens. The dye was dissolved until it reached a visual intensity comparable to successful prior experiments (~150 mg/L) (Figure S1) (McMahon 2022). Specimens remained in the staining tank for 24 h under grow lights (Agrobrite T5 - High Output Fluorescent Lighting System with T5 54 W/6400K bulbs) to promote growth and thus stain incorporation.

All 26 specimens bleached between 5 and 13 days after the calcein staining, shifting from pink to a white (Fig. 1). Specimens were then photographed to track bleaching, and either recovery or mortality. Recovery was defined as the return of pink surface tissue and was first observed on April 15 (94 days post-staining). Mortality was indicated by a persistent white to green coloration. Specimens were harvested on August 12th, 2022, November 23rd, 2022, and August 1st, 2023, either once they had largely recovered or had completely changed their hue to indicate mortality. Eighteen specimens partially or fully recovered, whereas eight did not recover and were classified as dead.

After collection, specimens were rinsed with freshwater, air-dried at room temperature, and shipped to the W.M. Keck Science Department of Claremont McKenna-Pitzer-Scripps Colleges (Claremont, California) for structural and geochemical analysis. Visual color assessment and fluorescence microscopy was used to identify post-stain skeletal growth. Of the 18 specimens that showed partial or full recovery, six were selected for further analysis based on sufficient skeletal growth during the experiment and the ability to fracture the specimen perpendicular to the growth axis to permit analysis. Of the eight specimens that died, four were selected for further analysis based on the ability to fracture the specimen to permit analysis (Table S1). The small sample size limits the inferential power of the statistical analysis. Further, a more robust skeleton aided in the fracturing process, for both living and dead specimens, and thus the subset of specimens analyzed might represent those specimens with the highest skeletal integrity of the full suite of specimens cultured.

Laboratory and data analysis

The ten specimens suitable for analysis were scored using a Dremel (300 Series) and vertically fractured perpendicular to the growth surface to preserve the calcite crystal structure. Fluorescence microscopy was used to locate the calcein stain, distinguishing the skeleton grown during the acclimation period from that grown post-bleaching event. The distance from the calcein stain to the outer growth edge of the specimen, representing the formerly living surface of the specimen, was measured three times, spread out across



B

Sample ID	1/12/22	1/27/22	4/15/22	5/24/22	6/08/22	6/21/22
72						
75						
76						
81						

Fig. 1 (A) Images of specimens on 11/7/21, one day after initial collection. (B) Timeline of bleaching and recovery in a subset of cultured CCA samples. Signs of bleaching are indicated by green and white

hue, while recovery in previously bleached samples is indicated by the reappearance of the pink hue

the surface, using digital calipers with a least count of 0.01 mm to quantify the extension rate.

Fractured specimens were etched for 40 to 60 min in a deionized-water sonic bath, dried at 40 °C for 24 h, mounted on aluminum scanning electron microscope (SEM) stubs,

secured with copper tape, and sputter-coated with Au/Pd for 2 min at 11 V. In six specimens (four recovered, two dead), multiple SEM images were stitched in Adobe Photoshop to create composite skeletal maps illustrating structural differences between wild and cultured skeleton. The fracturing

of the remaining four specimens did not lend themselves to composite skeletal maps. An additional non-bleached specimen from a prior experiment (McMahon 2022) served as a control (Figure S2). SEM imaging was conducted using a Hitachi SU-70 at 2,000 $\times$, 10 kV, and $\sim$ 8-mm working distance at Pomona College (Claremont, California). Images revealed a distinct transition zone of irregularly shaped cells. The distance from this transition zone to the outer edge of the skeleton was measured in the SEM images using ImageJ.

Mg and Ca weight% (wt%) were measured in wild and cultured skeletons using a Hitachi SU-70 SEM with a QuantaxTM Bruker EDS detector (15 kV, 12–13 mm working distance, > 10,000 cps). Energy channel calibration used a copper standard, and quantification employed P/B-ZAF standardless analysis. Expected Mg/Ca ratios (0.05–0.10) were based on prior coralline algae studies (Teichert et al. 2020). Wild-skeleton measurements targeted the oldest preserved skeletal material.

The Mg/Ca ratio derived from the wt% and thickness (μ m) of the cell wall, which is the inner layer of the elongated side of the cell wall, and the interfilament crystals, which are the vertically and/or diagonally oriented calcium carbonate crystals between cells, were measured in wild and cultured (recovered and dead) skeleton (Figures S3, S4). Fifteen measurements of the cell wall and interfilament crystal thickness in the wild skeleton, skeleton grown during the acclimation period, and skeleton grown post-bleaching event, were measured from the SEM images using ImageJ. Three to 15 measurements of the Mg/Ca ratio for the cell walls and interfilament crystals were taken in both the wild skeleton and skeleton grown post-bleaching event in each of the ten specimens.

Independent sample t-tests compared measurements in the skeletons grown in the wild versus the post-bleaching skeleton grown in culture and also the post-bleaching skeleton grown in culture in both specimens that died and those that recovered. ANOVA with post hoc Tukey tests evaluated differences among the wild, and both the acclimation and post-bleaching cultured skeleton. Prior to analysis, outliers were removed by identifying values outside of 1.5 times the interquartile range, and normality and equal variance were assessed using the Shapiro-Wilk normality test and Levene's test, respectively. Multiple measurements for a single specimen were averaged to avoid pseudoreplication, and only the mean values were statistically analyzed. All analyses were performed in Rstudio v2023.06.1. Since no difference in the cell wall and interfilament crystal Mg/Ca ratio was expected, these values were combined before analysis.

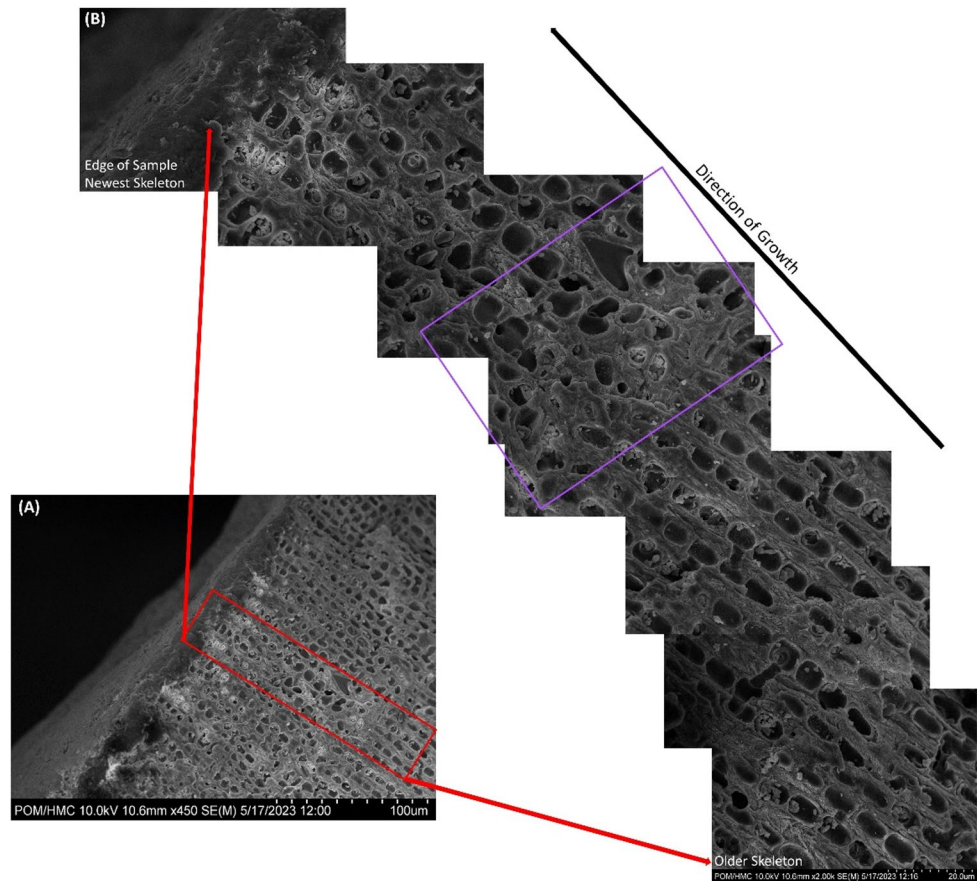
Results and discussion

All specimens exhibited bleaching shortly after the calcein staining procedure and transfer to the culturing tanks, with some later recovering (return of pink pigmentation) and others dying (persistent white–green coloration) (Fig. 1). Previous culturing experiments using similar acclimation and tank conditions did not induce bleaching (Anagnostou et al. 2019; McMahon 2022). Therefore, the bleaching event is attributed not to tank conditions but to acute stress associated with the calcein staining procedure, which occurred after specimens had acclimated. Light intensity was intentionally elevated during staining to promote calcification and stain uptake (Krieger et al. 2023a) and may have been higher than in previous experiments. Numerous studies show that intensified light exposure can induce bleaching in CCA (Figueiredo et al. 2000; Irving et al. 2004; Littler 1973; Kang et al. 2024), including in southern-hemisphere *Clathromorphum* (Calderon et al. 2024). This supports light-driven photoinhibition as the most likely trigger of the observed bleaching.

Among the specimens, skeletal extension from the calcein stain to the outer growing edge ranged from 140 to 380 μ m (Table S1). In the six specimens with SEM “maps,” a distinct transition zone was observed, characterized by irregular cell shapes, variable cell sizes, and partially infilled cell spaces (Fig. 2). The location of this transition zone relative to the outer edge matches the calcein-to-edge distance (Table S1), indicating that the irregular morphology visible in Fig. 2 formed after the bleaching event. In contrast, cells deposited before and after this zone exhibited more regular morphology. No comparable transition zone with irregular cell shapes was present in a non-bleached control specimen from a similar 2020 experiment (McMahon 2022; Figure S2). Together, these observations indicate that the irregular cells formed during or immediately following the bleaching event, rather than during the transition from the wild to the tanks. These results confirm that bleaching produced a temporary disruption in skeletal organization, yet calcification continued, consistent with prior work showing reduced but persistent photosynthesis and calcification in bleached CCA (Irving et al. 2004; Kang et al. 2024). Growth also occurred in specimens that later died, indicating that mortality was not preceded by cessation of calcification.

We quantified key skeletal properties in the CCA skeletons to evaluate the impact of the bleaching event (Table S1; Figures S3, S4). Both cell wall thickness and interfilament crystal thickness were significantly reduced in the skeleton grown post-bleaching relative to the skeleton grown in the wild (interfilament: $t(8) = -6.30$, $p < 0.001$; cell walls: $t(8) = -7.66$, $p < 0.001$; Fig. 3, Figure S3). These reductions indicate lower skeletal density (Chan et al. 2017b), a change

Fig. 2 (A) Overview and (B) map of the transition of skeleton grown in the wild (bottom right) to skeleton grown while being cultured (top left) within *C. compactum* specimen. Skeletal alteration during the transition area (bleaching event) is shown within the purple box



known to weaken CCA and increase susceptibility to grazing, bioerosion, and environmental stressors (Adey et al. 2013; Ragazzola et al. 2012). Such thinning likely reflects a physiological trade-off, enabling calcification to continue under stress but at the cost of reduced mechanical robustness (Chan et al. 2019; McCoy and Ragazzola 2014).

We also assessed whether the acclimation period affected skeletal development. An ANOVA with post hoc Tukey tests showed that the skeletal thickness immediately preceding the bleaching event—representing material deposited during acclimation—remained significantly thicker than that of the post-bleaching skeleton ($p=0.004$, 95% CI [0.30, 1.68] for interfilament crystals; $p<0.001$, 95% CI [0.12, 0.29] for cell walls) and statistically indistinguishable from the skeleton grown in the wild ($p=0.13$ and $p=1.00$, respectively; Table S1). This indicates that structural thinning began only after the onset of the bleaching event rather than during tank acclimation. Previous work using microCT similarly reported reduced density in cultured relative to wild skeletons, even in the absence of bleaching (Williams et al. 2021). The earlier findings likely reflect increased open cell space, whereas the present study demonstrates a reduction in the thickness of structural components themselves. Thus, the skeletal thinning is likely attributable to bleaching rather than acclimation to tank conditions.

No other parameters affected skeletal structure thickness after the transition zone in the cultured specimens. Thickness did not differ significantly between specimens that ultimately recovered and those that died (interfilament crystals: $t(6.38)=-0.22$, $p=0.83$; cell walls: $t(6.63)=-0.20$, $p=0.85$; Fig. 3). These results suggest that although specimens continued to calcify during bleaching, skeletal thinning did not progress to a critical threshold before mortality; instead, death appears to have occurred abruptly. For the individuals that survived, resumption of growth did not restore skeletal thickness to pre-stress levels. Additional work is needed to determine whether, and over what timescale, skeletal density can fully recover following severe stress.

No significant difference in Mg/Ca ratio was detected between skeleton grown in the wild and in the skeleton grown post-bleaching ($t(17.90)=-0.78$, $p=0.45$), nor between recovered and dead specimens within the cultured skeletons ($t(7.60)=0.19$, $p=0.85$; Fig. 3). In *C. compactum*, Mg incorporation into calcite typically increases with temperature (Williams et al. 2014). It can also vary with environmental conditions, including light levels, which modulate calcification rates (Williams et al. 2018). In other marine calcifiers, bleaching has had inconsistent effects on Mg/Ca ratios (Schoepf et al. 2014), in contrast to the lack of change observed here. Furthermore, specimens were

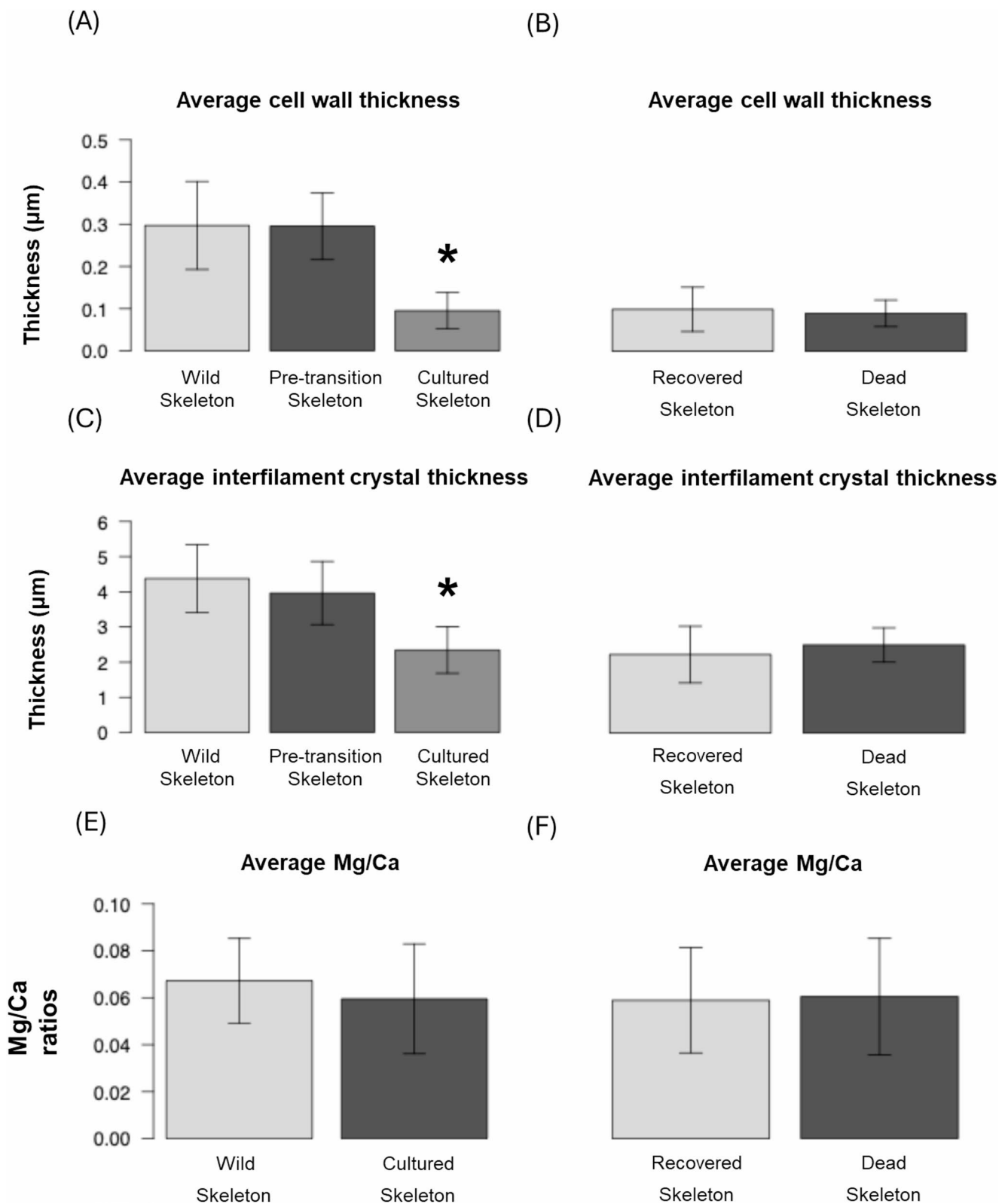


Fig. 3 Comparison of (A) average cell wall thickness in skeleton grown in the wild, during the acclimation period, and post-bleaching event, (B) average cell wall thickness in recovered and dead skeleton, (C) average interfilament crystal thickness in skeleton grown in the wild, during the acclimation period, and post-bleaching event, (D) average interfilament crystal thickness in recovered and dead skeleton, (E)

average Mg/Ca ratios in skeletons grown in the wild and post-bleaching event, (F) average Mg/Ca ratios in recovered and dead skeleton with percent change and standard deviation of averages represented by error bars (mean $\pm$ 95% CI). Significant differences (asterisks) between averages determined by post hoc Tukey tests

collected in the early winter and cultured at ambient temperature through the summer and the subsequent year. Despite this temperature variability, Mg/Ca ratio was stable. The absence of a detectable temperature effect on Mg content aligns with studies reporting weak or absent temperature–Mg relationships, with Mg/Ca instead linked to linear extension rates (Anagnostou et al. 2019; Krieger et al. 2023b). Collectively, these findings suggest that *C. compactum* maintained a stable internal Mg/Ca ratio across bleaching and culture conditions and showed no evidence of Mg loss via dissolution, even in specimens that died.

These findings provide evidence of the impact of bleaching on skeletal structure in an ecologically important mid- to high-latitude species of CCA. Likely induced by light stress during enhanced light exposure, bleaching produced a distinct transition zone characterized by a visible irregularity in cellular organization, not present in a non-bleached cultured specimen. Although some individuals recovered and others died, all bleached specimens showed reduced skeletal thickness after bleaching compared with wild-grown skeleton. In contrast, the study detected no significant difference in Mg/Ca ratio between wild and post-bleaching skeleton under the conditions and sample size examined. Thus, while the bleaching event did not specifically compromise the use of the CCA as a proxy archive, it does suggest that the CCA does not always faithfully document ambient seawater temperatures in the Mg/Ca content of its skeleton. Importantly, the reduction in skeletal structure thickness provides evidence of the impact of stressful environmental conditions on CCA and points to the increasing vulnerability of this species in a rapidly changing ocean.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-026-04882-x>.

Acknowledgements We thank Caitlin Cleaver and Phoebe Jekielek for collecting the specimens, Bowdoin undergraduates Jean Clemente, Alexis Mullen, Lucie Nolden, and Lemona Niu for experiment maintenance and carbonate chemistry analysis, Joe Tourtelotte for SCSC facilities assistance, and Henry Zucco for editorial feedback.

Authors' contributions SMB: Methodology, data curation, formal analysis, writing – editing; BW: Conceptualization, supervision, methodology, formal analysis, writing – review & editing; ADW: Conceptualization, supervision, writing – review & editing; KG: Methodology, writing – editing; HF: Methodology, writing – editing; ML: Conceptualization, supervision, writing – review & editing; All authors read and approved the final manuscript.

Funding Open access funding provided by SCEL, Statewide California Electronic Library Consortium. NSF OCE-MGG #2333620 to BW and #2028212 to ML supported this research. Maine Sea Grant NA18OAR4170103 to ML, BW, and ADW supported this research.

Data availability All data are included within this manuscript and Supplemental Information.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The approval of a research ethics committee was not required for this study as it deals with a non-endangered or otherwise regulated alga species.

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