

Modelling the
coralline algal
skeleton

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Potential and limitations of finite element modelling in assessing structural integrity of coralline algae under future global change

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Abstract

Coralline algae are important habitat formers found on all rocky shores. While the impact of future ocean acidification on the physiological performance of the species has been well studied, little research has focussed on potential changes in structural integrity in response to climate change. A previous study using 2-D Finite Element Analysis (FEA), suggested increased vulnerability to fracture (by wave action or boring) in algae grown under high CO₂ conditions. To assess how realistically 2-D simplified models represent structural performance, a series of increasingly biologically accurate 3-D FE-models that represent coralline algal growth were developed. Simplified geometric 3-D models of the genus *Lithothamnion* were compared to models created from computed tomography (CT) scan data of the same genus. The biologically accurate model and the simplified geometric model representing individual cells had similar average stresses and stress distributions, emphasizing the importance of the cell walls in dissipating the stress throughout the structure. In contrast models without the accurate representation of the cell geometry resulted in larger stress and strain results. Our more complex 3-D model reiterated the potential of climate change to diminish the structural integrity of the organism. This suggests that under future environmental conditions the weakening of the coralline algal skeleton along with increased external pressures (wave and bioerosion) may negatively influence the ability for coralline algae to maintain a habitat able to sustain high levels of biodiversity.

1 Introduction

Since the pre-industrial era CO₂ concentrations have risen by more than 100ppm (Ciais et al., 2013). The ocean has absorbed approximately 30% of the total anthropogenic CO₂ emissions (Rhein et al., 2013). This has led to a change in the carbonate chemistry of the ocean, resulting in a lowering of the carbonate saturation state and a decrease in ocean pH, a process termed “ocean acidification” (Caldeira

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and Wickett, 2003). Future projections suggest an additional average decrease in pH of between 0.13 (RCP 2.6) and 0.42 units (RCP 8.5) by the year 2100 (Pörtner et al., 2014). Calcifying organisms are at risk as the lower carbonate saturation state may affect the ability to calcify shells and skeletons (Diaz-Pulido et al., 2011; Fabricius et al., 2011; Kroeker et al., 2010). In response, ecosystem shifts are predicted to occur; for example sea-grasses and kelps may outcompete calcifying algae as the major habitat formers in shallow water habitats (Fabricius et al., 2011).

Rhodoliths (Fig. 1), non-geniculate free living (live and dead) coralline red algae (Foster, 2001), are an extremely diverse group of benthic calcifying organisms found from the polar to the tropical regions and low intertidal zones to 150 m deep (Foster, 2001). They are major contributors to the global inorganic carbon budget in shallow water ecosystems (Mackenzie et al., 2004). The largest rhodolith bed found on the Abrolhos shelf contributes roughly 5 % to the global calcium carbonate budget (Amado-Filho et al., 2012). Additionally these benthic ecosystems support a high level of biodiversity by forming structurally and functionally complex habitats (Nelson, 2009) for many organisms including polychaetes, crustaceans and molluscs (Foster, 2001), as well as being an important nursery grounds to commercial species including scallops (Grall and Hall-Spencer, 2003). Coralline algae biodiversity and habitat complexity are directly correlated; species richness and abundance of, in particular, arthropods, annelids and cnidarians, are known to increase as rhodolith size and branching increases (Foster et al., 2013). However coralline algae are ecologically fragile due to their slow growth rate of $\sim 1 \text{ mm yr}^{-1}$ (Freiwald and Henrich, 1994) and sensitivity to physical disturbances such as extraction and dredging.

Furthermore, as they form high Mg-calcite skeletons, the most soluble polymorph of calcium carbonate (CaCO_3) (Andersson et al., 2008), coralline algae are more susceptible to ocean acidification than other organisms that utilise different polymorphs of calcium carbonate. Consequently, a significant loss of rhodoliths from the North Atlantic by the year 2100 has been predicted (Brodie et al., 2014). However laboratory experiments have shown highly varied responses to elevated levels of CO_2 . Coralline

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algae (*Neogoniolithon* sp.) and calcareous green algae (*Halimeda incrassata*) exposed to increased CO₂ concentrations (606 and 903 ppm for 60 days) showed an increase in calcification (Ries et al., 2009); whereas another study on *Lithothamnion glaciale*, a cold temperate coralline algae, displayed a decrease in growth rate at elevated CO₂ conditions (589 and 755 μatm for three months) (Ragazzola et al., 2012), while also showing evidence for potential acclimation after ten months (Ragazzola et al., 2013).

Coralline algae have many pressures to withstand in their natural environments, including wave action and bioerosion, while maintaining a structurally and functionally complex habitat. Under elevated CO₂ conditions the algal skeleton appeared to be weakened (Ragazzola et al., 2012), thereby favouring erosion and breakage (Kamenos et al., 2013; Ragazzola et al., 2012).

Finite Element Analysis (FEA) is a technique that reconstructs the stress, strain and deformation in structures (Zienkiewicz et al., 2005). Originally developed for mathematical and engineering applications, it has recently become an established technique in zoology and palaeontology to understand morphology, function and evolution of hard tissue structures (Rayfield, 2007). Using material properties (Young's modulus and Poisson's ratio) and adequate boundary conditions (magnitude and direction of loading and constraints), mechanical performance of complex structures can be inferred. Ragazzola et al. (2012) were the first to use FEA in ocean acidification studies by creating simple 2-D FE-models of coralline algae to quantify the effect of elevated CO₂ on the skeleton of *Lithothamnion glaciale*. Specimens grown under CO₂ conditions simulating CO₂ predictions for the year 2050 were found to have larger cells and thinner cell walls that resulted in increased vulnerability to fracture compared to present day structures (Fig. 2a and b) as observed in the 2-D FE-model.

Simple 2-D models represent the mechanical performance of a cross-section of uniform thickness (1 μm) (Ragazzola et al., 2012) through the algal structure. Due to their simplistic nature, these models may have overestimated the distribution and magnitude of stress and hence future vulnerability of algal communities. Here we have developed a set of 3-D FE geometric models to represent different aspects of coralline

algae morphology and compared these models with a more biologically accurate 3-D FE-model generated from computed tomography (CT) data, allowing us to assess the trade-off between computing time (Andersen and Jones, 2006; Romeed et al., 2006) and the need for an appropriate representation of the structure. Finally, we use our improved understanding of the performance of the 3-D models to re-assess the impact of current and future ppm CO₂ induced changes to morphology on the ability of algal communities in maintaining a high level of biodiversity.

2 Materials and methods

2.1 Model geometry

Four 3-D FE-models with different coralline algal features were created based on the measurements and properties of Ragazzola et al. (2012) models. All 3-D geometric models were created and analysed in the Finite Element software package, Abaqus/CAE, v.6.10, (Simula, USA, Dassault Systèmes, //Simula, Providence, RI, USA), following the protocol established by Ragazzola et al. (2012).

Firstly, the 2-D models from Ragazzola et al. (2012) were expanded, using the extrude command in Abaqus, to create a 3-D model with the same area, all length and width dimensions (78.92 μm × 72.46 μm) were unchanged, but a depth of 80 μm was used instead of 1 μm. Size of the individual cells mirrored that of the 422 μm model of Ragazzola et al. (2012), with an individual cell height of 6.3 μm and width of 5.15 μm and an inter- and intra-wall thicknesses of 2.68 and 0.86 μm respectively. This structure is assigned the label “Corridor model” (Fig. 3a).

2.1.1 Compartmentalised (individual cell) model with current/422 μm CO₂ cell size

Although the cellular width and height in the Corridor model represented the dimensions recorded by Ragazzola et al. (2012) from SEM images, the cells are not

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represented as discrete entities and instead are represented as hollow calcite “tubes”. As algal cells grow apically, they form a lattice of individual cells, hence a second model, “Compartment model” (Fig. 3b) was created in which cell walls were added in the Z direction to create discrete cellular spaces. All dimensions apart from the depth of the individual cells and divisions between cells in the z direction were the same as the corridor model. It was assumed the depth of the cell was the same as the width (5.15 μm) and the divisions between the cells in the z direction were the same as the inter cell wall divisions (2.68 μm).

2.1.2 Biologically realistic model

Computed tomography (CT) scans of *L. glaciale* derived from the TOMCAT beamline at the Swiss Light source, Switzerland (see Ragazzola et al., 2012) were imported into *Avizo* V8.0 (VSG) software package. Each scan was 150 projections over 180° using a 15 keV energy beam with UPLAPO 10 \times objective. The field of view was 1.5 mm \times 1.5 mm and the pixel size was 0.74 mm \times 0.74 mm. A 3-D cube of similar dimensions (80 μm \times 80 μm \times 80 μm) as the geometric models was created but instead capturing the actual morphology of the rhodolith (known as the “Biological model”) (Fig. 3c). The scans were thresholded in *Avizo* and then exported to *Hypermesh* (v.11; part of the *Hyperworks* package from Altair, MI, USA) to create FE-models, which were analysed in *Abaqus* v6.10.

2.1.3 Compartmentalised (individual cell) model with 2050/589 μatm CO_2 cellular size

A final model, “the OA model” (Fig. 3d), was created by adjusting the cell size and spacing to represent the dimensions of the future 589 μatm CO_2 model as a 3-D and compartmentalised structure with overall dimensions (74.99 μm \times 77.2 μm \times 80 μm), individual cell dimensions (11.7 μm \times 7.99 μm \times 7.99 μm) and intra and inter-cell wall dimensions (0.685 and 0.829 μm) respectively. This future predicted CO_2 model was

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compared to the performance of the 3-D compartment model with current CO₂ ppm cell size.

In order to compare the 2-D to 3-D geometric models, the corridor model was meshed with 4-node linear, hexagonal elements. As tetrahedral elements were better at capturing the complex geometry of the Biological model, all models were then meshed with 4-node linear tetrahedral elements in order to be compared to the Biological model and to each other.

In keeping with Ragazzola et al. (2012), all models were assumed to be composed of a linearly elastic, isotropic, homogeneous material with a Young's Modulus of 36 GPa and a Poisson ratio of 0.31 (properties of calcite) (Tanur et al., 2010). Even though these material properties do not accurately represent the heterogeneities in the specimen and their material properties this approach gives a comparative insight into how different geometries affect the overall strength of a structure.

A load pressure of 20 000 Pa, assumed to simulate boring by organisms, was applied to the top left corner, 40 μm along the external surface and down the left surface of the models. Whereas constraints were applied to the bottom right corner, all along the bottom surface and 40 μm up the right hand surface, to simulate the attachment of the structure to the rest of the thallus (Ragazzola et al., 2012) (Fig. 4).

In order to compare the impact of predators on the different 3-D geometric models, stress and strain results were calculated. Stress results were also visually mapped onto the models as scaled colour plots. Stress, generated by the applied load (force) on a given area, is represented by the von Mises stress, a function of each of the principle stresses that represents tensile or compressive stress (Rayfield, 2007). Average stresses were calculated by dividing the von Mises stress by the element size to account for differing number of elements between models. Total strain energy refers to the energy stored in a system as a load is applied, which is a useful variable to record in mineralized structures as the more strain in a system leads to a larger amount of potential energy available for fracture (Gordon, 1978).

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Stress and strain energy are linearly dependent on surface area and volume respectively (Dumont et al., 2009), hence the applied pressure was rescaled for the biologically realistic model to rule out the effect of increased Mg-calcite volume on modelling stress and strain. To account for the increase in volume of calcite between the 2-D and the 3-D model, as strain energy is dependent on volume, the strain energy was calculated for the 3-D model using the following equation, outlined by Dumont et al. (2009);

$$U_{B^*} = (V_B/V_A)^{1/3}(F_A/F_B)^2 U_B \quad (1)$$

where U_{B^*} is the total strain energy for model B corrected for calcite volume, V_A and V_B are the volumes for the models A and B respectively, F_A and F_B are the loads applied to the two models and U_B is the total strain energy for model B.

The von Mises stress was displayed graphically on the model, with warm colours (red/orange) indicating areas of high stress and cool colours (blue) indicating areas of low stress, while average stress values and total strain energies can be found in Table 1.

3 Results

A similar stress distribution was observed in the 2-D and 3-D geometric model (Corridor model) (Fig. 5a and b), with areas of high stress occurring along the intra-cell walls and adjacent to the constrained surface. The average von Mises stress of the two models was very similar (Table 1), indicating that the simple 2-D model (Fig. 5a) was an accurate representation of the stress in a simple 3-D geometric model (Fig. 5b). As expected, the total strain energy in the 3-D model was over 500 × higher than the 2-D model, showing that the 3-D model with a larger volume was able to store more than the relative amount of strain energy compared to the 2-D model.

Once the complexity of the 3-D model was increased to better represent the natural structural complexity, differences between the simple 3-D model (Corridor model) and

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the more complex models became evident (Fig. 6a–c). In the compartmentalised model of current CO₂ conditions (Fig. 6b), both, the average stress and total strain energies were lower than the Corridor model (63 and 76 % respectively) (Table 1). The addition of cellular walls in the Z direction removed regions of peak stress near the constraints as stresses now dissipated throughout the structure, stabilising the model.

The results of the comparison between the 3-D geometric models (the Corridor and Compartment model) and the realistic model of similar dimensions generated from CT scans (the Biological model) showed that a similar average stress, strain energy (Table 1) and stress distribution (Fig. 6b and c) was observed between the compartmentalised model and the biologically realistic model.

As the compartmentalised model was similar in performance to the biologically realistic model, we used this model to assess the impact of ocean acidification (Fig. 2c and d). The change in wall thickness and cell size in the 589 µatm/2050 model led to a near doubling of average stress and a doubling of the total strain energy (Table 1). This increase in strain energy was less suggested using the simple 2-D models, which predicted an increase in average stress of 309 % and strain energy of 1421 %.

4 Discussion

Ragazzola et al. (2012) used 2-D FE-models to predict if changes to coralline algae cellular morphology induced by higher CO₂ concentrations generate a structure that might less able withstand stresses compared to current specimens. They predicted that increased CO₂ and resulting ocean acidification will create a structure more susceptible to fracture in response to environmental stressors such as wave action and boring. This 2-D model was the first step in assessing the structural and mechanical consequences of high CO₂-induced changes to growth structure, but it is important to note that it represented a 2-D approximation of a complex 3-D structure. Here our results showed that a 3-D extrapolation of the 2-D FE-model (Corridor model) generated comparable patterns and magnitudes of average stress to the 2-D model. However, once the

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complexity of the 3-D model was altered to approximate cellular compartments and compared to a biologically realistic model generated from SRXTM data, it became clear that stress and strain energy magnitudes in the simple 2-D and 3-D models were an over-estimation.

5 Coralline algae grow apically with lateral cell fusion being very common (Irvine and Chamberlain, 1994). This creates a vast network of individual cells able to oppose stress in all directions (Gordon, 1978). The importance of these structures is highlighted by the geometric model with compartments (the Compartment model) being the most stable of the geometric structures assessed and also most comparable,
10 in terms of stress distribution and magnitudes of average stress and total strain energy, to the biologically realistic model. This highlights the importance of geometry changes to the distribution and magnitude of stress. This occurrence was also observed by Romeed et al. (2006) who previously found that changes in the geometry between their 2-D and 3-D models of a restored premolar tooth also affected their displacement and profile stresses.
15

Creating the FE-model of the biologically realistic structure (the Biological model) from SRXTM data was a time consuming process compared to the user effort required to generate the compartmentalised geometric model (the Compartment model). As these different models produced very similar measures of average stress (2.75×10^{10} compared to 2.74×10^{10} Pa for the geometric and the biological model respectively), comparable measures of total strain energy (0.00427 compared to 0.00521 pJ) and a similar stress distribution, we propose that the compartmentalised geometric model presented a time efficient opportunity to manipulate geometric features to test hypotheses of mechanical performance and structural integrity.
20

25 Hence this model was used to assess the impact of ocean acidification changes to the cell growth on structural integrity. When the cellular size of the 3-D model was adjusted to reflect 589 μ atm growth conditions, the structure was less “efficient” than the structure under current environmental conditions, with a higher average stress and total strain energy. It is important to note though that the increase in stress

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and total strain energy magnitude was less pronounced than that suggested by the 2-D models, indicating that the extra cellular walls aided in stabilising the thinner cell walls of the model. This finding was in agreement with other work showing that microstructural features affect the mechanical properties of cellular solids (Gibson, 2005). For example, wood has a stiffness to weight ratio equal to steel, which is partly due to the arrangement of cells in a honeycomb structure (Gibson et al., 2010). Hence these features provide habitat forming organisms with a larger structural integrity to withstand external pressures and the ability to live in a highly dynamic environment such as the coastal shelf.

Although our geometric and biological models show congruence, they are still simplifications of the heterogeneities in the algal skeleton. A factor which was not considered in this study is the potential effect of changing material properties due to global change on the algal skeleton. Material properties are affected by the concentration of Mg in the skeleton (Ma et al., 2008), which is dependent on temperature (Kamenos et al., 2008) and potentially pH (Ragazzola et al., 2013; Ries, 2011). Mg incorporated into the calcite lattice increases the lattice distortion, which causes an increase in the sliding resistance and deformation resistance to crystals (Wang et al., 1997). Ma et al. (2008) found that due to a much larger difference in mol% of MgCO_3 (just below 40%), the high Mg-calcite polycrystalline matrix of the tooth of a sea urchin had a significantly higher elastic modulus (E) and hardness (H) value than both synthetic calcite and the single crystalline needles.

Sea surface temperatures in the North Atlantic are predicted to rise 2.5°C by the end of the century (Rhein et al., 2013). This rise in temperature corresponds to a 3% increase in mol% of MgCO_3 (Kamenos et al., 2008). As a 3% change in mol% of MgCO_3 is within the natural variation between specimens (Ragazzola et al., 2013), we suggest such a mol% change in MgCO_3 will not significantly impact the material properties and hence affect the skeleton. However Ma et al. (2008) also suggested the large difference in material properties wasn't due to just the difference in mol% of

MgCO₃ but also due to the orientation and uniform size of the crystals. This illustrates that Mg/Ca ratios are not the only factor which affects material properties.

Proteins are also known to affect material properties as the incorporation of organic macromolecules reduces the brittleness and enables plastic deformation (Berman et al., 1988; Ma et al., 2008; Wang et al., 1997; Weiner et al., 2000). The presence of chitin and collagen within the skeleton of *Clathromorphum compactum* aids calcification and increase skeletal strength (Rahman and Halfar, 2014). Implementing accurate material properties specific for specimens grown under a wide range of conditions into the model would allow a more accurate assessment of whether phenotypic variability in material properties has the potential to counteract structural changes in response to ocean acidification.

Using these more biologically accurate models, we have confirmed previous results that future climate change will lead to a loss in the structural integrity of coralline algae. We have shown that by increasing the complexity of a simple 2-D geometric model to a 3-D geometric model we can obtain informative data on the effect of ocean acidification on the structural integrity of the coralline algal skeleton, without need for complex real biological models derived from CT scanning that take ample computer time to construct and analyse. As the oceans are becoming more acidic, with concurrent calcification pressure, it is vital to understand the potential effect of ocean acidification on the skeletons of these habitat forming organisms to infer whether they are able to maintain habitats in the future. As coralline algae are major habitat formers, with the diversity and abundance of species dependent on their structural complexity, weakening of the skeleton under high CO₂ conditions will affect the organisms that rely on coralline algae as a habitat with important consequences for marine ecosystems. Our model results, along with bioerosion, rising sea levels (Rhein et al., 2013) and predicted increases in frequency and intensity of storm surges (Knutson et al., 2010) strongly suggest that coralline algae will be under more intense environmental pressure in future CO₂ scenarios.

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It is important to note that recent long term studies have shown calcifying organisms acclimating to ocean acidification for example cold water corals sustaining growth rates (Form and Riebesell, 2012) or coralline algae decreasing growth rates to maintain cell wall thickness (Ragazzola et al., 2013). The consequence of this sustained growth on the material properties and structural integrity has not been assessed and poses an open question with regards to their ability to provide habitats in the future.

Author contributions. Leanne Melbourne and Julia Griffin carried out the experiments under the guidance of Daniela Schmidt and Emily Rayfield. Leanne Melbourne prepared the manuscript with contributions from all co-authors.

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Table 1. Mesh type, average von Mises stress and total strain energy of all models.

Model	Mesh type	Number of Elements	Average von Mises Stress (Pa)	Total Strain Energy (pJ)
2-D	Quad	6520	1.67×10^{11}	0.0 008 908
3-D corridor model	hexagonal	116 759	1.72×10^{11}	0.1 110 610
3-D* corridor model	hexagonal	116 759		0.478 533
3-D corridor model	tetrahedral	2.13×10^6	7.46×10^{10}	0.0 174 947
Compartment model	tetrahedral	3.44×10^6	2.75×10^{10}	0.0 042 730
Biologically realistic model	tetrahedral	2.11×10^6	2.74×10^{10}	0.0 052 086
422 μatm 2-D model	Quad	6520	1.67×10^{11}	0.0 008 908
589 μatm 2-D model	Quad	1916	5.17×10^{11}	0.0 126 584
422 μatm compartmentalised	tetrahedral	3.44×10^6	2.75×10^{10}	0.0 042 726
589 μatm compartmentalised	tetrahedral	1.71×10^6	4.98×10^{10}	0.0 088 109

* Strain energy corrected for calcite volume.

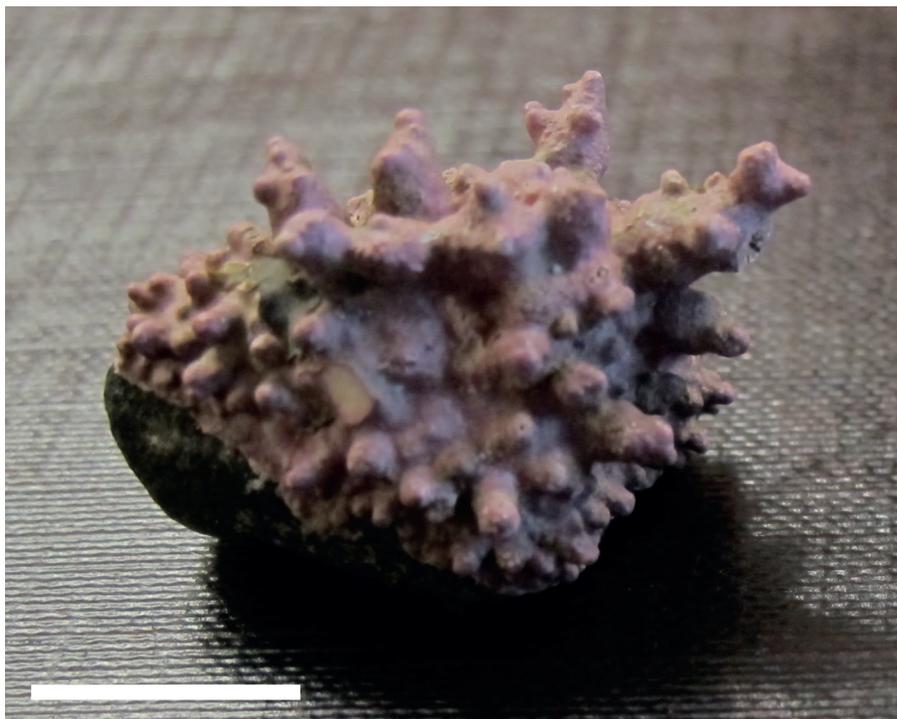


Figure 1. A *Lithothamnion glaciale* specimen in crustose form from Loch Creran, Oban, Scotland; Scale = 1 cm.

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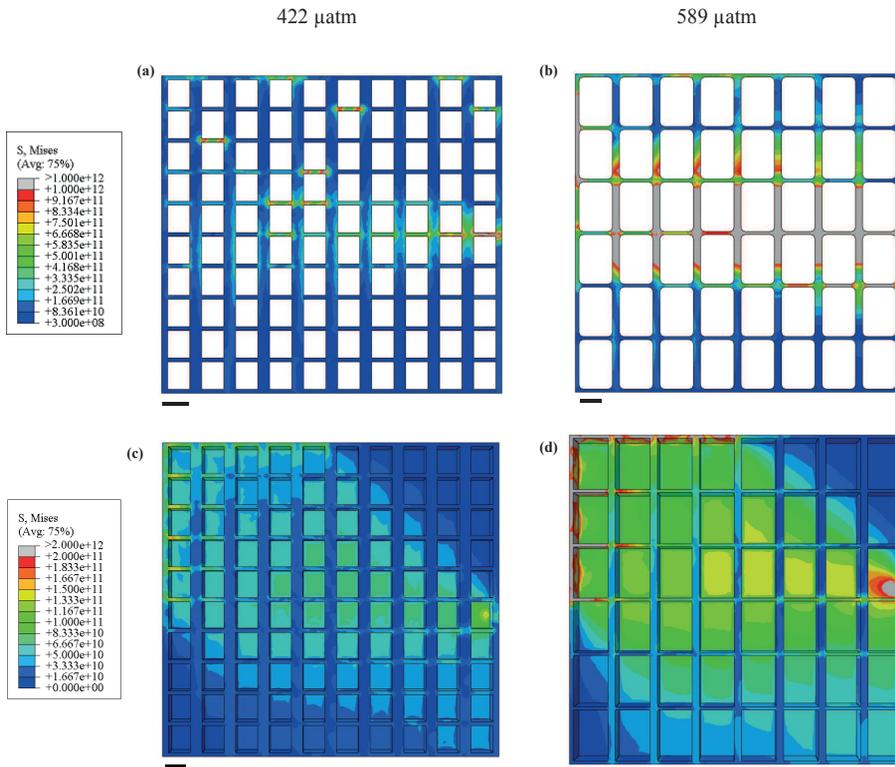


Figure 2. The effect of elevated CO_2 on the *Lithothamnion glaciale* structure. All models are subjected to the same loads and boundary conditions and measurements taken from Ragazzola et al. (2012). Von Mises Stresses are projected onto the 2-D finite element model (a, b) and the 3-D compartmentalised models (c, d). Warm colours indicate areas of high stress, while cooler blue colours indicate areas of low stress. Units = Pa.

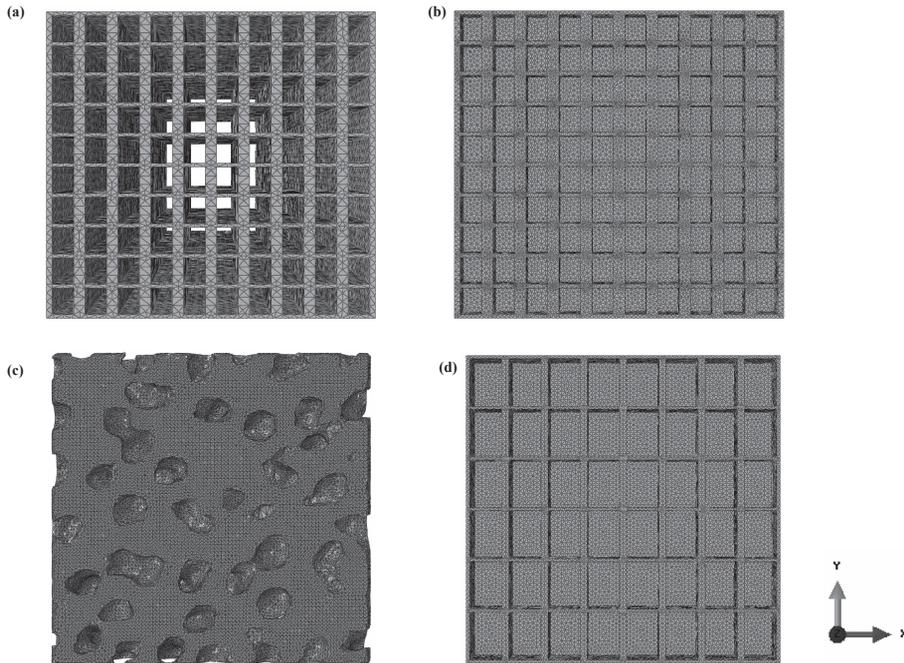


Figure 3. The four computer derived models; **(a)** the corridor model, a simple 3-D model; **(b)** the compartment model, a compartmentalised model; **(c)** the biological model, the biologically realistic model; **(d)** the OA model, the compartmentalised model under $p\text{CO}_2$ conditions simulating the year 2050.

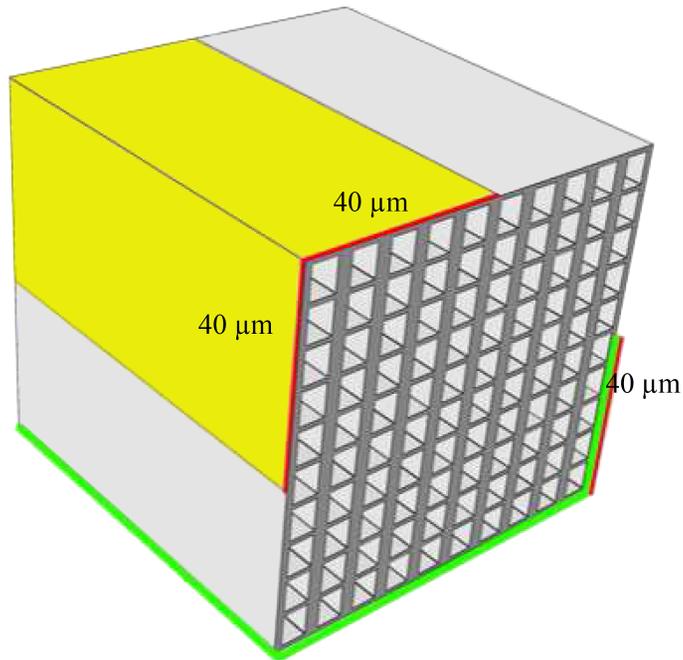


Figure 4. Loads and boundary constraints. All models had the same loads and constraints applied. Loads, representing wave erosion, were applied to the top left hand corner along a strip $40\ \mu\text{m}$ wide at the external top left side of the model (yellow surface). Constraints were applied to the bottom right corner (opposite corner to load) along a strip $40\ \mu\text{m}$ wide up the right hand side of the model and over the whole of the bottom model (green lines).

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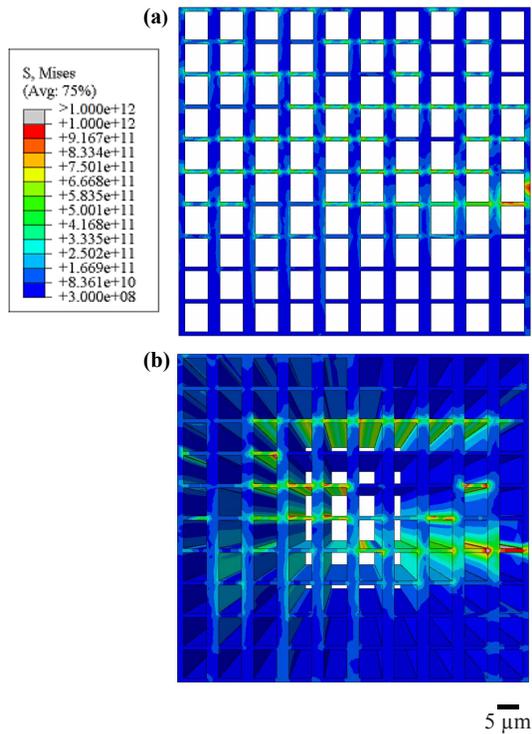


Figure 5. 2-D (a) vs. 3-D (b) comparison of the *Lithothamnion glaciale* structure based on Ragazzola et al. (2012) measurements. Units = Pa.

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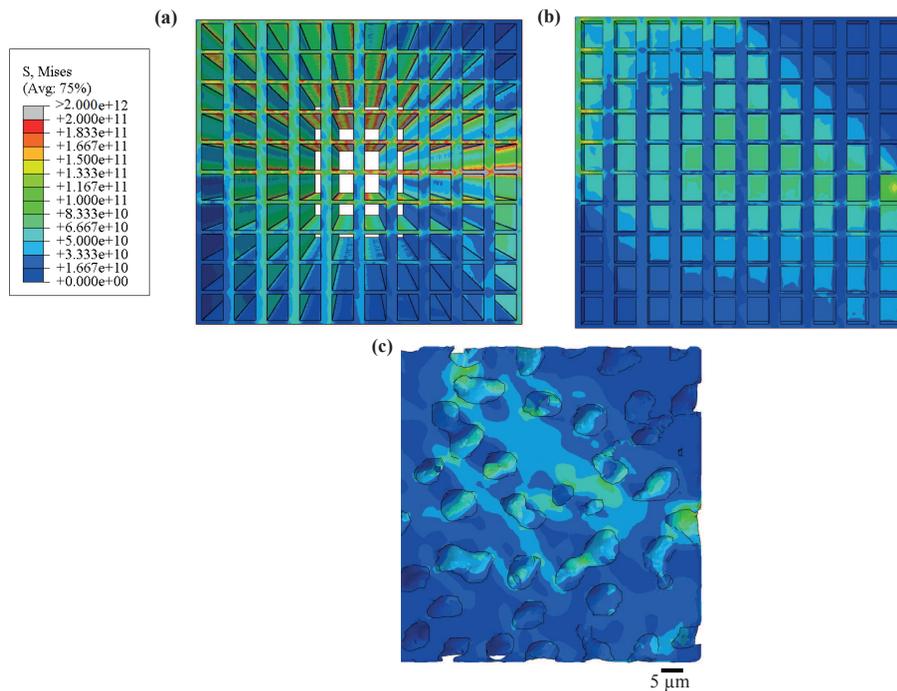


Figure 6. Comparison of all 3-D models. **(a)** The 3-D corridor model, **(b)** the compartmentalised model, and **(c)** the biologically realistic model. Units = Pa.

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