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The importance of wave exposure on the structural integrity of rhodoliths

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ABSTRACT

The structure (both gross morphology and internal cellular) of rhodoliths (free-living forms of coralline algae) are important factors in the ability of rhodoliths to create complex habitats. Using Finite Element Analysis, models of the internal structure of rhodoliths have been interrogated to assess how changes to the cellular structure affect structural integrity. These models are accurate in their portrayal of the internal skeleton, yet they fail in other ways. Specifically, they lack accurate environmental loads and material properties (Young's modulus), which form the basis of an accurate quantification of the structural integrity of rhodoliths. Here we measure the material properties of rhodoliths and quantify the hydrodynamic forces acting on them. Applying correct material properties and hydrodynamic forces, our results show that rhodoliths experience larger stresses than previously modelled. Water velocities representing storm surges cause internal stresses exceeding experimentally derived breakage stresses. As the intensity and frequency of storm surges are predicted to increase, the forces generated by them will result in breakage and hence affect their role as habitat builders.

1. Introduction

Rhodoliths, free-living non-geniculate (lack of non-calcified sections) coralline algae, are important habitat formers in the shallow marine environment, due to their densely branched 3D structure (Fig. 1). The aggregation of rhodoliths creates structurally and functionally complex beds that support a high level of biodiversity (Biomaerl, 1999), including commercial important species of scallops and fish larvae (Biomaerl, 1999; Kamenos et al., 2004).

Rhodoliths are coastal ecosystem engineers. Their morphology and subsequently bed distribution are highly affected by the coastal environment. In a latitudinal transect, it has been shown that changes in size, branch thickness and rhodolith shape mainly occur geographically than between species (Carro et al., 2014). Additionally, morphology can change within the same beds. For instance, rhodolith volume and branching density generally decreases with water depth (Bahia et al., 2010; Steller and Foster, 1995). Temperature and light are both first order environmental factors known to control rhodolith bed distribution (Foster, 2001), with substrate and hydraulic energy acting as a secondary control (Bosence and Pedley, 1982). For rhodoliths water flow must be within optimal ranges for growth. Too slow and rhodoliths are smothered by silt, but too fast and rhodoliths are susceptible to breakage (Foster, 2001). Rhodolith breakage can lead to the formation of coralline gravels (Bosence and Pedley, 1982). Rhodolith beds in Brittany, France are found in areas where mean current velocity ranges from 0.02 to 0.73 m s^{-1}, with the lowest percentage of rhodolith cover (< 59% covered) occurring in areas of water velocities exceeding 0.50 m s^{-1} (Dutertre et al., 2015). How often a rhodolith turns, due to water motion or bioturbation, is a factor that controls rhodolith shape, as a decrease in turning leads to more discoidal rather than spheroidal shapes (Steller and Foster, 1995). On the other hand rhodolith movement is important for survival. In general, the reduction in turning through decreasing wave-induced water velocity with depth or distance from land can reduce the size of rhodolith beds (Steller, 1993). This pattern can be reversed when more optimal conditions occur further away from land, due to environmental factors such as sedimentation, salinity and nitrate concentration also affecting bed distribution (Amado-Filho et al., 2007; Dutertre et al., 2015; Steller and Foster, 1995).

Rhodolith internal structure and material properties, which affect structural strength, are also affected by environmental conditions. Cellular structure changes to form larger cells with thinner cell walls in response to experimentally elevated temperature and CO_2 levels (Ragazzola et al., 2012). Finite element (FE) simulations demonstrate

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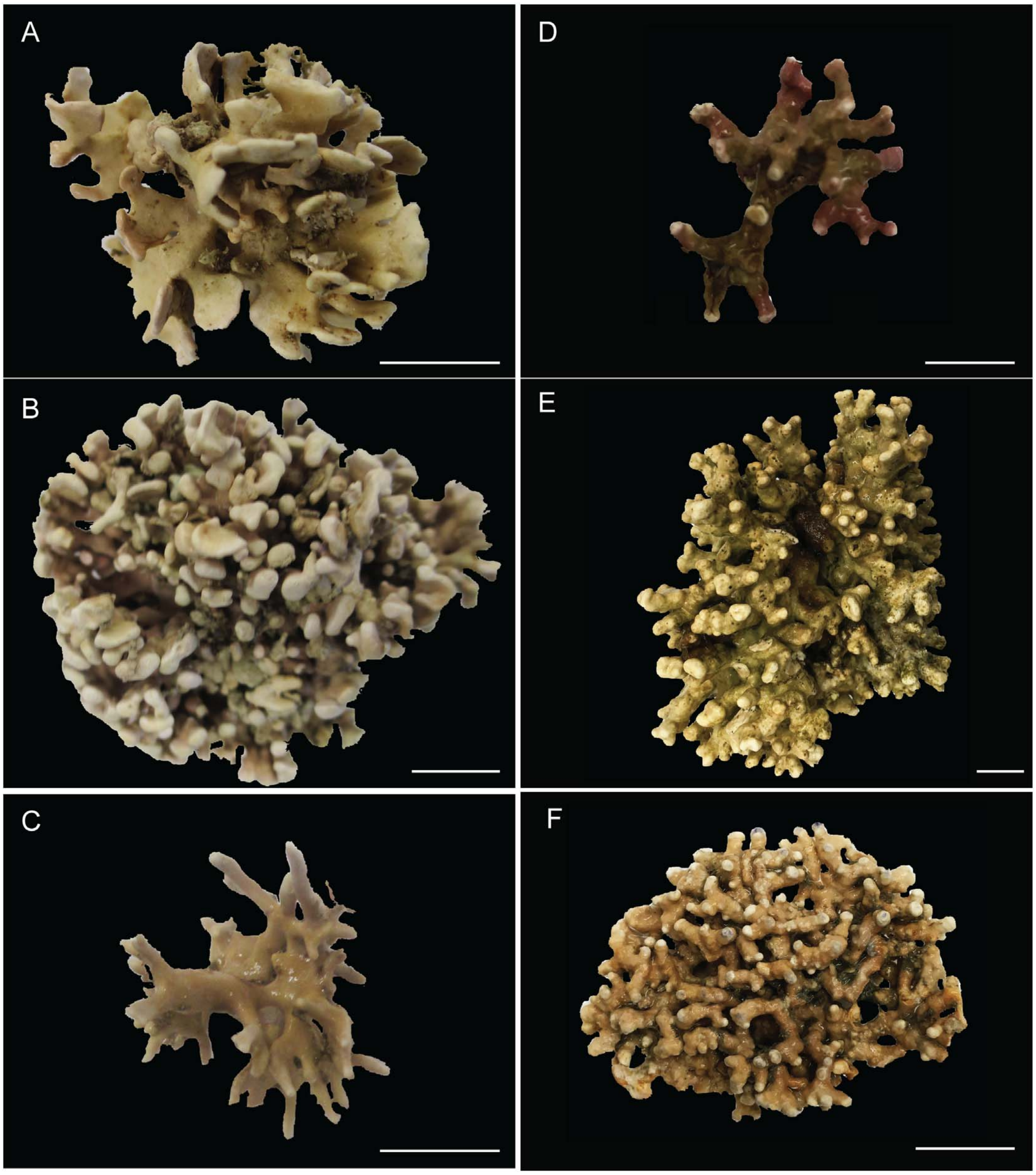

Fig. 1. Rhodoliths of varying morphologies of *Lithopyllum margaritae* (A–C) and *Phymatolithon calcareum* (D–F). Open branched (D), Spheroidal (E) and discoidal (F). Scale bar 1 cm.

that these growth changes reduce the structural integrity of the rhodolith, potentially making it more susceptible to breakage (Melbourne et al., 2015; Ragazzola et al., 2012). It is important to note that a longer exposure of 10 months resulted in acclimation of the organism and growth in the experimental material similar to control specimens (Ragazzola et al., 2013). Rhodoliths form high Mg-calcite skeletons (Moberly, 1968) and the amount of magnesium (Mg) in the skeleton is also affected by the environment (Halfar et al., 2000; Kamenos et al., 2008). Warmer temperatures result in a higher incorporation of magnesium into the skeleton compared to the colder winter temperatures creating alternating bands of high and low magnesium. Increasing CO_2 levels are suggested to reduce Mg incorporation resulting in the loss of this distinct banding (Ragazzola et al., 2013; Ragazzola et al., 2016). On the other hand, one study has shown how future CO_2 conditions have had no effect on the Mg incorporation of rhodoliths (Kamenos et al., 2013). Changes in Mg content are thought to affect the hardness of calcite in echinoderms, as higher concentrations of Mg lead to a harder material (Wang et al., 1997). These structural and material changes therefore have the potential to affect rhodolith structural integrity and ecosystem function.

Finite element models based on the internal growth structure of rhodoliths are ideal to assess their structural integrity (Melbourne et al., 2015; Ragazzola et al., 2012). However, in order to make meaningful predictions in quantifying the risk of possible breakage, FE simulations need to incorporate accurate rhodolith material properties and use hydrodynamic forces and water velocities that rhodoliths are exposed to. Fragmentation is the main form of rhodolith propagation (Irvine and Chamberlain, 1994). However, smaller fragments are more susceptible to smothering by silt (Hall-Spencer and Moore, 2000; Wilson et al., 2004), while rhodolith beds composed of smaller fragments will alter the composition of the associated fragments (Grall and Hall-Spencer, 2003). Given the importance of rhodolith size, wave exposure on rhodolith movement and morphology (Marrack, 1999; Scoffin et al., 1985; Steller and Foster, 1995) and the likelihood of more intense and frequent storm surges under climate change (Elsner et al., 2008; Knutson et al., 2010), it is paramount to quantify these hydrodynamic forces and the breakage limits of rhodoliths.

The aim of this study is to quantify the material properties (breaking stress, Young's modulus) and drag coefficients for varying morphologies of rhodoliths from Falmouth, UK and the Gulf of California, Mexico.