

# The bioprotective properties of the blue mussel (*Mytilus edulis*) on intertidal rocky shore platforms

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## ABSTRACT

Biogeomorphological processes are an important component in the geomorphic evolution of rocky coasts. Sessile organisms, including those which form dense biological covers, enhance and/or retard weathering and erosion. The common blue mussel (*Mytilus edulis*) is found on rocky shores in many parts of the world, typically forming extensive beds several centimetres thick. Yet, unlike other canopy forming marine organisms (e.g., seaweeds), the influences of mussels on processes of rock breakdown lack quantitative analysis. This study assesses the potential of *M. edulis* to act as a biogeomorphic agent through weathering experiments and field trials on a mudstone shore platform in Wales, UK.

Monitoring on the shore platform showed that daily near-surface temperature maxima, range and short-term variability were lower on surfaces colonised by *M. edulis* compared to those that were bare. This was supported by laboratory simulations which showed that (artificial) mussel beds consistently reduced the internal (sub-surface) temperature of rock samples during 'low-tide' periods. As mechanical rock weathering processes are influenced by surface and subsurface temperature regimes, it is inferred that these stabilising effects may translate to a reduction in the efficiency of particular rock breakdown processes. Rock hardness (Equotip Piccolo) measurements collected from the shore platform support this assertion as mussel-colonised surfaces were found to be significantly harder than bare surfaces, indicating they had experienced less breakdown during exposure to intertidal weathering and erosion. A supplementary field experiment based on the disintegration of gypsum 'domes' as an indirect measure of water/wave motion both within and outside of mussel beds further indicates that mussels may act as bioprotective agents by reducing turbulence at the rock surface.

Overall, this study presents the first empirical evidence of mechanisms by which mussels may protect intertidal rocks from weathering and erosional processes through the moderation of near-surface microclimate regimes and water motion in temperate environments. Importantly, compared to other canopy forming species, such as seaweeds, the observed dampening effects of *M. edulis* are likely only small in magnitude. However, as mussels can dominate the surfaces of rocky shores at certain tidal heights, they may act as locally important geomorphic agents that warrant further consideration as one component of the collective effect of bioprotective and bioerosive species in these environments. Further work is now needed to examine the geomorphic roles of mussel beds on a variety of other rock types, and the extent to which their impacts vary in time and space in relation to other biological, chemical and physical agents of change.

## 1. Introduction

Marine organisms are increasingly recognised for the important role they play in the geomorphic evolution of rocky coasts. Direct and indirect processes of bioerosion and bioprotection operating at a range of spatial and temporal scales are known to enhance or retard rock breakdown, contributing to the development of rock landforms and landscapes in coastal environments (Davidson et al., 2018; Moura et al.,

2012). For example, rock-boring micro-organisms and marine animals have been observed to create µm–cm scale bioerosive features that facilitate meso-scale erosional processes, such as the loosening of boulders on rocky shore platforms (Naylor et al., 2012). In contrast, marine organisms that form dense canopies and encrustations on the surfaces of rocks, such as seaweeds and barnacles, are thought to reduce the efficiency of certain forms of mechanical weathering through the dampening of near-surface microclimatic regimes (Coombes et al.,

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2013b, 2017; Gowell et al., 2015; Scrosati and Ellrich, 2018).

Despite these advances in understanding of rocky shore biogeomorphology, processes of bioprotection and the influences of marine organisms on rock breakdown are still relatively understudied (Carter and Viles, 2005; Coombes, 2014). This includes the common blue mussel, *Mytilus edulis*, which is particularly widespread throughout the cooler waters of the Northern and Southern Hemispheres (Seed and Suchanek, 1992) including the shores of the British Isles (Fig. 1). *M. edulis* can form dense beds several centimetres thick and kilometres in length. Like some other coastal macro-organisms (e.g., seaweeds), the spatial extent of mussel aggregations on rocky shores around the world makes them an important focus of research. Although some work has been done on mussels as rocky shore ‘ecosystem engineers’, including their influence on rock-surface microclimates (Jurgens and Gaylord, 2016, 2018; Seuront et al., 2018), very little has been done on their biogeomorphological roles. Recently, removal experiments on a very soft intertidal cohesive platform in Argentina have shown that mussel (*Brachidontes rodriguezii*) cover can limit substrate erosion via heating-cooling, wetting-drying, and salt crystallisation effects (Gonzalez et al., 2021). However, there is limited understanding of how these bioprotective processes may operate on different lithologies and in temperate environments. In these context, the impacts of mussel beds on rock-surface weathering and erosion regimes, and how this translates to rock breakdown, remain relatively unknown.

To address this research gap, a combination of field experiments and laboratory simulations were developed to quantify the bioprotective potential of *M. edulis* for the first time. Similar to canopy forming seaweeds (Gowell et al., 2015) and encrusting barnacles (Coombes et al., 2017), we hypothesised that *M. edulis* beds moderate rock breakdown by

decreasing the efficiency of mechanical weathering processes via thermal dampening (i.e., the reduction of temperature variability) during air-exposed low-tide periods, and by buffering the impacts of water movement during high-tide periods. Using a combination of field and laboratory experiments, and using surface hardness as a proxy for weathering state, we reveal significant differences in physical rock properties between mussel-colonised and bare areas of intertidal rock on our study platform. Overall, we suggest that such differences reflect spatially variable weathering regimes that are moderated, at least in part, by covers of blue mussels.

## 2. Materials and methods

### 2.1. Field site

Field experiments were conducted on an intertidal shore platform between Amroth and Wiseman’s Bridge, Pembrokeshire (South Wales), UK (51°43’38”N, 4°40’32”W). Here, gently WSW-dipping strata assigned to the South Wales Lower Coal Measures Formation (319–318 million years BP) is exposed in 30-m high sea-cliffs and an extensive platform which consists of interbedded grey mudstone, dark-grey siltstone, and medium-grey fine-grained heterolithic sandstone (Falcon-Lang, 2015). According to the MarLin wave exposure categories,<sup>1</sup> the shore platform is on an “exposed” coastline. The open coast faces away from the prevailing westerlies in a southeastern direction, and has a fetch of approximately 70 km. Although the coastline can experience strong winds, it is sheltered to the south by Monkstown headland and Caldy Island. The intertidal zone has a gentle gradient and a width of 200–250 m. The tidal regime is semidiurnal and macrotidal (7–8 m mean spring tidal range).

Extensive beds of *M. edulis* occur throughout the intertidal zone, covering much of the shore platform (Fig. 2). The shore platform is also colonised to a lesser extent by barnacles (*Semibalanus balanoides*) in the upper intertidal zone, and by honeycomb worms (*Sabellaria alveolata*), which form reefs in patchy distributions in the lower intertidal zone. We investigated the effects of *M. edulis* beds on weathering processes by examining and comparing areas with 95–100% mussel cover and those without any mussels; ‘colonised’ plots are defined as areas with mussels covering at least a 30-cm radius with 95–100% cover and a thickness of >3 cm, while ‘bare’ plots are defined as areas of bare rock without mussels or other macro-organisms present within a 50-cm radius.

Data were collected across the shore platform from six sites (Sites 1 to 6). These sites were at a similar elevation (mid-intertidal zone) and approximately 60 m apart. At each site, within a 5 m × 5 m area, data were collected in three or four pairs of randomly selected colonised and bare plots (Table 1). Paired plots within each site were 1–3 m apart. Rock surface hardness and mass strength (surface rebound) data were recorded at a pair of plots at each site. In addition, the material loss of gypsum domes during tidal inundation was recorded at two sets of paired colonised and bare plots at each site as a measure of relative water motion. The strength and hardness of rock materials have been used as an indicator of the efficiency of weathering processes in a number of terrestrial and coastal studies (e.g., Chelli et al., 2010; Coombes et al., 2013a; Feal-Pérez and Blanco-Chao, 2012; Mol and Viles, 2010; Moses et al., 2014; Pappalardo et al., 2016, 2018; Stephenson and Kirk, 2000). Furthermore, the dissolution of samples of plaster exposed to tidal flows has been successfully used to evaluate the effect of mussels on water motion and abrasion on shore platforms (Gonzalez et al., 2021). At Sites 1 and 2, an additional pair of representative colonised and bare plots was used to collect near-surface temperature data. The effects of canopy forming marine organisms on near-surface temperatures have been used as an indicator of variable weathering regimes in a number of previous studies (Gonzalez et al.,

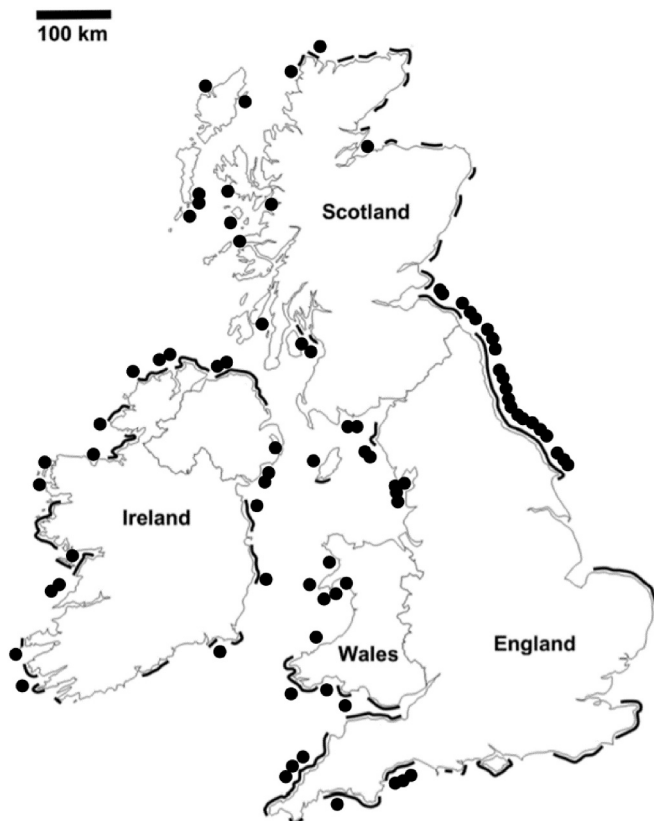


Fig. 1. Great Britain and Ireland distribution of rocky shore platforms (thick black line, modified from Fig. 4.2 in Moses, 2014) and *M. edulis* on exposed eulittoral rock (black dots, biotope data based on records in the UK Marine Recorder database downloaded from <https://jncc.gov.uk/our-work/marine-recorder/>, accessed 12.11.21).

<sup>1</sup> <https://www.marlin.ac.uk/glossarydefinition/waveexposure>

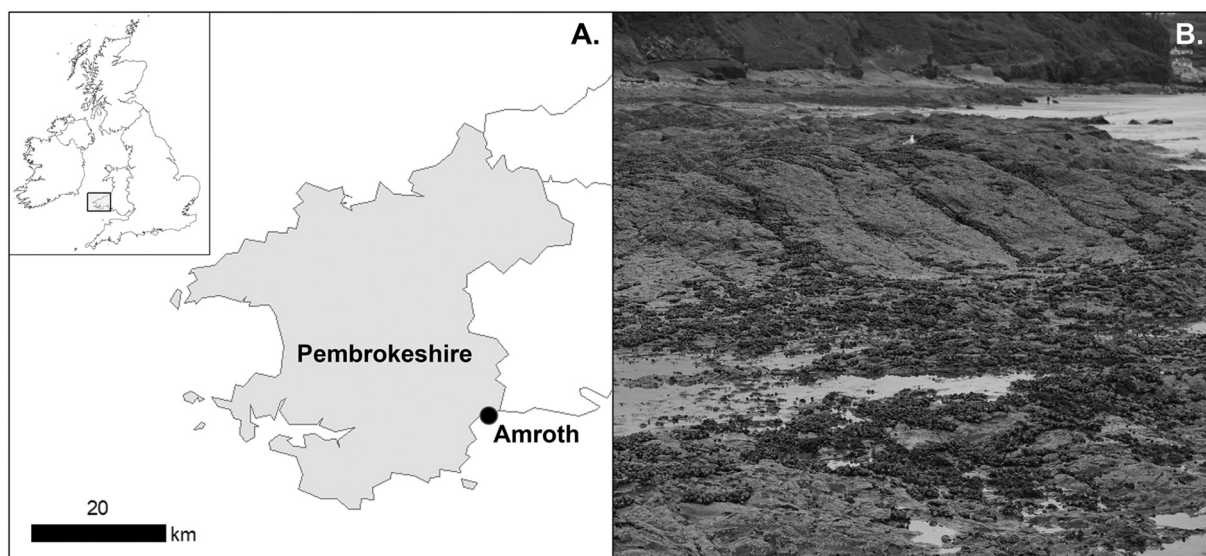


Fig. 2. (A) Location of Amroth Beach, Pembrokeshire, Wales, UK, and (B) the study shore platform.

Table 1

Summary of data collected at the field sites and in the laboratory.

	Type of data	Method	Sites	No. of plots per site	No. of measurements
Field study	Near-surface rock temperature ( $^{\circ}\text{C}$ )	iButton Thermochrons	1–2	2 (1 $\times$ bare and 1 $\times$ colonised)	Recorded at 30-min intervals over 21 d in each plot.
	Material loss during tidal inundation (g)	Weight change of gypsum domes	1–6	4 (2 $\times$ bare and 2 $\times$ colonised)	Weight change of two domes attached to each plot after two full tidal cycles.
	Rock surface hardness (HL)	Equotip Piccolo 2 (D-type)	1–6	2 (1 $\times$ bare and 1 $\times$ colonised)	30 measurements per plot
	Rebound Coefficient (Q)	Schmidt Hammer (N-type)	1–6	Note, rock surface hardness and mass strength data were collected in the same plots.	20 measurements per plot
	Subsurface rock temperature ( $^{\circ}\text{C}$ )	Thermistor probes	NA	NA	Recorded at two depths (10 mm and 20 mm below the surface) in four sample blocks (2 bare, 2 mussel-covered) at 1-min intervals during a 6-h low-tide simulation repeated three times.

2021; Gowell et al., 2015; Scrosati and Ellrich, 2018).

The field measurements were conducted during the summer (June and July) of 2014. This time of year was chosen because mechanical weathering processes, i.e., insolation weathering and salt crystallisation, are thought to be most efficient when average diurnal temperature ranges and wetting-drying cycles are most intense (Coombes et al., 2013b; Stephenson and Kirk, 2001).

## 2.2. Near-surface temperature (field measurements)

A temperature logger (Maxim® DS1921G iButton Thermochron) housed in a protective plastic casing was attached to the substrate in a pair of bare and mussel-colonised plots at Sites 1 and 2 using marine epoxy (Plastic Padding® Marine Epoxy). In the colonised plots, a 2-cm<sup>2</sup> area was cleared of mussels and other macro-biology so that the temperature loggers could be secured directly to the substrate (Fig. 3); caution was taken to ensure that the surrounding mussel bed was not damaged. The bare plots were already clear of mussels and other macro-organisms. As the loggers were small and flat (17.4 mm in diameter, 5.9 mm in thickness), they recorded air temperature near the surface of the substrate, and between the rock and the surrounding mussel bed which had an approximate thickness of 3 cm (Gonzalez et al., 2021). The loggers have an operating range of  $-30$  to  $70$   $^{\circ}\text{C}$ , a resolution of  $0.5$   $^{\circ}\text{C}$ , and an accuracy of  $\pm 0.5$   $^{\circ}\text{C}$ . The same devices have previously been used in weathering research including on the influence of organisms on thermal regimes (e.g., Coombes et al., 2013b; Gowell et al., 2015; Sternberg et al., 2011). The loggers were pre-programmed to measure the near-surface rock temperature at 30-min intervals over 21 days

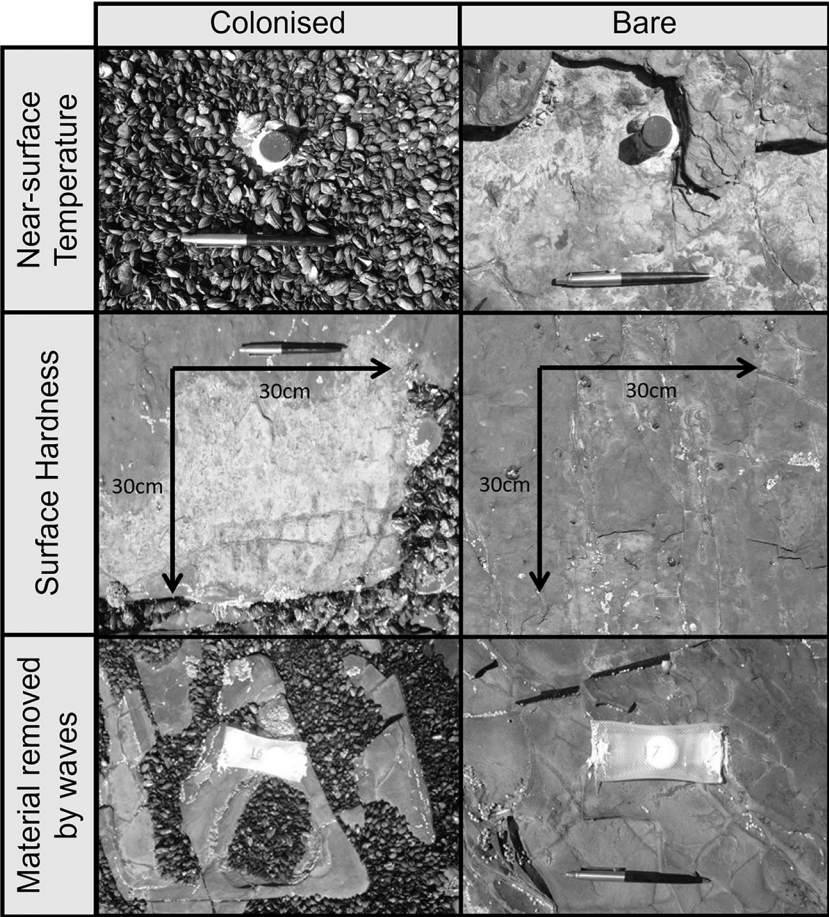
between 25th June and 15th July 2014. During this period, the tidal range varied between 3.1 m and 7.0 m.

From the four continuous time-series datasets from each plot, the daily temperature maxima ( $T_{\text{max}}$ ), daily temperature range ( $T_{\text{range}}$ ), and daily highest rate of change in temperature over consecutive 30-min periods ( $T_{\Delta 30}$ ) were calculated for each of the 21 measurement days. Within site comparisons of  $T_{\text{max}}$ ,  $T_{\text{range}}$ , and  $T_{\Delta 30}$  between the bare and colonised plots were made using graphical representations.

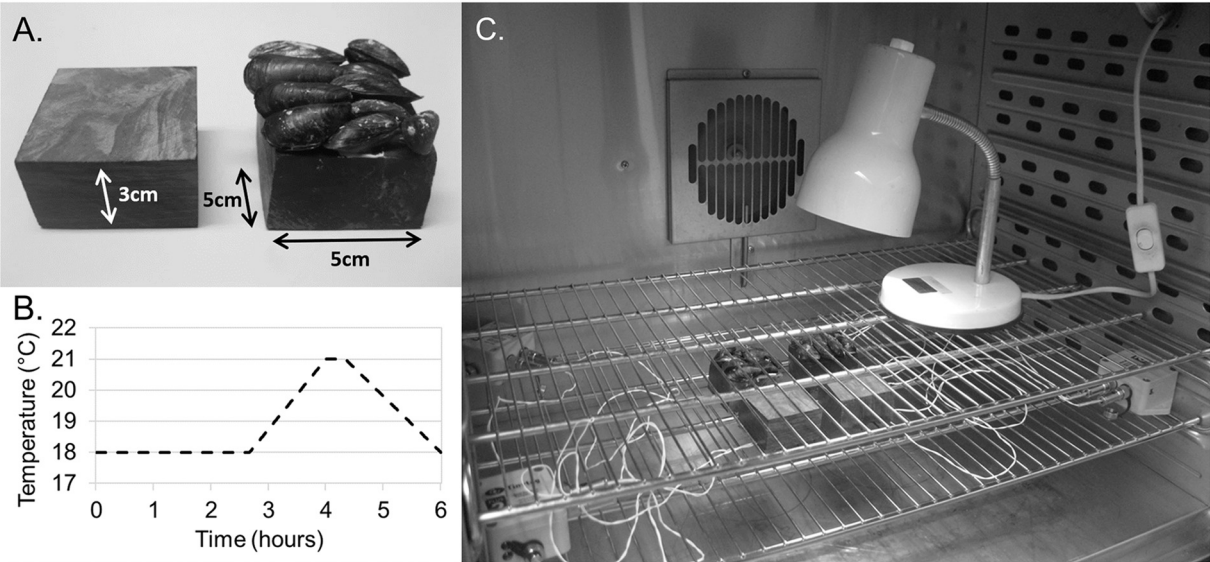
## 2.3. Rock subsurface temperature (laboratory measurements)

To supplement the near-surface temperature measurements made in the field, the influence of *M. edulis* covers on the internal (subsurface) temperature of rock was monitored in a laboratory simulation (e.g., Coombes et al., 2017). For this, four uniformly sized sample blocks of mudstone (50 mm  $\times$  50 mm  $\times$  30 mm) were cut from platform material collected from the field site. The top surfaces of two of the blocks were covered with ‘artificial mussels’ created using empty mussel shells collected from the field and filled with gypsum to mimic the mass of a living mussel (Fig. 4A). Living mussels were not used primarily for simplicity, as these would have likely died when subjected to laboratory conditions, and because our approach also enabled easy experimental replication (e.g., Coombes et al., 2017; Gowell et al., 2015). On each ‘mussel-covered’ block, ten artificial mussels were attached using a small amount of marine epoxy to achieve a 95–100% cover comparable to the colonised plots in the field. The tops of the other two blocks were left uncovered so as to simulate a bare plot. All of the remaining faces of the four blocks were coated in polyurethane varnish so that water could





**Fig. 3.** Examples of colonised and bare plots used to measure near-surface temperature over a 21-d period (top row), rock hardness (middle row), and material loss over two tidal cycles (bottom row).



**Fig. 4.** Preparation and procedure for laboratory-based measurement of subsurface rock temperature: (A) Examples of a bare and artificially mussel-covered test block; (B) Climate regime of a model summer's day simulated in the climate chamber; (C) A view of the set-up within the climate chamber during simulations, showing the positions of the bare and colonised blocks, the four Tinytags, and the daylight lamp.

only be absorbed and lost from the top surfaces, to replicate parts of the in-situ shore platform (e.g., Coombes, 2011; Gowell et al., 2015; Smith and McGreevy, 1983). Each block had 1- and 2-cm-deep holes (each 3.5

mm wide) drilled into their undersides for the insertion of thermal probes.

The blocks were first submerged in a solution of artificial seawater

(EU standard salt crystallisation text mix) for 12 h to achieve a suitable level of saturation. After submersion, two flexible lead thermistor probes (PB-5009-0 M6, Gemini Co., UK) connected to a Tinytag Plus 2 temperature logger (TGP-4520, Gemini Co., UK) were inserted into the pre-drilled holes to measure temperature 1 cm and 2 cm from the exposed surface. The four (wet) blocks were then placed in an APT.Line KBF 115 Binder climate chamber (BINDER, Tuttlingen, Germany) pre-programmed to simulate a simplified, model summer's day in south-west Wales (Fig. 4B-C). For this, meteorological data for 11th August 2014 were obtained from the Milford Haven weather station located 25 km from the field site, when low tide occurred around midday (11:54 am). Over the course of a 6-h simulation, the climate chamber was programmed to cycle between 18 °C and 21 °C with a constant relative humidity of 80%, approximating low-tide conditions on the shore platform on a hot summer's day.

During the simulated exposure periods, a full-spectrum daylight lamp was placed inside the climate chamber and positioned above the four experimental blocks to better simulate the warming of rock via insolation (Gowell et al., 2015; Smith et al., 2005; Warke and Smith, 1998). During the simulation, the thermistor probes were pre-programmed to measure the subsurface temperatures (at 1- and 2-cm depths) of the blocks at 1-min intervals. Once the blocks had undergone a full cycle in the climate chamber, the internal temperature readings were downloaded using Tinytag Explorer 4 software (SWCD-0040, Gemini co., UK) and compared between mussel-covered and bare blocks. The laboratory experiment (12 h submersion followed by 6 h exposure within the climate chamber) was repeated three times using the same sample blocks.

#### 2.4. Rock Hardness

Two types of surface rebound devices—an Equotip Piccolo 2 (D-type) and Silver Schmidt Hammer (N-type)—were used to collect surface hardness and rebound data at the six sites established along the study shore platform. Unlike previous studies that have used either the Equotip (e.g., Aoki and Matsukura, 2007a; Burningham and Knight, 2020) or the Schmidt Hammer (e.g., Moura et al., 2012; Stephenson and Kirk, 2000), both devices were used to generate complementary datasets of different rock properties (Aoki and Matsukura, 2007b; Pappalardo et al., 2018). Specifically, the Equotip Piccolo 2 (D-type), with its low impact energy (11 Nmm), is more sensitive to surface hardness variations (Coombes et al., 2013a; Viles et al., 2011), whereas the Silver Schmidt Hammer (N-type), with a much higher impact energy (2.207 Nm), provides an indication of bulk rock strength based on surface rebound measurements (Goudie, 2006). The Equotip expresses hardness as a 'Leeb' value (HL) and has a resolution of 1 HL and an accuracy of  $\pm 4$  HL. The Schmidt Hammer expresses compressive strength as a physical rebound coefficient ('Q') and has a resolution of 0.5 Q and an accuracy of  $\pm 1$  Q. Thus, as a function of rock elasticity, Equotip data (Leeb) were used to detect subtle differences in surface hardness associated with weathering processes (Aoki and Matsukura, 2007b) while the Schmidt Hammer data (Q) were used as an indicator of rock mass strength variations (Strzelecki, 2017). The obtained Q values were primarily used to test for spatial homogeneity in rock mass properties to ensure valid hardness comparisons between the different study plots. This approach contrasts with previous studies that have used the Schmidt Hammer as a direct indicator of the influences of other rocky shore species on sub-surficial rock-weathering (e.g., Pappalardo et al., 2018).

Hardness data and Schmidt Hammer rebound values were collected across the study shore platform in a pair of bare and mussel-colonised plots at Sites 1 to 6. Readings were only taken on flat or gently sloping rock surfaces to avoid errors associated with rock edges, which can strongly affect Schmidt Hammer reliability (Viles et al., 2011). Overall, 12 square plots (30 cm  $\times$  30 cm) were measured using both devices (Equotip and Schmidt Hammer) across the six sites, each consisting of one colonised and one bare plot (Fig. 3). The bare plots were

studied under the assumption that they had been clear of any mussel colonisation for at least several seasons (with no evidence of prior attachment) and, most likely, for a longer period of time. Before measurement, the colonised plots were cleared of any mussels or other macro-biology. In addition, both the colonised and bare plots were brushed clean of any sand or other material. As moisture can affect the reliability of Equotip and Schmidt Hammer readings (Desarnaud et al., 2019; Sumner and Nel, 2002; Viles et al., 2011), both the bare and colonised plots were allowed to dry for at least 2 h after they were initially exposed by the tide before any measurements were taken. When the surfaces were dry, 30 Equotip measurements were taken in each plot using the single impact (SIM) method (Wilhelm et al., 2016). The test surfaces were then smoothed using a carborundum stone before 20 Schmidt Hammer measurements were recorded (Aydin, 2009; Niedzielski et al., 2009). The carborundum stone was used as surface irregularities can result in a loss of impact energy before the plunger tip of the Schmidt Hammer reaches the rock surface, thereby reducing reliability (Williams and Robinson, 1983). This was done after the Equotip measurements, as this device is more sensitive to surface irregularities indicative of subaerial weathering processes, which may otherwise be destroyed by the Schmidt Hammer impact (Feal-Pérez and Blanco-Chao, 2012; Viles et al., 2011). Care was taken when using both devices to ensure that repeat impacts on the same spot of the rock were avoided, which can also affect the reliability of readings (Aydin, 2009). After each plot was measured, the Schmidt Hammer was calibrated using a test anvil to avoid measurement error.

The rebound values (Q) collected using the Schmidt Hammer as an indicator of rock mass strength were log-transformed to correct for non-normality. An analysis of variance (ANOVA) and post-hoc Tukey tests were then performed on the transformed data to compare the rebound values between the 12 plots across the six sites (6  $\times$  bare and 6  $\times$  colonised). One site (Site 5) was found to have significantly different rebound values compared to the other sites, indicating different bulk properties (see Section 3.2). Therefore, the hardness data collected using the Equotip at this site were excluded from further analysis to avoid potential confounding effects. The Equotip hardness data (excluding Site 5) could not be corrected for unequal variance, even when data transformation was applied. As such, a non-parametric Mann-Whitney U test was used to assess the difference between the pooled hardness data from the colonised and bare plots (Wilhelm et al., 2016).

#### 2.5. Material loss during tidal inundation

The dissolution/breakdown of gypsum has been used as a relatively accurate yet inexpensive means of studying how wave- and tide-induced forces influence the recruitment and survival of canopy forming organisms (e.g., D'Amours and Scheibling, 2007; Jonsson et al., 2006), and how wave exposure affects the morphology of marine animals (Molloy and Bolton, 1996). Rock and plaster 'discs' experimentally attached to shore platforms and exposed to the tide have also been successfully used to assess water flow and abrasion, including the influence of mussel cover (Gonzalez et al., 2021; Trudgill, 1975). Here, at each of the six sites along the shore platform (Sites 1 to 6), a 3.5-cm-diameter cast gypsum 'dome' was attached to the substrate of each of two colonised plots and two bare plots, giving a total of 24 domes. The domes, which were cast in uniform silicone moulds before being oven dried at 600 °C for 24 h, were created using a water:gypsum ratio of 1:1.85 (Jonsson et al., 2006; Molloy and Bolton, 1996). Once dried, the domes were sanded down until they were of equal weight ( $15 \pm 1$  g) to ensure uniformity prior to exposure, which can otherwise lead to variable responses to water motion (Molloy and Bolton, 1996). The domes were placed in individual rectangular, plastic mesh bags (5 cm  $\times$  12 cm) which enabled them to be securely attached to the rock surface and exposed to local hydrodynamic conditions caused by tides and waves (Trudgill, 1975). The mesh bags also limited abrasion by mobile sand and excluded grazing organisms (D'Amours and Scheibling, 2007). All of

the mesh bags were attached to the rock substrate using marine epoxy at a similar tidal height, orientated so their longest edge was parallel to the shoreline (Fig. 3). To ensure valid comparisons, the domes were attached 3 m apart and away from any larger-scale morphological features that might affect water flow over the platform, meaning that the pairs attached to colonised and bare surfaces were exposed to comparable hydrodynamic conditions.

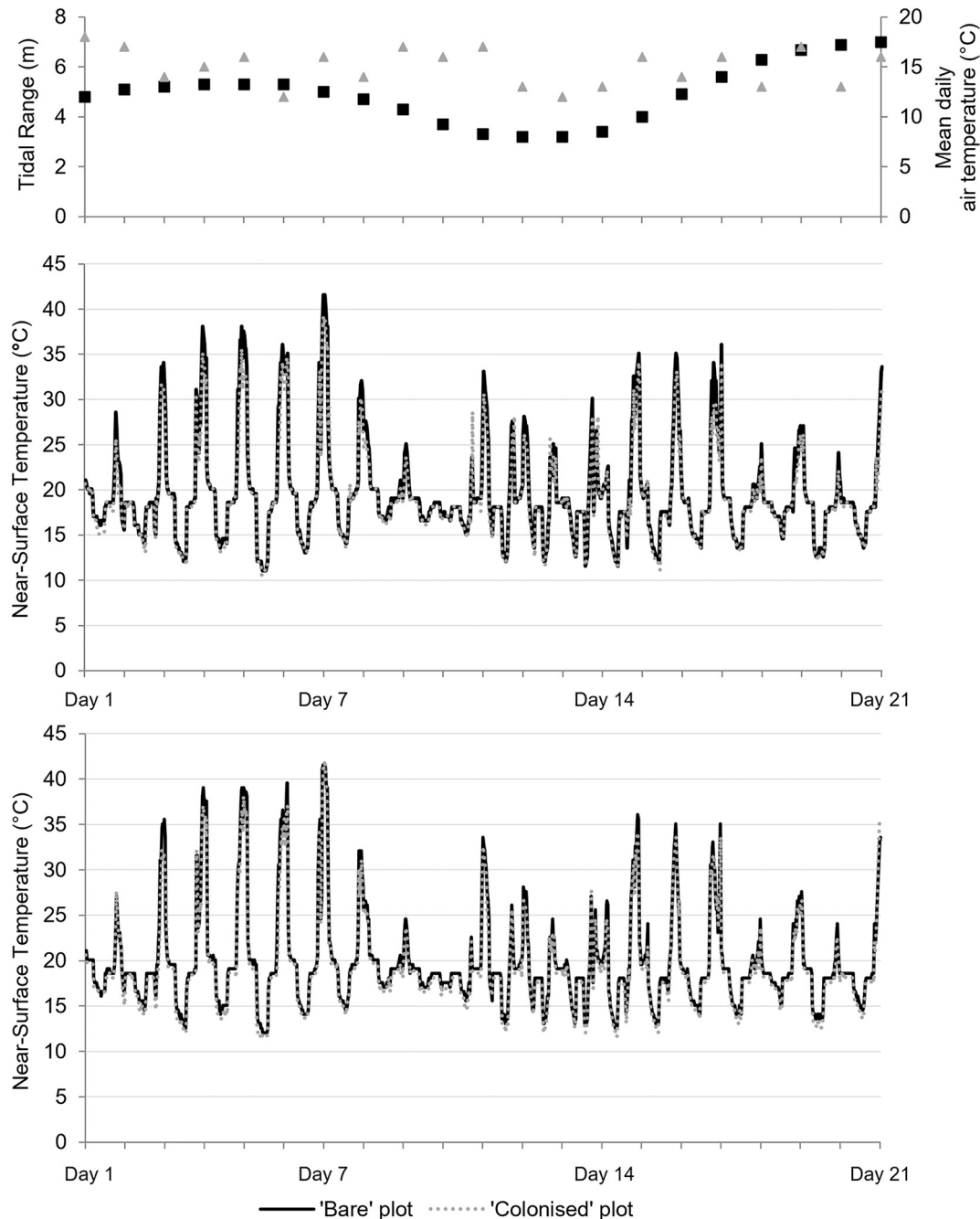
All of the gypsum domes were left for two full tidal cycles between 14th and 15th July 2014. The length of exposure was decided on the basis of a pilot study, which showed that there was an increased risk of the mesh bags dislodging or the domes completely disintegrating when exposed for longer periods. After being exposed, the gypsum domes were carefully removed and dried to a constant weight in a laboratory oven at

600 °C for 24 h. The difference between the initial weights of the domes and their weights after tidal exposure was then determined as a relative measure of material breakdown in response to water motion. A matched paired *t*-test was subsequently performed on the data to determine whether there was a difference between the weight loss of domes attached to the colonised plots ( $n = 12$ ) and bare plots ( $n = 12$ ).

### 3. Results

#### 3.1. Near-surface and internal temperature regimes

Time-series data of near-surface temperature collected from the shore platform at Amroth Beach are shown in Fig. 5 and differences in



**Fig. 5.** Daily mean tidal range (m, black squares) and mean daily air temperature (°C, grey triangles) at Amroth Beach over 21 d (25.06.14–15.07.14) during the field experiment (Top). Near-surface temperature (°C) of a colonised (grey dashed) and bare (black solid) plot at Site 1 (middle) and Site 2 (bottom) on the shore platform taken at 30-min intervals over the 21-day period.



$T_{\max}$ ,  $T_{\text{range}}$ , and  $T_{\Delta 30}$  between bare and colonised plots at Sites 1 and 2 are shown in Fig. 6. Over the measurement period,  $T_{\max}$  was consistently higher at the bare plots compared to the colonised plots across both sites; on only one occasion (Day 12, Site 1) was the opposite trend observed. On average,  $T_{\max}$  was between 1.3 and 1.7 °C (4–6%) higher in the bare plots compared to the colonised plots. The bare plots also typically had higher  $T_{\text{range}}$  values compared to the colonised plots; over 21 days across the two sites,  $T_{\text{range}}$  was on average 1.3 °C (8%) higher in the bare plots compared to the colonised plots. Differences in  $T_{\Delta 30}$  between the bare and colonised plots were more variable. For instance, there were 14 occasions over 21 days across the two sites where  $T_{\Delta 30}$  was greater in the colonised plots compared to the bare plots, although  $T_{\Delta 30}$  was typically greater in the bare plots, with differences ranging up to 7.5 °C. Over the 21-d study period,  $T_{\Delta 30}$  was on average 0.5–1.3 °C (8–17%) higher in the bare plots compared to the colonised plots.

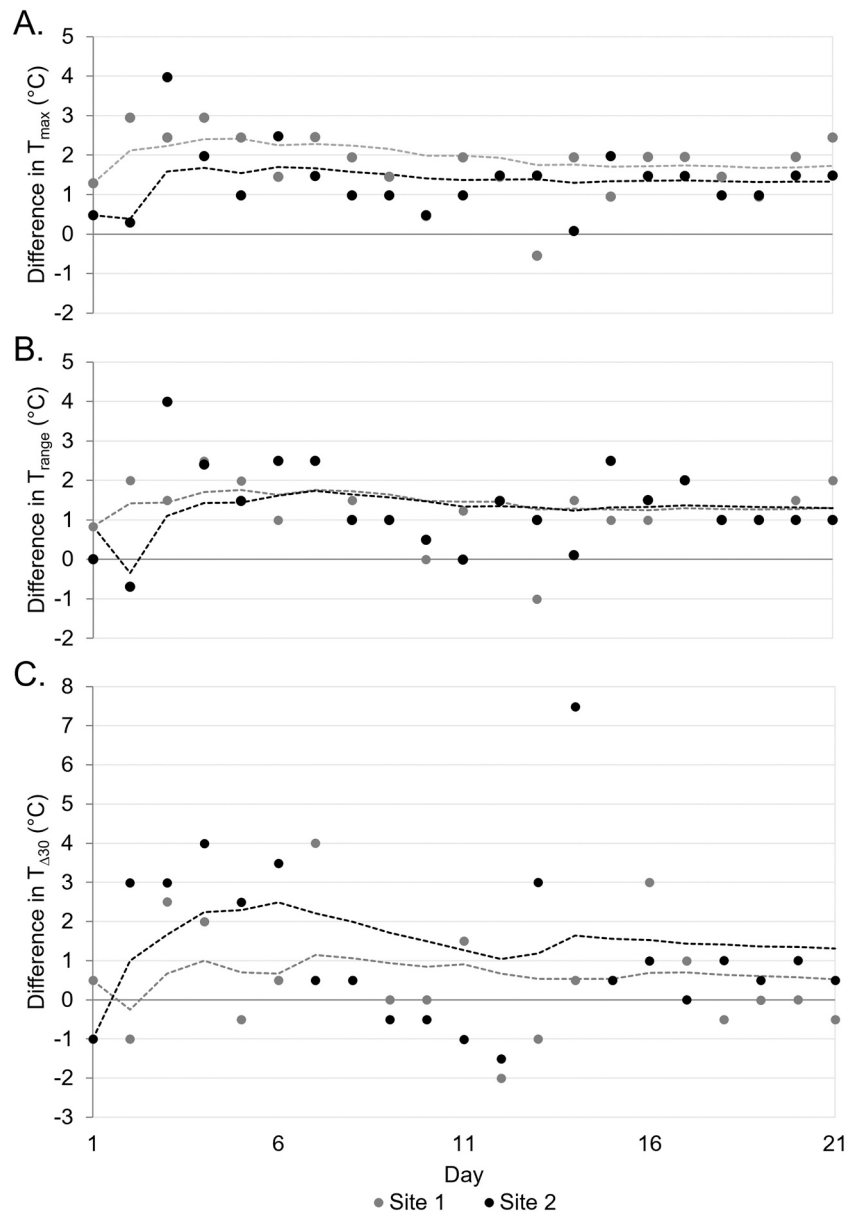
Complementary to the field data, the results of the laboratory simulation showed that the subsurface temperatures of the mussel-covered rock samples were consistently lower than the bare rock

samples, both at 1-cm and 2-cm depths below the surface (Fig. 7A). The bare and mussel-covered rock samples began the simulation with comparable internal temperatures (room temperature, approximately 23 °C), but diverged as the samples were initially cooled and then heated during the simulation. After approximately 210 min, the differences in the internal temperatures of the bare and mussel-covered rock samples stabilised at 0.65 °C and 0.70 °C at the 1-cm and 2-cm depths, respectively (Fig. 7B). Excluding some initial fluctuations during the first ~20 min of the simulations, the thermal gradient (i.e., the difference between the two depths) was consistently higher in the bare samples than the mussel-covered samples, averaging 0.099 °C and 0.045 °C, respectively, over the three low-tide simulations (Fig. 7C).

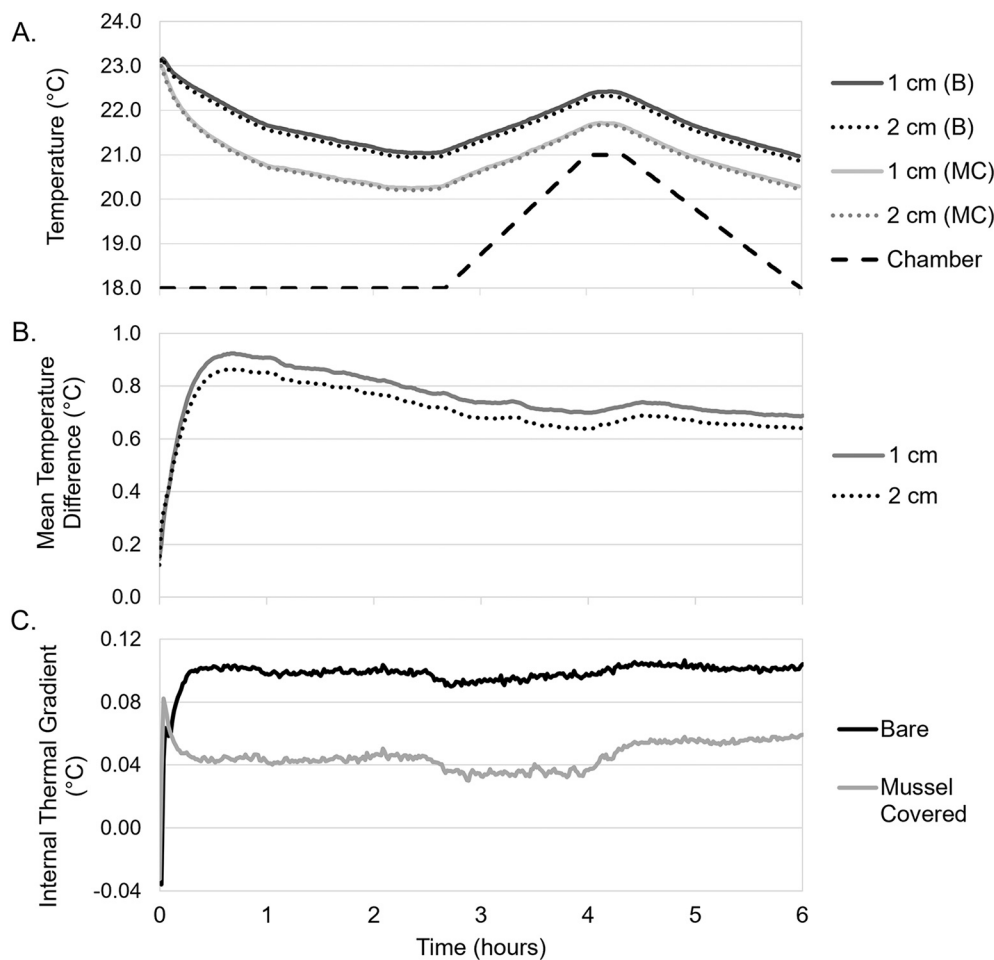
### 3.2. Rock hardness

#### 3.2.1. Rebound Coefficient (Schmidt Hammer, Q)

A two-way ANOVA was used to compare log-transformed Silver Schmidt Hammer data (Q values) between bare and mussel-colonised



**Fig. 6.** Differences in (A)  $T_{\max}$ , (B)  $T_{\text{range}}$ , and (C)  $T_{\Delta 30}$  between bare and mussel-colonised plots (i.e., bare minus colonised) at Site 1 (grey) and Site 2 (black). Cumulative moving averages of  $T_{\max}$ ,  $T_{\text{range}}$ , and  $T_{\Delta 30}$  for Site 1 (grey dashed line) and Site 2 (black dashed line) are also shown.



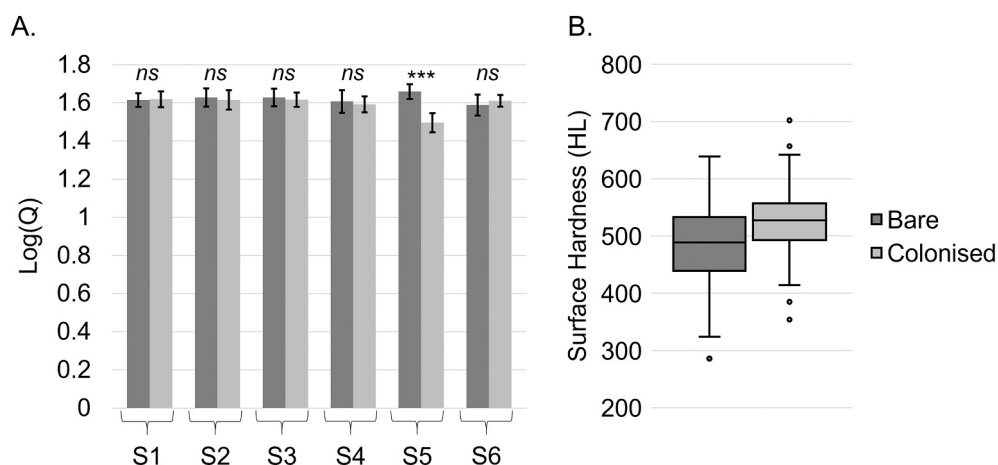
**Fig. 7.** Averaged time-series data of three, 6-h simulations of a 'model summer's day' showing: (A) internal rock temperatures (°C) at 1-cm (solid lines) and 2-cm (dotted lines) depths from the surface of mussel-covered (MC, light grey) and bare (B, dark grey) test blocks; (B) mean temperature difference between the mussel-covered and bare test blocks at 1-cm (solid line) and 2-cm (dotted line) depths; (C) mean thermal gradient between 1- and 2-cm depths in the bare (black solid line) and mussel-covered (grey solid line) samples.

plots at the six sites. The two levels of the test (site and colonisation state) showed significant interactive effects ( $f(5) = 20.7$ ,  $p < 0.001$ ). Based on post-hoc Tukey tests, rebound values were comparable between all the plots (bare and colonised) at Sites 1, 2, 3, 4, and 6 ( $p > 0.05$ ). At Site 5, however, rebound values were significantly lower in the colonised plot compared to the bare plot ( $p < 0.001$ ) (Fig. 8A). Furthermore, the colonised plot at Site 5 had significantly lower rebound values than all the other plots at Sites 1, 2, 3, 4, and 6 ( $p < 0.001$ ); and the bare plot at Site 5 had significantly higher rebound values than the plots at Sites 4 and 6 ( $p < 0.05$ ). Based on these results,

we excluded Site 5 from the surface hardness analysis (Section 3.2.2) so that any differences in surface hardness between the remaining sites, as measured using the Equotip, could be more confidently attributed to mussel cover rather than any underlying differences in bulk rock properties.

### 3.2.2. Surface hardness (Equotip, HL)

The pooled Equotip hardness (HL values) data (excluding Site 5, see Section 3.2.1) were analysed using a non-parametric Mann-Whitney  $U$  test. This revealed that the rock-surface hardness of the colonised plots



**Fig. 8.** (A) Log-transformed mass rock strength (Schmidt Hammer Q) of paired bare (dark grey) and mussel-colonised (light grey) plots at six different sites (S1–S6) along the study shore platform [mean  $\pm$  standard deviation (SD),  $n = 20$ ; statistical significance of Post-hoc Tukey test comparing differences between paired plots within sites: not significant (ns),  $p < 0.001$  (\*\*\*)]; (B) Boxplot showing the distribution of pooled surface hardness (Equotip HL) data for bare and mussel-colonised plots at Sites 1, 2, 3, 4, and 6 ( $n = 150$ ; note that data from Site 5 were excluded owing to the significantly different rock mass properties revealed by the Q rebound data analysis).



was significantly higher than in bare plots; the median hardness of the colonised plots was 527.5 HL compared to 489 HL in the bare plots ( $U = 7229.5$ ,  $n_1 = n_2 = 150$ ,  $p < 0.001$ ) (Fig. 8B).

### 3.3. Gypsum disintegration by water motion

In almost all cases, the gypsum domes secured to bare plots lost more material than those secured to colonised plots (Fig. 9). Domes secured to bare plots lost on average 8.4% (equivalent to 0.33 g) more material than those secured to colonised plots, and this difference was statistically significant overall ( $t(11) = 3.64$ ,  $p < 0.004$ ). The greatest difference in weight loss occurred at Sites 4 and 6, where the domes secured to the bare plots lost 17.2% and 15.3% more material than those secured to the colonised plots, respectively.

## 4. Discussion

### 4.1. Influence of mussel cover on rock-surface and internal (subsurface) thermal regimes

*M. edulis* cover had a marked influence on near-surface rock temperatures over both diurnal and minute-hour timescales. Temperature extremes and fluctuations were dampened on the colonised surfaces compared to adjacent areas of uncolonised rock (Figs. 5 and 6). This indicates that the implied bioprotective potential of other common intertidal species associated with thermal dampening, such as seaweeds and barnacles (Cartwright and Williams, 2014; Coombes et al., 2017; Gowell et al., 2015; Scrosati and Ellrich, 2018; Watt and Scrosati, 2013), can be extended to *M. edulis*. This finding complements observations of the thermal-dampening effects of mussel beds on rocky shores in the US and Australia (e.g., Jurgens and Gaylord, 2016, 2018; Seuront et al., 2018), and in Argentina where *B. rodriguezi* covers were found to buffer substrate surface temperatures on a cohesive rock platform (Gonzalez et al., 2021). As with other canopy-forming and encrusting species, lower near-surface temperatures within mussel beds are likely associated with shading effects and enhanced moisture retention and evaporative cooling relative to bare rock (Coombes, 2014; Coombes et al., 2013b). The results of our laboratory simulations further support this, whereby the surface-cooling effects of mussels measured in the field were found to translate to reductions in internal rock thermal cycling and dampened near-surface thermal gradients. Importantly, such thermal effects have been shown to influence rock breakdown rates under laboratory conditions (Gowell et al., 2015) and have been linked to platform erosion rates in the field (Gonzalez et al., 2021), although establishing direct causative links remains a challenge.

In comparison to other studies on the bioprotective properties of intertidal species, the magnitude of the dampening effect of *M. edulis* was relatively low (Table 2). For example, Coombes et al. (2013b) found that seaweed canopies on concrete and rock surfaces in South West

England reduced average  $T_{\max}$ ,  $T_{\text{range}}$ , and  $T_{\Delta 30}$  values by between 25% and 78% compared to uncolonised surfaces. In comparison, corresponding measures for *M. edulis* on the platform at Amroth Beach were between 4% and 17%. Based on this, *M. edulis* beds are likely less efficient bioprotectors compared to canopy-forming seaweeds, at least with respect to thermal dampening in temperate climates. This is linked to differences in the nature of the covers formed by different organisms, as mussel encrustations are less effective at retaining moisture during low-tide periods compared to often thicker canopy-forming seaweeds. Nevertheless, given that mussels typically colonise different areas and tidal heights to canopy-forming and other encrusting species, mussels should be considered a potentially important component of the 'mosaic' of biogeomorphic agents on rocky shores. For example, on temperate coasts, *M. edulis* beds may have comparatively high geomorphic relevance in the mid-tide zone, whilst some species of seaweed (e.g., *Fucus* spp.) and barnacles (e.g., *Chthamalus* spp.) may be most important at lower and higher tidal positions. Furthermore, biotic thermal dampening may be enhanced under hotter, more variable climate conditions, with Gonzalez et al. (2021) reporting surface thermal differences in the order of 7–12 °C between mussel-colonised and cleared plots in Argentina.

Importantly, differences in both the methods used and the morphological traits of study organisms likely explain the contrasting thermal dampening effects of different species reported in other studies (e.g., Coombes et al., 2013b, 2017; Gonzalez et al., 2021; Gowell et al., 2015; Jurgens and Gaylord, 2016). These include differences in (1) the morphology of the biological covers (e.g., canopy/encrustation thickness and organism density); (2) the substrate type examined with respect to thermal properties; (3) the study location, tidal height, and local climatic conditions (including simulated climates in laboratory experiments); (4) the spatial and temporal scales of measurement from which thermal measures are derived (e.g., hourly, diurnal, seasonal, inter-annual variability); (5) the type and replicability of the study (e.g., laboratory simulations vs. field measurements); and (6) the measurement instruments used (e.g., infra-red camera vs. different types of dataloggers) and where they are positioned (e.g., loggers attached to the surface vs. loggers embedded within the substrate so they are flush to the surface). For example, the thickness of a biological cover will strongly influence the magnitude of any thermal dampening effects, with thicker canopies having a greater influence in the case of seaweeds (Coombes et al., 2013b). The *M. edulis* beds observed in our study were relatively thin (~ 3 cm, i.e., one individual thick) compared to some types of biological cover examined elsewhere. This includes the *Mytilus californianus* beds examined by Jurgens and Gaylord (2016) who found that 6–10-cm-thick agglomerations reduced monthly near-surface thermal maxima by 10–15 °C compared to bare rock on the east and west coasts of the US. Greater effort is needed, therefore, to standardise research methods, experimental approaches, and reported metrics in biogeomorphic studies to improve comparability. This should help enable the relative and combined bioprotective roles of rocky intertidal communities to be evaluated with greater confidence.

### 4.2. Significance for rock coast weathering regimes

The thermal stabilising effect of *M. edulis* demonstrated in the field and in the laboratory has implications for rock weathering processes as fluctuations and extremes in temperature and humidity are known to influence the efficiency of mechanical weathering processes on rocky shores (Coombes, 2011; Hemmingsen et al., 2007; Kanyaya and Trenhaile, 2005; Mottershead, 2013; Trenhaile, 2006). As well as the extent and rate of rock drying (Coombes and Naylor, 2012; Stephenson and Kirk, 2000), it has been suggested that biological covers that modify the magnitude and frequency of thermal fluctuations during low-tide periods can modulate salt crystallisation processes and thermal fatigue (Gonzalez et al., 2021; Mottershead et al., 2003; Moura et al., 2012). Here, alongside the evidence of thermal buffering by *M. edulis*, the rock

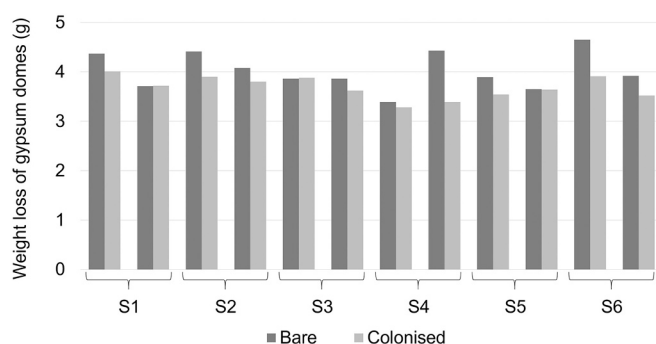


Fig. 9. Weight loss (g) of gypsum domes attached to paired bare and mussel-colonised plots at six different sites (S1–S6) along the study shore platform during two tidal cycles (14th and 15th July 2014).

**Table 2**

Comparison of the mean percentage and absolute differences in temperature metrics between bare rock and rock colonised by canopy-forming and encrusting intertidal species.

	Type of biological cover	Species	Substrate	Reference	Bare vs. colonised difference in $T_{\max}$		Bare vs. colonised difference in $T_{\text{range}}$		Bare vs. colonised difference in $T_{\Delta 30}$		Bare vs. colonised difference in internal thermal gradient ( $^{\circ}\text{C}$ )
					%	$^{\circ}\text{C}$	%	$^{\circ}\text{C}$	%	$^{\circ}\text{C}$	
Field Study	Mussels	<i>Mytilus edulis</i>	Mudstone	This study	4–6	1.3–1.7	8	1.3	8–17	0.5–1.3	–
		<i>Mytilus californianus</i>	(Not reported)	Jurgens and Gaylord (2016)	–	10–15 <sup>b</sup>	–	–	–	–	–
		<i>Brachidontes rodriguezii</i>	Siltstone	Gonzalez et al. (2021)	–	7–12 <sup>a</sup>	–	–	–	–	–
	Seaweed	<i>Fucus</i> spp.	Limestone and Concrete	Coombes et al. (2013b)	25	1.4–5.4	56	4.3	78	–	–
Labo-ratory Study	Mussels	Artificial <i>M. edulis</i>	Mudstone	This study	–	–	–	–	–	–	0.054
	Seaweed	Artificial seaweed	Mudstone	Gowell et al. (2015)	–	3–4	–	–	–	–	–
	Barnacles	<i>Chthamalus</i> spp.	Granite,	Coombes et al. (2017)	–	5.96 <sup>c</sup>	–	–	–	1.63 <sup>c</sup>	0.13 <sup>d</sup>
			Limestone, Concrete		–	1.59 <sup>c</sup>	–	–	–	0.70 <sup>c</sup>	0.16 <sup>d</sup>
					–	5.54 <sup>c</sup>	–	–	–	1.95 <sup>c</sup>	0.07 <sup>d</sup>

<sup>a</sup> Average difference in monthly rather than daily near-surface thermal maxima.

<sup>b</sup> Temperature difference over a 3-h air-exposure period.

<sup>c</sup> Temperatures recorded 10 mm from the rock surface.

<sup>d</sup> Average difference in internal thermal gradients measured between 5-mm and 10-mm depths rather than 10-mm and 20-mm depths as used in this study.

hardness data obtained using the Equotip show that mussel-colonised surfaces were significantly harder than adjacent areas of bare rock, independently of any differences in rock mass strength inferred from the Schmidt Hammer rebound values. This implies that the mussel-colonised surfaces have been exposed to less intense weathering regimes (probably over periods of years to decades) and/or that mussels facilitate surface hardening via some other mechanisms (Blanco-Chao et al., 2007; Chelli et al., 2010; Pappalardo et al., 2018; Stephenson and Kirk, 2000). These mechanisms may relate to the mussel cover itself or to other associated bio-geological features that differ from areas of bare rock (e.g., differences in the type and extent of microbial colonisation). The study by Gonzalez et al. (2021), which reports strength reductions directly following the experimental removal of mussels, implies that the significant differences in surface hardness we measured between the bare and mussel-colonised plots could be linked to mussel presence/absence. Similar differences in Equotip hardness data between bare and colonised surfaces of mudstone have been reported in laboratory simulations examining the influence of (artificial) seaweed cover on rock breakdown (Gowell et al., 2015). In contrast, Pappalardo et al. (2018) found that rock hardness measured using the Equotip was significantly lower on surfaces of sandstone colonised with barnacles compared to adjacent areas of bare rock, which they interpret as being indicative of barnacles being surficial bioeroders.

In addition to surface hardness, our use of gypsum domes as a simple proxy of relative water motion further implies that deteriorative processes associated with turbulence (e.g., abrasion, dissolution, and wave impact) are dampened to some extent within mussel beds, and supports similar findings described by Gonzalez et al. (2021). This is further supported by detailed evidence of wave attenuation by mussel beds, although direct cause and effect relationships remain difficult to establish (Donker et al., 2013).

At the community level, the cooler and wetter conditions maintained by canopy-forming and encrusting species may facilitate other forms of biological weathering and erosion including bioabrasion by grazing molluscs (e.g., Andrews and Williams, 2000; Trudgill, 1988; Vidal et al., 2013) and bioerosion by rock-boring microorganisms and marine animals (e.g., Naylor et al., 2012; Trudgill, 1987; Trudgill and Crabtree, 1987). Furthermore, there is some evidence to suggest that moisture retention by biological covers may enhance chemical forms of rock breakdown in the intertidal zone (e.g., Jayakumar et al., 2010; Jayakumara and Saravanane, 2009; Moura et al., 2012), although direct

evidence for this remains limited (Coombes, 2014). Nevertheless, based on our rock surface hardness measurements, the balance between protective and deteriorative influences likely falls on the side of the former in the case of *M. edulis* on our study platform.

More research is now needed to determine the factors that influence the biogeomorphological impacts of mussels and other marine organisms in different environments and across varying timescales (Kennedy et al., 2017). This might include rock type (e.g., Coombes et al., 2013b); shore position and orientation (e.g., Watt and Scrosati, 2013); wave regimes and wave exposure; species morphological and functional traits (e.g., cover thickness, spatial extent, life-history dynamics, etc.); disturbance regimes (e.g., Coombes et al., 2013; Denny, 1995; Hunt and Scheibling, 2001; Pocklington et al., 2017; Viles et al., 2008); and process variability over seasonal to multi-decadal timescales (e.g., Kennedy et al., 2017; Scrosati and Ellrich, 2018). More broadly, given the recognised challenges of establishing scale linkages in rock weathering research (Viles, 2001), the geomorphic implications of the—often indirectly measured—weathering and erosion influences of mussels and other rocky shore species for shore topography and dynamics require further work. Alongside additional data on rock properties in association with biological colonisation, topographical surveys (including remote sensing, photogrammetry, and UAV surveys) (e.g., Burningham and Knight, 2020; Lathlean et al., 2017), erosion/downwearing monitoring (e.g., Gómez-Pujol et al., 2007; Kanyaya and Trenhaile, 2005; Moura et al., 2012), laboratory simulations (e.g., Coombes and Naylor, 2012; Gowell et al., 2015), and modelling (e.g., Davidson et al., 2018; Naylor et al., 2012; Wang et al., 2014) could all prove useful avenues for future study.

## 5. Conclusions

This study provides the first evidence of the bioprotective role of the common blue mussel (*M. edulis*) on temperate rocky shores. On average, the daily-temperature maxima ( $T_{\max}$ ), temperature range ( $T_{\text{range}}$ ), and highest rate of temperature change ( $T_{\Delta 30}$ ) in summer were 4–6%, 8%, and 8–17% lower, respectively, in the mussel-covered patches on the shore platform compared to adjacent areas of bare rock. Our laboratory simulation further demonstrates that such thermal-buffering effects propagate at least 2 cm into the rock surface. Rates of material disintegration were also significantly lower within mussel beds in association with reduced water motion. Collectively, we suggest these influences at

least partly explain our main finding that mussel-colonised areas were significantly harder than bare areas, indicating that mussels have a bioprotective role on this platform..

In comparison to other intertidal species, the magnitude of the thermal dampening effect of mussels was relatively low under the specific experimental conditions of this study. However, given that mussels can be the dominant cover type at certain tidal heights (i.e., the mid-shore) on many temperate and tropical shores, they likely act as at least locally important biogeomorphic agents. Future work should focus on elucidating the net effect of intertidal species as bioprotective agents on rocky shores (i.e., the balance of mechanical, biological, and chemical effects) as well as exploring the controls of key variables on the magnitudes and relative influences of these effects in space and time.

## Data availability

Datasets related to this article can be found at <https://doi.org/10.5287/bodleian:JVpr9yDp1>, hosted at Oxford University Research Archive (Baxter, 2021).

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## Declaration of Competing Interest

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.

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