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Foul-weather friends: Modelling thermal stress mitigation by symbiotic endolithic microbes in a changing environment

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Abstract :

Temperature extremes are predicted to intensify with climate change. These extremes are rapidly emerging as a powerful driver of species distributional changes with the capacity to disrupt the functioning and provision of services of entire ecosystems, particularly when they challenge ecosystem engineers. The subsequent search for a robust framework to forecast the consequences of these changes mostly ignores within-species variation in thermal sensitivity. Such variation can be intrinsic, but can also reflect species interactions. Intertidal mussels are important ecosystem engineers that host symbiotic endoliths in their shells. These endoliths unexpectedly act as conditionally beneficial parasites that enhance the host's resistance to intense heat stress. To understand how this relationship may be altered under environmental change, we examined the conditions under which it becomes advantageous by reducing body temperature. We deployed biomimetic sensors (robomussels), built using shells of mussels (Mytilus galloprovincialis) that were or were not infested by endoliths, at nine European locations spanning a temperature gradient across 22 degrees of latitude (Orkney, Scotland to the Algarve, Portugal). Daily wind speed and solar radiation explained the maximum variation in the difference in temperature between infested and non-infested robomussels; the largest difference occurred under low wind speed and high solar radiation. From the robomussel data, we inferred body temperature differences between infested and non-infested mussels during known heatwaves that induced mass mortality of the mussel Mytilus edulis along the coast of the English Channel in summer 2018 to quantify the thermal advantage of endolith infestation during temperature extremes. Under these conditions, endoliths provided thermal buffering of between 1.7 degrees C and 4.8 degrees C. Our results strongly suggest that sustainability of intertidal mussel beds will increasingly depend on the thermal buffering provided by endoliths. More generally, this work shows that biomimetic models indicate that within-species thermal sensitivity to global warming can be modulated by species interactions, using an intertidal host-symbiont relationship as an example.

Keywords : biophysical model, climate change, mussels, mutualism, thermal tolerance

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INTRODUCTION

Globally, extreme temperature events have risen in frequency, strength and duration (e.g., Oliver et al., 2018) and are predicted to become more severe with intensifying climate variability (Fischer et al., 2010; Rahmstorf et al., 2011). Recently, extended periods of anomalously high temperatures such as heatwaves have driven significant ecological changes (e.g., Hughes et al., 2017; Smale et al., 2019; Wernberg et al., 2013). Given the serious consequences for biodiversity and ecosystem functioning, there is increasing interest in understanding variability in within-species thermal tolerance; we have yet to understand why some individuals survive when conspecifics succumb to abrupt temperature increases. The appreciation of such within-species variability will aid the prediction of long-term responses by species as a whole. Identifying the full capacity of species to survive heatwaves and extreme heat stress events may offer crucial insights into the stability of their ecological, and socio-economic functions.

Intertidal ecosystems are among the most productive of ecosystems, supplying vital services such as food production, stabilization of shorelines, capture of ‘blue carbon’, water clearance, nutrient turnover and acting as nurseries for high-trophic level taxa (e.g., Costanza et al., 1997; Macreadie et al., 2019; Raffaelli et al., 2012). Due to their daily exposure to both aerial and marine conditions and their low thermal inertia compared to open-ocean waters, these ecosystems are particularly vulnerable to extreme climatic events such as heatwaves and coldwaves (Halpern et al., 2008). Heatwaves in particular, have drastic deleterious effects on intertidal ecosystems globally. Heatwave-induced mass mortalities, local extinctions and range contractions of numerous key benthic habitat-forming species (e.g., corals, seagrasses, macroalgae, bivalves) have resulted in depleted local biodiversity, reduced carbon sequestration and weakened natural coastal defences (Arias-Ortiz et al., 2018; Holbrook et al., 2020). The damage caused by heatwaves also reduces the socioeconomic value of these

ecosystems by reducing recreational activities and tourism (e.g., Smale et al., 2019; Stillman, 2019) with major direct economic damage to recreational, artisanal and commercial fisheries (e.g., FAO, 2020; Li et al., 2019).

Mussel die-offs induced by heatwaves exemplify the severe economic and ecological effects of extreme heat events. Intertidal mussels are dominant ecosystem engineers that provide crucial habitat, supporting biodiversity and underpinning myriad ecosystem functions and services. For example, evidence from the NE Pacific coast and from southern African rocky shores shows that hundreds of associated species (e.g. invertebrates, small fish and algae) depend on mussel aggregations (Nicastro et al., 2020; Suchanek, 1985). Their dense mono- and multi-layered beds remain moist and thermally benign during low tides and offer protection against wave action during high tide (Helmuth et al., 2016). The loss of mussel beds associated with recent warming trends has resulted in the decline of species richness and the alteration of community structure (Harley, 2011).

Numerous experimental and observational studies have shown that symbiotic interactions, both parasitic and mutualistic, have dramatic effects on the host organism (Chomicki et al., 2020; Firth et al., 2017). Such interactions can alter the host's experience of environmental stress by altering the host phenotype (Feldhaar, 2011), with consequences for host fitness (i.e., survival and fecundity). When the host species is an ecosystem engineer, such as a mussel, these interactions can have significant knock-on effects at population, community and ecosystem levels (Fellous et al., 2009). As thermal stress intensifies under climate change, the effect of symbionts on the temperature tolerance of their hosts will be particularly important. Parasites can drive considerable alterations to both their host's thermal performance optima (Gehman et al., 2018) and thermal preferences (Macnab et al., 2012). In turn, mutualisms can favour survival following exposure to heat stress (Brumin et al., 2011; Feldhaar, 2011). Because gradual warming and the increased stress of extreme heat events

will challenge individuals with and without symbionts, mutualistic relationships will have a major role in setting within-species thermal variability (Feldhaar, 2011).

Critically, the nature of symbiotic associations is context dependent; a single symbiotic species can have both positive and negative effects depending on the biotic/abiotic environment in which the interaction occurs (e.g., Altizer et al., 2013; Harvell et al., 2009; Nowakowski et al., 2016; Sauer et al., 2018). The gradual change between symbiotic states may confer a suite of novel traits to the host organism thus offering it ecological opportunities (*sensu* Janson et al., 2008) that would otherwise be unavailable. This is the case for the widespread symbiosis between shell-degrading endolithic cyanobacteria and intertidal mussels (Zardi et al., 2016). Until recently, numerous studies have described a multitude of negative (lethal and sub-lethal) effects of endolith corrosion in mussels (Marquet et al., 2013), stressing the parasitic nature of this relationship (Zardi et al., 2009). Endoliths are metabolically dependent on the host for CO_2 released during shell degradation, which they use for photosynthesis (Garcia-Pichel et al., 2010). As a result, endoliths can affect the host's energetic budgeting through their boring activity at the expense of byssal attachment strength, growth and reproduction (Kaehler et al., 1999; Marquet et al., 2013; Ndhlovu et al., 2021; Nicastro et al., 2018; Zardi et al., 2009). Importantly, recent results have shown that shell corrosion caused by endoliths mitigates the thermal stress experienced by their mussel hosts; mussels with corroded shells experience significantly lower body temperatures leading to significant increases in survival (up to 50%) during heatwaves compared to conspecifics that are not affected by endoliths (Zardi et al., 2016). Such conditional help (*sensu* Fellous & Salvaudon, 2009) is triggered by reduced absorption of solar energy by mussel shells that are whitened by endolithic boring (Gehman et al., 2019; Zardi et al., 2016).

Despite a growing number of studies reporting the incidence and effects of phototrophic shell-degrading endoliths in a variety of taxa and habitats, the key environmental factors that determine the nature of the relationship remain unknown. This study aims at understanding the limits of endolith-mediated protection against thermal stress across

environments. Such knowledge is pivotal to the development of realistic, large-scale predictions of how mussel beds will respond to environmental change and the consequences to their related ecosystem and socio-economic value. To achieve this, we built biomimetic temperature loggers using the shells of *Mytilus galloprovincialis* that were either heavily infested or not infested by endoliths. These were then deployed in the field across a wide latitudinal range (i.e., 37°N to 59°N) to assess changes in endolithic thermal buffering in a variable environment and to identify the drivers of the maximum temperature differences between non-infested and infested mussels. Data from the biomimetic temperature loggers and high-resolution weather data were then used in Generalized Linear Mixed Models to identify the environmental factors influencing the cooling effect of endoliths on mussel populations. We subsequently used the model to identify maximum body temperature differences between infested and non-infested mussels under the known conditions of a heat wave-induced mortality event of *Mytilus edulis* that occurred along the north French coast in summer 2018. In parallel, we assessed whether non-infested mussels warm up faster than infested individuals as expected for dark ectotherms vs paler ones (Moyen et al., 2019; Porter et al., 1969).

METHODS

Drivers of the maximum temperature difference between non-infested and infested mussels

Biomimetic temperature loggers (robomussels) are used to mimic the thermal characteristics of living mussels (Helmuth et al., 2010; Helmuth et al., 2016). In this study, robomussels were deployed at multiple locations across a wide latitudinal range and environmental gradient along North Atlantic shores to quantify differences in body temperatures of mussels with and without endoliths when exposed to natural variability in meteorological conditions. All robomussels were assembled using the emptied shells of *Mytilus galloprovincialis* (shell length

153 4-5 cm) sampled at Viana do Castelo (Portugal; 41°42'0.94"N, 8°51'25.59"W) from wave
154 exposed intertidal rocky shores composed of granite. Mussels were sampled within a
155 monolayered bed (i.e. all individuals attached directly to the substratum) in a sun-exposed
156 area (i.e. surfaces with limited shading, exposed to solar radiation 60 % of the day). Shells
157 were either non-infested (Group A; Zardi et al., 2009) or heavily infested by endoliths (Group
158 D; Fig. 1a); Group A shells have clean, intact periostracum and distinct periostracal striation,
159 Group D shells are severely pitted and deformed, and the outer striations on the periostracum
160 are almost completely absent. Robomussels were made by placing a temperature logger
161 (iButtons®, DS1922, Maxim Integrated Products, Dallas Semiconductor, USA, resolution =
162 0.5 °C, accuracy = 0.5 °C) between two empty mussel valves filled with silicone sealant and
163 leaving it to dry at air temperature for 48 hours before being deployed in trials (Nicastro et al.,
164 2012). Endoliths in infested shells were killed by keeping the mussel shells in boiling water for
165 an hour before assembling them (Zardi et al., 2016). Loggers recorded temperatures at 30-
166 min intervals from 1st August to 13th September 2017, for a period of 42 days at nine sites (Fig.
167 1b; Supplementary Table S1). Data were lost from Plymouth (UK) due to robomussels being
168 vandalised. For one site (Aberffraw, UK), deployment was done the following summer, from
169 28th July to 18th September 2018. At each site, three to six pairs of infested and non-infested
170 robomussels were glued to the substratum (Z-spar Splash zone, A-788) in the mid mussel
171 zone on a relatively flat slope, orientated like a living solitary mussel (i.e., longitudinal axis
172 oriented parallel to the substratum with the ventral side facing the substratum) and equidistant
173 from each other (approximately 10 cm).
174 At each site, average estimates of robomussel intertidal height were calculated using the
175 temperature logger profiles and tables of tidal heights (Gilman et al., 2006; Harley et al., 2003).
176 These profiles clearly reveal when robomussels are first inundated by the returning tide
177 through a sudden sharp drop in temperature. The time of tidal inundation was used to calculate
178 the Effective Shore Level (ESL) using the XTide software (https://flaterco.com/xtide/). Tidal
179 predictions were obtained for nearby maritime ports (Supplementary Table S2). For every

robomussel pair, we retrieved all tidal levels that were associated with a temperature drop of >8°C in 30 min during incoming tides. We chose this threshold, which corresponds to a 5.33°C drop in 20 min, to ensure reliability of ESL estimates while maximising the probability of finding at least one drop during the study period (Gilman et al., 2006). We calculated the mean ESL (± standard deviation; SD) for each robomussel pair (Supplementary Table S3). ESLs were used to determine when mussels were exposed/submerged. However, ESLs can vary daily due to surge and wave exposure, which might lead to the misidentification of exposed/submerged periods. To ensure that temperature data were correctly attributed to periods of submergence or aerial exposure, we kept data that were recorded above the upper limit of a buffer zone (mean ESL + 0.3 m) or below the lower limit of a buffer zone (mean ESL - 0.3 m). Temperature data during submergence were used as a control, as we expect no differences in temperature between non-infested and infested robomussels when submerged. We used Linear Mixed Effects models (LMEs; using 'nlme' R package; Pinheiro et al., 2020) to test this. After adding robomussel identity as a random effect and controlling for autocorrelation (autoregressive model of order 1), we found that non-infested mussels were, on average, significantly warmer than infested ones during aerial exposure (mean difference = 0.36°C, SD = 2.04, t = -2.14029, p = 0.0323) whereas we did not find a significant difference during submergence (t = -1.62900, p = 0.1033). Therefore, we kept only temperature data during emergence for further analysis.

Using robomussels as proxy for mussel body temperature (Helmuth et al., 2010; Helmuth et al., 2016), we expected the maximum difference between non-infested and infested mussels (calculated as non-infested minus infested temperatures for each robomussel pair) to vary geographically during emergence due to site-specific meteorological conditions. Meteorological variables that are considered determinants of the body temperature of invertebrates (i.e. air temperature, wind speed, precipitation, relative humidity, and solar radiation (Helmuth, 1998)) were obtained from nearby weather stations (Supplementary Table

206 S4). However, we excluded three of our nine study sites from this analysis because solar
207 radiation was not measured at these sites during the study period (Supplementary Table S4).
208 Weather station data in the United Kingdom (Met Office, 2019a, 2019b, 2019c), France and
209 Portugal were provided by the Centre for Environmental Data Analysis (CEDA;
210 http://data.ceda.ac.uk/badc/ukmo-midas-open/data/), Météo-France
211 (https://donneespubliques.meteofrance.fr/) and Instituto Portugês do Mar e da Atmosfera
212 (IPMA; https://www.ipma.pt/en/otempo/obs.superficie/), respectively.

213 We used Generalized Linear Mixed Models (GLMMs; using 'lme4' R package; Bates et
214 al., 2015) to test for effects of daily values of (i) mean air temperature (°C), (ii) mean wind
215 speed (m s^{-1}), (iii) total precipitation (mm), (iv) mean relative humidity (%), and (v) total (global)
216 solar radiation (J m^{-2}) on the daily maximum difference in temperature between non-infested
217 and infested robomussels during emergence. Meteorological variables were averaged (or
218 summed for solar radiation and precipitation) within robomussel pair-specific periods of
219 emergence. The identity of individual pairs of robomussels was included as a random factor
220 nested within study site to account for inter- and intra-site variance. Because our dependant
221 variable was non-normally distributed (positively skewed), we used GLMMs with a Gamma
222 distribution and excluded the few days during which non-positive temperature differences
223 were found between paired robomussels. We applied a log link function to stabilize the
224 variance of residuals. We fitted all models (i.e. all combinations of response variables) using
225 maximum likelihood and selected the best candidates based on the lowest value of Akaike
226 Information Criteria corrected for finite sample size (AICc) and Akaike weights, which give a
227 measure of the relative support for each model (Akaike, 1974; Burnham et al., 2002). We
228 considered models with $\Delta AICc < 2$ as competitive and, for the sake of parsimony, we retained
229 the model with the least number of parameters. Based on this model, we extrapolated daily
230 maximum differences in body temperature between non-infested and infested mussels under
231 a range of meteorological conditions likely to be encountered on the shore.

Quantifying the thermal advantage of infestation during a heatwave-induced mussel mortality event

To assess the extent of thermal buffering provided by endoliths during extreme hot weather conditions, we used the meteorological data at Wimereux, France, during summer 2018 where mass mortality events of *Mytilus edulis* occurred following heatwaves (Seuront et al., 2019). Nine heatwaves (ranging from moderate to severe; see Table 2) were identified based on air temperature, following Hobday et al. (2018). We extracted meteorological data during these periods and predicted the daily maximum temperature difference between non-infested and infested mussels based on the previously selected model.

Assessing heating rate and maximum body temperature during aerial exposure

Temperatures recorded by robomussels were used as proxy of the body temperatures of living mussels. To assess whether non-infested mussels warm up faster and reach higher body temperatures than infested ones during aerial exposure, we calculated the rate of change in body temperature as well as the maximum and near-maximum (95^{th} percentile) body temperature for each robomussel during aerial exposure for every tidal cycle. We calculated the average rate of change in body temperature during one tidal cycle using the slope of the linear regression between temperature and time data (converted to °C h^{-1}). A positive slope indicates that robomussels were warming up while a negative one indicates that robomussels were cooling down. We assessed potential differences between non-infested mussels and infested ones using Linear Mixed Effects models with robomussel identity included as a random effect.

RESULTS

The thermal buffering effect of infestation depends on solar radiation and wind speed

Five candidate models were retained, with the number of selected meteorological parameters varying from two to four (Table 1). When compared to the null model (i.e., assuming no effect of any meteorological parameters; Table 1), these models exhibit a better fit (Table 1). The two best models (i.e., those with the lowest AICc values) showed similar relative support (Akaike weights > 0.2; Table 1) and, for the sake of parsimony, we selected the simplest one (i.e., using solar radiation and wind speed; Table 1) for further analysis. The results suggest that solar radiation ($t = 8.609$, $p < 0.0001$) and wind speed ($t = -3.181$, $p = 0.00147$) are the main drivers of the maximum difference in body temperature between non-infested and infested mussels. The selected model appropriately reproduced measured temperature differences, albeit slightly underestimating the difference at high temperatures (Supplementary Fig. S1). On average, daily total solar radiation during emergence increased from northern to southern sites with greater variability measured at the three northernmost (NEB, SKA and ABE) and intermediate (WIM) sites considered (Fig. 1c). Daily mean wind speed showed the opposite trend; decreasing to the south and again with greater variability measured at the three northernmost sites. Note that the southernmost site (VIL) was more exposed to wind than the other southern site (MON) during the study period. Geographically, the cooling effect of microbial endoliths (expressed as the maximum difference in body temperature between non-infested and infested robomussels predicted from the selected model using solar radiation and wind speed averaged over the study period) showed a gradient decreasing from southern (VIL and MON) to intermediate (WIM) and northern (NEB, SKA and ABE) sites (Fig. 1d). However, there was no clear pattern with latitude among the closest sites (e.g., MON and VIL). Confidence intervals of predictions (Fig. 1d) are shown in Supplementary Fig. S2 and the relationship between measured temperature differences and weather data is shown in Supplementary Fig. S3.

Prediction of body temperature differences between non-infested and infested mussels during heatwaves

283 In summer 2018 at Wimereux, based on the model that uses solar radiation and wind speed
284 (see Table 1 and prediction surface in Fig. 1d), we predicted a cooling effect of microbial
285 endoliths (i.e., the temperature difference between non-infested and infested mussels) of 4.21
286 to 4.77°C during June heatwaves (which were classified as moderate to strong), of 2.75 to
287 4.14°C during July heatwaves (which were classified as moderate to severe), and of 1.67 to
288 3.97°C during August heatwaves (which were classified as moderate to strong; estimates are
289 plotted on the prediction surface in Fig. 1d and confidence intervals are provided in Table 2).
290 During most of these heatwaves, mussels were exposed to high solar radiation (noticeably
291 higher than the conditions observed on average in southern sites like MON and VIL) and
292 moderate wind speeds (similar to the conditions observed on average at all sites except ABE
293 and MON; Fig. 1d). For one heatwave (10th August) that occurred under moderate solar
294 radiation and high wind speed, the predicted temperature difference was rather low and similar
295 to the ones predicted for northern sites (NEB, SKA and ABE).

296

297 **Non-infested mussels warm up faster and reach higher body temperatures than**
298 **infested mussels**

299 During periods of aerial exposure, non-infested robomussels warmed up faster than infested
300 ones ($t = -1.982$, $p = 0.0475$; mean rate of change = 0.38 and 0.28 °C h^{-1}, SD = 1.75 and 1.45,
301 respectively; Fig. 2a). Non-infested robomussels also reached higher maximum temperatures
302 than infested ones ($t = -4.477$, $p < 0.0001$; mean maximum temperature = 22.93 and 22.07°C,
303 SD = 7.5 and 6.6, respectively; Fig. 2b). We obtained similar results when comparing near-
304 maximum (95th percentile) temperatures ($t = -4.098363$, $p < 0.0001$; mean near-maximum
305 temperature = 22.47 and 21.69°C, SD = 7.31 and 6.45, respectively for non-infested and
306 infested ones; Fig. 2c).

307

DISCUSSION

We observed striking reductions in temperature in endolithically corroded robomussels compared to uncorroded ones in intertidal habitats, across large geographical areas exposed to a wide range of oceanographic and climatic conditions. Given that the biomimics used in this study have been extensively shown to be an accurate tool for recording organismal body temperature in their natural environment (e.g., Fitzhenry et al., 2004; Helmuth et al., 2016; Seabra et al., 2015), our results can effectively be interpreted as a marked cooling effect in infested mussels compared to non-infested mussels. Intraspecific variability in body temperature has to be accounted for in order to interpret and predict responses of the species to climatic change across biogeographic ranges. This is relevant not only for the individuals themselves, but also for the ecosystem as it provides crucial insights into the future stability of mussel beds and their role as ecosystem engineers that support myriad species, and a range of ecosystem functions and services.

We identify daily-mean wind speed and daily-total solar radiation as the environmental variables with the strongest influence on the within-site thermal buffering effects of endoliths. This is in agreement with previous work showing how body temperatures of intertidal ectothermic animals are primarily controlled by non-climatic heat sources, solar heating and re-radiation as opposed to climatic heat sources, i.e. air and water temperatures (e.g., Helmuth, 2002; Marshall et al., 2010). Our results show a negative relationship between the two key variables, suggesting that the seasonality of wind and solar radiation most likely will shape the implications of our results. While the highest wind speeds typically occur during winter, the peak in solar radiation usually occurs in summer when thermal heat stress is at its highest. This means that the maximum endolithic thermal buffering occurs in summer when it is also most ecologically meaningful. In summer, during heatwave conditions recorded at Wimereux in France, body temperature differences between non-infested and infested mussels ranged between 1.7°C and 4.8°C. Like other intertidal organisms, mussels live close

to the upper limit of their physiological thermal tolerance window and such a remarkable level of thermal buffering due to phenotypic variation has the potential to trigger changes at the population level, particularly in areas where the survival and physiological performance of mussels have already been affected by increasing temperatures. Our findings show that uncorroded individuals have significantly higher maximum body temperature and faster heating rates than those of corroded mussels. In particular, heating rate is known to have significant effects on cardiac thermal performance in intertidal mussels; recent studies show that faster heating rates significantly increase the heart's critical temperature (i.e., the temperature triggering a precipitous decline of heart rate; Moyen et al., 2019). Critically, these studies also emphasise the complexity of abiotic and physiological interactions. Heating rates significantly affect the cardiac thermal tolerance, of high- but not low-zone mussels, while heavy mussels tend to heat up faster compared to light weight mussels- but at the fast-heating rate only.

The heating rates recorded in our study are lower than those previously reported in natural populations (e.g., Miller et al., 2017) or in laboratory experiments (e.g., Moyen et al., 2019 and references therein) and are thus unlikely to significantly affect heart rates, at least under our study conditions. Additionally, all mussels used to build robomussels were collected from the same site and mussel zone and had similar shell length, excluding any potential effect of body mass. Nevertheless, given the determinant role of intertidal height on mussel cardiac thermal tolerance, further investigation is needed to assess the effect of endolithic corrosion on heating rates and heart rates throughout the intertidal distribution of mussels and for different body masses. Framed in a more theoretical context, our results show that endoliths provide their host mussels with a *key innovation* (i.e., thermal buffering) that potentially offers an ecological opportunity, opening previously unexploited niches. Key innovations (termed "*ad hoc* novelty" in Feldhaar, 2011; Miller, 1949) are features that allow a species to interact with the environment in a different way and thus may provide the capacity, otherwise unavailable,

to exploit available resources (Galis, 2001; Hunter, 1998; Rabosky, 2014). For instance, in tropical dendrobatid poison frogs, the evolution of bright coloration as an advertisement of unprofitability to predators, reduces the function and thus the need for predator-induced "hiding" behaviour, thus offering novel habitat opportunities (Arbuckle et al., 2015; Santos et al., 2003; Summers, 2003). Another example is that of archer fish (*Toxotes* spp.) in which the evolved capacity to fire jets of water from their mouths to dislodge insects perched on overhanging foliage has opened access to new prey resources (Burnette et al., 2015; Schuster et al., 2006). Key innovations have been mainly investigated in an evolutionary context and are often described as a key and eventually an essential stimulus for adaptive radiation through "*the evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms*" (Futuyma et al., 1988).

However, key innovations can be obtained through faster or even non-evolutionary routes. For instance, a variety of genome-engineering approaches have been used to reduce the proportion of black found on dairy cattle coats aiming at decreasing radiative heat gain, a contributing feature to heat stress (Maga, 2020). Similarly, alteration of a host's life history traits triggered by symbionts may become advantageous under certain environmental conditions; fast-tracking the host to higher fitness levels that would otherwise be accessible only through slower microevolutionary steps (Fellous & Salvaudon, 2009). Alternatively, symbiont-induced phenotypic changes may provide new functions allowing the host to reach higher levels of fitness unlikely to be attainable through mutation. Shell colour in intertidal mussel is reasonably plastic, however, the distinctive shell whitening caused by the eroding activity of endoliths extends beyond the range of such plasticity. This pronounced phenotypic change provides mussels with a higher degree of thermal buffering that is most likely unreachable through adaptive mutation. It has been suggested that endolithic thermal buffering might be indicative of a transition towards mutualism in the endolith-mussel relationship (Gehman & Harley, 2019; Zardi et al., 2016). Indeed, most mutualisms have evolved from wholly parasitic associations and conditionally beneficial parasites are

intermediate stages in a transient relationship triggered by changes in the biotic/abiotic environment (Fellous & Salvaudon, 2009). The ecological advantages of endolithic infestation are likely to be increasingly important in an era of global warming and more frequent and intense heatwaves. On the other hand, recurred storm strikes are also predicted to increase potentially raising mortality rates in infested mussels as they are more weakly attached to rocky shores than non-infested mussels. Critically, the ecological advantages of mussels with corroded shells will vary spatially and temporally. Our results suggest that these benefits will potentially peak in summer and at lower latitudes when and where intense solar radiation maximises relative differences in body temperature between corroded and uncorroded mussels.

In order to standardise our experimental design, all robomussels used were built using *M. galloprovincialis* shells sampled from a single location in southern Portugal. In reality, our study sites supported different mussel species, including *M. galloprovincialis*/*M. edulis* hybrids in the UK and northern France (Bierne et al., 2003), raising the possibility that endolithic communities and the cooling effect observed *in M. galloprovincialis* robomussels may not apply to other species. Recent evidence indicates that endolithic community composition and the thermal benefits they confer are similar among hosts. *Perna perna*, with an aragonite shell and *M. galloprovincialis*, with aragonite and calcite shell layers, co-exist in South Africa. Despite differences in shell and periostracum structure (Bers et al., 2010), severely infested mussels of the two species support the same endolith species (Ndhlovu et al., 2020). Most importantly, both mussels exhibit the same degree of thermal buffering by endoliths under a variety of environmental conditions (Zardi et al., 2016). Together these findings support the abundant literature highlighting the generalist, nonspecific, nature of endolithic corrosion (e.g., Golubic et al., 2005) and strongly suggest that thermal stress mitigation by symbiotic endolithic microbes does not apply to *M. galloprovincialis* only.

Mussel mass mortalities have repeatedly been reported globally and are often attributed to heatwaves (Harley, 2008; Petes et al., 2007; Suchanek, 1985; Tsuchiya, 1983). During the heatwave on the northern French coastline in August 2018, large numbers of empty mussel shells were washed ashore (Seuront et al., 2019). Interestingly, a close examination to over 1200 randomly shells collected following this mass mortality event show that the vast majority of them (96 to 100%) had no sign of infestation (Seuront, unpublished data, see Supplementary Material Figure S4). Although such observations cannot quantify or confirm the protective roles of endoliths, they complement previous field manipulative experiments in different regions showing that, during heat waves, the moderation of solar heating by endoliths results in significantly lower mortality rates (Gehman & Harley, 2019; Zardi et al., 2016). Interestingly, large-scale sampling covering a wide latitudinal range (ca. 28-37^{o}N) along the coasts of Portugal and Morocco revealed a strong gradient of increasing endolithic infestation of *M. galloprovincialis* towards lower latitudes, presumably due to the enhancement of endolith photosynthetic activity through greater light availability and decreased cloud cover towards the equator (Lourenço et al., 2017). Importantly, *M. galloprovincialis* is the only *Mytilus* spp. along this coast, eliminating potential confounding effects between endolith frequency and host identity. Likewise, higher levels of shell corrosion at lower latitudes is unlikely due to latitudinal or geographic changes in endolithic species. Endolithic community composition does not differ significantly between *M. galloprovincialis* from native (Portugal) and invasive (South Africa) regions nor from *P. perna* shells from different bioregion along 1000s km of the South African coast (Marquet et al., 2013; Ndhlovu et al., 2019). Most importantly, our results indicate that endolithic corrosion is higher at lower latitudes where its beneficial effects are enhanced and most beneficial to the host. Will climate-associated thermal stress push the endolith-mussel relationship towards a long-lasting mutually beneficial association? This seems possible as heatwaves are increasing in intensity, frequency and duration and these trends are expected to strengthen under future climatic changes (Perkins-Kirkpatrick et al., 2020; Smale et al., 2019). Further work is required to

437 evaluate if the cooling effect of endoliths has a significant impact on mussel fitness and if the
438 average fitness of corroded hosts, across all possible environments, is higher than that of
439 uncorroded individuals. Such an approach will also be key to testing the validity of near-future
440 conditions under which mussels shift their ecological niche to one whereby endoliths are more
441 often advantageous or might even evolve endolith dependence, losing the ability to live without
442 their symbionts.
443
444 Although hosts and symbionts have coupled life cycles, they can respond differently to
445 environmental changes. Thus, the response of host–symbiont interactions to climate warming
446 may largely depend on the performance of each interactor and the influence of the symbiont
447 on host performance (Gehman et al., 2018; Lafferty et al., 2003). In this context, mussel
448 survival may increasingly benefit from the thermal buffering provided by endolithic shell
449 erosion, which is predicted to increase as a result of ongoing ocean acidification and warming
450 rates (Reyes-Nivia et al., 2013; Tribollet et al., 2009). A further complication lies in the fact that
451 the endoliths infesting mussel shells comprise a community, the composition of which alters
452 in time and space (Ndhlovu et al., 2019; Pittera et al., 2014). Nevertheless, the generalist
453 nature of endoliths and their ubiquitous erosion of marine calcifying organisms
454 already stretched to the limits of their thermal tolerances strongly suggest that they will have
455 a key influence on the ability of many intertidal ecosystems to maintain their ecological
456 functions.
457

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TABLES

Table 1. Main drivers of the maximum difference in body temperature between non-infested and infested mussels. Results are shown for all best candidate models (ΔAICc < 2) as compared to the null model, along with associated Akaike weights (relative support of each model). The selected model (least number of parameters) is indicated in bold.

Meteorological parameters (estimated coefficients±SE)	AICc	ΔAICc	Akaike weights
Intercept(0.51±0.35) + AT(-0.03±0.02) + SR(0.05±0.005) + WS(-0.04±0.01) + Rdm(SD=0.24)	1845.13	0	0.28
Intercept(0.09±0.16) + SR(0.05±0.005) + WS(-0.04±0.01) + Rdm(SD=0.24)	**1845.34**	**0.21**	**0.25**
Intercept(0.66±0.36) + SR(0.04±0.007) + RH(-0.006±0.004) + WS(-0.04±0.01) + Rdm(SD=0.24)	1845.88	0.75	0.19
Intercept(0.94±0.48) + AT(-0.02±0.02) + SR(0.05±0.007) + RH(-0.005±0.004) + WS(-0.04±0.01) + Rdm(SD=0.25)	1846.14	1.02	0.17
Intercept(0.50±0.35) + AT(-0.03±0.02) + SR(0.05±0.005) + PR(0.002±0.005) + WS(-0.04±0.01) + Rdm(SD=0.24)	1847.01	1.88	0.11
null	1969.24	124.12	0

Abbreviations: Solar Radiation (SR), Relative Humidity (RH), Wind Speed (WS), Air Temperature (AT) and Precipitation (PR), Random factor (Rdm; robomussel identity nested within locations).

Table 2. Meteorological conditions during heatwaves identified in 2018 at Wimereux, France. Heat waves were identified based on air temperature during summer 2018, and were classified from moderate to extreme: “These events were classified as moderate (78.1%) to strong (21.9%) in June, moderate (67.8%), strong (23.1%), severe (7.0%) and extreme (2.0%) in July, and moderate (63.0%), strong (30.9%) and severe (6.2%) in August.” (from Seuront et al. 2019). Maximum temperature differences between non-infested and infested mussels

732 were predicted based on wind speed and solar radiation using the model selected in the
733 present study.

Date (in 2018)	Mean daily wind speed ($m.s^{-1}$)	Mean daily total solar radiation ($MJ.m^{-2}$)	Predicted max. temperature differences (°C) (95% confidence intervals)
June 28 to 30	4.54	28.160	4.26 (1.15)
July 05 to 07	2.48	26.006	4.14 (1.12)
July 23 to 25	2.61	24.433	3.80 (1.11)
August 01 to 08	2.67	25.350	3.97 (1.11)
June 23	2.81	26.610	4.21 (1.13)
June 26	4.41	30.270	4.77 (1.17)
July 13	3.12	18.510	2.75 (1.08)
July 17	5.95	28.350	4.06 (1.17)
August 10	8.95	13.340	1.67 (1.12)

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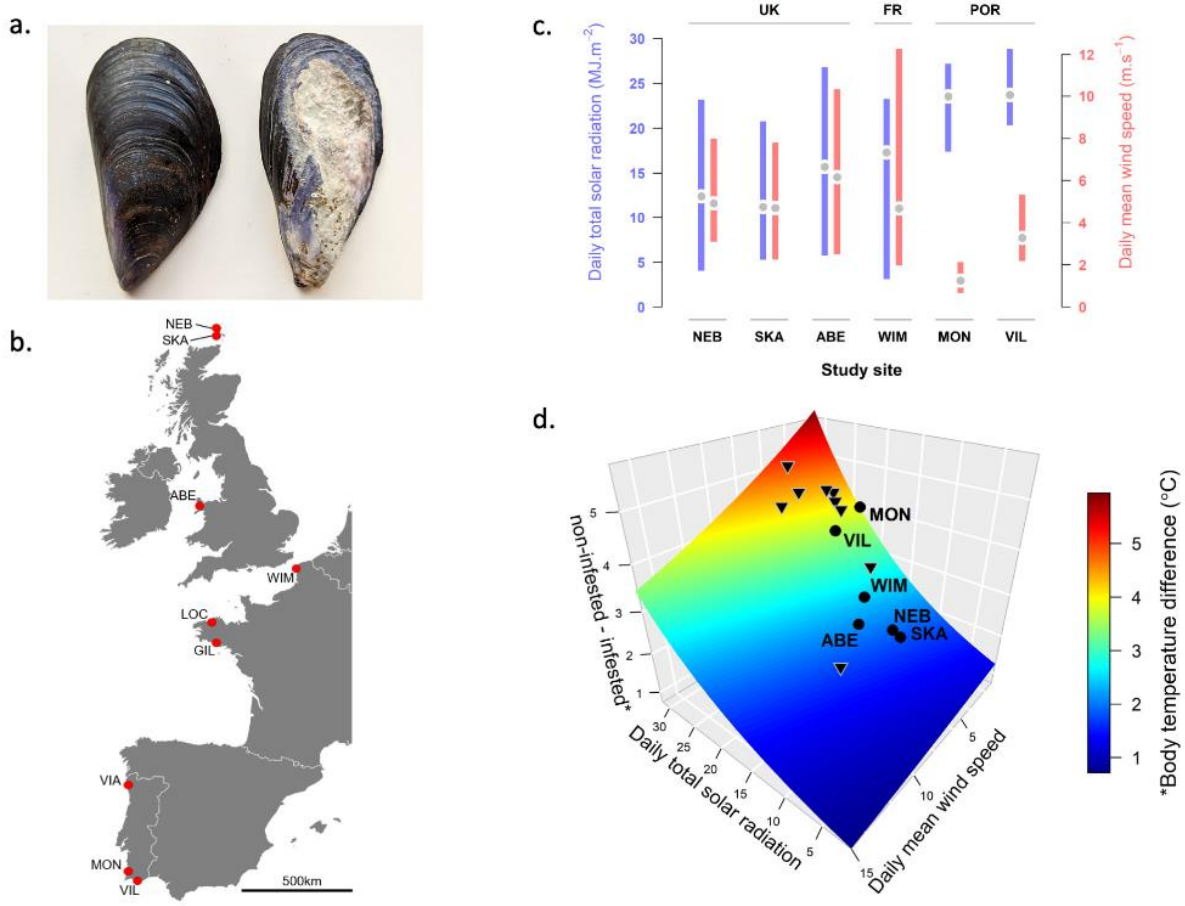
736 **FIGURE LEGENDS**



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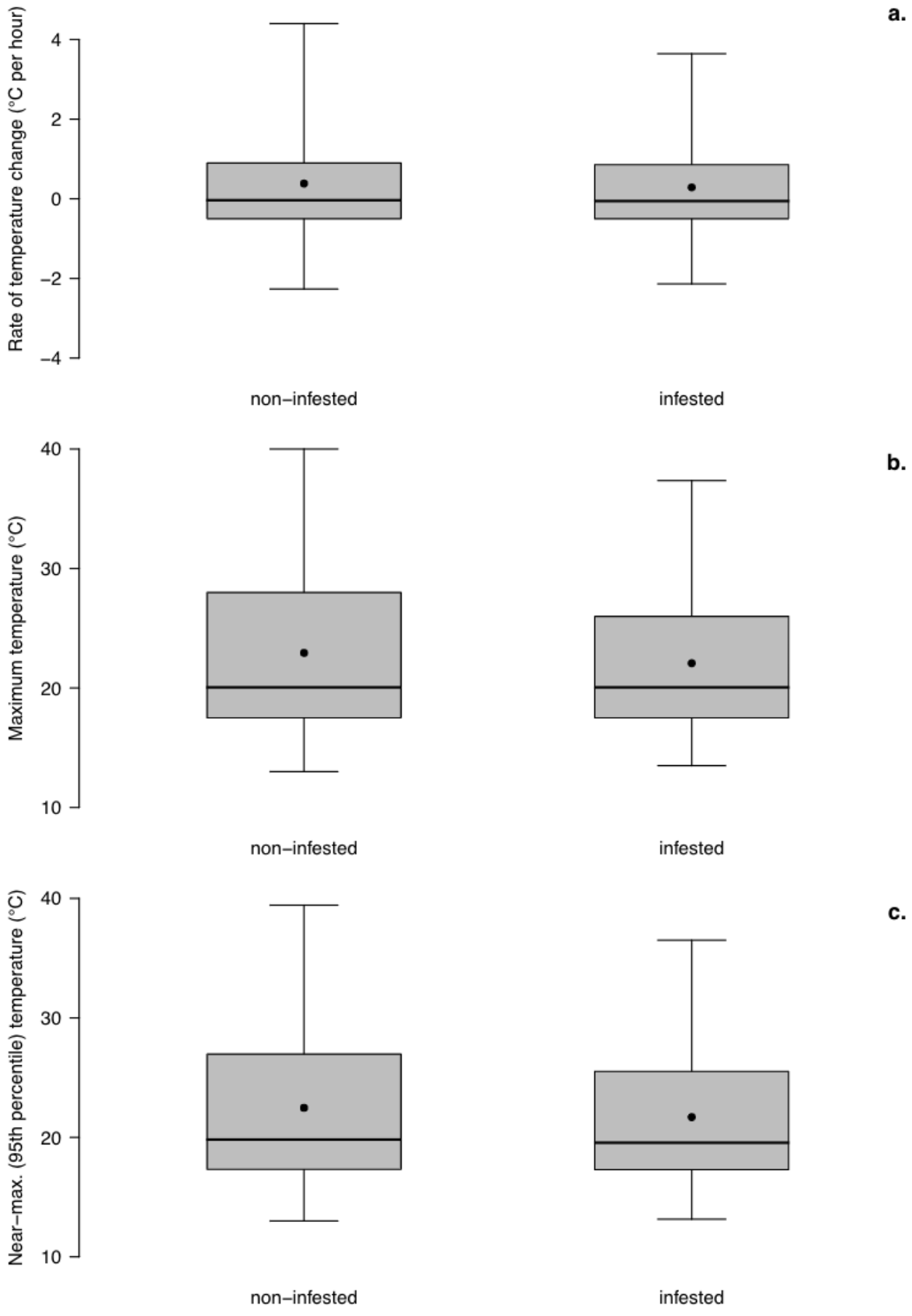
738 **Fig. 1.** (a) Example of non-infested and infested mussels. (b) Study sites where mussels were
739 deployed. (c) Daily total (global) solar radiation (blue) and mean wind speed (red) during
740 emergence at (from north (left) to south (right)) Nebo Geo (NEB), Bay of Skaill (SKA) and
741 Aberffraw (ABE), United Kingdom (UK), Wimereux (WIM), France (FR) and, Monte Clerigo
742 (MON) and Vilamoura (VIL), Portugal (POR). Coloured bars indicate 2.5th and 97.5th
743 percentiles and grey points are the median values. (d) Prediction surface of maximum
744 temperature differences in body temperature between non-infested and infested mussels (see
745 Supplementary Fig. S2 for a 2D representation with confidence intervals): The daily maximum
746 difference increases with increasing solar radiation and decreasing wind speed (units are
747 displayed in panel c). Black points indicate the mean expected difference for each site using
748 data averaged over the study period and triangles indicate the mean expected difference
749 during nine heatwaves identified at Wimereux during summer 2018 (confidence intervals are
750 between +/-1.08°C and +/-1.15°C for predictions during heatwaves; see Table 2).

Pre-proof accepted version of Zardi, G.I., Monsinjon, J.R., McQuaid, C.D., Seuront, L., Orostica, M., Want, A., Firth, L.B. and Nicastro, K.R., 2021. Foul-weather friends: Modelling thermal stress mitigation by symbiotic endolithic microbes in a changing environment. *Global Change Biology*, *27*: 2549-2560.



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752 **Fig. 2. Comparison of the temperature response between non-infested and infested**
753 **mussels.** (a) Average rate of change in body temperatures and (b) maximum or (c) near-
754 maximum (95th percentile) temperatures (per tidal cycles) during emergence. Means (black
755 dots), medians (central bars), 2.5th and 97.5th percentiles (respectively, lower and upper bars),
756 and 25th and 75th percentiles (grey boxes) are shown.
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