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Symbiotic endolithic microbes reduce host vulnerability to an unprecedented heatwave

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ABSTRACT

Heatwaves are increasingly severe and frequent, posing significant threats to ecosystems and human well-being. Characterised by high thermal variability, intertidal communities are particularly vulnerable to heat stress. Microbial endolithic communities that are found in marine calcifying organisms have been shown to induce shell erosion that alters shell surface colour, lowering body temperatures and increasing survival rates. Here, we investigate how the symbiotic relationship between endolithic microbes and the blue intertidal mussel *Mytilus edulis* mitigates thermal stress during the unprecedented 2022 atmospheric heatwave in the English Channel. Microbial infestation of the shell significantly enhanced mussel survival, particularly higher on the shore where thermal stress was greater. Using data from biomimetic temperature loggers, we predicted the expected thermal buffer and observed differences up to 3.2 °C between individuals with and without symbionts under the known conditions of the heat wave-induced mortality event. The ecological implications extend beyond individual mussels, affecting the reef-building capacity of mussels, with potential cascading effects for local biodiversity, carbon sequestration, and coastal defence. These findings emphasize the importance of understanding small-scale biotic interactions during extreme climate events and provide insights into the dynamic nature of the endolith-mussel symbiosis along a parasitic-mutualistic continuum influenced by abiotic factors.

1. Introduction

Heatwaves (HWs) are prolonged periods of anomalously high temperatures. They rank among the most lethal natural disasters, resulting in human fatalities and the deterioration of ecosystems, with irreversible impacts for the ecological and societal benefits they ensure (Smith et al., 2021, 2023). Over the last century, heatwaves have been more frequent, intense and long lasting with increasingly severe impacts (Holbrook et al., 2019). Critically, model predictions reveal that, extreme and very extreme heat waves (World Health Organization. Regional Office forE, 2021) that are considered rare today are likely to be the norm under ongoing climate change scenario (Sen Gupta et al., 2020).

Intertidal communities worldwide are particularly and increasingly threatened by thermal stress caused by HWs (Mieszkowska et al., 2021; Raymond et al., 2022; Seuront et al., 2019). Because their thermal regimes are affected by both oceanographic and atmospheric conditions, intertidal habitats are among the most thermally fluctuating and stressful ecosystems worldwide (Tomanek and Helmuth, 2002). Intertidal organisms typically experience large variation in temperature (associated also with alterations of oxygen availability, pH and salinity, changes) over time scales of seconds to hours (Lathlean et al., 2016; Monteiro et al., 2017; Zardi et al., 2013). Furthermore, within a shore, spatial thermal gradients can be more extreme than those across broader latitudinal scales (Helmuth et al., 2016; Wang et al., 2020). The deleterious ecological and economic impacts of heat waves in intertidal ecosystems are seen worldwide and are affecting a wide range of biological process and species (Oliver et al., 2019; Raymond et al., 2022; Zardi et al., 2021). Heat wave-induced mass mortalities, local

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extinctions and range contractions of several habitat-forming species (such as macroalgae, seagrasses, corals, bivalves) have led to a decline in local biodiversity, decreased carbon sequestration, weakened natural coastal protection, diminished socioeconomic value due to reduced recreational activities and tourism, and significant direct economic damage to recreational, artisanal, and commercial fisheries (e.g., Gulland et al., 2022; Seuront et al., 2019; Smale et al., 2019; Zardi et al., 2021).

Importantly, species are not exposed to HWs in isolation, but together with other species in their community which include mutualists, competitors and predators (McPherson et al., 2021; Michaud et al., 2022). Mounting evidence shows that understanding how these small-scale, species interactions among ecosystem components may modulate the large-scale impact of extreme climatic events is fundamental to comprehensively grasping the effects of contemporary climate change at relevant organismal scales (Monsinjon et al., 2021; Ross et al., 2022; Zardi et al., 2021).

A pivotal example is that of the symbiosis between endolithic microbes and mussels. Endolithic microbes are ubiquitous in marine calcifying organisms. In intertidal ecosystems, shell degrading microbial endoliths have been documented across various bioregions, spanning from cold temperate to sub-tropical/tropical conditions (Lourenço et al., 2017; Ndhlovu et al., 2019; Zardi et al., 2021). Recent studies have showed how mussel shell erosion caused by endolithic activity mitigates the thermal stress faced by their mussel hosts by changing shell surface colour, resulting in a considerable increase in survival rates during heatwaves (Gehman and Harley, 2019; Zardi et al., 2021). In particular, the whitening of the outer shell layer induced by the microbes enhances the reflectance of solar irradiance (albedo), subsequently diminishing the portion of solar energy absorbed by the shell and, ultimately the body temperature of the host (Gehman and Harley, 2019; Zardi et al., 2016).

In this study, we investigated how thermal mitigation by symbiotic endoliths affected survival rates of the intertidal mussels *Mytilus edulis* at two sites along the English Channel during the unprecedented mid-July 2022 atmospheric heatwave (Guinaldo et al., 2023; Lu et al., 2023). Critically, this record-breaking heatwave coincided with midday low tides when intertidal organisms are aerially exposed. Temperature extremes during aerial exposure generally far exceed those experienced during submersion and have been linked to mass mortality in a variety of taxa and habitats (Kolzenburg et al., 2019; Saada et al., 2016; Zardi et al., 2011).

2. Methods

2.1. Survival

The effect of endolithic infestation on mussel survival during a period of extreme heat was assessed by enumerating live and dead mussels at two sites along the French and English coasts of the English

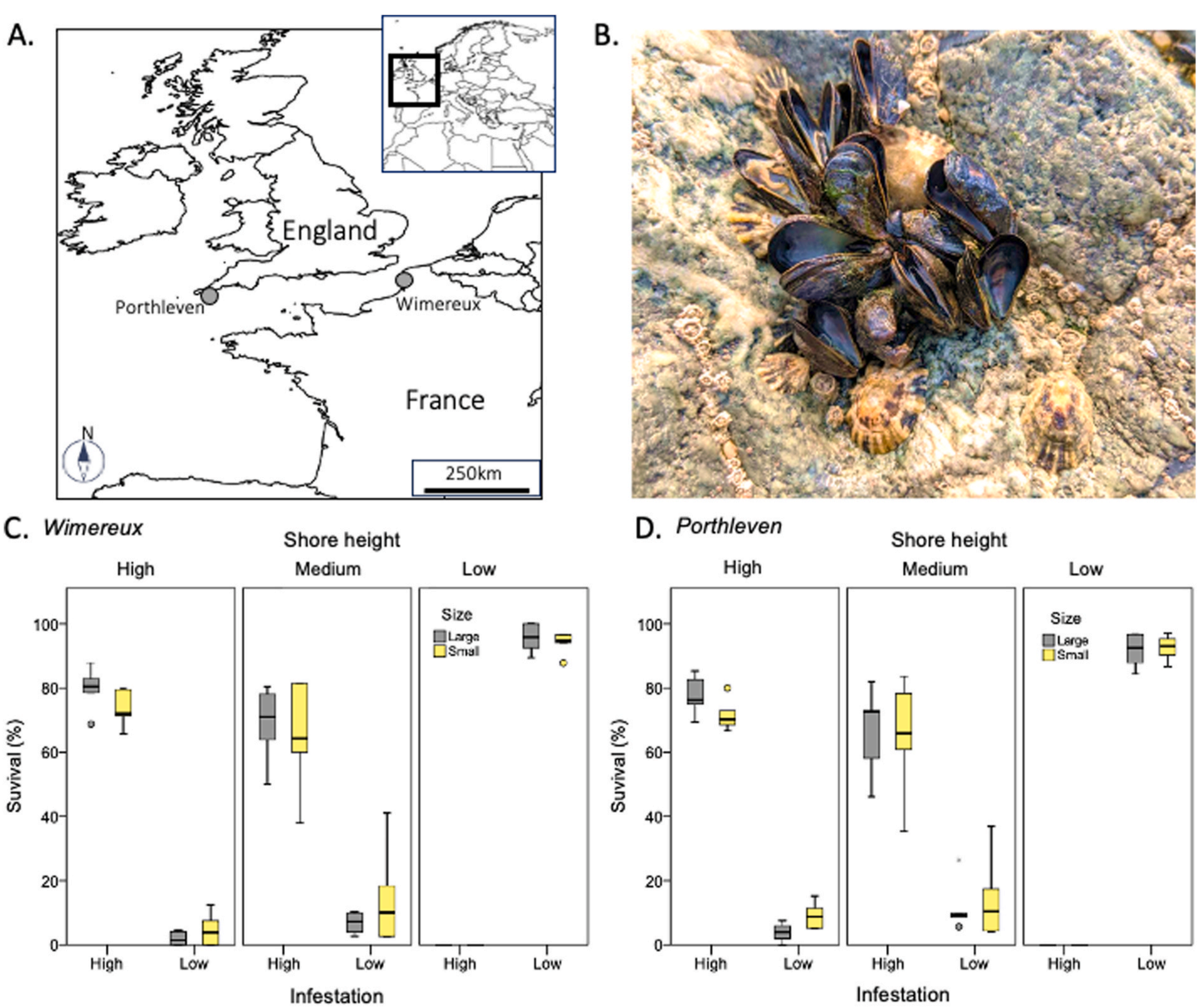

Fig. 1. (A) Map of the study site. (B) Example of a heat-induced mussel. mortality in the high shore at Porthleven. Survival rates of mussel population for each intertidal height and size class are plotted for (C) Wimereux and (D) Porthleven. Note that no highly infested mussels were recorded on the low shore.

Channel immediately following the mid-July 2022 atmospheric heatwave (Guinaldo et al., 2023). The sites were Porthleven in the UK (50°4′54.32"N, 5°19′2.29"W) sampled on July 18th, 2022, and Wimereux, (50°45′5.22"N, 1°35′42.91"E) in France, sampled July 20, 2022 (Fig. 1A). Three days before our mortality assessment, the average maximum air temperature at these sites surpassed 34 °C and coincided with coinciding with midday low tides (https://www.accuweather.com/).

Because incidence of endoliths is largely determined by solar radiation and abrasion due to waves (Zardi et al., 2016), we selected sites with similar exposure to solar radiation (surfaces with limited shading that are likely to be exposed to solar radiation 60% of the day) and similar wave exposure (i.e., lack of protecting structures in front of the area, with similar orientation towards incoming waves, and shoreline angle).

At each site, 6 quadrats (25cm × 25 cm) were haphazardly placed in the high, mid and low mussel zones (18 quadrats in total). All mussels inside each quadrat were separated into one of two size classes: small (0.5–3 cm in shell length) and large (3.1–6 cm in shell length). In each quadrat, the total number of live and of recently dead mussels were counted. In order to ensure that only recent mortalities were included in the survey, only shells still containing soft tissue and with a shiny inner nacreous layer were used (Fig. 1A). The insides of mussel shells become heavily fouled within a month after death (Kaehler, 1999) and all such shells were discarded. To assess mortality, the status of each mussel was visually checked and upon foot probing, unresponsive mussels (i.e., no valve closure) were recorded as dead. We categorized mussel infestations into two distinct groups, namely low and high infestation, based on the severity of shell corrosion, as assessed in Zardi et al. (2009)). The low infestation group included shells with clean, intact periostracum and distinct outer lines, as well as shells with a central portion of the surface eroding, resulting in outer striations on the periostracum becoming indistinct. The high infestation group, on the other hand, comprised shells with erosion spreading past the central portion, leading to the appearance of grooves and pits on the shell surface, as well as shells that were heavily pitted and deformed, with outer striations on the periostracum almost completely absent.

At each location, the effects of infestation and size were tested using a 3-way ANOVA with shore height, infestation and size class. Since the assumption of homoscedasticity (Levene's test) was not met for the 3-way ANOVA, a 2-way ANOVA was run instead for each shore height separately, with infestation (low, high) and size class (small, large) as fixed factors and survival rate as the dependent factor.

2.2. Thermal buffer

We predicted the expected thermal buffer (i.e., the daily maximum temperature difference between clean and infested mussels) at our two sites using a published model (Zardi et al., 2021). Briefly, the model was based on data from biomimetic temperature loggers (robomussels) built using the shells of *Mytilus* spp. that are either heavily infested or not infested by endoliths. Robomussels were deployed in the field across a wide latitudinal range (i.e., 37°N to 59°N) to assess changes in endolithic thermal buffering under variable environmental conditions and to identify the drivers of the maximum temperature differences between non-infested and infested mussels. Data from the robomussels 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. Finally, the model was used to identify maximum body temperature differences between infested and non-infested mussels under the known conditions of a heat wave-induced mortality event of intertidal mussels. Input data are daily mean wind speed and total solar radiation. We extracted those from the closest weather stations: Weather Station ID: ISAINT5775 (Nico 62,280) 3.7 km from Wimereux and Weather Station ID: IMULLION3 (Mullion, Cornwall, England) 6.5 km from Porthleven.

3. Results

3.1. Survival

On average, 40.7%, 38.6% and 89.5% of mussels survived the heatwave on the high, mid and low shore respectively, with the two sites showing comparable survival rates (Fig. 1 C, D). There were no highly infested mussels on the low shore, these data were not included in the analyses. At Porthleven, on the high and mid shore, regardless of the size class (size: $F_{1,20} = 0.001$ $p = 0.99$ and $F_{1,20} = 0.06$, $p = 0.813$ for mid and high shore respectively, Fig. 1) infestation had a significant effect on mussel survival rates (infestation: $F_{1,20} = 101.9$, $p < 0.001$ and $F_{1,20} = 1449.3$, $p < 0.001$ for mid and high shore respectively). At Wimereux, a similar pattern was observed with consistently higher survival rates for highly infested individuals across size classes and shore heights (infestation: $F_{1,20} = 25.8$, $p < 0.001$ and $F_{1,20} = 1319.7$, $p < 0.001$ for mid and high shore respectively).

3.2. Thermal buffer

During the 2022 HWs at Porthleven, daily mean wind speed ranged from 0.693 to 1.493 m s^{-1} and total solar radiation from 15207.93 to 19895.73 J m^{-2}, resulting in a daily maximum thermal buffer between 2.554 and 3.146 °C (Fig. 1S, see Supplementary Material Table 1S for confidence intervals). At Wimereux, daily mean wind speed ranged from 0.178 to 0.531 m s^{-1} and total solar radiation from 18678.6 to 27775.8 J m^{-2}, resulting in a daily maximum thermal buffer between 3.071 and 4.920 °C.

4. Discussion

Our results show that thermal stress mitigation by symbiotic endoliths significantly increased survival rates of the intertidal blue mussel *Mytilus edulis* during the 2022 all-time record atmospheric heatwave. The thermoregulatory effect of endolithic infestation was more pronounced higher on the shore, where mussels spend more time exposed to air and experience temperature extremes during aerial exposure that generally far exceed those encountered during submersion (e.g., Helmuth et al., 2016; Monsinjon et al., 2021; Nicastro et al., 2023; Zardi et al., 2021; Zardi et al., 2011). As a result, endolithic thermal mitigation for the host organism, was greatest where it was most required.

Importantly, the consequences of thermal mitigation by endolithic symbionts extends beyond the individual host and has ecosystem-level implications. Intertidal mussels, such as *M. edulis*, are crucial reef-building bioengineers in the intertidal zone. By reducing stress and enhancing habitat complexity, they influence resource availability, promote biodiversity persistence, and support ecosystem processes like primary productivity and nutrient cycling (Commito and Dankers, 2001; Nicastro et al., 2012; Suchanek, 1985). Additionally, intertidal mussels serve as a direct food source, provide nursery habitats, contribute to waste treatment and assimilation, and help mitigate coastal erosion (e.g., Hattam et al., 2015). Consequently, the effects of endolithic corrosion on mussel bioengineering can have diverse consequences for ecosystem functioning and services. For example, recent evidence demonstrates that the thermal advantages provided by endoliths to the intertidal reef-building mussel *Mytilus galloprovincialis* also extend to the invertebrate community that utilizes mussel beds as their habitat (Zardi et al., 2023).

These findings have significant implications in the context of global warming, where the occurrence, duration, and intensity of heat waves are widely acknowledged to be on the rise (Perkins-Kirkpatrick and Lewis, 2020). The significance of environmental temperature, long acknowledged in biology, now gains fresh attention amid human-induced climate change which alters global average and extreme temperature patterns worldwide. While mobile species have the ability to alleviate temperature stress by relocating to areas with more favourable temperatures (Hayford et al., 2015; Reid and Harley, 2021), sessile or highly sedentary foundation species like mussels lack this capability and are particularly susceptible to the impacts of heatwaves. For such organisms, small-scale variations in topography, such as the orientation, angle, and physical features of their substrates that provide shade, can influence absorbed solar radiation and subsequently affect their body temperature (Miller et al., 2009; Seabra et al., 2011). In addition to abiotic features, inter- and intra-specific interactions within the ecosystem can significantly modulate the effects of thermal stress (Helmuth, 2002; Lathlean et al., 2016; Nicastro et al., 2010). For instance, Darwin (1959)) noted that many distributional patterns along temperature gradients appeared to depend more on species interactions rather than solely on the direct impact of temperature. According to the prevailing theory, a species' reaction to spatial or temporal fluctuations in temperature is influenced by two factors: the direct effects on the characteristics of individuals and populations within that species, and the indirect effects caused by alterations to the distribution, abundance, and behaviour of other species including competitors, predators, parasites, and mutualists (Curd et al., 2021; Dunson and Travis, 1991; Helmuth, 1998; Kordas et al., 2011; Nicastro et al., 2020). In the past decade, the ecological significance of thermal mitigation of host body temperatures by endolithic symbionts has been highlighted through empirical and modelling studies across different systems and taxa (Monsinjon et al., 2021; Zardi et al., 2021). The effects of a symbiotic species can vary from positive to negative depending on the specific biotic and abiotic environment in which the interaction takes place (e.g., Altizer et al., 2013; Harvell et al., 2009; Nowakowski et al., 2016; Sauer et al., 2018). Initially, numerous studies highlighted a range of lethal and sub-lethal negative effects of endolithic corrosion on mussels, emphasizing the parasitic nature of this relationship (Marquet et al., 2013; Zardi et al., 2009). The boring activity of endoliths can affect the host's energy allocation, leading to reduced byssal attachment strength, growth, and reproduction (Kaehler and McQuaid, 1999; Marquet et al., 2013; Ndhlovu et al., 2021; Nicastro et al., 2018; Zardi et al., 2009). In contrast, more recent studies have focused on the positive aspects of endolithic symbiosis, particularly in terms of thermal mitigation. While it is intriguing to consider the possibility that the positive effects of endoliths could indicate a transition towards mutualism, this idea remains purely speculative at this stage. It is nevertheless noticeable that numerous mutualistic relationships have evolved from initially parasitic interactions, highlighting the significance of parasites that offer conditional benefits as pivotal transitional stages in this evolutionary progression (e.g., Fellous and Salvaudon, 2009).

Taken together, studies of the endolith-mussel symbiosis suggest that the nature of the relationship shifts along a parasitic-mutualistic continuum depending on biotic and abiotic factors, with, for instance, negative consequences of endolithic corrosion prevailing during storms, resulting in increased dislodgement of mussels due to weakened attachment strength, while endoliths provide assistance to their hosts during periods of intense heat stress (e.g., the cooling effect reported here of nearly 5 °C during the intense heatwave that occurred at Wimereux in July 2022). Quantifying and monitoring the beneficial ecological effects of endolithic thermal buffering is key to improving predictions of the resilience of mussel beds under future thermal conditions and the preservation of the services they provide.

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CRediT authorship contribution statement

Gerardo I. Zardi: Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Jonathan R. Monsinjon:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Laurent Seuront:** Writing – review & editing, Resources, Methodology. **Nicolas Spilmont:** Writing – review & editing, Resources, Methodology. **Christopher D. McQuaid:** Writing – original draft, Resources, Methodology. **Katy R. Nicastro:** Writing – original draft, Resources, Investigation, Formal analysis, Conceptualization.

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.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106622.

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