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ORIGINAL PAPER

Latitudinal incidence of phototrophic shell-degrading endoliths and their effects on mussel bed microclimates

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Abstract Aggregations of organisms commonly benefit their members by mitigating the effects of predators and environmental stresses. Mussel aggregations also form important intertidal matrices that support associated infaunal communities, the structures of which are largely shaped by the conditions within the interstitial spaces. Intertidal mussels are frequently parasitized by phototrophic endoliths that infest the shell and have thermoregulatory effects on both solitary and aggregated mussels by changing shell albedo. A large-scale sampling was carried out May–June 2016 along Portuguese and Moroccan shores to investigate a latitudinal gradient of endolithic infestation of the intertidal mussel *Mytilus galloprovincialis.* Endolithic infestation increased towards lower latitudes most likely as a response of greater light availability. Additionally, artificial beds of either 100% non-infested or infested biomimetic mussels were used to test whether infestation alters the temperature and humidity of the interstitial spaces within beds, and if mussels surrounded by infested mussels experience lower body temperatures than those surrounded by non-infested ones. Conditions within beds of infested mussels were significantly cooler and more humid than in non-infested beds and individuals in the centre of infested mussel beds experienced significantly lower body temperatures. Under a scenario of warming climate, endolithic infestation of mussel beds might thus represent an ecological advantage not only for *M. galloprovincialis* as a species but also for the associated communities.

Introduction

Organisms commonly form groups that mitigate either rates of predation or environmental stresses. Such aggregations have long been described as evolutionarily advantageous as the members benefit from increased survivorship and reproductive success, but the advantages of protection against predators and environmental conditions are balanced against the need to compete for resources and the possibility of increased risk of disease (Parrish and Edelstein-Keshet 1999; Fellous and Salvaudon 2009). Intertidal marine organisms frequently form patchy or very dense aggregations to cope with harsh environmental conditions. By aggregating, sea snails minimise desiccation stress and experience a reduction in dislodgement caused by water movement (e.g. Feare 1971; Garrity 1984; Rojas et al. 2013). Similarly, mussel beds improve individual growth and resistance to waves (van de Koppel et al. 2008).

As bioengineers, mussels are important to the functioning of intertidal ecosystems. Mussel beds provide shelter, substratum and food resources; they increase habitat complexity and alter intertidal humidity and temperature conditions (Ricciardi et al. 1997; Thiel and Ullrich 2002; O'Donnell 2008; Nicastro et al. 2012), thus enhancing

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species richness and species density and shaping trophic networks (Ricciardi et al. 1997; Christianen et al. 2016). The thermoregulatory effects of these aggregations are particularly relevant in the context of climate change. Intertidal mussels inhabit areas within a strong terrestrial–marine gradient, where they are exposed on a daily basis to dramatic environmental changes (Helmuth et al. 2006, 2016; Lathlean et al. 2016a) and live close to their thermal tolerance limits, potentially facing mass mortalities and population extinctions driven by rising temperatures (Jones et al. 2010; Harley 2011). Moreover, the thermal environment of mussel aggregations is not static but undergoes small-scale variations due to species-specific behaviour (Nicastro et al. 2012) or interactions among distinct micro-habitat components (Helmuth 1998). For example, gaping (periodic valve movement during emersion) by the brown mussel *Perna perna* leads to decreased temperatures and increased humidity within mussel aggregations (Nicastro et al. 2012). Similarly, shading by neighbours results in distinct microclimates for solitary or aggregated mussels (Helmuth 1998) and wind-induced convection may lower mussels' body temperatures (Helmuth et al. 2011). Additionally, it has also been shown that the body temperature of individual mussels is altered by the action of endolithic parasites (Zardi et al. 2016).

Phototrophic endolithic parasitism is a widespread phenomenon in mussels. Photosynthetic endoliths are metabolically dependent on their hosts as they excavate the host shell through chemical dissolution, converting carbonate ions from calcite into carbon dioxide, which they require for photosynthesis (Garcia-Pichel et al. 2010). This chemical dissolution degrades the outer layer of mussel shells leading to localised shell discolouration (i.e. shell whitening, Kaehler 1999). With extreme infestation events, shell whitening may cover the entire shell (Kaehler 1999). Such white discolouration enhances solar reflectivity, diminishing the absorbed energy, eventually leading to a reduction of mussel body temperature (Zardi et al. 2016). Although the cooling effect of endolithic parasitism has been shown for mussels within aggregations and in solitary individuals (Zardi et al. 2016), how infestation alters environmental conditions within mussel beds and whether endolith-induced cooling extends to neighbouring mussels have never been studied. Interestingly, the prevalence of infestation on mussels may differ greatly locally and regionally, dictated by factors that damage the outer layer of the shell (e.g. sand erosion) and light availability (Kaehler 1999; Zardi et al. 2009; Marquet et al. 2013; Ćurin et al. 2014). Mussels in wave-exposed sites exhibit higher endolithic infestation than mussels in bays, presumably because sediment load caused by waves removes the outer layer of mussel shells (i.e. the proteinaceous periostracum), facilitating endolithic infestation (Zardi et al. 2009). At small scales, endolithic infestation on mussels has also been shown to differ significantly between shaded and non-shaded areas, with greatest incidence of infestation where irradiance is strongest (Zardi et al. 2009). Thus, environmental variables that control light availability at a larger scale than within the intertidal habitat, such as cloud cover, may dictate geographical patterns of endolithic infestation. Light availability follows a latitudinal gradient, increasing towards lower latitudes as cloud cover decreases (Wetherald and Manabe 1980; Warren et al. 1986), setting the context for the aims of our study.

Here, we explore large-scale infestation severity to understand whether endolithic infestation follows a latitudinal gradient and investigate the thermal properties of infested and non-infested beds of the mussel *Mytilus galloprovincialis*. Specifically, we tested the following hypotheses: (1) degree of infestation increases as latitude decreases, (2) mussel beds made up of infested individuals exhibit decreased temperatures and increased humidity within the interstitial spaces and (3) mussels surrounded by infested mussels experience lower body temperatures than those surrounded by non-infested mussels.

Materials and methods

Study area and model species

The study targeted the temperate intertidal mussel *Mytilus galloprovincialis* collected from 12 sites distributed along ~1000 km of the southwestern (SW) and southern Portugal coastlines and the Atlantic coast of Morocco

Table 1 Sampling locations, organised from north to south; 1–4 Portugal; 5–12 Morocco

Location	Code	Coordinates
Malhão	1	37°46′56.47″N; 08°48′08.30″W
Castelejo	2	37°06′08.09″N; 08°56′44.99″W
Vilamoura	3	37°04′19.70″N; 08°07′19.71″W
Farol	4	36°58′29.38″N; 07°51′42.51″W
Larache	5	35°11′48.14″N; 06°09′30.61″W
Rabat	6	34°01′57.26″N; 06°50′27.96″W
Sidi Bouzid	7	33°13′06.11″N; 08°34′23.19″W
El Beddouza	8	32°32′42.33″N; 09°16′55.34″W
Essaouira	9	31°30′42.78″N; 09°46′24.31″W
Imsouane	10	30°50′24.43″N; 09°49′21.92″W
Mirleft	11	29°35′06.58″N; 10°02′50.78″W
El Ouatia	12	28°30′05.58″N; 11°20′06.38″W

(from Malhão, SW Portugal, site 1, 37°46′56.47″N 08°48′08.30″W to El Ouatia, southern Morocco, site 12, 28°30′05.58″N 11°20′06.38″W; Table 1). Sampling took place in May–June 2016. All locations were moderately exposed intertidal rocky shores, experiencing low tide at approximately the same time of day. Only monolayered mussel beds (i.e. mussels attached directly to the substratum) in sun-exposed areas (i.e. surfaces exposed to solar radiation 60% of the day; Zardi et al. 2009) were considered.

Degree of infestation along Portugal and Morocco

At each site, three quadrats (15 cm × 15 cm) were haphazardly sampled from areas with 100% mussel cover in the centre of the *M. galloprovincialis* zone. Mussels were measured and separated into 10-mm size classes according to shell length (SL) and the degree of endolithic infestation was evaluated following the classification of Kaehler (1999): Group A, shells with clean, intact periostracum and distinct periostracal striations; Group B, shells with central portion of surface eroding, outer striations on periostracum becoming indistinct; Group C, shells with erosion spreading past central portion, grooves and pits appearing on the shell surface; Group D, shells heavily pitted and becoming deformed, outer striations on periostracum almost completely absent; Group E, shells extremely pitted, deformed and brittle, eventually with holes.

The effect of infestation on the thermal properties of mussel bed microclimates

The effects of infestation on mussel bed interstitial spaces were investigated by deploying temperature and humidity data-loggers (hygrochron iButtons DS1923, Maxim Integrated Products, Dallas Semiconductor, USA) inside infested or non-infested beds. These provided relative humidity measurements with a resolution of 0.04% and temperature accuracy of ±0.5 °C and resolution of 0.0625 °C. Loggers were deployed in artificial mussel beds made up of either 100% non-infested (Group A, clean treatment) or heavily infested (Group D, infested treatment) biomimetic mussels. Biomimetic mussels mirror thermal properties of living mussels (Helmuth and Hofmann 2001) and were used to artificially create mussel beds. They were made by filling empty mussel valves (SL 45 ± 5 mm) with silicone sealant and left to dry at ambient temperature for at least 48 h. The beds ($n = 3$ per treatment) were circular (diameter of ca. 16 cm), made up of biomimetic mussels (n ~60), arranged vertically, with the umbo of each mussel on the substrate, to mimic their natural position on the shore. Partially rigid, white PVC net (mesh size 1 cm) was placed under and around the beds to prevent biomimetic mussels from falling (see Nicastro et al. 2012). Prior to the experiment, to ensure that all artificial beds were exposed to the same environmental conditions (temperature and light), artificial mussel beds were kept in the dark overnight and immersed in water (ca. 18 °C) for 15 min. After emersion, two loggers were immediately inserted into the centre of each bed, recording temperature and humidity data every 5 min. Mussel beds were then placed on white horizontal boards and aerially exposed to ambient sunny conditions for 80 min. The experiment was run twice (on the 17th and 19th August, 2016, referred to as day 1s and day 2s, respectively), during high sun elevation (12–15 h) and clear sky conditions at CCMar—Centre of Marine Sciences, Faro, Portugal. Each trial was conducted with different mussel beds to avoid pseudo-replication.

The effect of infestation-induced cooling on the body temperatures of neighbouring mussels

The effect of cooling on neighbouring mussel body temperatures was investigated using robomussels. Robomussels were built similar to biomimetic mussels, described above, with the addition of a temperature data-logger (thermochron iButton DS1921G, Maxim Integrated Products, Dallas Semiconductor, USA; accuracy ±1 °C, measurements in 0.5 °C increments) embedded in the inner silicone content. By having a temperature data-logger inside, robomussels capture mussel body temperature (see Helmuth and Hofmann 2001). Loggers were set to record robomussel body temperatures every 5 min. Clean or infested robomussels were deployed in the centre of 100% clean or infested biomimetic mussel beds. Clean or infested robomussel treatments were tested separately on three distinct days each (clean robomussels: 10th and 17th September and 6th October 2016, referred to as day 1c, day 2c and day 3c, respectively; infested robomussels: 11th and 16th September and 5th October 2016, day 1i, day 2i and day 3i), under clear sky conditions and high sun elevation (12–14 h) at CCMar—Centre of Marine Sciences, Faro, Portugal. Each mussel bed ($n = 6$ clean and $n = 6$ infested beds) had a robomussel positioned in the centre and was kept in the dark overnight. Prior to the experiment, mussel beds were immersed in water (ca. 18 °C) for 15 min and immediately placed on white boards aerially exposed to ambient sunny conditions for 80 min after emersion. New mussel beds were arranged for each trial to avoid pseudo-replication.

Data analyses

The incidence of endoliths was analysed based on the proportion (%) of each degree of infestation (Group A–E) for each site and size class. Spearman's rank correlation was used to evaluate the relationship between infestation frequency (%) and latitude of sampling sites. To avoid bias due to uneven distribution of size classes, a Spearman's rank correlation exclusively for mussels belonging to the size class that was common in all quadrats and all sites (SL 20–30 mm) was performed.

Data on temperature and humidity of interstitial spaces in mussel beds were analysed separately using two-way nested ANOVAs with bed (clean or infested) as a fixed factor, bed replicate (three levels) as a random nested factor and either temperature (^{o}C) or humidity (% relative humidity) as the dependent variable. Temperatures experienced by clean and infested robomussels were analysed separately using one-way ANOVA with bed (clean or infested) as a fixed factor. The two-way nested ANOVAs and one-way ANOVAs were undertaken for two time points (i.e. 40 and 80 min of sun exposure, representing the mid- and end-points of each experiments).

Data were tested for the prerequisites for parametric analysis (Shapiro's and Cochran's tests) and were analysed using STATISTICA v7.0 software (StatSoft, Tulsa, USA). When normality or homoscedasticity requirements were not met, analyses were run with PERMANOVA module (Anderson 2001; McArdle and Anderson 2001), which does not require prior assumptions. In this case, pair-wise tests were performed using 999 permutations.

Results

Severity and prevalence of infestation of *Mytilus galloprovincialis* increased with shell length (SL) throughout the study area (Fig. 1). Mussels ranging up to 40-mm SL (size classes 0–10, 10–20, 20–30 and 30–40 mm) were present at all locations (in at least one quadrat) and highlighted a tendency for more severe infestations towards southern locations (e.g. 0% infestation of Group C at site 1, the most northerly site, and 67% at site 12, in the extreme south, for the 0–10 mm size class). Initial infestation (Group B) was generally present in the smallest size class (0–10 mm SL) except for sites 3, 4, 10 and 11 (Group B infestation started at 10–20 mm SL). Additionally, shells with high levels of erosion and pitting (Group D) were found at all sites except two of the northernmost sites, 2 and 3. Site 1 was the only site where endolith-induced shell fractures were detected (Group E; two mussels, 0.2% occurrence in size class 10–20-mm SL).

Infestation significantly increased at lower latitudes (Spearman's rank correlation: $rs = -0.82$, $n = 36$, $P < 0.0001$; Fig. 2). This was also true when only the common size class was considered (20–30-mm SL; Spearman's rank correlation: $rs = -0.66$, $n = 36$, $P < 0.0001$; Fig. 2). Overall, sites 3 and 11 showed the lowest (2%) and highest (98%) proportion of endolithic infestation, respectively.

The interstitial spaces in clean (non-infested) mussel beds were warmer and less humid than in infested mussel beds (Fig. 3, Table S1 in Electronic Supporting Material, ESM). In general, temperatures in both mussel bed treatments increased through time while humidity decreased. Initial temperature varied between 22.5 and 23.6 °C on day 1s and 20.5 and 21.1 °C on day 2s. Relative humidity (RH) ranged 87.8–91.9 and 92.8–95.6% on day 1s and day 2s, respectively. Changes in temperature and humidity gradually decreased towards the end of the experiments, generally reaching a plateau at approximately 70–75 min. By the end of the experiment, interstitial temperatures in non-infested and infested beds had increased on average 78 and 72.3% respectively, while relative humidity decreased on average 55.1 and 52.4%. Clean mussel beds generally showed higher temperatures and lower relative humidity than infested beds. At 40 min, non-infested mussel beds exhibited significantly higher temperatures (on average 2.9 °C higher; $P < 0.05$ in both cases; Table S1 in ESM) and lower relative humidity (on average 12.7% RH lower; day 1s $P < 0.01$; day 2s $P < 0.05$; Table S1 in ESM) than infested beds. At 80 min, temperature and relative humidity of non-infested and infested beds did not differ significantly ($P > 0.05$ in both cases; Table S1 in ESM).

Clean and infested robomussels experienced lower temperatures when placed in beds composed of infested mussels, than when surrounded by clean, non-infested ones (Figs. 4, 5, Table S2 and Table S3 in ESM). At the start of the experiments (time 0 min), clean robomussel body temperatures ranged between 19.5–21.0 °C (day 1c, 20.0–20.5 °C; day 2c, 20.0–21.0 °C; day 3c, 19.5–20.5 °C), and increased by an average of 102 and 93.8% in non-infested and infested beds, respectively, by the end of the experiment (Fig. 4). At 40 min, clean robomussels deployed in non-infested beds exhibited significantly higher temperatures than those in infested beds (on average 2.2 °C higher; day 2c and day 3c $P < 0.05$; Table S2 in ESM), except on day 1c ($P > 0.05$, Table S2). Generally, after 80 min non-infested robomussels continued to reach higher temperatures when surrounded by non-infested mussels than by infested ones (on average 2.5 °C higher; day 2c and day 3c $P < 0.05$; Table S2 in ESM), again with the exception of day 1c ($P > 0.05$; Table S2 in ESM). At the end of the experiment, non-infested robomussel body temperatures reached 43.1 or 42.2 °C (day 1c), 42.8 or 40.5 °C (day 2c) or 37.1 or 34.4 °C (day 3c) in clean and infested mussel beds, respectively.

Infested robomussels displayed similar trends, although with lower overall temperatures. Initial body temperatures (time 0 min) of infested robomussels varied between 19.0 and 20.5 °C (day 1i, 19.5–20.0 °C; day 2i, 19.0–19.5 °C; day 3i, 20.0–20.5 °C) and increased on average 88.6 and 81.8% in non-infested and infested beds, respectively, at

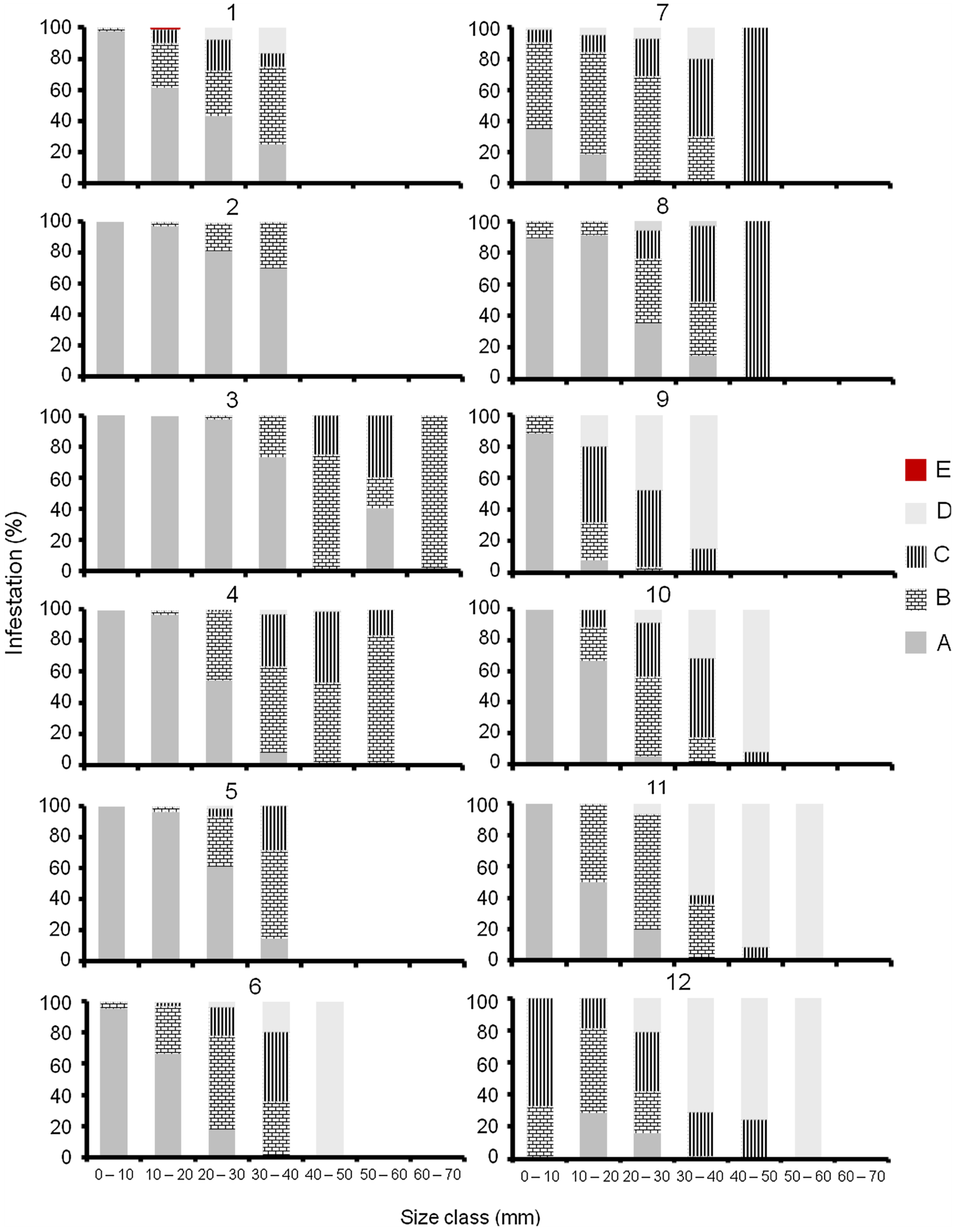

Fig. 1 Incidence of endoliths along Portuguese and Moroccan coasts. Proportion (%) of shells infested grouped into 10-mm size classes and classified as distinct degrees of infestation severity (Group A, shells with clean, intact periostracum, to Group E, shells extremely pitted, deformed and brittle, eventually with holes). Sites are arranged north to south from 1 to 12 (1–4 Portugal; 5–12 Morocco). Group E infestation was only found at site 1, in mussels ranging 10–20-mm

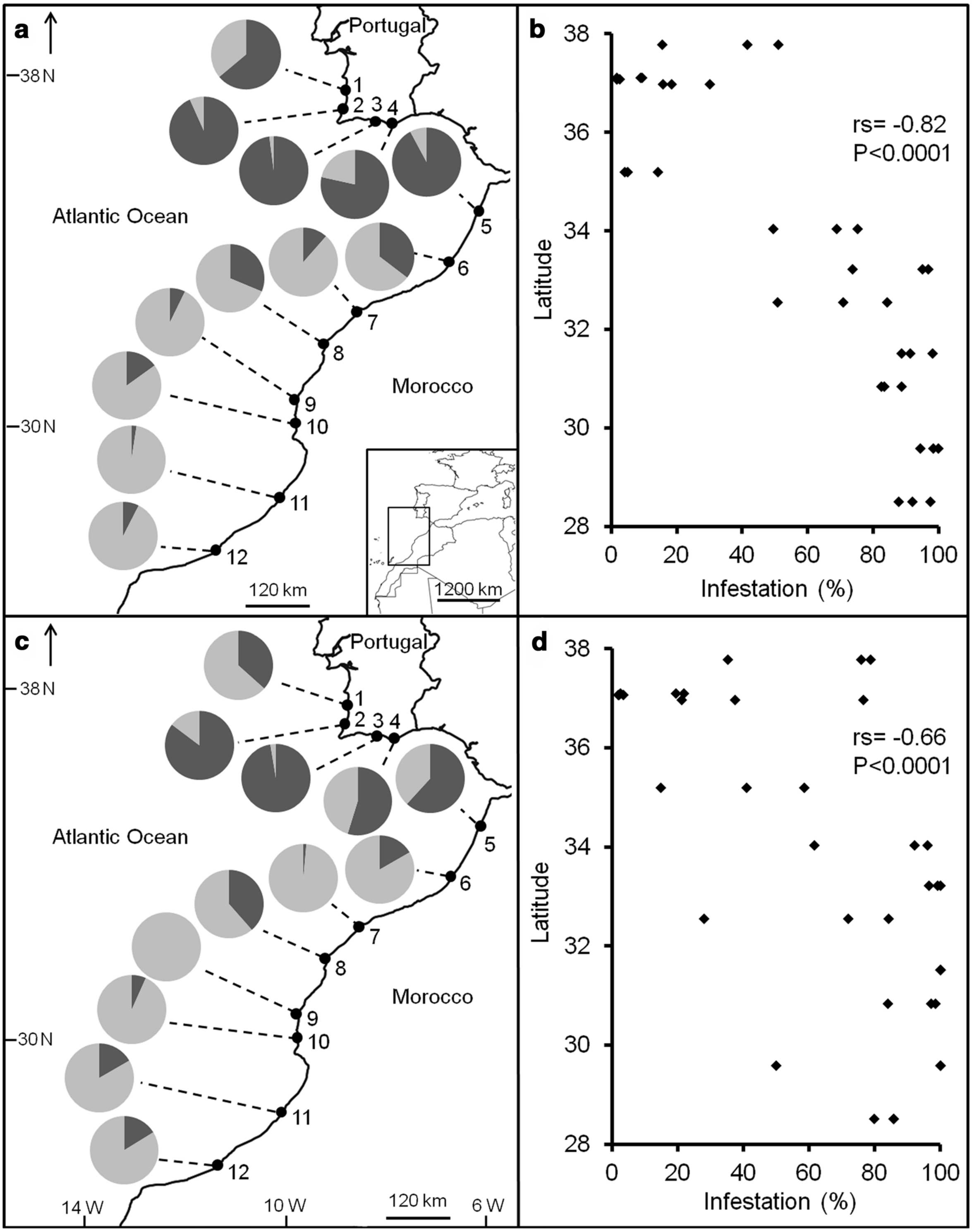

Fig. 2 Frequency of endolithic infestation at sites, location codes as in Table 1. *Light grey* indicates proportion of infested shells: (**a**) all size classes and (**c**) 20–30-mm size class only. Correlation between frequency of infestation and latitude: (**b**) all size classes and (**d**) 20–30-mm size class only

the end of the experiment (Fig. 5). Significantly higher temperatures were experienced by infested robomussels in clean mussel beds than by those in infested mussel beds at 40 min (on average 2.1 °C higher; day 1i $P < 0.05$ and day 2i $P < 0.01$; Table S3 in ESM) except on day 3i ($P > 0.05$; Table S3 in ESM). Infested robomussels remained

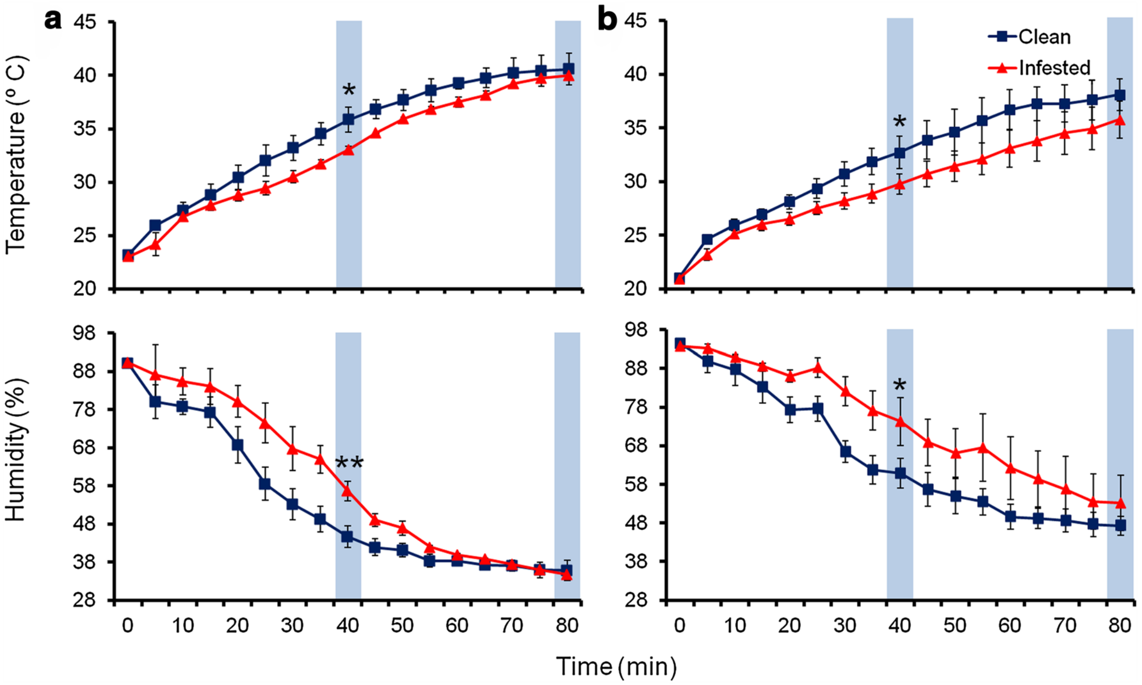

Fig. 3 Effect of mussel bed infestation on mean temperature and humidity ($n = 3$; ±SD) within mussel bed interstitial spaces. Results separated by day: **a** day 1s, **b** day 2s. *Top panels* represent temperature (°C) and *bottom panels* represent relative humidity (%). *Shade areas* depict statistical analyses performed at mid- (40 min) and endpoints (80 min) of the experiment. Statistical significance is represented by *($P < 0.05$) or **($P < 0.01$)

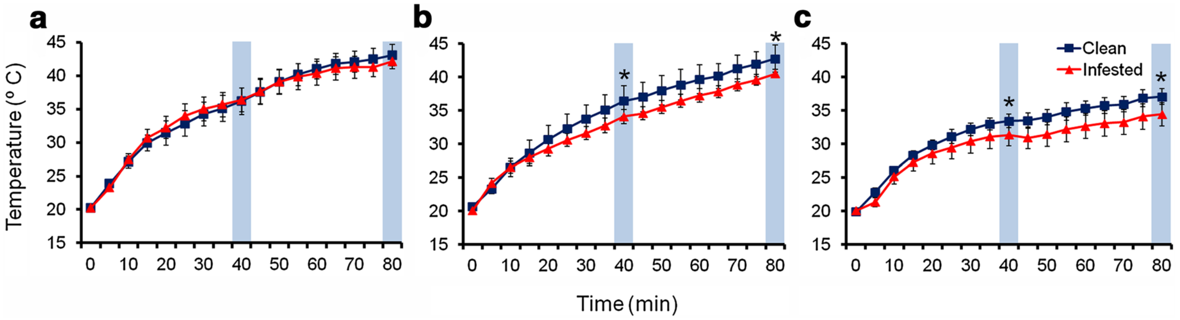

Fig. 4 Effect of mussel bed infestation on mean body temperature of clean robomussels ($n = 6$; ±SD). Results separated by day: **a** day 1c, **b** day 2c, **c** day 3c. *Shaded areas* depict statistical analyses performed at mid- (40 min) and endpoints (80 min) of the experiment. Statistical significance is represented by *($P < 0.05$)

significantly warmer in non-infested mussel beds than in infested ones at the end of the experiment (80 min; on average 1.9 °C warmer, day 1i $P < 0.01$ and day 2i $P < 0.05$; Table S3) except during the last trial (day 3i, $P > 0.05$; Table S3 in ESM). Moreover, at 80 min, infested robomussels reached on average 39.6 or 37.5 °C (day 1i), 36.3 or 34.8 °C (day 2i) or 36.4 or 35.6 °C (day 3i) depending on whether they were surrounded by clean or infested mussels, respectively.

Discussion

This study showed that endolithic infestation of *Mytilus galloprovincialis* significantly modifies the interstitial environment of mussel beds and that the cooling effect provided by phototrophic endoliths extends to neighbouring mussels. Furthermore, intertidal sampling along Portuguese and Moroccan shores revealed a strong gradient of increasing endolithic infestations at greater shell lengths and lower latitudes.

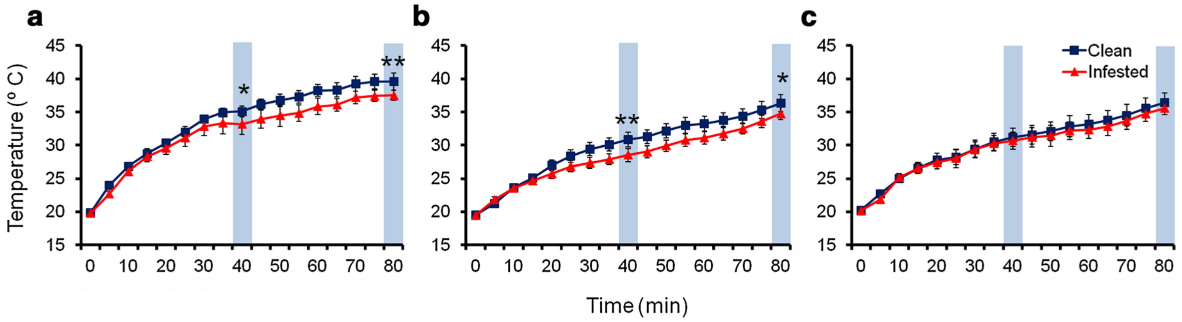

Fig. 5 Effect of mussel bed infestation on mean body temperature of infested robomussels ($n = 6$; ± SD). Results separated by day: **a** day 1i, **b** day 2i, **c** day 3i. *Shaded areas* depict statistical analyses performed at mid (40 min) and end (80 min) points of the experiment. Statistical significance is represented by *($P < 0.05$) or **($P < 0.01$)

Parasitic relationships have been documented in a wide range of taxa and their side-effects include changes in host size, shape, colour and behaviour (e.g. Poulin 1995; Mouritsen and Poulin 2002). Previous studies have shown that parasitic shell-degrading endoliths significantly reduce mussel condition index, reproductive output, shell and attachment strength and, at sites where their incidence is particularly high, they can be responsible for mass mortalities (e.g. Kaehler and McQuaid 1999; Zardi et al. 2009; Marquet et al. 2013; Ćurin et al. 2014). Surprisingly, during periods of intense heat stress, shell-degrading endoliths can also have beneficial thermal effects, decreasing the body temperature of mussels (Zardi et al. 2016). This cooling effect is related to shell discolouration. At an initial stage, shells become white through physical damage or removal of the outer layer (periostracum), due to the contact between adjacent mussels or the abrasion by sediment in the water (Kaehler 1999). After initial damages to the periostracum, endolithic infestation increases shell whitening through chemical dissolution and possibly through re-deposition of carbonates (Garcia-Pichel et al. 2010). Advantageous effects of parasitism are not exclusive to mussels. For example, the parasitic trematode *Maritrema* sp. enhances survival of the marine snail *Zeacumantus subcarinatus* by increasing the host's thermal tolerance (Bates et al. 2011). Here, we further revealed that the thermoregulatory effect of endolithic infestation extends beyond individual mussels to the mussel bed interstitial microclimate. The whitening of mussel shells by endolithic infestation increases reflectance of solar irradiation, reducing the absorption of solar energy, thereby reducing the temperatures of individual mussels and of mussel beds (Zardi et al. 2016). This cooling property, a direct by-product of solar reflectance, leads to greater interstitial relative humidity by reducing evaporative losses. Mussels low on the shore in our study area are typically emersed for ~80 min (pers. obs.). Higher on the shore, aerial exposure lasts longer and exposure to sun irradiance will lead to mussel beds with even lower relative humidities and higher temperatures than those we report, potentially enhancing the importance of the cooling effect offered by infested mussel beds. Most intertidal organisms live close to their thermal tolerance limits and face mass mortality as temperatures rise (Sagarin et al. 1999; Stillman and Somero 2000; Somero 2002; Harley 2008; Jones et al. 2010). The bioengineering protection offered by mussel beds to an array of intertidal organisms (Thiel and Ullrich 2002; O'Donnell 2008) is likely to be enhanced by endolith-induced improvements in humidity and temperature. Such small scale habitat amelioration could be particularly important under climate warming scenarios.

In this study, we demonstrate that the advantages of endolithic infestation to members of mussel aggregations extend beyond the cooling of the individual hosts (see Zardi et al. 2016), ameliorating the environment of nearby mussels. Our results showed that mussels surrounded by infested mussels experience lower body temperatures than those with non-infested neighbours, indicating a thermoregulatory effect of neighbouring conspecifics and their role as an element of an individual's thermal environment. A similar thermoregulatory effect of neighbouring individuals has been described from mixed species mussel beds, as *Perna perna* a gaping species (i.e. one that opens and closes the valves during emersion) releases water, cooling the non-gaping species *Mytilus galloprovincialis* (Lathlean et al. 2016b).

Overall non-significant differences detected during the experiments undertaken on day 1c (non-infested robomussels on non-infested and infested beds) and day 3i (infested robomussels on non-infested and infested beds) were most likely due to high variability in wind speed (Table S4 in Electronic Supporting Material, ESM), as solar radiation, cloudiness and air temperature were similar. Indeed, wind speed counteracts the effects of increases in air temperature and solar radiation, reducing the exposure to warming experienced by mussels (Helmuth et al. 2011). The fact that the difference between body temperatures of mussels living in clean or infested mussel beds is erased by high wind variability could indicate that the temperature amelioration caused by wind differs with the level of infestation of mussel beds. Nonetheless, under conditions of low wind variability, the cooling effect was observed regardless of whether the robomussel considered was non-infested or infested.

Our results not only support previous studies demonstrating that endolithic infestation is highly size dependent (larger mussels display greater infestation severity, Kaehler 1999; Kaehler and McQuaid 1999; Zardi et al. 2009; Marquet et al. 2013), they provide novel insights into the large-scale geographical distribution of endolithic infestation. Light increases as cloud cover decreases towards lower latitudes (Wetherald and Manabe 1980; Warren et al. 1986) and this is consistent with clearer skies and thinner clouds towards our southern sampling locations (http://neo.sci.gsfc.nasa.gov/dataset_index.php#energy). Because photosynthetic endoliths are highly dependent on light, greater endolithic infestation at southern locations could be explained by greater light availability at these sites. These results fit well with previous research showing that infestation in intertidal microhabitats varies with light availability. The intertidal mussel *M. galloprovincialis* is less infested in shaded places than in sun-exposed surfaces (Zardi et al. 2009). While endolithic infestation could be a by-product of wave action due to enhanced shell abrasion (Kaehler 1999; Zardi et al. 2009), our locations were topographically similar (i.e. all wave-exposed intertidal rocky shores) with no obvious differences in wave action (see also Marquet et al. 2013). Studies are needed on the variation in endolith species composition over large spatial scales to fully comprehend whether it plays a significant role over latitudinal gradients, because endoliths possess a range of functional roles and inhabit different parts of mussel shells (Mao Che et al. 1996; Ćurin et al. 2014; Peharda et al. 2015), potentially causing distinct degrees of infestation. However, the low diversity of endoliths identified for *M. galloprovincialis* in distant regions as Portugal and South Africa (Marquet et al. 2013) suggests that the endolithic communities in this study are unlikely to differ significantly.

Greater mussel endolithic infestation towards lower latitudes, where intertidal organisms are exposed to drier and warmer environments, might counterbalance the expected negative effects (e.g. mass mortalities) associated with climate change. Because conditions within beds of infested mussels are ameliorated and individuals in the centre of infested mussel beds experience significantly lower body temperatures, the greater endolithic infestation detected here at lower latitudes might result in an ecological advantage during, for example, heat waves. On the other hand, rising sea temperatures and ocean acidification might facilitate endolithic infestation, as mussel shells suffer periostracum loss and become weaker under warmer temperatures and lower pH (Gazeau et al. 2014). While it remains unknown whether the cooling effect of endolithic infestation will override the sub-lethal and lethal effects of parasites on mussels, this parasitic relationship might act as a thermal buffer, not only for members of the aggregations but also for their associated infauna.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The research was carried out following the applicable international, and/or institutional guidelines for the sampling and transport of the species.

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