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ORIGINAL PAPER

Parasitism by endolithic cyanobacteria reduces reproductive output and attachment strength of intertidal ecosystem engineers

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Abstract

Mussels are ecological engineers in intertidal communities; they affect coastal species richness by increasing habitat spatial complexity, buffering against environmental extremes, and providing protection from predators. Parasitic activities of endolithic cyanobacteria on mussels weaken their shells, requiring the expenditure of energy on shell repair, with potential indirect effects on organisms that rely on mussels as habitat providers. Given the seasonality of reproduction and the need for strong attachment during winter storms, we examined the consequences of redirecting energy for shell repair to two other energetically expensive processes: reproduction and byssal attachment. We examined seasonality in the effects of cyanobacterial infestation on reproduction and attachment strength in two intertidal mussels, the indigenous *Perna perna* and the invasive *Mytilus galloprovincialis* from the south coast of South Africa, using both qualitative and quantitative analyses. Reproductive effects were examined by measuring the weight of mussel gonads and the density of eggs within each gonad for co-occurring infested and non-infested mussels, while attachment strength was measured for mussels exhibiting different levels of infestation. Endolithic infestation was found to affect reproduction by reducing the mass of gonads, but not the density of eggs within them. Attachment strength was closely correlated with the degree of endolithic infestation, with very infested mussels requiring much less force to detach them from the substratum than mussels with low or no infestation. Thus, endolithic infestation affected mussel fitness directly, by increasing the probably of mortality through wave dislodgement and by reducing reproductive output.

Keywords Parasite · Ecological engineer · Reproduction · Attachment strength

Introduction

Ecosystem engineers are important to communities and studying factors that influence their fitness provides insight into potential indirect effects on their dependent communities. Intertidal mussels are important bioengineers on rocky shores where they enhance biodiversity by supporting complex assemblages of epifauna and infauna (Seed and Suchanek 1992; Zardi et al. 2007). Apart from providing architectural complexity, mussel beds offer habitat with profoundly modified environmental conditions, particularly in terms of heat and desiccation stress (Jones et al. 1994; Karatayev et al. 2002; Borthagaray and Carranza 2007; Arribas et al. 2014). As filter feeders, mussels are responsible for recycling nutrients in the water column, they are responsible for increasing sedimentation and act as important biological indicators for environmental stress (Karatayev et al. 2002; Borthagaray and Carranza 2007). Factors that influence mussel fitness directly or indirectly are likely to have indirect effects on the fauna that are dependent on mussels and their engineering ability.

Wave action in intertidal communities is one of the main factors affecting mussel survival (Seed and Suchanek 1992; Zardi et al. 2007). Because they inhabit wave-swept environments, intertidal mussels need to be able to withstand the

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forces exerted by waves. They achieve this by producing byssal threads for attachment to the substratum. Byssal threads are silky fibres made of proteins that are produced by mussels to use as holdfasts to the substratum (Carrington and Gosline 2004). Byssal attachment can be very strong, but individual byssal threads have a relatively short life (Moeser and Carrington 2006) and need to be replaced constantly. Their production can be very rapid (Blattenbauer et al. 2012) and mussels can produce varying numbers and thicknesses of byssal threads depending on the season, salinity, mussel size and the hydrodynamic stress experienced at the time of production (Young 1985; Seed and Suchanek 1992; Blattenbauer et al. 2012). The process is energetically expensive and, as such, it can have indirect effects on other fitness-related traits. It has been estimated that mussels use about 8–15% of their total energy expenditure in byssus production (Moeser and Carrington 2006; Zardi et al. 2009), which can conflict with other energetic process, such as reproduction or growth (Zardi et al. 2009; Ndhlovu et al. 2021). Reproduction in particular is extremely energetically costly, and attachment strength can be energetically constrained during the reproductive season, making mussels more vulnerable to waves and the risk of dislodgment (Carrington 2002). These energetic trade-offs can be significantly influenced by spatial and temporal variations in the availability of energy (e.g., Zardi et al. 2007).

An additional constraint on mussel energetics is the need for shell repair, particularly in response to the damage caused by endolithic cyanobacteria that corrode the shell (Kaehler and McQuaid 1999). Endolithic cyanobacteria are ubiquitous colonisers of organic and inorganic substrates in terrestrial, freshwater and marine environments (Golubic et al. 2005; Pernice et al. 2020) and use the calcium carbonate of mussel shells as a source of carbon during photosynthesis. Shell damage due to endolithic parasitism can be so severe as to lead to mortality through shell collapse (Kaehler and McQuaid 1999) and this can account for as much as 50% of total mortality (Kaehler and McQuaid 1999; Marquet et al. 2013). Endolithic infestation also leads to the re-direction of energy to shell repair and in doing so, significantly reduces scope for growth (Ndhlovu et al. 2021). Previous studies have provided snapshots of the consequences of endolithic corrosion on the development of reproductive tissue and attachment strength (Kaehler and McQuaid 1999; Zardi et al. 2009), while the long-term effects of endolithic infestation on attachment strength and reproduction throughout the entire reproductive cycle remain unknown. In this study, we assessed the effects of endolithic infestation on two coexisting intertidal musses species. We examined possible trade-offs between the energy demands of endolithic infestation, byssal attachment and reproduction over a period of 11 months.

Because both reproduction and the need for stronger or weaker byssal attachment are seasonal, we focussed on the seasonal effects of endolithic cyanobacterial infestation on the reproductive output of mussels and on how different levels of infestation in mussels affect their attachment strength to the substratum. To test the hypothesis that endolithic cyanobacteria will have a negative influence on reproduction and attachment strength in mussels, we addressed the following questions: (1) Does endolithic infestation have a negative effect on the reproductive output of individual mussels? This was tested by measuring density of eggs in the gonad and the gonadosomatic index of female mussels. (2) Does endolithic infestation have a negative effect on the strength of mussel attachment to the substratum? This was tested by measuring *in situ* attachment strength of individuals with varying infestation levels.

Methods

Reproductive output

To investigate the effects of cyanobacterial infestation on mussel reproductive output, reproduction was measured using two different methods: (1) histological assessment which involved calculating the density of fully developed female mussel eggs (eggs per unit area) and (2) calculating the gonadosomatic index of female mussels. Before analysis, individuals were categorised into one of the five levels of infestation described by Kaehler (1999). Group A are shells with clean, intact periostracum and distinct outer periostracal striations; Group B are shells with eroding central surface portion and the outer growth lines becoming hazy; Group C are shells with signs of erosion spreading past the central portion with grooves and pits appearing on shell surface; Group D are shells heavily pitted and becoming deformed, outer striations becoming virtually absent; Group E are shells extremely pitted, deformed and brittle, eventually developing visible holes. All samples were collected from mono-layered mussel beds in the mid-intertidal at moderately wave-exposed rocky shores and at sun-exposed sites. Mono-layered mussel beds are very common in this system with multi-layered beds being rare and to avoid any confounding effect, all mussels were collected from mono-layered beds only.

Histology

Heavily infested female *Perna perna* and *Mytilus galloprovincialis* (Level E, $n = 10$) and non-infested (level A, $n = 10$) mussels of 3.5–4.5 cm shell length were collected from

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Brenton-on-Sea. To ensure that the peak periods of reproduction identified by Zardi et al. (2007) as April and January for *M. galloprovincialis* and *P. perna* respectively were sampled, mussels were collected every two months for the first 6 months of the experimental period in 2017 (August, October, and December) and every month of the second part of the experimental period in 2018 (January–June). Samples were collected in the mid-mussel zone and stored in 70% ethanol. In the laboratory, the reproductive status of each individual was determined by taking a small portion of gonad (~0.1 g) tissue cut from the middle region of the mantle lobe and fixing it in Bouin's solution for histological examination. The remaining gonad tissue and the rest of the body were dried at 60 °C for two days. The fixed gonad tissue was dehydrated in ascending concentrations of alcohol, washed in xylene, and then embedded in paraplast. Since the reproductive tissues of both mussel species are homogeneously distributed around the mantle (Lowe et al. 1982; Ndzipa 2002), only a Section (6 μm^2) was cut from each sample and stained with haematoxylin and eosin. A representative section through the gonad tissue was used to determine the reproductive status of each individual using a light microscope fitted with a camera. Photographs of the female gonad were taken using a light microscope (Olympus BX50) with a camera (Olympus SC30) installed on the microscope, with a scale bar inserted for each photograph. The density of eggs was calculated by counting the number of eggs per unit area in each photograph and is referred to here as gamete density.

Gonadosomatic index (GSI)

To investigate the effects of cyanobacteria infestation on mussel reproductive output, each individual female mussel used in the histological study was later dissected, and the gonads separated from the body tissue. Gonads and the body tissues were dried in an oven at 60 C for 48 h. To measure the reproductive condition of mussels, the gonadosomatic index (GSI) was estimated. The GSI was calculated by multiplying the mantle gamete fraction which was calculated from assigning a grid of 64 points on a photo of gonads taken following the histology methods described above. The gamete fraction was calculated as the number of points that fell on developing or ripe eggs divided by the total number of points. The GSI was then calculated by multiplying the mantle gamete fraction by the dry weight of gonads, tissue that was reproductive, and then dividing that by the total dry body weight, including the mantle (Roff 1993; Zardi et al. 2007).

$$\text{GSI} = (\text{mantle gamete fraction} \times \text{weight of gonads})/\text{dry body weight}$$

To compare non-infested and infested mussels for both species, we compared GSI for infested and non-infested mussels in each month. GSI was also compared when mussels had their peak reproductive periods, which was January 2018 for both species. Comparing GSI for peak periods was done to compare maximum reproductive output rather than fluctuations of gonad tissue development.

Attachment strength

Perna perna and *Mytilus galloprovincialis* individuals were each categorised into one of the five levels of infestation described by Kaehler (1999), as above. For each species, we measured the *in situ* attachment strength of 20 individuals from each level of infestation. All measured individuals were from mono-layered mussel beds and were attached directly to the substratum. All measurements were done in a moderately wave-exposed intertidal rocky shore and at sun-exposed sites at Brenton-on-Sea. Samples measured were from mono-layered mussel beds in the mid- intertidal and mussels ranged between 3.5 and 4.5 cm in shell length for each species. A handheld drill was used to bore a 2 mm wide hole near the posterior margin of the shell and a fishhook was inserted into the hole. The fishhook was connected with a fishing line to a spring scale (Chatillon–N.Y.–U.S.A.–MODELIN- 25). The scale was gradually pulled normal to the surface of the rock until dislodgement occurred. The spring scale recorded kilograms, to convert kilograms to the Force (N) required to dislodge the mussel, a conversion of 1 kg = 9.81 N was used. Tested individuals were separated by at least 20 cm to avoid any dislodgement effects from adjacent mussels (Nicastro et al. 2010).

Statistical analysis

All data fulfilled the pre-requisites for parametric analysis (Shapiro–Wilk test, $p > 0.05$). To compare density of mussel eggs and GSI between non-infested and infested mussels, data were analysed using a Two-way ANOVA with two factors, status (2 levels—infested and non-infested) as a fixed factor and month (9 levels) as a random factor. To compare attachment strength for different levels of infestation, a Two-way model 1 ANOVA with Species (2 levels, *Mytilus galloprovincialis* and *Perna perna*), Infestation (5 levels, A–E) and their interaction was used.

Results

Reproductive output

Histology (*Perna perna*)

There was an increase in gamete density starting from the month of August through to January when the highest

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densities were recorded (Fig. 1). From the month of February gamete density fluctuated through to June. A density of more than 30 eggs per unit was recorded in all months throughout the study period. There was a significant month × status interaction, with the differences between infested and non-infested animals depending on the month (ANOVA, $F_{8162} = 8.616$, $p < 0.05$). During December and the peak reproductive month of January, the density of gametes in the gonad was significantly higher for non-infested than infested mussels (Post hoc, TUKEY HSD, $p < 0.05$), otherwise the differences were non-significant.

Histology (*Mytilus galloprovincialis*)

Mytilus galloprovincialis showed less clear seasonality in reproduction, with very little variation among months in gamete density. This was particularly true for infested individuals (Fig. 2). There was a significant month × status interaction (ANOVA, $F_{8162} = 6.42$, $p < 0.05$), with August and January being the only months when gamete densities for non-infested mussels were significantly higher than for infested mussels (Posthoc, TUKEY HSD).

Gonadosomatic index

Perna perna

The gonadosomatic index (GSI) fluctuated throughout the study period. There were two peaks for GSI, with the highest peak in the month of January (austral summer) and a second, smaller peak in April (autumn). On average, non-infested mussels showed peak value of 0.25 and infested mussels recorded an average peak of 0.15 in January (Fig. 3). Soon after the January peak there was a sharp decline in GSI,

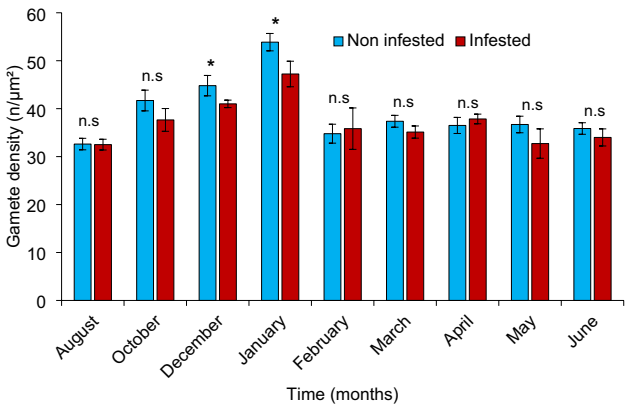

Fig. 1 Gamete density for non-infested and infested *Perna perna* mussels, collected from Brenton on sea on the south coast of South Africa (values are mean ± SD)

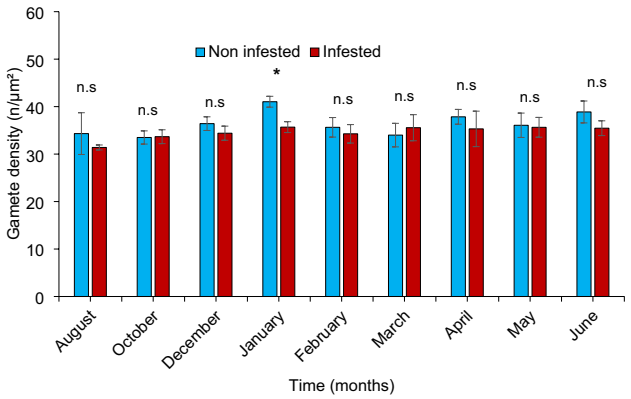

Fig. 2 Gamete density for *Mytilus galloprovincialis* mussels for non-infested and infested mussels, collected from Brenton on sea along the south coast of South Africa (values are mean ± SD)

presumably indicating spawning, and then GSI started to increase from March till it reached the second peak in April. There were significant effects on GSI of month (ANOVA, $F_{8162} = 9.264$, $p < 0.05$) and status (ANOVA, $F_{1162} = 13.217$, $p < 0.05$). There were significant effects on GSI of month (ANOVA, $F_{8162} = 9.264$, $p < 0.05$) and Status (ANOVA, $F_{1162} = 13.217$, $p < 0.05$), but also of the month × status interaction (ANOVA, $F_{8162} = 4.079$, $p < 0.05$). Non-infested mussels had significantly higher GSI values than infested individuals, but only when values were at their highest, in January (Post hoc, TUKEY HSD, $p < 0.05$).

Mytilus galloprovincialis

The gonadosomatic index (GSI) fluctuated throughout the study period, again with two peak periods. The first was in August (spring) when non-infested mussels showed a mean peak of 0.29 and infested mussels recording 0.24 (Fig. 4). A second peak in GSI occurred in April (autumn), with both

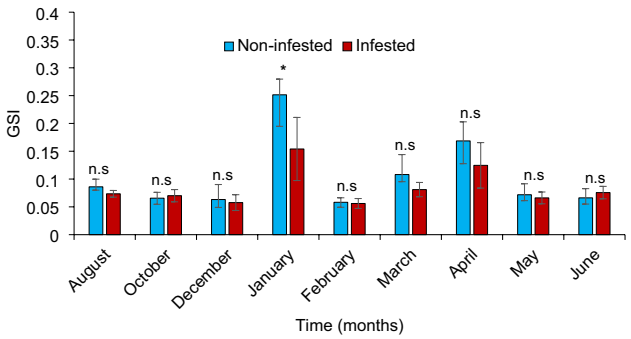

Fig. 3 Gonadosomatic Index for *Perna perna* mussels for non-infested and infested mussels, collected from Brenton on sea along the south coast of South Africa (values are mean ± SD). n.s = non-significant, * = significant

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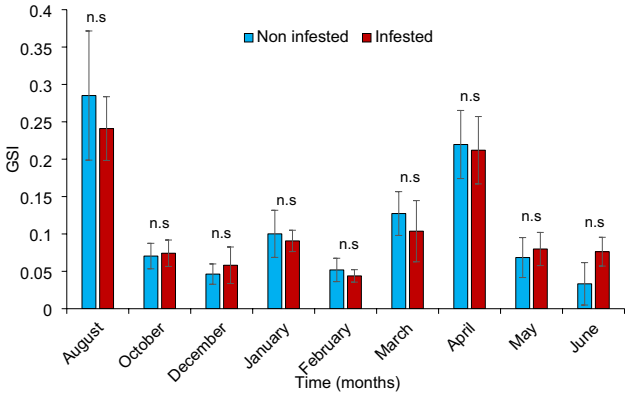

Fig. 4 Gonadosomatic Index for *Mytilus galloprovincialis* mussels for non-infested and infested mussels, collected from Brenton on sea along the south coast of South Africa (values are mean ± SD). n.s = non-significant, * = significant

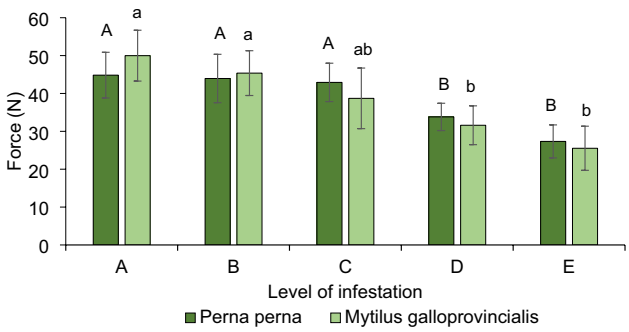

Fig. 5 Attachment strength of different levels of infestation for *P. perna* and *M. galloprovincialis* mussels (values are mean ± SD). Homogenous groups within species are indicated by upper case letters for *P. perna* and lower-case letters for *M. galloprovincialis*

infested and non-infested mussels recording just below 0.25 (Fig. 4). There was a significant effect of month on GSI (ANOVA, $F_{8162} = 5.236$, $p < 0.05$), but not of status, probably because of the high variability around the mean values (ANOVA, $F_{1162} = 1.76$, $p = 0.221$). There was, however, a significant interaction between month and status (ANOVA, $F_{8162} = 5.83$, $p < 0.05$), with differences in GSI levels being significant in some months (June), but not others (Posthoc, TUKEY HSD).

A Pearson correlation coefficient computed to assess the linear relationship between gonad density and GSI showed that there was no correlation between GSI and the density of eggs $r(178) = 0.217$, $p > 0.05$ with the equation ($y = 9.0198 \times - 10.632$) obtained (Supp. Mat. Fig. S1).

Attachment strength

There was a significant interaction of Species and Infestation (ANOVA, $F_{4190} = 3.887$, $p < 0.05$). For *M. galloprovincialis*, levels A–B were not significantly different from each other but were both greater than for levels D and E (ANOVA, TUKEY HSD, $p < 0.05$, Fig. 5) with level C being significantly different from neither of these two groups. The pattern for *P. perna* differed only in detail; levels A, B, C were significantly different from levels D and E (ANOVA, TUKEY HSD, $p < 0.05$, Fig. 5). This shows that the more infested a mussel becomes, the less force is required to be detach it from the substratum.

Discussion

Endolithic cyanobacteria act as parasites to mussels by continuously eroding their shells, although recent research has indicated that this may lead to advantages when mussels are under heat stress as infestation reduces shell albedo (Zardi et al. 2016, 2021; Gehman and Harley 2019). Our results show that colonisation of the shell by endolithic cyanobacteria potentially reduces aspects of mussel fitness by having a negative effect on reproduction, measured as GSI and the density of eggs within the ovary (gamete density), and on attachment to the substratum. Infested mussels had low gamete density and low GSI in the month of January compared to non-infested mussels during the period of maximum reproductive effort, and attachment strength to the substratum decreased with the level of infestation. As level of infestation broadly coincides with mussel size, this means that it is the individuals subject to greater drag and lift forces (Kaehler 1999; Zardi et al. 2009) that are most negatively affected by endoliths.

Reproductive output

Factors, such as temperature, food quality and quantity, are known to affect reproduction in mussels (Wacker and Von Elert 2003; Petes et al. 2007; Fearman et al. 2009), and intertidal mussels are subject to considerable environmental stress, including wave action and exposure to heat and desiccation stress during low tide (Helmuth and Hofmann 2001; Schneider 2014). In our case, however, both mussel species were collected from mixed-species beds at the same location where they experienced the same environmental conditions. The fact that the timing of spawning differed between them suggests that endogenous factors are important. For both species there was a significant interaction of month and status. Reproduction in mussels is well known to follow seasonal cycles (Fearman et al. 2009), but in this case, seasonality differed between our species, as previously shown by (Zardi et al. 2007). The influence of infestation was only significant in months when there was a high density of eggs, just before spawning, when infested mussels had lower densities than non-infested mussels. In

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the case of *Mytilus galloprovincialis*, the results followed the same trend as for *P. perna*, showing a strong influence of infestation in months when there were high gonad densities. Throughout the whole study period, neither mussel species had zero-density, showing that there were always eggs present, although their numbers fluctuated from month to month. Likewise, the gonadosomatic index (GSI) fluctuated throughout the study period for both mussel species and both showed a major and a minor spawning event. Reproduction can be altered by reducing the size (mass) of the gonads or by reducing the density of eggs (gametes) within the gonad, but the size of eggs (gametes) did not differ between infested and non-infested mussels (Ndhlovu, unpubl. data). There was no correlation between GSI and the density of eggs (Supp. Mat. Fig. S1), which means that reproduction was altered by reducing the size (mass) of gonads.

Parasitic larval trematodes have been shown to reduce the population density of salt marsh snail *Cerithidea californica* by castrating the snails (Lafferty 1993; Lafferty and Kuris 2009) and two trematode parasites are known to reduce the competitive ability of *P. perna* mussels (Calvo-Ugarteburu and McQuaid 1998). In the case of endolithic cyanobacteria, the need to channel energy into shell repair is reflected in reduced GSI for *P. perna* and gamete density for both mussel species. This mirrors the effects of endoliths on mussel Scope for Growth (the available energy that can be used to support growth and reproduction), which is significantly reduced in infested mussels (Ndhlovu et al. 2021).

Attachment strength

As for reproduction, endolithic infestation negatively affected attachment to the substratum for both mussel species. For *P. perna*, the effects of infestation resulted in a significant reduction in attachment strength at infestation level D and higher (see also Marquet et al. 2013). Thus, the early stages of infestation did not inflict sufficient damage to elicit a discernible reduction in byssal attachment strength. The effect was quicker to manifest in *M. galloprovincialis*, with a significant reduction in attachment strength at infestation level C and above. Although the difference between species was relatively minor, the fact that the effects of infestation on attachment strength become discernible at an earlier stage for *M. galloprovincialis* aligns well with the different attachment strategies of the two species. *P. perna* adopts a resistance approach to dealing with wave action, channelling energy into attachment by growing more and stronger byssal threads than *M. galloprovincialis*, which adopts a resilience approach involving weaker attachment and greater mobility when dealing with wave action (Zardi et al. 2007). The difference becomes important in terms of competitive interactions between the two (Robinson et al. 2005; Rius and McQuaid 2006, 2009).

Previous studies have looked at how factors such as hydrodynamic stress affect mussel attachment strength (Hunt and Scheibling 2001; Zardi et al. 2007; Nicastro et al. 2010), but other factors also influence byssus production, including temperature, salinity, and seasonality (Young 1985; Lachance et al. 2008). The reduction in byssal attachment in heavily infested mussels means they are likely to exhibit a reduction in life-long fitness, through greater vulnerability to mortality by dislodgement. At the same time, abrasion and strong wave action also facilitate initial infestation through damage to the periostracum (Kaehler 1999) so that the effects of endoliths are likely to be stronger where/when mussels are most vulnerable.

Infestation by endolithic cyanobacteria has been shown to have positive effects on host mussels by reducing heat uptake (Zardi et al. 2016; Gehman and Harley 2019), but this is balanced against increased mortality rates and reduced fitness through negative effects on Scope for Growth, specifically reproductive output, and attachment strength. Such effects of cyanobacterial infestation not only pose direct effects to their hosts, but they are likely to have indirect consequences for the many other organisms that are dependent on the ecological engineering qualities of mussels for their survival.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-022-04023-0.

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Author contributions AN, GZ and CDM: conceived the ideas. GZ, CDM and AN: designed the methodology. AN: collected the data; AN, KN and GZ: analysed the data. AN, KN, GZ and CDM: led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

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

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Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Research Reference Number: RES2019/30.

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