

Article

Biogeographical Patterns of Endolithic Infestation in an Invasive and an Indigenous Intertidal Marine Ecosystem Engineer

Aldwin Ndhlovu ¹, Christopher D. McQuaid ^{1,*}, Katy Nicastro ², Nathalie Marquet ², Marcos Gektidis ³, Cristián J. Monaco ^{1,4} and Gerardo Zardi ¹

¹ Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa; aldwynstav@gmail.com (A.N.); cristianmonaco@gmail.com (C.J.M.); zardi73@yahoo.it (G.Z.)

² CCMAR-CIMAR–Associated Laboratory, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal; katynicastro@gmail.com (K.N.); nmarquet@gmail.com (N.M.)

³ Independent Researcher, Frankfurt, D-60325 Frankfurt, Germany; mail@gektidis.de

⁴ Southern Seas Ecology Laboratories, School of Biological Sciences and The Environment Institute, University of Adelaide, Adelaide 5005, Australia

* Correspondence: c.mcquaid@ru.ac.za

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Abstract: By altering the phenotypic properties of their hosts, endolithic parasites can modulate the engineering processes of marine ecosystem engineers. Here, we assessed the biogeographical patterns of species assemblages, prevalence and impact of endolithic parasitism in two mussel species that act as important ecosystem engineers in the southern African intertidal habitat, *Perna perna* and *Mytilus galloprovincialis*. We conducted large-scale surveys across three biogeographic regions along the South African coast: the subtropical east coast, dominated by the indigenous mussel, *P. perna*, the warm temperate south coast, where this species coexists with the invasive Mediterranean mussel, *M. galloprovincialis*, and the cool temperate west coast dominated by *M. galloprovincialis*. Infestation increased with mussel size, and in the case of *M. galloprovincialis* we found a significantly higher infestation in the cool temperate bioregion than the warm temperate region. For *P. perna*, the prevalence of infestation was higher on the warm temperate than the subtropical region, though the difference was marginally non-significant. On the south coast, there was no significant difference in infestation prevalence between species. Endolith-induced mortality rates through shell collapse mirrored the patterns for prevalence. For *P. perna*, endolith species assemblages revealed clear grouping by bioregions. Our findings indicate that biogeography affects cyanobacteria species composition, but differences between biogeographic regions in their effects are driven by environmental conditions.

Keywords: Biogeographical region; *Mytilus galloprovincialis*; *Perna perna*; rocky shores; parasite

1. Introduction

Scientific literature on microbial endolithic life dates back for over a century [1]. Most studies have focused on the key role played by endoliths in geologically and ecologically important processes including the formation of biokarsts and acting as pathogens in hard corals, e.g., [2,3]. Endolithic heterotrophs (fungi) and phototrophs (cyanobacteria and algae) actively erode and penetrate hard minerals by biochemical dissolution, causing bioerosion and significantly affecting sedimentation processes [4]. Only relatively recently have the effects of endoliths on living organisms been studied [5,6]. The eroding activity of photosynthetic endoliths can cause severe erosion of the shells of molluscs, including those of important ecosystem bioengineers such as mussels, e.g., [7]. The impact of endolithic boring activity extends beyond the outermost layer of the mussel shell with a wide range of severe and

often lethal effects. Critically, endolithic cyanobacteria have a parasitic relationship with the mussels they colonise [8] as they are hypothesised to affect their hosts negatively through their eroding activity while being metabolically dependent on the host for CO₂ released during shell degradation and using it for photosynthesis [9].

Along southern African shores, two mussel species act as important ecosystem engineers in the intertidal habitat, *Perna perna* and *Mytilus galloprovincialis*. *M. galloprovincialis* is the most successful marine invasive species in southern Africa. It is believed that this invasion began in the late 1970s, probably via ballast water, on the south-west coast of South Africa [10]. From there, the species quickly expanded its distributional range along roughly 2800 of kilometres of the southern African shores [11]. Its northern limit is between the northern border of Namibia and southern Angola, while its eastern limit lies on the south-east coast of South Africa. Both range boundaries coincide with transitions between temperate and subtropical bioregions, where high water and air temperatures prevent further expansion as shown in Figure 1; [12]. *P. perna* dominates the east coast and coexists and competes with *M. galloprovincialis* on the southern warm-temperate coast [13]. It is absent from more than 1000 km of the cold-temperate west coast due to the cold, upwelled waters of the Benguela system (Figure 1). North of there, it colonises rocky shores in central Namibia and extends along the west coast of Africa to the southern Iberian Peninsula and into the Mediterranean Sea as far as the Gulf of Tunis [14].

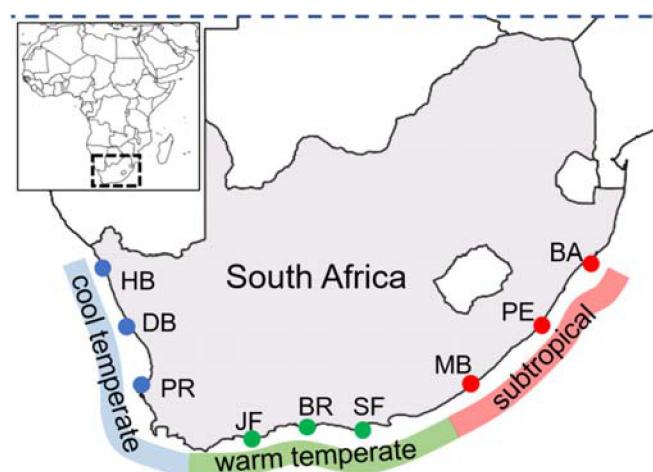


Figure 1. Overall prevalence of endolithic infestation along the cool temperate, warm temperate and subtropical bioregions of South Africa. Proportion of infested mussels (level A–E) shown in black. Full site names in Table 1.

Table 1. List of study sites.

Bioregion	Site	Codes	Coordinates
Subtropical	Ballito	BA	29.53°N; 31.22°E
	Port Edward	PE	31.03°N; 30.24°E
	Morgans Bay	MB	32.71° N; 28.34°E
Warm temperate	St. Francis Bay	SF	34.21°N; 24.84°E
	Brenton-on-Sea	BR	34.08°N; 23.02°E
	Jongensfontein	JF	34.42°N; 21.38°E
Cool temperate	Paternoster	PR	32.81°N; 17.87°E
	Doring Bay	DB	31.78°N; 18.23°E
	Hondeklip Bay	HB	30.31°N; 17.27°E

Several studies have investigated the effects of phototrophic endolithic parasitism on *M. galloprovincialis* and *P. perna* in South Africa [7,15]. However, these works are limited to the south warm-temperate coast. There, these two bioengineers form extensive assemblages dominating

the rocky intertidal habitat showing partial habitat segregation, with *M. galloprovincialis* dominating the upper shore, while the indigenous species dominates the lower mussel zone. The mid-mussel zone is characterised by mixed populations of the two species [16]. A wide variety of biotic and abiotic factors play a crucial role in establishing and maintaining across- and along-shore patterns of abundance of *M. galloprovincialis* and *P. perna*, moderating the dynamics of their coexistence reviewed in [14]. Among biotic factors, shell-boring endoliths exert significant pressure. Endolithic infestation occurs in both *M. galloprovincialis* and *P. perna*, however higher prevalence have been observed in the invasive species probably due to the greater thickness of the protective outer proteinaceous layer, or periostracum of the indigenous species [8], since comparisons between species was based on individuals at the same shore level. Along South African shores, infestation frequencies for these two mussels' range between 50% and 100% [15]. Such intense infestation can have devastating consequences for mussel populations. Endoliths weaken the shell dramatically and endolith-induced shell collapse can be responsible for almost 60% of total mortality [15,17]. Higher mortality rates attributed to parasitism in *M. galloprovincialis* can affect its ability to compete with *P. perna* [8].

Endoliths also have a wide range of sub-lethal effects. The repair of damaged parts of the shell is energetically demanding [18]. The essential need to maintain an integral shell comes at the expense of significantly lower health status (condition index), growth and byssal attachment strength [8]. The lethal effects of endolithic excavation can be enhanced by other concomitant disturbances. Mussels with shells weakened by endolith boring activity are more vulnerable to predation and the hydrodynamic stress imposed by wave action [19] as well as human pedestrian disturbance. At high trampling intensities, the effect is particularly strong for *M. galloprovincialis*, which suffers significantly higher mortality rates than *P. perna* [20].

Unexpectedly, recent results have shown that during periods of intense heat stress, endolithic infestation can provide benefits to mussels. Endolithic infestation increases shell whitening through the chemical dissolution and subsequent re-deposition of calcium on the outside of the shell [9]. Such shell discolouration enhances reflectance of solar irradiation, reducing the absorption of solar energy and reducing mussel body temperatures [21]. Most importantly, during extreme heat stress resulting from intense solar radiation, parasitised individuals exhibit mortality rates 49% lower than those of uninfected individuals [21]. For *M. galloprovincialis*, it has been shown that the thermal mitigation provided by endoliths extends beyond individual mussels to the mussel bed interstitial microclimate. Mussels with infested neighbours experience lower body temperatures than those surrounded by non-infested mussels [22]. The bioengineering protection offered by *M. galloprovincialis* beds to the infauna associated with mussel beds is likely to be enhanced by endolith-induced improvements in humidity and temperature. Such small-scale habitat amelioration is ecologically important at organismal scales [22] and could be particularly significant under climate warming scenarios.

Given that the two host mussels occur across very large geographical areas, we asked whether the levels and consequences of endolithic infestation reflect the effects of biogeography on endolith species composition. We did this by addressing three main questions: (1) does endolithic species richness differ among bioregions? (2) Does the identity of the host drive parasite diversity? (3) Do the rates of cyanobacteria infestation and mortality due to infestation differ across bioregions?

2. Methodology

The study was conducted across three major temperature-defined coastal marine biogeographical regions in South Africa: the eastern subtropical, southern warm temperate and western cool temperate bioregions (Figure 1). Three sampling sites separated on scales of 100 s of km within each bioregion were selected. Within each site, two locations approximately 300 m apart were selected. Each of the two species occurs in two of the three bioregions. *Perna perna* and *Mytilus galloprovincialis* occur in the subtropical and cool temperate bioregions respectively and co-exist in the warm temperate bioregion. All samples were collected from moderately wave-exposed intertidal rocky shores and at sun-exposed sites.

2.1. Prevalence of Endolithic Infestation

At each location, we identified areas of 100% mussel cover within the mid-mussel zone and collected 5 haphazardly identified individuals of each species from each of 4 size classes (20–30, 31–40, 41–50 and 51–60 mm), from these areas. All individuals were healthy, lacking lesions or other indications of poor health. In the laboratory, each of these mussels was assigned a level of infestation following Kaehler [7]: Group A, shells with clean, intact periostracum and distinct outer periostracal striations; Group B, shells with eroding central surface portion and the outer growth lines becoming hazy; Group C, erosion of shells spreading past the central portion with grooves and pits appearing on shell surface; Group D, shells heavily pitted and becoming deformed, outer striations becoming virtually absent; Group E, shells extremely pitted, deformed and brittle, eventually developing visible holes. This allowed us to estimate prevalence, the number of individuals of the host species infected with the parasite (level B–E) divided by the number of hosts examined and expressed as a percentage [23,24].

2.2. Identification of Endolithic Organisms

At each location, heavily infested (Group D or E) mussels of each species present were collected ($n = 5$ for each species). *M. galloprovincialis* and *Perna perna* were collected from the cool temperate bioregion and subtropical bioregion respectively while both mussel species were sampled in the warm temperate bioregion. Collected mussels were immediately preserved in 4% formalin and transported to the laboratory. In the laboratory, shells were cleaned with a scalpel to remove all epibionts and the soft tissue inside the valves. Cleaned shells were stored in 4% formalin.

To process the samples, each shell was broken into smaller pieces and placed in 3% HCl for 30 min to dissolve the calcium carbonate. Under a low power stereomicroscope, the emerging endoliths were transferred to a drop of immuno-mount (Shandon), on a glass slide using fine forceps. After selecting all visible endolithic colonies, the immuno-mount drop was covered gently with a glass slide. All prepared slides were viewed under a Zeiss Axio Imager Z2, Apotome with a Normaski lens (40x). Photographs, including a scale bar, were acquired for each endolith colony and used for endolith identification, based on descriptions in the published literature.

2.3. Lethal Effects of Endolithic Infestation

At each location, quadrats (50 cm × 50 cm; $n = 8$) were placed in the mid-mussel zone in an area with 100% mussel cover. Within each quadrat, dead mussels exhibiting extreme infestation levels (group E in which a fracture hole around the site of adductor muscle attachment was visible) were counted. To ensure that mortality had occurred recently, only mussel shells with a shiny nacreous layer were counted [15,17].

2.4. Data Analyses

To test whether geography has an influence on cyanobacterial infestation, for each mussel species, the overall prevalence of infested mussels (i.e., infestation categories B–E were pooled) was analysed using a three-way nested ANOVA (Analysis of Variance) with bioregion (fixed factor, three levels) and site nested into bioregion (random, three levels) and size (fixed factor, four levels) as factors.

To test whether species have similar infestation levels where they co-occur on the south coast, the overall proportion of infested mussels was analysed using a three-way ANOVA with species (fixed factor, two levels), site (random factor, three levels) and size (fixed factor, four levels) as factors.

To test whether bioregion has an effect on species richness of cyanobacteria, we ran separate two-way nested ANOVAs for each species as species was not orthogonal. The factors were bioregion (fixed, two levels), site (random, three levels) nested in bioregion, with the number of cyanobacterial species as the dependent variable. For the warm temperate bioregion, a further two-way ANOVA was run to test for differences in cyanobacterial species richness between coexisting mussel species,

with species (fixed, two levels) and site (random, three levels) as the factors. To visualise similarities and differences in endolithic communities among bioregions and between species on the south coast, a series of non-metric multidimensional scaling (nMDS) ordinations based on presence-absence of species were plotted based on the Bray–Curtis matrix. SIMPER (Similarity Percentage) analysis was used to identify the % contribution of each endolithic species to the Bray Curtis dissimilarity metric.

We tested the effects of bioregion on mussel mortality rates due to infestation using separate 2-way nested ANOVAs for each species with bioregion (fixed, two levels) and site (random, three levels) nested in bioregion as the factors.

To compare mortality rates between mussel species on the south coast, we used a two-way nested ANOVA with species (fixed, two levels) and site (random, three levels) as factors.

All univariate analyses were run using Statistica 13 (Statsoft). Data were transformed where necessary to fulfil the assumption of homogeneous error variances (Cochran's test) and post-hoc comparisons were performed using Tukey HSD tests. nMDS plots were created using PRIMER-E v6.

3. Results

3.1. Prevalence of Infestation

In the cool temperate bioregion, the prevalence of infestation in *M. galloprovincialis* ranged between 96% at DB and 100% at HB and PR (Figure 1). In the subtropical bioregion, the prevalence of infestation in *P. perna* ranged between 70% at BA and PE and 95% at MB. In the warm temperate bioregion, the two mussel species showed similar levels of infestation at all sites, with individuals from JF showing the highest levels of infestation (>98% infestation) for both species.

Infestation severity increased with size in the subtropical bioregion. At BA, PE and MB mussels in the size ranges 21–30 cm and 31–40 cm exhibited level A infestation. The same trend was observed on the warm temperate bioregion (SF, BR) with the exception of mussels from JF, where only the smallest size class 21–30 cm showed no infestation. In the cool temperate bioregion (PR, HB), mussels exhibited infestation at levels B to E, except for the smallest size class at DB, which exhibited level A severity (Figure 2).

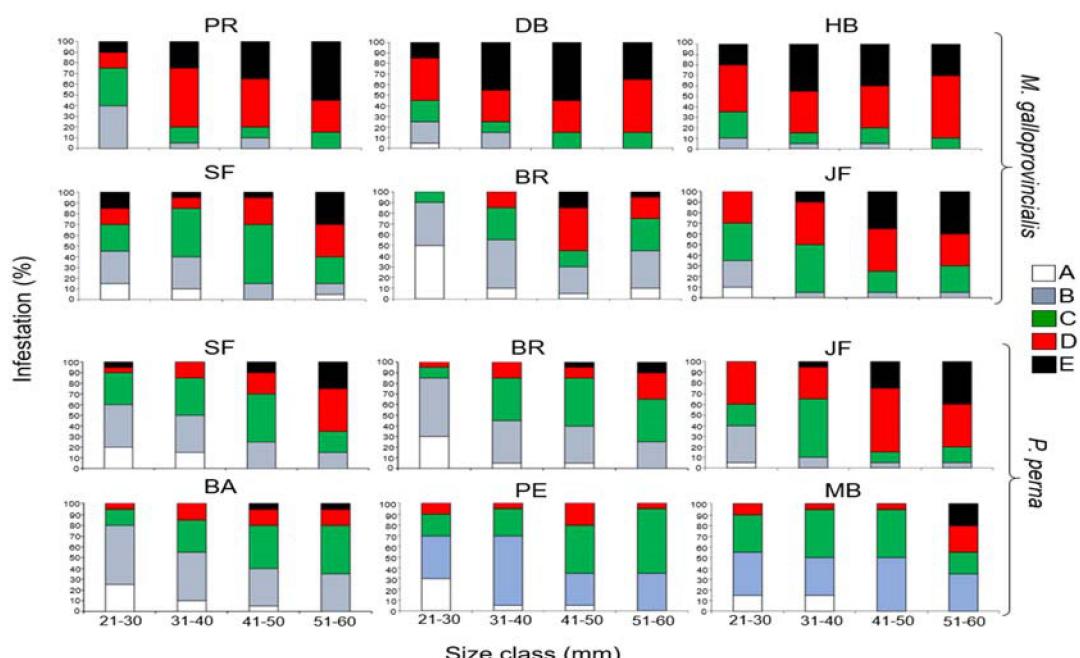


Figure 2. Prevalence of infestation (%) of mussel shells categorised by degrees of infestation severity for each site (Groups/levels A–E), grouped into 10 mm size classes for all three bioregions in South Africa.

3.2. Cool Temperate vs Warm Temperate Bioregion—*M. galloprovincialis*

In the cool temperate bioregion, infestation rates were higher than in the warm temperate bioregion (bioregion: $F_{1,24} = 8.467; p < 0.05$; Figure 3A). In the warm temperate bioregion, infestation levels in JF were significantly higher than those at BR and SF [site (bioregion): $F_{2,24} = 6.486; p < 0.05$].

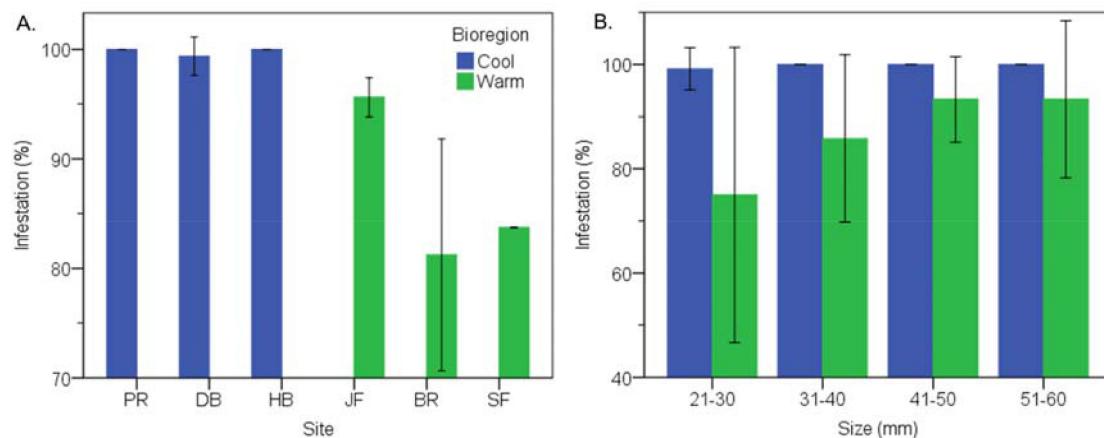


Figure 3. Overall prevalence of infestation (%; $\pm 95\%$ CI) for *Mytilus galloprovincialis* along the cool temperate and warm temperate bioregions. Data grouped by (A) site with size classes pooled and (B) by size class with sites pooled.

Infestation increased with size with smaller mussels exhibiting less severe infestation than bigger ones (size: $F_{3,24} = 6.743; p < 0.05$; Figure 3B), although this was less clear for the cool temperate bioregion than the other bioregions. Furthermore, the prevalence of infestation in large shells was similar between bioregions.

3.3. Subtropical vs Warm Temperate Bioregion - *Perna perna*

There was no significant difference in the prevalence of infestation between the two bioregions (bioregion: $p = 0.916$; Figure 4A). Larger mussels (41–50 mm, 51–60 mm) had more severe infestation than smaller individuals (21–30 mm, 31–40 mm; size: $F_{3,24} = 12.16, p < 0.05$; Figure 4B). Although infestation increased with mussel size at all sites, the effect was stronger at some sites than others [site (bioregion)*size: $F_{12,24} = 4.22, p < 0.05$; Figure 4B].

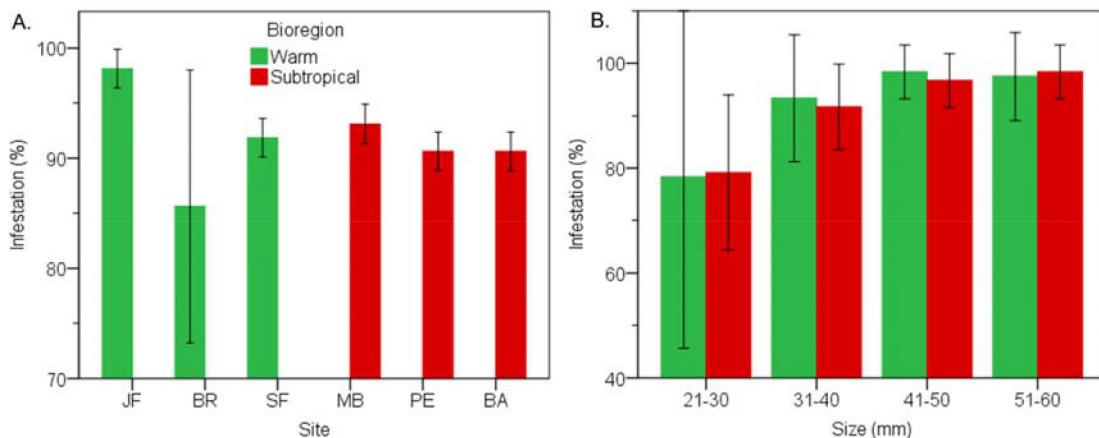


Figure 4. Overall prevalence of infestation (%; $\pm 95\%$ CI) for *Perna perna* along the subtropical and warm temperate bioregions. Data grouped by (A) site with size classes pooled and (B) by size class with sites pooled.

3.4. Warm Temperate Bioregion—*M. Galloprovincialis* vs *P. Perna*

There was no significant difference in the prevalence of infestation between the two species (species: $p = 0.132$; Figure 5). There was a significant site*size interaction (ANOVA: $F_{6,24} = 9.91$; $p < 0.05$). At all sites, both species showed an increase in infestation with increasing mussel length, but the effect was stronger at BR. Smaller mussels (21–30 mm, 31–40 mm) were less infested than bigger mussels (41–50 mm, 51–60 mm) with 100% infestation rates in size classes 41–50 mm and 51–60 mm (post hoc TUKEY HSD (honest significant difference); Figure 5B). For both species, the prevalence of infestation at BR was 60% for hosts belonging to the smaller size classes and this level increased to more than 75% for bigger size classes (Figure 5B).

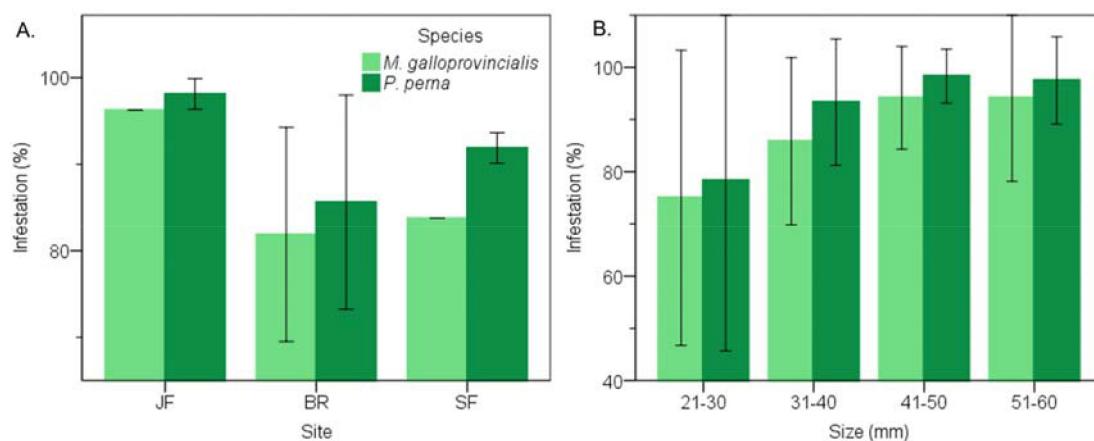


Figure 5. Overall prevalence of infestation (%; $\pm 95\%$ CI) for *Perna perna* and *Mytilus galloprovincialis* along the warm temperate bioregion where both species coexist. Data grouped by (A) site with size classes pooled and (B) by size class with sites pooled.

3.5. Cyanobacteria Species Composition

Overall, a total of eight species of endolithic cyanobacteria were identified across all bioregions (Table 2). Each site had between five and eight species with five of the species being common to all nine sites.

Table 2. List of identified endolithic species in all study sites for each species. Full site names refer to Table 1.

Cyanobacterium Species	<i>Mytilus Galloprovincialis</i>					
	HB	DB	PR	JF	BR	SF
<i>Hyella balani</i> (Lehman 1903)	X	X	X	X	X	X
<i>Mastigocoleus testarum</i> (Lagerheim 1886)	X	X	X	X	X	X
<i>Solentia stratosa</i> (Ercegovic 1932)	X	X	X	X	X	X
<i>Plectonema terebrans</i> (Bornet & Gomont, 1889)	X	X	X	X	X	X
<i>Hyella caespitosa</i> (Bornet & Flahault 1889)	X	X	X	X	X	X
<i>Hormathonema violaceo-nigrum</i> (Ercegovic 1930)	X					
<i>Kyrrhutrix dalmatica</i> (Ercegovic 1929)	X	X	X	X	X	X
<i>Hormathonema luteo brunneum</i> (Ercegovic 1930)	X	X	X	X		

Cyanobacterium species	<i>Perna perna</i>					
	JF	BR	SF	MB	PE	BA
<i>Hyella balani</i> (Lehman 1903)	X	X	X	X	X	X
<i>Mastigocoleus testarum</i> (Lagerheim 1886)	X	X	X	X	X	X
<i>Solentia stratosa</i> (Ercegovic 1932)	X	X	X	X	X	X
<i>Plectonema terebrans</i> (Bornet & Gomont, 1889)	X	X	X	X	X	X
<i>Hyella caespitosa</i> (Bornet & Flahault 1889)	X	X	X	X	X	X
<i>Kyrrhutrix dalmatica</i> (Ercegovic 1929)	X	X	X			
<i>Hormathonema luteo brunneum</i> (Ercegovic 1930)	X					

3.6. Cool Temperate vs Warm Temperate Bioregion—*Mytilus Galloprovincialis*

In the non-metric multi-dimensional scaling (nMDS) plot, there was distinct clustering by bioregion with only partial overlap (Figure 6A). The species that contributed most to regional differences were *Hormathonema violaceo nigrum* (SIMPER; 27.78%), found only in the cool temperate region, and *Hormathonema luteo brunneum* (26.85%) being common to all sites in the cool temperate bioregion but present at only one site (JF) in the warm temperate bioregion.

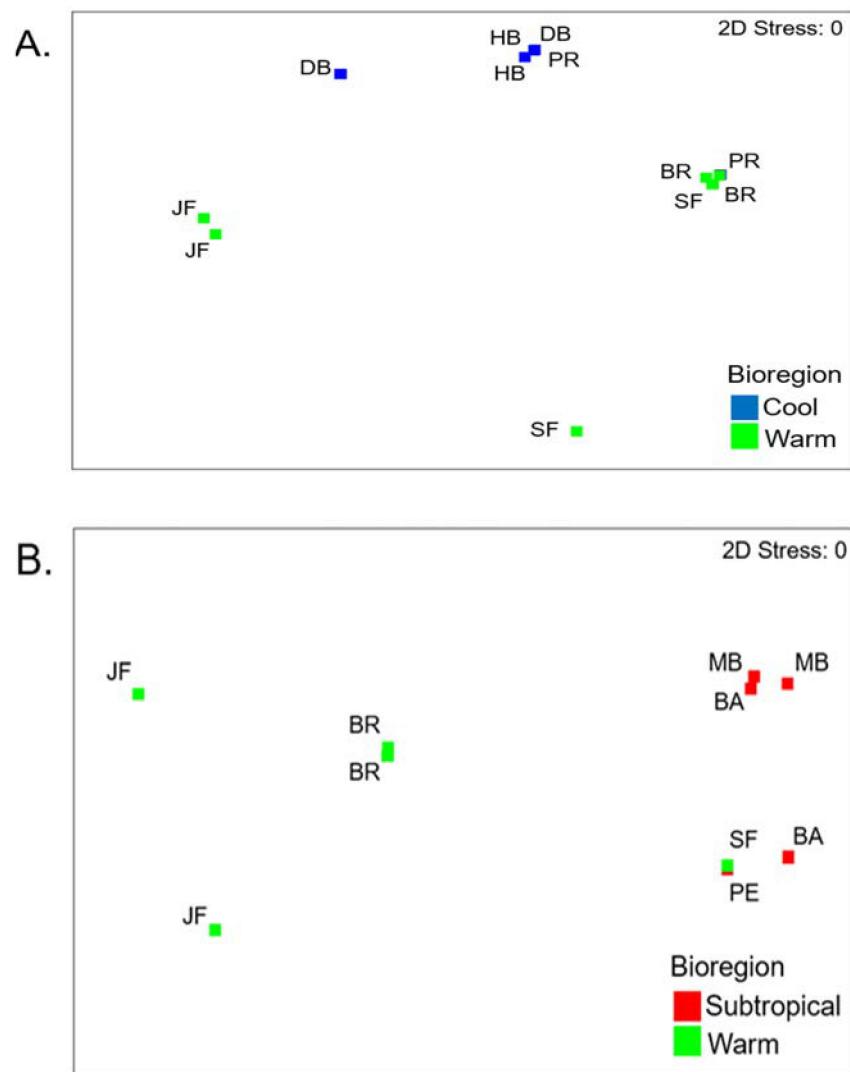


Figure 6. Cont.

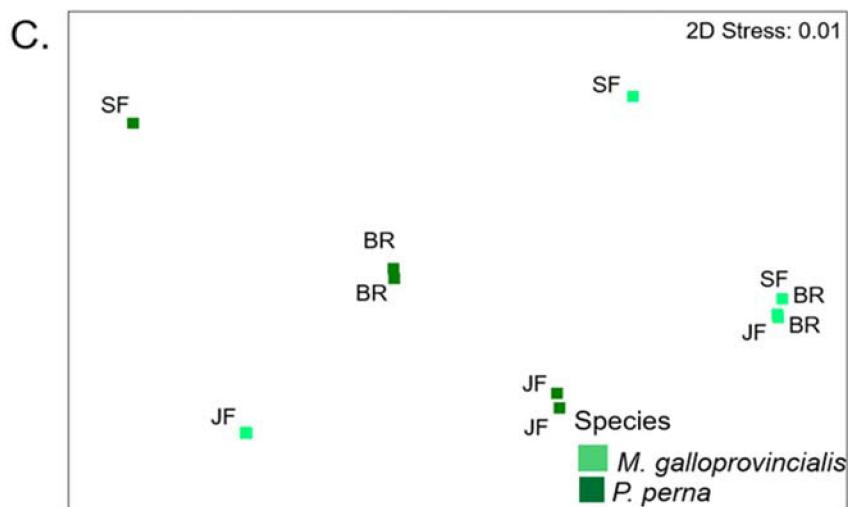


Figure 6. Non-metric multidimensional scaling (NMDs), based on presence-absence of cyanobacterial species using Bray–Curtis distance for (A) *Mytilus galloprovincialis*, (B) *Perna perna*, (C) the two mussel species within the warm temperate bioregion.

No significant effect of bioregion on species richness was detected (ANOVA, bioregion: $p = 0.192$). Eight endolith species were identified in mussel shells collected in the cool temperate and seven species from the warm temperate bioregion, with *Hormathonema violaceo nigrum* being unique to the cool temperate bioregion.

3.7. Subtropical vs Warm Temperate Bioregion—*Perna Perna*

Endolithic community composition displayed clear-cut grouping by bioregion, with the exception of SF (Figure 6B) where *Hormathonema luteo brunneum* was absent from some shells. Five and seven species were identified from the subtropical and warm temperate bioregions respectively, with *H. luteo brunneum* and *K. dalmatica* being unique to warm temperate shores, contributing 67.6% and 10.8% respectively to the overall difference between the two regions (SIMPER). *Mastigocoleus testarum* contributed a further 21.62%.

Samples from the warm temperate region displayed higher cyanobacterial richness than the subtropical bioregion (bioregion: $F_{1,6} = 11.604, p < 0.05$). The maximum number of species identified in a single shell on the subtropical east coast was five, while in the warm temperate bioregion seven species were identified, with *Hormathonema luteo brunneum* and *Kyrthutrix dalmatica* being unique to this bioregion.

3.8. Warm Temperate Bioregion—*Mytilus Galloprovincialis* vs *Perna Perna*

The nMDS plot did not reveal a clear difference in the cyanobacterial community composition between the two mussel species where they co-occurred (Figure 6C). The analysis indicated an acceptable stress level (stress = 0.01) and displayed partial overlap between samples from the two host species. *Hormathonema luteo brunneum* and *Kyrthutrix dalmatica* accounted for the highest contributions, 54.59% and 45.41% respectively (SIMPER) with both species being found more frequently in the shells of *M. galloprovincialis*. Collectively, seven endolith species were identified from the two mussel species with *H. luteo brunneum* being unique to *M. galloprovincialis* samples. There was no effect of mussel species (species: $p = 0.423$) on cyanobacteria species richness, though richness did differ significantly among sites (site: $F_{2,6} = 29.875, p < 0.05$).

3.9. Lethal Effects of Endolithic Infestation

For *M. galloprovincialis*, sites in the cool temperate bioregion had significantly higher mortality rates (mean five dead mussels/m²) than the warm temperate bioregion (mean one dead mussel/m²; Figure 7A,B; $F_{1,42} = 136.5$; $p < 0.05$).

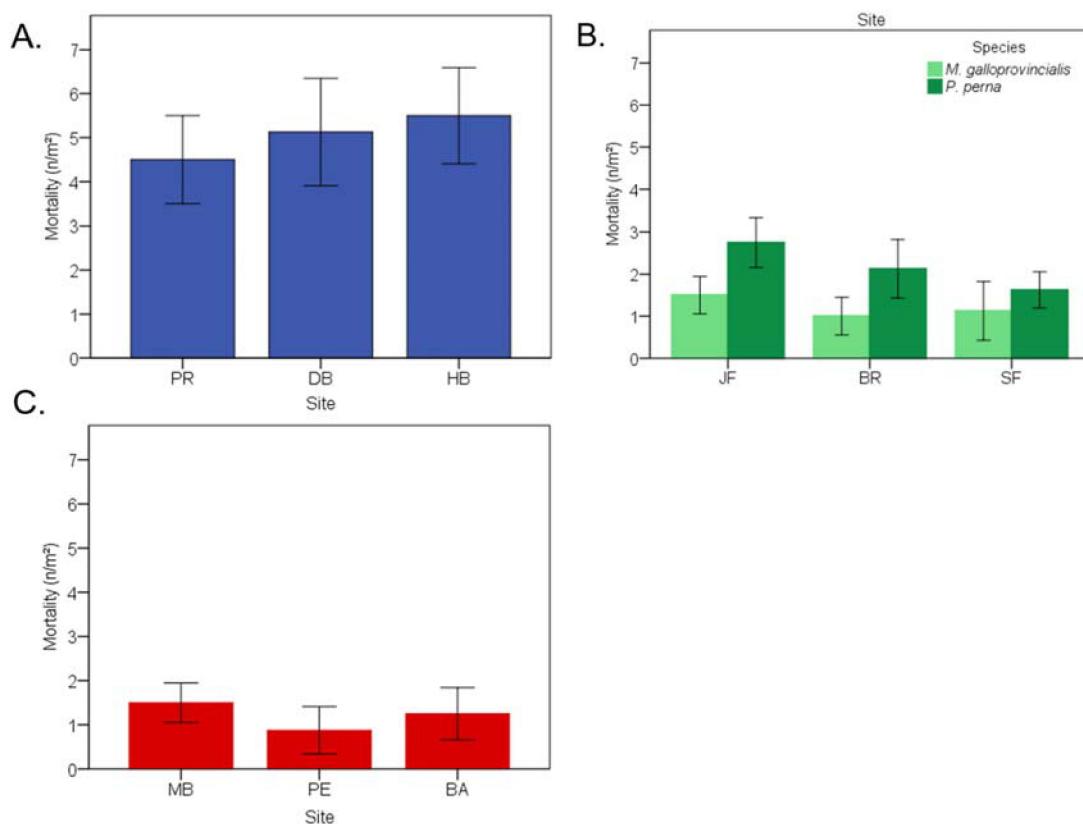


Figure 7. Mean endolithic induced mortality (\pm 95% CI) within the three coastal bioregions of South Africa (A) Cool Temperate, (B) Warm Temperate, (C) Subtropical bioregion. In the warm temperate bioregion, where both species coexist, two bars are plotted for each site, one for each mussel species.

In the subtropical bioregion, *P. perna* had an average mortality of 1.5 dead mussels/m², with an average of 2.1 in the warm temperate bioregion (Figure 7B,C). For this species, endolith induced mortality rates did not differ between the two bioregions (ANOVA: $F_{1,42} = 6.612$; $p = 0.062$). In the warm temperate bioregion, mortality rates for *P. perna* were significantly higher at JF than at SF ($p < 0.05$).

In the warm temperate bioregion, *P. perna* suffered higher rates of mortality than *M. galloprovincialis*, but the difference was marginally non-significant (species: $p = 0.054$; Figure 7A,B).

4. Discussion

Our results show that endolithic induced erosion is intense and ubiquitous in intertidal mussel aggregations across three distinct bioregions. Along approximately 2000 km of coastline, no mussel population had a prevalence of infestation lower than 75%, with infested individuals hosting between three and seven species of cyanobacteria each. These findings support previous works indicating that marine calcifying organisms are globally affected by endolithic parasitism [8].

An earlier study indicated that the invasive species *Mytilus galloprovincialis* showed more frequent infestation and endolith-induced mortality than the native *Perna perna*, giving endoliths a key role in the competitive balance between the two species [8]. Here, using different methods, we did not observe

a significant difference in the prevalence of infestation between the two where they co-occur, but the difference in endolith-induced mortality was only marginally non-significant (Figure 7; $p = 0.054$).

For *P. perna*, despite differences in terms of endolithic species composition and richness, mussels from the subtropical and warm temperate regions did not exhibit different levels of endolithic infestation or endolithic induced mortality. Phototrophic endoliths are extremely generalist parasites capable of eroding and penetrating various kinds of hard mineral substrates, including both carbonates and phosphates [25,26]. The generalist nature of endoliths [26] is the most likely explanation for the similar levels of infestation and shell fracture observed in *P. perna* samples. Interestingly, this was despite the fact that, in southern Africa, *P. perna* forms two distinct genetic lineages with a non-sister relationship [27] and different physiological tolerances [28]. The subtropical eastern and warm temperate southern bioregions of South Africa each supports only one of the two lineages [29], but we found no difference in infestation or mortality rates between the two.

M. galloprovincialis displayed a more complex biogeographic pattern than the indigenous species, with higher infestation rates along west, cool temperate shores (Figure 3), which in turn were associated with higher rates of endolith induced mortality (Figure 7). Comparisons of bioregions within each mussel species (*P. perna* south vs east, *M. galloprovincialis* south vs west) revealed similar levels of difference in endolithic species composition, yet *P. perna* showed no difference in endolithic effects between regions (Figure 7). Given this, we conclude that it is unlikely that there is a cause and effect relationship between endolithic species identity and infestation or mortality for *M. galloprovincialis*. Rather than a biogeographic effect of endolith species composition, we suggest that greater infestation and mortality on the west coast is an environmental effect, probably related to water conditions. The west coast of South Africa is powerfully affected by the Benguela upwelling system and there is abundant evidence that upwelling has a strong influence on the abundance, richness and dynamics of coastal communities [30–32]. Nevertheless, previous work along the Atlantic coasts of Portugal and Morocco suggests no direct effect of upwelling on the incidence of phototrophic shell-degrading endoliths [22], but a strong gradient of increasing endolithic infestations in *M. galloprovincialis* at lower latitudes. Together with our results this suggests that, on the cool temperate west coast, other environmental factors, indirectly related or unrelated to upwelling, enhance endolithic pressure or weaken mussels as hosts. Earlier studies have shown that wave action and solar radiation are key abiotic determinants of infestation, explaining variation in endolithic induced erosion and mortality across spatial micro- (i.e., shaded vs non-shaded areas along the intertidal) and meso- (sheltered bays vs wave exposed open coasts) scales [8]. The role played by environmental factors at different spatial scales acquires even more importance under climate change scenarios. Indeed, endolithic erosion is predicted to increase as a result of increased ocean acidification and warming rates [33,34]. If so, future environmental changes may alter the efficacy of ecosystem engineering by mussel aggregations by affecting endolith-modulated humidity and temperature regimes within mussel beds by affecting the host's physiological responses to a changing climate. Several aspects of endolith/mussel relationships remain unexplored. In particular, the effect of endolithic erosion on the hosts' immune system could have important ecological and conservation relevance that could be explored using flow cytometry and micro-Raman spectroscopy (e.g., [35]).

Overall, endolithic infestation is prevalent around this entire coast and responsible for significant mortality among larger/older mussels. Our results suggest that species richness among endolithic cyanobacteria along this coast is relatively low, with biogeography playing a role in determining the identity of species assemblages. Despite this, the clear difference between the south and west coasts in prevalence and induced mortality can be ascribed to environmental drivers, rather than endolith species composition. In addressing our initial questions, we found that endolithic species identity differed among bioregions, but with little effect on overall species richness; that host identity was not linked to parasite diversity and that mortality due to cyanobacterial infestation and endolith-induced mortality differed among bioregions, but only between the south and west coasts. Mussels are critical ecological engineers on rocky shores, providing architectural complexity and habitat for a wide range

of associated species. Our findings indicate that their ability to fulfil this role is powerfully influenced by the parasitic effects of endolithic cyanobacteria, which in turn respond to biogeography in terms of species composition and to environmental drivers in terms of their effects.

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