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ORIGINAL PAPER

Comparison of phototrophic shell-degrading endoliths in invasive and native populations of the intertidal mussel *Mytilus galloprovincialis*

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Abstract The intertidal mussel *Mytilus galloprovincialis* is a successful invader worldwide. Since its accidental introduction onto the South African west coast in the late 1970s, it has become the most successful marine invasive species in South Africa. One possible explanation for this phenomenon is that *M. galloprovincialis* suffers less from phototrophic shell-degrading endoliths in its invasive than in its native range. We assessed photoautotrophic endolithic pressure on *M. galloprovincialis* in native (Portugal) and invasive (South Africa) ranges. Invasive populations were more heavily infested than native populations. In Portugal, only the biggest/oldest mussels displayed endolithic erosion of the shell and the incidence of infestation was greater at higher shore levels where more prolonged exposure to light enhances endolith photosynthesis. In South Africa, even the smallest size classes of mussels were heavily infested throughout the shore. In Portugal, endolithic-induced mortality was observed at only one location, while in South Africa it occurred at all locations and at significantly higher rates than in Portugal. Important sub-lethal effects were detected in infested native mussels, confirming previous studies of invasive populations and suggesting an energy trade-off between shell repair and other physiological constraints. We observed a positive relationship between infestation rates and barnacle colonization on mussel shells, suggesting possible facilitation of barnacle settlement/survival by shell-boring pathogens. Identification of endoliths revealed common species between regions. However, two species were unique in the invasive range while another was unique in the native region. Different levels of endolithic infestation in the invasive and the native range were not explained by the effect of major environmental determinants

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(Photosynthetically Available Radiation and wave height). The results reject our initial hypothesis, indicating that invasion success of *M. galloprovincialis* is not simply explained by escape from its natural enemies but results from complex interactions between characteristics of the invaded community and properties of the invader.

Keywords Marine invasion · Endoliths · Parasitism · Bioerosion

Introduction

Biological invasions are widely recognized as a major threat to terrestrial, marine and freshwater biodiversity, causing annual economic losses amounting to billions of dollars worldwide (Pimentel et al. 2001; Prenter et al. 2004). Considerable attention is currently devoted to understanding invasion dynamics (e.g. Mack et al. 2000; Maron and Vilà 2001; Torchin and Mitchell 2004). In particular, there is major interest in identifying mechanisms that would allow the development of predictive models of invasive processes (Davis et al. 2000; Ruiz et al. 2000). This includes describing characteristics of invaders and invaded communities (including resources, the physical environment and natural enemies), and investigating their relationships (Parker et al. 1999; Shea and Chesson 2002; Torchin et al. 2002; Heger and Trepl 2003; Suarez and Tsutsui 2008).

Parasites are implicated as key factors in an increasing number of biological invasions (Prenter et al. 2004). They are seen as mediators of invasion success, either via direct effects on invader growth, reproduction or survivorship, or by indirectly mediating competitive and predatory interactions among native and invasive species (Torchin et al. 2001; Prenter et al. 2004). Although parasitism is widespread in marine systems, the extent to which parasites can mediate native-invader interactions is relatively unexplored (Torchin et al. 2002).

Endolithic organisms can cause serious bioerosion of the shells of molluscs, including important ecological engineering animals such as mussels. This can have both lethal and sublethal effects and the relationship between endolith and host can be considered to be a form of parasitism, sensu lato (Prenter et al. 2004). In this study, we compare the pressure of endolithic parasitism on *M. galloprovincialis*, one of the world's most successful invasive marine species (Lowe et al. 2000) in a country where it is indigenous (Portugal) and in South Africa, where it has been accidentally introduced and is now the most successful marine invader (Robinson et al. 2005).

Mytilus galloprovincialis is widespread in temperate zones worldwide (Hilbish et al. 2000) and is highly adaptable to different environments, possessing the broad physiological tolerances and high fecundity typical of many invasive species (Zardi et al. 2007, 2008; Nicastro et al. 2010). Over the past century, *M. galloprovincialis* has established populations in the United States, South Africa, Japan, and Hong Kong (Wilkens et al. 1983; Grant and Cherry 1985; Lee and Morton 1985; Geller 1999; Wonham 2004). Since its arrival on South African shores in the early 1970s (probably through ballast water; Grant and Cherry 1985), it has spread over 2,050 km of coastline, displacing the indigenous mussel *Aulacomya ater* and significantly altering the population structure and abundance of local mussel and limpet populations (Branch and Steffani 2004; Robinson et al. 2005). On the south coast of South Africa, *M. galloprovincialis* co-exists with the indigenous mussel *Perna perna* with partial habitat segregation in the lower eulittoral zone (Bownes and McQuaid 2006).

Endolithic microorganisms, including heterotrophs (fungi) and phototrophs (cyanobacteria and algae), actively penetrate hard minerals by biochemical dissolution contributing greatly to biodestruction processes (bioerosion) and sedimentation (Golubic et al. 1981). A few species of cyanobacteria are able to excavate carbonate minerals, from limestone to biogenic carbonates, including coral reefs, skeletal materials and molluscan shells (Tribollet 2007).

Although the existence of endoliths has been known since the twentieth century, only recently have their effects on living organisms been studied. Endoliths often have a parasitic relationship (sensu lato Prenter et al. 2004) with their live hosts, such as corals (e.g. Bentis et al. 2000; Golubic et al. 2005) and molluscs (e.g. Kaehler and McQuaid 1999; Alfaro et al. 2008; Zardi et al. 2009). In particular, the damage caused by phototrophic endoliths in bivalves was thought to be restricted to the outermost layer of the shell, the periostracum (Laukner 1983), but more recent studies have demonstrated that the boring activity of photosynthetic endoliths can cause extensive damage to the host. In mussel populations where endoliths are abundant, they can be responsible for almost 50 % of total mortality through shell collapse (Kaehler and McQuaid 1999). Endoliths also have significant sub-lethal effects. In South Africa, for example, endoliths negatively affect condition index (a general indicator of health status), shell growth and strength, and the byssal attachment strength of native (*P. perna*) and invasive (*M. galloprovincialis*) mussels (Kaehler and McQuaid 1999; Zardi et al. 2009).

The periostracum of mytilid shells possesses chemical and physical antifouling properties (Scardino et al. 2003; Wahl 2008; Bers et al. 2010). However, periostracum degradation caused by endoliths can degrade these defences and promote settlement of epibionts, directly affecting the host by increasing drag or interfering with filter feeding, or indirectly by modulating ecological interactions (Lesser et al. 1992; Wahl and Hay 1995; Wahl 2008).

Both the prevalence and intensity of endolithic infestations in mussels can vary over micro and meso spatial scales. In the intertidal, the frequency of endolith infestation is lower in bays than at open-coast sites where wave action is higher, possibly because of greater abrasion of the periostracum, while at smaller scales infection rates tend to be higher on the upper than the lower shore (Kaehler 1999). At smaller scales, photosynthetic endoliths depend on light availability, and infection rates are higher at sites exposed to high irradiance than in more shaded areas (Zardi et al. 2009).

We tested the hypothesis that the invasive success of *M. galloprovincialis* in South Africa is related to lower incidence of shell-degrading endoliths compared to populations from its native range. To assess this hypothesis we:

1. compared the degree of endolithic infestation and endolith-induced mortality of *M. galloprovincialis* in native (Portugal) and invaded (South Africa) ranges over small (intertidal) and large (latitudinal) spatial scales, identifying endoliths at the most infested locations in the native and invaded ranges;
2. determined sub-lethal effects (condition index, shell strength, attachment strength and cover by epibiotic barnacles) associated with endolithic parasitism of *M. galloprovincialis* in its native range (Portugal).

Finally, the role of environmental factors (Photosynthetically Available Radiation and wave height) in shaping infestation severity at the two geographical ranges was also investigated.

Materials and methods

Study locations

Four locations were selected in each of the native (Portugal) and invasive (South Africa) ranges of *M. galloprovincialis* (Table 1). At these locations, intertidal rocky shores are composed of limestone and granite (Table 1; Portugal: Carvalho et al. 1992; Da Silva et al. 1999; Boaventura et al. 2002; South Africa: Bownes and McQuaid 2006). Endolithic communities inhabit the outer few millimeters to centimeters of rocks exposed to the surface. Studies investigating the composition of endolithic communities living in different kind of rocky substrata (e.g. granite, limestone and sandstone) clearly indicate that communities do not cluster by rock type and that other site-specific characteristics (e.g. local climate and direction of exposure) and geography influence the specific microbial composition of endolithic communities (Friedmann and Ocampo-Friedmann 1984; Walker and Pace 2007).

Table 1 Sampling locations

Location	Code	Range	Coordinates	Rock type
Vilamoura	VL	Native	37°04′00″N; 8°06′00″W	Granite (man-made structures)
Malhão	MA	Native	37°13′00″N; 7°31′00″W	Limestone
Cascais	CS	Native	38°41′00″N; 9°24′00″W	Limestone
Viana do Castelo	VC	Native	41°55′00″N; 8°25′00″W	Granite
Robberg	RO	Invasive	34°06′00″S; 23°22′00″E	Granite
Oubosstrand	OB	Invasive	34°03′00″S; 24°12′00″E	Granite
Cape St Francis	CF	Invasive	34°13′00″S; 24°50′00″E	Granite
Cape Recife	CR	Invasive	34°01′60″S; 25°45′00″E	Granite

Geographical coordinates and rock type of each location in the native (Portugal) and the invasive (South Africa) range

At each location, we selected two rocky shore sites approximately 200 m apart. All locations had a similar orientation towards incoming waves, with no obstructing structures and lie on open stretches of exposed coast. Sampling was conducted between February and May 2011 during spring tides.

All mussels were collected in the lower eulittoral zone (referred to here as the mussel zone), which was divided horizontally into three equal sections: high, mid and low. Only the high and mid zones were sampled in South Africa because *M. galloprovincialis* is absent lower on the shore in the study area (Bownes and McQuaid 2006). Individuals were sampled within a monolayered bed (i.e. all mussels attached directly to the substratum) in a sun-exposed area (i.e. surfaces with limited shading, exposed to solar radiation >60 % of the day; Zardi et al. 2009).

Incidence of endoliths

Three haphazardly selected quadrats (15 cm × 15 cm) were collected from areas with 100 % mussel cover in each mussel zone, at each site. In the laboratory, mussels were measured (shell length), separated into 10 mm size classes and classified into five categories depending on the degree of endolith infestation, following 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 (Fig. 1S).

Lethal effects of endolithic infestation

Two 1 m × 1 m quadrats were placed haphazardly at each shore height at each site, in an area with 100 % mussel cover. When this was not possible because of mussel bed patchiness, four 25 cm × 25 cm quadrats adjacent to one another were used and the data were pooled. In each quadrat, the total number of recently dead mussels was counted. Shells of dead mussels can stay trapped in the mussel bed matrix and become heavily fouled within a month. To ensure that only recent mortalities were recorded, mussels with the inner nacreous layer of the shell still shiny were counted and all other shells were discarded. Of the total number of recently dead mussels, those dead due to endolithic infestation were identified. This is possible because endolith erosion around the site of the posterior adductor muscle causes shell collapse as the muscle contracts, resulting in a characteristic fracture hole (Kaehler and McQuaid 1999).

Identification of endolithic organisms

Four heavily infested mussels (Group D) from each geographic range were used to identify endoliths. All epibiotic organisms were carefully cleared from the shells with a scalpel and the upper layer of carbonate containing a "carpet" of epilithic algae was mechanically removed under a low power microscope (Zeiss V20 Stereomicroscope). The cleaned shells were fractured into smaller pieces and incubated for 30 min with HCl (3 %) to dissolve calcium carbonate. Shells were broken to increase contact between the acid and the shell. The exposed microendolithic layers were transferred to a drop of immuno-mount (Shandon) on a glass slide using slightly opened pincers. The operation was repeated until no more colonies were visible. The slides were viewed under a microscope (Zeiss Axio Imager Z2, Apotome) with Nomarski optics, where endolithic species were identified and compared qualitatively between the native and invasive ranges of *M. galloprovincialis.*

Sub-lethal effects of endolithic infestation in the native range

The most infested location in the native range (VC) was chosen to study the sub-lethal effects of endolithic infestation. Individual adult mussels (3–4 cm in shell length) belonging to Groups A (clean) and D (infested) were sampled haphazardly in the mid mussel zone.

Attachment strength

Infested (n = 15) and clean (n = 15) mussels were tested in situ for attachment strength following the methodology of Denny (1987). A small (2 mm) hole was drilled through the shell near the posterior margin, using a hand-held battery drill. A fishhook was then inserted through the hole and connected to a recording spring scale (Chatillon-N.Y.-U.S.A.-MODELIN-25) using fishing line. Mussels living within dense aggregations are primarily exposed to lift forces, which act perpendicularly to the substratum (Denny 1987) so the scale was steadily and uniformly lifted normal to the rock surface until dislodgment occurred after 1–3s. The force required to detach each mussel from the mussel bed was recorded in Newtons (N). Attachment strength was measured for mussels that were at least 20 cm apart in order to avoid any effects of previous measurements, such as byssal disruption.

Shell strength

Clean (n = 50) and infested (n = 50) mussels were tested for shell strength. The force required to crack the shell was measured using an automatic force gauge (SEIDNER® Form + Tester). The left valve of each mussel was placed horizontally on a plane surface. A load was applied continuously and without shock through a metal rod (5 cm in diameter) applied vertically at the point of maximum shell convexity on the mid-lateral surface of the shell. The force required to break the shell was recorded. Because of the small area of applied force, the measurement was interpreted as a relative, and not absolute, estimate of shell strength.

Condition index

The body tissues of clean (n = 50) and infested (n = 50) mussels were removed from their shells and dried to constant weight at 60 °C. Samples were weighed to the nearest 0.001 g and the condition index (CI) was calculated using the following equation from Davenport and Chen (1987):

$$\mathrm{CI} = [\text{dry flesh weight (mg) /dry shell weight (mg)}] \times 100$$

Relationship between endolithic infestation and barnacle epibiosis

Adult mussels (n = 150) were collected haphazardly from the mid mussel zone. In the laboratory, the left valve of each mussel was photographed and classified according to the severity of infestation (Groups A–E). The area of the whole shell and of the part covered by epibiotic barnacles (*Chthamalus montagui*) was measured using the software Image J (http://rsbweb.nih.gov/ij/). Percentage of barnacle cover (BC) was determined for each mussel using the following equation:

$$\mathrm{BC} = \left[\text{barnacle area}\left(\mathrm{mm}^2\right)/\text{whole shell area}\left(\mathrm{mm}^2\right)\right] \times 100$$

Environmental parameters

For each location, Photosynthetically Available Radiation (PAR) and wave heights from January to December 2010 were retrieved from satellite and Virtual Buoy® datasets respectively.

PAR refers to photon flux density (photons per second per square meter) between 400 and 700 nm of the spectral range and indicates the total energy available for photosynthesis. Monthly averaged data of PAR with a 9 km resolution were extracted from the Moderate Resolution Imaging Spectroradiometer-Aqua (MODIS-Aqua) dataset available from the National Aeronautics Space Administration (NASA) Goddard Earth Sciences (GES) Data and Information Services Center (DISC). Wave heights were obtained from data for Virtual Buoys® from the National Oceanic and Atmospheric Administration (NOAA) and based on the NOAA WAVE-WATCH III model (Tolman 1999, 2002). Estimated mean daily wave heights were calculated from hourly values and then used to calculate mean monthly values.

Statistical analyses

Data were transformed where necessary to fulfill the prerequisites for parametric analysis (Cochran's tests) and were analysed using ANOVA (GMAV software; University of Sydney, Underwood et al. 2002). Post-hoc comparisons were performed using SNK tests. When the requirements were not met even after data transformation, results were analysed using the PERMANOVA module (Anderson 2001; McArdle and Anderson 2001), which does not require either normality or homoscedasticity. Distance-based homogeneity of dispersion tests, tests of main effects and pair-wise tests on significant interactions were performed using 999 permutations.

Because of the lack of independence among data for levels of infestation, percentage of infested mussels for each size class were not analysed (Zardi et al.

2009). The proportion of infested mussels (i.e. all mussels from Group B to Group E) and the percentage of mussel mortality attributed to endoliths were analysed separately using a 3-way nested ANOVA (model 3) with geographic range (2 levels, native and invasive) as a fixed factor, location (4 levels) nested within range and site (2 levels) nested within location (both random factors). Only data from the mid and high shore were used for comparisons between South Africa and Portugal. Within each range, the proportion of infested mussels and the percentage of mussel mortality were tested separately for the effect of shore height. A 3-way nested ANOVA (model 3) was used with shore height as a fixed factor (3 levels for Portugal and 2 levels for South Africa) and location (4 levels) nested in shore height and site (2 levels) nested in location as random factors.

Data on the sub-lethal effects of endolithic infestation (attachment strength, condition index and shell strength) were analysed separately using a 1-way ANOVA with endolithic infestation (Group A or D) as a fixed factor. Percentages of barnacle cover were analyzed using PERMANOVA with infestation categories as a fixed factor with five levels (A–E). To reach an equal sample size, a random sub-sampling of 12 mussels (i.e. the smallest number of mussels in any category) was performed for all groups.

Data on averaged annual wave height and PAR were analysed separately using a 1-way ANCOVA (performed in STATISTICA 6) with geographic range (2 levels, native and invasive) as a fixed factor, wave height or PAR as covariate factors and averaged proportion of infested mussels at each location as the dependent factor. The assumption of homogeneity of regression slopes was tested prior to each ANCOVA. Because the covariant wave height did not comply with this assumption, a one-way ANOVA was performed instead, with geographical range as a fixed factor and wave height as the dependent factor.

Results

Incidence of endoliths

In Portugal, infestation severity was generally very low, but increased with shell length and with tidal height (Fig. 1). No mussels exhibited endolith-induced shell fractures (Group E).

Infestation was much higher at VC than at the other sites. Overall on the low shore a few mussels showed initial infestation (Group B), but at VC some endolith-induced erosion and pitting of the shell surface (Group C) was observed in mussels of 31–50 mm. Initial infestation occurred in smaller mussels (11–20 mm) at VC than at the other locations (31–40 mm at VL and 21–30 mm in length at MA and CS).

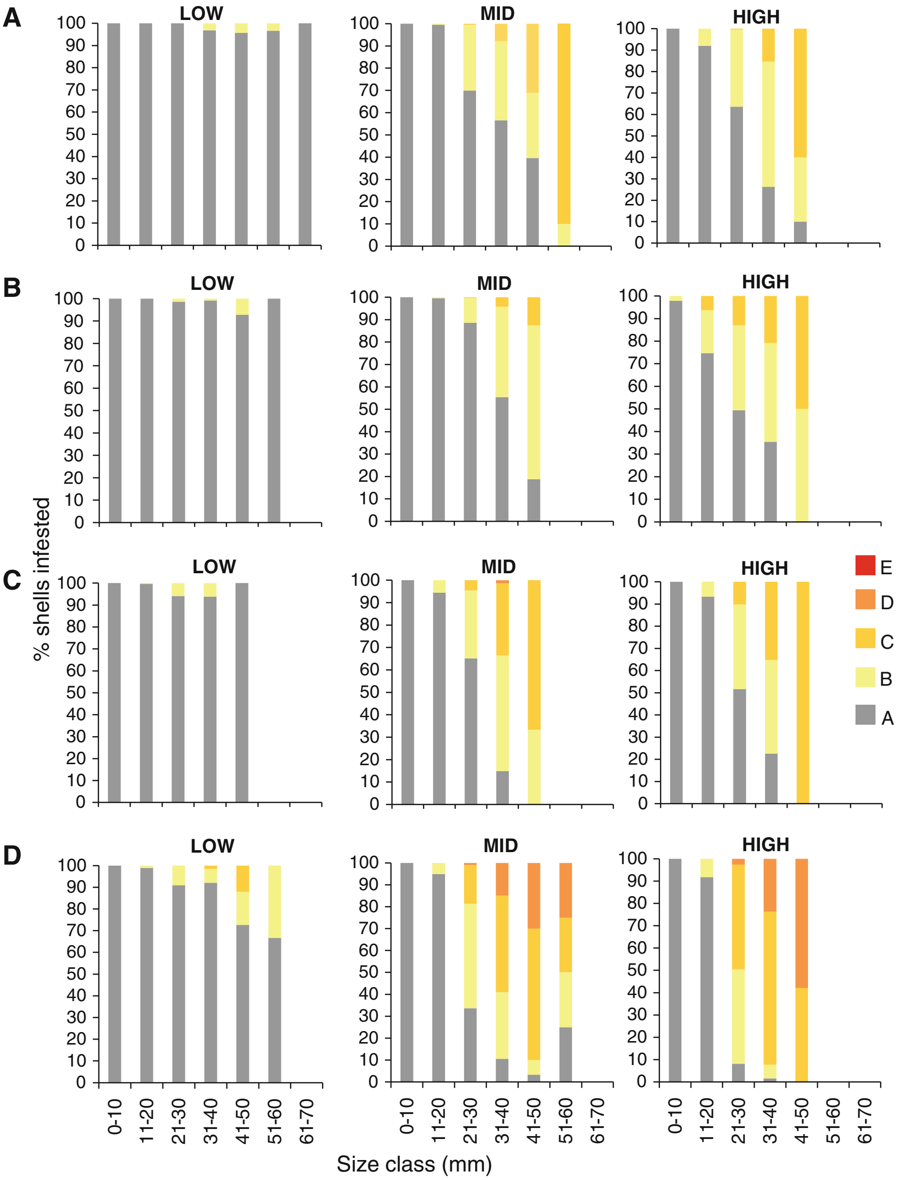
Broadly similar patterns of infestation were observed on the mid and high shore. On the mid shore initial infestation (Group B) occurred in mussels from 11 to 20 mm in length and at MA, CS and VC, more than 80 % of mussels >41 mm exhibited at least Group B deformation. Extremely pitted mussels (Group D) were observed only at VC and CS (from 21 to 30 mm and from 31 to 40 mm respectively). On the high shore even the smallest size classes showed signs of infestation at MA, with more than 90 % of mussels of 41–50 mm exhibiting Group B deformation at VL and MA and at least Group C deformation at CS and VC. Group D deformation was observed only at VC including >50 % of mussels of 41–50 mm.

In South Africa, infestation severity was much greater, again increasing with shell length at all shore heights (Fig. 2). In the high and mid shore of all locations, initial infestation (Group B) occurred in mussels belonging to the smallest size class and all mussels longer than 51 mm exhibited at least Group D deformation. On the high shore, Group E characteristics occurred in mussels of >31 mm at RO, OB and CR, and in mussels >41 mm at CF. Approximately 10 % of large mussels (51–60 mm in length) fell into Group D at all locations.

On the mid shore, endolith-induced shell fractures (Group E) occurred in size class 51–60 mm at OB and CR, and size class 41–60 mm at CF. At RO, mussels with Group D deformation were at least 31 mm long and more than 10 % of all mussels >51 mm exhibited this level of infestation.

ANOVA revealed that, in Portugal, infestation rates did not differ significantly between the high and mid shore, but were significantly lower on the low shore (Table 1S; ANOVA Model 3, $df = 2$, n = 72, $p < 0.05$; SNK test, $p < 0.05$; Fig. 3). However, on the high and mid shore of VL and CS, infestation rates differed between sites (ANOVA, [site (shore, location)], $df = 12$, n = 72, $p < 0.001$; SNK test, $p < 0.05$). In South Africa, no effect of shore height was detected (Table 2S; ANOVA Model 3, arcsine

Fig. 1 Incidence of endoliths in the native range. Percentages of shells exhibiting different degrees of infestation severity (Groups A-E), grouped into 10 mm size classes in the low, mid and high mussel zone at all locations in Portugal: **a** VL; **b** MA; **c** CS; **d** VC



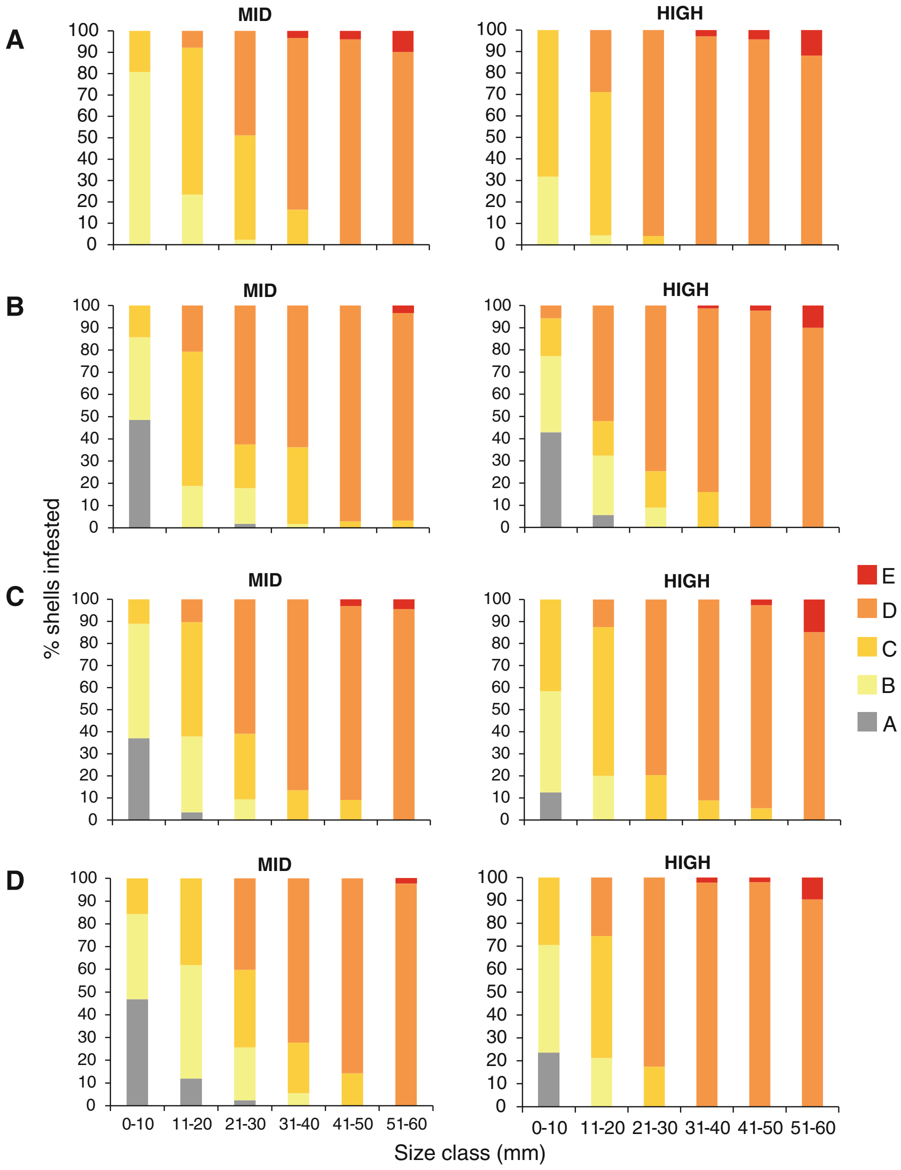
transformation, $df = 1$, n = 48, $p = 0.43$; Fig. 3). However, mid shore infestation rates at RO were significantly higher than at other mid shores (ANOVA, [location (shore)], $df = 6$, n = 48, $p < 0.01$; SNK test, $p < 0.05$).

Overall, mussels in the native range had a significantly lower infestation rate than individuals from the invasive range (Table 3S; ANOVA Model 3, arcsine transformation, $df = 1$, n = 96, $p < 0.001$; Fig. 3). Infestation rates also differed between sites at locations VL and MA in Portugal (ANOVA, [site (range, location)], $df = 8$, n = 96, $p < 0.001$; SNK test, $p < 0.05$).

Lethal effects of endolithic infestation

In Portugal, mussel mortality rates due to endolithic infestation did not differ with shore height (Table 4S; ANOVA Model 3, $df = 2$, n = 48, $p = 0.62$; Fig. 4). However, rates on the mid and high shore at VC were significantly greater than at all other locations (ANOVA, [location (shore)]; arcsin transformation;

Fig. 2 Incidence of endoliths in the invasive range. Percentages of shells exhibiting different degrees of infestation severity (Groups A–E), grouped into 10 mm size classes in the mid and high mussel zone at all locations in South Africa: **a** RO; **b** OB; **c** CF; **d** CR



$df = 9$, n = 48, $p < 0.001$); SNK test, $p < 0.05$). In South Africa, mortality rates were not significantly different between shore heights (Table 5S; ANOVA Model 3, arcsin transformation, $df = 1$, n = 32, $p = 0.10$), though in the mid shore at CR the two sites were significantly different (ANOVA, [site (shore, location)], $df = 8$, n = 32, $p < 0.05$; SNK test, $p < 0.05$).

Mortality attributed to endolithic infestation was significantly higher in mussel populations from the invasive than from the native range (Table 6S; ANOVA Model 3, arcsin transformation, $df = 1$, n = 64, $p < 0.01$). Within each region, VC and RO had significantly higher mortality rates than the other locations in Portugal and in South Africa respectively (ANOVA, [location (range)]; $df = 6$, n = 64, $p < 0.05$; SNK test, $p < 0.05$).

Identification of endolithic organisms

Four species of endolithic cyanobacteria occurred in both ranges: *Hyella balani* (Lehman 1903), *Plectonema terebrans* (Bornet & Flahault 1889), *Mastigocoleus testarum* (Lagerheim 1886), and *Solentia*

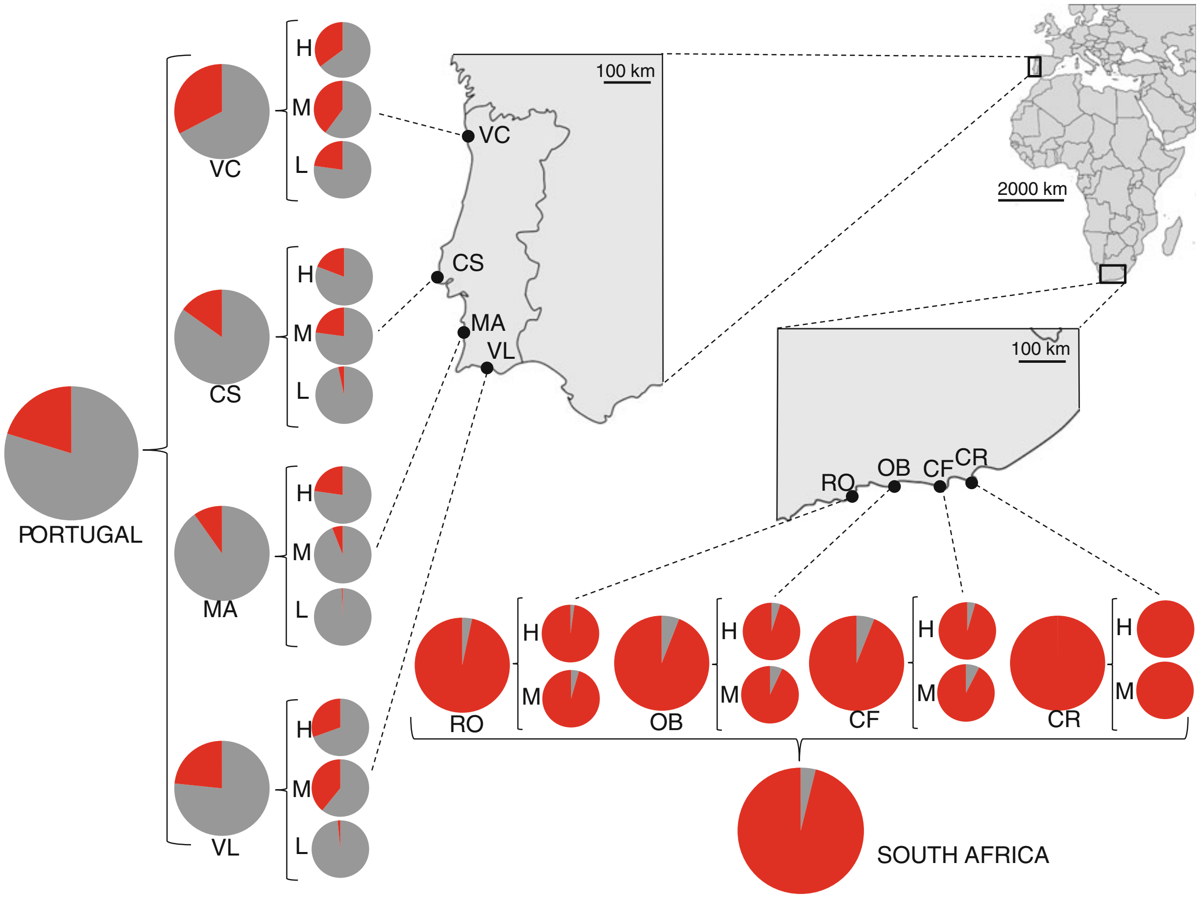


Fig. 3 Endolithic infestation frequencies. Infestation frequencies at each shore height in each location (sites pooled) in Portugal and in South Africa. *Red* indicates the proportion of infested shells. Shore level is averaged for each site and among sites for region

stratosa (Ercegovic 1932). *Hormathonema violaceo-nigrum* (Ercegovic 1932) was found only in mussels from Portugal, while *Hyella caespitosa* (Bornet & Flahault 1889) and *Kyrthutrix dalmatica* (Ercegovic 1929) were identified only in mussels from South Africa (Table 2, Figs. 5, 6, 7). Other endoliths were observed but they were not found in sufficient numbers or did not exhibit typical habitus for a definite taxonomic identification (Fig. 2S, 3S).

Sub-lethal effects of endolithic infestation in the native range

Clean mussels had significantly higher attachment strength (n = 30), shell strength (n = 100) and condition index (n = 100) than infested mussels (Table 7S-9S; ANOVA, $df = 1$, $p < 0.01$ in each case; Fig. 8a–c).

Percentage of barnacle cover increased with degree of infestation, with the highest cover recorded in Group D mussels (Table 10S; PERMANOVA, $df = 3, \mathrm{n} = 48, p\,(\mathrm{perm}) < 0.001$; Fig. 8d). The cover varied significantly between each category except between Groups A and B.

Environmental parameters

There was no significant covariate effect of PAR (Table 11S, ANCOVA, $df = 1$, n = 8, $p = 0.27$; Fig. 9a) on infestation intensity and the invasive range depicted higher infestation rates than the native Portuguese range. Wave height did not differ

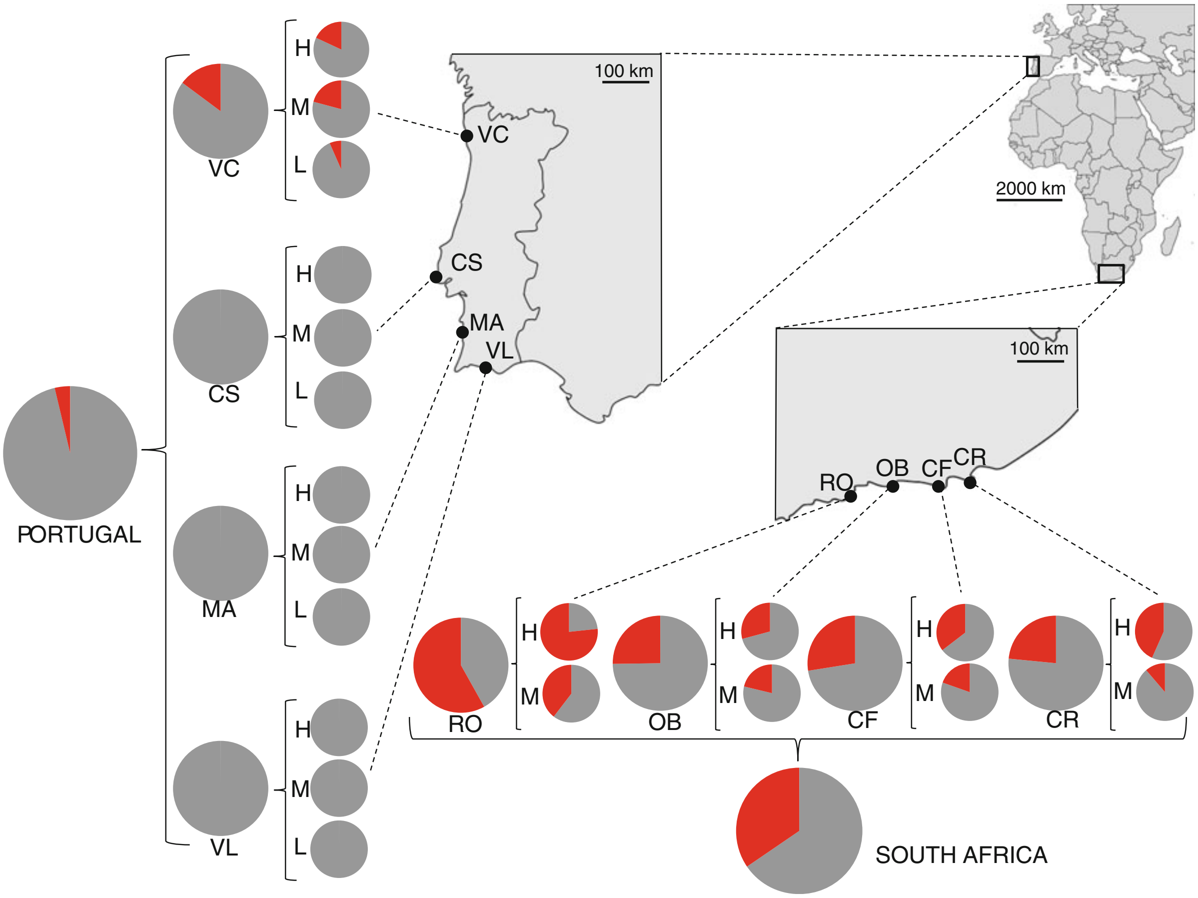


Fig. 4 Endolith-induced mortality frequencies. Mortality frequencies attributed to endolothic infestation at each shore height in each location (sites pooled) in Portugal and in South Africa. *Red* indicates the proportion of infested shells. Shore level is averaged for each site and among sites for region

significantly between geographical ranges (Table 12S, ANOVA, $df = 1$, $n = 8$, $p = 0.10$; Fig. 9b).

Discussion

In this study, we hypothesised that the success of *Mytilus galloprovincialis* as an invasive species in South Africa would be related to lower endolithic parasitism in the introduced range. In contrast, although we showed clear lethal and sub-lethal effects of endoliths, the data on photoendolithic parasitism fail to support our initial hypothesis. Both endolithic infestation and endolith-induced mortality rates were markedly higher in South Africa than in Portugal. Moreover, while infestation severity clearly increased with shell length, mussels were initially infested at much smaller sizes in the invasive range. Several factors may interact synergistically to enhance the effects of endoliths in the introduced populations.

Transportation of invading hosts and parasites to novel environments often results in a subsampling of a generally much larger pool in the native source populations, reducing the likelihood of introducing rare enemies and overestimating potential release from enemies (Colautti et al. 2004). Subsampling effect may be further enhanced by differential mortality of infected or parasitized propagules (Mitchell and Power 2003; Torchin et al. 2003) and by unfavorable environmental conditions during transport. Furthermore, dispersal vectors may predispose introduced species to invade without their native

Table 2 Identification of endolithic organisms

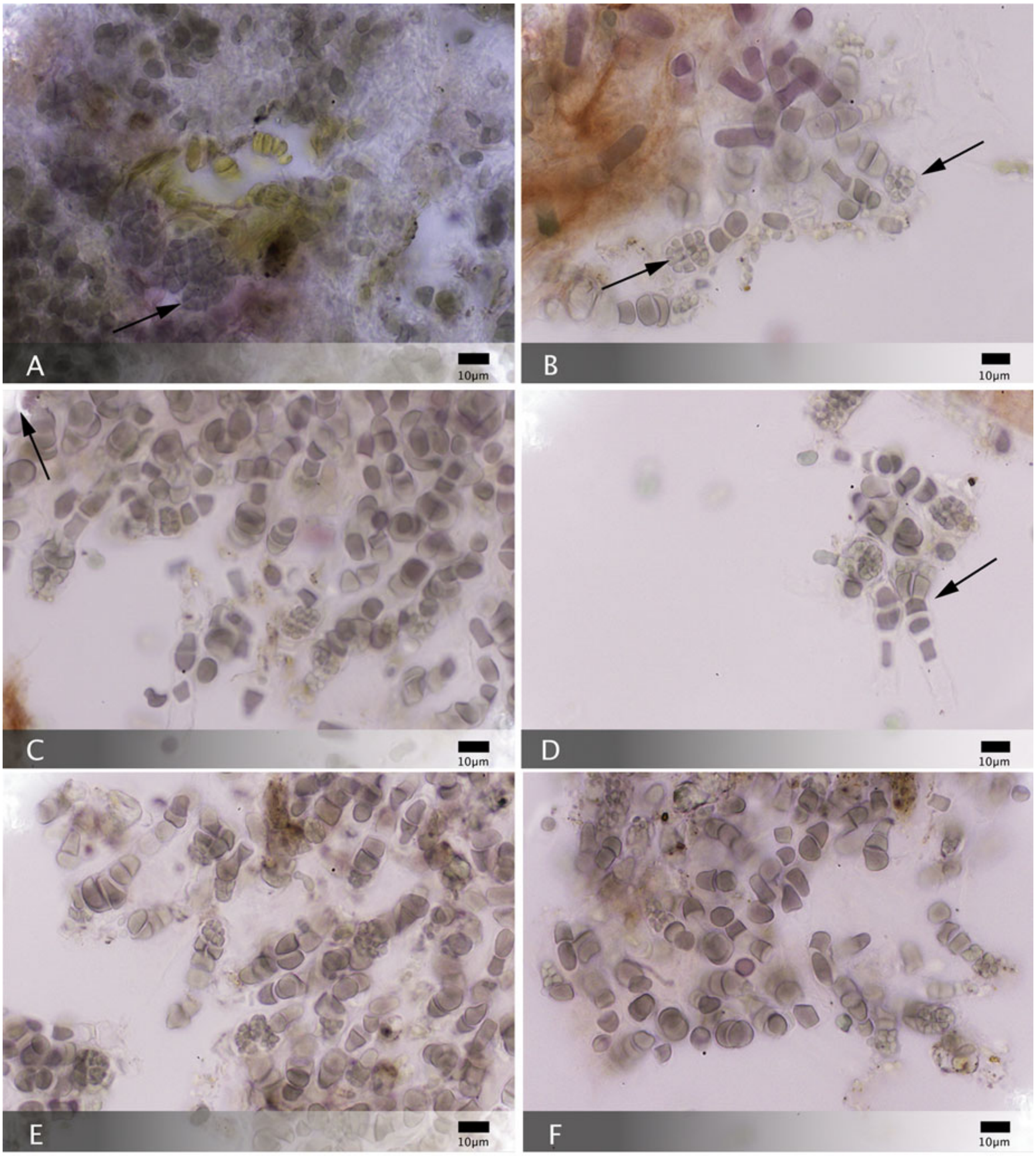
Species	Native	Invasive
Hormathonema violaceo-nigrum (Ercegovic 1932)	X	
Hyella balani (Lehman 1903)	X	X
Hyella caespitosa (Bornet & Flahault 1889)		X
Kyrthutrix dalmatica (Ercegovic 1929)		X
Plectonema terebrans (Bornet & Flahault 1889)	X	X
Mastigocoleus testarum (Lagerheim 1886)	X	X
Solentia stratosa (Ercegovic 1932)	X	X

Endolithic species identified in mussels from native (Portugal) and invasive (South Africa) range

parasites; for example, planktonic larval stages of aquatic invertebrates are rarely parasitized (e.g. zebra mussels, Molloy et al. 1997; Lafferty and Kuris 1996). In the 1970s, *M. galloprovincialis* invaded South African shores probably as planktonic larvae in ballast water (Grant and Cherry 1985) most likely lacking the parasites associated with adults. Therefore, even though some endoliths were common to both regions, it is likely that bioerosion observed in South African *M. galloprovincialis* shells results from the activity of native endoliths. In fact, once established, introduced species often acquire new assemblages of parasites over short periods of time (Poulin and Mouillot 2003). Specialist parasites often have complex life cycles that require multiple, specific intermediate hosts, whereas generalist parasites can affect a wide range of hosts (Torchin et al. 2002; Torchin and Mitchell 2004; Miller et al. 2008). Phototrophic endoliths can be considered as extremely generalist parasites because they can attack many kinds of hard mineral substrate, including both carbonates and phosphates (Golubic et al. 2005; Tribollet 2008). The generalist nature of endoliths, together with their presence in native South African mussel species (Kaehler 1999) could explain the lack of release from this type of parasite for *M. galloprovincialis* in this invasive situation.

Moreover, some of the endolithic species found in Portugal and in South Africa were different. In both native and invasive ranges all endoliths identified from *M. galloprovincialis* were phototrophic cyanobacteria. Kaehler (1999) described four endolithic cyanobacteria from the native mussel *Perna perna* on the south coast of South Africa, while we identified a total of seven species on *M. galloprovincialis*. One was unique to Portugal, two unique to South Africa and four were found in both countries (Table 2). Three of the species Kaehler (1999) identified from *P. perna* (*Plectonema terebrans, Hyella caespitos* and *Mastigocoleus testarum*) also occurred in *Mytilus galloprovincialis* from South Africa.

Characteristics of the invader, rather than of the parasites, can also be important in determining infestation rates. Invasion success is dependent on the size and source of introduced populations and on the frequency of introduction (Kolar and Lodge 2001; Suarez et al. 2005) and invasion filters are predicted to cause a reduction in post-invasion genetic diversity (genetic bottleneck; e.g. Cristescu et al. 2004; Golani et al. 2007). It has been suggested that, because of this, invasive species should be more vulnerable than native hosts to the effects of native enemies (Torchin et al. 2002; Prenter et al. 2004). Invasion bottlenecks may decrease the genetic diversity of polymorphic defenses that are essential in avoiding disease outbreaks (e. g. Lively 1999; Carr and Eubanks 2002). As a consequence, enemies will have stronger effects in the invaded range than in more genetically diverse native populations. However, recent studies of invasive populations found either no decline (e.g. Astenei et al. 2005; Wattier et al. 2007) or even an increase in genetic diversity (Kelly et al. 2006) highlighting important effects of the source and the history of an invasion for genetic diversity. Most importantly, it has been shown that when a reduction in post-invasion host genetic diversity is observed, it is not necessarily linked to enemy release from parasites in the invasive populations (Slothbouber Galbreath et al. 2010). In South Africa, the genetic structure of *M. galloprovincialis* is characterized by very low genetic variability (Zardi et al. 2007), confirming its recent arrival and suggesting low polymorphic defenses. It is likely that the endolithic communities inhabiting South African shores will have greater effects on the recent invader *M. galloprovincialis* than *P. perna*, which exhibits much greater genetic diversity (Zardi et al. 2007). A better understanding of the role of genetic variability in determining mussel defense abilities could come from investigating regions, such as northern Africa, where *M. galloprovincialis* is native, presumably has greater genetic diversity and also co-exists with *P. perna* (Abada-Boudjema and Dauvin 1995).



A Hormathonema violaceo-nigrum (Ercegovic 1932)
CL 2-8μm CW 2-5μm

B - F Hyella balani (Lehmann 1903)
CL 20 μm CW 4-8 μm

CL (Cell-length) | CL (Cell-width) | TL (Thallus-length) | TW (Thallus-width)

◀**Fig. 5** Microbial endoliths of *M. galloprovincialis*. *Arrows point* to typical packed cell cluster (**a**), sporangia (**b**), retouched area, where the original scale had been burned into the picture and then manually removed from the picture (**c**), thallus showing status typicus (**d**)

At micro (along the intertidal) and meso (exposed vs. sheltered sites) spatial scales, wave action has been proven to be a determinant factor in the endolithic infestation of mussels as it enhances periostracum abrasion, which in turn facilitates endolithic shell colonization (Kaehler 1999; Zardi et al. 2009). However, our results seem to exclude a determinant effect of hydrodynamic stress over larger geographical scales. Our data showed a tendency for South African locations to be subjected to higher waves than Portuguese ones, but these differences were not significant.

At smaller spatial scales, in Portugal, mean wave action did not differ greatly along the west coast, which is exposed to the prevailing northwest oceanic swell. On the south coast, wave conditions are less severe because of reduced exposure to the North Atlantic swell (Costa 1995). Low hydrodynamic stress experienced by intertidal mussels on the south coast (VL) could be responsible for moderate periostracum scouring and consequently the low endolithic activity observed at this location. Moreover, *M. galloprovincialis* is generally more abundant in the north of Portugal and mussel beds extend up to MHWN (Mean High Water Neap), while in central and southern regions (Boaventura et al. 2002) mussels are more scarce and generally below MTL (Mean Tide Level). Where abundance is high, tight packing of mussels is believed to increase abrasion by rubbing the valves against each other (Kaehler 1999). Additionally, mussels higher on the shore experience greater light exposure, which would enhance photosynthetic endolith activity.

In Portugal, infestation increased upshore. Other studies have shown the same pattern (Webb and Korrûbel 1994; Kaehler 1999) and linked this to greater erosion of the periostracum on the upper shore due to scour by wind-borne sand particles during low tide (Kaehler 1999). A more plausible explanation is the duration of light exposure. Mussels have lower infestation rates in shaded areas than in sun-exposed areas (Zardi et al. 2009), while higher on the shore, they spend more time out of water during which the boring activity of phototrophic endoliths is more pronounced (Gektidis et al. 2007). In contrast to Portugal, intertidal height did not have a significant effect on endolith abundances in South Africa, where infestation rates were so high (90–100 %) that they may have masked the effects of environmental gradients Similarly to wave action, and in contrast with previous studies indicating a clear enhancing effect of light on phototrophic endolithic activity (Gektidis et al. 2007; Zardi et al. 2009), our results do not show significant differences in PAR between South Africa and Portugal, thus excluding this environmental factor as a cause of high endolithic impact in invasive mussel populations.

Parasites can produce outbreaks that are responsible for mass mortalities (Harvell et al. 1999). However, the key pressure exerted by parasites on population dynamics and community structure may not be a result of catastrophic outbreaks, but of less virulent, persistent sublethal infections (Prenter et al. 2004; Ruesink and Trimble 2010). The sublethal effects caused by parasites can deeply affect invasion dynamics by modifying the interactions of native and invasive species with biotic and abiotic stresses (Hudson and Greenman 1998; Mouritsen and Poulin 2002; Hatcher et al. 2006). We found that, in the native range, endolithic infestation negatively affected attachment strength, shell strength and condition of *M. galloprovincialis*. Repairing shell damage caused by endoliths through secondary shell deposition is energetically costly, but essential and reduces the energy available for other physiological requirements such as reproduction and attachment (Geller 1990; Ambariyanto and Seed 1991; Kaehler and McQuaid 1999). This suggests an energy trade-off with negative consequences particularly under wave exposed conditions, where shell scouring (leading to endolith attack) and the risk of dislodgment are both high.

It is known that an intact shell maintains general fitness by reducing fouling (Scardino and de Nys 2004; Bers et al. 2010). In particular, surface microtopography of mytilid shells has been shown to have antifouling properties (Scardino et al. 2003). This can be explained by ‘attachment point theory’ which assumes that the adhesion strength of fouling organisms that are larger than the length scale of the surface topographical features would be reduced because fewer attachment points exist between the organism and the substrate. Conversely, organisms settling on

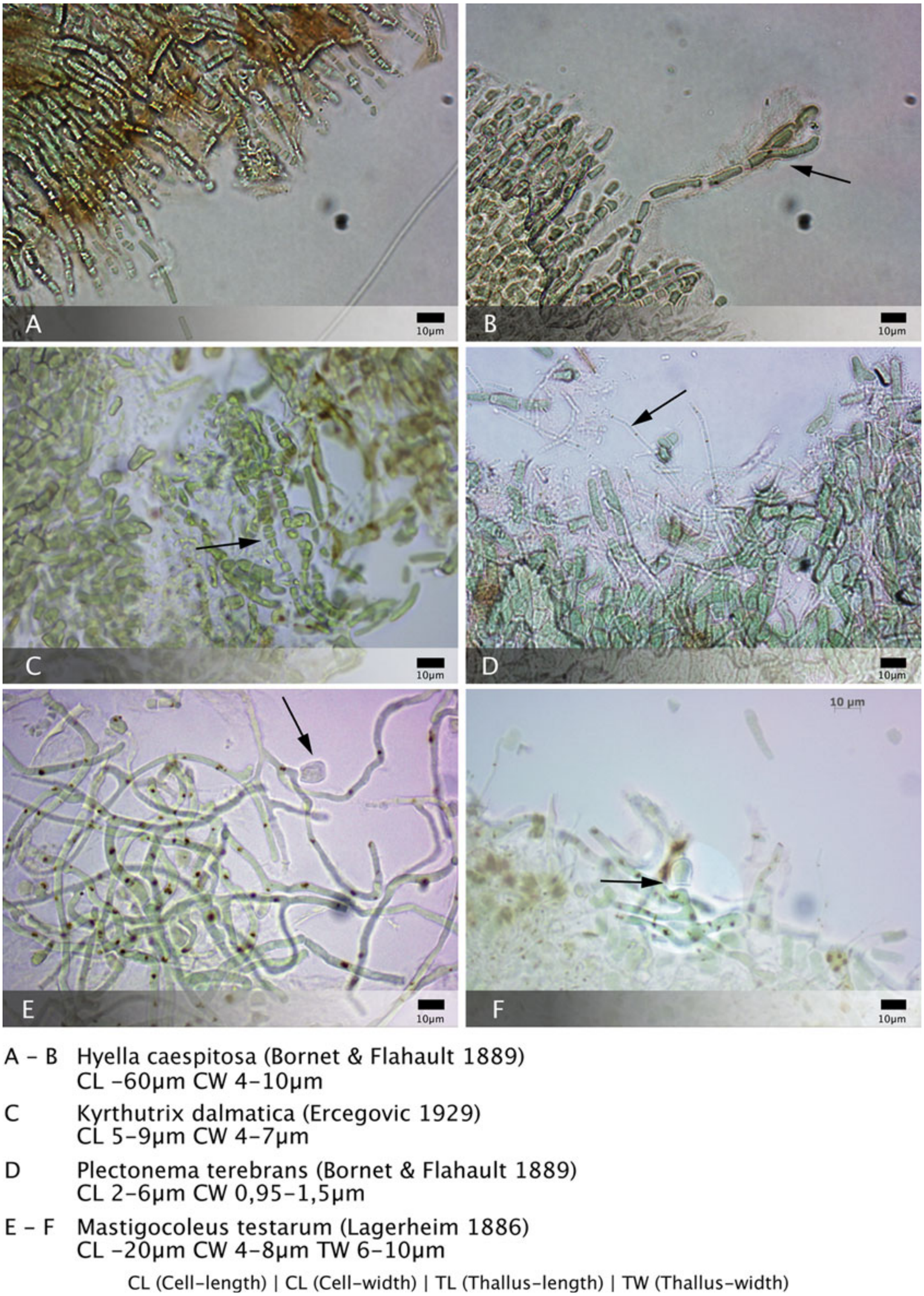


Fig. 6 Microbial endoliths of *M. galloprovincialis*. *Arrows point* to thallus with false branching (**a**, **b**), typical habitus of the thallus with loops (**c**), small filament of plectonema (**d**), heterocysts (**e**, **f**)

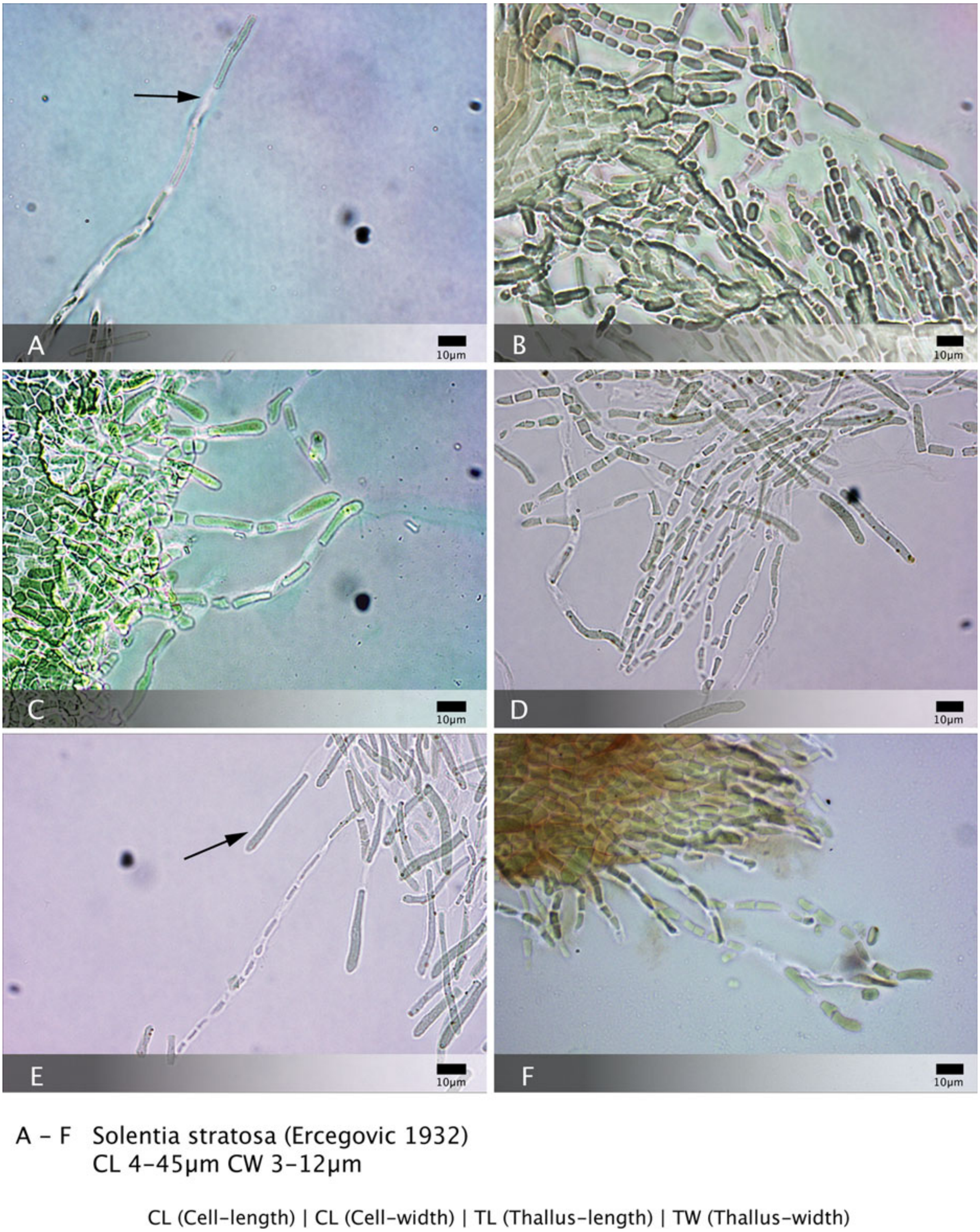


Fig. 7 Microbial endoliths of *M. galloprovincialis*. *Arrows point* to empty sheath behind terminal cell (**a**), elongated terminal cell (**e**)

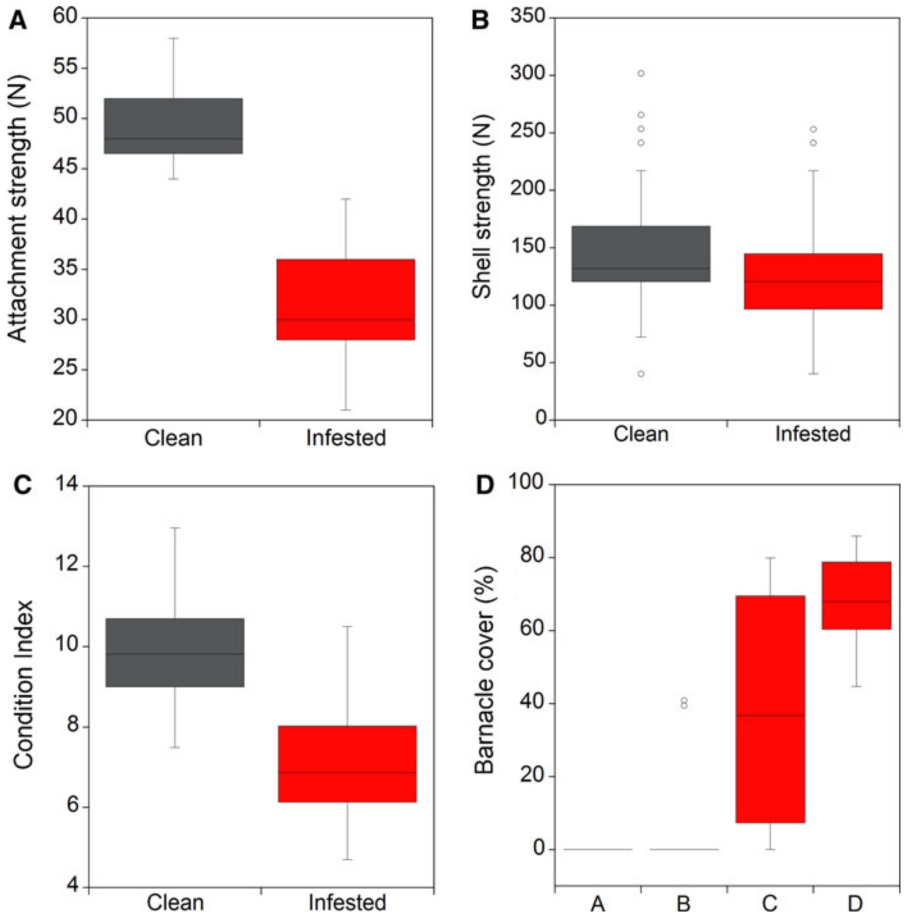


Fig. 8 Sub-lethal effects of endolithic infestation in the native range. **a** attachment strength **b** shell strength, **c** condition index in infested and clean mussels, and **d** barnacle cover for clean and infested shells

topographically modulated surfaces with topographic features larger than the organism's dimension would attach more strongly, as there would be more attachment points available for adhesion and hence greater resistance to hydrodynamic drag forces (Scardino et al. 2006, 2008, 2009a, b).

Being overgrown by epibionts may affect the host organism directly by increasing drag and interfering with filter feeding, or indirectly by modulating ecological interactions (Wahl 1997, 2008; Lesser et al. 1992; Wahl and Hay 1995). For example, the barnacle *Balanus improvisus* negatively affects the growth rate of *M. edulis*, increasing the risk of predation by the crab *Cancer maenas* and the recruitment of the boring polychaete *Polydora ciliata* (Wahl 2008). Here we show that heavily infested mussels were significantly more covered by barnacles than those with few or no endoliths, suggesting that endolith-induced destruction of shell microtopography and its anti-fouling characteristics facilitates barnacle settlers. This in turn would compound the negative effects of the endoliths themselves. However, we recognize that this may not be a cause and effect relationship, as endolithic infestation and barnacle settlement exhibit parallel, but independent responses to wave action, so that additional experiments would be needed to separate these two hypotheses.

For invasive species, parasites can be considered as ecological filters through which invaders must pass (Torchin and Mitchell 2004). Despite extremely high infestation rates, endoliths did not prevent *M. galloprovincialis* from becoming the most successful marine invasive species in South Africa (Robinson et al. 2005; Hanekom 2008). This suggests that the abilities of this invasive species, such as rapid growth rate (Griffiths et al. 1992), high fecundity (van Erkom

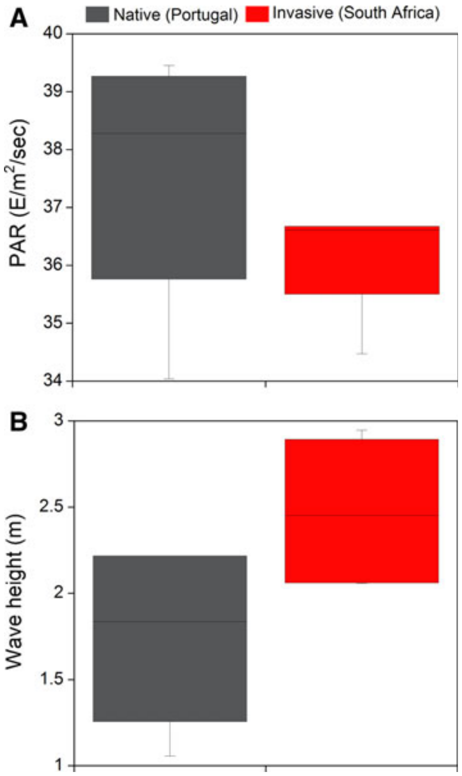


Fig. 9 Environmental parameters. *Box and whisker plots* showing annual averages for locations for the year January to December 2010 of **a** PAR and **b** wave height

and Griffiths 1991), high recruitment rate (Harris et al. 1998), resistance to desiccation (Hockey and van Erkom 1992) and sand stress (Zardi et al. 2006) are all hallmarks of a strong competitor that can overcome the limitations imposed by endolithic parasitism. Nevertheless, endoliths have a weakening or even lethal effect that may reduce the invasive potential of *M. galloprovincialis* where conditions such as wave action and light exposure enhance endolith activity or otherwise impose additional energetic demands.

Complex ecological patterns are unlikely to be reducable to simple explanations. For example, our findings for endoliths are in direct contrast to earlier findings showing that *M. galloprovincialis* in South Africa is much less subject to attack by platyhelminth parasites than the native mussel *P. perna* (Calvo-Ugarteburu and McQuaid 1998a, b). Further studies with (in particular) additional invasive and native populations would be valuable to corroborate our findings and could allow an explicit test for the role of parasite release in successful invasions. Studies of abundant or dominant invaders often reveal that one or more natural enemies with known impacts are conspicuously absent from the introduced population (Liu et al. 2007; DeWalt et al. 2004; Wolfe 2002). In contrast, other studies argue against a simple link between the success of an invasion and the hindering effects of enemies (Colautti et al. 2004; Hatcher and Dunn 2011; Ishtiaq et al. 2006; Pasternak et al. 2007).

Given the complexity of processes that underlie biological invasions, it should perhaps be no surprise that there is no simple relationship between the endolith escape and the vigour, abundance or impact of the invader. A full understanding of the dynamics of invasions and the impact of invasive species can be found only in the complex interactions between abiotic and biotic characteristics of the invaded community (native species) and abilities of the invader.

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