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Introduced marine ecosystem engineer indirectly affects parasitism in native mussel hosts

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Abstract The alteration of habitat structure by introduced ecosystem engineers imposes direct impacts on native biota but can also exert trait-mediated indirect effects. In this study, we show that the habitat structure provided by invasive Pacific oysters (*Crassostrea gigas*) can also indirectly affect parasitism in native blue mussels (*Mytilus edulis*). We conducted a 3-month field experiment, in which uninfected mussels were positioned at the bottom and top of two intertidal oyster reefs in the Wadden Sea. On one reef, we detected a significantly higher prevalence of parasitic copepods (*Mytilicola* spp.) in mussels positioned on top of oysters than in mussels at the bottom, but no difference in infection intensity. For trematodes (*Renicola roscovita*), a different pattern was observed, with higher prevalence (one reef) and significantly higher infection intensities (both reefs) in mussels positioned at the bottom of the oyster reef. We suggest that the contrasting pattern results from differences in parasite life cycles. *Mytilicola* spp. larvae spend 2–3 weeks in the water column before infecting their hosts and, therefore, mussels positioned at the top are exposed to higher numbers of planktonic larvae than mussels at the bottom. In contrast, infective trematode larvae spend less than 12 h in the water column and primarily infect mussels during low tide, which may explain higher prevalence and intensity of *R. roscovita* in mussels near the bottom of the oyster reef. Our results demonstrate that indirect effects leading to alterations of parasite-host interactions may be a more common but hitherto rarely considered impact of biological invasions.

Keywords Trait-mediated indirect effects · Invasive species · Ecosystem engineer · Parasite-host interaction · *Renicola roscovita* · *Mytilicola* · *Crassostrea gigas* · *Mytilus edulis*

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Introduction

Introduced species are considered as one of the greatest threats to ecosystem biodiversity and ecological communities worldwide (Elton 1958; Vitousek et al. 1996; Mack et al. 2000). In particular, invasive

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ecosystem engineers that create or modify physical habitat structure impose strong direct impacts on native biota, including effects on habitat and food availability, native species density and diversity, and changes in abiotic conditions (Jones et al. 1994, 1997; Crooks 2002). In addition to these direct effects, invasive ecosystem engineers may also affect other organisms in such ways that it has consequences for a third species. These indirect effects can be density-mediated, in which the habitat modifier indirectly influences a third species by altering the density of an intermediate species (density-mediated indirect effects (DMIEs); sensu Abrams 1995). For example, in north western America, the complex stem structure of invasive spotted knapweed (*Centaurea maculosa*) serves as new substrate for native spiders in grassland habitats, increasing densities of spider webs that, in turn, negatively affect densities of their insect prey (Pearson 2010). Simultaneously, habitat modifiers may affect a third species by altering the traits (e.g., behavioural, physiological, morphological, chemical) of an intermediate species (trait-mediated indirect effects (TMIEs); sensu Abrams 1995). For instance, in southeastern Australia, an ecosystem engineering species of invasive alga (*Caulerpa taxifolia*) is known to indirectly facilitate community diversity by modifying the burying behaviour of the clam *Anadara trapezia*, a native ecosystem engineer (Gribben et al. 2009). In *Caulerpa*-invaded habitats, clams could not burrow themselves completely, thereby providing rare hard substrate for colonizing species, resulting in an increase in abundance and richness of epibiont species compared to unvegetated sediments (Gribben et al. 2009). In addition, the availability of shelter within complex habitats created by invasive ecosystem engineers, can induce prey refuge behaviour that alters predator-prey encounter rates and thereby the risk of predation (Byers 2010; Pearson 2010; Eschweiler and Christensen 2011; Waser et al. 2015). Currently, evidence of DMIEs and TMIEs on predator-prey and competitive interactions imposed by invasive habitat modifiers is growing and helps to understand the full impacts of invasive species.

Other types of biological interactions that can be modified by invasive ecosystem engineers are less well-known. These also include parasite-host interactions, which can be altered in many different ways. For example, when invasive ecosystem engineers are introduced to new ecosystems, they can co-introduce parasites that can spill over to native species (Li et al. 2014; Goedknegt et al. 2017). Furthermore, invasive species are known to interfere with native parasite transmission cycles by predating on free-living infective stages or limiting their dispersal by providing physical obstructions (Bartoli and Boudouresque 1997; Thieltges et al. 2009; Welsh et al. 2014; Goedknegt et al. 2015). Much less is known on indirect effects that invasive ecosystem engineers can exert on parasite-host interactions. Most evidence on TMIEs on parasite-host interactions originates from native species in freshwater systems, where native predators affect traits of their prey, which in turn can determine how surviving prey can interact with parasites. For example, fish shoaling in response to predators can facilitate parasite transmission between individual fish, resulting in higher infection levels at locations with higher predation pressure (Stephenson et al. 2015). Similarly, predator-avoidance strategies of migrating water fleas can result in higher exposure to parasitic spores and, consequently, higher infection levels (Decaestecker et al. 2002). However, to our knowledge, no studies on altered parasite-host interactions as an indirect result of habitat modification by invasive ecosystem engineers exist.

Ecosystem engineers such as invasive oysters provide a suitable model system to study indirect effects of habitat modification on parasite-host interactions. These marine molluscs, in particular the Pacific oyster (*Crassostrea gigas* also known as *Magallana gigas*), have been introduced worldwide for aquaculture purposes (Ruesink et al. 2005). Once established in the wild after introduction, oysters create hard-substrate biogenic reefs and thereby modify the environment with consequences for other organisms and species interactions (Ruesink et al. 2005). In general, oysters (native and invasive) are known to provide predation refuge for prey hiding in the biogenic matrix created by the oysters, which can have indirect effects on predation strength (Grabowski 2004; Hughes and Grabowski 2006; Troost 2010). In Europe, invasive Pacific oysters co-exist with native mussels (*Mytilus edulis*) in dense aggregations termed oyssel reefs (Reise et al. 2017a; Troost 2010; Fig. 1). Mussel larvae use oysters as hard substrate for their settlement and can be found on top of the oyster reef, but also between the oysters. Moreover, mussels make use of the shelter provided by the three-dimensional matrix of oysters in order to escape predators. In

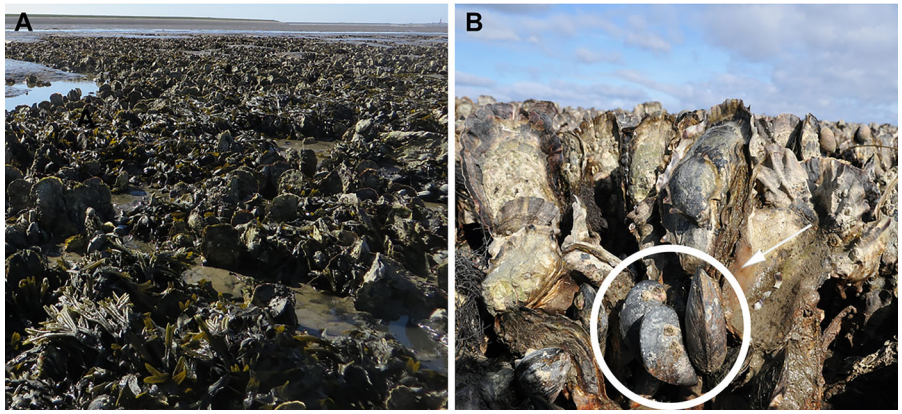

Fig. 1 **a** An oyssel reef in the Wadden Sea with **b** blue mussels (*Mytilus edulis*) hiding in the oyster matrix (*Crassostrea gigas*) indicated by the white circle and arrow

response to predation risk, mussels actively migrate to the bottom of the oyster matrix which significantly reduces mussel predation by crabs (Eschweiler and Christensen 2011; Waser et al. 2015). Hence, Pacific oysters exert TMIEs by creating complex habitats that initiate refuge seeking behaviour of mussels. However, this predation refuge is traded off against reduced foraging success suggested by decreased mussel condition at the bottom of the matrix (Eschweiler and Christensen 2011). The presence of invasive Pacific oysters is known to affect parasite infections in mussels by a mechanism referred to as *transmission interference* (Johnson and Thieltges 2010; Welsh et al. 2014; Goedknegt et al. 2016). As unsuitable hosts for trematodes, Pacific oysters significantly reduce the number of free-living trematode larval stages (cercariae) in the water column by filter feeding or trapping larvae on the complex rough shells (Thieltges et al. 2009; Welsh et al. 2014; Goedknegt et al. 2015). This transmission interference has been shown to reduce infection levels in native mussels placed on artificial oyster reefs compared to mussels situated on bare sediment (Thieltges et al. 2009). Consequently, mussels may experience reduced trematode infection levels when they hide at the bottom of the oyster matrix.

Hence, the presence of invasive oysters can affect parasite-host interactions on local scales, but it is not known whether the TMIEs observed for predator-prey interactions within the biogenic oyster matrix also affect parasite-host relationships on individual oyssel reefs. This also applies to native parasite-host interactions in which oysters serve as an alternative host for native parasites and which may also be affected via TMIEs induced by the oyster matrix. To investigate these potential indirect effects, we used a replicated large-scale field experiment conducted on two oyssel reefs in the south and north of the European Wadden Sea to investigate whether the habitat structure provided by invasive Pacific oysters can indirectly affect parasitism in native blue mussels. In the intertidal area of the Wadden Sea, two separate invasions of Pacific oysters in the north (island of Sylt 1986; Reise 1998, Reise et al. 2017a) and south (island of Texel 1983; Drinkwaard 1999) led to the transformation of native blue mussel beds into oyssel reefs were both species now co-occur (Troost 2010; Moehler et al. 2011; Reise et al. 2017b). In the south of the Wadden Sea, both molluscs are infected with the invasive parasitic copepod *Mytilicola orientalis* (Copepoda: Mytilicolidae) which was co-introduced with the Pacific oyster and recently spilled over to blue mussels (Pogoda et al. 2012; Goedknegt et al. 2017). In addition, a previously introduced congeneric species, *Mytilicola intestinalis*, only infects native blue mussels, and although established in the entire Wadden Sea, is almost absent in the south (Goedknegt et al. 2019). Both *Mytilicola* species have a direct life cycle with a free-living planktonic dispersal stage, which spends about 2–3 weeks in the water column before it resides in the intestines of its bivalve host (based on studies of *M. intestinalis*; Hockley 1951; Gee and Davey 1986a). Furthermore, blue mussels are infected with a range of native trematodes of which *Renicola roscovita* (Digenea: Renicolidae) is the most common species (Thieltges 2006; Goedknegt et al.

2019). This trematode species has a complex life cycle and uses the periwinkle *Littorina littorea* as first intermediate host, which achieves much higher densities on oyster reefs than on surrounding sand flats. From its gastropod host a short-lived free-living stage (< 1 day; Thieltges and Rick 2006) of *R. roscovita* emerges which subsequently infects blue mussels as second intermediate host. Birds serve as definitive host for this parasite (Werding 1969).

We focussed on these parasitic copepod and trematode species to investigate whether the refuge seeking behaviour of native blue mussels initiated by oysters can exert TMIEs on parasites by asking the following specific research questions: 1) Does the refuge-seeking behaviour of blue mussels and transmission interference by oysters affect parasite infection levels in blue mussels? 2) Does the resulting effect on parasite infection levels differ between parasites with direct (copepods) and complex (trematodes) life cycles? And 3) do the position in the matrix and parasite infection intensities affect mussel condition?

Materials and methods

Source of uninfected mussels

We used naturally uninfected blue mussels (*M. edulis*) to investigate the effect of the position in the oyster matrix on parasite infection levels. For the southern experimental location (Texel, The Netherlands), mussels (mean ± SE; 36.2 ± 0.4 mm) were collected from groynes located on the north-west shore of the Dutch mainland (52°52′42.37″ N, 4°42′25.60″ E; Fig. 2) on 7 July 2014. For the northern location (Sylt, Germany), mussels (38.0 ± 0.5 mm) originated from groynes situated on the west coast of Sylt (54°56′45.76″ N, 8°19′9.04″ E; Fig. 2) and were collected on 6 August 2014. Previous explorations had shown that the parasites *R. roscovita* and *Mytilicola* spp. seldom occur at these exposed source locations (confirmed by the dissection of 30 mussels at each source location; no infections found). Collected mussels were maintained in 75 L flow-through tanks at 18 °C under a 24 h light cycle (12 h light and 12 h dark) and fed three times per week with fresh *Isochrysis galbana* culture, or alternatively with Phyto-Feast® when fresh culture was unavailable. In addition, any epifauna (mostly barnacles) was carefully removed from the mussel shells to ensure that free-living stages of *R. roscovita* and *Mytilicola* spp. could infect mussels without being predated or physically obstructed by epifauna during the experiment (Johnson and Thieltges 2010).

Experimental locations

The experiment was conducted on Pacific oyster (*C. gigas*) reefs located near two islands at both ends of the Wadden Sea: Texel (south; reef area of about 12 ha, 53.0646° N, 4.5434° E) and Sylt (north; reef area of 6 ha, 55.0175° N, 8.2605° E Fig. 2). Background infection levels on these reefs have been acquired from previous morphological (and for *Mytilicola* spp. additional molecular) inspections (Goedknegt et al. 2019; Online Resource 1). Importantly, at the time of investigation the recently introduced copepod *M. orientalis* was pre-dominantly present in the southern (prevalence of 46.3%) and barely in the northern Wadden Sea (1.3%), while its congeneric *M. intestinalis* showed the reverse spatial pattern (12.5% in the south, 78.1% in the north; Goedknegt et al. 2019; Online Resource 1). For the trematode *R. roscovita* (prevalences: 86.3% in south and 98.8% in the north) infection intensity (± SE) is more than seven times higher in the north (178.9 ± 29.4 trematodes per infected mussel) in comparison to the south (25.9 ± 12.4; Goedknegt et al. 2019; Online Resource 1).

Vertical distribution of snails

To acquire knowledge on the vertical distribution of the first intermediate host of the trematode *R. Roscovita*, the density of common periwinkles *L. littorea* was measured at low tide on top and at the bottom of the oyster matrix. We determined snail density by haphazardly placing a 25 × 25 cm frame on the oyssel reef (Texel n = 10, Sylt n = 6). Within this frame, the top of the matrix (upper 10 cm) was first visually inspected for snails which were counted and removed. Subsequently, all oysters and mussels were detached from the area within the frame and the number of snails was counted that were found between the bivalves at the bottom of the matrix (approximately 10–20 cm depth from top of oyssel reef).

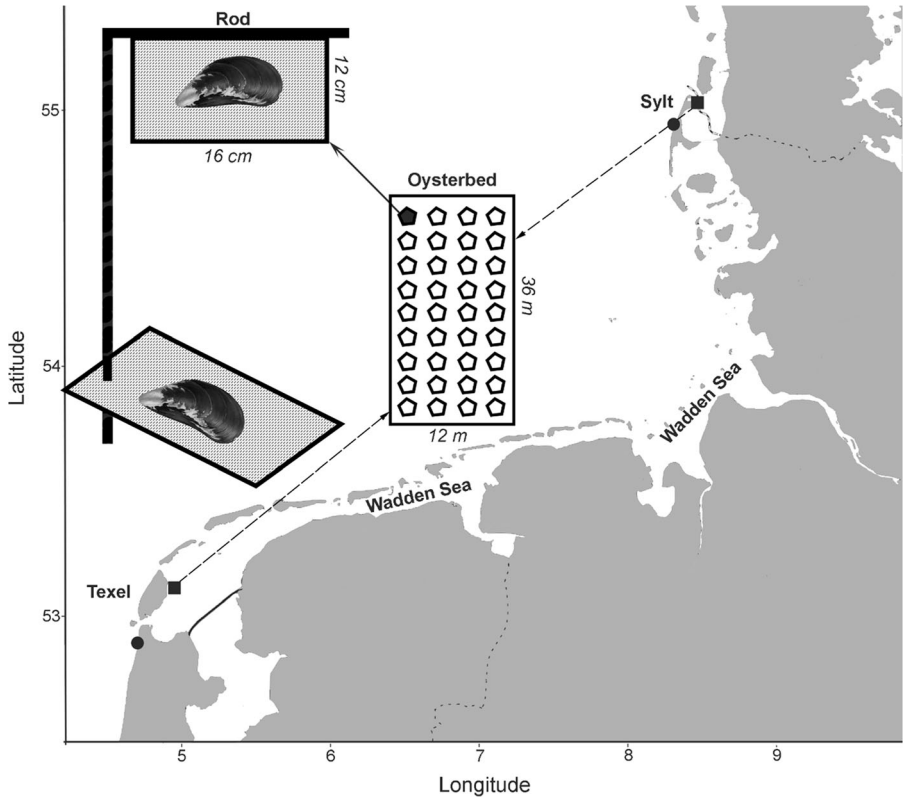

Fig. 2 Experimental set-up of the experiment on two oyssel reefs (squares), one in the south (Texel) and one in the north (Sylt) of the Wadden Sea. At each location, mussels originating from uninfected source locations (black dots) were individually added to two mesh bags attached to an iron rod that were positioned on the bottom and on the top of the oyster matrix. In total, 40 of these rods (pentagons) were placed within an area of 36 × 12 m (4 m distance among rods) on each oyssel reef

Experimental set-up

At both experimental locations, we placed uninfected mussels at the bottom and on top of the oyssel reef. Mussels were measured to the nearest 0.01 mm with digital calipers and placed individually into mesh bags made of PE (12 × 16 cm; 1 cm mesh size). Two mesh bags were then attached to an iron rod, with one bag positioned at the higher end of the rod on top of the oyster matrix and the other bag positioned at the lower end of the rod on the bottom of the oyster matrix (after carefully removing and replacing the matrix), with approximately 20 cm between both mesh bags (Fig. 2). At each location, 40 replicates of these rods were positioned in a rectangular field of 12 m × 36 m (10 rows of 4 rods, 4 m distance among rods) with similar oyster cover (Fig. 2). At termination of the experiment, dead mussels were counted and mesh bags with live mussels were frozen (− 20 °C) until later examination. The experiment commenced at the beginning of August 2014 and ended 4 months later in December. Due to bad weather conditions, some of the rods (n = 14) from Sylt could not be recovered until January 2015. To keep the infection time during the experiment at both locations as similar as possible, these 14 rods were excluded from the statistical analysis.

Parasite examination

Prior to dissection, we defrosted the mussels in random batches of 10 individuals. After measuring the mussel shell length with digital calipers to the nearest 0.01 mm, the mussel tissue was separated from the shell and searched for adult *Mytilicola* spp. that were retrieved from the tissue and collected in ethanol (96%). Adult *Mytilicola* individuals were later identified by using morphological characteristics described in Goedknegt et al. (2018). After this initial screening, the mussel tissue was compressed between glass slides

and examined under a stereo microscope (magnification 10–50×) to account for all *R. roscovita* metacercariae, and larval/juvenile *Mytilicola* spp., of which the latter could not always be identified on species level. As the share of unidentifiable larvae and juvenile *Mytilicola* in blue mussels was relatively large, we merged all *Mytilicola* individuals under *Mytilicola* spp. Finally, *R. roscovita* metacercariae and larval/juvenile *Mytilicola* spp. were left in the tissue, as these were too small to be removed from the mussel flesh.

Condition of mussels

After dissecting the mussels, the separated mussel flesh was frozen (− 20 °C for at least 24 h) and freeze-dried (48 h) to determine mussel tissue dry weight. We determined the condition index of mussels in a similar way as Eschweiler and Christensen (2011), who tested the effect of oyster TMIEs on predator–prey interactions, and used the formula $CI = DW/L^3$, where DW is the tissue dry weight (mg) and L the final shell length of a mussel (in cm, after Petersen et al. 2004).

Statistical analysis

All statistical analyses were conducted in the statistical software environment R (R Development Core Team 2015). Differences in snail density between matrix positions (bottom or top) at each location (Texel and Sylt) were tested with Student's t tests. Regarding the experiment, we used parasite data of individual mussels to model the effects of the position of mussels in the oyster matrix on the prevalence (the ratio of infected to sampled host species) and infection intensity (the mean number of parasites per infected host) of each of the parasite species (the copepods *Mytilicola* spp. and trematode *R. roscovita*) in mussels. Prevalence (characterized as parasite presence/absence in individual mussels) was modelled by using a generalized linear mixed model (GLMM; package lme4, Bates et al. 2015) following a binomial distribution, while for infection intensity (i.e., the number of parasites in infected mussels) a GLMM following a negative binomial distribution was used (package glmmADMB, Fournier et al. 2012). In both models, mussel position in the matrix, location and their interaction were regarded as fixed effects, and rod as random effect. Mussel Length (measured at the end of the experiment) was additionally included as a covariate in the infection intensity models, as *R. roscovita* intensity (Goedknegt et al. 2019) and *Mytilicola* spp. intensity (Grainger 1951; Goedknegt et al. 2017) are known to vary with mussel size.

We furthermore examined whether mussel condition as a decisive component of fitness was affected by the position in the oyster matrix and parasite infection levels (prevalence or infection intensity). We used linear mixed models (LMM, package lme4; Bates et al. 2015), with mussel condition as response variable. Position in the matrix, location, parasite infection parameters of both parasites (prevalence or infection intensity), and interactions (see Table 2) were included as fixed factors. Rod was again added as a random effect to the model.

P-values of all models were obtained by comparing the full model with reduced models without the fixed effect in question by means of likelihood ratio tests following Chi-square distributions. P-values 0.05 were considered as being significant. Raw data of the experiment parameters can be found in Goedknegt et al. (2020).

Results

Vertical distribution of snails

Both experimental locations varied in patterns of snail distribution within the oyster matrix structure. While for the northern location there was no significant variation in snail density with position in the oyster matrix (mean ± SE; top 440.0 individuals m^{-2} ± 29.1, bottom 450.7 ind. m^{-2} ± 26.3; Student's t test, $p = 0.791$), periwinkles were present at higher densities on top of the oysters (187.2 ind. m^{-2} ± 24.4 SE) compared to the bottom (104.0 ind. m^{-2} ± 12.2) of the oyster matrix in the south (Student's t test, $t = 3.044$, $p < 0.01$).

Mussel survival

At both locations survival of mussels was high. In total, 4 of the 80 mussels did not survive the experimental period at each site (Texel: n = 3 bottom, n = 1 top; Sylt: n = 2 both bottom and top).

Mussel infections

After 4 months, the surviving mussels were collected (n = 124 remaining, after removing the rods that were retrieved after the storm and all the dead mussels). These mussels harbored frequent infections with the copepod *Mytilicola* spp. (mean prevalence of both locations ± SE; 49.3% ± 0.7) and the trematode *R. roscovita* (89.6% ± 4.1).

On average, *Mytilicola spp*. infection rates of mussels at the bottom of the matrix were lower than mussels placed on top of the matrix ($\Delta_{Deviance}$ = 7.920, $p < 0.05$; Table 1). However, this pattern was only observed at the southern oyster bed, leading to an almost significant interaction term in the prevalence model of *Mytilicola* spp. (location * matrix interaction $\Delta_{Deviance}$ = 3.182, p = 0.074; Fig. 3). For *R. roscovita* infections the infection patterns were reversed, with significantly more infections at the bottom of the matrix. Again, this pattern was mainly driven by infections at the southern oyster bed, resulting in a significant interaction between matrix position and location ($\Delta_{Deviance}$ = 4.458, $p < 0.05$; Table 1).

The variation in infection prevalence with mussel position was also reflected in *R. roscovita* infection

Table 1 Results of GLMMs explaining variation in parasite prevalence and infection intensity in native blue mussels (*Mytilus edulis*) depending on location (southern vs. northern Wadden Sea), the position in the oyster matrix (top vs. bottom) and mussel length (for infection intensity models only).

Coefficients (Coeff.) and standard errors (SE) are shown for fixed effects, and variance (Var.) and standard deviations (SD) of random effects (rod) are shown for full models. The odd ratio (OR) with lower (LL) and upper limits (UL) are given for the binomial (prevalence) models only

Model	Parasite species	Fixed effects			Odd ratio			Random effects	
		Variable	Coeff.	SE	OR	LL	UL	Var.	SD
Prevalence	*Mytilicola* spp. (n = 124)	Intercept	− 0.007	0.427	0.993	0.430	2.293		
		Position (Bottom)	0.007	0.592	1.007	0.316	3.215		
		Location (South)	0.617	0.560	1.853	0.619	5.550		
		Position (Bottom)* Location (South)	− 1.138	0.795	0.251	0.053	1.192		
		Rod	–	–	–	–	–	0.183	0.428
	R. roscovita (n = 124)	Intercept	3.136	1.022	23.000	3.106	170.309		
		Position (Bottom)	− 0.738	1.261	0.478	0.040	5.658		
		Location (South)	− 2.071	1.085	0.126	0.015	1.058		
		Position (Bottom)* Location (South)	3.256	1.659	25.956	1.005	670.058		
		Rod	–	–	–	–	–	0	0
Infection intensity	*Mytilicola* spp. (n = 61)	Intercept	0.086	1.494	–	–	–		
		Position (Bottom)	− 0.058	0.327	–	–	–		
		Location (South)	− 0.013	0.300	–	–	–		
		Position (Bottom)* Location (South)	0.085	0.416	–	–	–		
		Mussel length	0.011	0.031	–	–	–		
		Rod	–	–	–	–	–	0	0.001
	R. roscovita (n = 110)	Intercept	3.875	1.433	–	–	–		
		Position (Bottom)	0.154	0.304	–	–	–		
		Location (South)	− 2.836	0.333	–	–	–		
		Position (Bottom)* Location (South)	0.524	0.403	–	–	–		
		Mussel length	0.014	0.030	–	–	–		
		Rod	–	–	–	–	–	0.281	0.530

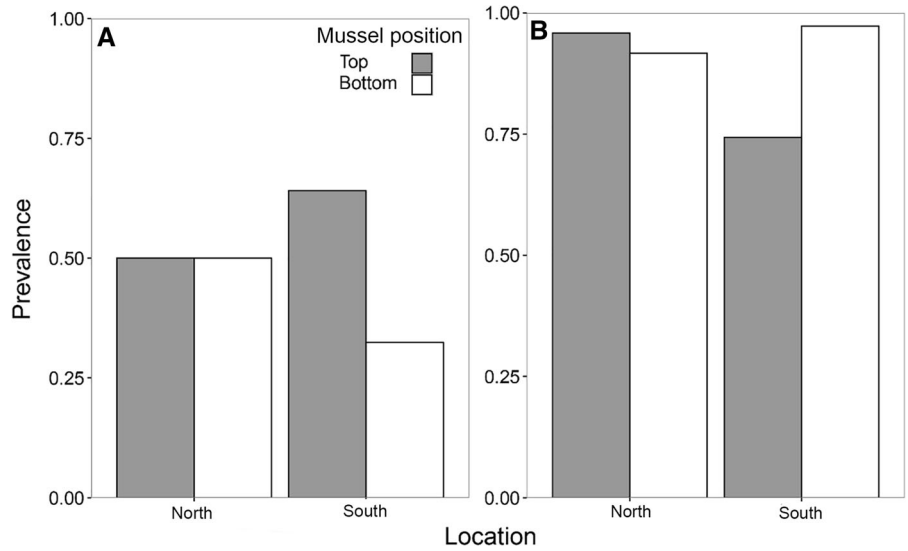

Fig. 3 Prevalence of **a** the parasitic copepod *Mytilicola* spp. and **b** the trematode *Renicola roscovita* at the top and bottom of the oyster matrix at both experimental locations

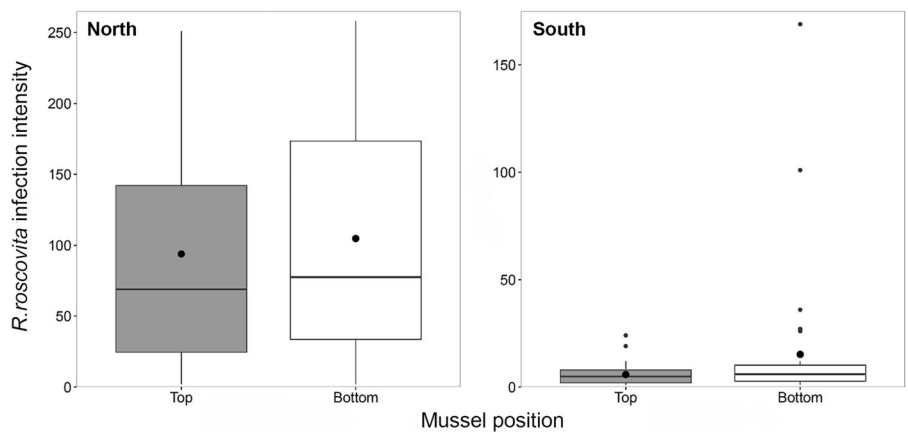

Fig. 4 Mean infection intensity (± SE) of the trematode *Renicola roscovita* at the top and bottom of the oyster matrix at the northern and southern location. The boxes represent the interquartile range, the whiskers denote the lowest and highest values within the 1.5 interquartile range, the black line in each box denotes the median, the large black dots represent the mean condition indices of each group and the smaller dots outside the boxes are outliers

intensity, as the number of metacercariae was significantly higher in infected mussels at the bottom relative to mussels positioned on top of the oyster matrix ($\Delta_{Deviance} = 6.708$, $p < 0.05$; Table 1). However, this statistical result was driven by the two southern mussels with relatively high infection intensities compared to the population background (Fig. 4). Such values are well within the range of observed infection intensities (Fig. 4) and since there were no biological or methodological reasons to remove these mussels, the analysis is based on the complete data set including those two specimens. Although the interaction term was not significant ($\Delta_{Deviance} = 1.676$, $p = 0.196$), the matrix position of mussels had a stronger effect at the southern location (Fig. 4), with several mussels at the bottom of the oyster matrix experiencing substantially higher infection levels (max to mean ratio of 11) than mussels at the top (max to mean ratio of 4). At the northern location mean infection levels where much higher but differed only by about 10% between matrix positions (max to mean ratio of 2 for both matrix positions; Fig. 4). In

contrast to trematode infections, *Mytilicola* spp. intensity in mussels was independent from the position in the matrix and did not differ between locations (Table 1). Finally, for both trematodes and copepods, mussel length was not a significant predictor in the infection intensity models ($p > 0.05$).

Mussel condition

Overall, mussels situated on top of the oyster matrix had significantly better condition indices than mussels at the bottom of the matrix in both the prevalence ($\Delta_{Deviance} = 26.863$, $p < 0.001$) and infection intensity models ($\Delta_{Deviance} = 17.967$, $p < 0.01$; Fig. 5). Mussel condition also differed between locations, with better condition of mussels at the southern compared to the northern location ($p < 0.01$ for both models; Fig. 5). Furthermore, in both models the difference in condition with position in the matrix was larger at the southern location than at the northern location, resulting in significant interactions with matrix position and location ($p < 0.01$ for both models). The condition of the mussels was not affected by infection by either parasite. However, there was a significant interaction of mussel position with *Mytilicola* spp. intensity ($\Delta_{Deviance} = 3.998$, $p < 0.05$; Table 2). While condition increased with higher *Mytilicola* spp. intensity for mussels positioned at the bottom of the matrix, the condition of mussels placed on top of the oyster matrix tended to decrease with *Mytilicola* spp. intensity (Online Resource 2).

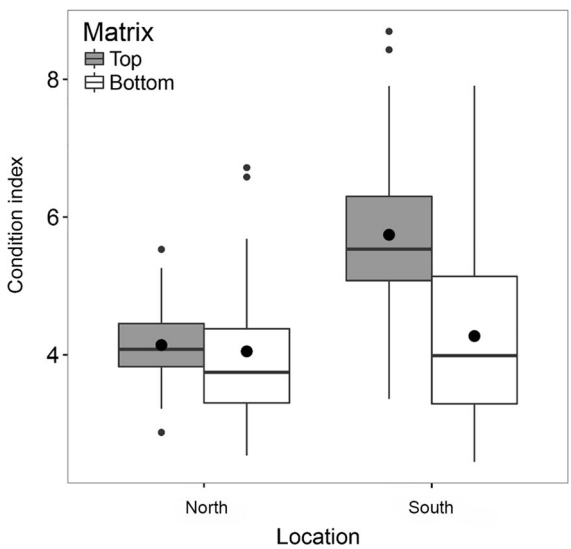

Fig. 5 Condition of mussels positioned on top (grey) and on the bottom (white) of the oyster matrix at the northern and southern location. The boxes represent the interquartile range, the whiskers denote the lowest and highest values within the 1.5 interquartile range, the black line in each box denotes the median, the large black dots represent the mean condition indices of each group and the smaller dots outside the boxes are outliers. Note the truncated y-axis

Discussion

In this study, we observed that an invasive ecosystem engineer can indirectly affect parasite-host interactions if the host adjusts its predator-avoidance behaviour to move deeper into the oyster reef structure. Our field experiment demonstrated that blue mussels at the top of an oyssel reef can experience different parasite infection levels than mussels situated at the bottom. Thus, mussels that hide to deeper layers in the oyster matrix to escape from predators (i.e., birds and crabs) also affect their parasite load. That predator presence can lead to behavioural changes of hosts which in turn result in alterations of parasite-host interactions has previously been documented in freshwater systems. Most of these studies observed that predator-avoidance behaviour leads to an increase in parasite infection levels. For example, female guppies that exert a higher tendency to shoal as a response to predators are infected with more directly transmitted monogenean parasites compared to male guppies which do not shoal under high predation pressure (Stephenson et al. 2015). Therefore, the degree of exposure to infected fish determined by sex-specific differences in shoaling behaviour is driving parasite infection levels in guppies. Interestingly, our study showed that the effect of escaping from predators on parasite infections can vary between different ecological conditions and can even lead to opposing patterns for different parasite groups. While infections by the parasitic copepod *Mytilicola* spp. decreased, trematode infections by *R. roscovita* were amplified. These results can be explained in the context of differential parasite exposure relating to interspecific differences in parasite life cycles.

Infection patterns of *Mytilicola* spp.

Mussels that were positioned on top of the oyster matrix had significantly higher prevalences of the

Table 2 Results of LMMs explaining variation in condition in blue mussels (*Mytilus edulis*) depending on the position in the oyster matrix (top vs. bottom), experimental location (north vs. south) and parasite infection level (prevalence or infection intensity for both parasite species *Mytilicola* spp. and *Renicola roscovita*). Coefficients (Coeff.) and standard errors (SE) are shown for fixed effects, and variance (Var.) and standard deviations (SD) of random effects (rod) are shown for full models

Model	Fixed effects			Random effects	
	Variables	Coeff.	SE	Var.	SD
Prevalence (n = 124)	Intercept	4.422	0.676		
	Position in matrix (Bottom)	− 0.186	0.866		
	Location (South)	1.609	0.311		
	Mytilicola spp. presence	− 0.544	0.686		
	R. roscovita presence	− 0.307	0.653		
	Position (Bottom) * Location (South)	− 1.373	0.437		
	Mytilicola spp. presence * *R. roscovita* presence	0.622	0.726		
	Position (Bottom) * *Mytilicola* spp. presence	0.063	0.433		
	Position (Bottom) * *R. roscovita* presence	0.054	0.838		
	Rod			0	0
	Residual			1.308	1.144
Infection intensity (n = 52)	Intercept	4.335	0.629		
	Position in matrix (Bottom)	− 0.152	0.923		
	Location (South)	1.803	0.552		
	Mytilicola spp. presence	− 0.131	0.220		
	R. roscovita presence	0.003	0.005		
	Position (Bottom) * Location (South)	− 2.089	0.745		
	Mytilicola spp. presence * *R. roscovita* presence	− 0.003	0.003		
	Position (Bottom) * *Mytilicola* spp. presence	0.562	0.301		
	Position (Bottom) * *R. roscovita* presence	− 0.006	0.005		
	Rod			0.219	0.468
	Residual			0.913	0.955

parasitic copepod *Mytilicola* spp. relative to mussels situated at the bottom of the oyssel reef. However, this pattern was only clearly detected at the southern location, suggesting that the observed patterns depended on the encountered ecological ramifications. For *Mytilicola* spp. infections this may reflect differences between the parasite species: *M. orientalis* was very rare at the northern location Sylt, whereas it was the dominant species at the southern location where *M. intestinalis* was very rare. It was already shown that even within *Mytilicola* species the interaction mechanisms with the host can differ between both locations (Feis et al. 2016, 2018), suggesting that larger differences could be expected between the species.

At the southern location, the observed pattern probably relates to the direct life cycle of the parasites, which involves a free-living phase in which larvae passively distribute in the water column for 2–3 weeks (Hockley 1951; Gee and Davey 1986a) until they reach their infective first copepodid stage that moves to deeper water layers by a photonegative response (Meyer and Mann 1950; Hockley 1951). Hence, production of larvae within the reef is decoupled from recruitment of infective larval stages, because earlier life stages leave the oyssel reef and new infections originate from outside the reef. As infective copepodids are mainly using the hosts' field of filtration and the strength of the host filtration current as settlement cues (Gee and Davey 1986b), the probability of successful infection of mussels on oyssel reefs is determined by the chance of encountering hosts. Therefore, it is likely that the highest concentration of *Mytilicola* spp. larvae would gather at the top of an oyssel reef where they first encounter filter feeding

hosts, resulting in higher prevalences of *Mytilicola* spp. in mussels positioned on top of the oyster matrix. Interestingly, a similar pattern has been observed in barnacle larvae, which, like *Mytilicola* copepodids, spend several weeks in the water column before settling on blue mussels. Densities of recently settled barnacles were 2–3 times higher on mussels placed on top of the matrix, compared to mussels situated on the bottom of the oyssel reef (Buschbaum et al. 2016). For barnacles as well as *Mytilicola* spp., the recruitment of larval stages from the water column will result in a decreased exposure of mussels at the bottom of the oyster matrix. Reduced exposure might only be a consequence of the physical structure of the reef but may also be further reduced due to dilution inside the matrix. Dilution of *Mytilicola* larvae can take place via the host competence of the Pacific oyster, which differs between both species of *Mytilicola*. For *M. orientalis*, the invasive Pacific oyster serves as the principle host, as this parasite-host relationship originates from the native range of both species (Mori 1935). Infective *M. orientalis* larvae searching for hosts are likely to infect the oysters and mussels they first encounter, resulting in lower infections of mussels living deep in the oyster matrix. In contrast, the mechanism for *M. intestinalis* is different, as this parasite does not seem to infect Pacific oysters in the Wadden Sea (Goedknegt et al. 2017) and artificial infections were thus far unsuccessful (Elsner et al. 2011; pers. comm. M. Feis). This suggests that, by being an incompetent host, the oyster may interfere with the transmission of larval stages of *M. intestinalis* by acting as a decoy, still filtering *M. intestinalis* larvae out of the water but remaining uninfected, thereby reducing the disease risk for mussels hiding in the matrix. In either way, competent or non-competent oysters reduce the risk of infection with *Mytilicola* spp. for mussels positioned deep in the oyster matrix. Whether the absence of a matrix position effect at the northern location, where *M. intestinalis* dominates, suggests that this effect is only relevant for *M. orientalis* or rather depends on other characteristics differentiating both sites remains to be investigated. In contrast to the vertical prevalence pattern, we did not observe significant differences in *Mytilicola* spp. intensity in native mussels depending on the position in the invasive oyster matrix. This suggests that encounter rates with infective larval stages may be higher at the top of the oyssel reef leading to a more even spread of infections, while larval stages inside the matrix have a reduced encounter rate leading to more aggregated distributions. Alternatively, the comparatively low infection levels with *Mytilicola* spp. building up during the experiment (mean infection intensity < 2) led to low statistical power to detect differences in infection intensities of mussels between the two positions in the oyster matrix.

Infection patterns of *R. roscovita*

The trematode *R. roscovita* showed different infection patterns in the oyster matrix compared to the copepods *Mytilicola* spp., with higher infection levels (in particular infection intensity) in mussels positioned at the bottom of oyssel reefs at the southern site. This result is contradicting our expectations, as we anticipated a strong effect of the oysters' transmission interference capacity which had been previously shown in field and laboratory studies (Thieltges et al. 2009; Welsh et al. 2014; Goedknegt et al. 2015) and which we expected to result in lower infection levels of mussels hiding in between the oysters. Probably the oysters still interfered in parasite transmission in our experiment, but this was overruled by other biological (e.g., down-ward orientated host-searching behaviour of *Renicola* spp. cercaria; Nicolaev et al. 2017), and hydrographical processes (e.g., differences current flow on top and between the oysters) that resulted in the observed vertical distribution pattern of trematodes in the oyster matrix. In contrast to the copepods, local recruitment of trematode larval infective stages mainly originates from within the oyssel reef, which can be ascribed to the complex life cycle of trematodes. The infection process of *R. roscovita* starts when free-living stages of the parasite (trematode cercariae) emerge from the first intermediate host, the periwinkle *L. littorea.* This host attains highest densities in oyster reefs in comparison to other intertidal habitats. As the free-living cercarial stage is short-lived (< 1 day and the infective period being < 12 h; Thieltges and Rick 2006) and locally produced by snails in very high numbers (Thieltges and Rick 2006; Thieltges et al. 2009), infections are expected to occur on small spatial scales in close vicinity to the first intermediate hosts. This explains why infection levels in second intermediate trematode hosts are usually positively correlated with the local density of (infected) snails (Thieltges 2007; Thieltges

and Reise 2007). Our data show that snail density was indeed reflected in the infection intensity in mussels, as snail density and infection intensity on natural oyssel reefs were both about three times higher in the northern (Sylt) compared to the southern (Texel) location. However, zooming in on the oyster matrix, the vertical distribution of snails did not relate to the trematode infection intensity in mussels. While trematode intensities were significantly higher in mussels positioned at the bottom of the oyster matrix, snail density was either higher on top of the matrix (southern location, Texel) or there was no significant difference between matrix positions (northern location, Sylt). It must be noted though, that we have only investigated the snail distribution in the oyster matrix at low tide, and high tide investigations might challenge these results. Without data on snail infection levels we can, however, not exclude the possibility that also infected snails aggregate at the bottom of the oyssel reef, e.g., as a result of parasite manipulation of the behaviour of infected snails (Curtis 1987).

Alternatively, hydrographical rather than biological processes may explain the higher infection levels of trematodes in mussels located on the bottom of the oyssel reef. Infection by marine trematodes are known to primarily occur at low tide, when large concentrations of infective stages accumulate and are trapped in small volumes of water such as tidal pools, maximizing contact with their second intermediate hosts and increasing transmission rates (Mouritsen and Jensen 1997; Mouritsen 2002a, b; Thieltges and Reise 2007; Koprivnikar and Poulin 2009). Similar trapping of cercariae likely occurs in the matrix of oyssel reefs so that mussels at the bottom are exposed to a higher density of infective stages and for a longer duration than mussels on top of the oyssel reef, resulting in higher infection levels in mussels at the bottom compared to the top of the matrix. Both biological and hydrographical processes are not mutually exclusive and future experiments will be needed to determine the relative strength of the processes responsible for the observed vertical infection pattern of the trematode *R. roscovita* in the oyster matrix. Spatial variation in the relative strength of these processes may underlie the observed difference in effect size between locations. Obviously spatial heterogeneity is much higher in the southern oyssel reef, especially in the bottom of the reef where particularly high infection intensities could be observed. This could suggest that infective cercarial stages were trapped in only a few pockets of the oyster matrix in the south. In the north, the much higher supply of cercaria might have masked such spatial heterogeneity and reef position effects in a density-dependent fashion. However, further studies will be needed to unravel the exact underlying mechanisms.

Mussel condition

Dwelling in deeper layers of the oyster matrix near the bottom does not only increase the risk of becoming infected by trematodes but also considerably lowers the availability of food particles, demonstrated by the significant lower condition of mussels positioned at the bottom of the oyssel reef. This is in agreement with results of Eschweiler and Christensen (2011) who also found reduced condition of mussels positioned at the bottom of oyssel reefs. We did not find a significant effect of *R. roscovita* intensity on condition index. This is surprising as *R. roscovita* is known to cause reductions in blue mussel condition (Stier et al. 2015). Possibly, the duration of our experiment was too short to detect a significant effect on the condition of the mussels. For *Mytilicola* spp. we did not detect an overall effect of infection intensity on mussel condition index but we detected a significant interaction of infection intensity with mussel position in the matrix. While mussel condition tended to increase with *Mytilicola* spp. intensity when mussels were placed at the bottom of the matrix, there was a slight decrease in infection intensity when mussels were placed on top of the oyster reef. Based on the fact that the found patterns are only driven by three points (two points at an infection intensity of 4 and one point at an infection intensity of 5) and low number of mussels with a high intensity of infection by copepods (see Online Resource 2), we are uncertain whether the found interaction pattern is actually real. Therefore, we consider this result as a statistical artefact and elude any biological significance. Finally, mussels significantly differed in condition between the two experimental locations, most likely caused by differences in environmental conditions and production between the northern and southern Wadden Sea.

Conclusions

In summary, our study shows that the biogenic matrix provided by invasive oysters does not only initiate TMIEs in the form of refuge seeking of native mussels which reduces crab predation and detrimental barnacle overgrowth (Eschweiler and Christensen 2011; Waser et al. 2015; Buschbaum et al. 2016) but that these indirect effects also extend to parasites: Refuge seeking behaviour in the oyster matrix reduces infections with parasitic copepods to a certain extent yet comes at the cost of an increased exposure to trematodes. These indirect effects of the invasive oysters are the net result of complex abiotic and biotic mechanisms related to the position of mussels in the oyster matrix as discussed above and thus apply to the scale of oyssel reefs. On larger spatial and temporal scales, oysters may also cause direct effects on parasites by transmission interference or parasite spillover which may ultimately affect background infection levels in the ecosystem. Hence, the net effect of invasive oysters on the ecosystem level may differ from their net effect on the scale of oyssel reefs. However, the magnitude of ecosystem-wide as well as ecsystem-specific impacts remains to be investigated.

Overall, the results of our study suggest that invasive ecosystem engineers can exert TMIEs on parasites, which is a novel mechanism of how invasive species can affect recipient ecosystems. Given the increasing evidence that ecosystem engineers in general can exert manifold indirect effects on species interactions and food webs (White and O'Donnell 2010; Sanders et al. 2014; Wetzel et al. 2016; Griffen et al. 2017; Mourant et al. 2017), it seems highly likely that many of these indirect effects will also trigger TMIEs (and also DMIEs) on parasites if they include changes in the behaviour or density of species that serve as hosts for parasites. Hence, indirect effects of invasive ecosystem engineers on parasite-host interactions in recipient ecosystems may be much more common than realized today and they possibly add significantly to the known diversity of impacts of invasive ecosystems engineers (Crooks 2002; Guy-Haim et al. 2018). Further research into the diversity and magnitude as well as the underlying mechanisms of indirect effects of invasive ecosystem engineers on parasitism is needed, and we hope that our study will spark further interest in this direction.

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Data accessibility Data is archived at https://data.4tu.nl/repository/, https://doi.org/10.4121/12826154.

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