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Invasive oysters as new hosts for native shell-boring polychaetes: Using historical shell collections and recent field data to investigate parasite spillback in native mussels in the Dutch Wadden Sea

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ABSTRACT

Biological invasions can have manifold effects on native biota, including impacts on species interactions in invaded ecosystems. Among those are effects on parasite-host interactions, for example in cases where invaders serve as a new host for native parasites, leading to an amplification of the parasite population which may ultimately result in increased infection levels in the original native hosts (parasite spillback). In this study, we investigated the potential spillback of the native shell-boring polychaete *Polydora ciliata* from invasive Pacific oysters (*Crassostrea (Magallana) gigas*) to native mussels (*Mytilus edulis*) in the Dutch Wadden Sea. A field survey in the intertidal revealed that the majority of *P. ciliata* can nowadays be found in the shells of live but also dead Pacific oysters and much less in shells of other potential host species: mussels and periwinkles (*Littorina littorea*). Using a unique historical shell collection based on long-term sampling programmes in the intertidal and subtidal of the western Dutch Wadden Sea, we compared *P. ciliata* infections in mussels before and after the invasion of the Pacific oyster by means of x-ray scans. Both for the intertidal and subtidal, we did not detect differences in prevalence of *P. ciliata* in mussels between pre- and post-invasion periods. This suggests that the invasion of the Pacific oyster may not have caused a strong spillback to mussels regarding *P. ciliata* and thus the invasion probably had little indirect infection-mediated effects on the condition and fitness of native mussels. Instead, the acquisition of native *P. ciliata* by the invasive oysters suggests that they may themselves be affected by the new infections and this may warrant further research.

1. Introduction

The invasion of species into marine ecosystems can have manifold effects on native biota, in particular in case of invading predators (Thomsen et al., 2014; Gallardo et al., 2016). Besides affecting predator-prey interactions, marine invasive species can also affect other species interactions such as the ones between parasites and their hosts (Prenter et al., 2004; Goedknecht et al., 2016). In general, invasive species often arrive without their native parasites which may give them a competitive advantage over native competitors (parasite release; Torchin et al., 2003; Blakeslee et al., 2013). However, once arrived in a new environment invasive species can acquire parasites native to their new habitats (parasite acquisition; Paterson et al., 2012). The addition of potential new hosts for the native parasites can lead to an amplification of their

population sizes and this, in turn, may result in an increase in infection levels in the original native hosts (parasite spillback; Kelly et al., 2009; Poulin et al., 2011; Telfer and Bown, 2012). Examples for such spillback effects are accumulating but empirical studies on the potential effects of invasive species on parasite-host interactions are still limited (Poulin et al., 2011; Telfer and Bown, 2012).

A marine invasion that has the potential to lead to parasite spillback is the invasion of the Pacific oyster (*Crassostrea (Magallana) gigas*) in Europe (Troost, 2010). The species had originally been introduced for aquaculture purposes and subsequently spread along the coasts of Europe (Troost, 2010; Herbert et al., 2016). The Pacific oyster has also invaded the Wadden Sea, beginning with first observations in 1983 on the island of Texel in the southern Wadden Sea (Troost, 2010). However, a massive spread of the oysters along the entire Wadden Sea occurred

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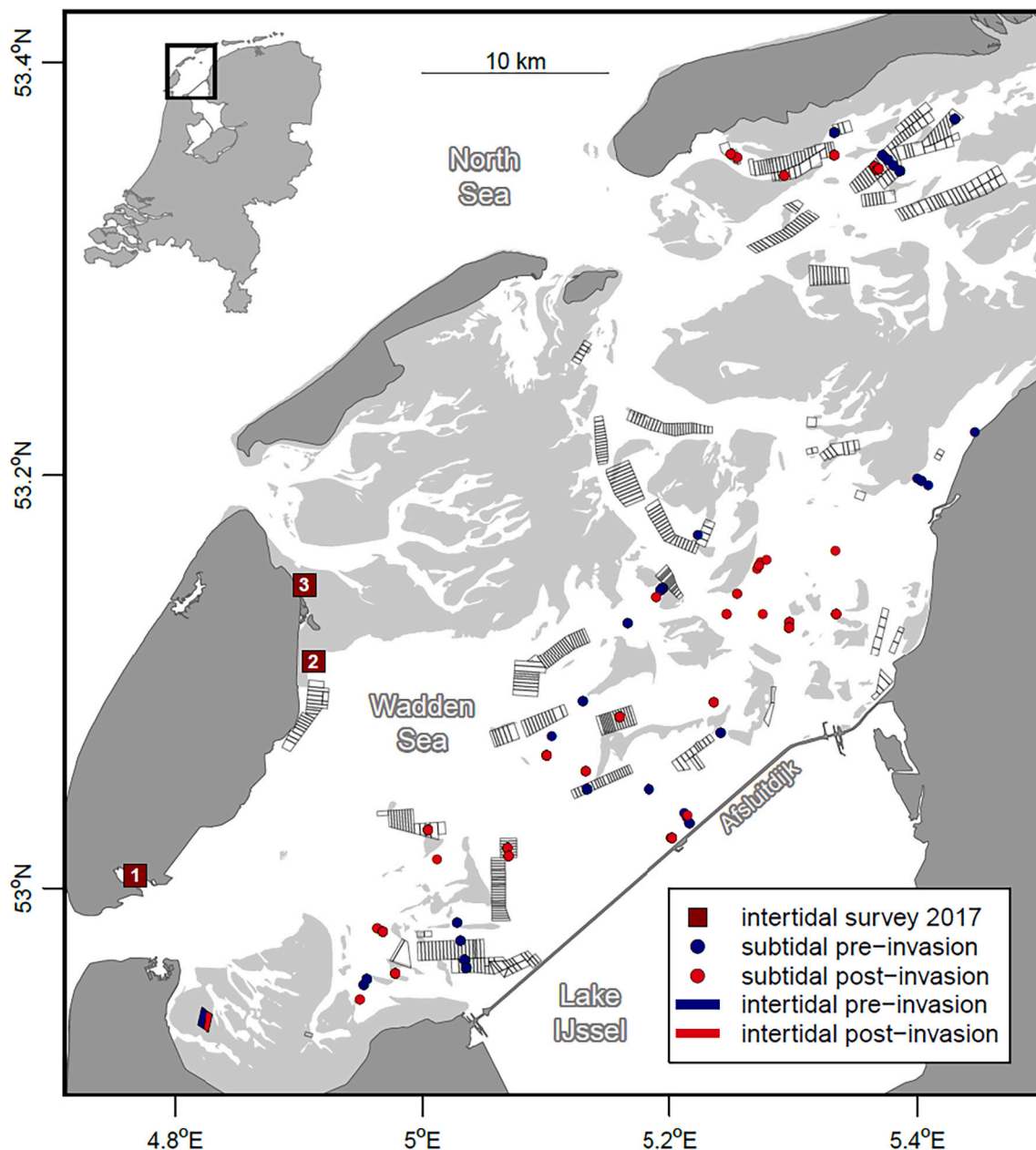


Fig. 1. Sampling locations of the three data sources used for this study: a) field collections of native blue mussels (*Mytilus edulis*) and periwinkles (*Littorina littorea*) and invasive Pacific oysters (*Crassostrea (Magallana) gigas*) at three mixed mussel and oyster beds (squares:1–3) in the intertidal along the east coast of the island of Texel in 2017; b) blue mussel shells from intertidal sites (stripes) from a historical shell collection from a long-term sampling programme on Balgzand; and c) blue mussel shells from subtidal sites (dots) from a historical shell collection from repeated large-scale surveys in the western Dutch Wadden Sea. Sites sampled before (blue) and after (red) the invasion of the Pacific oyster are shown. Light grey shading denotes intertidal and white shading subtidal areas. Mussel culture plots are indicated by black polygons. See text for details of the sampling procedures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

only after strong spatfall events in the early 2000s. Pacific oysters settled into existing intertidal beds of native blue mussels (*Mytilus edulis*), leading to the mixed mussel and oyster beds commonly observed in the intertidal along the entire Wadden Sea today (Troost, 2010; Waser et al., 2016; Reise et al., 2017b). The invasion of the Pacific oyster has diverse effects on native parasite-host interactions and among those is a potential spillback of the shell-boring polychaete *Polydora ciliata* to native molluscs (Goedknecht et al., 2019). This worm is a shell parasite that drills holes in the shells of epibenthic bivalves and gastropods, and infected organisms have to spend energy on repairing these holes (Kent, 1979). Infections reduce host condition and the strength of mussel and gastropod shells which in turn leads to increased predation by crabs

(Kent, 1979, 1981; Buschbaum et al., 2007). *P. ciliata* is a polydorid polychaete (Spionidae) with a pelagic larval stage and has probably a preference for mollusc hosts inhabiting the lower intertidal and subtidal (Michaelis, 1978; Warner, 1997; Buschbaum et al., 2007). In the Wadden Sea, the primary native hosts of *P. ciliata* are blue mussels and periwinkles (*Littorina littorea*; Thieltges et al., 2006). However, with the invasion of the Pacific oyster the worm has started to use the new oyster as an additional host (Thieltges et al., 2006; Goedknecht et al., 2019). Given the relatively thick shells of the oysters that offer many crevices, this new species seems to be an optimal host for the shell-boring polychaetes (Goedknecht et al., 2019).

However, quantitative data on the abundance of *P. ciliata* in native

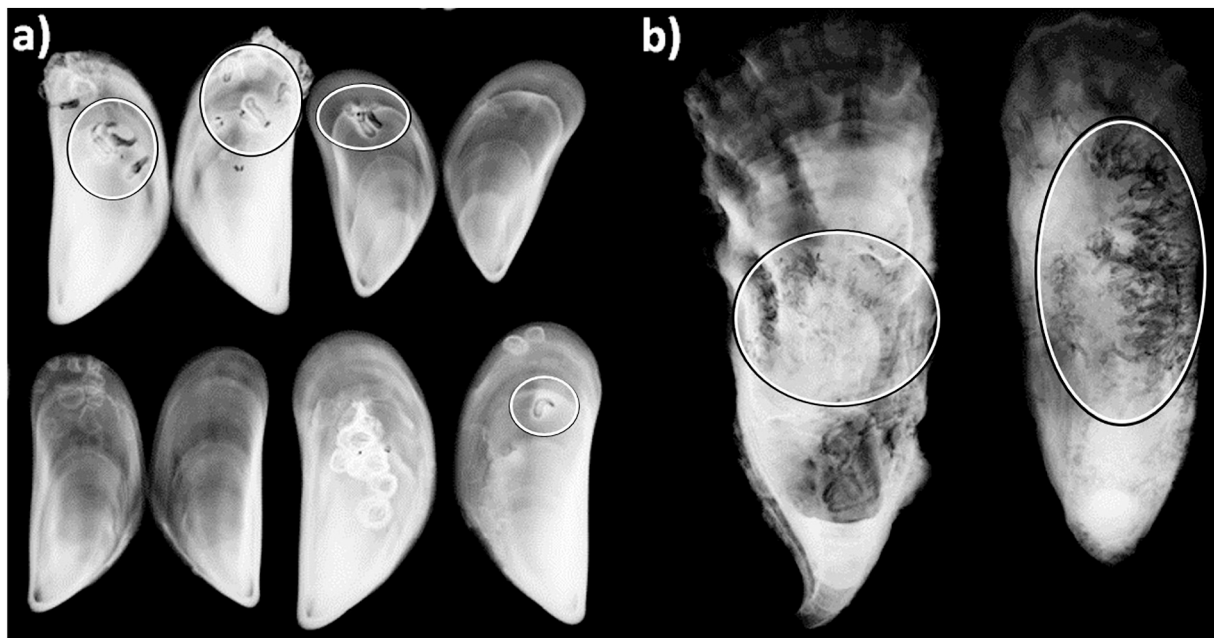


Fig. 2. X-ray scans showing burrows of the shell-boring polychaete *Polydora ciliata* (encircled areas) in individual valves of a) mussels (*Mytilus edulis*), also visible are barnacle stacks and base plates, and b) Pacific oysters (*Crassostrea (Magallana) gigas*).

and invasive hosts are missing to date. In addition, it is unknown whether the invasion of the Pacific oyster has led to an increase in infection levels of the worms in native mussels via a spillback effect. As Pacific oysters occur predominantly in the lower intertidal (Troost, 2010; Reise et al., 2017a), a potential spillback effect may be particularly strong in intertidal mussel and oyster beds. However, via larval dispersal of the polychaete, the invasion of the Pacific oyster may have also affected *P. ciliata* infections in subtidal mussels in the Wadden Sea. A spillback of the polychaete to mussels could have important implications given the pivotal ecosystem functions and services provided by mussels such as habitat provisioning and biological filtering and their economic value in mussel aquaculture in coastal ecosystems (Gosling, 1992; Buschbaum et al., 2009).

In this study, we investigated the potential spillback of the shell-boring polychaete *P. ciliata* from invasive oysters to native mussels in the intertidal (where all host species co-occur) and the subtidal (where the polychaete may thrive due to its preference for lower tidal levels) of the Dutch Wadden Sea. We first determined the current abundance and host use of the worm in native blue mussels (*M. edulis*) and periwinkles (*L. littorea*) as well as in invasive Pacific oysters (*C. gigas*) from the intertidal to identify its preferred host species. Then we investigated the infection prevalence of the worm before and after the invasion of the Pacific oyster, using shells from a historical shell collection from sampling programmes in the intertidal and subtidal of the western Dutch Wadden Sea.

2. Methods

We used three data sources for this study: a) collections of native blue mussels (*Mytilus edulis*) and periwinkles (*Littorina littorea*) as well as invasive Pacific oysters (*Crassostrea (Magallana) gigas*) from a field survey in the intertidal along the east coast of the island of Texel in the Netherlands in 2017; b) blue mussel shells from intertidal sites from a historical shell collection of a long-term sampling programme on a tidal flat close to Texel; and c) blue mussel shells from subtidal sites from a historical shell collection from repeated large-scale surveys in the western Dutch Wadden Sea (Fig. 1).

2.1. Field survey in 2017: current host use of *P. ciliata*

To identify the current abundance and host use of *P. ciliata* in the intertidal, we sampled native blue mussels (*M. edulis*) and periwinkles (*L. littorea*) as well as invasive Pacific oysters (*C. gigas*) on three mixed mussel and oyster beds along the east coast of the island of Texel (Fig. 1). On each mixed bed, eight samples were taken, using a metal frame of 15 × 15 cm, which was randomly thrown onto mussel/oyster patches. The content of each frame was removed, sieved in the field (1 mm mesh size), and all organisms transported to the laboratory. There, we first measured the total fresh weight of all individuals of each of the three species per sample (live individuals and dead shells were separated). Then all individuals of each species (live individuals and dead shells separately) from each sample were placed into a container with a 1:20 solution of ethanol and seawater to drive all worms out of their burrows (for details see Waser et al., 2020). After 12 h, all worms were retrieved from the containers and identified and counted. Worms were identified under a dissection microscope to avoid confusion with other *Polydora* species, in particular *P. cornuta*, which can occur on mixed mussel and oyster beds, not burrowing themselves into bivalve shells (Michaelis, 1978; Hartmann-Schröder, 1996; Radashevsky, 2005).

2.2. Historical shell collections: *P. ciliata* prevalence before and after oyster invasion

To compare infection levels of native mussels (*M. edulis*) with the shell-boring polychaete *P. ciliata* before and after the invasion of the Pacific oyster, we made use of two historical shell collections held by the NIOZ, one from intertidal and one from subtidal mussel samples. The intertidal mussel shells were obtained from a survey of macrozoobenthos in the Balgzand area near Den Helder, The Netherlands (Beukema and Dekker, 2007, 2020). The goal of this survey is to monitor macrozoobenthos population dynamics in the intertidal area over multiple years, taking 50 cores at 20 m intervals along 12 transects. For our study, we used samples from transect B of the aforementioned monitoring programme, as this was the only transect continuously containing blue mussels (Fig. 1). Intertidal mussel shells originated from samples taken in the years 1981 to 1987 (7 years) were used as samples from before the invasion of Pacific oysters on the mussel beds in the Wadden

Sea, and collections from the years 2010 to 2016 (7 years) were used as samples taken after the initial introduction and subsequent spread had taken place.

The subtidal mussel samples originated from a study of the subtidal macrobenthos in the western Dutch Wadden Sea performed in the early 1980's (pre-invasion), and in 2008 (post-invasion) in the same area. The pre-invasion samples were taken between September 1981 and July 1982 along 45 transects perpendicular to the direction of tidal channels, at a depth ranging from 0 to 10 m (Dekker, 1989). Sampling was done using a 0.2 m² Van Veen-grab and a 0.2 m² modified flushing sampler (van Arkel and Mulder, 1975), both modified for subtidal sampling from a boat. For the Van Veen grab, no more than 8–10 cm of sediment were collected for each sample to avoid deeper living organisms. The flushing sampler was adjusted to sample 40 cm of sediment as in the Wadden Sea macrobenthic infauna rarely lives deeper than about 30 cm. Per station, three flushing sampler samples and one Van Veen-grab sample were taken (Dekker, 1989). The post-invasion samples were taken in October 2008, when the same sampling region was re-visited and sampled by means of a 0.06 m² Reineck box corer (Dekker and Drent, 2013). Samples were counted if the core reached a depth of at least 15 cm. The mussel shells from both surveys have been kept in a shell collection at NIOZ, and we took mussels collected in the pre-invasion and post-invasion periods from roughly the same areas. Only very few locations contained mussels during both sampling campaigns so that paired comparisons were not possible, however, sampling locations during both periods overlapped to a reasonable extent (Fig. 1). For each mussel valve from the collection, the shell length was measured and then the valves were placed on a tray and an x-ray was taken to identify *P. ciliata* burrows inside of the shells (Fig. 2).

2.3. Statistical analyses

To investigate the current abundance and host use of *P. ciliata* in the intertidal, we used the field survey samples from 2017 and calculated the mean density of worms (ind. m⁻²) in live individuals and dead shells of native mussels and periwinkles as well as invasive Pacific oysters for each of the three locations. In addition, we calculated the mean total fresh weight (kg) of live individuals and dead shells of the three host species in the 15 × 15 cm samples per location and the mean relative density of *P. ciliata* in the three host species (ind. per kg host fresh weight). We used fully-factorial ANOVAs to investigate the effect of host species (mussels, periwinkles, oysters), shell status (dead or alive) and location (1–3), all added as fixed factors, on the three response variables (log(x + 1)-transformed). All raw data can be found in Waser et al. (2021).

As the x-rays taken from mussels from the historical shell collections did not provide numbers of worms per shell but only the presence or absence of worm burrows, we calculated the overall prevalence (%) of infections with *P. ciliata*. We did this separately for samples from the intertidal and subtidal for the periods before (pre-invasion) and after the invasion (post-invasion) of the Pacific oyster. In addition, we calculated the mean density of mussels (ind. m⁻²) and the density of infected mussels (ind. m⁻²) per habitat type and period. As the intertidal and subtidal samples originated from different sampling campaigns and slightly different periods, we tested for differences between pre- and post-invasion periods separately for each of the two habitats. Differences in prevalence between pre- and post-invasion periods were tested using Fisher's Exact Tests, differences in the density of mussels were tested using *t*-tests after log-transformation of the data. The density of infected mussels per habitat type and period only served an illustrative purpose and we did not statistically test for differences between periods due to the absence of replication. All raw data can be found in Waser et al. (2021).

Table 1

Results of fully-factorial ANOVA analyses on the effect of location (1–3), host species identity (periwinkles, mussels, oysters), shell status (dead or alive) on the abundance of *P. ciliata* (ind. m⁻²), the mean total fresh weight (kg) of live individuals or dead shells of the three host species in the 15 × 15 cm samples per location, and the relative density of *P. ciliata* in the different host species (ind. per kg host fresh weight). *N* = 3 locations, 8 sampling frames each. Significant results are indicated in bold letter type.

	df	MS	F	p
<i>Polydora</i> abundance				
Location	2	0.62589	1.11266	0.33189
Species	2	21.57041	38.34601	<0.001
Status	1	8.75369	15.56155	<0.001
Location*Species	4	2.7869	4.9543	<0.001
Location*Status	2	0.16012	0.28465	0.753
Species*Status	2	1.04023	1.84923	0.162
Location*Species*Status	4	0.87387	1.55348	0.191
Error	126	0.56252		
Host weight per sample				
Location	2	0.005857	5.5305	0.005
Species	2	0.192997	182.2345	<0.001
Status	1	0.095275	89.962	<0.001
Location*Species	4	0.00467	4.4092	0.002
Location*Status	2	0.003106	2.9332	0.057
Species*Status	2	0.021492	20.2931	<0.001
Location*Species*Status	4	0.00163	1.5387	0.194963
Error	126	0.001059		
Relative <i>Polydora</i> density per sample				
Location	2	0.15701	0.62764	0.535525
Species	2	5.41501	21.64646	<0.001
Status	1	1.86877	7.47041	0.007
Location*Species	4	1.19374	4.77196	0.001
Location*Status	2	0.06884	0.27518	0.760
Species*Status	2	0.04847	0.19374	0.824
Location*Species*Status	4	0.28983	1.15858	0.332
Error	125	0.25016		

3. Results

The data from the intertidal field survey in 2017 showed that the total density of *P. ciliata* significantly differed among host species and shell status (dead or alive; Table 1; Fig. 3). In general, highest density of *P. ciliata* was found in the shells of live Pacific oysters and worm abundance in live molluscs was higher than in dead shells (Fig. 3). However, the effect of host species identity differed between locations as indicated by the significant interaction term in the ANOVA (Table 1), resulting from relatively similar worm densities among the three host species at location 3 (Fig. 3). Oysters generally dominated in the samples in terms of total fresh weight but again this depended on location as well as on shell status (dead or alive) as indicated by the significant interaction terms (Table 1; Fig. 3). Similarly, relative worm densities tended to be highest in oysters, but this depended on location (Table 1; Fig. 3).

In the mussels from the historical shell collection, infection prevalence of *P. ciliata* in mussels from the intertidal was lower in the post-invasion (4.2%) than in the pre-invasion (10.2%) period, but this difference was not statistically significant (Fisher's Exact Test; *p* = 0.055; Fig. 4). In the subtidal samples, *P. ciliata* infection prevalence in mussels was not statistically different between the pre-invasion (9.4%) and the post-invasion (8.8%) periods (Fisher's Exact Test; *p* = 0.878; Fig. 4). Size frequency distributions of infected and uninfected mussels showed a similar size range of mussels present in the pre- and post-invasion periods for the subtidal, but a smaller size range (fewer large mussels) in the post-invasion compared to the pre-invasion period for the intertidal mussels (Fig. 5). Mussel density did not statistically differ between pre- and post-invasion periods in both intertidal (pre-invasion: 172.5 ± 47.9 SE ind. m⁻²; post-invasion: 272.1 ± 76.1; *t*-test; *t* = 1.086, *p* = 0.301) and subtidal samples (pre-invasion: 530.2 ± 200.4; post-invasion: 408.8 ± 99.4; *t*-test; *t* = 1.077, *p* = 0.286; Fig. 4). The relative density of infected mussels was similar in the pre- and post-invasion periods and

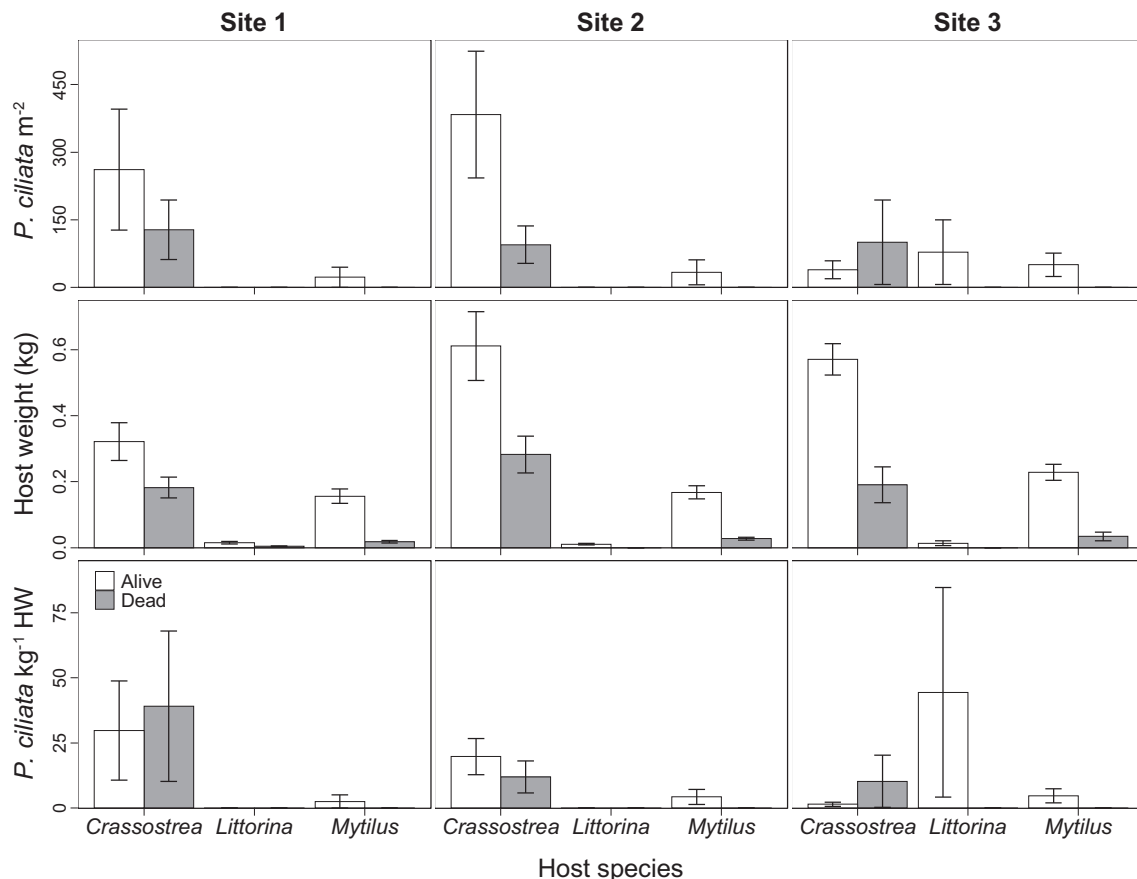


Fig. 3. Mean abundance (ind. m⁻²) \pm SE of the shell-boring polychaete *Polydora ciliata* in live individuals (white) and dead shells (grey) of invasive Pacific oysters (*Crassostrea (Magallana) gigas*), native periwinkles (*Littorina littorea*) and blue mussels (*Mytilus edulis*) at three locations (1–3) in the intertidal along the east coast of the island of Texel in 2017. Also shown are the mean total freshweight (kg) \pm SE of the three hosts species in the samples taken per location and the mean density of *P. ciliata* (ind. Per kg host fresh weight) \pm SE in the three host species per location. $N = 8$ frames of 15 \times 15 cm per mixed bed.

generally lower in the intertidal than in the subtidal (Fig. 4; not formally tested due to lack of replication and different sampling designs).

4. Discussion

The field survey revealed that invasive Pacific oysters have become the dominant host for the native shell-boring worm *P. ciliata* on intertidal flats in the Wadden Sea in terms of the total density of worms in this host species. This was not simply resulting from a higher biomass of oysters than mussels on the sample scale, instead the higher relative density of *P. ciliata* in oysters compared to mussels indicated that there were more worms per unit biomass in oysters than in mussels. It is easy to imagine that the thick shells of Pacific oysters probably provide a better habitat for the worms than the relatively thin and also much smaller shells of mussels and periwinkles. Similarly, Pacific oysters seem to be the only suitable host to date in the Wadden Sea for the recently discovered invasive shell-boring polychaete *Polydora websteri*, which is much larger than the native *P. ciliata* and thus probably depends on a thicker shell (Waser et al., 2020). However, whether the high abundance of *P. ciliata* in Pacific oysters results from a higher survival of worms in oyster shells or whether it is the result of a preference of larval stages of the worm to settle on Pacific oysters is not known and needs further study.

Interestingly, *P. ciliata* density was also relatively high in dead shells of Pacific oysters while the worms were more or less absent in dead shells of mussels and periwinkles. The settlement onto shells of dead oysters has also been observed in the related species *P. websteri* infecting Eastern oysters (*Crassostrea virginica*) in the US (Clements et al., 2018).

In general, oysters produce an adhesive structure that allows individual oysters to cement their shells to each other. This capability often leads to clusters of attached, vertically positioned oysters, in the long term, resulting in the development of biogenic reefs which do not tend to easily disintegrate, even after the death of individual oysters (Reise et al., 2017b; Clements et al., 2018). Hence, Pacific oysters provide a suitable habitat for *P. ciliata* even after death, as dead oysters will still be embedded in the extensive reef matrix. In contrast, the much lighter and less attached shells of mussels and periwinkles will be a less stable habitat for the worms, as there is a higher chance for shells of dead individuals of getting washed away or get buried by sedimentation processes. The high suitability of both live and dead Pacific oysters as a habitat for *P. ciliata* echoes findings on the distribution of general epibenthic fauna in oyster reefs which also tends to use both types of oyster structures to a similar extent (Norling et al., 2015). The high spatial and temporal stability of both dead and live Pacific oysters within the reefs probably facilitates local *P. ciliata* densities and also makes them less affected by changes in the population density of (live) oysters caused by mass mortality events which can occur for example in strong winters (Fey et al., 2010; Büttger et al., 2011; Reise et al., 2017a).

Although *P. ciliata* density peaked in Pacific oysters, we also observed that the effect of host species identity interacted with location as indicated by relatively similar densities of *P. ciliata* among host species at one (Site 3) of the three intertidal locations. We can only speculate about the underlying mechanisms but one of the potential reasons for differences in polychaete density could be differences in host size among locations. *Polydora ciliata* prevalence and infection levels in individual hosts are known to be positively correlated with host size,

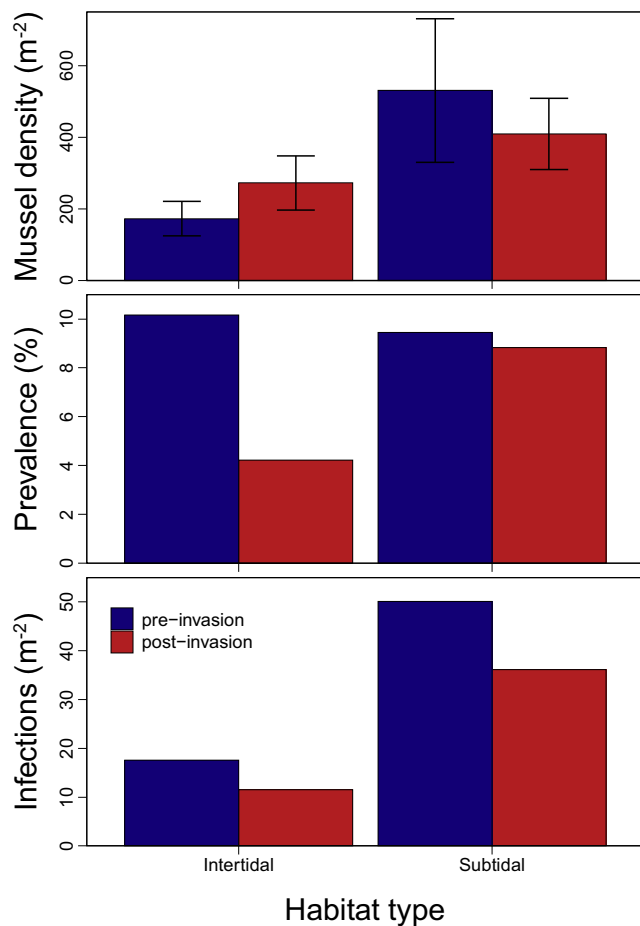


Fig. 4. The shell-boring polychaete *Polydora ciliata* in shells of blue mussels (*Mytilus edulis*) from historical shell collections from sampling programmes in the intertidal and subtidal of the western Dutch Wadden Sea before (blue) and after (red) the invasion of the Pacific oyster (*Crassostrea (Magallana) gigas*). Shown are the mean density of mussels (ind. m⁻²) ± SE, the prevalence (%) of mussels infected with *P. ciliata* as well as the density of infected mussels (ind. m⁻²) per habitat type and period. $N = 319$ (pre: 177; post: 142) and 503 (pre: 254; post: 249) mussels for intertidal and subtidal habitat samples, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

which is itself correlated with host age and thus exposure time to settling larval stages of the worms (Ambariyanto and Seed, 1991; Warner, 1997; Goedknecht et al., 2019). However, we cannot conclude whether host size played a role in explaining differences in *P. ciliata* abundance among locations in our study as we did not measure the size of individual hosts in the field survey. Another potential driver for heterogeneities in local *P. ciliata* densities in the intertidal could be tidal level as the worms are known to increase in abundance towards lower tidal levels, probably related to feeding time and emersion sensitivity (Warner, 1997; Buschbaum et al., 2007). However, tidal level is not likely to explain differences in *P. ciliata* densities in our study as all three mixed mussel and oyster beds were positioned at approximately similar tidal levels in the lower intertidal.

Given the fact that density of *P. ciliata* was highest in Pacific oysters and that oyster shells probably provide a highly suitable habitat for the worms, it seems likely that the oysters could have caused a spillback effect and lead to an increase of infections with *P. ciliata* in native mussels since their appearance in the Wadden Sea. However, our data from the historical shell collections did not provide any strong support that such a spillback effect has occurred as there were no statistical differences in prevalence between the pre- and post-invasion periods,

both in the intertidal and the subtidal. Despite no significant differences between the two time periods, the prevalence of *P. ciliata* in the intertidal was actually lower in the post-invasion period than before the invasion of the Pacific oyster. This low prevalence of *P. ciliata* was probably simply related to the fact that there were fewer larger mussels in the post-invasion period as indicated by the size frequency distribution. Given the known positive relationship of *P. ciliata* infections with host size (Ambariyanto and Seed, 1991; Warner, 1997; Goedknecht et al., 2019), the lack of larger mussels in the post-invasion samples is likely leading to a lower overall prevalence. In contrast, for the subtidal samples, the size distribution of mussels was very similar in both periods and prevalence was more or less identical in both periods, suggesting the absence of a spillback effect. However, we acknowledge that our x-ray method did not provide intensity measures of infections with *P. ciliata* for the pre- and post-invasion periods. Hence, we cannot rule out that polychaete intensity (but not prevalence) has changed. The lower infection prevalence of *P. ciliata* in intertidal mussels from the post-invasion (4.2%) compared to the pre-invasion period (10.2%), although marginally non-significant ($p = 0.055$), may suggest that infection levels in native intertidal mussels have decreased after the arrival of the Pacific oyster. If this would also hold true for infection intensities, it would suggest that the invasive oysters can exert a dilution effect, e.g. by attracting infective larval stages of the polychaetes and thus lowering infection levels in native mussels. However, experimental research will be needed to identify a potential dilution effect. With the existing results to date we can only conclude that the invasion of the Pacific oyster does not seem to have caused marked changes in the abundance of *P. ciliata* in mussels in the Wadden Sea.

In general, *P. ciliata* infections are known to reduce host condition and the strength of shells which increases predation pressure (Kent, 1979, 1981). With regard to the Pacific oysters, however, *P. ciliata* seems to have no considerable effect on oyster populations (Lemasson and Knights, 2019). Presumably, the relatively large and thick oyster shells provide ample of habitat for the polychaete, so that even high infection loads do not cause a significant impact on the oyster's performance. Hence, it is rather unlikely that *P. ciliata* plays a significant factor in the invasion success of Pacific oysters in the coastal waters of Europe.

Although we did not observe a spillback effect caused by the Pacific oyster, about 10% of the mussels were still affected by *P. ciliata* infections and are thus affected by the negative effects of infections. However, it remains to be studied whether this has any population level consequences and whether it affects the production efficiency of mussels from a shellfish aquaculture perspective. The latter, in turn, may also itself affect *P. ciliata* abundances as it is common practice to harvest seed mussels that have been placed onto subtidal culture plots after two to three years (Smaal et al., 2021). This is much shorter than the life-time of natural beds which can exist for many years to decades as known from intertidal populations (van der Meer et al., 2019). Hence, the culture practices may reduce the temporal exposure of mussels in culture plots and thus help prevent the build-up of high abundances of *P. ciliata*. Unfortunately, there were too few mussels from culture plots (see Fig. 1) in our data set to investigate a potential effect of mussel culture practices on *P. ciliata* infections in mussels, but this may warrant further study in the future.

In conclusion, while the invasive Pacific oyster has become the main host for the native shell-boring polychaete *P. ciliata*, we could not detect a spillback effect to the native mussel population in the Wadden Sea, which limits the indirect impact of the invasive oysters on mussels. However, Pacific oysters can cause a multitude other direct and indirect effects on parasite-host interactions in native biota (e.g. Goedknecht et al., 2016, 2019, 2020) which calls for further research on the ecological consequences of this prominent invader of European coastal ecosystems.

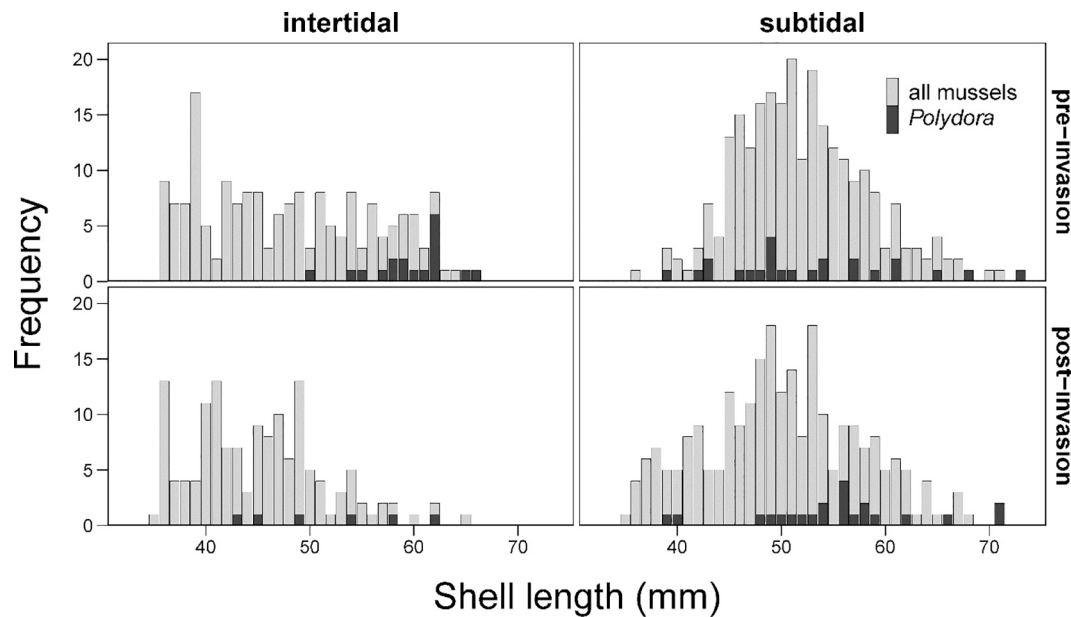


Fig. 5. Frequency distribution of the shell length (mm) of the blue mussel (*Mytilus edulis*) shells investigated from historical shell collections from sampling programmes in the intertidal and subtidal of the western Dutch Wadden Sea before (above) and after (below) the invasion of the Pacific oyster (*Crassostrea (Magallana) gigas*). Mussels infected with the shell-boring polychaete *Polydora ciliata* are indicated in black.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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