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ORIGINAL ARTICLE

Alien parasitic copepods in mussels and oysters of the Wadden Sea

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Abstract Molluscan intestinal parasites of the genus *Mytilicola*, specifically *M. intestinalis*, were initially introduced into bivalves in the North Sea in the 1930s. It was presumably introduced from the Mediterranean with ship-fouling mussels, then attained epidemic proportions in *Mytilus edulis* in the 1950s and is now widely established in the North Sea region. *Mytilicola orientalis* was co-introduced with Pacific oysters to France in the 1970s and in the southern North Sea in the early 1990s. Its main host *Crassostrea gigas* has massively invaded the Wadden Sea with a concomitant decline in mussels. To explore whether introduced mytilicolid parasites could play a role in the shifting dominance from native mussels to invasive oysters, we analysed 390 mussels and 174 oysters collected around the island of Sylt in the northern Wadden Sea. We show that *M. intestinalis* has a prevalence >90% and a mean intensity of 4 adult copepods in individual mussels with >50 mm shell length at all sheltered sites. By contrast, none were found in the oysters. However, at one site, we found *M. orientalis* in *C. gigas* with a prevalence of 10% and an intensity of 2 per host individual (August 2008). This constitutes the most northern record in Europe for this Pacific parasite until now. Alignments of partial sequences of the mitochondrial cytochrome oxidase I (COI) gene and the nuclear internal transcribed spacers (ITS) and 18S rDNA sequences each show a distinct difference between the two species, which confirms our morphological identification. We suggest that the high parasite load in mussels compared to oysters may benefit the continued expansion of *C. gigas* in the Wadden Sea.

Keywords Introduced species · Mussels · Mytilicola · Oysters · Parasites · Wadden Sea

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Introduction

Invasions of alien species have become a major process of change in marine coastal ecosystems (Ruiz et al. 1997; Reise et al. 2006; Rilov and Crooks 2009). Parasites may have two different effects on this global process. On the one hand, introduced species often escape from their native parasites during transport and when founder populations are rather small (Torchin and Lafferty 2009). In addition, parasites with complex life cycles seldom encounter all necessary hosts in a recipient ecosystem and thus are rarely co-introduced (Torchin et al. 2003), and native parasites tend to infest alien hosts only at low numbers (Krakau et al. 2006). This parasite release is assumed to generally facilitate invasive hosts.

On the other hand, with transfers of organisms for aquaculture and to some extent also with ships or the aquaria trade, diseases and parasites have been introduced with occasionally disastrous effects when they infest naïve (previously unexposed) host species in a recipient coastal region (Cook et al. 2008; Minchin et al. 2009; Pillay 2004).

Particularly, oyster stocks have been strongly affected by introduced disease agents (Andrews 1980; Wolff and Reise 2002). Many of these parasites mature and reproduce on or in a single host, and spores or larvae disperse to the next host individual (direct life cycle). This makes their invasion more likely compared to parasites with complex life cycles which depend on the presence of all hosts to become established. Parasitic copepods of the genus *Mytilicola* exemplify the type of invasive parasites with direct life cycles. They inhabit the guts of molluscs and disperse via larval stages to infect other host individuals (Lauckner 1983; Gotto 2004). In European seas, *M. intestinalis* has been described from the mussel *Mytilus galloprovincialis* in the Adriatic Sea by Steuer (1902). On the Atlantic coast, it appeared in *M. edulis* in England and in the German Bight in the 1930s (Caspers 1939; Korringa 1968) and is believed to have been imported with mussels fouling ship hulls (Korringa 1968).

However, for British waters, Eno et al. (1997) have not included *M. intestinalis* as an introduced species, based on a pers. comm. by M. Gee "that its biology suggests that it is a boreal species" (p. 12). This remark seems to be derived from results in Gee and Davey (1986), showing that development can be completed at temperatures below 18°C albeit at slow rates. We follow Korringa (1968) who assumes it as very unlikely that this highly conspicuous parasite has been overlooked in North Sea mussels prior to the 1930s, and thus regard *M. intestinalis* as an introduced rather than being a cryptogenic species.

From 1949 to 1951, an epidemic was observed at the North Sea coast, and *M. intestinalis* was blamed for massive mortality in *M. edulis* with a severe impact on the mussel fishery (Korringa 1968). Although this parasite evidently can harm its host (e.g. Meyer and Mann 1950; Williams 1969; Mann 1979; Theisen 1987), doubts have been raised as to whether *M. intestinalis* has been the causal agent for the observed mortality in the mussel epidemic or as to whether it merely had spread coincidentally at that time (Dethlefsen 1975; Lauckner 1983).

A second *Mytilicola* species, *M. orientalis*, has been described by Mori (1935) from the Pacific oyster *Crassostrea gigas* and mussels in the Inland Sea of Japan, and this species was first introduced with its host *C. gigas* to the Pacific coast of North America in the 1930s and to France in the 1970s (Katkansky et al. 1967; His 1977; His et al. 1978; Lauckner 1983; Grizel 1985). On the European Atlantic coast, it has spread further to the Netherlands and Ireland (Stock 1993; Holmes and Minchin 1995) and has also been introduced with *C. gigas* into the Mediterranean Sea (Clantzig 1989). Although it was initially feared that *M. orientalis* could initiate an epidemic similar to the one assumed with *M. intestinalis* in 1949–1951, this has not yet been observed, and harm to the host *C. gigas* seems to be small (Deslous-Paoli and Héral 1988; De Grave et al. 1995; Steele and Mulcahy 2001).

In the northern Wadden Sea, the typical hosts for these two parasites co-occur. While the mussels *M. edulis* are native, the oysters *C. gigas* have recently been introduced. Regular imports of young Pacific oyster *C. gigas* for sea ranching at Sylt island have occurred since 1986, and the oysters subsequently invaded mussel beds in that area (Reise 1998; Diederich et al. 2005). The question arose as to whether *C. gigas* could displace the native mussels (Diederich 2005, 2006; Nehls et al. 2006). Direct competition between mussels and oysters for space and food has been suggested (Troost 2009), but it also seems likely that indirect competition mediated by differential parasite loads among the two host species (apparent competition) could be another contributing factor (Krakau et al. 2006).

The aim of our study was to investigate mussels and oysters for the presence of the two parasitic copepod species and to quantify the respective infection levels in their hosts. To test the selectivity of the infestation, we experimentally investigated the host specificity of *M. intestinalis* in mussels and oysters. Due to ambiguous features of species identification mentioned in the literature (Stock 1993, Gotto 2004), we sequenced parts of the nuclear rDNA and one mitochondrial gene to genetically verify species determination based initially on morphological features only.

Materials and methods

Sampling area

The 390 individuals of *Mytilus edulis* and 174 of *Crassostrea gigas* examined in this study were sampled at six sites around the island of Sylt in 2007 and 2008 (Fig. 1, Tables 1 and 2). The intertidal sampling sites in the north and in the south are disconnected by a dam from the island to the mainland since 1927. Sampling site 3 at the exposed beach refers to mussels attached to groins. All other mussels and the oysters collected were living on sediment in the low tidal zone and at one site in the shallow subtidal zone. The subtidal mussels collected in August 2007 were dredged at a depth of 1–2 m, while the ones collected in May 2008 were collected by hand at a depth of about 0.5 m during extreme low tide. Regarding the two sites sampled for both mussels and oysters, the oyster bank was approximately 500 m from the mussel bank at site 2, whereas mussels and oysters co-occurred in a mixed assemblage at site 6. For every host individual, the infestation of *Mytilicola* spp. was recorded to determine the mean prevalence (% of host individuals infected) and the mean intensity (mean number of parasite individuals per

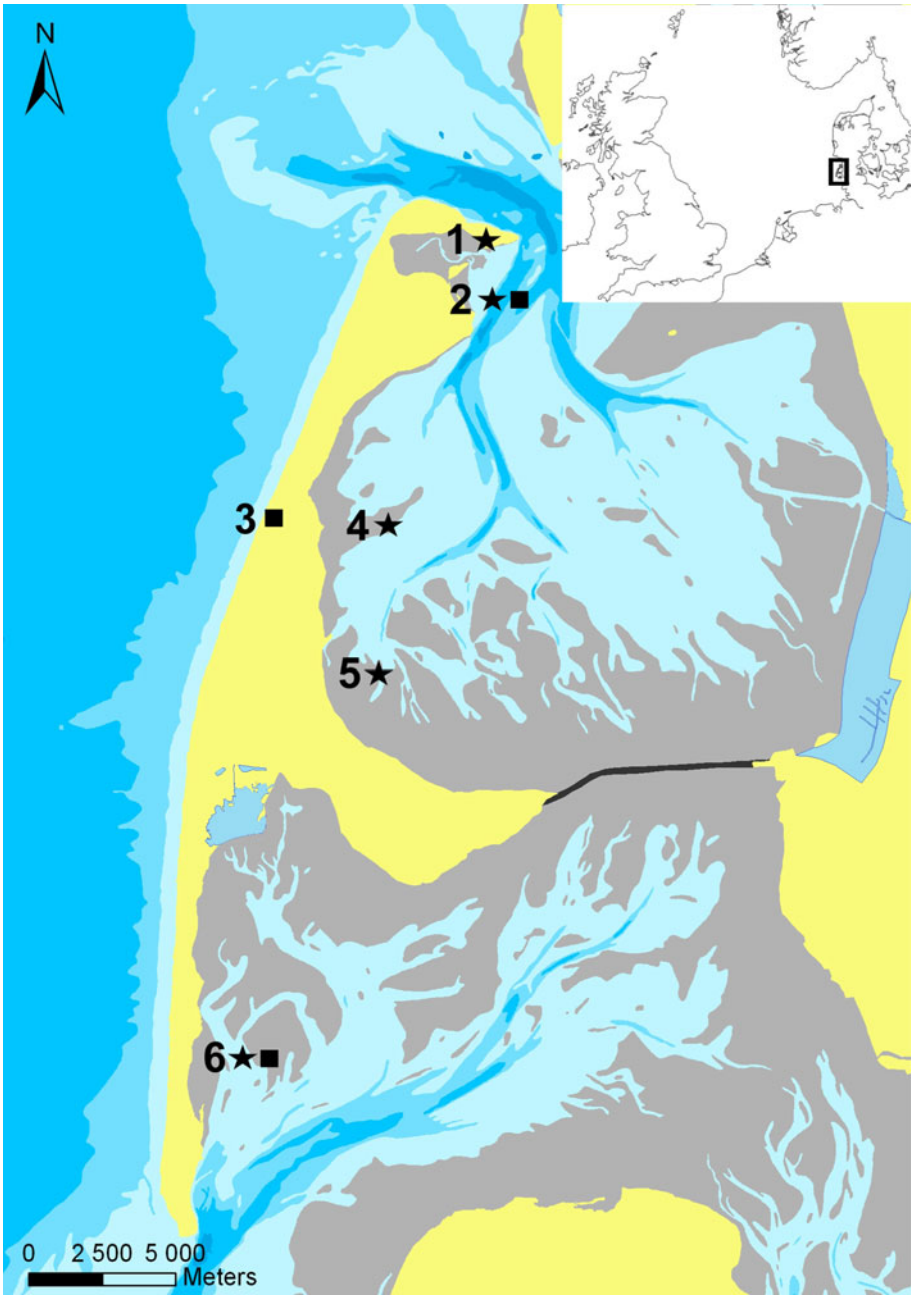

Fig. 1 Sampling sites of mussels (*squares*) and oysters (*asterisks*) around the North Sea island of Sylt. *1* Ellenbogen, *2* List, *3* Kampen, *4* Leghörn, *5* Munkmarsch, *6* Puan Klent. *Grey shaded* areas indicate the intertidal zone

Table 1 *Crassostrea gigas* investigated for intestinal copepods with locality (see Fig. 1), date, number, shell length (mean ± standard deviation) prevalence (% of host individuals infected) and intensity (mean ± standard deviation)

Site	Date	Oysters n	Shell length (mm)	Prevalence (%)	Intensity ± SD
1	May 2008	30	95.3 ± 28.4	0.0	0.0
2	August 2007	19	80.8 ± 26.5	0.0	0.0
2	August 2008	55	91.0 ± 21.5	0.0	0.0
4	May 2008	10	128.1 ± 20.0	0.0	0.0
5	May 2008	30	107.0 ± 24.7	0.0	0.0
6	August 2008	30	106.2 ± 22.1	10.0	1.7 ± 0.6

Only *Mytilicola orientalis* was found in *C. gigas*

Table 2 *Mytilus edulis* investigated for intestinal copepods with locality (see Fig. 1), date, number, shell length (mean ± standard deviation) prevalence (% of host individuals infected) and intensity (mean ± standard deviation)

Site	Date	Mussels n	Shell length (mm)	Category	Prevalence (%)	Intensity ± SD
2	August 2007	30	24.1 ± 3.9	Small	33.33	1.60 ± 0.97
2	August 2007	30	38.1 ± 5.1	Medium	63.33	4.05 ± 2.98
2	August 2007	30	57.6 ± 6.4	Large	90.00	4.48 ± 3.32
2*	August 2007	30	72.7 ± 6.4	Large	93.33	8.07 ± 4.75
2*	May 2008	30	70.3 ± 8.1	Large	86.67	3.81 ± 2.95
2*	August 2008	120	68.0 ± 8.1	Large	93.30	5.28 ± 3.53
3	August 2007	30	35.7 ± 3.1	Medium	3.33	1.0 ± 0.18
3	May 2008	30	32.7 ± 1.6	Medium	0.0	0.0 ± 0.0
6	August 2007	30	60.1 ± 4.2	Large	93.33	4.18 ± 3.25
6	August 2008	30	66.5 ± 3.7	Large	96.67	3.72 ± 2.76

Only *Mytilicola intestinalis* was found in *M. edulis* *subtidal, all others intertidal

infected host individuals) of the two copepods in each host population.

Mussels were divided into three shell length categories: small (<30 mm), medium (30–50 mm) and large (>50 mm; cp. Meyer and Mann 1950). These categories have previously been shown to be positively correlated with prevalence and intensity of *M. intestinalis* (e.g. Dethlefsen 1975). Due to the fact that the last recruitment event in *C. gigas* had occurred in summer 2006, small oysters were not available and random samples were taken.

After mussels and oysters were opened, the visceral mass was taken out and squeezed between two glass plates. Only adult stages of *Mytilicola* spp. were counted. These are readily detected due to their size and intensive red colour.

To detect statistically significant differences in infection levels, prevalence and intensity data were compared using chi-square test and analysis of variance (ANOVA), respectively.

Infection experiment

In order to test the host specificity of *M. intestinalis* with regard to *M. edulis* and *C. gigas*, a pilot study was conducted from the beginning of September to the beginning of November 2008. We infected previously uninfected individuals (medium-size mussels from site 3 and oysters from site 2, recipient mussels and oysters) by keeping them together in treatments with highly infected large blue mussels (from site 2, donor mussels) for 2 months. Recipient mussels were marked and could readily be distinguished by their size. The average rate of infection of recipient mussels and oysters and donor mussels was determined before the experiment commenced with samples of $n = 30$ for each host species (see Tables 1 and 2, samples from 2008). Epibionts of mussels were removed prior to the experiment.

Twelve aquaria (20 l) were used, each containing 10 donor mussels. Recipient mussels and oysters were exposed to infected mussels separately to prevent mutual interference. Therefore, six treatments were used for the infection of mussels and 6 for the infection of oysters. Of the recipient mussels and oysters, 6 individuals were added to each treatment. The bivalves were kept in oxygenated sea water filtered with a gravel filter. Every day, 3 l of each tank were renewed. Once every week, the whole tank was filled with fresh filtrated sea water. Previously uninfected mussels and oysters ($n = 20$ each) were kept as a control in unfiltered seawater. Water temperature remained at 15°C during the entire experiment. After 2 months, all individuals were simultaneously taken out of the water and stored at 4°C until dissection within 2 weeks. Cooled storage is assumed to have no effect on the intensity of the infestation (Dethlefsen 1972).

Genetic species differentiation

For the genetic differentiation of the species, the DNA of 5 specimens of *Mytilicola intestinalis* and 2 of *M. orientalis* was extracted using the Qiagen DNeasy Blood and Tissue Kit. From this extracted DNA, the sequences of the 18S rDNA, the internal transcribed spacers (ITS) of the rDNA and sequences of the 5′ part of the mitochondrial cytochrome c oxidase I (COI) gene were determined after amplification using polymerase chain reaction (PCR). Due to its length, the 18S sequence was divided into 3 overlapping parts which were separately amplified using three sets of forward and reverse primers. All primers used are specified in Table 3. The annealing temperature was set to

Table 3 Name and sequence of primers used for PCR amplification and sequencing

Primer name	Sequence 5′ → 3′	Reference
COI f	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
COI r	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)
ITS1 f	TCCGTAGGTGAACCTGCGG	White et al. (1990)
ITS4 r	TCCTCCGCTTATTGATATGC	White et al. (1990)
18S f	TACCTGGTTGATCCTGCCAG	Huys et al. (2006)
18S 554 f	AAGTCTGGTGCCAGCAGCCGC	Huys et al. (2006)
18S 1150 f (p2)	ATTGACGGAAGGGCACCACCAG	Huys et al. (2006)
18S 614 r	TCCACCTACGAGCTTTTTAACC	Huys et al. (2006)
18S 1282 r	TCACTCCACCAACTAAGAACGGC	Huys et al. (2006)
18S r	TAATGATCCTTCCGCAGGTTCAC	Huys et al. (2006)

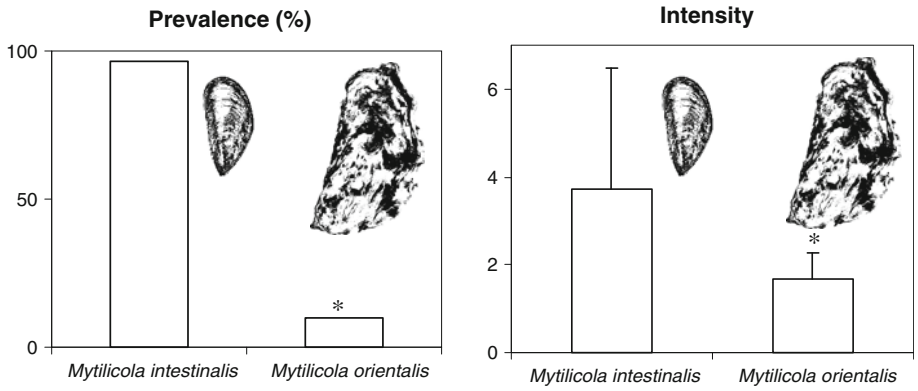

Fig. 2 Prevalence and intensity of *Mytilicola intestinalis* in its host *Mytilus edulis* and of *M. orientalis* in its host *Crassostrea gigas* at sampling site 6 in August 2008 (see Fig. 1, Tables 1 and 2). $n = 30$ for each *asterisk* statistically significant difference

57°C for the 18S primers and to 50°C for the COI and ITS primers. The PCR products were purified using the Qiagen QIAquick PCR Purification Kit and sent to Eurofins MWG Operon for sequencing. The three parts of the 18S sequence were manually rejoined to one sequence of 1,728 base pairs based on the overlapping regions. The sequences are available in GenBank under the accession numbers HM775187–HM775206.

The 18S rDNA, the COI and the ITS sequences of *M. intestinalis* and *M. orientalis* were inserted into an alignment using ClustalX (Higgins and Sharp 1988). Based on this alignment, the percentage of differing bases was calculated. All three genomic regions were determined in both *M. orientalis* individuals analysed. Regarding *M. intestinalis*, COI and ITS sequences were obtained from all five individuals while for the 18S sequencing, only two individuals were used.

Results

Infection levels in mussels and oysters

Almost all mussel populations were infected with *M. intestinalis*, and all mussels were free of *M. orientalis* (Tables 1 and 2). Prevalence and intensity were generally high in large mussels (>90% and approx. 4 parasites/host), and only medium mussels from the exposed shore of the island (site 3) had very low infection values (Table 1). In contrast, oysters were free of *M. intestinalis*, and *M. orientalis* was found only at a single sampling site (Fig. 1, site 6; 54.7917°N, 8.3056°E). At this site, infection levels of *M. intestinalis* in mussels were significantly higher than of *M. orientalis* in oysters (Fig. 2; prevalence: $\chi^2 = 45.3$; intensity: $F_{59} = 44.3$, $P < 0.001$).

Experimental infections

This pilot experiment yielded no infection of oysters but a noticeable infection of previously uninfected mussels (recipient mussels). Approximately, half of the recipient mussels in each aquarium were infected (mean prevalence 45.6 ± 7.2%, $n = 35$) with one or two *M. intestinalis* in each mussel (mean intensity 1.3 ± 0.3). After the experiment, the donor mussels used for the infection had a prevalence of 93.3% and an intensity of 5.3 ± 3.5. (The control mussels, previously uninfected but kept in unfiltered seawater, unexpectedly showed similar infection rates (prevalence 30.0% and intensity 1.7 ± 0.9). Again, oysters remained uninfected.)

Table 4 Inter- and intraspecific sequence differences determined in *M. intestinalis* and *M. orientalis*

Sequence	Base pairs	Interspecific (%, min/max)	*M. intestinalis* intraspecific (%)	*M. orientalis* intraspecific (%)
18S	1,744	1.20/1.26	0.0	0.06
COI	628	16.08/16.40	0.0	0.64
ITS	515	14.17	0.0	0.19

For interspecific values, minimal (min) and maximal (max) values are shown

Genetic species differentiation

A comparison of the *M. intestinalis* and *M. orientalis* sequences obtained showed notable differences regarding intra- and interspecific variation. Intraspecifically, no sequence variation existed between the analysed individuals of *M. intestinalis* (based on five individuals for the COI and ITS sequences and two individuals for the 18S region). For the two *M. orientalis* individuals analysed, intraspecific variations were found in all three sequences, although they are well under 1% (Table 4).

The interspecific differences are much higher. Regarding the conserved 18S sequence, they exceed 1%. For COI and ITS, both sequence markers with higher mutation rates, differences above 10% were determined.

During our investigations, we noticed that morphological identification features mentioned by Stock (1993) and Gotto (2004) are problematic. The caudal rami are said to be strongly divergent in *M. intestinalis* and almost parallel in *M. orientalis*. According to our observations, this feature is not reliable because *Mytilicola* can actively pull on the caudal rami causing them to lie parallel or to spread them out until they lie at a 180° angle to each other. We found the dorsal appendages to be the most suitable feature for identification: they are short and rounded in *M. intestinalis* and distinctly pointed and elongated in *M. orientalis* (Fig. 3).

Discussion

In the northern Wadden Sea, we found a heavy infestation of native mussels *Mytilus edulis* by the intestinal mytilicolid copepod *Mytilicola intestinalis,* indicating that this introduced parasite has become well established since the first record in 1970 (Dethlefsen 1972), while still absent in 1950 and 1965 (Meyer and Mann 1950; Theisen 1966). Prevalence and intensity in 2003–2004 (Thieltges et al. 2006, 2008) and in 2007–2008 (this study) have been at a similarly high level. In the invasive Pacific oyster *Crassostrea gigas*, we found no *M. intestinalis.* However, at a single site in the south of the island of Sylt, far away from the local oyster culture lot in the north of the island, we found for the first time oysters infected with *M. orientalis*. The nearest previously reported occurrence is the Rhine Delta in the Netherlands (Stock 1993), approximately 570 km along the North Sea shore in south-western direction. We speculate that this parasite may have just arrived at this northern most location for this Pacific species in Europe, although this site has not been screened previously. Thus, the sweeping invasion of *C. gigas* in the northern Wadden Sea presumably took place in the absence of this parasite burden.

The presence of both parasitic copepods was confirmed by the molecular analyses. Avise (2000) suggests <1% for intraspecific and >1% for interspecific COI variation. We found differences of >1% even in the conserved 18S sequence while COI sequences differed between *M. intestinalis* and *M. orientalis* by around 16%. Thus, even when the limit of 1% for species differentiation based on COI variation may be low, our results reveal a clear genetic distinction between both species and point to a not very close phylogenetic relationship. This is supported by a comparison with a GenBank entry of the 18S sequence of a third species of the Mytilicolidae, *Trochicola entericus* (Acc-No. AY627006). Differences between *M. intestinalis*

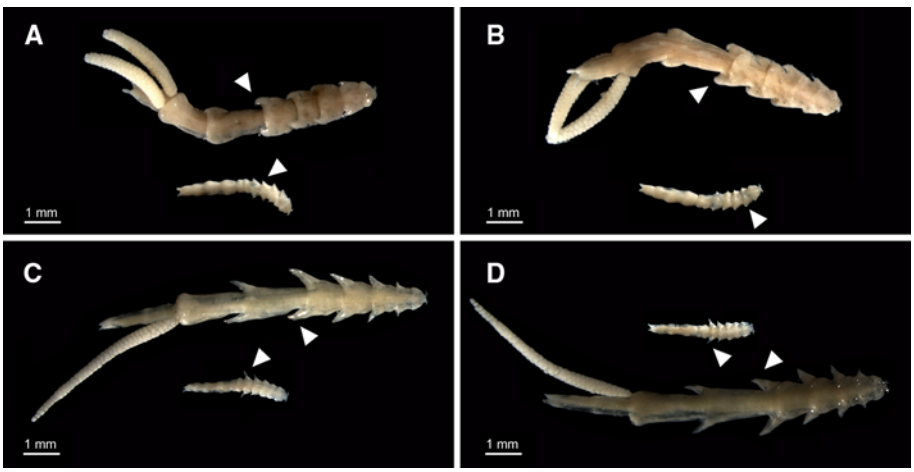

Fig. 3 *Mytilicola intestinalis* (**a**, **b**) and *M. orientalis* (**c**, **d**) in dorsal (**a**, **c**) and ventral (**b**, **d**) view. Female with egg sacks (one missing in *M. orientalis*), and dwarf male in each figure. Loss of the intense *red* colour due to ethanol fixation. Note the dorsal protuberances (*arrowheads*) as a distinct differential character

and *T. entericus* (1.32%) were higher than between *M. intestinalis* and *M. orientalis* (max. 1.26%).

Lauckner (1983) reviewed the host spectra of *M. intestinalis* and *M. orientalis,* listing a number of bivalve species and even some gastropods. Mytilids may even occasionally harbour both species concurrently in southern France (His 1977). However, *M. intestinalis* has not been recorded from Pacific oysters, except in a study by Aguirre-Macedo and Kennedy (1999) who refer to this species occurring throughout the year in *C. gigas* collected at the Exe estuary in southern England. This is in contrast to our observations since we did not find *M. intestinalis* in the 174 oysters screened for parasites, although all oysters were collected at sites where *M. intestinalis* occurred abundantly in mussels, often found in aggregates with the oysters. By referring to the above mentioned problem in species identification, we suggest that the only myticolid copepod in the intestine of *C. gigas* is *M. orientalis*.

Our experimental infections support our field observations that oysters are unsuitable as a host for *M. intestinalis*, as we yielded a high prevalence in mussels whereas the oysters remained free of this parasite. (The unexpected infection of mussels kept separate from mussels with *M. intestinalis* was most likely due to the fact that the water supply system for the flow-through tanks of the experiment has its incurrent syphon not far away from a subtidal mussel bed which is heavily infected by *M. intestinalis.*) Nevertheless, this pilot experiment may indicate that Pacific oysters are not infected by *M. intestinalis.* Unfortunately, we could not get enough *C. gigas* with *M. orientalis* to conduct the reverse infection experiment.

That *M. orientalis* was encountered only at a single site in *C. gigas* near the southern tip of the island was unexpected because the only oyster farm in the region is near the northern tip of the island, and this company regularly imports young oysters from Irish sources where *M. orientalis* has already been reported to infest *C. gigas* (Holmes and Minchin 1995; Steele and Mulcahy 2001). The sites in the north and south of Sylt are separated by a dam connecting the island with the mainland (see Fig. 1). Natural dispersal has to take a route all along the exposed shore of the island where *C. gigas* does not occur, and this amounts to a distance of at least 50 km, mostly against the residual currents. Thus, maybe it is more likely that *M. orientalis* has arrived in the northern Wadden Sea by spreading from the south within a *C. gigas* population which originates from cultures in the delta area of the Netherlands. Site 6 is located in an area with intensive mussel cultures with seed mussels taken from various sources. Pacific oysters could have been transferred together with mussels.

According to the literature, *M. intestinalis* has little or no effects on mussel growth and reproduction performance when intensity is low, but negative effects are evident at the intensities of 3 and higher (Meyer and Mann 1950; Gee and Davey 1986; Theisen 1987). Likewise, *M. orientalis* does not harm its host *C. gigas* at low intensities (Steele and Mulcahy 2001), but has a negative effect at the intensities of 3 and more (Odlaug 1946; Katkansky et al. 1967; Deslous-Paoli 1981). At the sampling site where both parasites occur, *M. intestinalis* has an intensity of about 4 in *M. edulis*, while that of *M. orientalis* was only about 2 in *C. gigas*. Thus, mussels are likely to suffer from its intestinal parasite, while the oysters are probably not. This suggests that the invasive oysters may have a competitive advantage over the native mussels in the northern Wadden Sea as a result of their unequal parasite burdens. However, differential loads with parasitic copepods are not the only competitive advantage of oysters. They may also be less susceptible to predators (crabs, shrimp, starfish), presumably due to their firm attachment, flat shape when small and with a sturdy shell when larger (own observation). And they also show low burdens of trematode parasites which regularly infect the native mussels (Krakau et al. 2006). The differential infestation of native mussels and invasive oysters with mytilicolid parasites may thus have contributed to the success of the oyster invasion. However, this difference may be attributed to the fact that *M. orientalis* has arrived very recently, six decades after the introduction of *M. intestinalis* in the North Sea region and nearly four decades after *M. intestinalis* was first found where we now have encountered *M. orientalis*. Future studies will have to show whether *M. orientalis* can attain the same level of infestation in *C. gigas* as *M. intestinalis* does in *M. edulis*.

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