Infestation of oysters and mussels by mytilicolid copepods: differences between natural coastal habitats and two offshore cultivation sites in the German Bight

By B. Pogoda[1,2], S. Jungblut[1], B. H. Buck[2,3,4] and W. Hagen[1]

[1]*Marine Zoology, University of Bremen, Bremen, Germany;* [2]*Alfred Wegener Institute for Polar and Marine Research (AWI), Bremerhaven, Germany;* [3]*Institute for Marine Resources (IMARE), Bremerhaven, Germany;* [4]*Applied Marine Biology, Bremerhaven University of Applied Sciences, Bremerhaven, Germany*

Summary

The aim of this study was to determine the macro-parasitic infestation level of oysters from the southern German Bight focussing on copepods of the genus *Mytilicola*. *Crassostrea gigas*, *Ostrea edulis* and *Mytilus edulis* were collected at five locations: three nearshore sites in the eastern Wadden Sea and two offshore cultivation sites in the German Bight. To reveal seasonal variations one sampling site was investigated in winter and summer. At the nearshore sites, *Mytilicola orientalis* was regularly detected in *C. gigas*. Prevalences ranged between 32.3% and 45.1%, intensity between 3.0 ± 0.6 and 8.2 ± 1.5. Infestation rates of *C. gigas* within the southern German Bight decreased from west to east: Apparently, *M. orientalis* has started its range extension along the German coast with gradual retardation eastwards but generally followed the invasion route of its main host, the Pacific oyster. Interestingly, we detected not only *M. intestinalis* but also *M. orientalis* as an intestinal parasite in *M. edulis*, which has sofar not previously been described as host within this region. We conclude that *M. orientalis* is flexible in its host choice. Furthermore, in the eastern Wadden Sea infestation rates of oysters and mussels by copepods are similar. These results deviate from the patterns observed for the northern Wadden Sea in terms of infestation level and host specificity. No macro-parasites were found in oysters and mussels from the offshore sites. This absence can be considered as potentially beneficial for aquaculture activities in the open ocean in terms of stamina and physiological performance.

Introduction

The Pacific oyster *Crassostrea gigas* was introduced into Dutch tidal backwaters in the 1970s (Andrews, 1980; Chew, 1990; Ruesink et al., 2005) to substitute depleted stocks of the European oyster *Ostrea edulis* and to reanimate declining oyster fisheries. The further invasion by *C. gigas* within the North Sea region developed from west to northeast along the German coast as a result of the prevailing current regime and the transport of pelagic oyster larvae (Wehrmann et al., 2000) but also through direct import for aquaculture purposes in the German Wadden Sea on the shores of the Island of Sylt. In contrast, the European oyster is considered to be extinct in German waters since it was extremely diminished by overexploitation, diseases and severe winters (Wehrmann et al., 2000). The species has not been found along the German coastline for the past half century. Populations of *O. edulis* still exist in the Danish Limfjord, in Norway and around Ireland but they are under threat or decline in all

these regions (OSPAR, 2009). Some former Wadden Sea habitats of the European oyster and even more excessively wild mussel banks of *Mytilus edulis* are now more or less dominated by the invading Pacific oyster (Diederich, 2006; Schmidt et al., 2008).

Since the beginning of the 1980s *Crassostrea gigas* spat was imported to Germany (Meixner, 1973; Neudecker, 1984) and environmental requirements of the species were investigated along the German coast. Various biotic and abiotic parameters affected fitness and health such as hypoxia, anoxia, symptoms of eutrophication as well as outbreaks of oyster parasites (Jackson et al., 2001): Wild and farmed oysters are subject to various diseases caused by macro- and micro-parasites such as copepods, trematodes, nematodes, polychaetes, and protozoans (e. g. Katkansky and Warner, 1968; Montes, 1990; Motes and De Paola, 1996; Aguirre-Macedo and Kennedy, 1999; Carnegie et al., 2000). Among others, two of these parasites, the intestinal mytilicolid copepods *Mytilicola orientalis* and *M. intestinalis* are introduced species in the North Sea: *M. orientalis* was introduced to the southern North Sea in the 1990s together with its main host, the Pacific oyster, whereas its congener *M. intestinalis* was initially introduced to the North Sea in the 1930s and is a long-established common parasite of the indigenous blue mussel *Mytilus edulis* in this region (e.g. Dethlefsen, 1975; Lauckner, 1983; Davey, 1989; Buck et al., 2005; Thieltges et al., 2008). The concrete effects of *Mytilicola orientalis* and *M. intestinalis* on their specific hosts are still under discussion. Low condition indices of mussels and oysters, low ability of recover after spawning and mass mortalities along the coasts of The Netherlands and Germany have been related to high infestation rates (Katkansky et al., 1967; Korringa, 1968; Paul, 1983). Other investigations reported no effects by mytilicolid infestations (Chew et al., 1965) or only at times of unfavourable environmental conditions (Campbell, 1970; Gee et al., 1977).

In the German Wadden Sea (northern and eastern parts) high infestation rates of native mussels *M. edulis* by parasitic copepods of the species *Mytilicola intestinalis* have been observed (e.g. Buck et al., 2005; Krakau et al., 2006; Elsner et al., 2010). Interestingly, investigations on the parasite burden at offshore locations in the North Sea could not detect any macro-parasites in mussels (Buck et al., 2005; Buck, 2007; Brenner, 2010). In case of oysters, Pacific oysters in the northern Wadden Sea were not infested by *M. intestinalis* and the infestation of oysters by *Mytilicola orientalis* was remote: *M. orientalis* was only found with a low prevalence and intensity at one single site close to the Island of Sylt

(Elsner et al., 2010). In the eastern part of the Wadden Sea, infestation of oysters with mytilicolid copepods has not been examined so far.

From an economic point of view, today, mussels (*M. edulis* and *M. galloprovincialis*) as well as the Pacific oyster (*C. gigas*) are the most important species in European shellfish production. There is also a respectable market for the European oyster *O. edulis* (FAO, 2009). As oysters represent high-value seafood products an aesthetic appearance of shell – especially on the half-shell market – and meat is rather important (FAO, 2011). Parasite infestations could reduce harvests and severely deplete local populations. Some macroparasites could also evoke a deteriorated morphological appearance. Understanding the development of infestation patterns is therefore crucial for the successful site-selection in oyster cultivation. In addition to ecological and economic advantages of offshore oyster cultivation (Pogoda et al., 2011) such cultures would further benefit from an absence of parasites, as observed for blue mussels (Buck et al., 2005; Buck, 2007; Brenner, 2010).

The aim of this study was to record the presence and describe the infestation levels and host specificity of macroparasites, particularly of the two parasitic copepod species (*Mytilicola orientalis* and *M. intestinalis*) in oysters from the eastern Wadden Sea and from two offshore cultivation sites. To demonstrate the general existence of parasitic copepods and other macro-parasites in shellfish at the investigated sites, the native mussel *M. edulis* was also sampled. As these mussels, originating from sub- and intertidal habitats, are commonly infested by macro-parasites, *M. edulis* was considered to be a useful reference organism. Furthermore, one nearshore site was investigated in winter as well as in summer to reveal potential seasonal variations of the parasite burden in oysters and mussels.

Therefore, we investigated parasite infestations (i) in *C. gigas* and *M. edulis* at three nearshore wild banks located in the eastern Wadden Sea and (ii) at two offshore cultivation sites in the German Bight.

Materials and methods

Sampling sites and investigated bivalves

Examinations on macro-parasite infestations were carried out with oysters and mussels from five different sites (Fig. 1): three intertidal nearshore sites (former mussel banks which were transformed to wild oyster reefs) and two offshore sites (cultivation experiment): Site 1 *Juister Watt* (JW) is located in the western part of the German East Frisian Wadden Sea near the Island of Juist (53°38.5′N, 006°56.5′E). Site 2 *Dornumer Nacken* (DN) is located about 8 nautical miles (nmi) east of site 1, south of the western tip of the Island of Langeoog (53°41.9′N, 007°28.1′E), and site 3 *Kaiserbalje* (KB) another 10 nmi further to the east, southeast of Mellum island (53°38.7′N, 008°16.0′E). Oysters and mussels collected at these sites originate from bottom habitats, which fall dry several hours per day. The offshore test site *Nordergründe* (NG) (site 4) was located in the outer Weser estuary (53°51.0′N, 008°04.0′E), 9 nmi off the coast (offshore classification by Ryan, 2005) as part of an official testing area, which was established for the multi-use research of offshore aquaculture within offshore wind farms (Buck, 2007; Pogoda et al., 2011). The planned offshore wind farm 'Nordergründe' (Energiekontor, 2011) will be realized about 1 nmi off the test site. The offshore test site *Butendiek*

Fig. 1. Map of the German Bight and the East Frisian Wadden Sea with sampling sites: 1 Juister Watt (JW), 2 Dornumer Nacken (DN), 3 Kaiserbalje (KB), 4 Nordergründe (NG), 5 Butendiek (BD)

(BD) (site 5) was located 15 nmi west of the North Frisian island of Sylt (54°59.1′N, 007°54.4′E), within the area of the planned wind farm 'Butendiek' (Buck et al., 2008). For the offshore cultivation experiments juvenile oysters were obtained from commercial hatcheries (Pogoda et al., 2011).

In total, 296 oysters (*Crassostrea gigas*) of 50–230 mm size were collected from the nearshore sites (Table 1). As *Mytilus edulis* acted only as a reference organism it was collected in lower numbers (Buck et al., 2005; Thieltges et al., 2006; Jungblut, 2011). In total, 60 mussels of 40–50 mm size were collected from the nearshore sites (Table 1). Due to the absence of the European oyster along the German coast *O. edulis* samples were only evaluated from the offshore cultivation experiments (Table 1). At the offshore sites juvenile oysters (*C. gigas* and *O. edulis*) were transferred to oyster lanterns for cultivation in April 2004 and 2007. At site 4 (NG) oyster lanterns were fixed to rigid steel rings welded to large offshore marker buoys, specifically constructed for offshore aquaculture research on shellfish candidates: *C. gigas*, *O. edulis*, *M. edulis* (Brenner et al., 2007; Pogoda et al., 2011). At site 5 (BD) oyster lanterns were fixed to steel frames attached to metal piles of a former research platform of the Federal Maritime and Hydrographic Agency. Culture plots at sites 4 and 5 were permanently submerged. After a six-month growth period in offshore waters 50 oysters of *C. gigas* and *O. edulis* (per site and species) were recollected for macro-parasitic investigations in October 2004 and 2007 (Table 1). Data on macro-parasitic infestation of *M. edulis* from offshore site 4 (same sampling date) has been found by Brenner (2010).

Analysis of parasite infestation and condition index

Length, width and height of each animal were measured with a calliper to the nearest 0.1 mm. Oysters and mussels were then opened by cutting the adductor muscle. The soft body was separated from the shell and dried on absorbent paper for 10 s. before weighing (wet mass [WM] of meat).

Table 1
Studying the infestation rates of mollusks at inshore and offshore sites. Sampling dates, sample sizes and ranges of key environmental parameters during the sampling period

Site	Site classification	Salinity range[1]	Temperature range [°C][1]	Sampled individuals [n]			Sampling time
				Crassostrea. gigas	Ostrea edulis	Mytilus edulis	
1 Juister Watt (JW)	Nearshore	24.3–31.4	−1.7–23.2	87	–	15	May 2011
2 Dornumer Nacken (DN)	Nearshore	24.6–31.2	−1.7–22.9	71	–	15	February 2011
3 Kaiserbalje (KB) winter/summer	Nearshore	7.8–30.8	−1.5–23.9	68/70	–	15/15	December 2010/June 2011
4 Nordergründe (NG)	Offshore	23.1–33.6	3.1–19.6	50	50	15[2]	October 2007
5 Butendiek (BD)	Offshore	30.8–33.1	2.8–18.9	42	50	–	October 2004

[1]BSH (2011).
[2]Mussels analyzed by Brenner (2010).

Digestive gland and rectum were inspected separately to detect and extract *Mytilicola* individuals as a whole. Adult individuals can be detected easily due to their size and bright red colour (Elsner et al., 2010). Most of the extracted copepods were stored in alcohol for detailed species determination. Some female individuals with developed nauplii in their egg sacs were reared in seawater to observe larval development. To ease investigations, parts of the soft body (digestive gland with rectum, muscle, gills, connective tissue) were squeezed separately between glass compressoria. Smaller *Mytilicola* individuals and further macro-parasites were then identified under the stereomicroscope. Parasite infestation was documented in terms of prevalence and mean intensity. Prevalence is defined as the percentage of infested host individuals within a certain group. Mean intensity (mI) signifies the mean number of parasites living in one host, while *n* of uninfested hosts is excluded.

$$mI = mI_i / mI \sum \qquad (1)$$

mI_i = sum of total parasites of species *i*.
$mI\sum$ = sum of total hosts infected with parasites of species *i*.
Shells of oysters and mussels were inspected for the presence of shell-boring polychaetes. Shells were then oven dried for 48 h at 65°C and weighed (dry mass [DM]) to calculate the condition index (CI) according to Davenport and Chen (1987):

$$CI = WMmeat(g) * 100 / DM \ shell \ (g) \qquad (2)$$

Determination of mytilicolid copepods to species level was performed using detailed descriptions by Dethlefsen (1985), Gee and Davey (1986) and Elsner et al. (2010). Additional parasite species were identified following Lauckner (1980, 1983), Grizel (1985) and Watermann et al. (1998). For trematodes and shell-boring polychaetes only the prevalence was recorded (Thieltges et al., 2006).

Statistical analysis

Means, standard errors of the mean (mean ± SE) and confidence intervals (mean ± conf. interv.) of condition indices and intensities were calculated using MS-Excel software. Data were also tested for normality with MS-Excel software. Differences between sites were analyzed with two-tailed Mann–Whitney tests using GRAPHPAD PRISM 5.0 with significance levels of P < 0.05.

Results

Individuals of *Crassostrea gigas*, *Ostrea edulis* and *Mytilus edulis* were examined to assess and compare their parasite burdens at nearshore and offshore sites in the German North Sea. The study focused on the dominant macro-parasites described for these species: intestinal mytilicolid copepods of the genus *Mytilicola*, namely the species *M. intestinalis* and *M. orientalis*.

At the nearshore sites (1–3), *M. orientalis* was detected in the Pacific oyster *C. gigas* and, interestingly, *M. intestinalis* as well as *M. orientalis* in the blue mussel *M. edulis*. Furthermore, another parasitic copepod of the genus *Modiolicola*, metacercaria of unidentified trematode species as well as unidentified nematode species and the bristle worm *Polydora ciliata* (Polychaeta) were detected in the Pacific oysters from the nearshore sites. In addition, *Renicola roscovita* (Trematoda) was detected in the blue mussel as a further macro-parasite at the nearshore sites (Table 2). No macro-parasites were detected in oysters from offshore cultivation (sites 4–5).

In the blue mussel *M. edulis* both parasitic copepods *M. intestinalis* and *M. orientalis* (Fig. 2) were detected at all nearshore sites. Prevalence was first calculated for infested mussels that carried only one mytilicolid species (Table 2) (Fig. 3a): For *M. intestinalis* prevalence ranged between 13.3% (site 2), 26.7% (site 1) and 33.3% (site 3), for *M. orientalis* between 20.0% (sites 2, 3) and 26.7% (site 1). As both parasite species were found in some individuals, prevalence was also calculated for mussels infected by *M. intestinalis* and *M. orientalis*: It ranged between 6.7% (sites 1, 3) and 13.3% (site 2). In total, 46.7% (site 2) to 60.0% (sites 1, 3) of blue mussels were infested by mytilicolid copepods (*M. intestinalis*, *M. orientalis*, or both species). Mean intensity ranged between one and two individuals for both species at all sites (Fig. 3b). No significant differences could be observed. For a seasonal comparison of mytilicolid infestation site 3 was investigated twice: in summer *M. intestinalis* showed a lower prevalence (20.0%) while *M. orientalis* reached a higher prevalence (33.3%) as compared to the first sampling in winter (Fig. 3a). Also deviating from the winter scheme described above, no mussels were infested by both species at the same time in summer and the total prevalence was slightly lower than in winter (53.3%). Mean intensities were one copepod per mussel for both mytilicolid species during summer, also somewhat lower than in winter (Fig. 3b).

The parasitic copepod *M. orientalis* occurred in *C. gigas* at all nearshore sites: Its prevalence ranged between 32.4% (site

Table 2
Prevalence (P) and mean intensity (mI ± conf. Interv.) of macro-parasitic species in oysters (*C. gigas* and *O. edulis*) and mussels (*M. edulis*) at three intertidal nearshore sites and two offshore sites employing suspended culture systems

				Parasites										
				Copepoda						Trematoda		Polychaeta	Nematoda	
				Mytilicola intestinalis		*Mytilicola orientalis*		*Modiolicola* sp.		*Renicola roscovita*	other	*Polydora ciliata*		
Site	Site Classification	Host		P [%]	mI	P [%]	mI	P [%]	mI	P [%]	P [%]	P [%]	P [%]	mI
1 (JW)	Nearshore	Crassostrea gigas		0	0	37.9	8.2 ± 1.5	0	0	0	48.3	2.3	5.8	1.6 ± 0.5
		Mytilus edulis		26.7	1.4 ± 0.3	26.7	2.0 ± 0.7	0	0	50.1	0	0	0	0
2 (DN)	Nearshore	Crassostrea gigas		0	0	45.1	4.6 ± 0.8	0	0	0	0	11.3	7	2.4 ± 3.1
		Mytilus edulis		13.3	1.3 ± 0.3	20	1.8 ± 0.7	0	0	0	0	0	0	0
3 (KB)	Nearshore	Crassostrea gigas	Winter	0	0	32.4	2.9 ± 0.6	8.8	1.2 ± 0.4	0	0	0	16.2	1.2 ± 0.6
			Summer	0	0	37.1	3.0 ± 0.6	0	0	0	54.3	8.6	4.3	1.0 ± 0.0
		Mytilus edulis	Winter	33.3	2.0 ± 0.3	20	1.5 ± 0.5	0	0	73.3	0	0	0	0
			Summer	20	1.0 ± 0.0	33.3	1.0 ± 0.0	0	0	0	0	0	0	0
4 (NG)	Offshore	Crassostrea gigas		0	0	0	0	0	0	0	0	0	0	0
		Ostrea edulis		0	0	0	0	0	0	0	0	0	0	0
5 (BD)	Offshore	Crassostrea gigas		0	0	0	0	0	0	0	0	0	0	0
		Ostrea edulis		0	0	0	0	0	0	0	0	0	0	0

3), 37.9% (site 1) and 45.1% (site 2) (Fig. 4a). Mean intensity (mI) decreased from 8.2 ± 1.5 in the west (site 1) to 4.6 ± 0.8 in the central eastern Wadden Sea (site 2) and to 3.0 ± 0.6 in the east (site 3) (Table 2) (Fig. 4b). Significant differences could be found between site 1 and site 2 ($P < 0.05$) and between site 1 and site 3 ($P < 0.05$). The seasonal comparison revealed no significant differences for the parasite infestation in oysters: Summer sampling at site 3 showed a prevalence of 37.1% and the same intensity in winter (three copepods per oyster).

No correlation could be observed between condition index (CI) and parasite infestation (intensity) of the examined oysters (Fig. 5a–c). Non-infested Pacific oysters showed essentially the same CI at all nearshore sites (15.5 ± 4.4 at site 1, 15.7 ± 3.4 at site 2 and 16.1 ± 3.6 at site 3). The CI of infested Pacific oysters ranged between 14.9 ± 4.2 (site 1), 15.1 ± 4.0 (site 2) and 15.8 ± 3.8 (site 3) with no significant differences ($P > 0.05$) between the nearshore sampling sites but a weak tendency of an increasing condition from west to east. In general, mean condition values of infested oysters showed no significant differences ($P > 0.05$) to the CI of not infested oysters.

To allow a better comparison of oyster size data regarding parasite burden we sorted the oysters into three defined size classes: S (≤ 100 mm), M (100–150 mm) and L (>150 mm) (Table 3). Site 1 (JW) and site 2 (DN) show similar patterns with highest prevalence in size class M, followed by S and L. At site 3 (KB), highest prevalence was observed in size class L, followed by M and S. Intensity did not show significant differences according to host size, except size class S showed significantly higher intensity at site 1 compared to site 2 ($P < 0.05$) and site 3 ($P < 0.005$). Mussels and offshore-cultivated oysters of both species were not separated into different size classes, all individuals belonged to size-class S.

Larval development of *Mytilicola orientalis*

Mytilicola orientalis females with completely developed nauplii in their egg sacs were found during the examination of Pacific oysters from site 2. After extracting an intact *M. orientalis* individual from the rectum of the oyster, the outer membrane surrounding the egg sacs broke and swimming nauplius larvae could be observed. A total of 70 nauplii were collected and put in a beaker with artificial seawater, which was exchanged every 2 days. Larvae were maintained at 15° C and larval development could be observed successfully for 2 weeks. After passing the first developmental stages (Fig. 6a,b) most larvae died. However, at least one individual reached the infective stage (first copepodite stage). Some individuals of each stage were conserved in alcohol for subsequent examinations.

Discussion

High abundances of the Pacific oyster in the Wadden Sea raised the question, if *Crassostrea gigas* could outcompete and replace the native blue mussel *Mytilus edulis* (Diederich, 2006; Schmidt et al., 2008; Markert et al., 2010). For a successful comparison of these species it is important to distinguish between direct competition (e.g. food and space) and indirect competition, for example parasite burdens, which were in the focus of this study. Knowledge on parasite burdens in relation to their geographical variations is a relevant factor, as the absence of macro-parasites, for example at offshore locations,

is an important (market-related) quality feature in shellfish production (Buck, 2007).

The effects of the parasitic copepods *Mytilicola orientalis* and *M. intestinalis* on their specific hosts are still under discussion. Lower condition indices of infested oysters and mussels have been reported, as well as *Mytilus* extinctions in the Netherlands and Germany have been related to infestations with *M. intestinalis* (Katkansky et al., 1967; Korringa, 1968). Also, a lower ability of recovery after spawning was observed for mussels (Paul, 1983). In contrast, other investigations found no effects in case of an infestation of oysters by *M. orientalis* (Chew et al., 1965) or negative effects were detected only in times of severe environmental conditions (Campbell, 1970; Gee et al., 1977): low food supply, severe winters and high infestation rates beyond 25 copepod individuals per host. Lower amounts of parasites could not be related to host size or gonad development, while seasonal cycles and other environmental factors caused greater effects on host condition. Long-term studies suggested that mytilicolid copepods should not be classified as harmful parasites but rather live as commensals in mussels and oysters (Gee and Davey, 1986; Davey and Gee, 1988; Davey, 1989; Steele and Mulcahy, 2001). Our study did not reveal any correlation between infestation rate and condition index of oysters and mussels of the eastern Wadden Sea, which in turn supports the concept of commensalism: At the western site we found three oyster individuals infested by more than 20 mytilicolid copepods and condition indices of host animals ranged between 9 and 20, which is well within the observed range of uninfested oysters. Small and medium size classes showed highest prevalences of *M. orientalis* at sites 1 and 2. In contrast, at site 3 a constant increase of prevalence with increasing size classes was observed. Intensity decreases from west to east in every size class. Within a sampling site, intensities decrease with increasing size class. As recruitments of *Mytilicola* are local and irregular phenomena (Robledo et al., 1994), parasitization can differ over years. Aguirre-Macedo and Kennedy (1999) observed much higher prevalences and intensities in the same size classes in 1995 in the Exe estuary (Great Britain) than in 1996. However, patterns of intensity regarding the oysters' age classes were similar for both years. Older oysters contained more parasites per individual than younger ones (Aguirre-Macedo and Kennedy, 1999), which could not be confirmed for every size class in this study.

Interestingly, recent studies suspected furthermore that heavily infested mussels could provide a competitive advantage for invasive and less infested Pacific oysters, which could enhance their successful distribution along the North Sea coast and eventually the outcompeting of the indigenous mussel (Diederich, 2005; Diederich et al., 2005; Krakau

Fig. 3. Prevalence (a) and intensity (b) of mytilicolid copepods in the blue mussel *Mytilus edulis* at the nearshore sites (*n* = 15 per site and sampling). No macro-parasites were observed at offshore site NG (Brenner, 2010)

et al., 2006; Schmidt et al., 2008; Elsner et al., 2010). However, Markert et al. (2010) did not observe any suppression of *M. edulis* in the eastern Wadden Sea, even if former mussel beds had transformed to *Crassostrea* reefs. Mean abundance of *M. edulis* (individuals m^{-2}) was even higher within the oyster reef than in the surrounding *Mytilus* bed. The fact that mussel shell size tended to be smaller in oyster reefs was not interpreted as a disadvantage, as mussels in turn benefit from their sheltered position between robust oyster shells, protected from predation by birds (Markert et al., 2010). Additionally, our study did not reveal different infestation levels for oysters and mussels: Parasite burdens in mussels and oysters of the eastern Wadden Sea showed prevalences for *M. orientalis* in *C. gigas* between 32% and 45% at all investigated nearshore sites. Mean intensities ranged between three and eight parasites per host decreasing from west to east. Prevalences of mytilicolid copepods in *M. edulis* ranged
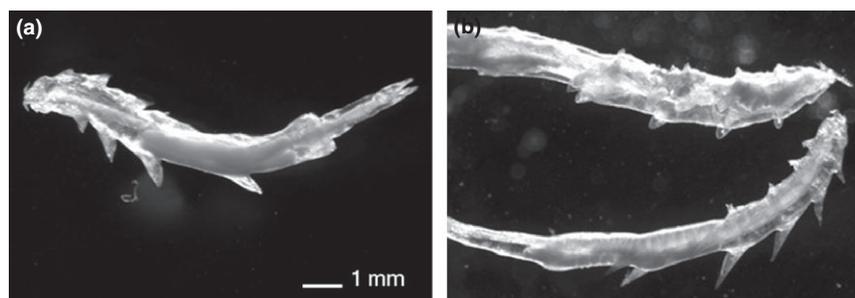

Fig. 2. (a) *Mytilicola orientalis* female with sharp dorsal appendages, (b) *Mytilicola intestinalis* female with rounded dorsal appendages (top) and for comparison *Mytilicola orientalis* (below)
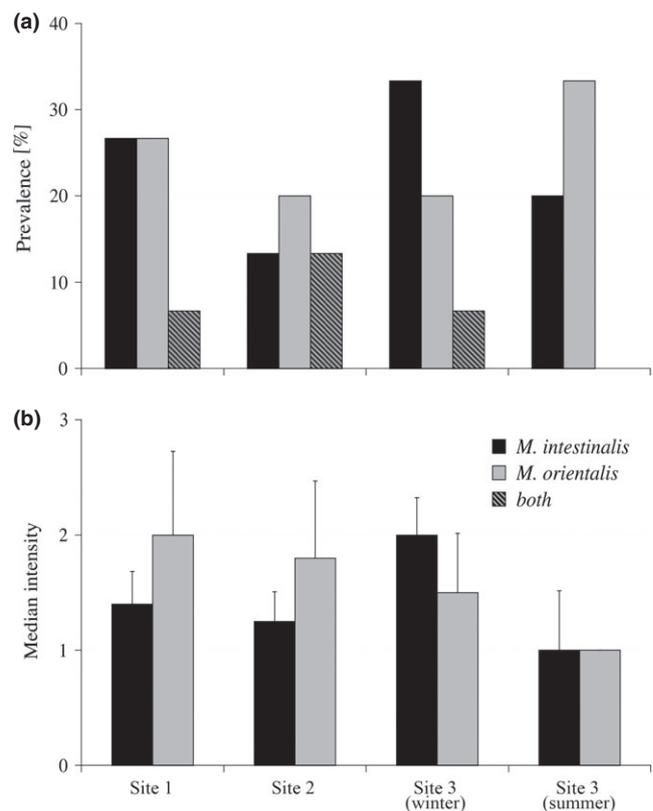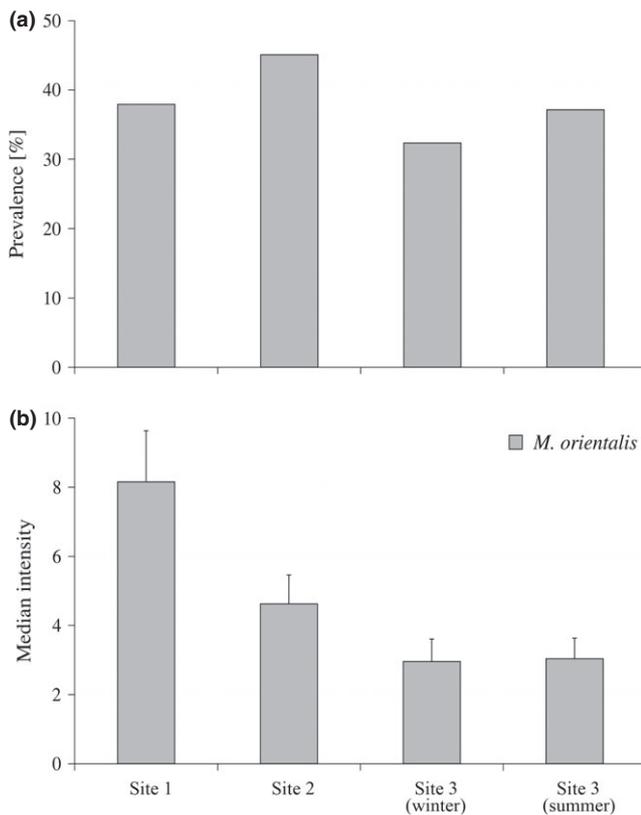
Fig. 4. Prevalence (a) and intensity (b) of the mytilicolid copepod *Mytilicola orientalis* in the Pacific oyster *Crassostrea gigas* at the nearshore sites ($n \approx 70$ per site and sampling). No macro-parasites were observed at the offshore sites ($n \approx 50$ per site)
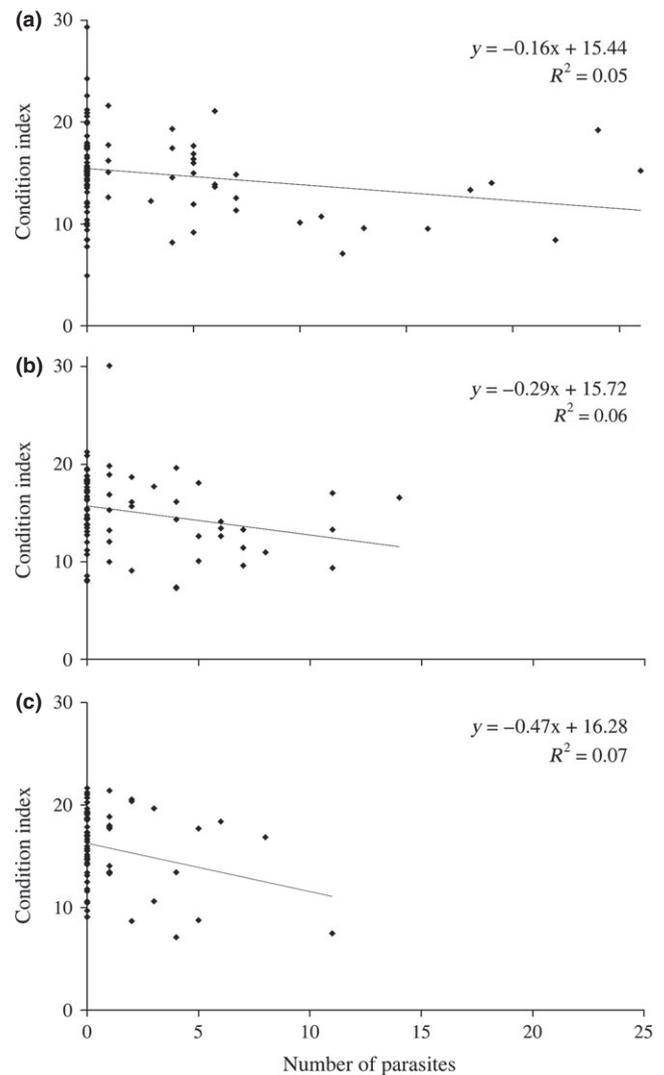

Fig. 5. Non-significant relation of condition index and number of parasites in the Pacific oyster *C. gigas* at nearshore sites from west to east: site 1 (a), site 2 (b) and site 3 (winter) (c) ($n \approx 70$ per site and sampling). No macro-parasites were observed at the offshore sites ($n \approx 50$ per site)

between 45% and 60% with intensities around two parasites per host. This is in substantial contrast to studies conducted in the northern Wadden Sea (Krakau et al., 2006; Thieltges et al., 2006, 2008; Elsner et al., 2010), where the infestation with mytilicolid copepods in terms of prevalence and intensity was nine times higher in *M. edulis* than in *C. gigas*. Prevalence of *M. intestinalis* in *M. edulis* was around 90% and the intensity was approx. four parasites per host. In contrast, prevalence and intensity of *M. orientalis* in *C. gigas* were very low: 10% prevalence at one single site (0% at all other sites) and the intensity was two parasites per host (Elsner et al., 2010).

Furthermore, clear host specificity has been observed in the northern Wadden Sea: *M. orientalis* was only found in *C. gigas*, while *M. intestinalis* occurred only in *M. edulis* (Elsner et al., 2010). In contrast, in the eastern Wadden Sea both species, *M. intestinalis* and *M. orientalis*, were found in *M. edulis*. This is the first widespread record of *M. orientalis* in *M. edulis* in Europe. In other regions, e.g. the Pacific east coast and Sea of Japan, *M. orientalis* is known to parasitize on a variety of hosts: *C. gigas*, *Ostrea lurida*, *M. edulis*, *M. californianus*, *M. crassistesta*, *Crepidula fornicata* (Katkansky et al., 1967; Grizel, 1985). In Europe, only the Pacific oyster had been infested so far. In experiments, *M. orientalis* had shown a clear preference for infecting *M. edulis* instead of the oyster *O. lurida* (Bradley and Siebert, 1978). *M. edulis* has also been the most infected host in Canadian and US waters (Odlaug, 1946; Bernard, 1969). Stock (1993) was the first scientist who found very few *M. orientalis* individuals in mussels of the East Scheldt, Netherlands. Therefore, it is

not surprising that *M. orientalis* has now been detected in *M. edulis* in the North Sea, too.

The question arises, whether *M. orientalis* has only recently started to infest the indigenous blue mussel in the North Sea region? Or has it been overlooked in former studies that focused on the common parasite of the blue mussel:

Table 3
Prevalence (P) and mean intensity (mI) of *M. orientalis*-infestations in Pacific oysters from nearshore sites, separated in different size classes*: S $\leq$ 100 mm, M = 100–150 mm, L > 150 mm

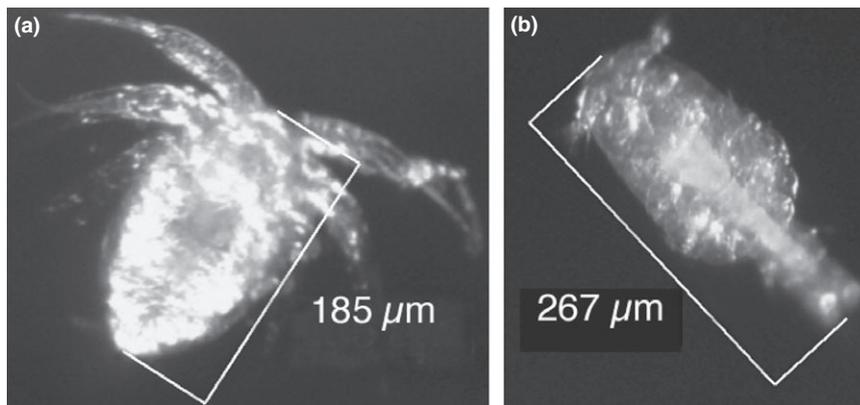| Site #	Size class*	n	P [%]	mI [ind^{-1}]
1	S	54	38.9	9.0 ± 7.2
	M	22	50.0	6.8 ± 6.3
	L	11	9.1	4.0 ± 0.0
2	S	46	43.5	4.2 ± 3.8
	M	13	76.9	5.4 ± 3.2
	L	12	16.7	5.5 ± 0.7
3	S	50	28.0	3.3 ± 3.2
	M	9	33.3	2.7 ± 2.1
	L	9	55.6	2.2 ± 1.3

Fig. 6. Larval stages of *Mytilicola orientalis*. (a) Nauplius larvae 3 h after hatching and leaving the egg sac, (b) after 72 h. Only one individual was observed and documented to reach this stage

M. intestinalis (Buck et al., 2005; Krakau et al., 2006; Thieltges et al., 2006, 2008; Brenner, 2010)? To distinguish *M. orientalis* from *M. intestinalis* complete animals need to be examined under the stereomicroscope. If mytilicolid copepods are detected in compressed preparations, species determination is usually impossible. Squeezed individuals of *M. orientalis* could have been misidentified and recorded as *M. intestinalis*. In 2004 and 2005 no mytilicolid copepods have been found in Pacific oysters of the northern Wadden Sea and *M. intestinalis* was only detected in *M. edulis* (Krakau et al., 2006; Thieltges et al., 2006). However, oysters and mussels were always examined by compressing the soft body parts between glass plates, as described above. In British waters *M. intestinalis* was reported to infest *C. gigas* (Aguirre-Macedo and Kennedy, 1999), but soft parts were also squeezed before examination. In our study only *M. orientalis* was found to infest *C. gigas*. This parasite was mentioned first by Elsner et al. (2010) for the North Sea region. They extracted *Mytilicola* individuals before squeezing and found *M. orientalis* in *C. gigas* but not in *M. edulis*.

On the one hand, the appearance of the Pacific oyster and its parasitic copepod in the North Sea may have initiated the recent infestation of the indigenous blue mussel with the introduced parasite. On the other hand, introduced Pacific oysters might divert parasite burdens taking pressure off native shellfish species (Krakau et al., 2006). The occurrence of other parasite species in the investigated oysters and mussels support this hypothesis: *C. gigas* was host to at least five different species (metacercariae of trematodes were not identified to species level as well as nematodes), *M. edulis* hosted only three different species. This is also in contrast to findings in the northern Wadden Sea where *C. gigas* was host to only two parasite species, *M. edulis* to nine species. Hence, in our study *M. edulis* exhibits lower parasite richness than *C. gigas* and also lower than that of *M. edulis* from the northern Wadden Sea. But due to the fact that not all parasites could be identified to species level it can only be seen as a trend, which requires additional thorough investigations.

Aquaculture activities along the North Sea coastline form the vector of introduction of several invasive species, e.g. Pacific oysters and their subsequent biogeographic distribution. First settlements of the Pacific oyster in the western part of the German Wadden Sea have been recorded in 1996 (Wehrmann et al., 2000). The further expansion of *C. gigas* is apparently related to natural distribution processes via larval drift (Nehring, 2006): pelagic stages of oyster larvae are carried northeast along the German coast as a result of prevailing current systems (Wehrmann et al., 2000). Subsequently, the invasion of *C. gigas* shows a clear northeastward direction beginning in the Netherlands, where spat of Pacific oysters was imported for aquaculture activities from the 1960′s on (Wehrmann et al., 2000, 2009; Brandt et al., 2008; Schmidt et al., 2008). *M. orientalis*, a common parasite of the Pacific oyster was co-introduced to the southern North Sea in the 1990′s (Elsner et al., 2010). Observed infestation rates of *M. orientalis* in *C. gigas* decrease from west to east: Hence, *M. orientalis* may have started the succession along the German coast with retardation, but essentially follows the invasion pattern of its main host.

From an economic point of view the absence of macro-parasites in shellfish products is certainly favourable. Oysters are commonly eaten raw and consumers would dislike the appearance of e.g. parasitic copepods, as they are easy to recognize due to their bright red colour and size (up to 25 mm). This is an issue, as it would result in a serious decrease of the oysters′ value. In contrast, mussels are cooked before consumption and copepods loose their colour and are no longer easy to detect.

Recent studies on macro-parasite body burdens by Buck et al. (2005) and Brenner (2010) reported a zero infestation rate of blue mussels at offshore locations in the North Sea. These observations can also be confirmed in this study for oysters. No macro-parasites have been detected in the European and Pacific oysters from the offshore cultivation sites. Absence of trematodes at offshore locations can be explained by their complex life cycle: they usually infest intertidal gastropods as first intermediate hosts (e.g. *Littorina littorea* and *Hydrobia ulva*) (Lauckner, 1984; Jensen and Mouritsen, 1992; Huxham et al., 2001; Bordalo et al., 2011). Due to the absence of these exclusively coastal organisms the parasite′s life cycle cannot be completed in offshore regions (Buck et al., 2005). Mytilicolid copepods and shell-boring polychaetes (e.g. *Polydora ciliata*) are abundant in inshore waters (Kent, 1981; Davey, 1989; Ambariyanto and Seed, 1991; Thieltges et al., 2006). Their short planktonic larval phase restricts successful the dispersion to coastal waters and larvae drifting away from the coast are bound to die in the absence of potential hosts (e.g. predation and starvation), which are only available at very few selected culture locations (Buck et al., 2005). An experimental study conducted in British waters also showed that young *C. gigas* (<25 mm) were not infested by *M. intestinalis* and few infestations occurred in

individuals around 45 mm (Dare, 1981). Furthermore, some parasites are known to occur only in mature molluscs (Thieltges et al., 2006). This implies, that spat oysters even if received from coastal regions with known parasite infestation would not yet be infested when transferred to offshore cultivation sites for grow-out.

Conclusions and outlook

(1) This study emphasizes the commercial advantages of offshore shellfish cultures with regard to parasite burdens: no macro-parasites have been found in the Pacific oyster *Crassostrea gigas* and the European oyster *Ostrea edulis* at the offshore sites.

(2) Furthermore, this study shows that the infestation of nearshore oysters and mussels with the parasitic copepod *Mytilicola orientalis* decreases geographically from west to east and therefore, the distribution of *M. orientalis* follows the invasion pattern of its main host, the Pacific oyster *C. gigas*. With regard to the formerly existing distribution gap of the invading Pacific oyster, we assume that the co-invasion of *M. orientalis* along the North Sea coast is not yet completed and abundances might still increase in the northeastern region.

(3) In the eastern Wadden Sea infection levels in oysters and mussels are similar, whereas in the northern Wadden Sea the parasite burden on mussels is much higher than that on oysters. We expect that parasite setting in the northern Wadden Sea will shift to similar infection levels as observed in this study for the eastern Wadden Sea region.

(4) *Mytilicola orientalis* also infests the native blue mussel *M. edulis* in the eastern Wadden Sea. Subsequently, the former described host specificity of *M. orientalis* for *C. gigas* is no longer valid for the North Sea.

Following ICES criteria for sustainable and environmentally friendly aquaculture shellfish transfers for aquaculture purposes on regional, national and international scales should be minimized and monitored continuously. These practices fostered the invasion of hitchhiking organisms, e.g. parasitic copepods, in the past (ICES, 2010) and will increase environmental and economic problems with introduced marine species in the future (Torchin et al., 2002).

References

Aguirre-Macedo, M. L.; Kennedy, C. R., 1999: Diversity of metazoan parasites of the introduced oyster species *Crassostrea gigas* in the Exe estuary. J. Mar. Biol. Ass UK. **79**, 57–63.

Ambariyanto; Seed, R.1991: The infestation of *Mytilus edulis* Linnaeus by *Polydora ciliata* (Johnston) in the Conwy Estuary, North Wales. J. Molluscan Stud. **57**, 413–424.

Andrews, J. D., 1980: A review of introductions of exotic oysters and biological planning for new importations. Mar. Fish. Rev. **42**, 1–11.

Bernard, F. R., 1969: The parasitic copepod *Mytilicola orientalis* in British Columbia bivalves. J. Fish. Res. Board Can. **26**, 190–191.

Bordalo, M. D.; Ferreira, S. M.; Jensen, K. T.; Pardal, M. A., 2011: Trematode fauna of *Hydrobia ulvae* (Gastropoda: Prosobranchia) in a eutrophic temperate estuary. J. Mar. Biol. Ass. UK **91**, 913–921.

Bradley, W.; Siebert, A. E., 1978: Infection of *Ostrea lurida* and *Mytilus edulis* by the parasitic copepod *Mytilicola orientalis* in San Francisco Bay, California. The Veliger **21**, 131–134.

Brandt, G.; Wehrmann, A.; Wirtz, K. W., 2008: Rapid invasion of *Crassostrea gigas* into the German Wadden Sea dominated by larval supply. J. Sea Res. **59**, 279–296.

Brenner, M., 2010: Assessing the health of blue mussels (Mytilus edulis) for site selection of cultivation areas: potential and constraints of applied parameters. ICES CM/F **13**, 1–7.

Brenner, M.; Buck, B. H.; Koehler, A., 2007: New concept combines offshore wind farms, mussel cultivation. Glob. Aquac. Adv. **10**, 79–81.

BSH, 2011: The Operational Circulation Model BSHcmod. Bundesamt für Seeschifffahrt und Hydrographie (BSH). Hamburg, Germany.

Buck, B. H., 2007: Farming in a high energy environment: potentials and constraints of sustainable offshore aquaculture in the German Bight (North Sea). Rep. Polar Mar. Res., Bremerhaven **543**, 1–217.

Buck, B. H.; Thieltges, D. W.; Walter, U,.; Nehls, U.; Rosenthal, H., 2005: Inshore – Offshore comparison of parasite infestation in *Mytilus edulis*: implications for Open Ocean Aquaculture. J. Appl. Ichthyol. **21**, 107–113.

Buck, B. H.; Krause, G.; Michler-Cieluch, T.; Brenner, M.; Buchholz, C. M.; Busch, J. A.; Fisch, R.; Geisen, M.; Zielinski, O., 2008: Meeting the quest for spatial efficiency: progress and prospects of extensive aquaculture within offshore wind farms. Helgol. Mar. Res. **62**, 269–281.

Campbell, S. A., 1970: The occurrence and effects of *Mytilicola intestinalis* in *Mytilus edulis*. Mar. Biol. **5**, 9–95.

Carnegie, R. B.; Barber, B. J.; Culloty, S. C.; Figueras, A. J.; Distel, D. L., 2000: Development of a PCR assay for detection of the oyster pathogen *Bonamia ostreae* and support for its inclusion in the Haplosporidia. Dis. Aquat. Org. **42**, 199–206.

Chew, K. K., 1990: Global bivalve shellfish introductions. World Aquacult. **21**, 9–22.

Chew, K. K.; Sparks, A. K.; Katkansky, S. C., 1965: Preliminary results in the seasonal size distribution of *Mytilicola orientalis* and the effect of this parasite on the condition of the Pacific oyster, *Crassostrea gigas*. J. Fish. Res. Bd. Canada **22**, 1099–1101.

Dare, P. J., 1981: The susceptibility of seed oysters of *Ostrea edulis* L and *Crassostrea gigas* Thunberg to natural infestation by the copepod *Mytilicola intestinalis* Steuer. Aquaculture **26**, 201–211.

Davenport, J.; Chen, X., 1987: A comparison of methods for the assessment of condition in the mussel (*Mytilus edulis* L). J. Moll. Stud. **53**, 293–297.

Davey, J. T., 1989: *Mytilicola intestinalis* (Copepoda: Cyclopoida): a ten year survey of infested mussels in a Cornish estuary, 1978–1988. J. Mar. Biol. Ass. UK **69**, 823–836.

Davey, J. T.; Gee, J. M. 1988: Mytilicola intestinalis, a copepod parasite of blue mussels. In: Disease processes in marine bivalve molluscs. W. S. Fisher (Ed.). Special Publication, American Fisheries Society, **18**, pp. 64–73.

Dethlefsen, V., 1975: The influence of *Mytilicola intestinalis* Steuer on the meat content of the mussel *Mytilus edulis* L. Aquaculture **6**, 83–97.

Dethlefsen, V., 1985: *Mytilicola intestinalis* parasitism. In: Identification leaflets for diseases and parasites of fish and shellfish no 24. C. J. Sindermann (Ed). ICES, Copenhagen, pp. 4.

Diederich, S., 2005: Differential recruitment of introduced Pacific oysters and native mussels at the North Sea coast: coexistence possible? J. Sea Res. **53**, 269–281.

Diederich, S., 2006: High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. J. Exp. Mar. Biol. Ecol. **328**, 211–227.

Diederich, S.; Nehls, G.; van Beusekom, J. E. E.; Reise, K., 2005: Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? Helgol. Mar. Res. **59**, 97–106.

Elsner, N. O.; Jacobsen, S.; Thieltges, D. W.; Reise, K., 2010: Alien parasitic copepods in mussels and oysters of the Wadden Sea. Helgol. Mar. Res. **65**, 299–307.

Energiekontor, 2011: Official homepage of the project developer Energiekontor. Available at: www.energiekontor.de (accessed February 2011).

FAO, 2009: The State of World Fisheries and Aquaculture – 2008 (SOFIA). FAO Fisheries and Aquaculture Department, pp. 176.

FAO, 2011: Fisheries and Aquaculture Information and Statistics Service – Available at: www.fao.org/fishery/aquaculture/en (accessed January 2011).

Gee, J. M.; Davey, J. T., 1986: Stages in the life-history of *Mytilicola intestinalis* Steuer, a copepod parasite of *Mytilus edulis* (L), and the effect of temperature on their rates of development. J. Conseil **42**, 254–264.

Gee, J. M.; Maddock, L.; Davey, J. T., 1977: The relationship between infestation by *Mytilicola intestinalis*, Steuer (Copepoda, Cyclopoida) and the condition index of *Mytilus edulis* in South-west England. J. Cons. Int. Explor. Mer. **37**, 300–308.

Grizel, H., 1985: *Mytilicola orientalis* Mori, parasitism. In: Identification leaflets for diseases and parasites of fish and shellfish, No 20. Sindermann CJ (Ed). ICES, Copenhagen, pp. 4.

Huxham, M.; Maitland, D.; Mocogni, M., 2001: Respiration rates in *Littorina littorea* infected with three species of digenean parasite. J. Mar. Biol. Ass. UK **81**, 351–352.

ICES, 2010: Report of the Working Group on Marine Shellfish Culture of the International Council for the Exploration of the Sea. Available at: www.ices.dk/workinggroups/ViewWorkingGroup. aspx?ID = 168 (accessed October 2011).

Jackson, J. B. C.; Kirby, M. X.; Berger, W. H.; Bjorndal, J. A.; Botsford, L. W.; Bourque, B. J.; Bradbury, R. H.; Cooke, R.; Erlandson, J.; Estes, J. A.; Hughes, T. P.; Kidwell, S.; Lange, C. B.; Lenihan, H. S.; Pandolfi, J. M.; Peterson, C. H.; Steneck, R. S.; Tegner, M. J.; Warner, R. R., 2001: Historical overfishing and the recent collapse of coastal ecosystems. Science **293**, 629–638.

Jensen, K. T.; Mouritsen, K. N., 1992: Mass mortality in two common soft-bottom invertebrates, *Hydobia ulvae* and *Corophium volutator* – the possible role of trematodes. Helgol. Meeresunters. **46**, 329–339.

Jungblut, S., 2011: Macroparasites in Pacific oysters (*Crassostrea gigas*) of the East Frisian Wadden Sea, Germany, with focus on copepods. Bachelor Thesis, University of Bremen, pp. 38.

Katkansky, S. C.; Warner, R. W., 1968: On the unusual occurrence of the copepod *Mytilicola orientalis* in the digestive diverticulae of the Pacific oyster, *Crassostrea gigas*. J. Invertebr. Pathol. **12**, 475–476.

Katkansky, S. C.; Sparks, A. K.; Chew, K. K., 1967: Distribution and effects of the endoparasitic copepod *Mytilicola orientalis*, on the Pacific oyster, *Crassostrea gigas*, on the Pacific coast. Proc. Natl. Shellfish Assoc. **57**, 50–58.

Kent, R. M. L., 1981: The effect of *Polydora ciliata* on the shell strength of *Mytilus edulis*. J. Cons. Int. Explor. Mer **39**, 252–255.

Korringa, P., 1968: On the ecology and distribution of the parasitic copepod *Mytilicola intestinalis* Steuer. Bijdr. Dierkd. **38**, 47–57.

Krakau, M.; Thieltges, D. W.; Reise, K., 2006: Native parasites adopt introduced bivalves in the North Sea. Biol. Invasions **8**, 919–925.

Lauckner, G., 1980: Diseases of Mollusca: Gastropoda. In: Diseases of marine animals. O. Kinne (Ed). Vol I Biologische Anstalt Helgoland, Hamburg, pp. 311–424.

Lauckner, G., 1983: Diseases of Mollusca: Bivalvia. In: Diseases of marine animals. Vol II Introduction, Bivalvia to Scaphopoda. O. Kinne (Ed). Biologische Anstalt Helgoland, Hamburg, pp. 477–961.

Lauckner, G., 1984: Impact of trematode parasitism on a North Sea tidal flat. Helgol. Meeresunters. **37**, 185–199.

Markert, A.; Wehrmann, A.; Kröncke, I., 2010: Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). Biol. Invasions **12**, 15–32.

Meixner, R., 1973: Erfahrungen bei der vertikalen Aufzucht von Pfahlmuscheln und Austern in den deutschen Küstengewässern. Neue Erkenntnisse auf dem Gebiet der Aquakultur. Arbeiten des Deutschen Fischerei-Verbandes **16**, 175–179. [In German].

Montes, J., 1990: Development of *Bonamia ostreae* parasitosis of flat oyster (*Ostrea edulis* L.) from Galicia, northwest Spain. In: Pathology in marine science. T. C. Cheng and F. O. Perkins (Eds). Academic Press, New York, pp. 223–227.

Motes, M. L.; De Paola, A., 1996: Offshore suspension relaying to reduce levels of *Vibrio vulnificus* in oysters (*Crassostrea virginica*). Appl. Environm. Microbiol. **62**, 3875–3877.

Nehring, S., 2006: NOBANIS – Invasive Alien Species Fact Sheet – *Crassostrea gigas*. Online Databas of the North European and Baltic Network on Invasive Alien Species (NOBANIS). Available at: http://www.nobanis.org (accessed on January 2011).

Neudecker, T., 1984: Untersuchungen des Einflusses von Aufzuchtverfahren und standortbedingten Umweltfaktoren auf den Abwachs von Mollusken. BMFT FB- M 84-001, ISSN 0340-8868. [In German].

Odlaug, T. O., 1946: The effect of the copepod *Mytilicola orientalis* upon the Olympia oyster, *Ostrea lurida*. Trans. Am. Microsc. Soc. **65**, 311–317.

OSPAR, 2009: Background document for *Ostrea edulis* and *Ostrea edulis* beds. Biodiv. Ser. **428**. OSPAR Commission, pp 22 (accessed February 2011).

Paul, J. D., 1983: The incidence and effects of *Mytilicola intestinalis* in *Mytilus edulis* from the Rías of Galicia, North West Spain. Aquaculture **31**, 1–10.

Pogoda, B.; Buck, B. H.; Hagen, W., 2011: Growth performance and condition of oysters (*Crassostrea gigas* and *Ostrea edulis*) farmed in an offshore environment (North Sea, Germany). Aquaculture **319**, 484–492.

Robledo, J. A. . F.; Santarém, M. M.; Figueras, A., 1994: Parasite Loads of Rafted Blue Mussels (*Mytilus galloprovincialis*) in Spain with special reference to the copepod, *Mytilicola intestinalis*. Aquaculture **127**, 287–302.

Ruesink, J. L.; Lenihan, H. S.; Trimble, A. C.; Heiman, K. W.; Micheli, F.; Byers, J. E.; Kay, M. C., 2005: Introduction of non-native oysters: ecosystem effects and restoration implications. Ann. Rev. Ecol. Evol. Syst. **36**, 643–689.

Ryan, J. 2005: Offshore Aquaculture – Do we need it, and why is it taking so long? Intern Salmon Farmers Ass (Ireland). Expert workshop on "Sustainable Aquaculture", DG JRC European Comm, Institute for Prospective Technological Studies, 17–18 Jan 2005, Seville, Spain.

Schmidt, A.; Wehrmann, A.; Dittmann, S., 2008: Population dynamics of the invasive Pacific oyster *Crassostrea gigas* during the early stages of an outbreak in the Wadden Sea (Germany). Helgol. Mar. Res. **62**, 367–376.

Steele, S.; Mulcahy, M. F., 2001: Impact of the copepod *Mytilicola orientalis* on the Pacific oyster *Crassostrea gigas* in Ireland. Dis. Aquat. Org. **47**, 145–149.

Stock, J. H., 1993: Copepoda (Crustacea) associated with commercial and non-commercial Bivalvia in the East Scheldt, The Netherlands. Bijdr Dierkd **63**, 61–64.

Thieltges, D. W.; Krakau, M.; Andresen, H.; Fottner, S.; Reise, K., 2006: Macroparasite community in molluscs of a tidal basin in the Wadden Sea. Helgol. Mar. Res. **60**, 307–316.

Thieltges, D. W.; Hussel, B.; Hermann, J.; Jensen, K. T.; Krakau, M.; Taraschewski H., ; Reise, K., 2008: Parasites in the northern Wadden Sea: a conservative ecosystem component over 4 decades. Helgol. Mar. Res. **62**, 37–47.

Torchin, M. E.; Lafferty, K. D.; Kuris, A. M., 2002: Parasites and marine invasions. Parasitology **124**, 137–151.

Watermann, B.; Die, I.; Liebe, S. 1998: Krankheiten der Miesmuschel (*Mytilus edulis*) an der ostfriesischen Küste:VII. Tagung der Deutschen Sektion der European Association of Fish Pathologists (EAFP) Krankheiten der Aquatischen Organismen. 23–25 Sept 1998 Schmallenberg-Grafschaft. pp. 177–187.

Wehrmann, A.; Herlyn, M.; Bungenstock, F.; Hertweck, G.; Millat, G., 2000: The distribution gap is closed – first record of naturally settled Pacific oysters *Crassostrea gigas* in the East Frisian Wadden Sea, North Sea. Senckenb. Marit. **30**, 153–160.

Wehrmann, A.; Markert, A.; Esser, W.; Narkus, S.; Rabe, K.. 2009: Management der Bioinvasion der Pazifischen Auster (*Crassos-*

trea gigas). Sachbericht Projekt 25/05 der Niedersächsischen Wattenmeer-Stiftung, pp.198.

Author's address: Marine Zoology, University of Bremen, P.O. Box 330440, 28334 Bremen, Germany.
E-mail: bernadette.pogoda@uni-bremen.de