

Parasites in the northern Wadden Sea: a conservative ecosystem component over 4 decades

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Abstract We investigated potential changes in the metazoan endoparasite fauna in the northern Wadden Sea during the past 4 decades by compiling published studies, reports and original data. During the time considered, the parasite fauna has remained basically the same. Only a few changes in parasite species presence occurred that resulted from changes in host distribution and abundance. The introduction of potential host species had little effect on the parasite community because no alien parasites were concomitantly introduced and the native parasites show low prevalence and intensity in these novel hosts. Eutrophication and effects of phased-out hunting may not have had clear bottom-up or top-down effects on the parasite community because of various confounding factors. Parasites depending on several host species may only be subject to strong population changes if all hosts are affected in a unidirectional way. This, however, is rather unlikely to happen in a coastal ecosystem subject to multiple pressures. Hence, parasites appear to be a relatively conservative component of the northern Wadden Sea.

Keywords Alien species · Climate · Trematodes · *Profilicollis* · *Mytilicola* · Invertebrates · Birds · Long-term · Marine parasitism

Introduction

Endoparasites are an intrinsic but hidden part of coastal ecosystems (Sousa 1991; Mouritsen and Poulin 2002). They affect host individuals, populations, and communities in various ways and thus alter food web structures and ecosystem functioning (Mouritsen and Poulin 2002, 2005; Thompson et al. 2005). In coastal invertebrates, the dominant metazoan parasite group are digenetic trematodes with complex life cycles (Fig. 1). First intermediate hosts are mostly gastropods in which the parasites multiply and cercariae develop. The free-living cercariae infect a second intermediate host, most often a bivalve, crustacean, or fish. When these hosts are consumed by a final host—fish, bird, or mammal—the cycle is completed. In the vertebrate hosts, the trematodes mate and produce eggs that infect the first intermediate invertebrate host. Birds play a dominant role as final hosts in coastal ecosystems with a wide shallow or tidal zone (Mouritsen and Poulin 2002). Besides trematodes, two other important groups of parasites in invertebrates of nearshore systems are acanthocephalans that utilize birds as final hosts and crustaceans as intermediate hosts (Nicholas 1973; Fig. 1) and copepods which have direct life-cycles (Lauckner 1980). To a lesser extent, invertebrates can also be infected by nematodes and cestodes (Lauckner 1980, 1983).

Although important constituents of coastal ecosystems, few parasite inventories have been accomplished. Most parasitological studies have been concerned with parasite communities in single host species and only some studies

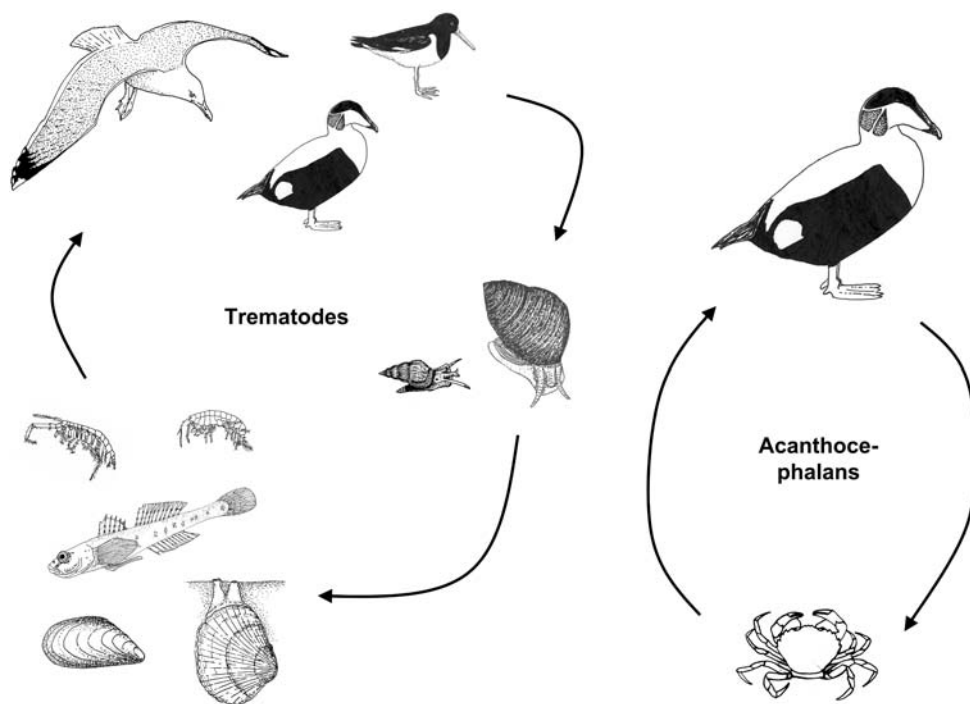
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Fig. 1 Life cycles of typical parasites in the northern Wadden Sea. Trematodes utilize mainly gastropods as first intermediate hosts and a range of invertebrates and fish as second intermediate hosts. Final hosts are mostly birds but some parasites also use fish and marine mammals. Acanthocephalans utilize crustaceans as intermediate hosts and birds as final hosts. In some cases fish and marine mammals can also serve as final hosts



have considered multi-species host communities in coastal regions (e.g. Kesting et al. 1996; de Montaudouin et al. 2000; Zander et al. 2000, 2002; Zander and Reimer 2002; Thieltges et al. 2006a). Even less is known on the long-term development of parasite faunas in changing coastal ecosystems. Pollution (Möller 1987; Khan and Thulin 1991), eutrophication (Reimer 1995; Kesting and Zander 2000), loss and introduction of host and parasite species (Krakau et al. 2006; Taraschewski 2006), and ambient temperature levels (Poulin 2006; Poulin and Mouritsen 2006) are known to influence parasite transmission and communities. Since coastal ecosystems are especially subject to habitat loss, overfishing, introductions, eutrophication, pollution and climate change (Valiela 2006), parasite communities are likely to reflect these changes. Parasites could be affected by these changes either directly, e.g. through acting on their free-living infective stages or indirectly by alterations in their host spectrum. Thus, changes in environmental settings can be expected to lead to (1) gain or loss of parasite species and/or (2) increased or decreased infection levels in the hosts.

In the northern Wadden Sea, first parasitological studies were conducted in the 1960s on the periwinkle *Littorina littorea* (Werding 1969) and the cockles *Cerastoderma edule* and *Cerastoderma lamarckii/glaucum* (Lauckner 1971). These studies were continued and expanded on other host species but unfortunately few of the data collected have been published and the original data are mostly not available. However, some of the earlier data can be found in journal publications and in notes published in the annual

reports of the Biologische Anstalt Helgoland (1973–1995/1996). This allows comparison with recent quantitative data published on certain host species. In addition to published data, there are some original data available that await analysis. Although not covering all parasites and hosts present in the area, the available data encompass the major host groups (gastropods, bivalves, crustaceans, birds) of the local system. By compiling the available information and data we aim to (1) identify long-term changes in the parasite fauna of the region and (2) find explanations for potential changes. Although, the available data are restricted in terms of scope and data quality we think it to be valuable due to the rarity of long-term parasitological data sets.

In the course of the last 4 decades, some major changes of relevance to parasites in the ecosystem of the northern Wadden Sea have occurred: (1) a notable warming trend of air and water temperatures can be observed in the Wadden Sea region since the 1980s (Oost et al. 2005); (2) eutrophication first increased and recently decreased again with a notable peak in green algal mats in the late 1980s to early 1990s (Reise and Siebert 1994; Beusekom et al. 2005); (3) introduced species, most notably the razor clam *Ensis directus/americanus* (Armonies and Reise 1999), Pacific oysters *Crassostrea gigas* (Diederich et al. 2005; Nehls et al. 2006) and American slipper limpets *Crepidula fornicata* (Thieltges et al. 2003), increased in population size, while the native *Corophium volutator* locally declined since the 1970s (Reise et al. 1994; and unpublished data) and most recently, the mussel *Mytilus edulis* also (Nehls et al. 2006); (4) fishery on mussels varied over time and

have mostly turned to bottom cultures since the 1980s, and shrimp fishery has gradually moved from tidal basins of the Wadden Sea to the outer coast (Marencic 2005); (5) hunting on coastal birds and seals was phased out and populations increased (Lotze 2005) although in most recent times, shellfish eating birds are subject to decline (Blew and Südbeck 2005). Since these changes are likely to directly or indirectly affect parasites, we hypothesize major alterations in the parasite fauna of the northern Wadden Sea during the last 4 decades.

Methods

Literature survey

We compiled published data on parasites in invertebrates around the island of Sylt in the northern Wadden Sea (Germany) by searching journal publications on parasites from the region and browsing the yearly reports of the Biologische Anstalt Helgoland (1973–1995/96). Only qualitative and quantitative data that allowed comparison with recent data were collected. For the following host species suitable data were available: *L. littorea*, *Hydrobia ulvae*, *C. edule*, *M. edulis*, *Carcinus maenas*. In addition to parasite species records, we collected reports on mass mortality events caused by parasites in the area.

Crab parasite study

Shore crabs (*C. maenas*) were collected in August 2004 around the island of Sylt. Intertidal crabs were collected on a mussel bed at the entrance of “Königshafen” (“Diedrichsenbank”). With the help of a small net, 25 crabs (35–66 mm) were randomly sampled. Subtidal crabs were collected at two localities from a research vessel with a dredge. In the “Lister Ley” at the entrance of “Königshafen”, 15 crabs (18–62 mm), and at “Schweinebucht”, 59 crabs (16–66 mm), were randomly taken as a sub-sample from the total number of crabs obtained with the dredge. To acquire trematode metacercariae, the digestive gland was removed and digested with pepsin. Afterwards, the number of metacercariae was counted under a dissection microscope. Acanthocephalans could be directly observed close to the stomach and were counted.

Eider parasite study

Common eiders (*Somateria mollissima*) were collected dead on the beaches of the island of Sylt within two different sampling periods, 1972–1976 and 1993–1998. All eiders were deep-frozen for later analysis. Age (juvenile/adult) and sex of each individual was determined. Corpses

were dissected and gallbladder, kidney as well as stomach and intestine, investigated for parasites. For acanthocephalans, total number of individuals per host was recorded. For trematode parasite species, only presence–absence data were noted. Data for two trematode species groups were available, Himasthlinae and Rencolidae.

Statistical analysis

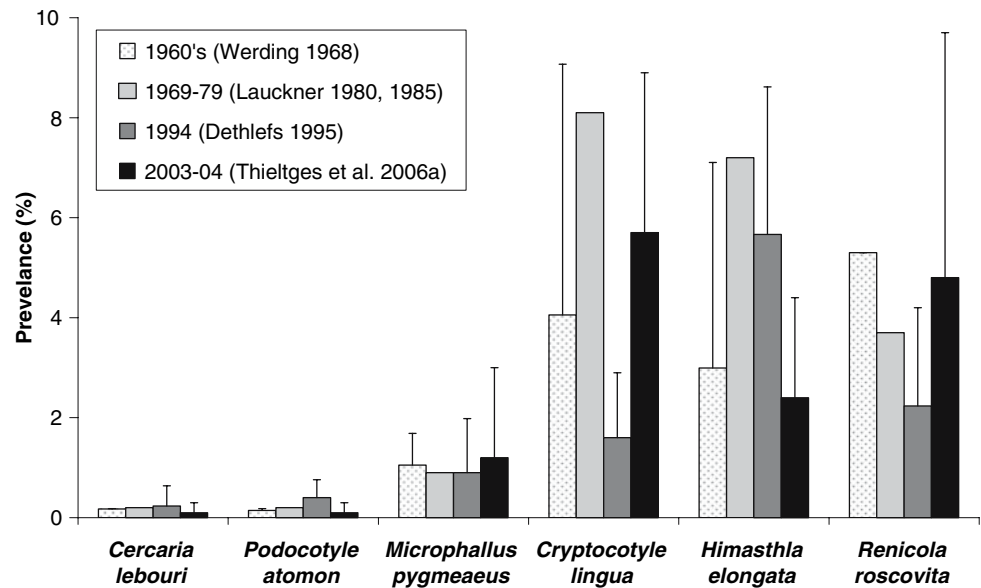
Since the data taken from the literature was of different quality in terms of individual and spatial replicates we refrained from a rigid statistical analysis and only analysed the data qualitatively. The eider parasite data were statistically investigated. Differences in acanthocephalan infection levels between time periods as well as between ages and sexes were tested with a two-factorial crossed ANOVA design with time period and age/sex as fixed factors. Due to the unbalanced nature of the data (different no. of investigated birds per factor level), we used type III SS for the analysis (Shaw and Mitchell-Olds 1993). Differences in prevalence of trematodes between time periods were tested for each age/sex separately using *G*-tests. All data are presented as prevalence (% of individuals infected from the total sample) and intensity (no. of parasite individuals per infected host).

Results

Littorina littorea

For the periwinkle (*L. littorea*), four data sets were obtained from the literature. Werding (1969) studied parasites of *L. littorea* at two sites on Sylt island in the 1960s [2,831 individuals (ind.)]. Lauckner (1980, 1985) investigated snails from several sites on tidal flats around Sylt Island during the period 1969–1979 (30,811 ind.). Dethlefs (1995) dissected snails from three sites around Sylt in 1994 (745 ind.) and Thieltges et al. (2006a) investigated snails from six sites around the island of Sylt in 2003/2004 (1,090 ind.). For Werding (1969), Dethlefs (1995) and Thieltges et al. (2006a), standard deviations were available or calculated from the raw data; no standard deviations were available for the data from Lauckner (1980, 1985). The parasite community in the snails was similar among the data sets (Fig. 2). Three species (*Cercaria lebouri*, *Podocotyle atomon*, *Microphallus pygmaeus*) were rare (prevalence < 1%) in all periods while three others (*Cryptocotyle lingua*, *Himasthla elongata*, *Renicola roscovita*) were common (>2%) (for life cycles of the different parasites see Thieltges et al. 2006a). Generally, there was a high variability in the data as indicated in the large standard deviations. No general increasing or decreasing trend could be observed in species presence and infection levels.

Fig. 2 Prevalence (%) + SD of trematode parasites in periwinkles (*L. littorea*) collected in different time periods. No SD available for data from Lauckner (1980, 1985)



Hydrobia ulvae

The mud snail (*H. ulvae*) was reported to be infected by a high diversity of trematodes (12 species) in 1986, with a total prevalence of 4.2% in approx. 600 ind. collected at a single locality in “Königshafen” (Lauckner 1995/96). Thieltges et al. (2006a) reported a mean prevalence of $9.9 \pm 5.5\%$ in snails from four sampling sites (1,681 ind.) collected in 1997 with a similar trematode species richness (12 species). Microphallidae, Echinostomatidae and Notocotylidae were the dominant taxa in both studies. For life cycles of the different parasites see Thieltges et al. (2006a).

Cerastoderma edule

For common cockles (*C. edule*), only semi-quantitative data could be obtained from earlier studies. Lauckner (1971) published a parasite species list and some additional semi-quantitative data obtained from investigating 6,000 cockles from tidal flats around Sylt Island in the late 1960s (Table 1). For recent years, quantitative data are available from 1,400 cockles obtained from four sites around the island of Sylt in 2003/2004 (Thieltges and Reise 2006). Most species are the same in both periods and seem to have been relatively stable in terms of infection levels. Two species (*Labratrema minimus* and *Monorchis parvus*) were not recorded by Lauckner (1971) and can be considered to be newcomers. *Meiogymnophallus minutus* showed a strong decreasing trend. It occurred in all cockles investigated in the earlier period (Lauckner 1971, 1990) but only at one locality in low numbers in today's cockles (Thieltges and Reise 2006). For life cycles of the parasites see Thieltges and Reise (2006).

Table 1 Parasite species occurring in cockles (*Cerastoderma edule*) in the late 1960s (Lauckner 1971) and in 2003/2004 (Thieltges and Reise 2006)

Parasite species	Lauckner (1971)	Thieltges and Reise (2006)	Trend
First int. hosts			
<i>Gymnophallus choledochus</i>	×	×	=
<i>Labratrema minimus</i>	0	×	+
<i>Monorchis parvus</i>	0	×	+
Second int. host			
<i>Himasthla elongata</i>	×	×	=
<i>H. continua</i>	×	×	=
<i>H. interrupta</i>	×	×	=
<i>Renicola roscovita</i>	×	×	=
<i>Psilostomum brevicole</i>	×	×	=
<i>Meiogymnophallus minutus</i>	×	×	-
<i>Gymnophallus gibberosus</i>	×	×	=

0 absent, × present. Trends in infection levels are indicated as follows: + increasing trend, - decreasing trend, = infection levels similar

Mytilus edulis

Lauckner (1987) reported *H. elongata* and *R. roscovita* to be the dominant trematode parasites (occurring as metacercariae) in blue mussels (*M. edulis*). This is still valid today, with highest prevalence in *R. roscovita* (96%) followed by *H. elongata* (27%) (Thieltges et al. 2006a; see this publication for life cycles). High prevalences (approx. 100%) of total metacercarial infections (species identity was not determined) were also reported by Dethlefsen (1972) from mussels collected at two sites in the List tidal basin. Although no samples were taken around Sylt Island, the parasitic copepod *Mytilicola intestinalis* was probably absent

in 1939 and 1950 since mussels from other North-Frisian localities were found to be free of this parasite (Table 2). In 1969/1970, the species appeared in mussels and increased in prevalence and abundance until today (Table 2). For life cycles of the parasites see Thieltges et al. (2006a).

Carcinus maenas

For shore crabs (*C. maenas*), one published data set was obtained from 1989 (Lauckner 1990a). Recent data were collected in 2004 as described above. Infection levels of the acanthocephalan, *Proflicollis botulus*, were similar in both periods and ranged from 1.1 to 3.3 ind. per host (Table 3). Infection levels of the trematode *Maritrema subdolum* were always higher than that for the trematode *Microphallus claviformis*. The latter species showed considerable spatial heterogeneity in infection levels in the intertidal data from 1989 (Table 3).

Somateria mollissima

No differences in infection levels with the acanthocephalan *P. botulus* could be observed in common eiders (*S. mollissima*) between the time periods (Table 4) (Fig. 3). However, the analysis indicated differences in parasite load within the factor age/sex (Table 4). Prevalences in the two trematode groups considered were not significantly different between the periods as indicated by *G*-tests (Fig. 4). For life cycles of eider parasites see Thieltges et al. 2006b.

Mass mortality events

Several mass mortality events of the hosts reported in this paper have been reported from the area (Table 5). In most mass mortality events, trematodes were suspected to be the causative agent. In one case, acanthocephalans were suspected to be involved. Most mass mortality events occurred during summer and occurred during high ambient temperatures.

Discussion

Similar parasite fauna

The composition of the parasite fauna in the northern Wadden Sea today seems to be similar to the one several

decades ago. The same parasite species were recorded in the host species and parasite species richness and infection levels remained similar. Since the parasites have complex life cycles, they integrate several trophic levels and taxonomic groups within an ecosystem. The arising complexity and interconnectivity may level out any direct effects of environmental changes on parts of the life cycles leading to relatively persistent parasite–host systems. However, this only works as long as the biotic compartment of an ecosystem remains the same. Changes in the host species composition have profound indirect impacts on parasite–host systems since the parasites usually show high host specificity (Lauckner 1980, 1983b). If a host species is lost from the system, the life cycle of a parasite species cannot be completed and the parasite species may eventually become locally extinct. This is evident in cockles (*C. edule*) that were regularly infected with high numbers of the trematode *M. minutus* in the 1960s and 1970s (Lauckner 1971, 1990b). Today, this parasite species can only be observed locally with low intensities (Thieltges and Reise 2006). The first intermediate host for this species is the bivalve, *Scrobicularia plana*, which was common in the earlier period, almost absent in the 1980s, with some recovery observed since the late 1990s (Reise, unpublished data). In addition, the final hosts of this parasite (oystercatchers *Haematopus ostralegus*) show a recent decline (Blew and Südbeck 2005), thus, probably further preventing the completion of the life cycle. The opposite effect can also happen, when new host species colonize an area. Today, two trematode species (*L. minimus*, *M. parvus*) occur in cockles (*C. edule*), which were not present in the 1960s and 1970s. Both species utilize fish as intermediate and/or final hosts and occur in Mediterranean, French Atlantic and British waters (Maillard 1975; Sannia et al. 1978). Changing fish distributions and migrations during the last 30 years (Ehrich and Stransky 2001; Perry et al. 2005) may have carried these parasites into the northern Wadden Sea. Native mussels fouling on ship hulls and translocations of mussels for aquaculture purposes were probably involved in the successive introduction of the parasitic copepod *M. intestinalis* from southern to northern European localities (Korringa 1968). Since females of *M. intestinalis* produce only few eggs (200–300) and larval dispersal appears to be limited (Korringa 1968), it probably took a while for the local population in the Wadden Sea to spread throughout

Table 2 Records of the parasitic copepod *M. intestinalis* in mussels (*M. edulis*) between 1939 and 2004 as indicated in the literature

Time	Prevalence	Intensity	No. of sites	Source
1939	Probably absent	×	Only samples from other North-Frisian sites	Caspers (1939)
1950–1953	Probably absent	×	Only samples from other North-Frisian sites	Meyer-Warden and Mann (1954)
1969–1970	2.5%	1.5 ± 0.7	2	Dethlefsen (1972)
2003–2004	68.4 ± 25.7%	3 ± 1.7	6	Thieltges et al. (2006)

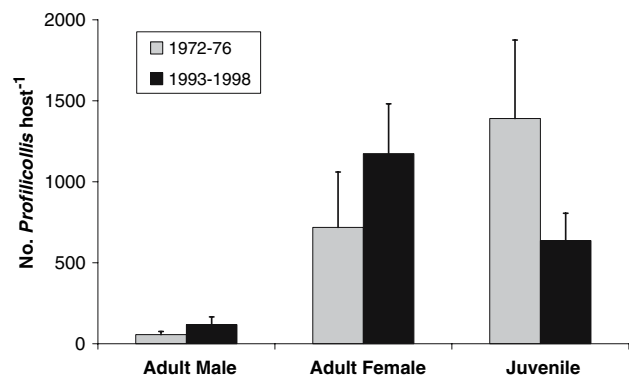
Table 3 Parasites recorded in shore crabs (*C. maenas*) in two periods: 1989 (Lauckner 1990) and 2004 (this study)

Date	Tidal level	Name of locality	n	Carapax width (mm)	Mean carapax width (mm)	<i>M. claviformis</i> (max)	<i>M. subdolum</i> (max)	<i>P. botulus</i> (max)	Reference
June 1989	Intertidal	Frischwassertal	10	>25	Approx. 30	173	2.8	3.3	Lauckner (1990)
June 1989	Intertidal	Schiessplatz	22	>25	Approx. 30	4,087	31.9	1.4	Lauckner (1990)
June 1989	Subtidal	Lister Ley at Königshafen	337	10–65	Approx. 35	No data	No data	2.3	Lauckner (1990)
June 1989	Subtidal	Lister Ley at Königshafen	369	10–65	Approx. 35	No data	No data	2.3	Lauckner (1990)
August 2004	Intertidal	Diedrichsenbank	25	35–66	55.3	506.9 ± 746.3 (3,104)	21.7 ± 36.9 (148)	2.5 ± 2.5 (10)	This paper
August 2004	Subtidal	Lister Ley at Königshafen	15	18–62	38.9	378.8 ± 684.2 (1,964)	9.4 ± 24.8 (89)	1.1 ± 1.3 (4)	This paper
August 2004	Subtidal	Schweinebucht	59	16–66	42.7	352.7 ± 823.9 (4,063)	15.8 ± 39.3 (223)	2.2 ± 3 (13)	This paper

Table 4 Results of two-factorial crossed ANOVA analysis testing for differences in infection levels of the acanthocephalan *P. botulus* in eiders (*S. mollissima*)

	dF	MS	F	P
Time	1	0.08	0.13	0.72
Age/sex	2	15.94	24.06	<0.001
Time × age/sex	2	0.38	0.59	0.56
Error	95	0.67		

No. of individuals investigated—1972–1976: adult male (17), adult female (8), juveniles (10); 1993–1998: adult male (31), adult female (17), juvenile (18)

**Fig. 3** Number of the acanthocephalan *P. botulus* in eiders (*S. mollissima*) (+SD) collected in two different time periods

the entire region and to finally include the area around Sylt where it now seems to be firmly established.

The introduction of now very abundant species like American razor clams (*Ensis americanus*), Pacific oysters (*C. gigas*), and American slipper limpets (*C. fornicata*) (Armonies and Reise 1999; Diederich et al. 2005; Thieltges et al. 2003) has not entailed arrivals of new parasites (Krakau et al. 2006). This is possibly due to the fact that invaders tend to leave behind their parasites in their native ranges since other necessary hosts in the life cycles are rarely co-introduced and hence missing in the new areas (“enemy release hypothesis”) (Torchin et al. 2003; Taraschewski 2006). Native trematode parasites infect oysters and clams, but to a lower extent than natives, and thus play only a minor role in their life cycles (Krakau et al. 2006). No trematode parasites were found at all in *C. fornicata* (Thieltges et al. 2004). However, future species introductions may import new parasites into the system, such as the one that has occurred with Erythrean invaders into the Mediterranean Sea (Galil 2000). Due to the strong populations of *E. americanus*, *C. gigas* and *C. fornicata* in the northern Wadden Sea, and a concomitant decline in native mussels *M. edulis* (Nehls et al. 2006), a large share of the present mollusc fauna is not or poorly integrated into the local parasite web.

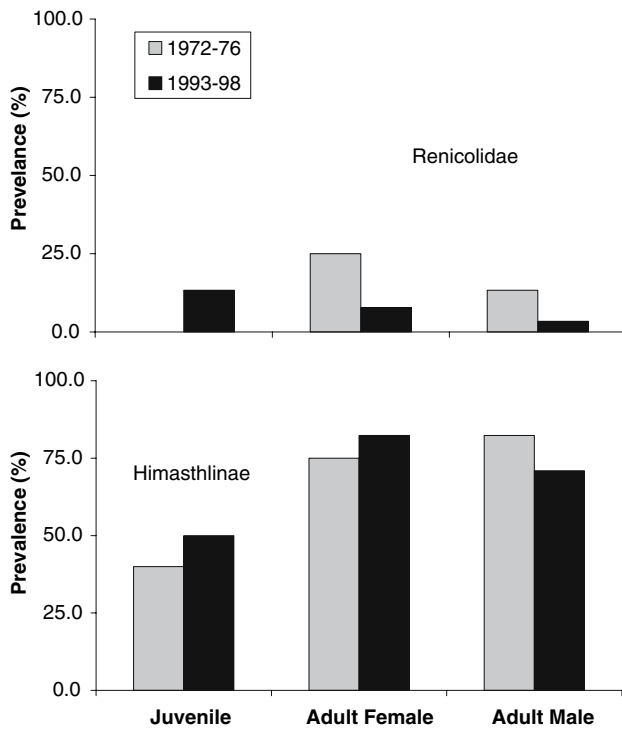


Fig. 4 Prevalence (%) of the trematode groups Renicolidae and Himasthinae in eiders (*S. molissima*)

Parasites and bottom-up and top-down control

Although pollution (Möller 1987; Khan and Thulin 1991), eutrophication (Reimer 1995; Zander 2002) and ambient temperature levels (Poulin and Mouritsen 2006; Poulin 2006) are known to influence parasite transmission and communities, we could not observe major alterations of the parasite fauna. This may indicate that the indirect effects of the composition of the host community on the parasite fauna override any direct effects of temporal changes in abiotic factors. However, especially eutrophication may be of high importance for parasite communities. It is often involved in bottom-up control of marine systems since eutrophication leads to an increasing primary production with a subsequent increase in benthic biomass, which then attracts birds and other predators (Posey et al. 1995; Cloern 2001; Beukema et al. 2002). Since benthic invertebrates act as intermediate hosts and birds and other predators as final hosts for parasites, this should result in a vicious circle leading to high parasite species richness and infection levels in eutrophicated systems. However, in the northern Wadden Sea, there is no clear evidence of eutrophication eliciting bottom-up effects to consumers relevant as parasite hosts. In the Skallingen area, Jensen (1992) could not detect a long-term increase in the intertidal macrobenthic fauna. Around Sylt, it has been suggested that some larger macrobenthic invertebrates have attained an elevated

Table 5 Mass mortality events reported in the northern Wadden Sea where parasites were probably involved

Time	Host	Parasite	Locality	Additional stressor	Reference
Summer 1983	<i>L. littorea</i>	Trematodes (esp. <i>R. roscovia</i>)	Königshafen	High temperatures	Lauckner (1983)
Summer 1985	<i>L. littorea</i>	Trematodes	Königshafen	High temperatures	Lauckner (1994)
May–June 1990	<i>H. ulvae</i>	Trematodes (<i>M. claviformis</i> , <i>M. subdolum</i>)	Hojer	High temperatures	Jensen and Mouritsen (1992), Mouritsen and Jensen (1997)
1992/1993	<i>C. edule</i>	Trematodes (<i>G. gibberosus</i>)	Königshafen	?	Lauckner (1992, 1994)
Summer 2004	<i>C. edule</i>	Trematodes (<i>G. choledochus</i>)	Königshafen	High temperatures	Thielges 2006
May–June 1990	<i>C. volutator</i>	Trematodes (<i>M. claviformis</i> , <i>M. subdolum</i>)	Hojer	High temperatures	Jensen and Mouritsen (1992), Mouritsen and Jensen (1997)
Summer 1986	<i>C. maenas</i>	Trematodes (<i>M. subdolum</i> , <i>M. similis</i>)	Königshafen	Probably high temperatures	Lauckner (1986)
Winter 1993/1994	<i>C. maenas</i>	Acanthocephalans (<i>P. botulus</i>)	Subtidal	Low temperatures	Lauckner (1994)

? not indicated in publication

abundance, particularly mussels (Reise et al. 1989, 1994), but the latter became subject to heavy human exploitation and more recently seem to have declined due to repeated recruitment failure. This has been attributed to a prevalence of mild winters which give an advantage to mussel predators such as shorecrabs *C. maenas* and starfish *Asterias rubens* (Nehls et al. 2006). Also, in the southern Wadden Sea, most bivalve populations are more affected by varying winter severity than eutrophication (Beukema and Dekker 2005). Temperature may also play an important role for parasites but the observed recent warming trend is probably too subtle (less than 1°C) to cause any observable effects.

Besides abiotic factors, biotic factors may also be important in the long run. While bottom-up regulation is usually considered in the context of eutrophication in coastal waters, top-down effects attained particular attention due to the loss of conspicuous predators because of hunting and fishing down the food web (Pauly et al. 1998; Jackson et al. 2001; Lotze et al. 2005). The complex life cycles of parasites of coastal systems are inherently linked to top predators. Thus, a loss of final hosts not only entails a relief from predation pressure but is also accompanied by a possible relief from parasitism for intermediate hosts. This may be an important long-term consequence for intertidal ecosystems such as the Wadden Sea with an intensive human exploitation having, e.g., caused a notable decrease in coastal birds in the eighteenth and nineteenth century and followed by a subsequent recovery due to bird protection programs (Wolff 2005; Lotze 2005). In this context, trematodes may be seen as exacerbating the effects of predation by the effects of parasitism, lowering secondary production in the intertidal zone. This may lead to an enhanced top-down regulation. However, most of the losses due to hunting and fishing in the Wadden Sea and the adjacent North Sea have already taken place prior to our period of investigation making it difficult to trace changes in the parasite fauna during the last 4 decades. The native oyster *Ostrea edulis* became commercially extinct in the 1920s and then vanished altogether from the northern Wadden Sea (Lotze 2005). Large and abundant fish such as sturgeon and rays disappeared in the 1930s and 1950s, respectively, and never came back. In contrast, seals and coastal birds did recover from former hunting pressure and as important final hosts, may have had a positive effect on parasite populations. However, again there are confounding effects. Seals, although generally increasing, have crashed in 1988 and 2003 to half of their population size in the Wadden Sea region (Reijnders et al. 2005, 2006). Mollusc-feeding birds such as eiders *S. mollissima* and oystercatchers *H. ostralegus* became more abundant until the 1990s but then declined more recently (Blew and Südbeck 2005). Thus, the overall top-down effects on the parasite populations may have lacked a clear trend over the past 4 decades.

Contingency and mass mortality events

Although relatively persistent during the time period investigated, there was considerable spatial variability between sampling localities, for example, indicated by the high standard deviations in the parasites of periwinkles (*L. littorea*) (Fig. 2). Also in crabs (*C. maenas*), differences between sampling sites could be observed within sampling periods (Table 3). Spatial heterogeneity in parasite infection levels is well known (Shaw and Dobson 1995; Wilson et al. 2002). In coastal ecosystems it results from a variety of factors, e.g. the presence and density of upstream hosts (the preceding host in the life cycle) (Hechinger and Lafferty 2005; Fredensborg et al. 2006), host density (Thieltges and Reise 2007), host size (Jensen et al. 1999) and habitat (Thieltges and Reise 2007; Thieltges 2007). To lead to high infection levels, a multitude of different events have to come together. All hosts (intermediate and final) have to be present in sufficient numbers and at least some of them must be infected by parasites. Suitable conditions for transmission of infective stages must be met before an infection can occur. Hence, contingency seems to be an important constituent of parasite population dynamics. This may explain why parasite-induced mass mortality events occur only locally and occasionally. Besides a high parasite load in the hosts, another prerequisite for mass mortality events seems to be an additional environmental stressor. Most mass mortalities reported in the past have been associated with warm ambient temperatures (Table 5). For example, higher than normal air and water temperatures in spring 1990 led to a strong increase in parasite burden and a subsequent mass mortality event in the mud snail (*H. ulvae*) acting as first intermediate host and in the amphipod *C. volutator* acting as second intermediate host for microphallid trematodes (Jensen and Mouritsen 1992; Mouritsen and Jensen 1997). It is too early to detect a potential increase in mass mortalities during the last decades with a notable warming trend due to the little data available. However, an increase of such events seems likely under climate change scenarios.

Parasites as environmental indicators

That we were unable to detect major alterations in the parasite fauna, although a range of environmental changes had occurred during the last 4 decades, seems to be contradictory to attempts to use parasites as environmental indicators (Lafferty 1997; Marcogliese 2005). As discussed above, environmental changes in our local system were multiple, often obscured by many confounding factors and thus far from unidirectional. This probably prevented major alterations in the parasite fauna. Studies where only single environmental factors changed during decades, alterations were

observed in the parasite fauna (e.g. Kesting and Zander 2000). Hence, parasites may only be useful as sensitive environmental indicators when environmental changes are few and unidirectional.

Interestingly, effects of changes in environmental factors seem to be mediated by indirect effects on hosts rather than direct effects on the parasites. For example, eutrophication in the Baltic Sea has led to alterations in the host fauna and subsequently to major changes in the parasite fauna, mainly due to losses of host species (Kesting and Zander 2000; Zander and Reimer 2002). The importance of the composition of host communities for parasite faunas is further indicated by positive correlations between host and parasite diversity (Hechinger and Lafferty 2005). Hence, parasite diversity is probably a good indicator for the diversity and complexity of the local host fauna. However, changes must be quite dramatic (loss or gain of host species) to detect any changes in the parasite fauna as, for example, observed in cockle parasites.

There are, of course, methodological difficulties in detecting effects of environmental changes on parasite faunas. While it is relatively easy to detect the gain or loss of parasite species in a local parasite fauna, identifying changes in infection levels in the hosts is much more difficult. As discussed above, spatial heterogeneity in infection levels is already usually high within single years and contingent events may locally lead to extremely high infection levels, thus adding considerable within-year variability. To capture inter-annual trends, within the noise of this high intra-annual variability, is a challenge. Well-designed sampling strategies are needed for sensitive long-term studies to detect changes in infection levels besides observing alterations in the parasite species composition.

Conclusions

The parasite fauna in the northern Wadden Sea has remained basically the same during the past 4 decades. The few changes in parasite species presence observed resulted from changes in host distribution and abundance. Introduced alien host species had little effect on the parasite community because no alien parasites were concomitantly introduced and the native parasites show low prevalence and intensity in these novel hosts. In the context of human aided biotic globalisation, parasites with complex life cycles constitute a conservative ecosystem component. Presumably, some changes occurred on much longer time scales than data are available, notably by the loss of conspicuous predators because of hunting and fishing down the food web. The recent warming trend in water temperatures has probably been too subtle to detect any effects. Eutrophication and effects of phased-out hunting may not have had clear bottom-up or top-down effects on the parasite

community because of various confounding factors. Parasites depending on several host species may only achieve strong population changes if all hosts are affected in a unidirectional way. This, however, is rather unlikely to happen in a coastal ecosystem subject to multiple pressures. Well-designed long-term studies are needed to detect future changes in the parasite fauna. Climatic warming may cause an increase in the frequency of mass mortality events and immigrants from the south may enrich the parasite fauna in the northern Wadden Sea in the future.

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References

- Armonies W, Reise K (1999) On the population development of the introduced razor clam *Ensis americanus* near the island of Sylt (North Sea). *Helgol Meeresunters* 52:291–300
- Beukema JJ, Dekker R (2005) Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. *Mar Ecol Prog Ser* 287:149–167
- Beukema JJ, Cadée GC, Dekker R (2002) Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. *J Sea Res* 48:97–110
- Beusekom J van, Bot P, Göbel J, Hanslik M, Lenhart H-J, Pätsch J, Peperzak L, Petenati T, Reise K (2005) Eutrophication. In: Essink K et al (eds) Wadden Sea quality status report 2004. Wadden Sea ecosystem 19. Common Wadden Sea Secretariat, Wilhelmshaven, pp 141–154
- Blew J, Südbeck P (eds) (2005) Migratory waterbirds in the Wadden Sea 1980–2000. Wadden Sea ecosystem 20. Common Wadden Sea Secretariat, Wilhelmshaven
- Caspers H (1939) Über Vorkommen und Metamorphose von *Mytilicola intestinalis* Steuer (Copepoda paras.) in der südlichen Nordsee. *Zool Anzeiger* 126:161–171
- Cloern JE (2001) Our evolving conceptual model of the coastal eutrophication problem. *Mar Ecol Prog Ser* 210:223–253
- de Montaudouin X, Kisielewski I, Bachelet G, Desclaux C (2000) A census of macroparasites in an intertidal bivalve community, Arcachon Bay, France. *Oceanol Acta* 23:453–468
- Dethlefs B (1995) Reproduktion der Strandschnecke *Littorina littorea* (L.) im Wattenmeer bei Sylt. Diplomarbeit. Universität Hamburg, Hamburg
- Dethlefsen V (1972) Zur Parasitologie der Miesmuschel (*Mytilus edulis* L., 1758). *Ber Dt Wiss Komm Meersforsch* 22:344–371
- Diederich S, Nehls G, van Beusekom JEE, Reise K (2005) Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? *Helgol Mar Res* 59:97–106
- Ehrich S, Stransky C (2001) Spatial and temporal changes in the southern species component of North Sea bottom fish assemblages. *Senckenb Maritima* 31:143–150
- Fredensborg BL, Mouritsen KN, Poulin R (2006) Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail—from small to large scale. *Mar Biol* 149:275–283
- Galil BS (2000) A sea under siege—alien species in the Mediterranean. *Biol Invasions* 2:177–186

- Hechinger RF, Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proc Biol Sci* 272:1059–1066
- Jackson JBC et al (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Jensen KT (1992) Macrozoobenthos on an intertidal mudflat in the Danish Wadden Sea: comparisons of surveys made in the 1930s, 1940s and 1980s. *Helgol Meeresunters* 46:363–376
- Jensen KT, Mouritsen KN (1992) Mass mortality in two common soft-bottom invertebrates, *Hydrobia ulvae* and *Corophium volutator*—the possible role of trematodes. *Helgol Meeresunters* 46:329–339
- Jensen KT, Castro NF, Bachelet G (1999) Infectivity of *Himasthla* spp. (Trematoda) in cockle (*Cerastoderma edule*) spat. *J Mar Biol Assoc UK* 79:265–271
- Kesting V, Zander CD (2000) Alteration of the metazoan parasite fauna in the brackish Schlei fjord (Northern Germany, Baltic Sea). *Int Rev Hydrobiol* 85:325–340
- Kesting V, Gollasch S, Zander CD (1996) Parasite communities of the Schlei fjord (Baltic coast of northern Germany). *Helgol Meeresunters* 50:477–496
- Khan RA, Thulin J (1991) Influence of pollution on parasites of aquatic animals. *Adv Parasitol* 30:201–238
- Korringa P (1968) On the ecology and distribution of the parasitic copepod *Mytilicola intestinalis*. *Steur Bijdr Dierk* 38:47–57
- Krakau M, Thielges DW, Reise K (2006) Parasites in introduced bivalves—implications for a coastal ecosystem. *Biol Invasions* 8:919–925
- Lafferty KD (1997) Environmental parasitology: what can parasites tell us about human impacts on the environment? *Parasitol Today* 13:251–255
- Lauckner G (1971) Zur Trematodenfauna der Herzmuscheln *Cardium edule* und *Cardium lamarcki*. *Helgol Meeresunters* 22:377–400
- Lauckner G (1980) Diseases of Mollusca: Gastropoda. In: Kinne O (ed) *Diseases of marine animals vol I, general aspects, protozoa to gastropoda*. Wiley, New York, pp 311–424
- Lauckner G (1983a) Auswirkungen des heißen Sommers 1983 auf die Trematodenfauna der Strandschnecke *Littorina littorea*. In: *Jahresbericht Biologische Anstalt Helgoland 1983*. BAH, Hamburg, pp 11–12
- Lauckner G (1983b) Diseases of Mollusca: Bivalvia. In: Kinne O (ed) *Diseases of marine animals vol 2, Introduction, Bivalvia to Scaphopoda*. Biologische Anstalt Helgoland, Hamburg, pp 477–961
- Lauckner G (1985) Populationsdynamik mariner Mollusken und ihrer eigenen Parasiten. In: *Jahresbericht Biologische Anstalt Helgoland 1985*. BAH, Hamburg, pp 11–13
- Lauckner G (1986) Einfluss von Trematodeninfestationen auf Überleben und Wachstum der Strandkrabbe *Carcinus maenas*. In: *Jahresbericht Biologische Anstalt Helgoland 1986*. BAH, Hamburg, pp 11–12
- Lauckner G (1987) Effects of parasites on juvenile Wadden Sea invertebrates. In: Tourgaard et al (eds) *Proceedings of the fifth international Wadden Sea symposium*. National Forest and Nature Agency, Esbjerg, pp 103–121
- Lauckner G (1990a) Populationsdynamik parasitengeschädigter Strandkrabben (*Carcinus maenas*) im Nordsylder Wattenmeer & *Carcinus*-Parasiten: Demonstration ihrer Pathogenität im Langzeitexperiment. In: *Jahresbericht Biologische Anstalt Helgoland 1990*, BAH, Hamburg, pp. 19–23
- Lauckner G (1990b) Parasiten—ihr Einfluss im Ökosystem Wattenmeer. In: Lozan et al, *Warnsignale aus der Nordsee*. Parey, Berlin, Hamburg, pp 219–230
- Lauckner G (1992) Parasitenbedingtes Herzmuschel-Massensterben im Königshafen bei List auf Sylt. In: *Jahresbericht Biologische Anstalt Helgoland 1992*, BAH, Hamburg, pp 31–33
- Lauckner G (1994) Parasiten als bestandregulierender Faktor im Watt. In: Lozan et al, *Warnsignale aus dem Wattenmeer*. Blackwell, Berlin, pp 144–149
- Lauckner G (1995/96) Bedeutung der Parasiten in der Fauna des Wattenmeeres. In: *Jahresbericht Biologische Anstalt Helgoland 1995/96*, BAH, Hamburg, pp 69–76
- Lotze HK (2005) Radical changes in the Wadden Sea fauna and flora over the last 2,000 years. *Helgol Mar Res* 59:71–83
- Lotze HK et al (2005) Human transformations of the Wadden Sea ecosystem through time: a synthesis. *Helgol Mar Res* 59:84–95
- Maillard C (1975) *Labratrema lamirandi* (Carrere, 1937) (Trematoda, Bucephalidae) parasite de *Dicentrarchus labrax* (L., 1758). Création du genre *Labratrema*. Cycle évolutif. *Bull Mus Natl Hist Nat* 193:69–80
- Marcogliese DJ (2005) Parasites of the superorganism: are they indicators of ecosystem health? *Int J Parasitol* 35:705–716
- Marencic H (2005) Fishery, hunting. In: Essink K et al (eds) *Wadden Sea quality status report 2004*. Wadden Sea ecosystem 19. Common Wadden Sea Secretariat, Wilhelmshaven, pp 49–57
- Meyer-Waarden P-F, Mann H (1954) Der Befall von *Mytilus edulis* durch *Mytilicola intestinalis* in den deutschen Wattgebieten 1950–1953. *Ber Dtsch Wiss Komm Meeresforsch* 8:347–362
- Möller H (1987) Pollution and parasitism in the aquatic environment. *Int J Parasitol* 17:353–361
- Mouritsen KN, Jensen KT (1997) Parasite transmission between soft-bottom invertebrates: temperature mediated infection rates and mortality in *Corophium volutator*. *Mar Ecol Prog Ser* 151:123–134
- Mouritsen KN, Poulin R (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* 124:101–117
- Mouritsen KN, Poulin R (2005) Parasites boost biodiversity and change animal community structure by trait-mediated indirect effects. *Oikos* 108:344–350
- Nehls G, Diederich S, Thielges DW, Strasser M (2006) Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? *Helgol Mar Res* 60:135–143
- Nicholas WL (1973) The biology of Acanthocephala. *Adv Parasitol* 11:671–706
- Oost A, Becker G, Fenger J, Hofstede J, Weisse R (2005) Climate. In: Essink K, Dettmann C, Farke H, Laursen K, Lürßen G, Marencic H, Wiersinga W (eds) *Wadden Sea quality status report 2004*, Wadden Sea ecosystem 19:75–82
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1998) Fishing down marine food webs. *Science* 279:860–863
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- Poulin R (2006) Global warming and temperature-mediated increases in cercarial emergence in trematode species. *Parasitology* 132:134–151
- Poulin R, Mouritsen KN (2006) Climate change, parasitism and the structure of intertidal ecosystems. *J Helminthol* 80:183–191
- Posey M, Powell C, Cahoon L, Lindquist D (1995) Top down vs. bottom up control of benthic community composition on an intertidal flat. *J Exp Mar Biol Ecol* 185:19–31
- Reijnders PJH et al (2005) Marine mammals. In: Essink K et al (eds) *Wadden Sea quality status report 2004*, Wadden Sea ecosystem 19. Common Wadden Sea Secretariat, Wilhelmshaven, pp 305–318
- Reijnders PJH, Brasseur SMJM, Abt K, Siebert U, Stede M, Tougaard S (2006) Aerial surveys of harbour seals in the Wadden Sea in 2006: puzzling results. *Wadden Sea Newsletter* 2006-1
- Reimer LW (1995). Parasites especially of piscine hosts as indicators of the eutrophication in the Baltic Sea. *Appl Parasitol* 36:124–135
- Reise K, Siebert I (1994) Mass occurrence of green algae in the German Wadden Sea. *DHZ Suppl* 1:171–188

- Reise K, Herre E, Sturm M (1989) Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. *Helgol Meeresunters* 43:417–433
- Reise K, Herre E, Sturm M (1994) Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. *Helgol Meeresunters* 48:201–215
- Sannia A, James B (1978) The occurrence of *Cercaria cerastodermae* I Sannia, James, and Bowers, 1978 (Digenea: Monorchiiidae) in populations of *Cerastoderma edule* (L.) from commercial beds of the lower Thames estuary. *Z Parasitenkd* 56:1–11
- Shaw DJ, Dobson AP (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. *Parasitology* 111:S111–S133
- Shaw RG, Mitchell-Olds T (1993) ANOVA for unbalanced data: an overview. *Ecology* 74:1638–1645
- Sousa WP (1991) Can models of soft-sediment community structure be complete without parasites? *Am Zool* 31:821–830
- Taraschewski H (2006) Hosts and parasites as aliens. *J Helminthol* 80:99–128
- Thieltges DW (2006) Parasite induced summer mortality in common cockles *Cerastoderma edule* by the trematode *Gymnophallus choledochus*. *Hydrobiologia* 559:455–461
- Thieltges DW (2007) Habitat and transmission—effect of tidal level and upstream host density on metacercarial load in an intertidal bivalve. *Parasitology* 134:599–605
- Thieltges DW, Reise K (2006) Metazoan parasites in intertidal cockles *Cerastoderma edule* from the northern Wadden Sea. *J Sea Res* 56:284–293
- Thieltges DW, Reise K (2007) Spatial heterogeneity in parasite infections at different scales in an intertidal bivalve. *Oecologia* 150:569–581
- Thieltges DW, Strasser M, Reise K (2003) The American slipper-limpet *Crepidula fornicata* (L.) in the Northern Wadden Sea 70 years after its introduction. *Helgol Mar Res* 57:27–33
- Thieltges DW, Strasser M, Beusekom JEE van, Reise K (2004) Too cold to prosper – winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. *J Exp Mar Biol Ecol* 311:375–391
- Thieltges DW, Krakau M, Andresen H, Fottner S, Reise K (2006a) Macroparasite community in molluscs of a tidal basin in the Wadden Sea. *Helgol Mar Res* 60:307–316
- Thieltges DW, Hussen B, Baekgaard H (2006b) Endoparasites in common eiders *Somateria mollissima* from birds killed by an oil spill in the northern Wadden Sea. *J Sea Res* 55:301–308
- Thompson RM, Mouritsen KN, Poulin R (2005) Importance of parasites and their life cycle characteristics in determining the structure of a large marine food web. *J Anim Ecol* 74:77–85
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421:628–630
- Valiela I (2006) *Global coastal change*. Blackwell, Oxford
- Werdning B (1969) Morphologie, Entwicklung und Ökologie digener Trematoden-Larven der Strandschnecke *Littorina littorea*. *Mar Biol* 3:306–333
- Wilson K, Bjornstad ON, Dobson AP, Merler S, Poglajen G, Randolph SE, Read AF, Skorpung A (2002) Heterogeneities in macroparasite infections: patterns and processes. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek D, Dobson AP (eds) *The ecology of wildlife diseases*. Oxford University Press, Oxford, pp 6–44
- Wolff WJ (2005) The exploitation of living resources in the Dutch Wadden Sea: a historical overview. *Helgol Mar Res* 59:31–38
- Zander CD (2002) The influence of eutrophication on parasite communities in the Baltic Sea. In: *Proceedings of the tenth international congress of parasitology, ICOPA, vol 10*, pp 247–253
- Zander CD, Reimer L (2002) Parasitism at the ecosystem level in the Baltic Sea. *Parasitology* 124:119–135
- Zander CD, Reimer LW, Barz K, Dietel G, Strohbach U (2000) Parasite communities of the Salzhaff (Northwest Mecklenburg, Baltic Sea) II. Guild communities, with special regard to snails, benthic crustaceans, and small-sized fish. *Parasitol Res* 86:359–372
- Zander CD, Koçglu Ö, Skroblies M, Strohbach U (2002) Parasite populations and communities from the shallow littoral of the Orther Bight (Fehmarn, SW Baltic Sea). *Parasitol Res* 88:734–744