Parasitism at the ecosystem level in the Baltic Sea

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SUMMARY

The Baltic Sea is characterized by organisms that can tolerate brackish water. Because of the Sea's history during glacial times, its flora and fauna (and also their parasites) can be traced to marine, freshwater and genuine brackish elements beside glacial relics. Snails, planktonic copepods, benthic amphipods and isopods are important intermediate hosts of diverse helminths; in addition polychaetes, bivalves and fishes may also act as final hosts. The most important final hosts, beside fishes, were seals and birds; these were able to disperse the parasites over the whole of the Baltic. Decreasing salinity from west to east limits the distribution of many parasites. Several marine and genuine brackish water species have almost spread over the whole Baltic. Freshwater species, however, have a lower tolerance than marine species and are only rarely found in the western part. A serious problem in the Baltic is eutrophication which can lead to massive abundances of generalist parasites, in host populations as well as host individuals. The final stage of this influence can cause a general decrease of host abundance and, as a consequence, of all kinds of parasites, due to oxygen deficiency. In comparison with the species spectrum of other brackish waters in Europe, the Baltic presents some endemic parasites as well as sharing parasite species with the Mediterranean and even the Black Sea.

Key words: Brackish water, distribution, tolerance, eutrophication, species spectrum.

INTRODUCTION

The Baltic Sea is of very recent origin; its status as a brackish water body goes back no longer than 3500 years. Therefore, evolutionary processes did not have sufficient time for spectacular specialisation. The Baltic is a shallow sea enclosed by land and has only a restricted connection from the Kattegat to the North Sea. From there salinity decreases from 30–20‰ to only 3–1‰ in the Bothnian Bay and the Gulf of Finland in the east (Fig. 1). A sharp decrease in salinity follows in the areas of the Belt Sea, the Sound and the south-west Baltic (Kiel Bight 20–14‰, Mecklenburg Bight 14–10‰), up to the shallow Bank of Darss (19 m deep). This is the limit between the Western and the huge area of the Central Baltic with an almost uniform surface salinity of 8–6‰. Salinity increases again in the depths and, together with the decline in temperature, creates a boundary layer. Therefore, an exchange of surface and deep layers is severely restricted, which causes oxygen deficits in the depths. Only sporadically (last time in 1994) can water bodies from the North Sea overcome the Bank of Darss and provide the deep Central Baltic with oxygen-saturated water for a short time period.

The aim of this article is to examine parasite–host relationships in the Baltic Sea as an extreme environment. Whereas changes of salinity are natural phenomena to which organisms can adapt over a long time, man-made eutrophication has only been in effect since the last century and has become a great problem in the Sea. The influences of salinity and eutrophication will be dealt with in the context of parasite abundance. The specialists among the parasites deserve special attention, because their occurrence in the Baltic Sea is expected to be restricted, in comparison to other waters. We follow the concept of Holmes & Price (1986), furthered by Zander (1998*a*, 2001), which discerns parasite populations and communities at different hierarchical levels: individual hosts (infrapopulation or infracommunity), host populations (component), group of ecologically similar host species (guild) and all stages of a species or all organisms of an ecosystem, respectively (suprapopulation or supracommunity). Because not all existing hosts (as well as parasites) may be recorded, the supracommunity can barely be analyzed and, therefore, can only be considered theoretically. The best approach may be to compile as many analyzed guilds as possible in order to characterize the ecosystem level. This is done in regard to possible processes of co-evolution in the greatest brackish sea of northern Europe.

PARASITE FAUNA AND ITS ORIGIN

Like all other organisms of the Baltic (Remane, 1958), the parasite communities are also composed of marine, brackish and freshwater elements. This composition does not mean that marine hosts are only infected by marine parasites, freshwater hosts only by freshwater parasites, and so on. The fact is that in the Baltic all groups of hosts and parasites are

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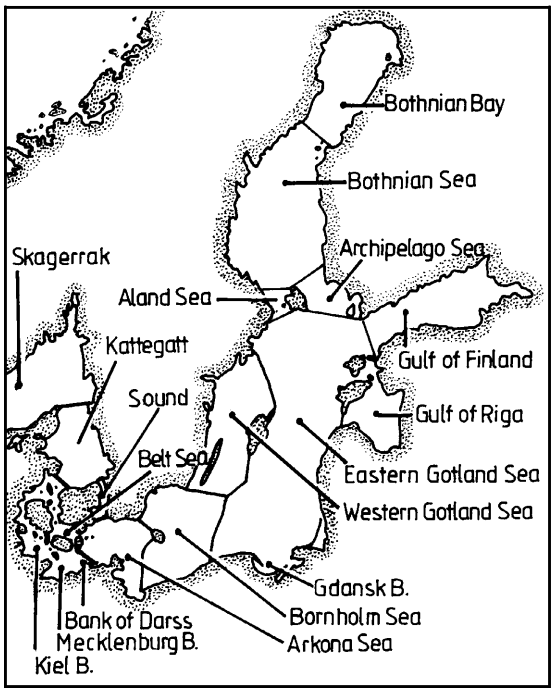


Fig. 1. Map of the Baltic Sea which is divided into several main areas according to salinity. Beginning in the Kattegat (30–20‰ S) salinity decreases until the Bank of Darss rapidly. Arkona Sea, Bornholm Sea, Western and Eastern Gotland Sea comprise the huge Central Baltic Sea with a salinity of 8–6‰. These low values decrease to a freshwater level at the end of the Bothnian Bay and the Gulf of Finland.

thoroughly mixed. Consequently, one can find many generalists and only some specialists among the parasites of this sea.

The marine elements are represented by many helminths and copepods. Several species of Digenea which are common in the Atlantic and North Sea also tolerate brackish waters. The intertidal fish parasite *Podocotyle atomon* (James, 1970) lives in the sublittoral of the Baltic. *Cryptocotyle lingua* infects fish as second intermediate host and birds as the final host (Stunkard, 1930). The digenean group of Hemiurida, (e.g. *Brachyphallus crenatus*) are obvious by their planktobenthic way of life (see below), which is also observed in the brackish Baltic (Reimer, 1970). Abundant cestodes of marine origin include *Bothriocephalus* spp. which have become specialized to several fish as final hosts (Renaud & Gabrion, 1984). Characteristic marine representatives among nematodes include *Anisakis simplex* from whales and *Hysterothylacium aduncum* from fishes. Common Acanthocephala are *Echinorhynchus gadi* in fish or *Corynosoma strumosum* in birds (Reimer, 1969). *Lernaeocera branchialis* is an example of a marine copepod found in Kiel Bight; the larvae may even be found in the Mecklenburg Bight (Arntz, 1972; Lüthen, 1989).

The number of species of freshwater origin is clearly lower because their existence depends on the occurrence of distinct intermediate hosts or, alternatively, the capture of replacement hosts (Holmes, 1990). The bird digenean *Diplostomum spathaceum*, widespread in fresh water causing blindness in many fish intermediate hosts, depends also in brackish water on the occurrence of the snail *Radix ovata* (Zander *et al*. 2000). The bird cestode *Schistocephalus solidus* has become specialized to its second intermediate host, the stickleback *Gasterosteus aculeatus*. Parasitic freshwater nematodes include *Raphidascaris acus* which is widespread in freshwater fish (Moravec, 1994) and regularly found in the Baltic, in flatfish, eels or sprats (Reimer & Walter, 2000). *Pomphorhynchus laevis* (Acanthocephala) matures in freshwater fish (Hine & Kennedy, 1974) as well as in several fish of the Baltic (Lüthen, 1989). *Caligus lacustris* (Copepoda) was found in the Schlei fjord (Kesting & Zander, 2000), Arkona Sea (Kozikowska, 1957; Schwarz 1960) and Gdansk Bight (Grabda, 1962). This parasite is also known from the Black and Kaspian Sea (Petrushewskij, 1957).

Genuine brackish water parasites are difficult to distinguish from marine parasites. One of their characteristics is a more abundant presence than closely-related species of marine origin. The digenean *Cryptocotyle concavum* is common in the Baltic and other brackish waters; its first and preferred second intermediate hosts (the snail, *Hydrobia stagnalis* and the fish, *Pomatoschistus microps*) are also genuine brackish water species. The digeneans *Aphalloides timmi*, also in *P. microps*, and *Acanthostomum balthicum* in *Syngnathus typhle* may also be representatives of this category (Reimer, 1971; Reimer *et al*. 1996; Zander, Reimer & Barz, 1999), as well as the copepod *Thersitina gasterostei* living in the gill chamber of *Gasterosteus aculeatus* (Hildebrand & Scharberth, 1992; Zander & Westphal, 1991).

The nematode *Ascarophis arctica* may be a glacial relic (Fagerholm & Berland, 1988) which must have immigrated into the Baltic, together with its main host, the sculpin *Myoxocephalus quadricornis*, from the Barents Sea. The most peculiar non-native parasite of the Baltic is the eel nematode *Anguillicola crassus* which uses the brackish milieu as a bridge between the rivers of continental Europe and those of Scandinavia on its way of dispersal (Reimer *et al*. 1994).

Several parasites of the Baltic or closely-related species can also be found in other European brackish waters, e.g. off the French Atlantic and Mediterranean coasts as well as in the Black and Asov Seas (Bauer, 1987; Reimer *et al*. 1996). Certain species found in the Baltic Sea also occur in the Black Sea (e.g. *Asymphylodora demeli*), and other species occur also in France (e.g. *Brachyphallus crenatus*). The distribution patterns may possibly be influenced by the history of the Tethys Sea (Gibson & Køie, 1991; Reimer *et al*. 1996) as well as by the Parathethys in

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its extension during the Oligocene, when the regions of the Black and North Seas as well as the Baltic Sea were connected. The parasitic copepod, *Thersitina gasterostei*, was not only found in the Black, Caspian, White Seas but also off the coasts of Canada (Yamaguti, 1963). Endemic species of the Baltic Sea like *Aphalloides timmi*, *Acanthostomum balthicum* or possibly *Magnibursatus caudofilomentosa* may be the result of speciation events after the isolation of this sea, followed decreasing salinities as a natural barrier.

Regarding faunistic patterns, the composition of parasitic species of the Baltic does not differ principally from that of free living organisms with a majority of marine elements in both groups. The category of genuine brackish water species has strong taxonomic affinities to those of other European brackish waters which is in accordance with non-parasitic species which can even be distributed world-wide (Remane, 1958). Albeit its short existence the Baltic Sea has evolved some endemic parasite species which all are genuine brackish water species.

CHARACTERISTIC LIFE CYCLES IN THE BALTIC SEA

Here, one should consider the functional types of hosts in the brackish Baltic Sea; these guarantee the existence of parasites. Marine mammals, birds and fish are highly mobile hosts which contribute to the dispersion of parasites. According to Holmes & Price (1986) parasites of birds are allogenic ones which are transferred from the terrestrial to the aquatic environment. If fish are final hosts, the parasites are autogenic elements. Fish as well as invertebrates can also be intermediate hosts.

The helminth parasites present characteristic cycles which need several intermediate hosts (Fig. 2). For transmission to the next host it is very important whether the host lives in open water or on the bottom. *Podocotyle atomon* presents a characteristic benthic cycle of digeneans which starts in the snail *Littorina saxatilis*, continues in benthic crustaceans like gammarids and isopods which are actively infected by creeping cercariae and ends in benthic fish like gobies or flatfishes. The digenean group of Hemiurida show a planktobenthic cycle from snails to planktonic copepods to pelagic fish or fish larvae which later may have a bottom-dwelling way of life. The digenean, *Cryptocotyle* spp., finally attain birds which are infected by consuming fish where the metacercariae encyst normally on the skin and fins. An exception is the microhabitat of *C. concavum* in the common goby, *Pomatoschistus microps*: the cercariae penetrate the gills and encyst in the kidney (Zander *et al*. 1984; Kreft, 1991).

Deviations of the general cycle are numerous in the Baltic Sea. *Asymphylodora demeli* which infect generally snails, mussels or polychaetes as intermediate hosts and fishes as final hosts, can shorten the life cycle by maturing in polychaetes (Reimer, 1973); the same phenomenon was found by Vaes (1974) in brackish waters of the Belgian coast. In a similar way, *Proctoeces maculatus* can already mature in mussels instead of flatfish, *Bunocotyle cingulata* in *Hydrobia ventrosa* (Reimer, 1961). *Parvatrema affinis* which normally finish its life cycle in birds do not leave its first intermediate host, *Macoma balthica* (Fig. 2). *Aphalloides timmi* regularly ends its life cycle in the second host, the common goby, *Pomatoschistus microps*. Microphallids of brackish waters present a great variability in life cycles: they must reach birds as final hosts – normally by benthic crustaceans as second host, but *Microphallus claviformis* and *M. pygmaeus* may infect birds directly by snails, where metacercariae can encyst; *M. claviformis* may include additionally fish as third host (Reimer, 1963; Kesting, Gollasch & Zander, 1996) (Fig. 2). This alteration enlarges the spectrum of final hosts from crustacean-eating to snail- and fish-eating birds.

Other helminth groups have often simpler life cycles. Cestoda present 2- or 3-host cycles, terminating in fish or birds; but probably only birds are infected by benthic crustaceans in the Baltic (Fig. 2). Tapeworms of freshwater origin, e.g. the bird parasite *Schistocephalus*, infect fish species of marine origin like gobies and cod (Reimer & Walter, 1993; Zander & Kesting, 1996) though the second host are in fresh water solely three-spined sticklebacks, *Gasterosteus aculeatus*. Nematodes need either 2 or 3 hosts (Fig. 2). Remarkably, a more complicated web prevails in the nematode *Hysterothylacium*, which can be directly transferred to fish by benthic crustaceans but also by smaller fish, or several invertebrates like ophiurids, copepods, polychaetes, ctenophores or chaetognaths (Køie, 1993). In similar ways eels are infected by *Anguillicola crassus* via planktonic copepods or by fish of which the pipefish, *Syngnathus typhle*, is the most frequent second intermediate host in the Baltic Sea (Reimer *et al*. 1994). No acanthocephalan is known from the Baltic, which deviates from the characteristic 2- (e.g. *Echinorhynchus*) or 3-host cycles (e.g. *Corynosoma*) (Fig. 2).

Remarkable are some cycles by which fish are infected by fish; besides the already mentioned nematodes, the digenean *Acanthostomum balthicum* is unique because it is transferred from small fish like gobies to the pipefish, *Syngnathus typhle* (Fig. 2).

Regarding patterns of ontogeny, successful parasites of the Baltic Sea often show great flexibility in altering life cycles (microphallids) which may even lead to cycles without vertebrate hosts (*Asymphylodora demeli*), and use a wide spectrum of paratenic hosts (*Hysterothylacium*). Parasites of extreme environments such as brackish water have better possibilities of existence when alternative ways of on-

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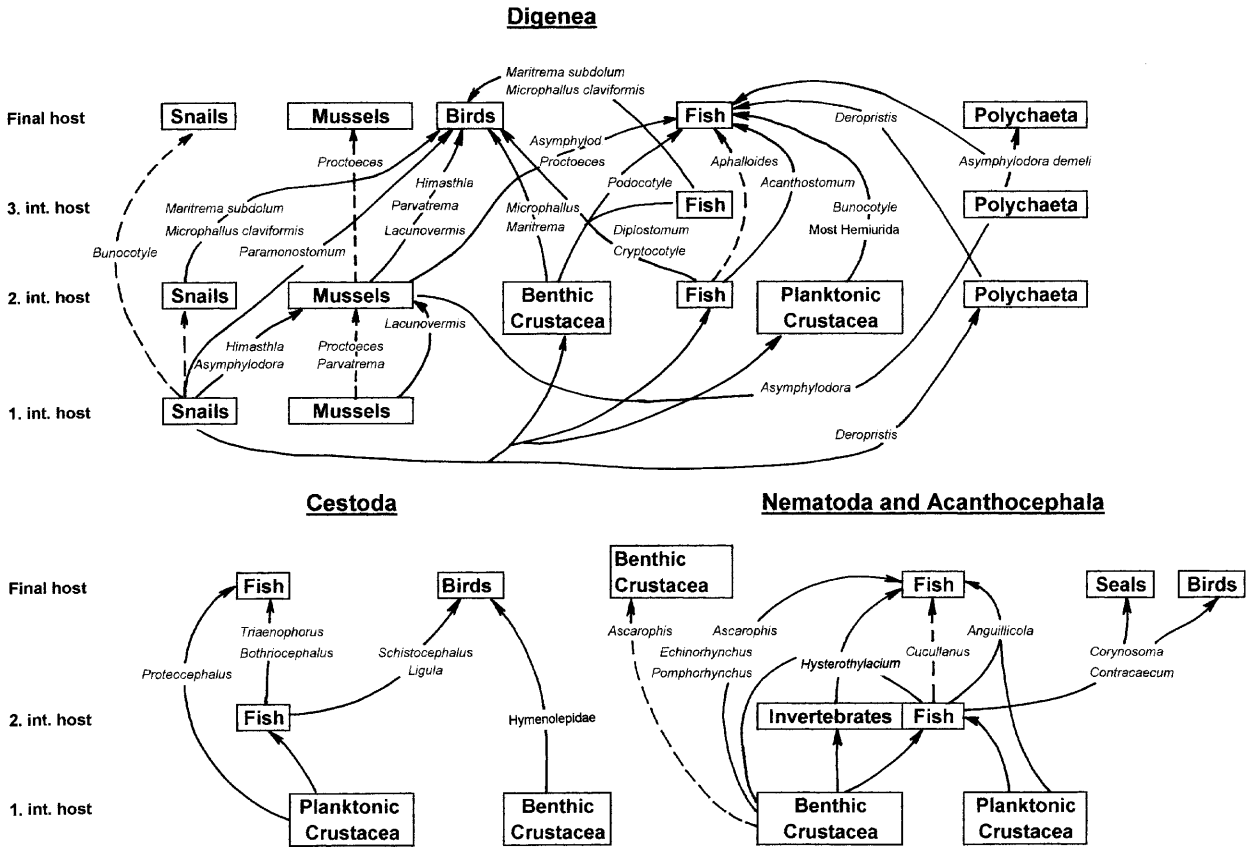


Fig. 2. Life cycles of parasites from the 4 most important helminth groups. The ways of digeneans are highly inhomogeneous because brackish water can lead to omission of second, to infect third intermediate hosts or to remain and mature in paratenic hosts (dashed lines).

togenetic development are adopted. Galaktianov (1985) reported *Microphallus* spp. from the White Sea which metacercariae encyst already in their first hosts, *Littorina rudis*, obviously as an adaptation of the short ice-free season in the year.

INFLUENCE OF HOSTS

Gastropods are first and, also sometimes, second intermediate hosts of most digeneans (Fig. 2). In the Baltic, the number of snail species is clearly lower than in the North Sea and is associated with a lower number of parasite species. However, the fresh water gastropods *Radix ovata* (up to 8) and *Theodoxus fluviatilis* (up to 15‰ salinity) can survive in brackish water. These species harbour not only fresh water digeneans like *Diplostomum spathaceum* but also brackish water species like *Asymphylodora demeli* (Zander *et al*. 2000). As many as 18 digenean species can live in *Hydrobia ulvae* and *H. ventrosa* from the Baltic Sea (Reimer, 1971).

In the brackish Baltic, digenean parasites are less specialised to snail species than in marine and freshwater environments. *Psilochasmus oxyuris* can infect as many as 6 snail species as intermediate hosts, *Asymphylodora demeli* is found in as many as 8 intermediate hosts, *Microphallus papillorobustus* in 4 (Reimer 1973; Kesting *et al*. 1996; Strohbach, 1999; Zander *et al*. 2000) (Table 1). The bird parasite, *Cryptocotyle lingua*, normally develops in the periwinkle, *Littorina littorina*, but was in the Baltic Sea also found in *L. saxatilis* and 3 *Hydrobia* species (Reimer, 1970, 1995). This broad host spectrum may induce cases of host capture (Holmes, 1990), also known from fish hosts. The fish digenean, *Podocotyle atomon*, which infects *Littorina saxatilis* in the North Sea, is also found in *Littorina littorea* in the Baltic, e.g. in the Schlei Fjord, Kiel Bight (Kesting *et al*. 1996) (Table 1). Remarkably, we did not find in the non-native (neozoon) *Pomatopyrgus jenkinsi* from New Zealand, a relative of *Hydrobia*, within many thousand specimens as infected one (Kesting & Zander, 2000).

Bivalves may be first and second intermediate as well as final hosts. Four host species are common in the Baltic: *Mytilus edulis*, *Macoma balthica*, *Cerastoderma edule* and *C. lamarcki*, whereas the non-native *Mya arenaria* is very rarely infected (Markowski, 1936; Pekkarinen, 1988; Reimer & Pohl, 1989; Junge, 1993). The digeneans, *Asymphylodora demeli*, *Himasthla* spp. and *Lacunovermis macomae* are very conspicuous because of their high prevalences in *Macoma balthica* or *Cerastoderma lamarcki*. Two turbellarians may occur, *Urostoma cyprina* in *Mytilus edulis* and *Paravortex cardii* in *Cerastoderma* spp. and *Macoma balthica*.

Annelids are parasitized by protozoans and by

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Table 1. Presence of digeneans in gastropods from 5 Baltic localities: B = Blank Eck, F = West Fehmarn, SC = Schlei (Kiel Bight); D = Dahmeshöved, S = Salzhaff (Mecklenburg Bight)
(According to Kesting, Gollasch & Zander, 1996; Strohbach, 1999; Zander *et al*. 2000.)

	Snail hosts										
Parasites	*Littorina saxatilis*	*Littorina littorea*	*Littorina obtusata*	*Hydrobia ulvae*	*Hydrobia ventrosa*	*Hydrobia neglecta*	*Zippora membranacea*	*Turboella conspicuosa*	*Limnaea ovata*	*Theodoxus fluviatilis*	Number of hosts
Cryptocotyle concavum				S, F, D	S. F. D						2
C. lingua	B, D			S							2
Aphalloides timmi				S, F	F						2
Acanthostomum balthicum				S	S						2
Psilochasmus oxyuris	SC	SC	SC	S, F	S, F		S				6
Bunocotyle cingulata				S							1
Magnibursatus caudofilamentosa							S				1
Asymphylodora demeli	S			S, F, D	S, F, D	F	S	F	S	S	8
Paramonostomum alveolatum				S	S						2
Podocotyle atomon	S, SC, B	SC									2
Maritrema subdolum				S, SC, F, D	S, SC, F, D	SC, F					3
Microphallus claviformis				S, SC, F	S, SC, F	SC					3
M. papillorobustum				F, D	S, SC, F	F		F			4
M. pygmaeus	S, B, D						S				2
Cotylurus cornutus									S	S	2

Table 2. Number of fish hosts of some abundant parasites of the German coasts of the Baltic Sea.
(According to Palm, Klimpel & Bucher (1999).)

Group	Species	Origin	Number of host spp.
Digenea	*Podocotyle atomon*	marine	27
	Brachyphallus crenatus	marine	18
	Diplostomum spathaceum	freshwater	15
Cestoda	*Bothriocephalus scorpii*–plerocercoids	marine	19
Nematoda	*Hysterothylacium aduncum*	marine	19–26
Acanthocephala	*Echinorhynchus gadi*	marine	20
	Pomphorhynchus laevis	freshwater	16

digeneans. *Asymphylodora demeli* can infect *Hediste dervisicolor*, *Alkmaria romijni* and *Spirorbis granulatus*, which act as second intermediate hosts. Additionally, *H. diversicolor* can also serve as final host of this digenean in the Baltic Sea (Reimer, 1973), and therefore replaces fishes (Fig. 2). *Neanthes virens* is the only second intermediate host of the eel parasite *Deropristis inflata*. Metacercariae of *Himasthla* sp. were found in *Arenicola marina* and also in *H. diversicolor*. Again, a non-native species of the Baltic, *Marenzelleria viridis*, remained uninfected (n = 109).

Planktonic crustaceans are very important intermediate hosts of digeneans of the group Hemiurida, cestodes and nematodes (Fig. 2). Strohbach (1999) found several calanoid copepods (*Acartia*, *Centropages*, *Eurytemora*, *Paracalanus* and *Temora* spp.) to be hosts of tapeworm and nematode larvae in Kiel and Mecklenburg Bight. The very abundant cyclopoid, *Oithona*, was only infected in the Schlei Fjord but not in the open Kiel and Lübeck Bight (Kesting *et al*. 1996). Copepods with lower abundance seem to be more heavily infected than common ones. They are also intermediate hosts for the important fish parasite *Ichthyophonus hoferi* (Fungi).

Benthic crustaceans are also important intermediate hosts of several helminth parasites. In particular, species of gammarids (Amphipoda), idotheids and sphaeromids (Isopoda) – being the preferred prey of fish or birds – can be heavily infected by larvae of helminth parasites (Skroblies, 1998). *Carcinus maenas* is the only host of the bird digenean *Microphallus primas*. Other specializations may not have evolved in parasites of benthic crustaceans, though preference of single species usually changes from locality to locality. *Gammarus salinus* seems to be less infected by cercariae of *Podocotyle atomon* or microphallids than other *Gammarus* species. *Maritrema subdolum* is an abundant parasite of *Idothea chelipes* or *I. granulosa* whereas *I. balthica* is hardly infected (Skroblies, 1998; Zander *et al*. 2000). Procercoids of the bird tapeworm family Hymenolepidae were also found in *Gammarus* spp. (Reimer, 1969; Zander & Döring, 1989; Gollasch & Zander, 1995; Strohbach, 1999). Acanthellae of acanthocephalans regularly infect gammarids and isopods (Gollasch & Zander, 1995; Strohbach, 1999). In the Baltic Sea, *Crangon crangon* is an occasional host of digenean metacercariae though metazoan parasites were never found in North Sea specimens (Gollasch *et al*. 1996).

Fish may be hosts of helminths but also of parasitic protozoans, crustaceans and of an annelid (*Piscicola*). Besides genuine fish parasites, the Baltic Sea also includes many parasites of birds and marine mammals which are transferred by fish as intermediate or paratenic hosts. The component community of small-sized fish from the Salzhaff (Mecklenburg Bight) like *Pomatoschistus microps* (Gobiidae) can attain as much as 16 parasite species, *Gasterosteus aculeatus* 20, and *Pungitius pungitius* (Gasterosteidae) 18 (Zander *et al*. 2000).

The number of generalist parasites is numerous on the German Baltic coasts of Schleswig-Holstein and Mecklenburg-Vorpommern, e.g. *Podocotyle atomon* can infect as much as 27 different fish hosts (Palm, Klimpel & Bucher, 1999) (Table 2). Recent investigations revealed the low presence or even absence of this parasite in *Gobius niger*, obviously because metacercariae cysts are not digested when these are ingested together with the second intermediate hosts, benthic crustaceans (Zander & Kesting, 1996; Zander *et al*. 1999).

Certain fish species may be the main hosts for a particular parasite and other fish species can serve as occasional hosts which are infected in clearly lower abundance probably due to different levels of co-evolution (Zander, 2001) (Table 3). Whereas *Aphalloides timmi* is restricted to gobies, the gill-inhabiting *Magnibursatus caudofilomentosa* is not only present in sticklebacks but also in gobies and in the brood pouches of *Syngnathus typhle* (Zander, unpublished). Obviously, among the small-sized fish of the Salzhaff (Mecklenburg Bight) *Proteocephalus percae* is present in gobies whereas *P. filicollis* is restricted to sticklebacks (Zander *et al*. 1999).

The specific parasites of smaller and larger fish hosts (Table 4) comprise in the Baltic Sea 7 digeneans, 8 cestodes, 2 nematodes and 4 copepods.

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Table 3. Prevalences (%) of 8 selected specialist parasites in small-sized fish hosts of the Salzhaff, Mecklenburg Bight.
(The main hosts are underlined. According to Zander (2001).)

Parasites	Hosts								Number of hosts	Specifity index (Rohde, 1993)
	Gobius niger	*Gobiusculus flavescens*	*Pomatoschistus minutus*	*Pomatoschistus microps*	*Gasterosteus aculeatus*	*Pungitius pungitius*	*Spinachia spinachia*	*Syngnathus typhle*		
Apatemon gracilis		2		35					2	0·973
Aphalloides timmi			7	52					2	0·941
Acanthostomum balthicum				0·6	8		7	59	4	0·877
Bunocotyle cingulata		2				26			2	0·964
Magnibursatus caudofilimentosa					38	1			2	0·987
Schistocephalus solidus	1		1	0·6	3				4	0·705
Schistocephalus pungitii						12			1	1
Thersitina gasterostei					71	8	10	1	4	0·911

Table 4. Parasite specialists of several fish species from the Baltic Sea

Hosts	Parasites			
	Digenea	Cestoda	Nematoda	Copepoda
Pomatoschistus microps	*Aphalloides timmi*			
Pomatoschistus microps	*Apatemon gracilis*, metacercaria			
Gasterosteus aculeatus	*Magnibursatus caudofilamentosa*	*Schistocephalus solidus*, plerocercoid		*Thersitina gasterostei*
Pungitius pungitius		*Schistocephalus pungitii*, plerocercoid		
Spinachia spinachia		*Diplocotyle olrikii*		
Syngnathus typhle	*Acanthostomum balthicum*			
Myoxocephalus scorpius		*Bothriocephalus scorpii*		
Myoxocephalus scorpius		*Prosorhynchus squamatus*		
Zoarces viviparus			*Hysterothylacium auctum*	
Anguilla anguilla	*Deropristis inflata*	*Bothriocephalus claviceps*	*Anguillicola crassus*	*Ergasilus gibbus*
Anguilla anguilla		*Proteocephalus macrocephalus*		
Pleuronectes flesus	*Aporocotyle simplex*			*Acanthochondria cornuta*
Pleuronectes flesus				*Lemaeocera branchialis*, larva
Pleuronectes limanda	*Proctoeces maculatus*			
Psetta maxima		*Bothriocephalus* cf. *gregarius*		

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Table 5. Specifity of helminth parasites in bird hosts. S = number of species; x/y = number of parasite species found only in the respective bird group/number of parasite species found only in 1 host species; Anatidae I = Anserini, Tadornini, Anatini; Anatidae II = Aythyini, Mergini, Somateriini

		Birds													
Parasites	S	Gaviidae 1	Podicipedidae 3	Phalacrocoracidae 1	Ardeidae 1	Anatidae I 6	Anatidae II 9	Charadriidae 2	Scolopacidae 7	Laridae 4	Sternidae 1	Rallidae 1	Species restricted species	Group restricted species	Infection stage or host
Digenea															
Diplostomatidae	7		1/0	1/0	1/0	1/0	0/1			0/1	1/0		5	2	Fish
Strigeidae	5				1/0		0/2			2/0			3	2	Molluscs and fish
Cyathocotylidae	1						1/0						1		Fish
Schistosomatidae	1									1/0			1		Cercariae
Renicolidae	4			1/0			0/1			0/1			1	2	Fish
Plagiorchidae	2					1/0				0/1			1	1	Chironomid-larvae
Gymnophallidae	4						0/2			1/0			1	2	Mussels
Microphallidae	9			1/1			1/2			?		1/0	3	3	Crustaceans
Eucotylidae	4					1/0	0/1		1/0			1/0	3	1	Molluscs
Notocotylidae	5					2/0						1/0	3		Metacercarial cysts on substrate
Psilostomatidae	2						0/1							1	Molluscs
Echinostomatidae	12		0/1	2/0	1/0	1/0	1/0			1/1			6	2	Molluscs and fish
Opisthorchiidae	1			1/0									1		Fish
Heterophyidae	4				1/0								1		Fish
Cestoda															
Pseudophylloidea	3	1/0		1/0									2		Fish
Tetrabothriidea	2	1/0								1/0			2		
Dilepididae	6			1/0	1/0				1/0	2/0			5		Fish
Davaneidae	1														?
Hymenolepidae	19		1/0			4/0	2/4	0/1		4/0			11	5	Oligochaetes, Molluscs, Crustacea
Amabiliidae	1		0/1											1	Copepods, Dragonfly-larv.
Nematoda															
Amidostomidae	3						0/2	1/0					1	2	Larvae
Heterakidae	1						0/1							1	Eggs, (Earthworms)
Anisakidae	3		1/0							0/1			1	1	Fish
Toxocaridae	1							1/0					1		Earthworms
Tetrameridae	1						1/0						1		Crustaceans
Streptocaridae	1						0/1							1	
Acuariidae	2		1/0							1/0			2		Amphipoda, (fish)
Ancyranthidae	1									1/0				1	
Capillariidae	6						2/1			1/0			3	1	Larvae, (Earthworms)
Acanthocephala															
Polymorphinae	4			1/0			0/1					1/0	2	1	Crustacea, Fish
Centrorhynchinae	1								1/0				1		
Plagiorhynchinae	1								0/1					1	

The nematode *Anguillicola crassus* is a non-native species which was imported from Asia to Europe in the late 1970s. Though adults are restricted to eels its larvae can occur in several intermediate fish hosts (Reimer *et al*. 1994).

Birds are important final hosts in the life cycles of several helminths (Fig. 2). Thirty six species out of 12 families of aquatic birds of the Baltic area turned out to be infected by 119 helminth species (Reimer, compiled in Reimer, 2002) (Table 5). Birds are highly mobile hosts that can collect their parasites in other climatic zones or even on other continents, resulting in a diverse mix of different elements in their parasite faunas. Digeneans of freshwater origin are mainly the Diplostomatidae, Strigeidae and Echinostomatidae, of which several species are found in fish as in intermediate hosts from the Mecklenburg and Kiel Bight (Reimer, 1970; Kesting *et al*. 1996; Kesting & Zander, 2000; Zander *et al*. 2000). Renicolidae and many species of Microphallidae and Gymnophallidae are of entirely marine, and Eucotylidae, of terrestrial origin. The cestodes, nematodes and acanthocephalans that were found are mostly limited to fresh waters. Dilepididae, Diplostomatidae (Digenea) or Polymorphinae (Acanthocephala) seem to be specialists of host families (Table 5). The majority of parasites are generalists which infect a lot of bird hosts. Among the helminths found the microphallids, *Levinseniella brachysoma* (16 bird host species) and *Maritrema subdolum* (13 bird species), as well as the heterophyid *Cryptocotyle concavum* (20 bird species) display the greatest host spectra. Several parasites with only 1 host are found among the Tetrabrothiidae, Dilepididae and Hymenolepidae (Cestoda) as well as the Acuariidae (Nematoda) (Table 5). It is not clear in every case whether these results are a consequence of co-evolution or of strict preference of distinct food (snails, crustaceans or fish) by the respective hosts. Most larvae of the above mentioned bird parasites are found in areas of lower salinity and can complete therefore their life cycle in brackish waters.

Regarding the patterns of biotic factors (hosts), Baltic parasites display loss or reductions of specialisation in a greater extent in comparison to marine and freshwater habitats. Even species which are not infected in other areas can become hosts in the Baltic Sea (*Crangon crangon*) which make host capture evident (Holmes, 1990). Non-native parasites (*Anguillicola crassus*) can find native hosts without difficulties. But in contrast, non-native hosts are not or only very seldom infected by Baltic parasites (*Pomatopyrgus jenkinsi*, *Mya arenaria* and *Marenziella viridis*).

INFLUENCE OF SALINITY

The brackish condition of the Baltic Sea is an obvious stress factor to all organisms, including parasites. In the central Baltic with salinity of only 6–8‰, the lowest number of species ('species minimum', Remane, 1958) is found. Generally, parasites depend on the salt tolerance of their hosts, the most restricted ones confine to the distribution of the parasite.

The restriction of parasites to certain areas of the Baltic depends mainly on the limits of the distribution of benthic, less mobile intermediate hosts, as well as on the tolerance of their own free larval stages. The cercariae of the bird digenean, *Cryptocotyle lingua* can exist down to salinities of 2‰ at temperatures below 10 °C, but higher temperatures reduce salinity tolerance to 8‰ and the life span to a maximum of 4 days (Möller, 1978). The distribution of intermediate hosts is probably more important for the presence of parasites than salinity. Thus, several snails of marine and fresh water origin are only found in parts of the Baltic, restricting the distribution of many digeneans (Table 6).

In other cases, the limits of the distribution of the first hosts can be further restricted but also enlarged by the next hosts. The first larval stages of the cosmopolitan *Derogenes varicus* are bound to *Natica snails* up to the Kiel Bight but may be exported with the help of currents to the Mecklenburg Bight in their second hosts, copepods, where they may be ingested by benthic fish (Table 6). Several migrating fish species are capable of transferring parasites like *Hemiurus luehei*, *Lecithaster confusus*, *Deropristis inflata* or *Diplostomum spathaceum* to areas where the salinity cannot be tolerated by the first hosts. The nematode, *Anisakis simplex*, was found repeatedly in fishes of the Baltic though euphausiids, their intermediate hosts, cannot exist below salinities of the Kattegat (Köhn & Gosselck, 1989). *Clupea harengus* migrate from feeding grounds in the North Sea where they prey also on infected krill to spawning grounds off Rügen or in the Oder Bight, Arkona Sea (Grabda, 1974). However, benthic fish like *Zoarces viviparus* in the Kiel Bight (Bucher, 1998) or 5 goby species in the Lübeck Bight were found to be infected by *A. simplex* (Zander, Strohbach & Groenewoldt, 1993; Zander & Kesting, 1996). The garfish, *Belone belone*, which migrates from the Atlantic Sea to spawn in the Central Baltic, harboured parasites like the marine cestodes *Ptychobothrium belones* and *Lacistorhynchus tenuis* as well as *Anisakis simplex* (Grabda, 1981).

The influence of salinity may be best recognized by the comparison of host populations from different localities along the salt gradient. Whereas highly mobile fish species are not suited to such analyses, resident benthic fish like the eelpout, *Zoarces viviparus*, are very suitable (Table 7). The population of the Lübeck Bight possesses the most marine parasite species (Zander, 1991). Gdansk Bight is the other extreme, with the most fresh water species (Markowski, 1938; Sulgostowska, Jerzewska &

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Table 6. Distribution limits of some digeneans in the Baltic Sea according to the distribution of their hosts
(According to diverse authors.)

Parasites	First host	Restricted distribution of first host	Second host	Restricted distribution of second host	Second or Third host beyond distribution limits	Locality of record
Marine species						
Derogenes varicus	*Natica* spp.	Kiel Bight	Calanoid copepods		Gobiidae, *Zoarces*	Lübeck Bight
Deropristis inflata	*Bittium reticulatum*	Lübeck Bight	*Neanthes virens*	Kiel Bight	*Anguilla anguilla*	Gdansk Bight
Hemiurus luehei	*Philine denticulata*	Lübeck Bight	Calanoid copepods		*Gadus morhua*	Bornholm
H. communis	*Retusa truncatula*	Bornholm	Calanoid copepods			
Lecithaster confusus	*Odostomia rissoides*	Mecklenburg Bight	Calanoid copepods		*Clupea harengus*	Arkona Sea
L. gibbosus	*Odostomia* spp.	Mecklenburg Bight	Calanoid copepods			
Magnibursatus caudofilamentosa	*Zippora membranacea*	Arkona Sea	Calanoid copepods			
Brachyphallus crenatus	*Retusa obtusa*	Gotland	Calanoid copepods			
Podocotyle atomon	*Littorina saxatilis*	Bornholm	Amphipoda, Isopoda			
Cryptocotyle lingua	*Littorina littorea*	Bornholm	Fish			
Microphallus primas	*Hydrobia ulvae*	Bothnian Bay	*Carcinus maenas*	Bank of Darss		
M. pygmaeus	*Littorina saxatilis*	Bornholm				
Freshwater species						
Diplostomum spathaceum	*Radix ovata*	8‰, Arkona Sea	Fish		*Gadus morhua*	Öresund
Cotylurus cornutus	*Radix ovata*	8‰, Arkona Sea	*Theodoxus fluviatilis*	15‰, Lübeck B.		

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Table 7. Prevalences (%) and origin of helminth parasites of *Zoarces viviparus* from 5 areas of the Baltic Sea

Parasite	Salinity Authors N hosts	Kiel Fjord 14–18‰ Möller, 1975 1112	Lübeck Bight 10–14‰ Zander, 1991 36	Salzhaff 10–12‰ Reimer & Walter, 1998 191	Gdansk Bight 7‰ Markowski, 1938 550	Gdansk Bight 7‰ Sulgostowska *et al.* 1990 280	Riga Bight 5–6‰ Vismanis *et al.* 1980 191
Gyrodactylus medius	freshwater				21		22
Diplostomum spathaceum M.	freshwater			25		50	4
Cardiocephalus longicollis M.	freshwater			11			10
Cryptocotyle concavum M.	brackish	50		4			
Acanthostomum sp. M.	brackish			3			
Podocotyle atomon	marine	20	72	46			
Derogenes varicus	marine		3				
Eubothrium sp.	freshwater						0·5
Bothriocephalus sp. Plerocercoid	freshwater		28		3	0·7	1
Triaenophorus nodulosus	freshwater				11		
Caryophyllaeus sp.	freshwater				5		
Hysterothylacium auctum	marine	71	94	82	54	50	38
Ascarophis arctica	brackish	0·1		17	2		1
Metabronema canadense	freshwater						6
Raphidascaris sp.	freshwater				12		
Neoechinorhynchus rutili	freshwater		5		0·4		
Echinorhynchus gadi	marine	14	38	3	2	7	1
Echinorhynchus salmonis	freshwater				0·2		
Pomphorhynchus laevis	freshwater	0·6	3	8	9	48	0·5
Corynosoma semerme Acanthella	marine		30				33
Corynosoma strumosum Acanthella	marine			5	2		
Sum of species	marine	3	5	4	3	2	3
	brackish	2	0	3	1	0	1
	freshwater	1	3	3	8	3	7

Wicikoski, 1990), the Salzhaff having an intermediate position with the most brackish parasite species (Reimer & Walter, 1998). The most marginal localities, Kiel Fjord (Möller, 1975) and Riga Bight (Vismanis *et al*. 1980), may be influenced by special factors and are not as persuasive as the other localities.

The same phenomena observed over large spatial scales can also be acting over short distances in isolated waters of the Baltic, e.g. in the Schlei Fjord (Kiel Bight) which is characterized by great freshwater influx (Kesting *et al*. 1996). The numbers of metazoan parasite species change from the innermost station in the Fjord (salinity 3‰) with 2 marine, 1 brackish and 7 freshwater species, through a middle station (6‰, 'species minimum') with 4, 3 and 6 species respectively, to the outer Station (15‰) near fjord entrance with 5 marine, 4 brackish and 3 fresh water species (Kesting & Zander, 2000). Here, also prevalence and intensity of the digenean *Cryptocotyle concavum* clearly increase with increasing salinities (Zander *et al*. 1984). This effect may be influenced and varied by hydrographical, topographical and biotic factors (Reimer, 1970).

Regarding the patterns of the main abiotic factor, salinity, in the Baltic Sea, the distribution of parasites is limited along the gradient from west to east. This phenomenon depends on the respective tolerance of their hosts and is found to be least in parasites which are generalists. The rule of 'species minimum' which is claimed for free living species at salinities of 6–8‰ (Remane, 1958) seems to be not absolutely valid for parasites, probably due to their ability to switch to several hosts.

INFLUENCE OF EUTROPHICATION

Eutrophication is an anthropogenic stress factor, caused by an increased influx of organic wastes, especially nitrate and phosphate which stimulates plant growth. This favours production throughout the trophic chain, and parasites can also profit from the increased abundance of their hosts. The Orther Bight off west Fehmarn (Kiel Bight) is a very shallow water with a maximal salinity of 11–12‰. Although a great stock of benthic algae provide high assimilation rates, low oxygen saturations of 50–60 % on the bottom in summer document the high deposition rate of organic detritus. Benthic crustaceans like *Idothea chelipes* attain densities of 28 individuals/m^2 on the bottom and more than 250 on a *Fucus* plant in summer. These can be infected at prevalences as high as 85 % and at intensities as high as 202 per host, with a mean of 88 metacercariae by the digenean *Maritrema subdolum* (Skroblies, 1998). This creates a high infection potential for birds that feed on crustaceans. The Orther Bight, therefore, has been designated as a habitat serving as a centre of epidemics (Lauckner, 1994). Because of the restricted mobility of infected isopods, their availability for birds is greatly increased.

Three localities in the western Baltic, characterized by clear differences in oxygen deficiencies, could be compared with respect to the digenean *Cryptocotyle concavum* which encysts in the kidneys of the goby, *Pomatoschistus microps* (Zander, 1998*b*). The lowest values of oxygen content were measured in the Orther (Kiel) Bight, followed by Salzhaff, then by Dahmeshöved (Mecklenburg Bight). The highest infection levels were found in the Salzhaff, attaining a maximum of 2300, and a mean of 430 metacercariae per fish, whereas in the Orther Bight, these values were 347 and 112 metacercariae, and in Dahmeshöved even lower (Zander, 1998*b*). These infection rates were promoted by different levels of eutrophication which influence the densities of the herbivorous first intermediate host, *Hydrobia* spp.

The localities Blank Eck in the Kiel Bight (15‰ salinity) and Dahmeshöved in the Lübeck Bight (11‰ salinity) differ in terms of eutrophication, as indicated by oxygen saturation: in Blank Eck oxygen saturation only drops below 100 % in autumn but in Dahmeshöved it is below 100 % over almost the whole year. The parasite fauna of 4 goby species from Blank Eck was a little poorer in species numbers and showed clearly lower prevalence and intensities, but attained higher diversity indices and evenness values than in Dahmeshöved (Zander & Kesting 1996) (Table 8). Also, the prevalence and parasite density of benthic crustaceans of Dahmeshöved by far surpassed the values from Blank Eck, whereas infection of planktonic crustaceans hardly differed between localities (Strohbach, 1999). This results from better conditions for herbivores and generalist parasites which may increase species richness and parasite density but decrease diversity indices. Only in *Littorina saxatilis* was the opposite result found, with periwinkles in Blank Eck attaining higher prevalences and parasite densities than in Dahmeshöved, which is explained by their smaller component community than in mud-snails.

Another way of using parasites as indicators of environmental influences is to calculate the regression of parasite prevalences versus host specificity (Zander, 1993). The idea is that specific parasites are favoured in more pristine habitats where their number is higher than in affected habitats where the generalists with many hosts prevail. Regarding the respective prevalences (y-axis in Fig. 3), parasites with only 1 host may prevail in pristine habitats over parasites with more hosts (x-axis in Fig. 3). In eutrophic waters, where generalists dominate over specialists, the reverse may be the result. The regression line in oligotrophic waters is therefore, negative, whereas in eutrophic habitats the slope of the regression line increases and indicates the level of eutrophication. The comparison of the habitats in Kiel and Lübeck Bights resulted in a clearly stronger

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Table 8. Comparison of levels of parasite infection in 4 host groups from Blank Eck (Kiel Bight, less eutrophicated) and Dahmeshöved (Lübeck Bight, eutrophicated). Hs = Shannon-Wiener index, J = index of equibility.
(According to Strohbach (1999), Zander & Kesting (1996).)

	Littorina saxatilis		Planktonic copepods		4 *Gammarus* spp.		4 gobiid fishes	
Parameter	Blank Eck	Dahmeshöved	Blank Eck	Dahmeshöved	Blank Eck	Dahmeshöved	Blank Eck	Dahmeshöved
Mean prevalence (%)	4·1	0·4	5·5	6·1	1·2–5·0	5·6–16·2	0·2–21·0	0·6–61·0
Mean intensity (N)			1·0	1·0	1·0–1·6	1·0–5·0	1·0–23·4	1·0–16·8
Parasite density (N/m²)	3·1	0·4	78	55	59	1921		3·8
Species Numbers (S)	3	2	11	12	14	9	4–9	3–10
Diversity (Hs)	0·17	0·09	1·95	2·08	1·67	1·52	0·78–1·74	0·55–1·62
Evenness (J)	0·15	0·13	0·81	0·83	0·63	0·69	0·48–0·89	0·45–0·70

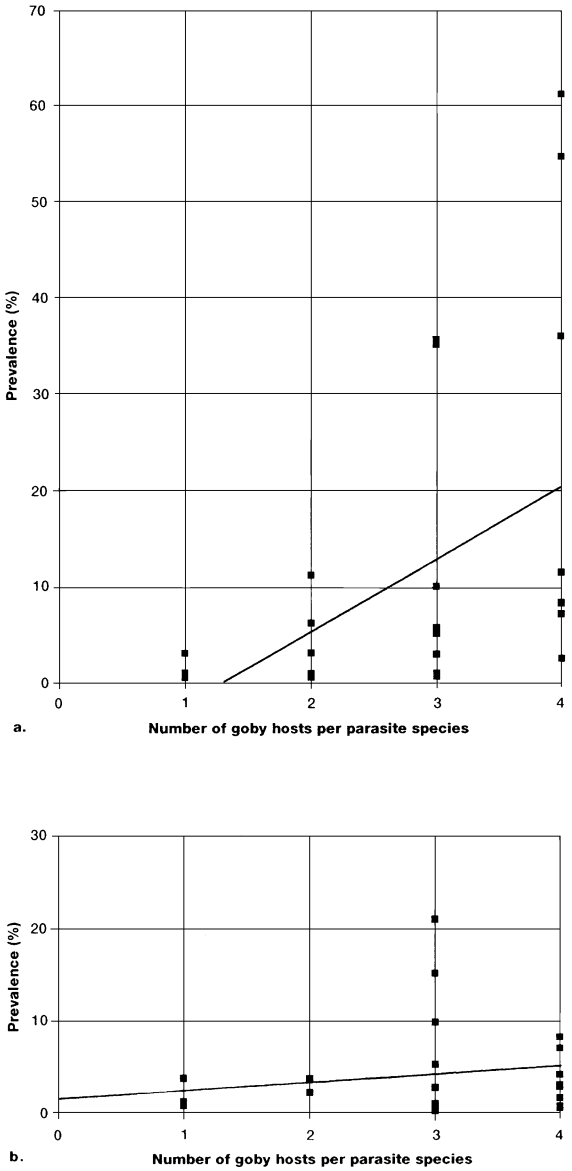


Fig. 3. Correlation of prevalence and number of infected goby (Gobiidae, Pisces) hosts at the sites of Lübeck Bight (a) and Kiel Bight (b), Germany. (From Zander, 1998*a*).

positive regression in Dahmeshöved than in Blank Eck (Fig. 3), which corresponds to what was expected based on prevalence values (Zander & Kesting, 1996).

Long-term changes by eutrophication were studied in mud snails, *Hydrobia ventrosa*, from the Wismar Bight (Mecklenburg Bight) and the Strela Sound (Arkona Sea) over nearly 30 years (Reimer, 1995). In particular the digeneans, *Microphallus claviformis* and *Paramonostomum alveatum* but also *Cryptocotyle concavum*, clearly increased in prevalence during this time of increasing eutrophication. Other parasites like *Asymphylodora demeli* or *Maritrema subdolum* showed minor changes, or none.

A faunal impoverishment over a period of 15 years was also found in the Schlei Fjord, which is strongly polluted in its inner parts, where lower salinity

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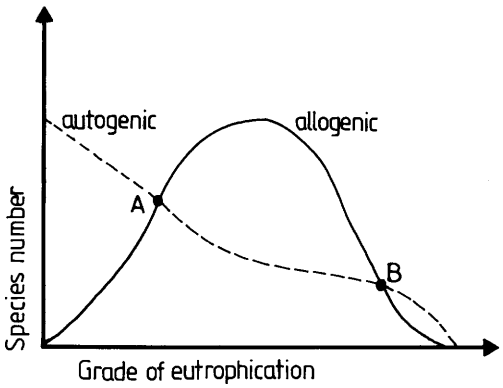


Fig. 4. Model of the relation of allogenic and autogenic parasite species numbers along the scale of increasing eutrophication. A and B = points of dominance alteration of the two categories. (From Zander, 1998*a*).

prevails (Kesting & Zander, 2000). The number of fish parasites decreased in Selk (2‰ salinity) from 8 to 4 species, in Haddeby (4‰) from 8 to 6 and in Missunde (6‰) from 11 to 6, whereas in the outer locality of Olpenitz (15‰) species numbers remained almost the same (10 or 11). Only during the 3 years from 1991 to 1994, did the numbers of parasites of snail, crustacean and fish hosts decrease in Missunde (from 18 to 8 species) with the number of potential host species among these groups dropping from 21 to 14.

The last example from the Schlei Fjord stresses the indicator properties of the parasite community of an ecosystem. Similar results attained Sulgostowska, Banaczyk & Grabda-Kabzubska (1987) in comparing parasite faunas of flatfish from Gdansk Bay during almost 50 years where the releaser was not only eutrophication but also chemical pollution. Clear signs of strongly eutrophic systems are: low number of parasite species, because less tolerant species vanish; predominance of generalists, because special hosts are extincted; predominance of planktonic parasites like tapeworms and hemiurid digeneans over benthic ones, because free water offers better oxygen supply than the bottom; predominance of parasites with direct development – like copepods or monogeneans – over those with complex cycles, because these are only dependent to one or few hosts (Overstreet & Howse, 1977; Kesting, 1996; Zander, 1998*a*). In oligotrophic waters, autogenic parasite species (see above) dominate. The more a water body is eutrophic, the more herbivores and carnivores profit from the increased plant growth and attract birds to rest and prey on them. The single hosts may be more heavily infected when the density increases, as consequence of better possibilities of parasite larvae to meet their hosts (Fig. 4). Finally, the number of allogenic parasite species decreases in extremely eutrophic waters because the environment becomes unattractive for birds, as a consequence of overall species impoverishment.

Regarding the patterns of eutrophication, parasites can profit from it in the first stage as indicated by increasing prevalences and intensities of hosts. In the second stage, oxygen deficiency influences hosts and parasites, at first on the bottom and thereafter also in the free water (Schlei Fjord). When a sufficient oxygen supply is guaranteed, as in very shallow habitats where exchange with the air is easy, higher levels of eutrophication may have an increased promoting effect not only on plants, but also on herbivores and parasites (Salzhaff, Orther Bight). This process differs from the effect of chemical pollutants which reduce parasite prevalence and intensity already with the start of their influence leading finally to lethality (Khan & Thulin, 1991). Only low doses of chemical pollutants can sometimes result in higher infection rates as a consequence of immunosuppression in the hosts.

CONCLUSIONS

The composition of parasite communities in the Baltic Sea is influenced by a complex of static and dynamic factors. The brackish condition with decreasing salinities from west to east means a strong stress to hosts as well as parasites, which excludes stenohaline marine and freshwater species. Beside some relic elements, the host species differ hardly from those of the North Sea or the adjacent freshwaters, respectively. Several non-native invertebrates which had immigrated from other continents were not infected by Baltic parasites whereas non-native parasites find native species as hosts without difficulty. These reactions may be evidence for the lack of co-evolution between the partners. The parasite communities of the Baltic Sea comprise especially euryhaline species of marine and freshwater origin. In contrast to hosts, several parasites are found outside the Baltic Sea only in other European brackish waters or have developed to endemic species.

Because brackish water is an extreme environment in which organisms tolerate lower or changing salinities, parasites have developed special adaptations which guarantee their successful existence in such an extreme environment. Therefore, some generalisations from effect of brackish water can be made (Zander 1998*a*): (1) Relaxation of host specificity. Parasites which infect only 1 host in marine or fresh water, infect several host species in brackish habitats. This is valid for many snails but also other hosts. (2) Exploitation of new hosts, e.g. *Crangon crangon* which is not infected at all in the adjacent North Sea. (3) Reduction or elongation of life cycles, as seen in several species of Microphallidae (Digenea) (Fig. 2). (4) Adaptation to genuine brackish-water species as hosts which is best explained by the rare co-evolution in the Baltic Sea of the digenean, *Cryptocotyle concavum*, with the gobiid fish, *Pomato-*

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schistus microps, where the parasite captures a new microhabitat.

In summary, the structure of the parasite community in the Baltic Sea is the result of the tolerance of parasites to low salinities, of the distribution and the dispersion of their hosts, of the possibility to alter the life cycles and sometimes of the co-evolution with hosts. The results from the brackish Baltic Sea can be a model for other environments where extreme intensities of abiotic factors prevail.

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