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Comparative studies on goby (Teleostei) parasite communities from the North and Baltic Sea

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Abstract The parasite communities of three goby species from the marine North and the brackish Baltic Sea were compared. The samples of summer 1992/93 from Helgoland, Lübeck and Kiel Bight comprised a parasite spectrum of 4–5 in *Pomatoschistus microps*, 2–3 in *P. pictus* or 3–8 parasite species in *Gobiusculus flavescens*. The highest numbers were found in Kiel Bight whereas those of Helgoland and Lübeck Bight differed between 3 and 7, respectively. In comparing the species identity of the studied localities the value was intermediate in *P. microps*, low in *P. pictus* and zero in *G. flavescens*. Values of prevalence and abundance were clearly lower in Helgoland than in Baltic localities. The prey of Helgoland goby populations comprised meio- and macrobenthos in *P. microps*, predominantly macrobenthos but also meiobenthos and some plankton in *P. pictus*, and predominantly plankton and some benthos in *G. flavescens*. Former studies (Zander in *J Zool Syst Evol Res* 32:220 1994) revealed a greater variability of prey choice in the Baltic. The greater parasite richness in the Baltic compared with that of Helgoland, may lie on better adaptations of genuine brackish components, lower defence mechanisms of hosts as a consequence of lower salinity, and greater variability in habitat choice. The effect of several filters on the colonisation of parasites in hosts is submitted here in a model.

(see Zander and Reimer 2002). In contrast, studies of small-sized fish from the North Sea were only rarely conducted (Möller-Buchner 1987; Hammerlynck et al. 1989; Groenewold et al. 1996). Among these fish, gobies (Gobiidae) are well-suited to get information on the structure and dynamics of parasite communities. These species are short-living, which grow up rapidly until they spawn in the second year and die off after that time. Most species live on the bottom (*Pomatoschistus microps*, *P. minutus*, *P. pictus*, *Gobius niger*) and a few live suprabenthically above the bottom (*Aphia minuta*, *Gobiusculus flavescens*). The larvae appear in huge swarms in the free water and switch to bottom life at a size of 15–20 mm (*P. microps*, *P. pictus*, *G. niger*) or 40 mm (*P. minutus*). These different times of stay in the free water can mirror the way of infections by parasites from diverse habitats (Marcogliese 2002; Zander et al. 1993, 2000; Zander 2004).

The North Sea is a characteristic marine ecosystem with salinities of 33–35‰ (Becker 1990). The Baltic Sea is the greatest brackish Sea in Europe, which presents a salinity gradient from west (Kattegat) to almost limnetic situations in the northeast (Bothnian Bay) and in the east (Gulf of Finland) (Matthäus 1996). Additionally, the North Sea is characterised by constant salinity and by periodical tidal oscillations, the Baltic Sea by greater fluctuations of salinity and water levels released by the direction of winds whereas tides are of prime importance in the Kattegat. Species richness of plants and animals is higher in the North Sea than in the Baltic, where only a part of the marine organisms has adapted to the lowered and fluctuating salinity. They form together with limnetic, genuine brackish and migratory elements the Baltic biocenosis (Remane 1958).

According to Bush et al. (1990) the parasite communities of fish are less rich than those of aquatic birds and mammals because endotherms need for their greater metabolism more food, which can be infected by parasite larvae. Also marine and freshwater fish differ in community richness. This is due to a greater mobility of the first group, which may lead the hosts to several

Introduction

Fish parasites of the brackish Baltic Sea, especially of small-sized hosts, had been investigated to a great extent

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habitats with a greater number of diverse parasites (Holmes 1990). The investigation of the brackish Baltic resulted in species-rich parasite compound and infra communities which can attain the range of marine fish parasites (Zander and Reimer 2002).

Therefore, it seemed be of interest to compare the parasite communities of identical hosts, which were sampled in an identical season in North and Baltic Sea. It was to expect that the parasite numbers are higher in the marine North Sea than in the brackish Baltic. The opportunity to resolve this assumption was afforded by material from Helgoland caught in July/August 1992 when adults were still present. It could be compared with samples from Dahmeshöved (Lübeck Bight), Blank Eck and Westerbergen (Kiel Bight), SW Baltic. The hosts comprised three goby species: *Pomatoschistus microps*, *P. pictus* and *Gobiusculus flavescens*, which present different ways of life—on the bottom, on the bottom with sojourns into the free water, and in the suprabenthic layer, respectively (Zander 1997).

The aims of this study are to compare species spectrum, prevalence and abundance of North and Baltic Sea parasites in the three mentioned goby species. These may result in new knowledge about the mechanisms of infection and the evolution of parasite–host relationships.

Material and methods

The gobies were caught in July and August of 1992 or 1993. *P. microps* from Helgoland were sampled in the ecotone of the sand-filled grooves of the beachrock in a water depth of 0.2–0.5 m during low tide by hand nets with a straight edge and of 1 mm mesh-size. *P. pictus* and *G. flavescens* were caught at the walls of the Vorhafen during Scuba dives at a depth of 2–6 m using round hand nets with a mesh-size of 1 mm. The locality of Dahmeshöved (Lübeck Bight near Grömitz, Zander et al. 1993) lies below the lighthouse and comprises a sandy beach, which continues underwater in a bottom of sand, pebbles and sometimes great boulders. Salinity was between 9‰ and 15‰. *P. microps* were caught in the shallow water, *P. pictus* and *G. flavescens* at a depth of 3–6 m using the same gear as in Helgoland. Blank Eck lies eastward of Kiel (Kiel Bight, near Heiligenhafen, Zander and Kesting 1996) where salinity was between 11‰ and 17‰. The bottom structure was similar to that of Dahmeshöved, therefore the same methods were used to sample *P. pictus* and *G. flavescens*. Because no *P. microps* were caught in Blank Eck this host was sampled between pebbles in the shallow muddy sand bottom of Westerbergen (West Fehmarn, Kiel Bight, 11–16‰ S, Zander et al. 2002). Numbers of investigated fish presents Table 1. The samples from Blank Eck and Dahmeshöved are a lesser part of material that was already analysed by a 2-year study (Zander and Kesting 1996) but formerly not evaluated in the special mode as

Table 1 Prevalence of parasites in goby hosts from Helgoland in comparison with gobies from the Baltic Sea

	Helgo-land <i>Pomatoschistus microps</i>		Wester-bergen <i>n</i> = 14	Dahmes-höved <i>Pomatoschistus microps</i>		Helgo-land <i>Pomatoschistus pictus</i>		Blank Eck <i>n</i> = 30	Helgo-land <i>Gobiusculus flavescens</i>		Blank Eck <i>n</i> = 60
	<i>n</i> = 99	<i>n</i> = 15		<i>n</i> = 17	<i>n</i> = 38	<i>n</i> = 97	<i>n</i> = 75		<i>n</i> = 97		
Benthic versus planktonic ssp.											
<i>Cryptocotyle concavum</i>											
<i>Cryptocotyle lingua</i>											
<i>Apatemon gracilis</i>	15.1	100.0	100.0						19.6		21.7
<i>Aphalloides timmi</i>			7.1								
<i>Podocotyle atomon</i>	5.0	6.7	42.9						20.6		6.7
<i>Brachyphallus crenatus</i>			35.7						2.1		3.3
<i>Lecithaster confusus</i>			57.1						1.0		1.7
<i>Asymphylodora demeli</i>									2.1		5.0
<i>Ligula pavlovskii</i>										1.3	
<i>Proteocephalus</i> sp.											
<i>Bothriocephalus scorpii</i>									4.1		6.7
<i>Hysterothylacium</i> sp.	4.0	33.3		10.5		6.0	6.7		4.1		1.7
<i>Contracaecum</i> sp.	1.0	20.0		2.6						2.7	
<i>Echinorhynchus gadi</i>							6.7				
<i>Caligus elongatus</i>	4	4	5	2					4.0		1.7
Number of species (S)	3/1	3/1	5/0	1/1		2/0	3		3		8
Benthic/planktonic spp.	23.2	100.0	100.0	10.5		58.8	20.0		0/3		3/5
Total prevalence		0.44							8.0		36.7
Sørensen-index									0		

Benthic versus planktonic species mean the habitat of parasite before infecting the goby host

here. The caught fish were fixed immediately after the catches in 4% formalin.

In the laboratory, at first, skin, fins, eyes and gills of the fish were inspected intensively for ectoparasites. Then, the body cavity was opened and also inspected, liver and gonads were twitched by fine needles. The alimentary tract was removed and opened along its total length, its content analysed for prey organisms and parasites. Several parasites were cleared by lactate acid in order to get better sights of inner organs for destination. The ingested prey was assorted to relevant taxa and presented as frequency of occurrence, i.e. the percentage of predators which had fed on the respective component.

For analyses of interspecific host comparisons, the Sørensen-index was calculated in order to gain results about species identity and the Student's *t*-test to prove statistical significance. Ecological parameters were used according to Bush et al. (1997): prevalence is the number of host population infected by parasites, abundance is the mean number of parasites in a host population. The classification of core and satellite species follows Zander et al. (2000) with values of abundance: > 2 = core species, $0.6-2$ = secondary species, $0.2-0.6$ = satellite species, < 0.2 rare species.

Results

Only six parasite species were present in gobies from Helgoland: the digenean *Cryptocotyle concavum* and *Podocotyle atomon*, the cestode *Proteocephalus* sp., the nematode *Contracaecum* sp. and *Hysterothylacium* sp., and the copepod *Caligus elongatus*. *Pomatoschistus microps* harboured as much as four of them, whereas in *Gobiusculus flavescens* three and in *Pomatoschistus pictus* only two were found (Table 1). In comparison with the Baltic localities the number of parasite species is almost equal as in Helgoland, with the exception of *G. flavescens*, which presents clearly higher parasite numbers in the Baltic. The species identity (Sørensen-index) is

moderate between North and Baltic Sea *P. microps* and low in *P. pictus* whereas the populations of *G. flavescens* were not at all identical albeit its relatively high species spectrum in the Baltic (Table 1).

Cryptocotyle lingua attained in Helgoland highest prevalence in *P. microps* (15%, Fig. 1). The next frequent parasite was *Hysterothylacium* sp. in *P. pictus* with 10%. The other seven host-parasite combinations remained below 5%. Only *Contracaecum* sp. was present in all three hosts, *Hysterothylacium* sp. in two, *P. microps* and *P. pictus*. Only single host species were infected by *Cryptocotyle lingua* and *Podocotyle atomon* (*P. microps*) or by *Proteocephalus* sp. and *Caligus elongatus* (*G. flavescens*) (Fig. 1).

The goby populations from Helgoland attained low prevalence in comparison to those from Dahmeshöved and Kiel Bight (Westerbergen or Blank Eck) (Table 1). Total prevalence of 100% presented *P. microps* from the two Baltic localities depending on the total prevalence of the digenean *Cryptocotyle concavum*. The other two hosts reached highest values in the Lübeck Bight.

The values of abundance follow those of prevalence but can be remarkably high in Baltic *P. microps* which were infected with *Cryptocotyle concavum* (Table 2). Their status is, therefore, that of core species which is also valid for this parasite in *P. pictus*. In contrast, *Cryptocotyle concavum* is only secondary species in *G. flavescens*, which presented no core species. Secondary species were also *Podocotyle atomon* in Baltic *P. microps* and *G. flavescens*, and *Aphalloides timmi*, *Apatemon gracilis* and *Hysterothylacium* sp. in *P. microps* from Westerbergen (Kiel Bight). Differences of abundance values between Helgoland and Baltic gobies were with one exception clearly significant according to Student's *t*-test (Table 2). The exception was found between *P. pictus* from Helgoland and Dahmeshöved, which may not be significant because of very low parasite numbers in both localities.

The prey spectra of the goby hosts from Helgoland differ clearly (Fig. 2). The frequency analysis indicates that *P. microps* prefers partly meiobenthos

Fig. 1 Prevalence values of two digenean, one cestodan, 2 nematode and one crustacean parasites in three gobiid fish hosts from Helgoland, North Sea

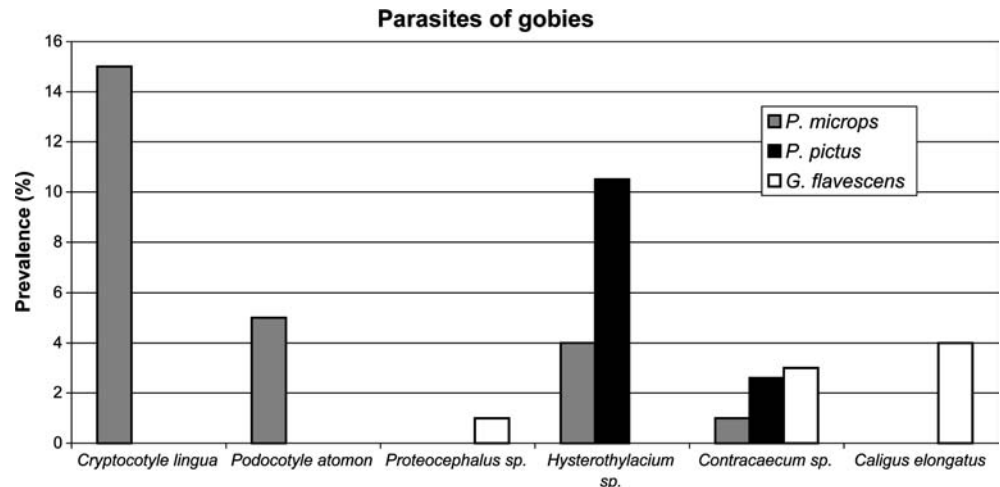


Table 2 Abundance of parasites in goby hosts from Helgoland in comparison with gobies from the Baltic Sea

	Allogenic versus autogenic				Pomatoschistus microps				Pomatoschistus pictus				Gobiusculus flavescens					
	Helgo-land		Wester-bergen		Dahmes-höved		Blank Eck		Helgo-land		Dahmes-höved		Helgo-land		Dahmes-höved		Blank Eck	
<i>Cryptocotyle concavum</i>					75.67 ^a	193.00 ^a	3.17 ^a	0.02										
<i>Cryptocotyle lingua</i>	0.18				0.14													
<i>Apatemon gracilis</i>					1.07 ^b													
<i>Aphalloides timmi</i>					1.63 ^b													
<i>Podocotyle atomon</i>	0.06				0.28													
<i>Brachyphallus crenatus</i>																		
<i>Lecithaster confusus</i>																		
<i>Asymphyllodora demeli</i>																		
<i>Ligula pavlovskii</i>																		
<i>Proteocephalus</i> sp.																		
<i>Bothriocephalus scorpii</i>																		
<i>Hysterothylacium</i> sp.	0.05				0.79 ^b		0.06	0.07										
<i>Contracaecum</i> sp.	0.01				0.40		0.03	0.07										
<i>Echinorhynchus gadi</i>																		
<i>Caligus elongatus</i>																		
<i>P</i> of <i>t</i> -test between Helgoland and Baltic populations					< 0.01	< 0.001	> 0.5	< 0.001										< 0.001

Allogenic versus autogenic parasite mean whether the parasite completes the life cycle in a foreign or in the same habitat
^a core species, ^b secondary species

(harpacticoids), partly macrobenthos (gammarid amphipods, isopods like *Idothea* and *Jaera*). All specimen of *P. pictus* ingested amphipods (gammarids and corophiids) but half of them also ingested harpacticoids. In contrast, *G. flavescens* forages mostly plankton from the free water, all specimen had fed on calanoids and more than half also on other plankton (cladocerans, chaetognaths, cypris- and nauplii-larvae) whereas benthos was ingested only in very low frequency.

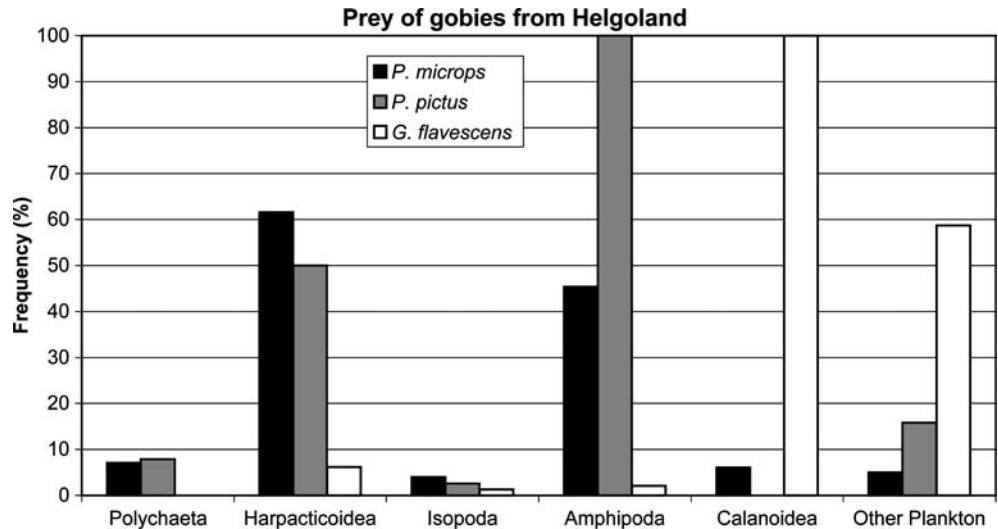
Discussion

The extreme differences between parasite communities of North and Baltic Sea gobies are caused by a complex of reasons. Generally, the North as well as the Baltic Sea are lying in the boreal climate area, the Baltic is an appendage of the North Sea connected by Skagerak and Kattegat. This juncture makes an exchange of organisms together with their parasites possible, either by water flows or by the transport of seabirds and sea mammals. Therefore, when Holmes (1990) concept of screens and filters is followed, the geographical handicap seems to be not very effective. A more important factor is rather the decreasing salinity of the Baltic Sea from marine conditions in the west to limnetic ones in the east.

Obviously, lower salinity in the Baltic is a main factor, which can reduce the number of species successively upto a minimum at 5–8‰ S (Remane 1958). From that point the species number increases again onto limnetic conditions because many fresh water species can tolerate low salinity. In contrast, Kesting and Zander (2000) found that parasite species number is relatively high at the point of species minimum and explained this phenomenon by greater tolerance of parasites than of hosts to lower and changing salinity. Decreasing salinity stops stenohaline marine species, these are partially replaced by genuine brackish water organism (Remane 1958), which are also represented by parasites (Zander 1997). Such species are more successful in brackish water than related marine species as is, e.g. demonstrated by the frequency of the digenean *Cryptocotyle concavum* which excels *C. lingua*. Other brackish parasites found here are the digenean *Asymphyllodora demeli*, *Apatemon gracilis* and *Aphalloides timmi*, a specialist, as well as the cestode *Ligula pavlovskii*. Therefore, the distribution of Baltic parasites seem to depend more likely on the adaptation abilities of their hosts, which are often more restricted than those of parasites (Zander and Reimer 2002). The evolution of Baltic parasites rather proceeded in widening the host spectrum which was facilitated by weaker defence mechanisms under osmotic stress in brackish water (Zander 1997).

Remarkably, more parasite species than in Dahmeshöved or Blank Eck were found in the north-situated Flensburg fjord as a consequence of higher salinity (11–20‰ S, Josten 2004) and in the semi-enclosed Salzhaff lagoon, Mecklenburg Bight (9–12‰ S) as a consequence of high eutrophication (Zander et al. 1999, 2000).

Fig. 2 Frequency values of important prey components ingested by three gobiid fish from Helgoland, North Sea. Polychaetes are predominantly nereids, Isopoda comprise *Idothea* and *Jaera*, Amphipoda *Gammarus* and *Corophium*, other plankton mostly cladocerans but also cypris-, nauplius-larvae and *Sagitta*



Eutrophication has a multiplying effect on parasite numbers which was acknowledged, e.g., in the Salzhaff and also at other localities like Westerbergen (Fehmarn, Zander et al. 2002). The eutrophication is also higher in Dahmeshöved than in Blank Eck (Zander and Kesting 1996, 1998; Zander 2002). High species numbers of parasites were related to increasing host density as a consequence of strong growth of algae and a surplus of detritus, which are prey especially for intermediate hosts (Zander 1997). If eutrophication changes to an extreme level, environmental conditions, especially oxygen content, becomes increasingly disadvantageous for the existence of organisms and, consequently, species numbers decrease again (Zander 1997; Kesting and Zander 2000). Increasing host density has the effect that parasite density grows exponentially (Zander et al. 2002). Also the entire North Sea is strongly eutrophicated, Helgoland presents conditions which are similar to those found in Dahmeshöved (Gerlach 1990; Blessin 1992). Nevertheless, in the present study species numbers are highest in Blank Eck and Westerbergen but additionally high in *Gobiusculus flavescens* from Dahmeshöved. Also prevalence and abundance are higher in the Baltic localities than in Helgoland. These results seem to depend on the way of life of hosts and the accessibility of parasite larvae from intermediate hosts.

The life history of gobies are important filters for the colonisation of parasites. These hosts can be characterised by their preferred habitat: *P. microps* is an obligate bottom dweller which preys mostly on benthos, *P. pictus* is a bottom dweller which also makes sojourns into the suprabenthos and ingests benthos and some plankton, *G. flavescens* inhabits the suprabenthos and mostly picks up plankton (Zander 1994, present study). These different ways of life can be confirmed by the respective parasite spectrum, which was predominantly benthic in *P. microps* and *P. pictus* but planktonic in *G. flavescens* (Table 1). As an exception, the life cycle of *Contracaecum* sp., which is assumed to infect planktonic copepods

and Cirripedia larvae, can be considered (Køie 1995). *G. flavescens* also feeds benthos in times of plankton shortness in the Baltic (Zander 1994) and may then be infected by *Podocotyle atomon* and *Echinorhynchus gadi* transferred by amphipods, and by *Cryptocotyle concavum*, the cercariae of which are released from benthic mud snails, *Hydrobia* spp.

Host specificity of parasites is frequently found in marine habitats, especially in snails which are first intermediate hosts of digeneans. This specificity can be lowered in brackish waters like the Baltic (Zander 1997, 2001). Thus, *Cryptocotyle lingua* infects only *Littorina littorea* in the North Sea, but also *Hydrobia ulvae* in the Baltic (Zander et al. 2000). *Asymphylogora demeli* is found in as many as six snail hosts from the Salzhaff and in four from Westerbergen (Zander et al. 2000, 2002). But *Podocotyle atomon* infects only *Littorina saxatilis* in the North as well as Baltic Sea though the snail changes its habitat from the supralittoral to the sublittoral zone in brackish waters. This flexibility is a way for parasites to succeed in the extreme environment.

The same reason is responsible for rare narrow host-parasite relationships in the Baltic Sea with special evolutionary alterations. From the present investigation three cases of genuine brackish water species can be emphasised: *Aphalloides timmi* presents a shortened life cycle and lives in the body cavity of *P. microps*, which is second intermediate and final host (Reimer 1970). *Asymphylogora demeli* can attain maturity not only in diverse fish species, its final hosts, but also in the second intermediate host, the polychaete *Hediste diversicolor* (Reimer 1973). *Cryptocotyle concavum*, cercariae of which infect skin and fins of diverse fish as intermediate hosts, colonises in *P. microps* the kidney where it encysts. As much as more than thousand metacercariae can be found in this organ without that the host seeming to be harmed (Zander et al. 1984, 2000; Zander 1997). This is a case of optimal adaptation of a genuine brackish water

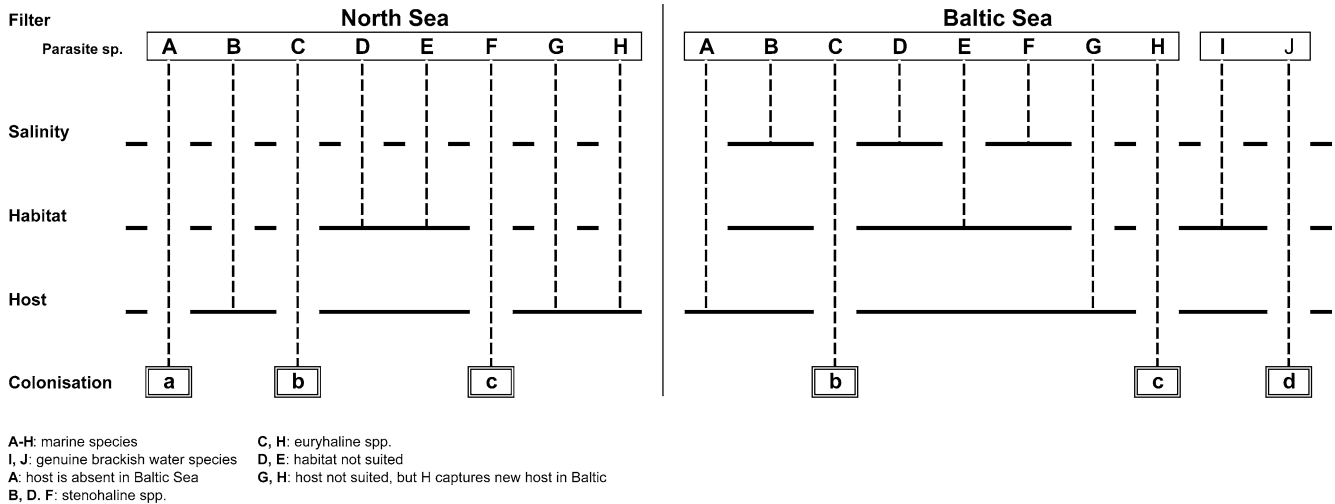


Fig. 3 Model of the effect of several filters as handicaps for the colonisation of hosts by parasites in North and Baltic Sea. A–J parasite species of which I and J occur only in the Baltic, a–d host species. *Solid lines* filters which are partly open, *dashed line* course of parasites onto their hosts. For other explanations see text

parasite to its intermediate host. The presence of *Apatemon gracilis* in *P. microps* may be promoted by the absence of *C. concavum* on fins (Zander et al. 1999). Remarkably, this parasite is not distributed in the free North Sea and was only found in the coastal waters and in the estuary of Elbe river (Derksen 1978, Möller-Buchner 1981). In other small-sized hosts, this parasite can together with the related *C. lingua* injure the mobility if the fins are heavily infected.

Studies that compare other fish hosts from habitats of North and Baltic Sea, Helgoland and Kiel Bight, were made on the digenean of dabs (*Limanda limanda*) and cods (*Gadus morhua*) (Køie 1983, 1984). The species identity (Sørensen-index) of the benthic dab had a value of 0.31 and that of the pelagic and suprabenthic cod only 0.20. This can confirm the present results on gobies where the benthic *P. microps* had the highest and the suprabenthic *G. flavescens* the lowest species identity. This result seems to be surprising if one assumes that benthic parasites are bound stronger to their habitats than pelagic ones, which can be distributed by currents. In contrast, it needs a great quantity of plankton prey in order to be infected because parasite density of plankton is very low (Golasch and Zander 1995; Strohbach 1999; Josten 2004), whereas that of benthos is high (Kesting et al. 1996; Strohbach 1999; Zander et al. 2000, 2002). Especially in eutrophicated localities, the discrepancy of plankton and benthos is obvious because among planktonic copepods rare species attain the highest infection rates (Strohbach 1999, Josten 2004) whereas at the bottom the abundant amphipods and isopods are the main transmitters of digeneans, acanthocephalans and nematodes (Zander et al. 1993, 2002).

Therefore, the mechanisms of infection depend on extreme factors like alteration of salinity and eutrophication, way of life of hosts, especially preferred habitats of foraging, reproduction and resting. A model (Fig. 3) presents the effect of several filters, which leads to the actual parasite species spectrum in the North as well as Baltic Sea. As filters may operate lowered salinity, linkage to habitat and suited hosts. A–J mark the parasite species that occur in the respective area (supra community), I and J only in the Baltic because these may be genuine brackish water species. A, C and H are euryhaline species, of which A represents a species whose host may be stenohaline and, therefore, absent in the Baltic. B, D, and F are stenohaline and filtered out in lower salinities. In reverse, B, G and H do not find their special hosts in the North Sea that may be present in the Atlantic, but H captures a new host in the Baltic. D, E and I are lost in consequence of an unsuited habitat which can restrict both, parasite as well as host (Fig. 3). Unsuited habitat can mean wrong medium or substrate as well as eutrophication. By this course through the filters, only three species or groups of species, respectively, with special ecological patterns can exist in the respective two areas. Other possible factors which influence the composition of the parasite community are stressed by Bush et al. (2003) and Zander (2005). Thus, the presence of more parasites in the Baltic Sea than in the North Sea may be due to better adaptations of parasites in the Baltic by genuine brackish water species, capture of new hosts as a consequence of their weaker defence systems and more variability of habitat choice during prey search of hosts. The latter point was clearly demonstrated by the parasite spectrum of the Baltic *G. flavescens*.

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