Ecology of Host Parasite Relationships in the Baltic Sea

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The Baltic Sea is one of the greatest brackish waters, and for 7000 years it has been affected by the influx of haline waters from the North Sea. Many marine and some fresh water organisms have adapted to its lower salinity. Some organisms, referred to as genuine brackish water species, predominate over their near relatives in this environment. All these elements are also present among parasites, which differ in the degree of specialization to their hosts. Analyses of parasite communities, especially those of small fish hosts, reveal characteristics which differ from communities in the marine milieu: (a) suspension of specifity, (b) new hosts, (c) reduction in the number of hosts in life cycles, and (d) adaptation to genuine brackish water hosts. The view of the Baltic Sea as a species-poor but balanced ecosystem is also valid for parasites. The Baltic Sea is endangered by the high level of eutrophication, as the organisms are not adapted to its consequences. The study of parasite communities reveals such threatening conditions for the respective environments.

Introduction

Parasites are organisms that depend metabolically upon other organisms as they draw off energy from them. Because they receive only a small proportion of the host's energy, the parasite can remain on the host for a long time while the host itself remains alive. This is the major difference between parasites and predators, which kill their prey. Parasites are therefore smaller than their hosts and also have shorter reproduction times.

Parasites may nevertheless damage their hosts. This damage may even lead to the death of host, but this is generally not advantageous to the parasite because of its metabolic dependence. Parasites are optimally adapted to life on or in the hosts and often develop morphological and physiological characteristics that render them specialists on a specific host in a specific organ (Dogiel 1964). In many cases several individuals of a parasite species infest a single host, especially when they clearly differ in size from the host, and when intraspecific competition is low. The dispersal over the host population is a negative binomial one, which results in high infestation ratios of host specimens with either few or many parasite numbers but low infestion ratios of host specimens, with middle parasite numbers (Crofton 1971).

The basic questions of ecology – "Where do we find organisms?" "How many are present?" and "Why do we find them here?" (Krebs 1994) – are also those of ecological parasitology. This means that an ecologist compiles all the factors leading to optimal conditions for their existence. The habitat is the sum of abiotic (climatic) factors which may create a multifactorial hypervolume. It is a characteristic of parasites that they must be described both by their macrohabitat, i.e., the habitat of its host, and by their microhabitat, i.e., the site where parasites live on or in the host. Additionally, an organism plays a dis-

tinct role within the community, where it exists in a distinct habitat, and therefore its interactions with other organisms create a dynamic system, which is called ecological niche; this means the exploitation of nature by an organism (Pianka 1994). Intraspecific competition is the most effective factor in determining the extent of the niche. Therefore abiotic factors and certain biotic factors such as symbionts, predators, and prey are the conditions for existence and create the theoretical niche; competitors for resources present the conditions that make it a realized niche (Hutchinson 1957). These two interdependent factors determine the ultimate conditions for the distribution of organisms, including that of parasites (Zander, unpublished).

Characteristic Abiotic Conditions of the Baltic Sea and the Composition of its Parasite Fauna

The Baltic Sea is characterized by decreasing salinity from the Skagerak to the northeastern, which is limnetic. The huge central Baltic east of the Darsser Schwelle to the Bothnian Sea and the Gulf of Finland shows a very uniform surface salinity of 6–8‰. In the western Baltic there is a more rapid decrease from 30‰ to 10‰ from Skagerrak to Kattegat and the Belt Sea. The organisms living here have adapted to these extreme conditions, which are increased by alterations in the salinity due to hydrographic effects (Remane 1958). Plants and animals in the Baltic live mainly in marine habitats; some are found in limnetic environments, and this is also true for parasites (Reimer 1970). A third group are the genuine brackish water inhabitants, which are in fact also marine organisms but are better competitors to relatives in the brackish than in the marine milieu. The forth category includes species such as that perform spawning migrations between marine and limnetic environments. While no migratory parasites are known, these are also represented in the genuine brackish water group (Zander et al. 1984).

The second problem for Baltic organisms is the increasing eutrophication (Nehring and Ærtjeberg 1996). The characteristic vertical stratification of the Baltic presents increasing salinity but oxygen deficiency with depth. Because there is no mixing of surface water of lower salinity with heavier deep water of higher salinity, oxygen is not tranferred from the surface to the deep. Consequently the bottom of the central Baltic obtains sufficient oxygen only after heavy storms from the northwest that transport wa-

ter from the North Sea and displaces the oxygen-poor water in the deep layers; instances of this occurred in 1962, 1976, and 1993 (Rheinheimer 1995; Matthäus 1996). Increasingly eutrophication also causes oxygen deficiencies in shallow waters (Gerlach 1996).

At first, eutrophication favors the existence of plants and simultaneously of herbivores. On the other hand, herbivorous snails and crustaceans are the major intermediate parasite hosts. Therefore parasites can profit from eutrophication (Reimer 1995). However, oxygen deficiency may reduce their populations, either indirectly by affecting hosts or directly by affecting free stages of parasites.

Thus the Baltic communities depend upon two stressors: first, decreasing salinity as a natural factor to which the organisms have had time to adapt; second, eutrophication and its consequences, an anthropogenic factor to which the organism have not had time to adapt.

The Regional Parasite Fauna

The regional fauna of the entire Baltic consists of several geographic elements as described above (Remane 1958). The parasites have their distribution boundaries in the Baltic Sea where these or their hosts can no longer tolerate the changing salinity due to the lack of adaptations of osmoregulation. If the parasite is bound to a specific host, its distribution is coterminous with that of the host.

Marine Species

The digenetic trematode *Derogenes varicus*, which lives in several fish species, is distributed worldwide but is limited in the Baltic to the Öre-Sund, which is also the boundary of its first intermediate hosts, snail species of the genus *Natica* (Køie 1983). Specimens are occasionally found in the Lübeck Bight, perhaps as the result of drifting of the second intermediate hosts, copepods, into this area (Strohbach, unpublished). The related *Brachyphallus crenatus* infests the snail *Rissoa* spp., which is more tolerant to freshwater and is therefore also found in fishes of the "Frisches Haff" (Fig. 1). Another digenean, *Podocotyle atomon*, infests first *Littorina saxatilis*, which lives in the North Sea at the high water level but in the Baltic in the sublittoral and is distributed as far as Bornholm. This is also the boundary of the presence of *P. atomon* in fishes (Fig. 1). *Littorina littorea*, whose distribution is limited to Rügen, is the

Fig. 1. Map of the Baltic Sea with the investigation sites and the distribution boundaries of some parasites. Sites: *1*, Schlei; *2*, Blank Eck; *3*, Dahmeshöved; *4*, Salzhaff; *5*, Westerbergen. Distribution boundaries: *Bo.sc*, *Bothriocephalus scorpii*; *Br.c.*, *Brachyphallus crenatus*; *Cr. li.*, *Cryptocotyle lingua*; *Di*, *Deropristis inflata*; *He*, *Hemiurus luehei* and *H. communis*; *Le*, *lecisthaster confusus*; *Po.a.*, *Podocotyle atomon*; *Pr.c.*, *Prosorhynchus crucibilis*. *Solid lines*, confirmed boundaries; *broken lines*, assumed borders. (From Reimer 1970)

characteristic first intermediate host of the digenean *Cryptocotyle lingua*, an important bird parasite (Fig. 1). In the Baltic it is also found in substitute hosts such as *L. saxatilis* and the genuine brackish water snail *Hydrobia ventrosa* (Strohbach, unpublished, Zander et al., unpublished). The cestodan *Bothriocephalus scorpii* is also widely distributed as far as Gdansk Bight (Fig. 1).

Among nematodes *Hysterothylacium aduncum* is a widely distributed parasite of fishes, especially cods. It is distributed as far as Gdansk Bight and is unspecialized to several intermediate hosts, including crustaceans, polychaetes, echinoderms, chaetognaths, and even ctenophores (Køie 1993). Another representative of this group, *Anisakis simplex*, infests several mammals as final hosts and is more specialized to the first intermediate hosts, Euphausiacea. These crustaceans occur in the Kattegat but do not penetrate further into the Baltic. Nethertheless, the parasites have been found in several small fishes which are second intermediate hosts from the Mecklenburg Bight (Zander et al. 1993; Zander et al. unpublished). It is still unknown which crustaceans are the first intermediate hosts in the western Baltic. The acanthocephalian *Echinorhynchus gadi* is a species that is distributed throughout the world and is unspecialized regarding both intermediate hosts (benthic crustaceans) and final hosts (fishes), where it lives in the intestinal tract. It is found as far as the central Baltic and the Gulf of Finland (Reimer and Walter 1993).

Limnetic Species

The limnetic group is not as frequent as the marine group. The digenean *Diplostomum spathaceum* develops in the fresh water snail *Lymnaea stagnalis* as first host, in eye lenses of fishes as second intermediate host, and in the intestinal tract of gulls as final host. Because the snails can also exist in brackish water of lower salinity these parasites are found in several fish species of the coastal Baltic such as in the Greifswalder Bodden (Reimer 1970), Salzhaff (Zander et al. unpublished), and Schlei fjord (Kesting et al. 1996). The cestodan *Schistocephalus solidus* occurs in several birds as final hosts which prey on the three-spined stickleback *Gasterosteus aculeatus*; this fish is the special second intermediate host in fresh waters. In the Baltic it is found also in the western parts but prevails in gobiid fishes there (Zander et al. 1993). The famous blood-sucking eel parasite *Anguillicola crassus* (Nematoda), which has been introduced to European freshwaters from East Asia, can still exist in the western Baltic at salinity of about 12‰, where it infests several fish as intermediate and transport hosts (Reimer et al. 1994). A similar distribution is described for the acanthocephalians *Pomphorhynchus laevis* and *Neoechinorhynchus rutili* (Zander et al. 1993).

Brackish Water Species

Parasites of the brackish water group are characterized by their great abundance in hosts, which are

also genuine brackish water species, although they are also present in lower abundance in some other hosts. Therefore among the unspecialized acanthocephalians and nematodes no species can be attributed to these groups. Among digeneans *Cryptocotyle concavum*, *Aphalloides timmi*, *Maritrema subdolum*, and *Microphallus claviformis* use the snail *H. ventrosa* as first intermediate hosts. The second intermediate host of *C. concavum* is the common goby *Pomatoschistus microps*, which is also a genuine brackish water species. The larvae penetrate into the kidney, the special microhabitat of this host, where they can accumulate to more than 2000 cysts (Zander 1996). In other goby and stickleback species *C. concavum* penetrates only the skin, as do usually other marine *Cryptocotyle* species. Final hosts are several birds. This is also true for *M. subdolum* and *M. claviformis* which generally infest benthic crustaceans as second intermediate hosts. In the Baltic *M. claviformis* larvae, however, remain in the first host and directly reach birds that feed on snails. *A. timmi* follows another path of development by infesting the final special host, the common goby *P. microps*, directly after leaving the snails and without building up a resting stage (Reimer 1970).

The Local Parasite Fauna or Compound Community

Following the general concept of parasite communities (Holmes and Price 1986), the compound community level includes all parasites of an ecosystem. It comprises the parasites of the regional fauna which are adapted to the abiotic and biotic factors of the respective habitat (Holmes 1990). The sampling site of Dahmeshöved, Lübeck Bight (Fig. 1), with salinity of 9–13‰, has been investigated in regard to parasites since 1987. Between 1992 and 1996, 21 parasites were found in five goby species (Gobiidae, Teleostei; Zander unpublished). In the Kiel Bight the sampling site of Blank Eck (Kiel Bight; Fig. 1), with salinity of 11–16‰, only 13 parasite species were present in these small fish hosts. This finding was unexpected because it is common in brackish water that the higher the salinity is, the more species occur (Remane 1958). The true reason for these results presumably lies in the differences of eutrophication, which is higher in Dahmeshöved than in Blank Eck (Zander and Kesting 1996).

Regarding the life cycles, the first developmental stages of fish parasites exist in snails and/or planktonic and benthic crustaceans. Eleven goby parasites from Dahmeshöved have also proven to be present in these invertebrates, which additionally harbour several species for which birds are final hosts (Table 1). The other species live either in other invertebrates which have not been investigated or have not yet been found, especially if they live in calanoid copepods. Some digenean species which infest fish as intermediate hosts are transferred to fish-preying birds or seals (Table 1). The brackish water digenean *M. claviformis*, which is very frequent in other localities, is not present at Dahmeshöved although the intermediate hosts, mud snails (*Hydrobia* spp.), are very abundant. Snail-preying birds which are final hosts are probably not attracted by this sampling site.

In aquatic ecosytems small fishes play an important role in the transfer of helminth parasites from the first intermediate to final hosts, most of which are larger fishes or birds and mammals (Zander and Westphal 1991). The small-size fishes are effective mediators between these two levels because birds and mammals which may feed on tiny planktonic copepods or small snails are rare (Fig. 2).

Parasites' success, however, decreases during their life cycle as a result of mortality loss, which is higher the more intermediate hosts are included in the respective cycles. In Dahmeshöved the density of hosts and of infested hosts have been measured in order to calculate this loss (Zander unpublished). Four abundant parasites, three digeneans and a nematode, were traced from several intermediate host levels to final hosts. Host density and total parasite density were low in the periwinkle snail *L. saxatilis* and the goby but higher in mud snails, *Hydrobia* spp., and highest in gammarid crustaceans (Fig. 3). The difference in host and parasite densities was high in snails (2 or 1.5 tenth power), middle in gammarids (1 tenth power), and low in gobies (<1 tenth power). While parasite larvae in snails produce and shed constantly new cercariae which penetrate the next host, crustaceans harbor only single parasites. Therefore the distribution of parasites in various host groups is, in mathematical terms, the product of infestation rate and infestation intensity of the former host, which should be nearly the same to ensure success in the next host. The life cycle of *P. atomon* demonstrates this as it begins in *L. saxatilis* with very low infestation rates (but extreme high infestation intensities), is continued in gammarids with relative high values, and ends in gobies with the highest values (Fig. 3). Whereas *P. atomon* is transferred to gobies by ingestion of gammarids, the cercariae of the bird parasite *C. concavum* actively penetrate the fish hosts and thus may attain greater infestation rates.

Table 1. Parasite compound community at Dahmeshöved (from Strohbach, unpublished; Zander et al. 1993; Zander and Kesting 1996)

Parasites	Snails	Crustaceans		Cockles	Fishes		Birds and/or seals
		Benthic	Planktonic		Intermediate host	Final host	
Digenea							
Cryptocotyle concavum	×				×		(×)
Cryptocotyle lingua	×				×		(×)
Aphalloides timmi	(×)				(×)	×	
Acanthostomum balthicum	(×)				×	(×)	
Brachyphallus crenatus	(×)		(×)			×	
Derogenes varicus	(×)		(×)			×	
Lecithaster confusus	(×)		(×)				
Lecithaster gibbosus	(×)		(×)				
Apatemon gracilis	(×)				×		(×)
Podocotyle atomon	×	×				×	
Asymphylodora demeli	×			(×)		(×)	
Maritrema subdolum	×	×					×
Microphallus papillorobustum	×	×					(×)
Microphallus pygmaeus	×	(×)					(×)
Notocotylidae gen. sp.	×						(×)
Cestoda							
Schistocephalus solidus			?		×		(×)
Bothriocephalus scorpii			?		×		(×)
Hymenolepsis sp.		×					(×)
Tetrarhynchidae gen. sp.			(×)		×	(×)	
Nematoda							
Hysterothylacium sp.		×	?		×	×	
Contracaecum sp.			(×)		×		(×)
Anisakis simplex			(×)		×		(×)
Raphidascaris acus		(×)			×	(×)	
Ascarophis arctica		×				×	
Acanthocephala							
Echinorhynchus gadi		×				×	
Pomphorhynchus laevis		×				×	
Neoechinorhynchus rutili		×				×	
Corynosoma sp.		×			×		(×)
Polymorphus minutus		(×)			*		(×)
Bivalvia							
Glochidium larvae					×		

×, parasite detected; (×), parasite not detected; ?, parasite not clearly destined; *, parasite detected but host is wrong

The Parasite Fauna of Ecological Equivalents or Guild Community

The guild community comprises the parasites of a host guild, a group of species which are similar in their way of life and ecological niches (Zander 1994). Coexistence in a single ecosystem is therefore possible only when specific conditions prevail, for example, a surplus of resources, which prevents competition. The gobies of the Baltic Sea comprise a guild which exploit the prey supplies of both the benthic and the pelagic environment, depending on the season (Zander unpublished). Snails and benthic and planktonic crustaceans may be other guilds, of which single species play similar roles as parasite hosts.

The five species of the goby guild from Dahmeshöved (Fig. 1) comprise the identical parasite spectrum albeit at differing prevalences (infestation ratios) (Table 2). The absence of single parasites in some of the host species may be caused either by differences in the specific defense systems of the host or by coevolutionary adaptations of parasite and host. These characteristics can also be used to calculate a correlation between the presence of parasites in one or in more hosts and the respective prevalence (Fig. 4). This correlation proves significant in four species of the goby guild from Dahmeshöved (Fig. 1) because an increase from monotopic
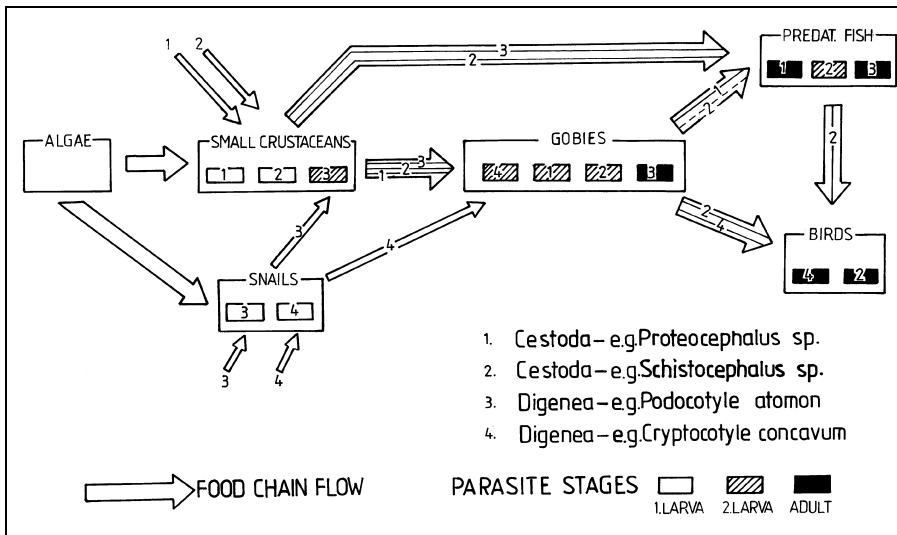
Fig. 2. The role of gobies as mediators of parasite transfer from first-level hosts, snails and crustaceans, to third-level hosts, predatory fishes or higher vertebrates. (From Zander and Westphal 1991)

(parasites in one host) to oligotopic (in two or three hosts) and polytopic (in all four hosts) has been ascertained (Zander and Kesting 1996). This means that the appearance of specialists is less than that of generalists, as is characteristic for eutrophic freshwaters (Wisniewski 1957).

In brackish waters largely the same conditions prevail as in freshwaters, but a characteristic of brackish water parasites is the generalization of specialists elsewhere. The plerocercoids of the tapeworm *S. solidus* are generally bound to the three-spined stickleback as the only intermediate host but is found in the Baltic in at least three goby species. This phenomenon of breakdown of specialization is explained by the osmoregulatory stress caused by the low salinity to which inhabitants of brackish waters are exposed (Kennedy 1975). On the other hand, some parasites reduce their characteristic developmental cycle, as does the bird digenean *M. claviformis* which encysts even in the first intermediate host, mud snails *H. ventrosa*, and not only in its second hosts, benthic crustaceans (Kesting et al.

1996; Reimer 1963). The opposite effect is caused by parasites that extend the number of intermediate hosts such as the digenean *M. subdolum*, which is also found in fishes of brackish water (Reimer 1963).

The Parasite Fauna of a Host Population or Component Community

The parasite component community comprises all parasites of a host population (Holmes and Price 1986) and is therefore restricted to a special area or site. The number of parasite species of component communities is generally lower than that in guild communities. Regarding the goby guild community from Dahmeshöved in 1992-1993 with 12 parasite species (Table 2), the relationship of component to guild community is 0.87 for *Pomatoschistus minutus*, 0.67 for *Gobiusculus flavescens*, 0.50 for *Gobius niger*, and 0.25 for *Pomatoschistus pictus*. When prevalences, the proportions of parasite-bearing hosts (Margolis et al. 1982), are considered, the single host species is seen to be susceptible to various parasites. Additionally, prevalences reveal the importance of single parasites in host species and in the ecosystem. The goby hosts from Dahmeshöved (Fig. 1) show clear differences between parasites with high and low prevalences in 1992-1993. Values higher than 60% characterize "core species," 40–60% "secondary species," of 5–40% "satellite species," and below 5% "rare species" (Holmes and Price 1986). Following this concept, we found only a single core species (*Hysterothycium* sp. in the black goby *Gobius niger*) and a single secondary species (*C. concavum* in the
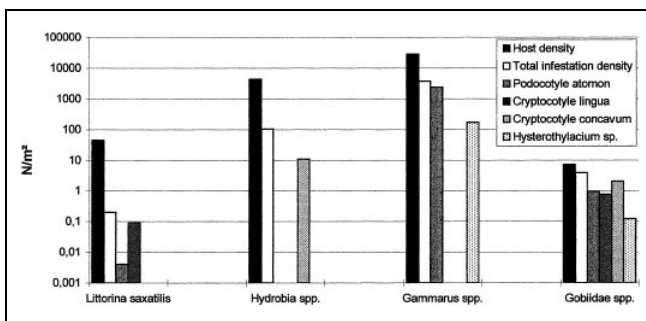

Fig. 3. Density of parasites and their hosts at different developmental stages at the site Dahmeshöved, Lübeck Bight, Schleswig-Holstein

Table 2. Abundance of parasites in four goby hosts from Dahmeshöved

Parasite species	Author	Auto- vs. allogenic	Planktonic vs. benthic	Goby hosts			
				G. flavescens	*P. minutus*	*P. pictus*	*G. niger*
Digenea							
Cryptocotyle concavum	(Creplin 1825)	allo	benth	0.828	0.353	3.446	0.082
Cryptocotyle lingua	(Creplin 1825)	allo	benth	0.007	0.530		3.391
Podocotyle atomon	(Rudolphi 1802)	auto	benth	1.008	0.066	0.300	
Asymphylodora demeli	Markowski 1935	auto	benth	0.009			
Cestoda							
Schistocephalus sp.		allo	plankt		0.031		
Nematoda							
Anisakis cf. simplex	(Rudolphi 1809)	allo	plankt	0.007	0.010		0.060
Hysterothylacium cf. auctum	(Rudolphi 1802)	auto	benth	0.085	0.116	0.025	2.013
Contracaecum sp.		allo	plankt		0.023		0.157
Acanthocephala							
Pomphorhynchus laevis	(Müller 1776)	auto	benth		0.011		
Polymorphus minutus	(Goeze 1782)	auto	benth	0.010	0.006		
Acanthella-larvae		auto	benth		0.031		0.062
Bivalvia							
Glochidium larvae		auto	benth	0.006			
Number of parasite species: 12		7–5	3–9	8	10	3	6

painted goby *P. pictus*); all other 25 host-parasite interactions were of lesser importance.

This finding is not always supported by the corresponding intensity values (Zander and Kesting 1996), i.e., the number of parasites in a host (Margolis et al. 1982). To emphasize the importance of parasites it is therefore better to use the parameter of abundance, which is the product of prevalence and intensity (Table 2). Abundance is thus the mean parasite number of a whole host population (Margolis et al. 1982) and may express a greater importance of parasite species above a value of 0.6, which is attained, for example, by the product of 60% prevalence and an intensity of 1. An abundance greater than 1 would express a still greater importance as this value would mean that every host of an average population is infested. Regarding this limit, the parasite communities of gobies from Dahmeshöved present five host-parasite combinations which are dominant (Table 2). In the sand gobies *P. minutus* no parasite appears to be important, while the other three hosts are characterized by one or two dominant parasite species which are generally different: three digeneans and one nematode.

Prevalence is well suited for obtaining comparative information on the environmental quality of different localities. The gobies in the site of Dahmeshöved attain higher values than those of Blank Eck in the Kiel Bight (Fig. 1; Table 3). It was to be expected that the slightly higher salinity in Blank Eck would cause a higher infestation, but the degree of eutrophication, which is lower at this site, probably plays a more decisive role for the infestation of hosts (Zander and Kesting 1996).
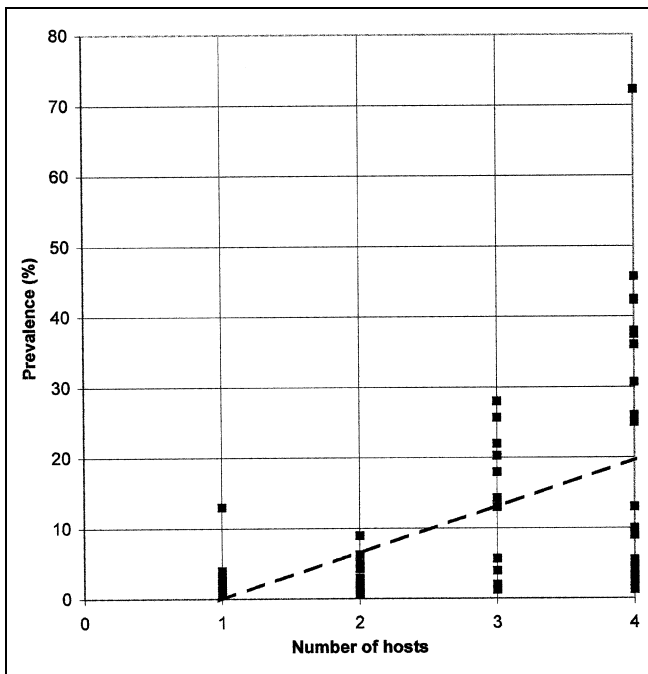

Fig. 4. Correlation of prevalence and number of infested goby hosts at the site Dahmeshöved, Lübeck Bight, Schleswig-Holstein. Results of the years 1992–1996

Additionally, analyzing component communities may provide information on the source of parasites from different habitats or microhabitats. Due to the developmental cycles stages of aquatic parasites can originate at final hosts from the terrestric environment (allogenic parasites) or at aquatic final hosts (autogenic parasites; Esch et al. 1988). Aquatic environments with many autogenic parasites are considered rather oligotrophic because they are not attractive for birds (Esch 1971). The opposite is true for eutrophic waters, which are frequently visited by birds that shed the eggs of parasites and also feed on intermediate hosts in these waters. The ratio in Dahmeshöved (Fig. 1) is 7 autogenic to 5 allogenic species (Table 2); when all host-parasite relationships are considered, there are 14 autogenic and 13 allogenic combinations. This result indicates an almost balanced situation, which guarantees the existence of parasites of both categories in this eutrophic water.

The classification according to planktonic vs benthic parasites refers to the source of the parasite's last habitat before infesting the respective host. This enables the analysis of a rather smaller scale of the environment (Zander and Kesting 1996). In hosts such as benthic and suprabenthic fishes these probably feed on various prey from either subhabitat, depending on which prey is in greater supply (Zander 1994). The study of the parasite community of gobies from Dahmeshöved found three planktonic and nine benthic parasites (Table 2). This result is disproportional but documents that both groups are present, including the planktonic with parasites which change hosts. Conditions for existence are therefore probably still advantageous (Zander and Kesting 1996). In another site, the inner Schlei fjord (Fig. 1), the heavy eutrophic situation results in the total vanishing of benthic parasites and the existence of only few planktonic parasites with one-host cycles (Kesting 1996). Thus parasite communities are best suited to stress the situation of the respective environment.

The Parasite Fauna of a Host Individuum or Infracommunity

The infracommunity comprises all parasites of a host specimen. They underlie the processes of coexistence vs competition because they prefer the same or similar microhabitats to a great extent. Therefore the number of parasite species of infracommunities is far lower than in component communities. Regarding the results from Dahmeshöved in 1992-1993, the 12 parasite species of the goby guild community or the 10 species of the component community of the sand goby *P. minutus* is reduced to maximally 3 species in a host individual with a maximum in the one-parasite group (Table 3). In the site of Blank Eck still lower values are found (Zander and Kesting 1996). The reasons may involve the intensity with which a parasite species infests a host, the size of host, the immunity system of host, or, very importantly, the seasonality of both host and of parasite. In other investigation sites as in Westerbergen (Fig. 1) and in the inner Schlei fjord (Fig. 1) the infracommunities present identical situations because no more than 3 parasite species exist in a host; this is charactersitic in freshwater infracommunities (Kennedy 1990). In contrast, in the site Salzhaff (Fig. 1) infracommunities of the common goby *P. microps* show 7 parasite species, those of the nine-spined stickleback *Pungitius pungitius* 5, and those of the three-spined stickleback *G. aculeatus* 9 parasite species (Zander et al., unpublished). This situation corresponds somewhat to the marine environments where, for example, in rock perches *Sebastes nebulosus* as many as 13 parasite species are found (Holmes 1990). These differences between gobies, sticklebacks, and rock perches are caused by the different sizes of these hosts, because larger ones offer more habitats or niches than smaller ones.

Special Patterns of Parasites in the Baltic Sea

The parasites of brackish waters show other characteristics in addition to morphological and physiological adaptations. Corresponding to specialities of freely living organisms (Remane 1958), parasites of this environment differ from those of their relatives in marine and limnetic habitats. These differences are especially in characteristics of life cycles, which may compensate the extreme abiotic conditions. They are dealt with in terms of four topics (Zander 1998):

Suspension of Specifity

The plerocercoid larvae of the tapeworm *S. solidus* live in fresh waters only in the three-spined stickleback *G. aculeatus*, while it is dissolved by the nine-spined stickleback *P. pungitius* (Orr et al. 1969)

Table 3. Prevalence of parasite infracommunities in four goby hosts from Dahmeshöved (D) and Blank Eck (B)

	G. flavescens		P. minutus		P. pictus		G. niger	
	D	B	D	B	D	B	D	B
1 parasite	0.34	0.11	0.29	0.06	0.44	0.07	0.51	0.34
2 parasites	0.18	0.06	0.05	0.02	0.05	0.01	0.18	0.03
3 parasites	0.01		0.01				0.03	
Total prevalence	0.53	0.17	0.35	0.08	0.49	0.08	0.82	0.37

which is the special host for the related *S. pungitii*. In the Baltic Sea the gobies *G. flavescens*, *P. minutus*, and *P. microps* are even more important hosts for *S. solidus*. The gobies have probably not developed defense mechanisms against this parasite because they are not present in fresh waters and therefore encounter no natural hosts there. This characteristic of parasites may correspond to the extension of habitats presented by freely living organisms of brackish waters (Remane 1958).

New Hosts

The brown shrimp *Crangon crangon* is found in marine sites such as the North Sea without metazoan parasites. In several sites of the Baltic Sea, for example, Schlei fjord, Westerbergen, and Dahmeshöved (Fig. 1), this species is infested by the digeneans *P. atomon* and *M. subdolum* (Gollasch et al. 1996). This means an enlargement of the host spectrum to predators of these shrimps which are larger than other benthic crustaceans and can bear more metacercariae. Additionally, *M. subdolum* can enlarge its characteristic life cycle by including fishes as third intermediate hosts, so-called transport hosts. These are able to extend the spectrum of final hosts to fish preying birds (Reimer 1963).

Reduction in Life Cycles

The effect of the reduction in life cycles is opposite to that of enlargement, as shown by microphallid digeneans, the cercariae of which remain and encyst in the first intermediate hosts, snails (Kesting et al. 1996; Reimer 1963). Consequently *M. claviformis* and *M. subdolum* can also reach snail-preying birds. The latter parasite may therefore alter its life cycle, with the inclusion of two to four hosts.

Adaptation to Genuine Brackish Water Species as Hosts

Characteristic brackish water species include the goby *P. microps*, the peracarid crustaceans *Idothea chelipes*, *Sphaeroma hookeri*, and *S. rugicauda*, *Gammarus zaddachi*, and *G. duebeni*, the copepod *Eurytemora hirundo*, and the mud snail *Hydrobia stagnalis*. These species harbour in the Schlei fjord at the point of "minimum of species" (Remane 1958) the most parasites (Kesting et al. 1996; Zander and Westphal 1991). The bird parasite *C. concavum* generally infests the snail *H. ventrosa* as first and the common goby *P. microps* as second intermediate host, where the cercariae encyst in the kidney and not, as in other fishes, in skin and fins (Zander et al. 1984). While a maximum of hundred cysts are found on the skin, several thousand can exist in the kidney without affecting the vitality of the common goby. This phenomenon is regarded as a unique coevolutionary adaptation of host and parasite in the brackish water.

The Baltic Sea is a young ecosystem, with the present condition of lowered salinity having developed over the past 7000 years. Today a balanced community exists comprising only a small spectrum of species without strength connections (Remmert 1992). However, 7000 years may be a sufficiently long period for coevolution which, as in the exemple of the common goby and *C. concavum*, can even mean a process of specialization: special host, special microhabitat, and no harm to host. The decreasing salinity therefore cannot be the only decisive factor in the existence of parasites.

Effects of Eutrophication

In contrast to the situation with lowered salinity, eutrophication is a very modern problem caused by human activity: the increased input of phosphates

and nitrates by farming, domestic wastes, and burnt traffic exhaust (Nehring and Ærtjeberg 1996). In the yearly succession of plants and animals, and their mineralization by bacteria, an excessive growth of algae in spring may cause large oxygen deficiencies after their death. This situation affects the existence of other organisms, including parasites (Kesting 1996).

An initial effect of eutrophication lies in promoting the existence of herbi- and detritovores, which are preferred intermediate hosts (Fig. 5). In the case of oxygen deficiency, however, which is often combined with the rise of toxic substances, its effect may be negative such as that of other stressors, for example, chemical wastes. Stressors affect not only hosts but also free stages of parasites, for example, miracidia and cercariae of digeneans and free larvae of cestodans, nematodes, and acanthocephalians. Additionally, the effect of stressors on host and parasite may differ, with the consequence that the host harmed by its reduced immune defense is better infested by parasites which are less harmed. This creates a network of interactions, including several feedback effects (Fig. 5).

The degree of eutrophication is indicated by the biological oxygen demand, i.e., the oxygen value of a sample measured after 5 days of darkness. The investigation sites of Kiel and Lübeck Bight, Blank Eck, and Dahmeshöved (Fig. 1) clearly differ in their oxygen balance, and fewer periods of oxygen
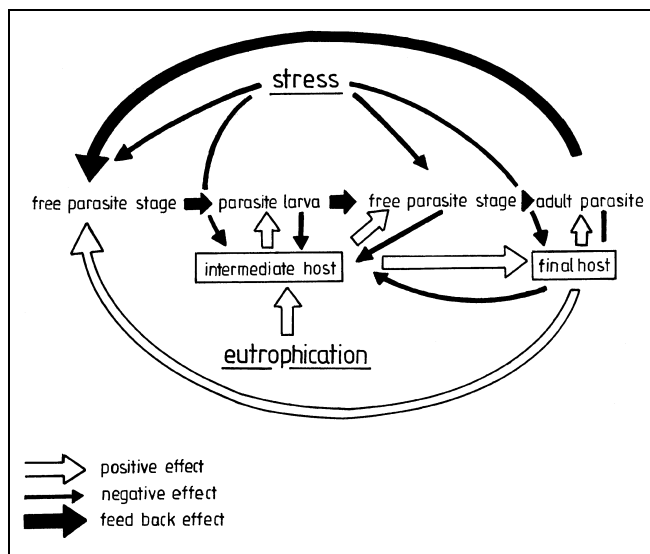

Fig. 6. Model of alteration in the number of allogenic and autogenic parasite species due to increasing eutrophication. *Points A,B*, the dominance of the two parasite groups alters. (From Zander 1998)

deficiency are found, for example, in Blank Eck than in Dahmeshöved (Zander and Kesting 1996). This may be the reason that the density of herbivores in Blank Eck, and with this the prevalence of parasites, is lower. Additionally, parasite diversity and equity is higher than in Dahmeshöved, where some parasite species can dominate. The surprising result of investigations in the inner Schlei fjord, which is exposed to a very strong oxygen deficiency, is a surplus of autogenic parasites in a species-poor community (Kesting 1996). This situation is also characterized by an almost total absence of benthic parasites due to anaerobic conditions in the benthal region. The conclusion is that increasing eutrophication will progressively reduce the numbers of allogenic parasites, most of which have complicated life cycles (Fig. 6). The last parasites under the extreme effect of this stressor are autogenic, planktonic ones because the free water may still provide better conditions, such as those found in the inner Schlei fjord (Kesting 1996). The ultimate result of increasing eutrophication is the vanishing of all hosts and, thus, all parasites (Fig. 6).

Fig. 5. Model of reinforcemant effect of parasite infestation on intermediate herbivorous hosts and carnivorous final host after eutrophication or stress by wastes. In this case the parasite is a digenan, after omitting the second free parasite stage the model is also valid for other helminths. (From Zander 1998)
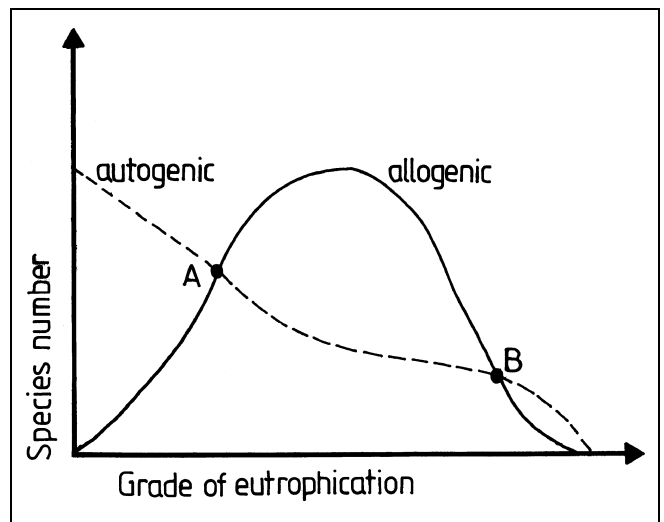
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