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Parasite communities of the Salzhaff (Northwest Mecklenburg, Baltic Sea) II. Guild communities, with special regard to snails, benthic crustaceans, and small-sized fish

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Abstract Metazoan parasites of guilds of benthic snails and crustaceans and of four fish families – Gobiidae, Gasterosteidae, Syngnathidae, and Zoarcidae – were investigated off the brackish Salzhaff area (Southwest Baltic) in the semienclosed Salzhaff and the near Rerik Riff in the free Baltic. Comparisons revealed greater similarities in parasite populations and communities within the fish guilds than between them. According to an evaluation of the core-/satellite-species concept using abundance values, the most important parasites of fish were some generalists, such as *Cryptocotyle* spp., *Podocotyle atomon*, and *Diplostomum spathaceum*, as well as some specialists, such as *Acanthostomum balthicum*, *Thersitina gasterostei*, and *Aphalloides timmi*. These specialists revealed high degrees of prevalence in their main hosts and lower degrees in one or two by-hosts. Additional importance is assigned to parasites that cause harm to their hosts due to their large size, e.g., *Schistocephalus* spp., or via massive infestation, e.g., several digenean metacercariae. Because specialists were more prominent in snails and fish from the Rerik Riff, the correlation of host numbers with prevalence resulted in only a slight increase instead of a more rapid rise in regression among crustaceans and fish from the entire Salzhaff, where the generalists were more prevalent. The selected host guilds demonstrated the entire life cycles of three digeneans (*P. atomon*, *A. balthicum*, *A. timmi*), one acanthocephalan (*Echinorhynchus gadi*), and one nematode (*Hysterothylacium* sp.). The prevalence increased in these cycles from host level to host level and attained relatively high values in all guilds. The parasite fauna of the Salzhaff area is influenced by eutrophication stress, which leads to a high level of productivity and, consequently, to great densities in primary consumers such as snails and crustaceans. These are attractive for several secondary consumers such as fish and birds, which is the reason for the existence of at least 24 autogenic and 20 allogenic parasite species at this locality. The slight surplus of the first category indicates a yet-balanced environment in the investigation area.

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Introduction

Modern ecologic parasitology differentiates the respective communities of these organisms according to the following levels: the infracommunity, i.e., the parasites of a host specimen; the component community, i.e., the parasites of a host population; the guild community, i.e., the parasites of several ecologically similar hosts; and the supracommunity, i.e., the parasites of an ecosystem (Holmes and Price 1986; Bush et al. 1997; Zander 1998). In part I of this investigation (Zander et al. 1999) of the Salzhaff area of Northwest Mecklenburg, German Baltic coast, we focused on the infracommunities and component communities of fish, especially on representatives of the Gobiidae, Gasterosteidae, Syngnathidae, and Zoarcidae. These studies revealed high degrees of prevalence and intensity in fish hosts for 36 parasites, among which the digeneans were represented by 15 species. Though their hosts are small, infracommunities may involve as many as 7 parasite species in common gobies, *Pomatoschistus microps*, and this number is surpassed by three-spined sticklebacks, *Gasterosteus aculeatus*, which can harbor as many as 9 species (Zander et al. 1999). High degrees of prevalence have been recorded not only for parasite generalists but also for some specialists. These results clearly indicate the special situation in the Salzhaff, which differs from those in other Baltic localities in the Lübeck and Kiel Bight (Zander and Kesting 1996, 1998). The causes may lie in the increased eutrophication in the very shallow Salzhaff, which is well supplied with oxygen and is therefore an attractive area for several types of birds preying on diverse aquatic organisms.

Some problems that were not investigated in part I were addressed in the present study. The diverse fish species are important second intermediate or final hosts in the Salzhaff area that, depending on their way of life, may be differently infested by larval parasite stages. Because representatives of the four fish families Gobiidae, Gasterosteidae, Syngnathidae, and Zoarcidae are ecologically similar with regard to their habitat and prey preferences, these groups can also be compiled as guilds (Root 1967) or ensembles (Fauth et al. 1996). Therefore, it might be of interest to elaborate the intra- and interguild differences among them as a means of testing their indicator properties. These fish are also well suited for evaluation of their importance in the parasites' life cycles. They serve as hosts for very tiny parasites such as trichodinans as well as for large cestodes. The latter occur only singly or in very low numbers, whereas metacercariae of *Cryptocotyle concavum* can infest their hosts by the hundreds or even thousands (Zander 1999).

In the present investigation we also concentrated on the parasites of benthic organisms, which are represented especially by snails and peracarid crustaceans. These are important intermediate hosts for several fish and bird parasites (Reimer 1970; Zander et al. 1994; Kesting et al. 1996) and can also be compiled as guilds. Because these organisms are mainly herbivores and detritivores, their population densities may follow the level of eutrophication. It should be assumed that this factor also influences the density of distinct parasite stages, as has been found in a yet more eutrophicated location in western Fehmarn, Ostholstein (Skroblies 1998). Therefore, the study of parasite life cycles might yield better qualitative and quantitative data if it were approached at different host levels. Because supracommunities can be analyzed only incompletely, evaluation of guild communities might provide a good means of comprehending the parasite fauna on a level higher than that represented by component communities. These investigations of several guild communities enable analysis of the suprapopulations of some parasites and may include at least sections of the parasite supracommunity of the Salzhaff.

Materials and methods

The field investigations were carried out predominantly in the entire Salzhaff and off the Rerik Riff, which lies directly at the entrance to the Salzhaff but in the free Baltic (Fig. 1 in Zander et al. 1999). The samples were taken in May, June, July, and September of 1995 and 1996 and represent the host levels of snails, benthic crustaceans, and fish, especially small-sized groups such as gobies, sticklebacks, and sea needles as well as the larger eelpouts.

The oxygen level was measured electronically from water samples that had been obtained from the surface or directly above the bottom. Specimens of water for testing of biological oxygen demands (BOD_5) were kept in brown bottles and measured at 5 days after sampling. The animals were caught in the entire Salzhaff from a depth of 2–3 m using a small dredge from a boat and were then sorted and fixed in 70% ethanol (benthic crustaceans) or 10% kohrsolin (fish). The snails and a smaller portion of fish were sampled in the 0.2- to −0.5-m shallow water immediately near the shore. To obtain quantitative samples of *Hydrobia* spp. a small net of 0.2-m breadth was drawn a distance of 0.5 m across the sediment. Live snails were transported to the laboratory, where they were kept at 8 °C until their parasitologic analysis. In addition, a smaller batch of fish was kept alive for several hours before they were killed just prior to preparation. The animals of the Rerik Riff were caught at a depth of 3 m using a small hand net (snails), quantitative gear (benthic crustaceans; Dietel 1997), and large hand nets (fish) together with scuba gear. The samples were fixed as described above.

All potential hosts were determined to the species level and carefully examined for parasites using a stereomicroscope. For inspection, smaller snails were squeezed between two glass slides and the shells of larger snails were broken, after which the entrails were examined, especially the digestive glands and gonads. Benthic crustaceans were twitched segment by segment to reveal parasites in the coelomic cavity and muscles. The fish were prepared as previously described by Zander et al. (1999). Parasites were separated from their hosts and identified, mostly to the species level. They were treated with lactic acid to clear the organs for better identification.

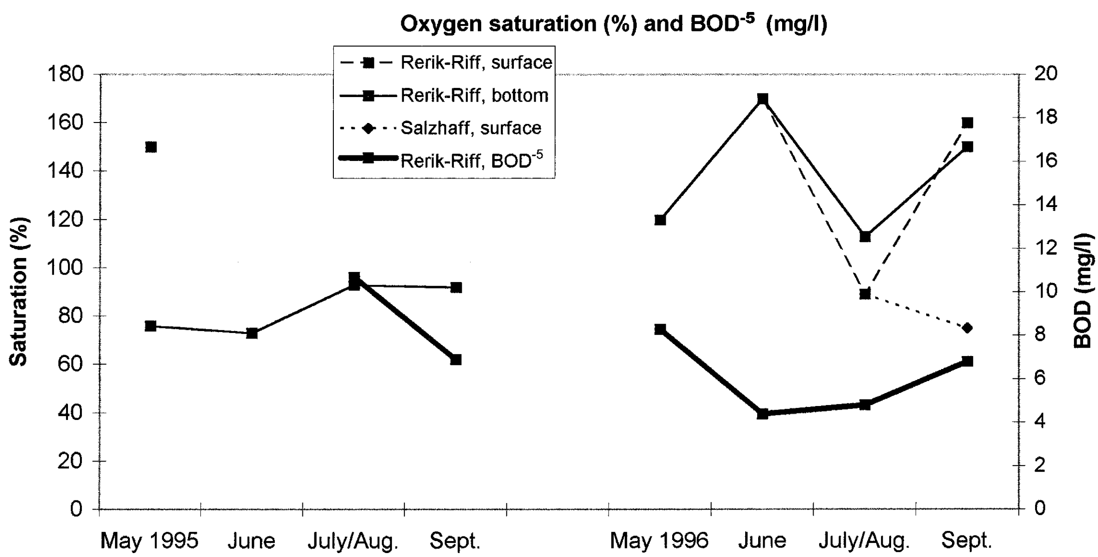


Fig. 1 Oxygen saturation (%) and BOD_5 (mg/l) values determined during two investigation periods in the Salzhaff area

The importance of parasites is judged by an altered core-/satellite-species concept (Holmes and Price 1986) according to their abundance, which is the product of the prevalence – the part of a host population that is infested – and the mean intensity – the mean number of parasites in a host population. The scores are divided into the following categories: > 2 core species, 0.6–2 secondary species, 0.2–0.6 satellite species, and < 0.2 rare species. In addition, a subdivision of the parasites according to size is done as follows: microparasites consist of protozoans and metacercariae of digeneans; meioparasites comprise most digeneans, nematode larvae, and copepods; macroparasites consist of adult nematodes, acanthocephalans, and cestodan plerocercoids from the gut; and megaparasites comprise cestodan plerocercoids from the body cavity.

The gut contents of fish were additionally used for analysis of the ingested prey, which was identified to relevant taxonomic units. As a parameter the frequency of occurrence was calculated, which compiles the parts of fish in which the respective prey item was found.

Some terms should be explained. The guild concept (Root 1967) was combined with geographic and taxonomic patterns of populations described by Fauth et al. (1996) into an integrated concept. Thus, guilds from the same community are "local guilds"; additionally, when the species are related they are "ensembles," which correspond to the "Lebensorttyp" described by Riedl (1970). These terms characterize the host populations. The concept of the parasite-community levels infracommunity, component community, and supracommunity (Esch et al. 1975) was extended by the guild community (Zander 1998), which is the parasite community of a host guild, local host guild, or ensemble; the guild population is the corresponding term for a host population (Dietel 1997). According to Esch et al. (1988), autogenic species are parasites that spend their whole lives in one environment and allogenic species are parasites that change from the aquatic to the terrestrial environment.

As statistical parameters, mean values and standard deviations as well as linear regressions and correlation coefficients were calculated. We calculated the Soerensen indices for species identity and the Renkonen indices for dominance identity; these indices can attain values ranging between 0 and 1, with the limit for moderate concordance being 0.6.

Results

Abiotic factors

The temperatures and levels of salinity found in the area of investigation from spring to late summer have been described in part I of this study (Zander et al. 1999). According to the season, the temperature ranged between 9° and 20 °C and the salinity varied between 0.85% and 1.20% in 1995 and 1996. The oxygen content presented low saturation values in 1995 and higher values in the spring of 1996, whereas in summer the entire Salzhaff showed clear undersaturation (Fig. 1). The BOD_5 was very high but decreased in the summer of 1996 to lower values.

Snails

Seven snail species were found in the Salzhaff area, and all were infested with the exception of *Littorina littorea*. In all, 18 digenean species infested snails, with the prevalence mostly being 1% or 2%, but several values surpassed the 10% level (Table 1). The mud snails *Hydrobia ulvae* and *H. ventrosa* harbored as many as 11 parasites, whereas the 2 snail species of limnetic origin, *Theodoxus fluviatilis* and *Lymnaea balthica*, contained only 2 species. The usual well-known specificity for snail hosts was reduced in this study, as most parasites occurred in two or more hosts and *Asymphylodora demeli* were even found in six different snail species (Table 1). Remarkably, *Cryptocotyle lingua* was not found in its

Table 1 Parasite spectrum and prevalence of snail hosts

Host species	*Littorina saxatilis*	*L. littorea*	*Zippora membranacea*	*Hydrobia ulvae*	*H. ventrosa*	*Theodoxus fluviatilis*	*Lymnaea ovata*	Number of hosts
Parasite species								
Numbers, 1995/1996	191/250	23/0	224/165	382/158	817/826	0/21	0/21	
Cryptocotyle concavum				< 0.01/0.02	0.01/0.01			2
C. lingua				< 0.01/0.01				1
Aphalloides timmi				< 0.01				1
Acanthostomum balthicum				/0.06	/ < 0.01			2
Psilochasmus oxyuris			< 0.01	/0.01	< 0.01/ < 0.01			3
Himasthla sp.				/0.02	/0.01			2
Bunocotyle cingulata				/0.01				1
Magnibursatus caudofilamentosa			0.02/0.17					1
Asymphylodora demeli	0.05/0.21		0.04/0.04	/0.01	0.01/0.01	/0.09	/0.09	6
Paramonostomum alveatum				/0.02	/0.04			2
Notocotylidae gen. sp.					0.03/0.01			1
Podocotyle atomon	0.02/0.02							1
Maritrema subdolum				0.01	< 0.01/0.02			2
Microphallus claviformis				0.03/0.07	0.03/0.08			2
M. papillorobustum					< 0.01/00.01			1
M. pygmaeus	/ < 0.01		< 0.01					2
Levinseniella sp.				< 0.01/0.03	/0.01			2
Cotylurus cornutus						/0.14	/0.14	2
Total	0.07/0.24	0	0.06/0.21	0.05/0.27	0.08/0.15	/0.24	/0.24	
Double infestation				< 0.01/0	0/0.02			
Number of parasite spp.	3	0	4	11	11	2	2	

specific host, *L. littorea*, but occurred at low levels of prevalence in *H. ulvae*. Double infestation was found only in *Hydrobia* spp., but only at low degrees of prevalence (Table 1).

Quantitative data on population density were obtained on two *Hydrobia* spp. from the bottom water of the Salzhaff as well as the deeper Rerik Riff (Table 2). It is evident that *H. ventrosa* dominated in the shallow Salzhaff locality, attaining peak numbers of $>3{,}000/\text{m}^2$. In the Rerik Riff the opposite situation was found, as *H. ulvae* clearly dominated over *H. ventrosa* (Table 2). From these data we calculated density values as high as 480 parasites/m^2 but mostly recorded >100 parasites/m^2 for *H. ventrosa*. The most abundant parasite was the bird digenean *Microphallus claviformis*, whereas *Maritrema subdolum*, *A. demeli*, and *C. concavum* were found at far lower densities (Table 2).

Crustaceans

The investigations of benthic amphipods and isopods, species of the genera *Gammarus* and *Idothea*, were concentrated in the entire Salzhaff in 1995 and in the Rerik Riff in 1996. Obviously, the Salzhaff populations attained far higher levels of prevalence than did those in the Rerik Riff (Table 3). The most dominant parasites in the Salzhaff were *Podocotyle atomon* in *G. locusta* and *G. salinus*, *M. subdolum* in *I. granulosa*, and *Levinseniella brachysoma* in *G. locusta*. The latter host harbored as many as six parasite species and presented the highest total prevalence (85%). In contrast, *I. granulosa* attained a value of 78% for the prevalence of *M. subdolum*, which was the only parasite detected in this host (Table 3). *P. atomon* infested the most hosts, including three *Gammarus* spp. and *I. balthica*, whereas the nematode *Hysterothylacium* sp. was present at low prevalence only in *G. locusta*.

Prevalence and abundance values were far lower in crustaceans of the Rerik Riff (Table 3). *G. salinus* harbored the most parasites ($n = 7$), whereas the *Idothea* spp. were not infested in this habitat. The highest values were recorded for *L. brachysoma* (32%) and *P. atomon* (18%) in *G. zaddachi*; all other parasites attained prevalence values of $<10\%$.

Density values were recorded for crustaceans from the Rerik Riff populations (Table 4). Young specimens of *Gammarus* spp. measuring <6 mm in body size dominated, but *G. salinus, G. oceanicus*, and *I. balthica* also formed considerable populations. The density value recorded for parasitized hosts was highest in *G. salinus*, predominantly due to infestation by *P. atomon* and *L. brachysoma*, which also occurred at high density in young *Gammarus* spp. (Table 4). All other parasites were of lesser importance. In contrast to the situation in the Salzhaff, in the Rerik Riff, *L. brachysoma* (67 infested hosts/m^2), and *P. atomon* (31 infested hosts/m^2) were by far the most abundant parasites, showing a high infestation potential (Table 4).

Fish

The component communities of fish comprised 36 parasites, of which 15 species were digeneans, 7 were cestodes, and 6 were nematodes (Table 1 in part I, Zander et al. 1999). The importance of single parasites of 10 fish hosts differed according to their respective abundance values (Table 5). A total of 12 core-species combinations were found that involved 7 parasites, of which both *C. concavum* and *P. atomon* infested 3 different hosts each. Although prevalence values were $<60\%$, the combinations *Aphalloides timmi*/*Pomatoschistus microps* and *P. atomon*/*Gasterosteus aculeatus* or *Spinachia spinachia* involved core species. The present secondary-species category comprised 7 combinations, of

Table 2 Density (n/m^2) of *Hydrobia* spp. and several of their parasites

Species	Site Date	Salzhaff May 1995	Salzhaff Sept. 1995	Rerik Riff Sept. 1995	Salzhaff June 1996	Salzhaff Sept. 1996
H. ulvae		82	87	860		13
H. ventrosa		602	1563	57	3197	1027
Parasite density *H. ulvae*		4	4	43		4
Parasite density *H. ventrosa*		48	125	5	480	154
C. concavum (H. ulvae)		1	4		< 1	
C. concavum (H. ventr.)		16	1	32	10	
C. lingua (H. ulvae)		1	4		< 1	
A. timmi (H. ulvae)		< 1	< 1	4		
A. balthicum (H. ulvae)						1
A. balthicum (H. ventr.)					16	5
A. demeli (H. ulvae)						< 1
A. demeli (H. ventr.)		6	15	1	32	10
M. subdolum (H. ulvae)		1	1	9		
M. subdolum (H. ventr.)		3	8	< 1	64	21
M. claviformis (H. ulvae)		2	2	26		1
M. claviformis (H. ventr.)		18	47	2	256	12
Levinseniella cf. *brachysoma (H. ulvae)*		< 1	< 1	4		< 1
Levinseniella cf. *brachysoma (H. ventr.)*					32	10

Table 3 Parasite spectrum and prevalence of crustacean hosts

Salzhaff 1995	Host species	*Gammarus locusta*	*G. salinus*	*G. zaddachi*	*G. juv.*	*Idothea granulosa*	*I. balthica*	Number of hosts
Parasite species	Numbers	114	246	17	50	221	747	
P. atomon		0.31	0.26	0.10			0.05	4
M. subdolum		0.07				0.78	0.10	3
M. claviformis								0
L. brachysoma		0.38	0.11	0.03				3
Hysterothylacium sp.		0.01						1
Ascarophis arctica		0.17	0.13	0.03				3
Echinorhynchus gadi		0.05	0.01					2
Total		0.85	0.43	0.16	0	0.78	0.13	
Double infestation		0.14	0.08				0.02	
Number of parasite spp.		6	4	3	0	1	2	
Rerik-Riff 1996								
Parasite species	Numbers	148	433	22	647	12	224	
P. atomon		0.03	0.08	0.18				3
M. subdolum			0.002	0.05				2
M. claviformis		0.03	0.01					2
L. brachysoma			0.09	0.32	0.07			3
Hysterothylacium sp.			0.01					1
A. arctica		0.03	0.01	0.05				3
E. gadi		0.03	0.01	0.05				3
Total		0.12	0.21	0.65	0.07	0	0	
Double infestation		0.01	0.01	0.14	0.002			
Number of parasite spp.		4	7	5	1	0	0	

Table 4 Density (n/m^2) of benthic crustaceans from the Rerik Riff and several of their parasites

	Host species						
	G. locusta	*G. salinus*	*G. zaddachi*	*G. juv.*	*I. granulosa*	*I. balthica*	Sum
Host density	109	319	16	476	9	165	1094
Infestation density	13	67	10	33	0	0	123
P. atomon	3	25	3				31
M. subdolum		1	1				2
M. claviformis	3	3					6
L. brachysoma		29	5	33			67
Hysterothylacium sp.		3					3
A. arctica	3	3	1				7
E. gadi	3	3	1				7

which 6 attained low prevalence values but high levels of intensity (Table 5). Therefore, prevalence values could range between 20% and 58% and the corresponding intensity levels were 7.0 (*Tylodelphis*) and 3.1 (*Hysterothylacium*). As many as 16 host-parasite combinations attained the level of satellite species (Table 5), their prevalence values varying between 9% and 33% according to the classification of Holmes (1991). All hosts except for *Gobius niger* as well as all important groups of parasites and their ontogenetic stages were involved. *P. atomon* and *C. concavum* were detected in several hosts.

The remaining 40 parasite-host combinations were classified as rare species. Among these, the cestodans *Schistocephalus pungitii* and *S. solidus* were remarkable in that they were the only parasites that represented the category megaparasites, which were not present at the higher levels (Table 5). These parasites infested 4 hosts (also *G. niger* and *P. microps*), which corresponds to 10% of the rare species. The core, secondary, and satellite species were mostly micro- and meioparasites, but 1 secondary, 2 satellite, and 11 rare species were macroparasites, representing 14%, 13%, and 28%, respectively, of these parasite-host combinations.

The parasite communities of fish hosts were first compared according to their interguild identities, which mostly attain a moderate level (Table 6). Values for species identity that surpassed the 0.6 level of greater similarity were found between *G. niger* or *P. microps* and *P. minutus*, between *G. aculeatus* and *Pungitius pungitius*, and between *Syngnathus typhle* and *Nerophis ophidion*.

Table 5 Classification of core/satellite species on the basis of abundance

Parasite	Host	Prevalence	Intensity	Abundance	Parasite size category	Harm to host
Core species: abundance > 0.2						
C. concavum	*Pomatoschistus microps*	0.99	102.8	**101.8**	Micro	Kidney cysts
C. concavum	*Gobius niger*	0.94	59.3	**55.7**	Micro	Skin/fin cysts
C. lingua	*G. niger*	1.00	19.5	**19.5**	Micro	Skin/fin cysts
Thersitina gasterostei	*Gasterosteus aculeatus*	0.71	23.2	**16.5**	Meio	Gill parasite
M. caudofilamentosa	*G. aculeatus*	0.73	19.3	**14.1**	Meio	Gill parasite
C. concavum	*Syngnathus typhle*	0.87	16.2	**14.1**	Micro	Skin/fin cysts
P. atomon	*Zoarces viviparus*	0.83	11.2	**9.3**	Meio	Gut parasite
A. timmi	*P. microps*	0.52	12.1	**6.3**	Meio	Body fluid sucker
Diplostomum spathaceum	*Z. viviparus*	0.67	4.7	**4.7**	Micro	Blur of eye lens
P. atomon	*G. aculeatus*	0.57	8.0	**4.6**	Meio	Gut parasite
P. atomon	*Spinachia spinachia*	0.57	4.3	**2.4**	Meio	Gut parasite
A. balthicum	*S. typhle*	0.64	3.4	**2.2**	Micro-Meio	Cysts/prey partit.
Secondary species: abundance > 0.6–2						
Hysterothylacium sp.	*Z. viviparus*	0.58	3.1	**1.8**	Macro	Gut parasite
Tylodelphis sp.	*G. aculeatus*	0.20	7.0	**1.4**	Micro	Blur of eye lens
Apatemon gracilis	*P. microps*	0.35	3.7	**1.3**	Micro	Skin/fin cysts
C. concavum	*P. minutus*	0.30	3.6	**1.1**	Micro	Skin/fin cysts
Bunocotyle cingulata	*Pungitius pungitius*	0.25	4.1	**1.0**	Meio	Gut parasite
C. concavum	*Gobiusculus flavescens*	0.26	3.3	**0.9**	Micro	Skin/fin cysts
Cardiocephalus longicollis	*G. aculeatus*	0.21	4.5	**0.9**	Micro	Brain
Satellite species: abundance > 0.2–0.6						
Brachyphallus crenatus	*G. aculeatus*	0.29	2.0	**0.6**	Meio	Gut parasite
Pomphorhynchus laevis	*Z. viviparus*	0.33	1.7	**0.6**	Macro	Gut parasite
T. gasterostei	*S. spinachia*	0.27	2.0	**0.5**	Meio	Gill parasite
Proteocephalus filicollis	*G. aculeatus*	0.24	1.8	**0.4**	Macro	Gut parasite
P. atomon	*G. flavescens*	0.21	1.7	**0.4**	Meio	Gut parasite
P. atomon	*P. minutus*	0.15	2.7	**0.4**	Meio	Gut parasite
C. concavum	*Z. viviparus*	0.08	4.8	**0.4**	Micro	Skin/fin cysts
P. atomon	*P. pungitius*	0.19	1.4	**0.3**	Meio	Gut parasite
A. demeli	*P. minutus*	0.18	1.6	**0.3**	Meio	Gut parasite
P. atomon	*Nerophis ophidion*	0.15	1.7	**0.3**	Meio	Gut parasite
C. longicollis	*Z. viviparus*	0.25	1.0	**0.3**	Micro	Brain
A. arctica	*Z. viviparus*	0.17	1.8	**0.3**	Meio	Gut parasite
Anguillicola crassus	*S. typhle*	0.10	2.9	**0.3**	Meio	Gill parasite
D. spathaceum	*G. aculeatus*	0.16	1.3	**0.2**	Micro	Blur of eye lens
C. concavum	*G. aculeatus*	0.15	1.4	**0.2**	Micro	Skin/fin cysts
C. lingua	*P. microps*	0.09	2.7	**0.2**	Micro	Skin/fin cysts
Rare species: abundance < 0.2 among other parasite-host combinations						
Schistocephalus pungitii	*P. pungitius*	0.12	1.2	**0.1**	*Mega*	Absorption
S. solidus	*G. aculeatus*	0.03	1.0	**0.03**	*Mega*	Absorption

Dominance identities presented yet lower values; therefore, no similarity was indicated (Table 6). Extremely low was the Renkonen index calculated between the two sea needles.

The interguild comparisons revealed similarities only in the species spectra of Zoarcidae and Syngnathidae and moderate values for Zoarcidae and Gobiidae or Gasterosteidae (Table 7). In contrast, dominance identities were extremely low, even attaining zero in the comparison of Syngnathidae and Gasterosteidae. Therefore, it was of interest to calculate an interguild analysis in which all species of a guild would be compared together. Though the number of common parasite species was low in four species of Gobiidae and three species of Gasterosteidae but was high in two Syngnathidae (Table 7), the species identity was relatively high in Gobiidae and Syngnathidae but differed more strongly within the Gasterosteidae. In contrast, the dominance identity was relatively low, especially in Syngnathidae (Table 7).

Supracommunity

Several parasites could be traced along different host levels that included 11 digeneans, 2 nematodes, and an acanthocephalian. Remarkably, *P. atomon* and *Acanthostomum balthicum* were found in the primary, secondary, and final hosts at increasing levels of prevalence when the respective main hosts were regarded (Table 8). In contrast, the prevalence of *M. claviformis* decreased from the first to the second intermediate host. The second intermediate hosts of *Magnibursatus caudofilomentosa*, probably harpacticoids, and those of *A. demeli*, probably bivalves and polychaetes, were not investigated in this study. The latter species represents a

Table 6 Comparison of parasite component communities by the Soerensen (*top*) and Renkonen indices (*bottom*). Numbers of parasite species are indicated

	G. niger	*G. flavescens*	*P. minutus*	*P. microps*
G. niger	**10**	0.53	0.63	0.54
G. flavescens	0.59	**9**	0.56	0.56
P. minutus	0.52	0.56	**9**	0.64
P. microps	0.57	0.57	0.43	**16**

	G. aculeatus	*P. pungitius*	*S. spinachia*
G. aculeatus	**20**	0.74	0.44
P. pungitius	0.50	**18**	0.48
S. spinachia	0.29	0.35	**7**

	S. typhle	*N. ophidion*
S. typhle	**8**	0.67
N. ophidion	0.14	**7**

Table 7a Comparison of parasite guild communities – interguild values: Soerensen (above) and Renkonen indices (below). Parasite species numbers of the guild are indicated

	Gobiidae	Gaster-osteidae	Syngna-thidae	Zoarcidae
Gobiidae	**21**	0.56	0.39	0.56
Gasterosteidae	0.01	**25**	0.46	0.44
Syngnathidae	0.10	0	**10**	0.67
Zoarcidae	0.11	0.17	0.11	**11**

Table 7b Comparison of parasite guild communities – infraguild values

	Common species (*n*)	Common species (%)	Soerensen index	Renkonen index
Gobiidae	5	0.24	0.59	0.38
Gasterosteidae	7	0.24	0.40	0.23
Syngnathidae	5	0.62	0.62	0.14

phenomenon that is also characteristic of microphallid digeneans: they do not leave their first intermediate hosts (Table 8). The great differences observed in the prevalence of *C. concavum* and *C. lingua* between the first and second intermediate host were also remarkable. A similar result was recorded for the nematode *Hysterothylacium* sp. between the intermediate host and the final host.

The correlation of parasite prevalence with the total numbers of their hosts involved the host levels snails, benthic crustaceans, and fish. In snails we found a Poisson-like distribution, which is strengthened by the almost equivalent mean values and variance ($y = 4.2 \pm 5.1$; Fig. 2); the linear regression was not significant. The prevalence values recorded for parasites infesting two and six hosts were the highest, which allows the assumption of even a negative binomial distribution. The respective analysis of benthic crustacean parasites and their hosts resulted in a linear regression with a steep increase that did not quite reach significance ($0.1 > P > 0.05$; Fig. 3). However, it indicated that parasite generalists with four or five hosts attained the highest prevalence values (mean 20%). The distribution of fish parasites presented nonuniform results according to the respective site of origin. The distribution of parasites from the Salzhaff showed a linear regression with a steep increase that was significant ($P < 0.05$; Fig. 4). An exception might be found in the two-host-group, which displayed some high values, obviously due to specialists such as *Thersitina gasterostei* and *Magnibursatus caudofilamentosa*, which infested not only the main host at high levels of prevalence but also secondary

Table 8 Main hosts in the development cycles of some parasite species from the Salzhaff. Numbers represent the respectively highest prevalence

	Snails	Benthic crustaceans	Fish – interm. host	Fish – final host
Digenea				
	H. ulvae (2)			
C. concavum	*H. ventrosa* (1)		*P. microps* (99)	
C. lingua	*H. ulvae* (< 1)		*G. niger* (94)	
P. atomon	*L. saxatilis* (2)	*G. locusta* (31)		*Z. viviparus* (83)
A. timmi	*H. ulvae* (< 1)		*P. microps* (52)	*P. microps* (52)
	L. saxatilis (21)			
A. demeli	*Z. membranacea* (4)[a]			*P. minutus* (18)
B. cingulata	*H. ulvae* (1)			*P. pungitius* (25)
M. caudofilamentosa	*Z. membranacea* (17)			*G. aculeatus* (73)
A. balthicum	*H. ulvae* (6)		*S. typhle* (64)	*S. typhle* (64)
M. subdolum	*H. ventrosa* (2)[a]	*I. granulosa* (78)		
	H. ulvae (7)[a]			
M. claviformis	*H. ventrosa* (8)[a]	*G. salinus* (3)		
Levinseniella sp.	*H. ulvae* (3)	*G. locusta* (38)		
Nematoda				
Hysterothylacium sp.		*G. locusta* (1)		*Z. viviparus* (58)
A. arctica		*G. locusta* (17)		*Z. viviparus* (17)
Acanthocephala				
E. gadi		*G. zaddachi* (5)		*Z. viviparus* (8)

[a] These species are primary as well as secondary intermediate hosts

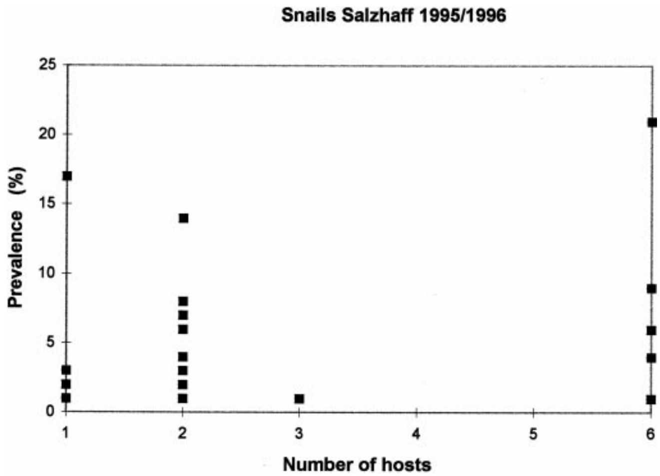


Fig. 2 Prevalence of six snail hosts from the Salzhaff area as correlated with the number of hosts a single parasite had infested. The significance level is >0.1

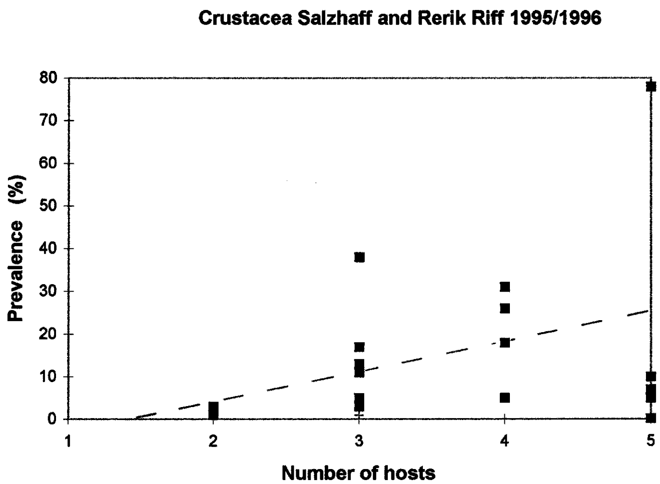


Fig. 3 Prevalence of five benthic crustacean hosts from the Salzhaff area as correlated with the number of hosts a single parasite had infested. The significance level is near 0.05; the *broken line* marks the course of regression

hosts at low degrees of prevalence. However, the mean prevalence of the two-host-group cut the regression line at a low level. The parasites of fish from the Rerik Riff showed a Poisson-like distribution ($y = 24.6 \pm 25.0$) because the two- and ten-host groups presented the highest prevalence values (Fig. 5); the linear regression was not significant ($P > 0.1$).

To obtain information about the pathways of transfer of parasites to the fish hosts we analyzed the frequency of prey species in four Gobiidae and three Gasterosteidae species. In the early spring, planktonic as well as benthic copepods dominated in most species, but Gammaridae played an even greater role in *G. niger* and *S. spinachia* (Figs. 6, 7). In the late spring the copepods were gradually substituted by polychaetes and chironomid larvae. Gammarids and chironomids also dominated in the summer, when *Idothea* was additionally important for *G. niger* and *S. spinachia* (Figs. 6, 7).

Discussion

Guild population

The concept of guild populations (Dietel 1997) and guild communities (Zander 1998) may have several advantages. The snails are composed of herbivorous and detritivorous species from different families of differing origin; the Hydrobiidae and Littorinidae are marine organisms and the Lymnaeidae and Neritidae are limnetic elements; these are local guilds that form an ensemble of benthic grazers. All species investigated in this study behaved as hosts in the same manner; prevalence values that were produced only by digeneans were low but the corresponding levels of intensity were extremely high. This was obvious in the case of *Littorina littorea*, whose numbers were too small for us to find a low rate of infestation, as did Reimer (1995) in the Salzhaff.

Benthic peracarid crustaceans are also herbivorous and detritivorous, and some isopods can additionally be scavengers. The idotheids and gammarids are also local guilds that can be summed up as an ensemble. Whereas gammarids are especially abundant on filamentous algae such as *Ceramium*, *Ectocarpus*, or *Enteromorpha*, *Idothea* spp. are instead found on *Fucus* or *Zostera* (Anders and Möller 1983; Schiro 1993; Nordhaus 1998; Böhme 1999). A special difference may lie in the vertical distribution of *I. granulosa*, which is found mostly in the shallow Salzhaff, and *I. balthica*, which may exist in shallow as well as deeper environments (Dietel 1997). However, deeper localities such as the Rerik Riff indicate a lower degree of infestation by *I. balthica* and by *Gammarus locusta* and *G. salinus*.

The investigated fish are members of four families that are respective local guilds and may form an ensemble of feeders on crustaceans from bottom water as well as free water. Adult gobies live on the bottom, the exception being *Gobiusculus flavescens*. Zander (1994) has found that the prey organisms of five goby species are identical during distinct seasons but differ during other seasons. The present study reveals that the food spectrum of the suprabenthic *G. flavescens* includes a considerable number of benthic gammarids, but not chironomids, as in other gobies. The stickleback species conform with regard to their suprabenthic way of life, preferring gammarids and chironomids; *Spinachia spinachia* differs slightly from the other two species in that it feeds only seldom on copepods. The two sea-needle species are characteristic of the mesophytic environment and feed predominantly on suprabenthic mysids or benthic crustaceans from the plants. The presence of the digenean *Acanthostomum balthicum* in *Syngnathus typhle* indicates that this sea needle also preys on smaller fish, which are intermediate hosts for the former. In contrast, *Zoarces viviparus* is not small like the other species investigated, growing as large as 30 cm. It moves by winding on the substrate and is a characteristic benthic feeder of gammarids and isopods (Zander 1991).

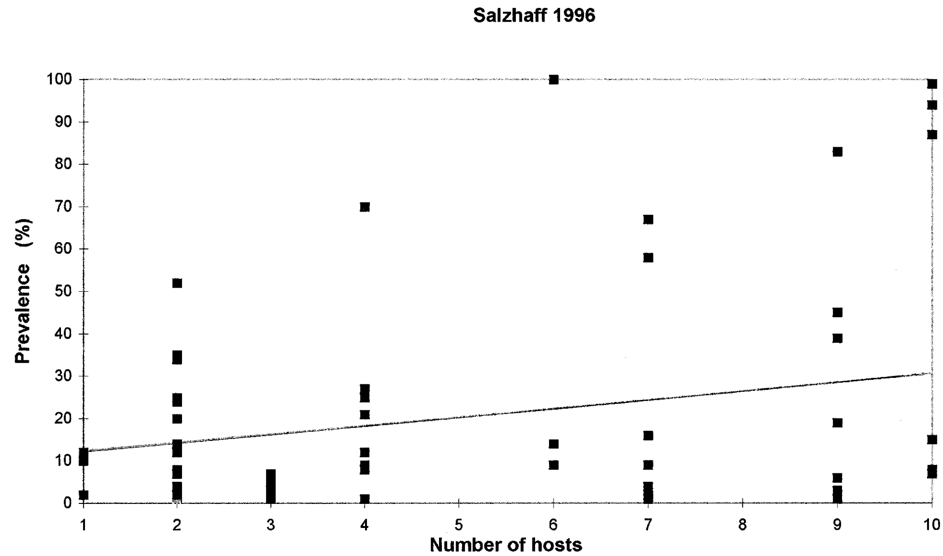


Fig. 4 Prevalence of ten fish hosts from the entire Salzhaff as correlated with the number of hosts a single parasite had infested. The significance level is <0.05; the *solid line* marks the course of regression

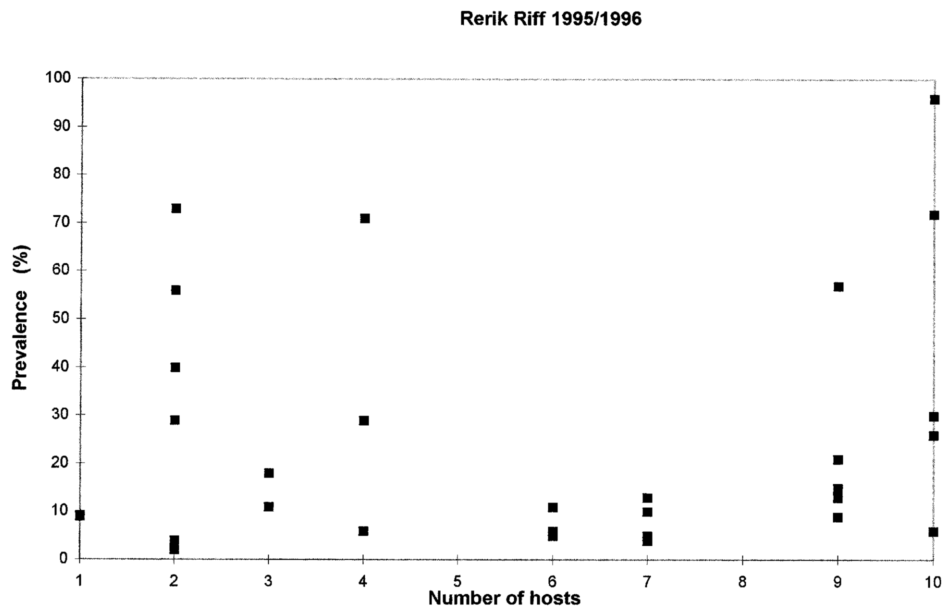


Fig. 5 Prevalence of ten fish hosts from the Rerik-Riff as correlated with the number of hosts a single parasite had infested. The significance level is >0.1

The species identity agreed, at least within gobies, to an almost moderate degree, though the numbers and proportions of common parasite species detected in Gobiidae and Gasterosteidae were relatively low. In contrast, the value recorded for syngnathids was high, obviously due to the paucity of members of this guild. However, this guild showed the lowest values for dominance identity, which may indicate divergent evolutionary pathways for the two sea needles with regard to resistance against different parasites. Their intraguild values were mostly greater than those recorded for different guilds, the only exception being the gasterosteids as compared with the syngnathids. The reason for this exception may lie in several similarities found between special members of these guilds, i.e., between *G. aculeatus* and *S. typhle*.

Guild community

Because the ensembles of snails, benthic crustaceans, and fish present at least three different host levels for parasites, they may provide a good overview of the parasite fauna of the Salzhaff area without the investigator's being forced to analyze the supracommunity, which would require considerably greater effort than the analysis of selected guilds. Comparisons of guild populations can indicate the grades of specificity of different guild members by placing emphasis on the main host. The guild community may enable clarification of the dominant parasites and may describe the distribution of specialists versus generalists in an ecosystem along the axis of the numbers of hosts within a guild.

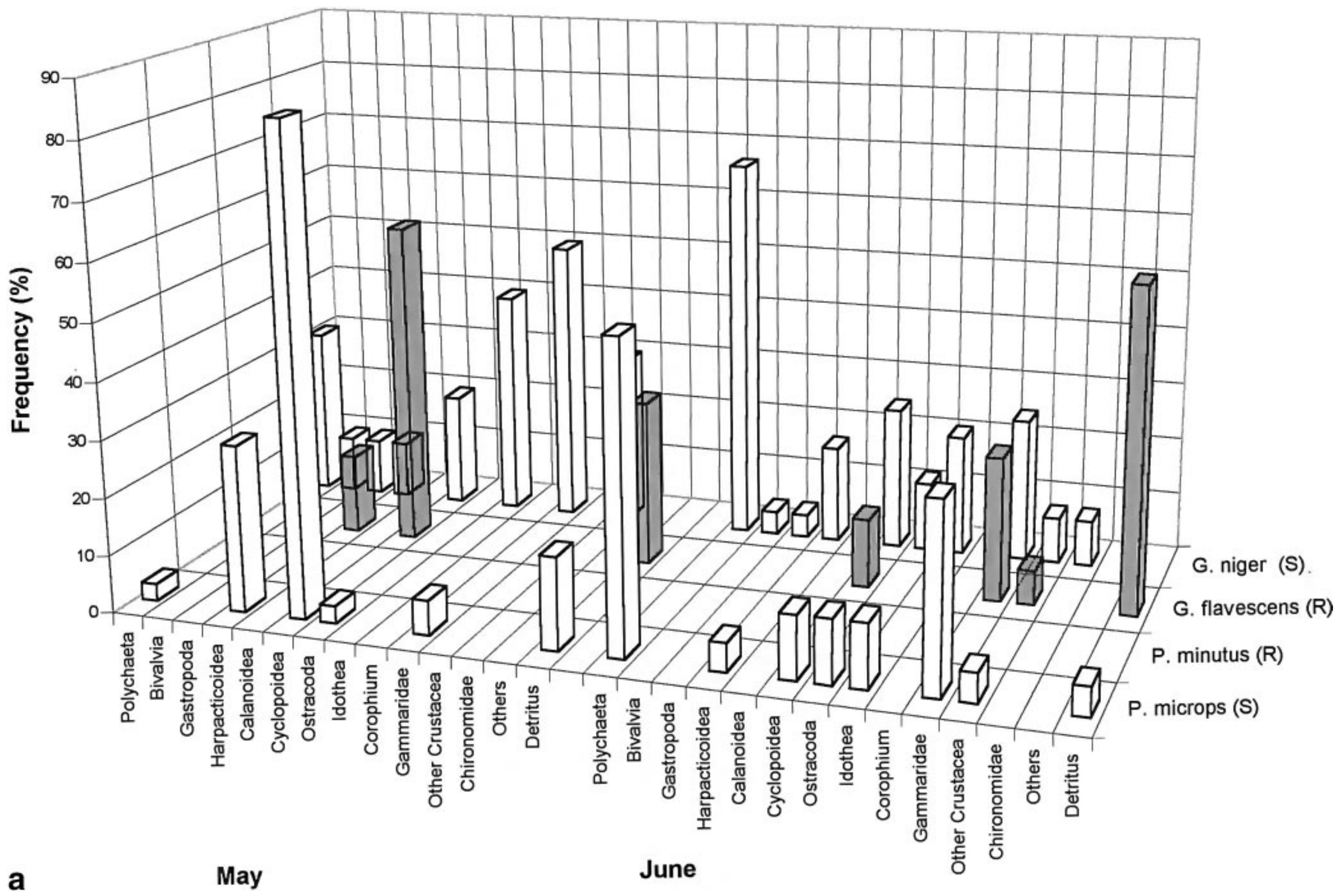
The high population densities of *Hydrobia* spp. imply a high infestation potential, which can reach as many as

480 infested mud snails/m^2; most of these species harbor the bird digenean *Microphallus claviformis*. The parasites may produce 20–100 cercariae every day and, in spite of great losses, these are sufficient for infestation of the second intermediate hosts at high degrees of prevalence. Strohbach (1999) also found high values in the muddy environment off Westerbergen (Kiel Bight), where *H. ventrosa* dominated as the host and *Asymphylodora demeli* and *Maritrema subdolum* were the dominant parasites. In the sandy bottoms of Dahmeshöved (Lübeck Bight), where *H. ulvae* dominated over *H. ventrosa*, the infestation densities were clearly lower (Strohbach 1999). The local differences observed in the presence of major parasite species may mainly depend on the composition of sediments, which influence the composition of the snail communities.

The density and infestation density of benthic crustaceans are more difficult to compare due to the different environments involved. Strohbach (1999) found a maximum of 71,800 benthic gammarids/m^2 in a shallow mussel belt off Dahmeshöved (Lübeck Bight) and observed 7,600/m^2 off Blank Eck (Kiel Bight). Skroblies (1998) reported detecting 75 gammarids and 280 idotheans per 100 g dry weight (corresponding to an area of 1 m^2) in *Fucus vesiculosus* and 50 gammarids and 225 idotheans per 100 g dry weight in *Enteromorpha intestinalis*. The corresponding values reported from the *Zostera* substrate of the Salzhaff (Dietel 1997) are considerably lower than the results recorded by Strohbach (1999). Skroblies (1998) found *I. chelipes*, *G. locusta*, and *G. salinus* to be the most important hosts and determined *M. subdolum*, *Levinseniella brachysoma*, and *Podocotyle atomon* to be the most important parasites, which could attain prevalence values exceeding 60%. Hence, infestation densities of *M. subdolum* can attain >3,500/m^2 only in *I. chelipes*, as in the Westerbergen environment, which was therefore characterized by Skroblies (1998) as an epidemiotope in the sense of Lauckner (1994).

Quantitative analysis of the importance of parasites was especially propagated by Holmes and Price (1986) and Holmes (1991), who created the core-/satellite-species concept for this group of organisms. The effect of parasites should be judged, first, according to the host population and, second, according to the host community; these correspond to the component population, the guild population, and the suprapopulation. Holmes (1991) fixed core species at prevalence values of >60% and challenged that the prevalence and intensity must be positive correlated. The use of abundance as calculated in the present investigation seems to be very advantageous because it regards the two above-mentioned pa-

Fig. 6a, b Frequency analysis of the food spectrum of four gobiid species. **a** Results obtained during May and June of 1996. **b** Results obtained during August and September of 1996



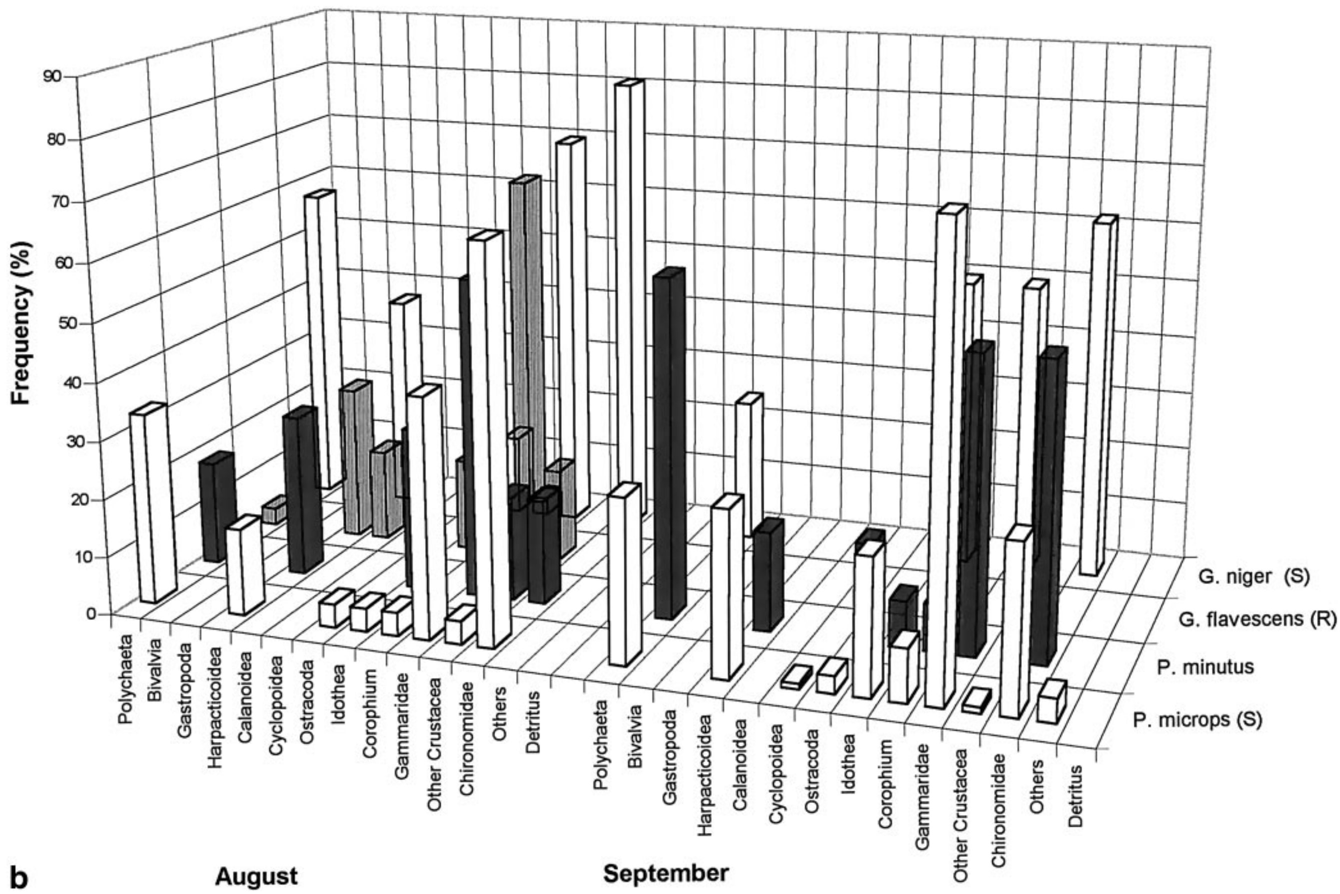
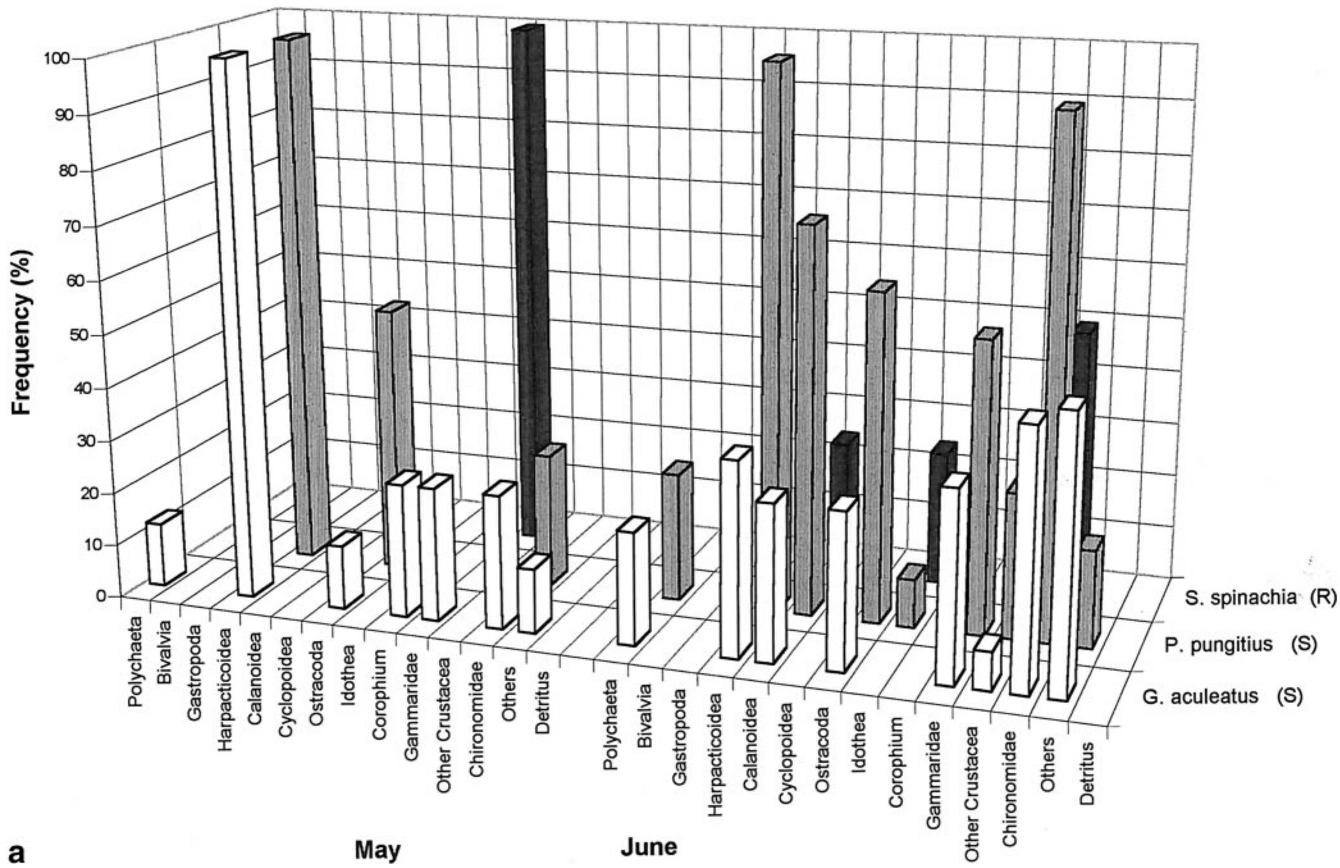


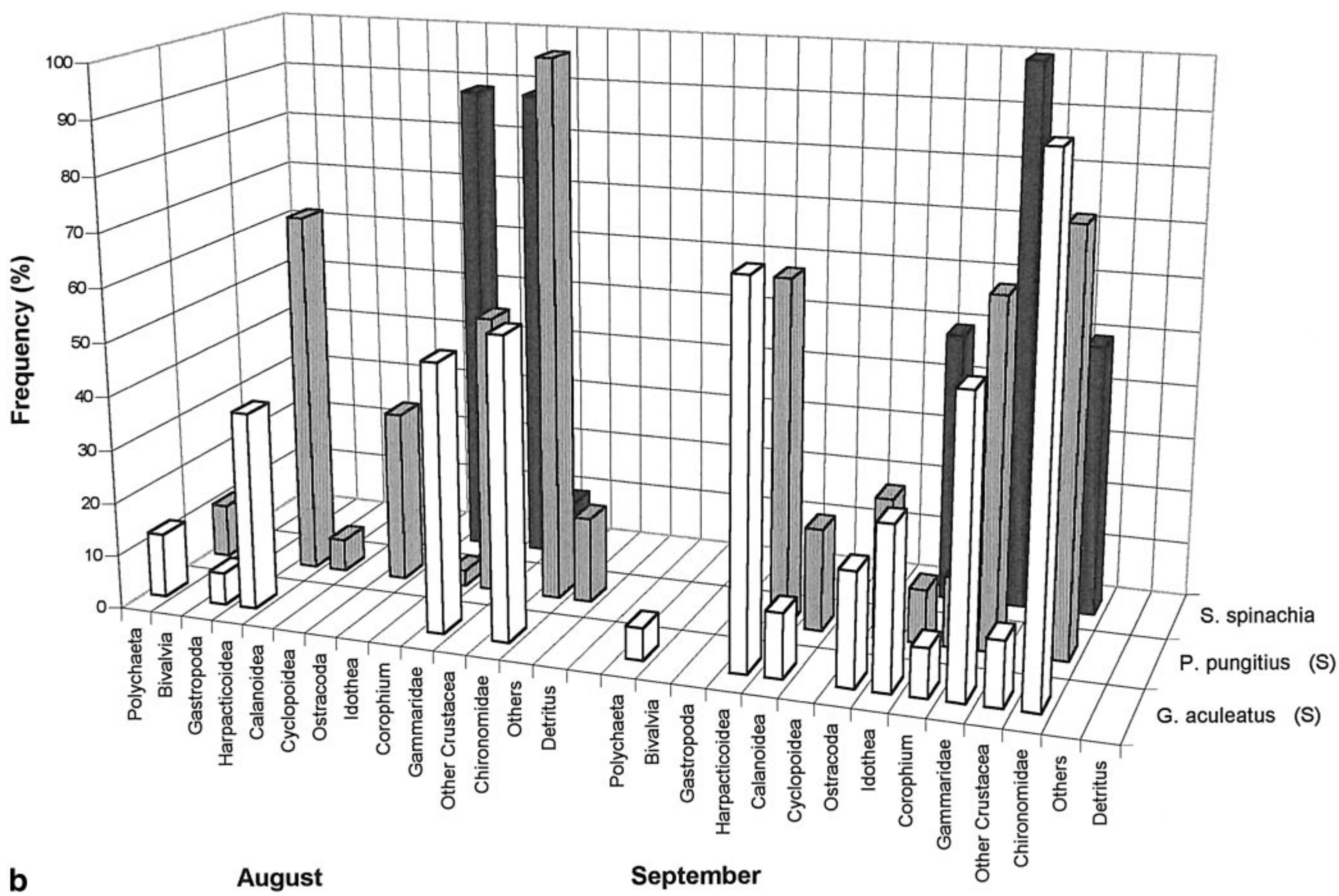
Fig. 6b

rameters simultaneously. The limit of an abundance value of 2 for core species demands, e. g., a prevalence of 60% and a minimal intensity of 3.4, which seems to be a proper value. It is also possible that some core species have prevalence values lower than 60% but higher levels of intensity. Thus, other host-parasite combinations with a prevalence of 60% cannot surpass the satellite-species level of 0.6 abundance when the intensity value is only 1. The problem of differing body sizes among parasites is clearly revealed in the group of rare species because it also includes some cestodes, which belong to the megaparasites. Some of them can attain one-third of the host's body weight and must have considerable influence on the host specimen and population. Their status as only rare species must therefore be revised.

Another decisive factor from which the importance of parasites can be judged is the harm they cause to the host. The majority of core and secondary species are inactive metacercarian cysts. These can lead to restriction of mobility, especially when the pectoral fins are heavily infested, as was the case in *Gobius niger* parasitized by *Cryptocotyle* spp. According to Shchepkina (1981), metacercariae of *C. concavum* are responsible for the winter mortality of *G. melanostomus*. The cercariae of digeneans can kill fish larvae when they try to penetrate them (Maillard et al. 1980; Lauckner 1984). Also, gut-dwelling parasites, which are mostly absorbers of digestive juice, were abundant among core species. These represented the most abundant category on the satellite-species level. The eelpout *Z. viviparus* is the most receptive host because it can accumulate them due to its large size and longevity (Zander 1991). Gill parasites and organisms that influence the function of the eyes or brain are present in all categories. Megaparasites such as *Schistocephalus* spp. cause deterioration of the swimming performance, reduction in the weight of the liver, displacement of the heart and liver, and inhibition of gonad maturation (Arme and Owen 1967) as well as inducing changes in behavior that make the hosts more available to fish-preying final hosts (Milinski 1985).

Surprisingly, in snails a despecialization of parasites was ascertained that followed the trend in brackish waters that had been found in the secondary hosts of the cestode *S. solidus*, which in the Baltic infests not only *Gasterosteus aculeatus*, as in fresh water, but also several goby species (Zander 1998). Though snails are very specific digenean hosts in fresh and marine waters, in the Salzhaff as many as six diverse snail species were infested by *A. demeli*, as were three snail species by *Psilochasmus oxyuris*. This is partially the result of an additional infestation by cercariae, which are less specific than miracidia. However, the parasites of crustaceans were generalists but their levels of prevalence differed clearly between the Salzhaff and the deeper Rerik Riff, obvi-


Frequency (%)
S. spinachia (R)
P. pungitius (S)
G. aculeatus (S)
Polychaeta
Bivalvia
Gastropoda
Harpacticoidea
Calanoidea
Cyclopoidea
Ostracoda
Idothea
Corophium
Gammaridae
Other Crustacea
Chironomidae
Others
Detritus
a
May
June


Frequency (%)
S. spinachia
P. pungitius (S)
G. aculeatus (S)
Polychaeta
Bivalvia
Gastropoda
Harpacticoidea
Calanoidea
Cyclopoidea
Ostracoda
Idothea
Corophium
Gammaridae
Other Crustacea
Chironomidae
Others
Detritus
b
August
September

◀

Fig. 7a, b Frequency analysis of the food spectrum of three gasterosteid species. **a** Results obtained during May and June of 1996. **b** Results obtained during August and September of 1996

ously due to the decreasing vertical distribution of larval parasites as indicated by *Idothea* spp.

The trend of parasites to have main hosts and by-hosts was especially apparent in fish. *Thersitina gasterostei* and *Magnibursatus caudofilamentosa* or *A. timmi* and *Apatemon gracilis* are not simply restricted to *G. aculeatus* or to *Pomatoschistus microps*, respectively, but also appear in other stickleback or goby species, albeit at far lower levels of prevalence. However, not all parasites infesting one host or a few hosts are specialists; they may also be generalists such as the acanthocephalans. This phenomenon may be attributable to the rare appearance of these parasites in Salzhaff fish that was also observed in crustaceans and may lead to a special threshold for infestation.

Therefore, the dispersion of prevalence values in fish with regard to their corresponding host numbers can result in a random distribution, as in the Rerik Riff, or an increasing line, as in the Salzhaff. In the Rerik Riff, specialists dominate only in a few hosts, as do generalists in many hosts. In the Salzhaff, generalists prevail that can attain low as well as high values of prevalence (*P. atomon*, *A. demeli*, *C. concavum*). The intermediate scale (5–6 hosts) presented mostly low levels of prevalence. Considering that parasite specialists are more sensitive to environmental stress, such dispersion patterns are well suited to indicate the status of the respective ecosystem. It is not surprising that the corresponding regressions of snails, which are generally specialists, followed the pattern of Rerik Riff fish, whereas the dispersion of benthic crustaceans, which are rather generalist hosts, followed that of Salzhaff fish. According to Zander and Kesting (1996) and Zander (1999), the higher the eutrophication grade, the steeper the slope of the correlation. Obviously, the water exchange is greater in the free Baltic at the Rerik Riff than in the semienclosed Salzhaff.

Suprapopulation and community

The observed reduction in free-living cercariae of several Digenea implies a greater importance for infestation by prey. The prey spectrum of gobiid and gasterosteid species includes many intermediate hosts, which may transfer larval parasite stages; gammarids and idotheids are very important prey organisms that harbored several digeneans, acanthocephalans, and nematodes. The role of copepods, polychaetes, and chironomid larvae, which are frequently also the prey of gobies and sticklebacks, in the Salzhaff is not yet clear because these were not investigated parasitologically. It is well known that calanoid and cyclopoid copepods can harbor cestode procercoids as well as hemiurud metacercariae (Reimer 1970; Gollasch and Zander 1995; Strohbach 1999), and harpacticoids can harbor metacercariae of *M. caudofilamentosa*. Nereid polychaetes are neoteneous hosts of *A. demeli* (Reimer 1973), but only a *P. microps* caught in 1997 in the Salzhaff harbored an ingested nereid together with 11 cysts of *A. demeli*. It should be assumed that the ingestion of gastropods of the genus *Hydrobia* may cause the presence of microphallid metacercariae in fish; their chances of survival is also not yet clear. Unexpectedly, the levels of prevalence of *Hysterothylacium* sp. (probably *H. auctum*) in crustaceans were very low in comparison with other Baltic localities (Skroblies 1998; Strohbach 1999). This nematode was frequently found in *Z. viviparus*, which can accumulate extremely high numbers as previously found in a specimen from the Lübeck Bight (Zander 1991).

The high levels of prevalence observed for five microphallid species in snails and benthic crustaceans indicate that birds are very frequent visitors in the Salzhaff. These, as well as four other bird digeneans that are found there only in snails, increase the number of allogenic parasites that have been found in fish hosts alone (Zander et al. 1999). In summation, 20 (45%) allogenic and 24 (55%) autogenic parasite species were found in the Salzhaff area. According to Reimer (unpublished data), who investigated parasites of cod, eel, and flounder as well as those of bivalves and polychaetes, as many as 26 allogenic (34%) and 51 autogenic (66%) parasite species exist in the Salzhaff. This may indicate a relative advantage in terms of environmental quality according to the criteria of Esch et al. (1988). Zander and Kesting (1996) found an even better situation in a Kiel Bight locality, where the parasite community of gobies showed lower species numbers than did that in a more stressed locality of Lübeck Bight (Zander 1999). However, the oxygen content in the Salzhaff and Rerik Riff indicated undersaturation on several occasions and revealed a high biological oxygen demand, which is a valuable measure of eutrophication. Its degree is especially high due to the influx of phosphorus and nitrogen into the Salzhaff area from heavily polluted tributaries (Köhn et al. 1991; Gosselck and von Weber 1997).

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