ORIGINAL PAPER

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Four-year monitoring of parasite communities of the southwest Baltic

III. Parasite species diversity and applicability of monitoring

Abstract The parasite infrapopulations of five goby species (*Pomatoschistus minutus*, *P. pictus*, *P. microps*, *Gobiusculus flavescens* and *Gobius niger*) were investigated during spring, summer and autumn of the years 1997–2000. In total, 34 parasite species were found: 17 Digenea, 6 Nematoda, 5 Cestoda, 3 Acanthocephala, 2 Protozoa, and 1 Monogenea. The dominant parasites were the digeneans *Podocotyle atomon* and *Cryptocotyle concavum*, which represent different ecological groups in terms of their modes of transmission, either indirectly by prey or directly by larvae. The relationship between the parasite *Cryptocotyle concavum* and the host *P. microps* is a special one which results in a mean intensity of several hundred cysts (max. 1,329) which settle in the kidney. The diversity of the parasite component community was highest in autumn, but low in spring and summer, with the exception of *P. microps* for which high values were already found in spring when direct parasites were disregarded. These results depend on the respective seasonal variation in species, some of which occur in huge numbers in some hosts. The diversity of the prey parasite assemblage is higher in *Pomatoschistus microps* and *Gobius niger* than in the whole parasite spectrum; the other hosts present the opposite trend. A combination of the island theory of biogeography as modified for parasite infection with the theory of screens and filters leads to a model which considers three handicaps or distances for parasite colonisation: genetic, phylogenetic and ecological. Long-term investigations, as performed here over a time-span of 4 years, can detect more than 80% of parasite species in single hosts after 3 years, and in the whole goby guild after 2 years. Long-term investigations can be useful for finding rare parasites, in analysing parasite diversity, and for determining the seasonality of parasites.

Introduction

In part I of this series, the investigations were focused on the structure and dynamics of the parasite communities which infected populations of five gobiid fish species from the southwestern Baltic (Zander 2003). Hosts were the small, short-lived species *Pomatoschistus microps*, *P. minutus*, *P. pictus*, *Gobiusculus flavescens* and *Gobius niger*. In total, 34 parasite species were found, but only a few of these were recurrently dominant in the hosts. The digeneans *Cryptocotyle concavum* and *Podocotyle atomon* were, at any season, core species in most hosts; the digenean specialists *Apatemon gracilis* and *Aphalloides timmi* were additionally abundant in *Pomatoschistus microps*, and *Podocotyle atomon* was replaced in *Gobius niger* by the nematode *Hysterothylacium* sp. The parasite communities revealed strong changes within the years 1997–2000 as well as between seasons, only *G. niger* presented rather homogeneous communities. The dominant parasites attained their maximum values at different seasons. These were influenced by the respective infection densities of the intermediate hosts. Therefore, it was concluded that the composition of parasite component communities was predominantly determined by the respective ways of life of the parasites, as well as of host species, and especially of their feeding habits (Zander 2003).

Part II (Zander 2004) focused on the structure and dynamics of infracommunities of the same goby hosts. Values of intensities peaked in summer and were lowest in autumn. Six parasite species, and especially *Podocotyle atomon* and *C. concavum*, decisively structured the infracommunities. In consequence, rare parasite species can settle only by chance. The number of parasite species usually increased with the growth of their short-living hosts.

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The present study deals with the structure and extent of infrapopulations, which can reveal the diversity of communities. Diversity indices may indicate a successive infection by an accumulation or aggregation of some species in parasite component communities during the course of a year. Therefore, it is of special interest in the present investigation to analyse the diversity differences of two groups of parasites, the direct and indirect (transferred by prey) species.

Finally, in consequence of the results of all parts of these investigations, the applicability of such long-term studies of parasite communities should be valued. Formerly, at least 2 years of sampling were necessary for determining the maximum number of parasite species in a component community (Zander et al. 1993). Whether a single host species, a group of species or the whole host community is better suited for monitoring may depend on the repective environmental conditions (Zander and Reimer 2002).

Materials and methods

As already described in part I (Zander 2003), the areas of investigation lie on the German Baltic coast and comprise: (1) the upper littoral of the Lübeck Bight at the lighthouse of Dahmeshöved, and (2) the shallow beach of the Salzhaff in northwestern Mecklenburg. Both localities lie in the mixomesohaline range of salinity. Dahmeshöved was visited in spring (May or June), summer (July) and autumn (September) in the years 1997–2000. At these times, the gobies *Pomatoschistus minutus*, *P. pictus*, *Gobiusculus flavescens* and *Gobius niger* were present. The Salzhaff was visited only in spring 1997–2000 in order to obtain specimens of *P. microps* which is very abundant there. In winter, the gobies emigrate into deeper water.

The numbers of caught fish are identical to those in part I and are presented there in Table 1 (Zander 2003). They were caught in the sublittoral of Dahmeshöved in a boulder and pebble ground of 3–6 m depth, about 200 m from the beach, and on a 0.2–0.5 m deep sand bottom at the beach at Salzhaff. The fish were caught in Dahmeshöved by means of SCUBA using a round hand net of 0.4 m in diameter and 1 mm mesh size. They were caught in the Salzhaff by a hand net with the same diameter and mesh size but with an even, strengthened margin.

In order to obtain the parasites, the fish were inspected externally, including the mouth and gill chamber, and were opened ventrally in order to remove the inner organs. The liver was squeezed between slides, the gonads teased apart with needles and the gut prepared by an incision along its total length. Its contents were then removed and carefully checked for parasites and ingested prey. Finally, the body cavity and kidney were inspected. The parasites were determined mostly to the species level, which was facilitated by clearing in lactate acid

The nomenclature follows the levels of communities and populations of Bush et al. (1997) and Zander (1997): infrapopulation indicates individuals of a parasite species in a single host; component population indicates individuals of a parasite species in a host population; guild population indicates individuals of a parasite species in a group of ecologically similar hosts; suprapopulation indicates individuals of a parasite species in all intermediate and final hosts. Direct parasites are those species which search actively for their host, whereas indirect parasites are transferred via the prey, which is an intermediate host.

Species richness is simply the number of species (*S*) found in a host population. Diversity describes the relationships of the ratios of all parasites found in a host population. It is calculated here using the Shannon-Wiener index (Hs), based on abundances and expressed as evenness (or equitability) which is the quotient of Hs and ln *S* (= maximum possible value of Hs):

$$E = -\sum (p_i \times \ln p_i)/\ln S \qquad (1)$$

(where p_i = ratio of parasite i in a host population).

Evenness values were calculated for the individual years between 1997 and 2000, as well as seasons, which are summarised from all 4 years. Evenness values > 0.6 mean a greater part of the homogeneity, of > 0.7 a high homogeneity. The χ^2-test and Student's *t*-tests were used for statistical comparisons.

Results

Parasite spectrum

All parasite species found in the goby hosts are listed in Table 1: 2 species of Protozoa, 1 of Monogenea, 17 of Digenea, 5 of Cestoda, 6 of Nematoda and 3 of Acanthocephala were found. Direct infection by larval stages is characteristic for 11 parasite species, most (23 species) are transferred indirectly by prey.
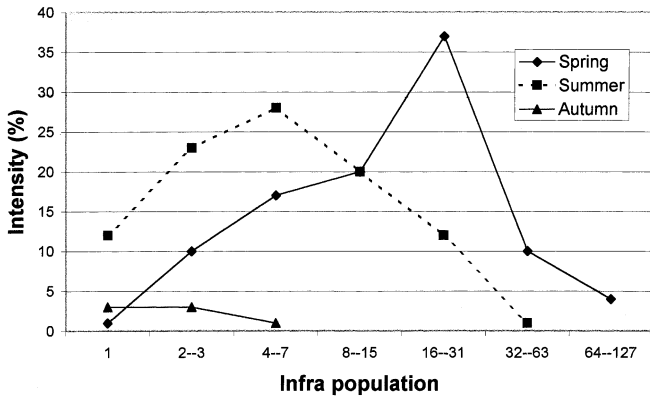
Infrapopulations

Only a few parasite species were so abundant that infrapopulations could be analysed. *Cryptocotyle concavum* was most abundant in *Pomatoschistus microps* and *P. pictus*, *Podocotyle atomon* in *P. pictus*, *P. minutus* and *Gobiusculus flavescens*. Additionally, *Aphalloides timmi* and *Apatemon gracilis* were of greater importance in *P. microps* (Figs. 1, 2, 3, 4, 5). The infrapopulation of *Podocotyle atomon* was largest in spring when the maximum values were also greatest; these values decreased in summer and become unimportant in autumn (Figs. 1, 2, 3). *C. concavum*, in contrast, attained its maximum values in *P. pictus* in autumn following very low levels in spring and low levels in summer (Fig. 4). The infection of *P. microps* by *C. concavum* already

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Table 1 List of parasites found in five goby host species from Dahmeshöved from 1997 and 2000. *D* Parasites which infect directly, *P* parasites which infect indirectly by prey organisms. *Ligula pawslovskii* was formerly misidentified as *Schistocephalus solidus* (I thank Prof. Dr. Tomas Scholz, Ceske Budejovice, Czech Republic, for having clarified this problem)
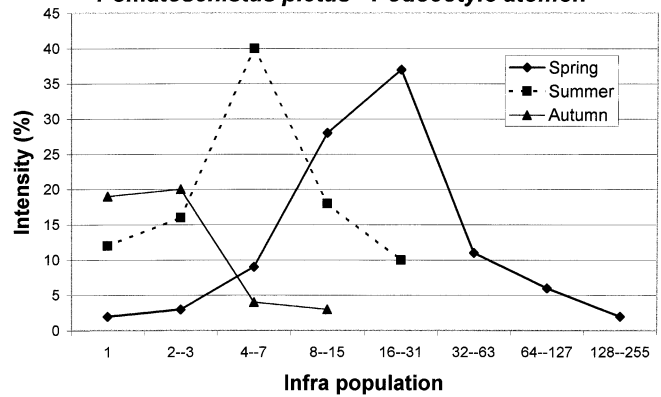
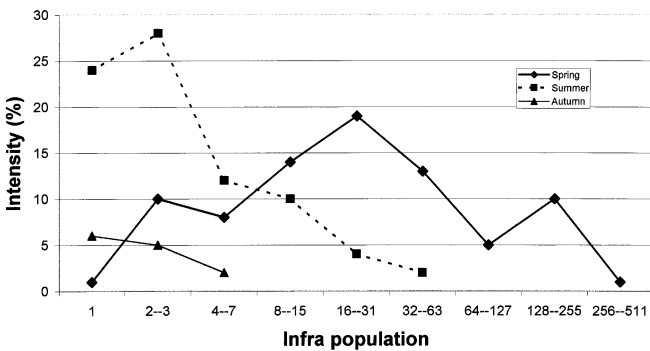|		D/P			D/P
Protozoa	*Trichodina* sp.	D	Cestoda	*Ligula pawslovskii*	P
	Myxozoa indet.	D		*Ligula* sp.	P
Monogenea	*Gyrodactylus* sp.	D		*Bothriocephalus sp.*	P
Digenea	*Cryptocotyle concavum*	D		*Proteocephalus percae*	P
	C. lingua	D		Procercoid larvae	P
	Apatemon gracilis	D	Nematoda	*Hysterothylacium* sp.	P
	Acanthostomum balthicum	D		*Contracaecum* sp.	P
	Podocotyle atomon	P		*Anisakis simplex*	P
	Plagioporus alacer	P		*Cucullanellus minutus*	P
	Aphalloides timmi	P		*Raphidascaris acus*	P
	Asymphylodora demeli	P		*Ascarophis arctica*	P
	Brachyphallus crenatus	P	Acanthocephala	*Acanthocephalus anguillae*	P
	Derogenes varicus	P		*Echinorhynchus gadi*	P
	Hemiurus communis	P		*Pomphorhynchus laevis*	P
	Lecithaster confusus	P			
	L. gibbosus	P			
	Magnibursatus caudofilimentosa	P			
	Diplostomum spathaceum	P			
	Tylodelphis podicipina	P			
	Cardiocephalus longicollis	P			

Fig. 1 Infrapopulation of *Podocotyle atomon* in *Gobiusculus flavescens* over three seasons during 1997–2000. The numbers of parasites are arranged along the *x*-axis logarithmically to the base 2
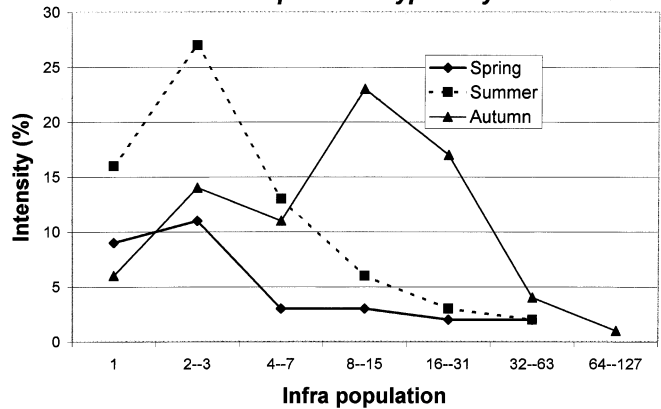

Fig. 3 Infrapopulation of *Podocotyle atomon* in *Pomatoschistus pictus* over three seasons during 1997–2000. The numbers of parasites are arranged along the *x*-axis logarithmically to the base 2


Fig. 2 Infrapopulation of *Podocotyle atomon* in *Pomatoschistus minutus* over three seasons during 1997–2000. The numbers of parasites are arranged along the *x*-axis logarithmically to the base 2

Fig. 4 Infrapopulation of *Cryptocotyle concavum* in *Pomatoschistus pictus* over three seasons during 1997–2000. The numbers of parasites are arranged along the *x*-axis logarithmically to the base 2

Fig. 5 Infrapopulation of four parasite species in *Pomatoschistus microps* over spring during 1997–2000. The numbers of parasites are arranged along the *x*-axis logarithmically to the base 2
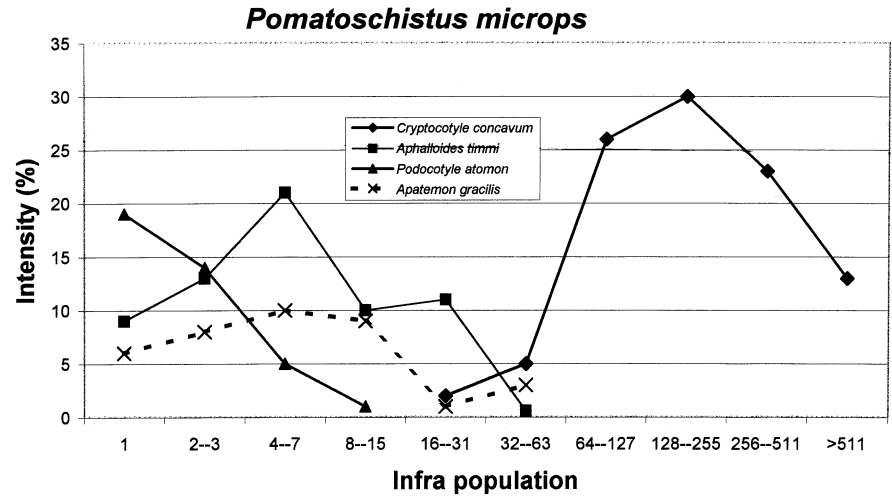
Table 2 χ^2 test to determine the association between the seasonal values of selected parasite infrapopulations from 1997 to 2000. Probability values (*P*) of <0.05 are considered to present strong alterations within the investigated years

Host species	Parasite species	Season	Mean	±SD	χ^2	*P*
Pomatoschistus microps	*Cryptocotyle concavum*	Spring	277.2	249.0	315.3	<0.001
	Aphalloides timmi	Spring	7.9	7.8	11.4	0.01
	Apatemon gracilis	Spring	11.2	21.6	5.2	>0.05
	Podocotyle atomon	Spring	2.3	2.0	1.4	>0.1
Pomatoschistus minutus	*Podocotyle atomon*	Spring	15.7	20.3	284.9	<0.001
		Summer	4.9	7.0	24.2	<0.001
		Autumn	2.3	1.5	1.3	>0.1
Pomatoschistus pictus	*Podocotyle atomon*	Spring	26.5	33.2	78.4	<0.001
		Summer	4.2	3.1	0.3	>0.1
		Autumn	2.2	1.7	1.5	>0.1
	Cryptocotyle concavum	Spring	6.4	9.5	8.8	<0.05
		Summer	4.4	6.9	4.8	>0.1
		Autumn	13.4	17.5	12.5	<0.01
Gobiusculus flavescens	*Podocotyle atomon*	Spring	19.7	15.4	7.1	>0.05
		Summer	7.6	7.9	6.5	>0.05
		Autumn	1.1	0.3	0.03	>0.1

surpassed the values of all other hosts in spring. A maximum of 1,349 cysts was found in the kidney of a specimen (Fig. 5). However, *Podocotyle atomon* was present in *P. microps* only in low numbers and was still surpassed by *Apatomon gracilis* and especially *by Aphalloides timmi* (Fig. 5).

Lack of homogeneity was significant for several host-parasite systems when the respective seasons of the four

Fig. 6 The diversity of the parasite communities of five goby hosts from the southwest Baltic at different seasons during the years 1997–2000 expressed as evenness. The *numbers* mark the respective parasite species numbers. To the *left* are all parasites, to the *right* only prey (indirect) parasites
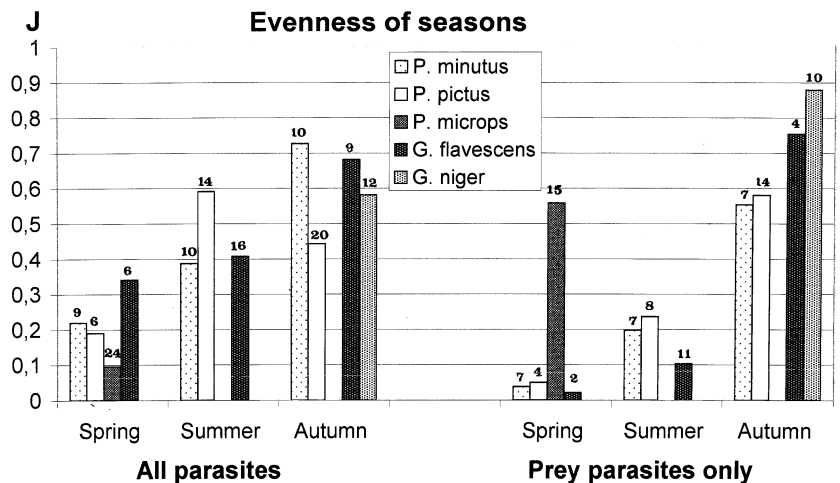
Fig. 7 The diversity of the parasite communities of five goby hosts from the southwest Baltic in the years 1997–2000 including three seasons, respectively, expressed as evenness. The *numbers* mark the respective parasite species numbers. To the *left* are all parasites, to the *right* only prey (indirect) parasites
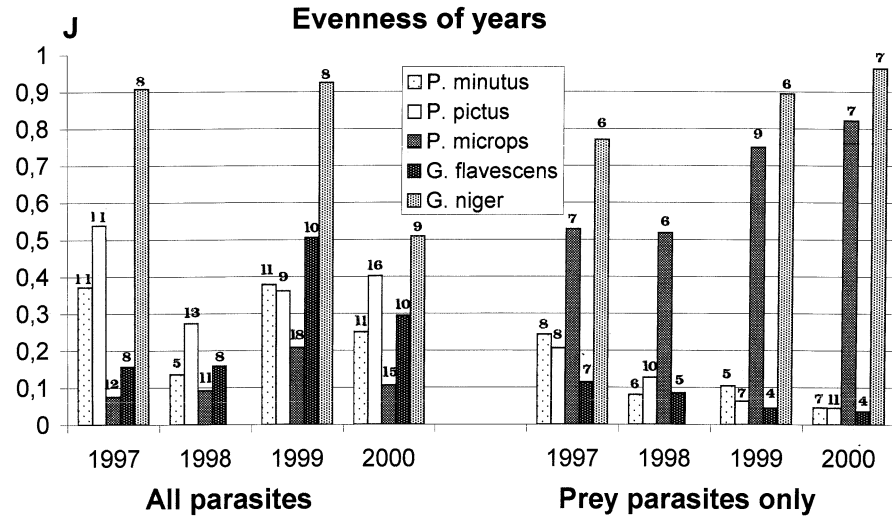
years of investigation were compiled (Table 2). No differences were found in the mean numbers of *Podocotyle atomon* in *G. flavescens* and partially in *Pomatoschistus pictus* and *P. minutus*. Obviously, all values from autumn, when this parasite is rare, appeared to be homogeneous. In contrast, *C. concavum* was the parasite which was rather homogeneous in *P. pictus* in summer. *Aphalloides timmi* and *Podocotyle atomon* were homogeneous in spring samples of *P. microps*, but *Apatemon gracilis* and *Podocotyle atomon* were not (Table 2).

Parasite species diversity

Diversity, expressed using evenness values, was calculated for the whole parasite community as well as separately for those parasites with indirect infection ("prey parasites") (Figs. 6, 7). Only *Gobiusculus flavescens* (summer) and *Pomatoschistus minutus* (autumn) surpassed the limit value of 0.6, whereas *P. pictus* and *Gobius niger* rarely attained this mark in summer and autumn. If only prey parasites were considered,

P. microps attained a value of 0.5 in spring, whereas no species surpassed a value of 0.3 in summer (Fig. 6). Under these premises, *Gobiusculus flavescens* and *Gobius niger* present a high level of homogeneity in autumn, whereas *P. pictus* remained below 0.6.

If single years were considered, only *Gobius niger* attained very high evenness values, in 1997 and 1999, and, if direct parasites were omitted, also in 2000 (Fig. 7). *P. microps* surpassed the limit of 0.6 in 1999 and 2000 if only prey parasites were considered. All other hosts attained low or even very low values. This is due to the restriction of samples from these hosts to spring (*P. microps*) or autumn (*G. niger*), whereas the other gobies were represented in three seasons. These also attained very low values when only prey parasites were considered.

Taking into consideration all parasites, the evenness values of single years for three seasons agreed in *Gobiusculus flavescens* and *P. pictus* but not in *P. minutus*, and differed if direct parasites were excluded (Table 3). If parasites from these three hosts were combined, no differences were found in the respective

Table 3 Relationship between parasite community diversity and the component and guild levels (*t*-test). The results are differentiated between the respective seasons over 4 years as well as between single years with three seasons. Probability values (*P*) of < 0.05 are considered to present greater relationship

Host	Evenness of seasons				Evenness of years			
	Mean	± SD	*t*	*P*	Mean	± SD	*t*	*P*
Pomatoschistus microps					0.65	0.13	9.8	< 0.01
Pomatoschistus minutus	0.26	0.21	2.1	> 0.1	0.12	0.07	3.5	0.05
Pomatoschistus pictus	0.29	0.22	2.3	> 0.1	0.11	0.06	8.2	< 0.05
Gobiusculus flavescens	0.29	0.33	1.5	> 0.1	0.07	0.03	4.4	< 0.05
Gobius niger					0.88	0.08	19.0	< 0.01
All hosts:								
Spring	0.36	0.12	5.2	< 0.05				
Summer	0.18	0.06	5.5	< 0.05				
Autumn	0.69	0.13	9.0	< 0.05				
All hosts:								
1997					0.27	0.15	3.5	< 0.05
1998					0.20	0.18	2.2	> 0.05
1999					0.24	0.29	1.6	> 0.1
2000					0.24	0.38	1.4	> 0.1

seasons over the 4 years. Combining the whole parasite spectrum over the course of 4 years, the characteristic values of the hosts mostly agreed, as did the values for single years; if direct parasites were excluded, the values disagreed for all three seasons of 1998, 1999 and 2000 (Table 3).

Pomatoschistus microps and *Gobius niger* showed a trend to increasing evenness if direct parasites were disregarded, whereas the other hosts showed decreasing values under this premise. This trend was observed for seasons as well as for years (Figs. 6, 7).

The number of parasite species (*S*) ranged between 6 and 24 over seasons and between 8 and 18 over years (Figs. 6, 7). Host species with higher values seemed to increase diversity indices when direct parasites were omitted. This was especially obvious in *P. microps* in spring but also in *P. pictus* in autumn. Exceptions to this trend were only found in summer (*P. pictus*, *Gobiusculus flavescens*). However, correlations were found neither between evenness and number of parasites nor between the ratios of direct to indirect parasite numbers. This result requires a more complex explanation for higher or lower values of these parameters.

Applicability of monitoring

The evaluation of parasite species numbers over the 4 years from 1997 to 2000 was performed using the additive method. In terms of their respective ratios, *Pomatoschistus pictus*, *P. microps* and *Gobiusculus flavescens* attainedat most 50% of all parasites found in the 1st year. *Gobius niger*, *P. minutus*, and especially the combined goby guild, surpassed this ratio (Fig. 8). In the 2nd year, more than 70% was attained by *P. pictus*, *P. minutus* and *Gobiusculus flavescens*, and more than 80% by the combined goby group from Dahmeshöved, and especially by the whole goby guild. The values for the 3rd year add mostly to more than 90%; only the ratios of *P. minutus* and *Gobius niger* were lower. *Gobius*

niger contributed no new parasite species to the guild in the course of any year. In *Gobiusculus flavescens*, the increase was finished in the 3rd year, whereas *Gobius niger* presented no new parasites in the 2nd year but a greater increase in the 4th. *P. minutus* was remarkable by a continual increase over all years.

Discussion

The present investigations covered a period of 4 years including three seasons. This conforms with former investigations at Lübeck and the Kiel Bight (Zander et al. 1993; Zander and Kesting 1996). The parasite species spectrum of the whole goby guild during the 1st and 2nd years surpassed that of all single component communities. This resulted in >80% parasites in guild communities in the 2nd year, whereas, with the exception of *Pomatoschistus pictus*, component communities only attained this limit after the 3rd year. One can, therefore, emphasise that guild communities must be analysed over at least 2 years, as more parasites are present than in single hosts, and, due to a greater host species spectrum, more rare parasites are found. But *P. microps*, which attained the greatest parasite number (24), clearly demonstrates the necessity for sampleing for longer than 2 years, at which time only 15 species were found. Therefore, recent short investigations of this host resulted in finding only 16 parasite species (Salzhaff, 2 years, Zander et al. 1999) or 14 (West Fehmarn, 1 year, Zander et al. 2002).

Sampling over several seasons was also of special advantage for detecting rare parasites. The presence of many parasites is restricted to distinct times. Thus, even the highly abundant *Podocotyle atomon* or *Cryptocotyle concavum* may be rare species in autumn and spring, respectively. Nevertheless, *C. concavum* already dominated the infracommunity of *P. microps* in spring, when other hosts had low (*P. pictus*) or very low abundance values (Zander 2004). The seasonal changes in *C. con-*

Fig. 8 The ratio of parasite species found yearly from 1997 to 2000 presented as an additive ratio. Considered are five single goby host species and two goby guilds—a combination of four species from Dahmeshöved and a combination of four species from Dahmeshöved with *Pomatoschistus microps* from Salzhaff
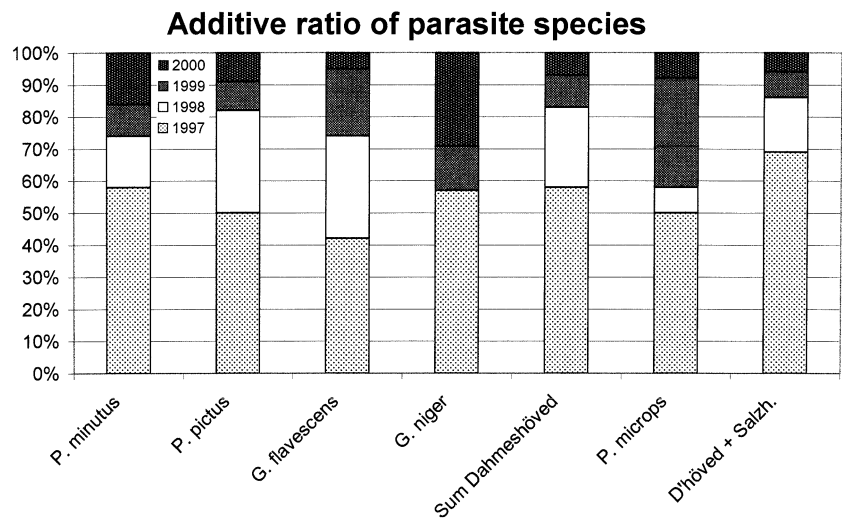
cavum in *P. microps* from the Salzhaff (Zander et al. 1999) revealed lower intensities in summer due to the massive appearance of the young of the year at this time, whereas in autumn, spring and late spring the intensities were similar. *G. niger* from the same locality had an infection maximum of this parasite in autumn, with a slight decrease in other seasons. This may not only be due to the seasonal appearance of young fish, but also to the presence of competing *C. lingua* which peaked in late spring. It is assumed that very heavy infections by both parasite metacercariae in the skin and fins, especially the pectoral fins, cause restricted mobility which make these fish easier prey for fish predators (Zander et al. 1999). On the other hand, low (*P. microps*) or almost lacking (*Gobius niger*) infection by *Podocotyle atomon* could be confirmed at this locality. The absence of *C. concavum* in *Gobiusculus flavescens* and *P. minutus* in autumn is a consequence of the suprabenthic life of these young gobies during this season, as they are hardly reached by cercariae. The adults of these species die off in summer, in contrast to *P. pictus* which spawn again in autumn (Zander 1994). Former investigations at Dahmeshöved and Blank Eck (Kiel Bight) revealed this trend, although the investigation time was shorter than in this study (Zander and Kesting 1996). Additionally, the availability of infective stages was also seasonally adjusted. For example, in the Schlei Fjord *Podocotyle atomon* metacercariae peak in benthic crustaceans in spring and *C. concavum* cercariae in *Hydrobia* snails in summer (Kesting et al. 1996). June is a month in which planktonic copepods are scarce, and all goby species prefer amphipods which are highly infected with *Podocotyle atomon* (Zander et al. 2002).

Judging the species diversity of parasite communities is a very complicated matter because such values depend not only on the ratios of parasite numbers but also on the number of species present. This may be the reason why the present results differ from those which were previously found in Dahmeshöved and the Kiel Bight (Zander and Kesting 1996). Thus, only *P. minutus* surpassed the threshold values of evenness (0.6) in 1992 and 1993 in Dahmeshöved, whereas in the Kiel Bight higher values were attained by gobies, with the exception of *Gobius niger*. This result was interpreted as being due to lower environmental stress near Blank Eck of the Kiel Bight (Zander and Kesting 1996). Obviously, the former results were influenced by the low numbers of parasites found in *P. pictus* (three or four) and *G. niger* (five or six), whereas the present results clearly show higher parasite species numbers. A further reason is that the intensity of parasites, even of *Podocotyle atomon* and *C. concavum*, was lower in 1992 and 1993, probably due to increasing environmental stress in the times thereafter. In both studies, evenness was significantly positively correlated with diversity; however, the number of parasite species in the present investigation is no longer significantly correlated with diversity. The differing results for diversity between the whole parasite spectrum and those parasites which are transferred by prey only

stresses the role of direct and indirect parasites. Direct parasites may be better suited to stabilising the parasite community of *P. minutus*, *P. pictus* and *Gobiusculus flavescens* in which prey parasites can be accumulated, whereas only infestation with direct parasites makes the communities of *P. microps* and *Gobius niger* rather instable. *G. niger* and *P. microps* are also the representatives of the goby guild which are mostly bottom dwelling. This is additionally influenced by the longer lifespan of *G. niger*, and may also be the decisive factor for the highly eutrophic Salzhaff environment from which the *P. microps* of this study originated. In this locality, the infection of *G. niger* by *C. concavum* and *C. lingua* was very high in the fins and skin (Zander et al. 1999), which argues for their accumulation over longer periods. Therefore, one can conclude that the most important elements for attaining the parasite diversity found in short-lived gobies are parasites which infect directly via their larvae.

Holmes and Price (1986) hypothesised that the infection of hosts by parasites is comparable with the colonisation of islands by invaders (MacArthur and Wilson 1967). Thus, the host immune system corresponds to the distance of islands to the mainland from which the invaders come, and the size of the host to island size. This can also be valid for short-lived hosts such as four of the five gobies species, and additionally for their intermediate hosts. These hosts are comparable to uninhabited islands where all organisms have become extinct after catastrophes or strong disturbances. As a consequence, the young of hosts should be at first colonised by r-selected organisms with a high reproductive rate and high population growth (Odum 1969). In addition, strong disturbance and high population growth are also agents which generally create low diversity (Huston 1979). Low values such as those found here are, therefore, in full accordance with this model. Specialist parasites are not always K-selected, but they can enrich the respective community with additional species beyond the host guild level. According to Poulin (1997), communities with specialists are richer in species than those with only generalists. This is confirmed here by *P. microps*, which is the only goby host with at least a specialist and a site specialist.

Parasites with complicated life cycles and multiple host changes, especially Digenea, Cestoda, Acanthocephala and Nematoda, may be compared with migrating species, e.g. anadromous and katadromous fish or birds of passage, which visit different ecosystems. According to Margalef (1963) these reproduce in less mature habitats (high P/B values) but can exist more successfully in mature habitats (low P/B values) which present greater diversity. However, parasites may grow until maturation in several hosts, and can survive as resting stages, e.g. as metacercaria, plerocercoids, L3 or acanthella in intermediate hosts. The Baltic gobies, which can be intermediate as well as final hosts, present high P/B values due to their small size and high reproductive ratio (Zander and Hagemann 1986); these values

Fig. 9 A model of parasite infection under the influence of three handicaps. *Above* Genetic distance is effective at the level of the component populations via the individual immune systems; the *arrows* mark the different availabilities of hosts by parasites. *Middle* Phylogenetic distance is effective at the level of the guild populations via the respective specific immune systems; additionally two handicaps are indicated—successful colonisation and maturation. The *arrows* mark the different availabilities of hosts by parasites. *Below* Ecological distance is effective at the level of the suprapopulations within a community via host characteristics such as life cycles and resource use; the ensembles (Fauth et al. 1996) represent the respective host group of a parasite life cycle, e.g. of a digenean; different intermediate host guilds guarantee a high infection possibility of final host guilds. The *arrows* mark the different availabilities of hosts by parasites
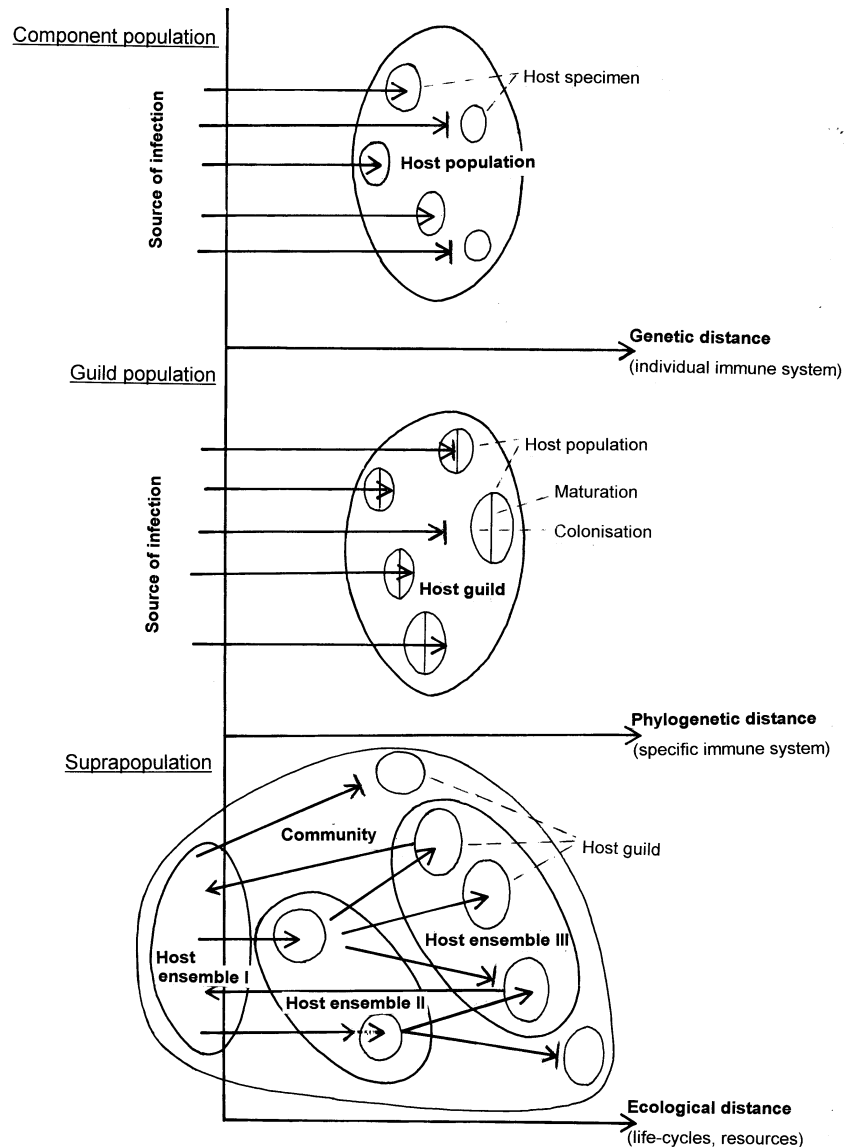
decrease in other final hosts such as predatory fish or birds as a consequence of increasing size.

According to Bush et al. (2003), not only a single host specimen, but also the whole host population can be compared with an island. Thus, the mode of colonisation can be considered differently in the component, guild and suprapopulation levels. The colonisation mechanisms which are influenced by screens and filters (Holmes 1990) can be combined with the model of (island) distances. Three categories have to be distinguished: (1) genetic distance, whereby the parasite population is influenced by the respective defence systems of the host specimen; (2) phylogenetic distance, whereby it is influenced by the varying defence systems of host species; and (3) ecological (ontogenetic) distance, whereby it is influenced by the respective ways of life and cycles of several host guilds (Fig. 9). Phylogenetic distance is not only responsible for the colonisation of parasites, but also for the successive steps in their mat-

uration. In the future, the distances or handicaps at these three levels may be calculated and arranged in three-dimensional graphs. These, together with the ecosystem parameters, may then be used to characterise the ecological niche of a single parasite species.

The advantage of the long-term monitoring of parasite communities in short-lived fish lies in three important aspects: (1) rare parasite species can be better detected, (2) the data on species diversity can be better analysed, and (3) the seasonality of infracommunities can be more clearly determined when the results from several years in succession are taken into consideration. For such an understanding, only 2 years is not sufficient, and investigations which comprise at least 3 years are more successful.

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