The importance of gobies (Gobiidae, Teleostei) as hosts and transmitters of parasites in the SW Baltic

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ABSTRACT: The parasite fauna of five goby species (Gobiidae, Teleostei) was investigated in the Baltic Sea during the period 1987 to 1990. 13 parasite species were found in samples from the Lübeck Bight: *Bothriocephalus scorpii, Schistocephalus* sp. (Cestoda); *Cryptocotyle concavum, Cryptocotyle lingua, Podocotyle atomon, Derogenes varicus* (Digenea); *Hysterothylacium* sp. (cf. *auctum*), *Contracaecum* sp., *Anisakis simplex* (Nematoda); *Corynosoma* sp., *Echinorhynchus gadi, Neoechinorhynchus rutili, Pomphorhynchus laevis* (Acanthocephala). The number of parasite species were: 10 in the sand goby *Pomatoschistus minutus*, 8 in the black goby *Gobius niger*, 7 in the two-spotted goby *Gobiusculus flavescens*, 6 in the common goby *Pomatoschistus microps*, and 5 in the painted goby *Pomatoschistus pictus. Neoechinorhynchus rutili* occurred only in *P. minutus*, and *Corynosoma* sp. only in *G. niger*. The extent to which the gobies were parasitized clearly depended on the respective ways of life and, moreover, on the kind of prey ingested by the hosts. Additionally, the age of the hosts might be important. The highest rate of parasitism, more than 60 %, was reached by *Hysterothylacium* sp. in *G. niger* and by *Cryptocotyle concavum* in *P. microps*. Infestation incidence lay mostly below 40 % which means a satellite species status (Holmes, 1991). The number of parasite species was highest in summer; the highest intensities of single parasites occurred in spring *(Podocotyle atomon)* or autumn *(Cryptocotyle concavum)*. *Bothriocephalus scorpii, Hysterothylacium* sp. and *Podocotyle* infested their juvenile hosts very early, but only *Hysterothylacium* was accumulated by *G. niger* during its whole life span, whereas *Bothriocephalus* persisted also in older gobies in low intensities. The cercariae of *Cryptocotyle* spp. penetrate actively into their hosts; all the other parasites named were transmitted in larval form by prey organisms which consisted mainly of planktonic and benthic crustaceans. The gobies were final hosts for only 5 parasites; but two species may be transmitted to larger fish, and 6 species to sea birds or mammals. The parasite community of the five gobies may possibly be taken to characterize the ecological quality of the environment of the Lübeck Bight.

INTRODUCTION

Teleosts of the family Gobiidae play an important role within the ecosystems of the North and Baltic Seas (Fonds, 1973; Hesthagen, 1977; Thormann & Wiederholm, 1983; Evans, 1984; Zander & Hagemann, 1986; Zander, 1988; Hamerlynck et al., 1990). Regarding food chains, the gobies are secondary consumers and are themselves prey for larger fish (Markowski, 1935; Arntz, 1974), sea birds (Hartwig & Söhl, 1975; Doornbos, 1984) and seals (Behrens, 1985; Sievers, 1989). Their availability to fish eating predators implies that they are important transmitters of parasites which perform their life cycles in several hosts (Zander et al., 1984; Zander & Döring, 1989). Within the complicated cycles

of digeneans, cestodes and nematodes, the gobies are frequently second intermediate hosts (Zander, 1988; Zander & Westphal, 1991).

It was Reimer (1970), in particular, who propagated the investigation of parasites in the Baltic Sea. He studied the helminths of 47 invertebrates as well as those of 27 fish species, with regard to morphology, ontogeny and taxonomy, thereby discovering new life cycles and areas of distribution. Several authors thereafter studied the parasitic faunas of single fish hosts (e.g. Möller, 1975; Køie, 1983), or the host spectra of single parasites (Køie, 1979; Zander et al., 1984).

Therefore it might be of interest to now provide a detailed study of parasites in a certain area of the Baltic Sea. Five goby species from the shallow waters of the Lübeck Bight were regarded as hosts. These may be called a guild (Root, 1967). The helminths of the taxa Digenea, Cestoda, Acanthocephala and Nematoda are considered, because their abundances as parasites are highest. The studies focussed on the following: (1) Analysis of the helminth species in regard to incidences and specificities within the goby guild. (2) Tracing of developmental cycles, including thereby the first and second invertebrate intermediate hosts. (3) Knowledge of structure and dynamics of a fish-parasite community in brackish waters. (4) Elaboration of parameters of a parasite community in order to characterize the respective habitat.

The five hosts are *Gobius niger* L., which is the only longer-living goby on this site with a short pelagic period, and four species that live approx. one year: *Pomatoschistus minutus* (Pallas), 6–7 cm long, a large species with a longer larval period; *Pomatoschistus microps* (Krøyer) and *Pomatoschistus pictus* (Malm) with shorter pelagic phases; and *Gobiusculus flavescens* (Fabricius) which lives suprabenthically during its whole life. All the investigated fishes were caught between 1987 and 1990, some *G. niger* before 1987. The studies were complemented by studies on specimens of snails (*Littorina* and *Hydrobia*), on planktonic and benthic Crustacea (*Gammarus, Jaera)* which were all collected during 1990. These investigations may provide further information on the structure and dynamics of the Lübeck Bight ecosystem which has been under observation since 1983 (Zander & Hagemann, 1986, 1987; Melander, 1989; Zander & Döring, 1989; Zander, 1990; Zander, 1991).

INVESTIGATION SITE, MATERIAL AND METHODS

Investigation site

Diverse host organisms were collected near the beacon of Dahmeshöved situated between the sea resorts of Kellenhusen and Dahme, Lübeck Bight, Baltic Sea. This site has been covered since 1983 by SCUBA investigations on the role of small-size fish within the Baltic ecosystem. A stony pier extends from the beach approximately 30 m in an easterly direction and then continues for about 100 m in a northerly direction parallel to the shore. Its foundation lies in 2–3 m water depth. The pier is adjacent to a wide sand bottom, followed by a clay ecotone with pebbles and boulders in 5–6 m water depth.

Water temperature and salinity values fluctuate during the course of a year, as was found earlier (Zander, 1990): Salinity is between 9 and 15‰; water temperature reaches 20 °C at the most (Fig. 1).
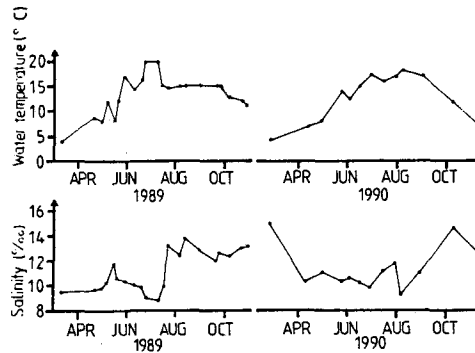
Fig. 1. Seasonal fluctuations of water temperature (above) and salinity (below) at Dahmeshöved during 1989 and 1990

Methods

The gobies were caught every 4–6 weeks from early spring to late autumn at the pier and in the clay ecotone by means of SCUBA and by hand-nets (Table 1). The fish were fixed in 4 % Formalin for further examinations. The plankton was sampled directly at the pier by pouring 100 l seawater through a net of 55 µm mesh; in summer 1990 some qualitative samples were added. The concentrated organisms were fixed in 4 % Formalin. Benthic crustaceans were quantitatively obtained by scratching an area of 156 cm² from the *Mytilus* girdle of the pier. The aufwuchs together with its mobile fauna was collected in a plastic-bottle and fixed in 4 % Formalin directly after the diving operation. The snails were collected at a water depth of 2–3 m. By means of a measuring rope, several areas of 0.25 m² were marked where all *Littorina saxatilis* were counted. The *Hydrobia* spp. were quantitatively sampled by means of a hand net, 20 cm wide and of 1 mm mesh, which was drawn over 0.5 m on the sand substrate. All snails were transported alive to the laboratory for further examinations.

The fixed fish were measured, wet weighed and intensively inspected externally, including the gills. Then the body cavity was opened, the intestinal tract cut off at the esophagus and the end of the rectum, externally inspected and finally opened in full

Table 1. Numbers of five goby species in the samples off Dahmeshöved examined in the years 1983–1990

Species Year	Before 1987	1987	1988	1989	1990	Sum
Pomatoschistus minutus		84	138	107	177	506
Pomatoschistus pictus			1	1	25	27
Pomatoschistus microps				75	3	78
Gobiusculus flavescens			10	135	16	161
Gobius niger	34	1	7	22	39	103
Sum	34	85	156	340	260	875

length. The content of the intestinal tract was transferred to investigation dishes, the prey organisms classified according to the relevant taxonomical units, and the parasites determined to the species level. Additionally, the body cavity, liver and kidney were inspected for parasites.

The copepods were selected from the plankton samples and transferred to a fluid consisting of 70 % ethanol, 25 % water and 5 % glycerine, completed by 1–2 drops of borax-carmine. The identification of species and their infestation with parasites was carried out under a microscope. The taxonomical classification of parasites is difficult, so that only "larval stages" were determined. The snails were investigated alive; the shells of *L. saxatilis* were broken by pliers, the visceral mass drawn onto a microscope slide. Regarding *Hydrobia,* 10 specimens were simultaneously pressed between 2 microscope slides and examined in the original medium. The sporocysts, rediae or cercariae present were at first studied alive, but were then transferred to a mixture of alcohol-glycerine, and determined as far as possible to the species level. The benthic crustaceans were selected from the aufwuchs samples which contained mainly *Mytilus edulis.* In particular, *Gammarus* spp. and *Jaera albifrons* were investigated to discover whether these harbour parasite larvae or cysts. Those found were also classified as far as possible to the species level.

The following indices were calculated:

(1) **E v e n n e s s**

$$J = \frac{H_s}{\ln S},$$

where H_s = Shannon-Wiener Index, S = number of species.

(2) **R e n k o n e n   I n d e x**

$$RI \% = 100 \cdot (pr_1 + pr_2 \ldots + pr_n),$$

where pr_{1-n} = the minor values of two compared hosts regarding infestation by parasite species 1 to n.

(3) **S p e c i f i c i t y   I n d e x** according to Rohde (1982)

$$SI = \Sigma \frac{\times (i, j)}{n(j) \cdot h(i, j)} : \Sigma \frac{\times (i, j)}{n(j)},$$

where x(i,j) = number of parasite specimen of species i in host species j; n(j) = number of host specimen of species j; h(i,j) = range of host species j infested by parasite i.

(4) **A f f i n i t y   I n d e x**

$$AI = N(i, j) \cdot \frac{1}{B(j) \cdot B(i, j)},$$

where N(i,j) = part of double infestation with parasite species i; B(j) = part of infested hosts of species j; B(i,j) part of host species j parasitized by species i.

RESULTS

Spectrum of parasite species

The mean incidence of parasitic infestation (percentage of infested hosts) of the five goby species fluctuated during the period 1989 and 1990 between 85 % *(Pomatoschistus*

microps) and 40 % *(Pomatoschistus minutus)*. As the other three species were infested to at least 64 % *(Gobiusculus flavescens)*, the sand goby is at the bottom of this scale (Fig. 2). Within the goby guild, 13 parasites were found (Fig. 3):

Cestoda: *Bothriocephalus scorpii* (Müller, 1776)
         Schistocephalus sp.
Digenea: *Podocotyle atomon* (Rudolphi, 1802)
         Cryptocotyle concavum (Creplin, 1825)
         Cryptocotyle lingua (Creplin, 1825)
         Derogenes varicus (Müller, 1784)
Nematoda: *Hysterothylacium* sp. (cf. *auctum* (Rudolphi, 1802)
         Anisakis simplex (Rudolphi, 1809)
         Contracaecum sp.
Acanthocephala: *Echinorhynchus gadi* Müller, 1776
         Pomphorhynchus laevis (Müller, 1776)
         Neoechinorhynchus rutili (Müller, 1780)
         Corynosoma sp.

High infestation incidences are only found in a few parasite-host systems, e.g. *Cryptocotyle concavum* in *P. microps; Cryptocotyle lingua* in *Gobius niger; Podocotyle*
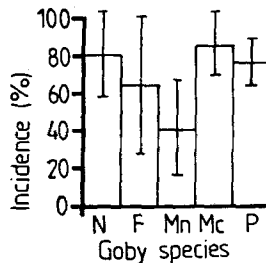

Fig. 2. Mean infestation incidence (%) of 5 goby species: N = *G. niger*, F = *G. flavescens*, Mn = *P. minutus*, Mc = *P. microps*, P = *P. pictus*. The vertical bars give the mean standard deviations

atomon in *G. flavescens*, *P. minutus* and *Pomatoschistus pictus; and Hysterothylacium* sp. in *G. niger* (Fig. 3). Only one host was infested by *N. rutili (P. minutus)* or by *Corynosoma* sp. *(G. niger)*; only two hosts by 4 parasite species (Fig. 4). However, *Hysterothylacium* sp. and *Podocotyle atomon* are present in all five gobies, whereas *Bothriocephalus scorpii* was found in all species excepting *P. microps* (Fig. 4).

    Infestations of *P. minutus* were investigated in several cycles of more than three years. From 1988, the parasite spectrum comprising 6 species changed to comprise 8 in 1989, of which 4, however, were new and 2 had vanished. The parasite fauna of the sand goby of 1990 is identical with that of 1988. This may mean that the investigation of two-year cycles is sufficient to record the parasites of a host.

Seasonal incidence and intensity of infestation

    The two-axes graphs, used here for the presentation of the incidence as well as the intensity of infestation, illustrate the importance of the respective parasites (Figs 5–7). Intensive investigations were carried out on *Pomatoschistus minutus* covering three and
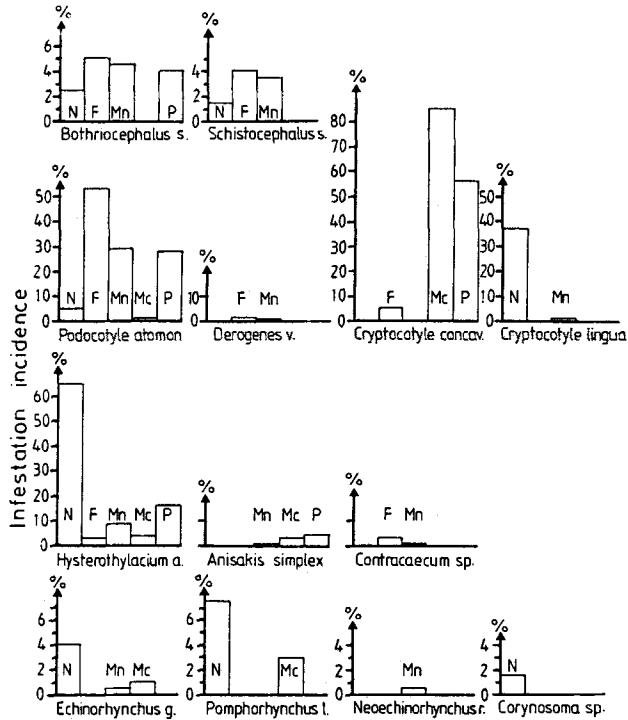
Fig. 3. Infestation incidence (%) of goby hosts by 13 different parasite species. Gobies: N = *G. niger*, F = *G. flavescens*, Mn = *P. minutus*, Mc = *P. microps*, P = *P. pictus*
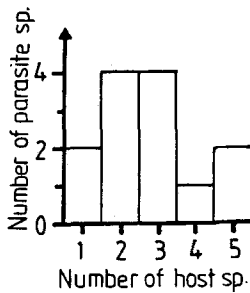

Fig. 4. Specificity of 13 parasite species according to their presence in 1–5 goby hosts

a half years (Fig. 5). *Podocotyle atomon* was the most abundant parasite in late spring and in summer with a maximal incidence of 95–98 % and intensity of 95 %. *Bothriocephalus scorpii* was found in spring and autumn at low rates of intensity; the other cestode, *Schistocephalus* sp., was present at a relatively high incidence rate in late summer and autumn. *Hysterothylacium* occurs during the whole year but at a low rate of intensity (Fig. 5). The other parasites play only a minor role; however, *P. minutus* is the goby host with the widest parasite spectrum (Fig. 11 f).
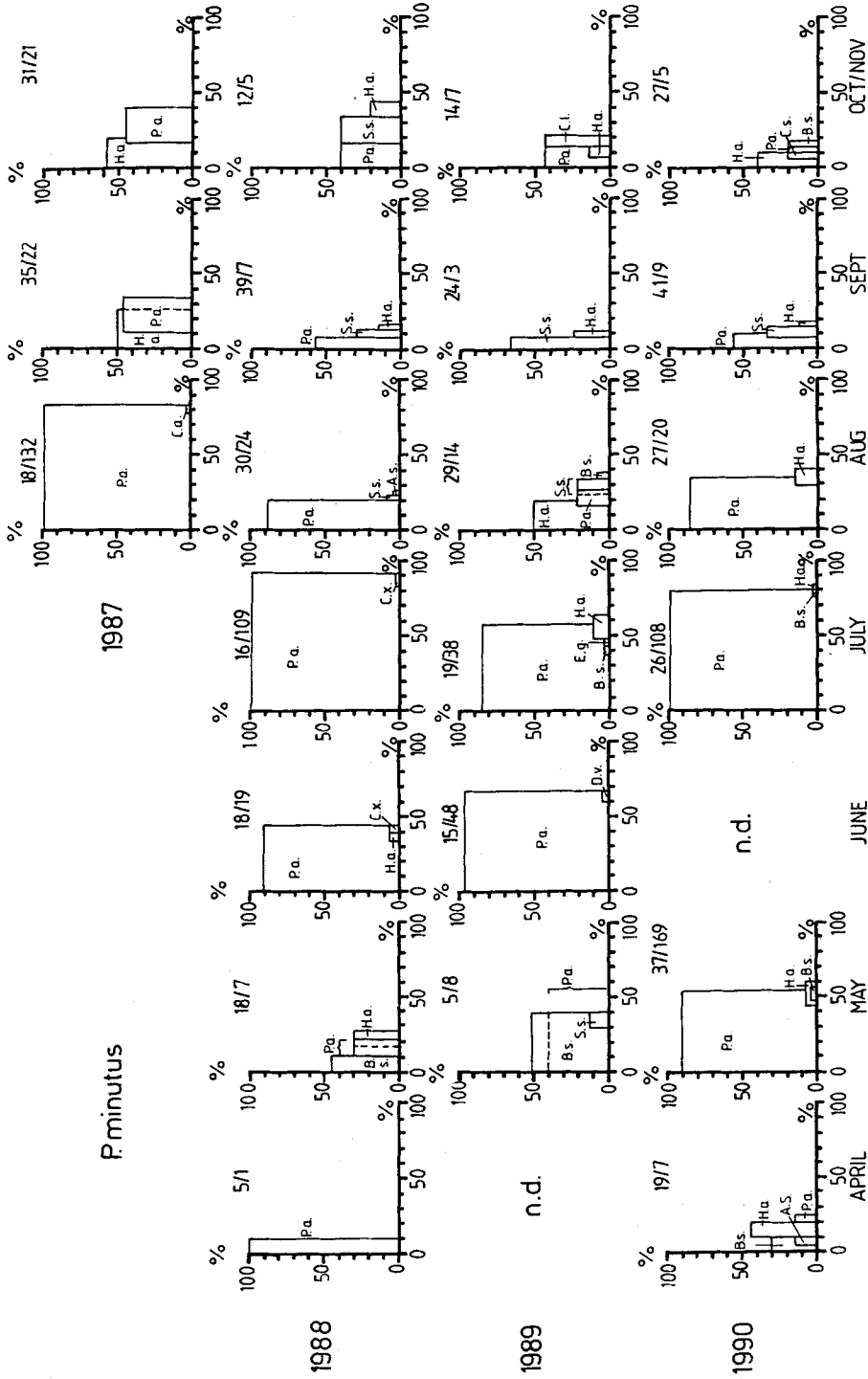
Fig. 5. Seasonal prevalence (X-axes) and infestation intensity (Y-axes) of helminth parasites in *P. minutus* during 1987–1990. Number of hosts/ total number of parasites are indicated. Parasites: A.s. = *Anisakis simplex*; B.s. = *Bothriocephalus scorpii*; C.c. = *Cryptocotyle concavum*; C.l. = *C. lingua*; C.s. = *Contracaecum* sp.; C.x. = *Corynosoma* sp.; D.v. = *Derogenes varicus*; E.g. = *Echinorhynchus gadi*; H.a. = *Hysterothy-lacium* sp.; N.r. = *Neoechinorhynchus rutili*; P.a. = *Podocotyle atomon*; P.l. = *Pomphorhynchus laevis*; S.s. = *Schistocephalus* sp.
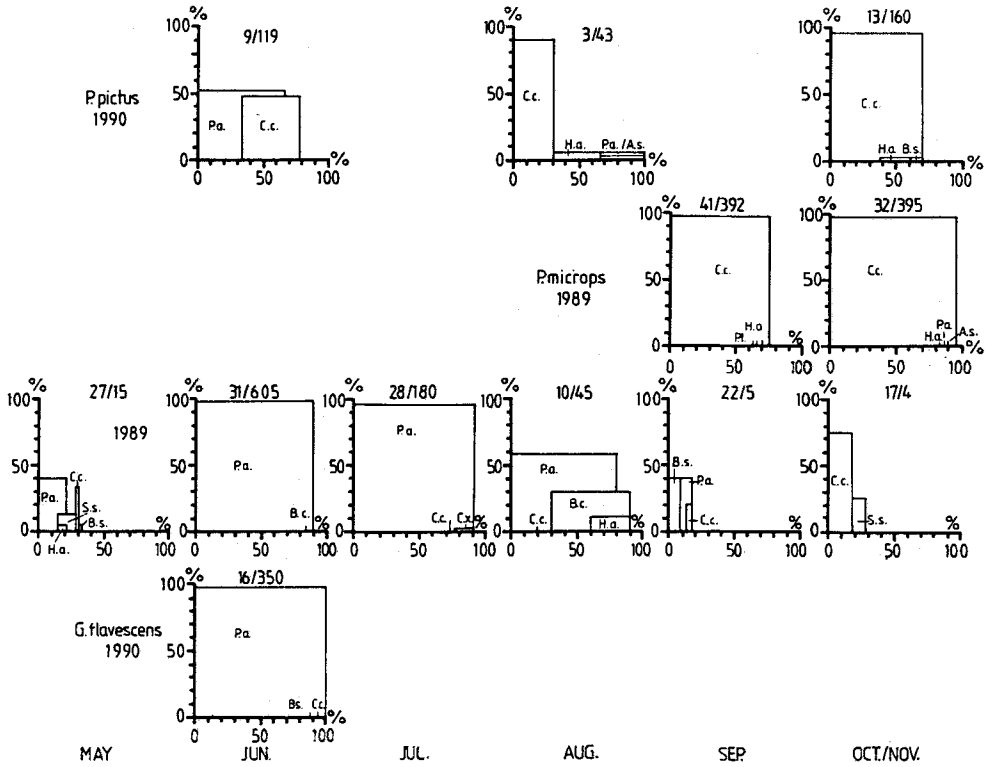
Fig. 6. Seasonal prevalence (X-axes) and infestation intensity (Y-axes) of helminth parasites found in *P. pictus*, *P. microps* and *G. flavescens* in 1989 and/or 1990. Number of hosts/total number of parasites are indicated. For explanation of abbreviations denoting parasites, see Fig. 5
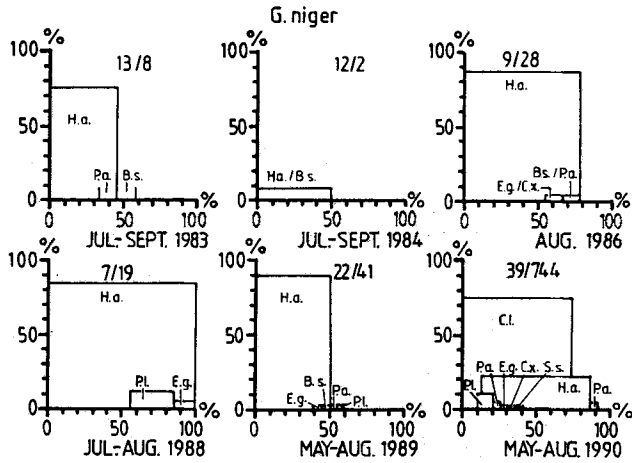

Fig. 7. Infestation incidence; (X-axes) and infestation intensities (Y-axes) of helminth parasites in *G. niger* investigated over 6 years. Number of hosts/total number of parasites are indicated. For explanation of abbreviations denoting parasites, see Fig. 5

G. flavescens presents the same trends as *P. minutus* regarding infestation with *P. atomon* but with even higher intensities (Fig. 6). Additionally, *Cryptocotyle concavum* is regularly found during the whole year but at low rates of incidence. This parasite dominates in the kidneys of *Pomatoschistus microps* which are riddled with metacercarial cysts in autumn, and in *Pomatoschistus pictus* where they settle mainly in the skin (Fig. 6). *P. pictus* reveals seasonal changes in its parasite community: *P. atomon* and *C. concavum* are present in a balanced relation in spring, whereas *C. concavum* dominates in summer and autumn with continuously increasing intensity. Other parasites are seldom present in *P. pictus* (Fig. 6).

Gobius niger is the only longer living species of the goby guild from Dahmeshöved. During the six years investigated, it was found in summer and sometimes also in spring (Fig. 7). *Hysterothylacium* sp., determined as *Hysterothylacium auctum* when adult, occurs frequently and intensively. *Podocotyle atomon,* however, plays only a minor role. In 1990, dermal cysts of *Cryptocotyle lingua* were highly apparent (Fig. 7). Remarkably, 3 Acanthocephala were found to infest *G. niger* which is the only intermediate host for *Corynosoma* sp.

Burden of parasite specimens

Pomatoschistus pictus and *Gobius niger* reveal a mean infestation rate of 13 parasite specimens, *Pomatoschistus microps* of 10, *Gobiusculus flavescens* of 8, but *Pomatoschistus minutus* clearly differs from the other gobies in harbouring only 2 parasites (Fig. 8). The reasons may lie in the respective seasonalities of the parasite species (Fig. 9). *Podocotyle* is very abundant in *G. flavescens* but also in *P. pictus* and *P. minutus* in spring and early summer, whereas *Cryptocotyle* is found with high intensities in *P. microps* and *P. pictus* during summer and autumn (Fig. 9).
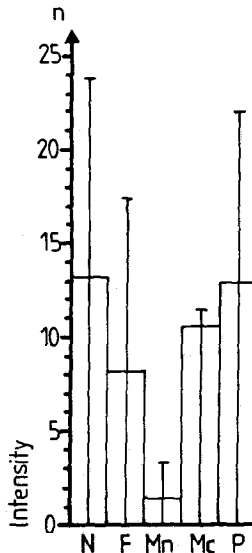

Fig. 8. Infestation intensity during 1989 and 1990 expressed as mean number of parasites per goby species (x-axis: N = *G. niger,* F = *Gobiusculus flavescens,* Mn = *P. minutus,* Mc = *P. microps,* P = *P. pictus*). The solid line scale gives the standard deviations
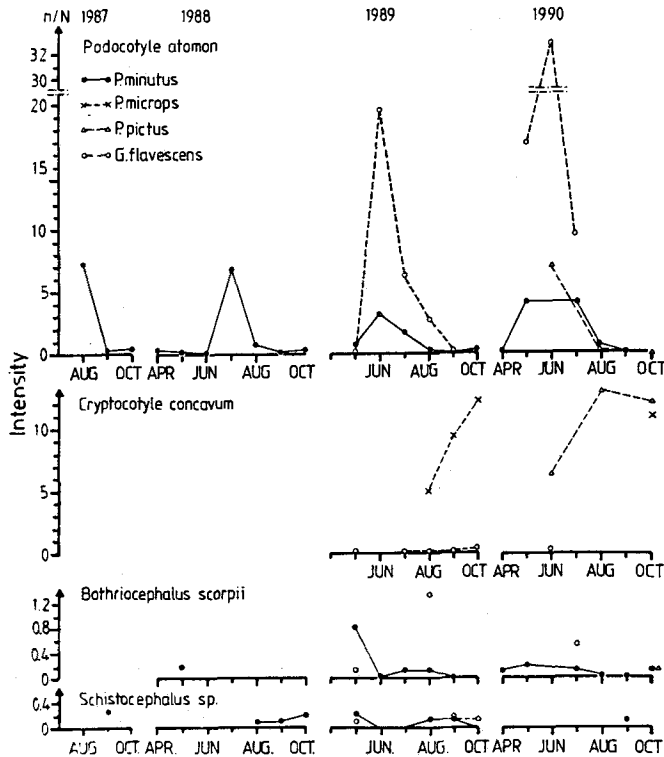
Fig. 9. Seasonal fluctuations in the infestation intensity of four parasite species in four goby hosts
during 1987–1990 related to the total number of investigated hosts

    The two cestodes are of much lesser abundances than the digeneans. *Bothrio-cephalus scorpii* seems to have maximal values in May *(P. minutus)* or in summer *(G. fla-vescens* [Fig. 9]). *Schistocephalus* sp. infests *G. flavescens* in spring as well as in autumn, at a low but almost identical level.

    Selected examples of the single host-parasite relationship are presented in Figure 10. *Podocotyle atomon* is present in *G. flavescens* and *P. minutus,* usually with 4–7 individuals, whereas *Cryptocotyle concavum* is concentrated in *P. microps* with 8–15 specimens. Some *G. flavescens* were found to be infested by more than 128 *P. atomon,* or some *G. niger* by more than 128 *Cryptocotyle lingua* (Fig. 10).

Species burden and diversity

    The relation of parasite species to the number of all host individuals was studied, whether these were infested or not, which creates relatively low values (Fig. 11). *Pomatoschistus minutus* bears the highest burden in late spring, but the lowest in April and autumn. However, *Gobiusculus flavescens* as well as *Pomatoschistus pictus* surpass these values in summer and autumn (Fig. 11a). The mean species burden of 1989 and 1990 is highest in *Gobius niger,* attaining, as in *P. pictus* and *Pomatoschistus microps,* more than 1, but lowest in *P. minutus* with the value of only 0.5 (Fig. 11b).
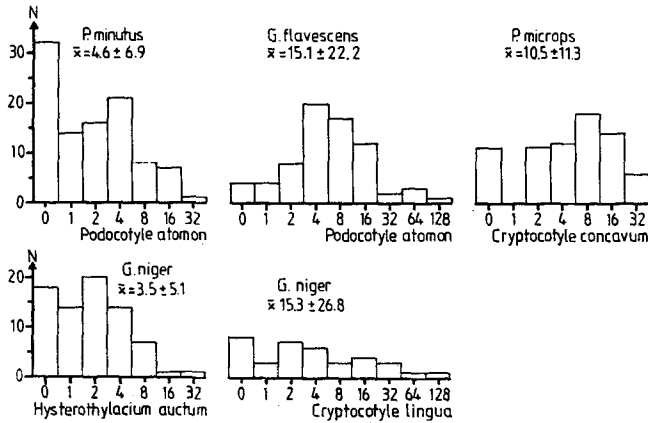
Fig. 10. Distribution of host specimens depending on increasing parasite intensities which are arranged on a geometrical scale. x̄ = mean rate of intensity ± standard deviation

Regarding evenness, a contrasting tendency to that of the species burden is visible (Fig. 11c). The only exceptions are *G. flavescens* in August and *P. pictus* in June, when high species burden as well as high evenness values occur. The mean evenness of 0.6 of *P. minutus* may demonstrate a balanced parasite community in this host (Fig. 11d). The mean values of the other gobies are clearly lower, indicating especially in *G. flavescens* and *P. microps,* unbalanced parasite communities (Fig. 11d).

The highest numbers of parasite species were found in *G. flavescens* in May 1989 (5), whereas they were lower (2–3) in the other hosts or in other months (Fig. 11e). Minimal values are found every summer in *P. minutus;* these are combined with different evenness values in the individual years. The sum of all parasites which occur in the course of a year is greater than that found in the monthly samples (Fig. 11f). This means that the parasites change during the seasons in a species-specific manner: *P. minutus* thus harbours up to 10, but *P. pictus* only 5, parasites (Fig. 11f).

Parasites of hosts of different age groups

An analysis of parasites in the different size classes of *Pomatoschistus minutus, Pomatoschistus microps* and *Gobius niger* seems to be opportune, considering the sufficient number of specimens of these species present (Fig. 12). The sizes of hosts and the extent to which they are parasitized are significantly correlated in *G. niger* and *P. minutus* but not in *P. microps,* where the larger specimens are parasitized to a lesser extent than the smaller ones (Fig. 12a). The same trend is visible when the intensities of *Cryptocotyle concavum* are considered (Fig. 12b). *Podocotyle atomon* may be a pioneer species in *P. minutus,* as are *C. concavum* in *P. microps* and *Hysterothylacium* in *G. niger* (Fig. 12b). Additionally, an increasing number of parasites occur in the larger size classes with low intensities (Fig. 12c). The number of parasite species increases during the growth of *G. niger* as well as of *P. minutus,* whereas evenness decreases as a result of the dominance of the main parasites (Fig. 12d). In *P. microps,* however, the different sized classes do not present clear differences.
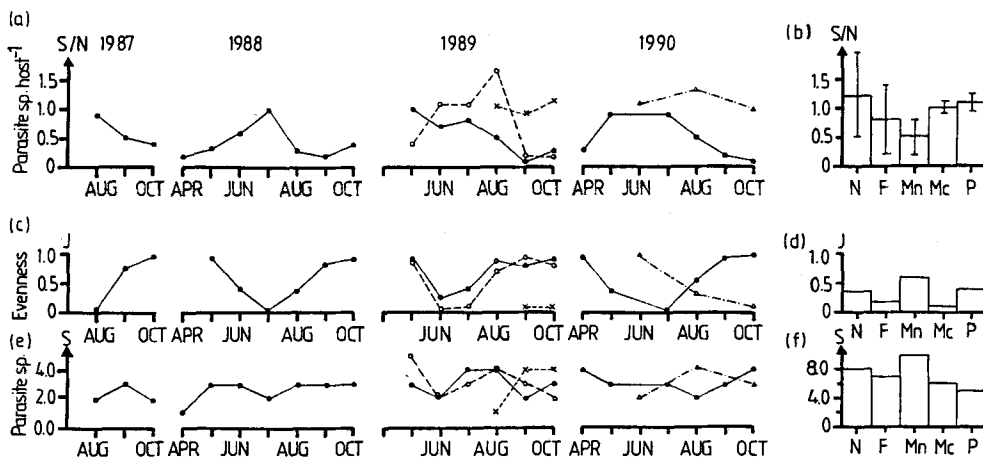
Fig. 11. Seasonal fluctuations (a, c, e) and mean values (b, d, f) of helminth parasites in five goby hosts during 1989/1990. a and b: parasite species burden; c and d: evenness; e and f: number of parasite species. Bars in Fig. 11 b give standard deviations. Gobies: N = *G. niger*, F = *G. flavescens*, Mn = *P. minutus*, Mc = *P. microps*, P = P. pictus. Symbols: full circles = *P. minutus*, open circles = *G. flavescens*, crosses = *P. microps*, triangles = *P. pictus* (see Fig. 9)

Macro- and microhabitats

The cladograms of the Renkonen indices indicate highest similarities between *Pomatoschistus microps* and *Pomatoschistus pictus*, and also between *Gobiusculus flavescens* and *Pomatoschistus minutus* in the species composition of parasites (Fig. 13). The same trends are apparent when intensities are compared and, in the case of *P. microps/P. pictus*, when infestation incidence is regarded. All three parameters reveal the special position of *Gobius niger* (Fig. 13). However, *P. pictus* presents also accords with *P. minutus* and *G. flavescens* with regard to incidence of infestation. Therefore the painted goby may probably play an intermediate role within the goby guild.

A further analysis follows Rohde (1982) who calls the habitat of host the macrohabitat, and the site within the host where the parasite lives the microhabitat. By means of the specificity index, slight preferences are found here for distinct goby hosts by the 13 parasites, because no value lies below 0.6 (Table 2). The maximal value of 1 calculated for *Cryptocotyle lingua* in *G. niger* means that the black goby is preferred by this parasite. *Hysterothylacium* sp. and *Podocotyle atomon* which are present in all 5 gobies reveal higher indices with regard to density, but lower indices with regard to frequency (Table 2). This may lie in the strong preference for *G. niger* by the nematode and for *G. flavescens* by the digenean. The lowest indices are found in *Bothriocephalus scorpii* whose infestation rates are almost identical, with the exception of *G. niger*. In most cases, only one host is preferred: *P. microps* by *Cryptocotyle concavum*, *G. flavescens* by cestodes, and *G. niger* by 3 of the 4 acanthocephalan species. This was already demonstrated by the respective infestation incidence (Fig. 3).

The microhabitats conform in 9 of the 13 parasites in all goby hosts. *B. scorpii* and *Neoechinorhynchus rutili* are found in the stomach, *Derogenes varicus* in the midgut, and
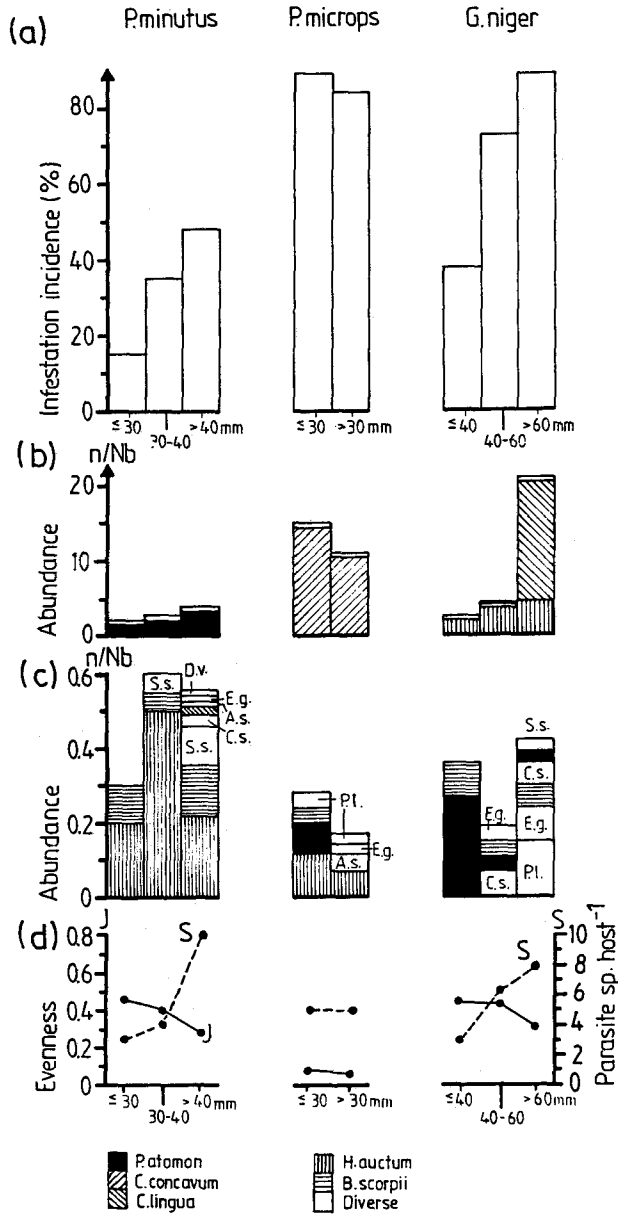
Fig. 12. Infestation of different size classes of three goby species. a: infestation incidence; b: infestation intensity of infested host specimens; c: infestation intensity of infested host specimens by rare parasites; d: numbers of parasite species per host (S) and evenness (J). Abbreviations denoting rare parasites: A.s. = *Anisakis simplex*, C.s. = *Contracaecum* sp., D. v. = *Derogenes varicus*, E.g. = *Echinorhynchus gadi*, P.l. = Pomphorhynchus laevis, S.s. = *Schistocephalus* sp.
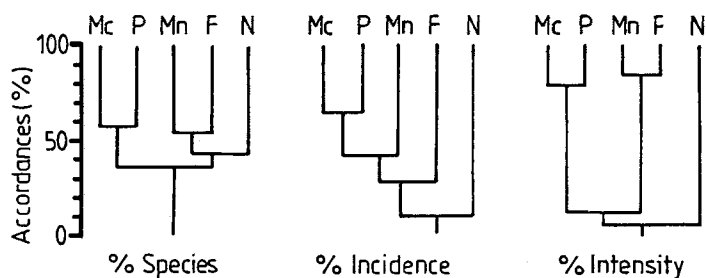
Fig. 13. Relationships of five goby hosts by means of the Renkonen index, regarding numbers, incidence and intensity of joint parasite species. Gobies: Mc = *P. microps*, P = *P. pictus*, Mn = *P. minutus*, F = *Gobiusculus flavescens*, N = *Gobius niger*

Pomphorhynchus laevis and *Echinorhynchus gadi* in the rectum, whereas *Corynosoma* sp. builds up cysts on the outer wall of the rectum. *Anisakis simplex* and *Contracaecum* sp. settle in the body cavity, mostly on the liver, whereas *Schistocephalus* sp. fills out this space almost completely. The parasite may reach one third of the weight of its host. Among the four most abundant parasites, *P. atomon* prefers the midgut but is sometimes found also in the stomach of *P. minutus* and *G. flavescens* (Fig. 14). A greater microhabitat spectrum is displayed by *Hysterothylacium* sp. which is mostly found in the midgut but also in stomach, rectum and, in *G. niger*, in the body cavity (Fig. 14). Whereas in *P. microps*, *C. concavum* infests exclusively the kidney, in *P. pictus* and *G. flavescens* it is found on fins and skin as black spots; only also few penetrate the kidney of *P. pictus* (Fig. 14). *C. lingua* seems to prefer the pectoral fins of *G. niger* (Fig. 14).

The affinity index describes the probability of the existence of several parasites in a host specimen (Table 3). Not only species with high abundances, such as *Hysterothylacium* and *P. atomon*, but also the less abundant *Bothriocephalus*, present high affinities

Table 2. Specificity indices of 13 helminth parasites and of the total parasite community of 5 goby species from Dahmeshöved, regarding intensities (SI-I) and incidences (SI-E)

| Species	SI-I	SI-E	(SI-I + SI-E):2
Bothriocephalus scorpii	0.67	0.66	0.67
Schistocephalus sp.	0.68	0.71	0.70
Derogenes varicus	0.83	0.88	0.85
Podocotyle atomon	0.80	0.67	0.74
Cryptocotyle concavum	0.75	0.77	0.76
Cryptocotyle lingua	1	1	1
Hysterothylacium sp.	0.94	0.76	0.85
Anisakis simplex	0.73	0.76	0.74
Contracaecum sp.	0.90	0.92	0.91
Echinorhynchus gadi	0.77	0.76	0.77
Pomphorhynchus laevis	0.86	0.87	0.87
Neoechinorhynchus rutili	1	1	1
Corynosoma sp.	1	1	1
Community index (SIC)	0.84	0.83	0.84
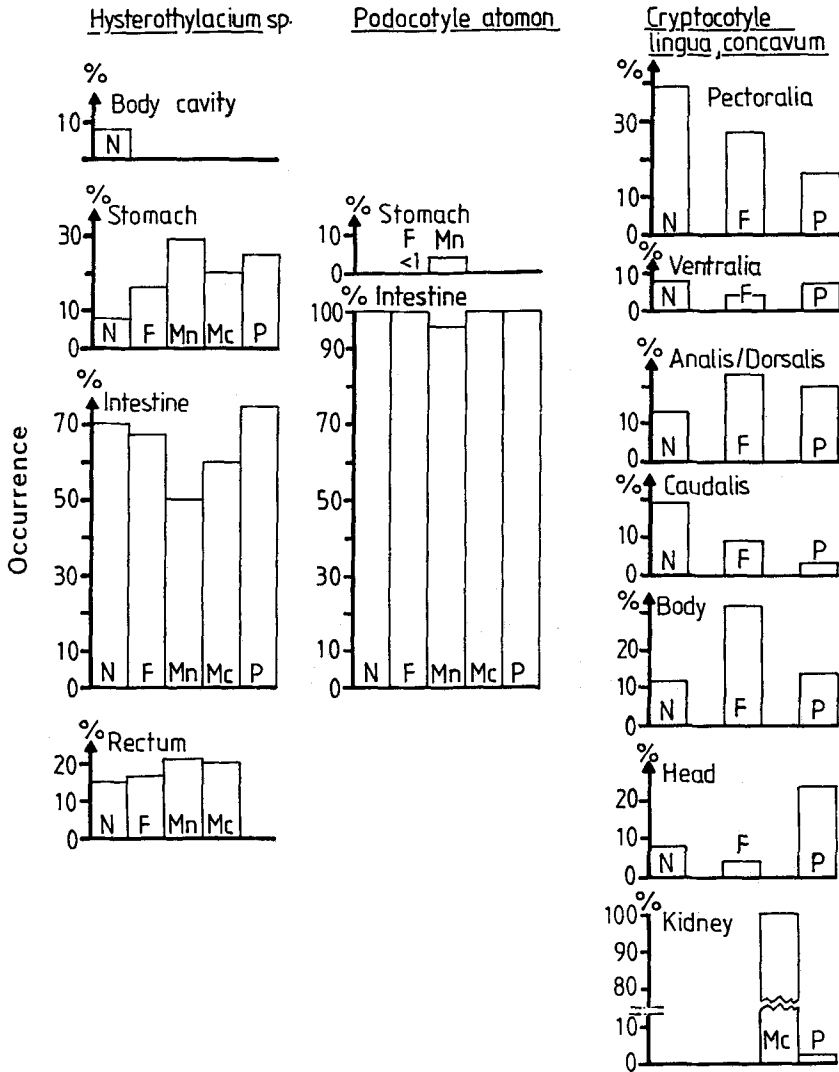
Fig. 14. Preferred microhabitats of four frequent parasites in five goby hosts: N = *G. niger*, F = *G. flavescens*, Mn = *P. minutus*, Mc = *P. microps*, P = *P. pictus*

to other parasites-which means frequent associations. *C. concavum* reveals an intermediate position because it appears in masses but in only three of five hosts. The same is true for *P. laevis* and *E. gadi*, whereas all other parasite species show low affinities (Table 3).

Infestation of invertebrate intermediate hosts

Figure 15a presents the abundance of planktonic copepods in Dahmeshöved during 1990. Two maxima, one in spring and a very high one in autumn, are characteristic. The

Table 3. Affinity indices (AI) of 12 helminth parasites found in five goby species and of the total goby guild (AIG) in Dahmeshöved

Parasite species	Host species					
	P. min.	P. mic.	P. pic.	G. flav.	G. nig.	AIG
Bothriocephalus scorpii	0.19		0.22	0.30	0.17	0.18
Schistocephalus sp.	0.08			0.05	0.12	0.05
Derogenes varicus	0.07			0.14		0.04
Podocotyle atomon	0.19	0.14	0.26	0.19	0.15	0.19
Cryptocotyle concavum		0.14	0.37	0.13		0.13
Cryptocotyle lingua					0.18	0.04
Hysterothylacium sp.	0.19	0.22	0.34	0.17	0.25	0.23
Anisakis simplex		0.17				0.03
Contracaecum sp.	0.10			0.22		0.06
Echinorhynchus gadi	0.05	0.14			0.24	0.09
Pomphorhynchus laevis		0.17			0.22	0.08
Corynosoma sp.					0.24	0.05

maximal infestation with cestode larvae, which were lacking in the beginning and the middle of the year, followed the peaks of their hosts (Fig. 15b). The copepod guild, comprising 7 calanoids and the cyclopoid *Oithona similis,* revealed a varying composition during the course of 1990: *Arcatia bifilosa* was most abundant during times of low densities but *O. similis* at times after the maxima; *Eurytemora hirundoides* prevailed at the beginning and end of 1990 (Strohbach, 1991). Highest infestation ratios were found at times of low copepod abundance (Fig. 15b). Procercoids of cestodes, but also nematode larvae, were the most frequent parasite stages observed, whereas oncospheres predominantly occurred before and after the periods of copepod dominance (Fig. 15b).

A. *bifilosa* and *E. hirundoides* which were present at a rate of 14–15 % during the year harboured the most parasites (Fig. 16). *Arcatia discaudata* and *Paracalanus parvus* were also relatively highly infested with cestode larvae, as was *Centropages hamatus* with nematodes. *O. similis* displayed the lowest infestation rate, though its ratio within the copepod guild was 57 % (Fig. 16).

Benthic crustaceans were investigated between May and November 1990 in order to find larval stages of digeneans, acanthocephalans and nematodes (Fig. 18). Some of the parasites common in snails were also discovered in gammarids as metacercariae: *Podocotyle atomon* and probably Microphallidae; additionally, *Hysterothylacium* sp. larvae and acanthellae are found. The isopod *Jaera* also harbours *Hysterothylacium* sp. in its body cavity (Fig. 18b, d).

Snails were investigated between August and November 1990. The density of *Littorina saxatilis* presented a maximum in autumn, when 55 specimens per square meter were counted (Fig. 17a). The infestation incidence changed only slightly due to increasing infestation by shell-destroying *Polydora ciliata,* whereas the ratio of digeneans decreased in autumn (Fig. 17b); *Cryptocotyle lingua* vanished at the end of the investigation time. The abundance of the mud snails, *Hydrobia* spp. which were dominated by *Hydrobia ulvae,* was highest in late summer and decreased thereafter (Fig. 17c). Thus incidences and intensities of digenean sporocysts and rediae decreased in autumn after
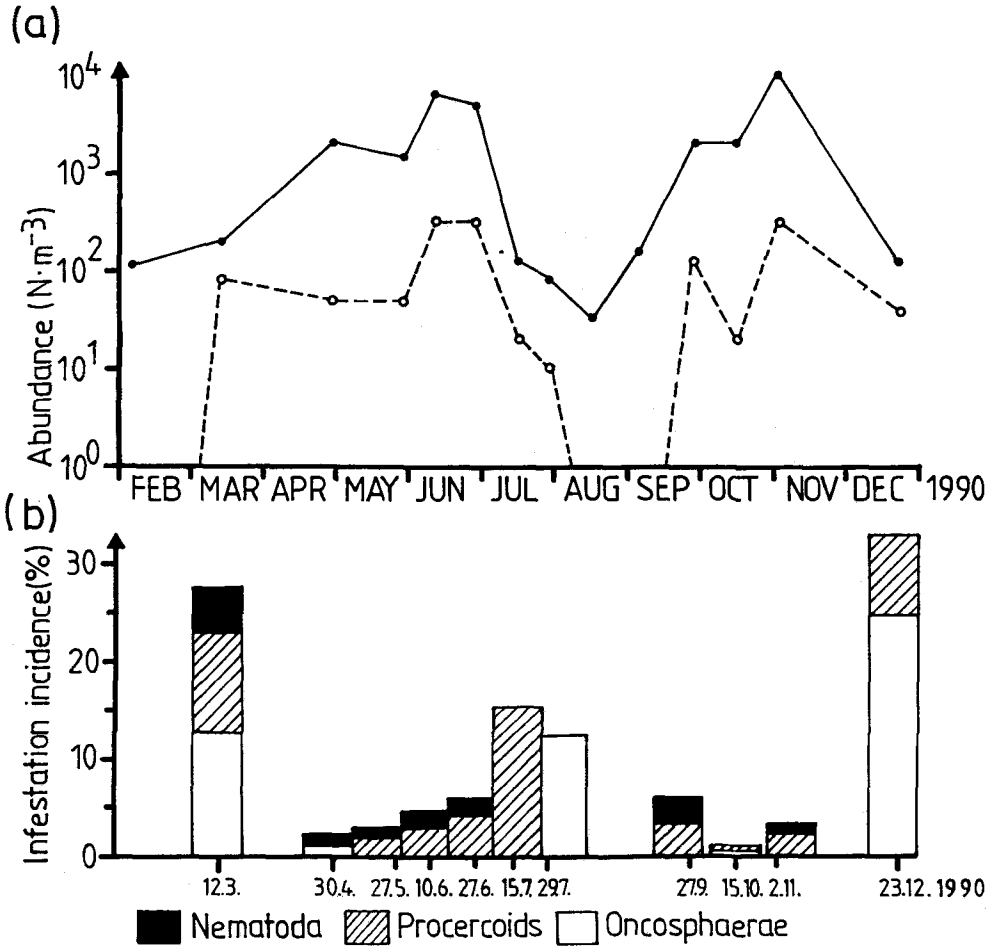
(a)

(b)

Fig. 15. Seasonality of planktonic copepods and their parasites from Dahmeshöved during 1990. a: abundances (N m⁻³) of all (solid line) and infested (broken line) copepods. b: Prevalences (%) of cestode and nematode larvae

being maximal in late summer (Fig. 17d). *Cryptocotyle concavum* prevailed in mud snails, whereas *Maritrema syntomocyclus* and *Himasthla* sp. II were less conspicuous.

The density and infestation density of gammarids of 18 000 m⁻² and 5000 m⁻², respectively, were extremely high; these values were clearly lower in *Jaera albifrons* (Fig. 18a, c). Regarding gammarids, *P. atomon* was the dominant parasite in spring, *Hysterothylacium* sp. in summer, and thereafter the Microphallidae with a maximal incidence of 25 % in November (Fig. 18b). Acanthella larvae also occur in late summer, reaching maximal values in October. *Hysterothylacium* sp. is the only helminth parasite found in *J. albifrons*, where it attains higher rates of infestation than in gammarids, in summer (Fig. 18d).
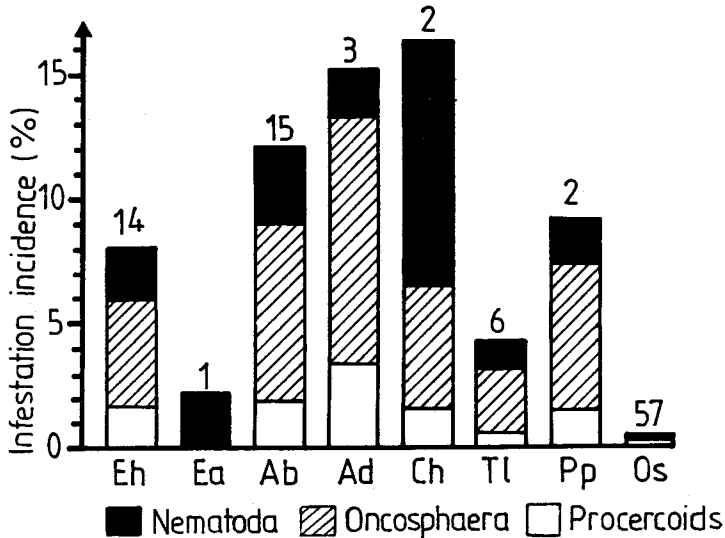
Fig. 16. Infestation incidence of helminth larvae in 8 copepod species from the plankton samples of 1990 in Dahmeshöved. The numbers above the columns mean the parts of the respective species within the copepod guild: Ab = *Acartia bifilosa*, Ad = *A. discaudata*, Ch = *Centropages hamatus*, Ea = *Eurytomora affinis*, Eh = *E. hirundoides*, Os = *Oithona similis*, Pp = *Paracalanus parvus*, Tl = *Temora longicornis*

Prey of gobies

The prey spectrum of *Pomatoschistus minutus* comprised 25 components, 13 of which occurred in all four years of investigation (Fig. 19). With regard to the frequency of occurrence, gammarids prevailed in all years whereas other components such as harpacticoids, *Mytilus* or polychaetes were preyed on, at the most, by 10 % of the sand gobies.

Gammarids dominated also in *Pomatoschistus microps* whose prey was completed by *Mytilus*, harpacticoids or isopods, the frequencies of which amounted to approx. 30 % (Fig. 20). Gammarids and also some planktonic components such as calanoid copepods and cypris larvae are also preferred by *Pomatoschistus pictus* (Fig. 20). Of lesser frequencies are harpacticoids, *Jaera* or the suprabenthic Mysidacea.

Gammarids, calanoids and cypris-larvae were also of greatest importance in *Gobius-culus flavescens* (Fig. 20). Whereas gammarids attained 70 % and calanoids 50 % in 1989, the latter component was preyed on by 90 % *G. flavescens* in 1990, when 70 % gobies ingested gammarids or cypris larvae. Hunting of suprabenthic mysids is probably of lesser success in *G. flavescens* than in *P. pictus* (Fig. 20).

As *Gobius niger* has been sampled since 1983, the values of several years have been combined in two groups and compared with those of 1990 (Fig. 21). The prevailing components are gammarids of all three time groups. *Jaera, Idotea*, polychaetes, and *Mytilus* attained high, but changing, frequencies. This was also true for *Corophium* in 1990 (Fig. 21).

The prey of the respective goby species can be related to the way of life of the fish.
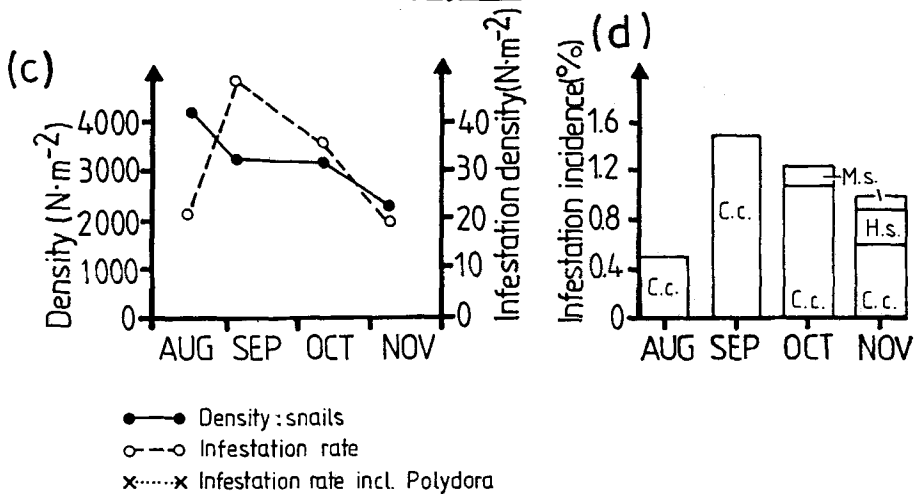
Littorina saxatilis
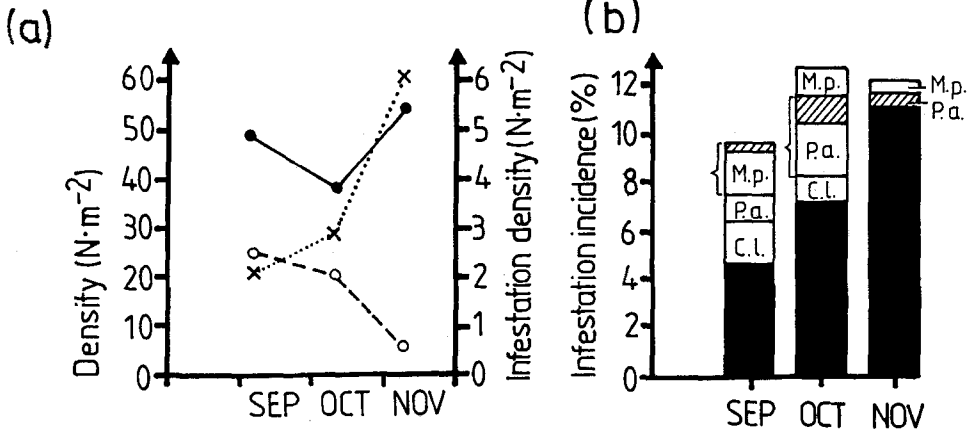
Hydrobia ulvae

Fig. 17. Densities (N m^{-2}), infestation densities (N m^{-2}) and prevalences (%) of *Littorina saxatilis* and *Hydrobia ulvae* from Dahmeshöved during late summer and autumn 1990. Black columns = *Polydora ciliata*, hatched boxes = double infestation by *P. ciliata* and digeneans. Parasites: C.c. = *Cryptocotyle concavum*, C. l. = *C. lingua*, H.s. = *Cercaria himasthlinarum*, M.p. = *Microphallus pygmaeus*, M.s. = Maritrema sp. P.a. = *Podocotyle atomon*

Whereas *P. minutus*, *P. microps* and *G. niger* prefer benthic prey organisms, the appearance of gammarids in the suprabenthic *G. flavescens* results from a shortage of planktonic copepods in the summer months. *P. pictus*, however, is a benthic species which also hunts planktonic prey, by shooting very fast from the bottom into the free water column.
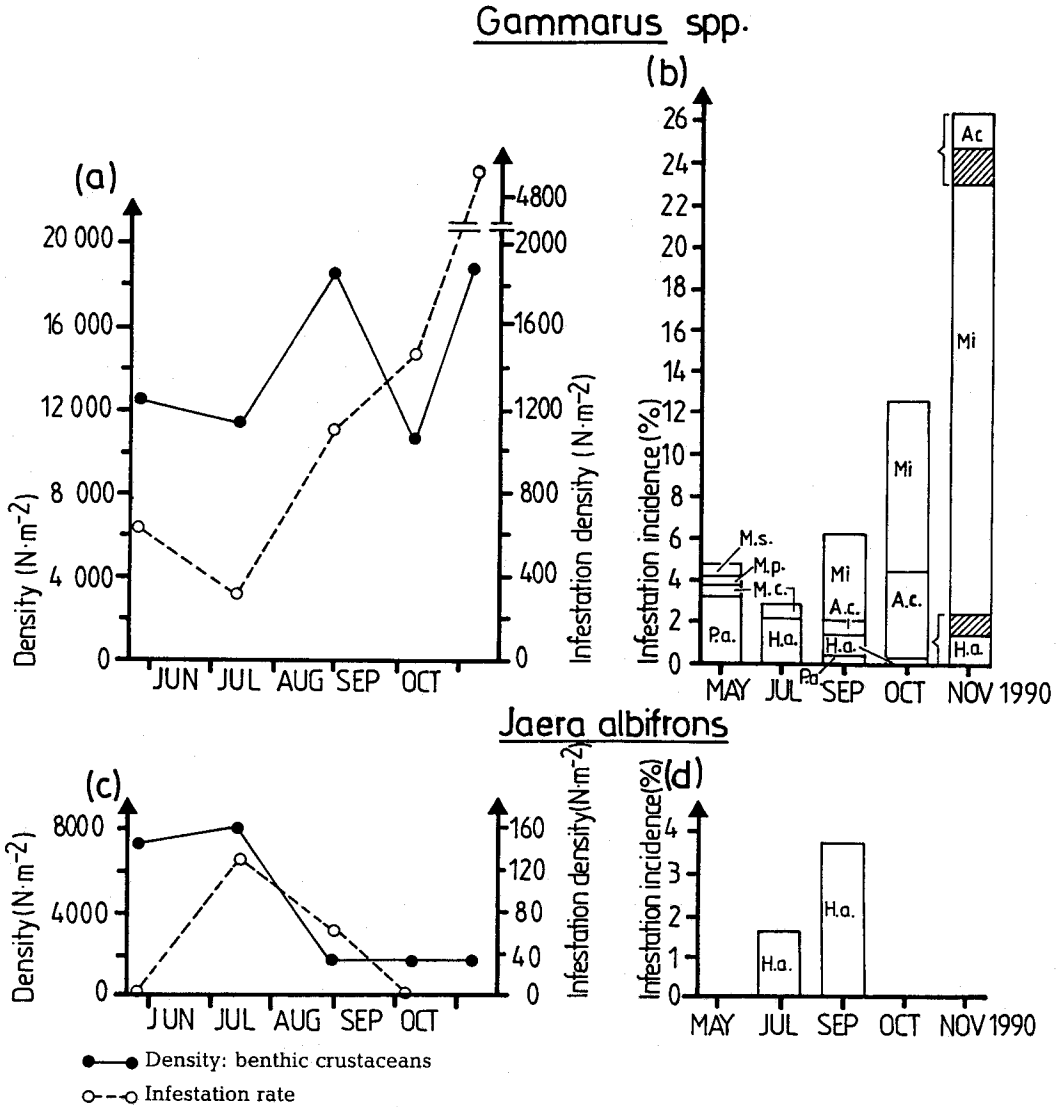
Gammarus spp.

Fig. 18. Densities (N m^{-2}), infestation densities (N m^{-2}) and prevalences (%) of *Gammarus* spp. and *Jaera albifrons* during 1990. Hatched boxes = double infestation of *Hysterothylacium* sp. and Microphallidae. Other parasites: Ac = Acanthella larvae, H.a. = *Hysterothylacium* sp., M.c. = *Microphallus papillorobustum*, M.s. = *Maritrema* sp., Mi = diverse Microphallidae, P.a. = *Podocotyle atomon*

DISCUSSION

Structure of parasite community

The present investigations on five goby species from the Lübeck Bight may give new insight into the parasite community structures. Only 13 helminth species were found,
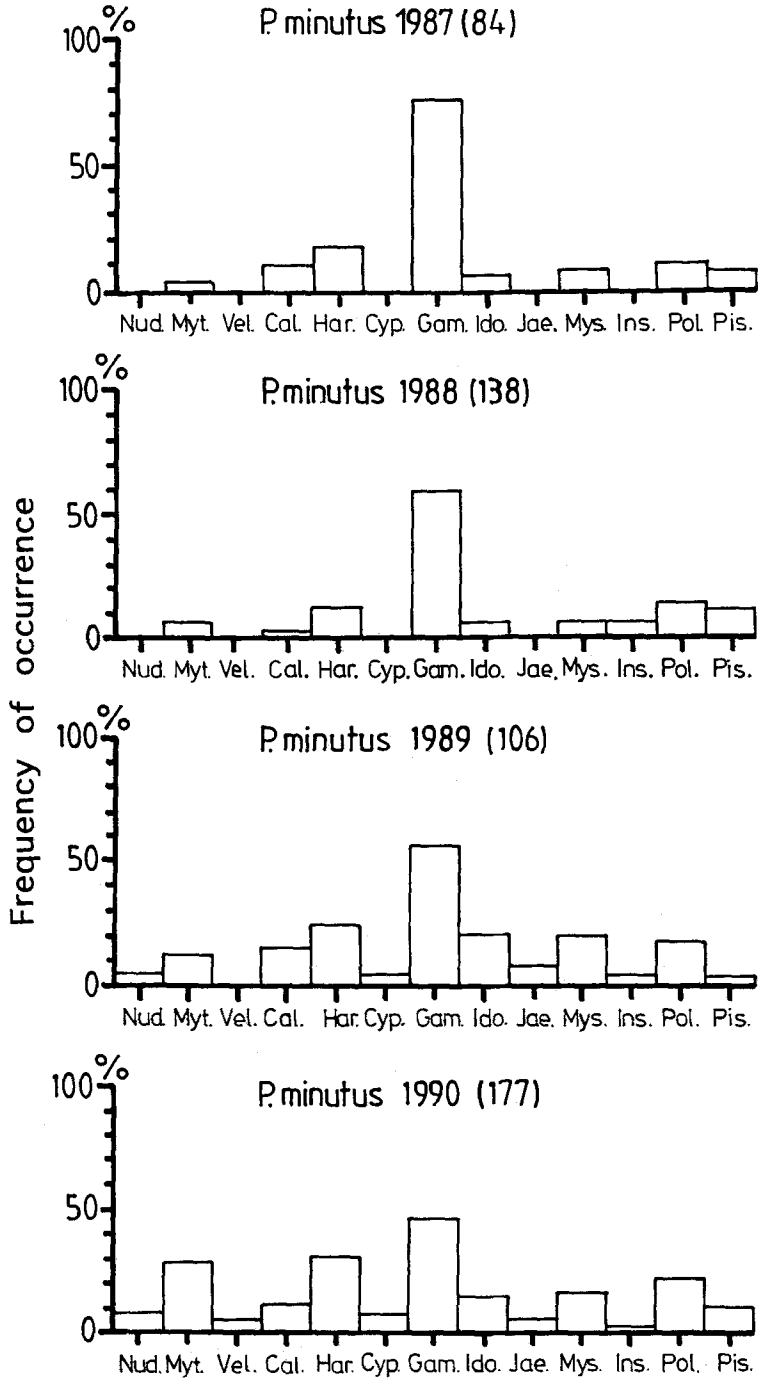
Fig. 19. Frequencies of occurrence of prey components ingested by *P. minutus* in 1987–90. In parentheses: numbers of investigated fish. Explanation of abbreviations in Fig. 21
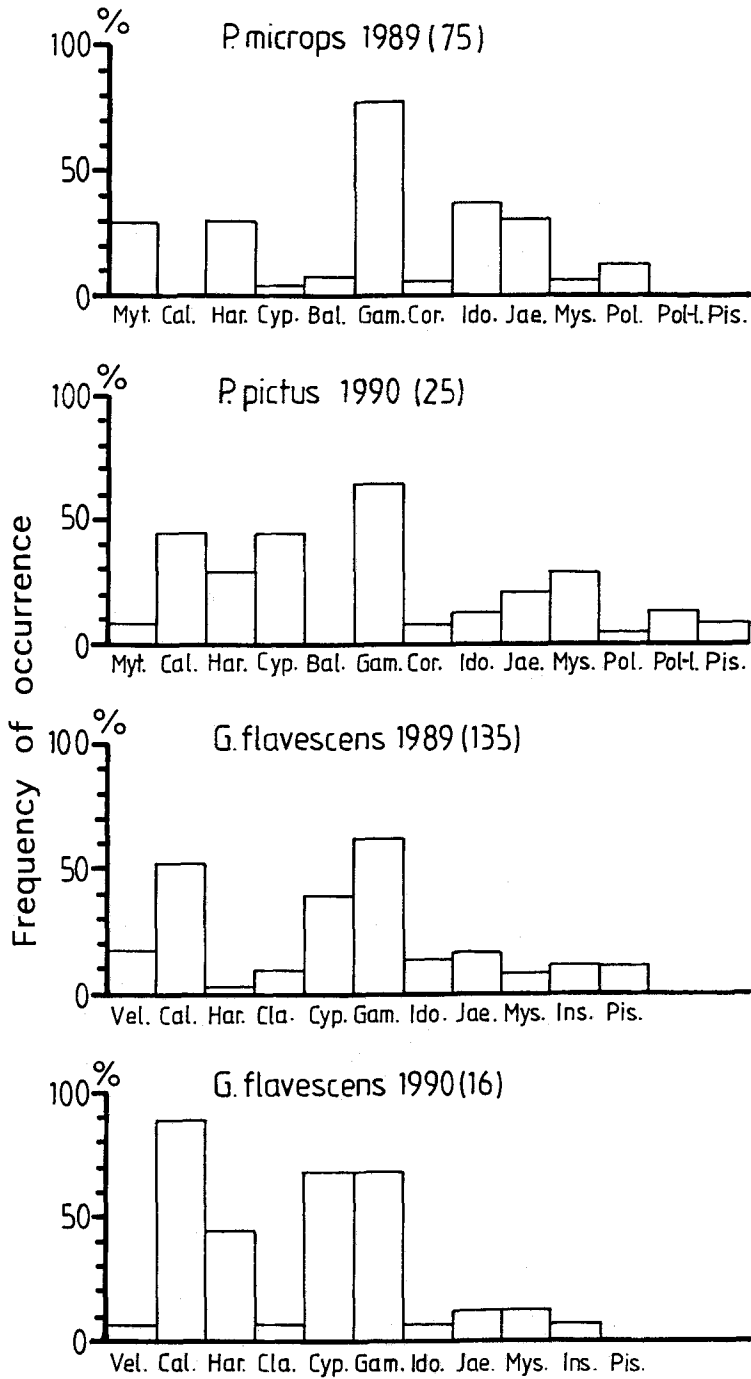
Fig. 20. Frequencies of occurrence of prey components ingested by *P. microps* and *G. flavescens* during 1989 and 1990. In parentheses: numbers of investigated fish. Explanation of abbreviations in Fig. 21
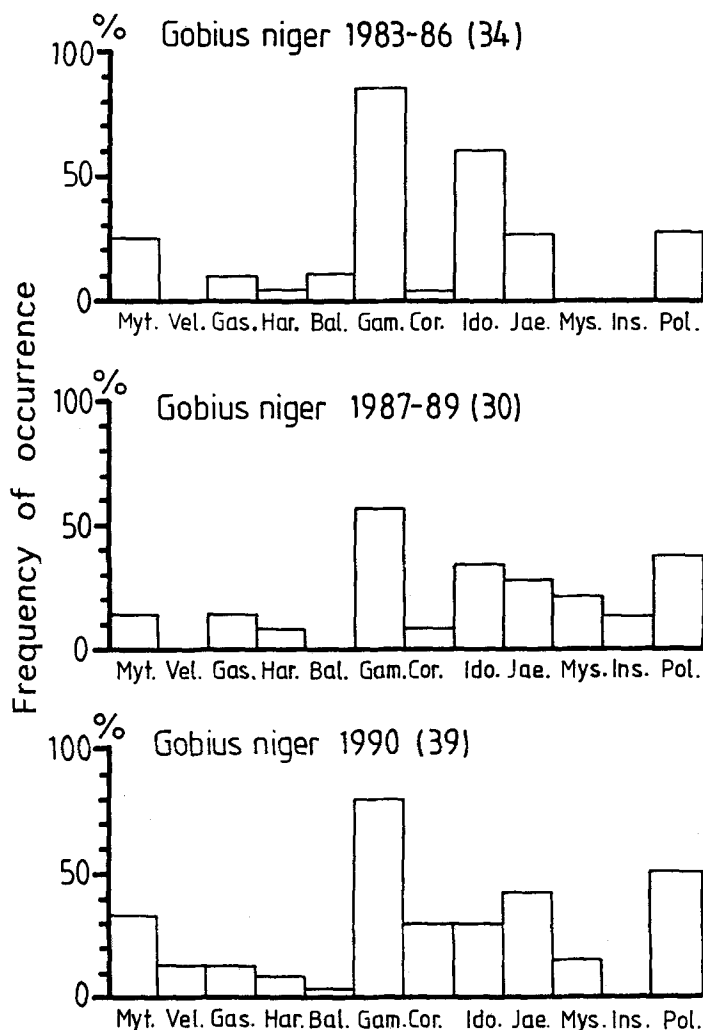
Fig. 21. Frequencies of occurrence of prey components ingested by *G. niger* during 1983–1990. In parentheses: number of investigated fish. Abbreviations: Bal. = Balanidae, Cal. = Calanoidea, Cla. = Cladocera, Cor. = *Corophium*, Cyp. = Cypris larvae, Gam. = Gammaridae, Gas. = Gastropoda, Har. = Harpacticoidea, Ido. = *Idotea*, Ins. = Insecta, Jae. = *Jaera*, Mys. = Mysidacea, Myt. = *Mytilus*, Nud. = Nudibranchia, Pis. = young fish, Pol. = Polychaeta, Pol-l. = Polychaeta larvae, Vel. = veliger larvae

which is apparently due to low salinities, a number which is lower than at marine sites (Möller-Buchner, 1987; Holmes, 1989) or limnetic habitats (Wootton, 1976; Möller-Buchner, 1987). Thus, these results follow the brackish water rules of species minimum (Remane, 1958). Only 8 helminth parasites were found in the eelpout *Zoarces viviparus* from the Lübeck Bight, which comprises species identical to those found in this investigation (Zander, 1991). The goby host with the highest species burden (10) is *Pomatoschistus minutus*; the least species (5) were found in *Pomatoschistus pictus*. However, when

incidences are regarded, *P. minutus* clearly differs from the other gobies with a mean of only 40 % and with the lowest individual and species burden. Diversity being high, a balanced composition of parasite species can be assumed in the sand goby. In contrast, the other goby hosts reveal a higher incidence of infestation, higher species and especially individual burdens, combined with lower diversities.

The metacommunities (Esch et al., 1988) are in part similar *(Pomatoschistus microps/ P. pictus, P. minutus/Gobiusculus flavescens)* but in part, of very low conformity *(Gobius niger/*all other hosts, *P. microps/P. minutus)*. *P. pictus* may have relations to the *P. minutus/G. flavescens* group which is probably due to the respective kind of prey foraging. *G. flavescens* lives suprabenthically; at a size of 30 mm, *P. minutus* changes its life style to a benthic way of life (Zander & Hagemann, 1986, 1987) and is therefore exposed to cestode bearing copepods over longer periods of time than *P. microps* or *G. niger* (Zander, 1979).

The high rates of specificity of some parasites must be related to the reduced host species number as displayed by the goby guild from Lübeck Bight. *Neoechinorhynchus rutili* attains the maximum value of 1 in *P. minutus,* but is a euryhaline fresh-water parasite (Bykhovskii, 1964) found also in the Schlei fjord, which has a clear salinity gradient (Zander & Westphal, 1991). It is probably transported from fresh or low brackish water into the Lübeck Bight. *Corynosoma* sp., the specifity index of which is 1 in *G. niger,* may exist only in longer living hosts as it is found also in the eelpout of the Lübeck Bight (Zander, 1991). The third parasite species with an index of 1 is *Cryptocotyle lingua,* which should live on pelagic fish hosts (Sindermann & Farrin, 1962) and not on epibenthic ones like *G. niger.* In contrast to *P. minutus* from Lübeck Bight, *P. minutus* of the Schlei fjord was not infested by this digenean, whereas *P. microps* was, to a low degree (Kreft, 1991).

An important factor governing parasite settlement is the dependence of each kind of prey on the respective habitat as well as on the life span of the host. Additionally, the rivalry or affinity between parasite species, evaluated here with a new index, also influences the infestation ratios. *Hysterothylacium* sp. and Podocotyle atomon, both of which display a widespread occurrence as well as high intensities, reveal great affinities as does *Bothriocephalus scorpii* which occurs in very low abundances. The parasite supracommunity (Esch et al., 1988) of the 5 gobies from the Lübeck Bight may, therefore, be ranged in the middle of the scale between isolation and interaction (Holmes & Price, 1980, see below). The selection of different microhabitats by *Cryptocotyle concavum* or *C. lingua* depends presumably to a lesser degree on competition with other parasite species than on coevolution with their respective hosts. This is particularly demonstrated by *C. concavum* which settles in the skin of most of its hosts, but in the kidney of *P. microps* (Zander et al., 1984; Kreft, 1991; Zander & Westphal, 1991).

The structure of a parasite community is strongly influenced by the ratios of satellite, secondary and core species (Hanski, 1982; Holmes, 1989). Holmes (1991) proposed to separate these groups at the 40 or 60 % level, respectively, and claimed a positive correlation between infestation incidence and mean intensity. This correlation is given in the Lübeck Bight community with a significance of 0.001 (Fig. 22). Regarding the traditional classification of dominance, 5 (= 8 %) of 65 parasite-host combinations are eudominant and 3 (= 5 %) are dominant (Fig. 23a). According to Holmes (1991), only *Hysterothylacium* sp. in *G. niger* and *C. concavum* in *P. microps* are core species (3 %); but 32 host-parasite combinations (= 42 %) have only a satellite status (Fig. 23b).
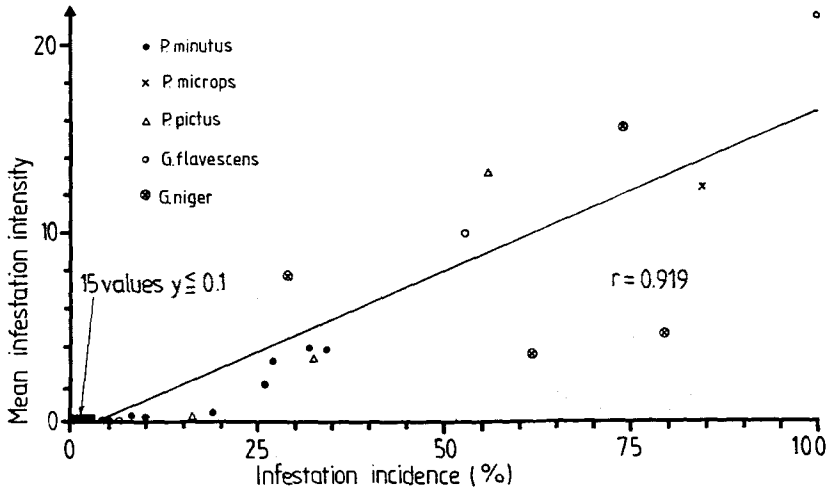
Fig. 22. Correlations of extensities (X-axis) and mean intensities (Y-axis) of 36 goby-parasite relationships in Dahmeshöved during 1989/90

Fig. 23. Frequencies (%) of 65 possible goby-parasite combinations arranged on the scale of the respective infestation incidences (%). The zero mark on the Y-axes means the undetected goby-parasite systems in Dahmeshöved. a: rates of infestation subdivided on the basis of the dominance scale; b: rates of infestation subdivided on the basis of the satellite-/core-species scale (Holmes, 1991)

Bush & Holmes (1986) found among water birds more specialists than generalists in the category of core species. In this investigation, the two types are equ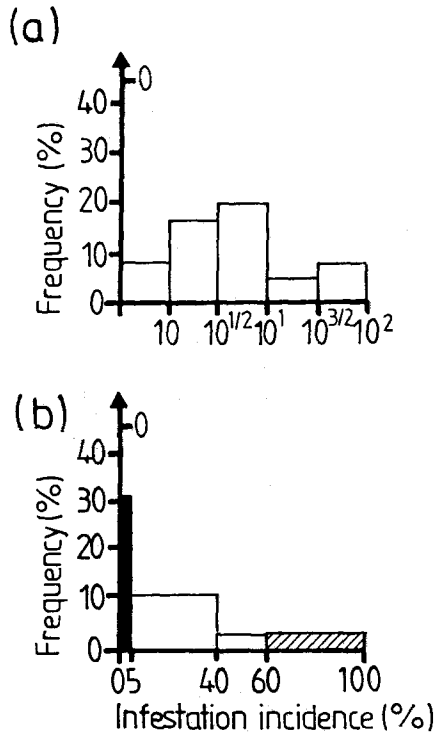al in numbers. *C. concavum* displays a balanced parasite-host relationship in the kidneys of *P. microps* but not in *P. pictus* where it more frequently occurs on the skin, as found also in *P. minutus* from the Schlei fjord (Kreft, 1991). *Hysterothylacium* sp., a core species in *G. niger* but a secondary or satellite species in the other gobies, apparently needs longer living hosts to be accumulated, as was demonstrated earlier in eelpout *Z. viviparus* from the Lübeck Bight (Zander, 1991). In contrast, *P. atomon*, a core species in *Z. viviparus*, is only a satellite in *G. niger*. This disagreement can be solved by direct observations of gammarids bearing *Podocotyle*-cysts in *P. minutus*, *P. microps* and *G. niger* which often pass through the intestinal tracts without excysting. In *G. flavescens*, however, these metacercariae excyst in every observed case.

According to the investigation in the Schlei fjord, *Neoechinorhynchus* is a core species in *Z. viviparus*, a secondary species in *Gasterosteus aculeatus*, but a satellite species in *P. minutus* and *P. microps* (Zander & Westphal, 1991).

The dynamics of parasite community

The clear seasonality of *Podocotyle atomon* is apparent because in springtime it especially infests *Gobiusculus flavescens* and *Pomatoschistus minutus* to a high degree. Similar results are also found by Kreft (1991) in *Pomatoschistus microps* or *Gasterosteus aculeatus* in the Schlei fjord where this parasite reveals maxima, not only in spring but also in autumn.

An autumnal maximum of *P. atomon* is not proved in the Lübeck Bight probably due to the population composition of juveniles only in the *Pomatoschistus* and *Gobiusculus* species and the invulnerability of *Gobius niger* to this parasite. However, *Cryptocotyle concavum* attains autumnal maxima in the Lübeck Bight as well as in the Schlei fjord but at the latter site with much higher numbers of parasites (Kreft, 1991).

All the other parasites found in the Lübeck Bight show no clear seasonalities. A maximum of species burden occurs in summer, followed by a decrease in parasite species richness. This may be caused by the death of adult gobies as well as by the low infestation ratios of young gobies. This assumption is supported by the increasing number of parasites in the larger size classes of *P. minutus* and *G. niger*, the largest species of the goby guild. Pioneer parasite species, such as *Bothriocephalus scorpii*, are also present in older gobies whereas *Hysterothylacium* sp. decreases in number in larger *P. minutus* and *P. microps*. The same trend is found in *G. niger* and *G. flavescens* which are infested as juveniles by *P. atomon*. Identical results were attained by Kreft (1991) on *P. atomon* in gobies and sticklebacks of the Schlei fjord. *G. niger* is able to accumulate *Hysterothylacium* sp. during its whole life span. This is also true of *G. aculeatus* of the Elbe and Eider rivers (Möller-Buchner, 1987). A similar, extreme accumulation, which may influence the health situation of the hosts has been described in *Zoarces viviparus* from the Lübeck Bight (Zander, 1991). In cases where the younger fish are more severely infested than the adults, one may assume direct or indirect mortality, as is found in sticklebacks which are more easily caught by predators when they bear parasites (Milinski, 1985). It is assumed that *Gasterosteus aculeatus* with dermal cysts of *C. concavum* have a shorter life span

than uninfested specimens of the same age group (Zander et al., 1984; Kreft, 1991).

Thus, fluctuations in the parasite communities observed in the five gobies of the Lübeck Bight may express the special adaptations of the respective host species.

Life cycles

It was not possible in every case to trace the total life cycle of goby parasites in the Lübeck Bight. Thus, early life stages of nematodes, acanthocephalans and cestodes can only be roughly determined. In contrast to digeneans, the first intermediate hosts of other parasites are not species-specific but, at the most, group-specific: Cestoda live in planktonic copepods; acanthocephalans and nematodes in benthic peracarids; nematodes, sometimes also in planktonic copepods. Regarding *Podocotyle atomon*, the results on this species in the Lübeck Bight are identical with those on the same species in the Schlei fjord where it infests, among peracarids, mostly *Idotea chelipes* (Kreft, 1991).

The first intermediate hosts of digeneans in the Lübeck Bight are *Littorina saxatilis* for *P. atomon* and *Cryptocotyle lingua; Hydrobia ulvae* for *Cryptocotyle concavum*. These host specifities may differ from area to area, because *C. lingua* in the Schlei fjord preferably infests *Littorina littorea*, whereas *C. concavum* is found there in *Hydrobia ventrosa* and *H. neglecta* (Zander et al., 1984; Kreft, 1991).

The gobies themselves are second intermediate hosts to *Cryptocotyle* spp., cestodes, nematodes and *Corynosoma* sp. in the Lübeck Bight. Only the cercariae of *Cryptocotyle* spp. penetrate into their hosts actively, whereas all other parasites are transmitted by the

Table 4. Evaluation of the parasite community of five goby hosts from Dahmeshöved by means of four parameters: I. Auto-/allogeny; steps – 0 = autogenic, goby is final host; 0.5 = autogenic, goby is intermediate host; 1 = allogenic. II. Affinities to other parasites; 0 = affinity index (AI) is greater than 0.1; 0.5 = AI is between 0.06 and 0.10; 1 = AI is smaller than 0.06. III. Infestation incidence; 0 = satellite species; 0.5 = secondary species; 1 = core species. IV. Specializations; 0 = one goby species is infested; 0.5 = 2–3 goby species are infested; 1 = 4–5 goby species are infested

| Parasite species | Category | | | | Sum | Mean |
	I	II	III	IV		
Bothriocephalus scorpii	0.5	0	0	1	1.5	0.4
Schistocephalus sp.	1	1	0	0.5	2.5	0.6
Derogenes varicus	0	1	0	0.5	1.5	0.4
Podocotyle atomon	0	0	0.5	1	1.5	0.4
Cryptocotyle concavum	1	0	1	0.5	2.5	0.6
Cryptocotyle lingua	1	1	0.5	0.5	3.0	0.8
Hysterothylacium sp.	0.5	0	1	1	2.5	0.6
Anisakis simplex	1	1	0	0.5	2.5	0.6
Contracaecum sp.	1	0.5	0	0.5	2.0	0.5
Echinorhynchus gadi	0	0.5	0	0.5	1.0	0.3
Pomphorhynchus laevis	0	0.5	0	0.5	1.0	0.3
Neoechinorhynchus rutili	0	1	0	0	1.0	0.3
Corynosoma sp.	1	1	0	0	2.0	0.5
Sum	7.0	7.5	3.0	7.0		6.2
Parasite community	0.54	0.58	0.23	0.54		0.48

prey organisms of the fish (Zander et al., 1984; Zander & Döring, 1989; Kreft, 1991; Zander, 1991; Zander & Westphal, 1991). On the other hand, gobies are natural prey for larger fish, sea birds and seals. Therefore, their additional role in the food web is that of transmitters of parasites to the final hosts (Zander, 1988; Zander & Döring, 1989). *Bothriocephalus scorpii* and *Hysterothylacium* sp. are in this way transferred to predatory fish species (Möller & Anders, 1986). Presumably, *Hysterothylacium* sp. is able to mature in the larger and longer living *Gobius niger*. This is also true for this nematode in *Zoarces viviparus* from the Lübeck Bight (Zander, 1991). All other parasites found in gobies are adapted to homoiothermic final hosts, mostly sea birds. Only *Anisakis simplex* and *Contracaecum* sp. are frequently found in seals (Reijnders et al., 1981), and *Corynosoma* sp. in cormorants (Reimer, 1969) and seals (Helle & Valtonen, 1981). Therefore, only 3 of the 13 parasites of gobies from the Lübeck Bight are allogenic species, in the sense of Esch et al. (1988), which means that they display at least a periodic absence from the aquatic habitat.

The gobies are final hosts for 2 Digenea and 3 Acanthocephala species. These are also transmitted by crustaceans which are the main food of the gobies (Zander & Döring, 1989; Zander 1990). They present a rich resource of *Podocotyle atomon,* several acanthocephalans and *Hysterothylacium* sp. for gobies, as well as Microphallidae for birds. As *Contracaecum* larvae have been recognized in some *Gammarus* specimens, the way gobies are infested is clear now. Additionally, the succession of *P. atomon, Hysterothylacium* sp. and acanthocephalans, at first in crustaceans and thereafter in gobies, reveals the season-dependent life cycles of these parasites.

Characterization of the Lübeck Bight by means of the parasite community

The Baltic Sea is for the greatest part a brackish sea in which the organisms are adapted to low salinities. Its community has attained a stable status though only a few organismic interactions have developed (Remmert, 1989). The low salinity has also the effect of a filter on parasites (Kennedy, 1991) which is intensified when more than one host is involved in the life cycles. Therefore, the Lübeck Bight which is characterized by salinities of 8–12 ‰ influences the macrohabitats of a parasite more decisively than the microhabitats (in the sense of Rohde, 1982). This implies that only few specializations can be expected such as, for example, the microhabitat of *Cryptocotyle concavum* in the kidney of its second intermediate host *Pomatoschistus microps*. This parasite-host relationship is considered to be a progressive coevolution in the brackish milieu (Zander et al., 1984). All other goby-helminth interactions of the Lübeck Bight may be founded on "host capture" (Holmes & Price, 1980), as intermediate hosts bearing parasite larvae are the common prey of these fish, especially *Gammarus* spp. with metacercariae of *Podocotyle atomon*. According to former investigations, *Gammarus* specimens were not infested until they reached a length of 9 mm (Zander & Döring, 1989). In this investigation, however, 5 mm-large specimens were found with cysts of this digenean, this size being preferred as prey by *Pomatoschistus minutus* (Zander, 1990). Additionally, small *Gammarus* spp. harbour a rich association of diverse helminth larvae, which also cause the transmission of nematodes and acanthocephalans (Zander & Döring, 1989; Zander, 1991).

Using the island theory (MacArthur & Wilson, 1967), Holmes & Price (1980) compare the colonization of hosts by parasites with the colonizing of islands by invaders. Accord-

ing to Holmes & Price (l.c.), the number of microhabitats offered by the hosts corresponds to the size of the island, and the difficulties surrounding parasite settlement such as, for example, immune defense of the host, correspond to the distance of the islands from the continent (Esch et al., 1988). The resulting coevolution of parasite and host may be a point of equilibrium such as in the island theory when newly invading parasites can only replace others that die out because all the existing niches are densely packed. This point of equilibrium has not yet been reached by parasites of the Baltic Sea, although some coevolutive developments can be recognized: some parasites prefer distinct micro-habitats; single infestation occurs instead of mass infestation in some cestodes and acanthocephalans; and tolerance of different parasite species begins to develop.

The present results from the Lübeck Bight differ from those on some sea fishes (Holmes, 1989, 1991) or some freshwater fishes (Kennedy, 1989, 1991) in comprising more microhabitats than only that of the intestinal tract. Additionally, these investigations focussed on brackish water where parasite communities are only scantly known. Table 4 tries to use numerically the single parameters discussed above for a characterization of the parasite community of the Lübeck Bight. As a result, a value in the middle of the interactive scale (Holmes & Price, 1980) is attained. This may emphasize the thesis of Remmert (1989) who calls the Baltic Sea a balanced ecosystem. The utilizability of the regarded criteria must be proved in the future, especially with regard to brackish habitats. This calculation goes even further than the results of Möller-Buchner (1987), which are based on the diversities of the parasite communities of sticklebacks studied in order to analyse the quality of the Elbe and Eider rivers.

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