Eel parasite diversity and intermediate host abundance in the River Rhine, Germany

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SUMMARY

European eels (*Anguilla anguilla*) from 2 sampling sites on the Rhine river (near Karlsruhe and near Worms) were investigated with respect to their parasite communities. Nine different metazoan species were found to live in and on the eels. The highest number of species was recorded from the intestine, which contained up to 6 different helminths. Among these, acanthocephalans were the most prevalent worms with the eel-specific parasite *Paratenuisentis ambiguus* as the dominant species of the intestinal component communities at both sites. Comparing the intestinal parasites from eels caught near Karlsruhe with those from Worms, the acanthocephalans showed a significantly lower abundance at Worms. A significantly lower mean number of intestinal helminth species as well as a significantly lower Brillouin's Index was found at Worms compared with Karlsruhe. This difference could be related to the abundance of the respective intermediate crustacean hosts. At the sampling site Worms the amphipod *Corophium curvispinum* was the dominant crustacean. Additionally, only the isopod *Jaera istri* and the amphipod *Dikerogammarus villosus* were found. All these crustacean species have only recently colonized the Rhine river system via the Main-Danube canal, built in the early 1990s. They are not known to act as intermediate hosts for any of the acanthocephalans found in the eels. The site near Karlsruhe exhibited a higher crustacean diversity, including *Asellus aquaticus* and different species of the genus *Gammarus*, which are all known intermediate hosts for the acanthocephalans found. Therefore, changes of eel parasite diversity can be correlated with the appearance of invading crustacean species (neozoans).

Key words: *Anguilla anguilla*, parasites, acanthocephalans, crustaceans, diversity, neozoans.

INTRODUCTION

Immigration of species is known to cause serious problems in the receptive ecosystems. Probably the best known free-living migrating species from aquatic biotopes worldwide is the zebra mussel *Dreissena polymorpha*. In the USA the appearance of zebra mussels in Lake St Clair in 1988 (Herbert, Muncaster & Mackie, 1989), possibly introduced by ballast water of a ship from the Black Sea area, has alerted both conservationists and business people because of possible long-term economic and ecological effects (Garton & Haag, 1993). *D. polymorpha* has a great impact on limnic biotopes as it can numerically dominate the benthic community due to its free-swimming veliger larvae (Garton & Haag, 1993).

It is also known that migrating fish species and fish species introduced as a result of generally increased stocking and management of freshwater fish (Kennedy, 1993*a*) have in part severely altered aquatic communities. Recently it was shown, by using data from 1995, that the eel parasite community of the river Rhine, consisting of a total of 9 metazoan species, included 4 species that were introduced into German eel populations within recent years from various regions of the world (Sures *et al*. 1999*a*). Eel parasite species introduced to Europe and which have achieved considerable attention are the swim bladder nematode *Anguillicola crassus* introduced from the far East (Taraschewski *et al*. 1987), the gill monogeneans *Pseudodactylogyrus anguillae* and *P. bini* originating from Tawain (Buchmann, Mellergard & Køie, 1987), and the intestinal acanthocephalan *Paratenuisentis ambiguus*, an endemic eel parasite of brackish waters along the east coast of the USA (Samuel & Bullock, 1981; Taraschewski *et al*. 1987). Due to its harmful effects on eels (Molnár, Székely & Baska, 1991; Würtz, Taraschewski & Pelster, 1996; Würtz & Taraschewski, 2000) *A. crassus* has become the most studied introduced eel parasite as demonstrated by a still increasing number of investigations (e.g. Ashworth & Kennedy, 1999; Sures, Knopf & Taraschewski, 1999*b*; Kelly, Kennedy & Brown, 2000; Sures, Knopf & Kloas, 2001).

Although eel parasite community structure (e.g. Kennedy, 1995; Barker, Marcogliese & Cone, 1996;

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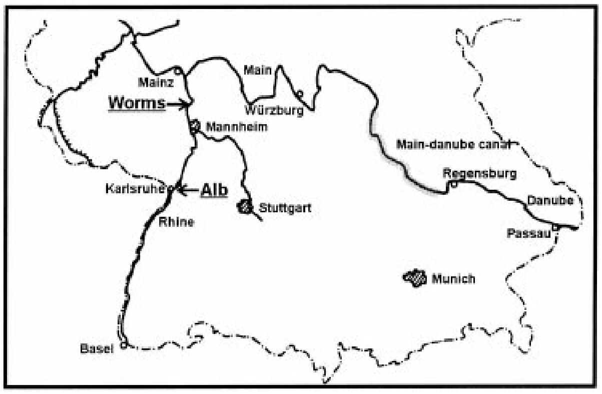

Fig. 1. Location of the sampling sites along the River Rhine.

Marcogliese & Cone, 1996; Kennedy *et al.* 1996; Kennedy, 1997; Schabuss *et al.* 1997; Kennedy *et al.* 1998; Sures *et al.* 1999*a*) as well as parasite biodiversity in general (Bush, Aho & Kennedy, 1990; Esch, Bush & Aho, 1990; Poulin, 1996) have been of growing interest to ecological parasitologists in recent years, the role of macro-invertebrates as necessary intermediate hosts for a number of helminths, e.g. most of the acanthocephalan species, was seldom considered. In respect of the River Rhine 468 macro-invertebrate species were recorded in the years 1986–1995 (Schöll, Becker & Tittizer, 1995). After the inauguration of the Main-Danube canal in 1992 that connects the Danube system with the Rhine system (Fig. 1), several ponto-caspian amhpipod and isopod species including e.g. *Corophium curvispinum*, *Dikerogammarus villosus* and *Jaera istri* have recently started to migrate from the confluence of the rivers Rhine and Main into northern and southern parts of the Rhine river system (Tittizer, 1996; Tittizer & Banning, 2000).

Thus, the present study was designed to determine species richness and diversity of helminths of European eels from two sampling sites of the River Rhine whilst simultaneously considering also the distribution of particular macroinvertebrates (crustaceans) known to act as intermediate hosts for different helminths.

MATERIALS AND METHODS

Study area and organism collection

Eels were collected by electrofishing at 2 sites on the River Rhine in July and August 1999. One is located near Karlsruhe: the other site was approximately 80 km in the north, near the city of Worms (Fig. 1). Eels were sampled in the main stream at both sites which were similar in flow rate, stream width and substratum. At the site Worms 35 eels (size: $57{\cdot}2 \pm 7{\cdot}0$ cm, weight: 331 ± 183 g) were collected (Worms). Another 19 eels (size: $60{\cdot}7 \pm 5{\cdot}6$ cm, weight: 382 ± 126 g) were caught near the confluence of the small river Alb and the river Rhine (Alb). The fish were brought back alive to the laboratory, killed and examined immediately for metazoans as described by Sures *et al.* (1999*a*).

At the eel sampling sites samples of the macro-invertebrates were taken in several years between 1995 and 1999. At Worms crustaceans were collected by hand from stones taken from the embankment with a claw arm. Near the site Alb approximately 3 km upstream the river Alb macro-invertebrate samples were taken with sieves from the choreotopes lethal, psamal, phytal and akal (time sampling, 10 min, 2 persons). Additional data about the crustaceans at the site Alb in the river Rhine were provided by the environmental protection agency (Karlsruhe) after crustaceans were collected by hand from stones. The animals were immediately fixed in ethanol and the crustaceans were determined using a stereobinocular according to the method described by Nagel (1989).

Determination of intestinal helminth community structure and statistical treatment

The terms prevalence, mean intensity and abundance were used according to the usage of Bush *et al.* (1997). Measures of community structure and similarity for the intestinal helminths were those used by Kennedy (1993*b*) and Sures *et al.* (1999*a*). The Mann-Whitney U-test was employed to determine significant differences among the diversity characteristics of the intestinal infra-community.

RESULTS

Composition of the parasite community

Data on the parasites found in and on the eels from the sampling sites are summarized in Table 1. At both sites highest prevalences were exhibited by the gill monogeneans *P. bini* and/or *P. anguillae* and the swim bladder nematode *A. crassus*. As most eels were heavily infested by both monogenean species the species were not separated. Therefore the prevalence given in Table 1 summarizes the data for eels parasitized with either both or one of both *Pseudodactylogyrus* species. Six different species of intestinal helminths were present in the fish: 3 acanthocephalan species (*Paratenuisentis ambiguus*, *Pomphorhynchus laevis* and *Acanthocephalus anguillae*), the nematode *Raphidascaris acus* and the cestodes *Bothriocephalus claviceps* and *Proteocephalus macrocephalus*. *P. laevis* and *P. macrocephalus* were present only in eels from Alb.

Macro-invertebrates

The abundance of the crustaceans around Worms and near the site Alb (rivers Alb and Rhine) between the years 1995 and 1999 is summarized in Table 2. At the site Worms the crustacean fauna only comprises 3 species in 1999, all originating from the

Table 1. Prevalence (P) in percent, Mean Intensity (MI) (±S.D.), and Abundance (A) (±S.D.) of the parasites of eel from 2 sites along the River Rhine

Location		Worms			Alb		
Parasite	Site*	P	MI	A	P	MI	A
Anguillicola crassus	SB	94·3	8.6 (13·4)	8·1 (13·2)	89·5	9·1 (7·4)	8·6 (7·5)
Paratenuisentis ambiguus	I	14·3	29·8 (44·8)	4·3 (18·7)	36·8	16·3 (26·3)	6·0 (17·2)
Acanthocephalus anguillae	I	2·9	2·0†	0·1 (0·3)	15·8	4·0 (2·6)	0·6 (1·7)
Pomphorhynchus laevis	I	–	–	–	15·8	1·0 (0·0)	0·2 (0·4)
Raphidascaris acus	I	2·9	5·0†	0·1 (0·9)	26·3	4·8 (4·8)	1·3 (3·1)
Bothriocephalus claviceps	I	5·7	5·0 (5·7)	0·3 (1·5)	15·8	1·7 (1·2)	0·3 (0·7)
Proteocephalus macrocephalus	I	–	–	–	15·8	4·7 (2·5)	0·7 (1·9)
Pseudodactylogyrus sp.	G	94·3	N.D.	N.D.	89·5	N.D.	N.D.

* SB, swim bladder; I, intestine; G, gills.
N.D., Not determined.
–, Not found.
† Only 1 eel infected.

Table 2. Abundance of crustacean macro-invertebrates at the sampling sites

Location	Worms*			Alb (River Alb)†				Alb (River Rhine)‡			
	95	96	99	96	97	98	99	95	96	97	98
Asellus aquaticus	–	–	–	226	106	61	2	–	–	–	1
Jaera istri	–	–	720	–	–	3	1	–	–	–	–
Echinogammarus berilloni	–	–	–	–	–	–	–	1	1	–	–
Echinogammarus ischnus	2	–	–	–	–	–	–	–	4	3	2
Gammarus tigrinus	153	7	–	–	–	–	–	1	2	1	1
Gammarus pulex	–	–	–	6	64	51	166	2	2	2	2
Gammarus roeseli	–	–	–	2	12	8	15	–	–	–	–
Gammarus fossarum	–	–	–	–	–	13	24	1	–	–	–
Dikerogammarus villosus	1	312	470	6	–	4	–	–	–	3	7
Corophium curvispinum	12390	3880	2600	–	–	–	–	2	2	2	–

* Individuals/m².
† Individuals/10 min sampling.
‡ Estimated frequency according to Knöpp (1955), with 1 (single occurrence of a species) to 7 (massive occurrence).

ponto-caspian region with *C. curvispinum* being the dominant species. Whilst *Gammarus tigrinus* has become extinct, there was a clear increase in the abundance of *Dikerogammarus villosus* and *Jaera istri*. Both amphipod species as well as the isopod are not known to act as intermediate hosts for intestinal parasites.

At both sites near Alb a higher number of crustacean species was found compared with Worms. The abundance of the 3 gammarids *Gammarus pulex*, *G. roeseli* and *G. fossarum* increased from 1996 to 1999 whilst the numbers of *Asellus aquaticus* and *J. istri* decreased in the river Alb. Although not present in the river Alb, *G. tigrinus* was detected in the river Rhine near Karlsruhe from 1995 until 1998. In the same period the abundance of both *Echinogammarus* species decreased whilst that of *D. villosus* increased. Additionally, also *C. curvispinum* and *A. aquaticus* were detected. *G. pulex* occurred throughout the years in low numbers.

The gammarids *G. pulex*, *G. roeseli* and *G. fossarum* are intermediate hosts for *P. laevis*, found only at Alb whereas *G. tigrinus* is the intermediate host for *P. ambiguus*. The isopod *A. aquaticus* is used as the intermediate host for *A. anguillae* and *A. lucii*. However, although the invading crustaceans have reached the Rhine near Karlsruhe, there are still macroinvertebrates used as intermediate hosts for the acanthocephalans found in the eels.

Intestinal component community structure

Summarized data on the intestinal helminth component community structure are given in Table 3. The sampling site Alb showed a higher diversity (Shannon-Wiener and Simpson's Index) than Worms. The evenness at Worms reached about 30 % of the maximum theoretical value whereas Alb showed a considerably higher evenness. Accordingly, the Berger-Parker index was lower for eels from Alb compared with Worms. At both sites *P. ambiguus* dominated the intestinal component communities. Sörensen Index revealed a similarity between the sites Alb and Worms of 67 %.

Table 3. Comparison of the diversity characteristics of the intestinal helminth component communities of eels from the River Rhine

	Worms	Alb
No. of eels	35	19
No. of species	4	6
Shannon-Wiener Index	0·42	1·11
S-W Evenness	0·30	0·62
Simpson's Index	1·23	2·12
Berger-Parker Index	0·90	0·67
Dominant species*	*Pa*	*Pa*

* *Pa*, *Paratenuisentis ambiguus*.

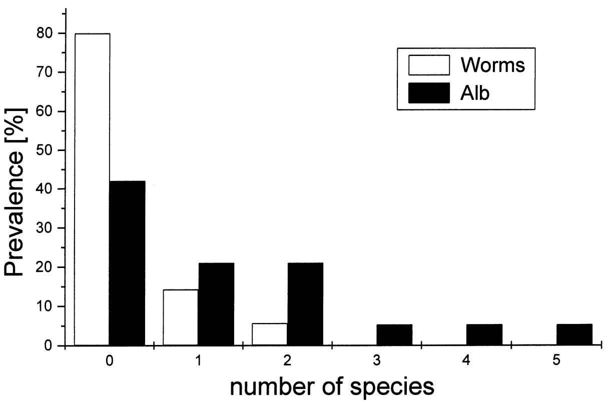

Fig. 2. Prevalence of coexistent helminth species in the intestine of eels from 2 sampling sites of the River Rhine.

Table 4. Comparison of the diversity characteristics of the intestinal infra-community of helminth of eels from the River Rhine

		Worms	Alb
No. of eels		35	19
No. of helminths	$\bar{x}$	4·7	9·1*
	S.D.	18·9	21·2
No. of helminth species (all eels)	$\bar{x}$	0·3	1·3*
	S.D.	0·6	1·5
	Max	2	5
No. of helminth species (infected eels only)	$\bar{x}$	1·3	2·2
	S.D.	0·5	1·3
Brillouin's Index (all eels)	$\bar{x}$	0·02	0·22*
	S.D.	0·08	0·33
	Max	0·37	1·02
Brillouin's Index (infected eels only)	$\bar{x}$	0·10	0·38*
	S.D.	0·17	0·36

* Significantly different (U-test, $P \leqslant 0{\cdot}05$).

Intestinal infra-community structure

The composition of the intestinal infra-community was analysed and the results are presented in Fig. 2 and Table 4. The prevalence differs markedly between the sampling sites (Fig. 1). At Worms 80% of the eels were uninfected, whereas only 40% of the eels from Alb had no intestinal helminths. The highest number of coexistent worms was 2 at Worms but 5 at Alb. Accordingly, the mean number of helminth species was approximately 4 times higher at Alb than at Worms (Table 4). Values of Brillouin's diversity index were significantly lower (U-test, $P \leqslant 0{\cdot}05$) at Worms compared with Alb, indicating the higher diversity at the latter site.

Statistical analysis revealed a significantly lower (U-test, $P \leqslant 0{\cdot}05$) number of helminths and helminth species, as well as significantly lower abundance for all intestinal helminths except for *B. claviceps* at Worms compared with Alb.

DISCUSSION

The parasitological examination of the eels from the river Rhine revealed a total of 9 different metazoan parasite species. This number is similar to that of a recent study of the parasite community of eels in the river Rhine (Sures *et al.* 1999*a*), as well as to corresponding data from Belgium (Schabuss *et al.* 1997), Denmark (Køie, 1988), England (Kennedy, 1993*b*, 1997), Ireland (Conneely & McCarthy, 1986), and Italy (Kennedy *et al.* 1996, 1998). In the present study, the eels were infected neither by eye flukes (such as metacercariae of *Diplostomum* spp.) nor by parasitic crustaceans (like *Ergasilus* spp.) which frequently infest freshwater eels (Kennedy, 1974; Conneely & McCarthy, 1986; Køie, 1988).

The most prevalent helminths were eel-specific parasites like *A. crassus*, *P. ambiguus* and *Pseudodactylogyrus* spp. The swim bladder nematode *A. crassus* was found in approximately 90% of the eels, a level slightly higher when compared with other studies on the occurrence of *A. crassus* in Europe. Würtz, Knopf & Taraschewski (1998) and Sures *et al.* (1999*a*) reported prevalences between 60 and 80% for the river Rhine near Karlsruhe. Thus, it seems that *A. crassus* may reach a prevalence in eels in the River Rhine of 100% in the near future. The rapid and successful spread of *A. crassus* across the European continent, which is still going on, was assisted by both human activity (Belpaire *et al.* 1989; Kennedy & Fitch, 1990), and the excellent colonization ability of the nematode (Kennedy & Fitch, 1990). The life-cycle of this nematode involves copepods and other crustaceans as intermediate hosts (De Charleroy *et al.* 1990; Kennedy & Fitch, 1990; Moravec & Konecny, 1994; Knopf *et al.* 1998). About 30 fish species are known to serve as paratenic or metaparatenic hosts, assisting the spread of *A. crassus* (Haenen & Van Banning, 1991; Thomas & Ollevier, 1992; Moravec & Konecny, 1994; Székely, 1994, 1995, 1996; Sures *et al.* 1999*b*). At least 1 species of aquatic snail (Moravec, 1996), but also amphibians and aquatic insects (Moravec & Škoriková, 1998), can act as paratenic hosts. In

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addition to its low intermediate and paratenic host specificity, the nematode's ability to survive and reproduce in eels under many conditions accelerate its spread (Kennedy & Fitch, 1990; Knopf *et al*. 1998; Kirk, Lewis & Kennedy, 2000).

In the present study the highest number of different parasite species was recorded from the intestine of eels, which contained up to 6 different helminths. Among these, acanthocephalans were the most prevalent worms with *P. ambiguus* as the dominant species of the intestinal component communities. However, there was a significant difference concerning infection of eels with this acanthocephalan between Worms and Alb. The abundance as well as the prevalence of *P. ambiguus* was much lower at Worms. At this site the amphipod community was dominated by *C. curvispinum*, a crustacean which is not yet known to act as an intermediate host for acanthocephalans. The specific intermediate host for *P. ambiguus*, the amphipod species *G. tigrinus* was frequently detected at the sampling site Alb in the river Rhine until 1998 which is in contrast to the crustacean community near Worms, where *G. tigrinus* seems to have gone extinct. Until 1995 *G. tigrinus* was one of the most abundant crustaceans in the whole Rhine river (Bernauer, Kappus & Jansen, 1996; Tittizer, 1996). Subsequently the abundance dropped down most likely due to a decreasing salinity of the river. At the same time a massive invasion and spread of the ponto-caspian crustacean species occurred, spreading from the confluence of the rivers Rhine and Main to both northern and southern areas of the Rhine system (Tittizer, 1996; Kelleher *et al*. 1998; Tittizer & Banning, 2000). Consequently also the prevalence of *P. ambiguus* in eels caught near Karlsruhe seems to have decreased. In 1995 *P. ambiguus* had a prevalence between 40 and 57% with a mean intensity (mean $\pm$ S.D.) of up to 41·6 $\pm$ 43·9 (Sures *et al*. 1999*a*) which was approximately 2·5 times higher than the intensity in the present study. Additionally, a study on the diet of eels showed that *C. curvispinum* was the most important prey for eels in the Lower Rhine even if *C. curvispinum* and *G. tigrinus* occurred in similar abundances (Kelleher *et al*. 1998). Thus, even if *G. tigrinus* is abundant, the prevalence and intensity of *P. ambiguus* would decrease as the amphipod became a less important food item for eel. Furthermore, in the River Alb near the confluence with the Rhine the abundance of *Asellus aquaticus* dropped down whilst that of *G. pulex* and *G. fossarum* increased. This shift may be due to an increase of water quality. However, the isopod as well as the *Gammarus* species are important intermediate hosts for acanthocephalans, which is in contrast to the crustaceans occurring at Worms.

The intestinal component-communities exhibited a low diversity and were dominated by the eel specific worm *P. ambiguus*. At the sampling site Alb, diversity indices were higher than at Worms. Consequently the evenness reached higher, and the dominance lower, values. Considering the data from 1995 (Sures *et al*. 1999*a*), diversity was markedly higher at Alb in the present study. This higher diversity is most likely related to a decrease of *P. ambiguus* and an increase of *A. anguillae* and *P. laevis*. Comparing the diversity characteristics of the eels caught in the River Rhine with data from Italian lakes (Kennedy *et al*. 1996), the potential to build up a diverse community does not appear to be realized for the eels investigated here. The evenness reaches only up to 64% and less, whereby values of up to 100% were described for lakes in Italy (Kennedy *et al*. 1996). Thus, there is a high potential for a more diverse helminth community of the eels from the River Rhine.

The present study has revealed changes in the helminth communities in eels over time and between different places. The low parasite diversity found at the sampling site Worms may reflect the influence of immigrating amphipod species which tend to dominate the amphipod communities in the River Rhine near the confluence of the rivers Main and Rhine. The data provide a baseline, as the need for more sustained long-term measurements remains (Kennedy, 1997), to distinguish natural parasite community changes (background fluctuations) from fluctuations due to changing communities of the respective intermediate hosts.

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