Long-term investigation of the composition and richness of intestinal helminth communities in the stocked population of eel, *Anguilla anguilla*, in Neusiedler See, Austria

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SUMMARY

Data from a long-term study of the intestinal helminth parasite community of eels, *Anguilla anguilla*, stocked into the shallow eutrophic Neusiedler See, Austria, were collected over an 8 year period (1994–2001). In total, 720 eels from 2 sampling sites were examined. The parasite community showed characteristics similar to those in the natural eel populations in rivers of the UK and mainland Europe: it was species poor, with only 5 species (*Acanthocephalus lucii*, *Acanthocephalus anguillae*, *Raphidascaris acus*, *Proteocephalus macrocephalus*, *Bothriocephalus claviceps*) comprising the component community and a maximum infracommunity richness of 4 species. Over the period, the intestinal parasite community of the sampling site in Illmitz, which was originally dominated by *A. lucii*, changed. As levels of *A. anguillae* increased to a point at which it dominated the community, diversity increased whilst dominance of a single species decreased. By contrast the community in the southern sampling site remained rather constant with a continuous high infection level of *A. anguillae* and low abundance of *A. lucii*. Both acanthocephalan species exhibited higher infection levels in larger eels and in different seasons of the year and the infection parameters were significantly different between the years of study. The significant differences in the infection levels of the 2 acanthocephalan species at the 2 sampling sites were surprising as both acanthocephalan species use the same intermediate host, *Asellus aquaticus*, and the sampling sites were in close proximity and were similar in terms of water quality, host size and invertebrate abundance. Differences in the fish communities of the 2 sampling sites and eel movements rather than interspecific competition are discussed as possible explanations for the differences in the parasite communities of the 2 sampling sites.

Key words: *Anguilla anguilla*, parasite community, diversity, *Acanthocephalus lucii*, *Acanthocephalus anguillae*.

INTRODUCTION

Long-term studies on host–parasite systems are generally rare in parasitology though of crucial importance to better understanding of many aspects of parasite ecology (Kennedy, 1993). This is also the case in fish parasite systems and most of the published data on the intestinal helminth communities in European eels, *Anguilla anguilla*, have been obtained from short-term investigations that have extended over 3 years or less (Kennedy *et al*. 1997; Schabuss *et al*. 1997; Sures *et al*. 1999; Kennedy, 2001; Sures & Streit, 2001; Norton, Lewis & Rollinson, 2003). In general, these studies have shown that intestinal helminth communities of eels in the UK and mainland Europe are isolationist in character, exhibiting low densities, low species diversity, with low richness and high dominance, usually by a single acanthocephalan or nematode species. Only a few publications (Kennedy, 1993, 1997; Kennedy *et al*. 1998; Kennedy & Moriarty, 2002) describe long-term changes in composition and richness of eel parasites.

Most of the investigations were carried out in small (Kennedy, 1993, 1997) or large rivers (Kennedy *et al*. 1998; Sures *et al*. 1999; Sures & Streit, 2001; Kennedy & Moriarty, 2002; Norton *et al*. 2003) and data about parasite communities in eels from lakes are very rare (Moravec, 1985; Køie, 1988*a*, *b*). Such data as do exist were obtained from naturally occurring eel populations. The data presented here are the results of an 8-year investigation into the composition and structure of intestinal helminth communities in eels from 2 sites in Neusiedler See, Austria.

The eel stock in Neusiedler See, like in many other lakes of Central and Eastern Europe, is based on

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allochtonous populations and has been maintained by regular massive stocking since 1958 (Herzig *et al.* 1994). This therefore represents the first study of the intestinal parasite community of a stocked, unnatural eel population and the Neusiedler See could be used as a model for other water bodies in Europe where eel is not naturally occurring, for instance Lake Balaton, Hungary (Herzig *et al.* 1994).

Furthermore, since the establishment of the trans-boundary national park Neusiedler See-Seewinkel between Austria and Hungary in 1993, stocking of eels has been prohibited. The eel population was therefore predicted to decline and was expected to become extinct within 10 years due to the ongoing fishery (Herzig *et al.* 1994). As the samples were taken from 1994 to 2001 this appeared to provide a unique opportunity to compare the dynamics of the intestinal parasite community of the declining, stocked host population in Neusiedler See with stable, natural eel populations as in Lough Derg, Ireland (Kennedy & Moriarty, 2002) and the river Tiber, Italy (Kennedy *et al.* 1998).

MATERIALS AND METHODS

Study areas and organism collection

The Neusiedler See (47°45′N 16°48′E) is the largest, westernmost steppe lake in Europe. The basin of this shallow, eutrophic lake covers an area of 321 km^2 across the Austrian-Hungarian border. The mean depth of the lake is 1·2 m and the water temperatures can reach more than 30 °C during summer. A dense reed belt (*Phragmites communis*) encircles the lake and covers more than 50% of the lake area (180 km^2). The average conductivity in the reed belt lies between 2000 and 4000 μS and the salinity can reach 2 g/l (Wolfram *et al.* 2001; Herzig, Kubecka & Wolfram, 2002). Eels were collected by electrofishing in the course of an ecological investigation of the fishery of the reed belt (Wolfram *et al.* 2001) at 2 different sampling areas, located about 5 km apart from each other: in the bay of Illmitz and in the southern part of the lake (Fig. 1). Wherever possible samples were taken at least once a year at both localities, but as sampling had to fit into the fishery ecological investigation it was more frequent in some years at one sampling area (1995 and 1996 in Illmitz and 1997 and 1998 in the southern area) whereas no samples were taken in others (1999 and 2000). Sampling spanned a period of 8 years from 1994 to 2001 and a total of 19 samples were taken. Details of sample times and sample sizes are given in Table 1. Sampling was normally restricted to spring (March to May), summer (June to August) and autumn (September to November) as the freezing of the lake rendered electrofishing impossible in winter. The number of eels per sample ranged from 5 to 68 (mean 37·9±14·4 S.D.).

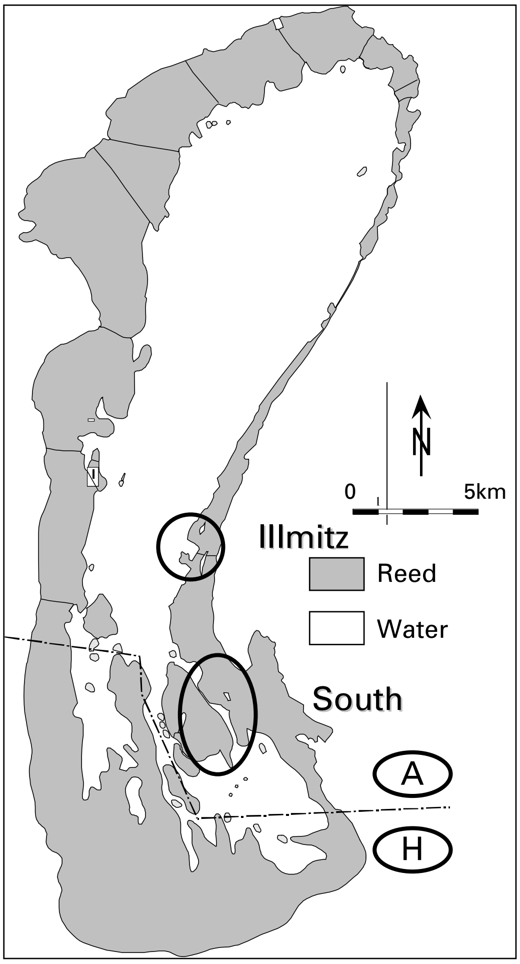

Fig. 1. Eel sampling areas in the bay of Illmitz and in the southern part of Neusiedler See (after Wolfram *et al.* 2001). A, Austria; H, Hungary.

A total of 424 eels were caught in the bay of Illmitz (mean size: 39·8±10·5 cm, mean weight: 119±107 g, sex ratio male to female 1:5) and 296 specimens in the southern area of the lake (mean size: 43·2±9·3 cm, mean weight: 141±105 g, sex ratio male to female 1:11). The fish were transported to the laboratory alive and their weight (±0·1 g) and length (±0·1 cm) were recorded. The eels were killed by decapitation, the abdomens were opened, the fish were sexed according to the appearance of the gonads (Tesch, 1977) and the swimbladders and intestines were removed and examined for helminth parasites by standard methods (for details see Schabuss *et al.* (1997)). The detailed data and results concerning the swimbladder nematode *Anguillicola crassus* will be presented in a separate paper. All endo-helminths in each eel were identified to species and counted.

Determination of helminth community structure and statistical treatment

In order to describe the parasite population structure, the terms prevalence (P%), mean intensity (MI)

Table 1. Dates of fishing, sample sites, season and number of eels examined (*n*)

Sampling site	Date	Season	*n*
Illmitz	25 April 1994	Spring	19
	23 March 1995	Spring	23
	27 April 1995	Spring	40
	3 August 1995	Summer	54
	2 November 1995	Autumn	39
	28 April 1996	Spring	68
	19 June 1996	Summer	29
	20 October 1996	Autumn	37
	25 August 1997	Summer	33
	26 September 1998	Autumn	41
	1 May 2001	Spring	41
South	27 April 1996	Spring	5
	24 May 1997	Spring	39
	19 June 1997	Summer	61
	1 August 1997	Summer	50
	25 August 1997	Summer	30
	27 April 1998	Spring	38
	26 September 1998	Autumn	39
	2 May 2001	Spring	34

and abundance (AB) were used according to Bush *et al*. (1997). The measures of community structure and similarity for the endoparasitic helminths detected were those employed in previous investigations (Kennedy, 1993, 1997; Sures *et al*. 1999; Kennedy & Moriarty, 2002; Norton *et al*. 2003). The measures of component community structure were Simpson's index (1/D), the Shannon Wiener index ($H' \log_2$), Evenness [$H'/\log_2(S)$], and the Berger Parker dominance index (BP). Infracommunity parameters were Brillouin's index and the mean number of species and individuals of the helminths per eel. All indices were calculated according to Magurran (1988). The ratio of variance to mean abundance was used as an index of dispersion. The effects of year, season and host length on prevalence, mean intensity and abundance of *A. lucii* and *A. anguillae* and on the number of species and number of helminth parasites per eel were explored with an Analysis of Variance (ANOVA, General Linear Model Procedure available in SPSS 10.0). Year (1994, 1995, 1996, 1997, 1998 and 2001), season (spring, summer, autumn) and size class (<30, <40, <50 and >50 cm) were entered as categorical predictors and individual host length (L) as a covariate. Significance was accepted for $P \leqslant 0{\cdot}05$.

RESULTS

Composition of the parasite community

During the 8-year study, a total of 720 eels was examined with overall 6014 helminth specimens found in the intestines. The intestinal helminth community of eels in Neusiedler See was composed of 5 species (Table 2): 2 acanthocephalan species, 2 cestode species and 1 nematode. As the prevalence, mean intensity and abundance of the parasite species *A. lucii*, *A. anguillae* and *P. macrocephalus* were significantly different ($P < 0{\cdot}001$) between the 2 sampling sites and the acanthocephalans represented the vast majority of the parasite community, the 2 locations were analysed separately. In Illmitz, the highest values of prevalence, mean intensity, mean and relative abundance from 1994 to 1998 were recorded for *A. lucii* in each year. The relative abundance of *A. lucii* as a proportion of the total number of all helminth species decreased from 0·95 in 1995 to 0·3 in 1998 and stayed at this low level until 2001. The relative abundance of *A. anguillae*, which exhibited the second highest infection levels until 1998, increased from 0·01 in 1995 to 0·57 in 2001 and became the most prevalent and abundant intestinal helminth species in Illmitz in 2001. The 2 cestode and especially the nematode species occurred at low levels of infection throughout the study period. In the southern sampling site *A. anguillae* exhibited the highest levels of infection from 1996 to 2001, whereas *A. lucii* constantly occurred at rather low values of prevalence, mean intensity and abundance. The 2 cestode and the nematode species occurred at even lower levels than in Illmitz.

The effects of host size, season of sampling and year of study on helminth communities

As the 2 acanthocephalan species dominated the parasite community, the influence of host length, season of sampling (spring, summer, autumn) and year of study on the prevalence, mean intensity and abundance of *A. lucii* and *A. anguillae* from the 2 sampling sites was tested for statistical significance. The results of the general linear model are presented in Table 3. All 3 parameters had a significant influence on the infection levels of *A. lucii* and *A. anguillae*. Concerning the year of study *A. lucii* was significantly more prevalent ($P \leqslant 0{\cdot}05$) and abundant ($P \leqslant 0{\cdot}05$) in 1996 in Illmitz, whereas there was no significant difference in the infection levels of *A. lucii* in the southern part of the lake. In Illmitz, *A. anguillae* was significantly more abundant ($P \leqslant 0{\cdot}001$) and prevalent ($P \leqslant 0{\cdot}001$) and showed higher mean intensities ($P \leqslant 0{\cdot}05$) in 2001 than in all other years. In the southern sampling area *A. anguillae* showed significantly higher values of abundance ($P \leqslant 0{\cdot}01$) and mean intensity ($P \leqslant 0{\cdot}001$) in 1998.

The prevalence ($P \leqslant 0{\cdot}001$), mean intensity ($P \leqslant 0{\cdot}01$) and abundance ($P \leqslant 0{\cdot}001$) of *A. lucii* in Illmitz were significantly higher in autumn than in spring or summer, whereas in the southern sampling site *A. lucii* showed higher values of abundance ($P \leqslant 0{\cdot}05$) and prevalence ($P \leqslant 0{\cdot}05$) in spring than in summer and autumn. *A. anguillae* exhibited significant higher abundance ($P \leqslant 0{\cdot}01$) and mean intensity ($P \leqslant 0{\cdot}01$)

Table 2. Prevalence (P%), mean intensity (MI) ± standard deviation (S.D.), mean abundance (± S.D.) and relative abundance of each helminth species as a proportion (p_i) of the total number of all helminth species in the intestines of eels from 2 sites in Neusiedler See

(s^2/x, variance over mean ratio; *, numbers too small for calculation of S.D. to be meaningful.)

	Illmitz						South			
Year	1994	1995	1996	1997	1998	2001	1996	1997	1998	2001
Acanthocephalus lucii										
P%	21·1	52·6	67·9	54·6	48·8	58·5	40·0	13·3	13·0	29·4
MI	3·8	7·4	12·3	6·7	2·5	10·8	1·5	5·3	3,1	1,7
S.D.	4·3	9·7	21·8	7·4	1·4	10·9	*	7,2	1,9	1,3
AB	0·8	3·9	8·3	3·7	1·2	6·3	0·6	0,7	0,4	0,5
S.D.	2·4	7·9	18·8	6·4	1·6	9·9	*	3,2	1,2	1,0
p_i	0·88	0·95	0·87	0·64	0·3	0·39	0·17	0,1	0,02	0,07
s^2/x	7·0	16·2	42·6	11·1	2·0	15·4	1·3	14,0	3,7	2,1
Acanthocephalus anguillae										
P%		3·9	21·6	39·4	36·6	80·5		65,0	72,7	73,5
MI		1·3	3·5	2·8	2·6	11·7		9,7	25,3	7,2
S.D.		0·5	3·0	2·0	2·3	12·5		11,8	38,6	7,0
AB		0·1	0·8	1·1	1·0	9·4		6,3	18,4	5,3
S.D.		0·3	2·0	1·8	1·9	12·2		10,6	34,8	6,8
p_i		0·01	0·08	0·19	0·24	0·57		0,87	0,97	0,75
s^2/x		1·5	5·2	3·1	3·6	15·7		17,7	65,6	8,7
Bothriocephalus claviceps										
P%	5·3	0·6	11·9	15·2	26·8	7·3	20·0	3,3	3,9	20,6
MI	2·0	1·0	1·9	2·0	2·6	1·7	15·0	1,5	2,7	1,7
S.D.	*	*	1·5	2·2	3·3	1·2	*	0,8	1,5	0,8
AB	0·1	0·0	0·2	0·3	0·7	0·1	3·0	0,1	0,1	0,4
S.D.	0·5	0·1	0·8	1·1	2·0	0·5	*	0,3	0,6	0,8
p_i	0·12	0·002	0·02	0·05	0·18	0·01	0·83	0,01	0,01	0,11
s^2/x	2·0	1·0	2·9	3·8	5·7	2·1	15·0	1,8	3,2	1,7
Proteocephalus macrocephalus										
P%		9·6	5·2	24·2	22·0	19·5		2,2	1,3	8,8
MI		1·5	2·4	2·8	4·6	2·9		6,5	3,0	2,3
S.D.		1·3	2·6	2·6	5·0	1·5		7,1	*	2,3
AB		0·1	0·1	0·7	1·0	0·6		0,1	0,0	0,2
S.D.		0·6	0·8	1·7	2·9	1·3		1,3	0,3	0,9
p_i		0·03	0·01	0·12	0·25	0·03		0,02	0,002	0,03
s^2/x		2·4	4·7	4·4	8·6	3·0		12,4	3,0	3,8
Raphidascaris acus										
P%		1·3	1·5	3·0	2·4	2·4		0,6	7,8	8,8
MI		1·0	12·5	1·0	3·0	1·0		15,0	1,5	3,3
S.D.		*	16·3	*	*	*		*	0,8	1,2
AB		0·0	0·2	0·0	0·1	0·0		0,1	0,1	0,3
S.D.		0·1	2·1	0·2	0·5	0·2		1,1	0,5	1,0
p_i		0·003	0·02	0·01	0·02	0·002		0,01	0,01	0,04
s^2/x		0·99	23·07	1·00	3·00	1·00		15,00	1,80	3,41
No. of eels examined										
	19	156	134	33	41	41	5	180	77	34
No. of helminths										
	17	637	1292	190	161	675	18	1313	1469	227

in spring than in summer and autumn in both sampling sites.

There was no significant difference in the length frequency of eels from the 2 sampling areas, but significant differences ($P \leqslant 0{\cdot}001$) in length were found between the years of the study. The average length of eels increased slightly from 1994 to 2001. In Illmitz, *A. lucii* recorded significant higher mean intensity ($P \leqslant 0{\cdot}05$) in eels from 40–49·9 cm than eels smaller 30 cm and in the southern sampling site, eels larger 50 cm showed significantly higher prevalence ($P \leqslant 0{\cdot}01$), mean intensity ($P \leqslant 0{\cdot}05$) and abundance ($P \leqslant 0{\cdot}01$) than all other size classes. *A. anguillae* exhibited in Illmitz higher abundance ($P \leqslant 0{\cdot}01$) and prevalence ($P \leqslant 0{\cdot}01$) in eels larger than 50 cm than in fish smaller 30 cm. In the southern area *A. anguillae* showed higher abundance ($P \leqslant 0{\cdot}01$) and mean intensity ($P \leqslant 0{\cdot}01$) in eels larger than 50 cm than hosts

Table 3. Results of the general linear model examining effects of year, season and host length (L) on prevalence, intensity and abundance of *A. lucii* and *A. anguillae* in eel from 2 sampling sites in Neusiedler See (ANOVA tests)

	Illmitz						South					
	A. lucii			*A. anguillae*			*A. lucii*			*A. anguillae*		
Effect	D.F.	χ^2	*P*	D.F.	χ^2	*P*	D.F.	χ^2	*P*	D.F.	χ^2	*P*
Prevalence		($r^2=0,11$)			($r^2=0,32$)			($r^2=0,29$)			($r^2=0,10$)	
Year	5	1·4	<0·001	5	4·2	<0·001	3	1·3	<0·001	3	1·2	0·001
L	1	0·9	<0·05	1	0·2	0·22	1	0·9	<0·05	1	1·4	<0·01
Season	2	3·1	<0·001	2	0·8	<0·01	2	4·4	<0·001	2	1·1	<0·01
Intensity		($r^2=0,16$)			($r^2=0,26$)			($r^2=0,22$)			($r^2=0,26$)	
Year	1	1060·0	<0·001	4	135·8	0·07	3	70·2	0·06	2	9893·7	<0·001
L	5	1328·9	<0·05	1	128·3	0·15	1	141·1	<0·05	1	2512·8	<0·05
Season	2	2670·6	<0·001	2	1·5	0·98	2	16·1	0·55	2	7046·5	<0·001
Abundance		($r^2=0,17$)			($r^2=0,32$)			($r^2=0,19$)			($r^2=0,26$)	
Year	5	1421·4	<0·001	5	531·4	<0·001	3	66·8	<0·001	3	7533·6	<0·001
L	1	1380·8	<0·001	1	26·0	0·20	1	56·1	<0·01	1	2929·5	<0·01
Season	2	3594·6	<0·001	2	13·0	0·45	2	143·2	<0·001	2	9580·3	<0·001

Table 4. Diversity characteristics of the intestinal component communities of helminths of eels from 2 sites in Neusiedler See

(Data for whole year combined. *A. l.*, *Acanthocephalus lucii*; *A. a.*, *A. anguillae*; *B. c.*, *Bothriocephalus claviceps*.)

	Illmitz						South			
	1994	1995	1996	1997	1998	2001	1996	1997	1998	2001
No. of species	2	5	5	5	5	5	2	5	5	5
No. of helminths	17	637	1292	190	161	675	18	1313	1469	242
Shannon-Wiener index	0·52	0·36	0·79	1·49	2·07	1·22	0·65	0·74	0·27	1·27
S-W Evenness	0·52	0·16	0·34	0·64	0·89	0·53	0·65	0·32	0·12	0·55
Simpson's index	1·26	1·11	1·32	2·18	4·02	2·10	1·38	1·32	1·07	1·73
Berger Parker index	0·88	0·95	0·87	0·64	0·30	0·57	0·83	0·87	0·97	0·75
Dominant species	*A. l.*	*A. l.*	*A. l.*	*A. l.*	*A. l.*	*A. a.*	*B. c.*	*A. a.*	*A. a.*	*A. a.*
Ratio *A. l.*: *A. a.*	15 : 0	76 : 1	11 : 1	3·4 : 1	1·3 : 1	0·7 : 1	3 : 0	0·1 : 1	0·02 : 1	0·1 : 1

in the size classes of < 30 and < 40 cm and the prevalence was significantly lower ($P \leqslant 0·01$) in eels smaller than 30 cm than in all other size classes. Overall, the average size of eels increased slightly throughout the study period, both acanthocephalan species exhibited higher infection levels in larger eels and in a certain season and the infection parameters were significantly different between the years of study.

Component community profiles

Summarized data on the helminth component community structure of the 2 sampling areas for each year are shown in Table 4. Except in 1994 in Illmitz and 1996 in the southern area where the number of eels examined was very low, all 5 species were present at both sites in each year of the study. The Simpson's index, Shannon-Wiener index and Evenness varied in Illmitz from the lowest values in 1995 to maximum values in 1998. The diversity parameters were lower and varied to a smaller extent from 1996 to 2001 in the southern sampling site. The Berger Parker dominance index in Illmitz showed, after a high dominance of *A. lucii* from 1994 to 1996, a decrease from 1997 to 1998 and in 2001 *A. anguillae* dominated the component community. In the southern area *A. anguillae* remained the dominant species at a rather constant high level throughout the investigation. The small sample of 1996 when *B. claviceps* was the dominant species may be atypical. The species ratio between *A. lucii* and *A. anguillae* in the intestinal parasite community in Illmitz decreased drastically from a maximum value of 76 : 1 in 1995 to a value of 0·7 : 1 in 2001, whereas the ratio in the southern area remained rather constant from 1997 to 2001. The 2 acanthocephalan species represented the vast majority (in average > 80%) of the helminths found in the intestines of eels throughout the study.

Table 5. Diversity characteristics of the intestinal infracommunities of helminths of eels from 2 sites in Neusiedler See

(Data for whole year combined. x, mean; Max, maximum; *, numbers too small for calculation of S.D. to be meaningful.)

	Illmitz						South			
	1994	1995	1996	1997	1998	2001	1996	1997	1998	2001
No. of eels	19	156	134	33	41	41	5	180	77	34
No. of helminths (all eels)										
x	0·9	4·1	9·6	5·8	3·9	16·5	3·6	7·3	19·1	7·1
S.D.	2·4	7·9	19·6	7·9	5·2	19·1	*	11·9	34·9	7·8
No. of species (all eels)										
x	0·3	0·7	1·1	1·4	1·4	1·7	0·6	0·8	1·0	1·4
S.D.	0·5	0·7	0·8	0·9	1·1	0·8	*	0·7	0·7	0·9
Max.	1	3	3	3	4	4	2	3	3	4
No. of species (infected eels only)										
x	1·0	1·2	1·5	1·7	1·9	1·8	1·5	1·2	1·3	1·6
S.D.	*	0·4	0·6	0·7	0·8	0·7	*	0·5	0·5	0·7
Brillouin's index (all eels)										
x	0	0·03	0·11	0·20	0·23	0·29	0·09	0·06	0·07	0·17
S.D.	*	0·10	0·18	0·22	0·27	0·29	*	0·17	0·16	0·24
Max.	0	0·62	0·85	0·66	0·79	0·83	0·17	0·97	0·83	1·00
Brillouin's index (infected eels only)										
x	0	0·05	0·14	0·26	0·32	0·31	0·09	0·09	0·10	0·20
S.D.	*	0·13	0·20	0·23	0·27	0·28	*	0·20	0·18	0·25

Table 6. Prevalence (%) of coexisting helminth species in the intestine of eels from 2 sampling sites in Neusiedler See

(Data for whole year combined. *A. l.*, *Acanthocephalus lucii*; *A. a.*, *A. anguillae*.)

	Illmitz						South			
	1994	1995	1996	1997	1998	2001	1996	1997	1998	2001
0 species	73·7	42·3	25·4	21·2	29·3	4·9	60·0	31·1	26·0	11·8
1 species	26·3	48·1	44·0	30·3	24·4	36·6	20·0	55·6	50·6	44·1
2 species	0	9·0	27·6	39·4	29·3	46·3	20·0	11·1	22·1	35·3
3 species	0	0·6	3·0	9·1	14·6	9·8	0	2·2	1·3	5·9
4 species	0	0	0	0	2·4	2·4	0	0	0	2·9
% of eels infected with *A. l.* and *A. a.*	0	3·2	17·9	33·3	26·8	48·8	0	10·6	13·0	29·4

Infracommunity profiles

The composition of the helminth infracommunity of the eels from the 2 sampling sites for each year is presented in Table 5. The mean number of helminths species and specimens per eel (all eels) and the Brillouin's index increased in Illmitz from a minimum value in 1994 to a maximum in 2001. In the southern sampling site a similar trend was obvious, but the values of the diversity parameters were lower compared to Illmitz. The prevalences (%) of coexisting helminth species in the intestine of eels are shown in Table 6. The percentage of uninfected eels decreased in Illmitz from 74% in 1994 to 5% in 2001 and in the southern area from 60% in 1996 to 12% in 2001. Throughout the 8 years of study the individual eel harboured an increasing number of helminth species in each year and in Illmitz in 2001 more fish were infected with 2, 3 or 4 species than with 0 or 1 species. The percentage of eels infected with both acanthocephalan species increased with each year in both sampling sites (Table 6). The number of species and the number of helminth parasites per eel were significantly correlated with the year of study, season of sampling and host length. In Illmitz, the number of species was significantly higher ($P \leqslant 0{\cdot}001$) in each year than in the previous year, significantly more species ($P \leqslant 0{\cdot}05$) were recorded in autumn than in spring or summer and eels larger than 50 cm harboured significantly more species ($P \leqslant 0{\cdot}05$) than the smaller size classes. In the southern sampling site significantly more species ($P \leqslant 0{\cdot}05$) were found in

2001 than in all other years, the number of species was higher ($P \leqslant 0{\cdot}001$) in spring than in summer or autumn and eels larger than 50 cm harboured more ($P \leqslant 0{\cdot}05$) and eels smaller 30 cm significantly less ($P \leqslant 0{\cdot}001$) species than all other size classes.

The number of intestinal helminth specimens per eel in Illmitz was significantly higher ($P \leqslant 0{\cdot}01$) in 2001 than in all other years except 1996, more parasites ($P \leqslant 0{\cdot}01$) were found in autumn than in spring or summer and eels in the size class from 40 to 49·9 cm and larger than 50 cm harboured significantly more ($P \leqslant 0{\cdot}01$) parasites than eels smaller than 30 cm. In the southern sampling site significantly more ($P \leqslant 0{\cdot}05$) parasites were found in 1998 than in all other years, the number of helminths was higher ($P \leqslant 0{\cdot}001$) in spring than in summer or autumn and eels larger than 50 cm harboured more parasite specimens ($P \leqslant 0{\cdot}01$) than all other size classes.

DISCUSSION

The intestinal helminth parasite community of the stocked eel population in Neusiedler See showed characteristics similar to those in natural eel populations in rivers of the UK and mainland Europe (Kennedy, 1993; Kennedy *et al.* 1997, 1998; Sures *et al.* 1999; Sures & Streit, 2001; Kennedy & Moriarty, 2002). The component community consisted of 5 helminth species, all of these species have previously been reported from eels in Europe. This number of species is comparable with data on the intestinal parasite fauna reported for eels from rivers in Belgium (Schabuss *et al.* 1997), Germany (Sures *et al.* 1999; Sures & Streit, 2001), Ireland (Kennedy & Moriarty, 2002), Italy (Kennedy *et al.* 1997), Portugal (Saraiva & Eiras, 1996) and the Netherlands (Borgsteede *et al.* 1999). Higher component community richness (9, 11, 8 and 8 species) was reported from England (Kennedy, 1993, 1997; Norton *et al.* 2003) and Italy (Kennedy *et al.* 1998), respectively.

The intestinal parasite community in both sampling sites in Neusiedler See was heavily dominated by acanthocephalans. Such domination of a community by an acanthocephalan is a common characteristic of intestinal helminth communities in eels and has been reported from the UK and mainland Europe (Kennedy, 1990; Schabuss *et al.* 1997; Kennedy *et al.* 1998; Sures *et al.* 1999; Kennedy & Hartvigsen, 2000; Sures & Streit, 2001; Kennedy & Moriarty, 2002).

Within the 8 years of study significant changes in the structure and diversity of the parasite community in Neusiedler See were observed. The parasite community in Illmitz was heavily dominated by *A. lucii* from 1994 until 1998 but in 2001 *A. anguillae* dominated the parasite community, after increasing continuously from 1995 onwards. The diversity indices increased and more eels were infected with more parasite species with each year of the study. In the southern sampling site, the community structure remained rather constant with a continuous domination of *A. anguillae* and a very low proportion of *A. lucii*-infected eels. The diversity characteristics increased with each year but to a lower extent than in Illmitz. Comparing the component community of eels in Neusiedler See with the investigation in Lough Derg, Ireland (Kennedy & Moriarty, 2002), it is obvious that the Shannon-Wiener index and Simpson's index in Neusiedler See exhibited higher values (maximum 2·07 and 4·02 respectively) and varied over a higher range than in Lough Derg (maximum values 0·30 and 1·15). The Berger Parker dominance index in Illmitz decreased from a maximum value of 0·95 to a minimum of 0·3 and the dominating species changed within the study period, whereas in Lough Derg the high domination of *A. lucii* ranging from 0·93 to 1·0 remained constant throughout the 18 years of study. Thus the diversity in Neusiedler See was higher and varied to a higher extent between years than in Lough Dergh, while the dominance of a single species was lower and decreased throughout the study. The diversity in Neusiedler See was more similar to diversity characteristics reported from component communities of the 13-year study on the river Clyst (Kennedy, 1993) and short-term studies from coastal lagoons in Italy (Kennedy *et al.* 1997), the river Rhine (Sures *et al.* 1999; Sures & Streit, 2001) and the rivers Thames and Test (Norton *et al.* 2003).

On the intestinal helminth infra-community level, a higher maximum number of species per eel (4 species), similar mean number of species and mean Brillouin's index values, and lower mean number of parasites per eel were recorded in Neusiedler See compared to results from Lough Derg. The number of eels infected with 0 or 1 parasite species decreased and the percentage of eels infected with 2 or more species increased in both sampling sites in Neusiedler See throughout the 8 years of study, whereas the number of eels uninfected or with a single-species infection remained at a rather constant high level in Lough Derg. Results of the investigations on the eel parasite community of the River Tiber (Kennedy *et al.* 1998) showed lower diversity characteristics of the infracommunity than in Neusiedler See.

This increase in richness and diversity is very surprising as the eel population was predicted to decline and become extinct within 10 years after the prohibition of eel stocking in 1993 (Herzig *et al.* 1994). The infection levels and the diversity of the parasite community did not decline as a reaction to the predicted changes in the host population. So the question arose whether the eel population was in decline at all. Recent results from fish ecological investigations of the reed belt showed that despite a slight decrease in the eel population between 1994 and 1997, the eel stock in 2002 was at a similar level as in the early 1990s (Wolfram *et al.* 2001; Wolfram & Mikschi, 2003). In contrast to the findings of this study, the results of the fish ecological investigations showed that the length frequency distribution of eel did not change from 1988 to 2002 and the average size of eels did not increase (Wolfram *et al.* 2001; Wolfram & Mikschi, 2003). There was no decrease of specimens in the smaller size classes and small eels (<15 cm) were caught regularly until 2002, indicating constant illegal stocking.

Corresponding to such ongoing illegal stocking measures probably by local fishermen, the host population did not decrease after 1993. Thus, the characteristics of the intestinal parasite community reflected the unchanged eel population and moreover we observed an increase in helminth parasite diversity over the last decade.

The most important factors associated with the infection parameters of the dominating acanthocephalans in the 2 sampling sites in Neusiedler See were the year of study, season of sampling and length of eels.

In this study, we found a clear relationship between the parasite infection parameters and host size on both a total length and size-class basis. The influence of host length on parasite infection levels has been reported from various studies where larger eels harboured more parasites than smaller ones (Dogiel, Petrushevski & Polyanski, 1958; Moravec, 1985; Conneely & McCarthy, 1986; Molnar, Szekely & Perenyi, 1994; Schabuss *et al.* 1997; Poulin, 2000; Lefebvre *et al.* 2002; Audenaert *et al.* 2003), but various factors like sample size and size range of hosts are also of major importance and not all parasite species exhibit a correlation between intensity of infection and host size (see Poulin (2000) for a critical review). This accumulation of parasites in larger specimens is explained by a longer exposure time of older (=larger) eels to the parasite, a larger host area (intestine size) for parasite establishment, a higher degree of consumption of infected prey with increasing host size and a differential efficiency of the parasite transmission between intermediate and paratenic hosts (Poulin, 2000; Lefebvre *et al.* 2002). Moravec (1985) assumed that the intermediate host *Asellus aquaticus* is the main source of *A. lucii* infection for smaller eels, but their proportion in the food of large eels gradually decreases with increasing proportion of forage fish. Gut analyses showed that eels in Neusiedler See mainly feed on aquatic insects (Odonata, Coleoptera, Ephemeroptera and Trichoptera representing more than 50% of the food items throughout the year) and on *Asellus aquaticus* especially in spring, whereas planktonic animals and fish are of minor importance (Herzig *et al.* 1994; Wolfram *et al.* 2001). Eels in Neusiedler See become piscivorous at a size larger than 50 cm. As there are few eels in Neusiedler See with a body length exceeding 60 cm due to high population density and intensive fishing (Herzig *et al.* 1994; Wolfram *et al.* 2001; Wolfram & Mikschi, 2003), *Asellus aquaticus* seems to be the main source of infection with *A. lucii* and *A. anguillae* in this lake and eels larger than 50 cm seem to continue to feed intensively on this isopod. In this study the host length also had significant influence on the mean number of parasites and mean number of parasite species per eel. Norton *et al.* (2003) and Conneely & McCarthy (1986) reported a significant influence of eel length on the number of parasite species per eel, but no correlation between eel size and number of parasites per eel has been found in their study. The higher number of helminth species and specimens in larger eels in Neusiedler See may indicate a consumption of an increasing amount and variety of intermediate hosts with increasing host size.

Within this study, significant differences in the infection levels of both acanthocephalan species between the seasons of sampling were observed. *A. anguillae* exhibited significantly higher abundance and mean intensity in spring in both sampling sites. *A. lucii* recorded in Illmitz showed significantly higher abundance and mean intensity in autumn, whereas in the southern sampling site this parasite species displayed the highest values of abundance and prevalence in spring. Moravec (1985), Conneely & McCarthy (1986) and Kennedy *et al.* (1998) reported seasonality of parasite infections in eels, but not for acanthocephalans. Kennedy & Moriarty (2002) reported higher abundance of *A. lucii* in May, July and August, but noted that the increase in abundance is very dependent upon the values found in a single month and alternative samples in the same month can produce very different patterns of dispersion. Kennedy & Moriarty (1987) recorded lowest levels of abundance and prevalence of *A. lucii* and *A. anguillae* in March and April with an increase to a peak in mid-summer, a decrease in July and an increase again in autumn. A variety of ecological factors seem to account for the seasonal patterns and between-site variations in eel parasite infections (Conneely & McCarthy, 1986). Eels exhibit marked seasonality in their activity patterns and feeding intensity and temperature-related changes in feeding habits rather than physiological synchronization of parasite and host life-cycles are more likely to be responsible for the increased parasitizing of eels in certain seasons (Conneely & McCarthy, 1986). The gut analyses of the eel in Neusiedler See showed that eels were feeding more intensively in April and June while the feeding intensity decreased in summer and autumn and *Asellus aquaticus* was consumed intensively especially in spring (Herzig *et al.* 1994). This feeding behaviour of eel in Neusiedler See could explain the higher infection rate for acanthocephalans and the higher number of helminth species and specimens in spring in the southern sampling area. In Illmitz, however, the maximum infection level of

A. lucii was recorded in autumn and it seemed that this parasite utilized eel at a different time of the year than in the southern sampling site. Other ecological factors, like a different population cycle of *A. aquaticus* or different cycles in recruitment and reproduction of the parasite may influence the transmission of *A. lucii* in Illmitz.

The significant differences between the 2 sampling sites concerning the infection levels of *A. lucii* and the increasing infection of eel with *A. anguillae* in Illmitz are surprising. Both species use *Asellus aquaticus* as their intermediate host and the 2 sampling sites were in close proximity and were similar in terms of water quality, host size and invertebrate abundance (Wolfram *et al*. 2001). Neither acanthocephalan species are eel specialists: the preferred final host of *A. lucii* is the perch (*Perca fluviatilis*) and that of *A. anguillae* is the chub (*Leuciscus cephalus*). As the chub is absent in the Neusiedler See (Herzig *et al*. 1994; Wolfram *et al*. 2001), eel might be the preferred definitive host of *A. anguillae* as in Lough Derg (Kennedy & Moriarty, 1987, 2002).

Results of the fish ecological investigation of the reed belt showed that the fish community of the 2 sampling sites is different. Perch were more abundant in Illmitz than in the southern sampling area (Wolfram *et al*. 2001). Thus, the higher prevalence, mean intensity and abundance of *A. lucii* in Illmitz compared to the southern sampling site could be explained by the higher number of *A. lucii* introduced to the community by perch. Kennedy & Moriarty (2002) observed changes in the relative abundance of *A. lucii* and *A. anguillae* in Lough Derg and attributed these changes to differences in infection levels in different parts of the lake and to changes in the movement patterns of eels in the Lough. An increased movement of eels from areas with high abundance of *A. anguillae*, like in the southern sampling site, into the bay of Illmitz might be a cause for the increasing infection of eels with *A. anguillae* in this area.

Kennedy (1992) reported competition between *A. lucii* and *A. anguillae* in eels such that *A. anguillae* populations are depressed by its congener, whereas Kennedy & Moriarty (1987) could not detect competitive displacement or resource partitioning in space or time between these two acanthocephalans, but still considered that exploitation competition might occur. In this study it seems that in the southern sampling site, the proportions of the 2 species remained fairly constant over the period and both congeneric species of acanthocephalans co-exist in apparently stable equilibrium in eels. In Illmitz, however, the observed changing proportions and species ratios of *A. lucii* and *A. anguillae* and the increasing number of eels infected with both species, seem to reflect the differences in the fish community and eel movements into this sampling site rather than competition as *A. lucii* is reported to be the stronger competitor (Kennedy, 1992). However, resource partitioning in time might be possible in this sampling site, as indicated by the maximum infection levels of *A. lucii* in autumn and *A. anguilla* in spring.

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