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Long-term stability in the richness and structure of helminth communities in eels, *Anguilla anguilla*, in Lough Derg, River Shannon, Ireland

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Abstract

A data set on intestinal helminth parasites was collected in the course of an 18 year investigation into the biology of eels in Meelick Bay, Lough Derg, River Shannon. This was used to test two hypotheses relating to the composition and structure of intestinal helminth communities, namely that eels in large rivers do not harbour richer and more diverse communities than those in small rivers but that community composition and structure are more stable over time than in small rivers. The helminth community was species poor, with only six species comprising the component community and a maximum infracommunity richness of three species. The community was overwhelmingly dominated by the acanthocephalan *Acanthocephalus lucii*, reflecting the importance of its intermediate host *Asellus aquaticus* in the eels' diet. The remaining helminth species contributed to species richness but made very little contribution to community diversity. Population levels of *Acanthocephalus lucii* fell and remained low between 1992 and 2000, probably reflecting increased movement of eels from other parts of the lough into Meelick Bay. Diversity values were low, but similar to those reported from other rivers in Britain and Europe. The results provided support for both hypotheses and indicated that in respect of richness, diversity and dominance, the helminth communities of eels in the River Shannon were typical of, and comparable to, those of other large rivers throughout Europe.

Introduction

Studies on the intestinal helminth communities of eels *Anguilla anguilla* in freshwater have shown them to be isolationist in character, exhibiting low species richness and diversity (Kennedy, 1990, 1993, 2001; Schabuss *et al.*, 1997; Kennedy *et al.*, 1998; Sures *et al.*, 1999; Kennedy & Hartvigsen, 2000; Sures & Streit, 2001). There is often considerable spatial and temporal variation in community composition between and within localities but community structure seems to remain fairly constant and there is some evidence that the communities may be saturated (Kennedy & Guegan, 1994) and that there is a limit to infracommunity richness (Kennedy & Guegan, 1996). These generalizations apply not only to the British Isles, where many of these investigations were undertaken. but also to continental Europe (Schabuss *et al.*, 1997; Sures *et al.*, 1999).

Two issues have arisen from these ecological studies that have yet to be completely resolved. Firstly, Kennedy (1993, 1997) has shown that component communities in small rivers can not only vary in richness over time but also be amongst the richest such communities known from eel helminths. By contrast, eels in large rivers do not appear to harbour richer or more diverse helminth

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communities even though such rivers may have a large catchment area, be very productive and harbour a rich free-living biota (Saraiva & Eiras, 1996; Schabuss *et al.*, 1997; Sures *et al.*, 1999; Sures & Streit, 2001). Indeed, Sures *et al.* (1999) drew specific attention to the low diversity and high dominance of eel helminth communities in the River Rhine, and queried why the potential to build up a diverse community does not appear to have been realized. There is a clear need for more studies on large rivers to clarify this issue. The second issue relates to community stability. Kennedy (1993) tested the hypothesis that parasite communities in a small river would be particularly variable in composition and subject to change over time. His findings supported the hypothesis that community composition was unstable, but indicated that community structure was fairly stable. A second long-term study on a small river (Kennedy, 1997) confirmed these findings. An investigation of long-term changes in helminth communities of eels in the River Tiber suggested that they were much more stable over time than those in small rivers (Kennedy *et al.*, 1998). This, however, is the only long-term study of eel helminth communities in a large river and there is a clear need for further studies to test this suggestion.

The data presented here are the results of an 18 year investigation into the composition and structure of helminth communities in eels of Lough Derg on the River Shannon, Ireland. They were undertaken as part of a long-term research programme studying the eel populations themselves. Some aspects of the parasitological findings have already been published (Kennedy & Moriarty, 1987; Kennedy, 1992) but these focused on interspecific interactions between acanthocephalan species within the community. The findings presented in this paper address issues of community composition and structure and aim specifically to test two hypotheses: that helminth communities in eels in large rivers are not richer or more diverse than those in small rivers, and that helminth communities in eels in large rivers are more stable over time than those in small rivers.

Materials and methods

The River Shannon is the largest river system in Ireland. It drains a catchment of some 11,700 km^2 and the river itself is 250 km long (McCarthy *et al.*, 1999). The gradient is naturally low, but flow is controlled for hydroelectric purposes. Lough Derg is the largest (11,635 ha) and most downstream of the lakes through which the Shannon flows and it is the site of the most productive eel fishery in the Republic of Ireland. The lough has been subject to increasing eutrophication (Flanagan & Toner, 1975; Bowman, 2000).

The parasites occurred as a natural infection in eels, and all samples were taken by fyke nets set in fixed places in one part of the lough only, in Meelick Bay (see Moriarty (1983) for details of location and sampling). At the commencement of the long-term programme in 1983, samples were taken monthly between March and November, but over the course of time the numbers of samples per year declined although an attempt was made to try and ensure that samples were taken in May, July and August or the months nearest to these. Representative sub-samples of 14 eels (wherever possible) were retained for parasitological investigation in every year up to 2001, although those from 1998 were subsequently lost in the post. Details of preservation and examination of eels are given in Kennedy & Moriarty (1987) and Kennedy (1993).

The measures of community structure adopted were those employed in previous investigations (Kennedy, 1993, 1997; Kennedy *et al.*, 1998; Sures *et al.*, 1999) in order to facilitate comparisons with the results of other studies. Component community parameters determined were Simpson's index (as 1/C), the Shannon-Weiner index, Evenness and the Berger-Parker dominance index. Infracommunity parameters were Brillouin's index (log n) and the mean numbers of species and individuals per eel. All indices were calculated as defined in Magurran (1988). Terms for describing populations are used as in Bush *et al.* (1997). The ration of variance to mean abundance was used as an index of dispersion. Correlations between indices were tested with Spearman's rank correlation coefficient. Because population levels showed clear seasonality, annual comparisons were based either on all data combined over all months for the year or on data from the same, or closest, months in each year.

Results

The intestinal helminth community of eels in Meelick Bay was composed of six species (table 1), all of which have previously been recorded from Ireland. The most prevalent species, and the only one present in all years and samples, was the acanthocephalan *Acanthocephalus lucii*, which is not an eel specialist. *Acanthocephalus anguillae* occurred in all years except 1999 and 2001, but at

Table 1. Prevalence of the intestinal helminth species in eels in Lough Derg.

Year	*A.l*	*A.a.*	*A.c.*	*R.a.*	*P.t.*	*B.c.*	No. of eels
1983	82.6	12.2	0	0	1.7	1.7	115
1984	80.1	15.9	0	3.2	0	1.1	94
1985	88.4	7.0	0	3.5	1.2	3.5	86
1986	78.1	8.8	0	8.8	3.5	1.4	73
1987	97.3	15.7	1.4	4.1	2.0	1.4	146
1988	88.0	37.3	2.7	5.3	8.0	5.3	75
1989	85.8	14.1	0	0	2.6	1.3	78
1990	95.0	27.5	0	7.5	15.0	5.0	40
1991	87.5	27.1	0	0	4.2	1.1	48
1992	55.8	2.3	0	2.3	2.3	0	43
1993	72.4	10.3	0	0	0	17.2	29
1994	60.8	4.3	0	2.2	4.3	4.3	46
1995	65.8	15.2	0	1.3	0	3.8	79
1996	32.2	10.2	0	0	0	5.1	59
1997	66.0	1.9	0	7.5	0	5.7	53
1999	94.7	0	0	0	0	0	38
2000	65.0	5.0	0	0	0	5.0	20
2001	100.0	0	0	5.9	0	11.7	17

Data for the whole year combined. *A.l.*, *Acanthocephalus lucii*; *A.a.*, *A. anguillae*; *A.c.*, *A. clavula*; *R.a.*, *Raphidascaris acus*; *P.t.*, *Paraquimperia tenerrima*; *B.c.*, *Bothriocephalus claviceps*.

lower levels of prevalence and these fluctuated rather erratically from year to year. The eel specialist *Bothriocephalus claviceps* occurred in all years except two, but, with the exception of 1993, always at low levels of prevalence. Prevalence levels of the eel specialist *Paraquimperia tenerrima* and the generalist *Raphidascaris acus* were also generally low, and their occurrence rather erratic and especially from 1992 onwards. The scarcest species in the community was *Acanthocephalus clavula*, which occurred in only two of the 18 years and then at low levels of prevalence. The prevalence of *A. lucii* declined from 1992 onwards, and *P. tenerrima* virtually disappeared from the samples after 1992, being recorded only in 1994.

The high prevalence levels of *A. lucii* were matched by high abundance values (table 2). This species exhibited the highest relative and absolute levels of abundance of any species in the community: all the remaining species, including *A. anguillae* which exhibited the second highest levels of prevalence, occurred at very low levels of relative and absolute abundance. It is clear that the whole community is overwhelmingly dominated by *A. lucii*. The relative abundance of this species varied within very narrow limits, from 0.933 to 1.00, giving structural stability to the community. Absolute abundance changed dramatically from 1992 onwards. From 1983 to 1991 mean abundance of *A. lucii* fell below 20 in only one year (1989) and exceeded 30 in three years, but from 1992 to 1996 abundance never exceeded 10. There were slight increases in abundance from 1997 to 2000, but even over this period mean values never exceeded 20. Not until 2001 did abundance reach pre-1992 levels of 30. Changes in maximum intensity values showed a similar pattern: they peaked in 1983 and 1984 and only fell below 100 once, in 1989, between 1983 and 1991. From 1992 to 2000 maximum intensity only exceeded 100 in one year (1997), but it reached its highest post-1992 level in 2001.

The decline in abundance of *A. lucii* from 1992 onwards is equally apparent when data for the three richest months only are considered separately (table 3). Prevalence and abundance levels were higher in most months over the period 1983 to 1991 than in the same months over the period 1992 onwards. During the earlier period the high values for the dispersion index in most months suggests the presence of some heavily infected eels in the samples, also indicated by the maximum intensity values in table 2. From 1992 to 2000, prevalence and abundance values could be high in individual months and attain levels comparable to those in the earlier period, e.g. May 1997, but in most months they were far lower. It does appear, furthermore, that in this second period prevalence and abundance values were comparable to those in the first period in one month in each year, though not of necessity in the same month. Values in other months in the same year could be very low (compare May 1997 values with those for July and August 1997). The increase in abundance from 1997 onwards (table 2) is less apparent in table 3. It appears 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 (table 4). The decline in the levels of over dispersion was, however, confirmed. Maximum values were recorded in July 1983 and August 1988, and minimal values in August 1996 and 1997. By 2001 parameters had returned to the pre-1992 levels.

High relative abundance values for *A. lucii* can be interpreted as high values of the Berger-Parker dominance index and, as might be predicted from such high values, component community diversity was low

Table 2. The relative abundance of each helminth species as a proportion (pi) of the total number of all helminth species in the intestines of eels in Lough Derg.

	Parasite species						No. of parasites		
Year	*A.l.*	*A.a.*	*A.c.*	*R.a.*	*P.t*	*B.c.*	Total	x	Max
1983	0.993	0.004	0	0	0.001	0.002	4087	35.5	301
1984	0.985	0.011	0	0.003	0	0.001	2678	28.5	478
1985	0.994	0.002	0	0.002	0.001	0.001	2554	29.7	177
1986	0.981	0.003	0	0.011	0.004	0.001	1886	25.8	256
1987	0.987	0.007	0.001	0.003	0.001	0.001	4824	33.0	210
1988	0.971	0.021	0.001	0.002	0.004	0.001	2110	28.1	193
1989	0.975	0.020	0	0	0.003	0.002	1027	13.2	82
1990	0.971	0.012	0	0.003	0.012	0.002	1468	36.7	142
1991	0.972	0.022	0	0	0.004	0.002	1135	23.6	146
1992	0.939	0.023	0	0	0.038	0	396	9.2	94
1993	0.963	0.014	0	0	0	0.023	273	9.4	83
1994	0.982	0.023	0	0.003	0.006	0.006	327	7.1	84
1995	0.953	0.037	0	0.005	0	0.005	558	9.4	74
1996	0.933	0.046	0	0	0	0.021	235	3.9	70
1997	0.978	0.001	0	0.016	0.005	0	935	17.6	144
1999	1.000	0	0	0	0	0	422	11.1	91
2000	0.989	0.007	0	0	0	0.004	272	13.6	92
2001	0.995	0	0	0.003	0	0.002	619	36.4	192

Data for the whole year combined. *A.l., Acanthocephalus lucii*: *A.a., A. anguillae*; *A.c., A. clavula*; *R.a., Raphidascaris acus*; *P.t., Paraquimperia tenerrima*; *B.c., Bothriocephalus claviceps*; x, mean; max, maximum.

Table 3. Abundance of *Acanthocephalus lucii* in eels in Lough Derg.

	May				July				August			
Year	%	x	SD	s/x	%	x	SD	s/x	%	x	SD	s/x
1983	100.0	35.6	28.0	22.1	100.0	47.6	64.8	88.3	93.7	27.3	31.1	35.4
1984	92.8	35.2	36.5	37.8	83.3	10.0	9.7	9.9	71.4	10.9	12.5	14.2
1985	100.0	62.0	54.4	47.8	100.0	28.1	32.6	37.9	100.0	15.6	19.3	23.8
1986	100.0	36.0	32.9	30.2	85.7	19.1	14.0	10.4	100.0	22.2	19.3	16.9
1987	100.0	37.1	33.1	29.5	100.0	37.1	36.8	36.6	100.0	16.7	15.2	13.8
1988	100.0	34.8	26.6	20.4	100.0	21.8	21.5	21.2	*100.0	54.8	53.5	52.4
1989	92.8	15.7	9.2	5.4	100.0	5.6	3.8	2.7	*71.4	15.8	21.8	30.1
1990	*100.0	56.8	24.0	10.1	84.6	33.3	39.6	47.2	100.0	22.8	24.1	25.5
1991	*71.4	11.5	12.9	14.5	*100.0	31.7	32.8	34.3	85.7	24.8	37.6	56.9
1992	*42.8	5.9	11.1	20.7	71.4	14.2	24.9	43.8	46.7	6.7	18.3	50.2
1993	*64.3	4.5	5.6	7.0	No sample taken				73.3	13.6	21.7	34.6
1994	*35.7	2.2	3.8	6.6	77.3	9.4	17.9	35.2	60.0	8.3	9.8	11.6
1995	92.8	24.6	22.1	19.8	62.5	5.2	10.7	22.0	45.2	3.3	6.8	14.1
1996	25.0	2.0	4.0	8.0	52.6	7.1	12.4	21.7	22.8	2.8	3.1	3.4
1997	100.0	61.0	40.4	26.7	66.7	1.9	2.9	4.4	38.8	0.7	1.1	1.6
1999	95.0	18.6	21.9	25.7	88.8	3.3	4.1	5.1	No sample taken			
2000	No sample taken				No sample taken				65.0	13.5	20.4	30.7
2001	100.0	36.2	48.1	64.0								

*Sample taken in nearest month.
%, prevalence; x, abundance; SD, standard deviation; s, variance.

(table 5). Both Shannon-Weiner and Simpson's diversity indices indicate low diversity with all Shannon-Weiner values close to zero and all Simpson's values close to one. Evenness values were accordingly very low. There is no indication of the division of the data into two periods as far as component community diversity is concerned since values for the indices are similar both before and after 1992. The diversity indices varied over a very narrow range, reflecting the narrow range of variation in the Berger-Parker dominance index. The Shannon-Weiner index varied from 0 to 0.298 and Simpson's from one (the minimal possible value) to 1.15. The correlation between the two indices is positive and highly significant ($rs = 0.96, P < 0.01$). The overall picture is of a component community exhibiting heavy dominance by one species and so very low diversity, but one that is very stable and in which diversity varies within very narrow limits.

This stability was confirmed at the infracommunity level (table 6). The mean number of species per eel ranged from 0.7 to 1.7 per eel, and the maximum never exceeded three. Mean species richness per eel was generally lower in the 1992–2000 period, when values were below one in 6 of the 8 years, whereas all values exceeded one pre-1992. The proportion of eels with 0 or one species also differed between the two periods: prior to 1992, the maximum was 0.75 and 7/9 values were below 0.7. From 1992 onwards only one value (in 1993) was below 0.7 and all the rest were above 0.8. The mean number of helminths per eel was very variable, but all the highest values were recorded pre-1992. Mean Brillouin's index was always low, confirming low infracommunity diversity, but here again it varied over a very narrow range from 0 to 0.162, and there was no clear division into two periods. The maximum value of 0.922 was recorded in 1987, but this differed little from the maximum of 0.835 reported in 1997. The distinction between the two periods disappears when infected eels only are considered as the highest values of 0.635 and 0.377 were reported from 1992 and 1995 respectively, and, whilst the lowest value was recorded in 1999, the next lowest value was recorded from 1983. In 2001 values for mean numbers of species and helminth individuals had returned to pre-1992 levels, whereas Brillouin's index and the proportion of eels with 0/1 species remained at post-1992 levels. Overall, infracommunities are characterized by low species richness and diversity, with the lower values from 1992

Table 4. Frequency distribution of the number of *Acanthocephalus lucii* in eels in Lough Derg in alternative samples in July.

		No. of individuals per eel								
Year	No. of eels	0	1–12	13–25	26–50	51–100	101–200	Max.	x	s/x
1984	12	2	5	4	1	0	0	29	10.0	9.9
	14	0	4	1	4	3	2	199	57.6	69.9
1989	14	0	12	2	0	0	0	13	5.6	2.7
	14	1	4	5	1	3	0	82	26.4	24.2

Max, maximum; x, mean; s, variance.

Table 5. Component community diversity of the intestinal helminth communities of eels in Lough Derg.

Year	Shannon-Weiner (H′)	Evenness	Simpson (1/C)	Berger-Parker
1983	0.048	0.035	1.01	0.993
1984	0.088	0.064	1.03	0.985
1985	0.044	0.027	1.01	0.994
1986	0.115	0.071	1.04	0.981
1987	0.086	0.048	1.03	0.987
1988	0.158	0.089	1.06	0.971
1989	0.133	0.096	1.05	0.975
1990	0.150	0.093	1.06	0.970
1991	0.146	0.105	1.01	0.972
1992	0.221	0.159	1.13	0.939
1993	0.180	0.164	1.08	0.963
1994	0.114	0.071	1.04	0.982
1995	0.266	0.168	1.10	0.952
1996	0.298	0.099	1.15	0.932
1997	0.102	0.025	1.04	0.978
1999	0.000	0.000	1.00	1.000
2000	0.068	0.061	1.02	0.989
2001	0.039	0.014	1.01	0.995

Data for whole year combined.

onwards reflecting the increase in the proportion of eels with 0 or one parasite species only, i.e. exhibiting zero diversity.

Discussion

By any standards, the River Shannon must be considered a large river. Nevertheless, the intestinal helminth community of eels in Meelick Bay comprised only six species. All of these have previously been reported from Ireland. Even by the standards of the impoverished fauna of Ireland, this is not a rich community. Intestinal helminth component community richness values from eels have been reported as 9 from Lough Corrib (Conneely & McCarthy, 1986), 9 from the Dunkellin River (Callaghan & McCarthy, 1993) and 7 from Lough Erne (Evans & Mathews, 1999). Higher values have also been reported from smaller rivers in

Table 6. Diversity characteristics of the intestinal infracommunities of helminths of eels of Lough Derg.

Year and month	No. of species x	No. of species SD	No. of species Max	No. of helminths x	No. of helminths SD	No. of helminths Max	Brillouin's Index x	Brillouin's Index SD	Brillouin's Index Max	B.I. infected eels only x	B.I. infected eels only SD	Prop. 0/1	No. of eels
1983 (Jun)	1.3	0.8	3	69.1	81.5	242	0.029	0.092	0.392	0.086	0.151	0.67	18
1984 (Jul)	1.1	0.7	2	10.6	9.9	29	0.074	0.146	0.451	0.296	0.138	0.75	12
1985 (Sep)	1.4	0.5	2	33.5	25.1	105	0.056	0.099	0.322	0.183	0.093	0.69	13
1986 (Jun)	1.4	0.5	2	79.1	79.0	258	0.056	0.084	0.201	0.138	0.086	0.54	11
1987 (Jun)	1.7	0.7	3	56.9	62.2	210	0.104	0.224	0.922	0.201	0.282	0.38	25
1988 (May)	1.7	0.7	3	36.7	27.4	85	0.162	0.169	0.478	0.325	0.179	0.36	15
1989 (Jul)	1.3	0.5	3	5.6	3.8	13	0.085	0.142	0.367	0.296	0.057	0.71	14
1990 (Aug)	1.5	0.5	2	22.4	38.2	140	0.158	0.209	0.537	0.316	0.191	0.50	14
1991 (Jun)	1.5	0.6	3	31.2	32.3	127	0.089	0.142	0.405	0.223	0.144	0.60	20
1992 (Jul)	0.7	0.6	2	15.1	27.1	94	0.045	0.170	0.635	0.635	–*	0.92	14
1993 (Aug)	1.1	0.8	3	15.0	22.2	83	0.084	0.159	0.513	0.252	0.188	0.67	15
1994 (Jul)	0.9	0.6	3	9.6	18.0	84	0.039	0.105	0.366	0.215	0.165	0.82	22
1995 (Aug)	0.8	0.8	3	3.7	7.5	35	0.126	0.190	0.567	0.377	0.095	0.81	18
1996 (Jul)	0.7	0.7	2	7.1	12.5	46	0.036	0.095	0.367	0.230	0.119	0.84	19
1997 (Jul)	0.9	0.8	3	2.3	3.4	13	0.066	0.196	0.835	0.282	0.225	0.85	21
1999 (May)	1.0	0.0	1	18.6	21.9	91	0.000	0.000	0.000	0.000	0.000	1.00	21
2000 (Aug)	0.8	0.6	2	13.6	20.6	72	0.012	0.038	0.130	0.124	–*	0.90	20
2001 (May)	1.2	0.5	3	36.4	48.0	192	0.019	0.057	0.201	0.167	–*	0.88	17

*Numbers too small for calculation to be meaningful.
Data shown for the richest month only. x, abundance; SD, standard deviation; max, maximum; prop. 0/1, proportion of eels with 0 or 1 species.

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England, with a maximum of 9 from the River Clyst (Kennedy, 1993) and 11 from the River Otter (Kennedy, 1997). On the other hand, species richness in the River Shannon is comparable with values from the large rivers of the continent, with values of 5, 6, 8 and 6 being reported respectively from the Scheldt (Schabuss *et al.*, 1997), Este (Saraiva & Eiras, 1996), Tiber (Kennedy *et al.*, 1998) and Rhine (Sures *et al.*, 1999). Thus, the results of this study support the first hypothesis, namely that communities are not richer in large rivers.

Two of the species found, *P. tenerrima* and *B. claviceps*, are eel specialists, but they made very little contribution to community diversity. *Acanthocephalus clavula* uses eel as its preferred host, but can infect a range of fish. Both this species and the generalist *R. acus* also made little contribution to community diversity. In Ireland, *A. anguillae* appears to be an eel specialist in the absence of its preferred definitive host *Leuciscus cephalus* from the island (Lyndon & Kennedy, 2001), but its abundance, although not prevalence, was always very low and it also made little contribution to community diversity. The dominant species and the one that made the maximum contribution to diversity was the acanthocephalan *A. lucii*. This shows a preference for *Perca fluviatilis* as its definitive host, and in the River Shannon 80.5% of perch were infected with a maximum value of 229 parasites per fish (C.R. Kennedy, unpublished).

Such domination of a community by a non-specialist acanthocephalan is a common characteristic of intestinal helminth communities in eels. In a survey of 50 British and Irish localities Kennedy (1990) found that 60% were dominated by a generalist species and the single most common dominant species was *A. lucii*. All the Irish localities studied to date have been dominated by an acanthocephalan, the great majority by *A. lucii* also. Exceptions do occur, but rarely: in the southwest of England eel helminth communities may be dominated by eel specialist nematodes. On the continent also it is common to find acanthocephalans dominating the eel helminth communities in large rivers: for example, *A. clavula* in the Tiber (Kennedy *et al.*, 1998), *A. lucii* and *A. anguillae* at different sites in the Scheldt (Schabuss *et al.*, 1997) and the introduced specialist *Paratenuisentis ambiguus* in the Rhine (Sures *et al.*, 1999). Here again, the Shannon fits the pattern of the large European rivers.

Component community diversity values in the Shannon were very low. Values of Simpson's index in the River Otter ranged from 1.64 to 5.5, and Shannon-Weiner values from 0.71 to 1.83 (Kennedy, 1997). Equivalent values from the River Clyst were, respectively, 1.28 to 2.67 and 0.44 to 1.04. All the values from the Shannon fell below these and there was no overlap at all. Values of Simpson's index for the Scheldt were lower, but values for the Shannon-Weiner index were higher (Schabuss *et al.*, 1997) than those from the Shannon and there was again no overlap between them. Values of both indices were higher in the Rhine (Sures *et al.*, 1999) and here again there was no overlap with values for the Shannon. Thus, diversity values from the Shannon are far more closely comparable to those reported from the larger European rivers than to those from the smaller ones.

By contrast, infracommunity species richness values in the Shannon are relatively high with mean values frequently exceeding many of those reported from the Rivers Clyst and Otter (Kennedy, 1993, 1997) and the Tiber (Kennedy *et al.*, 1998) and Rhine (Sures *et al.*, 1999). The maximum value of 3 recorded in the Shannon is the normal maximum for eels everywhere (Kennedy & Guegan, 1996), although this can occasionally be exceeded as in the River Rhine system where a maximum of 5 was reported by Sures & Streit (2001). Mean values of Brillouin's index are comparable to those reported from the above rivers, but values of Brillouin's index from infected eels only are on the whole slightly lower than those from the River Clyst (Kennedy, 1993) and the River Rhine (Sures *et al.*, 1999), which are similar to each other. Maximum values often exceed those reported from the River Tiber (Kennedy *et al.*, 1998), but tend to be lower than values reported for the other rivers, albeit that they are of a similar order of magnitude. The temporal ranges of all community parameters recorded from eels in the Shannon are much narrower than those reported from the Rivers Clyst and Otter (Kennedy, 1993, 1997), and the intestinal helminth community there exhibits a level of stability in structure that is comparable to the eel helminth community in the River Tiber, the only other large river for which a long-term community data set exists (Kennedy *et al.*, 1998). The findings from the River Shannon therefore support the view that intestinal helminth communities in eels are similar in diversity structure right across Europe (Kennedy *et al.*, 1998; Kennedy & Hartvigsen, 2000).

Dominance of helminth communities by a generalist acanthocephalan is a fairly characteristic feature of intestinal parasite communities of eels (Kennedy & Hartvigsen, 2000). The River Rhine is exceptional in that the community is dominated by the specialist eel acanthocephalan *P. ambiguus*. This unusual situation may reflect the fact that this is an introduced species from North America and the unique physio-chemical and biological conditions in the Rhine (Sures & Streit, 2001). The greater the degree of dominance the more likely the community is to be stable over time, since the irregular occurrences of other species which occur at low abundance will have little or no impact on community diversity or indeed on other community parameters except species richness. The overwhelming dominance of the intestinal helminth communities of eels in the Shannon by *A. lucii* is only an extreme example of this. It is common to find the proportion of eels with 0 or 1 helminth species only being much higher in other localities than in the Shannon (at least until 1992). The communities in the Shannon are very similar in many respects to those reported from eels in the River Tiber (Kennedy *et al.*, 1998): these were overwhelmingly dominated by *A. clavula*, such that other species including eel specialists also contributed little or nothing to community diversity, as opposed to richness. Community structure here was also very stable over an interval of 16 years although community richness changed. Mean species richness of helminth communities in the Tiber eels was lower because the proportion of eels with 0 or 1 species was much higher than in the Shannon.

Even when the absolute abundance of *A. lucii* in eels in the Shannon changed, as they did from 1992 onwards, helminth community structure was relatively little

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affected: this must reflect the fact that the relative abundance of *A. lucii* did not change whilst the other species were too uncommon to make any significant contribution to community structure. The reasons for the decline of *A. lucii* from 1992 onwards and its increase again in 2001 are not yet clear. In the 1980s, eels in Meelick Bay were known to specialize in feeding on *Asellus aquaticus* (Moriarty, 1986), which is the intermediate host for both *Acanthocephalus lucii* and *A. anguillae*. These two species compete in eels (Kennedy & Moriarty, 1987; Kennedy, 1992) such that *A. anguillae* populations are depressed by its congener. The third congener, *A. clavula*, uses *Asellus meridianus* as its intermediate host. There is therefore no likelihood that the decline in abundance of *Acanthocephalus lucii* can be attributed to interactions with its congeners. Eel populations in Ireland, as in the rest of Europe, declined during the 1980s and in subsequent years as elver runs declined (Moriarty, 1992; Moriarty & Decker, 1997) but it is hard to see how this could explain the decline in abundance of *A. lucii* or *A. anguillae*. There is no evidence that the eels in Meelick Bay have changed their dietary preference as there was no significant difference between years over the period 1982 to 1999 in the frequency of *Asellus* in the eels' diet (C. Moriarty, unpublished). There is also no evidence that levels of *A. aquaticus* in the Bay have declined (Moriarty, unpublished). Indeed, in view of the increasing eutrophication of the lake (Flanagan & Toner, 1975; Bowman, 2000), it is more likely numbers of *A. aquaticus* would have increased. No single dramatic event is known to have occurred in 1992, and there is no precise correlation between changes in the physico-chemical conditions in the Lough and *Acanthocephalus lucii* abundance. The trophic status of the Lough has been the subject of investigation over the period of this study (Bowman, 2000). Levels of phosphorous, chlorophyll and phytoplankton were relatively low in the early 1970s, but began to increase at the end of the decade and notably high levels were recorded in 1991/1992. By 1999, levels had fallen again and were similar to those in the early 1970s. This fall in levels was attributed to a combination of a reduction in phosphorous input resulting from improved waste water treatment and the appearance and population explosion of the zebra mussel *Dreissena polymorpha* in 1996 (Minchin & Moriarty, 1997).

A more likely likely explanation for the change in *A. lucii* abundance is that it actually reflects changes in the movement patterns of eels in the Lough. Moriarty (1983) drew attention to the fact that the eel population in Meelick Bay was not resident but was in a state of constant flux over the warm summer months: exceptionally low recaptures of tagged eels suggested that eels were moving freely in and out of the Bay. It is possible, therefore, that from 1992 onwards there was a greater movement of eels in the Lough and a change in the patterns of movements such that eels from other regions of the Lough where *A. lucii* was absent or uncommon moved into Meelick Bay. Movements of eels of this nature would also explain the differences in parasite dispersion patterns evident in the same month. Meelick Bay itself is not homogenous with regard to substrate (Moriarty, 1986), and other parts of the Lough differ with respect to physico-chemical conditions and substrate (Flanagan & Toner, 1975). These different regions will support different invertebrate populations and so eels feeding there can be expected to acquire different species of parasite. Such movement of eels could explain the erratic appearance of the least common helminth species in Meelick Bay, as the helminth communities of these immigrants would reflect conditions in the areas from which they had originated, where communities may be different in composition or relative abundance. The River Shannon is very variable in physical conditions along its length and even Lough Derg itself is not a single, homogenous basin (McCarthy *et al.*, 1999).

Overall, however, the results of this study of the intestinal communities of eels in the River Shannon have confirmed that such communities are not richer or more diverse than those in small rivers. They have also confirmed the hypothesis that such communities in large rivers are more stable in structure than those in small rivers. The characteristic features of all these communities from large rivers is the overwhelming dominance by an acanthocephalan species, the identity of which may change from river to river, and the consequent insignificant contribution of the other species to community diversity and structure, though not to richness. In these respects, the intestinal helminth communities of eels in the River Shannon are comparable to, and typical of, those of the other great rivers of Europe.

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