# Richness and diversity of intestinal metazoan communities in brown trout *Salmo trutta* compared to those of eels *Anguilla anguilla* in their European heartlands

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SUMMARY

The hypothesis that intestinal helminth communities in freshwater brown trout are dissimilar in composition and structure to those in the European eel was tested by an analysis of component communities from 72 localities and of infracommunities from 34 localities in the British Isles and Norway. Derived indices were then compared with published data from eels. Composition of helminth communities differed considerably between the two hosts as a group of 4 species occurred commonly in trout and so gave greater predictability to the community composition. These 4 species were trout specialists and in 97% of the localities a trout specialist dominated the community rather than a generalist acanthocephalan as is typical for eels. By contrast all measures of community structure and indices of richness and diversity indicated that helminth communities in trout were isolationist in character, species poor and exhibited low diversity at both component and infracommunity levels. All values of indices for trout helminth communities were strikingly similar to those obtained from eels. Evidence of interspecific interactions within the trout helminth communities and a limit of 4 to infracommunity species richness further enhanced the similarities and suggested a common determinant of community structure. The hypothesis was thus supported in respect of species composition but refuted in respect of community structure.

Key words: trout, eel, helminth community, species richness, diversity, competition.

## INTRODUCTION

Intestinal helminth communities of freshwater fish exhibit low species richness and diversity when compared to similar communities in aquatic birds (Kennedy, Bush & Aho, 1986). They also fit into the category of isolationist, as opposed to interactive, communities as defined by Holmes & Price (1986). A series of studies on helminth communities of the European eel, *Anguilla anguilla*, and the American eel *A. rostrata* have demonstrated that intestinal helminth communities in European and American, as opposed to Australian (Kennedy, 1995), eels are unpredictable in composition and isolationist in nature (Kennedy, 1990; Marcogliese & Cone, 1993, 1996, 1998; Barker, Marcogliese & Cone, 1996). Other detailed studies have revealed that helminth community structure, though not composition, remained relatively constant in time and space (Kennedy, 1993, 1997; Kennedy *et al*. 1998) and in relation to enhanced salinity (Kennedy *et al*. 1997). Communities in eels in freshwater were frequently dominated by a species of acanthocephalan and were fundamentally isolationist in nature even though negative interactions did occur between some pairs of acanthocephalan species (Bates & Kennedy, 1991; Kennedy, 1992). The communities appeared to reach a saturation level of richness (Kennedy & Guégan, 1994, 1996) and there appeared to be a limit to the number of niches available in the intestine.

At an early stage in the series of investigations, Kennedy (1990) posed 2 questions: (1) whether the conclusions drawn to date applied to helminth communities of eels in general and throughout their range and (2) whether similar conclusions could be applied to intestinal helminth communities in other species of freshwater fish. Effectively, the questions suggested the possibility that there were general patterns in helminth community composition and structure in freshwater fish and so common determinant factors. Subsequent research has answered the first question, as it is now clear that communities in European eels are similar throughout their range (Kennedy *et al*. 1998) and similar to those in the American eel (Marcogliese & Cone, 1998) but the second question remains unanswered. Some data are available on intestinal helminth communities in other fish species, both temperate and tropical (Kennedy, 1995; Nie, 1995; Kennedy & Pojmanska, 1996; Salgado-Maldonado & Kennedy, 1997), but few present data on infracommunities and so this specific question has not been addressed so far. In

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1990 Kennedy did suggest that intestinal helminth communities of salmonids might be similar to those of eels, basing the suggestion on published accounts of component communities and inspection rather than on detailed investigations. Several subsequent studies have tended to confirm this suggestion, including those of Hartvigsen & Halvorsen (1993), Hartvigsen & Kennedy (1993) and Dorucu *et al.* (1995), but only that of Molloy, Holland & Poole (1995) has actually presented infracommunity data. This small-scale study indicated communities low in species richness and diversity and so similar to eels, but it remains far from clear how representative the values are or to what extent the conclusions can be applied to brown trout elsewhere.

The aims of this present paper, therefore, are to present the results of detailed and concentrated investigations of intestinal helminth communities in brown trout at both component and infracommunity levels using both published and original data, and then to compare the findings with those from European eels by using the same methods of analysis over a large geographical scale. Trout are believed to have recolonized the British Isles and Norway following the last glaciation around the same time as eels, so the species are comparable in respect of length of time they have inhabited the region (Guégan & Kennedy, 1993), and both are also in their respective heartlands (Kennedy & Bush, 1994). The specific objective was to test the hypothesis that intestinal helminth communities in brown trout in freshwater are not similar in composition and structure to those in European eels.

## MATERIALS AND METHODS

Data on helminth communities were obtained from 2 sources. Component community data (*sensu* Bush *et al.* 1997) have been published for a number of localities, but in many cases species lists are incomplete and not all species were identified or counted. Published data on 38 localities were selected on the basis of there being sufficient information to determine component community richness (CCR) and to calculate dominance indices (Table 1). Additional data on component and infracommunities were obtained from a further 34 localities (Table 2) from the authors' own collections. Some of these data have been published previously. Data were included regardless of method of collection, sample size, host size and sex, year or season. Regions sampled included England, Ireland, Scotland, Wales and Norway and habitats included lakes, reservoirs and rivers. Samples were taken from all parts of these regions to avoid any complications arising from species at the edge of their range or any island effects.

Fish were examined, and parasites treated, by standard methods and according to a consistent laboratory protocol that was also adopted for parasitological investigations of eels (Kennedy, 1993, 1997), or as described in appropriate publications. Only data from helminths of the alimentary tract were considered. Terminology is as defined by Bush *et al.* (1997). Measures of community structure adopted were those specifically designed to facilitate comparison with data from eels (Kennedy, 1990, 1993, 1996, 1997). Measures of component community structure are: the total number of helminth species in a sample (CCR), the Berger-Parker Dominance Index (BP), Simpson's Index (SI) as (1/D) and the Shannon-Wiener Index (SW). Measures of infracommunity structures adopted are: mean number of species per eel (ICR mean) and maximum number (ICR max.), mean number of helminth individuals per eel (NI mean), mean Brillouin's Index per eel (infected and uninfected) (BI mean) and maximum (BI max) and percentage of the sample harbouring 0 or 1 species of helminth. Indices are defined and calculated as in Magurran (1988) using natural logarithms ($\log_2$) as appropriate. These same indices and abbreviations were used by Kennedy (1993) and Kennedy & Guégan (1996) in their studies of eel parasite communities.

Student's *t*-tests were used for determining significance of differences in means. The parametric correlation coefficient *r* was used for linear correlations and $2 \times 2$ contingency tables were used to examine potential interspecific associations. Data are summarized as median, 25 % and 75 % quartiles and range.

## RESULTS

### *Sample validation*

In respect of component community data obtained from the published literature (Table 1), there were no significant correlations between N, here used also as a measure of sampling effort, and CCR ($r = 0{\cdot}181$, $n = 38$, N.S.) or BP ($r = -0{\cdot}084$, $n = 38$, N.S.). Comparison of BP values by sample size also confirms a lack of relationship between N and BP (for $N > 20$, mean BP $= 0{\cdot}735 \pm 0{\cdot}191$ S.D., $n = 22$: for $N < 20$, mean BP $= 0{\cdot}734 \pm 0{\cdot}176$ S.D., $n = 15$: $P > 0{\cdot}05$, N.S.). The mean BP was also independent of habitat type (for lakes, mean BP $= 0{\cdot}776 \pm 0{\cdot}157$, $n = 27$; for reservoirs, mean BP $= 0{\cdot}723 \pm 0{\cdot}204$, $n = 7$: $P > 0{\cdot}05$, N.S.). There were too few rivers (3) to be included in this comparison. It can therefore be concluded that since neither sample size nor habitat type influence CCR or BP it is valid to use the whole data set without any subsequent control for sample size/effort.

In respect of component community data from the authors' collections (Table 2), there was similarly no significant correlation between N and CCR ($r = -0{\cdot}095$, $n = 34$, N.S.), nor was there any

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Table 1. Summary data for helminth communities in brown trout from 38 localities in the British Isles

(Species names are given in full in Table 3. (Key: L, lake; R, river; Res, reservoir; N, number of trout in sample; CCR, no. of helminth species in the component community.))

| Locality | Country | *n* | CCR | Berger-Parker Dominance Index | Dominant species | Reference |
|---|---|---|---|---|---|---|
| L. Corrib | Ireland | 26 | 11 | 0·72 | *C. metoecus* | Conneely & McCarthy (1988) |
| L. Bunaveela | Ireland | 285 | 4 | 0·72 | *P. laevis* | Molloy *et al.* (1995) |
| L. Feeagh | Ireland | 264 | 3 | 0·56 | *P. laevis* | Molloy *et al.* (1995) |
| R. Shournagh | Ireland | 242 | 3 | 0·45 | *P. laevis* | Fitzgerald & Mulcahy (1983) |
| L. Padarn | Wales | 30 | 10 | 0·61 | *A. clavula* | Powell (1966) |
| R. Terrig | Wales | 252 | 6 | 0·47 | *C. farionis* | Ataur Rahim (1981) |
| L. Watten | Scotland | 27 | 3 | 0·62 | *Cy. truncatus* | Lyndon *et al.* (1997) |
| L. Toftingall | Scotland | 39 | 2 | 0·99 | *Cy. truncatus* | Lyndon *et al.* (1997) |
| L. Calder | Scotland | 23 | 2 | 0·99 | *E. truttae* | Lyndon *et al.* (1997) |
| L. Yarrows | Scotland | 45 | 3 | 0·43 | *E. truttae* | Lyndon *et al.* (1997) |
| L. Hempriggs | Scotland | 27 | 3 | 0·67 | *E. truttae* | Lyndon *et al.* (1997) |
| L. Fhearna | Scotland | 24 | 4 | 0·79 | *E. truttae* | Lyndon *et al.* (1997) |
| L. Ascaig | Scotland | 21 | 3 | 0·83 | *E. truttae* | Lyndon *et al.* (1997) |
| L. Ruathair | Scotland | 33 | 1 | 1·0 | *Eu. crassum* | Lyndon *et al.* (1997) |
| L. Leir | Scotland | 24 | 2 | 0·88 | *E. truttae* | Lyndon *et al.* (1997) |
| L. Sletill | Scotland | 24 | 2 | 0·84 | *E. truttae* | Lyndon *et al.* (1997) |
| L. Strathbeg | Scotland | 402 | 5 | 0·93 | *C. metoecus* | Bwathandi (1984) |
| L. Lomond | Scotland | 8 | 3 | 0·7 | *Eu. crassum* | Dorucu *et al.* (1995) |
| L. Maragan | Scotland | 35 | 5 | 0·65 | *C. farionis* | Dorucu *et al.* (1995) |
| R. Fillan | Scotland | 18 | 4 | 0·4 | *C. farionis* | Dorucu *et al.* (1995) |
| Aurs Barn | Scotland | 10 | 4 | 0·52 | *E. truttae* | Dorucu *et al.* (1995) |
| Carbeth Res. | Scotland | 20 | 4 | 0·42 | *E. truttae* | Dorucu *et al.* (1995) |
| L. Awe | Scotland | 20 | 3 | 0·79 | *Eu. crassum* | Dorucu *et al.* (1995) |
| L. Jaw | Scotland | 10 | 5 | 0·7 | *N. rutili* | Dorucu *et al.* (1995) |
| L. Cochno | Scotland | 3 | 1 | 1·0 | *N. rutili* | Dorucu *et al.* (1995) |
| L. Leven | Scotland | 3 | 1 | 1·0 | *Eu. crassum* | Dorucu *et al.* (1995) |
| Secret L. | Scotland | 1 | 3 | 0·93 | *N. rutili* | Dorucu *et al.* (1995) |
| Hill L. | Scotland | 7 | 0 | 0 | — | Dorucu *et al.* (1995) |
| L. Rannoch | Scotland | 19 | 3 | 0·53 | *E. truttae* | Dorucu *et al.* (1995) |
| Brunscrooks L. | Scotland | 4 | 3 | 0·71 | *Eu. crassum* | Dorucu *et al.* (1995) |
| Talla Res. | Scotland | 15 | 4 | 0·92 | *E. truttae* | Dorucu *et al.* (1995) |
| L. Venachar | Scotland | 2 | 2 | 0·8 | *Eu. crassum* | Dorucu *et al.* (1995) |
| Carron Valley Res. | Scotland | 22 | 2 | 0·85 | *C. farionis* | Dorucu *et al.* (1995) |
| Whiteadder Res. | Scotland | 19 | 4 | 0·65 | *E. truttae* | Dorucu *et al.* (1995) |
| Fruid Res. | Scotland | 9 | 3 | 0·74 | *E. truttae* | Dorucu *et al.* (1995) |
| L. Garry | Scotland | 7 | 3 | 0·67 | *E. truttae* | Dorucu *et al.* (1995) |
| Slapton L. | England | 9 | 3 | 0·74 | *C. tenuissima* | Kennedy unpublished |
| Hanningfield Res. | England | 56 | 5 | 0·96 | *Eu. crassum* | Wootton (1973) |

correlation between N and SW ($r = 0{\cdot}013$, $n = 34$, N.S.). Comparison of sample indices by sample size again reveals a lack of relationship (for $N > 20$, $n = 16$ and BP mean $= 0{\cdot}811 \pm 0{\cdot}149$, SI mean $= 1{\cdot}164 \pm 0{\cdot}448$ and SW mean $= 0{\cdot}481 \pm 0{\cdot}283$: for $N < 20$, $n = 18$ and BP mean $= 0{\cdot}854 \pm 0{\cdot}123$, SI mean $= 1{\cdot}403 \pm 0{\cdot}193$ and SW mean $= 0{\cdot}425 \pm 0{\cdot}270$: all $P$ values $> 0{\cdot}05$ and N.S.). Comparison of indices by habitat also reveals no significant differences (for lakes $n = 17$, BP mean $= 0{\cdot}846 \pm 0{\cdot}147$, SI mean $= 1{\cdot}37 \pm 0{\cdot}354$ and SW mean $= 0{\cdot}424 \pm 0{\cdot}279$: for reservoirs $n = 10$, BP mean $= 0{\cdot}806 \pm 0{\cdot}152$, SI mean $= 1{\cdot}59 \pm 0{\cdot}477$ and SW mean $= 0{\cdot}418 \pm 0{\cdot}312$: all $P$ values $> 0{\cdot}05$ and N.S.). It can therefore be concluded that since neither sample size nor habitat influence CCR, BP or diversity it is valid to use the whole data set regardless of the value of N.

In the case of infracommunity data there were no significant correlations between N and ICR mean ($r = 0{\cdot}135$, $n = 34$, N.S.), ICR max ($r = 0{\cdot}03$, $n = 34$, N.S.), BI mean ($r = 0{\cdot}061$, $n = 29$, N.S.) or BI max ($r = 0{\cdot}005$, $n = 29$, N.S.). It was therefore considered valid to use the whole combined data set regardless of sample size or habitat.

Comparison between mean component community parameters (Table 2) for the UK and Norway (UK values first: BP $0{\cdot}793 \pm 0{\cdot}229$ and $0{\cdot}829 \pm 0{\cdot}143$ respectively; SI $1{\cdot}362 \pm 0{\cdot}499$ and $1{\cdot}415 \pm 0{\cdot}344$: SW $0{\cdot}417 \pm 0{\cdot}574$ and $0{\cdot}466 \pm 0{\cdot}259$) indicated no significant differences ($P > 0{\cdot}05$). At infracommunity level differences between the UK and Norway in ICR mean ($1{\cdot}328 \pm 0{\cdot}529$ and $1{\cdot}321 \pm 0{\cdot}470$) and BI mean ($0{\cdot}171 \pm 0{\cdot}116$ and $0{\cdot}117 \pm 0{\cdot}122$ respectively) were also not significant ($P > 0{\cdot}05$). It was therefore considered valid to combine UK and Norwegian samples in a single data set.

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Table 2. Summary indices for intestinal helminth communities of brown trout in 34 localities in the British Isles and Norway

(All data from British Isles from Kennedy (unpublished) and from Norway from Hartvigsen (unpublished). (Key: E, England; W, Wales; I, Ireland; S, Scotland; No, Norway; Re, reservoir; L, Lake; Ri, river; N, number of trout; CCR, component community richness; BP, Berger Parker Dominance Index; SI, Simpson's Index; SW, Shannon-Wiener Index; ICR, infra community richness; NI, number of helminths per fish; BI, Brillouin's Index; %0/1, % of fish with only 0 or 1 species; N.C., not calculable. Species abbreviations as in Table 3.))

| | | | Component Community | | | | Infra Community | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *n* | CCR | BP | SI | SW | ICR mean ± S.D. | ICR max | NI mean ± S.D. | BI mean ± S.D. | BI max | %0/1 |
| Argal Re | E | 7 | 4 | 0·91*Euc* | 1·2 | 0·3 | 1·43 ± 0·78 | 2 | 8 ± 7·3 | 0·164 ± 0·18 | 0·459 | 42·8 |
| Avon Dam Re | E | 18 | 2 | 0·93*Ct* | 1·15 | 0·12 | 1·42 ± 0·50 | 2 | 25·9 ± 22·7 | 0·158 ± 0·19 | 0·509 | 55·5 |
| Burrator Re | E | 31 | 4 | 0·79*Cf* | 1·56 | 0·7 | 1·16 ± 0·97 | 3 | 15·4 ± 13·4 | 0·248 ± 0·22 | 0·633 | 29·0 |
| Colliford Re | E | 27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100·0 |
| Crowdy Re | E | 43 | 5 | 0·75*Cm* | 1·72 | 0·67 | 1·3 ± 0·79 | 3 | 30·1 ± 48·8 | N.C. | | 65·1 |
| Meldon Re | E | 16 | 4 | 0·65*Cf* | 2·14 | 0·72 | 1·25 ± 0·77 | 3 | 7·9 ± 8·1 | 0·153 ± 0·29 | 0·421 | 68·7 |
| Stithians Re | E | 13 | 4 | 0·93*Cf* | 1·16 | 0·27 | 0·77 ± 0·78 | 2 | 32·2 ± 84·9 | 0·01 ± 0·02 | 0·062 | 84·6 |
| Upper Tamar Re | E | 30 | 1 | 1·0*Cm* | 1·0 | 0·0 | 0·39 ± 0·49 | 1 | 0·9 ± 1·6 | 0 | 0 | 100·0 |
| Venford Re | E | 12 | 3 | 0·77*Ct* | 1·59 | 0·62 | 1·83 ± 0·71 | 3 | 25·5 ± 30·7 | 0·364 ± 0·27 | 0·874 | 16·7 |
| Malham Tarn L | E | 30 | 2 | 0·99*Euc* | 1·02 | 0·02 | 0·93 ± 0·24 | 2 | 13·8 ± 0·9 | 0·009 ± 0·04 | 0·184 | 28·0 |
| Cowsic Ri | E | 71 | 3 | 0·86*Ct* | 1·32 | 0·56 | 1·18 ± 0·87 | 3 | 28·8 ± 32·6 | 0·194 ± 0·25 | 0·741 | 45·9 |
| Exe Ri | E | 25 | 4 | 0·79*Ct* | 1·55 | 0·68 | 1·28 ± 0·32 | 3 | 16·7 ± 23·7 | 0·13 ± 0·19 | 0·527 | 60·0 |
| Gara Ri | E | 24 | 3 | 0·94*Ct* | 1·13 | 0·26 | 1·87 ± 0·74 | 3 | 43·3 ± 92·6 | 0·179 ± 0·24 | 0·950 | 33·3 |
| Otter Ri | E | 12 | 4 | 0·87*Pl* | 1·29 | 0·31 | 1·75 ± 0·75 | 3 | 26·7 ± 17·8 | 0·225 ± 0·27 | 0·841 | 41·7 |
| Swincome Re | E | 73 | 3 | 0·85*Ct* | 1·35 | 0·52 | 1·54 ± 0·93 | 3 | 68·2 ± 150·1 | 0·178 ± 0·25 | 0·709 | 47·5 |
| Craig Goch Re | W | 13 | 3 | 0·65*Nr* | 1·97 | 0·78 | 1·92 ± 0·86 | 3 | 17·0 ± 13·8 | 0·316 ± 0·31 | 0·803 | 38·0 |
| Inchiquinn L | I | 9 | 4 | 0·96*Et* | 1·09 | 0·21 | 1·55 ± 0·53 | 2 | 90·9 ± 172·6 | 0·166 ± 0·23 | 0·531 | 44·4 |
| Shannon Ri | I | 7 | 3 | 0·9*Al* | 1·22 | 0·21 | 1·43 ± 0·78 | 3 | 22·6 ± 21·8 | 0·162 ± 0·28 | 0·682 | 71·4 |
| Dunalastair Re | S | 13 | 4 | 0·53*Et* | 2·43 | 0·97 | 2·38 ± 0·65 | 4 | 18·7 ± 12·9 | 0·415 ± 0·25 | 0·967 | 0 |
| Langvatn L | No | 28 | 2 | 0·66*Cyt* | 1·81 | 0·64 | 0·78 ± 0·74 | 2 | 2·1 ± 2·4 | 0·084 ± 0·18 | 0·499 | 82·1 |
| Skogsfjord L | No | 6 | 1 | 1·0*Euc* | 1·0 | 0 | 0·5 ± 0·55 | 1 | 3·3 ± 5·1 | 0 | 0 | 100·0 |
| Spilderdalsvann L | No | 17 | 2 | 0·58*Euc* | 1·86 | 0·68 | 0·88 ± 0·33 | 1 | 5·8 ± 6·3 | 0 | 0 | 100·0 |
| Dankervag L | No | 30 | 3 | 0·59*Euc* | 2·03 | 0·76 | 1·03 ± 0·49 | 2 | 8·8 ± 11·6 | 0·048 ± 0·149 | 0·580 | 86·6 |
| Rakkfjord L | No | 21 | 4 | 0·8*Cm* | 1·49 | 0·59 | 2·05 ± 0·38 | 3 | 69·6 ± 99·3 | 0·394 ± 0·159 | 0·764 | 4·7 |
| Øsjodalsvann L | No | 42 | 4 | 0·74*Cm* | 1·68 | 0·77 | 1·78 ± 0·81 | 3 | 8·4 ± 10·9 | 0·246 ± 0·25 | 0·805 | 40·4 |
| Rotvab L | No | 12 | 4 | 0·75*Cf* | 1·72 | 0·75 | 1·75 ± 1·05 | 4 | 19·6 ± 36·6 | 0·246 ± 0·27 | 0·798 | 41·7 |
| Strind B L | No | 8 | 3 | 0·72*Euc* | 1·69 | 0·63 | 1·12 ± 0·35 | 2 | 15·5 ± 10·8 | 0·035 ± 0·99 | 0·278 | 87·5 |
| Sandn B L | No | 11 | 2 | 0·98*Euc* | 1·03 | 0·70 | 0·73 ± 0·47 | 1 | 6·9 ± 8·8 | 0 | 0 | 100·0 |
| Vatn 4B L | No | 33 | 7 | 0·98*Cm* | 1·04 | 0·18 | 1·23 ± 0·87 | 4 | 39·7 ± 73·4 | N.C. | | 54·5 |
| Vatn 5B L | No | 20 | 5 | 0·85*Cm* | 1·34 | 0·42 | 1·65 ± 0·81 | 3 | 480·0 ± 621 | N.C. | | 50·0 |
| Vatn 6B L | No | 28 | 4 | 0·98*Cm* | 1·04 | 0·07 | 1·5 ± 0·89 | 3 | 91·9 ± 140·7 | N.C. | | 64·3 |
| Vatn 7B L | No | 32 | 3 | 0·94*Cm* | 1·13 | 0·25 | 1·66 ± 0·91 | 3 | 327·4 ± 467·2 | N.C. | | 53·1 |
| Kvanntavann L | No | 37 | 2 | 0·96*Cm* | 1·13 | 0·26 | 1·15 ± 0·61 | 2 | 10·0 ± 6·4 | 0·101 ± 1·87 | 0·653 | 74·1 |
| Stokkedalsvann L | No | 129 | 2 | 0·91*Cm* | 1·23 | 0·29 | 2·0 ± 0 | 2 | 26·1 ± 43·0 | 0·129 ± 0·062 | 0·237 | 0 |

Table 3. Intestinal helminth component community composition in brown trout in 72 localities in the British Isles and Norway

| Species | Abbreviation | Status | Occurrence | | Dominance | |
|---|---|---|---|---|---|---|
| | | | *n* | % | *n* | % |
| *Bunodera luciopercae* | | Perch S | 1 | 1·4 | 0 | 0 |
| *Crepidostomum farionis* | *Cf* | S | 47 | 67·1 | 9 | 12·8 |
| *Crepidostomum metoecus* | *Cm* | S | 29 | 41·4 | 11 | 15·7 |
| *Sphaerostoma bramae* | | Cyprinid G | 1 | 1·4 | 0 | 0 |
| *Cyathocephalus truncatus* | *Cyt* | S | 15 | 21·4 | 3 | 4·2 |
| *Eubothrium crassum* | *Euc* | S | 42 | 60·0 | 14 | 19·4 |
| *Proteocephalus neglectus** | | S | 6 | 8·6 | 0 | 0 |
| *Camallanus lacustris* | | Perch S | 1 | 1·4 | 0 | 0 |
| *Cucullanus truttae* | | S | 2 | 2·8 | 0 | 0 |
| *Cystidicoloides tenuissima* | *Ct* | S | 15 | 21·4 | 7 | 9·7 |
| *Procapillaria salvelini* | | S | 14 | 20·0 | 0 | 0 |
| *Raphidascaris acus* | | G | 6 | 8·6 | 0 | 0 |
| *Acanthocephalus clavula* | | Eel S | 3 | 4·2 | 1 | 1·4 |
| *Acanthocephalus lucii* | *Al* | Perch S | 3 | 4·2 | 1 | 1·4 |
| *Echinorhynchus truttae* | *Et* | S | 25 | 35·7 | 16 | 22·2 |
| *Neochinorhynchus rutili* | *Nr* | S | 17 | 24·3 | 4 | 5·7 |
| *Pomphorhychus laevis* | *Pl* | S | 5 | 7·7 | 4 | 5·7 |

* Now considered a synonym of *P. exiguus*.

### *Component community composition*

Altogether 17 species were recorded from the 72 localities included in the survey (Table 3). Three further species, *Rhabdochona* sp., *Proteocephalus percae* and *Acanthocephalus anguillae* have been recorded from brown trout in other studies (Kennedy, 1974; Holland & Kennedy, 1997) making the regional species richness (RSR) 20. The maximum CCR was 11 (Table 1), or 55·5% of RSR. No species occurred in all localities. Only 2 species, *Crepidostomum farionis* and *Eubothrium crassum*, occurred in more than 50% of the localities (Table 3) and only 4, these 2 plus *C. metoecus* and *Echinorhynchus truttae*, in more than 33·3%: all these 4 species are trout specialists. By contrast 9 species (52·9%) occurred in fewer than 10% of the localities. Some of these were accidentals like the *Perca fluviatilis* specialist *Camallanus lacustris*, some were generalists like *Sphaerostoma bramae* but some were rarely found trout specialists such as *Cucullanus truttae*. Thus there were a number of species that occurred at low frequency that gave an unpredictable element to the community and a smaller number that occurred at higher frequency and gave a degree of predictability and continuity to the community composition.

Several species could dominate the community (Table 3), but the most frequent dominant species was the acanthocephalan *E. truttae* (at 22·2%) followed by *E. crassum* (19·4%). In 96·9% of the localities the dominant species was a trout specialist and acanthocephalans dominated 37% of the localities. However, no single species or group exhibited overwhelming dominance.

### *Component community diversity*

The majority of localities harboured at least 1 species of helminth, but component communities were characteristically poor with CCR exceeding 4 in only 13·9% localities (Tables 1 and 2). The median value of CCR was 3 and the maximum 11, which value was approached on only 1 occasion. Communities were generally dominated by a single species, almost invariably a specialist, and in only 15·7% infected localities did the BP Index fall below 0·6. The median value was 0·79 and 75% of the values were above 0·55. Median value of SI was 1·33 and of SW 0·52, with maxima of 2·43 and 0·97 respectively (Table 2). The majority of values (75% quartile) fell below 1·69 and 0·7 respectively. The majority of component communities could therefore be described as species poor, being heavily dominated by a single species and exhibiting low diversity.

### *Infracommunity diversity*

The characteristics of the infracommunities were generally similar to those of the component communities, and the range and distribution of indices were similar whether all samples, or only samples where $N > 30$, were considered (Table 4). The majority of fish (56%) contained 1 or 0 helminth species (Tables 2 and 4). Mean numbers of individuals and species per fish were also low, with medians of 22·6 and 1·3 respectively although maximum values rose as high as 480 and 2·38 (Table 4). The maximum value of ICR never exceeded 4 in any of the 795 fish and 34 localities (Fig. 1). These low values of ICR and NI in turn resulted in low

Table 4. Summary distribution of intestinal helminth infracommunity indices of *Salmo trutta*

(Figures in parentheses are comparable values for eels from the River Clyst, taken from Kennedy (1993). Abbreviations as in Table 2. 1. All samples included ($n = 34$), 2. Samples of 30 and greater only ($n = 12$).)

| Index | Min. | 25 % | Median | 75 % | Max |
|---|---|---|---|---|---|
| ICR Mean | | | | | |
| 1. | 0 (0) | 1·03 (0·23) | 1·3 (0·67) | 1·65 (1·11) | 2·38 (1·14) |
| 2. | 0·39 | 1·03 | 1·18 | 1·66 | 2·0 |
| NI | | | | | |
| 1. | 0 (0) | 8·0 (0·17) | 22·6 (1·04) | 32·2 (2·94) | 480·0 (10·3) |
| 2. | 0·9 | 8·4 | 15·4 | 39·0 | 327·0 |
| BI mean | | | | | |
| 1. | 0 (0) | 0·035 (0·036) | 0·158 (0·093) | 0·246 (0·150) | 0·415 (0·158) |
| 2. | 0 | 0·048 | 0·153 | 0·194 | 0·248 |
| BI max | | | | | |
| 1. | 0 (0) | 0·184 (0·001) | 0·531 (0·009) | 0·764 (0·203) | 0·967 (0·986) |
| 2. | 0 | 0·237 | 0·580 | 0·741 | 0·805 |
| % 0/1 | | | | | |
| 1. | 0 (0) | 40·4 (75·0) | 53·1 (92·0) | 82·1 (99·2) | 100·0 (100·0) |
| 2. | 0 | 40·0 | 53·0 | 82·0 | 100·0 |

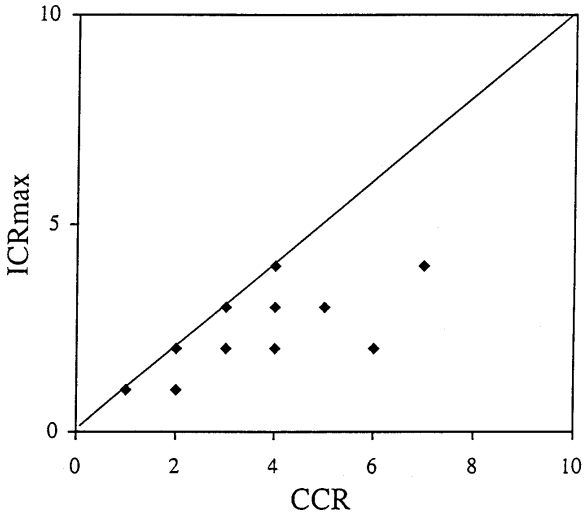


Fig. 1. Relationship between infracommunity richness and component community richness for intestinal helminths of brown trout from the 34 localities listed in Table 2.

values of mean BI, with a median of 0·158 and a maximum of 0·415. Absolute values of BI max showed a median of 0·531 and a maximum of 0·967 (Table 4). The majority of infracommunities could thus be described as species poor and exhibiting low diversity.

Only 3 fish harboured 4 species of helminth (0·02 %). Although there was a significant correlation between ICR max and CCR ($r = 0·758$, $P < 0·001$) at higher values of CCR the relationship departed from linearity (Fig. 1) and became asymptotal.

### *Associations*

Inspection of the data set suggested only 1 interspecific association: a negative one between *E. crassum* and *C. metoecus*. Both species inhabit the pyloric caeca of trout. Analysis of this association by locality (all localities included) suggested a significant negative association ($n = 74$, $X^2 = 9·95$, $P < 0·01$). An even more significant result was obtained from an analysis by infra-community (all fish included) ($n = 711$, $X^2 = 12·87$, $P < 0·001$).

## DISCUSSION

The fundamental objective of the present investigation was to determine whether the intestinal helminth communities of freshwater eels, with their low diversity and isolationist nature were characteristic of that species only, or whether intestinal helminth communities in other species of freshwater fish were similar to those in eels. Brown trout were selected for a comparison for a number of reasons, both practical and biological. A number of studies have been published on their parasite fauna, so it was anticipated that there would be several data sets available for analysis. We had also a number of data sets ourselves from both the British Isles and Norway. On the biological side, trout are like eels in that they are believed to be one of the first fish species to recolonize northern Europe after the last glaciation and so they are not only old inhabitants of the region (Guégan & Kennedy, 1993) but they have also inhabited it for similar periods of time. A corollary of their being indigenous is that both species could be studied in their heartland (Kennedy & Bush, 1994). On the other hand, the two species differ in several important respects. They are both migratory species, but eels are catadromous whereas trout are anadromous. They are both omnivorous in diet, but eels are benthic in habit and nocturnal feeders whereas trout are mid-water in habit and either diurnal or crepuscular. Particularly important

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to this study is the fact that they belong not only to different families but also to different orders. There are thus no phylogenetic grounds for predicting any similarity in composition and/or structure of their helminth communities, and so no need to control for phylogeny in any comparisons. Therefore, any similarity in patterns observed must be ecologically based. We are aware of the possibility of there being other nested patterns within the data set, but it is not our intention to address them at this time.

The basis for any prediction of similarity, or otherwise, between intestinal helminth communities in eels and trout is weak and to some extent conflicting. Kennedy *et al*. (1986) identified brown trout as harbouring the richest intestinal helminth community of all the 9 species investigated by them. A mean value of 0·316 for Brillouin's Index was recorded for a helminth infracommunity in 1 locality, whereas the then highest mean value recorded for eels was 0·188. Brillouin's Index max., mean number of species and mean number of individuals were also higher in infracommunities in trout than in eels. Nevertheless, Kennedy (1990) did suggest that there might be similarities in helminth community structure between the 2 host species in respect of low richness and diversity, high dominance and an isolationist nature. Subsequent published data by Hartvigsen & Halvorsen (1993) suggested that whilst helminth communities in trout might be species poor, they might also be more predictable in structure. Data from other authors including Hartvigsen & Kennedy (1993) and Dorucu *et al*. (1995) have also tended to suggest that component communities in trout exhibit low species richness and diversity, with a high level of dominance often by a species of acanthocephalan. Molloy *et al*. (1995) actually calculated Brillouin's Index values for intestinal helminth communities in western Ireland and recorded mean values ranging from 0·04 to 0·19 and mean values for SR ranging from 0·56 to 1·47. These values are very much more within the range reported for eels by Kennedy *et al*. (1986) rather than for trout. The values quoted for trout by these authors were based on data from only 3 localities, but the communities otherwise exhibited lower richness than those in aquatic birds and tropical eels (Kennedy, 1995).

The present investigation covered a much larger number and range of localities. Although it was deliberately restricted to the heartland to maximize the likelihood of finding rich helminth communities and minimize the likelihood of exchange of species (Kennedy & Bush, 1994), it was also designed to include part of the European mainland so minimizing any possible island effects resulting from sole reliance on data from the British Isles. Restriction to the heartland also facilitated comparison with helminth communities in eels. Within the heartland, a deliberate attempt was made to obtain data from as large a number of localities as possible, spanning the area from North Norway to the West of Ireland, and from a wide range of habitat types. The emphasis throughout has been on number and diversity of sampling localities to ensure valid estimates of the median values of the selected indices and their ranges. Analyses by habitat suggest that none of the indices differed significantly between lakes and reservoirs. No attempts were made to obtain samples of trout that were comparable in respect of size or sex of fish: helminth community diversity may well be influenced by these parameters and there may be such nested patterns within the data set but it is not our intention to examine them here. The intent was instead to include a diversity of fish sizes. Sample effort was measured by sample size and N values were clearly very small in some cases. Sample size is generally determined by practical and pragmatic considerations but again our interest was in covering the possible range of the indices being measured. It is noticeable in this context that the 3 richest and most diverse infracommunities were reported from localities with small values of N (Dunalastair where $N = 13$, Rakkfjord where $N = 21$ and Vennford where $N = 12$). Moreover, (1) the lack of any significant correlations between N and the helminth community parameters measured at both component and community infracommunity levels, (2) the lack of any significant difference in mean index values between large and small samples, and (3) the similarity in range, quartile and median values for all samples and for large samples only all confirm the validity of combining the data sets and including all samples regardless of sample size. For the purposes of this investigation, it was considered more valuable to focus on the range of community parameters whilst recognizing that some sample sizes are smaller than is generally desirable.

There can be no doubt that at both component and infracommunity levels all indices of diversity are low. The median dominance value is high, whilst SI and SW values are low. At infracommunity level, values of ICR, NI, BI mean and BI max are all also similarly low whilst the proportion of trout with 0 or 1 species only is high. Thus intestinal helminth communities in trout are species poor and exhibit low diversity compared to, for example, aquatic birds (Kennedy *et al*. 1986). In these respects they are similar to communities in eels. Indeed, it is startling just how similar the characteristics of the helminth communities in these two species of host are (see Table 4, where trout values are compared with those from eels of the R. Clyst). Values of community parameters from the R. Otter (Kennedy, 1997) are of similar orders of magnitude to those of the R. Clyst, though on occasion individual values may be higher or lower. For example, ICR mean in the Otter was higher at 2·2, NS max was the same as the Clyst and BI mean was slightly higher at 0·415

and BI max slightly lower at 0·96. Thus, the median or mean and maximum values of all diversity parameters are very closely similar in both host species.

There are also indications that interspecific interactions may play a role in structuring the helminth communities within both species of hosts. Bates & Kennedy (1990, 1991) have provided experimental evidence for interactions between the species of acanthocephalans that live in the intestines of eels, and Kennedy (1992) has further provided field evidence for such interactions. In the present study, there was strong presumptive evidence for negative interactions between *Crepidostomum metoecus* and *Eubothrium crassum* in trout, both of which inhabit the pyloric caecae. The nature of the relationship between ICR max and CCR is also compatible with the role of interactions and suggests the communities may be saturated (Kennedy & Guégan, 1994; Srivastava, 1999). Furthermore, Halvorsen & Macdonald (1972) have suggested the possibility of negative interactions between *C. metoecus* and *Cyathocephalus truncatus*.

There are of course some differences in the composition of the intestinal helminth communities in the two species of fish. Although RSR = 20 for both fish species, there is a far more recognizable group of common (i.e. frequently occurring) helminth species in trout which are specialists and which give greater predictability to the community composition than in eels. Such a group of common species was also noted by Hartvigsen & Halvorsen (1993). Other, rare species comprised the unpredictable element in the community composition. Specialists dominated 96·9% of trout communities although maximum frequency of dominance by any one species, by the acanthocephalan *E. truttae*, was only 22·8%, and 28·5% of communities were dominated by digeneans (*Crepidostomum* spp.). In eels, by contrast, only 50% of localities were dominated by a specialist, and the maximum frequency of dominance by a single species, the acanthocephalan *Acanthocephalus lucii* was 32% (Kennedy, 1990). Digeneans dominated only 2·1% of communities. Acanthocephalan generalists were the most frequent dominant species within eels. In respect of dominance, trout helminth communities were more similar to those in the American eels *A. rostrata* which were also generally dominated by specialists (Marcogliese & Cone, 1998).

Thus intestinal helminth communities of trout and eels in freshwater are in fact very similar, despite the differences in composition, and the hypothesis of dissimilarity in structure is refuted. These conclusions are based on a large enough number of samples across the heartland of both species to be fairly sure that the conclusions apply to each throughout their entire ranges. Their intestinal helminth communities are richer than those in some species such as carp *Cyprinus carpio* in its heartland (Nie, 1995) and in Europe (Kennedy & Pojmanska, 1996). This may relate to the more specialized diet of carp as well as to its introduced status in Europe (Kennedy & Guégan, 1994). Thus, it would seem that intestinal helminth communities in eels may be typical of the communities in freshwater temperate fish species, though not of necessity in tropical fish species. Low richness and diversity, together with isolationist natures, are indeed characteristic of the helminth communities in the oldest freshwater fishes in their European heartland, i.e. of the species and regions in which maximum richness and diversity would be expected (Kennedy & Bush, 1994). In view of the high degree of similarity in structure observed in this study between intestinal helminth communities in trout and eels, the question must be raised of whether there are common determinants of community structure and in particular whether there is some factor setting a limit to the number of niches in the intestine (Kennedy & Guégan, 1996). The relationship between ICR max and CCR for intestinal helminths of both brown trout and eels is also very similar indeed, suggesting saturated communities (Srivastava, 1999) with similar ICR limits of 4. Saturation suggests the action of interspecific competition (Srivastava, 1999), and evidence for such interactions has been found in the intestinal helminth communities of both host species. The alternative explanation for these similarities of chance (Rohde, 1998) is not so easy to accept given the large differences in community composition and in host phylogenies and host ecology.

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