FOLIA PARASITOLOGICA 42: 29–35, 1995

The ecology of endoparasitic helminth infections of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in Scotland

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Key words: trout, endoparasitism, helminths, ecology

Abstract. Two hundred and forty brown trout (*Salmo trutta*) and 49 rainbow trout (*Oncorhynchus mykiss*), obtained from 21 locations in Central Scotland between October 1990 and August 1993, were examined for endoparasitic helminth infections. *Crepidostomum farionis* (Digenea) was the most widely distributed helminth species, followed by *Eubothrium crassum* (Cestoda), *Diphyllobothrium dendriticum* and *D. ditremum* (Cestoda), *Neoechinorhynchus rutili* (Acanthocephala), *Echinorhynchus truttae* (Acanthocephala), *Eustrongylides* sp. (Nematoda), *Capillaria salvelini* (Nematoda), *Cyathocephalus truncatus* (Cestoda), *Raphidascaris acus* (Nematoda) and *Cystidicola farionis* (Nematoda), in that order. The prevalences and intensities of each helminth infection were recorded. No evidence was found to indicate that even fish with the highest worm burdens (e.g. 339 plerocercoids of *Diphyllobothrium* spp.) were experiencing any obvious morbidity. An analysis of pairs of associations between species of helminths revealed a significantly positive association between *N. rutili* and *C. farionis* ($P < 0.01$). The results are discussed in terms of patterns in helminth communities in freshwater fish.

Earlier studies of parasitic infections of trout in the British Isles have focussed on morphological and taxonomic aspects of the different types of parasite, with particular attention being paid to those species associated with disease in their fish hosts (Duguid and Sheppard 1944, Wootten 1973, Betterton 1974, Hickey and Harris 1974). More recently, emphasis has been placed on the circumstances which may have influenced the origins and evolution of trout-parasite relationships. For example, Kennedy (1978) noted that the diversity of parasite species harboured by the trout living in various lakes increased in relation to increasing surface area. He concluded that large lakes contained greater habitat diversity than small lakes and so harboured a greater variety of invertebrate hosts of parasites dependent on indirect life-history patterns. These ideas were developed further by Kennedy et al. (1991) and Hartvigsen and Kennedy (1993) in a consideration of the role of habitat in determining the diversity of trout parasites. The trophic status of lakes has also been related to the complexity of fish-parasite faunas (Wisniewski 1958, Esch 1971, Chubb 1979, 1980, 1982).

Few surveys have been carried out on the regional distribution of helminth parasites of fish in Central Scotland, an area with abundant and varied bodies of freshwater richly stocked with brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*). The oldest of these water bodies dates from about 15000 years BP when Scotland was being released from the grip of the Ice Age (Ratcliffe 1977). One such survey was carried out by Copland (1957), who investigated the parasite fauna of fish, including trout, in Loch Lomond and another by Bwathondi (1984) who identified thirteen species of helminths from a sample of 402 brown trout caught in Strathbeg.

The objectives of the investigation described in present paper were to study the distribution and abundance of species of endoparasitic helminths in Scottish brown and rainbow trout, with emphasis on (1) the intensity of the infections, (2) interspecific associations between helminth species in the communities and (3) the status of the trout in the helminths' life cycles. The reasons for conducting the investigation were threefold. First, recent theory has indicated that for macroparasites intensity is the variable that exerts most influence over the regulation of host-macroparasite interactions (Anderson and Gordon 1982), including parasite-induced morbidity and mortality. Secondly, much effort is being made to identify the processes that generate and stabilize communities of helminth species in fish (Esch et al. 1990). Thirdly, it is of interest to determine the importance of trout in the survival of the species of helminth found in association with them.

MATERIALS AND METHODS

A total of 289 trout (240 brown trout, *Salmo trutta* L., 1758, and 49 rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792)) were obtained from 21 different locations in Central Scotland between October 1990 and August 1993. Some were caught with gill nets or hand nets and some were acquired from sport fishermen. Lengths and weights of fish were recorded and sex was determined. Many of the fish were examined for the presence of endoparasitic helminths immediately after capture, but some were frozen at –20°C and then thawed before examination. Fish eyes, gills, stomach, intestine, pyloric caeca, liver, pancreas, swim bladder, spleen and kidneys were examined. All helminths recovered were identified by reference initially to publications by Chubb et al. (1987), Kennedy (1974) and Brown et al. (1986) and the number of helminths per fish was counted. If helminths could not be identified quickly, they were fixed in AFA (Pritchard and Kruse 1982), stained by using Malzacher's staining technique and mounted before taxonomic keys were consulted. Routine statistical procedures were used for investigation of the data collected during the survey, provided that samples of at least 18 trout had been studied from each location. The customary method of investigating associations, by means of the log-odds ratios for 2 × 2 contingency tables, was hampered somewhat by very low prevalences of some of the parasites. In order to accommodate the systematic effect of location, a GLIM analysis was carried out which included "Location" in the model. Thus the results would summarise the association by an average value (over locations) of the log-odds ratio. This metric takes a value zero for complete independence with positive and negative values respectively denoting positive and negative associations.

A total of 6192 helminths representing 10 species from 10 genera (Table 1) were obtained from the 289 fish examined

Table 1. The species of endoparasitic helmints found in *Salmo trutta* (brown trout) and *Oncorhynchus mykiss* (rainbow trout) from freshwater bodies in Central Scotland.

Parasite	Species status	Host Status	Microhabitat
Phylum PLATYHELMINTHES			
Class Trematoda			
Crepidostomum farionis (Müller, 1784)	AU	DH	Posterior intestine and pyloric caeca
Class Cestoda			
Order Spathebothriidea			
*Cyathocephalus truncatus** (Pallas, 1781)	AU	DH	Pyloric caeca
Order Pseudophyllidea			
Diphyllobothrium dendriticum (Nitzsch, 1824)	AL	IH_2	Body cavity
Diphyllobothrium ditremum (Creplin, 1825)	AL	IH_2	Body cavity
Eubothrium crassum (Bloch, 1779)	AU	DH	Pyloric caeca and anterior intestine
Phylum ACANTHOCEPHALA			
Class Eoacanthocephala			
Neoechinorhynchus rutili (Müller, 1780)	AU	DH	Intestine
Class Palaeacanthocephala			
Echinorhynchus truttae (Schrank, 1788)	AU	DH	Intestine
Phylum NEMATODA			
Order Dioctophymidea			
Eustrongylides sp.	AL	IH	Encysted in musculature or body cavity
Order Trichuridea			
*Capillaria salvelini** (Polyanskii, 1952)	AU	DH	Pancreas and posterior intestine
Order Ascarididea			
*Raphidascaris acus** (Bloch, 1779)	AU	DH	Encysted in liver
Order Spiruridea			
*Cystidicola farionis** (Fischer, 1798)	AU	DH	Swim bladder

Abbreviations: (*) not observed in rainbow trout during the course of this survey, AU - autogenic species, AL - allogenic species (see Esch et al. 1988); see Kennedy (1974) and Chubb (1979, 1980, 1982) for checklists of helminth infections in freshwater fishes, DH - definitive host, IH - intermediate host, IH_2 - second intermediate host.

during the survey. The specific identity of the nematode placed in the genus *Eustrongylides* (Table 1) remains problematic (Kennedy and Lie 1976).

RESULTS

Prevalence of helminth infections

Information about the number of trout examined and the prevalences of the 10 species of helminth are given in Table 2. Overall, *Crepidostomum farionis* was found to be the most widely distributed species of helminth; not every individual fluke was examined but all those inspected in detail were judged to belong to this species. *Diphyllobothrium* spp., *Echinorhynchus truttae, Eubothrium crassum,* and *Neoechinorhynchus rutili* were the most widely distributed, in that order, after *C. farionis* (Table 2).

Intensity of helminth infections

Intensities of infections (the number of worms per infected fish; Margolis et al., 1982) are given in Table 3. Some heavy infections were recorded, for example, 339 plerocercoids of *Diphyllobothrium* spp. and 118 adult *N. rutili*, 105 adult *E. truttae* and 100 *C. farionis*

Table 2. The prevalence (%) of endoparasitic helminth infections in *Salmo trutta* (brown trout) and *Oncorhynchus mykiss* (rainbow trout) in Central Scotland.

Location	n	A	B	C	D	E	F	G	H	J	K
Loch Lomond (NS3597)	8	-	-	12.5	25	37.5	-	-	12.5	-	-
Loch Maragan (NN4027)	35	74.2	-	68.5	45.7	2.8	-	-	14.2	2.8	-
River Fillan (NN3726)	18	33.3	5.5	22.2	-	5.5	-	-	-	-	-
Aurs Burn (South Glasgow)	10	10	90	40	-	10	-	-	-	-	20
Carbeth Reservoir (NS 5379)	20	15	15	10	10	10	-	-	-	-	-
Loch Awe (NN0722)	20 4*	-	-	10	100 75	65 25	-	-	5	-	-
Dunalastair Reservoir (NN7158)	15	-	26.6	33.3	60	66.6	6.6	-	-	-	-
Jaw Loch (NS4975)	10	50	-	50		10	30	-	-	10	-
Cochno Loch (NS4976)	3	100	33.3	-	33.3	-	-	-	-	-	-
Loch Leven (NN0960)	3 2*	-	-	-	33.3	33.3	-	-	-	-	-
Secret Loch	1 1*	+	-	+	-	-	+	-	-	+	-
Hill Loch (NS5647)	7 1*	-	-	-	57	-	-	-	-	-	-
Loch Rannoch (NN 5957)	19 7*	- 14.2	57.8 71.4	15.7 14.2	57.8 42.8	63.2 100	- -	5.2 -	- -	- -	- -
Bruncrooks (NS 4879)	4	25	-	25	25	25	-	-	-	-	-
Talla Reservoir (NT 1121)	15	-	93.3	40	26.6	33.3	33.3	20	6.6	-	
Loch Venachar (NN5705)	2	-	-	50	50	100	-	-	-	-	-
Loch Rusky (NN6103)	13*	30.7	-	15.3	-	15.3	-	7.6	-	-	-
Carron Valley Reservoir (NS 6983)	22	-	18.2	13.6	13.6	-	-	4.5			
Whiteadder Reservoir (NT6563)	19	10.5	78.9	36.8	15.7	5.2	-	5.2	-	-	36.8
Fruid Reservoir (NT0919)	9	-	88.8	55.5	22.2	11.1	-	33.3	-	-	
Lake of Menteith (NN5700)	21*	-	-	-	33.3	-	-	-	-	-	-

Abbreviations: n = number of fish examined. Percentage of infected fish with (A) *Neoechinorhynchus rutili,* (B) *Echinorhynchus truttae,* (C) *Crepidostomum farionis,* (D) *Diphyllobothrium* spp., (E) *Eubothrium crassum,* (F) *Cyathocephalus truncatus,* (G) *Eustrongylides* sp., (H) *Capillaria salvelini,* (J) *Raphidascaris acus,* (K) *Cystidicola farionis.* (*) rainbow trout, (+) infected, (-) no worms found.
Grid references taken from the Ordinance Survey Gazetteer of Great Britain, third edition (1992).

Table 3. Intensity of endoparasitic helminth infection in *Salmo trutta* (brown trout) and *Oncorhynchus mykiss* (rainbow trout) in Central Scotland.

Location	n	A		B		C		D		E		F		G		H		J		K	
		X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X	X±SD	S^2/X
Loch Lomond	8	-	-	-	-	1	-	2.0±1.4	0.9	1.6±1.1	0.7	-	-	-	-	1	-	-	-	-	-
Loch Maragan	35	21.3±40.4	77.0	-	-	45.8±30.5	20.3	27.1±34.6	44.1	2	-	-	-	-	-	1.6±0.8	0.4	1	-	-	-
River Fillan	18	3.6±2.8	2.1	30	-	10.5±11.2	11.9	-	-	13	-	-	-	-	-	-	-	-	-	-	-
Aurs Burn	10	1	-	2.3±1.3	0.7	4.2±3.3	2.5	-	-	1	-	-	-	-	-	-	-	-	-	1	-
Carbeth Reservoir	20	2.6±1.5	0.8	7.6±5.5	3.9	4.0±1.4	0.5	1.5±0.7	0.3	8.0±9.9	12.2	-	-	-	-	-	-	-	-	-	-
Loch Awe	20	-	-	-	-	5.0±4.2	3.5	23.8±12.5	6.5	3.3±2.9	2.5	-	-	-	-	1	-	-	-	-	-
	4*	-	-	-	-	-	-	5.0±3.6	2.5	1	-	-	-	-	-	-	-	-	-	-	-
Dunalastair Res.	15	-	-	6.0±8.0	10.6	26.2±27.4	28.6	18.7±14.4	11.0	2.9±3.3	3.7	1	-	-	-	-	-	-	-	-	-
Jaw Loch	10	28.4±50.4	89	-	-	10.3±13.9	18.7	-	-	1	-	2.0±1.0	0.5	-	-	-	-	3	-	-	-
Cochno Loch	3	12.0±9.4	7.3	-	-	3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Loch Leven	3	-	-	-	-	-	-	4	-	1	-	-	-	-	-	-	-	-	-	-	-
	2*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Secret Loch	1	336	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	1*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Hill Loch	7	-		-	-	-	-	68.2±90.1	119	-	-	-	-	-	-	-	-	-	-	-	-
	1*	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-
Loch Rannoch	19	-	-	5.0±7.2	10.3	2.3±1.1	0.5	8.0±13.2	21.7	3.5±2.6	1.9	-	-	1	-	-	-	-	-	-	-
	7*	-	-	11.6±9.9	8.4	4	-	20.6±12.6	7.7	3.8±2.7	1.9	-	-	-	-	-	-	-	-	-	-
Burncrooks	4	-	-	-	-	2	-	1	-	5	-	-	-	-	-	-	-	-	-	-	-
Talla Reservoir	15	-	-	31.0±34.0	37.2	1.8±1.3	0.9	4.2±2.9	2.0	1.2±0.4	0.1	2.4±1.6	1.0	3.0±2.6	2.2	6	-	-	-	-	-
Loch Venachar	2	-	-	-	-	2	-	2	-	4.0±0.0	-	-	-	-	-	-	-	-	-	-	-
Loch Rusky	13	2.7±2.8	2.9	-	-	3.0±2.8	2.6	-	-	1.5±0.7	0.3	-	-	3	-	-	-	-	-	-	-
	*																				
Carron Valley Reservoir	22	-	-	1.2±0.5	0.2	9.6±10.0	10.4	2.3±2.3	2.3	-	-	-	-	1	-	-	-	-	-	-	-
Whiteadder Reservoir	19	1	-	11.3±13.1	15.2	11.5±9.9	8.5	11.3±17.0	25.4	5	-	-	-	1	-	-	-	-	-	5.4±3.1	1.7
Fruid Reservoir	9	-	-	12.2±10.9	9.7	6.6±5.9	5.2	1.0±0.0	-	2	-	-	-	2.6±2.8	3.0	-	-	-	-	-	-

Abbreviations: n = number of fish examined. Infection with (A) *Neoechinorhynchus rutili,* (B) *Echinorhynchus truttae,* (C) *Crepidostomum farionis,* (D) *Diphyllobothrium* spp., (E) *Eubothrium crassum,* (F) *Cyatocephalus truncatus,* (G) *Eustrongylides* sp, (H) *Capillaria salvelini,* (J) *Raphidascaris acus,* (K) *Cystidicola farionis.* (*) rainbow trout, (-) no worms found.

Table 4. The number of species of helminths found in individual *Salmo trutta* (brown trout) from seven locations in Central Scotland.

Location	n	0	1	2	3	4
Loch Maragan	35	1	7	16	10	1
River Fillan	18	10	4	4	-	-
Carbeth Res.	20	11	6	3	-	-
Loch Awe	20	-	7	10	3	
Loch Rannoch	19	2	5	5	5	2
Carron Valley Res.	22	12	9	1	-	-
Whireadder Reservoir	19	3	4	5	6	1

n - number of fish examined, 0 - number of fish with no infection, 1 - number of fish with one infection and so on.

Table 5. The results of an investigation of associations between pairs of helminth species in *Salmo trutta* (brown trout) from seven locations in Central Scotland.

Species pairs	Log odds ratio (±SE)	Odds ratio	Result
A/B	0.75±1.08	2.12	
A/C	1.16±0.58	4.99	P < 0.01
A/D	-1.30±0.78	0.27	
A/E	-0.74±1.31	0.47	
B/C	1.24±0.70	3.46	
B/D	0.27±0.69	0.76	
B/E	-0.75±0.85	0.47	
C/D	0.16±0.53	1.18	
C/E	0.78±0.79	2.19	
D/E	1.32±0.77	3.75	P < 0.10

A - *Neoechinorhynchus rutili*, B - *Echinorhynchus truttae*, C - *Crepidostomum farionis*, D - *Diphyllobothrium* spp., and E - *Eubothrium crassum*.
Note: positive association between pairs of species is denoted by a positive value for the log odds ratio and a negative association by a negative value.

in individual brown trout. It was noticeable that, where sufficient numbers of infected fish had been obtained (samples of 18 or more from the different locations; Table 2), the frequency distribution of numbers of worms per fish was overdispersed with the variance: mean ratio (S^2/x) >1 (Anderson and Gordon 1982). Although intensity of infection would be expected to influence host health and condition, direct observations made at the *postmortem* examination of whole fish did not indicate that even individual fish with the highest worm burdens were experiencing any overt morbidity. Furthermore, there was no evidence of any statistical correlation between host weight and worm burden.

Asociations between helminth species

The numbers of helminth species found in individual brown trout from the seven of the locations from which 18 or more fish were caught are shown in Table 4. The largest number of species found per fish was four. In cases where certain species were often found together or where species appeared not to coexist in the same host, the question arises as to whether these distributions are generated randomly or depend on either synergistic or antagonistic associations. The results of the log-odds ratio analysis to investigate estimates of the significance of association between pairs of helminth species in the brown trout from the seven locations (Table 4) is given in Tables 5 and 6. Clear evidence was obtained for a positive association between *N. rutili* and *C. farionis* ($P < 0.01$) in brown trout, regardless of their location, and some evidence for a possible positive association between *Diphyllobothrium* spp. and *E. crassum* was also found (Table 5). It needs to be emphasised, that the sensitivity of investigations of this sort are influenced by the level of infection. However, it should be noted that the associated pairs of species of helminths depend for their transmission on benthic and pelagic intermediate hosts.

DISCUSSION

The results from the current survey have added significantly to knowledge of the distribution and abundance of endoparasitic helminths infections in trout in Scotland (see Copland 1957, Bwathondi 1984). None of the species of helminths observed in the trout is a new host record, but it is only recently that *C. farionis* has been found in rainbow trout (Kennedy et al. 1991). Nor was evidence obtained to suggest that any of the infections was associated with significant morbidity or poor condition of their fish hosts.

The most interesting aspect of the study is the interpretation of the results in terms of helminth communities in freshwater fish in Great Britain (Esch et al. 1988). The results undoubtedly show considerable variation in the helminth communities from the trout sampled in reasonable numbers from seven of the 21 locations studied (Table 4). Kennedy (1990) pointed out that such variation remains largely unexplained, although after an analysis of several data sets, Esch et al. (1988) were able to suggest a range of ecological processes that could account for the observed diversity. One of the data sets investigated by Esch et al. (1988) dealt with brown trout taken from 9 locations in the British Isles. Two of these locations were from Scotland; three species of helminth were found in 20 trout from Loch Long and nine species were recovered from

Table 6. Characteristics of helminth communities in *Salmo trutta* (brown trout) from seven locations in Central Scotland.

	Locations						
Characteristics	LM	RF	CR	LA	LR	CVR	WR
Number of fish examined	35	18	20	20	19	22	19
Total no. of helminth species	6	4	5	4	5	4	7
No. of autogenic species	5	4	4	3	3	2	5
No. of allogenic species	1	0	1	1	2	2	2
Total no. of helminth individuals	2 076	107	58	502	193	42	331
Proportion of autogenic individuals	0.8	1	0.95	0.11	0.54	0.81	0.89
Proportion of allogenic individuals	0.2	0	0.05	0.89	0.46	0.19	0.11
Berger-Parker dominance index	0.52	0.39	0.39	0.89	0.45	0.69	0.51
Character of dominant species	AU	AU	AU	AL	AL	AU	AU
Identity of dominant species	Cre	Cre	Ech	Dip	Dip	Cre	Ech
Mean % similarity between indiv. fish (autogenic species)	39.5	7.5	3.3	25.7	18.1	3.9	33.6
Mean % similarity between indiv. fish (allogenic species)	20.2	0	0.5	13.8	13.8	1.3	1.8

Abbreviations: Cre - *Crepidostomum farionis*; Ech - *Echinorhynchus truttae*; Dip - *Diphyllobothrium* spp.; LM - Loch Maragan; RF - River Fillan; CR - Carbeth Reservoir; LA - Loch Awe; LR - Loch Rannoch; CVR - Carron Valley Reservoir; WR - Whiteadder Reservoir.

as few as 13 trout from Loch Dunalastair. In Table 1 of their paper Esch et al. (1988) describe the characteristics of the helminth communities in the populations of trout they studied. A similar description is presented in Table 6 for the trout sampled from seven locations during our survey. *Crepidostomum farionis* was the dominant species in the helminth communities in brown trout in 3 of the seven locations and *E. truttae* and *Diphyllobothrium* spp. in two each. There was little similarity between these results and those obtained by Esch et al. (1988), indicating the importance of the trout habitats in determining the structure of helminth communities (Kennedy 1978, Chubb 1980, 1982). The concept of the compatibility and encounter filters proposed by Combes (1990) also helps to explain how helminth communities might vary between populations of the same host species living in a relatively small geographical area. The physiological and immunological properties of the trout will determine whether helminths will survive in them and little variation is to be expected in this aspect of the trout-helminth relationship. The infective stages of compatible helminth species that trout actually encounter, however, will depend particularly on the role of the water body in the ecology of intermediate hosts and vectors.

Within helminth communities evidence of only one interaction was found between helminth species, namely the positive association between *C. farionis* and *N. rutili*. Perhaps one species improves either the establishment or survival of the other. The fact that both species are restricted to the gut throughout their time in trout indicates that some effect of the host's immune response may not be involved. This association and other aspects of *C. farionis* in trout (Table 6) merit further investigation.

Acknowledgements. MD is grateful to the Turkish Government for his financial support. It is a pleasure to thank the Fisheries Society of the British Isles for a grant to Ms Lorna Ballantyne who contributed much to the collection of hosts and helminths on which this paper is based. We also thank R.C. Stoddart and Margaret Mullin for technical help and Alan McGregor for his invaluable knowledge of the haunts and habits of Scotland's trout.

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Received 4 October 1994

Accepted 16 December 1994