

Interspecific interactions between Acanthocephala in the intestine of brown trout: are they more frequent in Ireland?

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SUMMARY

The aim of this paper was to test the hypothesis that when the 2 species of Acanthocephalan *Pomphorhynchus laevis* and *Acanthocephalus clavula* are found concurrently within the intestine of brown trout under field conditions, they have the potential to interact negatively. Evidence has shown that Acanthocephala are more likely to exhibit negative interactions with their own and other species, under both field and experimental conditions. Furthermore, the likelihood of these interactions is increased in Ireland because of the absence of certain definitive hosts and the fact that concurrent infections by two or more species of Acanthocephala are more commonly observed in fish. Data collected from wild and stocked brown trout and from 2 lakes provided an opportunity to compare the 2 potentially interacting helminth species in their fundamental and realized niche and several pieces of convincing evidence are provided here to support the hypothesis. A significant negative association between the numbers of each species found in individual fish was reported and this was consistent for both wild and stocked trout. Furthermore, an analysis of the proportions of low, moderate and high intensity infections in single and concurrent infections revealed a significant reduction in increasing intensities in concurrent infections compared to single infections. Finally, strikingly different patterns of niche inhabitation were observed, particularly for *P. laevis* in the presence of *A. clavula* in wild trout. Results from the niche width analysis also support the observations on average position in single and concurrent infections. The niche width of *P. laevis* when it co-occurred with *A. clavula* decreased markedly in high intensity infections compared to low intensity infections.

Key words: trout, Acanthocephala, interspecific interactions, niche shifts, Ireland.

INTRODUCTION

The role of interspecific interactions in structuring natural helminth parasite communities in the fish intestine remains a subject for debate (Poulin, 2001). Experimental data (Bates & Kennedy, 1990, 1991) have yielded significant and convincing evidence to support a role for competition between parasite species but data from the field remain more difficult to interpret (Kennedy, 1992). It has been suggested by several authors that Acanthocephala may have more of an impact upon intestinal parasite communities than other kinds of helminths (Price, 1980; Holland, 1987; Janovy, 2002). Ireland presents a useful zoogeographical situation for the exploration of parasite competition under field conditions due to the relatively depauperate nature of its fish fauna (Griffiths, 1997). It has indeed been suggested that interspecific competition may be more commonly observed in Ireland because Acanthocephalan species may be forced to share definitive hosts in the absence of their preferred definitive hosts from

that country (Lyndon & Kennedy, 2001). Some Acanthocephalan species co-occurrences in the same host and locality have been reported from Ireland whereas they seldom occur elsewhere. For example, *Pomphorhynchus laevis* and *Acanthocephalus clavula* are a very uncommon species combination in brown trout, *Salmo trutta* as the preferred definitive host of *A. clavula* is the eel *Anguilla anguilla* whilst brown trout is the preferred definitive host of *P. laevis* only in Ireland. Thus Kennedy & Hartvigsen (2000) recorded *A. clavula* in brown trout in only 3 of the 72 localities sampled in the British Isles and Norway, and there appears to be only a single record of the 2 species co-occurring in trout in Europe apart from Ireland (Dezfuli *et al.* 2001). By contrast, this combination of parasites and host has been reported from Ireland on 3 occasions in 2 localities (Conneely & McCarthy, 1984, 1988; Molloy, Holland & Poole, 1993; Byrne *et al.* 2002).

Discovery of an unusual situation in Ireland provided the opportunity to test the hypothesis that interactions are more likely when Acanthocephalan species are found in unusual hosts. This involved *P. laevis* and *A. clavula* in brown trout, and changing infection levels of the 2 species in 1 locality. In a

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sample of 549 brown trout derived from Lough Feeagh and Bunaveela lake in the west of Ireland in 1991 and 1992 the helminth community was observed to be dominated by a single Acanthocephalan species *P. laevis* (Molloy, Holland & Poole, 1995). Six years later *A. clavula* was observed in very high numbers in brown trout sampled from Clogher lake (adjacent to Lough Feeagh and Bunaveela lake) and in the absence of *P. laevis* (Byrne, 2000). In contrast, both single and concurrent infections of *P. laevis* and *A. clavula* were observed in wild and stocked trout from Lough Feeagh (Byrne *et al.* 2002).

Data collected from these 3 situations provided an opportunity to compare 2 potentially interacting helminth species in their fundamental and realized niche. Four pieces of evidence, both numerical and functional, are provided to test the hypothesis that *P. laevis* and *A. clavula* interact within the intestine of trout under field conditions. Firstly, numerical responses are explored in 3 ways (i) the observed frequencies of species co-occurrence are compared with the expected frequency of species co-occurrence using a null model generated from the actual prevalences of helminth species (Janovy *et al.* 1995) (ii) significant negative and positive associations are sought between species pairs in hosts (iii) the proportion of Acanthocephalan worms found in low, medium and high intensity infections are compared for single and concurrent infections in Lough Feeagh. Secondly, functional responses are explored by comparing the fundamental and realized niches of each parasite species in the intestine of trout.

MATERIALS AND METHODS

Site

The wild brown trout used in this study were taken from 2 lakes, Lough Feeagh and Clogher Lake in the west of Ireland (see Byrne *et al.* 2002).

Fish

The stocked brown trout used in this study were all taken from Lough Feeagh, and were the F1 progeny of wild sea trout broodstock taken from Lough Feeagh and maintained by the Marine Institute as part of their west coast sea trout broodstock programme (Poole *et al.* 2002). Thus, the brown trout stocked into Lough Feeagh were essentially genetically identical to the wild trout living there.

Beach seine netting was carried out, in accordance with the procedure described by Matthews *et al.* (1997), on 7 occasions in Lough Feeagh between April 1997 and November 1998. Netted fish were measured (fork length), and examined for the presence of tags. Due to the nature of the shoreline surrounding Clogher Lake, a combination of extremely soft mud substrate and reed beds, it was not possible

to beach seine this lake, so all fish samples were taken using gill nets.

Parasitological procedures

Most captured trout (wild and stocked) were transported to the laboratory alive where they were killed and frozen for subsequent parasitological examination. Details of which are reported by Byrne *et al.* (2002).

Niche determinants

Whilst the possibility of a post-mortem niche shift in either species after host death cannot be completely excluded, it does not appear likely since neither species is known to shift its niche over time or in relation to host stress (Kennedy, 1972; Kennedy & Lord, 1982; Kennedy, Broughton & Hine, 1976).

Parasites were assigned a percentage location, with 0% corresponding to the anterior oesophagus and 100% corresponding to the anus (see Byrne *et al.* 2002). Data from 5 different samples of worms were used to compare the niches occupied by *P. laevis* and *A. clavula*. For *P. laevis* a measure of the fundamental niche was derived from data collected from Lough Feeagh and Bunaveela Lake in 1991 and 1992 (Molloy *et al.* 1995). At this time, *P. laevis* was the only Acanthocephalan observed in the gut of a total of 549 brown trout sampled. It should be noted that unlike the data sets derived from the present study detailed information on the position of each individual worm and a measure of the intensity of infection in the fish it occupied is not available for this fundamental niche data set (see below). The other 4 samples were derived from fish sampled during the present study and included worms derived from single infections (in the absence of *A. clavula*) in wild and stocked fish from Lough Feeagh and worms found in concurrent infections (in the presence of *A. clavula*) in wild and stocked fish from Lough Feeagh.

The data on the fundamental niche of *A. clavula* are derived from fish sampled from Clogher Lake where *A. clavula* was the only Acanthocephalan observed in those fish during the present study. The other 4 samples mirror those described above for *P. laevis* and include worms found in single infections in wild and stocked fish from Lough Feeagh and worms derived from concurrent infections in wild and stocked fish from Lough Feeagh.

Niche width values were calculated using Culver's (1972) standardized Shannon-Wiener function, H' . The function describes the evenness of the distribution of a parasite along the intestine of its host and values for it range from zero where a parasite is present in only one section of the intestine to one where the parasite is present in all sections of the intestine.

Statistical analysis

One-way analysis of variance (ANOVA) was used to compare the lengths of wild trout from Clogher Lake and wild and stocked fish from Lough Feeagh. Spearman's rank correlation coefficient was used to examine the association between fish length and the numbers of *P. laevis* and *A. clavula* respectively. The null model for species density distributions as described by Janovy *et al.* (1995) was used to determine whether species density distributions in parasite species assemblages reveal regularly occurring species-to-species interactions. Actual prevalence values of each parasite species in an assemblage were compared to expected prevalence values generated by the model, allowing us to determine whether different helminth species co-occur more or less frequently than expected. χ^2 tests were used to compare observed and expected frequencies.

Spearman's rank correlation coefficient was used to examine the pair-wise associations between the intensity of the 4 most prevalent intestinal species between all fish hosts. In all cases double zeros (fish not infected by either species in a species pair) were excluded from the analyses.

The proportions of worms found in low, medium and high-intensity infections of each species of Acanthocephalan were compared in single and concurrent infections in fish from Lough Feeagh. The cut-offs were as follows: for *P. laevis* low 1–5 worms, medium 6–9 worms and high 10 or more worms; for *A. clavula* low 1–15 worms, medium 16–75 and high 76 or more worms. The parameters for low, medium and high-intensity infections of *P. laevis* and *A. clavula* were obtained by combining all of the intensity data for each species into a frequency histogram. Parameters were then assigned by visual examination of the frequency histogram. In the case of *A. clavula* low, medium and high-intensity infection categories were derived from the intensity data for Clogher Lake, where *A. clavula* was the only Acanthocephalan species present, thus the same parameters were used for Lough Feeagh and Clogher Lake. The proportions of worms at each infection intensity between single and concurrent infections were compared using χ^2 analysis.

Regression analysis was used to explore the relationship between fish length and the position of the individual parasites in the intestine for the 10 niche samples described above. One-way analysis of variance (ANOVA) was employed to compare the mean position of *P. laevis* between the different samples (fundamental versus realized niche in wild versus stocked trout). Two separate two-way analyses of variance (ANOVA) were then used to compare the average position of *P. laevis* in wild and stocked trout and the possible influence of parasite intensity upon the observed relationships. Two-way analysis of variance (ANOVA) was also used to compare the

mean position of *A. clavula* between the different samples (fundamental versus realized niche in wild versus stocked trout) and to also include parasite intensity as the second factor in the analysis.

RESULTS

A total of 540 trout sampled in 1997 and 1998 were examined from the 2 lakes – 161 from Clogher Lake, 257 wild trout and 122 stocked fish from Lough Feeagh. The component communities consisted of 11 metazoan species recorded from wild trout from Lough Feeagh, 10 species from the stocked trout and 9 species from wild trout caught in Clogher Lake. Of particular note, is the very high prevalence and intensity of *A. clavula* in fish from Clogher Lake and the absence of *P. laevis* (Table 1).

The mean length of the trout sampled from Lough Feeagh and Clogher Lake differed significantly with wild fish from Lough Feeagh being shorter than stocked fish from the same lake and wild fish from Clogher (*F* ratio = 279.8; D.F. = 2, 534; $P \leq 0.0001$) (Table 1). Spearman's rank correlation revealed a significant positive association between the length of fish and the number of *A. clavula* per fish in Clogher lake ($0.245 P \leq 0.01$) and for wild fish in Lough Feeagh ($0.200 P \leq 0.01$) but not for stocked fish from Lough Feeagh. In contrast, there was no association between the length of fish and the numbers of *P. laevis* for either of the fish samples derived from Lough Feeagh.

Observed frequency values of parasite species co-occurring in each fish sample (Lough Feeagh wild and stocked trout and Clogher Lake wild trout) were compared to the expected frequency values of species co-occurrence, which were generated using a null model. These observed and expected frequencies of co-occurrence were calculated for all parasite species in each sample and for the 4 most prevalent intestinal species in each sample. χ^2 tests showed no significant differences between the observed and expected frequencies of species co-occurrence with the exception of the total parasite sample for stocked trout ($\chi^2 = 77.59$; D.F. = 9; $P \leq 0.0001$) when the observed frequency was less than that of the expected.

Spearman's rank correlation coefficient revealed that for both wild and stocked trout there were highly significant negative correlations between *P. laevis* and *A. clavula* (Table 2). In addition, significant negative correlations were demonstrated between the two species of Acanthocephala and other helminth species. Of particular note was the cestode/Acanthocephalan interaction between *P. laevis* and *Eubothrium crassum* in wild fish from Feeagh and the very consistent finding of a significant negative correlation between *A. clavula* and *E. crassum* in wild and stocked trout from Feeagh and wild trout from Clogher.

Table 1. Percentage prevalence and the mean intensity (\pm S.D.) values for all helminth species recorded in trout (*Salmo trutta* L.) in each sample

(% prevalence, I, mean intensity.)

	L. Feeagh wild		L. Feeagh stocked		Clogher Lake	
	%	I (\pm S.D.)	%	I (\pm S.D.)	%	I (\pm S.D.)
Sample size	257		122		161	
Mean length (\pm S.D.)	14.8 (3.6)		21.1 (2.6)		16.4 (3.5)	
<i>Eubothrium crassum</i>	26.5	8.2 (8.6)	56.6	15 (36.9)	57.1	3.7 (3.8)
<i>Crepidostomum farionis</i>	45.9	17.3 (24.9)	22.1	9.2 (17.9)	77	56.5 (91.4)
<i>Pomphorhynchus laevis</i>	67.3	7.1 (9.1)	51.6	8.5 (10.9)	0	0
<i>Acanthocephalus clavula</i>	26.1	10.6 (18.7)	39.3	9.3 (15.9)	86.3	90.1 (93.2)
<i>Diphyllbothrium ditremum</i>	15.6	5.3 (6.2)	34.4	17.4 (38.9)	24.2	14.7 (24.8)
<i>Rhabdochona</i> sp.	18.7	6.4 (10.4)	13.1	3.6 (3.3)	6.8	20.9 (43.1)
<i>Cystidicola farionis</i>	3.9	10.2 (10.7)	7.4	6 (8.2)	0	0
<i>Anisakis</i> sp.	0.4	1	0	0	1.9	2.7 (2.9)
<i>Cystidicoloides tenuissima</i>	3.9	12.8 (17.6)	0.8	1 (0)	0	0
<i>Discocotyle sagittata</i>	13.2	1.8 (1.2)	13.9	2.1 (1.7)	1.2	1 (0)
<i>Salmincola salmoneus</i>	9.3	1.6 (1.2)	8.2	1.3 (0.5)	19.9	1.7 (1.1)
<i>Diphyllbothrium dendriticum</i>	0	0	0	0	1.9	45.7 (52)

Table 2. Spearman's rank correlation coefficients for the relationships between the four most prevalent intestinal helminth species in wild trout in each sample lake and for stocked trout in Lough Feeagh

(Double zeros, fish not harbouring either species in a pairwise association were excluded. Figures given below the diagonal are the actual sample sizes of fish harbouring at least 1 of the 2 species in a species pair.)

	<i>E. crassum</i>	<i>C. farionis</i>	<i>P. laevis</i>	<i>A. clavula</i>	<i>Rhabdochona</i> sp.
L. Feeagh wild					
<i>Eubothrium crassum</i>	—	-0.608**	-0.382**	-0.527**	
<i>Crepidostomum farionis</i>	165	—	-0.404**	-0.193*	
<i>Pomphorhynchus laevis</i>	201	217	—	-0.382**	
<i>Acanthocephalus clavula</i>	116	145	194	—	
L. Feeagh stocked					
<i>Eubothrium crassum</i>	—	-0.368**	-0.179	-0.486**	
<i>Crepidostomum farionis</i>	79	—	-0.411**	-0.035	
<i>Pomphorhynchus laevis</i>	90	74	—	-0.551**	
<i>Acanthocephalus clavula</i>	94	60	89	—	
Clogher Lake					
<i>Eubothrium crassum</i>	—	-0.169*		-0.222**	-0.005
<i>Crepidostomum farionis</i>	148	—		0.004	0.042
<i>Acanthocephalus clavula</i>	153	156		—	-0.057
<i>Rhabdochona</i> sp.	94	124		140	—

* $P < 0.05$; ** $P < 0.01$.

The proportions of worms in infections of different intensities are compared for single and concurrent infections for *P. laevis* and *A. clavula* (see Figs 1A, B and 2A, B). These figures demonstrate that in concurrent infections the proportion of worms in high intensity infections falls significantly compared to single infections and this trend is demonstrated for both species (*P. laevis* wild fish $\chi^2 = 98.6$ D.F. = 2 $P \leq 0.0001$; stocked fish $\chi^2 = 20.51$ D.F. = 2 $P \leq 0.0001$) (*A. clavula* wild fish $\chi^2 = 97.75$ D.F. = 2 $P \leq 0.0001$; stocked fish $\chi^2 = 39.7$ D.F. = 2 $P \leq 0.0001$).

Regression analysis revealed no evidence of a statistically significant relationship between the length of fish and the position of individual parasites in the intestine for 9 of the 10 samples of worms described below. In only 1 case was there evidence of a relationship, in concurrent infections of *A. clavula* with *P. laevis* in stocked fish ($R^2 = 0.331$, $F = 26.7$, $t = -5.7$ $P \leq 0.0001$).

The median positions of *P. laevis* are illustrated by means of box plots in Fig. 3. In the case of *P. laevis* in its fundamental niche, parasites have on average a posterior position but the widest range of all the

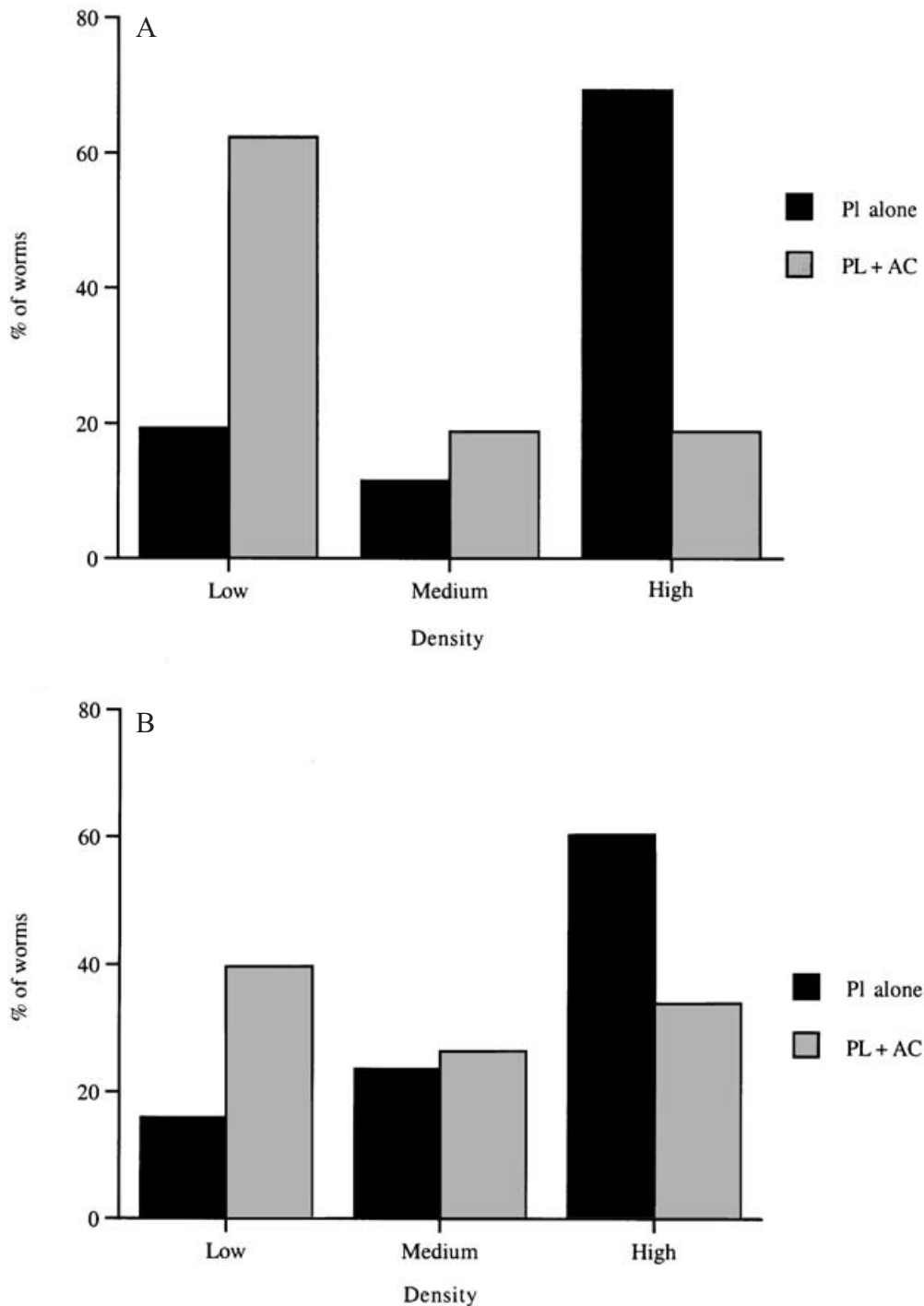


Fig. 1. (A) The proportion of low, medium and high-intensity infections of *Pomphorhynchus laevis* in single and concurrent (with *Acanthocephalus clavula*) infections in wild trout from Lough Feeagh. (B) The proportion of low, medium and high-intensity of infections of *P. laevis* in single and concurrent (with *A. clavula*) infections in stocked trout from Lough Feeagh.

5 samples. For parasites found in the absence of *A. clavula* in wild fish in Feeagh the situation is very similar with a slightly reduced range. In stocked fish, worms are on average less posteriorly situated and the 2 samples of *P. laevis* either alone or in the presence of *A. clavula* are quite analogous. The most striking difference can be observed in wild fish when *P. laevis* is found concurrently with *A. clavula*. In this situation, the worms are considerably more

posteriorly located, the minimum value is less anterior and the range is considerably reduced indicating that in the presence of *A. clavula*, *P. laevis* worms are situated in a much more posterior position and occupy a smaller proportion of the intestine.

One-way analysis of variance revealed that the mean position of *P. laevis* differs significantly between the 5 samples (F ratio = 43.8; D.F. = 4, 2431;

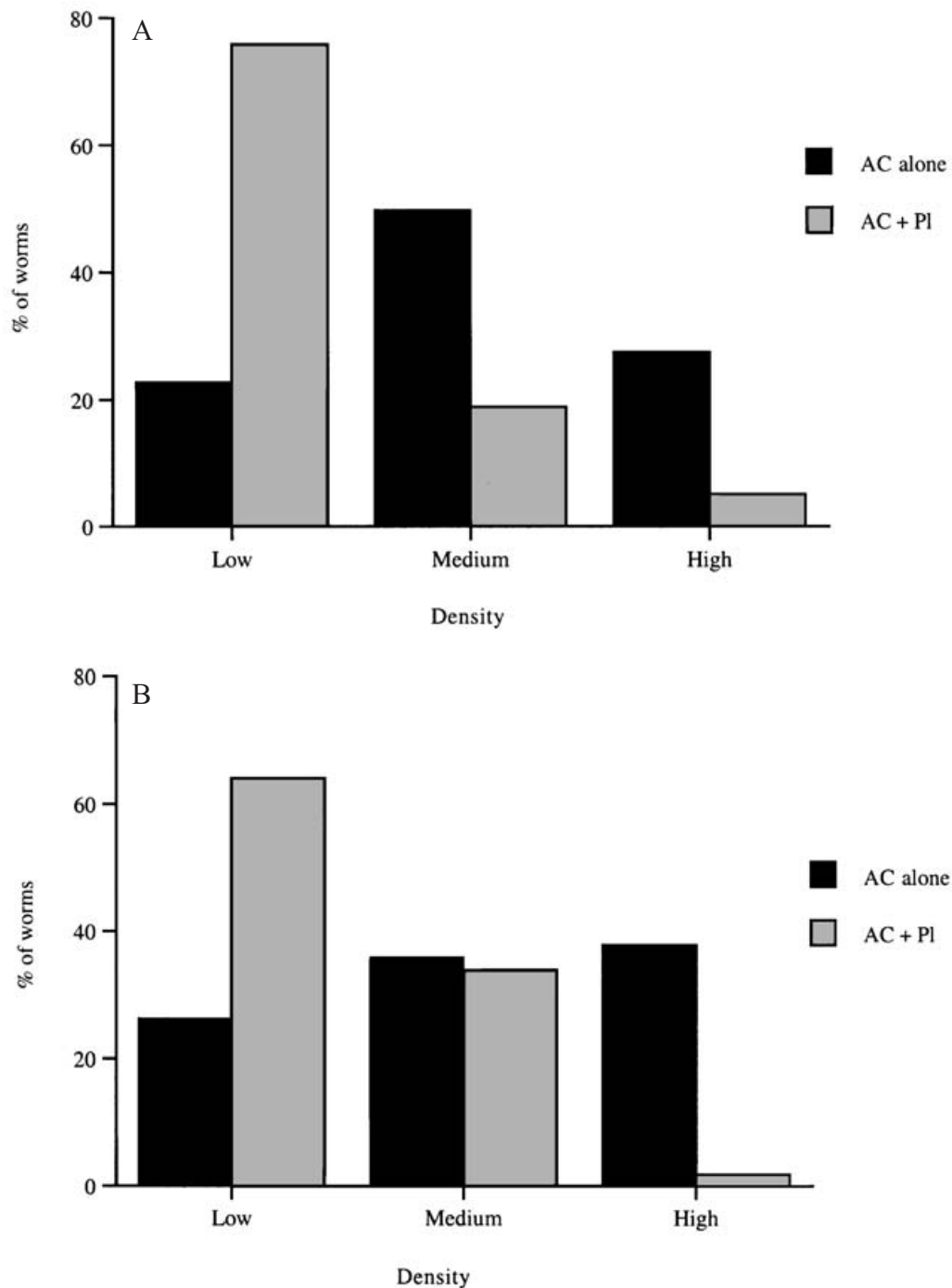


Fig. 2. (A) The proportion of low, medium and high-intensity infections of *Acanthocephalus clavula* in single and concurrent (with *Pomphorhynchus laevis*) infections in wild trout from Lough Feeagh. (B) The proportion of low, medium and high-intensity of infections of *A. clavula* in single and concurrent (with *P. laevis*) infections in stocked trout from Lough Feeagh.

$P \leq 0.0001$). Least square difference *post-hoc* tests demonstrated that the mean position of *P. laevis* in its fundamental niche did not differ significantly from worms derived from wild trout in single infections. In addition, *P. laevis* alone or in the presence of *A. clavula* in stocked trout showed no significant difference in mean position. All other comparisons were significantly different at the $P \leq 0.0001$ level.

As explained in the Materials and Methods section, no information on the relationship between intensity of infection and position was available for *P. laevis* in its fundamental niche, so for this reason intensity was not included as a second factor in the entire analysis of variance as it is below for *A. clavula*. Therefore, 2 separate two-way analyses of variance are performed – one concerning wild fish and comparing *P. laevis* in the presence and absence

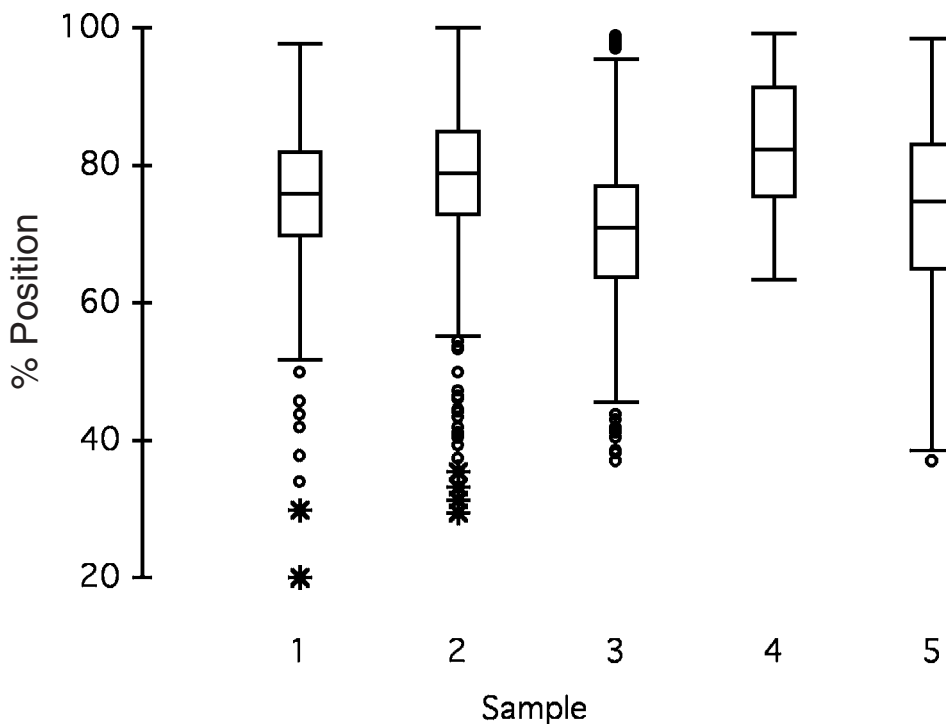


Fig. 3. A boxplot of the median position (\pm interquartile range and lowest and highest point) of *Pomphorhynchus laevis* for 5 different samples: (1) fundamental niche; (2) single infection of *P. laevis* in wild trout; (3) single infection of *P. laevis* in stocked trout; (4) *P. laevis* in concurrent infections with *Acanthocephalus clavula* in wild trout; (5) *P. laevis* in concurrent infections with *A. clavula* in stocked trout (Symbols \circ and * indicate worms in extreme positions).

of *A. clavula* and including the intensity of *P. laevis* as a second factor, the other concerning stocked fish and the same combination. For wild fish, the presence or absence of *A. clavula* was a significant factor ($F=13.34$; D.F. = 1, 1135; $P \leq 0.0003$), intensity of *P. laevis* was non-significant ($F=0.925$; D.F. = 2, 1135; $P=0.3966$) and the interaction between the presence or absence of *A. clavula* and intensity was significant ($F=3.38$; D.F. = 2, 1135; $P \leq 0.0343$). For stocked fish, only the presence or absence of *A. clavula* was significant ($F=4.14$; D.F. = 1, 517; $P \leq 0.016$), intensity of *P. laevis* was non-significant ($F=0.025$; D.F. = 2, 517; $P=0.8732$) and the interaction between presence or absence of *A. clavula* and intensity was also non-significant ($F=0.801$; D.F. = 2, 517; $P=0.4493$).

The median positions of *A. clavula* are illustrated in Fig. 4. A measure of the position of *A. clavula* in its fundamental niche in Clogher Lake demonstrates that, on average, worms inhabit a middle position in the intestine and have a wide range. This pattern is very similar in worms derived from wild fish from Lough Feeagh in the absence of *P. laevis*. In stocked fish, worms are, on average, slightly anterior to those from wild fish and the range is diminished. The median position of *A. clavula* worms in the presence of *P. laevis* in both wild and stocked fish is considerably posterior although the range remains the same (see Fig. 4). Therefore, the striking diminution in the range observed for *P. laevis* in the presence of *A. clavula* is not observed in this comparison.

A two-way analysis of variance was performed in order to compare the mean position of *A. clavula* between the 5 samples and to examine the influence of intensity of *A. clavula*. This revealed that position did differ significantly between the 5 samples ($F=59.1$; D.F. = 4, 10 335; $P \leq 0.0001$), intensity of *A. clavula* was non-significant ($F=0.139$; D.F. = 2, 10 335; $P=0.8702$) but the interaction between the two was significant ($F=3.64$; D.F. = 8, 10 335; $P \leq 0.003$). Furthermore, *post-hoc* tests on the differences between the mean position of the 5 samples showed that all samples differed significantly from each other with the exception of worms derived from stocked trout in the presence of *P. laevis* and worms in their fundamental niche from Clogher. These differences were significant at the $P \leq 0.0001$ level with the exception of parasites in their fundamental niche and parasites from wild fish in the absence of *P. laevis* ($P \leq 0.033$); and parasites from wild fish in absence of *P. laevis* and those derived from stocked fish in the presence of *P. laevis* ($P \leq 0.018$).

Niche width values for the total sample of *P. laevis* were 0.71 for wild trout and 0.8 for stocked trout (Table 3). When *P. laevis* co-occurred with *A. clavula*, niche width values for *P. laevis* decreased substantially from low to high intensity infections of *A. clavula* in both wild and stocked trout (Table 3). The niche width values for the total sample of *A. clavula* were comparable between the wild and stocked trout in Lough Feeagh and wild trout in

Table 3. Niche width values for *Pomphorhynchus laevis* and *Acanthocephalus clavula* in wild and stocked trout in Lough Feeagh and for *A. clavula* in Clogher Lake

(Niche width values are also presented for *P. laevis* when it co-occurs with *A. clavula* in low, medium and high-intensity infections in wild and stocked trout and for *A. clavula* when it co-occurs with *P. laevis* in low, medium and high-intensity infections in wild and stocked trout in Lough Feeagh.)

	Total	Low intensity	Medium intensity	High intensity
Lough Feeagh – Wild				
<i>P. laevis</i>	0.71	0.71	0.68	0.76
<i>A. clavula</i>	0.86	0.86	0.82	0.61
<i>P. l.</i> and low, medium high-intensity infection of <i>A. c.</i>		0.66	0.45	0.18
<i>A. c.</i> and low, medium high-intensity infection of <i>P. l.</i>		0.79	0.55	0.57
Lough Feeagh – Stocked				
<i>P. laevis</i>	0.8	0.75	0.74	0.76
<i>A. clavula</i>	0.79	0.8	0.72	0.54
<i>P. l.</i> and low, medium high-intensity infection of <i>A. c.</i>		0.62	0.66	0
<i>A. c.</i> and low, medium high-intensity infection of <i>P. l.</i>		0.66	0.6	0.66
Clogher Lake				
<i>A. clavula</i>	0.84	0.77	0.84	0.81

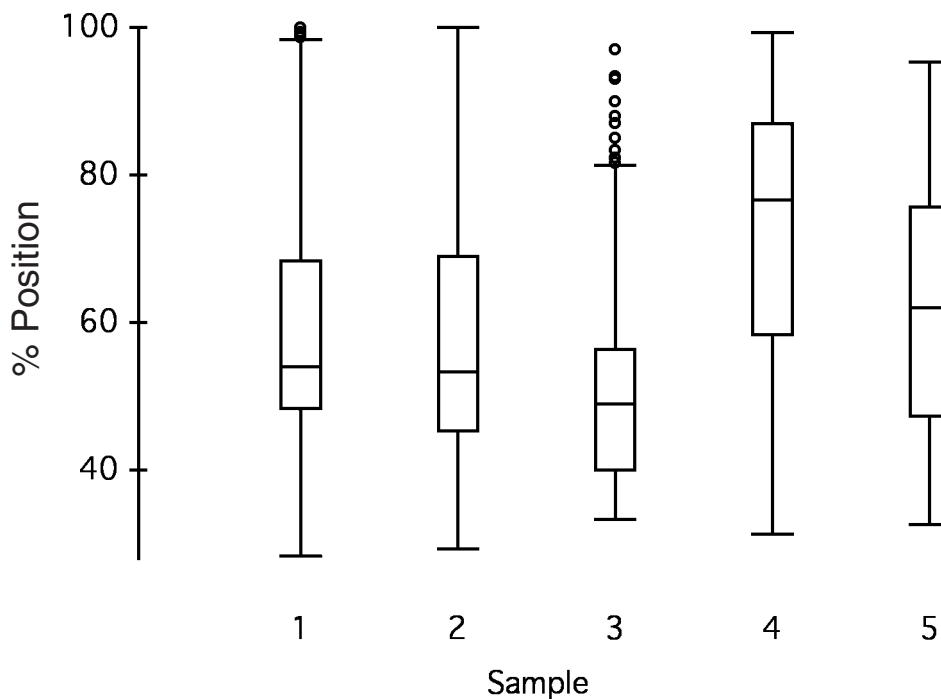


Fig. 4. A boxplot of the median position (\pm interquartile range and lowest and highest point) of *Acanthocephalus clavula* for 5 different samples: (1) fundamental niche; (2) single infection of *A. clavula* in wild trout; (3) single infection of *A. clavula* in stocked trout; (4) *A. clavula* in concurrent infections with *Pomphorhynchus laevis* in wild trout; (5) *A. clavula* in concurrent infections with *P. laevis* in stocked trout.

Clogher Lake. However, for high intensity infections the niche width value reported from Clogher Lake, 0.81, was substantially higher than the corresponding values reported from wild or stocked trout in Lough Feeagh. The niche width of *A. clavula* when it co-occurred with *P. laevis* decreased from low to high-intensity infections of *P. laevis* in wild trout but not to the same degree as observed for *P. laevis* in high-density concurrent infections. However, in stocked trout the niche widths of *A. clavula*

were comparable between low, medium and high-intensity infections of *P. laevis*.

DISCUSSION

The aim of this paper is to test the hypothesis that when the 2 species of Acanthocephalan *P. laevis* and *A. clavula* are found concurrently within the intestine of brown trout under field conditions that they have the potential to interact negatively. The

erection of this hypothesis within the present context is founded upon 2 important premises. Firstly, there is evidence to suggest that Acanthocephala are more likely than other groups of helminths to exhibit negative interactions with their own and other species, under both field (Chappell, 1969; Grey & Hayunga, 1980; Kennedy, 1992; Vidal-Martinez & Kennedy, 2000) and experimental conditions (Holmes, 1961, 1962a; Holland, 1984, 1987; Bates & Kennedy, 1990, 1991). Secondly, the likelihood of these interactions is increased in Ireland because of the absence of certain definitive hosts (Lyndon & Kennedy, 2001) and the fact that concurrent infections by 2 or more species of Acanthocephala are more commonly observed in aquatic hosts including fish (Kane, 1966; Kennedy, 1966; Conneely & McCarthy, 1984, 1986; Holland & Kennedy, 1998). For example, Kennedy & Moriarty (1987) observed stable populations of *Acanthocephalus lucii* and *Acanthocephalus anguillae* in eels over a 3-year period in Lough Derg. The data were difficult to interpret but the authors suggested that the observations were consistent with exploitation competition. This species combination was further explored in a greater range of localities by Kennedy (1992) and Kennedy & Moriarty (2002) and added further weight to the conclusion that the 2 species demonstrated evidence of competitive interactions under field conditions.

P. laevis and *A. clavula* are seldom found together in the same locality in brown trout outside Ireland (Kennedy & Hartvigsen, 2000; Dezfuli *et al.* 2001). Several convincing pieces of evidence are provided here to support the hypothesis that *P. laevis* and *A. clavula* interact under field conditions. Firstly, although the co-occurrences of the 2 species, based upon presence/absence data were not different from what one would expect by chance (i.e. neither species excludes the other from establishing) there was nevertheless evidence for a significant negative association between the numbers of each species found in individual fish and this was consistent for both wild and stocked trout. Furthermore, an analysis of the proportions of low, moderate and high-intensity infections in single and concurrent infections revealed a significant reduction in increasing intensities in concurrent infections compared to single infections. Finally, strikingly different patterns of niche inhabitation were observed, particularly for *P. laevis* in the presence of *A. clavula* in wild trout. The similarity in the position of both parasites in their fundamental niche compared to single infections in wild fish added particular weight to these observations. Results from the niche width analysis also support the observations on average position in single and concurrent infections. The niche width of *P. laevis* when it co-occurred with *A. clavula* decreased markedly from 0.66 in low-intensity infections to 0.18 in high-intensity infections. It is not

clear why the observations in stocked trout on the niche of *P. laevis* in concurrent infections with *A. clavula* did not mirror those of wild trout. Other comparative data on the biology of *P. laevis* in wild and stocked trout does reveal significant differences between the 2 parasite populations indicating that the *P. laevis* population in stocked trout had not attained stability within the timing of this natural experiment (see Byrne, 2000).

Documentation of niche shifts for cestode/Acanthocephalan combinations and concurrent Acanthocephalan infections has been provided from mammalian and fish hosts under field and experimental conditions and have been interpreted as evidence for interspecific interactions. For example, Chappell (1969) described concurrent infections of the cestode *Proteocephalus filicollis* and the Acanthocephalan *Neoechinorhynchus rutilii* in three-spined stickleback infected under natural conditions. He concluded that as their spatial distribution differed in concurrent infections the parasites exhibited competitive exclusion, possibly as a result of what is now described as interference competition (Dobson, 1985). As described for *Moniliformis dubius* and *Hymenolepis diminuta* in the rat intestine (Holmes, 1961; 1962a; Holland, 1984, 1987), the Acanthocephalan appeared to be the dominant competitor. In the white sucker, Grey & Hayunga (1980) also described the spatial displacement of the 'generalist' cestode *Glaridacris laruei* by the 'specialist' Acanthocephalan *Pomphorhynchus bulbocolli*. In these cestode/Acanthocephalan combinations the Acanthocephalan is identified as the dominant competitor with the cestode losing out in terms of space and/or size and reproductive output.

In Acanthocephalan combinations the situation is less clear cut. In the present study, both parasites exhibit changes in site in concurrent infections but the impact on *P. laevis* is more pronounced particularly with respect to its range. Significantly fewer high-intensity infections are found in concurrent infections for both species but in general terms intensity of *P. laevis* infection is low compared to infections in a preferred definitive host like chub in Britain (Brown, 1989). Bates & Kennedy (1990) demonstrated reductions in survivorship and the range of the intestine occupied by *A. anguillae* in the presence of *P. laevis* in experimentally infected rainbow trout. In this host-parasite combination the interaction was one-sided and *P. laevis* was unaffected.

Interestingly and mirroring the experience of Holmes (1962b) when he used the hamster-helminth system, Bates & Kennedy (1991) found no evidence of an interaction between *A. anguillae* and *P. laevis* in another, more natural host, the eel. In an earlier field-based study, also in Ireland, where single and concurrent infections of 2 Acanthocephalan congeners were explored in eels, 2 types of interactions

were observed (Kennedy, 1992). Changes in density were attributed to exploitation competition and shifts in site were attributed to interference competition whereby large numbers of *Acanthocephalus lucii* appeared to impede the posterior migration of *A. anguillae*. In the present study, our data do not indicate clearly whether this is exploitation or interference competition.

The findings reported here increase the number of freshwater Acanthocephalan species reported to be involved in interspecific competitive interactions to 4 out of the 6 present in the British Isles. Two of the competitive combinations, *A. lucii* and *A. anguillae* and *A. clavula* and *P. laevis* have now been reported from Ireland and the third, *A. anguillae* and *P. laevis* is believed to be responsible in part for the distribution of the 2 species in Ireland (Bates & Kennedy, 1990). It is never easy to demonstrate conclusively that interspecific competition occurs in field situations, but there appears now to be a *a priori* case for considering that Acanthocephalan species do compete in fish and that, as predicted, examples are more likely to be found in Ireland. Further work might well focus upon the remaining 2 species.

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