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# Utilization of brown trout *Salmo trutta* by *Acanthocephalus clavula* in an Irish lake: is this evidence of a host shift?

**C.J. Byrne[1], C.V. Holland[1]*, E. Walsh[1], C. Mulligan[1], C.R. Kennedy[2] and W.R. Poole[3]**

[1]Department of Zoology, Trinity College University of Dublin, Dublin 2, Ireland: [2]Department of Biological Sciences, Hatherly Laboratories, University of Exeter, Exeter, EX4 4PS, UK: [3]Marine Institute Salmon Management Service Division, Newport, Co. Mayo, Ireland

**Abstract**

The population biology of the fish acanthocephalan *Acanthocephalus clavula* was described from 161 wild brown trout, *Salmo trutta* sampled over a two-year period in Clogher Lake in the west of Ireland. Overall prevalence of the parasite was 86% and the mean abundance was 53 worms per fish. Despite the presence of large numbers of worms in the trout very few females (2%) attained full reproductive maturity. This suggests that trout is an accidental host. A sample of yellow eels, *Anguilla anguilla* was examined at a different time from the same lake. The prevalence of *A. clavula* was 97% and the average abundance was 8 worms per fish. In contrast to the situation in trout, the proportion of female worms attaining full reproductive maturity was 61% fulfilling the expected characteristic of a preferred definitive host. The possible explanations for the very high abundance of *A. clavula* in trout are discussed and include the influence of fluctuations in host populations, host diet and the absence of a potential competitor.

## Introduction

The preferred definitive host of the fish acanthocephalan *Acanthocephalus clavula* is the European eel *Anguilla anguilla* (Chubb, 1964; Kennedy & Lord, 1982). Outside Ireland, this parasite is rarely reported from brown trout. Kennedy & Hartvigsen (2000) reported it in only three of 72 localities sampled for trout from the British Isles and Norway. In northern Italy, *A. clavula* was recorded in trout in only one of three streams and then at a very low prevalence (Dezfuli *et al.*, 2001). In contrast, *A. clavula* has been recorded in trout on several previous occasions in Ireland (Conneely & McCarthy, 1984; 1988; Molloy *et al.*, 1993; Byrne *et al.*, 2002). Acanthocephala of freshwater fish are known to have a capacity to use a wide range of host species in some of which they can reproduce to a greater or lesser extent (Chubb 1964; Hine & Kennedy, 1974; Holmes *et al.*, 1977; Rauque *et al.*, 2003). In particular, the ability of an acanthocephalan to utilize brown trout as a 'colonization' host has been suggested as a useful adaptation to overcome natural barriers to dispersion (Lyndon & Kennedy, 2001). In Ireland, there is already evidence from two acanthocephalan host–parasite relationships of alternative host utilization in the absence of the preferred definitive host. *Pomphorhynchus laevis* infects brown trout (*Salmo trutta*) as a preferred definitive host in Ireland in the absence of chub (*Leuciscus cephalus*) and barbel (*Barbus barbus*) and accumulating evidence suggests that it constitutes a separate strain from that of the English and marine parasites (Kennedy *et al.*, 1978; Molloy *et al.*, 1995a; O'Mahoney, 2003). In Lough Derg, *Acanthocephalus anguillae* uses eels as a preferred definitive host in the absence of chub (Kennedy & Moriarty, 2002).

As part of a larger study on the infracommunities of wild and stocked trout, we discovered high abundances of *A. clavula* in brown trout and this enabled us to undertake an investigation of the status of this species as a host for

*Author for correspondence
Fax: 353 1 6778094
E-mail: cholland@tcd.ie

this acanthocephalan. We therefore report the results of a study of *A. clavula* in trout over a two-year period, together with data on the parasite in eels in Clogher Lake and then discuss the probable role of trout as a host.

## Materials and methods

### *Site and fish capture*

Brown trout and yellow eels were sampled from Clogher Lake (009°28′W 53°49.5′N) near Westport, Co. Mayo, Western Ireland. All trout were caught in floating gill nets set parallel to the shore overnight. Eels were caught in fyke nets.

### *Post-mortem and parasitological procedures*

Captured trout and eels were transported to the laboratory and frozen for subsequent parasitological examination. Fish were examined for helminths by standard methods (see Byrne *et al.*, 2002). Following a ventral incision from the anus to the lower jaw, the entire gut was removed, laid in a dissecting tray, and measured from the anterior end of the oesophagus to the anus. This facilitated accurate positioning of individual parasites in the intestine. Parasites were assigned a percentage location, with 0% corresponding to the anterior oesophagus and 100% corresponding to the anus. All parasites recovered (except the Acanthocephala) were fixed in 10% formalin solution. Acanthocephalans were first placed in tap water for 24 h to evert the proboscis. Then, 24 to 48 h after fixation, parasites were washed in 70% ethanol, before being transferred to fresh 70% ethanol with 4% glycerol for long term storage.

To examine the size and population biology of *A. clavula*, worms were removed from the alcohol–glycerol storage medium and weighed on a Mettler-Toledo AG245 balance (* 0.001 mg). All *A. clavula* were then measured to the nearest millimetre using electronic callipers. To sex them, the worms were placed on a glass slide, flooded with saline (0.9%) and cut in half, releasing the contents of the body cavity. In females, the single ligament sac containing the reproductive structures disintegrates once the ovary fragments, allowing eggs and ovarian balls to float free of the body cavity. Males were identified by the presence of cement glands and testes, which appear as small black ovoid structures when examined under the binocular microscope, and the absence of eggs and ovarian balls. Where necessary, contents of the body cavity were squeezed out using a fine forceps. The sex ratio of parasites from each fish was recorded. The maturity status of female parasites was assessed, using a three-stage classification system: stage 1, ovarian balls only; stage 2, ovarian balls and immature acanthors; stage 3, ovarian balls, immature acanthors, and mature acanthors (Bates & Kennedy, 1990). The measures of component community richness used were percentage prevalence, mean abundance and mean intensity, all calculated according to Bush *et al.* (1997). Due to the fact that abundance data was non-normal it was log $(n + 1)$ transformed prior to statistical analysis.

## Results

### *Prevalence and abundance of metazoan parasites in brown trout*

Nine species of metazoan parasite were recorded from the brown trout sampled from Clogher Lake (table 1). *Acanthocephalvs clavula* was the most prevalent and abundant species recorded.

### *Seasonal patterns of prevalence and abundance of* A. clavula *in brown trout*

The prevalence of *A. clavula* was very high in April (94%) and May (95%), dipped considerably in August (43%) and then reached 100% in November. Patterns of abundance were similar with a reduction in August and peak in November (see fig. 1).

### *Relationship between abundance of* A. clavula *and time of capture, age and sex of brown trout*

Analysis of variance was employed to examine the influence of host age and sex, year and month of sampling on the abundance of *A. clavula*. Month of host capture was found to be the only significant factor (F ratio = 14.5; df = 4,160; $P < 0.0001$).

### *Size, position and reproductive status of* A. clavula *in Irish brown trout*

The number of *A. clavula* individuals recovered ranged from 4264 in April to 183 in August. A total of 9690 worms

Table 1. Component community of metazoan parasites from brown trout sampled from Clogher Lake (1997–1998) (n = 161).

| Species | Site | % Prevalence | Mean abundance (± SD) | *pi* | Mean intensity (± SD) | Range | Variance to mean ratio |
|---|---|---|---|---|---|---|---|
| *Discocotyle sagittata* | G | 1.2 | 0.01 ± 0.1 | 0.00013 | 1 ± 0 | 0–1 | 0.01 |
| *Crepidostomum farionis* | IN | 77 | 32.8 ± 74.2 | 0.34755 | 56.5 ± 91.4 | 0–528 | 5506.8 |
| *Eubothrium crassum* | IN | 57.1 | 2.1 ± 4 | 0.02245 | 3.7 ± 3.8 | 0–23 | 11.5 |
| *Diphyllobothrium ditremum* | V | 24.2 | 3.6 ± 13.6 | 0.03785 | 14.7 ± 24.8 | 0–138 | 185.7 |
| *Diphyllobothrium dendriticum* | V | 1.8 | 0.85 ± 8.5 | 0.00902 | 45.6 ± 52 | 0–105 | 72.2 |
| *Rhabdochona* sp. | IN | 6.8 | 1.4 ± 12 | 0.0151 | 21 ± 43.1 | 0–147 | 144.1 |
| *Anisakis* sp. | IN | 1.8 | 0.05 ± 0.5 | 0.00053 | 2.6 ± 2.9 | 0–6 | 0.24 |
| *Acanthocephalus clavula* | IN | 86.3 | 53.2 ± 82.3 | 0.56383 | 90.1 ± 93.2 | 0–422 | 6774.2 |
| *Salmincola salmoneus* | G | 19.8 | 0.33 ± 0.8 | 0.00349 | 1.7 ± 1.1 | 0–5 | 0.65 |

IN, intestine; V, viscera; G, gills; *pi*, relative abundance as a proportion of the total number of all helminths of all species in trout.

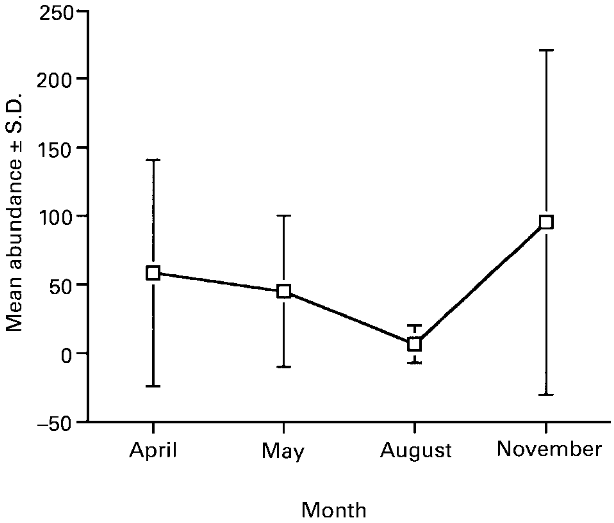


Fig. 1. Mean abundance (±S.D.) of *Acanthocephalus clavula* in brown trout sampled in April (n = 63), May (n = 39), August (n = 28) and November (n = 31) (1997–1998) from Clogher Lake.

were removed from all the trout sampled from Clogher Lake. The mean position (±S.D.) was 60.85% ± 14.61 with a minimum of 28.3 and a maximum of 100. A range of 71.7 indicates that the fundamental niche of the acanthocephalan was quite broad.

A sample of 296 *A. clavula* (from 34 fish) were selected from the total number of worms recovered in order to assess parasite size and reproductive status of female worms. Of these 296 worms, 191 were females and 105 were males. Parasites ranged in length from 2 to 6 mm and in weight from 0.1 and 0.9 mg. The mean lengths and weights of male and female parasites are shown in table 2. Male *A. clavula* were found to be significantly shorter (t = 14.43; df = 294; $P < 0.0001$) and weigh significantly less (t = 9.46; df = 294; $P < 0.0001$) than females. Female parasites demonstrated significant differences in length (F ratio = 11.96; df = 2,188; $P < 0.0001$) and weight (F ratio = 7.82; df = 2,188; $P < 0.005$) between months with heavier parasites in May and November compared to August and longer worms in May compared to both August and November. In contrast, male worms were significantly longer in May compared to August and November (F ratio = 3.96; df = 2,104; $P < 0.0219$) but showed no significant differences in weight between months.

Table 2. Average length (mm) and weight (mg) of *Acanthocephalus clavula* from brown trout and yellow eels sampled from Clogher Lake.

| | Trout | Eel |
|---|---|---|
| Mean weight ± SD | 0.34 ± 0.13 | 0.29 ± 0.24 |
| (all worms) (n) | 296 | 230 |
| Mean length ± SD | 3.55 ± 0.87 | 2.91 ± 0.90 |
| (all worms) (n) | 296 | 230 |
| Mean female weight ± SD | 0.39 ± 0.14 | 0.34 ± 0.27 |
| (n) | 191 | 158 |
| Mean male weight ± SD | 0.25 ± 0.09 | 0.205 ± 0.10 |
| (n) | 105 | 72 |
| Mean female length ± SD | 3.96 ± 0.74 | 3.15 ± 0.91 |
| (n) | 191 | 158 |
| Mean male length ± SD | 2.79 ± 0.51 | 2.39 ± 0.64 |
| (n) | 105 | 72 |

An investigation of maturity status of female worms revealed that 68% (n = 130) of all worms were stage 1 females, 30% (n = 57) were stage 2 females and 2% (n = 4) were stage 3 females. Worms were derived from fish sampled in May, August and November. Because of the very small number of stage 3 females identified, in order to analyse the data statistically the numbers of stage 2 and stage 3 females were combined (maturing females) and compared with the numbers of immature (stage 1) females. When the proportions of these two groups were compared for the three months of sampling, no statistically significant difference was found between the groups.

### *Comparative population biology of* A. clavula *from yellow eels sampled from Clogher Lake*

From a sample of 30 yellow eels *A. clavula* was the most prevalent and abundant helminth species recorded (table 3).

Two hundred and thirty individuals of *A. clavula* were randomly sampled from the total number of acanthocephala derived from the eels. The mean position (±S.D.) was 57.7% ± 21 with a minimum of 5 and a maximum of 100. The niche of the acanthocephalan was very broad with a range of 95. 158 worms were female and 72 were male. The average weight and length of these worms are shown in table 2. As was the case from trout, male *A. clavula* worms were significantly shorter (t = 6.34; df = 228; $P < 0.001$) and lighter (t = 5.23; df = 228; $P < 0.001$) than female worms. In a comparison between months, male worms showed no significant difference in length or weight between months but female worms derived from eels in June were significantly longer (t = 3.4; df = 156; $P < 0.001$) than those from September.

An investigation of maturity status of female worms revealed that 13% (n = 21) of all worms were stage 1 females, 26% (n = 41) were stage 2 females and 61% (n = 96) were stage 3 females. Worms were derived from fish caught in June and September but, when the proportions of the different stages of maturity were compared for the two months, there was no statistically significant difference between them.

## Discussion

Chubb (1964) provided evidence that *A. clavula* has the capacity to infect a range of fish definitive hosts but that a greater proportion of fully mature females was found in eels. For example, infections of this acanthocephalan in grayling (*Thymallus thymallus*), pike (*Esox lucius*) and roach (*Rutilus rutilus*) demonstrated the percentage of females with shelled acanthors to be 12.6%, 26.3% and 3.0%, respectively, in contrast to 43.4% in the eel. This agrees with the description by Lyndon & Kennedy (2001) of the eel as the preferred definitive host for *A. clavula*, pike a suitable host and roach an additional host. Lyndon

Table 3. Component community of metazoan parasites from yellow eels sampled from Clogher Lake (2002) (n = 30).

| Species | Site | % Prevalence | Mean abundance (±SD) | Mean intensity (±SD) | Range | Variance to mean ratio |
|---|---|---|---|---|---|---|
| *Acanthocephalus clavula* | IN | 97 | 7.7 ± 6.2 | 12.5 ± 5.8 | 0–22 | 5 |
| *Acanthocephalus lucii* | IN | 57 | 1.7 ± 2.4 | 3.3 ± 2.7 | 0–11 | 3.3 |
| *Acanthocephalus anguillae* | IN | 43.3 | 1.6 ± 2.4 | 3.5 ± 2.6 | 0–8 | 3.8 |

IN, intestine.

& Kennedy (2001) describe brown trout as a suitable host for *A. clavula* but its presence in trout is quite rare (see Kennedy & Hartvigsen, 2000) except in Ireland.

The population dynamics of the parasite in this single lake situation show a number of interesting anomalies. Firstly, the prevalence and abundance of the parasite is strikingly high and this is maintained over the two-year period of study. Data compiled from other sites in Ireland are shown in table 4 and indicate considerably lower prevalence and abundance. Secondly, the proportion of stage 3 females in the trout was very low indeed and these trout did not fulfil the description of a preferred host under these conditions. In fact the term 'secondary host' as described by Holmes *et al.* (1977) might be more appropriate. They describe a situation whereby the basic stock of parasites are maintained in one host species (primary host) from which it may spread to other species (secondary hosts or recipients). Reproduction may not occur to any great extent in these secondary hosts.

In contrast, data from eels revealed a pattern of stage 3 females commensurate with their status as a preferred definitive host. A third anomaly, which applied equally to both trout and eels, was the small size of the worms in both hosts. One would predict that worms might show little growth in trout but this would not be expected in the case of parasites obtained from the eels. Lyndon & Kennedy (2001) described gravid female worms weighing from 2.7 to 3.1 mg in eels − the weights described here are more analogous to those described from perch (*Perca fluviatilis*) (0.63 ± 0.02). It is important to note that the average weights of *P. laevis* from Irish brown trout were much lower (7 mg) (n = 731 but both males and females combined) (Molloy *et al.*, 1995a) compared to gravid female worms derived from English brown trout (mean 38.3 mg) (n = 10) (Lyndon & Kennedy, 2001). There is therefore a precedent for differences in acanthocephalan growth between the two geographical locations. Nevertheless, despite their smaller size, female *A. clavula* in Irish eels are capable of reaching full reproductive maturity in high numbers.

One explanation for the high numbers of *A. clavula* in trout in Clogher lake might be a decline in the eel population or in the population of the parasite in eels. There is evidence for a decline in eel populations in Ireland during the 1980s and in subsequent years as elver runs declined (Moriarty, 1992; Moriarty & Decker, 1997). Clogher Lake has not been sampled previously for trout or eel parasites but earlier work by Molloy *et al.* (1995b) in Lough Feeagh and Bunaveela lake found no evidence of *A. clavula* in trout in that adjacent river system. Therefore we do not have an earlier data set to determine whether *A. clavula* is declining in eels. Kennedy (1984) described the dynamics of a declining population of *A. clavula* in eels in a small river and found that recruitment and maturation of the parasite continued throughout the period of decline. Furthermore, the patterns of decline in eels were mirrored in flounder (*Platichthys flesus*), acting as an additional host and stone loach (*Noemacheilus barbatulus*) as an accidental host. This does not seem to be the case in Clogher Lake as the prevalence and abundance of the parasite in the sample of eels collected in 2001 was high, as was the number of fully reproductively mature females. In fact, in general terms, the intestinal community in eels confirmed the general pattern described from other locations in Britain and Europe – species poverty, low diversity and high dominance by a single species of helminth, usually an acanthocephalan (Kennedy, 1993, 1997; Kennedy *et al.*, 1998).

Another possible explanation could be the feeding behaviour of brown trout in this lake. The intermediate host of *A. clavula* is *Asellus meridianus* (Chubb, 1964) and it may be that trout were feeding intensively upon infected *Asellus* or the balance between aquatic invertebrate availability changed within the lake. Unfortunately, we do not possess data on parasite status of *Gammarus* and

Table 4. Comparative population parameters for *Acanthocephalus clavula* sampled from brown trout in Ireland.

| Site | % Prevalence | Mean abundance ± S.D. | n (trout) | Reference |
|---|---|---|---|---|
| Lough Corrib | 15% | NA | 133 | Conneely & McCarthy, 1988 |
| Burishoole river system | 7% (smolts) | 0.1 ± 0.2 | 72 | Molloy *et al.*, 1993 |
| | 23% (kelts) | 2 ± 0.2 | 17 | |
| Lough Feeagh | 26% (wild) | 3 ± 11.4 | 217 | Byrne *et al.*, 2002 |
| | 39.3% (stocked) | 4 ± 11 | 122 | |
| Present study | 86.3% | 53.2 ± 82.3 | 161 | |

NA, not available.

*Asellus* in this lake or in other lakes in the region. Data on the population dynamics of acanthocephalan parasites in their intermediate hosts is generally lacking from Ireland.

Perhaps the most plausible explanation for the epidemic proportions of *A. clavula* in Clogher Lake is the absence of *P. laevis* as a potential competitor. The two previous Irish studies, which provide quantitative data on the abundance of *A. clavula* and other parasite species, demonstrate that the numbers of *A. clavula* are considerably smaller than those encountered in Clogher Lake. *Pomphorhynchus laevis* was present in the smolts and kelts described from the Burishoole river system (Molloy *et al.*, 1993) and the wild and stocked trout from Lough Feeagh (Byrne *et al.*, 2002) (see table 4), in some cases in the same individual fish. Evidence for a competitive interaction between the two species *A. clavula* and *P. laevis* has now been reported on the basis of both numerical and functional responses (see Byrne *et al.*, 2003).

Although further investigation is desirable, this study has fulfilled its primary aim of determining the status of trout as a host for *A. clavula*. It has convincingly shown that brown trout is not an alternative preferred host of *A. clavula* and that there has in fact been no host shift: rather trout serve as a secondary host, and so as a potential colonization host *sensu* Lyndon & Kennedy (2001). It has also shown that under suitable environmental conditions an acanthocephalan can reach very high levels of abundance in a secondary host, even though the suprapopulation must be maintained by the smaller infrapopulations and flow of parasites through the preferred definitive host. The situation in Clogher Lake is thus similar in several respects to that in Cold Lake (Leong & Holmes, 1981), where the infrapopulation levels as measured by prevalence and abundance of *Metechinorhynchus salmonis* were higher in secondary host species, but the suprapopulation was maintained by the flow through the preferred hosts. Furthermore, a parallel situation to *A. clavula* in trout in Clogher Lake has been described for *P. laevis* in eels (Kennedy, 2001). The preferred definitive host of *P. laevis* is chub but this acanthocephalan was found to dominate the intestinal communities of eels in the River Culm over two separate years.

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