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The parasite community structure of stocked and wild brown trout (*Salmo trutta* L.).

by

Ciaran John Byrne

09 MAY 2001

Volume I of II

A thesis submitted in the fulfilment for the Degree of Doctor in Philosophy to Trinity College, University of Dublin.

October 2000

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DECLARATION

This thesis has not been submitted as an exercise for a degree at any other university. Except where stated, the work described therein was carried out by me alone.

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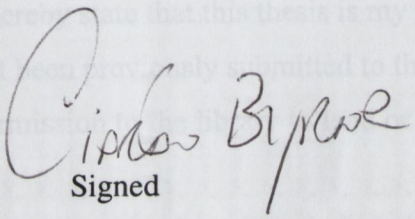

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Summary

The present study examined the parasite component and infracommunities of wild and stocked brown trout from an experimental fishery, Lough Feeagh and compared them to the parasite component and infracommunities of wild brown trout from an unmanaged wild trout fishery, Clogher Lake. This study also examined the process of establishment and development of the parasite communities in stocked brown trout, from the point of their first entry into Lough Feeagh, to the point where they contained mature parasite communities. To date, a large amount of the parasite community ecology literature pertaining to fish has focused on eels, and brown trout despite their status as dominant salmonid species in Europe have received comparatively little attention, also no studies have considered the parasite communities of wild and stocked brown trout.

The parasite component and infracommunities of wild and stocked brown trout from Lough Feeagh, and of wild brown trout from Clogher Lake were examined over a period of two years. The parasite community recorded for brown trout from Clogher Lake was found to be richer and more diverse than the parasite community recorded in brown trout from Lough Feeagh. Comparison of the parasite communities of wild and stocked brown trout revealed that for the total sample the two parasite communities were comparable in terms of composition but differed in terms of structure. The parasite community in stocked brown trout established and developed from a 'naïve' state into a mature parasite community over the course of seven months, from the first entry of stocked trout into Lough Feeagh in April to the final monthly sample taken in November. Differences in the behaviour and feeding ecology of stocked brown trout appeared to be the primary reason for the differences reported in the community structure between wild and stocked trout.

The microhabitat selectivity of the acanthocephalan species *P. laevis* and *A. clavula* were also compared between wild and stocked brown trout. *A. clavula* occupied a similar position in the intestine of wild and stocked trout, and its microhabitat

position was also comparable to that recorded for Clogher Lake, where it was the only acanthocephalan species present. In contrast the microhabitat selectivity of *P. laevis* differed between wild and stocked trout, it occupied a more anterior position in the intestine of stocked trout.

Examination of the population biology of *P. laevis* in trout demonstrated that in terms of parasite size brown trout in Ireland could be classified as a preferred definitive host for *P. laevis* in Ireland. Whereas, in terms of maturity status brown trout appear to fall into the second host category, suitable host. Comparison of the population biology *P. laevis* between wild and stocked trout revealed some striking differences. The majority of *P. laevis* in stocked trout were of stage I maturity, and none were mature, whereas for wild trout 20% of female worms were mature. The exact reason for this disparity in the maturity levels of *P. laevis* between wild and stocked trout is unclear.

Finally, examination of single and concurrent infections of *P. laevis* and *A. clavula* indicated that an interaction occurred between the two species. Indirect evidence from the prevalence and abundance values recorded for *A. clavula* from Clogher Lake also supported this theory. In contrast *A. clavula* did not appear to have any effect on the population biology and size of *P. laevis*. The differences in the size and population biology between *P. laevis* occurring alone and *P. laevis* co-occurring with *A. clavula* were possibly related to the fact that considerably fewer *P. laevis* co-occurred with *A. clavula* than occurred alone.

Chapter 1

Introduction, aims and literature review

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1.1 Introduction

In a landmark paper on the parasite community ecology of birds and fishes, Kennedy *et al.* (1986b) identified five factors essential to the production of a diverse helminth community. Subsequently in a series of papers (Kennedy, 1993a; Kennedy 1995; Kennedy and Guegan, 1996; Kennedy, 1997; Kennedy *et al.*, 1998) he examined the parasite community ecology of eels (*Anguilla anguilla*) from Britain, Australia and mainland Europe in detail. The parasite community ecology of resident brown trout (*Salmo trutta* L.) have also received particular attention given their status as dominant salmonid species in Europe (Kennedy and Burrough, 1978; Hartvigsen & Halvorsen, 1993; Molloy *et al.*, 1995a,b). More recently Kennedy and Hartvigsen (2000) attempted to characterise the parasite communities of brown trout. They identified a suite of four commonly occurring trout specialists which gave greater predictability to community composition.

Increasing levels of pollution, habitat decline, and over fishing have increased the importance of fish stocking as a fishery management option. However, no study has compared the parasite community structure, at any level, of wild and stocked brown trout from the same system. Poynton & Bennett (1985) compared parasites of wild brown trout and stocked rainbow trout in a Hampshire river but this study was limited by small sample sizes and no parasite community parameters were examined. McGuigan and Sommerville (1985) examined the effects of cage culture of rainbow trout on the parasite fauna of Lough Fad in western Scotland, however this study was more concerned with the aquacultural implications of cage culture rather than parasite community ecology or interactions between wild and stocked trout.

In the present study, the parasites of wild and stocked brown trout in an 'experimental' lake, Lough Feeagh, were examined at the infracommunity and component community levels over two years. The establishment and development of parasite communities in naïve stocked trout were also examined at the infra and component community levels from the time of the first entry of fish into Lough

Feeagh. These parasite communities were compared with the parasite infra and component communities of brown trout from an unmanaged wild trout fishery, Clogher Lake.

A number of studies have examined aspects of the biology of *Pomphorhynchus laevis* in experimental and natural infections in a range of fish hosts (Kennedy 1972a; Kennedy 1974a; Kennedy *et al.*, 1976; Kennedy and Rumpus, 1977; Kennedy *et al.*, 1978; Kennedy, 1996c). Kennedy *et al.* (1978) proposed that *P. laevis* existed as three separate strains, an English freshwater strain, an Irish strain and a marine strain. Several studies have examined the population biology of *P. laevis* in chub and barbel the preferred definitive host of the parasite in England (Brown, 1989; Bates and Kennedy, 1991b) but considerably less quantitative information is available on the Irish strain of *P. laevis*. Relatively few workers (Fitzgerald and Mulcahy, 1983; Conneely and McCarthy, 1984; Molloy *et al.* 1995b) have examined the population biology of *P. laevis* in brown trout in Ireland. In the present study the population biology of *P. laevis* in wild and stocked trout was compared in detail, further delineating the important characteristics of the Irish strain of *P. laevis*. In contrast to the study by Molloy *et al.* (1995b) detailed information on the relationship between the growth and reproduction of *P. laevis*, and its microhabitat selectivity was also provided.

Kennedy & Moriarty (1987) and Kennedy (1992) examined the site segregation and co-existence of the congeneric species *Acanthocephalus lucii* and *Acanthocephalus anguillae* in eels. In a further study Bates and Kennedy (1990, 1991b) examined the interactions between *P. laevis* and *A. anguillae* in rainbow trout and in their preferred definitive hosts, chub and eels, in controlled laboratory experiment. In the present study the acanthocephalans *P. laevis* and *Acanthocephalus clavula* were found to co-occur in Lough Feeagh, an observation not previously made by Molloy *et al.* (1995a,b), and were identified as potentially competitive species. The interactions between the two species were also examined.

1.2 Aims

1. To compare the parasite communities of wild and stocked brown trout at the infracommunity and component community levels. The null hypothesis was that no difference existed between the parasite communities of wild and stocked brown trout in Lough Feeagh.

2. To examine the establishment and development of the parasite communities of stocked trout in Lough Feeagh from the point of their first entry into the lake.

3. To investigate whether the parasite component and infra communities of brown trout were comparable between an experimental fishery – Lough Feeagh, and a totally wild fishery – Clogher Lake.

4. To investigate whether the parasite communities recorded for brown trout in this study were typical of those for the west of Ireland, and the rest of Europe.

5. To examine whether the microhabitat selectivity of two parasite species differed between wild and stocked brown trout, and between Lough Feeagh and Clogher Lake.

6. To investigate whether the population biology of *P. laevis* was comparable between wild and stocked brown trout.

7. To investigate whether the population biology of *P. laevis* in brown trout in Lough Feeagh was typical of the Irish strain as described by Molloy *et al.* (1995b).

8. To investigate the potential for interaction between the acanthocephalan species *P. laevis* and *A. clavula* in brown trout in Lough Feeagh.

1.3 Introduction to the main concepts involved in parasite community ecology

Parasitologists have known for a long time that the parasitic fauna of an animal host taken together with its environment, form an interacting ecological complex. In one of the earliest studies on helminth ecology, Dogiel and Petrushevski (1935) called this ecological complex a "parasitocoenosis". Although the origin of modern parasite ecology is accredited to the Russian investigator V. A. Dogiel (Dogiel, 1964), it was not until the seminal work by Holmes (1961, 1962a,b) on the interactions between the rat tapeworm *Hymenolepis diminuata* and the acanthocephalan *Moniliformis dubius*, that a quantitative approach to the study of helminth community dynamics became established in parasite community literature. Whereas Crofton (1971a,b) was largely responsible for the introduction of a quantitative approach to the study of helminth population dynamics.

In the intervening period a large body of publications have dealt with issues relating to parasite community ecology (Kennedy, 1993a, 1995, 1997b, Kennedy *et al.*, 1986a,b, 1997; Kennedy and Pojmanska, 1996; Kennedy and Hartvigsen, 2000; Dorucu *et al.* 1995; Marcogliese and Cone, 1991; Marcogliese and Cone, 1998; Bagge and Valtonen, 1999; Ibbeken and Zander, 1999). It soon became apparent that parasite populations and communities were organised at different hierarchical levels, that different processes operated at different levels, and quantification of the various hierarchical levels was essential for the understanding of parasite communities.

One of the first attempts to clarify the issues of level in parasite populations was by Esch *et al.* (1975) who developed the concepts of infrapopulation and suprapopulation. An infrapopulation was described as one that includes all of the parasites of a single species, in one host. A suprapopulation was defined as all parasites of a given species in all stages of development, within all hosts in an ecosystem. In a later study Riggs and Esch (1987) coined the term metapopulation to represent all of the infrapopulations sampled from a given host species within an

ecosystem, however more recently Bush *et al.* (1997) replaced the term metapopulation with the more accurate term component population.

The hierarchy developed for parasite community ecology follows the one initially developed for parasite populations. Thus, as an infrapopulation was defined as all of the parasites of a single species in one host, an infracommunity was defined as all of the infrapopulations within an individual host (Bush and Holmes, 1986). A component parasite community which is analogous to the component population, is defined as all of the infracommunities within a given host population (Holmes and Price, 1986). Similarly the supra community, which consists of all the parasite communities within an ecosystem (Holmes and Price, 1986) mirrors the supra population.

1.4 Examination of the main hypotheses associated with parasite community ecology

1.4.1 The island biogeography hypothesis

Whether parasite communities of fish have a predictable structure or are stochastic assemblages is a recurring question in fish parasite community ecology (Holmes, 1990; Kennedy, 1990, Aho and Bush, 1993). Kennedy (1978b) tested the correlation between selected physicochemical factors and the composition of the parasite fauna in British lakes. He found a positive correlation between the number of parasite species and lake size, and a negative correlation between the number of parasite species and lake altitude. However he was unable to find a correlation between the occurrence of specific parasite species and selected physicochemical variables. He concluded that it was individual factors and chance colonisation events that determined the species composition and therefore it was impossible to predict the parasite assemblage.

Using a different approach Kennedy (1978a) and Kennedy *et al.* (1986a) applied MacArthur and Wilson's island biogeographic model (1967) to parasites of

freshwater fish on close and remote islands. They found that there was no clear relationship between the size and position of the islands and the number of parasite species and parasite diversity. They also concluded that chance colonisation events were the major determinants of parasite species composition, and the parasite fauna on offshore islands does not agree well with the predictions of the island biogeographic theory. The island theory makes predictions about species number and diversity in relation to decreasing size and increasing remoteness of the island, but it does not consider species composition.

More recently Poulin and Morand (1999) examined the effect of geographical distances and similarity among parasite communities of conspecific host populations. They concluded that the geographical distance between component communities of fish parasites is often the best and most general predictor of the similarity in species composition. However, they warned that there were many factors which promote dissimilarity in the composition of parasite communities between lakes, and these may sometimes be stronger than those, such as geographical closeness which promote similarity (Kennedy *et al.*, 1991; Hartvigsen and Kennedy, 1993).

1.4.2 Examination of the rescue effect and carrying capacity hypotheses

It has been well established in free living community ecology that there are common and rare species and a positive relationship between the local abundance of species and their regional distribution (Nee *et al.*, 1991). Thus species which occur in high abundance in any one patch are to be found on more of the patches of the region. Hanski (1982) referred to common and rare parasite species and core and satellite parasite species. Hanski's core / satellite hypothesis considers that extinction rate on a patch is a declining function of the population size on that patch and the rate at which a full patch colonises empty patches may be an increasing function of population size on that patch. This has been termed the rescue effect hypothesis, the idea that emigrants from surrounding populations may reduce the possibility of local extinction (Bush and Kennedy, 1994).

Nee *et al.* (1991) disagreed with the rescue effect hypothesis as proposed by Hanski (1982), and instead proposed an alternative interpretation, the carrying capacity hypothesis. They suggested that species differ in their local carrying capacity and that a species that attains a larger patch population size will have a smaller extinction rate and or a larger colonisation rate than a comparable species with a smaller population size.

Hartvigsen and Halvorsen (1993) examined common and rare parasites of brown trout from four lakes in northern Norway. They also stocked hatchery reared salmon fingerlings into a recently cleaned earth pond. They showed that the regionally rare species were in some cases as abundant or more abundant than the regionally common species in some localities. This finding was not entirely in accordance with the predictions of Hanski (1982), that a region will contain widespread core species and satellite species that are rare both locally and regionally. They suggest that further research needs to be done to clarify the general applicability of the core satellite hypothesis. However the results from the salmon pond were in agreement with the rescue effect hypothesis. The core species *Crepidostomum metoecus* and the intermediate species *Crepidostomum farionis* were the first to infect the population of young salmon.

Kennedy (1984b, 1993a) examined the changes in composition and diversity of the intestinal helminth component and infracommunities of eels, *Anguilla anguilla*, from the River Clyst over a period of 13 years. He demonstrated that all the measures of infracommunity structure adopted in this study were sensitive to the changes in the helminth component community over the investigation period, but they varied over a smaller range than expected. He concluded that there were large changes in species composition and species richness over the period, but changes in community diversity were much smaller and suggested an underlying stability in community structure. This underlying stability reflects the rescue effect of eels colonising from the River Exe.

Bush and Kennedy (1994) examined the probability of parasite extinction in a range of hosts, due to the anthropogenic fragmentation of the host population and in the absence of host extinction. They concluded that extinction at the infrapopulation and infracommunity levels is both common and trivial and in the absence of complete host extinction, populations of the parasite in other fragments are likely to serve as sources for re-invasion (e.g. a rescue effect).

1.4.3 Examination of the phylogenetic and ecological hypotheses

Parasites are viewed as highly specific, but considerable variation in specificity occurs between and within parasite groups (Poulin, 1992). Choudhury *et al.* (1996) and Choudhury and Dick (1998) consider that parasite communities of fish are unpredictable and random assemblages, except for those parasites that are host specialists. Kennedy and Bush (1994) suggest that host-specific parasites should form a predictable set of species within that host's component parasite community, and closely related species are expected to share similar parasites. However many parasites may be associated with a host for reasons other than host specificity or relatedness among hosts. Host-generalist parasites can be shared among unrelated hosts that have similar ecology or feeding preferences.

Brooks (1980) proposed a phylogenetic approach to the understanding of parasite community structure, and based his conclusions on two assumptions. Firstly, that parasites are host specialists exhibiting genealogies congruent with those of their hosts and secondly, that parasite communities co-evolve as a unit, thus the phylogeny of hosts and parasites constrain the development and organisation of communities. This can be referred to as the co-speciation hypothesis. Holmes and Price (1980) vigorously countered Brook's argument that the organisation of parasite communities could only be understood by an analysis of the phylogenetic tracking between host and parasite. They stressed importance of colonisation, generalist parasites and biotic interactions in these parasites and thus advocated an ecological approach to the understanding of parasite community structure. A number of workers have attempted to assess the relative importance of phylogenetic and ecological determinants of

community structure with a view to improving the understanding of unpredictable communities (Kennedy and Bush, 1994; Vickery and Poulin, 1998; Lile, 1998; Sasal *et al.*, 1999a; Carney and Dick, 1999).

Bush *et al.* (1990) examined the community richness among intestinal parasitic helminth communities in fishes, herptiles, birds and mammals with respect to the comparative number of component species. They concluded that habitat of the host was more important in determining community richness than host phylogeny.

Knudsen *et al.* (1997), studying parasite communities in two sympatric morphs of arctic char in northern Norway, concluded that the considerable differences in parasite community structure and abundance between the two char populations were closely related to differences in the width and composition of the food niches between the morphs. They pointed out that the only recorded parasite species with a direct life cycle, and thus somewhat unaffected by host ecology (the copepod *Salmincola edwardsii*) had relatively similar abundance in the two morphs.

Similarly, studies by Kennedy (1990), Kennedy (1993a), Hartvigsen and Kennedy (1993) and Bergeron *et al.* (1997), on the communities of freshwater fish, and Lile (1998) on the helminth communities of four species of pleuronectid flatfish, considered ecological factors rather than the phylogenetic relationships of these hosts as the main influence on the composition and diversity of the helminth community. They suggested that stochastic processes, which were mainly ecological in nature, obscured predictability.

In contrast Salgado-Maldonado and Kennedy (1997) examined the richness and similarity of helminth communities in the tropical cichlid fish *Cichlasoma urophthalmus*, and considered the composition of the component community to be composed of phylogenetic and ecological elements. The specialist parasite species formed the phylogenetic component of the community and the generalist species formed the ecological component. They concluded that the phylogenetic element

played the major part in characterising the communities and was responsible for most of the similarity between them.

Similarly Blaylock *et al.* (1998) concluded that the parasite community of pacific halibut (*Hippoglossus stenolepis*) was more similar to those in other flatfishes than to ecological analogs and thus that phylogeny was an important determinant of community structure. Marcogliese and Cone (1998) suggested that there was a substantial phylogenetic component to parasite community structure in eels from the United Kingdom and Nova Scotia. Nie (1995) examined the communities of intestinal helminths of carp in the Yunnan province of southwest China. He concluded that as the lakes were ecologically and geographically isolated and some species of fish were lake-specific, host-parasite co-evolution was important in determining the parasite species composition.

Kennedy and Bush (1994) considered problems in pattern and scale in helminth communities of freshwater fish by examining them at different hierarchical and taxonomic scales. Communities were first examined at the level of the salmonid genera, focusing on the genus *Oncorhynchus* in its heartland in Canada, then in *Oncorhynchus mykiss* throughout its global range and finally in individual localities to which it has been introduced in Britain.

The authors demonstrated that in their heartland salmonid parasite communities were dominated by host specialists which formed the phylogenetic element, and conferred a degree of predictability (Kennedy and Bush, 1992; Hartvigsen and Halvorsen, 1993; Carney and Dick, 1999; Kennedy and Hartvigsen, 2000) and generalists formed the minority ecological element of the community. They also showed that as the distance *O. mykiss* was translocated from its heartland increased the number of generic specialists declined first, and then the number of salmonid specialists declined. The helminth community was thus composed of generalists and was increasingly species poor. Much of the variation in the system may in fact be ecological noise, which effectively masks underlying patterns (Sale and Guy, 1992).

Kennedy and Pojmanska, (1996) suggested that in addition to time, both ecological and phylogenetic factors contributed to the paucity of helminth communities in carp. Vickery and Poulin (1998) used mathematical modelling to investigate which evolutionary process influenced the likelihood of detecting an effect of host ecological characteristics on the richness of parasite communities in comparative analyses among related host species. They concluded that phylogenetic effects were likely to obscure ecological effects, except when the effects of host ecology were strong. Thus, because the composition of parasite communities tends to reflect their ancestry, the effect of host ecology will often be very difficult to detect.

It can be concluded from the literature reviewed above that there is still a large amount of debate surrounding the issues of phylogeny and ecology. A strong argument can be put forth to suggest that phylogenetic influences are the primary determinant of parasite community structure, however an equally strong argument can be put forth to counter this, and suggest that ecological processes are the primary determinants of parasite community structure. It appears that the best way forward is not to try and prove one theory over the other, but to examine parasite communities and establish the relative importance of phylogenetic and ecological processes as structuring forces.

1.4.4 The colonisation time hypothesis

Rohde (1978, 1979) examined the monogenean gill flukes of marine fishes in tropical waters and showed that individual fishes commonly harbour parasite communities numbering five to seven species, whereas, in cold seas fish species are known to have no monogeneans or only a single species. Price (1980) suggested that many parasite communities existed in this non-interactive phase, where an equilibrium number of parasites maintained by equal rates of colonisation and extinction has not yet been reached. Thus both workers subscribed to the time hypothesis which suggested that younger communities have fewer species than older communities because evolutionary time is required for the increase in species number.

Holmes and Price (1986) showed that one of the basic principles of the co-speciation hypothesis, that evolving host species carry with them parasite communities derived from their ancestors casts serious doubts on the application of the time hypothesis to host species-level component communities. A new species, unlike a new island does not start out devoid of parasites.

Bush *et al.* (1990) used the helminth parasites of vertebrate hosts to test a prediction of the time hypothesis, i.e. that phylogenetically older groups (e.g. fishes) would have greater species richness than phylogenetically younger groups (e.g. mammals). Patterns of community richness among intestinal parasitic helminth communities in fishes, herptiles, birds mammals were examined with respect to the comparative number of component species in a host population. They found little evidence that phylogenetic aspects played a major role in the development of helminth communities. Fish and herptiles had the least number of component species; and the number increased significantly in birds and then declined slightly in mammals, thus the pattern detected refuted the time hypothesis.

Holmes and Price (1986) suggested that the time hypothesis would apply to species recently introduced / colonising a new habitat. To this end Guegan and Kennedy (1993) examined the parasite community richness in British freshwater fish with a view to testing the colonisation time hypothesis. They revisited the data of Price and Clancy (1983) and recalculated the correlations between helminth species richness and host geographical area, using a different measure of species richness, controlling for the effects of sampling effort, and separating indigenous and introduced fish species. They showed that the relationship demonstrated by Price and Clancy (1983), that there was a significant positive correlation between the number helminth parasite species per host and the geographical range of the host fish species, was statistically correct. However, Price and Clancy (1983) interpreted the result as evidence for the applicability of the island biogeography theory, whereas Guegan and Kennedy (1993) suggested that the colonisation time hypothesis was the more correct explanation. They concluded that the helminth species richness was related to the time since the

fish host arrived in Britain, and that introduced species required a considerable time to acquire a helminth fauna derived from the native species even though their helminth communities were unsaturated (Kennedy and Guegan, 1994).

The concept, that the parasite fauna of introduced species was likely to be far less rich than the native fauna was explored by Kennedy and Bush (1994). They examined the helminth communities of the genus *Oncorhynchus* in its heartland in Canada, in *O. mykiss* throughout its global range, and finally in individual localities in Britain to which it had been introduced. They showed that as the distance *O. mykiss* was translocated from its heartland increased its parasite community became increasingly composed of generalists, and species poor, as both generic and salmonid specialists disappeared. However where native salmonids were present helminths may be acquired from them, depending on availability.

Kennedy and Pojmanska (1996) examined the richness and diversity of helminth parasite communities in common carp and three more recently introduced carp species. They concluded that the poor infra-communities in common carp reflect the fact that their helminth communities are composed mainly of specialists. They are not readily susceptible to invasion by specialists of other fish hosts, and that as introduced species, they have not had sufficient time to acquire many generalist helminths from native fish species. They also concluded that the fact that the data did not support the prediction of a difference in the helminth community richness between common carp and the more recently introduced carp species, does not refute the colonisation time hypothesis, but only suggests that more time is needed to acquire a richer parasite fauna.

1.5 Examination of the main processes involved in structuring parasite communities

1.5.1 Interactive versus isolationist parasite communities

Holmes and Price (1986) examined the character of parasite communities and synthesised current notions regarding competition niche and guild as they applied to the level of helminth infracommunities, and defined isolationist and interactive communities. Interactive communities are saturated equilibrial communities structured largely by biotic interactions with species evenly dispersed in resource space and responding to the presence of other guild members (Holmes and Price, 1986). Isolationist communities are unsaturated non-equilibrial communities with species individualistically dispersed in resource space and insensitive to the presence of other guild members. Holmes and Price (1986) presented the interactive / isolationist community hypothesis as a dichotomy, whereas Goater *et al.* (1987) interpreted interactive and isolationist communities as end points of a continuum.

Kennedy *et al.* (1986b) examined the fundamental differences between helminth communities in birds and fish. They concluded that helminth communities in fish were significantly poorer in numbers of species, individuals and diversity than such communities in birds. A number of factors were identified which they considered essential to the formation of a diverse parasite community, including complexity of the host alimentary canal, endothermy, host vagility, and the breadth and selectivity of the host diet. Fish, being ectothermic, less vagile than birds and having a simpler alimentary tract would be expected to have less diverse intestinal helminth communities. This study did not examine any exclusively marine fish species or tropical fish or bird species. It is likely that the same set of factors identified for temperate fish and bird species would lead to the production of diverse helminth communities in tropical species. In a series of papers Kennedy (1985, 1990, 1993a) demonstrated that the intestinal helminth communities of European eels, *Anguilla anguilla*, are species poor and characterised by low diversity and high dominance, i.e. that they are stochastic in composition and isolationist in structure.

More recently Kennedy and Hartvigsen (2000) endeavoured 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 brown trout were similar to those in eels. Thus, they set out to test the hypothesis that intestinal helminth communities in brown trout in freshwater were not similar in structure and composition to those found in European eels. The authors examined component community data on brown trout from seventy-two localities and infracommunity data on brown trout from thirty-four localities in the British Isles and Norway. They showed that a group of four species, which were trout specialists, occurred commonly in trout and so gave greater predictability to the community composition. In 97% of localities a trout specialist dominated the parasite community rather than an acanthocephalan generalist which was the situation with eels. The authors demonstrated that helminth communities in brown trout, similar to those in eels, were species poor, isolationist in character and exhibited low diversity. Thus, they concluded that the original hypothesis was correct in terms of species composition, but incorrect in terms of parasite community structure.

Kennedy (1995) showed that the richest parasite communities of tropical eels *Anguilla reinhardtii* were more diverse that those reported from any other species of fish, whether freshwater or marine, to date, and were comparable with the communities found in some species of aquatic birds. Salgado-Maldonado and Kennedy (1997) showed that the parasite communities of tropical cichlid fish *Cichlasoma urophthalmus* resembled those in Australian anguillids in respect of species richness and digenean dominance, but resembled the helminth communities of northern temperate fish in respect of low diversity, similarity and high dominance. In contrast Bush and Holmes (1986) considered the intestinal communities of lesser scaup ducks to be species rich, diverse, packed, interactive, equilibrial helminth communities.

1.5.2 Allogenic versus autogenic parasite communities

Esch *et al.* (1988) examined the colonisation strategies of helminth parasites and recognised two categories of helminths: autogenic species which mature in fish, and allogenic species which mature in vertebrates other than fish, and have a greater colonisation ability. They further divided fish helminth communities into three distinct groups. Salmonids, dominated by autogenic species, which were also found to be responsible for most of the similarity within and between geographic localities; cyprinids, dominated by allogenic helminth species, which also accounted for most of the similarity within and between localities; and anguillids whose helminth communities exhibit intermediate features with neither category consistently dominating or providing a clear pattern of similarity. They suggested that colonisation was a major determinant of helminth community structure, and that allogenic species are likely to have a greater colonising potential than autogenic species.

Kennedy *et al.* (1991) examined parasite community similarity between water bodies that were linked by fish transfer and concluded that anthropochore transfers of trout between reservoirs had little or no significance in the dispersal of parasites throughout the reservoirs. However they agreed with Esch *et al.* (1988) that the transfer of autogenic parasites by natural movements of fish will only occur very infrequently and probably under unusual circumstances and that allogenic parasites have a much greater colonising potential and ability. In contrast Hartvigsen and Halvorsen (1993) showed that the autogenic digenean *Crepidostomum metoecus* was the first parasite species to infect naïve salmon fingerlings.

Kennedy *et al.* (1989) examined the distributions of the freshwater fish acanthocephalans *Pomphorhynchus laevis* and *Acanthocephalus anguillae* and showed their distributions to be discontinuous and mutually exclusive both regionally and locally in the British Isles. They also showed that the distributions of both the intermediate and final hosts of both parasite species are far wider than those of the parasites themselves, thus providing evidence for the poor colonising potential of autogenic parasites.

However more recently Kennedy (1996c, 1997b) has shown that acanthocephalan parasites (although they are autogenic and require an arthropod intermediate host), are widely distributed throughout the British Isles and can persist at low population levels and can colonise new localities very readily. Lyndon and Kennedy (2000) have continued to challenge the paradigm that autogenic species are poorer colonisers than allogenic species, by a re-examination and interpretation of the distributions and host utilisation by the six acanthocephalan species using freshwater fish as their definitive hosts in the British Isles. They suggest that the ability of each species of acanthocephalan to use other hosts is crucial to the survival strategy of each species, and this colonisation host will give the parasite considerable potential and ability to overcome natural barriers to dispersal. An example of such a colonisation host is brown trout, which can be used by all species of acanthocephalan except *A. anguillae*; correspondingly this is the species with the most localised distribution of any acanthocephalan species in Britain (Kennedy *et al.*, 1989).

1.6 Examination of the role of competition in structuring parasite communities

Competition occurs whenever two or more organismic units use the same resources and when those resources are in short supply (Pianka, 1983). Competition can take one of two forms, exploitation or interference (Esch *et al.*, 1990). Exploitation competition is when the interaction of two populations or individuals is mediated indirectly, through inhibitory effects such as utilisation of a common resource. Halvorsen (1976) concluded that exploitation competition was uncommon among parasites, occurring only when intestinal parasites competed for limited food resources. Dobson (1985) suggested that the potential for exploitation competition existed in a large number of hosts where parasite co-occurrence is frequent enough. Interference competition occurs when two individuals or species are vying for the same resource and there is some form of direct confrontation or interactions that reduces access to the resource for one or both individuals or species (Esch *et al.*, 1990).

The outcomes of competition could be viewed in three ways, competitive exclusion, interactive site segregation and selective site segregation. Holmes (1973) reviewed the literature on coexistence of helminths, and concluded that interactive site segregation, or competition between species within a host that resulted in occupation of discrete microhabitats, was uncommon, competitive exclusion or competition that prevented co-occurrence in the same host individual, was moderately common while selective site segregation, or evolved differences between microhabitats of coexisting species, was very common. Awachie (1968) and Bwathondi (1984) demonstrated selective site segregation between *Crepidostomum metoecus* and *Crepidostomum farionis* in the intestine of brown trout.

Sousa (1994) acknowledges that heminth parasites can potentially interact in a variety of ways, both negative (Halvorsen and MacDonald, 1972) and positive (Dorucu *et al.*, 1995) but identifies the lack of studies identifying the precise mechanisms by which inferred interactions are occurring as a constraint on the development of general theory in this area.

These ideas are embodied in the competition hypothesis which states that competition has been an important organising force in parasite communities through evolutionary time and still acts in contemporary or ecological time (Holmes and Price, 1986). Whether competition leads to exclusion or niche shifts may well depend on what species are competing for, and the type of competition they use. Branch (1984) showed that competition for space, usually interference, frequently resulted in exclusion whereas competition for food, usually exploitation, often resulted in coexistence sometimes with niche diversification. Space as an absolute requirement cannot be shared whereas food is a relative requirement and can be shared. However space can be partitioned, resulting in resource partitioning rather than complete exclusion, which then increases the likelihood of exploitation competition occurring.

Holmes (1987) acknowledges that the existence of empty niches has been taken as evidence of isolationist communities, but interactions can still occur in such low

diversity systems. However current theory suggests that interspecific competition is uncommon and seldom plays a role in colonisation or extinction (Kennedy, 1985, 1992; Kennedy and Moriarty, 1987; Bates and Kennedy, 1990, 1991a,b; Salgado-Maldonado and Kennedy, 1997; Bagge and Valtonen, 1999).

Geets *et al.* (1997) tested the hypothesis that niche restriction leads to higher intraspecific contact and an enhancement of chance to mate, on two monogenean parasites of whitespotted rabbitfish. They showed that the niche breadths of the two species increase with their own abundance. Thus, they suggested that interspecific competition for space was low and that intraspecific factors could play an important role in the microhabitat choice of these gill parasites.

Interspecific interaction may lead to species exclusion, but there are several ways in which species can coexist. One way is by reducing the overall intensity of competition via aggregated utilisation of fragmented resources (Dobson, 1985; Morand *et al.*, 1999). Known as the aggregation model of coexistence this system assumes saturation and an equilibrium number of parasites per community. To test the model Morand *et al.* (1999) examined the effects of interspecific aggregation on the level of intraspecific aggregation among 36 communities of ectoparasites of marine fish. The results of the analysis gave support to one of the assumptions of the aggregation model of coexistence, which predicts that interspecific interactions are reduced relative to intraspecific interactions facilitating species coexistence.

Rohde (1991) examined intraspecific and interspecific interactions in low-density populations in resource rich habitats, namely parasites on the gills of tropical marine fish. He provides evidence that many niches are not utilised, and that the insignificant effects of potentially competing species on microhabitats and on infection intensities do not support the view that interspecific competition has great ecological / evolutionary importance. Rohde (1991) suggests that the observation of niche restriction leading to increased intraspecific contact is not to avoid competition but to find suitable sites for feeding and mating. Rohde and Heap (1998) contend that both

endo- and ectoparasites live in assemblages not structured by interspecific competition. However, although Lyndon and Kennedy (2000) agree that inter-specific competition is uncommon among freshwater fish acanthocephalans and seldom plays a role in colonisation or extinction, they do agree that inter-specific competition can occur. They predict that it is more likely to occur between species which share the same definitive host.

1.7 Examination of niche theory in terms of parasite community structure

The niche can be defined as an *n*-dimensional hypervolume, with multiple axes for all the variables contributing to the success of a given species (Hutchinson, 1957). Solbrig and Solbrig (1979) defined the fundamental niche as the hyperspace bounded by the values of the variables that organisms require to live. However organisms rarely occupy their fundamental niches. As a result of biotic interactions such as competition and predation most organisms occupy a subset of their fundamental niche, which is their realised niche.

A large number of workers have examined the niches of parasites in order to understand the structure and dynamics of parasite communities (Price, 1980, 1984; Rohde, 1979, 1998; Kennedy and Guegan, 1994, 1996; Zander *et al.*, 1999; Sasal *et al.*, 1999a). It has become clear that two opposing niche theories exist. Those who believe that there are empty or vacant niches and parasite communities are essentially unsaturated and exist in a non-equilibrium state (Morand *et al.*, 1999; Rohde, 1991; Price, 1980, 1984, 1990) and those who believe there may be a limit to the number of niches available and thus the potential for local saturation of helminth communities exists (Kennedy, 1990, 1993a; Kennedy and Guegan, 1994; 1996).

Kennedy (1990) first showed that the infracommunities of eels were always poorer than component communities and the number of intestinal helminths did not exceed three. He then showed (Kennedy, 1993a) that over a period of 14 years there were major changes in the component community of eels in a small river but very little

change in richness and diversity at infracommunity level, and concluded that the possibility of a fixed number of niches and an underlying constancy in the community structure exists.

Kennedy and Guegan (1994) examined the relationships between regional species richness and local species richness in respect of the helminth parasite communities of 32 species of freshwater fish in the British Isles. They concluded that local processes were operating increasingly independently of regional processes, thus regional richness was not a key determinant of local species richness, and knowledge of regional patterns does not improve local predictability. Srivastava (1999) demonstrated that a proportional relationship between local and regional richness, is evidence for an unsaturated community, thus as regional richness increases local richness also increases. Whereas, in a saturated community, one whose local species richness is limited largely by ecological processes, there will be no correlation between local and regional richness. Thus as regional richness increased the local richness curve reaches its asymptote and subsequently declines.

Kennedy and Guegan (1996) compared the frequency distributions of the number of helminth species per eel, and the relationships between maximum and mean infracommunity richness and component community richness, over time and space. They showed that in the single locality examined over time and in several localities examined at one time only, the relationship between maximum and mean infracommunity richness and component richness was curvilinear. Thus local species richness operated independently of regional species richness. They concluded the results could not be explained by supply-side ecology, pool exhaustion or transmission rates, but could be explained as infracommunity processes acting to impose a fixed limit to the number of species in an infracommunity. They suggest this limit is four species.

In contrast to the above study, Rohde (1998) showed that the curvilinear relationship between infracommunity and component community richness is a consequence of the

differential likelihoods of parasite species appearing in an infracommunity as determined by transmission rates and intrinsic lifespans. He concludes that 'processes operating at the infracommunity level are not necessary to explain the curvilinear relationship and that even communities much richer than those found in European freshwater fishes cannot be assumed to be saturated in the sense that further species cannot be added over evolutionary time'.

Morand *et al.* (1999) tested the effects of interspecific aggregation on the level of intraspecific aggregation among ectoparasites of marine fishes. They found a positive relationship between infracommunity species richness and total parasite species richness, thus supporting the view that infracommunities of parasites were not saturated by local parasite residents.

Sasal *et al.* (1999b) studied the structure of the parasite communities of digeneans of two families of teleost fishes of the Mediterranean Sea. They showed that potential microhabitats were vacant in the two host families studied, suggesting a lack of niche saturation, which they attributed to either little inter / intra specific competition or enough available space and resources within the host. Zander *et al.* (1999) examined the structure and dynamics of the parasite communities of ten species of littoral fish of the Salzhaff (Northwest Mecklenburg, Baltic Sea). They examined the theory of empty niches and substituted it with the assumption of variable niche widths. Geets *et al.* (1997) demonstrated that niche restriction would lead to higher intraspecific contact and an enhancement of the chances to mate.

1.8 Examination of the biology and ecology of freshwater fish acanthocephalans

1.8.1 Experimental infections involving freshwater acanthocephalans

The *P. laevis* – fish system has been widely used as a model for fish parasite interactions. Partly because *P. laevis* occurs as a natural infection in the alimentary canal of almost every species of British freshwater fish (Kennedy *et al.*, 1976) and

also in some marine fish (Gibson, 1972), also because its intermediate host, *G. pulex* (*G. duebeni* in Ireland) is widely distributed (Hynes, 1954, 1955a,b).

Kennedy (1972a) examined the effect of temperature, host starvation, and density of infection on the survival of *P. laevis* in goldfish, *Carassius auratus*. He showed that the density of infection had no effect upon the establishment of the parasite, which is in agreement with the findings of Awachie (1966), but a 12°C rise in water temperature reduced the recovery of parasites after one week by 30%. Host starvation resulted in *P. laevis* attaching in a more anterior position in the alimentary tract, and did not appear to have any noticeable effect on the establishment, and hence recruitment of the parasite.

In a follow on study, Kennedy (1974a) examined the mortality rate of *P. laevis* in goldfish, to determine whether it was related to population size. Infections with different population densities of *P. laevis* were given to fish on one occasion only, and on several occasions with different time intervals between infections. On the basis of these experiments he concluded that *P. laevis* mortality does not function as a feedback control and thus was relatively unimportant in regulating the population size of fish acanthocephalans.

Hine and Kennedy (1974) examined the growth rate of *P. laevis* in grayling, dace and chub in the laboratory. Results showed that *P. laevis* did not grow in grayling, but in dace they did grow and some worms became gravid after 60 days. For both hosts the size obtained was comparable to that recorded in the field. However results for chub showed that even after 170 days the largest parasite was only 7mm long and none became gravid. This result was contrary to the results obtained in the field, where chub is considered as the preferred definitive host of *P. laevis*. Overall they concluded that laboratory experiments supported the conclusion that there were three classes of hosts for *P. laevis*: unsuitable host (grayling), suitable host (dace) and preferred host (chub).

Kennedy *et al.* (1976) examined the distribution of *P. laevis* along the alimentary canal of several species of freshwater fish in experimental and natural conditions. They showed that the presence of cestodes in the region of the preferred site had no effect on the distribution of the parasite, and high intensity infections extended the parasites' distribution. Thus, they concluded that the distribution of *P. laevis* was determined by the process of liberation, activation and establishment of the parasite, and unsuitable chemical or feeding conditions only affect its growth not the position it occupies.

In a further series of experiments Kennedy *et al.* (1978) examined the status of brown trout and rainbow trout as hosts for *P. laevis*. Experimental results showed that rainbow trout was a much more suitable host for *P. laevis*, as it permitted greater infection levels and better parasite growth and maturation. The laboratory experiments complemented results from the field, which assigned rainbow trout to the group of preferred hosts, whereas brown trout was considered as a host where the parasite could make some growth, and occasionally mature.

Kennedy (1984a) and Munro *et al.* (1989) examined flounders as potential hosts for *P. laevis*. Kennedy (1984a) infected flounders with parasites from the river Avon, and showed that they grew but did not mature. In contrast *P. laevis* in flounders the Baltic Sea grew to a larger size, became sexually mature and occupied a different position in the intestine. He concluded that flounders were not a suitable host for the English freshwater strain of *P. laevis*, and that Baltic parasites constitute a different strain of *P. laevis* one which completes its entire lifecycle in the marine habitat. In support of this theory, Munro *et al.* (1989) showed that flounder in the tidal river Thames utilised a different intermediate host than flounder in the Avon system, and the reproductive status of *P. laevis* in the Thames flounders differed from the *P. laevis* / flounder system studied by Kennedy (1984a). Thus they concluded that the two *P. laevis* populations belonged to two subspecies or strains, the English freshwater strain and the marine strain.

However, in a later study Munro *et al.* (1990) compared the English freshwater and marine strains using molecular techniques. Their results provided evidence for considerable genetic homogeneity between the two strains of *P. laevis*, as was predicted. However they also identified some heterogeneity between the two forms using ribosomal DNA probes. This study provided some preliminary evidence for the possible genetic separation of the English freshwater and marine strains of *P. laevis*.

Brown (1986) examined the establishment and survival of *P. laevis* in primary and superimposed infections of rainbow trout. He showed that density dependant establishment and survival of *P. laevis* occurred in laboratory infected rainbow trout, such that the numbers of parasites which survive to reproduce within an individual host fish reach a ceiling level. This finding contrasted with the results of Kennedy (1972a, 1974a). However, the maximum number of parasites administered to fish by Kennedy (1972a, 1974a), 42, was below that for which marked density-dependence was observed in this study; also the parasites were contained in hosts in which they did not grow.

Bates and Kennedy (1990) examined the potential for interaction between *P. laevis* and *A. anguillae* in rainbow trout. They showed that at low intensity infections in rainbow trout there was a high degree of overlap in the range of intestine occupied by the two species and thus, no evidence for interspecific competition affecting either species. However at high intensity infections in rainbow trout the establishment of both species was unaffected by the presence or number of individuals of the other species, but the survivorship of *A. anguillae* was reduced in the presence of *P. laevis*. As the interaction was one sided, it was considered indicative of interference competition.

The experiments were repeated using chub, the preferred definitive host of *P. laevis*, and eel, the preferred definitive host of *A. anguillae* (Bates and Kennedy, 1991b). They showed that experimental results for chub, differed substantially from field data, in that both species showed low establishment and growth rates, thus it was not

possible to do any further experiments with this host. However no evidence of any interactions, competitive or otherwise, was found in mixed infections at low or high intensity in eels.

Bates and Kennedy (1991a) also examined site availability and density-dependent constraints on *P. laevis* in the intestine of rainbow trout. They showed that there was no significant change in the distribution of the parasite populations with time, which indicated that the favourable region for establishment had remained unchanged. They also failed to detect any manifestation of competition. More recently Kennedy (1999) showed that post cyclic transmission of *P. laevis* was possible from chub, minnow, bullhead and stoneloach even though they came from three families and differed in respect of their status and suitability as hosts for *P. laevis*. However, post cyclic transmission of gravid parasites could occur from bullhead but not from chub, which reflects the age and hence development of the proboscis bulb and the extent of the hosts encapsulation response, rather than the size or stage of maturity.

1.8.2 Examination of the distribution of *P. laevis* in the British Isles

Six species of acanthocephala been found as adults in the intestines of freshwater fish in the British Isles (Brown *et al.*, 1986). All six are also found on continental Europe, but only *Neoechinorhynchus rutili* also occurs in North America. Thus, the remaining five are on the edge of their distributional range in the British Isles. All six species colonised in the post-glacial period and have been found through Britain and Ireland (Kennedy, 1974b; Kennedy *et al.*, 1989; Holland and Kennedy, 1997).

Kane (1966) and Kennedy (1966) drew attention to the fact that for such a widespread and non-specific parasite, the distribution of *P. laevis* in Britain was extremely restricted when compared with its distribution and abundance in Ireland. *P. laevis* has been reported from a large number of lakes and rivers throughout Ireland (Kane, 1966; Kennedy and Fitzmaurice, 1971; Fitzgerald and Mulcahy, 1983; Conneely and McCarthy, 1984, 1988; Molloy *et al.*, 1995a; Byrne *et al.*, 1999). In contrast the distribution of *P. laevis* in England is extremely localised, and apart from a few

scattered records is confined to four main river systems, despite the fact that the distribution of both its intermediate and definitive hosts is far wider than that of the parasite itself (Kennedy *et al.*, 1989).

Hine and Kennedy (1974) identified three groups of fish based on their status of hosts of *P. laevis*. The natural or preferred hosts in which *P. laevis* attains its maximum size and gravid parasites are common; suitable hosts in which growth is possible and some parasites become gravid; and unsuitable hosts in which the parasites do not grow or mature. They demonstrated both in the laboratory and in the field that brown trout in England belonged to a group of hosts in which *P. laevis* can achieve some growth and occasional maturation.

In contrast, the frequent occurrence and heavy infection levels of *P. laevis* recorded from brown trout in Ireland (Conneely and McCarthy, 1984; Fitzgerald and Mulcahy, 1983; Molloy *et al.*, 1995a), would suggest that brown trout was acting as a preferred definitive host in this country. Hine and Kennedy (1974) suggest that in association with the geographical separation and isolation of mainland Britain and Ireland and the utilisation of different species of both intermediate and definitive hosts in each country, *P. laevis* in England and Ireland has evolved into separate strains. In Britain *P. laevis* uses *Gammarus pulex* as its intermediate host and chub and barbel as its preferred definitive hosts, and brown trout is considered as a secondary host. In contrast, in Ireland where chub and barbel are absent, and *Gammarus duebeni* is the dominant amphipod, *P. laevis* uses *G. duebeni* as an intermediate host and brown trout act as preferred definitive hosts.

Subsequently, Kennedy (1996c) demonstrated that the English freshwater strain of *P. laevis* could colonise and establish in a location from which its preferred definitive hosts, chub and barbel, were absent. Kennedy *et al.* (1986a) demonstrated an analogous situation when they examined the parasite communities of freshwater fish from Jersey, Channel Islands. They showed that the acanthocephalan *E. truttae* dominated the eel parasite community. This species is a more characteristic parasite

of salmonids, especially brown trout, but it has been reported from eels periodically (Kennedy, 1974b). On Jersey it was a normal parasite of eels, became sexually mature in them and dominated most of their communities. They suggested that in the absence of characteristic species of acanthocephalans found in eels such as *A. clavula* and *A. lucii*, their niche was occupied by *Echinorhynchus truttae*.

Kennedy (1984a) examined the status of flounders *Platichthys flesus* L., as hosts of *P. laevis*. He concluded that marine and Baltic parasites constituted a different strain of *P. laevis*, a marine strain, which completes its entire life cycle in the marine habitat and for which flounder is the preferred definitive host. In contrast to this, flounder was not even a suitable host for the English freshwater strain of *P. laevis*.

Kennedy *et al.* (1989) explained the discontinuous distribution of *P. laevis* in the British Isles in the following manner. They suggested that *P. laevis* arrived in Britain with continental cyprinids via the eastward-flowing rivers and the Thames-Rhine link, which existed in early post-glacial times, and that the distribution of *P. laevis* in England resulted from the stocking infected barbel from the river Thames into other rivers. The introduction of infected cyprinids into Ireland and the subsequent change of intermediate and definitive hosts, taken together with its geographical isolation was sufficient to exert the necessary selection pressure for *P. laevis* to evolve into a separate strain, thus explaining the distribution of the parasite in Ireland. Finally another *P. laevis* stock specialised in using flounders as hosts and marine gammarids as intermediate hosts, and this became the marine strain.

1.8.3 Examination of the microhabitat selection of freshwater fish acanthocephalans

A large number of studies have addressed the question of habitat selectivity of parasite populations (Holmes, 1973; Sukhedo and Sukhedo, 1994; Rohde, 1994; Buchmann and Uldal, 1997; Aznar *et al.*, 1997; Buchmann and Bresciani, 1998; Ellis *et al.*, 1999). Uldal and Buchmann (1996) showed that *Hexamita salmonis* preferentially occupied the pyloric region of infected rainbow trout, but occupied the entire length of the gut in heavy infestations. Sukhdeo (1991) examined the

relationship between intestinal location and fecundity in adult *Trichinella spiralis*, and concluded that the physico-chemical conditions of the anterior small intestine are optimal for the parasites reproductive fitness and this exerts a strong selective pressure on habitat selection behaviour. Similarly Barber and Crompton (1997) demonstrated that metacercariae of *Diplostomum phoxini* were unevenly distributed throughout the brains of minnows. They suggested that the parasite might have evolved to enhance its transmission to subsequent hosts, as individuals were aggregated in areas of the brain known to be involved in antipredator responses. Adamson and Caira (1994) considered how helminth specificity patterns are shaped during the course of evolution. They suggest that host ecology acts as an external factor affecting specificity. It predominates in parasites that interact minimally with the hosts physiological and immune systems, whereas co-evolutionary factors are more important in parasites that feed on host tissue or occur in extra-intestinal sites. Also they concurred that the role of competition in determining specificity is difficult to assess.

There has also been a large amount of work on the microhabitats of freshwater fish helminths, specifically acanthocephalans (Kennedy, 1984a, 1985; Crompton, 1973; Kennedy *et al.*, 1976; Kennedy and Lord, 1982; Uznanski and Nickol, 1982; Fitzgerald and Mulcahy, 1983; Bates and Kennedy, 1990, 1991a,b).

Kennedy (1972a) examined the effects of temperature, host starvation and density of infection on the establishment and survival of *P. laevis* in goldfish. He showed that *P. laevis* did not change its position in the intestine throughout the course of infection. However at low temperatures (6°C) the mean position of *P. laevis* was 5% nearer the anus, and at a density of thirty parasites per fish, the population was located about 3% nearer the oesophagus and in starved fish *P. laevis* was located 8% nearer the oesophagus. This was probably due to a wider anterior spread of the attachment zone under crowded conditions rather than a more anterior site being actively selected.

The results from this study contrasted with the results of Awachie (1966) who studied *Echinorhynchus truttae* and Tedla and Fernando (1970) who studied *Echinorhynchus salmonis*. They showed that a regular movement of acanthocephala down the intestine of the fish occurred during the course of the infection. Kennedy *et al.* (1976) examined the site selection of *P. laevis* in seven species of fish which vary in their status as hosts species. They showed that in both experimental and natural infections *P. laevis* exhibited a preference for a particular region of the alimentary canal, however in all cases parasite individuals occurred throughout the intestine. In cyprinid species the majority of individuals occurred in the anterior region of the intestine, in salmonids *P. laevis* were normally found in the region posterior to the pyloric caeca.

They agreed with the finding of Kennedy (1972a) that *P. laevis* did not move down the intestine during the course of infection, but instead remained at the site of first attachment. The failure of *P. laevis* to move down the intestine was attributed to its method of attachment, in particular the use of a proboscis bulb, which elicits an encapsulation response from the host's immune system. Thus, Kennedy *et al.* (1976) concluded that the distribution of *P. laevis* in the alimentary canal of fish is determined by the process of liberation, attachment and establishment of the parasites and it normally attaches in the first available space and remains there.

The microhabitat of *P. laevis* in flounder was examined by Kennedy (1984a) and Munro *et al.* (1989). Kennedy demonstrated that in the Baltic Sea *P. laevis* showed a very pronounced preference for, and was virtually confined to the rectum of flounders. However when flounders were infected with the English freshwater strain of *P. laevis* and when it occurred naturally in flounders in the River Avon, parasites were far less site specific and occupied a site significantly anterior to the rectum.

Munro *et al.* (1989) also examined the marine strain of *P. laevis* and showed that it occurred exclusively in the intestine and rectum, and that the highest density of worms occurred in the rectum. They showed that there was some variability in the

mean attachment position of worms in individual fish. The mean attachment position of *P. laevis* in individual fish was found to be closely related to the size of the parasite burden. Thus, as the intensity increased the mean position of the population shifted to more anterior positions. Both Kennedy (1984a) and Munro *et al.* (1989) found a large proportion of *P. laevis* in extra-intestinal sites, and in many cases an effective host immune response was mounted and parasites were encapsulated and lysed.

Kennedy and Lord (1982) examined the site specificity of *A. clavula* in a number of freshwater fish, as well as eels, the preferred definitive host, maintained experimentally under different regimes. They showed that *A. clavula* was consistently small and appeared to make little growth in perch and flounder, and no gravid females were found in either host, but in eels growth occurred and most females became gravid. In all three hosts *A. clavula* exhibited preference for a particular region of the intestine (which did not differ between the three host species), but they could survive over a much wider region.

In common with *P. laevis*, *A. clavula* did not change position throughout the course of an infection, and in high intensity infections the range of *A. clavula* was extended and the mean position was significantly more anterior than in single worm infections. The mean position of *A. clavula* did not change when the host was starved, maintained in 100% seawater with no acclimatisation, or with reduced aeration or at high temperature, thus, the authors concluded that *A. clavula* was a hardy species well adapted to its preferred definitive host, the eel.

Kennedy (1985) examined the site specificity and distribution of five species of freshwater acanthocephalans, and one marine species. He showed that each species exhibited a preference for a particular region of the intestine, and this preferred region changed in relation to host identity and sex and abundance of parasite. However, each species could inhabit most of the length of the intestine and in most cases there was a lot of overlap between the distribution of species in the same host. He concluded that at the level of the individual fish fidelity of site location and distribution was poor,

therefore, site specificity and segregation were most applicable at the population level.

In an Irish context, site selection by *P. laevis* was examined in salmon and brown trout (Fitzgerald and Mulcahy, 1983) and brown trout (Molloy *et al.*, 1995a,b). Fitzgerald and Mulcahy (1983) showed that unattached *P. laevis* had a slight preference for more posterior sites when compared to attached worms, and site selection for both male and female worms was similar. Molloy *et al.* (1995a,b) also showed that *P. laevis* occupied a more posterior region of the intestine.

Bates and Kennedy (1991a) examined the microhabitat selectivity of *P. laevis* in experimental rainbow trout when they were infected with fifty cystacanths each, every four weeks over a period of sixteen weeks. The aims of the experiment were to examine threshold density levels of *P. laevis*, and establish whether any density dependent constraints existed. They showed that there was no significant change in the distribution of the parasite population over the course of the infection. They suggested that the increase of intestine availability (possibly as a result of the growth of the fish host) might be sufficient to mask the effects of intraspecific competitive interactions.

1.8.4 Co-occurrence and interaction of fish parasites with special reference to freshwater fish acanthocephalans

Kennedy (1990) considered that the regular co-occurrence at substantial population densities of more than one helminth species would seldom occur in freshwater fish, and therefore interspecific competition was unlikely to be a major determinant of community structure. A number of other studies appear to give support to this theory, Kennedy (1993a) and Kennedy *et al.* (1997, 1998) examined eels in Britain and in Italy respectively, in all three studies a large proportion of eel hosts harboured one or zero helminth species. Also, in the case of the River Tiber, Kennedy *et al.* (1998) showed that parasite communities were dominated by the acanthocephalan *A. clavula*.

A number of other studies have also examined the potential for interspecific interactions in isolationist systems. Thomas (1964) examined the helminth parasites in brown trout, and found little evidence of competitive interactions. Halvorsen and MacDonald (1972) showed that when the cestode *Cyathocephalus truncatus* was present in the alimentary canal of brown trout, the digenean *C. metoecus*, whose normal preferred position is the anterior pyloric caeca, attached to the posterior pyloric caeca. Kennedy and Hartvigsen (2000) presented a strong evidence for negative interactions between the digenean *C. metoecus* and *Eubothrium crassum* in the intestine of brown trout, whereas, Conneely and McCarthy (1988) could not demonstrate any antagonistic interaction between these two species in the intestine of brown trout in Ireland.

Awachie (1968) demonstrated site segregation by the congeneric parasite species *Crepidostomum farionis* and *C. metoecus* along the alimentary canal of brown trout. Dorucu *et al.* (1995) examined endoparasitic helminth infections of brown trout in Scotland and demonstrated a positive association between the acanthocephalan *N. rutili* and the digenean *Crepidostomum farionis*.

Barger and Nickol (1999) examined the effect of the presence of *Pomphorhynchus bulbocolli* on the development of *Lepthorhynchoides thecatus* in amphipod intermediate hosts, in the laboratory. They showed that a significantly smaller number of *L. thecatus* reached the cyctacanth stage in co-infected amphipods, thus the number of *L. thecatus* in amphipods available for transmission to the definitive host was reduced. Barger and Nickol (1998) demonstrated that although *P. bulbocoli* and *L. thecatus* used the same intermediate host *Hyalella azteca*, differences in the fibrillar coats of the parasites resulted in segregation in the environment in a manner that affects transmission and occurrence in intermediate hosts. Dezfuli *et al.* (1999) showed that *P. laevis* co-occurred with the acanthocephalan *A. clavula* and the cestode *C. truncatus* in the intermediate host *Echinogammarus stammeri*, and amphipods with multiple infections constituted 28-32% of each monthly sample.

A number of studies have concentrated on the potential of acanthocephalans in freshwater fish in the British Isles to interact. Kennedy (1985) examined the site segregation of acanthocephalans in fish, with special reference to eels. He showed that each acanthocephalan species could inhabit most of the length of the intestine, in most cases there was considerable overlap in the distributions of species in the same host, but the mean position of each species differed significantly from that of any other, and at the level of the individual fish site fidelity was weak. Kennedy suggests that the normal situation in England is that only one species of acanthocephalan occurs in a locality, and if more than one species occurs, then one species dominated the acanthocephalan population in that locality. He concluded that as acanthocephalans are normally over dispersed, the probability of one fish harbouring large populations of two species of must be very low. Therefore, it would seem reasonable that two species of acanthocephalans could co-exist in the same host individuals without any interactions taking place between them.

In a later study Kennedy and Moriarty (1987) examined a population of eels from Lough Derg on the River Shannon which harboured two acanthocephalan species, *A. anguillae* and *A. lucii*. Throughout the study period *A. lucii* was the dominant acanthocephalan, it was overdispersed throughout the eel population and occurred most often as a single species infection. In contrast *A. anguillae* occurred most often as a multi-species infection and its distribution was close to random in most cases. They could find no evidence for interspecific competition, but showed that the pattern of infection in eels, where *A. lucii* completely dominated *A. anguillae* was consistent with Dobson's (1985) predictions on the results of exploitation competition. Thus, they showed that congeneric species of acanthocephalans could co-exist in an apparently stable equilibrium system in wild fish hosts.

Conneely and McCarthy (1986) demonstrated that negative correlations existed between *P. laevis*, *A. lucii* and *A. clavula*. In the case of *A. clavula* a significant negative correlation existed with *P. laevis* in a small sample of eels, which they suggested could be the result of competitive exclusion. Kennedy *et al.* (1989)

examined the distributions of *P. laevis* and *A. anguillae* in Britain and Ireland and showed that they were mutually exclusive. Joint occurrences of *A. anguillae* and *P. laevis* only occurred in the Shannon and Thames systems, and in most cases within these river systems their distributions were discrete with little or no overlap. Where there was limited overlap, in no case did both species co-occur in the one fish host. They suggested that competitive exclusion was responsible for the mutually exclusive distributions of *P. laevis* and *A. anguillae.*

In a series of laboratory experiments Bates and Kennedy (1990, 1991b) examined the potential interactions between *P. laevis* and *A. anguillae.* In the first experiment (Bates and Kennedy, 1990) rainbow trout were used as definitive hosts. They showed that in high intensity infections, establishment by both species was unaffected by the presence and number of individuals of the other species. However, the survivorship and the range of the intestine occupied by *A. anguillae* were reduced in the presence of *P. laevis*. The interaction was one-sided as *P. laevis* was unaffected by *A. anguillae,* this indicated that interference competition was taking place.

In the second experiment Bates and Kennedy (1991b) used the preferred definitive hosts of the two parasite species, chub for *P. laevis* and eel for *A. anguillae.* Unfortunately due to the poor establishment and growth of parasites in chub, laboratory infections were discontinued. Both species showed higher establishment rates in eels than in rainbow trout, but *A. anguillae* grew faster and matured to a greater extent than *P. laevis*. However no evidence of any interactions were found between *P. laevis* and *A. anguillae* in concurrent infections at low or high infection levels.

Lyndon and Kennedy (2000) suggest that interspecific competition between acanthocephalans of freshwater fish in Britain is uncommon, and seldom plays a role in colonisation, however they do not suggest that interspecific competition cannot occur. They believe that competition is likely to occur when two species co-occur in the same suitable definitive host but not preferred definitive host. To demonstrate this

they examined the definitive and intermediate host specificity of acanthocephalans in Britain and Ireland and predicted that interspecific competition was likely to be more common in Ireland, as species are forced into sharing suitable hosts in the absence of their preferred definitive hosts from that country. For example, they predict that the potential for competition between *P. laevis* and *E. truttae* would be high, as both species utilise the same intermediate host, and *P. laevis* also utilises trout as its preferred definitive host in the absence of chub.

1.9 Examination of the establishment and development of the parasite communities in wild and stocked fish

1.9.1 Examination of the establishment and colonisation of fish parasites

A number of laboratory studies have examined the establishment, survivorship, site selection, mortality and fecundity of parasites when they colonise fish hosts. Some were more concerned with ecological aspects of the relationship (Kennedy, 1972a, 1974a; Kennedy *et al.*, 1976; Kennedy and Lord, 1982; Brown, 1986; Munro *et al.*, 1989; Bates and Kennedy, 1990, 1991a,b), whereas others were concerned with the actual or potential commercial implications of parasite infestation (Kennedy and Fitch, 1990; Johnson and Albright, 1991; Bakke *et al.*, 1991; Uldal and Buchmann, 1996; Buchmann and Lyholt, 1995; Buchmann and Uldal, 1997; Buchmann and Bresciani, 1998).

A number of workers have also examined the colonisation and establishment of parasites in field situations. Kennedy (1996b) reviewed a long-term data set on the roach, rudd and perch populations in Slapton Ley. He showed that the introduction of *Ligula intestinalis* probably as a result of the colonisation of the lake by great crested grebes (*Podiceps cristatus* L.) greatly affected the dynamics of the cyprinid populations over the following twenty-five years. Kennedy (1996c) demonstrated the ability of the English freshwater strain of *P. laevis* to colonise and establish in brown trout in the absence of its preferred definitive hosts, chub and barbel. Lyndon and Kennedy (2000) reviewed examples of colonisation and extinction of

acanthocephalan parasites from a number of river systems over time, such as the disappearance and reappearance of *A. clavula* in eels in the River Clyst, and the sudden appearance of *N. rutili*. However Kennedy (1993b) cautioned that the potential for the introduction of fish parasites appeared to be much greater than the actuality. In this situation he was referring to the British Isles, but the caution is probably just as relevant to the introduction of fish parasites into a new lake or river system.

Some workers have examined the colonisation and establishment of parasites as a result of the introduction of fish hosts. Wootten (1973) suggested that the introduction of trout into Hanningfield reservoir introduced an oligotrophic element to an otherwise eutrophic parasite fauna. Similarly Kennedy (1978b) suggested that just as it was possible to recognise an oligotrophic and eutrophic lake fauna, it was also possible to recognise an oligotrophic and eutrophic parasite fauna, and once the trophic status of the lake was known it should be possible to predict the parasite species present. Kennedy *et al.* (1989) showed that the stocking of the rivers Avon and Severn with infected barbel from the river Thames led to the introduction of *P. laevis*.

Kennedy and Pojmanska (1996) examined the helminth communities of common carp and three other carp species, introduced into Poland. They concluded that the poor infracommunities in common carp reflected the fact that their helminth communities were composed mainly of specialists and that they were not readily susceptible to invasion of specialists of other fish host. They also suggested that as carp were introduced species they have not had enough time to acquire generalist helminths from native fish. Bergeron *et al.* (1997) examined the parasite fauna of brook trout in relation to lake morphometrics and the introduction of creek chub. They showed that two parasite species from creek chub were exchanged with brook trout and two parasite species from brook trout species were exchanged with creek chub.

Despite the relative wealth of literature pertaining to the establishment of parasites in laboratory experiments, in wild hosts in field investigations, and as a result of introductions of fish into new localities, very few studies exist on the establishment and development of parasite communities of naïve cultured fish in field situations.

Vidal-Martinez *et al.* (1998) used sentinel fish to examine the structuring processes of the macroparasite community of the tropical cichlid *Cichlasoma uropthalmus*. Three thousand uninfected cichlids were stocked into floating cages and introduced into a quarry in which a wild population of the same species was present. Results showed that seventeen macroparasite species were found in the wild cichlid population and after six months ten species were found in the caged cichlid population. They concluded that the structuring process of the macroparasite community of the tropical cichlid *C. uropthalmus* followed a predictable pattern because early infections of caged cichlids were by species which were more frequent and abundant in the wild population, whereas helminth with a low prevalence and abundance in the wild appeared later in the caged fish population.

The use of sentinel fish is more common in environmental pollution and ecotoxociology studies (Julshamn and Grahl-Nielsen, 1996; Dunier, 1996; Gibbons *et al.*, 1998; Fitzgerald *et al.*, 1999; Thompson *et al.*, 1999) however, Hartvigsen and Halvorsen (1993) used sentinel fish (although they referred to them as a tracer population) to examine the establishment of parasites in a population of naïve cultured salmon fingerlings. They stocked a small earthen fishpond fed by streams from two neighbouring lakes, with hatchery reared salmon fingerlings. Wild fish were prevented from entering. At the end of the stocking period salmon fingerlings were found to be infected with *C. metoecus*, considered to be a core species, and juvenile *Crepidostomum* which could not be identified to species level. Thus their results were in accordance with the predictions of the core-satellite model, namely that core species should have a superior colonising ability.

1.9.2 Comparison of the parasite communities in wild and stocked fish

Scholz (1999) suggested that parasites which cause little apparent damage in feral fish populations, may become causative agents of diseases of great importance in farmed fish, ultimately leading to pathological changes, decrease of fitness or reduction of the market values of the fish. He reviewed the current status of several important parasite species in cultured and feral fish. It is apparent that most of the scientific literature pertaining to the parasites of cultured fish focuses on the commercial implications of parasite infestation (Kahn *et al.*, 1990; Costello, 1993; Field and Irwin, 1994; Hoole, 1994; Buchmann *et al.*, 1995; Buchmann and Bresciani, 1997) and only a few have simultaneously considered the parasites of wild fish (Wootten and Smith, 1979; Bucke *et al.*, 1991; Tully, 1992; McVicar, 1997a,b; Todd *et al.*, 1997; Hendrick, 1998).

Most of these studies have concentrated on single parasite species, correspondingly there are very few studies that have examined the parasite communities of wild and cultured fish. In an early study, Aderounmu (1966) examined the parasite communities of brown trout from a lake and hatchery in Wales. A total of twelve parasite species was reported from brown trout in the lake, and only seven parasite species were recovered from the hatchery. Parasites with direct life cycles were more prevalent in the hatchery trout than the lake trout, which was consistent with the trout in the hatchery being kept at high stocking densities. It was suggested that the lower parasite burden and higher prevalence of direct life cycle parasites in parasites in hatchery trout was probably related to stocking density, diet, and parasite control measures applied in the hatchery.

Wootten (1973) examined the parasites of eight species of fish from Hanningfield Reservoir in Essex (including rainbow trout), and also juvenile rainbow trout from adjacent trout raceways. He showed that the parasite fauna of the juvenile rainbow trout from the adjoining raceways represented a reduced version of that of the adult fish from the reservoir.

Poynton and Bennett (1985) conducted a similar examination on the parasitic infections and interactions in wild and cultured brown trout and cultured rainbow trout from the river Itchen, Hampshire. They recorded 21 parasite genera from wild brown trout, 17 parasite genera from cultured brown trout and 5 parasite genera from cultured rainbow trout. The large differences in the number of genera recorded between the cultured brown trout and cultured rainbow trout was attributed to the management practices adopted on the fish farms: the rainbow trout farm was managed under intensive culture conditions, whereas the trout farm was kept in semi-natural conditions, closer to the wild situation. These results are consistent with those of Aderounmu (1966) and Wotten (1973).

Hartvigsen and Halvorsen (1993) examined the parasite communities of wild brown trout and stocked salmon fingerlings, and showed that the first parasite species to infect the salmon fingerlings were *C. metoecus* and *Crepidostomum* sp., however the authors did not compared the parasite communities of brown trout and stocked salmon fingerlings. Vidal-Martinez *et al.* (1998) compared the helminth communities of wild and stocked *Cichlasoma uropthalmus*, and showed that seventeen parasite species were recorded in wild *C. uropthalmus* and ten species were detected in the caged population after six months. Their results were consistent with those of Aderounmu (1966), Wootten (1973) and Poynton and Bennett (1985). However in this study fish were kept in floating cages and fed an artificial diet, they had free access to all planktonic copepod and their parasites but not to benthic intermediate hosts. The results from this study supported the core-satellite hypothesis proposed by Hartvigsen and Halvorsen (1993) such that early parasite infections of the caged cichlid population were by species that occurred with greater frequency and in greater abundance in the wild cichlid population.

McGuigan and Sommerville (1985) examined the effects of cage culture of rainbow trout on the parasite fauna of Loch Fad in western Scotland. They examined rainbow trout held in floating cages, feral rainbow trout, which had escaped from the floating cages and wild perch, roach, pike and stocked eels. There was no natural breeding

population of salmonids in the lough. They showed that strigeid metacercariae dominated the parasite fauna and represented over 90% of the total number of parasites recovered, but infection was lower in caged rainbow trout than in feral rainbow trout. Also, it was suggested that the protozoan pathogens discovered were probably introduced with stocked trout.

In a similar study Valtonen and Koskivaara (1994) examined the relationships between the parasite fauna of wild and cultured fish from two lakes and a fish farm in Finland. One of the lakes studied formed the water source for the fish farm and the other lake was the effluent recipient lake. The authors examined Atlantic salmon and brown trout from the fish farm, roach perch and whitefish from the lake which formed the water source and roach and perch from the effluent lake. Cultured fish harboured 14 parasite species, mostly protozoan generalists, nine species were found on salmon and twelve were found on brown trout. The proportion of parasite species common to both wild and cultured fish were 17% of the species from roach, 36% of those from perch, 47% of the species from whitefish. However they did not compare the parasite communities of one species of fish in both wild and stocked situations. They concluded that the source of parasites in the fish farm was the water supplying lake, but the fish farm was unlikely to effect the fish parasite fauna of the recipient lake.

Chapter 2

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2.1 Sample site descriptions

2.1.1 Burrishoole Catchment

The Burrishoole valley lies in a north-south direction, in the Nephin Beg mountain range, Co. Mayo (9^0 55' W 53^0 55' N). The freshwater catchment has a total area of 8,949ha (Fig 2.1). There are three main lakes, Lough Furnace (brackish water– 141ha), Lough Feeagh (410ha) and Bunaveela Lake (46ha), and a number of smaller lakes. The catchment is drained by approximately 45km of small shallow streams (Poole, 1994). The western side of the catchment is composed primarily of Dalradian schists, gneiss and quartzite (Whittow, 1974) leading to poorly buffered generally acidic runoff. The northern and eastern sides of the catchment have small outcrops of limestone and sandstone. Forestry, which covers approximately 31% of the catchment (2702ha), and mountain sheep farming, are the main land uses. Overgrazing by sheep has led to severe hillside erosion, resulting in increased peat siltation and acidification of streams, particularly in the western part of the catchment (Whelan, 1995).

2.1.2 Lough Feeagh

Lough Feeagh was chosen as the primary sample lake in the present study for a number of reasons. Firstly, although Molloy *et al.* (1993, 1995a) examined the parasite communities of trout in Lough Feeagh, the present study will facilitate a comparison, and thus provide an accurate picture of the changes occurring in the parasite communities of trout in Lough Feeagh over a five year period. The second main reason for choosing Lough Feeagh was the fact that the Salmon Research Agency of Ireland is based there, which meant that human resources, nets, boats and all of the other equipment and facilities required to make the project work were readily available.

Lough Feeagh is a low-lying, oligotrophic freshwater lake of glacial origin. The lake has an area of 410ha, maximum depth of 43m and is at an altitude of 14m above sea level. Lough Feeagh is joined to Lough Furnace by two narrow channels, the Salmon

Leap (natural) and the Millrace (man-made) (Fig 2.2). The lake is composed of a series of basins, the largest and deepest occupies the northern portion of the lake. A smaller basin lies south of this, and another shallower basin occupies the south-west corner of the lake. The southern portion of the lake is shallow (15–18m) and has an undulating bottom. The water of Lough Feeagh is neutral to acidic and distinctly coloured, due to peat siltation. The pH values range from 6.3 to 7.0, and conductivity values are around 80-90μS/cm (Poole, 1994). The lake temperature is continuously monitored at the Millrace and values are normally within the range of 3 – 20°C.

2.1.3 Bunaveela Lake

Bunaveela Lake lies on the north-eastern side of the main catchment. It has an area of 42ha, a maximum depth of 23m and lies at an altitude of 150m above sea level. There is one main inflow, the Fiddaunveela River, and one main outflow, the Goulaun River. The lake is naturally divided by a promontory sticking out from the eastern shore. The northern end of the lake is shallow with an average depth of 2-8m. The southern half is composed of three basins, the deepest of which is 23m. The geology around Bunaveela Lake is a mix of limestone and sandstone. The buffering effect of limestone and sandstone on the water boosts productivity and allows considerable numbers of molluscs and *G. duebeni* to inhabit the lake.

2.1.4 Clogher Lake

Clogher Lake was chosen as a comparison to Lough Feeagh, because it is in the same geographical region and it only contains wild brown trout. The lake lies in a north to south facing valley about 8km from Westport Co. Mayo and 6km from the Burrishoole catchment. The lake is relatively small 60ha and is at an altitude of 25m above sea level. Clogher Lake has one inflowing stream from the north and two outflowing streams to the south (Fig 2.3). The lake is surrounded by low-lying farmland, and it appears to be a lot richer than Lough Feeagh. Clogher Lake could probably be classified as a mesotrophic lake, although no environmental data is presently available to confirm this. The lakeshore is composed of soft marl, and reed

beds cover most of the shoreline, the reed beds are particularly prominent on the southern and eastern shores. This lake is owned and managed by the western region fisheries board.

2.2 Types of trout found in Lough Feeagh

2.2.1 Stocked Trout

The trout used in the present study were the F1 progeny of wild seatrout broodstock from Lough Feeagh which were being maintained by the Salmon Research Agency of Ireland as part of their West Coast sea trout broodstock programme. Thus, in this study the stocked trout were essentially genetically identical to wild trout in Lough Feeagh. A total of 5801 pond reared, one-year-old, brown trout were tagged using V. I. (Visible Implant) tags. 4167 were tagged in 1997, and 1634 were tagged in 1998. The visible implant tag combines the benefits of an external tag (easy to see in live fish) with the benefits of an internal tag (low biological effect). Transparent tissue found around the eye of the trout serves as a "window" for the visible implant tag. Tags are luminous coloured, flat rectangles approximately 2mm long x 1mm wide with alphanumeric characters (e.g. A51). Tags fluoresce when viewed under ultra violet light.

Trout were transferred in batches, from rearing ponds, into a large oxygenated holding tank. From the holding tank fish were transferred in smaller batches of 25–30, to an anaesthetic bath, where benzocaine (Ethyl p-Aminobenzoate, Sigma) was used to lightly anaesthetise them. A tag was "loaded" into the tip of the applicator, a modified syringe flattened at the tip with a protrudable plunger. The tip of the loaded applicator was inserted into the transparent tissue behind the left eye of the anaesthetised trout, and slowly removed while depressing the plunger. This caused the tag to be ejected from the tip of the applicator into the eye tissue.

Tagged trout were measured (fork length), had their tag number recorded, their adipose fin clipped off, and were put into an oxygenated recovery tank. Removal of the adipose fin is a quick way to identify a fish, which has been V. I. tagged. Ten days later all trout were examined for tag retention. In 1997 green and red coloured tags were used, and in 1998 red and orange coloured tags were used. In April 1997 tagged trout were released into Lough Feeagh. Red V. I. tagged trout (n=1667) were released at Tom Billy's Stream (Fig 2.2) and green V. I. tagged trout (n=2500) were released at Treanlaur Pier (Fig 2.2). In March 1998 both red and orange V. I. tagged trout (n=1634) were released into Lough Feeagh, as a single group at the Black River Bridge (Fig 2.2).

2.2.2 Wild Trout

Lough Feeagh contains resident and migratory wild trout: both spawn together in streams surrounding the lake and emergent fry are indistinguishable from each other. Electrofishing and beach seine netting surveys (Matthews *et al.*, 1997) have shown that most trout production takes place in the lake, with inflowing streams acting as spawning and nursery areas, and the lake acting as the first recruitment area which juvenile trout encounter. Resident trout (brown trout) mature in the lake and only migrate upstream to spawn. Iteroparity is frequent, with adults spawning at least two or three times before death. The majority of migratory trout (sea trout) in Lough Feeagh smoltify after two years, with the remainder smoltifying after three years. Recruitment to the sea takes place as spring migrating silvered smolts, and autumn migrating unsilvered juvenile trout. Migratory trout were also present in Bunaveela Lake, but in different proportions to Lough Feeagh. Migratory trout were less prevalent and only formed a small proportion of the total trout population in Bunaveela Lake.

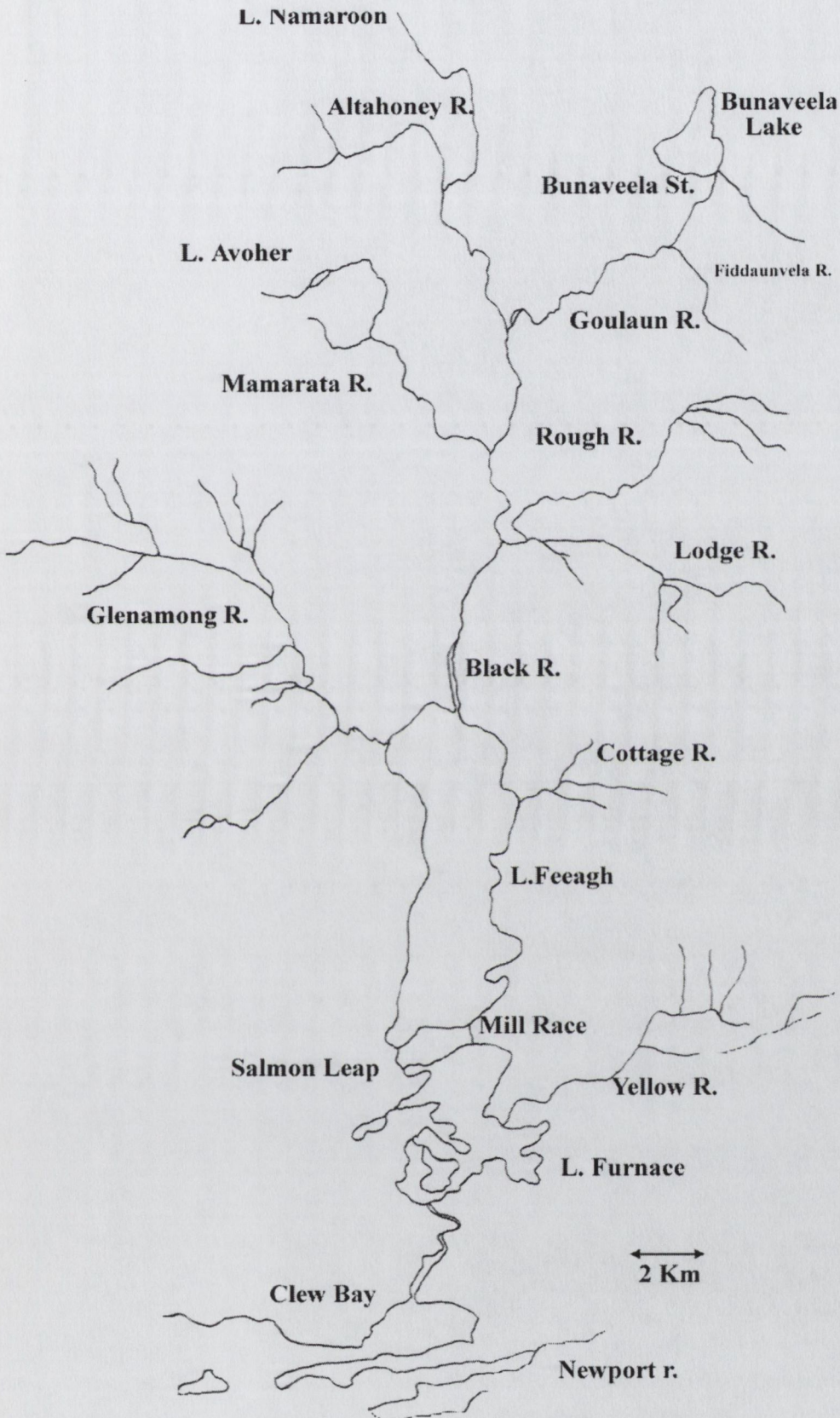

Figure 2.1 Map of the Burrishoole Catchment

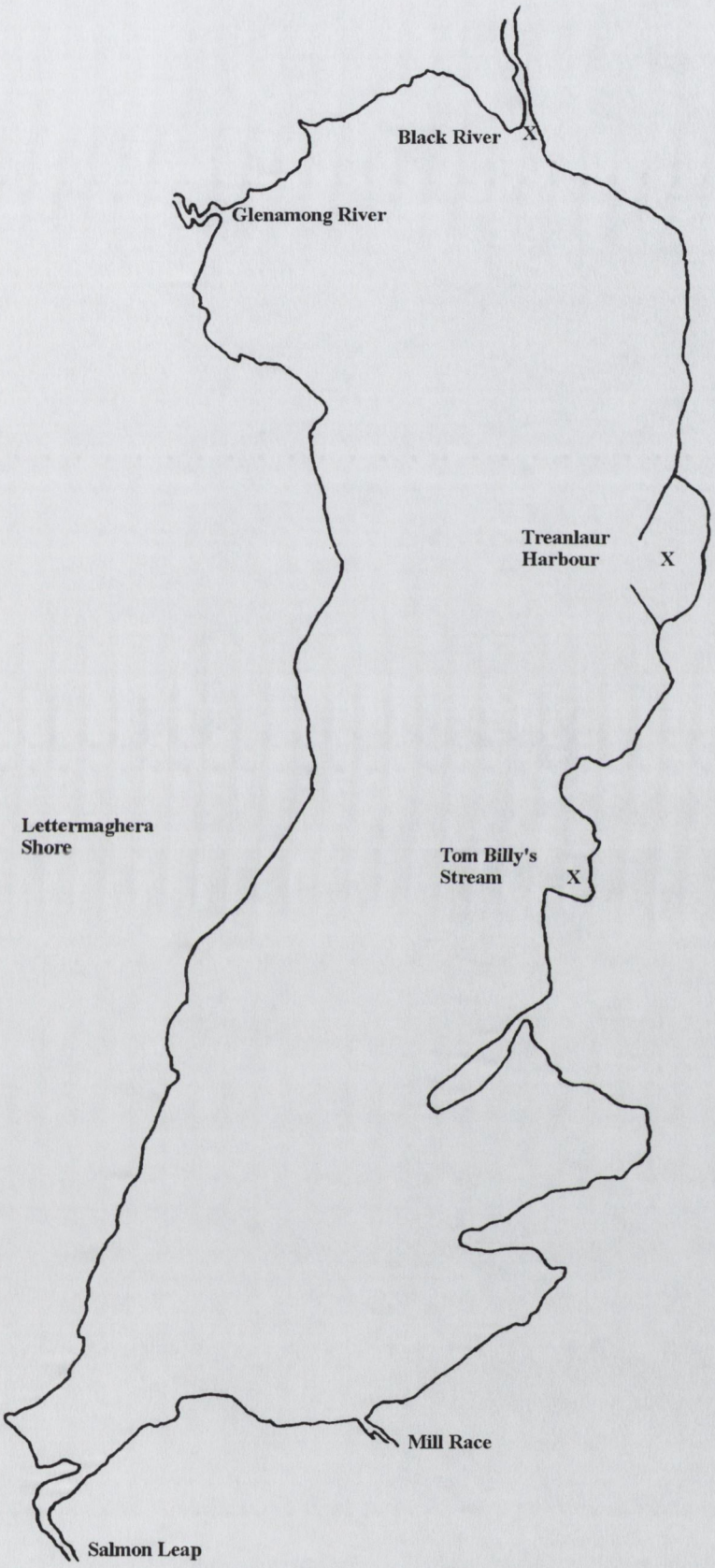

Figure 2.2 Map of Lough Feeagh showing fish release points and draft net sites.

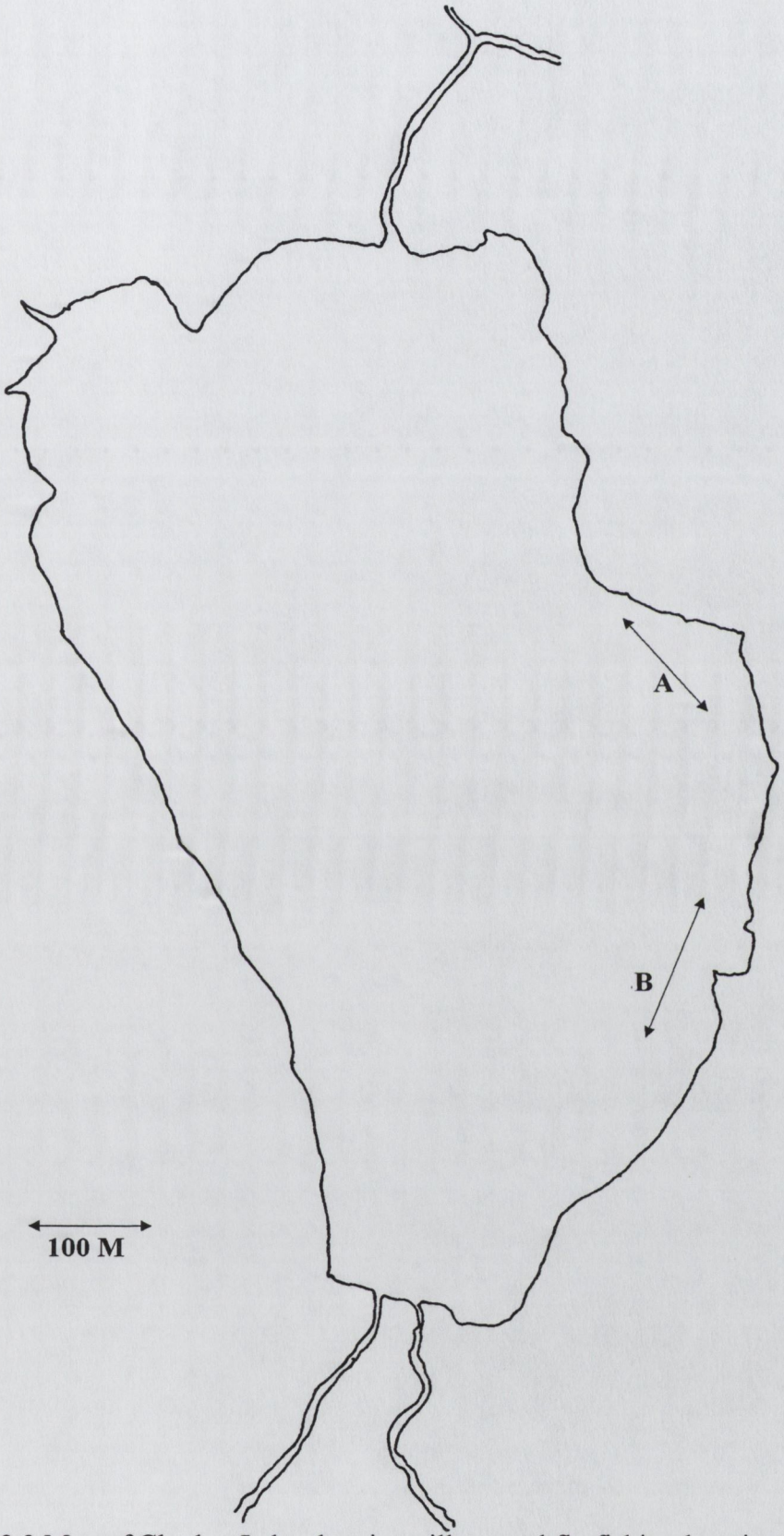

Figure 2.3 Map of Clogher Lake showing gill net and fly fishing locations (A, B).

2.3 Methods of fish capture

2.3.1 Lough Feeagh

Beach Seine Netting

Two methods were used to capture trout in Lough Feeagh, beach seine netting and fish traps. Beach Seine netting was carried out on seven occasions on Lough Feeagh between April 1997 and November 1998, and on one occasion on Bunaveela Lake in August 1998. Netting sites were generally slightly sloping sandy, silty bays, which were generally free from submerged obstructions such as boulders and tree stumps. Certain areas of the shoreline could not be sampled owing to repeated snagging of the net on submerged obstructions. Two nets were used over the course of the sampling program.

The first net (60m long x 3m deep) was constructed from 9mm half-mesh knotless nylon with 10m towlines attached at either end. The top rope had floats fitted at 1m intervals; the bottom rope was nylon with 0.5kg m^{-1} lead line. The second net (80m long by 3m deep) was constructed of 18mm knotless nylon with 10m towlines attached at either end. The top rope had floats at .75m intervals and an orange trawl float at the mid-point. The bottom rope was nylon with 0.5kg m^{-1} lead line. A holding bag 2.5m high, 2m wide and 2m long was fitted at the centre of this net.

The net was set by fixing a towline onshore, and allowing the net to unfurl over the transom of a lake boat which was rowed in a semi-circle around the targeted fish. Both towlines were then hauled simultaneously, drawing the net into a circle. The net was hauled in slowly, to allow water to pass through the mesh, and to prevent the lead line from rising off the lake bottom. When the net was near shore, the bottom lines were also pulled, drawing the net in under the fish and directing them back into the bag located in the central part of the net. Netted fish were measured (fork length), and examined for the presence of tags. The same procedure was used for both nets.

Fish Traps

Full upstream and downstream traps are present on Lough Feeagh. One set of traps (upstream and downstream) were located at the Millrace, and the other set at the Salmon Leap (see Fig 2.1). Migrating fish were channelled from the main water body into the holding tank associated with each trap. Holding tanks were examined on a daily basis, and a record was kept of all fish caught. In this way samples of downstream migrating trout smolts, both wild and stocked were obtained. A record was kept of all stocked trout that migrated downstream, and those which subsequently returned.

2.3.2 Clogher Lake

This lake is owned and managed by the Western Regional Fisheries Board as a wild trout fishery. Fishing on the lake is only permitted during open season, which runs from April to October, and during the fishing season all fish must be caught by fly-fishing. Special permission was obtained from the fisheries board to set gill nets in the lake on 3 occasions during the closed seasons of 1997/98 and 1998/99.

Gill Netting

A gill net is a single wall of webbing held vertically in the water by floats at the top and weights at the bottom. The net was composed of panels of light monofilament mesh with a 1" stretch diameter. The net was floated in shallow water, from the surface to 3m deep, parallel to the shore, approximately 50m offshore. In all cases the net was set parallel to a reed bed which was considered a refuge for fish. Initially the net was checked after four hours, however with no success after that length of time it was decided to leave the net overnight to optimise the catch.

Fly Fishing

All other samples from Clogher Lake could only be taken by rod fly-fishing.

In all cases for Clogher lake and for Lough Feeagh tests for selectivity between fishing methods were performed, however in no case were significant differences between fishing methods found to exist.

2.4 Sampling Protocol

2.4.1 Lough Feeagh

During 1997 samples of wild fish were taken on four occasions and samples of stocked fish were taken on three occasions (Table 2.1). Wild and stocked fish were taken in May, August and November, only wild fish were taken in April. It was not possible to take any wild fish in April 1998 as a result of the high water level in Lough Feeagh, due to unseasonable rainfall.

Samples were taken in so far as possible to reflect seasonal differences and also as a function of fish availability. Previous experience in Lough Feeagh has shown that sampling in January or February is unproductive and yields very few fish. Sampling in December was also inappropriate as many fish were in breeding condition and either had migrated, or were in the process of, migrating up the tributaries of the lake to spawning grounds. For these reasons November was considered as the winter sample. August was considered as the summer sample, and May was considered as the spring sample.

Stocked fish were put into Lough Feeagh early in April of 1997 and late in March of 1998, consequently the first samples of stocked fish for parasitological purposes were not taken until May, to allow the parasite community to develop. Further samples of stocked fish were taken in August and November of 1997 and 1998 (Table 2.1).

2.4.2 Clogher Lake

The lake is located in a separate catchment to Lough Feeagh and contains only wild trout. All samples were taken to reflect seasonal differences and also to mirror the

samples taken in Lough Feeagh. Samples were taken in April, May, August and November (Table 2.1). It was not possible to gill net fish for the November sample in 1998, consequently there is only one winter sample of wild trout in Clogher Lake. To compensate, an extra sample was taken in February of 1999, however when the data from this sample were examined it was considered more appropriate to include it with the April samples from 1997 and 1998 rather than the November sample from 1997.

Table 2.1 Sample details for wild and stocked trout in Lough Feeagh, and wild trout in Clogher Lake in 1997, 1998 and 1999.

Clogher Lake				
Wild trout	April	May	August	November
1997	21	17	21	31
1998	30	22	7	-
1999	12	-	-	-
Totals	**63**	**39**	**28**	**31**
Lough Feeagh				
Stocked trout	**April**	May	August	November
1997	-	21	15	25
1998	-	26	10	25
Totals		**47**	**25**	**50**
Lough Feeagh				
Wild trout	April	May	August	November
1997	60	32	56	14
1998	-	32	32	31
Totals	**60**	**64**	**88**	**45**

2.4.3 Combining Samples

After visual examination of the sample data it was decided to statistically test for any differences in the abundance in parasite species between years. If only minor differences were found to exist, samples from both years were combined. Analysis of variance was performed on log (x+1) transformed data for species abundance. Results are reported in Tables 2.2-2.4 for wild trout in Lough Feeagh, stocked trout in Lough Feeagh and wild trout in Clogher Lake. On the basis of the statistical results and

visual examination of the parasite data it was decided to combine all samples for both years.

Table 2.2 One-way analysis of variance (ANOVA) on log (x+1) transformed species abundance data for wild trout for each month from Lough Feeagh, (1997 / 1998).

Lough Feeagh Wild Trout	Species significantly different between years	F- Ratio	P- value
May	*S. salmoneus*	4.55	0.006
	Crepidostomum farionis	2.10	0.019
August	*D. sagittata*	4.83	0.002
November	*E. crassum*	4.80	0.0003
	D. ditremum	2.93	0.011

Table 2.3 One-way analysis of variance (ANOVA) on log (x+1) transformed species abundance data for stocked trout for each month from Lough Feeagh, (1997 / 1998).

Lough Feeagh Stocked Trout	Species significantly different between years	F- Ratio	P- value
May	All non-significant	~	~
August	*D. sagittata*	4.20	0.018
November	*D. sagittata*	3.22	0.021

Table 2.4 One-way analysis of variance (ANOVA) on log (x+1) transformed species abundance data for wild trout for each month from Clogher Lake, (1997 / 1998 / 1999).

Clogher Lake Wild Trout	Species significantly different between years	F- Ratio	P- value
April	*Rhabdochona* sp.	5.62	0.006
	D. dendriticum	7.22	0.002
May	*Crepidostomum farionis*	5.79	0.021
August	*Rhabdochona* sp.	3.75	0.038
	E. crassum	4.83	0.037

2.5 Post catching procedures

Fish captured in Lough Feeagh and Bunaveela Lake were transported back to the laboratory alive, except for the few fish that died from stress during transportation. This was not possible for Clogher Lake. Rod caught fish from Clogher Lake were kept under ice in a freezer box, and transported back to the laboratory as soon as possible after catching, which was not more than four hours. Fish caught by gill netting, spent a maximum of 20 hours "caught" before being transported back to the laboratory under ice.

Once in the laboratory all fish were measured (fork length ± 0.1cm) and weighed (± 0.1g). Scales were removed from all wild fish for ageing. Scales were removed from some stocked fish of known age, for validation purposes. All fish were photographed in a standard manner for morphometric analyses. Only wild and stocked one-year-old fish from Lough Feeagh were stomach flushed for dietary analyses. Fish were individually labelled, bagged and frozen. Fish from Lough Feeagh were killed using an excess of anaesthetic immediately prior to processing, and frozen immediately after processing. Fish from Lough Feeagh, which died during transportation were always processed first. Fish from Clogher Lake were kept on ice prior to processing and frozen immediately afterwards.

2.5.1 Ageing

Scales were mounted on a glass slide and covered. To improve clarity a drop of water was drawn under the coverslip before examination. The slide was placed in a microfiche reader, from this it was possible to examine the annuli and thus, age the fish. Back calculation techniques using the direct proportion method of LeCren (1947) which assumed a direct relationship between the radius of scale annuli and fish length, were used to determine the past growth of fish.

2.5.2 Dietary Analysis

Stomach contents of wild and stocked one-year-old trout were flushed out using a modified Seaburg (1957) stomach sampler. The fish was held facing downwards and a narrow plastic tube was inserted into its stomach. Water was pumped into the stomach, causing stomach contents to be evacuated. Stomach contents were preserved in 70% alcohol. Stomach contents were examined under a binocular microscope and all food items were identified as near as possible to the family level. Excess alcohol was removed and stomach contents were oven dried at 50°C for 24 hours, then weighed on an electronic balance (± 0.1mg).

2.5.3 Morphometric Analyses

Fish were laid out on a white board with the tail fin spread, where necessary slips of white paper were placed under fins to highlight them. A standard scale ruler was included, fish were numbered and then photographed using a tripod mounted Minolta Maxxum 35mm camera with a camera mounted flash. All fish were photographed in this manner. Photographs were digitised using a computer graphics tablet. From each photograph 34 landmark co-ordinates both conventional and truss measurements were recorded. Measurements were entered into a spreadsheet for further analysis.

2.6 Parasitological Examination

Fish were defrosted at room temperature and the general condition of the fish and any external lesions were noted. 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. Parasites were assigned a percentage location, with 0% corresponding to the anterior oesophagus and 100% corresponding to the anus.

The gut was initially rinsed with 0.9% saline, which was kept and separately examined for parasites. It was then systematically examined under the binocular microscope for the presence of parasites. Gills were individually removed from each fish, washed in saline and examined for parasites. Eyes were removed before fish were frozen and examined for the presence of eye flukes, which were treated according to the procedure of Shigin (1986).

The liver, spleen, heart, gonads and swim bladder were all removed and examined for parasites. The body cavity was examined to detect any parasites, which might be encysted there. Gonads, where present, were used to determine the sex of the fish. In females the ovaries were orange in colour and granular in appearance, as a result of eggs. In males the testis were a white colour and smooth in appearance. It was not possible to sex some juveniles as the gonads were not sufficiently well developed.

2.6.1 Treatment of Parasites

All parasites recovered were fixed in 10% formalin solution. Acanthocephalans were first placed in tap water for 24 hours to evert the proboscis. 24 to 48 hours after fixation, parasites were washed in 70% ethanol, and then transferred to fresh 70% ethanol with 4% glycerol for long term storage. Parasites were stored in sealed labeled glass tubes. A separate written record was kept of the number of parasites found and percentage locations of parasites occurring in the intestine.

2.6.2 Parasite Identification

Cestoda

Larval and adult parasites were examined under the binocular microscope where the three dimensional structure of the scolex could be clearly seen. Parasites were identified using the key by Chubb *et al.* (1987).

Acanthocephala

Temporary mounts of the parasite were prepared. Using a stage microscope the number of rows of hooks on the parasite's proboscis, and the number of hooks in each row were counted. From this, and the key by Brown (1986) it was possible to identify the parasite to species. Where necessary parasites were cleared in lactophenol, stained with Meyer's acid carmine, and differentiated in acid alcohol (4% hydrochloric acid and 70% ethanol).

Digenea

Parasites were cleared in lactophenol to facilitate examination of their internal structures. Temporary parasite mounts were prepared and examined under a stage microscope. Parasites were then identified using descriptions given by Dawes (1946).

Monogenea

As worms were quite large, examination under a binocular microscope was sufficient for identification. Descriptions given by Dawes (1946) were used for identification. In some cases worms were first cleared in lactophenol to facilitate examination of internal organs.

Copepoda

Copepods were examined under the binocular microscope and identified using the keys of Kabata (1969, 1979) and Fryer (1982).

Nematoda

All nematodes were initially cleared in lactophenol, and subsequently examined as temporary microscopic preparations in glycerine. For nematodes, effective clearing is essential, to allow for examination of the internal organs which are important for identification. Nematodes were identified using the descriptions provided by Moravec (1995).

2.6.3 Eye Fluke Procedure

A total of 99 fish were examined for the presence of eye flukes, 71 from Lough Feeagh and 28 from Bunaveela Lake. Due to time constraints it was not possible to examine any fish from Clogher Lake for the presence of eye flukes. In most cases it was not possible to examine eyes immediately after removal from the fish, so they were refrigerated at 4^{0}C. A maximum of three days elapsed before examination.

Eyes were incised under a binocular microscope and the lens capsule and vitreous humour were removed for examination. Once found, flukes were removed from the eye tissue and killed by immersion in tap water. The location of flukes within the eye, on the lens capsule or in the vitreous humour was noted. When all flukes were dead, tap water was replaced with acetic carmine stain. Flukes were immersed in acetic carmine until all had "taken up" the stain. The acetic carmine was removed and flukes were differentiated for a short period in acid alcohol. Flukes were then put through a dehydration series starting with 70% ethanol up to 80%, 90% and finally 95% ethanol (the clearing agent does not require absolute alcohol).

Flukes were placed into a small vial half full of 95% ethanol. An equal volume of the clearing agent dimethylphalate (DMP), which is denser than ethanol, was run down the side of the vial and deposited under the ethanol. Flukes align at the interface, and over the course of an hour, fall to the bottom of the vial. When all flukes have fallen, most of the liquid can be removed. Flukes were then placed dorsal side down on a glass slide, within a circle of Canada balsam. Excess DMP was drained away, and a

drop of "runny" Canada balsam was placed on each fluke, where necessary slides were gently heated on a hot plate. The orientation of the fluke was checked under a microscope. A coverslip was placed on the slide, bubbles were excluded by gentle heating. Slides were left to dry naturally. Once mounted flukes could be identified using the key of Shigin (1986).

2.6.4 Reproductive Status of Acanthocephalans

Parasites were removed from 70% alcohol, blotted on adsorbent tissue paper to remove excess moisture, and weighed on a Mettler-Toledo AG245 balance (± 0.001mg). For some *P. laevis* specimens, as a result of encapsulation by the host fish, it was necessary to dissect host intestinal tissue from the parasite proboscis prior weighing. Parasites were measured to the nearest millimetre using electronic callipers.

Worms were placed on a glass slide, flooded with saline (0.9%) and cut in half, where the contents of the body cavity were released. In females the single ligament sac containing the reproductive structures disintegrates once the ovary fragments, allowing eggs and ovarian balls float free of the body cavity. Where necessary contents of the body cavity were squeezed out using a fine forceps.

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. 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. Elaine O' Mahony weighed, measured sexed and staged the *P. laevis* worms (see acknowledgements).

All *A. clavula* recorded in this study have been fixed, preserved and retained for further examination. At some point in the near future, the size and population biology

A. clavula from Clogher Lake and from Lough Feeagh will be assessed in the same manner as was done for *P. laevis*.

2.7 Data Analysis

A range of descriptive statistics and analyses were used to examine the parasite data presented in this thesis. Analyses will be dealt with in sequential order.

2.7.1 Component community

For the component community, prevalence, mean abundance, mean intensity, variance to mean ratio and range values were presented for each parasite species. All terms were used in accordance with the definitions set out by Bush *et al.* (1997).

Prevalence

Prevalence is the number of hosts infected with one or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined for that parasite species. In this study prevalence values were expressed as percentages.

Mean abundance

Mean abundance is the total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of hosts of that species examined (including both infected and uninfected hosts). In all cases mean abundance values were reported in association with the standard deviation.

Mean intensity

Mean intensity is the average intensity of a particular species of parasite among infected members of a particular host species. Similar to the mean abundance values, in all cases mean intensity values were also reported in association with the standard deviation.

Variance to mean ratio

The variance to mean ratio was used to assess the aggregation of parasite numbers (Anderson and Gordon, 1982). A variance to mean ratio >1 implies overdispersion, a variance to mean ratio equal to one implies a random distribution and a variance to mean ratio <1 implies underdispersion of the data.

Range

The range was the difference between the minimum number of parasites recorded and the maximum number of parasites recorded.

Component Species

This term refers to any species which has a prevalence value of 10% or more. The term was used by Bush *et al.* (1997) as a means of arbitrarily dividing parasite communities into species which are not likely to have any effect on community structure (prevalence less than 10%) and those which are likely to have an effect on community structure (prevalence greater than 10%).

2.7.2 Infracommunity

As well as descriptive statistics, a number of ecological indices were used to describe parasite infracommunities in this thesis. All ecological indices were calculated according to the methodology described by Magurran (1988).

Mean species richness

The mean species richness was the total number of parasite species in/on each host in a sample divided by the total number of hosts (including uninfected hosts) in that sample. In all cases the mean species richness value was presented in association with the standard deviation.

Mean number of individuals

The mean number of individual parasites was the total number of individual parasites recorded in a sample divided by the number of hosts (including uninfected hosts) in that sample. Similarly, in all cases the mean number of individuals value was presented in association with the standard deviation.

Brillouin's index of diversity

This is a diversity index which is most appropriately used when the diversity of non-random samples or collections are being estimated. The Brillouin's index of diversity is used frequently in parasitological studies, where parasite communities have been completely censused. The parasites living on/in a single fish host represent a fully censused community. The index is calculated in the following manner:

$$HB = (\ln N! - \Sigma \ln n!) / N$$

Simpson's dominance index

This is an index which is weighted towards the abundances of the commonest species, rather than providing a measure of species richness. The Simpson's dominance index gives the probability of any two individuals drawn at random from an infinitely large community belonging to different species. The reciprocal form of Simpson's dominance index (1/D) is normally adopted. This ensures that the value of the index increased with increasing diversity. The index is calculated in the following manner:

$$D = \Sigma((n_i (n_i-1)) / (N(N-1)))$$

Berger-Parker index

The Berger-Parker index is also a dominance measure, it expresses the proportional abundance of the most important species. As with the Simpson's dominance index the reciprocal form of the Berger-Parker index (1/d) is normally adopted so that an

increase in the value of the index accompanies an increase in diversity and a reduction in dominance. The index is calculated in the following manner:

$$d = N_{max} / N$$

Shannon diversity index

This is a diversity index which assumes that individuals are randomly sampled from an infinitely large (that is effectively infinite) population. The index also assumes that all species are represented in the sample. The formula for the Shannon diversity index commences with a minus to cancel out the negative created by taking logs of proportions. Thus the index is calculated in the following manner:

$$H` = -\Sigma p_i \ln p_i$$

2.7.3 Analysis of Variance (ANOVA)

In this thesis one, two and three-way analyses of variance (ANOVA) were used to assess the significance of a given factor or factors on the measurement of a particular dependant variable. One-way analyses of variance (ANOVA) were used to assess the significance of the contribution of a single factor to the difference in variance observed between the mean of a number of samples. Similarly, two-way analyses of variance were used to assess the contribution of two factors and three-way analyses were used to assess the contribution of three factors to the differences in variance observed between the means of a number of samples. For all one-way analyses performed, post hoc tests were used to examine the differences between individual means. In all cases least squares difference post hoc tests were used, and results were only presented when significant. For two and three-way analyses of variance the interactions between individual factors were also assessed, again results for interactions were only presented when significant.

2.7.4 Contingency tables

Contingency tables were used on a number of occasions to examine the relationships between factors and frequencies of occurrence. However, when the mean intensities of the four most common parasite species in Lough Feeagh and the three most common parasite species in Clogher Lake were examined, the main assumption of the chi-squared test statistic, that the value in any individual cell should not fall below five, was violated. Thus, for these samples Fisher's exact test, which was not subject to any requirement for cell size, was used. This test could only be used on 2 x 2 contingency tables. Contingency tables were also used to compare the proportions of female *P. laevis* of stage I and II maturity between wild and stocked trout, and to compare the proportions of female *P. laevis* of stage I, II and III maturity occurring in single and concurrent infections with *A. clavula*.

2.7.5 Kendall's tau

The Kendall's tau correlation coefficient was used to examine the relationships in abundance between all possible combinations of species pairs in Clogher Lake, and for wild and stocked trout in Lough Feeagh. Kendall's tau (τ) is a non-parametric measure of association. The values of the correlation coefficient range from +1.0 to –1.0. A value near +1.0 indicates that as one variable increases the other variable increases in a similar fashion. A correlation coefficient near –1.0 indicates that as one variable increases the other variable decreases. If the correlation coefficient is low or close to zero, the two variables have little correlation.

2.7.6 Niches

Summary statistics

The distributions of four species (*P. laevis*, *A. clavula*, *Crepidostomum farionis* and *E. crassum*) along the length of the intestine in trout were examined in some detail. There was a particular focus on the distribution of *P. laevis* in Lough Feeagh. In all cases when distributions were examined a set of summary statistics were provided. Summary statistics provided a count of the number of individual worms examined

and the mean and median position values, (the mean position value was always presented in association with the standard deviation). In some cases due to the large number of parasites present, it was not possible to record an exact position along the intestine for each individual parasite. In such cases the number of individuals occurring along a specified length of the intestine was recorded. For the analysis of species distributions and for the construction of frequency histograms the midpoint of the specified range along the intestine was used. Thus, if 100 *Crepidostomum farionis* worms were recorded between the 50% and 60% locations of the intestine, for analysis and the construction of frequency histograms the mid-point, 55%, was used.

Summary statistics provided the lower (25%), upper (75%) quartile values and the interquartile range as well as the minimum and maximum location values of the parasite species along the intestine and the range of occurrence of that species along the intestine of trout. Finally the summary statistics also provided a measure of the skewness and kurtosis of the distribution.

Skewness is a measure of the asymmetry of a distribution about its mean. Positive skewness is indicative of a distribution with an asymmetric tail extending towards more positive values, and negative skewness is indicative of a distribution with an asymmetric tail extending towards more negative values. Kurtosis was used to characterise the relative peakedness or flatness of a distribution compared with the normal distribution. Negative kurtosis indicates a relatively flat distribution and positive kurtosis indicates a relatively peaked distribution.

Frequency Histograms

In all cases frequency histograms summarising the distributions of each species in a graphical manner, were presented. Frequency histograms were calculated by dividing the intestine into a number of discrete sections and recording the number of parasite individuals occurring in each section. In this study the intestine was divided into 50 discrete sections. Thus, the 24-25% section included all parasites recorded between

the 24% and 25.99% locations along the intestine, similarly the 26-27% section included all parasites recorded between the 26% and 27.99% locations along the intestine.

Niche width

The niche width values were calculated for the three species examined from Clogher Lake and for the four species examined from Lough Feeagh. Niche width values were calculated for each sample month and for the total sample, and for the parasite in low, medium and high intensity infections. Values were calculated using Culver's (1972) standardised Shannon-Wiener function, H'. This function describes the evenness of the distribution of a parasite along the intestine of its host. The function ranges 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.

Niche overlaps

The niche overlap values were calculated for each species pair of the three most prevalent intestinal species in Clogher Lake and of the four most prevalent intestinal species in wild and stocked trout in Lough Feeagh. Values were calculated according to the Morisita-Horn measure (Magurran, 1988), a quantitative similarity index. The main advantage of this index is that it is not strongly influenced by species richness and sample size, however it is sensitive to the intensity of the most abundant species. Values for the index fall between zero and one. When there is complete similarity, i.e. when the distributions of two species are identical, the index gives a value of one, and where the distributions of the two species are totally dissimilar and have no overlap the index gives a value of zero.

Chapter 3

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3.1 Organisation of chapter three

The component parasite community of wild trout in Clogher Lake was examined for each sample month (both sample years were combined). Component community parameters for the four most prevalent species (*Acanthocephalus clavula*, *Crepidostomum farionis*, *Eubothrium crassum*, *Diphyllobothrium ditremum*) were subsequently examined and finally summary characteristics for the component community were presented.

In the following section the abundance of the four most prevalent species were statistically examined in relation to the month and year of host capture, sex and age of the host fish. The parasite community was then examined at the infracommunity level. Firstly, the infracommunities of all parasites of trout in Clogher Lake were examined by sample month, and then in a similar manner the infracommunities of only the intestinal parasites in trout in Clogher Lake were examined by sample month.

The relationships in abundance of the three most prevalent intestinal species (*A. clavula*, *Crepidostomum farionis*, *E. crassum*) were examined using contingency tables. Kendall's tau correlation coefficient was used to examine relationships in abundance between all parasite species in Clogher Lake.

The intestinal distributions of *A. clavula*, *Crepidostomum farionis* and *E. crassum* were examined for the total sample and for each sample month. Frequency histograms showing the distribution of the parasite along the intestine, for the total sample and for each sample month have been provided for each of the three species. Accompanying each frequency histogram is a set of statistics summarising the distribution of that species. The distribution of each species was also examined when it occurred at low, medium and high intensity, and a set of summary statistics was provided in each case.

The Morisita-Horn quantitative similarity index was used to calculate the total niche overlap and niche overlap for each sample month for the three intestinal species. Finally the distribution of each (of the three intestinal) species was examined when it occurred at low, medium and high intensities of another species. Four combinations were examined, *E. crassum* at low, medium and high intensities of *A. clavula*. *A. clavula* at low medium and high intensities of *E. crassum* and *Crepidostomum farionis* at low, medium and high intensities of *A. clavula* and *E. crassum*. In all cases a set of statistics summarising the distributions of each of the three species along the intestine of trout have been provided.

3.2 Helminth component community in wild trout in Clogher Lake (1997 / 1998)

3.2.1 Examination of component community data for all wild trout in Clogher Lake

A total of nine parasite species were recorded in wild brown trout in Clogher Lake (Table 3.1). Three cestode species (*E. crassum*, *D. ditremum*, *Diphyllobothrium dendriticum*), two nematodes identified to genus level (*Anisakis* sp., *Rhabdochona* sp.), one acanthocephalan species (*A. clavula*), one digenean species (*Crepidostomum farionis*), one monogenean species (*Discocotyle sagittata*) and one copepod (*Salmincola salmoneus*).

Two cestodes, *D. ditremum*, *D. dendriticum* and one nematode *Anisakis* sp. were allogenic, and only occurred as larval forms in brown trout. The remaining parasite species were autogenic and occurred as adults in brown trout (Table 3.1). Five parasite species, *E. crassum*, *Crepidostomum farionis*, *A. clavula*, *D. ditremum* and *S. salmoneus* were component, the remaining four species were not. *A. clavula* had the highest component community values for prevalence, mean abundance, mean intensity.

3.2.2 Examination of component community data by month

The component parasite community of wild brown trout in Clogher Lake was examined by sample month for both years combined, and trends for the four most prevalent parasite species are also discussed. For this section results are presented in Tables 3.2-3.5 for each month (April, May, August and November). The prevalence, mean abundance and mean intensity of the four most prevalent species, *E. crassum*, *Crepidostomum farionis*, *A. clavula* and *D. ditremum* in wild trout in Clogher Lake are presented in Figure 3.1.

Prevalence

The highest values for all community parameters were recorded in November. *A. clavula* had the highest prevalence, mean abundance and mean intensity values (Fig

3.1). *D. sagittata* and *D. dendriticum* were only recorded in April and *Anisakis* sp. was only recorded in November. *Rhabdochona* sp. was absent in November.

Component Species

With the exception of *D. sagittata*, *D. dendriticum*, *Anisakis* sp., and *Rhabdochona* sp. all other species recorded in Clogher Lake were component species. *Rhabdochona* sp. was the only non-component species, which was recorded in more than one month. All remaining parasite species were component in all months. Six component species occurred in April, five in May, August and November.

Mean Abundance and Mean Intensity

A. clavula had the highest mean abundance and mean intensity in April, May, and November. *Crepidostomum farionis* had the highest mean abundance and mean intensity in August (Fig 3.1). Two species (one of which, was always *S. salmoneus*) had mean abundance values below one in all months. Three species (two of which, were always *E. crassum* and *S. salmoneus*) had mean intensity values below five in all months.

3.2.3 Examination of component community data for the four most prevalent species

E. crassum

No pattern was apparent for the community parameters of *E. crassum*. Prevalence was highest in April, lowest in May. Mean abundance values were similar in April and May, and decreased from August to November. Mean intensity and range values decreased from their peak in May to their lowest point in November (Fig 3.1).

Crepidostomum farionis

Prevalence of *Crepidostomum farionis* increased from August through November to a peak in April, and decreased again in May. The same pattern was observed for mean abundance and mean intensity values. Values for the range were lowest in August and highest in November.

A. clavula

All community parameters for *A. clavula* were highest in November, and decreased from April to August, except for prevalence, which was higher in May than April.

D. ditremum

Prevalence of *D. ditremum* rose from May to a peak in November, and decreased in April. All other community parameters were highest in April, decreased from May to August, and increased again in November.

3.2.4 Summary characteristics of the component community

The summary characteristics for the component community of wild trout in Clogher Lake are reported in Table 3.6. All months except April had 100% parasite infection. The component community of brown trout in Clogher Lake contained eight parasite species in April, and six parasite species in each of the three remaining months.

The total number of parasite individuals was highest in April, lowest in August and increased again in November. When corrected for sample size, November had the highest number of parasite individuals per fish, this decreased in April and May to its lowest in August.

November had the lowest number of autogenic species, April had the highest and May and August had an intermediate number. April and November had two allogenic species, May and August only had one. April had six component species; all other months had five. Six species recorded were considered as specialists of trout in Ireland.

The digenean *Crepidostomum farionis* dominated in August, and the acanthocephalan *A. clavula* dominated in the remaining months. The proportional abundance (*P*i) values varied between the months. Just under half of the total number of parasite species were accounted for by the dominant species in April, and over three-quarters of parasite individuals were accounted for by the dominant species in November. The

dominant species was an autogenic generalist parasite of trout in April, May and November and an autogenic specialist parasite of trout in August.

3.3 Statistical examination of the four most prevalent species in Clogher Lake

One-way analysis of variance (ANOVA) was used to examine the relationship between the abundance of the four most prevalent parasite species in Clogher Lake (*A. clavula*, *Crepidostomum farionis*, *E. crassum*, *D. ditremum*), the month and year of capture, sex of host fish and age of host fish. In all cases parasite abundance data was overdispersed, so all analyses were done on log (x+1) transformed data. In all cases only significant relationships have been shown.

3.3.1 Month and year of host capture

When the total fish sample was examined by month, significant differences were found in the abundance of *A. clavula* (F ratio = 19.0; df =3,157; $p \leq 0.001$) and *Crepidostomum farionis* (F ratio = 4.5; df = 3,157; $p \leq 0.005$). The mean abundance of *A. clavula* ranged from 95.19(± 125.4) in November to 6.64(± 13.7) in August, for *Crepidostomum farionis* the mean abundance ranged from 47.57(± 82.5) in April to 17.64(± 26.6) in August. The total fish sample was then divided by year, and examined by month. *A. clavula* was the only species which showed significant differences between months in 1997 (F ratio = 11.6; df = 3,86; $p \leq 0.0001$), and in 1998 (F ratio = 14.0; df = 2,68; $p \leq 0.0001$).

The abundance of the four parasite species in each sample month was compared between the two sample years. No significant difference in abundance was found for any of the species between the April 1997 and 1998 samples. The abundance of *Crepidostomum farionis* differed significantly between May 1997 and May 1998 (F ratio = 5.8; df = 1,37; p = 0.021), and the abundance of *E. crassum* differed significantly between August 1997 and August 1998 (F ratio = 4.8; df = 1,26; p = 0.037). For both *Crepidostomum farionis* and *E. crassum* mean abundance values

were higher in 1998. As there was only a November sample in 1997, it was not possible to compare between years.

3.3.2 Sex of host fish

When the relationship between the abundance of the four most prevalent species and the sex of the host fish was examined, no significant differences were found. Regardless of how the samples were divided, either by year or month, or by year and month no significant differences were reported in the abundance of the four species between male and female fish.

3.3.3 Age of host fish

The relationship between the age of host fish and the abundance of the four common species in Clogher Lake was also examined. The majority (91%) of fish sampled from Clogher Lake were from one to three years old, of the remaining fifteen fish, thirteen were four years old and two were five years old. For the total fish sample a significant relationship between age and the abundance of *Crepidostomum farionis* (F ratio = 3.0; df = 4,155; p = 0.012), and *D. ditremum* (F ratio = 4.9; df = 4,155; $p \leq 0.0003$) existed. In both cases the mean abundance increased with age. The mean abundance of *Crepidostomum farionis* was 19.45(± 32.27) in one year old fish and 62.21(± 123.86) in four old fish, the mean abundance of *D. ditremum* was 0.3(±1.04) in one year old fish and 10.64(±16.33) in four year old fish. When the relationship between age and abundance was examined by month for the total fish sample, a significant relationship was found for *D. ditremum* in April (F ratio = 8.4; df = 4,58; $p \leq 0.0001$) and May (F ratio = 3.0; df = 3,35; p = 0.0429). In November a significant relationship between age and the abundance of *Crepidostomum farionis* (F ratio = 6.1; df = 2,27; $p \leq 0.003$) was found.

The relationship between the abundance of the four parasite species and age was examined by year and by sample month within each year. A significant relationship between the abundance of *Crepidostomum farionis* and age was found for the total sample (F ratio = 4.0; df = 4,85; $p \leq 0.005$), the April (F ratio = 7.6; df = 4,19; p =

0.013) and November (F ratio = 6.1; df = 2,27; $p \leq 0.003$) samples in 1997. The abundance of *D. ditremum* was also significantly related to age in the May 1997 sample (F ratio = 4.8; df = 3,13; p = 0.019).

In 1998 the abundance of *D. ditremum* was significantly related to age for the total sample (F ratio = 5.0; df = 4,66; $p \leq 0.002$) and for the April sample (F ratio = 6.0; df = 4,37; $p \leq 0.001$). There was no significant relationships between the abundance of any of the four parasite species and age in May or August 1998.

In all cases the relationship between age and the abundance of *Crepidostomum farionis* and *D. ditremum* was a positive relationship, as age increased the abundance of both *Crepidostomum farionis* and *D. ditremum* increased. However, despite the fact that in many cases there were significant differences in the abundance of *Crepidostomum farionis* between fish of different ages, examination of raw data would suggest that these statistically significant differences do not have much biological significance. In most cases the differences were caused by the presence of one, or a few heavily infected individuals. Also, because of the relatively large sample sizes used in these analyses in many cases the smallest biological differences became statistically significantly different.

Table 3.1 Component Population data for all wild trout in Clogher Lake (1997 – 1998, $n = 161$).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	57.14	2.12(4)	3.71(3.8)	0 - 23	11.52
Crepidostomum farionis	IN	77.02	32.79(74.2)	56.54(91.4)	0 - 528	5506.8
Acanthocephalus clavula	IN	86.33	53.19(82.3)	90.11(93.2)	0 - 422	6774.2
Diphyllobothrium ditremum	V	24.22	3.57(13.6)	14.74(24.8)	0 - 138	185.7
Rhabdochona sp.	IN	6.83	1.43(12)	20.91(43.1)	0 - 147	144.12
Anisakis sp.	IN	1.86	0.05(0.5)	2.66(2.9)	0 - 6	0.24
Discocotyle sagittata	G	1.24	0.01(0.1)	1(0)	0 -1	0.01
Salmincola salmoneus	G	19.88	0.33(0.8)	1.66(1.1)	0 - 5	0.65
Diphyllobothrium dendriticum	V	1.86	0.85(8.5)	45.67(52)	0 - 105	72.18

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 3.2 Component Population data for wild trout in Clogher Lake in April ($n = 63$).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	63.49	2.25(3.2)	3.55(3.4)	0 – 15	4.6
Crepidostomum farionis	IN	82.54	47.57(82.5)	57.63(87.6)	0 – 498	143.04
Acanthocephalus clavula	IN	93.65	58.24(77.5)	62.19(78.5)	0 – 338	103.05
Diphyllobothrium ditremum	V	23.8	5.15(19.3)	21.73(35.4)	0 – 138	71.98
Rhabdochona sp.	IN	12.69	3.52(19.1)	27.75(49.6)	0 – 147	103.36
Discocotyle sagittata	G	3.17	0.03(0.2)	1(0)	0 – 1	0.99
Salmincola salmoneus	G	15.87	0.30(0.9)	1.90(1.3)	0 – 4	2.42
Diphyllobothrium dendriticum	V	4.76	2.17(13.5)	45.66(52)	0 – 105	84.33

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 3.3 Component Population data for wild trout in Clogher Lake in May (n = 39).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	48.72	2.26(4.3)	4.63(5.2)	0 - 23	2.05
Crepidostomum farionis	IN	69.23	28(62.7)	40.44(72.2)	0 - 340	140.18
Acanthocephalus clavula	IN	94.87	45.07(55.2)	47.51(55.6)	0 - 246	67.54
Diphyllobothrium ditremum	V	12.82	2.38(9.7)	18.6(22.6)	0 - 57	39.22
Rhabdochona sp.	IN	2.56	0.13(0.8)	5(0)	0 - 5	5
Salmincola salmoneus	G	25.64	0.33(0.6)	1.30(0.5)	0 - 2	1.16

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 3.4 Component Population data for wild trout in Clogher Lake in August (n = 28).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	57.14	2.18(3.7)	3.81(4.2)	0 - 16	6.19
Crepidostomum farionis	IN	85.71	17.64(26.6)	20.58(27.7)	0 - 14	40.19
Acanthocephalus clavula	IN	42.86	6.64(13.7)	15.50(17.7)	0 - 63	28.42
Diphyllobothrium ditremum	V	28.57	1.46(0.3)	5.13(3.4)	0 - 12	5.79
Rhabdochona sp.	IN	7.14	0.11(0.4)	1.50(0.7)	0 - 2	1.62
Salmincola salmoneus	G	14.29	0.21(0.6)	1.50(0.6)	0 - 2	1.51

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 3.5 Component Population data for wild trout in Clogher Lake in November (n = 31).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	54.84	1.61(2.1)	2.94(2)	0 - 7	2.63
Crepidostomum farionis	IN	67.74	22.45(94.3)	33.14(113.8)	0 - 528	395.71
Acanthocephalus clavula	IN	100	95.19(125.4)	95.19(125.4)	1 - 422	165.1
Diphyllobothrium ditremum	V	35.48	3.71(9.3)	10.45(13.6)	0 - 37	23.53
Anisakis sp.	IN	9.68	0.26(1.1)	2.66(2.9)	0 - 6	4.64
Salmincola salmoneus	G	25.81	0.48(1.2)	1.88(1.6)	0 - 5	2.74

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 3.6 Component Population characteristics of wild trout in Clogher Lake.

Characteristics	April	May	August	November
No. of fish examined	63	39	28	31
Percentage infected	98.4	100	100	100
No. of parasite species	8	6	6	6
Total no. of parasites	7514	3049	791	3835
No. of autogenic sp.	6	5	5	4
No. of allogenic sp.	2	1	1	2
No. of component sp.	6	5	5	5
No. of specialists sp.	6	4	4	4
*P*i of dominant sp.	0.49	0.58	0.62	0.77
Identity of dominant sp.	*A. clavula*	*A. clavula*	*Crepidostomum farionis*	*A. clavula*
Character of dominant sp.	Generalist, autogenic	Generalist, autogenic	Specialist, autogenic	Generalist, autogenic

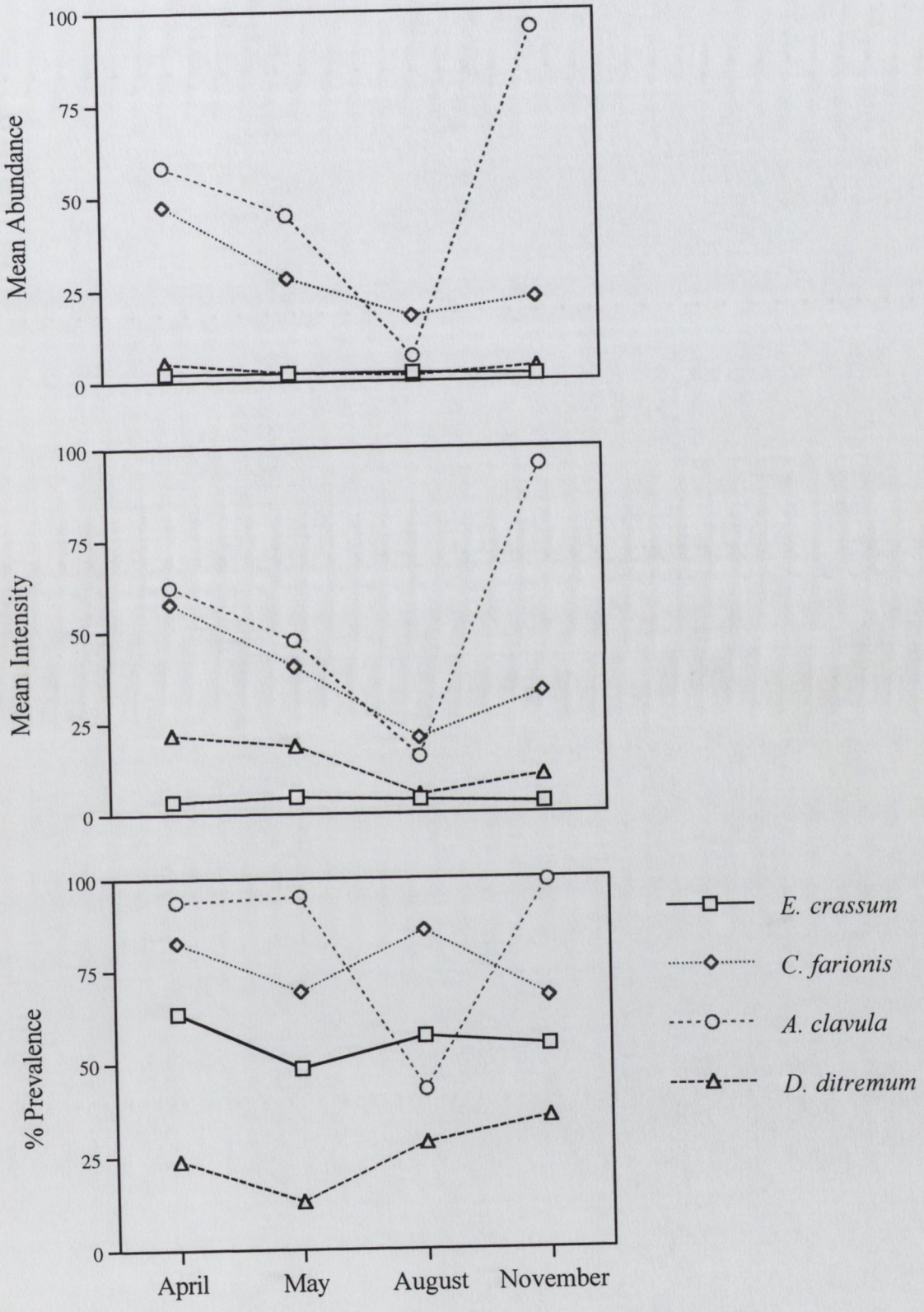

Fig 3.1 Prevalence, mean abundance and mean intensity of the four most common species in wild trout in Clogher Lake.

3.4 Helminth infracommunity in wild trout in Clogher Lake (1997/1998)

A total of 161 wild brown trout from Clogher Lake were examined, 63 fish were caught in April, 39 in May, 28 in August and 31 in November (Table 3.7). Mean species richness values ranged from 2.36 in August, the lowest value, to 3.0 in April, the highest value.

One-way analysis of variance (ANOVA) on log (x+1) transformed data for the number of parasite species per fish revealed significant differences in species richness between months (F ratio = 7.3; df = 3,157; $p = 0.04$). Least squares difference post hoc tests also revealed significant differences in the mean species richness between, April and May ($p = 0.043$), April and August ($p = 0.019$) and November and August ($p = 0.048$).

April was the only month in which uninfected fish occurred, in all other months at least one parasite species was recorded in each fish. The maximum number of species recorded decreased in the remaining months, with a maximum of six species recorded in May, and five in August and November (Table 3.7).

The highest mean number of parasite individuals was recorded in November and the lowest value was recorded in August (Table 3.7). One-way analysis of variance (ANOVA) on log (x+1) transformed data for the number of individual parasites per fish showed significant differences in the number of individuals between the months for the overall sample (F ratio = 7.7; df = 3,157; $p \leq 0.0001$). Least squares difference post hoc tests showed highly significant differences between the mean number of individuals occurring in August and in every other month, ($p \leq 0.0001$ in each case).

Brillouin's index of diversity was calculated for each month, and a similar pattern to that observed for the mean species richness was found, April had the highest index value and August had the lowest index value (Table 3.7). For a number of fish in each month it was not possible to calculate the index as a result of the large number of

parasite individuals, so a percentage of the most heavily infected fish had to be excluded from the calculations (Table 3.7). One-way analysis of variance showed no significant difference in the Brillouin's index between months for the overall sample (F ratio = 2.4; df = 3,127; p = 0.06). However, least squares difference post hoc tests show that there was a significant difference in the Brillouin's index between April and May (p = 0.02) and April and August (p = 0.02).

Three other indices were also calculated for each month and for the total sample, Simpson's dominance and Berger-Parker indices, which are dominance indices, and the Shannon diversity index (Table 3.7). The lowest values for both dominance indices and the highest value for the Shannon diversity index occurred in April. August had the next highest diversity value and the second lowest values for both dominance indices. November had the lowest diversity value, and also the highest value for the Simpson's dominance, however May had the highest value for the Berger-Parker index.

3.5 Helminth infracommunity of intestinal parasite species in wild trout in Clogher Lake (1997/1998)

The same suite of parameters used to examine the total parasite infracommunity in Clogher Lake was employed to examine the infracommunity of the intestinal parasite species. Mean species richness was highest in April and lowest in August (Table 3.8). One-way analysis of variance (ANOVA) on log (x+1) transformed data showed a significant difference in the intestinal parasite species richness between months (F ratio = 4.1; df = 3,157; $p \leq 0.007$) for the total sample. Least squares difference post hoc tests showed significant differences in the species richness between April and August ($p \leq 0.001$) and November and August ($p = 0.02$).

Fish uninfected with intestinal parasites occurred in April and August. The mean number of individuals recorded for each month was not substantially different from that reported for the total helminth infracommunity. November still had the highest mean number of individuals and August still had the lowest. One-way analysis of variance (ANOVA) on log (x+1) transformed data for the number of parasite individuals per fish showed significant differences between months (F ratio = 8.1; df = 3,157; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the number of parasite individuals per fish between August and every other month ($p \leq 0.0003$ in all cases).

Similar to the situation reported for the total helminth infracommunity April had the highest value for Brillouin's index, but the lowest value was reported in May (Table 3.8). One-way analysis of variance (ANOVA) showed a significant difference in the Brillouin's index between months for the total sample (F ratio = 4.1; df = 3,126; $p \leq 0.008$). Least squares difference post hoc tests showed significant differences in the Brillouin's index between April and May ($p = 0.01$), April and August ($p \leq 0.002$) and April and November ($p = 0.05$).

The Simpson's dominance, Berger-Parker and Shannon diversity indices were calculated for each month and for the total sample (Table 3.8). Results for the intestinal parasite infracommunity were comparable to those found for the total helminth infracommunity. November had the highest values for both dominance indices and the lowest values for the Shannon diversity index. April had the highest value for the Shannon diversity index and the lowest value for the Simpson's dominance index, but May had the lowest value for the Berger-Parker index (Table 3.8).

Table 3.7 Infracommunity parameters for all parasites of the total wild trout sample and monthly wild trout samples from Clogher Lake (1997-1998).

	Total Sample	April	May	August	November
Number examined	161	63	39	28	31
Mean sp. richness (± S.D.)	2.76(1.12)	3(1.91)	2.54(1.14)	2.36(0.87)	2.94(1.03)
Range	0 – 7	0 – 7	1 – 6	1 – 5	1 – 5
Mean no. individuals (± S.D.)	94.34(129.83)	119.27(139.8)	78.18(74.33)	28.25(36.58)	123.71(186.3)
Range	0 – 930	0 – 836	4 – 351	2 – 187	3 – 930
Brillouin's Index (± S.D.)	0.51(0.31)†	0.56(0.31)‡	0.43(0.32)β	0.35(0.28)ϕ	0.51(0.30)*f*
Simpson's Dominance Index (1/D)	0.44 (2.27)	0.40 (2.49)	0.46 (2.16)	0.45 (2.21)	0.63 (1.60)
Berger Parker Index (1/*d*)	0.74 (1.35)	0.71 (1.41)	0.82 (1.22)	0.76 (1.32)	0.80 (1.25)
Shannon Diversity Index	0.90	1.12	0.93	1.04	0.71

† *n* for Brillouins Index = 134; ‡ *n* for Brillouins Index = 47; β *n* for Brillouins Index = 36; ϕ *n* for Brillouins Index = 27; *f n* for Brillouins Index = 24.

Table 3.8 Infracommunity parameters for the intestinal parasites of the total wild trout sample and monthly wild trout samples from Clogher Lake (1997-1998).

	Total Sample	April	May	August	November
Number examined	161	63	39	28	31
Mean sp. richness (± S.D.)	2.31(0.82)	2.57(0.89)	2.15(0.67)	1.93(0.90)	2.32(0.60)
Range	0 – 5	0 – 5	1 – 4	0 – 4	1 – 3
Mean no. individuals (± S.D.)	90.43(128.09)	113.76(136.0)	75.46(74.10)	26.57(36.66)	119.52(187.2)
Range	0 – 930	0 – 836	4 - 351	0 – 187	3 – 930
Brillouin's Index (± S.D.)	0.43(0.28)†	0.68(0.28)‡	0.25(0.26)β	0.29(0.27)ϕ	0.43(0.26)*f*
Simpson's Dominance Index (1/D)	0.48(2.09)	0.44(2.28)	0.50(2.02)	0.51(1.96)	0.67(1.49)
Berger Parker Index (1/*d*)	0.58(1.70)	0.73(1.37)	0.60(1.67)	0.66(1.51)	0.83(1.21)
Shannon Diversity Index	0.88	0.97	0.79	0.85	0.57

† *n* for Brillouins Index = 135; ‡ *n* for Brillouins Index = 47; β *n* for Brillouins Index = 37; ϕ *n* for Brillouins Index = 27; *f n* for Brillouins Index = 24.

3.6 Examination of the relationships in intensity between the three most common intestinal parasite species in Clogher Lake.

Initially Chi squared analysis was going to be used to examine the relationship in intensity between the three most common intestinal parasite species in Clogher Lake, *E. crassum*, *A. clavula* and *Crepidostomum farionis*. The intensity of each species was coded numerically in the following manner. Zero was when the parasite did not occur in a fish, one when the parasite occurred at low intensity and two when the parasite occurred at high intensity. The ranges for low and high intensity infections for each of the three species are given below. The low and high range values used in this study were selected after a visual examination of the raw data. Other studies have recorded significantly higher parasite levels, for example Kennedy (1996a). However the range values selected for this chi squared analysis were considered to be appropriate to this study.

	Absent = 0	Low = 1	High = 2
E. crassum	No worms	1 – 2 worms	3+ worms
A. clavula	No worms	1 – 25 worms	26+ worms
C. farionis	No worms	1 – 20 worms	21+ worms

Once contingency tables were calculated it became apparent that it would not be possible to use Chi squared as the test statistic because in all cases the main underlying assumption of this test statistic, that the value in any individual cell should not fall below five, had been violated.

Fisher's exact test was used instead, as it is not subject to requirements for cell size. However, Fisher's exact test can only be used on 2 x 2 contingency tables, as a result two sets of contingency tables were prepared, the first set used presence / absence (0-1) data, and the second set used low / high intensity (1-2) data. Contingency tables for all combinations of the three most common intestinal parasite species were calculated for the total fish sample in Clogher Lake (Tables 3.9-3.11). None of the relationships

between *E. crassum*, *A. crassum* and *Crepidostomum farionis* for the presence / absence or low high intensity contingency tables were significant.

The relationship between *A. clavula* and *E. crassum* was examined using presence / absence and low / high intensity contingency tables (Table 3.9). The percentage of column totals showed that in 36.4% of cases when *A. clavula* was absent *E. crassum* was also absent. In 43.9% of cases *A. clavula* was present when *E. crassum* was absent and in 56.1% of cases both species co-occurred. When the percentage of column totals were examined for the low / high intensity contingency tables, *A. clavula* and *E. crassum* were present together in 60.5% of low intensity infections. In 39.5% of cases *A. clavula* occurred at low intensity when *E. crassum* occurred at high intensity. In 54.3% of cases when *A. clavula* occurred at high intensity so did *E. crassum* and in 45.7% of cases *A. clavula* occur at high intensity when *E. crassum* occurred at low intensity (Table 3.9).

Crepidostomum farionis / E. crassum

In a similar manner, the relationship between *Crepidostomum farionis* and *E. crassum* was examined using presence / absence and low / high intensity contingency tables (Table 3.10). Examination of the percentage of column totals showed that in 35.1% of cases when *Crepidostomum farionis* was absent so was *E. crassum*. In 45.2% of cases *Crepidostomum farionis* was present when *E. crassum* was absent and in 54.8% of cases they co-occurred (Table 3.10). When the low / high intensity contingency table was examined percentage of column totals showed that in 57.1% of cases *Crepidostomum farionis* and *E. crassum* co-occurred at low intensity and in 42.9% of cases when *E. crassum* occurred at high intensity *Crepidostomum farionis* occurred at low intensity. In 42.3% of cases *E. crassum* and *Crepidostomum farionis* co-occurred at high intensity (Table 3.10).

A. clavula / Crepidostomum farionis

In the final contingency table, the relationship between *A. clavula* and *Crepidostomum farionis* was examined using presence / absence and low / high

intensity infections (Table 3.11). Percentage of column totals showed that in 22.7% of cases when *A. clavula* was absent so was *Crepidostomum farionis*. In 23% of cases *A. clavula* was present when *Crepidostomum farionis* was absent, however in 77% of cases both species were present together. For the low / high intensity contingency table in 55.6% of cases when *A. clavula* was present at low intensity so was *Crepidostomum farionis* (Table 3.11). In 44.4% of cases, when *A. clavula* occurred at high intensity *Crepidostomum farionis* occurred at low intensity, and in 45.3% of cases both species co-occurred at high intensity (Table 3.11).

3.7 Examination of the relationships in abundance between all parasite species in Clogher Lake.

Kendall's tau was used to assess the relationships in abundance between all possible combinations of parasite species pairs for the total fish sample in Clogher Lake. Four species pairs were significantly correlated, and all had positive values for their correlation coefficients (Table 3.12). In all cases the significantly correlated species pairs were composed of the nematode *Rhabdochona* sp. and a cestode species, or two cestode species. *Rhabdochona* sp. was significantly correlated with all the cestode species present, and both larval cestode species (*D. ditremum*, *D. dendriticum*) were significantly positively correlated.

Table 3.9 Presence / absence and low / high contingency table for the total sample *of E. crassum / A. clavula* in Clogher Lake (n = 161).

Row Totals = *E. crassum*
Column Totals = *A. clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	8	61	69	1	26	16	42
	11.6	88.4	100		61.9	38.1	100
	36.4	43.9	42.9		60.5	45.7	53.8
	4.97	37.9	42.9		33.3	20.5	53.8
1	14	78	92	2	17	19	36
	15.2	84.8	100		47.2	52.8	100
	63.2	56.1	57.1		39.5	54.3	46.2
	8.7	48.4	57.1		21.8	24.4	46.2
Total	22	139	161	Total	43	35	78
	13.7	86.3	100		55.1	44.9	100
	100	100	100		100	100	100
	13.7	86.3	100		55.1	44.9	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.66 Fishers Exact Test = 0.25

Table 3.10 Presence / absence and low / high contingency table for the total sample of *E. crassum / Crepidostomum farionis* in Clogher Lake (n = 161).

Row Totals = *E. crassum*
Column Totals = *Crepidostomum farionis*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	13	56	60	1	24	15	39
	18.8	81.2	100		61.5	38.5	100
	35.1	45.2	42.9		57.1	57.7	57.4
	8.07	34.8	42.9		35.3	22.1	57.4
1	24	68	92	2	18	11	29
	26.1	73.9	100		62.1	37.9	100
	64.9	54.8	57.1		42.9	42.3	42.6
	14.9	42.2	57.1		26.5	16.2	42.6
Total	37	124	161	Total	42	26	69
	23	77	100		61.8	38.2	100
	100	100	100		100	100	100
	23	77	100		61.8	38.2	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.35 Fishers Exact Test = 1.00

Table 3.11 Presence / absence and low / high contingency table for the total sample of *A .clavula / Crepidostomum farionis* in Clogher Lake (n = 161).

Row Totals = *Crepidostomum farionis*
Column Totals = *A . clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	5	32	37	1	30	29	59
	13.5	86.5	100		50.8	49.3	100
	22.7	23	23		55.6	54.2	55.1
	3.11	19.9	23		28	27.1	55.1
1	17	107	124	2	24	24	48
	13.7	86.3	100		50	50	100
	77.3	77	77		44.4	45.3	44.9
	10.6	66.5	77		22.4	22.4	44.9
Total	22	139	161	Total	54	53	107
	13.7	86.3	100		50.5	49.5	100
	100	100	100		100	100	100
	13.7	86.3	100		50.5	49.5	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 1.00 Fishers Exact Test = 1.00

Table 3.12 Kendall's tau correlation coefficients for the total parasite sample in Clogher Lake (n = 161). Row one shows correlation coefficients, row two shows two tailed significance levels. Significant correlations have been presented in bold print.

	E. crassum	*C. farionis*	*A. clavula*	*D. ditremum*	*Rhabdochona* sp.	*Anisakis* sp.	*S. salmoneus*	*D. dendriticum*
E	**X**	-0.03	-0.1	0.10	0.14	-0.13	-0.10	0.14
		0.65	0.1	0.13	**0.04**	0.07	0.14	0.05
C		**X**	0.05	-0.01	0.11	0.04	0.11	0.8
			0.41	0.86	0.09	0.60	0.10	0.22
A			**X**	-0.01	0.01	0.03	0.09	0.83
				0.91	0.89	0.65	0.18	0.20
D				**X**	0.22	0.13	-0.06	0.28
					0.003	0.09	0.43	**0.001**
R					**X**	-0.37	0.18	0.34
						0.64	0.06	**0.001**
Ani						**X**	-0.15	-0.66
							0.85	0.39
S							**X**	-0.54
								0.48
Ddend								**X**

E = *E. crassum*; C = *C. farionis*; A = *A. clavula*; D = *D. ditremum*; R = *Rhabdochona* sp.; Ani = *Anisakis* sp.; S = *S. salmoneus*; Ddend = *D. dendriticum*.

3.8 Examination of the niches of the three most prevalent intestinal parasite species in Clogher Lake.

The niches occupied by the three most prevalent intestinal parasite species (*A. clavula*, *E. crassum*, *Crepidostomum farionis*) in trout from Clogher Lake were examined in detail. The distribution of each species along the intestine was calculated for the overall total sample (both years combined) and also for each sample month. In all cases a set of statistics summarising the distribution of parasites along the intestine have been provided.

3.8.1 *A. clavula*

The fundamental niche of *A. clavula* along the intestine of trout from Clogher Lake was examined first (Fig 3.2). This sample was then divided and the distribution of *A. clavula* was examined for each month (Figs 3.3-3.4), and for low, medium and high intensity infections (Figs 3.5). For analytical statistical purposes the single sample taken in February 1999 was kept separate.

3.8.2 Total sample of *A. clavula* examined by month

The number of *A. clavula* individuals recorded varied from greater than four thousand in April to fewer than two hundred in August. A total of 9690 worms were removed from the total fish sample in Clogher Lake (Table 3.13; Fig 3.2). The mean percentage position of worms along the intestine ranged from 55.61% in November to 61.29% in May, a difference of 5.68%. The percentage difference between the month with the highest median value (65.87% in August) and the month with the lowest median value (51.17% in November) was 14.7%, substantially larger than the range recorded for the mean values (Table 3.13; Fig 3.3; Fig 3.4).

In all months the maximum location of *A. clavula* along the intestine was 100%, the lowest minimum location, 28.3%, was recorded in April. Correspondingly April had the largest distributional range of *A. clavula* along the intestine, followed by August,

November and May. In all cases *A. clavula* occupied over 65% of the intestine (Table 3.13; Fig 3.3; Fig 3.4)

The interquartile range varied from 10.98% in November to 29.55% in May. Values for the upper 75% quartile ranged from 71% to 77.05% for April, May and August, but the value for November was considerably lower at 59.45%. Values for the lower 25% quartile were all similar and ranged from 45.82% in August to 50.48% in April.

Only November had a skewness value above one, which suggests that the distribution of *A. clavula* in this month had an asymmetric tail extending towards more positive values (Fig 3.4). November was also the only month which had a positive kurtosis value, all remaining months had negative kurtosis values.

One-way analysis of variance (ANOVA) was used to compare the mean percentage position of *A. clavula* along the intestine between sample months. A significant difference existed in the distribution of *A. clavula* between the months (F ratio = 53.3; df = 7,9682; $p \leq 0.0001$). Least squares difference post hoc tests showed which sample months had significantly different distributions from each other. Of the twenty-eight possible paired month combinations (for the eight sample months), there were significant differences between eleven. Results are presented in Appendix 1, Table 1.

3.8.3 Total sample of *A. clavula* examined by intensity of infection

Data for the distribution of *A. clavula* were then examined in three groups, low, medium and high, depending on the number of parasites infecting individual fish. Low intensity infection was when between one and fifteen worms infected a fish, medium intensity infection was when between sixteen and seventy five worms infected a fish and high intensity infection was when over seventy six worms infected a fish (Table 3.14; Fig 3.5).

Of the 9690 worms from the total sample in Clogher Lake, 522 were in low intensity infections, 2207 were in medium intensity infections and the remaining 6961 worms were in high intensity infections. The mean position of worms along the intestine was highest for worms in low intensity infections, 64.38%, and lowest for the worms in high intensity infections, 57.72%. The difference between the highest and lowest mean position was 6.66% which was similar to the difference between the highest and lowest mean positions when the total sample was examined by month.

For low and medium intensity infections, the mean percentage location along the intestine was higher than the highest percentage location along the intestine recorded when the total sample was examined by month (Table 3.13; Table 3.14). Values for the median follow the same pattern described for the mean, with low intensity infections having the highest percentage location along the intestine, 62.10%, and high intensity infections having the lowest percentage location along the intestine, 53.68%. However median values were within the range of values recorded when the total sample was examined by month (Table 3.13).

The minimum position along the intestine, 28.3% was recorded in low intensity infections; all three samples had a maximum position of 100%. The pattern for the range of occurrence of *A. clavula* in the intestine was similar to that recorded for the mean and median, with the low intensity infection having the largest range of occurrence and high intensity infection having the smallest range of occurrence.

Values for the 25% quartile were quite similar between low, medium and high intensity infections. The value of the 75% quartile for the high intensity infection was considerably lower than for either the low or medium intensity infection, although not as low as the value recorded for November when the total sample was examined by month (Table 3.14). Thus medium intensity infections had the largest interquartile range and high intensity infections had the smallest interquartile range.

Both low and medium intensity infections had positive skewness values below one, and negative kurtosis values. This indicated a relatively flat distribution, which approximated the normal distribution. However the high intensity infection had a skewness value above one and a positive value for kurtosis, which indicated a relatively peaked distribution with an asymmetric tail extending towards positive values (Table 3.14; Fig 3.5).

One-way analysis of variance (ANOVA) was used to examine the differences in the distribution of *A. clavula* along the intestine between low, medium and high intensity infections. A significant overall difference existed (F ratio = 117.7; df = 2,9687; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the distribution of *A. clavula* between medium and low ($p \leq 0.002$), high and low ($p \leq 0.0001$) and high and medium ($p \leq 0.0001$) intensity infections.

The niche width of *A. clavula* was calculated for the total sample (0.84) and for each month (April = 0.82, May = 0.83, August and November = 0.77). The niche width was smallest in August and November and largest in May, although values did not differ substantially from each other. The niche width was also calculated for low, medium and high intensity infections (Low = 0.77, Medium = 0.84, High = 0.81). Low intensity infections had the lowest value and medium intensity infections had the highest value, however all values were similar to those recorded for the monthly samples.

Table 3.13 Summary statistics for the distribution of *A. clavula* in the intestine of trout from Clogher Lake for the total sample and for each month.

	April	May	August	November	Total
Count	4264	1766	183	3477	9690
Mean (± S.D.)	60.85(14.61)	61.29(16.83)	59.63(17)	55.61(12.69)	59.03(14.67)
Median	56.25	56.09	65.87	51.17	53.99
Inter quartile Range	21.79	29.55	26.10	10.98	19.35
Minimum	28.3	34.78	31.73	32.98	28.3
Maximum	100	100	100	100	100
Range	71.7	65.22	68.27	67.02	71.7
Skewness	0.69	0.52	0.56	1.31	0.85
Kurtosis	-0.47	-0.95	-0.86	1.21	-0.22
Lower (25%)	50.48	47.5	45.82	48.47	48.43
Upper (75%)	72.27	77.05	71.93	59.45	67.77

Table 3.14 Summary statistics for the distribution of *A. clavula* in the intestine of trout from Clogher Lake at low (1-15 worms), medium (16-75 worms) and high (76+ worms) infection intensities.

	Low	Medium	High
Count	522	2207	6961
Mean (± S.D.)	64.38(15.36)	62.19(16.18)	57.72(13.83)
Median	62.10	57.49	53.68
Inter quartile Range	23.09	28.11	16.24
Minimum	28.30	29.72	34.43
Maximum	100	100	100
Range	71.7	70.28	65.57
Skewness	0.27	0.49	1.01
Kurtosis	-0.75	-0.89	0.21
Lower (25%)	51.81	48.81	48.32
Upper (75%)	74.90	76.92	64.60

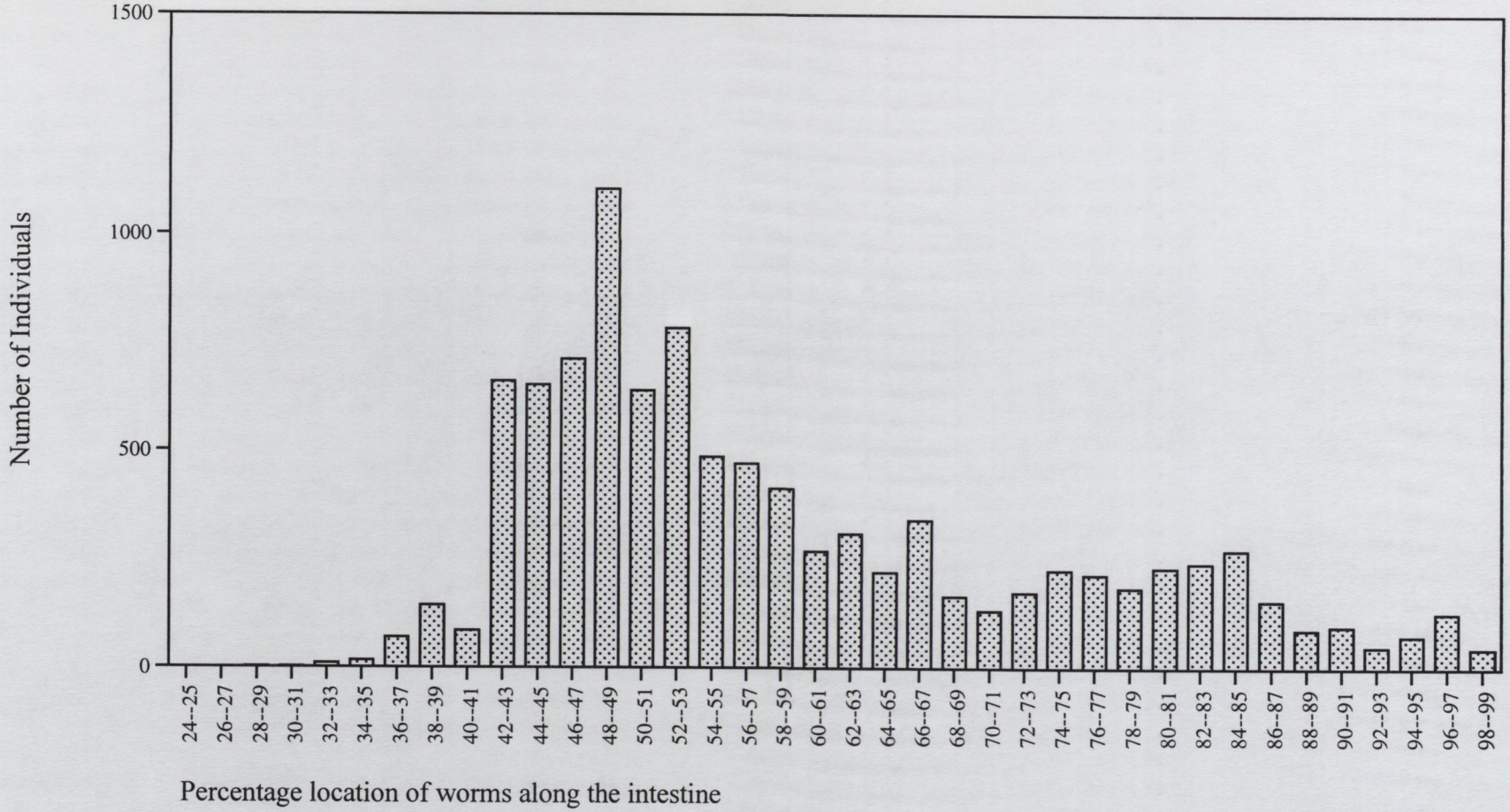

Fig 3.2 Fundamental niche of *A. clavula* along the intestine of trout from Clogher Lake.

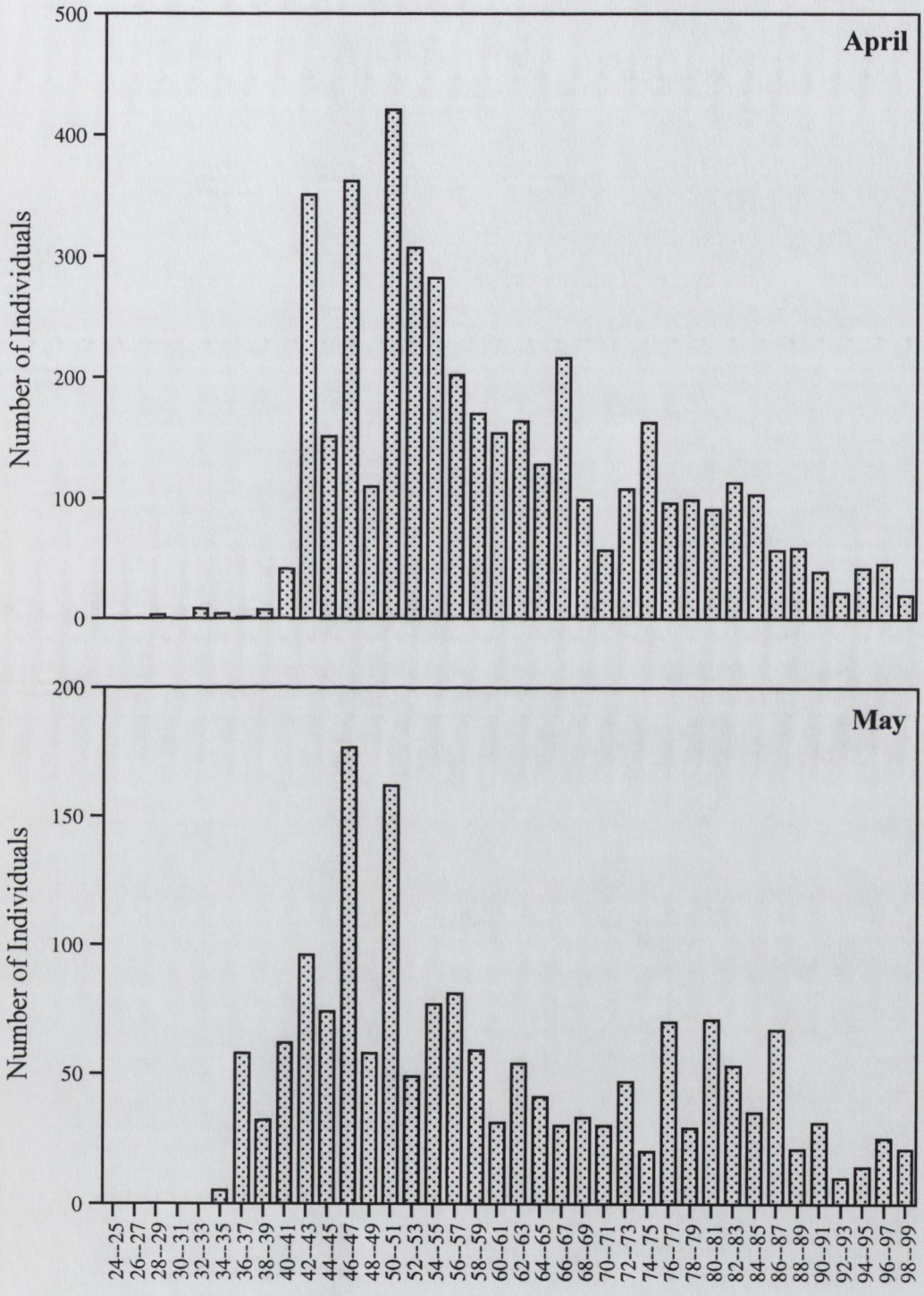

Fig 3.3 Niches for *A. clavula* along the intestine of wild trout in Clogher Lake in April and May.

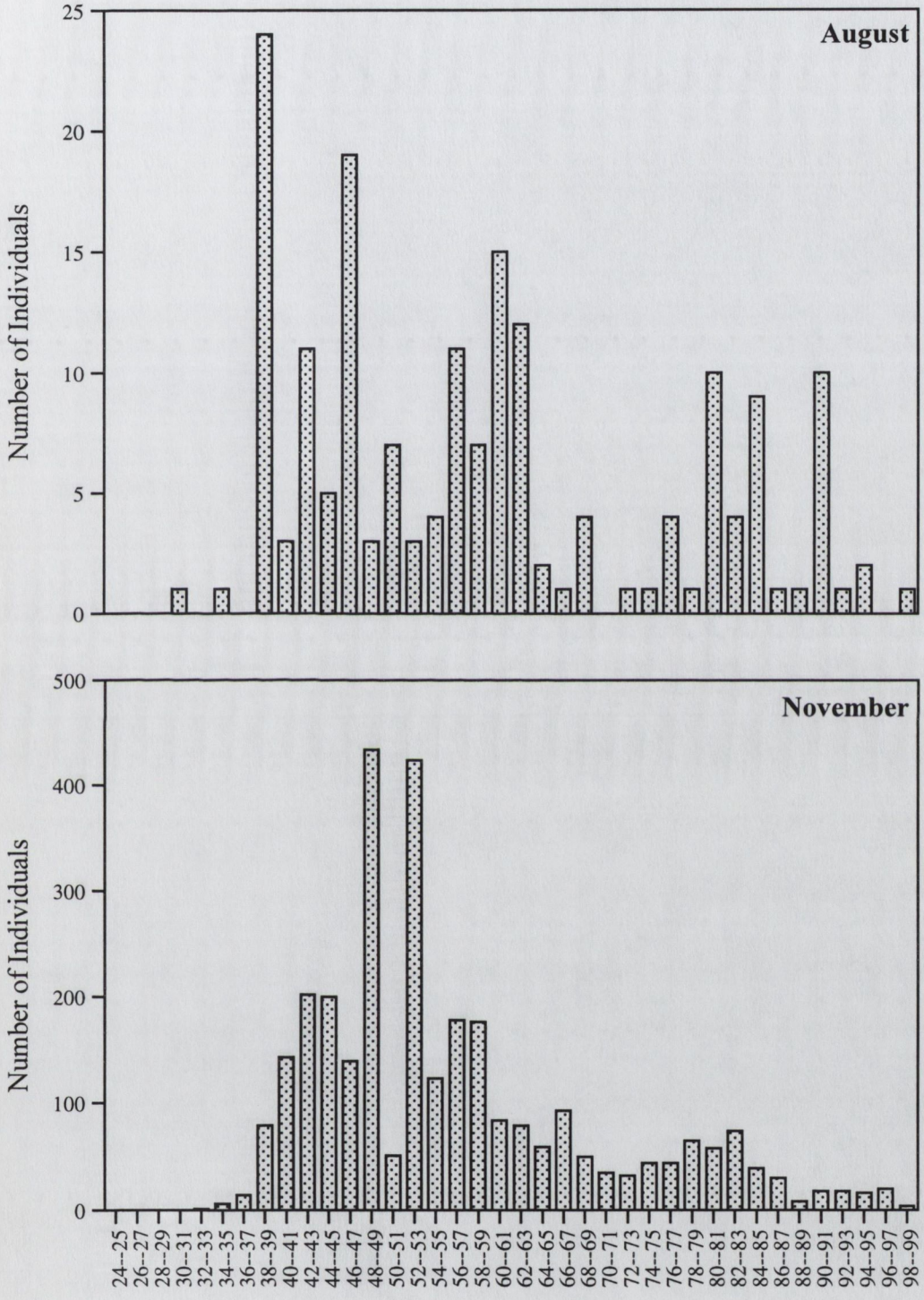

Fig 3.4 Niches for *A. clavula* along the intestine of wild trout in Clogher Lake in August and November.

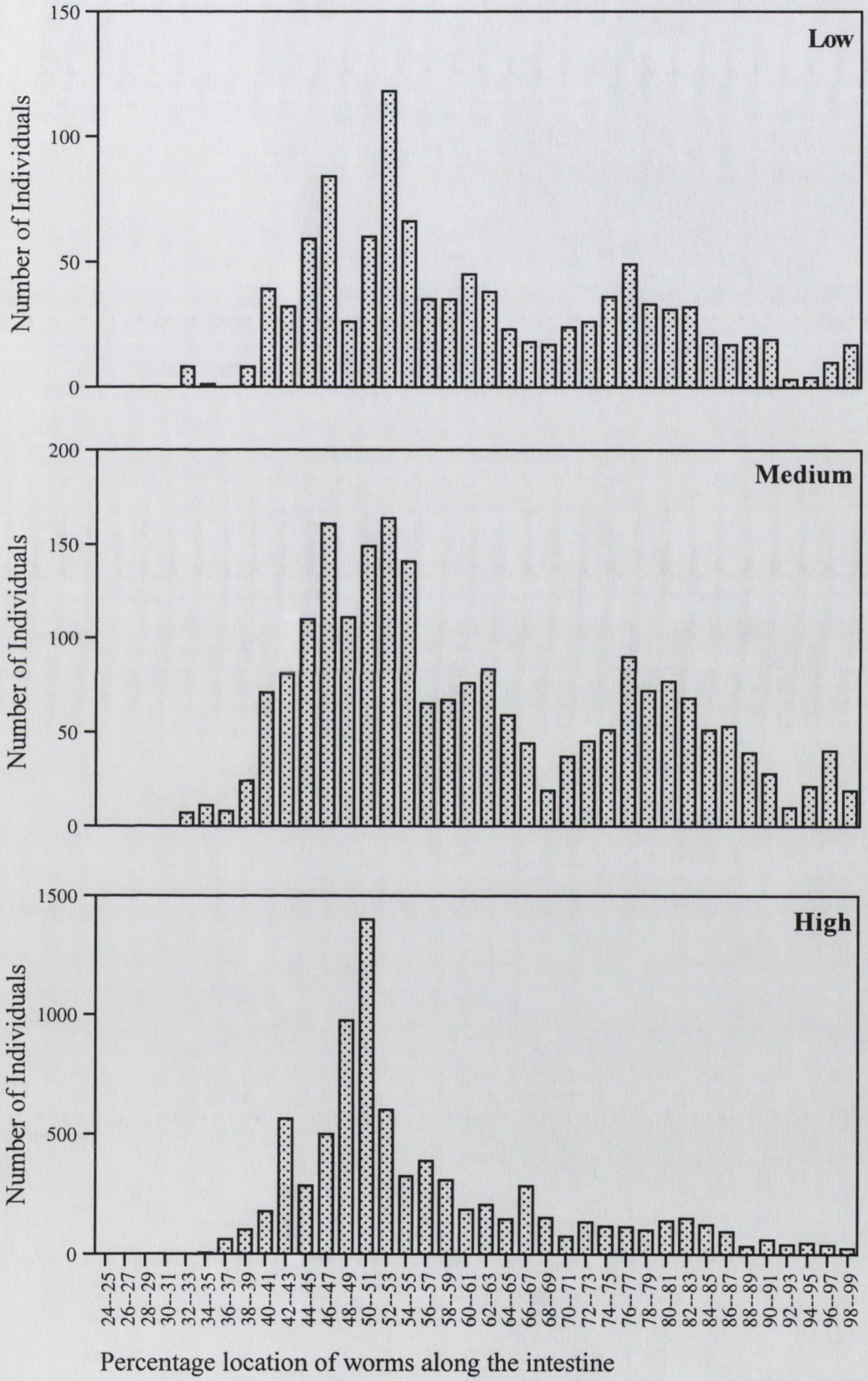

Fig 3.5 Niches of *A. clavula* in low intensity (1-15 worms), medium intensity (16-75 worms) and high intensity (76+ worms) infections along the intestine of trout from Clogher lake.

3.8.4 *Crepidostomum farionis*

Crepidostomum farionis in the intestine of trout from Clogher Lake was treated in the same manner as *A. clavula*. The distribution of the total sample of *Crepidostomum farionis* from all fish in Clogher Lake was first examined (Fig 3.6). The total sample was then examined by month, and also for low, medium and high intensity infections (Figs 3.7-3.9). The single sample of fish from February 1999 was kept separated during analytical statistical procedures.

3.8.5 Total sample of *Crepidostomum farionis* examined by month

A total of 6022 worms were found in the total sample in Clogher Lake, 3822 in April, 1038 in May, 489 in August and 673 in November. August had the highest mean position of *Crepidostomum farionis* along the intestine, 61.2%, and April had the lowest, 56.52%, a difference of 4.68%. May and November had intermediate values. The same pattern was evident for the median values, April had the lowest median position of *Crepidostomum farionis* along the intestine, 48.8% and August had the highest median position, 59.53%, a difference of 10.73%. Again May and November had intermediate values (Table 3.15). The range of median values recorded for *Crepidostomum farionis* was over twice the range recorded for the mean values (Table 3.15).

Maximum values of 100% were recorded for April and May and values of 98.87% and 98.63% were recorded for August and November respectively. The lowest minimum value, 30.58%, recorded in August was not considerably different from the minimum values recorded in any other month. The highest minimum value, 32.46%, was recorded in November, the month with the smallest range of occurrence. However the difference between the smallest range of occurrence of *Crepidostomum farionis*, in November, and the largest range of occurrence, in May, was only 2.88% (Table 3.15).

The interquartile range varied from 25.89% in November to 44.30% in May. In November the value of the 25% quartile was higher than the values recorded for all

other months, whereas the 75% quartile value was similar to the values recorded in April and August, resulting in a narrower interquartile range. The opposite situation arose in May where values for the 25% quartile were in line with the values recorded in August and April, but values for the 75% quartile were higher than in any other month resulting in a broader interquartile range (Table 3.15).

For all months the skewness value was positive and below one. Kurtosis was negative for all months. This suggests that *Crepidostomum farionis* had a similar type of distribution in all months, a flattened distribution which approximated normal (Table 3.15; Figs 3.7-3.8).

One-way analysis (ANOVA) of variance was used to compare the mean percentage position of *Crepidostomum farionis* for each sample month. A significant difference existed (F ratio = 16.0; df = 7,6014; $p \leq 0.0001$). Least squares difference post hoc tests showed which of the sample months had significantly different distributions from each other. Of the twenty-eight possible combinations of pairs of sample months (from the eight months in the total sample), seventeen were significantly different from each other (See Appendix 1, Table 2).

3.8.6 Total sample of *Crepidostomum farionis* examined by intensity of infection

The distribution of *Crepidostomum farionis* was examined when it occurred in low, medium and high intensity infections. An infection of *Crepidostomum farionis* was considered to be of low intensity when one to ten worms occurred in a fish, of medium intensity when eleven to thirty nine worms occurred in a fish and of high intensity when forty or more worms occurred in a fish.

For the total sample 227 worms were found in low intensity infections, 1036 in medium intensity infections and 4759 in high intensity infections. The mean location of *Crepidostomum farionis* varied from 56.28% in medium intensity infections to 68.70% in low intensity infections, a difference of 12.42%. The mean location of worms in low intensity infections was higher than that recorded for any month in the

total sample (Table 3.16). The lowest median value was recorded in high intensity infections and the highest median value was recorded in low intensity infections. In the case of high and medium intensity infections the median value was lower than that recorded for the mean but in the case of low intensity infections the median value was 5.59% higher than the mean value (Table 3.16). The difference between the highest and lowest median values was 24.29%, considerably higher than the difference between the highest and lowest values for the mean.

For low, medium and high intensity infections maximum values were above 99%. The lowest minimum value, 30.58% was recorded in medium intensity infections. The range of occurrence of *Crepidostomum farionis* was largest for medium intensity infections, however values were similar to the range of occurrence recorded for low and high intensity infections (Table 3.16; Fig 3.9).

Values for the 25% quartile were lowest for medium intensity infections and highest for low intensity infections. For the 75% quartile a similar pattern emerged, they were also lowest for medium intensity infections and highest for low intensity infections. The interquartile range decreased in size from low intensity infections to high intensity infections, the difference between the two was 11.72%. The interquartile range for medium intensity infections was intermediate between them.

The low intensity infection of *Crepidostomum farionis* had a negative skewness value, which suggests that there was an asymmetric tail extending towards negative values. For medium and high intensity infections the skewness value was positive and below one. Kurtosis values were negative in all cases, suggesting flatter type distributions.

One-way analysis of variance (ANOVA) showed significant differences in the distribution of *Crepidostomum farionis* between low, medium and high intensity infections (F ratio = 41.2; df = 2,6019; $p \leq 0.0001$). Least squares difference post hoc

tests showed significant differences between medium and low ($p \leq 0.0001$), high and low ($p \leq 0.0001$) and high and medium ($p = 0.028$) intensity infections.

The niche width values of *Crepidostomum farionis* for the total sample in Clogher Lake ranged from 0.69 in November to 0.82 in April. May and August had intermediate values of 0.76 and 0.78 respectively. Niche width values for low, medium and high intensity infections for the total sample of *Crepidostomum farionis* were 0.80, 0.82 and 0.82 respectively.

Table 3.15 Summary statistics for the distribution of *C. farionis* in the intestine of trout from Clogher Lake for the total sample and for each month.

	April	May	August	November	Total
Count	3822	1038	489	673	6022
Mean (± S.D.)	56.52(18.45)	59.30(21.27)	61.2(20.30)	60.65(15.81)	57.78(18.99)
Median	48.8	50	59.53	53.68	50.61
Inter quartile Range	29.32	44.30	38.85	25.89	32.29
Minimum	31.13	30.95	30.58	32.46	30.58
Maximum	100	100	98.87	98.63	100
Range	68.87	69.05	68.29	66.17	69.42
Skewness	0.74	0.47	0.09	0.73	0.62
Kurtosis	-0.65	-1.41	-1.37	-0.74	-0.92
Lower (25%)	43.06	41.67	40.42	50	42.85
Upper (75%)	72.38	85.97	79.26	75.89	75.14

Table 3.16 Summary statistics for the distribution of *C. farionis* in the intestine of trout from Clogher Lake at low (1-10 worms), medium (11-39 worms) and high (40+ worms) infection intensities.

	Low	Medium	High
Count	227	1036	4759
Mean (± S.D.)	68.70(22.11)	56.28(19.84)	57.70(18.51)
Median	74.29	52.04	50
Inter quartile Range	42.71	35	30.99
Minimum	33.48	30.58	32.61
Maximum	99.39	100	100
Range	65.91	69.42	67.40
Skewness	-0.34	0.42	0.71
Kurtosis	-1.34	-1.10	-0.81
Lower (25%)	45.63	39.35	43.8
Upper (75%)	88.34	74.35	74.79

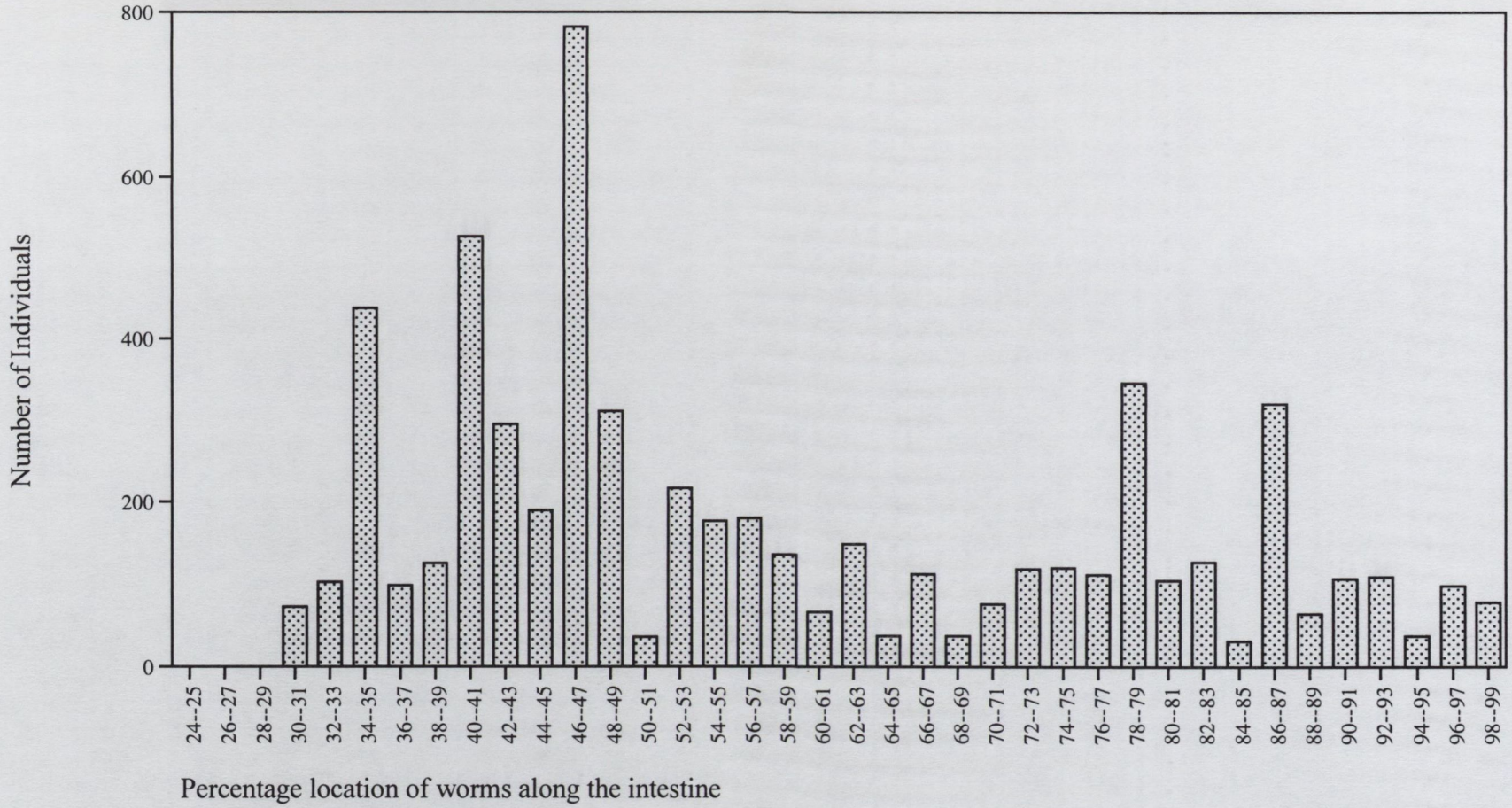

Fig 3.6 Fundamental niche of *Crepidostomum farionis* along the intestine of trout from Clogher Lake.

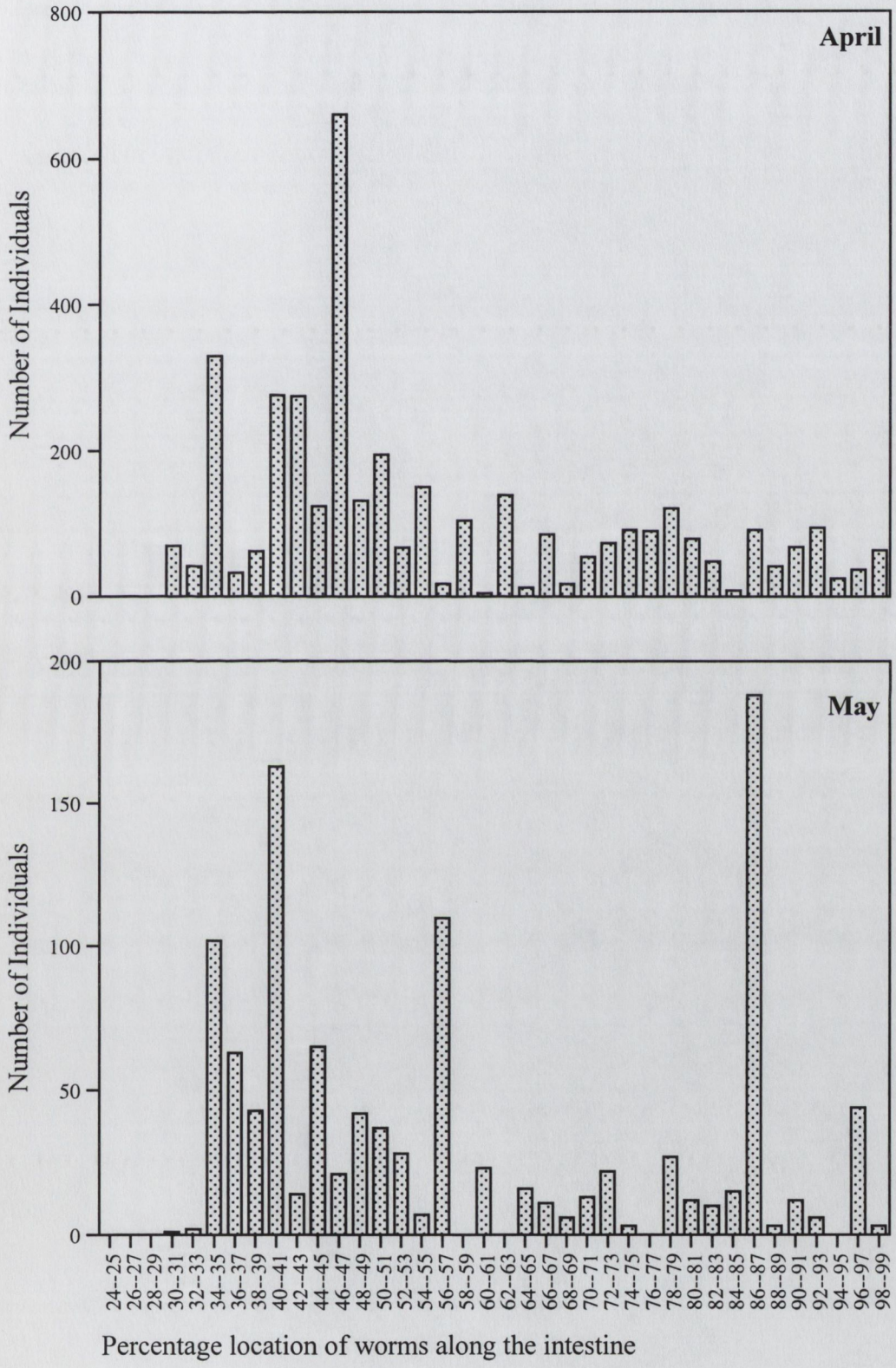

Fig 3.7 Niches for *Crepidostomum farionis* along the intestine of wild trout in Clogher Lake in April and May.

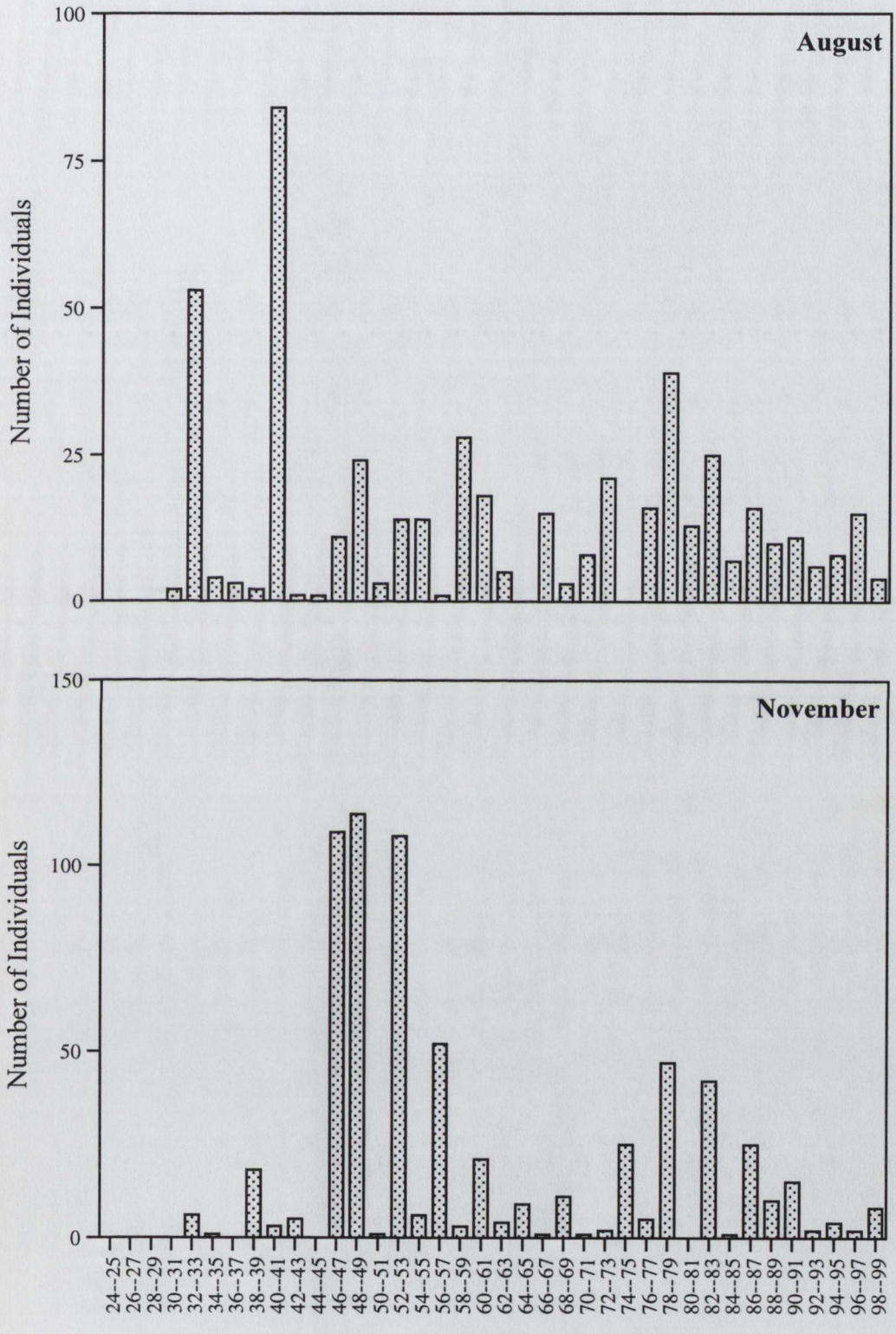

Fig 3.8 Niches of *Crepidostomum farionis* along the intestine of wild trout in Clogher Lake in August and November.

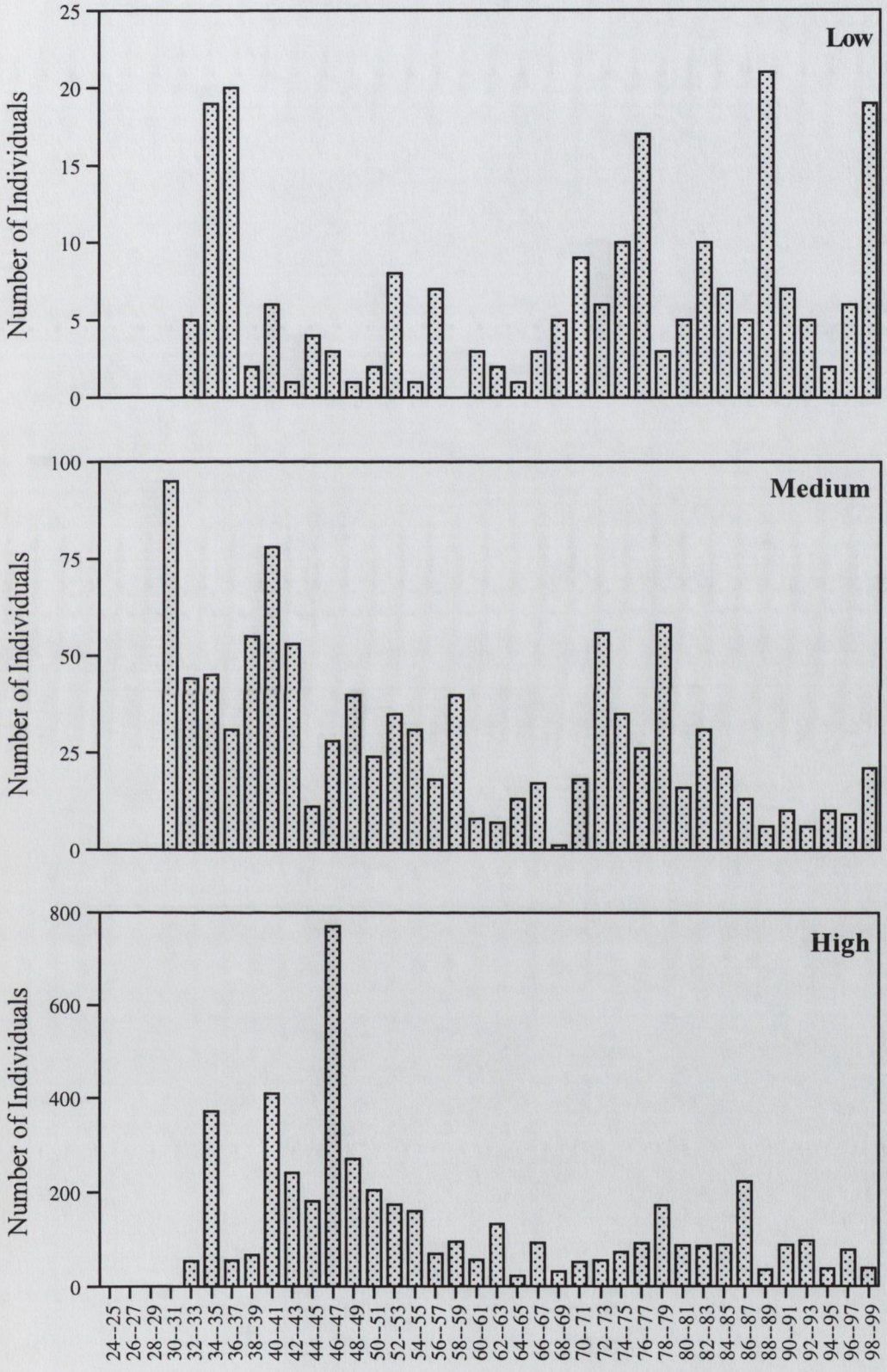

Fig 3.9 Niches of *Crepidostomum farionis* in low intensity (1-10 worms), medium intensity (11-39 worms) and high intensity (40+ worms) infections along the intestine of trout from Clogher Lake.

3.8.7 *E. crassum*

The distributions of *E. crassum* in all fish in Clogher Lake were first examined (Fig 3.10). The total sample was then divided and the distribution of *E. crassum* was examined by sample month (Figs 3.11-3.12), and in low, medium and high intensity infections (Fig 3.13). *E. crassum* in the single sample from 1999 were treated in the same manner as *A. clavula* and *Crepidostomum farionis*: they were kept separate during analytical statistical procedures.

E. crassum is a relatively large tapeworm of the upper intestine of trout. Its preferred location is inside the pyloric caeca, where it attaches itself by means of a scolex. The body of the worm can extend right down into the small intestine, unlike *Crepidostomum farionis* and *A. clavula* which are smaller parasites in the intestine. Therefore, in the following sections all percentage locations given are based of the position of the scolex.

3.8.8 Total sample of *E. crassum* examined by month

A total of 320 tapeworms were found in the total fish sample in Clogher Lake. 163 were found in April, 51 in May, 60 in August and 46 in November. The mean position ranged from 36.77% in August to 41.34% in April, a difference of 4.57% (Table 3.17). For all months median positions were lower than mean positions. Median positions were very consistent and only varied by 1%, from 36.17 in November to 37.17 in August (Table 3.17)

The maximum position of *E. crassum*, 92.04%, was recorded in April. The maximum positions recorded for *E. crassum* in the remaining months were substantially lower, 63.04% in May, 48.23% in August and 49.29% in November. Minimum values were a lot more homogenous, from 25.66% in April to 31.7% in November. The 24-25% location was generally where the stomach ended and the intestine began in most of the brown trout examined in this sample. As a result of the very high maximum position recorded in April this month had the largest range of occurrence, 66.38%. May had a range of occurrence approximately half that recorded in April, 33.52%,

and August and November had ranges approximately half that recorded in May, 17.8% and 17.59% respectively.

Interquartile ranges were comparable between the April and May samples, and the August and November samples. For three out of four sample months values for the 25% quartile were 35%, and for August it was 33.79%. The 75% quartile values for April and May were extended, but comparable. August had the lowest value for the 75% quartile (Table 3.17).

Skewness values for April and May were positive and above one, suggesting a distribution with an asymmetric tail tending towards positive values. Skewness values for August and November were positive and below one. Kurtosis values were positive for three of the four sample months, only November had a negative value for kurtosis; this month also had the smallest range of occurrence and least number of individuals (Figs 3.10-3.12).

One-way analysis of variance (ANOVA) on log (x+1) data was used to examine the differences between the distributions of *E. crassum* for each sample month. A significant difference existed (F ratio = 9.4; df = 7,312; $p \leq 0.0001$). Least squares difference post hoc tests showed which of the sample months had significantly different distributions from each other. Of the twenty-eight possible combinations of pairs of sample months from the eight months in the total sample, eleven were significantly different from each other (See Appendix 1, Table 3). February 1999 was significantly different from all other months.

3.8.9 Total sample of *E. crassum* examined by intensity of infection

The total sample of *E. crassum* in Clogher Lake was divided into low, medium and high intensity infections, in the same manner as done for *Crepidostomum farionis* and *A. clavula*. For *E. crassum* a low intensity infection was one worm, a medium intensity infection was two to four worms and a high intensity infection was five or more worms.

24 worms were found in low intensity infections in Clogher Lake, 98 were found in medium intensity infections and 198 were found in high intensity infections. The mean location was lowest in low intensity infections, 36.13% and highest in high intensity infections, 39.87%, a difference of 3.74%. Median values were all lower than the mean values and they ranged from 36.76% in high intensity infections to 35.85% in low intensity infections, a difference of 0.91% (Table 3.18).

The minimum values recorded were lowest for the low intensity infections and highest for the high intensity infections, but values were still comparable. However maximum values were lowest for the low intensity infections and considerably higher in medium and high intensity infections (Table 3.18). A difference of 48.84% existed between the highest and the lowest maximum value. The range of occurrence followed the same pattern. The smallest range of occurrence was for low intensity infections and the largest range of occurrence was for high intensity infections (Table 3.18; Fig 3.13).

Skewness values for medium and high intensity infections were positive and above one which indicated an asymmetric tail tending towards positive values. Low intensity infections had a negative skewness value below one suggesting a skew towards negative values (Table 3.18; Fig 3.13). Kurtosis values were all positive. They were substantially lower in low intensity infections than for medium or high intensity infections, which suggests more peaked distributions.

One-way analysis of variance (ANOVA) on log (x+1) data showed significant differences in the distributions of *E. crassum* in low, medium and high intensity infections (F ratio = 3.5; df = 2,317; $p = 0.031$). Least squares difference post hoc tests showed significant differences between high and low ($p = 0.034$) and high and medium ($p = 0.048$) intensity infections. No significant difference was found between medium and low intensity infections.

The restricted distribution of *E. crassum* in the intestine was reflected in the niche width values. The niche width of *E. crassum* was 0.52 in April, 0.49 in May, 0.47 in August and 0.49 in November. The overall value for H' was 0.58. The niche widths for low, medium and high intensity infections were 0.46, 0.52 and 0.56 respectively.

Table 3.17 Summary statistics for the distribution of *E. crassum* in the intestine of trout from Clogher Lake for the total sample and for each month.

	April	May	August	November	Total
Count	163	51	60	46	320
Mean (± S.D.)	41.34(12.09)	39.04(6.11)	36.77(4.35)	37.38(4.47)	39.50(9.26)
Median	36.51	36.57	37.17	36.17	36.3
Inter quartile Range	7.41	7.98	4.15	5.60	6.25
Minimum	25.66	29.52	30.43	31.7	25.66
Maximum	92.04	63.04	48.23	49.29	92.04
Range	66.38	33.52	17.8	17.59	66.38
Skewness	2.39	1.48	0.72	0.78	2.99
Kurtosis	5.68	2.48	0.18	-0.25	11.1
Lower (25%)	35	35	33.79	35	35
Upper (75%)	42.41	42.98	37.94	40.6	41.25

Table 3.18 Summary statistics for the distribution of *E. crassum* in the intestine of trout from Clogher Lake at low (1 worms), medium (2-4 worms) and high (5+ worms) infection intensities.

	Low	Medium	High
Count	24	98	198
Mean (± S.D.)	36.13(4.21)	37.87(8.5)	39.87(8.34)
Median	35.85	35.53	36.76
Inter quartile Range	3.80	5.73	7.98
Minimum	25.66	30.43	31.79
Maximum	43.2	87.84	92.04
Range	17.54	57.41	60.25
Skewness	-0.19	3.16	3.14
Kurtosis	0.34	12.92	14.82
Lower (25%)	34.09	33.3	35
Upper (75%)	37.89	39.03	42.98

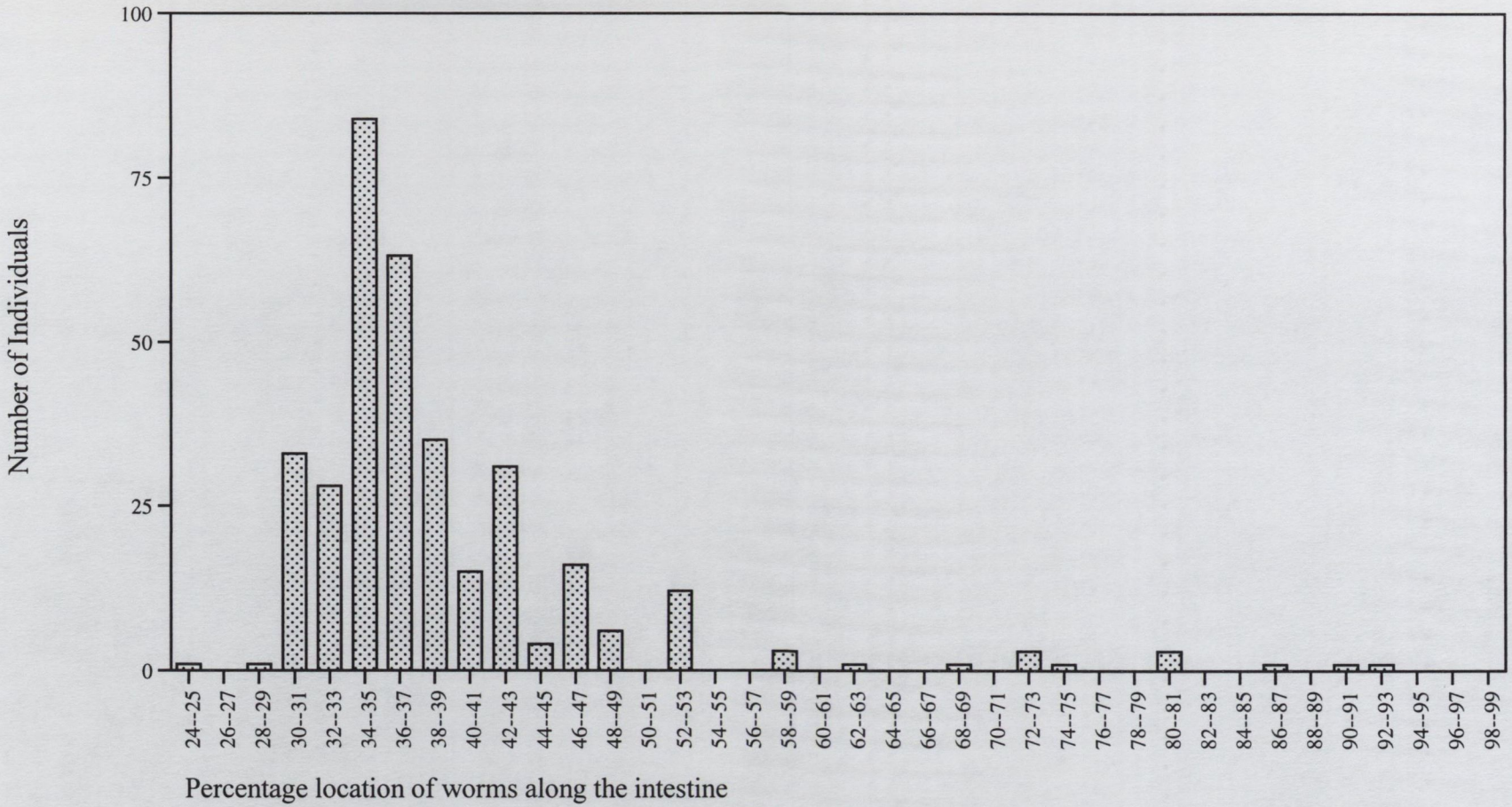

Fig 3.10 Fundamental niche of *E. crassum* along the intestine of trout from Clogher Lake.

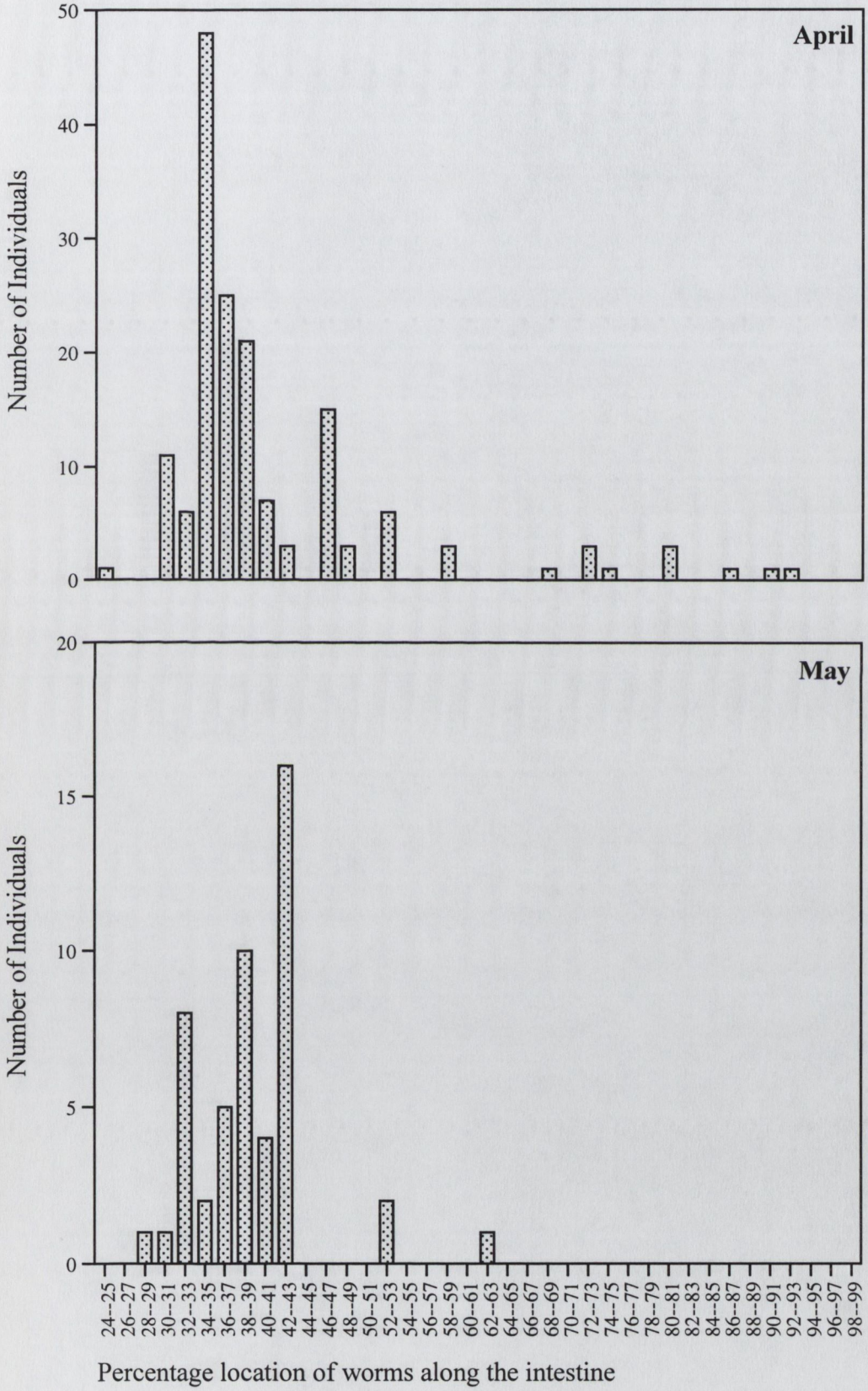

Fig 3.11 Niches for *E. crassum* along the intestine of wild trout in Clogher Lake in April and May.

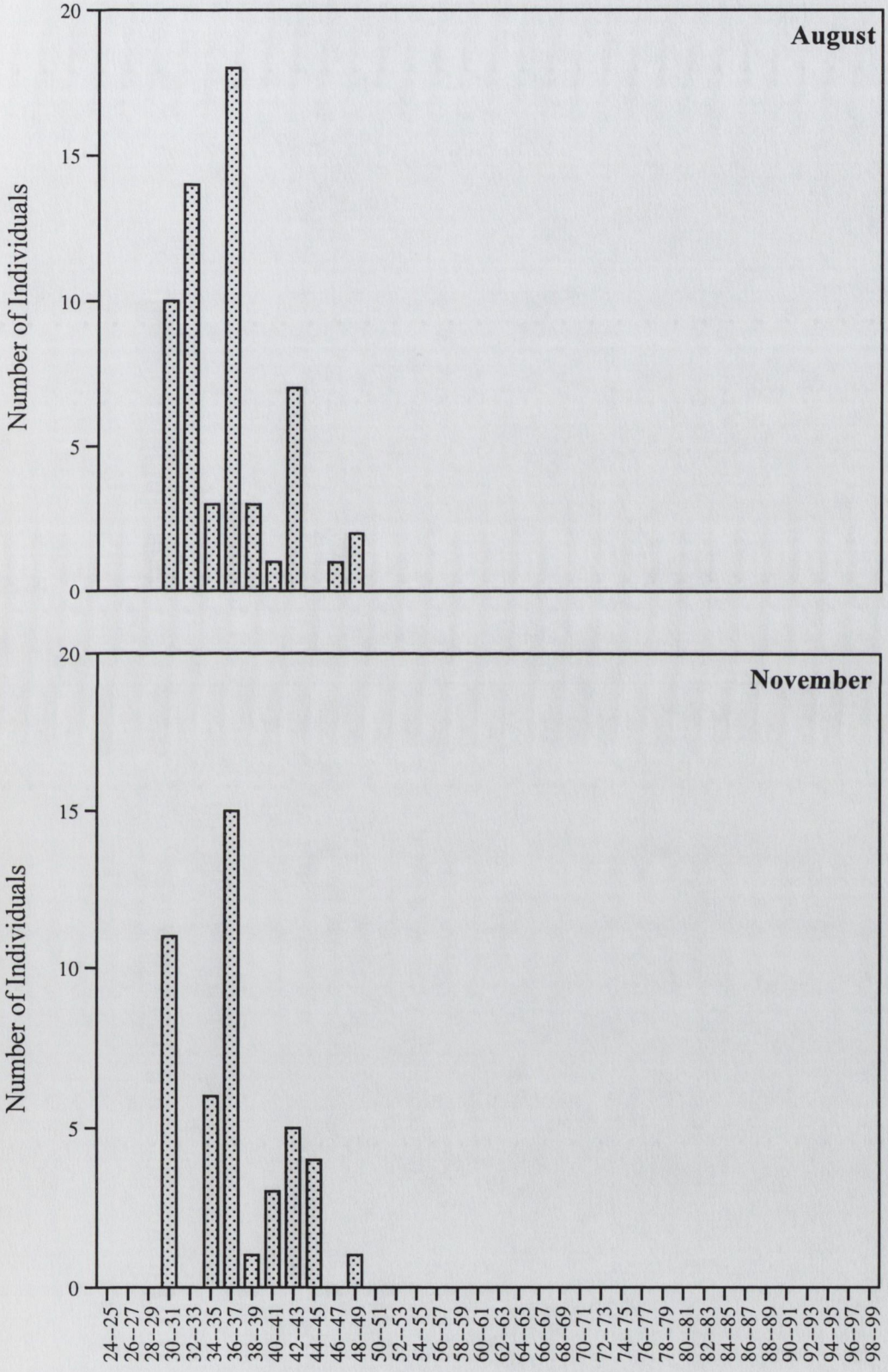

Fig 3.12 Niches for *E. crassum* along the intestine of wild trout in Clogher Lake in August and November.

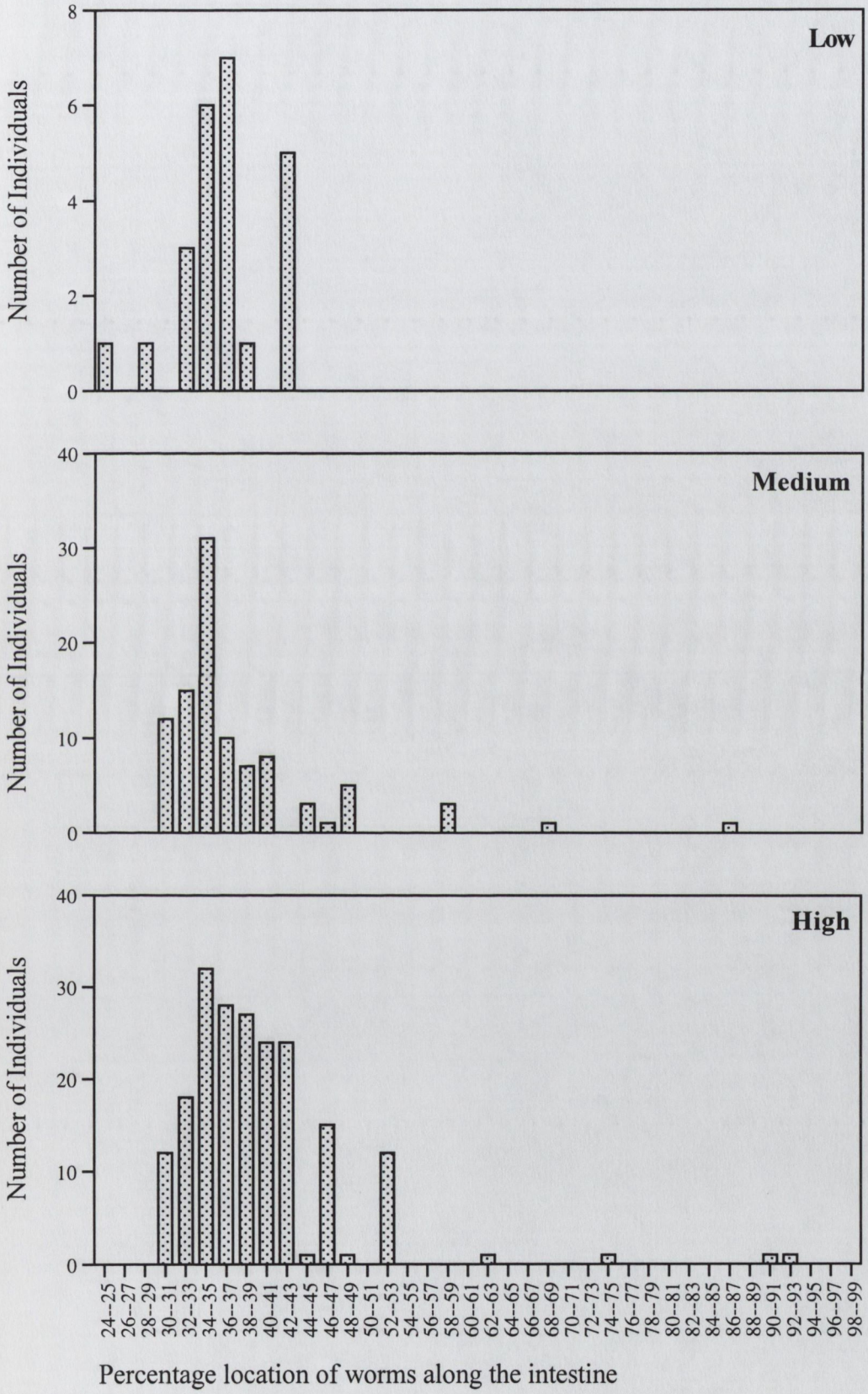

Fig 3.13 Niches of *E. crassum* in low intensity (1 worm), medium intensity (2-4 worms) and high intensity (5+ worms) infections along the intestine of trout from Clogher Lake.

3.9 Examination of the niche overlaps of the three most common species in Clogher Lake

A. clavula and E. crassum

When the total sample was examined by month the overlap between *A. clavula* and *E. crassum* was lowest in April, increased to a peak in August and decreased again in November (Table 3.19). However, overlap values for May and November were comparable. The niche overlap for the total sample, 0.23, was similar to the value recorded in May, but considerably lower than the highest value recorded in August (Table 3.19).

A. clavula and Crepidostomum farionis

Niche overlap values were high in April, decreased to their lowest point in August, and then peaked in November. The total niche overlap value, 0.78, was very similar to the peak value recorded in November, 0.8 (Table 3.19).

E. crassum and Crepidostomum farionis

Niche overlap values between *E. crassum* and *Crepidostomum farionis* increased from April to a peak in May. Values then decreased substantially in August and there was practically no overlap whatsoever in November (Table 3.19). The total niche overlap value, 0.53, was very similar to the value recorded in April.

Table 3.19 Niche overlaps of the three most prevalent parasite species in Clogher Lake, for each monthly sample and for the total sample, calculated using the Morisita-Horn quantitative similarity index.

Species	April	May	August	November	Total
A. clavula & *E. crassum*	0.10	0.19	0.38	0.16	0.23
A. clavula & *C. farionis*	0.67	0.55	0.33	0.80	0.78
E. crassum & *C. farionis*	0.52	0.63	0.28	0.05	0.53

3.10 Examination of the distribution of *A. clavula* when it occurred in low, medium and high intensity infections of *E. crassum.*

The distribution of *A. clavula* in the intestine of trout in Clogher Lake was examined when it co-occurred with *E. crassum* in low, medium and high intensity infections (Table 3.20). It was also compared to the distribution of *A. clavula* in low, medium and high intensity infections for the total fish sample in Clogher Lake (Table 3.14). A low intensity infection of *E. crassum* was considered to be one worm, a medium intensity infection was two to four worms and a high intensity infection of *E. crassum* was five or more worms.

23 *A. clavula* were found co-occurring with *E. crassum* in low intensity infections, 73 in medium intensity infections and 138 *A. clavula* co-occurred with *E. crassum* in high intensity infections. The mean position of *A. clavula* ranged from 80.46% in high intensity infections to 85.24% in medium intensity infections, a difference of 4.78% (Table 3.20). When compared with the total sample (Table 3.14), the mean locations of *A. clavula* in low, medium and high intensity infections of *E. crassum* were substantially higher. A difference of 16.08% existed between the highest mean location for the total sample and the lowest mean location for *A. clavula* in low, medium and high intensity infections of *E. crassum* (Table 3.20).

The median values of *A. clavula* in low, medium and high intensity infections of *E. crassum* were all higher than the mean values (Table 3.20). Median values of *A. clavula* ranged from 84.75% for high intensity infections to 90.69% for medium intensity infections. In contrast median values of *A. clavula* for the total sample were all lower than the mean, and ranged from 53.68% in high intensity infection to 62.10% in low intensity infections (Table 3.14).

The lowest minimum value recorded for *A. clavula* was 50%, for medium intensity infections of *E. crassum* (Table 3.20). The maximum value of *A. clavula* when it occurred in medium and high intensity infections of *E. crassum* was 100%, and

99.66% when it occurred in low intensity infections of *E. crassum* (Table 3.20). The maximum values of *A. clavula* for low, medium and high intensity infections in the total sample were 100%, in contrast the minimum values were all substantially lower than 50% (Table 3.14). Correspondingly the ranges of occurrence of *A. clavula* for all intensities of *E. crassum* (Table 3.20) were considerably lower than for the total sample of *A. clavula* in low, medium and high intensity infections (Table 3.14).

The interquartile ranges were broadly comparable between the total sample of *A. clavula* (Table 3.14) and *A. clavula* in low, medium and high intensity infections of *E. crassum* (Table 3.20). However, values for the 75% and 25% quartiles were completely different. Values for the 25% quartile of *A. clavula* co-occurring with *E. crassum* (Table 3.20) were more comparable with the values for the 75% quartile for the total sample of *A. clavula* (Table 3.14).

A. clavula had negative skewness values in low, medium and high intensity infections of *E. crassum*. It also had a negative kurtosis value for low and high intensity infections of *E. crassum* (Table 3.20; Fig 3.14). In contrast skewness values for the total sample were all positive, and only low and medium intensity infections had negative kurtosis values (Table 3.14; Fig 3.5).

The niche width of *A. clavula* was calculated when it occurred in low, medium and high intensity infections of *E. crassum*. The niche width of *A. clavula* was 0.83 in low, 0.67 in medium and 0.20 in high intensity infections of *E. crassum*. One-way analysis of variance (ANOVA) showed a significant difference in the niche width of *A. clavula* between low, medium and high intensities of *E. crassum* (F ratio = 6.1; df = 2,231; $p \leq 0.003$). Least squares difference post hoc tests a showed a significant difference in the niche width of *A. clavula* between high and low ($p \leq 0.001$), and high and medium intensities of *E. crassum* ($p = 0.011$).

3.11 Examination of the distribution of *E. crassum* when it occurred in low, medium and high intensity infections of *A. clavula.*

In a similar analysis to that described above the distribution of *E. crassum* was examined when it co-occurred with *A. clavula* in low, medium and high intensity infections (Table 3.21). It was then compared to the distribution of the total sample of *E. crassum* in low medium and high intensity infections (Table 3.18). A low intensity infection of *A. clavula* was one to ten worms, a medium intensity infection was eleven to seventy-six worms, and a high intensity infection was seventy-six or more worms.

Approximately 100 *E. crassum* were found at each level of *A. clavula* intensity. The mean location of *E. crassum* ranged from 39.03% in high intensity infections, to 40.34% in medium intensity infections, a difference of 1.13% (Table 3.21). These values compare favourably with the mean locations for *E. crassum* in low, medium and high intensity infections in the total sample (Table 3.18).

Median values for *E. crassum* in low, medium and high intensities of *A. clavula* were lower than mean values, and varied by only 0.57% (Table 3.21). They also compared favourably with the median values from the total sample of *E. crassum* in low, medium and high intensity infections (Table 3.18).

Minimum and maximum values for *E. crassum* in low, medium and high intensity infections of *A. clavula* (Table 3.21) were similar to the values reported for low, medium and high intensities of *E. crassum* in the total sample (Table 3.18), with one exception. The maximum value for *E. crassum* in the presence of *A. clavula* (Table 3.21) was considerably higher than the maximum value for *E. crassum* in the total sample (Table 3.18). Correspondingly, values for the range of occurrence of the two samples followed the same pattern.

Values for the interquartile range were broadly comparable between *E. crassum* in the presence of *A. clavula* (Table 3.21) and *E. crassum* occurring in low, medium and high intensities in the total sample (Table 3.18). 25% quartile values were 35% for *E. crassum* in low, medium and high intensity infections of *A. clavula*, and ranged from 33.3% to 35% for *E. crassum* in the total sample (Table 3.18). Values for the 75% quartile were also comparable between the two samples despite being slightly higher for *E. crassum* in the presence of *A. clavula*.

With the exception of *E. crassum* in low intensity infections in the total sample (Table 3.18), all skewness and kurtosis values for both samples were positive and above one (Fig 3.15; Fig 3.13). Suggesting peaked distributions with asymmetric tails extending towards positive values.

The niche width of *E. crassum* was 0.54 in low intensity infections, 0.13 in medium intensity infections and 0.26 in high intensity infections of *A. clavula*. Analysis of variance showed no significant overall difference in the niche width of *E. crassum* between low, medium and high intensity infections of *A. clavula*. However least squares difference post hoc tests showed a significant difference in the niche width of *E. crassum* between medium and low intensity infections of *A. clavula* ($p = 0.041$).

Table 3.20 Summary statistics for the distribution of *A. clavula* when it occurred in low (1 worm), medium (2-4 worms) and high (5+ worms) intensity infections of *E. crassum* in the intestine of trout from Clogher Lake.

	Low	Medium	High
Count	23	73	138
Mean (± S.D.)	84.23(14.99)	85.24(14.10)	80.46(14.69)
Median	87.55	90.69	84.75
Inter quartile Range	21.30	17.19	16.9
Minimum	56.39	50	42.9
Maximum	99.66	100	100
Range	43.27	50	57.1
Skewness	-0.82	-1.10	-0.88
Kurtosis	-0.79	0.19	-0.19
Lower (25%)	76.02	78.57	74.2
Upper (75%)	97.32	95.76	91.1

Table 3.21 Summary statistics for the distribution of *E. crassum* when it occurred in low (1-15 worms), medium (16-75 worms) and high (76+ worms) intensity infections of *A. clavula* in the intestine of trout from Clogher Lake.

	Low	Medium	High
Count	104	101	115
Mean (± S.D.)	39.15(7.41)	40.34(11.84)	39.03(7.81)
Median	36.76	36.57	36.19
Inter quartile Range	8.86	4.78	7.41
Minimum	25.66	30.59	30.48
Maximum	75	92.04	87.84
Range	49.34	61.45	57.36
Skewness	1.61	2.91	2.87
Kurtosis	3.95	8.09	12.3
Lower (25%)	35	35	35
Upper (75%)	43.86	39.78	42.41

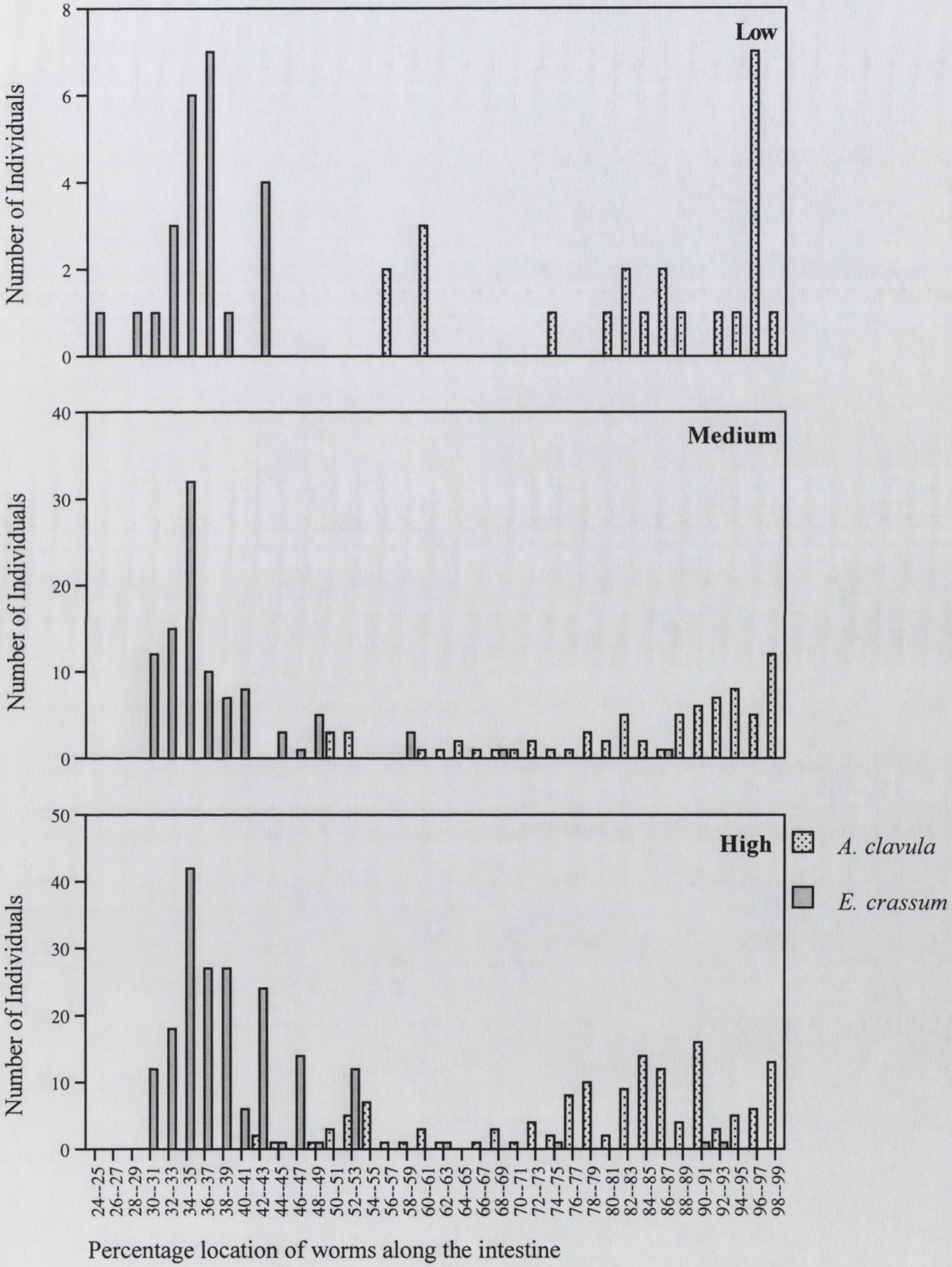

Fig 3.14 Niches of *A. clavula* at low intensity (1worm), medium intensity (2-4 worms), and high intensity (5+ worms) infections of *E. crassum* along the intestine of trout from Clogher Lake.

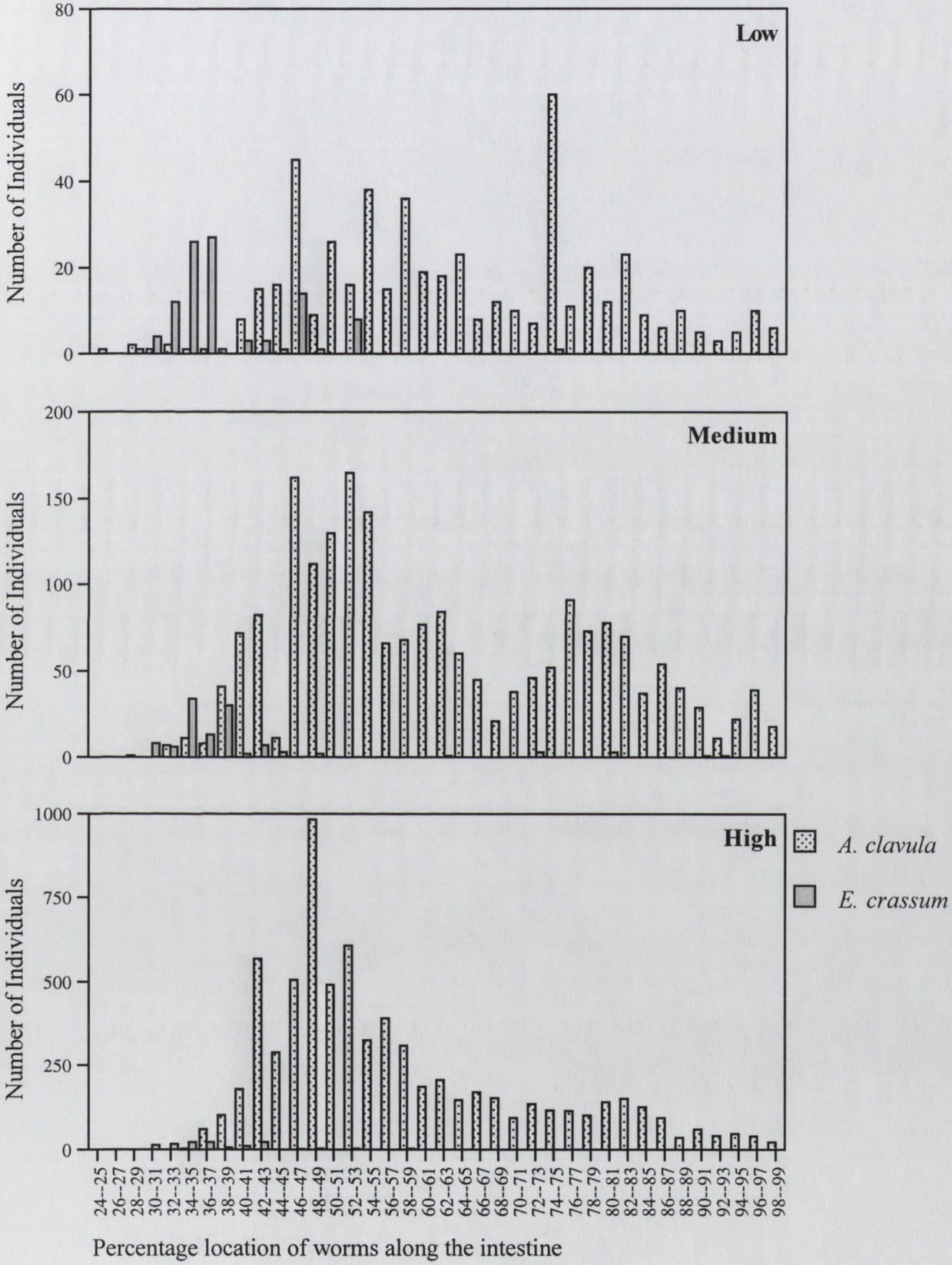

Fig 3.15 Niches of *E. crassum* at low intensity (1-15 worms), medium intensity (16-75 worms), and high intensity (76+ worms) infections of *A. clavula* along the intestine of trout from Clogher Lake.

3.12 Examination of the distribution of *Crepidostomum farionis* when it occurred in low, medium and high intensity infections of *A. clavula* and *E. crassum*.

The distribution of *Crepidostomum farionis* was examined when it occurred in low, medium and high intensity infections of *A. clavula* (Table 3.22) and *E. crassum* (Table 3.23). These distributions were also compared to the distribution of the total sample of *Crepidostomum farionis* when it occurred in low, medium and high intensity infections (Table 3.16).

3.12.1 *Crepidostomum farionis* in low, medium and high intensity infections of *A. clavula*

A total of 406 *Crepidostomum farionis* were found in low intensity infections, 944 in medium intensity infections and 4672 in high intensity infections of *A. clavula*. The mean location decreased from, 74.93% in low intensity infections to 56% in high intensity infections of *A. clavula*, a difference of 18.93% (Table 3.22; Fig 3.16) compared with a decrease of 12.42% from low to medium intensity infections for the total sample (Table 3.16).

Median values of *Crepidostomum farionis* for both samples decreased by approximately 25% from low to high intensity infections (Table 3.16; Table 3.22). Median values in low, medium and high intensity infections for both samples (Table 3.16; Table 3.22) were very similar.

Minimum and maximum values of *Crepidostomum farionis* for low, medium and high intensity infections for the total sample (Table 3.16) and for low, medium and high intensity infections of *A. clavula* (Table 3.22; Fig 3.16) were similar. Hence the range of occurrence of *Crepidostomum farionis* in the two samples was also similar. The largest difference in the range of *Crepidostomum farionis* between the total sample and *Crepidostomum farionis* in the presence of *A. clavula* was 2.83% for medium intensity infections.

The interquartile ranges for medium and high intensities of *A. clavula* (Table 3.22) were comparable with the corresponding values in the total sample (Table 3.16). However the interquartile range of *Crepidostomum farionis* in low intensity infections in the total sample (Table 3.16) was twice the value of the interquartile range of *Crepidostomum farionis* in low intensity infections of *A. clavula* (Table 3.22). Correspondingly, the 25% and 75% quartile values of *Crepidostomum farionis* were comparable for medium and high intensity infections for both samples (Table 3.16; Table 3.22).

Skewness values were positive and below one in medium and high intensity infections for both samples (Table 3.16; Table 3.22), and negative in low intensity infections for both samples. Kurtosis values were negative for all intensities of *Crepidostomum farionis* in the total sample (Table 3.16), and for *Crepidostomum farionis* in medium and high intensity infections of *A. clavula* (Table 3.22).

Niche width values were 0.82 in low intensity infections, 0.72 in medium intensity infections and 0.75 in high intensity infections of *A. clavula*. Analysis of variance showed no significant differences in the niche widths of *Crepidostomum farionis* between low, medium and high intensity infections of *A. clavula*.

3.12.2 *Crepidostomum farionis* in low, medium and high intensity infections of *E. crassum*

A total of 18 *Crepidostomum farionis* were found in low intensity infections of *E. crassum*, 59 in medium intensity infections and 140 in high intensity infections. The mean location ranged from 70.5% in low intensity infections to 77.24% in medium intensity infections, a difference of 6.74% (Table 3.23; Fig 3.17). The mean location of *Crepidostomum farionis* in low intensity infections in the total sample, 68.7% (Table 3.16) was comparable with the mean location of *Crepidostomum farionis* in low intensity infections of *E. crassum*, 70.5% (Table 3.16). However the mean locations of *Crepidostomum farionis* in medium and high intensity infections of *E.*

crassum were considerably higher than the mean locations for the corresponding intensities in the total sample of *Crepidostomum farionis* (Table 3.16).

Median values were higher than mean values for all intensities, and ranged from 73.9% in high intensity infections of *E. crassum* to 86.5% in medium intensity infections of *E. crassum* (Table 3.23). The median value of *Crepidostomum farionis* in low intensity infections of *E. crassum*, 74.77%, was comparable to the median value of *Crepidostomum farionis* in low intensity infections in the total sample, 74.29% (Table 3.16). However, median values of *Crepidostomum farionis* were considerably higher in medium and high intensity infections of *E. crassum* (Table 3.23; Fig 3.17).

Minimum values varied from 30.95% in low intensity infections to 37% in medium intensity infections of *E. crassum*, and maximum values varied from 97.96% in medium intensity infections to 100% in low intensity infections of *E. crassum*. Thus the range of occurrence was largest in low intensity infections, smallest in medium intensity infections and intermediate in high intensity infections of *E. crassum* (Table 3.23). Minimum and maximum values, and hence the range of occurrence of *Crepidostomum farionis*, were broadly comparable between low, medium and high intensity infections for both samples (Table 3.16; Table 3.23).

Values for the 25% quartile of *Crepidostomum farionis* increased from 42.85% in low intensity infections of *E. crassum* to 63.93% in high intensity infections, a difference of 21.08% (Table 3.23). In contrast values for the 25% quartile of *Crepidostomum farionis* for the total sample were highest in low intensity infections and lowest in medium intensity infections (Table 3.16). Values for the 75% quartile of *Crepidostomum farionis* decreased from 93.33% in low intensity infections to 85.65% in high intensity infections of *E. crassum* (Table 3.23). A similar pattern was found for the 75% quartile of *Crepidostomum farionis* in the total sample, although quartile values were considerably lower. The interquartile range of *Crepidostomum farionis* in

the presence of *E. crassum* (Table 3.23) and for the total sample (Table 3.16) decreased substantially from low to high intensity infections.

Kurtosis values were negative for all samples (Table 3.16; Table 3.23). Skewness values were negative for low, medium and high intensity infections of *E. crassum* suggesting a flattened distribution with an asymmetric tail tending towards negative values. Only the skewness value for low intensity infections of *Crepidostomum farionis* in the total sample was negative (Table 3.16).

Niche width values were 0.82 in low intensity infections, 0.43 in medium intensity infections and 0.57 in high intensity infections of *E. crassum*. Analysis of variance showed no significant overall difference in the niche width of *Crepidostomum farionis* between of low, medium and high intensity infections of *E. crassum*. However least squares difference post hoc tests showed that a significant difference existed niche widths of *Crepidostomum farionis* between medium and low intensity infections of *E. crassum* ($p = 0.049$).

Table 3.22 Summary statistics for the distribution of *C. farionis* when it occurred in low (1-15 worms), medium (16-75 worms) and high (76+ worms) intensity infections of *A. clavula* in the intestine of trout from Clogher Lake.

	Low	Medium	High
Count	406	944	4672
Mean (± S.D.)	74.93(15.51)	59.42(20.78)	56(18.13)
Median	75.37	51.73	50
Inter quartile Range	20.05	36.64	26.7
Minimum	30.95	33.41	30.58
Maximum	98.11	100	99.39
Range	67.16	66.59	68.81
Skewness	-0.79	0.57	0.76
Kurtosis	0.33	-1.10	-0.66
Lower (25%)	66.79	41.21	43.06
Upper (75%)	86.84	77.85	69.76

Table 3.23 Summary statistics for the distribution of *C. farionis* when it occurred in low (1 worms), medium (2-4 worms) and high (5+ worms) intensity infections of *E. crassum* in the intestine of trout from Clogher Lake.

	Low	Medium	High
Count	18	59	140
Mean (± S.D.)	70.50(24.81)	77.24(19.88)	72.08(15.72)
Median	74.77	86.5	73.91
Inter quartile Range	50.48	34.66	21.72
Minimum	30.95	37	35.4
Maximum	100	97.96	98.63
Range	69.05	60.96	63.23
Skewness	-0.37	-0.84	-0.56
Kurtosis	-1.35	-0.85	-0.24
Lower (25%)	42.85	56.31	63.93
Upper (75%)	93.33	90.97	85.65

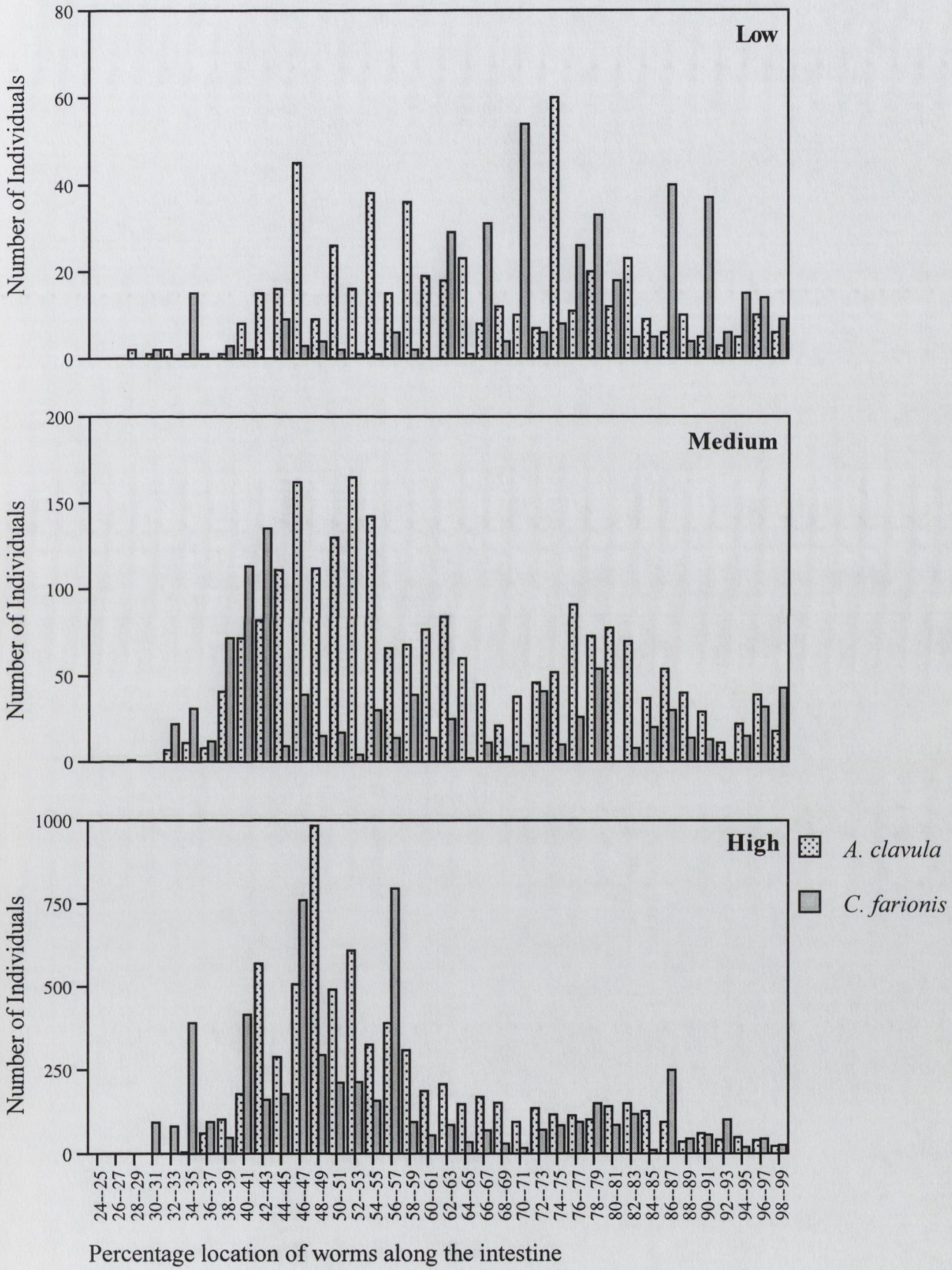

Fig 3.16 Niches of *Crepidostomum farionis* at low intensity (1-15 worms), medium intensity (16-75 worms), and high intensity (76+ worms) infections of *A. clavula* along the intestine of trout from Clogher Lake.

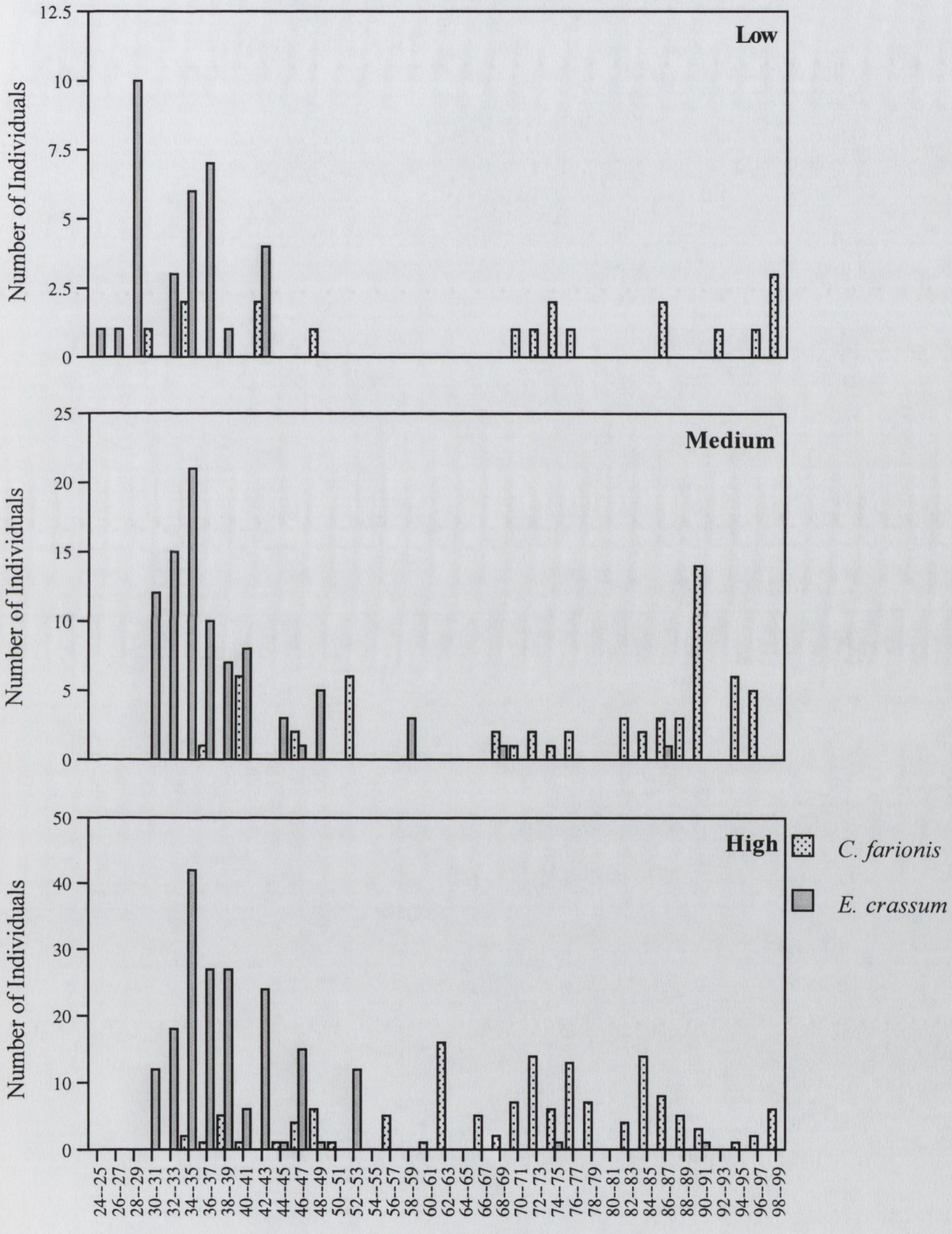

Fig 3.17 Niches of *Crepidostomum farionis* at low intensity (1worm), medium intensity (2-4 worms), and high intensity (5+ worms) infections of *E. crassum* along the intestine of trout from Clogher Lake.

3.13 Discussion

Q. Is the parasite community of brown trout in Clogher Lake characteristic of brown trout in western Ireland / Europe?

Nine parasite species were recorded in the component community in Clogher Lake. Of the nine species, two cestodes and one nematode were allogenic species and only occurred as larval forms, and five parasite species were component species. The acanthocephalan *A. clavula* had the highest prevalence overall, followed by *Crepidostomum farionis*, *E. crassum* and *D. ditremum*, and the highest values for all community parameters were recorded in November. In comparison Molloy *et al.* (1995a) recorded six parasite species from brown trout in Lough Feeagh. Only one allogenic species and three component species were recorded. Similar to Clogher Lake an acanthocephalan (*P. laevis*) had the highest prevalence followed by *E. crassum* and *Crepidostomum farionis*.

Byrne *et al.* (2000) recorded eleven parasite species from four lakes in Co. Donegal, with a maximum of nine parasite species recorded from one lake, Lough Owennamarve. Two species from this lake were allogenic, and seven were component species. The cestode *E. crassum* had the highest prevalence in this lake followed by *D. dendriticum* and *Crepidostomum farionis*. No acanthocephalan species were recorded. The prevalence and abundance values recorded for brown trout in Clogher Lake were considerably higher than any of the values recorded in Lough Feeagh or Bunaveela Lake by Molloy *et al.* (1995a), but were comparable to the values recorded for Lough Owennamarve.

The mean species richness value recorded for Clogher Lake was substantially higher than that recorded for Lough Feeagh or Bunaveela Lake, but was comparable to the value recorded in Lough Owennamarve (Table 3.24). The mean number of individuals recorded for the total sample in Clogher Lake was substantially higher

than the mean number of individuals recorded in Lough Feeagh, Bunaveela Lake and in Lough Owennamarve.

Table 3.24 Summary of the community characteristics for wild brown trout from four lakes in the west of Ireland**

	Clogher Lake§	Lough Feeagh†	Lake Bunaveela†	Lough Owennamarve‡
Total No. Species	9	6	5	9
No. of Component sp.	5	3	1	7
Mean Sp. Richness	2.76	0.87	0.86	3.1
Mean No. Individuals	94.34	8.5	3.3	49.5
Mean Brillouin's Index	0.51	0.09	0.07	0.48
Simpson's Dominance Index	0.44	N/A	N/A	0.48
Berger-Parker Index	0.74	N/A	N/A	0.56
Shannon Diversity Index	0.9	N/A	N/A	0.6

N/A = Not available for this Lake; ** = Standard deviation values have not been presented as they were not available for Lough Feeagh and Bunaveela Lake separately. § = Present study; † = Molloy *et al.*, 1995a; ‡ = Byrne *et al.*, 2000.

The Brillouin's index of diversity values for all trout in Clogher Lake and for infected trout only (0.43(±0.28)) were comparable to the values recorded for trout in Lough Owennamarve. All fish caught in Lough Owennamarve were infected with parasites, therefore the Brillouin's index recorded for infected fish only was the same as that for all fish. For Clogher Lake and Lough Owennamarve, the Brillouin's index values were substantially higher than the values reported for Lough Feeagh and Bunaveela Lake (Table 3.24). The mean Brillouin's index values reported for Clogher Lake and Lough Owennamarve were higher than any of the mean values reported by Kennedy and Hartvigsen (2000), but were within the maximum range of values recorded for the Brillouin's index. Whereas, the mean Brillouin's index values recorded for Lough Feeagh and Bunaveela Lake were comparable to the lowest mean Brillouin's index values reported by Kennedy and Hartvigsen (2000).

Simpson's dominance index, the Berger-Parker index and the Shannon diversity index were calculated for Clogher Lake, these indices were also calculated for Lough Owennamarve but not for Lough Feeagh or Bunaveela Lake. When compared with Lough Owennamarve, Clogher Lake had a lower value for the Simpson's dominance index and higher values for the Shannon diversity and the Berger-Parker indices.

Thus, the parasite community of trout in Clogher Lake showed a number of similarities with the parasite community recorded in Lough Owennamarve. In both cases nine species were found in the component community. Three allogenic species were recorded in Clogher Lake compared to two in Lough Owennamarve. The allogenic species common to both lakes were *D. dendriticum* and *Anisakis* sp. *D. ditremum* was also recorded from Clogher Lake but not from Lough Owennamarve, although it was present in the other lakes in the study. Five component species were recorded in Clogher Lake compared to seven component species in Lough Owennamarve. Three of the component species were common to both lakes, and both lakes had a larval *Diphyllobothrid* as a component species. Prevalence and abundance values were also comparable between the two lakes.

When infracommunity parameters were examined the mean species richness values and Brillouin's index values were comparable between the two lakes. However, diversity and dominance indices showed Clogher Lake to have greater diversity and less dominance than Lough Owennamarve. The greatest difference between both of these lakes was the overwhelming presence of the acanthocephalan *A. clavula* in Clogher Lake, and its complete absence in Lough Owennamarve. No acanthocephalan species was found in any lake in this study, whereas in Clogher Lake *A. clavula* was the dominant species in three out of four sample months, and had the highest overall prevalence, mean abundance and mean intensity. The large numbers of *A. clavula* and *Crepidostomum farionis* recorded in each sample were responsible for the difference in the mean number of individuals recorded between Clogher Lake and Lough Owennamarve.

The parasite community found in Clogher Lake was considerably richer than the communities recorded from Lough Feeagh and Bunaveela Lake by Molloy *et al.* (1995a). Three allogenic species and five component species were found in Clogher Lake compared to one allogenic species and three component species in Lough Feeagh, and no allogenic species and one component species in Bunaveela Lake. The two component species recorded in Lough Feeagh, *Crepidostomum farionis* and *E. crassum* were also component species in Clogher Lake. The component species recorded in Bunaveela Lake, *P. laevis* was not found in Clogher Lake.

The greatest differences between the three lakes were not in the number of allogenic or component species present but the substantial differences recorded in the prevalence, mean abundance and mean intensity values. All values were higher in Clogher Lake. When infracommunity parameters were considered, the mean species richness, the mean number of individuals and the Brillouin's index were also substantially higher in Clogher Lake.

On the basis of the two comparisons, it could be suggested that there are two types of parasite communities in trout in western Ireland. The first type which Clogher Lake and Lough Owennamarve typify, would be characteristic of more mesotrophic waters, giving rise to a greater diversity of parasite species, higher prevalence and abundance values and generally, a much richer and diverse parasite community. The second type which Lough Feeagh typifies, would be characteristic of more oligotrophic waters, resulting in species poor parasite communities, very low levels of diversity and low prevalence and abundance values. This situation presented here is consistent with the ideas of Esch (1971), who suggested that the trophic status of a lake determined the fish species present, which in turn determined the parasite species composition. In this case all the lakes contained brown trout, however it is likely that the invertebrate communities differed between the lakes. More invertebrate species and individuals were available for infection by parasites in Lough Owennamarve, thus giving rise to the richer parasite community recorded in trout. Marcogliese and Cone (1991) examined the metazoan parasites of salmon and brook trout in eight lakes in

Newfoundland, they also concluded that lake characteristics affected the parasite community.

The parasite community of trout from Clogher Lake can also be compared to trout parasite communities from Scotland (Dorucu *et al.*, 1995) and from Norway (Hartvigsen and Halvorsen, 1993). Hartvigsen and Halvorsen (1993) also recorded nine parasite species in the component community of brown trout from four lakes in northern Norway and Dorucu *et al.* (1995) recorded ten helminth species from trout in 21 locations in Scotland. When examined in more detail, a maximum of five parasite species were recorded in any single lake in northern Norway and a maximum of seven species were recorded from any lake in central Scotland. In Norway, two allogenic species were found, both only occurred in one lake, and a maximum of three component species were found in any single lake. In the Scottish study, two allogenic species were recorded, and the maximum number of component species recorded in any single locality was six. Three parasite species (*Crepidostomum farionis*, *E. crassum* and *Diphyllobothrium* sp.) were common to all three studies. The same three species were common to Clogher Lake and the lakes in Scotland, and five parasite species (*Crepidostomum farionis*, *E. crassum*, *D. dendriticum*, *D. ditremum* and *D. sagittata*) were common to Clogher Lake and the lakes in northern Norway.

Dorucu *et al.* (1995) showed that *Crepidostomum farionis* was the most widely distributed species in the Scottish lakes, and *Diphyllobothrium* sp., *E. truttae* and *E. crassum* were the next most widely distributed species. Similarly Hartvigsen and Halvorsen (1993) showed that the digenean *C. metoecus* was the most abundant species in three lakes and *E. crassum* was the most abundant species in the remaining lake. In Clogher Lake the four most prevalent species were *A. clavula*, *Crepidostomum farionis*, *E. crassum* and *D. ditremum*, in that order. When prevalence, mean abundance and mean intensity values were compared (mean abundance values were given in the Norwegian study, and mean intensity values were given in the Scottish study), Clogher Lake had higher values on average than either of the other studies.

Thus, it appeared that there was an element of similarity between the three lakes in terms of the composition of the parasite community, but the parasite community was richer in trout from Clogher Lake. These results are consistent with those of Kennedy and Hartvigsen (2000) who examined the component and infracommunity parameters of brown trout from a number of localities in the British Isles and Norway. They concluded that there was a suite of four trout specialists which occurred commonly, and gave a greater degree of predictability to the community composition.

Q. Is there a seasonal effect at the component community level?

In Clogher Lake a maximum of eight parasite species were recorded in April, and six were recorded in all other months. Five parasite species (*E. crassum*, *Crepidostomum farionis*, *A. clavula*, and *D. ditremum*) occurred in all months, and all were component species in all months. *D. sagittata* and *D. dendriticum* were only recorded in April, *Anisakis* sp. was only recorded in November and *Rhabdochona* sp. was absent in November.

D. sagittata and *D. dendriticum* both had prevalence values lower than 5%. However the mean intensity value for *D. dendriticum* was 45.66(±52), compared to a mean intensity value of 1(±0) for *D. sagittata*. It is likely that both species were present throughout the year, but present at extremely low levels. Kennedy and Moriarty (1987) suggested that the absence of the acanthocephalan *A. anguillae* from eel samples in winter months was also due to the population size having fallen, rather than the parasite actually disappearing over winter. Hine and Kennedy (1974) demonstrated that the population of *P. laevis* could be maintained at a low level by maturing through trout. They also suggested that the presence and abundance of the parasite at any site was related to the presence and abundance of the intermediate and definitive hosts, and the dietary preferences of the definitive host.

The fact that *D. dendriticum* occurred in only one month, with low prevalence and mean abundance values, and its ecological congener *D. ditremum* occurred in all

months with reasonable high prevalence and mean abundance values, could suggest that there was some type of interaction / exclusion occurring. Conneely and McCarthy (1988) recorded a similar pattern, *D. ditremum* occurred in all three sites and had a prevalence of 21.8% in Lough Corrib, whereas *D. dendriticum* only occurred in Lough Corrib, and had a prevalence of 5.3%. Byrne *et al.* (2000) also showed that *D. ditremum* had substantially higher prevalence, mean abundance and mean intensity values than *D. dendriticum* in three lakes where they co-occurred in western Ireland, but in one lake when *D. dendriticum* occurred at high prevalence, *D. ditremum* was absent. In contrast, Andersen and Valtonen (1992) showed that *D. dendriticum* was found in the greatest number of fish hosts and that it most commonly co-occurred with *D. ditremum*.

Hickey and Harris (1947) considered that trout become infected with *Diphyllobothrium* plerocercoids through preying on infected sticklebacks, Halvorsen (1970) agreed with this suggestion but also suggested that fish feeding on infected copepod intermediate hosts could acquire infection. However he concluded that trout represented a dead end in the life cycle of *D. dendriticum* and the three-spined stickleback was a more suitable host. Examination of the stomach contents of trout from Clogher Lake revealed that piscivoury was very uncommon, but feeding on planktonic copepods was reasonably common (Byrne, unpublished). Such dietary preferences could account for the lower prevalence and mean abundance values of *D. dendriticum* and the higher prevalence and mean abundance values of *D. ditremum*.

A similar situation occurred for *D. sagittata* and *S. salmoneus*. Both are ectoparasitic on trout and occur around the gill chamber area, *D. sagittata* favours the gill filaments and *S. salmoneus* favours the opercular cover. However *S. salmoneus* was present as a component species in all months in Clogher Lake, and *D. sagittata* occurred once in April. Conneely and McCarthy (1988) found *S. gordoni* and *D. sagittata* on trout from Lough Corrib. *S. gordoni* occurred in all three locations with a maximum prevalence of 24.1%, whereas *D. sagittata* only occurred in two locations with a maximum prevalence of 3.8%. In contrast Byrne *et al.* (2000) found *D. sagittata* in

three out of four lakes examined in Co. Donegal, and *S. salmoneus* in one lake. In the lake where *S. salmoneus* occurred, *D. sagittata* dominated. This is also a situation which requires further examination.

The absence of *Rhabdochona* sp. in the November sample was probably related to the diet of trout, and or the absence of infected intermediate hosts. The nematode was present as a component species with a high mean intensity value in April, but mean intensity values declined in May and August. Moravec (1995) suggested that there was no obvious annual maturation cycle for parasites in this genus, and that egg producing female nematodes were present throughout the fishing year. However, he suggested that life history patterns appeared to be mainly due to the availability of infected intermediate hosts.

Anisakis sp. utilise fish as intermediate hosts, their final hosts are marine mammals. Thus, the occurrence is *Anisakis* sp. in trout in November, is entirely consistent with it occurring in an autumn running sea trout returning from the sea. However, Clogher Lake does not support a migratory trout population *per se*. It is possible, but unlikely, that in winter flood conditions a small number of migratory sea trout harbouring *Anisakis* sp. reached Clogher Lake. However, *Anisakis* sp. has been previously reported from an entirely landlocked system in Ireland (Kane, 1966).

Prevalence values for four of the five component species recorded in Clogher Lake species showed no distinct seasonal pattern. Only the prevalence of *A. clavula* decreased substantially from May to August and the abundance of *A. clavula* and *Crepidostomum farionis* decreased significantly in August. This decline was followed by an increase in November, a dramatic increase in the case of *A. clavula*. Awachie (1965) examined the ecology of the acanthocephalan *E. truttae* in Wales. He showed that there was a clearly defined seasonal periodicity in the infection of the intermediate host *G. pulex*. The percentage of *G. pulex* infected dropped in the warmer months, until September when an upward trend in incidence corresponding to decreasing water temperatures occurred. Awachie also noticed a corresponding

midsummer drop in the degree of parasitisation of trout. It is likely that the same pattern occurred in Clogher Lake where *A. clavula* used the isopod *Asellus meridianus* as its intermediate host. Chubb (1964) considered the isopod *A. meridianus* to be the intermediate host of the *A. clavula*.

Andrews and Rojanapaibul (1976) examined the ecology of *A. clavula*, and showed that infected *A. meridianus* were present in all months, however they concluded that seasonal changes in water temperature could influence parasite population dynamics. In contrast Kennedy (1984b) could find no evidence of a seasonal cycle in the prevalence or abundance of *A. clavula* in eels. However, he did show that abundance increased every October, similar to the situation in Clogher Lake, and suggested that this was as a result of increased recruitment at this time.

Bwathondi (1976, 1984) examined the biology of *C. metoecus* in brown trout and demonstrated a clear annual seasonality. He showed that there was a winter / spring maximum and a minimum in August. Awachie (1968) demonstrated a similar drop in the prevalence and intensity of *C. metoecus* and *Crepidostomum farionis* in midsummer. He concluded that there was a close relationship between temperature and the life cycles of *Crepidostomum farionis* and *C. metoecus*, and at a temperature above 10°C these two species may not be able to establish themselves in trout. The results reported from Clogher Lake are in agreement with these findings.

Q. Is there a seasonal effect at the infracommunity level?

The midsummer decrease in component community parameters was also reflected at the infracommunity level. The lowest values for the mean species richness, mean number of individuals and Brillouin's index occurred in August, and differences in the mean species richness and mean number of individuals between months were significant. Similar to the situation demonstrated for mean abundance and mean intensity values, the range in the number of individuals recorded was also lowest in August, and increased substantially in November. The Brillouin's index decreased

from May to August, the Shannon diversity index increased slightly during the same period, and the Simpson's dominance and Berger Parker indices decreased.

The results for the infracommunity are in broad agreement with the pattern identified for the component community. Infracommunity parameters peaked in spring, decreased to their lowest point in mid summer and started to rise again in autumn. It would seem likely that the factors affecting seasonality at the component community level have the same effect at the infracommunity level. A number of workers have examined seasonality in parasite populations. In many cases only prevalence and abundance values were examined (Kennedy and Rumpus, 1977; Bwathondi, 1984; Kennedy, 1996c), and in other cases the seasonal occurrence of only one parasite species was examined (Awachie, 1968; Molloy *et al.*, 1995a,b; Kennedy, 1996c).

Few workers have examined parasite communities at the infracommunity level (Kennedy *et al.*, 1997; Marcogliese and Cone, 1998; El-Darsh and Whitfield, 1999; Kennedy and Hartvigsen, 2000) and even fewer workers (Vidal-Martinez *et al.*, 1998; Kennedy, 1997b) have examined seasonality at this level. Kennedy (1997b) showed that the infracommunity parameters of eels do not change significantly from month to month through the summer, and suggested that the apparent tendency of infracommunity parameters to decline in May / June was as a result of stochastic variation. However, results from this study were not directly comparable with those from Clogher Lake.

Q. Did the sex of the host fish affect the parasite community?

There was no significant relationship between the abundance of the four most prevalent parasite species in Clogher Lake and the sex of the host fish. The vast majority of the 161 fish sampled in Clogher Lake were in the 1+ to 3+ age category, only fifteen fish were older than this, therefore the fish sample was quite homogenous. The second factor, which I believe contributed to the lack of any relationship between the abundance of the four most prevalent species and host sex,

was the fact that trout sampled from Clogher Lake were resident brown trout. Consequently, male and female trout had essentially the same life history and feeding strategies.

To put this in context, in a migratory trout fishery, a small proportion of young male trout may remain and mature in the river or lake, these are called precocious males, the remaining trout migrate to sea or the estuary. Of the migrating trout, females predominate over males in many systems (Elliott, 1994). Some fish remain at sea for up to 18 months, but others, called finnock return after about six months. In many populations the majority of finnock are male fish (Elliott, 1994).

Accordingly, it is possible to have male and female fish of the same age, which have spent varying lengths of time at sea, and which are of different size classes and have different feeding ecologies. In this situation a difference in parasite prevalence and mean abundance between male and female fish could be expected.

Awachie (1965) could find no correlation between the sex of brown trout and the prevalence and abundance of *E. truttae*, similarly Molloy *et al.* (1995b) showed that the sex of the host fish had no significant effect on the abundance of *P. laevis*. In contrast, Conneely and McCarthy (1988) showed that there was a significant difference in the prevalence of *C. metoecus* between male and female trout in one site on the Corrib system, with female trout having a higher prevalence. However, for all other parasite at all other sites there was no significant difference in the prevalence or mean abundance between male and female trout. Bwathondi (1976) also recorded a higher prevalence of *C. metoecus* in spawning female trout and suggested that the reproductive hormones active during the spawning period may play a role in the resistance of trout to infection.

Q. Did the age of the host fish affect the parasite community?

Statistical examination of the four most prevalent and abundant species revealed that only *D. ditremum* and *Crepidostomum farionis* had any relationship with the age of the host. The abundance of *D. ditremum* was significantly related to the age of the host fish, for the overall sample, and the April and May samples. A number of other authors have demonstrated a relationship between host age and the prevalence and abundance of *Diphyllobothrium* plerocercoids (Hickey and Harris, 1947; Halvorsen, 1970; Halvorsen and Andersen, 1984; Conneely and McCarthy, 1988). However in these studies the authors have suggested that the increase in the abundance of *Diphyllobothrium* plerocercoids is related to the piscivory of the host fish, and heavily infected fish have accumulated aggregates of plerocercoids from smaller paratenic or transport hosts.

The situation in Clogher Lake was different, examination of stomach contents (Byrne, unpublished) revealed that very few fish were piscivorous. It appeared that infection of trout hosts was as a result of feeding on infected copepod intermediate hosts (Hoole, 1994), and that the greater size of older trout resulted in them eating greater quantities of copepods. However it was not possible to identify the copepods found in trout stomachs in Clogher Lake down to species level because in the majority of cases they had been partially or fully digested.

Kennedy *et al.* (1992) demonstrated that the widely accepted view that eels were almost exclusively benthic in habitat and feeding ecology was not strictly true. Examination of eel parasite communities led to the conclusion that eels of all sizes regularly fed upon planktonic copepods. A similar view is often suggested for trout, that they are planktivorous when young then change to a more benthic diet. It appears that trout of all ages in Clogher Lake were actively feeding on planktonic copepods. Kennedy (1996a) reported huge infestations of *E. crassum* in brown trout and concluded that they must ingest large numbers of copepods, the intermediate host for *E. crassum*. Also, the significant relationship between abundance of *D. ditremum* and

age in spring is probably closely related to the seasonal occurrence of the copepod intermediate hosts. Wyatt and Kennedy (1989) demonstrated that four copepod species found in Slapton Ley only occurred in abundance during discrete periods of the year.

The abundance of the digenean *Crepidostomum farionis* also increased with host age in Clogher Lake. Awachie (1968) also demonstrated an increase in the abundance of *Crepidostomum farionis* with increasing host age. However he also showed that the increase in abundance of *Crepidostomum farionis* only occurred up to a point, after which a decrease became apparent among the oldest and longest fish as they tended to adopt a more carnivorous diet, feeding on larger prey items. Thus, it appears that the increase in the abundance of *Crepidostomum farionis* with host age is related to the diet of the fish. *Crepidostomum farionis* utilises a range of invertebrate species as intermediate hosts, such as *G. pulex* (Awachie, 1968), the mayflies *Cloeon similo*, *Siphlonurus lacustris* (Bwathondi, 1984) and *Ephemera danica* (Brown, 1927). It is probable that as fish grow they consume greater quantities of infected intermediate hosts, resulting in an increased abundance of *Crepidostomum farionis* in older fish.

Q. Is the relationship between categories of intensity of the four most prevalent species significant?

The relationships between categories of intensity for *A. clavula*, *E. crassum* and *Crepidostomum farionis* were examined. For each species pair two contingency tables were prepared, one showing presence / absence data and the other showing low / high intensity data. There appeared to be a slightly positive relationship between the categories of intensity of *A. clavula* and *E. crassum*. In 36.4% cases when *A. clavula* was absent from a fish so was *E. crassum*, and in the majority of cases (56.1%) *A. clavula* occurred with *E. crassum*. For the low / high intensity data a similar relationship emerged, in 54.3% of cases when *A. clavula* was present at high intensity so was *E. crassum* and in the majority of cases (60.5%) both species co-occurred at low intensity.

It would probably be more informative to interpret the relationship between *E. crassum* and *A. clavula*, not so much as one which was positive, but one which was not negative. *E. crassum*'s preferred location in the intestine of trout is the anterior pyloric caeca (Halvorsen and MacDonald, 1972; Conneely and McCarthy, 1988) whereas *A. clavula* occurs over quite a wide range along the intestine (Kennedy and Lord, 1982) so there is little overlap between the species (see Table 3.19). Both species utilise different intermediate hosts, *E. crassum* uses a copepod (Kennedy, 1996a) and *A. clavula* uses an isopod (Chubb, 1964), consequently, dietary intake fails to explain the slightly positive relationship in the categories of intensity of *E. crassum* and *A. clavula*. It is likely that the slightly positive relationship was as a result of stochastic processes.

A similar relationship occurred between the categories of intensity of *Crepidostomum farionis* and *E. crassum*. In 35.1% of cases when *Crepidostomum farionis* was absent from a fish, so was *E. crassum*, and in the majority of cases (54.8%) when *Crepidostomum farionis* was present in a fish so was *E. crassum*. For the low / high intensity data, *Crepidostomum farionis* and *E. crasum* co-occurred at low intensity in 57.1% of cases and they co-occurred at high intensity in 42.3% of cases. The relationship between the categories of intensity of *Crepidostomum farionis* and *E. crassum* is also probably a result of stochastic processes.

The relationship between the categories of intensity of *A. clavula* and *Crepidostomum farionis* was also slightly positive. In this case both species occupied similar locations along the intestine, but used different intermediate hosts. Dorucu *et al.* (1995) demonstrated a positive association between the acanthocephalan *N. rutili* and *Crepidostomum farionis*. They suggested that the presence of one species may improve the establishment and or colonisation prospects of the other species. However, the exact nature of the relationship between *A. clavula* and *Crepidostomum farionis* is unclear, but the dietary preferences of trout possibly do have some part to play in it.

The stochastic nature of these relationships was reaffirmed when the Kendall's tau correlation coefficients were calculated for the total abundance of all species pairs. Coefficient values were negative between *A. clavula* and *E. crassum* and between *E. crassum* and *Crepidostomum farionis* and values were positive between *A. clavula* and *Crepidostomum farionis*. However, only four species pairs were significantly correlated. *Rhabdochona* sp. was significantly correlated with all three cestode species, and both of the larval *Diphyllobothrium* species were significantly correlated. In all cases the significant correlation coefficients were positive.

The most likely reason for the significant positive correlations between both of the larval *Diphyllobothrium* species and between *Rhabdochona* sp. and all of the cestodes is that they use similar intermediate hosts. Both of the larval *Diphyllobothrium* species and *E. crassum* use copepod intermediate hosts (Halvorsen, 1970; Kennedy, 1996a), but according to Moravec (1995) *Rhabdochona* sp. most probably uses a mayfly as an intermediate host. However, the significant positive correlation between *Rhabdochona* sp. and all of the cestode species, and the fact that there were the only significantly correlated species, suggests that fish were feeding on a common copepod intermediate host.

Therefore, it is likely that *Rhabdochona* sp. used a copepod intermediate host in Clogher Lake. Moravec (1995) identified nine species of *Rhabdochona*, of these nothing is known about the biology or life cycle of six species, and of the remaining three much of the work done on the life cycle was carried out in laboratory experiments. So it is possible that some species of *Rhabdochona* use copepod intermediate hosts.

Q. Is the niche occupied by *A. clavula* typical?

A. clavula has been reported from a number of fish hosts in Ireland (Holland and Kennedy, 1997) and Britain (Kennedy, 1974b). It is considered a specialist parasite of eels (Chubb, 1964), however Rojanapaibul (1977) reported that brown trout,

bullhead, grayling, gwyniad, perch, pike, roach and three-spined stickleback could all act as definitive hosts. Kennedy (1985) has shown that competition between *Asellus aquaticus*, the intermediate host of the acanthocephalans *A. anguillae* and *A. lucii* and *Asellus meridianus* the intermediate host of *A. clavula* has prevented *A. clavula* from occurring in the same locality as the other two *Acanthocephalus* species. Correspondingly, *A. clavula* was the only acanthocephalan species found in Clogher Lake. This situation was quite unusual as *A. clavula* was the dominant species in the trout population of Clogher lake, but eels are considered to be its preferred definitive host (Chubb, 1963, 1967; Kennedy and Lord, 1982). Also, Kennedy and Hartvigsen (2000) examined the parasite communities of trout in seventy-two localities in Britain and Norway, and in 97% of localities a trout specialist dominated the community.

For the total brown trout sample, the mean position of *A. clavula* along the intestine was approximately 59%, the maximum position recorded, 100%, corresponded to the anus, and the minimum position recorded, 28.3%, corresponded to the most anterior portion of the pyloric caeca. *A. clavula* occurred over 71.7% of the total length of the intestine. The distribution of *A. clavula* along the length of the intestine approximated a normal distribution. The niche width value recorded for the total sample was 0.84.

When the distribution of *A. clavula* along the intestine of trout was examined for each sample month, a similar pattern emerged. In each month the maximum position corresponded with the anus and the minimum position corresponded with the anterior portion of the pyloric caeca. The mean position of *A. clavula* moved in an anterior direction from May to November, but in all cases *A. clavula* occurred over at least 65.22% of the total length of the intestine. The distribution of *A. clavula* along the intestine approximated normal, except for November, where it was slightly positively skewed. Niche width values decreased from May to November.

The mean position of *A. clavula* in low, medium and high intensity infections moved in an anterior direction as the intensity of infection increased, however, at each intensity level *A. clavula* occurred over a minimum of 65.57% of the length of the

intestine. The distribution of *A. clavula* along the intestine approximated normal. Niche width values increased from low to medium intensity infections and decrease slightly in high intensity infections.

Thus, it can be concluded that *A. clavula* preferably occupied a middle position along the alimentary tract of trout, but site fidelity in individual fish was poor as *A. clavula* was found all along the intestine. Conneely and McCarthy (1988) reported similar findings for the location of *A. clavula* along the intestine of trout from Lough Corrib. They showed that *A. clavula* also occupied a more anterior position, but worms occurred all along the intestine. They also reported that *A. clavula* was found throughout the intestine of eels, but was most abundant in the middle section (Conneely and McCarthy, 1986). Kennedy and Lord (1982) examined the occurrence of *A. clavula* in a number of fish hosts and its preferred definitive host eels. Although it was not possible to compare mean positions of *A. clavula* between eels and trout directly, they also recorded *A. clavula* in a similar position in the intestine, and like the situation in trout, *A. clavula* had a preferred location but was capable of occurring all along the intestine.

There was a tendency for *A. clavula* to inhabit a more anterior position throughout the course of the year. The most posterior mean position was recorded in May and the most anterior mean position was recorded in November. A similar tendency for *A. clavula* to inhabit a more anterior position occurred with increasing infection intensity. In both cases the interquartile range and the deviation about the mean were smallest at the most anterior position, suggesting that the range of *A. clavula* contracted. Also, in high intensity infections the range of *A. clavula* was smaller than the ranges in medium or low intensity infections. Kennedy and Lord (1982) also recorded an anterior shift in mean position with increasing infection intensity, but they demonstrated an extension of the range of *A. clavula* at high infection intensities.

Kennedy and Moriarty (1987) examined the occurrence of *A. anguillae* and A. *lucii* in eels and suggested that most parasites bred in mid summer and were lost from their

hosts, and subsequent to this, recruitment to the next generation began. This pattern probably occurred for *A. clavula* in Clogher Lake. Therefore, in November, when a lot of recruitment had occurred, the mean intensity value for *A. clavula* was extremely high (the highest value recorded for any month) and this resulted in the observed anterior mean position in this month. The contraction in the range of *A. clavula* was probably related to the parasite recruitment / loss process. The loss of parasites probably resulted in the reduction in the range of occurrence, subsequently, recruitment to the next generation occurred, and this explains the higher mean intensity value and more anterior mean position. However, there was considerable variation in the mean positions and standard deviations between individual fish.

Q. Does the niche of *A. clavula* change in the presence of *E. crassum*?

The distribution of *A. clavula* along the intestine of trout in low, medium and high intensity infections was substantially different to the distribution of *A. clavula* when it co-occurred with *E. crassum* in low, medium and high intensity infections. Mean location values were considerably more posterior for *A. clavula* in the presence of *E. crassum*. Minimum location values were also considerably more posterior and consequently the range of occurrence was also reduced. Values for the interquartile range were similar between both groups, however the 25% quartile values recorded for *A. clavula* in the presence of *E. crassum* were actually higher than the 75% quartile values recorded for *A. clavula* alone. The niche width for *A. clavula* also decreased from 0.83 in low intensity infections of *E. crassum* to 0.67 in medium intensity infections and 0.20 in high intensity infections. Niche overlap values also showed that the niches of *A. clavula* and *E. crassum* were quite restricted. The highest overlap value, 0.38, was recorded in August. Niche overlap values recorded in all other months did not exceed 0.2. It can be concluded that the presence of *E. crassum* reduced the realised niche of *A. clavula* in the intestine of trout in Clogher Lake.

Interactions between cestodes and acanthocephalans in fish have been reported on a number of occasions (Crompton and Whitfield, 1968; Chappell, 1969; Grey and

Hayunga, 1980). Holmes (1961, 1962a,b) reported that the presence of the acanthocephalan *Moniliformis dubius* interfered with the ontogenic migration of the cestode *Hymenolepis diminuata*. Chappell (1969) and Grey and Hayunga (1980) examined the interactions between cestodes and acanthocephalans in fish and reported that in all cases the cestode was displaced by the acanthocephalan. However, in Clogher Lake it appears that the niche of the acanthocephalan was being affected by the presence of the cestode. The presence of *E. crassum* resulted in *A. clavula* occupying a more posterior position in the intestine of trout.

Q. Does the niche of *E. crassum* change in the presence of *A. clavula*?

Comparison of niche parameters revealed very little difference between the niches of *E. crassum* in low, medium and high intensity infections, and *E. crassum* co-occurring with *A. clavula* in low, medium and high intensity infections. Thus it can be concluded that *A. clavula* in low, medium or high intensity infections, appears to have no noticeable effect on the niche of *E. crassum* in trout. This finding is contrary to the findings of Chappell (1969) and Grey and Hayunga (1980).

Q. Is the niche of *Crepidostomum farionis* typical?

Many studies have recorded *Crepidostomum farionis* from brown trout in Ireland (Corbett, 1955; Kane 1966; Pippy, 1969; Fitzgerald and Mulcahy, 1983; Conneely and McCarthy, 1984, 1988; Molloy *et al.*, 1995a), however few have considered the microhabitat distribution of *Crepidostomum farionis* in brown trout (Thomas, 1957, 1958; Awachie, 1968; Bwathondi, 1984), and none have examined it in detail.

The mean location of *Crepidostomum farionis* in the total sample of fish in Clogher Lake was 57.78%. The maximum location of *Crepidostomum farionis*, 100%, corresponded to the anus, and the minimum location, 30.58%, corresponded to the anterior portion of the pyloric caeca, therefore approximately 70% of the intestine was occupied by *Crepidostomum farionis*. When monthly samples were examined the

mean position *Crepidostomum farionis* became more posterior from April to August, but in all cases a minimum of 66% of the intestine was occupied. Niche width values were also comparable between April, May and August but smaller for November. This month also had the smallest interquartile range and deviation about the mean, which corresponded with the reduced niche width. The mean position of *Crepidostomum farionis* also became more anterior as infection intensity increased, but similar to the situation for the monthly samples, a minimum of 65% of the intestine was occupied. Niche width values were comparable between low, medium and high intensity infections.

Crepidostomum farionis is normally considered to be a parasite of the hind-gut region of trout (Conneely and McCarthy, 1988). However, many of the studies which have recorded *Crepidostomum farionis* in the hind-gut of trout, have also recorded the congeneric species *C. metoecus* (Corbett, 1955; Conneely and McCarthy, 1988; Thomas, 1958). Awachie (1968) demonstrated that *Crepidostomum farionis* and *C. metoecus* exhibited site segregation along the length of the intestine of trout. *C. metoecus* preferentially occupies the pyloric caeca and anterior portion of the intestine, and *Crepidostomum farionis* is mostly found in the posterior portion of the intestine. However, in Clogher Lake *Crepidostomum farionis* was the only species found and worms had a preference for the middle section of the intestine, but worms occurred over a minimum of 66% of the intestine in any single month. Therefore, it is conceivable that the main reason for the more posterior distribution previously recorded for *Crepidostomum farionis* was the presence of *C. metoecus* in the anterior portion of the intestine.

The mean position of *Crepidostomum farionis* became more anterior as infection intensity increased, and from August to April. The more anterior mean position recorded in April was consistent with the higher mean abundance value recorded in this month. Correspondingly, as the mean abundance values decreased in May and August, mean positions became more posterior, however in November when the mean abundance value increased again, the mean position became more anterior.

Such anterior migration has also been reported in acanthocephalans (Kennedy and Lord, 1982), and it is generally associated with a greater spread of the parasite at higher levels of infection (Awachie, 1966; Muzzall, 1980). Similar to the situation with *A. clavula*, the anterior shift in the mean position of *Crepidostomum farionis* with increasing infection intensity was a population characteristic, because at the level of the individual fish parasites still occurred over the length of the intestine.

Q. Does the niche of *Crepidostomum farionis* change in the presence of *E. crassum*?

The distribution of *Crepidostomum farionis* in low intensity infections was very similar to the distribution of *Crepidostomum farionis* when it co-occurred with *E. crassum* in low intensity infections. Mean positions, niche width values and the interquartile ranges and deviations about the mean were comparable. However when the distribution of *Crepidostomum farionis* occurring in medium and high intensity infections was compared with *Crepidostomum farionis* co-occurring with *E. crassum* in medium and high intensity infections, a different pattern emerges. Mean positions were substantially more posterior for *Crepidostomum farionis* co-occurring with *E. crassum*. Interquartile ranges were comparable between the two groups, but values for the 25% quartile were also substantially more posterior for *Crepidostomum farionis* co-occurring with *E. crassum*. Niche width values were substantially smaller for *Crepidostomum farionis* co-occurring with *E. crassum*, and minimum location values for *Crepidostomum farionis* co-occurring with *E. crassum* in medium and high intensity infections also were more posterior. However, this shift in the mean position of *Crepidostomum farionis* when it co-occurred with *E. crassum* in medium and high intensity infections also appears to be a population characteristic, because in all cases nearly the entire intestine was occupied by *Crepidostomum farionis*, and niche overlap values were high.

Halvorsen and MacDonald (1972) demonstrated an interaction between the cestode *Cyathocephalus truncatus* and the digenean *C. metoecus* in brown trout. They showed

that *C. metoecus* preferentially occupied a more anterior position in the pyloric caeca when it occurred alone, but when it co-occurred with *C. truncatus* it showed a preference for the posterior pyloric caeca. Although two different species were involved in this example, the cestode *C. truncatus* occupied a similar location in the intestine to *E. crassum*, and *C. metoecus* and *Crepidostomum farionis* are closely related species. Kennedy and Hartvigsen (2000) also demonstrated a negative association between *E. crassum* and *C. metoecus* and interpreted this as strong presumptive evidence for interspecific interaction. In contrast, Conneely and McCarthy (1988) also found *E. crassum* and *C. metoecus* in the pyloric caeca of trout. They showed that the infection intensities of both species were not significantly positively or negatively correlated, and thus concluded that there was no antagonist relationship between the two species.

In Clogher Lake the substantial posterior shift of the mean position, and corresponding reduction in niche width of *Crepidostomum farionis* in the presence of *E. crassum* could be interpreted as evidence of an interspecific interaction. However, if such an interaction exists, it is only visible at the component community level, as at the infracommunity level *Crepidostomum farionis* occupies almost the entire intestine.

Q. Does the niche of *Crepidostomum farionis* change in the presence of *A. clavula*?

A comparison of the niche of *Crepidostomum farionis* when it co-occurred with *A. clavula* was also made. In this situation the mean and median location values, the range of intestine occupied by *Crepidostomum farionis* and the deviation about the mean were comparable between *Crepidostomum farionis* occurring alone at all intensities and *Crepidostomum farionis* co-occurring with *A. clavula* at all intensities. However, the interquartile range recorded for *Crepidostomum farionis* in low intensity infections was considerably larger than the interquartile range recorded for *Crepidostomum farionis* co-occurring with *A. clavula* in low intensity infections. The

difference in the interquartile ranges resulted from the 25% quartile value being much more posterior for *Crepidostomum farionis* when it co-occurred with *A. clavula*. In this situation such a difference is probably a result of stochastic variation.

In both groups there was a distinct anterior shift of the mean and median positions as population density increased, which suggests that *Crepidostomum farionis* in the presence of *A. clavula* is behaving in the same manner as the total sample of *Crepidostomum farionis*. This also supports the contention that there was no interspecific interaction between the two species. However, niche width values for *Crepidostomum farionis* did decrease from low to medium intensity infections of *A. clavula*, but they increased again in high intensity infections of *A. clavula*. Also, the magnitude of the decrease in niche widths was considerably smaller than the magnitude of the decrease in niche width values when *Crepidostomum farionis* co-occurred with *E. crassum*. Examination of niche overlap values also support the contention that there was no interspecific interaction between these species, as they had the highest overall niche overlap value and the highest overlap value in two out of four months.

In one of the few studies to consider the potential for interaction between digeneans and acanthocephalans, Dorucu *et al.* (1995) showed that a positive relationship existed between *Crepidostomum farionis* and *N. rutili*. They postulated that the positive interaction could result from one species improving the establishment or survival prospects of the other, or that the presence of both species in the intestine of trout may have implications for the immune response of the host. This supports the findings from Clogher Lake, also a positive, but not significant, correlation coefficient existed between *Crepidostomum farionis* and *A. clavula* in Clogher Lake.

Q. Is the niche of *E. crassum* typical?

Examination of niche data for *E. crassum* in Clogher Lake, showed that there was very little difference in the niche occupied by the parasite between sample months.

The preferred site was the anterior pyloric caeca, although examination of the range of occurrence suggests that some individuals occurred in the intestine. A similar situation was found for *E. crassum* in low, medium and high intensity infections.
It is generally accepted that the preferred location of *E. crassum* in the gut of trout is the anterior pyloric caeca (Halvorsen and MacDonald, 1972; Conneely and McCarthy, 1988; Kennedy, 1996a) and the results from Clogher Lake support this finding.

Kennedy (1996a) demonstrated that the infection of trout by plerocercoids of *E. crassum* commenced in spring and continued until July, that small plerocerciform parasites initially located in the intestine and then some moved into the pyloric caeca, while others (the majority in heavy infections) were lost from fish. A total of 320 *E. crassum* were recorded from the total sample of 161 trout from Clogher Lake, resulting in very low mean abundance and mean intensity values when compared to a mean intensity value of 84 reported by Wootten (1972). As a result, there was no obvious change in the niche recorded for *E. crassum* in trout throughout the year, or in low, medium and high intensity infections. The most posterior mean position was recorded in April and the range of occurrence was highest in April, *E. crassum* occurred along most of the intestine.

This could be interpreted as evidence that plerocerciform parasites initially occupied the intestine, and that some were lost from the fish (hence the range of occurrence over most of the intestine). Whereas, others migrated to the pyloric caeca (hence the more anterior mean position and restricted range in subsequent months – by that time mortality and subsequent loss had already occurred). More evidence for this theory comes from the fact that the range of occurrence of *E. crassum* decreased substantially and the mean position became more anterior in May and August. However, examination of mean intensity values for *E. crassum* showed that values increased from April to a peak in May and subsequently decreased in August, and the value recorded in August was higher than that recorded in April. Kennedy (1996a)

identified midsummer as the peak infection period of *E. crassum*, which could account for the higher mean intensity value in August.

The opposite situation may be equally true, that the change in the niche of *E. crassum* in April was in no way related to a spring recruitment of parasites. It was just a stochastic population event, and that the increased range of occurrence recorded in April and in high intensity infections, was as a result of random mortality and loss of the cestode from the fish. Because mean abundance and mean intensity values were consistently low for *E. crassum* in Clogher Lake, and there was no obvious pattern, it was not possible to definitively rule in, or rule out, either scenario.

Chapter 4

Examination of the infra and component communities of wild and stocked brown trout in Lough Feeagh

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4.1 Organisation of chapter four

One-way analysis of variance (ANOVA) was used to compare the total abundance data for each parasite species between sample years. For wild and stocked trout the total abundance of a number of parasite species were significantly different between years (see methods). However, for all parasite species which were significantly different raw data was examined visually and statistically (see methods chapter), and on the basis of these examinations it was decided to combine sample years.

The component parasite community of wild trout in Lough Feeagh was first examined for each sample month. Component community parameters for each parasite species were examined and summary characteristics for the component community were presented. In the following section the abundance of the four most prevalent species (*P. laevis*, *A. clavula*, *Crepidostomum farionis*, *E. crassum*) was statistically examined in relation to the month and year of host capture, sex and age of the host fish.

Stocked trout from Lough Feeagh were then examined in the same manner. The component parasite community was examined for each sample month and then parameters were examined for each parasite species. Finally summary characteristics for the component community in stocked trout were presented. The four most prevalent species (*P. laevis*, *A. clavula*, *Crepidostomum farionis*, *E. crassum*) were also statistically examined in relation to the month and year of host capture, sex of the host fish and the age of the host fish.

The component communities of wild and stocked trout in Lough Feeagh were then compared. They were first compared for the total sample and then for each sample month. Following this, the summary characteristics presented for the component community in wild and stocked trout were compared, and finally, the component communities of wild and stocked trout were compared by species.

The second part of the chapter deals with the infracommunities of wild and stocked trout in Lough Feeagh. First the helminth infracommunity for the total sample of wild trout was examined, then the infracommunities of only the intestinal parasite species were examined. Finally the relationships in intensity between the four most prevalent species (*P. laevis*, *A. clavula*, *Crepidostomum farionis*, *E. crassum*) were examined using contingency tables, and Kendall's tau was used to examine the relationships between all parasite species in Lough Feeagh.

The helminth infracommunities of stocked trout were examined in a similar manner. First the total helminth infracommunity was examined and then the infracommunities of only intestinal species were examined and finally contingency tables and Kendall's tau were used to examine the relationships in abundance between the four most prevalent species, and all parasite species, respectively. Finally, helminth infracommunities were compared between wild and stocked fish, firstly total infracommunities were compared and then the infracommunities of only intestinal helminths were compared.

4.2 Helminth component community in wild trout in Lough Feeagh

4.2.1 Examination of component community data for all wild trout in Lough Feeagh

Eleven parasite species were identified from wild brown trout in Lough Feeagh (Table 4.1): four nematodes, two identified to species level (*Cystidicola farionis*, *Cystidicoloides tenuissima*), and two identified to generic level (*Rhabdochona* sp., *Anisakis* sp.), two cestode species (*Eubothrium crassum*, *Diphyllobothrium ditremum*) two acanthocephalan species (*Pomphorhynchus laevis*, *Acanthocephalus clavula*), one digenean species (*Crepidostomum farionis*), one monogenean species (*Discocotyle sagittata*) and one copepod species (*Salmincola salmoneus*).

Two parasite species, *D. ditremum* and *Anisakis* sp. were allogenic, the remaining nine species were autogenic (Table 4.1). *D. ditremum* and *Anisakis* sp. were also the only two larval species present. When the overall parasite prevalence in wild trout in Lough Feeagh was examined, seven species were component, and four species, *Cystidicola farionis*, *Anisakis* sp., *C. tenuissima*, and *S. salmincola* were not.

The acanthocephalan *P. laevis* had the highest overall prevalence in wild trout in Lough Feeagh (Table 4.1). The digenean *Crepidostomum farionis* had the highest values for all remaining component community parameters, mean abundance, mean intensity, range, and variance to mean ratio. *Anisakis* sp. was randomly dispersed, all other species were over dispersed.

4.2.2 Examination of component community data by month

The component community data for wild trout in Lough Feeagh was examined by sample month, and trends for individual parasite species are also discussed. Results are presented in Tables 4.2 – 4.5 for each month (April, May, August, November). Figure 4.1 shows the prevalence, mean abundance and mean intensity of the four most prevalent species, *E. crassum*, *Crepidostomum farionis*, *P. laevis* and *A. clavula* in wild trout in Lough Feeagh.

Ten species were recorded in April and nine were recorded in all other months. *Cystidicola farionis* was absent in August. Two species were recorded in only one month, *Anisakis* sp. in April, and *C. tenuissima* in August. The remaining eight species were recorded in all months.

Prevalence

The highest values for all community parameters were recorded in May, *P. laevis* had the highest prevalence (Fig 4.1), and *Crepidostomum farionis* had the highest values for all remaining parameters. Prevalence of *Cystidicola farionis* and *Anisakis* sp. did not exceed 10% in any month. For all remaining species prevalence exceeded 10% in at least one month.

Component Species

Four component species were recorded in April, five in May, eight in August, and seven in November. Only *Crepidostomum farionis*, *P. laevis* and *A. clavula* were component species in all months.

Mean Abundance

Crepidostomum farionis had the highest mean abundance value in April and May, values exceeded ten. *P. laevis* had the highest mean abundance values in August and November (Fig 4.1). For all other parasites, in all other months, with the exception of *P. laevis* in May, mean abundance values were below five. Seven parasite species had mean abundance values below one in April, this decreased to five in May, three in August, and increased to four in November.

Mean Intensity

Crepidostomum farionis had the highest mean intensity values in April and May, *C. tenuissima* had the highest mean intensity value in August and *A. clavula* had the highest mean intensity value in November (Fig 4.1). Mean intensity values were variable, and no trends emerged. For example, in April, the nematode *Cystidicola*

farionis had a low prevalence value, a low mean abundance value and the second highest mean intensity value.

4.2.3 Examination of component community by parasite species

E. crassum

Values for all community parameters of *E. crassum* were lowest in April and increased throughout the year. The variance to mean ratio and range peaked in August: all other parameters peaked in November. Although November had the highest prevalence, mean abundance and mean intensity, values were not notably higher than August. Similarly, values for the range and variance to mean ratio recorded in August were not notably higher than those recorded in November.

Crepidostomum farionis

All community parameters for *Crepidostomum farionis*, with the exception of mean intensity, were lowest in November and increased throughout the spring. The mean intensity value was lowest in August. The prevalence peaked in April, and all other values peaked in May.

P. laevis

All community parameters for *P. laevis*, with the exception of the variance to mean ratio, were highest in May, and decreased steadily throughout the year. November had the highest variance to mean ratio value and the lowest prevalence value. April had the lowest values for all other community parameters

A. clavula

A. clavula had the lowest community parameters in April and the highest in May. August had lower values than November for all community parameters except prevalence, however prevalence values were similar between the two months.

4.2.4 Summary characteristics of the component community

Component community characteristics for wild brown trout in Lough Feeagh are summarised in Table 4.6. At least 95% of fish were infected with parasites in each month. No month had 100% infection.

Fish caught in May had the most parasite individuals, and fish caught in November had the lowest number of parasite individuals. All months had eight autogenic species, and only April had more than one allogenic species. The number of component species rose through the year, from four in April, to a peak of eight in August, and decreased to seven in November. Seven of the species recorded were considered specialists in trout.

Crepidostomum farionis was the dominant species in April and May. It accounted for over half the total number of parasite individuals recorded in April and over 25% of the parasite individuals recorded in May. *P. laevis* was the dominant species in the two remaining months, and accounted for 26% and 24% percent of the total number of parasite individuals recorded in August and November respectively (Table 4.6). The proportional abundance (*P*i) values recorded for *P. laevis* were much lower than the *P*i value recorded for *Crepidostomum farionis*. In all months the dominant species was autogenic, and a specialist parasite of trout in Ireland.

4.3 Statistical examination of the four most prevalent species in wild trout in Lough Feeagh

One-way analysis of variance (ANOVA) was used to examine the relationship between the abundance of the four most prevalent parasite species in wild trout in Lough Feeagh (*P. laevis*, *A. clavula*, *Crepidostomum farionis*, *E. crassum*) the month and year of host capture, the age of the host fish, and the sex of the host fish. In all cases parasite abundance data was overdispersed, so all analysis was done log (x+1) transformed data. In all cases only significant relationships have been shown.

4.3.1 Month and year of host capture

When the total fish sample was examined by month significant differences were found in the abundance of *Crepidostomum farionis* (F ratio = 11.0; df = 3,253; $p \leq 0.0001$) and *P. laevis* (F ratio = 6.7; df = 3,253; $p \leq 0.0003$). The mean abundance of *Crepidostomum farionis* ranged from 16.1(± 28.4) in May to 2.04(± 5.4) in November, mean abundance values for *P. laevis* ranged from 1.87(± 3.9) in April to 9.05(±11.8) in May. The total fish sample was then divided by year and examined by month. *P. laevis* was the only species which showed significant differences in abundance between months in 1997 (F ratio = 7.0; df = 3,158; $p \leq 0.0003$), and *Crepidostomum farionis* was the only species which showed significant differences in abundance between months in 1998 (F ratio = 20.0; df = 2,92; $p \leq 0.0001$).

The intensity of the four parasite species in each sample month was compared between the two sample years. As there was only one April sample, in 1997, it was not possible to compare between years. The intensity of *Crepidostomum farionis* differed significantly between May 1997 and May 1998 (F ratio = 10.9; df = 1,30; $p \leq 0.003$). The mean intensity of *Crepidostomum farionis* in May 1997 was 1.62(± 3.86) compared to a mean abundance value of 30.59(± 34.52) in 1998. No other species differed significantly between months in 1997 and 1998.

4.3.2 Sex of host fish

When the relationship between the abundance of the four most prevalent species and the sex of the host fish was examined only the abundance of *P. laevis* in April 1997 differed between the sexes (F ratio = 5.6; df = 1, 58; p = 0.026), females had more worms. For all other situations regardless of how the samples were divided, either by year or month or by year and month no significant differences were reported in the abundance of the four parasite species between male and female fish.

4.3.3 Age of host fish

The relationship between the age of host fish and the abundance of the four most prevalent species in Lough Feeagh was also examined. The sampling protocol for Lough Feeagh aimed to catch pond reared stocked fish and equivalent samples of wild fish, therefore the majority of fish were one to two years old. There were some smaller three year old fish and one fish which was four years old. For the total fish sample a significant relationship between age and the abundance of *P. laevis* (F ratio = 3.0; df = 3,253; p = 0.03) existed, in all cases older fish had greater abundance values for *P. laevis*. When the relationship between age and abundance was examined by month for the total fish sample, no significant relationships were found.

The relationship between the abundance of the four parasite species and age was examined by year and by sample month within each year. A significant relationship between the abundance of *P. laevis* and age was found for the total sample (F ratio = 3.1; df = 3, 158; p = 0.031) and the August sample (F ratio = 5.2; df = 1, 54; p = 0.011) in 1997. In 1998 a significant relationship existed between the total abundance of *Crepidostomum farionis* and age (F ratio = 3.8; df = 2, 92; p = 0.03) and the total abundance of *E. crassum* and age (F ratio = 6.8; df = 2, 92; p = 0.01). In both cases the abundance of *Crepidostomum farionis* and *E. crassum* increased with age. For the August sample there was a significant relationship between the abundance of *P. laevis* and age (F ratio = 5.2; df = 1,30; p = 0.01).

Table 4.1 Component Population data for all wild trout in Lough Feeagh (1997 – 1998, $n = 257$).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	26.45	2.17(5.7)	8.19(8.6)	0 – 38	14.96
Crepidostomum farionis	IN	45.91	7.95(18.9)	17.31(24.9)	0 – 143	44.91
Pomphorhynchus laevis	IN	67.31	4.76(8.2)	7.07(9.1)	0 – 80	14.11
Acanthocephalus clavula	IN	26.07	2.79(10.6)	10.64(18.7)	0 – 90	40.4
Diphyllobothrium ditremum	V	15.56	0.82(3.1)	5.28(6.2)	0 – 26	11.55
Rhabdochona sp.	IN	18.68	1.21(5.1)	6.35(10.4)	0 – 54	21.76
Cystidicola farionis	SB	3.89	0.36(2.7)	10.22(10.7)	0 – 31	7.11
Anisakis sp.	IN	0.39	0.003(0.1)	1	0 – 1	1
Cystidicoloides tenuissima	S	3.89	0.50(4.1)	12.8(17.6)	0 – 45	34.32
Discocotyle sagittata	G	13.23	0.24(0.7)	1.79(1.2)	0 – 6	2.28
Salmincola salmoneus	G	9.33	0.15(0.6)	1.63(1.2)	0 - 6	2.34

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.2 Component Population data for wild trout in Lough Feeagh in April (1997 – 1998, $n = 60$).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	8.30	0.30(1.4)	3.60(3.7)	0 -10	6.47
Crepidostomum farionis	IN	66.66	11.66(21.3)	17.50(24.1)	0 - 95	38.84
Pomphorhynchus laevis	IN	48.33	1.87(3.9)	3.86(4.9)	0 - 24	8.24
Acanthocephalus clavula	IN	15	0.66(2.5)	4.33(5.4)	0 - 18	9.79
Diphyllobothrium ditremum	V	8.33	0.23(1.3)	2.80(4)	0 - 10	7.33
Rhabdochona sp.	IN	51.66	4.42(9.9)	8.28(12.4)	0 - 54	22.18
Cystidicola farionis	SB	6.66	0.78(3.7)	15.66(7.5)	0 - 23	17.57
Anisakis sp.	IN	1.66	0.02(0.1)	1(0)	0 - 1	1
Discocotyle sagittata	G	8.33	0.10(0.4)	1.20(0.5)	0 - 2	1.25
Salmincola salmoneus	G	1.66	0.02(0.1)	1(0)	0 - 1	1

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.3 Component Population data for wild trout in Lough Feeagh in May (1997 – 1998, n = 64).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	17.19	1.06(3.6)	6.18(6.9)	0 - 22	12.25
Crepidostomum farionis	IN	50	16.10(28.4)	32.22(33.2)	0 - 143	50.13
Pomphorhynchus laevis	IN	90.63	9.05(11.8)	9.98(12)	0 - 80	15.32
Acanthocephalus clavula	IN	34.37	4.59(15)	13.36(23.4)	0 - 90	48.66
Diphyllobothrium ditremum	V	9.38	0.20(0.9)	2.17(2)	0 - 6	3.62
Rhabdochona sp.	IN	4.69	0.11(0.6)	2.33(1.5)	0 - 4	2.94
Cystidicola farionis	SB	6.25	0.61(3.9)	9.75(14.2)	0 - 31	25.09
Discocotyle sagittata	G	4.69	0.11(0.5)	2.33(0.6)	0 - 3	2.36
Salmincola salmoneus	G	15.63	0.28(0.9)	1.80(1.6)	0 - 6	2.76

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.4 Component Population data for wild trout in Lough Feeagh in August (1997 – 1998, n = 88).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	38.64	3.49(7.4)	9.03(9.6)	0 - 38	15.53
Crepidostomum farionis	IN	38.64	2.50(6.2)	6.47(8.6)	0 - 36	15.15
Pomphorhynchus laevis	IN	73.86	4.14(5.9)	5.60(6.2)	0 - 29	8.39
Acanthocephalus clavula	IN	27.27	2.63(8.9)	9.63(15.2)	0 - 72	30.11
Diphyllobothrium ditremum	V	15.91	1.26(4.2)	7.93(7.9)	0 - 26	14.21
Rhabdochona sp.	IN	6.82	0.17(0.8)	2.50(1.8)	0 - 5	3.4
Cystidicoloides tenuissima	S	11.36	1.45(7)	12.8(17.6)	0 - 45	33.62
Discocotyle sagittata	G	15.91	0.32(0.9)	2(1.1)	0 - 4	2.28
Salmincola salmoneus	G	10.22	0.18(0.6)	1.78(1.1)	0 - 4	2.22

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.5 Component Population data for wild trout in Lough Feeagh in November (1997 – 1998, $n = 45$).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	40	3.64(6.9)	9.11(8.5)	0 - 31	13.19
Crepidostomum farionis	IN	26.67	2.04(5.4)	7.66(8.3)	0 - 23	14.08
Pomphorhynchus laevis	IN	46.67	3.73(7.9)	8(10.2)	0 - 40	16.91
Acanthocephalus clavula	IN	26.66	3.31(0.5)	12.42(22.3)	0 - 79	46.93
Diphyllobothrium ditremum	V	33.33	1.62(3.8)	4.87(5.3)	0 - 16	8.84
Rhabdochona sp.	IN	17.77	0.53(1.3)	3(1.7)	0 - 5	3.38
Cystidicola farionis	SB	4.44	0.13(0.6)	3(0)	0 – 3	2.94
Discocotyle sagittata	G	26.66	0.44(1)	1.67(1.4)	0 – 6	2.41
Salmincola salmoneus	G	8.88	0.09(0.3)	1(0)	0 – 1	0.94

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.6 Component Population characteristics of wild trout in Lough Feeagh in 1997 – 1998.

Characteristics	April	May	August	November
No. of fish examined	60	65	88	45
Percentage infected	96.66	98.46	95.45	95.55
No. of parasite species	10	9	9	9
Total no. of parasites	1203	2056	1420	700
No. of autogenic sp.	8	8	8	8
No. of allogenic sp.	2	1	1	1
No. of component sp.	4	5	8	7
No. of specialists sp.	7†	7†	7†	7†
*P*i of dominant sp.	0.58	0.28	0.26	0.24
Identity of dominant sp.	*Crepidostomum farionis*	*Crepidostomum farionis*	*P. laevis*	*P. laevis*
Character of dominant sp.	Specialist, autogenic	Specialist, autogenic	Specialist, autogenic	Specialist, autogenic

† The acanthocephalan *P. laevis* is considered a specialist in trout in Ireland.

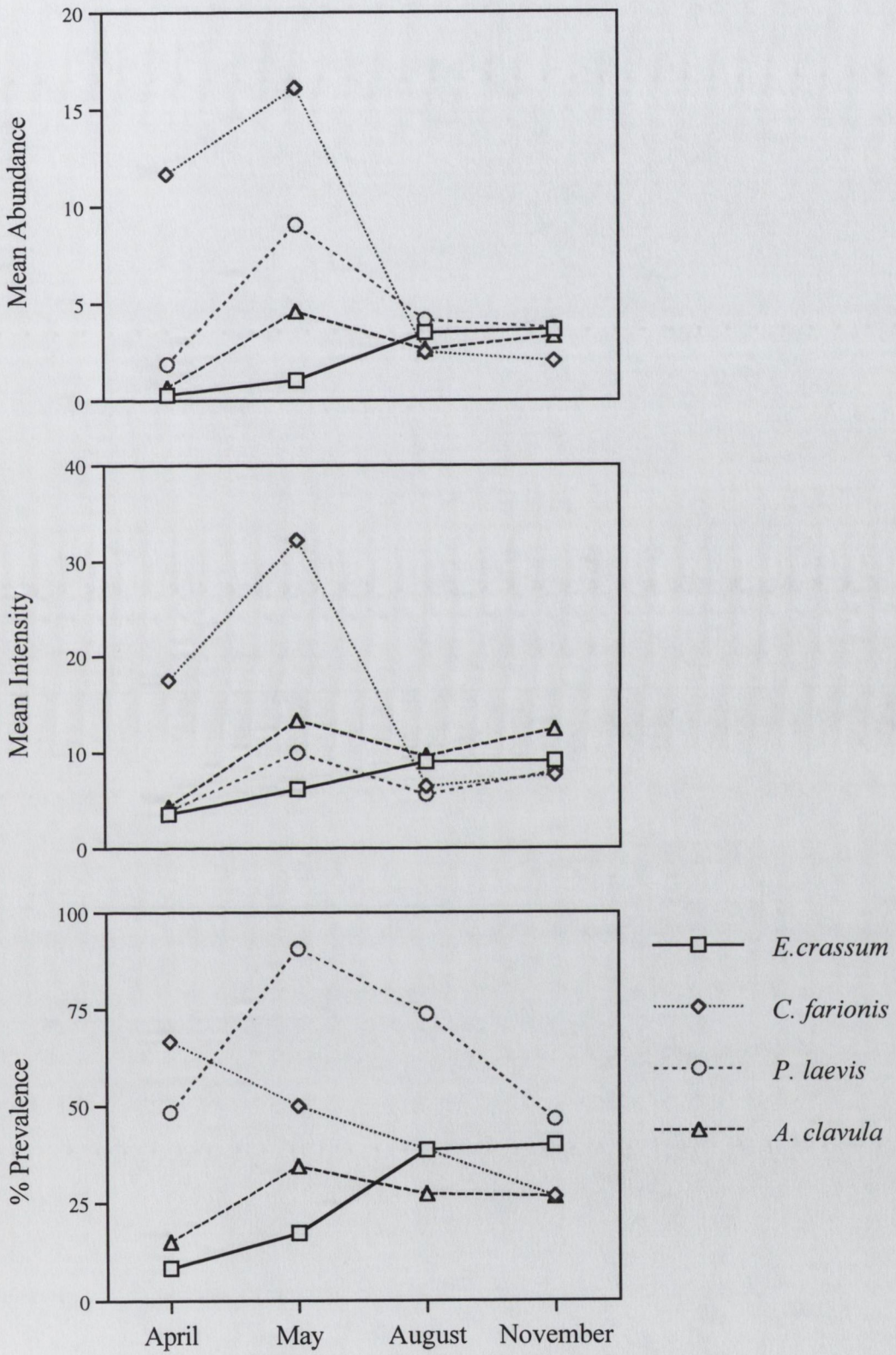

Fig 4.1 Prevalence, mean abundance and mean intensity of the four most common species in wild trout in Lough Feeagh.

4.4 Helminth component community of stocked trout in Lough Feeagh

4.4.1 Examination of component community data for all stocked trout

Ten parasite species were recorded in stocked trout in Lough Feeagh (Table 4.7). Three nematodes, one identified to genus level (*Rhabdochona* sp.) and two identified to species level (*Cystidicola farionis*, *C. tenuissima*), two acanthocephalan species (*P. laevis*, *A. clavula*), two cestode species (*E. crassum*, *D. ditremum*), one digenean species (*Crepidostomum farionis*), one monogenean (*D. sagittata*), and one copepod (*S. salmoneus*).

D. ditremum was the only allogenic species present, and also the only species which occurred in larval form (Table 4.7). All other parasites were autogenic and occurred as adults in brown trout. The nematodes *Cystidicola farionis* and *C. tenuissima*, and the copepod *S. salmoneus* were present as non-component species. The remaining seven species were component species. Only *S. salmoneus* had a prevalence value less than five percent.

E. crassum had the highest prevalence, mean abundance and range values in stocked trout in Lough Feeagh. *D. ditremum* had the highest mean intensity and variance to mean ratio.

4.4.2 Examination of component community data by month

Component community data for stocked fish in Lough Feeagh were examined by month and trends present in individual species are also discussed. Data for each month (May, August, November) are discussed, and presented in Tables 4.8- 4.10. Figure 4.2 shows the prevalence, mean abundance and mean intensity of the four most prevalent species in stocked trout in Lough Feeagh.

Four species were recorded in May, ten species in August, and nine in November. *C. tenuissima* only occurred in August. *P. laevis*, *A. clavula*, *Crepidostomum farionis*

and *E. crassum* were recorded in all months. The remaining five species were only recorded in August and November.

Prevalence

The highest prevalence value was recorded for *E. crassum* in November. For all other community parameters the highest values were recorded in August (Fig 4.2). *E. crassum* had the highest mean abundance and range values, and *D. ditremum* had the highest mean intensity and variance to mean ratio values. *A. clavula* had the highest prevalence value in May, and *E. crassum* had the highest prevalence value in August and November.

Component Species & Mean Abundance

There were two component species in May and eight in August and November. *A. clavula* had the highest mean abundance value in May, *E. crassum* in August, and *P. laevis* in November. Only *E. crassum* and *D. ditremum*, in August, had mean abundance values above ten. Two species had mean abundance values below one in May, this increased to six species in August, and dropped to three species in November.

Mean Intensity

A. clavula had the highest mean intensity value in May, *D. ditremum* in August, and *Crepidostomum farionis* in November (Fig 4.2). *Rhabdochona* sp., *D. sagittata*, and *S. salmoneus*, had mean intensity values below five in August and November. Mean intensity values for all remaining species exceeded five in at least one month.

4.4.3 Examination of component community by parasite species

E. crassum

The lowest values for all community parameters of *E. crassum* occurred in May, and the highest values, with the exception of prevalence, occurred in August. November had a slightly higher prevalence value than August.

Crepidostomum farionis

The highest values for all community parameters of *Crepidostomum farionis*, with the exception of prevalence, were recorded in November. The prevalence value was higher in August, but still comparable to the value recorded in November. Mean abundance values increased from May to November. Mean intensity, range and variance to mean ratio values, decreased from November through to August.

P. laevis

P. laevis had the highest values for all community parameters in November. All community parameters decreased in May, and were lowest in August.

A. clavula

The prevalence value recorded for *A. clavula* was highest in May. August and November had identical prevalence values. Values for all other community parameters of *A. clavula* were higher in August, and lower, but comparable for May and November.

4.4.4 Summary characteristics of the component community

The component community characteristics for stocked trout in Lough Feeagh are summarised in Table 4.11. Only 65% of fish were infected with parasites in May, compared with 100% infection in August and November.

The total number of parasite individuals recorded increased from May to November. Four autogenic species were recorded in May, this increased to nine species in August, and decreased to eight species in November. One allogenic species was recorded in August and November, none were recorded in May. Eight of the parasite species recorded were specialists in trout.

A. clavula was the dominant species in May, and *E. crassum* dominated in the remaining months. *A. clavula* had the highest *P*i value of any month, with 63% of the total number of parasite individuals being composed of the dominant species. *P*i

values decreased from May to November. In November only 21% of the total number of parasite individuals were composed of the dominant species. All dominant species were autogenic.

4.5 Statistical examination of the most prevalent species in stocked trout in Lough Feeagh

One-way analysis of variance (ANOVA) was used to examine the relationship between the abundance of the four most prevalent intestinal parasite species in stocked trout in Lough Feeagh (*P. laevis*, *A. clavula*, *Crepidostomum farionis*, *E. crassum*) and the month and year of host capture, the age of the host, and the sex of the host fish. In all cases parasite abundance data was overdispersed. Therefore, all analysis was performed on log (x+1) transformed data. In all cases only significant relationships have been shown.

4.5.1 Month and year of host capture

When the total sample of stocked trout in Lough Feeagh was examined by month significant differences in abundance between months existed for *E. crassum* (F ratio = 5.4; df = 2,119; $p \leq 0.006$), and *P. laevis* (F ratio = 11.3; df = 2,119; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the abundance of *E. crassum* between August and May ($p = 0.01$) and November and August ($p = 0.01$). For *P. laevis* significant differences existed between November and May ($p \leq 0.0002$) and November and August ($p \leq 0.001$).

The total sample of stocked fish was then divided by year and examined by month. Only the abundance of *P. laevis* was significantly different between months in 1997 (F ratio = 7.3; df = 2,58; $p \leq 0.003$). Least squares difference post hoc tests showed significant differences between November and May ($p = 0.03$) and November and August ($p \leq 0.002$). Mean abundance values for *P. laevis* in 1997 were 0.81(± 2.3) in May, 0.29(± 0.6) in August and 13.42(± 13.3) in November.

In 1998 the abundance values for *E. crassum* (F ratio 10.0; df = 2,58; $p \leq 0.0005$) and *P. laevis* (F ratio = 2.8; df = 2,58; $p \leq 0.008$) were significantly different between months. Least squared difference post hoc tests showed significant differences between August and May ($p \leq 0.004$) and November and August ($p \leq 0.0003$) for *E. crassum* and between November and May ($p = 0.03$) for *P. laevis*. Mean abundance values for *E. crassum* were 0.12(± 0.4) in May, 51.3(± 86.6) in August and 4.72(± 5.1) in November. For *P. laevis* mean abundance values were 1.42(± 2.6) in May, 0.5(± 1.3) in August and 5(± 8.8) in November.

The intensity values of the four parasite species in each month were compared between the two sample years. *E. crassum* and *Crepidostomum farionis* were only present in May 1998. *P. laevis* and *A. clavula* were present in May of both years, but neither species was significantly different between years. Only *E. crassum* was significantly different between August 1997 and August 1998 (F ratio = 5.0; df = 1, 23; $p = 0.04$). The mean intensity of *E. crassum* was 12.6(± 23.4) in August 1997 compared to a mean intensity of 51.3(± 86.6) in August 1998. Both *E. crassum* (F ratio = 7.1; df = 1, 48; $p = 0.01$) and *P. laevis* (F ratio = 5.4; df = 1, 48; $p = 0.03$) were significantly different between November 1997 and November 1998. Mean intensity values for *E. crassum* were 8.4(± 6.6) in November 1997 and 4.72(± 5.1) in November 1998. For *P. laevis* mean abundance values were 13.92(± 13.3) in November 1997 and 5(± 8.8) in November 1998.

4.5.2 Sex of host fish

The relationship between the abundance of the four most prevalent species and the sex of the host fish was examined. Only the abundance of *P. laevis* in November for the total sample differed between the sexes (F ratio = 4.1; df = 1, 48; $p = 0.04$), females had nearly three times more worms than males. For all other situations regardless of how the samples were divided, either by year or month or by year and month no significant differences were reported in the abundance values of the four parasite species between male and female fish.

4.5.3 Age of host fish

The relationship between the abundance of the four most common species and the age of the host fish was examined. The sampling protocol for Lough Feeagh was designed to catch pond reared stocked trout. As a result all fish in the stocked fish sample were either one or two years old. There was a significant difference between age and the abundance of *P. laevis* for the total sample of fish (F ratio = 16.5; df = 1,120; $p \leq 0.0001$). There was also a significant relationship between age and the abundance of *P. laevis* in 1998 (F ratio = 10.0; df = 1,59; $p \leq 0.004$). In all cases older fish had a higher abundance of *P. laevis*. There was also a significant difference between age and the abundance of *Crepidostomum farionis* for the 1998 sample (F ratio = 7.4; df = 1,59; p = 0.01). For *Crepidostomum farionis*, it was younger fish, which had higher abundance values.

Table 4.7 Component community data for all stocked trout in Lough Feeagh (1997 – 1998, $n = 122$).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	56.56	8.47(28.6)	14.97(36.9)	0 - 292	96.73
Crepidostomum farionis	IN	22.13	2.02(9.1)	9.15(17.9)	0 - 94	41.27
Pomphorhynchus laevis	IN	51.64	4.39(8.9)	8.51(10.9)	0 - 56	17.97
Acanthocephalus clavula	IN	39.34	3.66(10.9)	9.31(15.9)	0 - 84	32.36
Diphyllobothrium ditremum	V	34.42	5.98(24.1)	17.36(38.9)	0 - 191	97.25
Rhabdochona sp.	IN	13.11	0.48(1.7)	3.63(3.3)	0 - 12	5.95
Cystidicola farionis	SB	7.38	0.44(2.6)	6(8.2)	0 - 26	15.61
Cystidicoloides tenuissima	S	0.82	0.008(0.1)	1(0)	0 - 1	1
Discocotyle sagittata	G	13.93	0.29(0.9)	2.05(1.7)	0 - 7	3.08
Salmincola salmoneus	G	8.20	0.11(0.4)	1.3(0.5)	0 - 2	1.37

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.8 Component Population data for stocked trout in Lough Feeagh in May (1997 – 1998, $n = 47$).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	4.26	0.06(0.32)	1.5(0.7)	0 - 2	1.66
Crepidostomum farionis	IN	8.51	0.57(3)	5.4(8.3)	0 - 20	15.34
Pomphorhynchus laevis	IN	34.04	1.15(2.5)	3.38(3.3)	0 - 12	5.3
Acanthocephalus clavula	IN	44.68	3(6.1)	6.71(7.7)	0 - 28	12.41

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.9 Component Population data for stocked trout in Lough Feeagh in August (1997 – 1998, n = 25).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	88	28.08(59.2)	31.91(62.3)	0 - 292	124.87
Crepidostomum farionis	IN	32	1.28(2.6)	4(3.2)	0 - 10	5.11
Pomphorhynchus laevis	IN	20	0.36(0.9)	1.80(0.1)	0 - 4	2.29
Acanthocephalus clavula	IN	36	7.48(20.6)	20.77(31)	0 - 84	56.64
Diphyllobothrium ditremum	V	40	17.48(48.3)	43.70(70.3)	0 - 191	133.22
Rhabdochona sp.	IN	12	0.24(0.7)	2(0)	0 - 2	1.83
Cystidicola farionis	SB	8	0.08(0.3)	1(0)	0 - 1	0.96
Cystidicoloides tenuissima	S	4	0.04(0.2)	1	0 - 1	1
Discocotyle sagittata	G	20	0.40(1)	2(1.2)	0 - 4	2.29
Salmincola salmoneus	G	12	0.12(0.3)	1(0)	0 - 1	0.92

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.10 Component Population data for stocked trout in Lough Feeagh in November (1997 – 1998, n = 50).

Species	Site	% Prevalence	A (± S.D.)	I (± S.D.)	Range	S^2/X
Eubothrium crassum	IN	90	6.56(6.1)	7.29(6)	0 - 26	5.96
Crepidostomum farionis	IN	30	3.76(13.8)	12.53(23.4)	0 - 94	50.39
Pomphorhynchus laevis	IN	84	9.46(12)	11.26(12.3)	0 -56	15.25
Acanthocephalus clavula	IN	36	2.38(6.4)	6.61(9.4)	0 - 35	17.15
Diphyllobothrium ditremum	V	64	5.84(13.9)	9.13(16.5)	0 - 80	32.97
Rhabdochona sp.	IN	26	1.04(2.5)	4(3.5)	0 - 12	5.96
Cystidicola farionis	SB	14	1.04(4.1)	7.42(8.9)	0 - 26	15.77
Discocotyle sagittata	G	24	0.50(1.3)	2.08(1.9)	0 - 7	3.2
Salmincola salmoneus	G	14	0.20(0.5)	1.43(0.5)	0 - 2	1.43

IN = intestine; V = viscera; S = stomach; SB = swim bladder; G = gills.
A = mean abundance; I = mean intensity; S^2/X = variance to mean ratio.

Table 4.11 Component Population characteristics for stocked trout in Lough Feeagh in 1997 – 1998.

Characteristics	May	August	November
No. of fish examined	47	25	50
Percentage infected	65.96	100	100
No. of parasite species	4	10	9
Total no. of parasites	225	1389	1539
No. of autogenic sp.	4	9	8
No. of allogenic sp.	0	1	1
No. of component sp.	2	8	9
No. of specialists sp.	4†	8†	7†
*P*i of dominant sp.	0.63	0.51	0.21
Identity of dominant sp.	*A. clavula*	*E. crassum*	*E. crassum*
Character of dominant sp.	Generalist, autogenic	Specialist, autogenic	Specialist, autogenic

† The acanthocephalan *P. laevis* is considered a specialist in trout in Ireland.

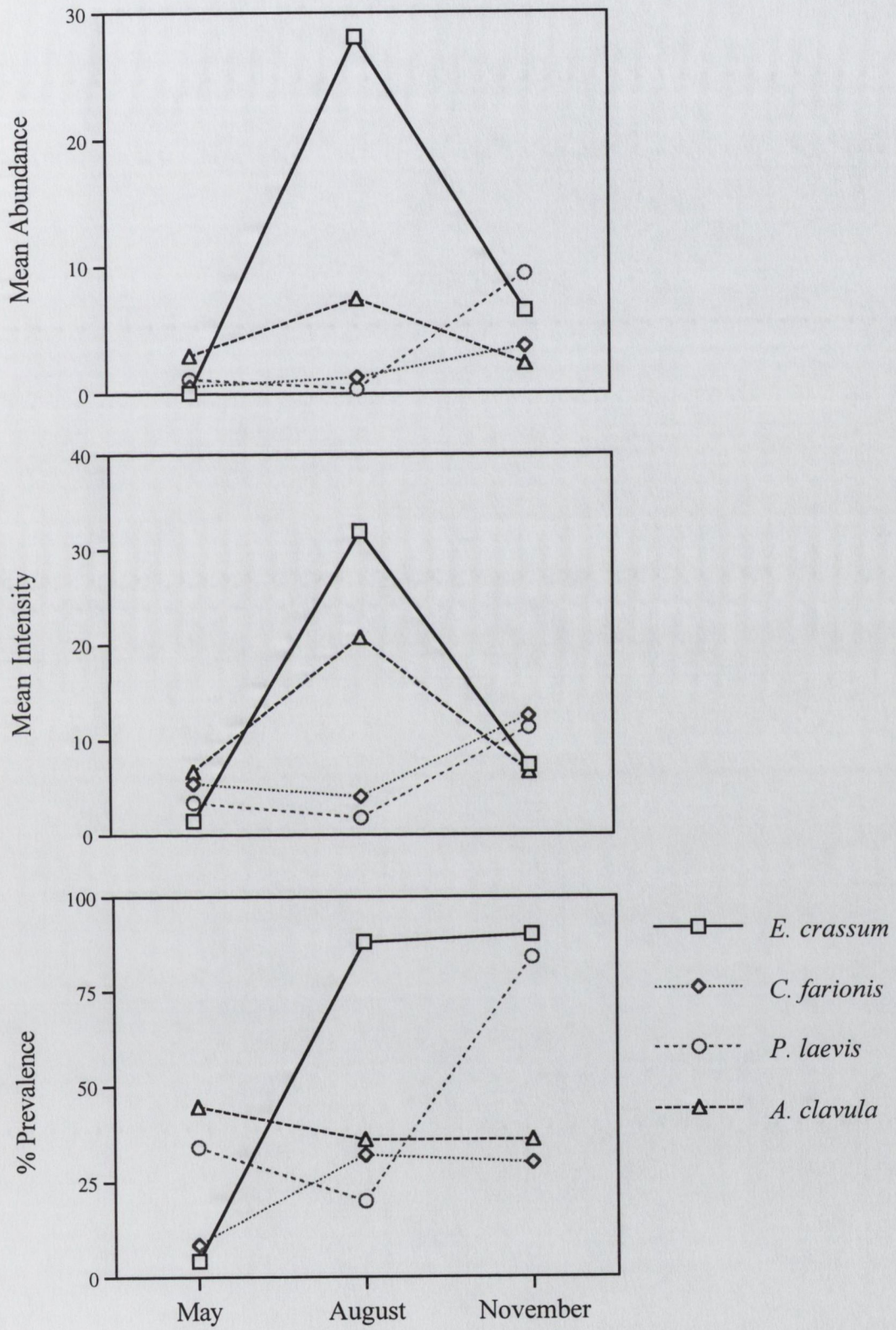

Fig 4.2 Prevalence, mean abundance and mean intensity of the four most common species in stocked trout in Lough Feeagh.

4.6 Comparison of the helminth component community in wild and stocked trout in Lough Feeagh

The helminth component communities of wild and stocked trout in Lough Feeagh were compared for the total sample (Table 4.1, for wild trout; Table 4.7, for stocked trout) and for each sample month, Tables 4.2-4.5 for wild trout and Tables 4.8-4.10 for stocked trout. Summary characteristics for the component communities of wild and stocked trout were also compared (Table 4.6; Table 4.11).

4.6.1 Comparison of component community data for the total sample of wild and stocked trout

Eleven parasite species were found in wild trout, ten species were found in stocked trout. *Anisakis* sp. only occurred in wild trout. The remaining ten species which comprised three nematodes species, two acanthocephalan species, two cestode species, one monogenean, one digenean and one copepod species were common to wild and stocked trout (Table 4.1; Table 4.7).

Two allogenic species *D. ditremum* and *Anisakis* sp. were present in wild trout, only *D. ditremum* was present in stocked trout. This was also the only species occurring in larval form in stocked trout (Table 4.7). Seven of the ten species recorded in stocked trout were component species, only the nematodes *Cystidicola farionis*, *C. tenuisssima* and the copepod *S. salmoneus* were non-component species. Seven of the eleven species recorded in wild trout were component species, again the nematodes *Cystidicola farionis*, *C. tenuissima* and the copepod *S. salmoneus* were non-component species, and the nematode *Anisakis* sp. was also a non-component species (Table 4.1).

Prevalence values varied widely between wild and stocked trout. Wild trout had the highest prevalence value for five species (*Crepidostomum farionis*, *P. laevis*, *Rhabdochona* sp., *C. tenuissima*, *S. salmoneus*), stocked trout had the highest prevalence values for the remaining five species (*E. crassum*, *A. clavula*, *D.*

ditremum, *Cystidicola farionis*, *D. sagittata*). In the case of *E. crassum* and *D. ditremum* prevalence values were over twice as high in stocked trout, however for *Crepidostomum farionis* and *P. laevis* prevalence values were substantially higher in wild trout. *E. crassum* had the highest prevalence value in stocked trout (Table 4.7) and *P. laevis* had the highest prevalence value in wild trout (Table 4.1).

Mean abundance values followed an identical pattern to prevalence values, for wild and stocked trout the same species had the highest mean abundance and prevalence values. The mean abundance, values of *E. crassum* and *D. ditremum* were nearly four times higher in stocked trout (Table 4.7), and the mean abundance of *Crepidostomum farionis* was nearly four times higher in wild trout (Table 4.1). *E. crassum* had the highest mean abundance value in stocked trout and *Crepidostomum farionis* had the highest mean abundance value in wild trout.

Wild trout had the highest mean intensity values for six species (*Crepidostomum farionis*, *A. clavula*, *Rhabdochona* sp., *Cystidicola farionis*, *C. tenuissima*, *S. salmoneus*) and stocked trout had the highest mean intensity values for the remaining four species (*E. crassum*, *P. laevis*, *D. ditremum*, *D. sagittata*). Stocked trout had the highest mean intensity values for both cestode species and one acanthocephalan species (*P. laevis*), whereas wild trout had the highest mean intensity values for all of the nematode species the one digenean species and the remaining acanthocephalan species (*A. clavula*). *D. ditremum* had the highest mean intensity value in stocked trout (Table 4.7) and *Crepidostomum farionis* had the highest mean intensity value in wild trout (Table 4.1)

The highest range of occurrence was recorded for *E. crassum* in stocked trout and *Crepidostomum farionis* in wild trout. All species, with the exceptions of *C. tenuissima* in stocked trout and *Anisakis* sp. in wild trout were overdispersed.

4.6.2 Comparison of component community data for wild and stocked trout by sample month

The component communities of wild and stocked trout (combined for both years) were compared for each sample month. Comparisons were only made between wild and stocked trout for May, August and November. No stocked fish samples were collected in April, therefore it was impossible to compare the April wild trout sample to anything. Data for each month are presented in Tables 4.3-4.5 for wild trout and Tables 4.8-4.10 for stocked trout.

May

Four species were recorded in stocked trout and nine species were recorded in wild trout. *E. crassum*, *Crepidostomum farionis*, *P. laevis* and *A. clavula* were common to wild and stocked trout. *D. ditremum*, *Rhabdochona* sp., *C. tenuissima*, *D. sagittata* and *S. salmoneus* were only present in wild trout.

Two acanthocephalan species, *P. laevis* and *A. clavula*, were component species in stocked trout, having prevalence values of 34.04% and 44.68% respectively. *D. ditremum*, *Rhabdochona* sp., *Crepidostomum farionis* and *D. sagittata* were non-component species in wild trout (Table 4.3). Stocked trout had a higher prevalence value for *A. clavula*, 44.68%, against 34.37% in wild trout. However the prevalence value for *P. laevis* was almost three times higher in wild trout (90.63%) than in stocked trout (34.04%) (Table 4.8).

Mean abundance and mean intensity values were substantially lower for all species recorded in stocked trout (Table 4.8). *A. clavula* had the highest mean abundance and mean intensity values in stocked trout and *Crepidostomum farionis* had the highest mean abundance and mean intensity values in wild trout. The mean abundance and mean intensity values for *A. clavula* in stocked trout were almost twice the values recorded for *P. laevis*. In wild trout *P. laevis* had the highest mean abundance value and *A. clavula* had the highest mean intensity value (Table 4.3).

August

Ten species were recorded in stocked trout in August, and nine species were recorded in wild trout. The nematode *Cystidicola farionis* was not recorded in wild trout. Eight of the ten species recorded in stocked trout and eight of the nine species recorded in wild trout were component species. The nematodes *Cystidicola farionis* and *C. tenuissima* in stocked trout and *Rhabdochona* sp. in wild trout were not component species. Only *Crepidostomum farionis*, *P. laevis* and *C. tenuissima* had higher prevalence values in wild trout, all remaining species had higher prevalence values in stocked trout. *E. crassum* had the highest prevalence value in stocked trout (Table 4.9) and *P. laevis* had the highest prevalence value in wild trout (Table 4.4).

Mean abundance values for *E. crassum*, *D. ditremum*, *Rhabdochona* sp., and *D. sagittata* were highest in stocked trout. In the case of *E. crassum* and *D. ditremum* mean abundance values were up to eight times higher in stocked trout. In wild trout only four species had mean abundance values higher than two, and the highest mean abundance value recorded, 3.49, was for *E. crassum* (Table 4.4). Three species had mean abundance values higher than two in stocked trout. *E. crassum* also had the highest mean abundance value in stocked trout, 28.08 (Table 4.9).

Mean intensity values for *E. crassum*, *D. ditremum* and *A. clavula* were also highest in stocked trout. Values were substantially higher than those recorded in wild trout. *C. tenuissima* had the highest mean intensity value in wild trout, 12.8 (Table 4.4) and *D. ditremum* had the highest mean intensity value for stocked trout, 43.70 (Table 4.9). Three species, *E. crassum*, *D. ditremum* and *A. clavula* had mean intensity values greater than twenty in stocked trout compared to one species *C. tenuissima* which had a mean intensity values greater than ten in wild trout.

November

The same nine species were recorded in wild and stocked trout in November. All nine species in stocked trout and seven of the nine species recorded in wild trout were component species. Only the nematode *Cystidicola farionis* and the copepod *S.*

salmoneus were not component species. All species, with the exception of *D. sagittata*, had higher prevalence values in stocked trout (Table 4.10). In the case of *E. crassum*, *P. laevis* and *D. ditremum* prevalence values were substantially higher in stocked trout, 50% higher for *E. crassum*, 37% higher for *P. laevis* and 31% higher for *D. ditremum*. *E. crassum* had the highest prevalence in stocked trout (Table 4.10) and *P. laevis* had the highest prevalence in wild trout (Table 4.5).

All species, with the exception of *A. clavula*, had higher mean abundance values in stocked trout. The mean abundance value for *A. clavula* was 3.31 in wild trout and 2.38 in stocked trout. Four species recorded in wild trout had mean abundance values lower than one, compared to two species with mean abundance values lower than one in stocked trout. *P. laevis* had the highest mean abundance values for wild and stocked trout.

E. crassum and *A. clavula* had higher mean intensity values in wild trout, for all other species mean intensity values were higher in stocked trout. The mean intensity value for *A. clavula* was almost twice as high in wild trout, whereas the mean intensity values for *E. crassum* in wild and stocked trout differed by only 1.82. The highest mean intensity value recorded in stocked trout was 12.53, for *Crepidostomum farionis* (Table 4.10), and the highest mean intensity value recorded for wild trout was 12.42, for *A. clavula* (Table 4.5).

4.6.3 Comparison of the component community characteristics between wild and stocked trout in Lough Feeagh

The component community characteristics of wild and stocked trout are presented in Tables 4.6 and 4.11 respectively. The smallest sample was twenty-five fish for stocked trout in August, in all other months the sample size was at least forty-five fish. The percentage of fish infected with parasites was reasonably consistent for wild fish, it ranged from 95.45% to 98.46%. In stocked fish the percentage of fish infected increased sharply from 65.96% in May to 100% in August and November (Table 4.11).

Nine parasite species were recorded in wild trout samples in May, August and November, in contrast only four species were recorded in stocked trout in May, but this increased to ten in August and decreased to nine in November.

The number of parasite individuals recorded in stocked trout increased from 225 in May, to 1389 in August and peaked at 1539 in November. In contrast the number of parasite individuals recorded for wild trout decreased from 2056 in May to 700 in November (Table 4.6). The decline in the number of individuals recorded between May and November was due to the fact that fewer fish were examined in November, and that the abundance values of a number of parasite species, including *Crepidostomum farionis* were lower.

One allogenic species, *D. ditremum* was present in wild trout samples in May, August and November and in stocked trout samples in August and November. *Anisakis* sp. was also present in wild trout in April. All remaining species were autogenic. Five component species were present in wild trout in May, compared to two in stocked trout. Eight component species were present in both trout groups in August, however in November the number of component species in wild trout decreased to seven while the number of component species in stocked trout increased to nine.

In wild trout *P. laevis* dominated in May, August and November (Table 4.6), whereas in stocked trout *A. clavula* dominated in May and *E. crassum* dominated in August and November (Table 4.11). The *P*i values for *P. laevis*, the dominant species in wild trout decreased from 0.28 in May to 0.24 in November. In contrast the *P*i value for *A. clavula* the dominant species in stocked trout in May was 0.63, and the *P*i values for *E. crassum* the dominant species in August and November were 0.51 and 0.21 respectively. With the exception of the May stocked trout sample, the dominant species were autogenic specialists in trout, *A. clavula* is considered a generalist in trout.

4.6.4 Comparison of the component community of wild and stocked trout in Lough Feeagh by species

E. crassum

In wild and stocked trout the prevalence values of *E. crassum* increased from May to November, however, in both cases prevalence values for August and November were similar. A similar pattern was found for the mean abundance values in wild trout. In stocked trout the mean abundance values increased from 0.06(± 0.32) in May to a peak of 28.08(± 59.2) in August and decreased to 6.56(±6.1) in November. Mean intensity values for wild trout followed the same pattern as mean abundance and prevalence values, increasing from May to November. Mean intensity values for stocked trout followed the same pattern as mean abundance values, increasing from May to a peak in August and decreasing in November.

Crepidostomum farionis

The prevalence of *Crepidostomum farionis* in wild trout decreased from 50% in May to 26.67% in November, in contrast the prevalence of *Crepidostomum farionis* in stocked trout increased from 8.51% in May to a peak of 32% in August and decreased again to 30% in November. Mean abundance values for *Crepidostomum farionis* in wild trout followed the same pattern as prevalence values and decreased from May to November. In stocked trout mean abundance values did exactly the opposite and increased from 0.57(± 3) in May to 3.76(±13.8) in November. Mean intensity values for wild and stocked trout decreased from May to August and increased in November. In wild trout mean intensity values decreased substantially from 32.22(±33.2) in May to 6.7(±8.6) in August and increased to 7.66(±8.3) in November. However in stocked trout mean intensity values decrease from 5.4(±8.3) in May to 4(±3.2) in August, but they increased to 12.53(±23.4) in November.

P. laevis

Prevalence and mean abundance values for *P. laevis* in wild trout decreased from May to November. In stocked trout the prevalence and mean abundance values of *P. laevis* decreased from May to August, but then increased substantially in November.

In November the prevalence and mean abundance values for wild trout were 46.67% and 3.73(±7.9) respectively, compared to prevalence and mean abundance values of 84% and 9.46(±12) in stocked trout. Mean intensity values for *P. laevis* in wild and stocked trout decreased from May to August and then increased in November. In May and August mean intensity values for *P. laevis* in stocked trout were lower than mean intensity values for *P. laevis* in wild trout, the opposite situation occurred in November.

A. clavula

Prevalence values for *A. clavula* in wild trout decreased from 34.37% in May to 26.66% in November, but mean abundance and mean intensity values decreased from a peak of 4.59(±15) and 13.36(±23.4) respectively in May to their lowest levels in August and increased again in November. In stocked trout the prevalence value decreased from 44.68% in May to 36% in August and November. Mean abundance and mean intensity values increased from May to a peak in August and decreased in November to levels almost identical to those in May.

4.7 Three-way analysis of variance examining the relationships between the intensity of each parasite species, the year and month of host capture and host status

Three way analysis of variance (ANOVA) with interactions was used to examine the relationship between the intensity of each parasite species and year of host capture, month of host capture and status of host fish (stocked or wild). In all cases analysis was performed on log (x+1) transformed data. For *E. crassum* there was a significant relationship between intensity and month of host capture (F ratio = 4.5; df = 3, 126; $p \leq 0.005$). There was also a significant relationship between intensity of *E. crassum* and the interaction between host status and month (F ratio = 4.0; df = 2, 126; p = 0.02).

When the same analysis was performed on log (x+1) transformed data for the intensity of *Crepidostomum farionis*, a significant relationship between the intensity and year of host capture existed (F ratio = 4.0; df = 1,134; p = 0.048). The interactions between month of host capture and year of host capture were significant (F ratio = 4.5; df = 2,134; p = 0.013) for the intensity of *Crepidostomum farionis*, as were the interactions between host status and month (F ratio = 4.2; df = 2,134; p = 0.017).

A significant relationship existed between the intensity of *P. laevis* and year of host capture (F ratio = 6.1; df = 1,225; p = 0.014). There was also a significant relationship between intensity and the month of host capture (F ratio = 4.2; df = 3,225; $p \leq 0.006$). The interaction between the status of the host fish and the month of capture was also significant for the intensity of *P. laevis* (F ratio = 5.1; df = 2,225; $p \leq 0.007$).

The intensity of the remaining parasite species was examined using three way analysis of variance with interactions, and only the relationship between the month of host capture and intensity for the nematode *Cystidicola farionis* was significant (F ratio = 3.7; df = 3,11; p = 0.045).

4.8 Helminth infracommunity in wild trout in Lough Feeagh

257 wild brown trout from Lough Feeagh were examined, 60 in April, 64 in May, 88 in August and 45 in November (Table 4.12). Mean species richness values ranged from 2.17 in April to 2.39 in November (Table 4.12). Mean species richness values recorded in May and August were very similar to the value recorded in November. Analysis of variance showed no significant difference between mean species richness and sample month.

In all months at least one fish remained uninfected with parasites. May and November had the largest range of infection with a minimum of zero species and a maximum of six species recorded in both months. In April and August a minimum of zero species and a maximum of five species were recorded (Table 4.12).

The highest mean number of parasite individuals was recorded in May. It was substantially higher than the value recorded in April, and nearly double the values recorded in August and November. August had the lowest mean number of individuals. One-way analysis of variance (ANOVA) on log (x+1) transformed data for the number of parasite individuals per fish showed significant differences between months for the overall sample (F ratio = 4.5; df = 3,253; $p \leq 0.005$). Least squares difference post hoc tests showed significant differences between the mean number of individuals occurring in May and every other month ($p = 0.023$ for April, $p \leq 0.0008$ for August and $p \leq 0.004$ for November).

Correspondingly the largest range in the number of parasite individuals recorded per fish was also in May, with a minimum of zero and a maximum of 238. Brillouin's Index was calculated for each sample month. Values for the index increased from April, the lowest value, to a peak in November. The Brillouin's index values reported for August and November were comparable (Table 4.12). For one fish in May it was not possible to calculate the Brillouin's index. as a result one fish with a large number of parasite individuals was excluded from the calculations (Table 4.12). One-way

analysis of variance showed no significant difference in the Brillouin's index between months for the overall sample (F ratio = 1.8; df = 3,251; p = 0.15), least squares difference post hoc tests also failed to show any significant difference in the Brillouin's index between any combination of months.

Simpson's dominance index, the Berger-Parker index and the Shannon diversity index were also calculated for the total sample and for each month (Table 4.12). Values for both dominance indices (Simpson's & Berger-Parker) decreased from April to November, and values for the Shannon diversity index increased from April to November. Therefore November had the lowest values for both dominance indices and the highest value for the Shannon diversity index, and April had the lowest value for the Shannon diversity index and the highest values for both dominance indices. Values for May and August were in between the two extremes.

4.9 Helminth infracommunity of intestinal parasite species in wild trout in Lough Feeagh

The same suite of parameters used to examine total parasite infracommunity in wild trout in Lough Feeagh was used to examine the infracommunity of only the intestinal species. In the intestinal parasite infracommunity November had the lowest mean species richness value and May and August had the highest values (which were identical) and April had a comparable but slightly lower value (Table 4.13). Analysis of variance on log (x+1) transformed data showed no significant difference in the intestinal parasite species richness between months for the total sample (F ratio = 2.1; df = 3,253; p = 0.09). Least squares difference post hoc tests showed significant differences in the mean intestinal parasite species richness between November and May (p = 0.03) and November and August (p = 0.02).

Fish uninfected with intestinal parasites occurred in all sample months. November had the smallest range of intestinal species, with a minimum of zero and a maximum of three, all remaining months had a maximum of four intestinal parasite species.
The mean number of individuals recorded in each month ranged from 13.27(± 15.49) in November to 30.92(±37.92) in May, values did not differ substantially from those reported for the total helminth community. The lowest mean number of parasite individuals was recorded in November and the highest was recorded in May. One-way analysis of variance (ANOVA) on log (x+1) transformed data for the number of parasite individuals per fish showed significant differences between months for the total sample (F ratio = 6.2; df = 3,253; $p \leq 0.0004$). Least squares post hoc tests showed significant differences in the number of parasite individuals per fish between May and every other month ($p \leq 0.01$ in all cases).

Brillouin's index, when calculated for intestinal species, was identical for April and May, increased to a peak in August and decreased to its lowest value in November (Table 4.13). It was not possible to calculate the Brillouin's index for one of the most heavily parasitised fish in May. One-way analysis of variance (ANOVA) showed no

significant difference in the Brillouin's index between months for the total sample (F ratio = 0.3; df = 3,252; p = 0.81). Least squares difference post hoc tests also showed no significant difference in the Brillouin's index between any months.

The Simpson's dominance index, Berger–Parker index and Shannon diversity index were calculated for each month and the total sample (Table 4.13). Both the Simpson's dominance index and the Berger-Parker index decreased from their highest point in April, to their lowest point in August and then increased again slightly in November. The Shannon diversity index followed the opposite pattern. It increased from the lowest value in April to a peak in August, and then decreased again in November. (Table 4.13). Values for the Berger-Parker index were very similar for April and May, as were values for the Simpson's dominance index (Table 4.13).

Table 4.12 Infracommunity parameters for all parasites of the total wild trout sample and monthly wild trout samples in Lough Feeagh (1997-1998).

	Total Sample	April	May	August	November
Number examined	257	60	64	88	45
Mean sp. richness (± S.D.)	2.31(1.23)	2.17(1.17)	2.33(1.24)	2.31(1.12)	2.39(1.33)
Range	0 – 6	0 – 5	0 – 6	0 – 5	0 – 6
Mean no. individuals (± S.D.)	20.93(26.36)	20.05(22.60)	32.13(39.78)	15.55(16.47)	16.14(16.88)
Range	0 – 238	0 – 101	0 – 238	0 – 79	0 – 75
Brillouin's Index (± S.D.)	0.39(0.33)†	0.32(0.28)	0.38(0.32)‡	0.43(0.33)	0.45(0.37)
Simpson's Dominance Index (1/D)	0.23 (4.35)	0.58 (1.74)	0.35 (2.84)	0.19 (5.35)	0.18 (5.64)
Berger Parker Index (1/*d*)	0.71 (1.40)	0.89 (1.13)	0.87 (1.15)	0.74 (1.35)	0.66 (1.52)
Shannon Diversity Index	1.75	1.26	1.28	1.80	1.86

† *n* for Brillouins Index = 256; ‡ *n* for Brillouins Index = 63.

Table 4.13 Infracommunity parameters for only the intestinal parasites of the total wild trout sample and monthly wild trout samples in Lough Feeagh (1997–1998).

	Total Sample	April	May	August	November
Number examined	257	60	64	88	45
Mean sp. richness (± S.D.)	1.89(0.92)	1.92(0.87)	1.97(0.89)	1.97(1.01)	1.58(0.81)
Range	0 – 4	0 – 4	0 – 4	0 – 4	0 – 3
Mean no. individuals (± S.D.)	19.36(25.37)	18.92(22.59)	30.92(37.92)	14.38(15.56)	13.27(15.49)
Range	0 – 236	0 – 101	0 – 236	0 – 75	0 – 79
Brillouin's Index (± S.D.)	0.30(0.28)†	0.28(0.25)	0.28(0.29)‡	0.34(0.30)	0.23(0.27)
Simpson's Dominance Index (1/D)	0.27(3.75)	0.45(2.24)	0.38(2.63)	0.22(4.65)	0.31(3.18)
Berger Parker Index (1/*d*)	0.83(1.21)	0.90(1.11)	0.89(1.11)	0.73(1.37)	0.83(1.21)
Shannon Diversity Index	1.5	1.05	1.11	1.60	1.23

† *n* for Brillouins Index = 256; ‡ *n* for Brillouins Index = 63.

4.10 Examination of the relationship in intensity between the four most common intestinal parasite species in wild trout in Lough Feeagh

The relationship in intensity between the four most prevalent intestinal parasites in wild trout in Lough Feeagh (*P. laevis*, *A. clavula*, *Crepidostomum farionis*, *E. crassum*) was examined using Fisher's exact test. Chi squared analysis was not used in Lough Feeagh for the same reasons it was not used in Clogher Lake, namely the main underlying assumption of the test statistic, that the value of any individual cell should not fall below five, was violated.

The intensity of each species was coded numerically. A zero value was recorded when a parasite did not occur in a fish, one was recorded when the parasite occurred at low intensity and two was recorded when the parasite occurred at high intensity. The range for low and high intensity infections for each species are given below.

	Absent = 0	Low = 1	High = 2
P. laevis	No worms	1 – 10 worms	11+ worms
A. clavula	No worms	1 – 25 worms	26+ worms
C. farionis	No worms	1 – 20 worms	21+ worms
E. crassum	No worms	1 – 2 worms	3+ worms

Fisher's exact test can only be used on 2 x 2 contingency tables, as a result two sets of contingency tables were prepared, the first set used presence / absence (0-1) data and the second set used low / high intensity (1-2) data. Contingency tables for all combinations of the four most prevalent intestinal parasite species were calculated for the total fish sample in Lough Feeagh (Tables 4.14-4.19).

The relationships in intensity between *Crepidostomum farionis* and *A. clavula* and between *E. crassum* and *Crepidostomum farionis* for the presence / absence contingency tables for the total sample of wild trout in Lough Feeagh were significant

(Tables 4.14-4.19). However for the low / high intensity contingency tables only the relationship between *Crepidostomum farionis* and *A. clavula* was significant.

P. laevis V *A. clavula*

The relationship between *P. laevis* and *A. clavula* was examined using presence / absence and low / high intensity contingency tables (Table 4.14). Percentage of column totals showed that in 33.2% of cases when *P. laevis* was absent *A. clavula* was also absent, and in 66.8% of cases *P. laevis* was present when *A. clavula* was absent. When the percentage of column totals were examined for the low / high intensity contingency tables, *P. laevis* and *A. clavula* were present together in 83.3% of low intensity infections. In all cases *A. clavula* occurred at high intensity when *P. laevis* was absent. In 16.7% of cases *P. laevis* occurred at high intensity when *A. clavula* occurred at low intensity, but in no case did both species co-occur at high intensity.

Crepidostomum farionis V *P. laevis*

In a similar manner the relationship between *Crepidostomum farionis* and *P. laevis* was examined using presence / absence and low / high intensity contingency tables (Table 4.15). Percentage of column totals showed that in 47.6% of cases when *P. laevis* was absent so was *Crepidostomum farionis*. In 57.2% of cases *Crepidostomum farionis* was absent when *P. laevis* was present, and in 42.8% of cases they occurred together. When the low / high intensity contingency table was examined percentage of column totals showed that in 72.9% of cases both species co-occurred at low intensity. In 27.1% of cases *Crepidostomum farionis* occurred at high intensity when *P. laevis* occurred at low intensity, and in 20% of cases both species co-occurred at high intensity.

E. crassum V *P. laevis*

The relationship between *E. crassum* and *P. laevis* was also examined using presence / absence and low / high intensity contingency tables (Table 4.16). Percentage of column totals showed that in 66.7% of cases when *E. crassum* was absent so was *P.*

laevis. In 33.3% of cases *E. crassum* present when *P. laevis* was absent, however in 76.9% of cases *P. laevis* was present when *E. crassum* was absent and in 23.1% of cases *P. laevis* and *E. crassum* co-occurred. When the low / high intensity contingency tables were examined percentage of column totals showed that in 31.3% of cases both species co-occurred at low intensity, and in 68.8% of cases *E. crassum* occurred at high intensity when *P. laevis* occurred at low intensity. In 37.5% of cases *P. laevis* occurred at high intensity when *E. crassum* occurred at low intensity and in 62.5% of cases both species co-occurred at high intensity.

Crepidostomum farionis V *A. clavula*

The relationship between *Crepidostomum farionis* and *A. clavula* was examined using presence / absence and low / high intensity contingency table (Table 4.17). In 58.9% of cases when *A. clavula* was absent *Crepidostomum farionis* was also absent, and in 41.1% of cases *Crepidostomum farionis* was present when *A. clavula* was absent. However in 59.7% of cases when *Crepidostomum farionis* was present *A. clavula* was also present. Percentage of column totals for the low / high intensity contingency table showed that in 71.4% of cases *Crepidostomum farionis* and *A. clavula* co-occurred at low intensity. In no case did *A. clavula* occur at high intensity when *Crepidostomum farionis* was absent. In 28.6% of cases *Crepidostomum farionis* occurred at high intensity when *A. clavula* occurred at low intensity, but in all cases both species co-occurred at high intensity.

E. crassum V *A. clavula*

The relationship between *E. crassum* and *A. clavula* was examined using presence / absence and low / high contingency tables (Table 4.18). In 74.2% of cases when *A. clavula* was absent *E. crassum* was also absent and in 25.8% of cases when *E. crassum* was present *A. clavula* was absent. In 28.4% of cases both species co-occurred. For the low / high intensity contingency tables in 17.6% of cases both species co-occurred at low intensity. In 82.4% of cases *E. crassum* was present at high intensity when *A. clavula* was present at low intensity. However in all cases when *A. clavula* occurred at high intensity *E. crassum* also occurred at high intensity.

E. crassum V *Crepidostomum farionis*

In the final combination the relationship between *E. crassum* and *Crepidostomum farionis* was examined using presence / absence and low / high contingency tables (Table 4.19). In 66.2% of cases when *E. crassum* was absent so was *Crepidostomum farionis*. In 33.8% of cases *E. crassum* was present when *Crepidostomum farionis* was absent. In 82.2% of cases *Crepidostomum farionis* was present when *E. crassum* was absent, and in 17.8% of cases both species co-occurred. For the low / high intensity contingency tables in 16.7% of cases both species co-occurred at low intensity, and in 83.3% of cases *E. crassum* occurred at high intensity when *Crepidostomum farionis* occurred at low intensity. In 33.3% of cases both species co-occurred at high intensity, and in 66.7% of cases *Crepidostomum farionis* occurred at high intensity when *E. crassum* occurred at low intensity.

4.11 Examinations of the relationships in abundance between all parasite species in wild trout in Lough Feeagh

Kendall's tau was used to assess the relationships in abundance between all possible combinations of parasite species pairs for the total wild trout sample in Lough Feeagh. Fourteen species pairs were significantly correlated, seven had positive values for their correlation coefficients and the remainder had negative values (Table 4.20). *E. crassum* was significantly positively correlated with *D. ditremum* and *D. sagittata*, and significantly negatively correlated with *Crepidostomum farionis*, *P. laevis* and *Rhabdochona* sp.. *Crepidostomum farionis* was significantly positively correlated with *A. clavula* and *Rhabdochona* sp. and significantly negatively correlated with *P. laevis*. *Rhabdochona* sp. was significantly negatively correlated with *P. laevis*, *A. clavula* and *D. ditremum*. The remaining three significantly correlated species pairs were all positively correlated.

Table 4.14 Presence / absence and low / high contingency table for the total sample of *P. laevis /A. clavula* in wild trout in Lough Feeagh (n = 257).

Row Totals = *P. laevis*
Column Totals = *A. clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	63	21	84	1	35	4	39
	75	25	100		89.7	10.3	100
	33.2	31.3	32.7		83.3	100	84.8
	24.5	8.17	32.7		73.1	8.7	84.8
1	127	46	173	2	7	0	7
	73.4	26.6	100		100	0	100
	66.8	68.7	67.3		16.7	0	15.2
	49.4	17.9	67.3		15.2	0	15.2
Total	190	67	257	Total	42	4	46
	73.9	26.1	100		91.3	8.7	100
	100	100	100		100	100	100
	73.9	26.1	100		91.3	8.7	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.88 Fishers Exact Test = 1.00

Table 4.15 Presence / absence and low / high contingency table for the total sample of *P. laevis / Crepidostomum farionis* in wild trout in Lough Feeagh (n = 257).

Row Totals = *Crepidostomum farionis*
Column Totals = *P. laevis*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	40	99	139	1	43	12	55
	28.8	71.2	100		78.2	21.8	100
	47.6	57.2	54.1		72.9	80	74.3
	15.6	38.5	54.1		58.1	16.2	74.3
1	44	74	118	2	16	3	19
	37.3	62.7	100		84.2	15.8	100
	52.4	42.8	45.9		27.1	20	25.7
	17.1	28.8	45.9		21.6	4.05	25.7
Total	84	173	257	Total	59	15	74
	32.7	67.3	100		79.7	20.3	100
	100	100	100		100	100	100
	32.7	67.3	100		79.7	20.3	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.18 Fishers Exact Test = 0.75

Table 4.16 Presence / absence and low / high contingency table for the total sample of *P. laevis /E. crassum* in wild trout in Lough Feeagh (n = 257).

Row Totals = *E. crassum*
Column Totals = *P. laevis*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	56	133	189	1	10	3	13
	29.6	70.4	100		76.9	23.1	100
	66.7	76.9	73.5		31.3	37.5	32.5
	21.8	51.8	73.5		25	7.5	32.5
1	28	40	68	2	22	5	27
	41.2	58.8	100		81.5	18.5	100
	33.3	23.1	26.5		68.8	62.5	67.5
	10.9	15.6	26.5		55	12.5	67.5
Total	84	173	257	Total	32	8	40
	32.7	67.3	100		80	20	100
	100	100	100		100	100	100
	32.7	67.3	100		80	20	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.09 Fishers Exact Test = 1.00

Table 4.17 Presence / absence and low / high contingency table for the total sample of *Crepidostomum farionis / A . clavula* in wild trout in Lough Feeagh (n = 257).

Row Totals = *Crepidostomum farionis*
Column Totals = *A . clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	112	27	139	1	25	0	25
	80.6	19.4	100		100	0	100
	58.9	40.3	54.1		71.4	0	64.1
	43.6	10.5	54.1		64.1	0	64.1
1	78	40	118	2	10	4	14
	66.1	33.9	100		71.4	28.6	100
	41.1	59.7	45.9		28.6	100	35.9
	30.4	15.6	45.9		25.6	10.3	35.9
Total	190	67	257	Total	35	4	39
	73.9	26.1	100		89.7	10.3	100
	100	100	100		100	100	100
	73.9	26.1	100		89.7	10.3	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.01 Fishers Exact Test = 0.01

Table 4.18 Presence / absence and low / high contingency table for the total sample of *A. clavula / E. crassum* in wild trout in Lough Feeagh (n = 257).

Row Totals = *E. crassum*
Column Totals = *A. clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	141	48	189	1	3	0	3
	74.6	25.4	100		100	0	100
	74.2	71.6	73.5		17.6	0	15.8
	54.9	18.7	73.5		15.8	0	15.8
1	49	19	68	2	14	2	16
	72.1	27.9	100		87.5	12.5	100
	25.8	28.4	26.5		82.4	100	84.2
	19.1	7.39	26.5		73.7	10.5	84.2
Total	190	67	257	Total	17	2	19
	73.9	26.1	100		89.5	10.5	100
	100	106	100		100	100	100
	73.9	26.1	100		89.5	10.5	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.75 Fishers Exact Test = 1.00

Table 4.19 Presence / absence and low / high contingency table for the total sample of *Crepidostomum farionis / E. crassum* in wild trout in Lough Feeagh (n = 257).

Row Totals = *E. crassum*
Column Totals = *Crepidostomum farionis*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	92	97	189	1	3	2	5
	48.7	51.3	100		60	40	100
	66.2	82.2	73.5		16.7	66.7	23.8
	35.8	37.7	73.5		14.3	9.52	23.8
1	47	21	68	2	15	1	16
	69.1	30.9	100		93.8	6.25	100
	33.8	17.8	26.5		83.3	33.3	76.2
	18.3	8.17	26.5		71.4	4.76	76.2
Total	139	118	257	Total	18	3	21
	54.1	45.9	100		85.7	14.3	100
	100	100	100		100	100	100
	54.1	45.9	100		85.7	14.3	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test < 0.004 Fishers Exact Test = 0.13

Table 4.20 Kendall's tau correlation coefficients for the total parasite sample in wild trout in Lough Feeagh (n = 257). Row one shows correlation coefficients, row two shows two tailed significance levels. Correlations with significant p-values have been presented in bold print.

	E	C	P	A	D	R	C F	Ani	C T	D S	S
E	**X**	-.15	-.101	0.03	0.46	-1.96	0.06	0.09	-0.01	0.21	-0.02
		0.004	**0.049**	0.56	**0.000**	**0.001**	0.31	0.15	0.89	**0.000**	0.69
C		**X**	-0.12	0.17	-0.10	0.18	0.08	-0.49	0.06	-0.49	0.10
			0.017	**0.001**	0.06	**0.03**	0.16	0.39	0.27	0.37	0.08
P			**X**	-0.06	-0.01	-0.24	0.07	0.6	0.02	0.02	0.07
				0.24	0.93	**0.000**	0.18	0.25	0.68	0.78	0.19
A				**X**	-0.00	-0.13	-0.07	-0.04	0.01	0.10	0.06
					0.95	**0.02**	0.24	0.56	0.91	0.07	0.28
D					**X**	-0.18	-0.08	-0.03	-0.03	-0.06	-0.03
						0.05	0.19	0.67	0.60	0.28	0.57
R						**X**	0.00	-0.03	-0.05	-0.01	-0.06
							0.99	0.63	0.40	0.85	0.31
C F							**X**	0.33	-0.04	-0.02	0.16
								0.000	0.54	0.79	**0.01**
Ani								**X**	-0.01	-0.02	-0.02
									0.84	0.70	0.75
C T									**X**	0.12	0.15
										0.06	**0.02**
D S										**X**	0.00
											0.96
S											**X**

E = *E. crassum*; C = *C. farionis*; P = *P. laevis*; A = *A. clavula*; D = *D. ditremum*; R = *Rhabdochona* sp.
C F = *Cystidicola farionis*; Ani = *Anisakis* sp.; C T = *C. tenuissima*; D S = *D. sagittata*; S = *S. salmoneus*.

4.12 Helminth infracommunity in stocked trout in Lough Feeagh

A total of 122 stocked brown trout from Lough Feeagh were examined, 47 in May, 25 in August and 50 in November (Table 4.21). Values for the mean species richness ranged from 0.91 in May, to 3.82 in November. The mean species richness value recorded for the total sample, 2.48 was comparable to the value recorded in August. One-way analysis of variance (ANOVA) showed significant differences in the mean species richness between months for the total sample (F ratio = 73.0; df = 2,119; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences between May and August, May and November and November and August ($p \leq 0.0001$ in all cases).

In August and November all fish were infected with at least one parasite species while in May a number of fish remained uninfected. The maximum number of species recorded increased from three in May to five in August, this increased again to a peak of seven in November. November had the largest range of parasite species, with a minimum of one species and a maximum of seven species (Table 4.21).

The mean number of individuals recorded increased by more than a factor of ten from 4.79 in May to a peak of 55.56 in August, and then decreased by almost a half to 30.78 in November. Analysis of variance on log (x+1) transformed data for the number of individual parasites per fish showed a highly significant difference between months for the total sample (F ratio = 28.1; df = 2,119; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the number of parasite individuals between May and August ($p \leq 0.0001$) and May and November ($p \leq 0.0001$). The largest range in number of parasite individuals recorded per fish was in August, with a minimum of three and a maximum of 449 (Table 4.21).

Brillouin's Index was calculated for each sample month, values for the index increased from 0.08 in May to 0.42 in August and they peaked at 0.81 in November. The index was approximately ten times larger in November than in May. The

Brillouin's index value for the total sample, 0.42 was identical to that recorded for the August sample (Table 4.21). One-way analysis of variance showed a highly significant difference in the Brillouin's index between months for the total sample (F ratio = 90.4; df = 2, 118; $p \leq 0.0001$). Least squares difference post hoc tests also showed significant differences between May and August, May and November and August and November ($p \leq 0.0001$ in all cases).

Simpson's dominance index, the Berger-Parker index and the Shannon diversity index were also calculated for the total sample and for each month (Table 4.21). Values for both dominance indices (Simpson's, Berger-Parker) decreased substantially between May and November. For the Simpson's dominance index the value recorded in November, 0.23, was exactly half the value recorded in May, 0.46, and August had an intermediate value. For the Berger-Parker index a similar decline occurred, although the value recorded for November, 0.56, was a little over half the value recorded in May, 0.93 and August also had an intermediate value (Table 4.21). Correspondingly values for the Shannon diversity index increased from 0.95 in May to 1.19 in August and 1.79 in November.

4.13 Helminth infracommunity of intestinal parasite species in stocked trout in Lough Feeagh

The same parameters were used to examine the intestinal infracommunity of stocked trout in Lough Feeagh as were used to examine the entire infracommunity. The mean species richness value recorded in May for the intestinal infracommunity, 0.91, was identical to the value recorded for the total infracommunity. Only intestinal parasite species were found in May. Mean species richness values for August and November were 1.92 and 2.66 respectively, both values were considerably lower than corresponding values for August and November in the total infracommunity.

One-way analysis of variance (ANOVA) showed significant differences between species richness and month for the total sample (F ratio = 48.5; df = 2,119; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in species richness between May and August ($p \leq 0.0001$), May and November ($p \leq 0.0001$) and August and November ($p \leq 0.0008$).

The mean number of individuals recorded in the intestinal infracommunity increased from 4.79 in May to 37.48 in August and decreased again to 23.2 in November (Table 4.22). The mean number of individuals recorded in May was identical to the total infracommunity (as only intestinal species were found in May), but the mean number of individuals recorded in August and November was lower than for the total infracommunity. However, as in the total infracommunity the mean number of individuals recorded in August was substantially higher than in May or November (Table 4.22).

One-way analysis of variance (ANOVA) on log (x+1) transformed data for the number of parasite individuals per fish showed significant differences between months for the total sample (F ratio = 20.4; df = 2,119; $p \leq 0.0001$). Least squares difference post hoc tests showed significant differences in the number of parasites

individuals per fish between May and August and May and November ($p \leq 0.0001$ in both cases).

Brillouin's index was calculated for the three sample months and the total sample. Values ranged from 0.08 in May to 0.25 in August and 0.59 in November. Again the value recorded in May was identical to the value recorded for the total infracommunity, but values recorded in August and November were lower. Similar to the total infracommunity, the Brillouin's index value for the total sample, 0.25 was identical to the Brillouin's index value for August (Table 4.22). One-way analysis of variance (ANOVA) showed significant differences in the Brillouin's index between months for the intestinal parasites species in the total sample (F ratio = 55.8; df = 2, 118; $p \leq 0.0001$). Least squares difference post hoc tests also showed that significant differences existed between May and August ($p \leq 0.007$) and also between May and November and November and August ($p \leq 0.0001$ in both cases).

Simpson's dominance index, the Berger-Parker index and the Shannon diversity index were calculated for the total sample and for each month (Table 4.22). All values recorded in May were identical to those in the total infracommunity for the reason outlined above. Values for the Simpson's dominance index increased from 0.46 in May to 0.61 in August and then decreased substantially to 0.28 in November. The Berger-Parker index was more consistent and decreased from May to November. However values for the Berger-Parker index for May (0.92) and August (0.86) were comparable. The Shannon diversity index followed a pattern diametrically opposed to that of the Simpson's dominance index. As the Simpson's dominance index increased from May to August and then decreased in November, the Shannon diversity index decreased from 0.95 in May to 0.69 in August and increased to 1.39 in November (Table 4.22).

Table 4.21 Infracommunity parameters for all parasites of the total stocked trout sample and monthly stocked trout samples from Lough Feeagh (1997-1998).

	Total Sample	May	August	November
Number examined	122	47	25	50
Mean sp. richness (± S.D.)	2.48(1.76)	0.91(0.83)	2.72(1.14)	3.82(1.47)
Range	0 – 7	0 – 3	1 – 5	1 – 7
Mean no. individuals (± S.D.)	25.84(52.14)	4.79(7.23)	55.56(101.67)	30.78(26.46)
Range	0 – 449	0 – 28	3 – 449	7 – 129
Brillouin's Index (± S.D.)	0.42(0.42)†	0.08(0.18)	0.42(0.27)‡	0.81(0.32)
Simpson's Dominance Index (1/D)	0.22(4.62)	0.46(2.16)	0.37(2.68)	0.23(4.30)
Berger Parker Index (1/*d*)	0.67(1.49)	0.93(1.07)	0.78(1.29)	0.56(1.71)
Shannon Diversity Index	1.70	0.95	1.19	1.79

† *n* for Brillouins Index = 120; ‡ *n* for Brillouins Index = 23.

Table 4.22 Infracommunity parameters for only intestinal parasites of the total stocked trout sample and monthly stocked trout samples in Lough Feeagh (1997-1998).

	Total Sample	May	August	November
Number examined	122	47	25	50
Mean sp. richness (± S.D.)	1.84(1.17)	0.91(0.83)	1.92(0.81)	2.66(0.91)
Range	0 – 5	0 – 3	1 – 4	1 – 5
Mean no. individuals (± S.D.)	19.03(33.50)	4.79(7.23)	37.48(63.01)	23.2(19.77)
Range	0 – 299	0 – 28	2 – 299	2 – 120
Brillouin's Index (± S.D.)	0.25(0.33)†	0.08(0.18)	0.25(0.24)‡	0.59(0.28)
Simpson's Dominance Index (1/D)	0.30(3.33)	0.46(2.16)	0.61(1.63)	0.28(3.52)
Berger Parker Index (1/*d*)	0.86(1.16)	0.92(1.01)	0.86(1.16)	0.66(1.53)
Shannon Diversity Index	1.35	0.95	0.69	1.39

† *n* for Brillouins Index =121; ‡ *n* for Brillouins Index = 24.

4.14 Examination of the relationship in intensity between the four most common intestinal parasite species in stocked trout in Lough Feeagh

As in the previous section the relationship in intensity between the four most prevalent intestinal parasite species in stocked trout in Lough Feeagh (*P. laevis*, *A. clavula*, *Crepidostomum farionis*, *E. crassum*) was examined using Fisher's exact test. The methodology and reasons for selecting Fisher's exact test as the test statistic have been outlined in the previous section. The ranges used to classify low and high intensity infections in Clogher Lake and in wild trout in Lough Feeagh were also used for stocked trout in Lough Feeagh.

A zero value was recorded when a parasite did not occur in a fish, one was recorded when the parasite occurred at low intensity and two was recorded when the parasite occurred at high intensity. The range for low and high intensity infections for each species are given below.

	Absent = 0	Low = 1	High = 2
P. laevis	No worms	1-10 worms	11+ worms
A. clavula	No worms	1 – 25 worms	26+ worms
C. farionis	No worms	1 – 20 worms	21+ worms
E. crassum	No worms	1 – 2 worms	3+ worms

Contingency tables for all combinations of the four most prevalent intestinal parasite species were calculated for the total fish sample in Lough Feeagh (Tables 4.23-4.28). Only the relationship between *E. crassum* and *P. laevis* for the presence / absence contingency table was significant. The relationships between all other species pairs for the presence / absence and for the low / high intensity contingency tables were not significant.

P. laevis V *A. clavula*

The relationship between *P. laevis* and *A. clavula* was examined using presence / absence and low / high intensity contingency tables (Table 4.23). Percentage of column totals showed that in 44.6% of cases when *P. laevis* was absent, *A. clavula* was also absent, and in 55.3% of cases *P. laevis* was present when *A. clavula* was absent. In 54.2% of cases *A. clavula* was present when *P. laevis* was absent, and in 45.8% of cases both species co-occurred. For the low / high intensity contingency table, percentage of column totals showed that in 85% of cases when *P. laevis* was present at low intensity *A. clavula* was also present at low intensity. Also in all cases when *A. clavula* was present at high intensity *P. laevis* was absent, and in no case did both species co-occur at high intensity.

Crepidostomum farionis V *P. laevis*

In a similar manner to above, the relationship between *Crepidostomum farionis* and *P. laevis* was examined using presence / absence and the low / high intensity contingency tables (Table 4.24). Percentage of column totals showed that in 81.4% of cases when *P. laevis* was absent *Crepidostomum farionis* was also absent. In 74.6% of cases *P. laevis* was present when *Crepidostomum farionis* was absent and in 25.4% of cases both species were present together. In 18.6% of cases *Crepidostomum farionis* was present when *P. laevis* was absent. For the low / high intensity contingency table, percentage of column totals showed that in 93.3% of cases both species co-occurred at low intensity, and in 6.67% of cases *Crepidostomum farionis* was present at high intensity when *P. laevis* was present at low intensity. In all cases *Crepidostomum farionis* and *P. laevis* co-occurred at high intensity.

E. crassum V *P. laevis*

The relationship between *E. crassum* and *P. laevis* was also examined using presence / absence and low / high contingency tables (Table 4.25). Percentage of column totals showed that in 54.2% of cases when *E. crassum* was absent *P. laevis* was also absent and in 45.8% of cases *E. crassum* present when *P. laevis* was absent. However in 66.7% of cases when *P. laevis* was present *E. crassum* was also present (Table 4.25).

For the low / high intensity contingency table, percentage of column totals showed that in 17.2% of cases *E. crassum* occurred at low intensity when *P. laevis* occurred at low intensity. In 82.8% of cases *E. crassum* occurred at high intensity when *P. laevis* occurred at low intensity. However in 30.8% of cases *P. laevis* occurred at high intensity when *E. crassum* occurred at low intensity, and in 69.2% of cases *P. laevis* and *E. crassum* co-occurred at high intensity.

Crepidostomum farionis V *A. clavula*

Percentage of column totals showed that in 83.8% of cases when *Crepidostomum farionis* was absent, *A. clavula* was also absent. In 68.8% of cases *A. clavula* was present when *Crepidostomum farionis* was absent, and in 31.3% of cases both species co-occurred. In 16.2% of cases *Crepidostomum farionis* was present when *A. clavula* was absent (Table 4.26). For the low / high intensity contingency tables *Crepidostomum farionis* and *A. clavula* co-occurred at low intensity in 91.7% of cases. In 8.33% of cases *Crepidostomum farionis* was present at high intensity when *A. clavula* was present at low intensity. In 33.3% of cases *Crepidostomum farionis* and *A. clavula* co-occurred at high intensity.

E. crassum V *A. clavula*

The relationship between *E. crassum* and *A. clavula* was examined using presence / absence and low / high intensity contingency tables (Table 4.27). In 37.8% of cases when *E. crassum* was absent *A. clavula* was also absent and in 62.2% of cases *E. crassum* was present when *A. clavula* was absent. In 47.9% of cases when *A. clavula* was present *E. crassum* was also present. For the low / high intensity contingency tables percentage of column totals showed that *E. crassum* and *A. clavula* co-occurred at low intensity in 36.4% of cases. In 63.6% of cases *E. crassum* was present at high intensity when *A. clavula* was present at low intensity. In no case did *A. clavula* occur at high intensity when *E. crassum* occurred at low intensity, but in 100% of cases *A. clavula* and *E. crassum* co-occurred at high intensity. (Table 4.27).

E. crassum V *Crepidostomum farionis*

In the final comparison the relationship between *E. crassum* and *Crepidostomum farionis* was examined using presence / absence and low / high intensity contingency tables (Table 4.28). In 45.3% of cases when *E. crassum* was absent *Crepidostomum farionis* was also absent and in 54.7% of cases *E. crassum* was present when *Crepidostomum farionis* was absent. However in 37% of cases *Crepidostomum farionis* was present when *E. crassum* was absent. For the low / high intensity contingency tables *Crepidostomum farionis* and *E. crassum* co-occurred at low intensity in 31.3% of cases, and in 68.8% of cases *E. crassum* occurred at high intensity when *Crepidostomum farionis* occurred at low intensity. In all cases *Crepidostomum farionis* occurred at high intensity when *E. crassum* occurred at low intensity, and in no cases did *Crepidostomum farionis* and *E. crassum* co-occur at high intensity (Table 4.28).

4.15 Examinations of the relationships in abundance between all parasite species in stocked trout in Lough Feeagh

Using the same technique as was used for wild trout; Kendall's tau was used to assess the relationships in abundance between all possible combinations of parasite species pairs for the total stocked trout sample in Lough Feeagh. Fourteen species pairs were significantly correlated and all had positive correlation coefficients (Table 4.29). *E. crassum* was significantly correlated with *P. laevis* and *D. sagittata* and highly significantly correlated with *D. ditremum*. *Crepidostomum farionis* was significantly correlated with *A. clavula* and *D. sagittata*. It was also highly significantly correlated with *Rhabdochona* sp. and *S. salmoneus*. *P. laevis* was highly significantly correlated with *D. ditremum*. *D. ditremum* was significantly correlated with two nematode species *Rhabdochona* sp. and *Cystidicola farionis*. It was also correlated with *D. sagittata* and highly correlated with *S. salmoneus*. *D. sagittata* was significantly correlated with *Rhabdochona* sp., and in the final relationship *S. salmoneus* was significantly correlated with the nematode *Cystidicola farionis*.

Table 4.23 Presence / absence and low / high contingency table for the total sample of *P. laevis* / *A. clavula* in stocked trout in Lough Feeagh (n = 122).

Row Totals = *P. laevis*
Column Totals = *A. clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	33	26	59	1	17	2	19
	55.9	44.1	100		89.5	10.5	100
	44.6	54.2	48.4		85	100	86.4
	27	21.3	48.4		77.3	9.09	86.4
1	41	22	63	2	3	0	3
	65.1	34.9	100		100	0	100
	55.3	45.8	51.6		15	0	13.6
	33.6	18	51.6		13.6	0	13.6
Total	74	48	122	Total	20	2	2
	60.7	39.3	100		90.9	9.09	100
	100	100	100		100	100	100
	60.7	39.3	100		90.9	9.09	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.36 Fishers Exact Test = 1.00

Table 4.24 Presence / absence and low / high contingency table for the total sample of *P. laevis / Crepidostomum farionis* in stocked trout in Lough Feeagh (n = 122).

Row Totals = *Crepidostomum farionis*
Column Totals = *P. laevis*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	48	47	95	1	14	0	14
	50.5	49.5	100		100	0	100
	81.4	74.6	77.9		93.3	0	87.5
	39.3	38.5	77.9		87.5	0	87.5
1	11	16	27	2	1	1	2
	40.7	59.3	100		50	50	100
	18.6	25.4	22.1		6.67	100	12.5
	9.02	13.1	22.1		6.25	6.25	12.5
Total	59	63	122	Total	15	1	16
	48.4	51.6	100		93.8	6.25	100
	100	100	100		100	100	100
	48.4	51.6	100		93.8	6.25	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.39 Fishers Exact Test = 0.13

Table 4.25 Presence / absence and low / high contingency table for the total sample of *P. laevis* / *E. crassum* in stocked trout in Lough Feeagh (n = 122).

Row Totals = *E. crassum*
Column Totals = *P. laevis*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	32	21	53	1	5	4	9
	60.4	39.6	100		55.6	44.4	100
	54.2	33.3	43.4		17.2	30.8	21.4
	26.2	17.2	43.4		11.9	9.52	21.4
1	27	42	69	2	24	9	33
	39.1	60.9	100		72.7	27.3	100
	45.8	66.7	56.6		82.8	69.2	78.6
	22.1	34.4	56.6		57.1	21.4	78.6
Total	59	63	122	Total	26	13	42
	48.4	51.6	100		69	31	100
	100	100	100		100	100	100
	48.4	51.6	100		69	31	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.03 Fishers Exact Test = 0.42

Table 4.26 Presence / absence and low / high contingency table for the total sample of *A . clavula / Crepidostomum farionis* in stocked trout in Lough Feeagh (n = 122).

Row Totals = *Crepidostomum farionis*
Column Totals = *A . clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	62	33	95	1	11	2	13
	65.3	34.7	100		84.6	15.4	100
	83.8	68.8	77.9		91.7	66.7	86.7
	50.8	27	77.9		73.3	13.3	86.7
1	12	15	27	2	1	1	2
	44.4	55.6	100		50	50	100
	16.2	31.3	22.1		8.33	33.3	13.3
	9.84	12.3	22.1		6.67	6.67	13.3
Total	74	48	122	Total	12	3	15
	60.7	39.3	100		80	20	100
	100	100	100		100	100	100
	60.7	39.3	100		80	20	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.07 Fishers Exact Test = 0.37

Table 4.27 Presence / absence and low / high contingency table for the total sample of *A. clavula* / *E. crassum* in stocked trout in Lough Feeagh (n = 122).

Row Totals = *E. crassum*
Column Totals = *A. clavula*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	28	25	53	1	8	0	8
	52.8	47.2	100		100	0	100
	37.8	52.1	43.4		36.4	0	34.8
	23	20.5	43.4		34.8	0	34.8
1	46	23	69	2	14	1	15
	66.7	33.3	100		93.3	6.67	100
	62.2	47.9	56.6		63.6	100	65.2
	37.7	18.9	56.6		60.9	4.35	65.2
Total	74	48	122	Total	22	1	23
	60.7	39.3	100		95.7	4.35	100
	100	100	100		100	100	100
	60.7	39.3	100		95.7	4.35	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.14 Fishers Exact Test = 1.00

Table 4.28 Presence / absence and low / high contingency table for the total sample of *Crepidostomum farionis / E. crassum* in stocked trout in Lough Feeagh (n = 122).

Row Totals = *E. crassum*
Column Totals = *Crepidostomum farionis*

	Presence / Absence				Low / High Intensity		
	0	1	Total		1	2	Total
0	43	10	53	1	5	1	6
	81.1	18.9	100		83.3	16.7	100
	45.3	37	43.4		31.3	100	35.3
	35.2	8.2	43.4		29.4	5.88	35.3
1	52	17	69	2	11	0	11
	75.4	24.6	100		100	0	100
	54.7	63	56.6		68.8	0	64.7
	42.6	13.9	56.6		64.7	0	64.7
Total	95	27	122	Total	16	1	17
	77.9	22.1	100		94.1	5.88	100
	100	100	100		100	100	100
	77.9	22.1	100		94.1	5.88	100

Count
% of Row Total
% of Column Total
% of Table Total

Fishers Exact Test = 0.51 Fishers Exact Test = 0.35

Table 4.29 Kendall's tau correlation coefficients for the total parasite sample in stocked trout in Lough Feeagh (n = 122). Row one shows correlation coefficients, row two shows two tailed significance levels. Correlations with significant p-values have been presented in bold print.

	E	C	P	A	D	R	C F	C T	D S	S
E	**X**	0.02	0.16	-1.38	0.46	0.12	0.04	0.13	0.19	0.5
		0.78	**0.03**	0.06	**0.000**	0.13	0.62	0.10	**0.01**	0.56
C		**X**	0.03	0.24	0.11	0.41	0.01	-0.46	0.20	0.27
			0.70	**0.003**	0.19	**0.000**	0.94	0.60	**0.02**	**0.001**
P			**X**	-0.12	0.25	0.01	0.10	-0.77	-0.06	0.08
				0.10	**0.001**	0.90	0.20	0.34	0.94	0.30
A				**X**	-0.13	0.01	0.12	-0.65	0.01	0.09
					0.87	0.90	0.14	0.44	0.94	0.29
D					**X**	0.25	0.17	0.12	0.18	0.27
						0.003	**0.04**	0.15	**0.03**	**0.001**
R						**X**	-0.11	-0.03	0.27	0.06
							0.23	0.70	**0.002**	0.53
C F							**X**	-0.25	0.13	0.37
								0.78	0.13	**0.000**
C T								**X**	-0.36	-0.27
									0.69	0.77
D S									**X**	0.13
										0.15
S										**X**

E = *E. crassum*; C = *C. farionis*; P = *P. laevis*; A = *A. clavula*; D = *D. ditremum*; R = *Rhabdochona* sp.; C F = *Cystidicola farionis*; Ani = *Anisakis* sp.; C T = *C. tenuissima*; D S = *D. sagittata*; S = *S. salmoneus.*

4.16 Comparison of the helminth infracommunities of wild and stocked trout in Lough Feeagh

A total of 257 wild trout and 122 stocked trout were examined. In May, 64 wild trout and 47 stocked trout were examined, in August 88 wild trout and 25 stocked trout were examined and in November 45 wild trout and 50 stocked trout were examined (Table 4.12; Table 4.21). An additional 60 wild trout were examined in April, but there was no corresponding sample of stocked trout.

Mean species richness values for wild trout increased from April to November, however the value recorded in August, 2.31, was slightly lower than but comparable to the value reported in May, 2.33. The mean species richness value reported in November was 2.39 (Table 4.12). In contrast the mean species richness value for stocked trout in May, 0.91 was much lower than the corresponding value for wild trout but the mean species richness values recorded in August and November, 2.72 and 3.82 respectively were substantially higher that corresponding values in wild trout. The range of species recorded in stocked trout increased from, 0-3 in May to 1-7 in November (Table 4.21), whereas the range in number of species recorded for wild trout decreased from 0-6 in May and November to 0-5 in August (Table 4.12). When mean species richness was compared between individual sample months for wild and stocked trout one-way analysis of variance (ANOVA) showed significant differences in May (F ratio = 46.2; $df = 1,109$; $p \leq 0.0001$) and November (F ratio = 31.1; $df = 1,93$; $p \leq 0.0001$).

The mean number of individuals recorded in wild trout decreased from 32.13(± 39.78) in May to 15.5(±16.47) in August and it increased to 16.14(±16.88) in November (Table 4.12). In contrast, the mean number of individuals recorded in stocked trout increased substantially from 4.79(±7.23) in May to 55.56(±101.67) in August and then decreased to 30.78(±26.46) in November. Wild trout had the highest mean number of individuals in May, but the situation was reversed for August and November. Similarly, wild trout also had the highest range of parasite individuals in

May (0-238) but stocked trout had the highest range of parasite individuals in August and November (3-449) and (7-129) respectively. One-way analysis of variance (ANOVA) on log (x+1) transformed data was used to compare the number of individuals between wild and stocked trout for each sample month. Significant differences existed in May (F ratio = 75.7; df = 1,108; $p \leq 0.0001$), August = (F ratio = 7.5; df = 1,111; $p \leq 0.007$) and November (F ratio = 22.5; df = 1,93; $p \leq 0.0001$).

Two sample t-tests and Mann-Whitney U-tests were used to compare the abundance of each parasite species found in wild trout with the abundance of the same species found in stocked trout (Tables 4.30-4.33). Two sample t-tests are parametric tests and were performed on log (x+1) transformed data whereas Mann-Whitney U-tests are non-parametric tests and were performed on untransformed data. Two sample t-tests showed significant differences in the abundance of *E. crassum*, *Crepidostomum farionis*, *D. ditremum* and *A. clavula* between wild and stocked trout when compared for the total sample (Table 4.30). However Mann-Whitney U-tests only showed significant differences in the abundance of *P. laevis* and *D. ditremum* between wild and stocked trout for the total sample (Table 4.30).

In May only four species were recorded in stocked trout and two sample t-tests showed significant differences in abundance between three of them (*E. crassum*, *Crepidostomum farionis*, *P. laevis*) and wild trout. Mann-Whitney U-tests showed no significant differences in the abundance of any parasite species between wild and stocked trout (Table 4.31). In August two sample t-tests showed significant differences in the abundance of *E. crassum*, *P. laevis* and *C. tenuissima* between wild and stocked trout, whereas Mann-Whitney U-tests only showed significant differences in the abundance of *D. ditremum* (Table 4.32). For the final sample month, November, two sample t-tests showed significant differences in the abundance of *E. crassum*, *P. laevis* and *D. ditremum* between wild and stocked trout, and Mann-Whitney U-tests only showed significant differences in the abundance of *E. crassum* between wild and stocked trout (Table 4.33).

Brillouin's index values for wild trout increased from 0.38(±0.32) in May to 0.45(±0.37) in November. However it was not possible to calculate the Brillouin's index of diversity for one heavily infected fish in May. In stocked trout values for the Brillouin's index followed a similar pattern increasing from 0.08(±0.18) in May to 0.81(±0.32) in November. It was not possible to calculate the index for two fish in August. Values for the index were substantially lower for stocked fish in May, comparable between wild and stocked fish in August, and substantially higher for stocked fish in November. Brillouin's index values were compared between wild and stocked trout for each sample month. One-way analysis of variance (ANOVA) showed significant differences in the value of the index between wild and stocked trout in May (F ratio = 35.3; df = 1,108; $p \leq 0.0001$) and November (F ratio = 31.4; df = 1,92; $p \leq 0.0001$).

Simpson's dominance index and the Berger-Parker and Shannon diversity indices were also compared between wild and stocked trout for the total sample and for each sample month. For Simpson's dominance index and the Berger-Parker index in both wild and stocked trout values decreased from May through to November (Table 4.12; Table 4.21). Corresponding to this decrease in dominance values for the Shannon diversity index for both wild and stocked trout increased from May through to November. However, in all cases for the Simpson's dominance index, and in May and August for the Berger-Parker index, values were higher for stocked trout. Berger-Parker index values were higher for wild trout in November (Table 4.12). For all sample months values for the Shannon diversity index (Table 4.21).

4.17 Comparison of the helminth infracommunities of intestinal parasite species between wild and stocked trout in Lough Feeagh

In this section the helminth infracommunities of only the intestinal parasite species were compared between wild and stocked trout (Table 4.13; Table 4.22). Mean species richness values for the intestinal helminth communities in wild trout were identical for May and August, 1.97 (±0.87) and 1.97(±1.01) respectively. Values decreased to 1.58(±0.81) in November. Mean species richness values for stocked trout were substantially lower than for wild trout in May (0.91(±0.83)), comparable to wild trout in August (1.92(±0.81)), and substantially higher than wild trout in November (2.66(±0.91)). One-way analysis of variance (ANOVA) showed significant differences in the mean number of intestinal parasite species between wild and stocked trout in May (F ratio = 40.2; df = 1,109; $p \leq 0.0001$) and November (F ratio = 35.7; df = 1,93; $p \leq 0.0001$). In wild trout four intestinal parasite species were recorded in May and August and three were recorded in November, in all months fish uninfected with parasites were recorded (Table 4.13). In contrast, three intestinal parasites species were recorded in stocked trout in May, four were recorded in August and five were recorded in November, and uninfected fish only occurred in May (Table 4.22).

The mean number of individuals recorded in wild trout decreased substantially from 30.92(±37.92) in May to 13.27(±15.49) in November. In stocked trout the mean number of individuals increased substantially from 4.79(±7.23) in May to 37.48(±63.01) in August and then decreased to 23.2(±19.77) in November. The mean number of individuals recorded in stocked trout was considerably higher than the number recorded in wild trout in August and November and considerably lower than the number recorded in wild trout in May (Table 4.13; Table 4.22). One-way analysis of variance (ANOVA) on log (x+1) transformed data showed significant differences in the number of individuals recorded in wild and stocked trout in May (F ratio =

73.1; df = 1,109; $p \leq 0.0001$), August (F ratio = 5.5; df = 1,111; $p = 0.021$) and November (F ratio = 18.5; df = 1,93; $p \leq 0.0001$).

Brillouin's index was also calculated for the intestinal species in wild and stocked trout. In wild trout values increased from May to a peak in August and decreased to their lowest levels in November (Table 4.13). In contrast to this Brillouin's index values for stocked trout increased from May to a peak in November. Brillouin's index values were considerably higher for stocked trout in November, but considerably higher for wild trout in May and August. One-way analysis of variance (ANOVA) only showed significant differences in Brillouin's index values between wild and stocked trout in August (F ratio = 9.6; df = 1,111; $p \leq 0.003$).

Simpson's dominance index and the Berger-Parker and Shannon diversity indices were also calculated for intestinal parasite species in wild and stocked trout. In wild trout both the Simpson's dominance index and Berger-Parker index decreased from May to August and increased again in November (Table 4.13). The Shannon diversity index increased from May to a peak in August and decreased again. In contrast in stocked trout the Simpson's dominance index increased from May to a peak in August and decreased in November. The Berger-Parker index decreased from May to November and the Shannon diversity index decreased from May to August and increased to a peak in November. Values for the Simpson's dominance index were higher for stocked trout in May and August, and higher for wild trout in November. Similarly values for the Berger-Parker index were also higher for wild trout in November, but higher for stocked trout in May and August, and finally values for the Shannon diversity index were higher in stocked trout in November (Table 4.13; Table 4.22).

4.18 Discussion

Q. Is the component community of Lough Feeagh comparable to the component community reported by Molloy *et al.* (1995a)?

Eleven parasite species were recorded in the component community of wild trout in Lough Feeagh. One nematode and one cestode were allogenic species and only occurred as larval forms, and seven species were component species. An acanthocephalan, *P. laevis*, had the highest prevalence overall and *Crepidostomum farionis* had the highest values for all other component community parameters. Molloy *et al.* (1995a) recorded six parasite species from the component community of trout in Lough Feeagh. They found one allogenic species and three component species. The acanthocephalan *P. laevis* also had the highest prevalence. All of the species recorded by Molloy *et al.* (1995a) were also recorded in this study. However, one acanthocephalan species, three nematode species and one copepod species were recorded in this study but not in the study of Molloy *et al.* (1995a).

Prevalence values for all species in this study were higher than those recorded by Molloy *et al.* (1995a). All mean abundance values were also higher for this study with the exception of the mean abundance of *D. ditremum*. Only one of the five new species recorded in this lake was allogenic, *Anisakis* sp. This genus normally utilises a marine fish as its intermediate host, and a marine mammal as its definitive host. It has previously been reported from freshwater fish in Ireland (Kane, 1966). Lough Feeagh has a large migratory trout component, so the presence of this parasite probably resulted from trout migrating to the estuary or to the sea. *Anisakis* sp. was found on one occasion and only one larval parasite was recovered. Consequently, the presence of *Anisakis* sp. in trout in Lough Feeagh can be considered a chance occurrence.

The nematode *C. tenuissima* also occurred in Lough Feeagh in only one month, August. However, it was a component species and had the highest mean intensity

value in this month. Conneely and McCarthy (1988) considered *C. tenuissima* to be typical of lotic situations. They suggested that the occurrence of this parasite in Lough Corrib was consistent with trout having recently spent some time in a lotic habitat. In Lough Feeagh, juvenile fish tend to interchange between lake and river until they reach about 2 years of age, when they migrate into the lake permanently. They are possibly using the rivers as a type of sheltered area. Therefore, the occurrence of *C. tenuissima* in a number of trout from Lough Feeagh in August, is consistent with the idea that juvenile trout were moving into and out of the lake. Thus, the presence of *C. tenuissima* in this study may be the result of the chance capture of juvenile trout which had migrated into the lake temporarily. It is likely that this nematode was also present in feeder streams surrounding Lough Feeagh during the study of Molloy *et al.* (1995a), but juvenile fish migrating into the lake were probably not caught.

The situation for the nematode *Rhabdochona* sp. was somewhat different. It occurred in all months, with a maximum prevalence of 51.66% in April. *Rhabdochona* sp. had a distinct seasonal pattern, it had an early spring peak, decreased throughout the summer, and started to increase again in winter. This suggests that temperature may have had some effect on its seasonal dynamics. The same seasonal cycle was reported for *Rhabdochona* sp. in Clogher Lake. Conneely and McCarthy (1988) suggested that *Rhabdochona* sp. was typical of lotic situations. They showed that *Rhabdochona* sp. had a prevalence of 9.8% in the river Drimneen and 0.8% in Lough Corrib. However, given that *Rhabdochona* sp. was found in Lough Feeagh in all months and in reasonable amounts, it would seem highly unlikely that it was present during the study of Molloy *et al.* (1995a) but not recorded. The alternative situation, that *Rhabdochona* sp. was present in trout in the feeder streams surrounding Lough Feeagh during the study of Molloy *et al.* (1995a) but never occurred in the lake, also seems unlikely, considering that *Rhabdochona* sp. occurred in all samples in this study.

Molloy *et al.* (1995a) examined fish from Bunaveela Lake, the other freshwater lake in the Burrishoole catchment, and they did not record *Rhabdochona* sp. Thus, a possible scenario is that there was a rescue effect from another population. Bush and Kennedy (1994) considered that localised parasite extinction in the absence of host extinction was a common and trivial event and that fragments of the population in other areas were likely to serve as sources of re-invasion. In this case the rescue effect could have resulted from a straying migratory salmonid introducing / reintroducing *Rhabdochona* sp. into Lough Feeagh. The absence of *S. salmincola* from Lough Feeagh during the study of Molloy *et al.* (1995a) was almost definitely a result of chance, as it was recorded in Bunaveela Lake. However, its prevalence in Bunaveela Lake was extremely low, 0.3%. It is likely that it was present in Lough Feeagh, but at a similarly low prevalence level, thus minimising the chance that it would be recorded.

A. clavula was the fourth most prevalent species in Lough Feeagh in this study, it had the second highest mean abundance value and was a component species in all months. It is highly unlikely that *A. clavula* was present in trout in Lough Feeagh during the study of Molloy *et al.* (1995a) but not recorded. Over the course of this study one sample of thirty eels was obtained from Lough Feeagh, *A. clavula* occurred in 60% of them. This prompts the question, was *A. clavula* always present in eels? On the basis of the answer from this we could ask 1) if *A. clavula* was not always present in eels, when and how did it arrive into Lough Feeagh?, 2) if *A. clavula* was always present in eels, what caused it to suddenly occur in trout in such large numbers.

On the basis of available evidence it is likely that *A. clavula* was always present in eels, in Lough Feeagh. *A. clavula* has been frequently reported from Ireland (Kane, 1966; Conneely and McCarthy, 1984, 1986, 1988). Molloy *et al.* (1993) reported *A. clavula* from autumn migrating smolts in the Burrishoole River. The two outflows from Lough Feeagh, the Millrace and the Salmon Leap flow into Lough Furnace, a brackish water lake with some tidal influence. The outflow from Lough Furnace is called the Burrishoole River, and it flows into the sea. Considering that *Asellus*

meridianus, the intermediate host of *A. clavula*, prefers moderately eutrophic freshwater (Hynes and Macan, 1960), and has not been widely reported from brackish water, that migrating smolts have been know to reduce feeding during migration (Fahy, 1985), and that the fish harbouring *A. clavula* were autumn migrating smolts (Molloy *et al.*, 1993). It would seem likely that these fish became infected with *A. clavula* in Lough Feeagh. Thus, we have tentative evidence that *A. clavula* occurred in brown trout in Lough Feeagh, and if it occurred in brown trout it is highly likely that it also occurred in eels, as eels are the preferred definitive host of *A. clavula* (Chubb, 1964; Kennedy and Lord, 1982). Therefore, it would seem likely on the basis of the available evidence that *A. clavula* always occurred in eels in the Burrishoole system.

This leads us to question two, if *A. clavula* was always present in eels in the Burrishoole catchment, why was it completely absent in trout during the study of Molloy *et al.* (1995a) and the fourth most prevalent species in this study. Kennedy (1984b) demonstrated a situation where the size and composition of a population of *A. clavula* in eels declined over a period of 4.5 years. He suggested that the cause of the decline was the decrease in abundance of *A. meridianus* as a result of interspecific competition with the congeneric species *A. aquaticus*. However *A. meridianus* was the only species of isopod recorded from Lough Feeagh in 1994 and 1997 (May, 1994; Boisson, 1997). Consequently, the findings of Kennedy (1984b) are not applicable in this case. However, the principle, that changes in the abundance of the intermediate host can affect the size and composition of an acanthocephalan population, is applicable.

Evidence from invertebrate studies carried out in 1994 (May, 1994) and 1997 (Boisson, 1997) suggest that the percentage of *A. meridianus* in the total number of invertebrates collected (excluding *G. duebeni*) at thirteen difference sites around the lake increased from 0.2% in 1994 to 5.6% in 1997. The virtual absence of *A. meridianus* in 1994 would probably have resulted in the population of *A. clavula* being lost from trout and severely declining in eels. However by 1997 the population

of *Asellus* had recovered to the point where trout became re-infected. Therefore, an explanation for the complete absence of *A. clavula* in trout in Lough Feeagh during the study of Molloy *et al.* (1995a) was that the population of *A. meridianus* had declined to the point where trout were no longer being infected. Accordingly, the appearance of *A. clavula* in trout in this study was as a consequence of the increased abundance of *A. meridianus*. Thus it appears that *A. clavula* was not a new introduction into the lake, as first thought.

The scenario outlined above appears to be the most likely explanation for the occurrence of *A. clavula* in large numbers in this study and its complete absence from the study of Molloy *et al.* (1995a). However, a number of factors are required to definitively confirm that the scenario outlined above is correct. Firstly, more comprehensive data on the parasites of eels in the lake, to confirm that *A. clavula* is indeed cycling through them, and secondly a long term study of trout, along the lines of that undertaken by Kennedy on Slapton Ley (1996b). It appears that Molloy *et al.* (1995a) examined trout at the end of one cycle, when *A. clavula* was missing and this study examined trout at the start of another cycle, in which the population of *A. clavula* had recovered or was recovering.

It can be concluded that the composition of the component communities was comparable between this study and the study of Molloy *et al.* (1995a). All the species recorded by Molloy *et al.* (1995a) were recorded in the present study, and in both cases *P. laevis* was the dominant species followed by *Crepidostomum farionis* and *E. crassum*. However in terms of richness, all values (with the exception of *D. ditremum*) were higher in the present study. The component community recorded in Lough Feeagh in this study could be considered a more abundant and intense version of the component community recorded by Molloy *et al.* (1995a). Regarding the five species which were only recorded in the present study, *Rhabdochona* sp. was potentially the only new introduction into the lake from another source.

Q. Is the infracommunity of wild trout in Lough Feeagh comparable to that recorded for Molloy *et al.* (1995a)?

When infracommunity results for the total sample were compared to those of Molloy *et al.* (1995a) all infracommunity values for this study were considerably higher (Table 4.34).

Table 4.34 Summary of the community characteristics for wild brown trout from three lakes in the west of Ireland*.

	Lough Feeagh†	Lough Feeagh‡	Clogher Lake†	Lake Bunaveela‡
Total No. Species	11	6	9	5
No. of Component sp.	7	3	5	1
Mean Sp. Richness	2.31	0.87	2.76	0.86
Mean No. Individuals	20.93	8.5	94.34	3.3
Mean Brillouin's Index	0.39	0.09	0.51	0.07
Simpson's Dominance Index	0.23	N/A	0.44	N/A
Berger-Parker Index	0.71	N/A	0.74	N/A
Shannon Diversity Index	1.75	N/A	0.9	N/A

N/A = Not available for this Lake; * = Standard deviation values have not been presented as they were not available for Lough Feeagh and Bunaveela Lake separately. † = Present study; ‡ = Molloy *et al.* (1995a).

However, Molloy *et al.* (1995a) reported that the number of individual parasites recovered from each fish varied considerably, and a range of 0-470 was recorded, whereas the largest range in the number of parasite individuals recorded for this study was 0-238. It can be concluded without any doubt that the helminth infracommunity recorded in wild and stocked trout in Lough Feeagh for this study was substantially richer than the helminth infracommunity recorded in wild brown trout in Lough Feeagh by Molloy *et al.* (1995a). These findings support the contention that the parasite community recorded in this study while similar in composition, was a richer and more intense version of the community recorded by Molloy *et al.* (1995a).

Q. Is the component community of Lough Feeagh comparable to the component community of Clogher Lake?

Examination of the component communities of Clogher Lake and Lough Feeagh suggest that there was a strong element of similarity between them (Table 4.34). Three allogenic species were found in Clogher Lake, and two were found in Lough Feeagh. An acanthocephalan species dominated in both lakes, and eight of the nine species recorded in Clogher Lake were also recorded in Lough Feeagh. Only the larval cestode *D. dendriticum* (Clogher Lake) and the nematodes *Cystidicola farionis* and *C. tenuissima* (Lough Feeagh) were found in one lake.

Clogher Lake had higher prevalence, mean abundance and mean intensity values for six of the eight species. *E. crassum* had a higher prevalence in Clogher Lake but lower mean abundance and mean intensity values and *Rhabdochona* sp. had a lower prevalence value in Clogher Lake and higher mean abundance and mean intensity values. All component community parameters were higher for *D. sagittata* in Lough Feeagh, in contrast all parameters for *S. salmoneus* were higher in Clogher Lake.

A number of workers have examined the issue of predictability in fish parasite communities (Kennedy, 1978a,b; Kennedy, 1990; Hartvigsen and Halvorsen, 1993). The general view is that there is a small degree of predictability in the composition of the helminth community, provided by the suite of salmonid specialists, but in most localities stochastic colonisation events play a major part. Esch *et al.* (1988) demonstrated that most component communities were dominated by a single species.

Kennedy and Hartvigsen (2000) demonstrated that four parasite species occurred commonly in the parasite communities of brown trout thus, giving a greater degree of predictability and that these four species were trout specialists. The findings from Lough Feeagh and Clogher Lake are in agreement with the general view. Although the composition of the component community of Clogher Lake and Lough Feeagh was similar, their component community structures differed.

In the previous chapter the component community of Clogher Lake was compared to the component community of Lough Feeagh as described by Molloy *et al.* (1995a) and to the component community of Lough Owennamarve from the Rosses in Co. Donegal (Byrne *et al.*, 2000). It was concluded that there was essentially two types of community, Clogher Lake and Lough Owennamarve characterised one type of component community, it was species rich, more diverse, and probably typical of more mesotrophic waters. Lough Feeagh characterised the second type of component community, it was less diverse, typical of oligotrophic waters, and most component community characteristics were lower.

On the basis of the evidence presented here it appears that Lough Feeagh has moved 'up the scale', and the dichotomous description of parasite communities proposed for Clogher Lake, Lough Owennamarve and Lough Feeagh (sensu Molloy *et al.*, 1995a) is no longer accurate. The component community in Lough Feeagh in this study has been described as a richer more abundant version of the component community described by Molloy *et al.* (1995a), but it was not as rich and abundant as that described for Clogher Lake.

Q. Is the infracommunity of wild trout recorded in Lough Feeagh comparable to that found in Clogher Lake?

When the infracommunities of Clogher Lake and Lough Feeagh were compared for the total sample only the value for the Shannon diversity index was higher in Lough Feeagh, all remaining parameters were substantially higher in Clogher Lake (Table 4.34). Clogher Lake had the highest mean species richness value and mean number of individuals for all months. Lough Feeagh had the highest Shannon diversity value in all months and the highest Brillouin's index value in August.

Examination of the component communities of Lough Feeagh and Clogher Lake led to the conclusion that the component community recorded for Lough Feeagh in this study was richer than that recorded for Lough Feeagh by Molloy *et al.* (1995a), but

not as rich as that recorded for Clogher Lake. Infracommunity results from the present study support this conclusion. The parasite infracommunity recorded for Lough Feeagh in this study was substantially richer than that recorded by Molloy *et al.* (1995a) but not as rich as that recorded for Clogher Lake. Thus, the infracommunity results support the contention that the original dichotomous classification of trout parasite community types in the west of Ireland was an oversimplification. Lough Feeagh is a dynamic lake in the

Kennedy (1997) demonstrated that infracommunity parameters for eels in the River Otter exhibited some variation between months. They were highest in April and lowest in June, but differences between each month were not significant. He concluded that such variation was as a result of stochastic processes. In Lough Feeagh and Clogher Lake infracommunity parameters also varied seasonally. The mean species richness, Brillouin's index and Shannon diversity index for Lough Feeagh were lowest in April and highest in November. In contrast the Simpson's dominance and Berger-Parker indices were highest in April and lowest in November. Thus there was a definite seasonal trend in infracommunity parameters in Lough Feeagh, but there was only a significant difference in the mean number of individuals between months. The highest mean number of individuals was recorded in May and lowest was recorded in August.

Q. Are the component communities of stocked and wild trout comparable in Lough Feeagh?

Eleven parasite species were recorded in wild trout and ten species were recorded in stocked trout. *Anisakis* sp. was the only species recorded in wild trout and not recorded in stocked trout. As previously discussed *Anisakis* sp. has been recorded in freshwater (Kane, 1966) and is normally associated with migratory fish, although it has also been reported from landlocked populations (Wootten and Smith, 1975), it is likely that the wild fish infected with *Anisakis* sp. had undertaken some form of migration. Only one allogenic species, *D. ditremum* was common to wild and stocked

trout. Three of the four non-component species recorded in wild trout were also non-component species in stocked trout.

Wild trout had the highest prevalence values for five of the ten parasite species they had in common. Stocked trout had substantially higher mean abundance values for *E. crassum* and *D. ditremum*, and wild trout had higher values for *Crepidostomum farionis*. This suggests that stocked trout were feeding on more planktonic organisms, probably planktonic copepods, which are the intermediate hosts of *E. crassum* and *D. ditremum* (Kennedy and Burrough, 1978), and wild trout were feeding on more benthic invertebrates, which are the intermediate hosts of *Crepidostomum farionis*.

A number of studies have examined the diets of wild and stocked fish (Sosiak *et al.*, 1979; O'Grady, 1983; Johnsen and Ugedal, 1986; Kelly-Quinn and Bracken, 1989a,b) and all have shown that stocked fish ultimately adopt a normal diet, although the length of time taken to do this differs. Sosiak *et al.* (1979) working on salmon parr and O'Grady (1983) working on brown trout demonstrated that stocked fish initially favoured food items on or near the surface of the lake. O'Grady (1983) also suggested that competition with resident fish might result in trout being forced from the benthic feeding areas and having to feed near the surface. Thus, stocked fish are considered to feed on more items on or near the surface resulting in higher prevalence and mean abundance values for *D. ditremum* and *E. crassum*.

Wild trout had the highest mean intensity values for six of the species they shared with stocked trout. Wild trout also had the highest mean abundance and prevalence values for four of them. Thus, it can be concluded that the composition of the total parasite component community of stocked brown trout was almost identical to that of wild trout, however in terms of community structure some differences existed.

Q. Is there a difference between the component communities of wild and stocked trout over the sample months?

When the component communities of the total samples of wild and stocked trout were compared, they were similar in terms of composition, but differed in terms of community structure. However, just examining the total component community does not give a clear picture of the processes which occurred. Stocked trout were put into Lough Feeagh in late March / early April, thus they had about one month to acclimatise and become infected with parasites, before the first sample was taken in May.

In May, four species were recorded in stocked trout and nine were recorded in wild trout. All four species were component species in wild trout and *P. laevis* and *A. clavula* were component species in stocked trout. The prevalence of *A. clavula* was higher in stocked trout, whereas, all component community parameters for *P. laevis* were higher in wild trout. *A. clavula* was the dominant species in stocked trout and *Crepidostomum farionis* was the dominant species in wild trout. *E. crassum* had the lowest component community parameters of any species in stocked trout.

It can be concluded that the parasite component community of wild fish in May was richer and more diverse than the component community of stocked fish. The parasite community recorded in stocked fish was made up of the four most prevalent species found in wild fish. This finding agrees with the findings of Hartvigsen and Halvorsen (1993) who showed that the parasite species infecting naïve salmon parr were the most prevalent species in the adjoining lake. Kennedy and Hartvigsen (2000) examined the intestinal helminth communities of brown trout from 72 localities in Ireland, England and Norway and identified a group of four specialists which occurred commonly in trout, and gave a greater degree of predictability to the parasite community. The results from stocked trout in May agree with the findings of Kennedy and Hartvigsen (2000).

Eight component species were recorded in wild and stocked trout in August. *E. crassum* had the lowest component community parameters in stocked trout in May, in August it dominated the community. The next most dominant species, the larval cestode *D. ditremum*, was not recorded in May. For both species all component community parameters were higher in stocked trout. The increase in the component community parameters of *E. crassum* and *D. ditremum* was consistent with a peak recruitment period in midsummer (Kennedy, 1996a), a similar increase was also seen in Clogher Lake. *A. clavula* was the dominant parasite species in stocked trout in May and August. Although the prevalence value recorded for *A. clavula* declined from May to August, the mean abundance and mean intensity values increased, whereas for *P. laevis* the prevalence and mean intensity values decreased substantially. All component community parameters were substantially higher for *P. laevis* in wild trout.

It can be concluded that the component communities of wild and stocked trout in August were similar in terms of composition, but different in terms of structure. The dominance of *E. crassum* and *D. ditremum* in stocked trout suggests they adopted a more planktonic diet than wild trout. The dominance of *P. laevis* over *A. clavula* in wild trout, and the dominance of *A. clavula* over *P. laevis* in stocked trout suggests that both groups of fish were feeding preferentially on different intermediate hosts. In contrast, O' Grady (1983) could not find any significant differences in the proportions of *Asellus* and *Gammarus* consumed by wild and stocked trout.

In November the same nine species were recorded in wild and stocked trout, all were component species in stocked trout and seven were component species in wild trout. With the exceptions of *D. sagittata* and *A. clavula* all species had higher prevalence, mean abundance and mean intensity values in stocked trout. Prevalence values for *E. crassum* in stocked trout were comparable between August and November, but mean abundance and mean intensity values decreased sharply. Kennedy (1996a) also demonstrated a large midsummer increase in *E. crassum* as a result of recruitment, followed by a large drop, which was as a result of parasite mortality. A similar

situation occurred for *E. crassum* in stocked trout, except in this case the prevalence value also increased from August to November. In comparison, all the component community parameters for *E. crassum* in wild trout were comparable between August and November. For *D. ditremum*, the situation was similar to that reported for stocked trout.

P. laevis was the dominant species in stocked trout in November, and all component community parameters recorded for *P. laevis* were higher than those recorded for *A. clavula*. In wild trout *P. laevis* had the highest prevalence and mean abundance values, and *A. clavula* had the highest mean intensity value. All component community parameters recorded for *P. laevis* were higher for stocked trout in November, whereas, for *A. clavula* the prevalence value was higher for stocked trout and the mean intensity and mean abundance values were higher for wild trout. Thus it can be concluded that the component community recorded for stocked trout in November was richer than that recorded for wild trout.

When the total parasite component communities were compared between wild and stocked trout, their compositions were comparable but their structures differed. Also, differences existed in the structure and composition of the component communities between wild and stocked trout over the sampling period, which examination of the total component community alone would not have revealed.

In May when the first sample of stocked fish was taken from Lough Feeagh, *A. clavula* was the dominant species followed by *P. laevis* and *Crepidostomum farionis*. *E. crassum* had the lowest values for all component community parameters. To produce such a pattern newly stocked fish must have been feeding on benthic isopods and amphipods, however dietary analysis of the stocked fish caught does not support this. The most common food group in the stomachs of newly stocked fish was dipterans, which suggests that fish were feeding at or near the surface. However there is some evidence to suggest stocked fish were also feeding on the benthos. Gravel

occurred in the diets of about 20% of stocked trout, and it occurred significantly more often than either *Asellus* or *Gammarus*.

In August *E. crassum* was the dominant species in stocked trout inLough Feeagh. Examination of mean abundance and mean intensity values suggest that there was a large amount of recruitment of *E. crassum* during this period, which is in agreement with the findings of Kennedy (1996a). Consequently, fish must have consumed large quantities of infected copepod intermediate hosts. It is likely that when put into Lough Feeagh in late March / early April trout initially fed on benthic organisms, principally because planktonic organisms were not present in sufficient quantities. This accounts for the greater abundance of *A. clavula*, *P. laevis* and *Crepidostomum farionis* recorded in stocked trout in May. As the water temperature increased, the abundance of planktonic organisms increased and stocked fish switched focus and fed intensively on them instead, hence the dominance of *E. crassum*. Wyatt and Kennedy (1988) demonstrated that a number of copepod species had distinct seasonal occurrences, and different species peaked in abundance from spring to autumn. It is likely that the same spring to autumn increases in abundance of planktonic copepods occurred in Lough Feeagh.

A number of other workers have examined the parasite communities of wild and stocked fish (Aderounmu, 1966; Wootten, 1973; Poynton and Bennett, 1985; Hartvigsen and Halvorsen, 1993), however few of them have examined community parameters in any detail. Aderounmu (1966) showed that twelve species were found in wild trout and seven species were found in hatchery reared trout. Similarly, Wootten (1973) demonstrated that the parasite fauna of stocked rainbow trout from the raceways in Hanningfield reservoir was a reduced version of the parasite community found in the adult fish from the reservoir.

Poynton and Bennett (1985) examined the parasitic infections of wild and cultured brown trout and cultured rainbow trout. This study was more concerned with the identity of parasite species and their potential interactions with cultured fish, rather

than parasite community dynamics. However, a total of 21 genera of parasite (protozoan and metazoan) were recovered from wild trout compared to seventeen genera from cultured brown trout and five genera from cultured rainbow trout. These findings while not directly comparable to the situation in Lough Feeagh, at least support the idea that initially stocked / cultured trout do not harbour as many species as wild trout.

McGuigan and Sommerville (1985) compared the parasite fauna of cultured rainbow trout, eels and wild fish in a eutrophic freshwater loch in the west of Scotland. They demonstrated that a number of differences existed in the prevalence and intensity values recorded for wild and stocked trout, for example strigeid metacercariae dominated the fauna of both wild and caged trout, but infection was lower in caged trout. The aim of this study was to examine the effects of intensive fish farming on a Scottish loch in terms of disease and parasites, correspondingly sample fish were maintained in cages, artificially fed and treated with therapeutic products when necessary. Thus, the results from this study support the findings from Lough Feeagh, although both studies were not directly comparable.

In a similar experiment Vidal-Martinez *et al.* (1998) compared the parasite communities of wild and caged *Cichlasoma urophthalmus* over a seven-month period. A total of 17 parasite species were recorded from the wild fish sample and ten species were recorded from the caged fish sample. A maximum of thirteen parasite species were recorded from the wild fish sample in April. The pattern demonstrated for caged fish was similar to that demonstrated for stocked trout in Lough Feeagh, in that the number of parasite species increased over the course of the study. Unlike the situation in Lough Feeagh the number of parasites recorded in caged fish in any month never equalled or exceeded the number of parasites recorded in wild fish. This study was also not directly comparable to the study in Lough Feeagh, as stocked *C. urophthalmus* were fed an artificial diet, and maintained in artificial cages. They had free access to all planktonic copepods and their parasites but not to benthic

intermediate hosts. Consequently, it would be impossible for caged *C. uropthalmus* to adopt a fully wild parasite fauna.

Q. Is there any difference in the abundance of parasites recorded between wild and stocked fish hosts of different ages?

A significant relationship existed between the abundance of *P. laevis* and age in wild and stocked trout, and *E. crassum* in wild trout. In all cases older fish had higher abundance values. There was also a significant difference in the abundance of *Crepidostomum farionis* between wild and stocked trout, however in wild trout older fish had higher abundance values but in stocked trout younger fish had higher abundance values.

In 1997 stocked trout were put into Lough Feeagh in early April. These fish formed the May, August and November trout samples. In 1998 a similar situation occurred, except that in 1998 a small number of stocked trout from 1997 were also caught. Thus, the significant relationship between age and *P. laevis* in stocked trout resulted from some 1997 fish being caught in 1998. Molloy *et al.* (1995a) and Kennedy (1972a) also reported that the abundance of *P. laevis* increased with host age. In contrast, Fitzgerald and Mulcahy (1983) demonstrated that *P. laevis* had the highest prevalence in 0+ trout and the highest intensity in 1+ trout and both values decreased with increasing host age. It is likely that changes in the quantity of intermediate hosts consumed by trout were responsible for the two different patterns.

The pattern recorded for *Crepidostomum farionis* in wild trout agrees with the findings of Awachie (1968). He demonstrated that the prevalence and mean intensity of *Crepidostomum* sp. increased with the age of the fish, and suggested that this was probably related to larger fish eating greater quantities of intermediate hosts. O'Grady (1983) suggested that stocked fish had a preference for surface food and they tended to concentrate on it. Results from the dietary survey carried out in Lough Feeagh, also suggest that recently stocked fish identified a particular food item, and then

concentrated heavily on it. Thus, recently stocked trout probably fed heavily on the intermediate host of *Crepidostomum farionis*. Also, when stocked fish were first put into the lake, they probably concentrated on benthic organisms as the spring increase in planktonic copepods had not yet occurred.

The mean abundance of *E. crassum* was significantly related to the age of the host fish. A similar situation was found for *D. ditremum* in Clogher Lake. The explanation for Clogher Lake, was that older fish were feeding on greater quantities of planktonic copepods. Kennedy *et al.* (1992) showed that eels while thought to be almost exclusively benthic, regularly fed on planktonic copepods. It appears that such a pattern also occurred for trout, in Clogher Lake and in Lough Feeagh.

Q. Is there any difference in the abundance of parasites between the sex of the host fish for wild and stocked trout in Lough Feeagh?

Only the abundance of *P. laevis* differed between male and female fish. This occurred for wild and stocked trout. The difference in the abundance of *P. laevis* between sexes occurred in April for wild trout, and in November for stocked trout. In both situations female fish had significantly more worms than male fish. Very few authors have examined component community parameters in relation to host sex. Molloy *et al.* (1995a,b) demonstrated that there was no significant relationship between host sex and the abundance of *P. laevis*. Similarly Awachie (1965) could find no correlation between the sex of trout and the prevalence and abundance of *E. truttae*.

Dezfuli *et al.* (1999) demonstrated that *P. laevis* showed no preference for host sex in the intermediate host (which is *Echinogammarus stammeri* in Italy). Conneely and McCarthy (1988) and Bwathondi (1976) only demonstrated a difference in prevalence between male and female trout for the digenean *C. metoecus*. The situation described in the previous chapter regarding the potential differences in life history strategy between male and female migratory trout, may account for the significant difference in the abundance of *P. laevis* between male and female wild trout in April.

However, as stocked trout had not migrated, the life history strategy of male and female fish would be similar. Perhaps as Bwathondi (1976) suggested female hormonal activity could have influenced the abundance of *P. laevis*, especially as the difference occurred in stocked trout in November, when fish begin to migrate upstream to breed. The other possibility that exists is that differences in the abundance of *P. laevis* between male and female stocked and wild fish occurred purely by chance.

Q. Is there any difference in the abundance of parasites recorded between months for wild and stocked trout in Lough Feeagh?

Crepidostomum farionis and *P. laevis* were the only species which showed significant differences in abundance between months in wild fish and *P. laevis* and *E. crassum* were the only species which showed significant differences in abundance between months in stocked fish. It appears that the inability of *Crepidostomum farionis* metacercariae to establish in fish, above a certain water temperature was responsible for the seasonal pattern reported for this species. Thus it is likely that temperature regulates the *Crepidostomum farionis* population. Awachie (1968) suggested that this regulation temperature was approximately 10°C.

The results from Lough Feeagh agree with those from Clogher Lake and those of Awachie (1968) and Bwathondi (1976, 1984). However, examination of temperature values in Lough Feeagh suggest that the maximum temperature at which metacercariae can establish is higher than 10°C. The mean temperature in Lough Feeagh was 12.1(± 2.2)°C in May, 17.1(±0.8)°C in August and 10.5(±1.3)°C in November. Considering that prevalence and mean intensity values increased from April to May, and that the mean temperature in May was approximately 12°C, it would seem likely that the maximum temperature at which establishment of metacercariae of *Crepidostomum farionis* could occur in Lough Feeagh was closer to 12°C.

For wild and stocked trout mean abundance and mean intensity values for *P. laevis* decreased from May to August. A similar situation was found for the dominant acanthocephalan species *A. clavula* in Clogher Lake, and it was concluded that seasonal changes in water temperature affected the parasites population dynamics (Andrews and Rojanapaibul, 1976). Kennedy (1972a) demonstrated experimentally that temperature adversely affected the initial establishment of *P. laevis* in goldfish. He demonstrated that mean percentage recovery of parasites after three weeks decreased substantially as the temperature increased. Considering that the mean temperature of Lough Feeagh was 17.1°C in August 1997, it is likely that temperature also affected the population dynamics of *P. laevis*.

The differences in the component community parameters recorded for *E. crassum* in stocked trout between month's resulted from their tendency to feed at or near the surface. Stocked trout were consuming large amounts of planktonic copepods, thus hence becoming infected with *E. crassum* (Byrne, unpublished). A similar pattern was observed for trout in Malham Tarn (Kennedy and Burrough, 1978). Kennedy (1996a) demonstrated that the peak infection period for *E. crassum* occurred in July, and that a large proportion of the *E. crassum* found were recently acquired plerocerciform cestodes. He also demonstrated that soon after the initial increase in and abundance in July, most of the pleroceriform worms were lost, resulting in a substantial decrease in abundance. The situation reported for stocked trout in Lough Feeagh followed exactly the same pattern.

Q. Are the helminth infracommunities of wild and stocked trout comparable?

The infracommunity patterns recorded for stocked trout reflect the fact that they were only put into the lake in spring. The mean species richness, mean number of individuals, and diversity indices all increased from May to August. Such an increase is consistent with the development of the helminth community in stocked trout.

When the total infracommunities for wild and stocked trout were compared, stocked trout had higher values for the mean species richness, mean number of individuals and the Brillouin's index, whereas wild trout had higher values for the Shannon diversity index and the Berger-Parker index. This would suggest that stocked trout had richer infracommunities than wild trout. However, examination of only the total sample does not reveal the underlying monthly pattern.

As might be expected, all infracommunity parameters with the exception of the Simpson's dominance and Berger Parker indices, were higher for wild trout in May. This was entirely consistent with the fact that stocked trout were recent arrivals into Lough Feeagh. They appeared to feed heavily on a few food substances and therefore their parasite infracommunities were heavily dominated by a few parasite species. In August, the highest values for the mean species richness, mean number of individuals, and the Simpsons dominance and Berger-Parker indices were recorded for stocked trout, and only the Brillouin's index of diversity and the Shannon diversity index were higher for wild trout. It appears that stocked trout had richer infracommunities but wild trout had more diverse infracommunities.

In November, all values except the Berger-Parker and Shannon diversity indices were higher in stocked trout. Thus, in November it appears that stocked trout had substantially richer and more diverse infracommunities. The helminth infracommunity went from being substantially lower than that recorded for wild trout in May, to being comparable with the infracommunity recorded for wild trout in August, and higher than the infracommunity recorded for wild trout in November. Examination of the total infracommunity parameters in isolation would not have revealed such a pattern.

As discussed for Clogher Lake very few workers have examined helminth infracommunities in any detail (Kennedy *et al.*, 1997; Marcogliese and Cone, 1998), similarly, few workers have examined the parasite communities of wild and stocked fish (McGuigan and Sommerville, 1985; Vidal-Martinez *et al.*, 1998) in any detail

and none have compared infracommunity parameters between wild and stocked fish. Vidal-Martinez *et al.* (1998) presented infracommunity data for wild *Cichlasoma urophthalmus* and some data for caged *C. urophthalmus*. They demonstrated that the mean species richness for caged *C. urophthalmus* increased from April to a peak in August and then remained constant. Although not directly comparable to the situation in Lough Feeagh, a similar type pattern was found for the mean species richness values of stocked trout.

Q. Is there a significant difference in the abundance of parasite species between wild and stocked trout?

Significant differences occurred in the abundance of *D. ditremum*, *E. crassum*, *A. clavula* and *Crepidostomum farionis* between the total samples of wild and stocked trout. In all months there were significant differences in the abundance of *P. laevis* and *E. crassum*, in two months there were significant differences in the abundance of *A. clavula* and in one month there was a significant difference in the abundance of *D. ditremum* between wild and stocked trout. Mann-Whitney U-tests revealed significant differences in the abundance of *D. ditremum* and *P. laevis* between the total samples wild and stocked trout. In August there was a significant difference in the abundance of *D. ditremum* between wild and stocked trout, and in November there was a significant difference in the abundance of *E. crassum* between wild and stocked trout.

The results from these analyses support the conclusions drawn from the discussion on the component community. Specifically, stocked trout appear to feed preferentially on organisms at or near the surface and hence their parasite component communities were heavily influenced by species which utilised planktonic intermediate hosts. Whereas wild trout appeared to adopt a more benthic diet, so their parasite component communities were heavily influenced by parasites which utilised benthic intermediate hosts.

Q. Are the relationships between the categories of intensity of the four most prevalent species in wild and stocked trout significant?

The relationship between categories of intensity of *P. laevis*, *A. clavula*, *Crepidostomum farionis* and *E. crassum* were examined for wild and stocked trout. There appeared to be a negative trend in the relationship between *P. laevis* and *A. clavula* in wild and stocked trout. However, the relationships between both species were not significant for the presence / absence or low / high intensity contingency tables for wild or stocked trout. Kennedy and Moriarty (1987) examined the co-existence of *A. lucii* and *A. anguillae* in Ireland. They showed that both species could co-occur, but *A. lucii* was the dominant species in all years. Bates and Kennedy (1990) showed that the survivorship and range of intestine occupied by *A. anguillae* was reduced in the presence of *P. laevis*, but the survivorship and range of *P. laevis* was not reduced in the presence of *A. anguillae*.

Similarly Kennedy (1985) demonstrated *A. clavula* and *P. laevis* exhibit clear site segregation. The apparent negative trend in the categories of intensity of *A. clavula* and *P. laevis* could support the idea that some type of inhibitory interaction is occurring, although the nature of such an interaction is far from clear.

There was a difference in the patterns of occurrence of *Crepidostomum farionis* and *P. laevis* in wild and stocked trout. In wild trout both species co-occurred in 42.8% of cases and in only 20% of cases did they co-occur at high intensity. Whereas in stocked trout both species only co-occurred in 25.4% of cases but in 100% of cases they co-occurred at high intensity. The differential feeding pattern of wild and stocked trout was probably responsible for the differences in the patterns of intensity recorded between the both species in wild and stocked trout. The differences in the pattern of intensity of *E. crassum* and *P. laevis* were probably also related to the differential feeding of wild and stocked trout. Stocked trout had much higher levels of *E. crassum* as a result of their more planktonic diets. This is supported by the fact that there was a significant relationship between *E. crassum* and *P. laevis* for the presence

/ absence contingency table for stocked trout. Kennedy (1985) suggested that there would be little overlap between the cestode *E. crassum* and *P. laevis*, as *E. crassum* occurred in the pyloric caeca and *P. laevis* had a more posterior distribution. This could account for the overall absence of any distinct patterns in the occurrence of *E. crassum* and *P. laevis* in the low / high contingency tables.

For wild trout the relationship between *Crepidostomum farionis* and *A. clavula* was significant for the presence / absence and low / high intensity contingency tables, and the trend appeared to be positive. In stocked trout both species only occurred together in 31.3% of cases, and for the low / high intensity tables they only co-occurred together at high intensity in 33.3% of cases. Dorucu *et al.* (1995) demonstrated a positive association between *Crepidostomum farionis* and the acanthocephalan *N. rutili*. Whether the association here is a genuine positive association or a result of chance is unclear. A similar positive type relationship occurred between *Crepidostomum farionis* and *A. clavula* in Clogher Lake but it was not significant, thus it was concluded in that case that the relationship was as a result of chance.

Differences in the pattern of occurrence of *E. crassum* and *A. clavula* between wild and stocked fish were reported. For wild fish both species occurred together in 28.4% of cases and for stocked fish both species occurred together in 47.9% of cases. For the low / high intensity contingency tables for wild and stocked fish both species co-occurred at high intensity in all cases. A similar pattern of occurrence was also found for *P. laevis* and *E. crassum*. In both situations *E. crassum* co-occurred with the acanthocephalan species much more frequently in stocked trout. This was related to the fact that stocked trout had a more planktonic diet which resulted in greater component community parameters being recorded for *E. crassum*.

For the low / high intensity contingency tables the relationship between *E. crassum* and the acanthocephalan species was similar for wild and stocked trout. When the cestode and acanthocephalan species did co-occur there did not appear to be any obvious relationship between them. The preferred position of *E. crassum* was the

pyloric caeca (Kennedy, 1996a). *A. clavula* occurred over the entire length of the intestine (Kennedy and Lord, 1982) and *P. laevis* had a more posterior distribution (Kennedy, 1985), however there was little overlap between the cestode and both acanthocephalan species, hence the lack of any obvious relationship.

The same situation occurred for *E. crassum* and *Crepidostomum farionis*. In wild trout both species co-occurred in 17.8% of cases, whereas in stocked trout both species co-occurred in 63% of occasions, again probably related to the more planktonic diet of stocked trout. However when both species did co-occur there appeared to be a negative type relationship. Halvorsen and McDonald (1972) demonstrated that a negative relationship between *C. truncatus* and *C. metoecus* and Kennedy and Hartvigsen (2000) suggested that a negative relationship existed between *E. crassum* and *C. metoecus*. These results, and those from Clogher Lake indicate that there may be some type of negative interaction between *E. crassum* and *Crepidostomum farionis*, although the exact nature of such an interaction is unclear.

Kendall's tau correlation coefficient was calculated for the total intensity of all species pairs. For wild trout, fourteen species pairs were significantly correlated, seven of these were significantly negatively correlated. For stocked trout, fourteen species pairs were significantly positively correlated. Six significant correlations were common for wild and stocked trout.

In Clogher Lake *Rhabdochona* sp. was significantly positively correlated with all cestode species, on the basis of these correlations it was suggested that *Rhabdochona* sp. used a copepod as an intermediate host. For wild trout in Lough Feeagh there was a significant negative correlation between *Rhabdochona* sp. and both cestode species, whereas for stocked trout there was significant positive correlation between *Rhabdochona* sp. and *D. ditremum*.

However, *Rhabdochona* sp. was also significantly negatively correlated with *A. clavula* and *P. laevis* in wild trout, and it was significantly positively correlated with

Crepidostomum farionis in wild and stocked trout. *Crepidostomum farionis* is known to use an ephemeropteran intermediate host (Brown, 1927; Bwathondi, 1984). Thus in Clogher Lake correlation coefficients would lead one to the opinion that *Rhabdochona* sp. utilised a copepod intermediate host, and in Lough Feeagh correlation coefficients would lead one to the opinion that *Rhabdochona* sp. utilised either a copepod or a mayfly, as an intermediate host (Moravec *et al.*, 1991). In contrast, *E. crassum* and *D. ditremum* were significantly positively correlated for wild and stocked trout, which supports the fact that they both use copepod intermediate hosts.

The significantly negative correlation between *Crepidostomum farionis* and *E. crassum* supports the results from the contingency tables, which suggested that there was some type of interaction occurring between these species. Also, for wild and stocked trout there was a significantly positive relationship between *Crepidostomum farionis* and *A. clavula*. This supports the results from the contingency tables, which suggested that that there was a type of positive relationship between these two species.

Results from the contingency tables suggested that *E. crassum* and *P. laevis* co-occurred more frequently in stocked trout. Stocked trout had a more planktonic diet and thus acquired greater quantities of *E. crassum*. Correlation coefficient values also supported this idea. *E. crassum* and *P. laevis* were negatively correlated in wild trout and positively correlated in stocked trout. The difference in the pattern of co-occurrence of *Crepidostomum farionis* and *P. laevis* between wild and stocked trout for the presence / absence and low / high contingency tables was also shown by their correlation coefficients. In wild trout *Crepidostomum farionis* and *P. laevis* were significantly negatively correlated whereas in stocked trout there was no significant relationship between the two species. A number of species pairs appeared to be significantly correlated for no other reason than chance, and as a result they will not be discussed.