The Ecology of the Family Chydoridae (Branchiopoda, Anomopoda) and its Application to Lake Monitoring

A thesis submitted to Dublin University for the degree of Doctor of Philosophy

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Declaration

I hereby certify that this thesis, submitted to the University of Dublin for the degree of Doctor of Philosophy, has not been submitted as an exercise for a degree at any other University. I also certify that the work described here is entirely my own, unless stated as otherwise.

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November, 1999.

Acknowledgements

I would like to thank my supervisor, Dr. Ken Irvine, for all his help and support over the last three and a half years, and for giving me the wonderful opportunity to work on Irish lakes. Also, Dr. Julian Reynolds and Dr. Norman Allott contributed much to my understanding of freshwater biology and answered many of my questions, for which I thank them. The two years spent sampling and driving around the country (in vans and boats!) would not have been nearly so enjoyable without my companions, Rossana Caroni, Jonathan White, and Gary Free. I would like to thank them and also Áine O Connor most sincerely for their patience and constant advice during the time spent in the freshwater lab, and while writing this thesis. Thanks also go to Ciarán Byrne who entertained us all in Newport, and is himself, an honorary Freshwater Biologist. I would also like to express my gratitude to all the postgraduates and staff in the Zoology Department, both past and present, for providing continuous distraction and a lot of entertainment. Other members of the Zoology Department helped me throughout the six years I have been with them, and have always been on hand with bright ideas, in times of crisis. They are Peter Stafford, Alison Boyce, Martyn Linnie, Marina Pearson and Richard Hollinshead, and my sincere thanks goes to all of them. We stayed with many people during our sampling trips throughout 1996 and 1997, and I would particularly like to thank the Robsons in Clifden House, the Joyces at Maam cross, the Mulchrones in Newport, the O'Gradys in Sligo and the Shackletons in Mullagh. Their hospitality, hot dinners and big breakfasts made the many sampling trips very enjoyable.

I would especially like to thank Chris (Dr. Troy!), Dad, Mum, Sorcha, Adam, Granny, Kate, Vera and Barry for everything. They have all provided me with unconditional support throughout my years in college, particularly in the last few months, and I suspect that they are nearly as happy as I am that this thesis is finished.

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Finally, I would like to extend my thanks to all the members of Dublin University Sub Aqua Club, who have ensured that a lot (if not the majority!) of my time in Trinity has been spent either underwater, or thinking about diving. My years spent on the committee (particularly as Diving Officer) taught me a lot and the fact that this thesis is finished owes much to my experiences while involved with DUSAC. Those of you fortunate enough to dive High Island in June of this year will realise what an inspiration it was! Thank you all.

Summary

Chydorids (Branchipoda, Anomopoda) were sampled from twenty nine Irish lakes between June 1996 and July 1997, in order to assess the usefulness of this group as indicators of lake ecological quality. The lakes represented a wide range of the physicochemical conditions found in Irish lakes, and thirty one species of Chydoridae were identified from a total of 260 samples. Multivariate analysis was used to elucidate relationships between the chydorids and their environment, and in particular, what aspects of the lakes system had strong effects on the chydorid community structure. It was found that the ecological quality of the twenty nine lakes could be characterised successfully by the chydorid communities sampled. The main factors affecting the community structures were found to be the trophic status of the lake, the acidity/alkalinity of the water, and the amount of physical disturbance in the littoral region. Several species (*Alona affinis, Alonopsis elongata, Chydorus sphaericus* and *Monospilus dispar*) were found to dominate the chydorid community in lakes which were under some kind of environmental stress, and in lakes where this stress was not so significant, the community was richer and more diverse. A dichotomous key, based on the dominant species of chydorid and the diversity of the community is described, which could be used to assess the ecological quality of a lake.

As spatial distributions of chydorids may affect how successful a classification scheme for lakes based on the chydorid community may be, two of the study lakes, Lough Inchiquin, Co. Clare, and Lough Maumwee, Co. Galway, were sampled intensively. The heterogeneity of the chydorid community, with respect to species distribution among several different microhabitats and also down the littoral zone with depth was examined and the two lakes proved to have quite different distribution patterns of chydorids. In Lough Inchiquin, the chydorid communities from different

substrata were quite distinct, and the chydorids were restricted to the top one and a half metres of the littoral zone. In contrast, there was not much distinction between chydorid communities associated with different substrata in Lough Maumwee, and the chydorids were not restricted to the top of the littoral zone. Lake morphometry seemed to have an important role in determining the heterogeneity of the chydorid community, and the ease with which the chydorids disperse among different substrates.

In order to investigate why some chydorid species become dominant in particular lake types, several autecological studies were conducted. The effects of temperature and pH on the egg development time of *Chydorus sphaericus, Alona affinis, Alonopsis elongata and Acroperus harpae* were tested, as well as the difference in population growth of *Alona affinis, Alonopsis elongata* and *Chydorus sphaericus*, cultured in four food mediums. As expected, temperature proved to be very important in determining the rate of egg development, although the extent to which a decrease in temperature brought about an increase in egg development time differed with each species. pH also proved to have a significant affect on egg development time, although this may have been due to fluctuations in the experimental chambers. Again, the extent of the effect depended on the species under examination. The population growth of each species was significantly affected by the type of food which they were supplied with. Some of these results can be used to explain observed differences in chydorid community structure between lakes of varying ecological quality.

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Introduction.

1.1 The biota of the littoral zone.

In the majority of lakes, the littoral zone is a very important part of the ecosystem, forming a crucial link between the land surrounding the lake and the openwater (Moss, 1988; Wetzel, 1983). The heterogeneous nature of the substrata (including macrophytes) of the littoral zone, combined with high productivity and food availability means that this zone can support a high diversity and biomass of life. This includes bacteria, protozoa, microcrustaceans such as copepods and cladocera, larger macroinvertebrates and fish, all of which can be involved in complex interactions with each other and the plants and substrata of their environment. An important group within this web are the chydorids, which are a cladoceran family. Most chydorids are found in association with littoral benthic substrates or macrophytes, although some species, such as *Chydorus sphaericus* and *Alona rectangula* are often found in open water plankton samples, although, even in this case, they may not be truly planktonic, as *Chydorus sphaericus* is often observed to be attached to filaments of algae when present in the open water (Havens, 1991; Fryer, 1968). Chydorids are thought to have an unselective diet of algae, epiphyton and detritus which is scraped or collected from the surface of plants, rocks or mud, using the second trunk limbs, and then passed via the third, fourth and fifth trunk limbs to the mouthparts. Adaptive radiation in the chydorids has led to a diverse range of feeding habits and although they are generally known as detritivores, each species has a particular way of feeding which is adapted for their lifestyle and some species have become scavengers (*Pseudochydorus globosus*) or parasites (*Anchistropus emarginatus*) (Fryer, 1968).

The chydorids are important components of the littoral (and hence the whole lake) food web, converting detritus and primary products into body matter, which is then consumed by invertebrate and vertebrate predators and even plants such as Bladderwort (Duigan & Kovach, 1991; Havens 1991; Rasmussen, 1988; Green, 1954). *Chydorus*

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sphaericus and *Alona guttata* were found to account for 9% of the littoral biomass in a eutrophic lake (Havens, 1991) and an assemblage of three chydorid species was found to have a secondary production of 684 mg m^{-2} y^{-1} in the River Thames, UK (Robertson, 1995). They can form dense populations comprising several thousands of animals and are therefore a potentially important food source for the next level in the food web. They are often found in the stomachs of fish (Fitzmaurice, 1977) and are also important food for invertebrate predators such as *Chaoborus* (Havens, 1991), chironomid larvae (Williams & Whiteside, 1978) and Odonata nymphs (Williams, 1983). Given their importance within the littoral zone, however, the literature concerning this family is relatively limited.

1.2 Introduction to the Chydorid family

Chydorids are small crustaceans belonging to the group known as Cladocerans or water fleas. The group was revised several years ago and split into four orders, Anomopoda, Haplopoda, Ctenopoda and Onychopoda (Dodson & Frey, 1991) although recent molecular evidence suggests that these four orders should be reassigned to the suborder level (in the order Cladocera), as they may be monophyletic (Hanner, 1997; Crease & Taylor; 1998). Either way, the term "Cladocera" as a general description is still widely used. The full classification of chydorids as it stands is:

Phylum Crustacea

    Class Branchiopoda

        Sub Class Diplostraca

           Order Anomopoda

           Family Chydoridae

The classification of the Chydorid family is constantly being updated and revised, mainly because of the realisation that some 'species' which were previously thought to

have a cosmopolitan world-wide distribution, are actually several similar species with more distinct geographical distributions (Frey, 1993; Duigan & Murray, 1987). The chydorids are split into several sub families: the Sayciinae, Eurycercinae, Aloninae and Chydorinae, the last three of which have representatives in Ireland (Duigan, 1992). The identification of chydorids is relatively easy as it does not usually require any dissections, and for most species it is based on the shape of the carapace, the rostrum and the postabdominal tail. A lack of keys specific to distinct areas has led to a reliance on keys which may not represent the true species assemblage of a region, and this has probably contributed to the notion that some species have very wide geographical distribution (Elias-Gutierrez *et al.*, 1997; Duigan & Murray, 1987).

The chydorids are small animals typically ranging from 0.2mm to 1 mm although some species (such as *Eurycercus* species) can grow to several millimetres in length. Like other cladocerans, the chydorids have a distinct head, protected by a head shield and a carapace composed of two valves that encloses the feeding appendages which are modified legs. They have two sets of antennae, the second of which is often the main swimming appendage, and they also have a large postabdominal claw or tail that is also used for propulsion, along with the first of the six sets of trunk limbs. Chydorids have a compound eye and an ocellus which is thought to be a light sensitive organ, and in some genera, the compound eye is reduced, or even absent (Fryer, 1968).

As with other cladocerans, the main reproductive strategy is parthenogenesis. For most of the year, the populations are almost entirely composed of females that reproduce asexually to produce more females. This means that they can build up large populations very quickly. Unlike other cladocerans, chydorids produce no more than two eggs (except in the sub-family Eurycerinae) and may only produce one egg in times of low food availability, old age or overcrowding (Keen, 1973). The link between

variable food availability and clutch size has been investigated in other cladoceran families, and it may be that the clutch size in the chydorids is uniform because there is less variability in the littoral food supply compared with open water habitats (Murugan & Job, 1982). The chydorids can reproduce sexually in response to environmental conditions, such as low winter temperatures or the drying out of water bodies in the summer. When this happens, some of the females produce males, which then mate with females to produce resting eggs that are enclosed within an ephippium. An ephippium is formed from the carapace of the chydorid, which thickens and hardens, and forms a resilient capsule with the eggs inside. These ephippia can survive for several years but usually hatch out once environmental conditions have eased and the population can be restored (Frey, 1982). In nearly all cases the ephippium enclose one egg, although two-egged ephippia have been found in some of the Chydorinae subfamily (Fryer & Frey, 1981).

1.3 The Chydorid family in Ireland

The first Irish study of chydorids was a monograph in 1867 written by Norman & Brady (Duigan, 1990). Since then, 41 species in 18 genera have been recorded in the country. A comprehensive survey of Irish chydorids was carried out by Duigan in 1984-1986, and the distribution of each species was recorded along with previous records, taxonomic comments and ecological notes (Duigan, 1992). This body of work provides a baseline for subsequent studies of Irish chydorids. Three geographically distinct groups of chydorid species were described in this 1984-1986 study; a western group found most commonly in the mountainous areas of Connemara, Wicklow and Donegal, a central plains group, and an indiscriminate group of species found countrywide (Duigan & Kovach, 1991). The Irish chydorids are thought to have a northern character, with some species being at their southern limit in the country. These include *Eurycercus*

glacialis, Alonopsis elongata, Chydorus ovalis, Rhynchotalona falcata and *Alona intermedia* (Duigan, 1992). As yet, no species of chydorids have been found which are restricted to Ireland, so the keys to British and French chydorids written by Scourfield & Harding (1958), and Amoros (1984) respectively, appear to be adequate for the identification of Irish species, although they may be out of date with regard to recent taxonomical revisions.

1.4 The ecological quality of lakes

Irish lakes are generally considered to be of good quality when compared to other EC countries, with more than 81% of 120 surveyed lakes recently surveyed falling into the oligotrophic to mesotrophic status according to a modifed version of the O.E.C.D. scheme (O.E.C.D., 1982) used by the Irish Environmental Protection Agency (Lucey, 1999). The fragility of freshwater ecosystems in the country is, however, beginning to become more apparent, with frequent reports in the national newspapers of fish kills and toxic algal blooms, and an overall trend of increasing eutrophication over the past thirty years. As with many of the world's freshwaters, the main threat to Irish lakes is primarily from non point nutrient sources particularly associated with run off from agriculture. Acidification from atmospheric pollution has affected some freshwaters in the east of Ireland (Farrell, Cummins & Boyle, 1997; Bowman 1991), and even in the absence of atmospheric pollution, acidification of freshwaters is becoming a problem in some catchments in the west of Ireland and is associated with coniferous afforestation (Allot *et al.*, 1990; 1997). The forthcoming European Directive (European Union Environment Council, 1998) establishing a framework for water policy which will require member states to establish monitoring schemes for their surface waters is therefore timely. The ultimate aim of this Directive is for all surface waters to have a high ecological quality.

The European Directive puts much emphasis on the term "Ecological Quality" of a waterbody, but opinions differ as to what this phrase actually means. This has become quite a subject for debate – so much so that a whole conference entitled "Freshwater Quality: Defining the Indefinable?" was devoted to the issue in 1995 (Boon & Howell, 1997). What seems to be the crucial issue is that 'quality' is a very subjective thing. In terms of the value to humans, a lake which may be considered relatively poor quality in one part of the world might be considered to be relatively pristine elsewhere. In a dystrophic or oligotrophic catchment, a small increase in nutrients may bring about a richer macrophyte community, and hence a more diverse benthos. Does this mean the ecological quality has increased, or decreased? Similarly for the inhabitants of a lake, some species such as the Rat Tailed maggot, *Eristalis tenax*, may thrive in lakes of a particular quality (which is therefore high to them) but which to other species such as the Atlantic Salmon, *Salmo salar*, is inhospitable (and therefore of low quality) (Maitland, 1997) . All these examples show that in any monitoring scheme, an understanding of what is being implied by "Ecological Quality" needs to be outlined at the start. One definition of Ecological Quality (or freshwater quality) is the extent to which a lake has changed compared with its natural baseline state (Battarbee, 1997) (i.e., a pristine lake would be of high ecological quality, and as disturbance and pollution increased, this quality would decrease). This implies that the natural state is one which is desirable and of a sustainable nature, which most limnologists, I think, would agree with.

The use of an index which uses a natural, baseline state as its starting point, however, has its difficulties. Lakes, by their nature, are dynamic and are continuously evolving, and so a baseline state may be hard to define. Perhaps the most useful starting point from which to define the baseline, natural state, would be the point in time when

anthropogenic influences were minimal and the use of the catchment around a lake was sustainable and having a neutral affect on its surroundings (Moss, Johnes & Phillips, 1997). This approach of defining ecological quality relative to the natural state of a lake is becoming more widely used, and reflects a change from "spatial state" assessments which compares lakes to each other, to a "state change" method which is based on monitoring of a water body and comparing it to its previous quality. The state-change approach removes some of the subjectivity from the classification of lakes, and can also enable realistic targets for water quality objectives to be set.

The indices to be used in a state change approach should be variables which can be traced over a long period of time and which will also be sensitive to slight changes in the ecological processes of the lake. While chemical and physical attributes such as nutrient concentrations, alkalinity, pH, maximum depth and retention time are well established variables for lake classification, the use of biological indicators has had less attention. In addition to measuring chemical and physical variables in lakes, the European Directive will also require biological factors be taken into consideration when monitoring. The use of macroinvertebrates to monitor river quality is widely accepted and is extensively utilised in Ireland to monitor rivers (Lucey *et al.*,1999). However, biotic indices for lake quality are still underdeveloped. A study of 27 biotic scores used in freshwaters found only two to be suitable for lake surveys (Resh & Jackson, 1993). Factors such as the effects of substrata, the extent of macrophyte coverage, the slope of the littoral region, and the seasonal variability of many taxa means that any relationships found between animal groups and lake ecological quality are likely to be complex and it is probably this complexity that has hindered the development of suitable biotic scores applicable to lakes.

The advantages of biological indices over other ones such as chemical measurements is that they provide a more integrated picture of the ecological condition of a lake, and are a product of the culmination of lake conditions prior to the sampling period (Hellawell, 1997). Any biological variable that preserves well in the lake sediments will have the advantage that any changes in the lake can be traced historically through cores and compared with present day populations. The use of diatoms and Chironomids in this regard have been well received and have been used to reconstruct histories of eutrophication (e.g. Lough Augher, Co. Tyrone; Anderson, 1989) and acidification (e.g. Round Loch, Scotland; Flower & Batterbee, 1983). In both cases diatom-based transfer functions were used to reconstruct changes in Total Phosphorus (TP) and pH respectively. This is done by studying modern diatom distributions in relation to TP or pH and constructing "training sets" which are used to calculate the optimum range of the particular variable for each taxon.

1.5 The use of Chydorids as biological indicators of ecological quality

As Cladocerans, and chydorids in particular, preserve extremely well in lake sediments, they may also be useful in the ongoing monitoring of lakes, as they can be used to reconstruct the history of lakes, with reference to their changing trophic status or acidification (Hann, Leavitt & Chang 1994; Hofman, 1987; Boucherle & Züllig, 1983; Whiteside, 1970; Harmsworth & Whiteside, 1968; Frey, 1960). Changes in macrophyte communities and fish stocks have also been inferred from such paleolimnological studies (Miskimmin, Leavitt, & Schindler, 1995; Leavitt, Carpenter, & Kitchell, 1989; Stansfield, Moss & Irvine,1989). Irish lakes have been the focus of several paleolimnological studies, using cladocerans (including chydorids) to reconstruct the lakes' history. Changes in the cladoceran communities of Lough Neagh, Northern Ireland has been attributed to water level changes and predation (Wood, Andrew &

Redfern, 1990) and a decline in cladoceran species diversity in the 1840's in Lough Garadice, Co. Leitrim was attributed to the construction of the Ballinmore-Ballyconnell canal (Wood *et al.*, 1996). Paleolimnological studies of cladoceran microfossils have also been conducted on Lough Ennell and Lough Owel in Co. Westmeath (Redmond, 1977) and Lough Leane in Co. Kerry (Douglas & Murray, 1987; Murray, 1979). In Lough Ennell, numbers of *Chydorus sphaericus* appeared to increase significantly as the lake became more enriched while in Lough Leane, large numbers of *Alona rectangula* coincided with a phase of disturbance in the watershed, which is indicated in the sediment cores by a large amount of organic matter.

With the chydorid family, therefore, there is the potential for their use as biological indicators of ecological quality. Further studies of the ecology and community dynamics of present day populations will help to strengthen the use of chydorids as paleoindicators (Nilssen & Sandøy, 1986), and ideally, the use of this group of animals to infer past historical events should be backed up with present day observations from the same region (training sets), as the ecology of species may change depending on geographical and climatic variation (Whiteside, 1970). Recovery of chydorid parts from surficial sediments provides a very useful record of present day (or recent) chydorid populations, without the complications brought about by seasonal and spatial variation and this has been utilised by several authors (Hofmann 1996; Whiteside, 1970; Harmsworth & Whiteside, 1968; Frey 1960) to compare lakes of different types and their chydorid communities.

If chydorids can be used as paleoindicators, then perhaps they should also be considered for inclusion into any lake monitoring scheme, which seeks to measure change in comparison to a baseline state. For inclusion in an integrated, rapid

monitoring scheme to be warranted, a biological variable should ideally have several characteristics:

1. *They should be present in all likely sampling sites (or lakes in this case).*

Chydorids are extremely common inhabitants of lakes, and while it is not possible to say that they occur in every single lake in the world, they are as likely to be as ubiquitous as any other group of animals. The evidence from distribution studies of chydorids leads to the conclusion that they are almost ubiquitous, and representatives of the family occur all over the world. Several monographs have documented their widespread distribution across Europe, and these provide a very useful baseline, from which other work can follow. Duigans's (1992) work in Ireland provides a useful description of the distribution of chydorid species across the country. Other countries with extensive literature include Italy (Margaritora, 1983; 1985), Romania (Negrea, 1983), Spain (Alonso, 1996) and Germany (Flössner, 1972). The chydorid fauna of the UK is also well described by various publications (Fryer, 1993; Fryer, 1985; Fryer & Forshaw,1979; Scourfield & Harding, 1966; Smyly, 1958). Whiteside (1970) carried out work on Danish chydorids from a paleolimnological point of view and this included some study of present day populations. Russia (and the USSR) has perhaps the most extensive literature about chydorids, with large publications by Smirnov (1996,1974, 1963 and1962).

2. *They should be quick to sample, with the minimum of equipment. A standard sampling method should have comparable results, irrespective of the sampling substrate.*

The recognised difficulty in sampling the littoral region quantitatively (Chengalath, 1982; Whiteside, Williams & White, 1978) has undoubtedly hindered studies of this area of the lake but has led to several novel sampling methods being developed by people studying chydorids (Campbell, Clark & Kosinski, 1982; Pennak, 1962; Whiteside & Williams, 1975). The most commonly used method however, is a sweep net of some description, which is quick, cheap and easy to operate. As the chydorids live in the littoral zone, a boat is not required which drastically cuts down on the sampling time. However, with so many species of chydorids inhabiting the littoral area of water bodies, it is likely that there is a high degree of segregation between microhabitats, and some papers have focused on this issue. In particular, the differences between vegetated areas and non vegetated areas have been studied, (Duigan & Kovach, 1994; Paterson, 1993; Chengalath, 1982; Quade, 1969; Smirnov, 1962) as well as different hard substrates such as sand, mud, etc (Duigan & Kovach, 1994; Robertson, 1990; Smirnov, 1962; Smyly, 1958). This may mean that samples taken over different substrates can not be compared effectively. Cumulative samples taken over a variety of substrates may lessen this problem (Duigan, 1992).

3. *Samples should be relatively easy to analyse, with regard to sorting and identification*

There can be no doubt that the sorting and identification of chydorids is quicker than that of many other biological samples, such as macroinvertebrates. In the case of Irish lakes, approximately 40 species have been identified from the country, which is

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significantly less than the total number of macroinvertebrate species likely to be found in the littoral region. The family in general, do not require dissection in order for identification to be made to species level, as is the case with chironomids or copepods for example. Therefore, the taxonomy, while tricky at the outset can be quickly mastered. While the taxonomy of Irish chydorids is well documented (Duigan, 1992) much of the taxonomic work on chydorids has, perhaps naturally, stemmed from regional studies and is hence rather patchy. This is compounded by the fact that many new species are being described from areas, such as Mexico (Ciros-Perez & Elias-Gutierrez, 1997), Australia (Smirnov, 1995) and Eastern Europe (Brancelj, 1997). Only recently have genetic studies been used as a tool to decipher the evolution and speciation of chydorids (Crease & Taylor, 1998; Hanner, 1997). Work carried out on the genetics of *Daphnia* has contributed a lot to the taxonomy of that group (Herbert & Finston, 1996; Herbert & Wilson, 1994), and similar work on the chydorids would definitely help clarify the taxonomy of the family, which would enhance faunisitic, zoogeographic and ecological studies.

4. *The group of animals as a whole should be sensitive to changes in the ecological quality of the lake (eg eutrophication or acidification, or habitat disturbance). Information about how the community is likely to change as the result of a certain factor can be obtained from present day populations sampled from a wide variety of lakes.*

There are several examples of studies of chydorid communities in relation to chemical and physical variables and lake type (Duigan & Kovach, 1994; Dodson,1992; Duigan & Kovach,1991; Stansfield, Moss & Irvine, 1989; Fryer 1985; Fryer, 1980; Whiteside, 1970; Whiteside & Harmsworth, 1967). In particular, chydorid assemblages and diversity have been shown to change with increasing eutrophication (eg, Whiteside,

1970) and acidification (eg Duigan & Kovach, 1994; Fryer, 1980). It has, therefore, been shown that this group of animals is sensitive to the type of waterbody they are inhabiting, and that the community composition is likely to change with different ecological conditions. The mechanisms behind these changes, are however, relatively understudied, as autecological work on chydorids is rare. What studies there are focus mainly on population dynamics such as birth rates, (Robertson, 1988; Meyers, 1984; Murugan & Job, 1982; Bottrell, 1975; Keen, 1973). Although species such as *Chydorus sphaericus* are included in autecological studies of the open water zooplankton (eg: Lundstedt and Brett, 1991), the roles that competition, predation and food availability play in the structuring of chydorid communities specifically has only been discussed in a handful of papers (eg: Williams, 1983; Williams & Whiteside, 1978). Some others stress that the chydorid community is more likely to be affected by habitat structure and the presence or absence of certain substrata, rather than the actual chemical quality of the water they live in (Quade, 1969; Fryer, 1968), and warn against trying to correlate elements of the chydorid community with certain chemical variables. However, if an increase in total phosphorus, or a decrease in pH brings about a change in the structure of the littoral environment (for example, changes the macrophyte coverage) then this will indirectly affect the chydorid community. The process, however, is initially driven by the chemical changes, and the change in the chydorid community can be related back to this. It does not seem unreasonable, therefore, to try to unravel the effect of water quality on the chydorid community, and whether the effect is direct or indirect is a further area for study, which may tell us a lot about the processes controlling the communities in the littoral zone.

In view of the forthcoming directive from the EU, the Irish Environmental Protection Agency (EPA) commissioned a two year project entitled "The Ecological Assessment of Irish Lakes", one of the aims of which was to assess which variables

should be including in a rapid monitoring scheme for Irish Lakes. This study of chydorids was funded under this project. As well as chydorids, data about chemical and physical variables, phytoplankton, zooplankton, profundal invertebrates and littoral macroinvertebrates were collected from about thirty lakes around Ireland (Irvine *et al.*, in press).

1.6 Outline of this thesis

The initial aim of this project was to assess the use of chydorids as indicators of ecological quality in Irish lakes and chapter 2 describes a study that was conducted over two years for this purpose. Twenty nine Irish lakes were sampled either monthly or quarterly, and the chydorids collected were then analysed to see whether they could be used to characterise certain lake types, particularly nutrient enriched or acidified lakes. If it transpires that the chydorids can be used to trace different environmental conditions across a wide range of lakes, then their inclusion in monitoring schemes could be warranted. Trends which are apparent over a range of environmental conditions (for example, changing community structure with increased nutrient status) can then be used to develop lake monitoring programs.

This study was conducted with the knowledge that the community of chydorids within a lake may differ significantly, depending on what habitat was sampled. This would obviously have consequences for any generalised conclusions about a lakes' community. Chapter 3, therefore, looks at two different lakes in detail and assesses whether general conclusions about the lake community are significantly affected by the spatial distributions of different species, and the various sampling methods used to collect chydorids.

Chapter 4 focuses on autecological studies conducted in the laboratory on four species, *Alona affinis, Chydorus sphaericus, Alonopsis elongata* and *Acroperus harpae*. The first three of these were identified in Chapter 2 as being very important components of the lakes' chydorid communities. The dominance of one or other of these species was found to be an important part of characterising a lake by its chydorid community, and assessing which environmental factor was having the greatest effect on the lakes. Experiments on reproductive rates under varying environmental conditions were conducted on these four species in order to assess why certain species become dominant in particular lake types. In addition, populations of each species were grown in different food sources, to see whether these species are really nonselective feeders, or whether some species do better with certain food sources than others. This would also have implications for the success of various species as food availability changes over the year. Chapter 5 is a general discussion of the factors affecting community structure, and what the results from the three preceeding chapters, combined with previous knowledge imply about the community strucure of chydorids.

Chapter 2.

An assessment of chydorids as indicators

of ecological quality.

2.1 Introduction

This chapter assesses the use of the chydorid family as indicators of lake ecological quality. The chydorids have many characteristics which make them suitable for biomonitoring – they are almost ubiquitous in Irish lakes, they are relatively easy to sample and identify, and they are limited to around 40 species in Ireland (Duigan, 1992), which makes the whole process less time consuming then similar surveys using macroinvertebrates, when in excess of 200 taxa may need to be considered. In addition to this, chydorids are well preserved in the sediments of lakes, which opens the possibility of long term historical studies (e.g. Boucherle & Züllig, 1990, Hofman, 1987; Whiteside, 1970; Frey, 1960).

Individual chydorid species or species assemblages which are characteristic of particular water bodies may be useful as indicators of ecological quality. Chydorid assemblages have been identified from many types of water bodies. A study of a swamp in North America showed a species assemblage characteristic of an acid bog lake which comprised eight species of chydorids (Anderson, Benfield & Buikema, 1977). In Ireland, work by Duigan (1992) and Duigan & Kovach (1991) identified seven chydorid assemblages which were differentiated by what type of substrate they frequented. Microcrustacean species on the Isle of Skye were also found to form distinct assemblages, depending on lake characteristics such as pH, catchment area, macrophyte diversity and the distance from the sea (Duigan and Kovach, 1994). A comprehensive study carried out on 77 lakes in Denmark by Whiteside (1970) classified lakes into clear water, ponds and bogs, or polluted water groups according to transparency, alkalinity, pH, depth, conductivity and area with chydorid assemblages characteristic of the three groups. Only two species were found to thrive in polluted waters, *Chydorus sphaericus* and *Alona rectangula*. A study in the Norfolk Broads used Whiteside's chydorid

groups to study the switch from submerged plant dominance to phytoplankton dominance in a eutrophic lake (Stansfield, Moss and Irvine, 1989).

Community analysis (such as species richness or species diversity) may also be useful for indicating water quality. Several workers have associated aspects of chydorid communities with various ecological and geographical variables. Increasing acidity has been used to explain poor species richness of chydorids by Carter (1971) and Fryer (1980). Other factors affecting species richness include habitat structure (Rundle & Ormerod 1991; Whiteside, Williams & White 1978; Smyly 1958), geographical location (Dodson,1992) and waterbody size (Dodson, 1992; Fryer,1985). A parabolic relationship between productivity and species richness was noted by Dodson (1992), with richness initially increasing as productivity increased until a certain point and in very productive lakes (eutrophic - hypertrophic) richness decreases. The relationship between chydorid species diversity (as calculated, for example, using the Shannon Diversity Index) and primary production is a complex one, and simple relationships may be uncommon (Whiteside and Harmsworth, 1967). It has been suggested that production in lakes could be directly correlated with numbers of chydorids (Harmsworth and Whiteside, 1968) but this is also a complex relationship involving other factors, such as seasonal cycles of species, macrophyte diversity and predation as important determinants of chydorid abundances.

As eutrophication is the main threat to the ecological quality of Irish lakes, the effect of nutrient status on species diversity, abundance and composition of the chydorid community was one of the prime focuses in this study. Some studies have been able to use cladoceran communites as indicators of changing trophic status in lake, but in these cases, it was based on microfossils obtained from the lake sediments, rather than present day populations (Mezquita & Miracle, 1997; Hofmann, 1996; Hann,

Leavitt & Chang, 1994; Whiteside, 1970). Increased nutrients into a lake are likely to affect the chydorid community in a number of ways. In the initial stages of nutrient enrichment, an increase in the diversity of the macrophytes (and hence substrate for the chydorids) and increased availability of food as periphyton may produce higher abundances and species richness of chydorids. With increased eutrophication, a switch from a plant dominated lake to a phytoplankton dominated lake may cause a decrease in the species richness owing to changes in the structure of littoral zone associated with the loss of macrophytes. Water clarity may decrease which could have implications for the benthic periphyton, and oxygen levels may also fluctuate. Changes in the invertebrate and vertebrate communites with increased nutrient enrichment would also be likely to have an effect on the chydorid communities. A eutrophic lake in which healthy macrophytes have decreased or died out would favour chydorids with a more planktonic lifestyle such *as Chydorus sphaericus*, which may use agglomerations of phytoplankton as its substrate. It has been recorded in the literature that some species thrive better in mesotrophic/eutrophic water bodies than in oligotrophic ones. In particular, high proportions of *Chydorus sphaericus* have been linked to productive lakes (Mezquita & Miracle, 1997; Hofmann, 1996; Duigan & Murray, 1987; Whiteside, 1970; Whiteside & Harmsworth, 1967). Other species associated with more productive waters include *Alona rectangula* and *Pleuroxus uncinatus*.

As acidification of lakes in some regions of Ireland is becoming more a cause for concern, the reaction of chydorid communities to low pH and low alkalinity was also studied. Acidification may affect chydorids either directly by debilitating some of their physiological and reproductive process, or indirectly, by altering the ecology of the lake, and the habitat structure in the littoral zone. Acidification may lead to a decline in productivity, because as the acidified water drains through a catchment, it mobilises aluminium ions. This leads to a precipitation of phosphate which then stays in the soil

(Moss, 1988). This decrease in production may favour species with a preference for oligotrophic waters. A change in the macrophyte community is also a likely result of acidification, as the community will become more dominated by acidophilic species of plants such as *Sphagnum*. This will have implications for the structure of the littoral zone, and hence, for factors such as the presence of refuges and the growth of epiphyton. If the acidification is severe enough to cause the reduction or loss of fish life, the whole food web of the lake is likely to be affected. Several studies have shown that species richness decreases in lakes with low pH (Rundle 1990; Fryer,1980; Carter,1971) although some authors report an increase in diversity as pH falls below 6.0 (Nilssen & Sandøy, 1986, Chengalath, 1982). Certain chydorid species such as *Chydorus piger, Alona intermedia* and *Alonopsis elongata* have been associated with low alkalinities (Duigan & Kovach, 1994; Duigan & Kovach, 1991; Fryer, 1980; Fryer & Forshaw, 1979; Whiteside, 1970).

As with most biological variables, direct correlations between chydorid communities and chemical or physical measurements are unlikely, as there are so many factors determining distributions and abundances of animals, particularly in the littoral zone. These include the effects of predation, competition, habitat structure and food availability, which are practically impossible to combine to form a single, comprehensive scale. The increasing use of multivariate techniques in ecological studies is perhaps a result of an increasing awareness of this complexity. Multivariate analysis allows data be analysed for trends without initially confining the data to specific environmental variables (the exception being Canonical Correspondance Analysis, CCA, which constrains the biological data to linear combinations of chosen environmental variables (Duigan & Kovach, 1994)). Some multivariate techniques have been developed specifically with ecological analysis in mind, such as TWINSPAN (Hill, 1979) which classifies species and samples according to similarities with each

other and presents the results in the hierarchical manner of a dendogram. DECORANA (Detrended Correspondance Analysis) is often used in conjunction with TWINSPAN, but it presents the data as an ordination plot in two dimensions (Hill, 1979). These two programs, along with Principal Component Analysis (PCA) and CCA are probably the most widely used multivariate techniques used for ecological assessments, particularly in the United Kingdom. Multidimensional Scaling (MDS) (specifically Non-metric MDS) is an ordination method which is beginning to become widely used for ecological data, particularly in the field of marine biology (Clarke & Warwick, 1994).

The basis of MDS is that a (dis)similarity matrix is constructed between all the samples, which allows them to be ranked according to how (dis)similar they are to each other. MDS then attempts to map the samples according to these ranks (Manly, 1986; Kruskal & Wish, 1978). For example, samples that are similar to another one will be placed close together on the ordination, while the two most dissimilar samples will be placed at the extremities of the plot. The ordination can be done in as many dimensions as required, which recognises the fact that some samples will be similar in some respects (and hence close together along one dimension) but not in others. The concept behind MDS is therefore quite simple, even though the algorithms used to fit the data to an ordination are complex, and this is probably the most advantageous aspect of MDS analysis. Comprehensive mathematical knowledge is not required in order to grasp the theory behind the method, and this makes interpretation and communication of the results easier. Several of the properties of MDS also make it very suitable for ecological data. As it ignores joint absences (i.e. it will skip over a species that is missing from two or more samples) when calculating the distance matrix, deletion of species is unnecessary because they will automatically be downweighted by the similarity measure used (usually Euclidean distance, Bray Curtis Index or Sorensen Index). For ease of interpretation, however, it might be better to remove rare species at the outset.

This is not the case for PCA analysis, where many species may have to be removed (fairly arbitrarily), in order for the algorithm to work. As MDS is based on ranked distances (rather than the actual data), it is particularly suited to data that is nonnormal, or is on an arbitrary, discontinuous scale. It also means that the presence of lots of gaps in the data (or zeros) will also be less of a problem in MDS than in other ordination techniques. Another advantage of MDS is that it requires few assumptions or decisions from the operator to be made (in contrast to TWINSPAN for example, which requires a decision to be made about what level the distinction between species and psuedospecies should be made – this can have quite large effects on the outcome of the analysis). This means that the method is relatively objective, and "the species and environmental data is allowed to tell their own story (under minimal model assumptions) before judging the extent to which one provides and explanation of the other" (Clarke & Warwick, 1994).

2.2 Methods

2.2.1 Study sites

The chydorid communities of 29 Irish lakes (Table 2.1) were studied between July 1996 and September 1997. The 29 lakes represented a wide range of physical, chemical and geological variables associated with Irish lakes, and a summary of these is given in Table 2.2. The chemical data which are used in the analysis were obtained as part of the Environmental Protection Agency project "The Ecological Assessment of Irish Lakes". Standard methods were used for collection and measurement of chemical variables and are given in Irvine *et al.*, (in press). Eleven of the lakes were sampled on a monthly basis (except over the winter, when sampling trips were not carried out in November, December or February)) while the rest were sampled approximately quarterly (July and September, 1996 and January, April, June, July and September, 1997).

Table 2.1. Irish lakes where chydorid committees were studied between July 1996 and September 1997. Numbers refer to their position on the map in Figure 2.1.

Lakes sampled monthly	Lakes Sampled quarterly (approx.)	
5.Lene, Co. Westmeath	19.Rea, Co. Galway	21.Gara South, Co. Leitrim
6.Owel, Co. Westmeath	20.Graney, Co. Clare	11. Oughter, Co. Cavan
2.Dan, Co. Wicklow	28.Ballycullinan, Co. Clare	9. Egish, Co. Monaghan
7.Ramor, Co. Cavan	27.Bunny, Co. Clare	8. Muckno, Co. Monaghan
24.Inchiquin, Co. Clare	26.Cullaun, Co. Clare	4. Mullagh, Co. Cavan
23.Lickeen, Co. Clare	25.Dromore, Co. Clare	1. Bray, Co. Wicklow
22.Doolough, Co. Clare	17.Lettercraffroe, Co. Galway	3. Poulaphouca, Co. Wicklow
18.Ballyquirke, Co. Galway	16.Maumwee, Co. Galway	
15.Moher, Co. Mayo	13.Talt, Co. Sligo	
14.Feeagh, Co. Mayo	12.Easky, Co. Sligo	
10.Gowna, Co. Mayo	21.Gara North, Co. Sligo	
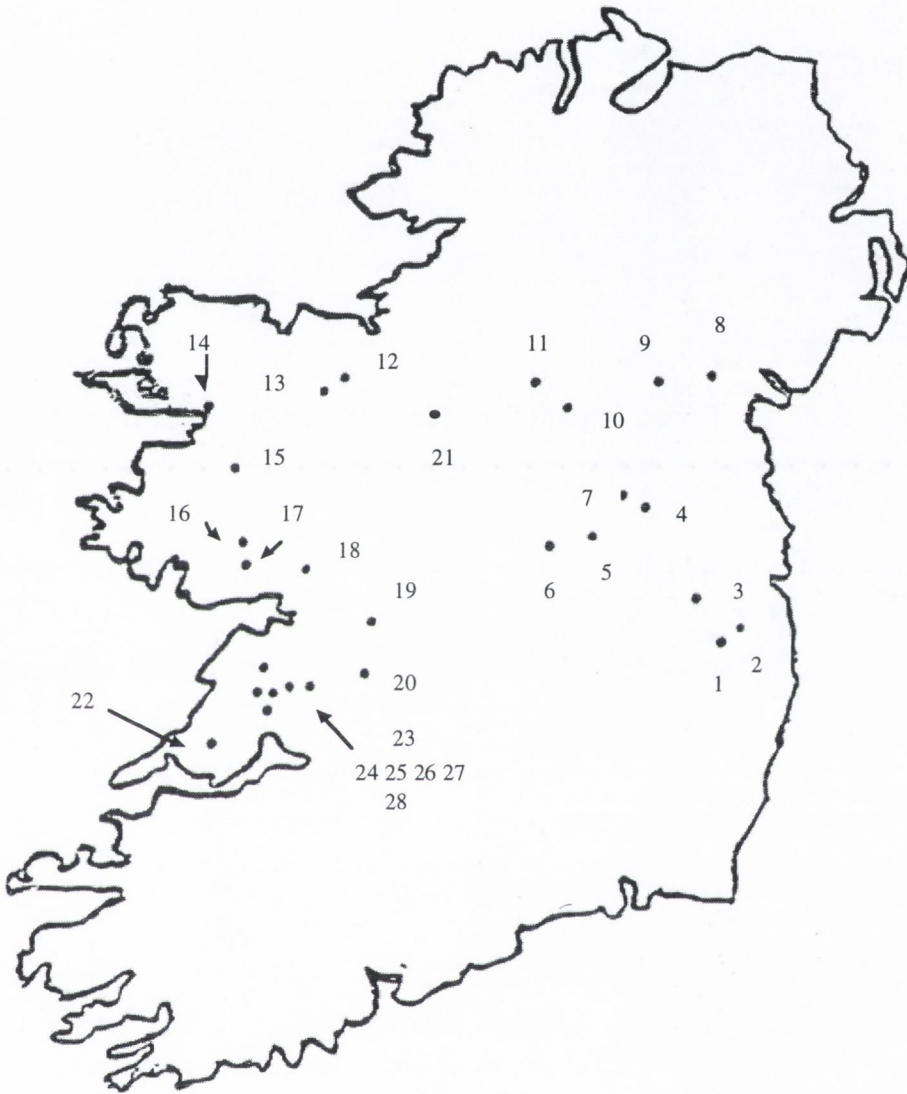
Figure 2.1 Map of Ireland showing the geographical location of the 29 lakes sampled.

For identification, see numbers in Table 2.1.

Table 2.2. Characteristics of the 29 lakes included in this survey. Mean and Median values are calculated for the period July 1996 – September 1997. Trophic status is classified according to the modifeid version of (O.E.C.D. 1982) used by the EPA (Lucey *et al*, 1990), according to maximum values of Chlorophyll *a*. O – oligotrophic, M – mesotrophic, E – eutrophic, H – hypertrophic. (Irvine *et al.*, 1999, in press).

Lake	County	O.S. Catchment	National Grid Ref.	Max depth (m)	Mean Depth (m)	Lake Area (Ha)
Ballycullinan	Clare	Fergus	R 293 862	10	3	5
Ballyquirke	Galway	Corrib	M 231 313	12	3	79
Bray	Wicklow	Dargle	O 137 161	46	20	25
Bunny	Clare	Fergus	R 373 966	13	1	102
Cullaun	Clare	Fergus	R 315 906	23	7	63
Dan	Wicklow	Avoca	O 151 037	38	14	105
Doolough	Clare	Annageeragh	R 124 721	15	3	127
Dromore	Clare	Fergus	R 346 859	19	6	53
Easky	Sligo	Easky	G 448 235	11	2	123
Egish	Monaghan	Erne	H 796 131	13	3	122
Feeagh	Mayo	Srahmore	F 964 007	45	15	406
Gara North	Sligo	Shannon Upper	G 709 013	16	?	?
Gara South	Rosscommon	Shannon Upper	M 711 962	5	1	203
Gowna	Cavan	Erne	N 287 894	15	4	1119
Graney	Clare	Shannon Lower	R 557 915	18	4	382
Inchiquin	Clare	Fergus	R 266 898	29	10	117
Lene	Westmeath	Boyne	N 520 682	23	8	424
Lettercraffroe	Galway	Corrib	M 059 374	16	2	84
Lickeen	Clare	Inagh	R 170 909	24	4	84
Maumwee	Galway	Corrib	L 975 486	8	2	27
Moher	Mayo	Owenwee	L 976 767	13	3	40
Muckno	Monaghan	Fane	H 856 175	27	6	364
Mullagh	Cavan	Boyne	N 677 854	8	2	35
Oughter	Cavan	Erne	H 341 075	14	2	1105
Owel	Westmeath	Inny	N 401 587	23	7	1029
Poulaphouca	Wicklow	Liffey	N 985 086	12	6	1974
Ramor	Cavan	Boyne	N 621 857	6	3	741
Rea	Galway	Kilcolgan	M 615 152	21	4	307
Talt	Sligo	Moy	G 399 149	41	9	95

Table 2.2 (continued)

Lake	Mean TP µg l⁻¹	Mean Chl *a* µg l⁻¹	Trophic status	Median pH	Mean Alkalinity (mg l⁻¹ CaCO₃)
Ballycullinan	30	20.96	E	8.21	183
Ballyquirke	20	10.85	M	7.84	48
Bray	10	20.72	E	4.92	-1
Bunny	<10	1.73	O	8.40	128
Cullaun	<10	2.49	O	8.35	152
Dan	10	1.33	O	5.00	0
Doolough	10	6.39	M	6.90	5
Dromore	20	9.66	M	8.25	158
Easky	<10	3.68	M	6.47	2
Egish	340	43.15	H	8.19	77
Feeagh	10	1.85	O	6.94	6
Gara North	30	9.15	M	8.33	144
Gara South	20	4.71	M	8.28	154
Gowna	40	22.22	E	8.00	63
Graney	10	10.09	M	7.55	26
Inchiquin	20	3.99	O	8.35	140
Lene	10	4.3	M	8.35	97
Lettercraffroe	10	8.3	E	5.86	1
Lickeen	20	15.36	E	7.58	21
Maumwee	<10	2.39	O	6.60	2
Moher	10	3.85	M	7.34	16
Muckno	30	11.3	M	7.91	45
Mullagh	60	42.45	H	7.97	52
Oughter	70	20.56	E	8.02	70
Owel	10	7.25	M	8.36	96
Poulaphouca	10	6.55	M	7.70	21
Ramor	80	53.08	H	8.13	50
Rea	10	3.27	O	8.41	106
Talt	<10	2.53	O	8.22	73

2.2.2 Sampling technique

Chydorids were sampled with a standard FBA 240 μm net which was swept over approximately 1 metre of the lake bed (which was disturbed by shuffling backwards over it for 12 seconds). The sample was washed from the net and preserved in 70% alcohol. The samples were taken from the littoral zone of each lake in a depth of approximately 30 cm. As the literature suggests that different chydorid species may have quite specific habitat preferences, a stony / gravely substrate was sampled in all the lakes where possible in order to have comparable results over all the lakes. Where possible, a plant bed was included in the sample site. The samples were taken from the same site on each visit. In the laboratory, chydorids were counted under a dissecting microscope using a Perspex disc with a grove cut around its circumference. Five ml subsamples were randomly extracted from the samples and the chydorids were counted and identified. Subsamples were examined until at least 50 individuals of the most common species were counted. Chydorids were identified according to Scourfield and Harding (1958), Amoros (1984) and Duigan (1992).

2.2.3 Statistical Analysis

Initially, the chydorid communites (Abundance, species richness and diversity, and individual species) of the lakes were analysed in relation to one environmental variable at a time. The Shannon Diversity Index was used to calculate chydorid species diversity:

$$\text{Shannon Diversity Index (H)} = -\sum_{i=1}^{s} p_i \ln p_i$$

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where p*i* is the proportional abundance of species *i* in the sample. Spearman rank correlations (Spearman's rho) were calculated for the relationship between the aspects of the chydorid communities and various physical and chemical variables.

Multivariate analysis was used to interpret what contribution several variables made to the observed patterns in the chydorid community. From this, an assessment of what the chydorid community can indicate about a lake and its characteristics was made. Multidimensional scaling (MDS) was used to "map" the different lakes in 2 dimensions according to the differences between their chydorid communities. (While the analysis was also carried out in three dimensions, it was found that the two dimensional ordination provided sufficient clarity). The differences were calculated using euclidean distances from the formula below:

$$ED_{jk} = \left[\sum_{i=1}^{I} (A_{ij} - A_{ik})^2 \right]^{0.5}$$

where A_{ij} is the value of the variable A_j (e.g.. Lough Ballyquirke) for species i (e.g. *Alona affinis*). (Clarke & Warwick, 1994). Several sets of data were analysed using Multidimensional Scaling:

- Chydorid communities represented by the proportional abundance of each species in the lake averaged over the 14 month sampling period. This allows the lakes to be separated according to both the species present and the proportion that these species are present in and takes into consideration winter and summer populations. Species with a proportional abundance less than 3% were omitted from the analysis (Section 2.3.6.1).
- Combinations of physical and chemical variables (such as TP, alkalinity, colour, temperature and littoral plants) to determine which combination produced a similar

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spread to the chydorid data (Section 2.3.6.2). These variables were log transformed where necessary and standardised to a normal distribution. This transforms all the various ranges of physical and chemical measurements to comparable scales. Principal Component Analysis can also be used for plotting the abiotic variables, but when the number of these variable is small, an MDS plot will be similar to a PCA plot (Clarke &Warwick, 1994).

- A presence/absence data matrix to see whether a species list with no quantitative element at all is useful (Section 2.3.6.3).

- Proportional abundances of each species samples over the summer (June, July and September, 1997) to see whether samples taken only over the summer can provide useful data (Section 2.3.6.4). As chydorids have peaks in their population abundances in the summer months from June to September, it may be that it is not necessary to include a winter sampling trip for their analysis.

- Proportional abundances of chydorids taken in September 1997, to assess the usefulness of only one month's sampling effort (Section 2.3.6.5). September was chosen for this analysis rather than the other summer months because this was when the highest species diversity was observed.

All lakes in the MDS analysis were given a two letter code so that lakes could be identified on the MDS plots (Table 2.3). Each of the MDS plots has a stress value which indicates how much difficulty there was in spreading out the data. A stress value greater than 0.3 indicates that the spread of data observed was nearly random, and therefore useless (Clarke & Warwick, 1994). An R^2 value is also given for each plot.

Table 2.3. The two letter codes attributed to each of the study lakes which was used in the multivariate analysis.

Lake	Label	Lake	Label	Lake	Label	Lake	Label
Ballycullinan	Bc	Easky	Ea	Lene	Le	Owel	Ow
Ballyquirke	Bq	Egish	Eg	Lettercraffroe	Lt	Poulaphouca	Po
Bray	Br	Feeagh	Fe	Lickeen	Li	Ramor	Ra
Bunny	Bu	Gara North	Gn	Maumwee	Ma	Rea	Re
Cullaun	Cu	Gara South	Gs	Moher	Mo	Talt	Ta
Dan	Da	Gowna	Go	Muckno	Mu		
Doolough	Do	Graney	Gr	Mullagh	Ml		
Dromore	Dr	Inchiquin	In	Oughter	Ou		

In conjunction with the MDS of the data, cluster analysis was also carried out to see how the lakes grouped according to the chydorids in them. Cluster analysis produces a hierarchical dendogram, with all the samples being grouped together at the top. Similar samples (or lakes in this case) are then clustered together and separated from dissimilar samples. These clusters can then be overlaid on the MDS plot to verify the results obtained and to see which lakes have similar characteristics. The use of the two techniques together clarify whether some samples were arbitrarily subdivided in the cluster analysis (e.g., if they are close together on the MDS plot). The cluster analysis used was again based on the euclidean distances between the lakes which were then put through an agglomerative hierarchical cluster analysis using between group average linkage.

2.3 Results

2.3.1 Baseline

A total of 260 samples were counted from the 29 lakes and 31 species of Chydoridae identified (Table 2.4 and 2.5). Although 41 species of chydorids have previously been recorded in Ireland, a few are not characteristic of water bodies large enough to be considered as lakes (e.g. *Eurycercus glacialis*) and others are extremely rare (e.g. *Tretocephala ambigua*). Some species such as *Alona affinis* and *Chydorus sphaericus* were found in almost all the study lakes, while others such as *Chydorus ovalis* and *Pleuroxus denticulatus* were found on only one occasion. The majority of lakes supported more than 10 species of chydorids, although some such as Poulaphouca, Egish and Easky had quite depauperate communities. Several lakes had very high species richness, especially Lough Moher and Lough Dromore, which were found to support 20 and 19 species respectively. The maximum number of species found at any one time was 11 from Lough Dan. *Chydorus sphaericus, Alona affinis, Alonopsis elongata, Monospilus dispar* and *Eurycercus lamellatus* dominated many samples and analysis of the data was heavily influenced by these five species.

Chydorid populations were maximal during the summer months and tended to die out over the winter. Graphs of abundances in the eleven lakes sampled monthly show a consistent pattern of summer peaks and low winter abundance (Figures 2.2-2.4). Several thousand individuals in one sample were not uncommon, particularly of the more dominant species such as *Chydorus sphaericus, Alona affinis* and *Alonopsis elongata*. In lakes that did support large winter populations (Ballycullinan, Dan, Lettercraffroe, Cullaun and Mullagh), it was these three species that made up a large proportion of the chydorid community.

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Table 2.4 Chydorid species found during the study period, number of lakes that each species was sampled from and the percentage occurrence of each species in the study lakes.

Chydorid species found	Number of lakes sampled from	Percentage Occurrence
Acroperus harpae (Baird, 1834)	25	86
Alona affinis (Leydig, 1860)	29	100
Alona costata Sars, 1862	26	89
Alona guttata Sars, 1862	7	24
Alona intermedia Sars, 1862	7	24
Alona quadrangularis (O.F. Müller, 1776)	10	34
Alona rectangula Sars, 1862	17	58
Alona rustica Scott, 1895	11	38
Alonella excisa (Fischer, 1854)	11	38
Alonella exigua (Lilljeborg, 1853)	11	38
Alonella nana (Baird, 1843)	14	48
Alonopsis elongata (Sars, 1862)	15	52
Anchistropus emarginatus Sars, 1862	4	14
Camptocercus rectirostris Schoedler, 1862	13	49
Chydorus ovalis Kurz, 1875	1	3
Chydorus piger Sars, 1862	9	31
Chydorus sphaericus (O.F. Müller, 1776)	28	96
Disparalona rostrata (Koch, 1841)	18	62
Eurycercus lamellatus (O.F. Müller, 1776)	21	72
Graptoleberis testudinaria (Fischer, 1848)	15	52
Leydigia leydigi (Schoedler, 1862)	3	10
Monospilus dispar Sars, 1862	21	72
Oxyurella tenuicaudis (Sars, 1862)	3	10
Pleuroxus aduncus (Jurine, 1820)	2	7
Pleuroxus laevis Sars, 1861	7	24
Pleuroxus denticulatus Birge, 1879	1	3
Pleuroxus trigonellus (O.F. Müller, 1785)	12	41
Pleuroxus truncatus (O.F. Müller, 1776)	11	38
Pleuroxus uncinatus Baird, 1850	11	38
Pseudochydorus globosus (Baird, 1843)	6	21
Rhynchotalona falcata (Sars, 1862)	15	52

Table 2.5 Chydorid species richness found in each of the study lakes.

Lake	Species richness	Lake	Species richness
Ballycullinan	13	Inchiquin	17
Ballyquirke	17	Lene	15
Bray	12	Lettercraffroe	15
Bunny	13	Lickeen	12
Cullaun	18	Maumwee	16
Dan	17	Moher	20
Doolough	8	Muckno	13
Dromore	19	Mullagh	13
Egish	6	Oughter	12
Easky	6	Owel	14
Feeagh	10	Poulaphouca	4
Gara (north)	13	Ramor	10
Gara (south)	18	Rea	11
Gowna	11	Talt	16
Graney	15		
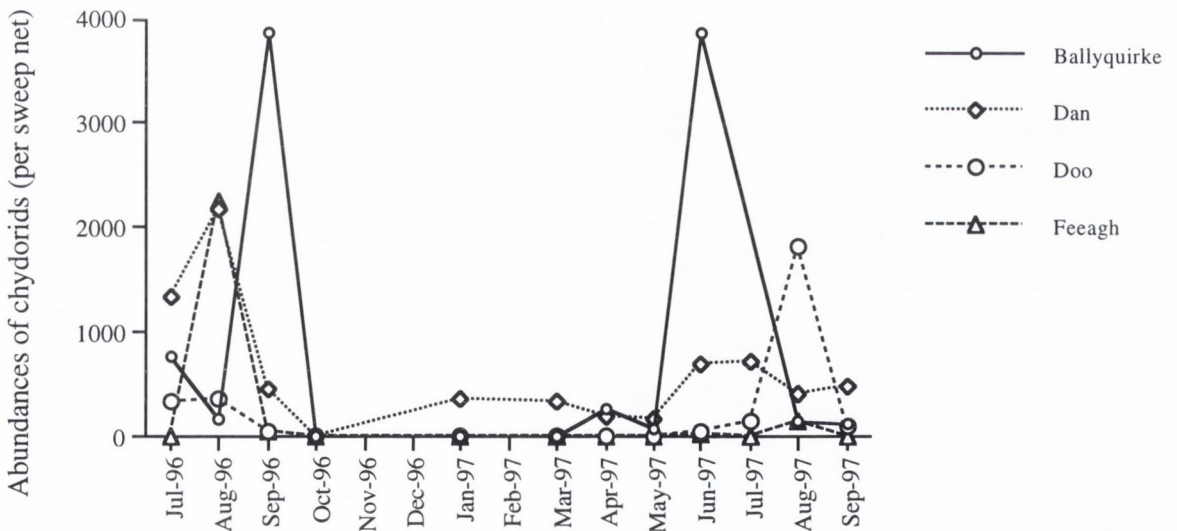
Figure 2.2. Chydorid abundances in Loughs Ballyquirke, Dan, Doo and Feeagh in samples taken over the 14 month sampling period.
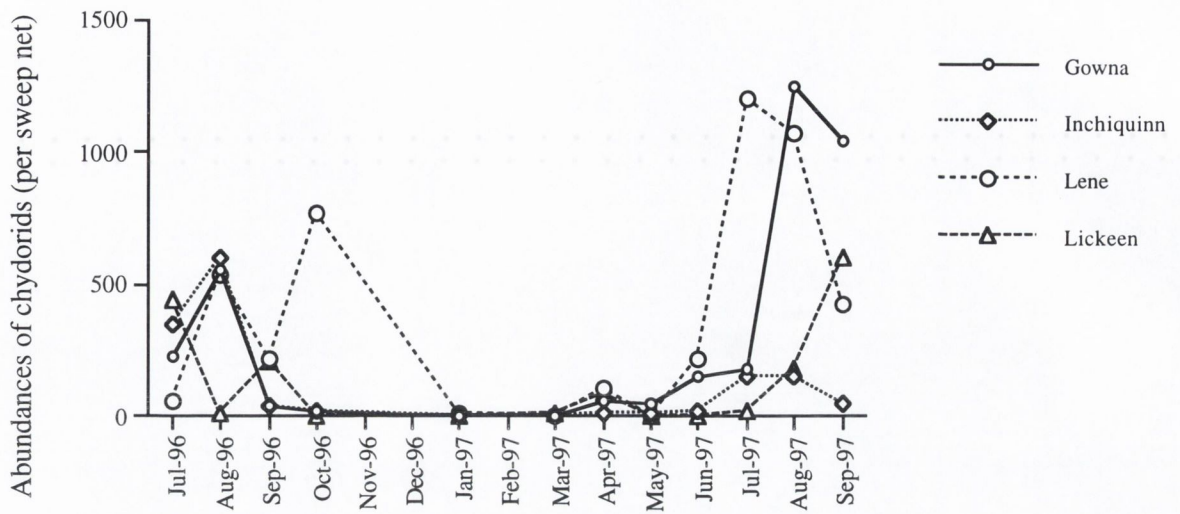
Figure 2.3. Chydorid abundances in Loughs Gowna, Inchiquin, Lene and Lickeen in samples taken over the 14 month sampling period.
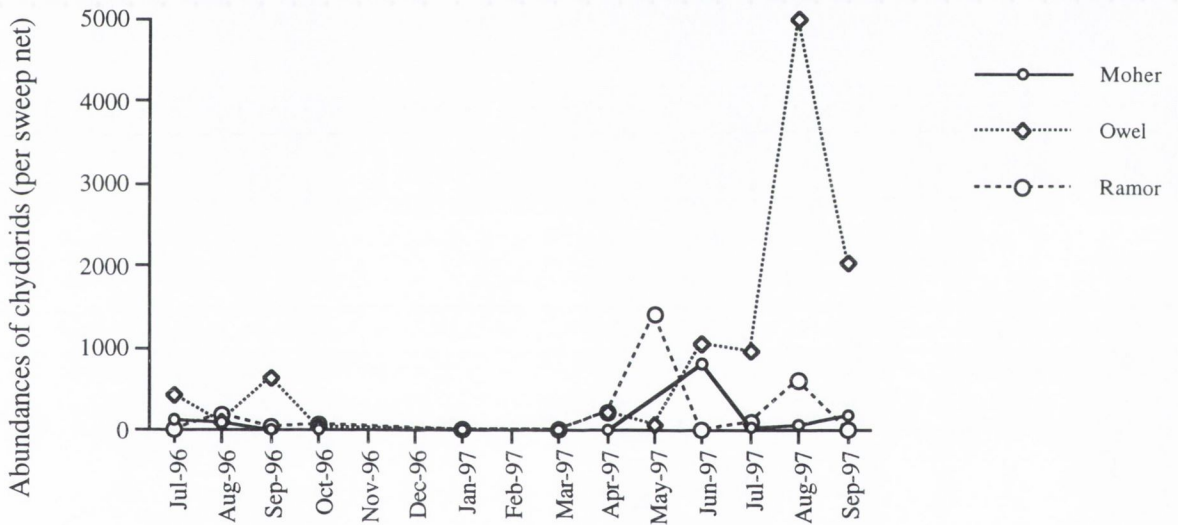
Figure 2.4. Chydorid abundances in Loughs Moher, Owel and Ramor in samples taken over the 14 month sampling period.

Species diversity (Shannon index) is higher in summer than in winter in all lakes. In winter the diversity is low either because there is no community at all or if there is, because it is usually dominated by one or two species (Figure 2.5).
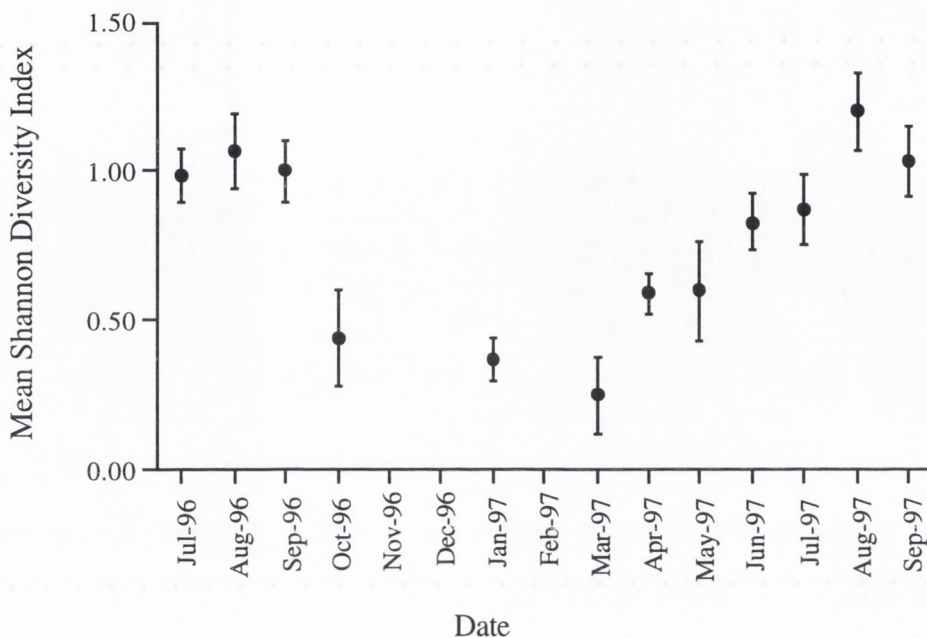
Figure 2.5. Mean Shannon diversity index (± s.e.) for all lakes over the 14 month sampling period (n=29). Gaps represent months when no samples were taken.

In order to get an overview of what physicochemical variables might affect the chydorid community and the species in it, Spearman rank correlation coefficients (rho) were calculated (Table 2.6 (a) & (b)) for the relationship between certain variables and the abundance, diversity and richness of the lakes chydorid communites, and also for individual species. As several of these physicochemical variables are themselves interrelated, it seemed sensible to split these variables into three main categories to see how they affected the chydorids. They were plant cover, nutrient enrichment, and pH / alkalinity.

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Table 2.6 (a). Spearman Rank correlation coefficients (rho) for relationships between chydorids (community variables and individual species) and physicochemical variables. Values marked with an asterisk are significant at 95% level. See text for discussion.

	Littoral plants	Mean TP µgl⁻	Mean Chl a mgl⁻¹	Mean Turbidity (NTU)	Mean Secchi depth (m)
Chydorid abundance	0.13	-0.06	0.01	-0.20	0.20
Species Diversity (Shannon)	0.40*	-0.33	-0.29	-0.36	0.29
Species richness	0.49*	-0.17	-0.12	-0.17	0.17
Acroperus harpae	0.29	0.23	0.26	0.21	-0.04
Alona affinis	-0.23	-0.17	-0.12	-0.01	-0.04
Alona costata	0.08	-0.35	-0.37	-0.38*	0.44*
Alona guttata	0.25	0.08	-0.07	-0.07	0.11
Alona intermedia	-0.02	-0.19	-0.26	-0.18	-0.08
Alona quadrangularis	0.14	0.24	0.12	0.25	-0.10
Alona rectangula	0.15	0.06	0.01	0.09	0.06
Alona rustica	0.05	-0.11	-0.26	-0.03	-0.19
Alonella excisa	0.02	-0.57*	-0.47*	-0.51*	0.46*
Alonella exigua	0.17	0.18	-0.04	0.12	-0.04
Alonella nana	0.23	-0.12	-0.16	-0.13	-0.07
Alonopsis elongata	-0.26	-0.79*	-0.62*	-0.59*	0.27
Anchistropus emarginatus	-0.08	-0.28	-0.25	-0.31	0.23
Camptocerus rectirostris	0.02	0.35	0.26	0.41*	-0.49*
Chydorus piger	0.00	-0.18	-0.27	-0.27	0.04
Chydorus sphaericus	0.29	0.58*	0.51*	0.52*	-0.23
Disparalona rostrata	-0.19	0.10	0.07	0.16	-0.16
Eurycercus lamellatus	0.54*	0.32	0.15	0.16	-0.04
Graptoleberis testudinaria	0.28	0.14	-0.02	-0.03	0.01
Monospilus dispar	0.01	-0.04	-0.22	-0.05	-0.13
Oxyurella tenuicaudis	0.06	0.32	0.29	0.20	0.04
Pleuroxus laevis	0.06	0.17	0.04	0.25	-0.20
Pleuroxus denticulatus	0.46*	0.10	-0.09	0.01	0.08
Pleuroxus trigonellus	0.36*	-0.10	-0.001	-0.10	0.13
Pleuroxus truncatus	0.48*	0.03	-0.08	-0.13	0.26
Pleuroxus uncinatus	-0.03	0.57*	0.56*	0.69*	-0.60*
Pseudochydorus globosus	0.06	0.17	0.11	0.04	-0.06
Rhynchotalona falcata	-0.01	-0.23	-0.36	-0.16	-0.02

Table 2.6 (b) Spearman Rank correlation coefficients (rho) for relationships between chydorids (community variables and individual species) and physicochemical variables. Values marked with an asterisk are significant at 95% level . See text for discussion.

	Mean Temp °C	Mean Oxygen mg l⁻¹	Mean Alkalinity l⁻¹ CaCO₃	Median pH	Mean Conductivity μs cm⁻¹
Chydorid abundance	-0.01	0.07	0.29	0.26	0.31
Species Diversity (Shannon)	0.01	-0.30	0.36	0.31	0.35
Species richness	0.20	-0.40*	0.28	0.17	0.29
Acroperus harpae	0.12	-0.37	-0.16	-0.25	-0.07
Alona affinis	-0.04	0.11	-0.15	0.00	-0.13
Alona costata	-0.08	-0.01	0.08	0.25	0.05
Alona guttata	0.27	-0.01	0.44*	0.36	0.42*
Alona intermedia	0.07	-0.12	-0.28	-0.28	-0.28
Alona quadrangularis	0.21	-0.42*	0.01	0.00	0.03
Alona rectangula	0.35	0.12	0.31	0.41	0.28
Alona rustica	-0.25	0.13	-0.32	-0.37*	-0.36
Alonella excisa	-0.32	0.26	-0.13	-0.01	-0.19
Alonella exigua	0.32	-0.17	0.19	0.16	0.21
Alonella nana	0.20	0.06	-0.14	-0.21	-0.13
Alonopsis elongata	-0.56*	0.39*	-0.35	-0.26	-0.43*
Anchistropus emarginatus	-0.06	-0.11	0.25	0.23	0.27
Camptocerus rectirostris	0.11	-0.38*	0.09	-0.01	0.12
Chydorus piger	-0.04	-0.17	-0.46*	-0.40*	-0.39*
Chydorus sphaericus	0.37	-0.30	0.43*	0.23	0.45*
Disparalona rostrata	0.05	-0.13	0.17	0.26	0.18
Eurycercus lamellatus	0.33	-0.62*	0.27	0.06	0.35
Graptoleberis testudinaria	-0.07	-0.16	-0.19	-0.11	-0.13
Monospilus dispar	-0.19	-0.03	-0.12	-0.01	-0.10
Oxyurella tenuicaudis	-0.16	0.14	0.05	0.07	0.07
Pleuroxus laevis	-0.22	0.07	0.23	0.18	0.23
Pleuroxus denticulatus	0.35	-0.38*	0.33	0.19	0.34
Pleuroxus trigonellus	0.35	-0.44*	0.30	0.10	0.28
Pleuroxus truncatus	0.38*	-0.52*	0.55*	0.32	0.57*
Pleuroxus uncinatus	0.15	-0.26	0.04	-0.01	0.06
Pseudochydorus globosus	-0.11	-0.27	-0.04	-0.05	0.05
Rhynchotalona falcata	-0.14	0.06	-0.17	-0.10	-0.18

2.3.2 Chydorids and Plant cover

Many species of chydorids use plants both as habitat on which to live and as a source of epiphytic food Plants may also act as a refuge for chydorids from invertebrate and vertebrate predators. For the analysis of the chydorid data, an index of plant cover provided a description of the plants in the area where samples were taken. This was categorised as follows:

1 - No plants in the sampling site or in sight of the sampling site.

2 - No plants in the sampling site, but some in the vicinity of the site.

3 - Small amounts of plants in the sample site.

4 - Rich monospecific plants in the sampling site.

5 - Rich littoral vegetation in sample site, of more than one species.

Vegetative cover at the sampling location in each lake is shown in Table 2.7. A significant positive correlation was found between the species diversity and species richness of the chydorid community and the extent of littoral vegetation (Table 2.6). An ANOVA carried out on the five groups showed there was a significant difference in the chydorid species diversities (F ratio = 5.7, d.f. = 4, $p<0.01$) , in particular the difference between groups 1 and 2, and 1 and 5 ($p<0.05$). The biggest distinction seems to be whether there were no plants at all (group 1) or some amount of vegetation (groups 4-5) (Figure 2.6). The differences among the higher end of the scale are not so marked. Group 3 is skewed by the presence of Lough Egish which has very low chydorid species diversity even though it has quite high macrophyte diversity in the sampling site. Without this lake, the differences between groups would probably be more marked.

Table. 2.7. Classification of lakes according to the scale devised for the littoral vegetation in the sites where the chydorid samples were taken from.

1	2	3	4	5
Bray	Ballyquirke	Egish	Dan	Ballycullinan
Doo	Bunny	Gara north	Gara south	Dromore
Easky	Cullaun	Lene	Gowna	Maumwee
Feeagh	Graney	Muckno	Inchiquin	
Oughter	Lettercraffroe		Moher	
Poulaphouca	Lickeen		Mullagh	
Ramor	Rea		Owel	
	Talt			
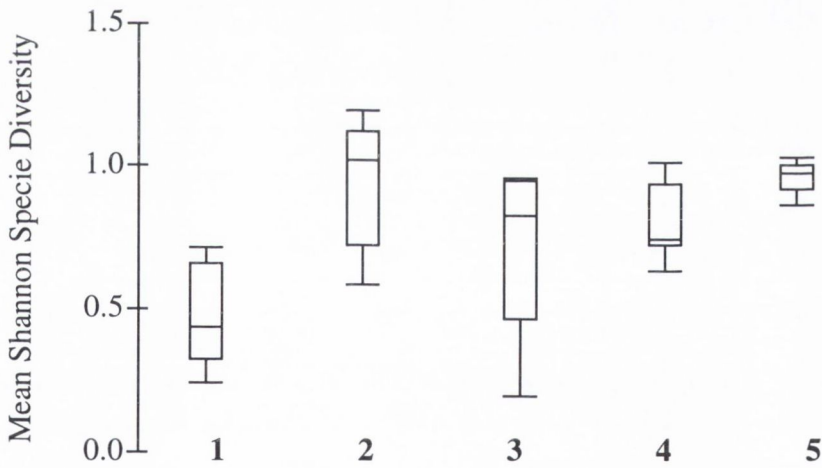
Figure 2.6. Boxplots of mean chydorid species diversity (Shannon index) found in 29 lakes classified 1-5 according to the scale for the littoral vegetation in the sampling site. (1 - no vegetation, 5 - rich, diverse vegetation). The boxes represent the lower and upper 25% quartiles with the median in the middle and the whiskers representing the spread of the data, not including outliers.

Eurycercus lamellatus, Pleuroxus denticulatus, Pleuroxus trigonellus and Pleuroxus truncatus were all found to be significantly correlated with the extent of vegetation in the sampling area, with the proportional abundance of each species increasing with vegetation cover. However, the results for *Pleuroxus denticulatus* and *Pleuroxus trigonellus* are based on very small number of animals.

2.3.3 Chydorids and nutrient enrichment

Species diversity varies over the range of TP measurements (Figure 2.7) but in lakes with a mean TP > 40μgl^{-1} (Gowna, Mullagh, Oughter, Ramor, Egish), species diversity drops off to below 1 on the Shannon Diversity Index. The lowest species diversity was recorded in Lough Egish, which had a mean TP of 340μgl^{-1}.

When classified according to chlorophyll *a*, there is also a decline in chydorid diversity in lakes with high nutrient status (Figure 2.8). It is, however, obvious that nutrient status by itself does not account for differences in the chydorid species diversity as several lakes with low concentrations of nutrients and chlorophyll *a* also have low species diversity. This is reflected in the correlation coefficients calculated between species richness and diversity, and total phosphorus (TP) and chlorophyll *a*, none of which were significant (Table 2.6). Species diversity may also be affected by other factors (which may or may not be affected themselves by eutrophication) such as pH, macrophyte diversity and habitat disturbance.

There is no obvious pattern in the relationship between TP and total chydorid abundance (Figure 2.9) except that none of the eutrophic lakes had very high abundances, as do none of the oligotrophic lakes. A similar relationship was also found between concentrations of chlorophyll *a* and total chydorid abundances (Figure 2.10).

Table 2.8. Mean total phosphorus and mean chlorophyll a measurements (± standard error) for each of the study lakes.

Lake	Mean Total Phosphorus µgl^{-1} ± standard error	Mean Chlorophyll a mgl^{-1} ± standard error
Ballycullinan	30 ±4	20.96 ±8.14
Ballyquirke	20 ±1	10.85 ±2.01
Bray	10 ±1	20.72 ±7.41
Bunny	<10 ±0.3	1.73 ±0.17
Cullaun	<10 ±0.3	2.49 ±0.54
Dan	10 ±1	1.33 ±0.25
Doolough	10 ±1	6.39 ±0.70
Dromore	20 ±3	9.66 ±2.76
Easky	<10 ±0.6	3.68 ±0.80
Egish	340 ±27	43.15 ±12.51
Feeagh	10 ±1	1.85 ±0.38
Gara North	30 ±2	9.15 ±2.61
Gara South	20 ±3	4.71 ±1.41
Gowna	40 ±3	22.22 ±2.52
Graney	10 ±1	10.09 ±1.84
Inchiquin	20 ±3	3.99 ±0.58
Lene	10 ±1	4.3 ±0.64
Lettercraffroe	10 ±1	8.3 ±2.43
Lickeen	20 ±1	15.36 ±3.22
Maumwee	<10 ±0.3	2.39 ±0.30
Moher	10 ±1	3.85 ±0.73
Muckno	30 ±3	11.3 ±2.13
Mullagh	60 ±6	42.45 ±10.01
Oughter	70 ±8	20.56 ±4.60
Owel	10 ±1	7.25 ±0.58
Poulaphouca	10 ±1	6.55 ±1.07
Ramor	80 ±11	53.08 ±14.44
Rea	10 ±1	3.27 ±0.81
Talt	<10 ±0.7	2.53 ±0.23
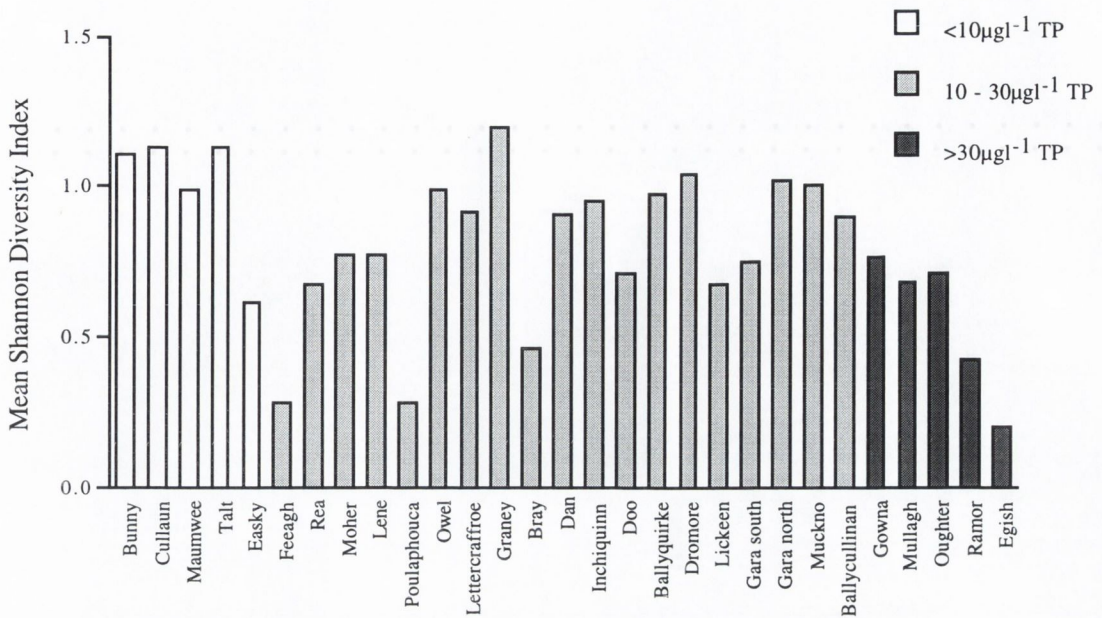
Figure 2.7. Mean Shannon diversity indices for 29 lakes ordered according to mean total phosphorus. The lakes are grouped according to the mean Total Phosphorus indicated in the legend.
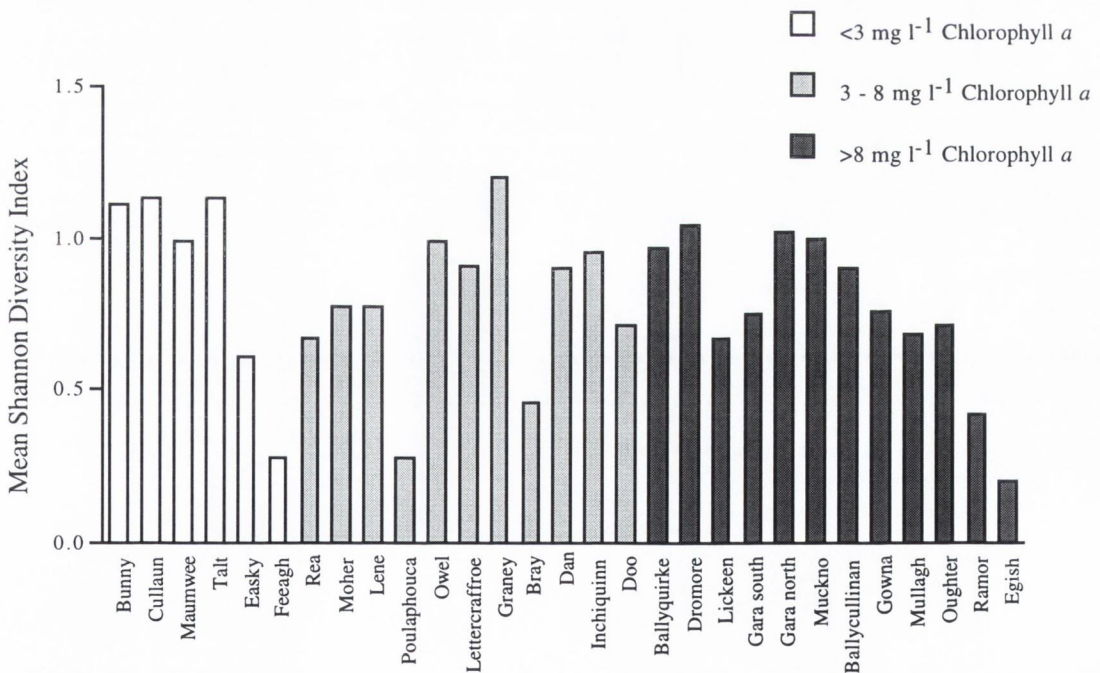
Figure 2.8. Mean Shannon diversity indices for 29 lakes ordered according to mean chlorophyll *a*. The lakes are grouped according to the mean Chlorophyll *a* indicated in the legend.
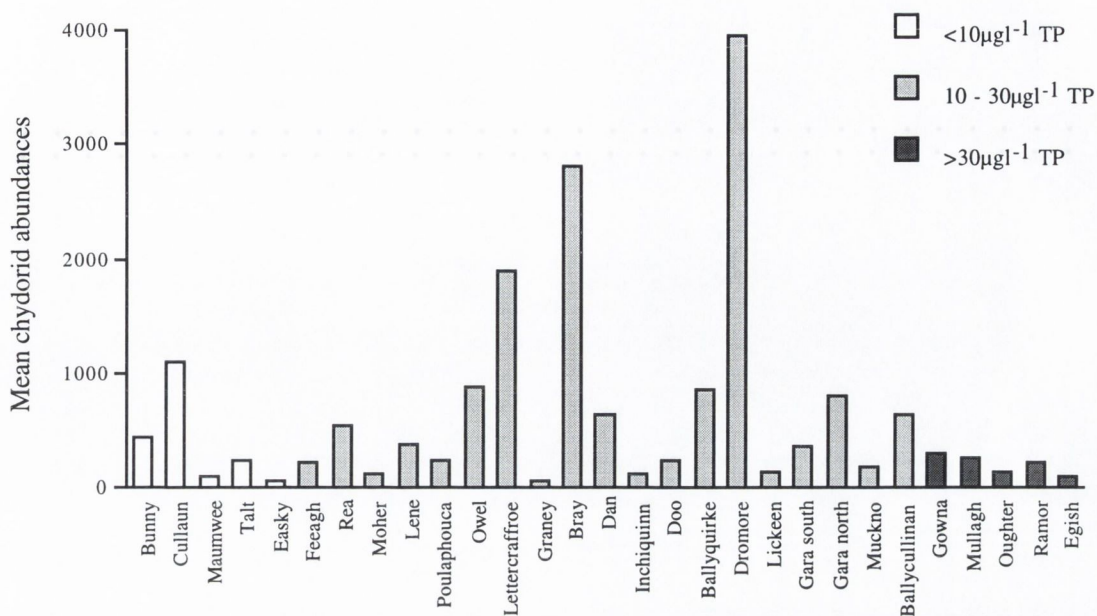
Figure 2.9. Mean abundance of chydorids (per sweep net) in 29 sample lakes ordered according to total phosphorus. The lakes are grouped according to the mean Total Phosphorus indicated in the legend.
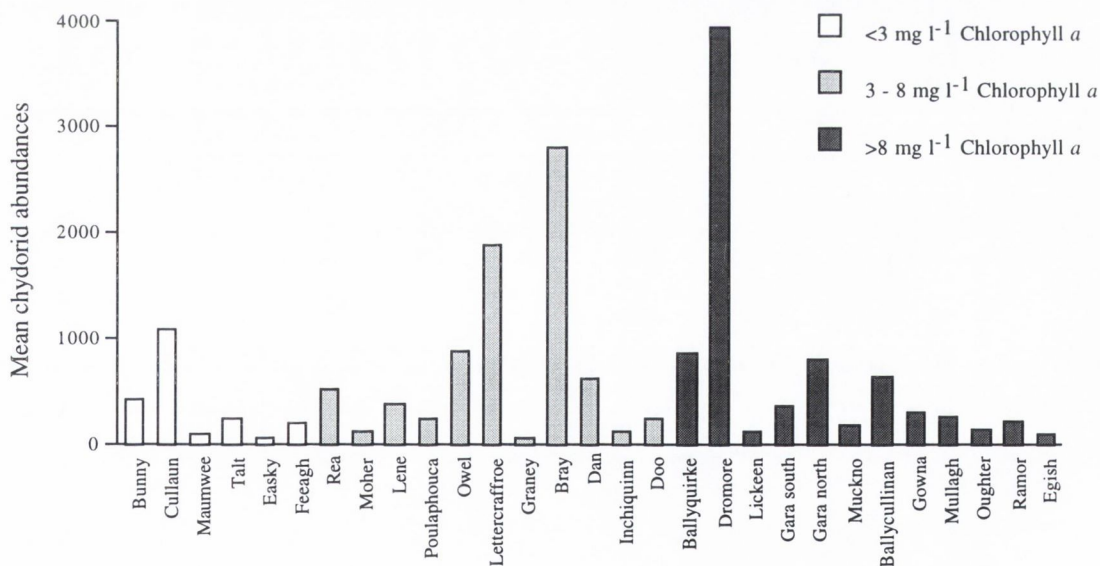
Figure 2.10. Mean abundances of chydorids (per sweep net) in 29 lakes ordered according to chlorophyll a. The lakes are grouped according to the mean Chlorophyll a indicated in the legend.

High proportions of *Chydorus sphaericus* were found in the more productive lakes in this study and there is a general trend of increasing *Chydorus sphaericus* with TP (Figure 2.11) (Spearman rho of 0.58, $p<0.05$). High proportions were also found in some lakes where TP was not very high (e.g. Lettercraffroe). *Chydorus sphaericus* was also significantly correlated with chlorophyll *a* and turbidity, which are closely associated with total phosphorus (Spearman rho 0.52 and 0.53 respectively).
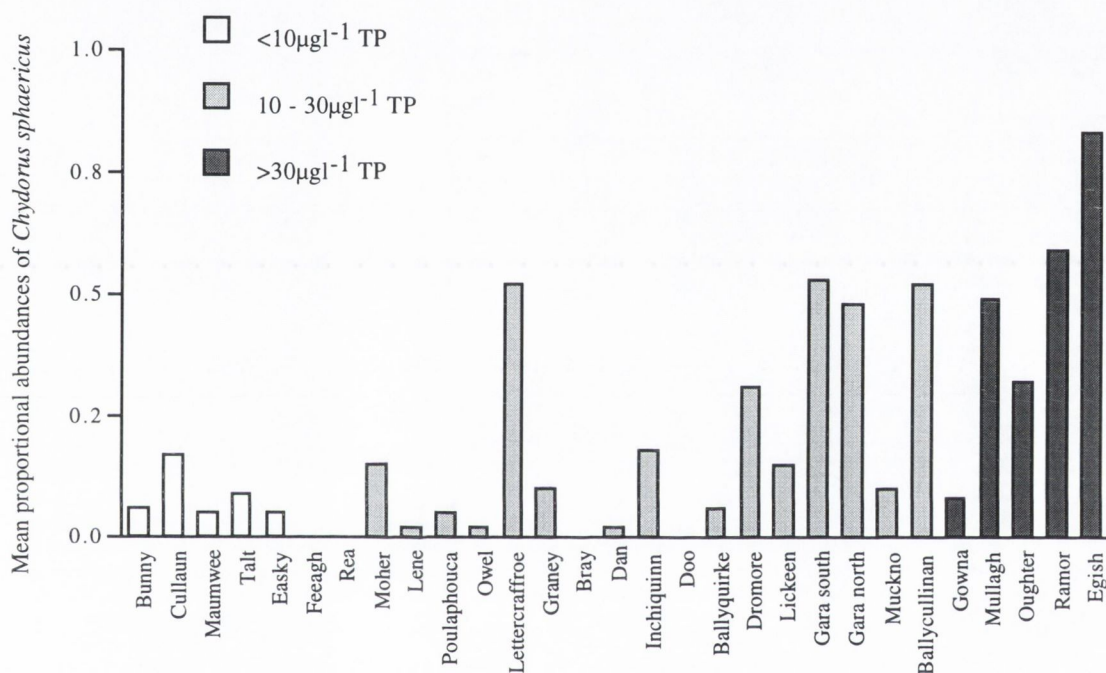
Figure 2.11. Mean proportional abundances of *Chydorus sphaericus* in lakes ordered according to mean total phosphorus. The lakes are grouped according to the mean Total Phosphorus indicated in the legend.

Another species which has previously been associated with nutrient enriched water bodies is *Alona rectangula* which was not found very often in this study, and when it was, it was never in high abundance and no significant correlations were found (Table 2.6 (a)). However, the proportional abundances of another species, *Pleuroxus uncinatus* was found to be significantly correlated with TP, chlorophyll *a* and turbidity (spearman rho 0.57, 0.56, 0.70 respectively) and was noticed to be abundant in individual samples with high levels of detritus. *Camptocercus rectirostris* also showed a

preference for nutrient rich, turbid water is as it had a significant positive correlation with turbidity (spearman's rho, 0.4) and secchi depth (negative correlation, spearman's rho, -0.50)

Two species in particular showed distinct associations with lakes with low trophic status and clear water: *Alonopsis elongata* and *Alonella excisa*. Both had strong negative correlations with TP, chlorophyll *a* and turbidity (Table 2.6 (a)). Figure 2.12 shows boxplots of the levels of TP and chlorophyll *a* in lakes where *Alonopsis elongata* is present and absent and pooled t-tests of the TP and chlorophyll *a* in lakes with or without *Alonopsis elongata* show significant differences ($p<0.1$, d.f.=27 for TP and $p<0.05$, d.f.=27 for chlorophyll *a*). *Alona costata* also showed a preference for clearer water, with significant correlations with turbidity (spearman's rho, -0.38) and secchi depth (spearman's rho, 0.45).
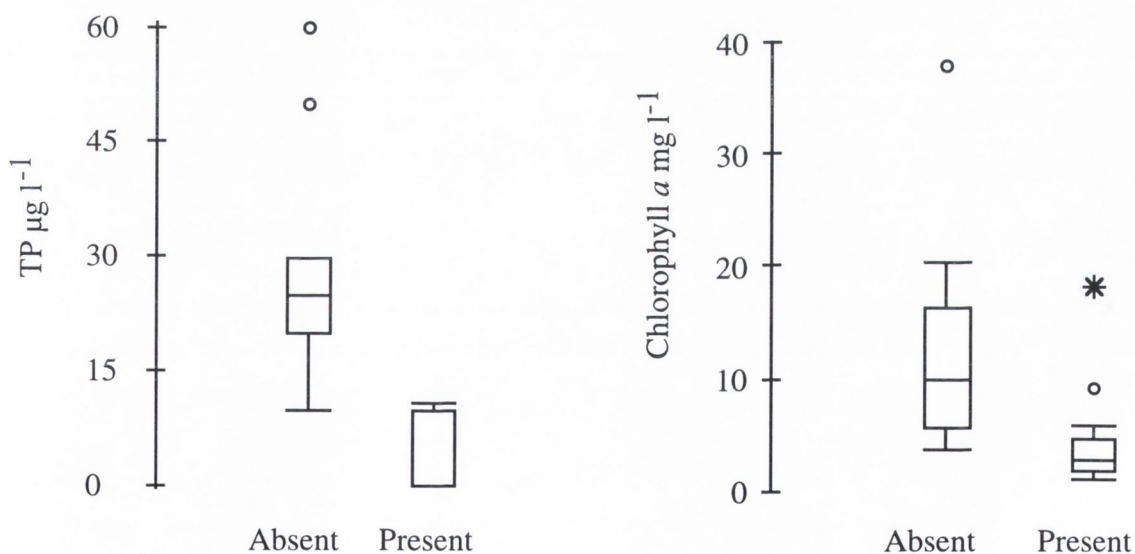
Figure 2.12. Total phosphorus and chlorophyll *a* measurements from lakes where *Alonopsis elongata* is present or absent. The boxes represent the upper and lower 25% quartile of the data and the whiskers represent the spread of the majority of the data, not including outliers. Outliers are represented by a circle or a star.

2.3.4 Chydorids and Alkalinity / pH.

There was no direct relationship found between chydorid diversity and low pH and alkalinity. Many of the lakes in this study with low pH and alkalinity measurements had quite high species diversity (Figure 2.13). The only visible trend was for low species diversity to occur in lakes with low alkalinity.
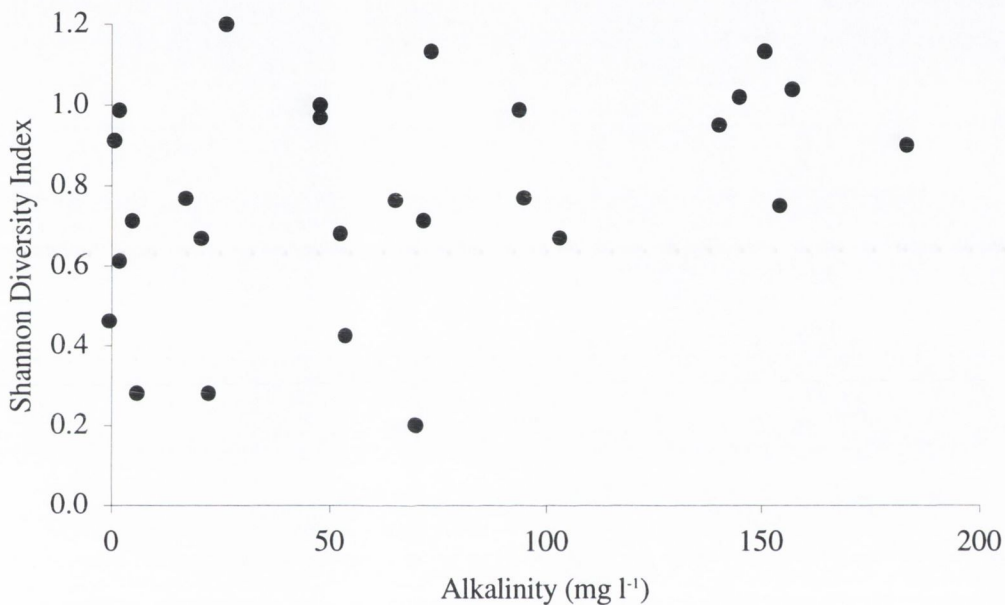
Figure 2.13. Shannon diversity index of chydorid communities in 29 lakes with varying alkalinity (mg l^{-1} of $CaCo_3$).

Proportional abundance of *Chydorus piger* were found to decrease significantly with increases in alkalinity, pH and conductivity (spearman's rho: -0.46, -0.42 and –0.39 respectively). *Alona rustica* also showed some association with soft water lakes, although the correlations were not significant at 95%. *Alonopsis elongata* was negatively correlated with conductivity, pH and alkalinity (spearman's rho: -0.43, -0.28 and –0.35) although only the value for conductivity was significant at 95%. *Alonopsis elongata* was frequently found to be the dominant chydorid in lakes with low alkalinities, although it was also found in some of the hard water lakes in Co. Clare

(Figure 2.14). Another interesting feature of *Alonopsis elongata* is its tendency to frequent water with low average temperatures, with the proportional abundances in a lake decreasing with increasing temperature (Spearman's rho –0.56). This is another indication of its preference for oligotrophic, upland lakes, with low pH levels and alkalinities.
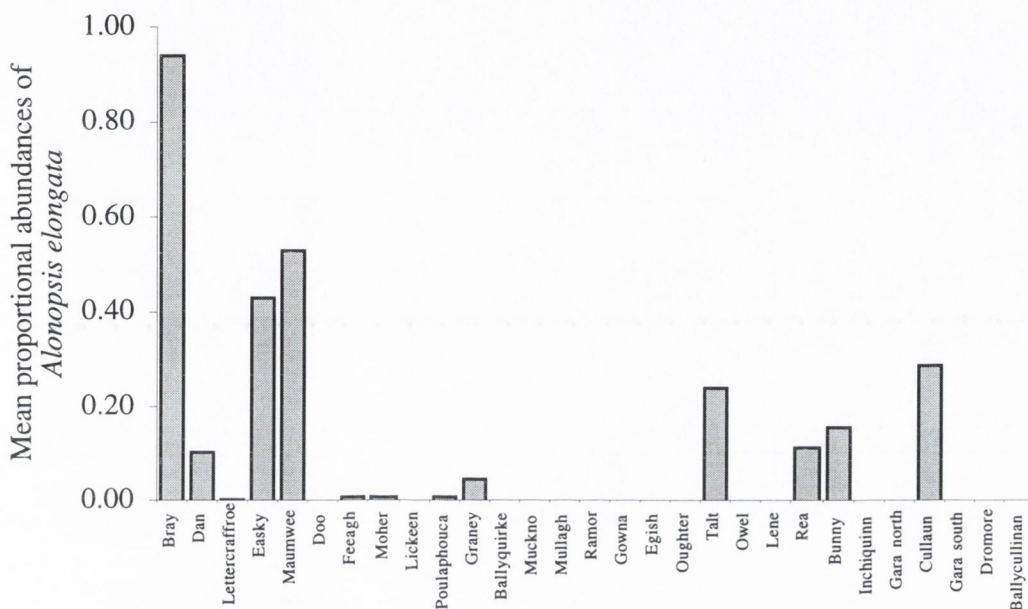
Figure 2.14. Proportional abundances of *Alonopsis elongata* in 29 sample lakes ordered left to right by increasing alkalinity mg l^{-1} of $CaCO_3$ (range from -0.63 to 182.88).

2.3.5 Rare species

Some of the species found in this study are considered to be rare and were only found on one or two occasion, so statistical analysis of these species would be invalid. However, their distribution is worth noting. For example, *Leydigia leydigi* was found in Lough Mullagh, Gara North and Oughter all of which are productive lakes (mean TP = 60 µg l^{-1}, 30 µg l^{-1} and 80 µg l^{-1} respectively). Another rare species *Oxyurella tenuicaudis* was only found in Lough Egish, Gara South and Cullaun. The first two of these lakes had a lot of mud and detritus at the sampling sites which fits in with

previous observations on the habitat preferences of this species. *Pleuroxus aduncus* was found on two occasions in Lough Dromore and Gara North. As *P. aduncus* has been associated with rich vegetation, the presence of the extensive macrophyte habitats in these lakes is probably why this species was found there.

2.3.6 Multidimensional scaling of chydorid data.

From the results of the univariate analysis above. it became obvious that many factors were working in conjunction with each other to produce the particular chydorid community found in each lake. Multivariate analysis was therefore used to separate out the important trends in the data.

2.3.6.1 Chydorid communites from 14 months sampling
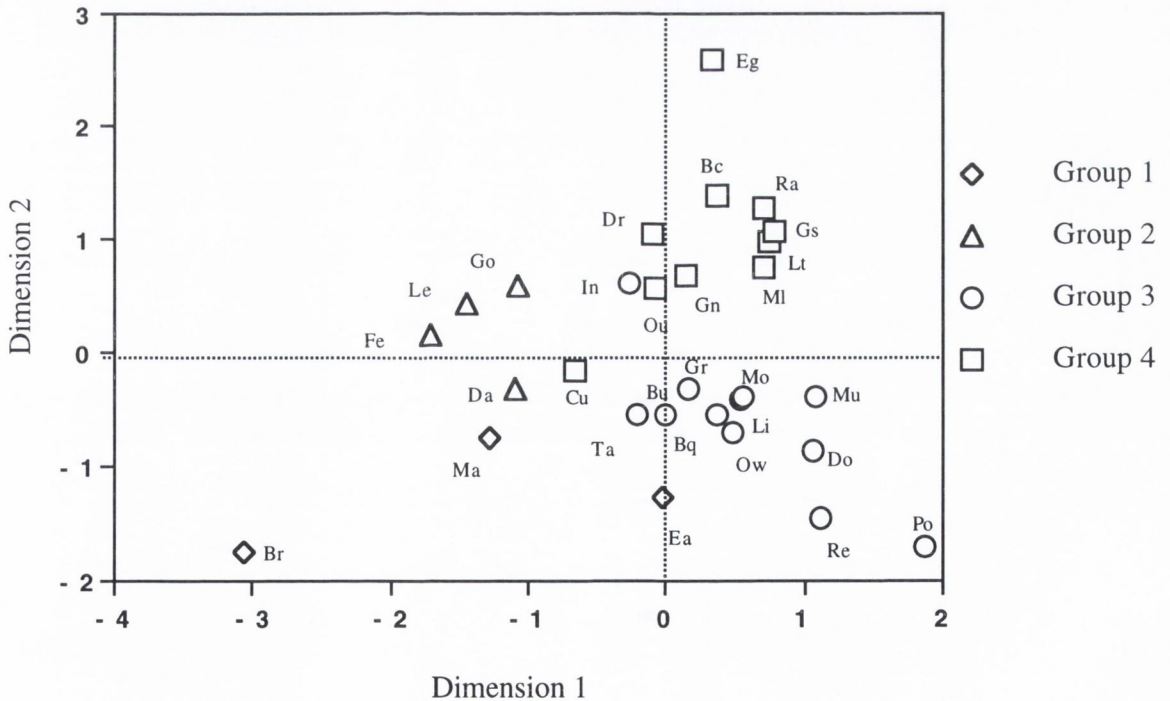
Figure 2.15. MDS plot of lakes based on euclidean distances between their chydorid communities from the 14 month sampling period. Stress = 0.17, R^2 = 0.88. Groups refers to the dendogram in Figure 2.16.

It can be seen from the MDS plot of the 14 month data set (Figure 2.15) that the lakes are spread out in three branches from the centre with Lough Egish, Bray and Poulaphouca at the extremities of the branches. While it is not possible to say what chemical or physical variables the dimensions represent, the more productive lakes are in the top half of the graph with the less productive lakes below the indicated line. Also, the lakes with low alkalinities are mostly found in the bottom left quarter and the lakes in the top right corner all have rich macrophyte beds. A cluster analysis of the same data split up the lakes into 4 groups: (Figure 2.16)

Group 4	**Group 3**	**Group 2**	**Group 1**
Dromore	Doo	Feeagh	Easky
Cullaun	Owel	Gowna	Maumwee
Egish	Moher	Dan	Bray
Oughter	Muckno	Lene	
Lettercraffroe	Lickeen		
Ramor	Bunny		
Mullagh	Ballyquirke		
Gara N	Inchiquinn		
Gara S	Talt		
Ballycullinan	Graney		
	Rea		
	Poulaphouca		
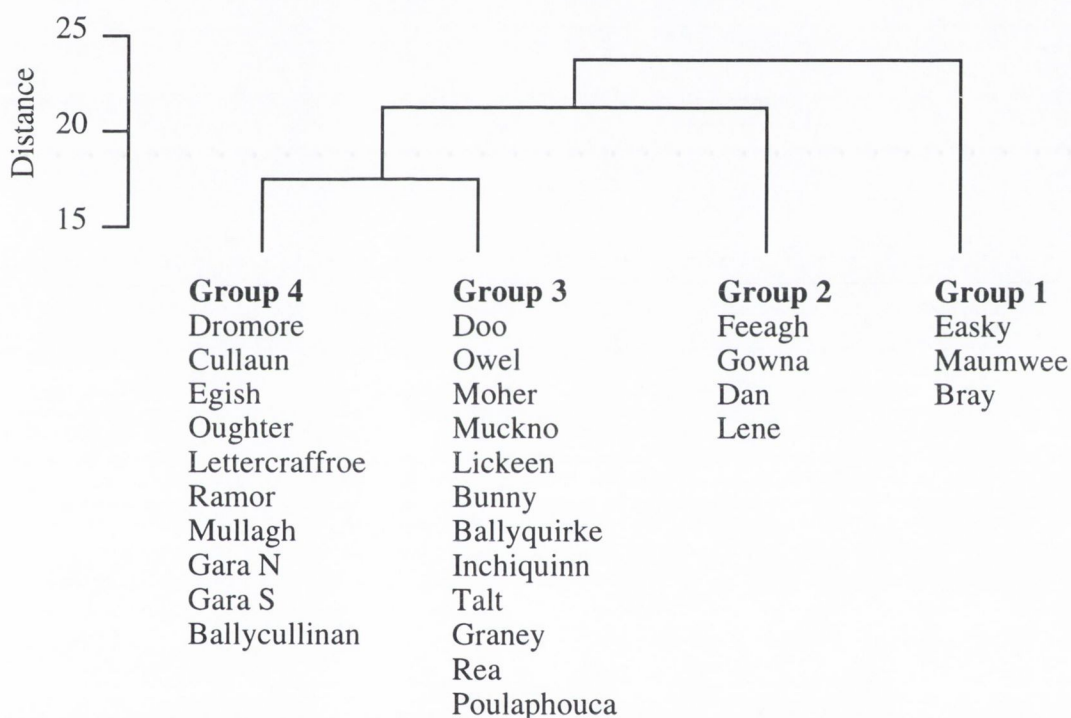
Figure 2.16. Dendogram of clusters produced from chydorid data from all lakes taken over the 14 month sampling period. Groups relate to the legend on the MDS plot of the same data (Figure 2.15).

After looking at the proportional abundances of the species in each lake, it becomes obvious that the lakes are spread according to one of four dominant chydorid

species. These were *Alonopsis elongata, Chydorus sphaericus, Alona affinis* and *Monospilus dispar.* The proportional abundances of these species is given in Table 2.9.

Table 2.9. Mean proportional abundances of four chydorid species in each sample lake which are also classified according to the groups in Figure 2.15.

Group	Lake	*Alonopsis elongata*	*Alona affinis*	*Monospilus dispar*	*Chydorus sphaericus*
1	Easky	0.43	0.46	0.00	0.05
1	Maumwee	0.53	0.10	0.04	0.05
1	Bray	0.94	0.01	0.02	0.00
2	Feeagh	0.01	0.03	0.49	0.00
2	Gowna	0.00	0.09	0.36	0.08
2	Dan	0.11	0.16	0.49	0.02
2	Lene	0.00	0.02	0.41	0.02
3	Doo	0.00	0.48	0.00	0.00
3	Owel	0.00	0.49	0.02	0.02
3	Moher	0.01	0.47	0.01	0.15
3	Muckno	0.00	0.55	0.01	0.01
3	Lickeen	0.00	0.48	0.00	0.15
3	Bunny	0.16	0.37	0.16	0.06
3	Ballyquirke	0.00	0.45	0.21	0.06
3	Inchiquin	0.00	0.08	0.03	0.18
3	Talt	0.24	0.26	0.00	0.09
3	Graney	0.05	0.31	0.05	0.10
3	Rea	0.11	0.73	0.01	0.00
3	Poulaphouca	0.01	0.93	0.00	0.05
4	Dromore	0.00	0.09	0.00	0.31
4	Cullaun	0.29	0.16	0.00	0.17
4	Egish	0.00	0.03	0.00	0.83
4	Oughter	0.00	0.18	0.16	0.32
4	Lettercraffroe	0.00	0.23	0.00	0.52
4	Ramor	0.00	0.20	0.01	0.59
4	Mullagh	0.00	0.26	0.00	0.49
4	Gara N	0.00	0.23	0.13	0.48
4	Gara S	0.00	0.21	0.00	0.53
4	Ballycullinan	0.00	0.08	0.00	0.52

Group one has high proportional abundances of *Alonopsis elongata*, Group 2 of *Monospilus dispar*, Group 3 of *Alona affinis* and Group 4 of *Chydorus sphaericus*. In

most cases, the lakes in each group are solely dominated by the one species that defines the group. In some cases such as Easky, Talt and Cullaun, however, there are two or more species which both have high abundance. For example, Lough Easky was clustered with the group dominated by *Alonopsis elongata* (Group 1) even though it also has high proportional abundances of *Alona affinis*. The position of Lough Easky on the MDS plot (Figure 2.15) shows that it is very close to the Group 2 lakes so the proportion of *Alona affinis* was taken into consideration when the dimensions were calculated. Similarly, Lough Cullaun has relatively high proportions of three species, *Alonopsis elongata, Alona affinis* and *Chydorus sphaericus* which is why it was positioned near the middle of the MDS plot. What is very evident is that three lakes on the extremities of the plot (Egish, Bray and Poulaphouca) are there because of the dominance of one chydorid species, *Chydorus sphaericus, Alonopsis elongata* and *Alona affinis* respectively. Towards the centre of the MDS plot, species diversity increases, and there is less dominance by one particular species.

2.3.6.2 Chemical and physical data

None of the combinations of abiotic variables produced a spread identical to that observed from the chydorid data (Figure 2.15). The most similar combination was with TP(μg l^{-1}), alkalinity (mg l^{-1}) and littoral plants (scale of 1 - 5) (Figure 2.17).
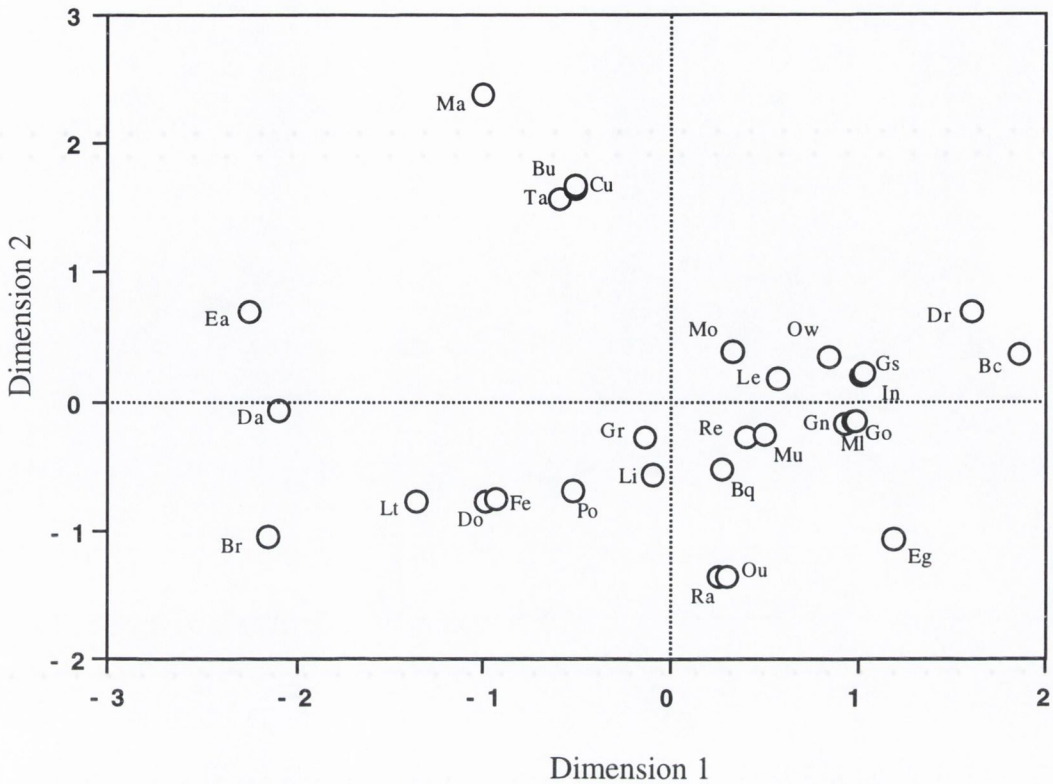
Figure 2.17. MDS plot of Total Phosphorus (μg l^{-1}), alkalinity (mg l^{-1}) and littoral plants (scale of 1 - 5). Stress = 0.15, R^2 = 0.90

As with the biotic plot, Lough Bray and Egish were at the extremities of the plot, and productive lakes were split from the less productive lakes by dimension 1 (in the chydorid plot, the productive lakes were split from the less productive ones by dimension 2). Lakes with rich littoral vegetation were grouped to the right of the graph and lakes with low alkalinities are towards the bottom left (except for Maumwee, whose rich littoral vegetation separates it from other lakes with low alkalinities). Although the lakes were orientated slightly differently from those in Figure 2.15, ordinating the lakes by their TP, alkalinity and littoral plants does produce a similar result to that using chydorid data.

2.3.6.3 Presence and absence of chydorid species

An MDS of the 29 lakes was carried out, with the euclidean distances calculated from scores of 1 where a species was present and 0 where it was absent (Figure 2.17).
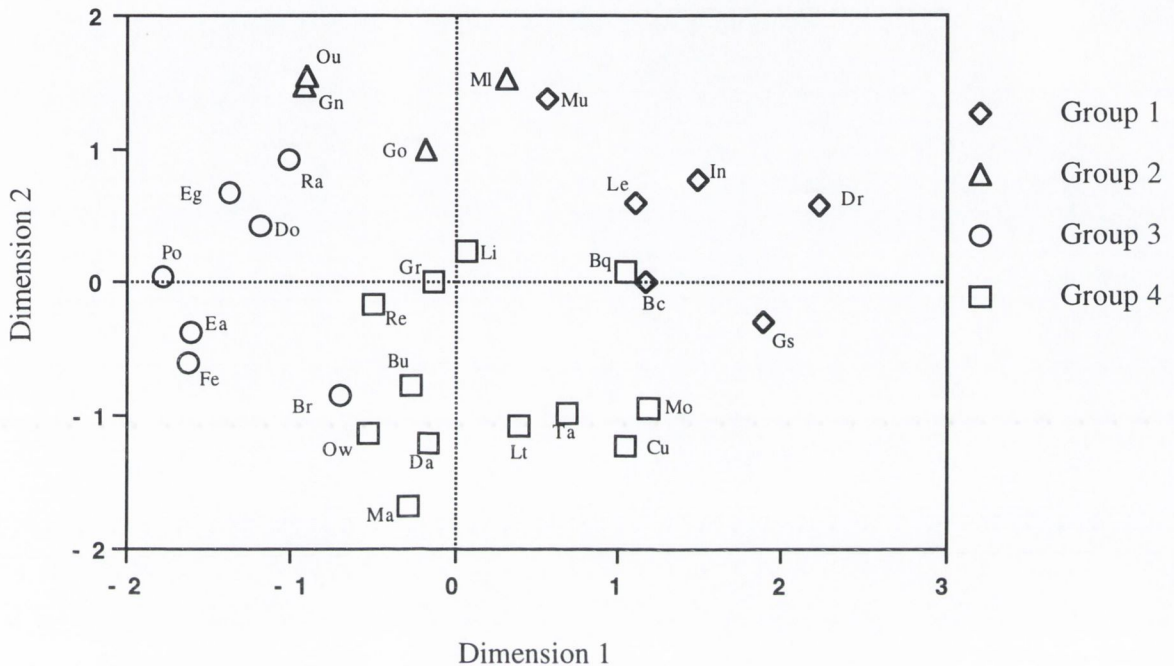
Figure 2.18. MDS plot of chydorid data based on euclidean distances calculated from presence/absence of all species. The groups refer to the dendogram (Figure 2.19). Stress = 0.25, R^2 = 0.63.

The presence/absence data produced less of a spread than when using the proportional abundance of chydorids, and the stress values for the ordination is quite high which means that the algorithm had difficulty plotting the data. Nonetheless, this method is useful to assess conditions that are associated with species poor chydorid communities. Again the plot is split top to bottom with the more productive lakes in the top half. The lakes with low alkalinities are in the bottom left quarter of Figure 2.18 and lakes with rich littoral vegetation are towards the right hand side of the plot. A cluster analysis of the data produces four groups with varying species richness (Figure 2.19). The four

groups have significantly different species richness (from an ANOVA, F ratio = 15.4, $p \leq 0.01$) (Table 2.10).

	Group 3	Group 2	Group 4	Group 1
	Doolough	Mullagh	Owel	Gara S
	Bray	Gara N	Moher	Dromore
	Ramor	Oughter	Dan	Ballycullinan
	Feeagh	Gowna	Maumwee	Lene
	Easky		Ballyquirke	Muckno
	Poulaphouca		Graney	Inchiquinn
	Egish		Bunny	
			Rea	
			Lickeen	
			Cullaun	
			Talt	
			Lettercraffroe	
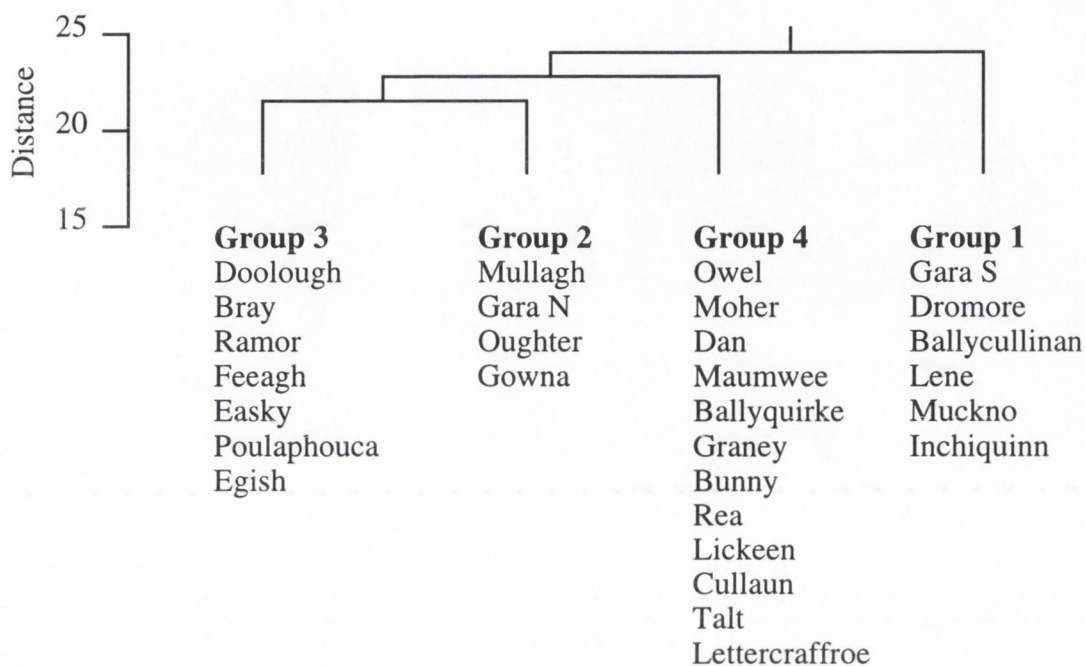
Figure 2.19. Dendogram of clusters produced using presence/absence of chydorid species. Groups relate to the legend on the MDS plot of the same data (Figure 2.18).

Table 2.10. Mean chydorid species richness (±standard error) of groups from cluster analysis (Figure 2.19) of 29 lakes, based on the presence or absence of 31 species.

Lakes	Group 1	Group 2	Group 3	Group 4
no. of lakes (n)	6	4	7	12
Mean species richness	15.8±1.0	12.3±0.5	8±1.1	15.3±0.7

Although the lakes in Group 3 are all quite different, they all have low species richness for one reason or another. From the MDS plot, it is apparent that the main

problems could be eutrophication (Egish and Ramor), low alkalinities (Bray and Easky) and a poor littoral environment with respect to plant cover (Poulaphouca and Doolough) . Lakes in Group 2 also have quite low species richness although not as extreme as the previous lakes. These four lakes are all productive lakes in the central lowlands and have high total phosphorus measurements (30 - 70 µgl⁻¹). This ties in with the earlier observation that increased TP in a lake reduces chydorid species richness and diversity. Groups 1 and 4 have similar species diversities but the lakes in Group 1 are more productive (10-30 µgl⁻¹ TP) then those in Group 4 (0-20 µgl⁻¹ TP). Another difference between the two groups is that the lakes in Group 1 have more extensive macrophytes, particularly reed beds.

2.3.6.4 Summer chydorid data
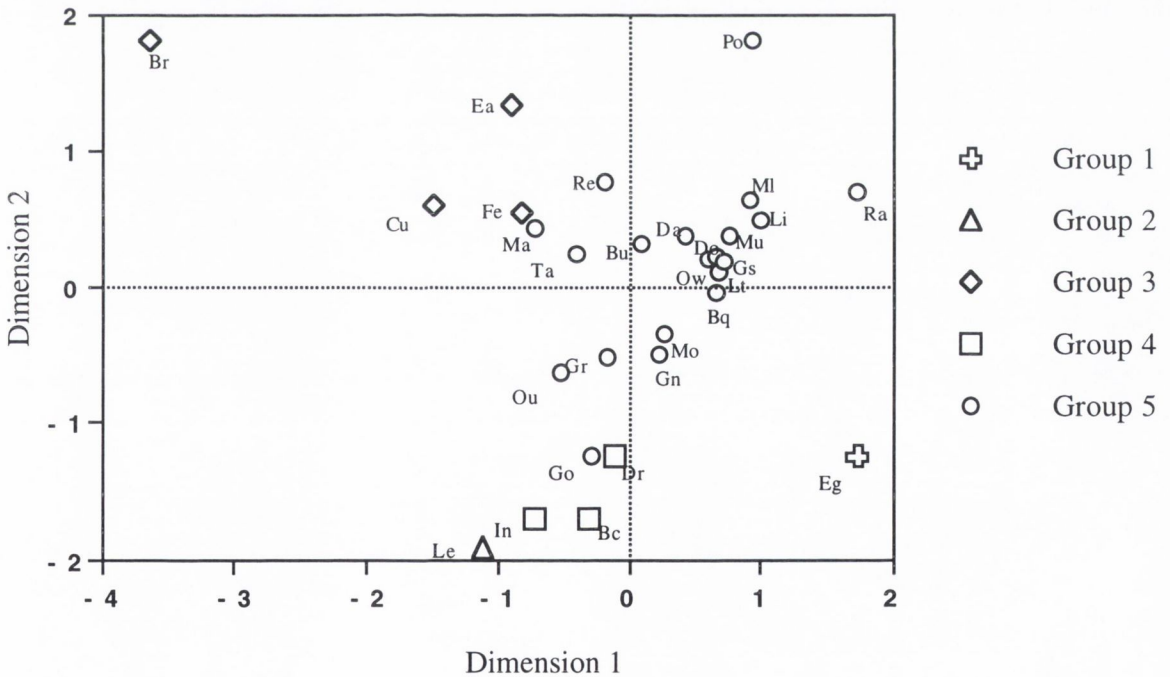
Figure 2.20. MDS plot of lakes based on the euclidean distances between their chydorid communities from June, July and September 1997. Groups refers to the dendogram (Figure 2.21). Stress = 0.19, $R^2 = 0.87$.

The MDS plot of summer chydorid data (Figure 2.19) showed a similar result to that obtained using data from 14 months, in that the same three lakes (Egish, Bray and Poulaphouca) are at the extremities of the plot. The more productive lakes are on the right hand side of the plot and lakes with low alkalinities are in the top left quarter.

Group 5		Group 4	Group 3	Group 2	Group 1
Moher	Maumwee	Ballycullinan	Easky	Lene	Egish
Doo	Talt	Dromore	Feeagh		
Owel	Bunny	Inchiquinn	Cullaun		
Graney	Dan		Bray		
Oughter	Rea				
Muckno	Ballyquirke				
Mullagh	Gara S				
Ramor	Gara N				
Poulaphouca	Lickeen				
Lettercraffroe					
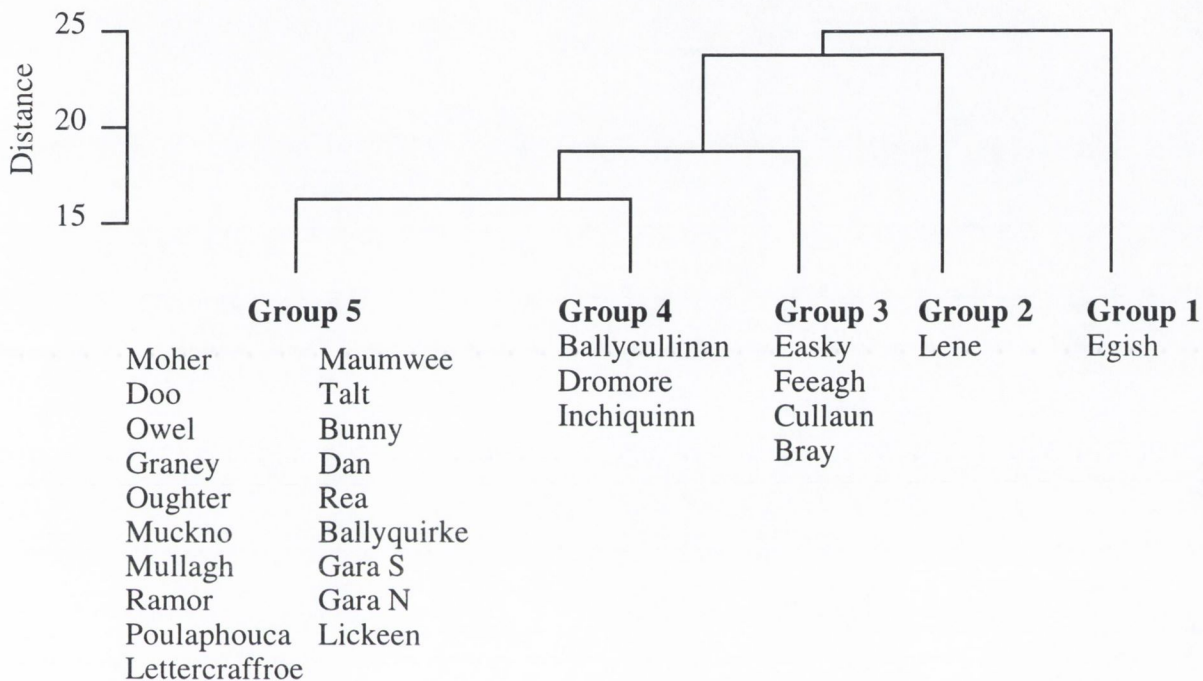
Figure 2.21. Dendogram of clusters produced using chydorid data from samples taken from all lakes in June, July and September 1997. Groups relate to the legend on the MDS plot of the same data (Figure 2.20).

The separation of lakes in the cluster analysis indicated that the groups are not so clearly defined as they were for the 14 month samples, with the majority of lakes being grouped together in group 5. However, some of the same dominant species again characterise the groups: *Alona affinis* (group 5), *Alonopsis elongata* (Group 3) and *Monospilus dispar* (Group 2). Some other species show high proportions as well: *Eurycercus lamellatus* (Group 1 and 4) and *Pleuroxus truncatus* (Group 4). While no group in particular had higher proportions of *Chydorus sphaericus*, lakes in the bottom

of the graph (e.g. Ballycullinan, Dromore, Inchiquin and Ballyquirke) had higher proportions of this species.

2.3.6.5 Chydorid data from one months sampling (September, 1997)
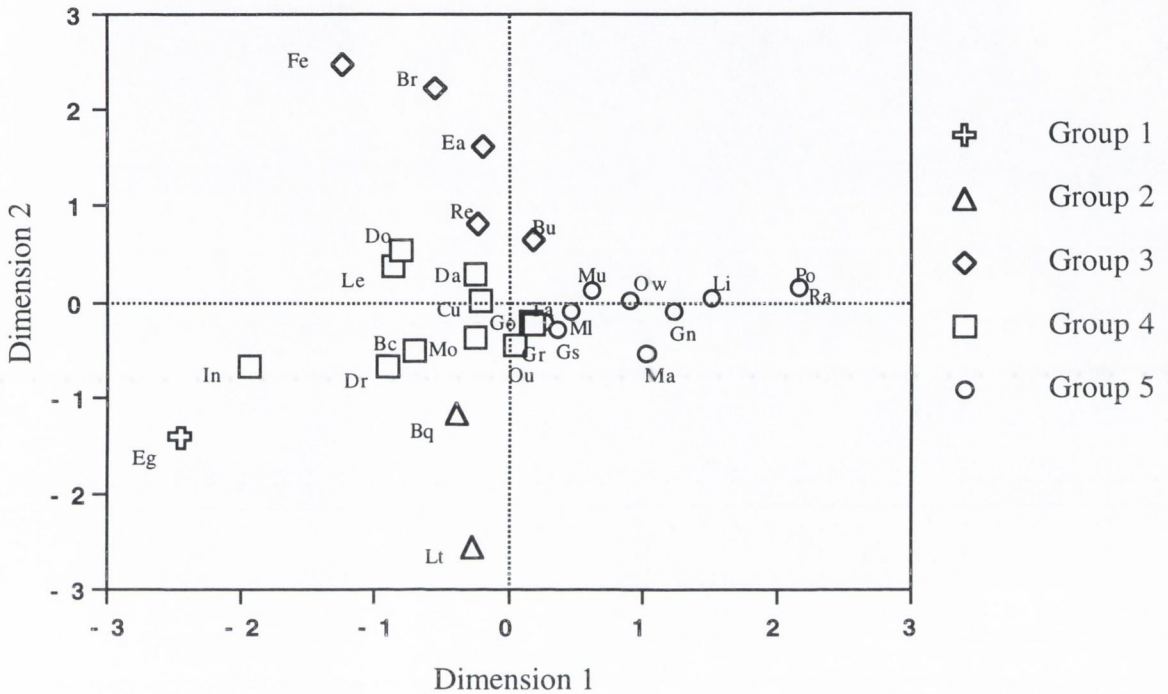
Figure 2.22. MDS plot of lakes based on the euclidean distances between their chydorid community from September 1997. Groups refer to the dendogram in Figure 2.23. Stress = 0.20, R^2 = 0.85.

The data from the September samples produced a different shaped MDS plot as there are four main branches instead of three. Lakes with low alkalinity were spread towards the top left of Figure 2.22 and lakes with rich vegetation were found near the bottom of the plot. The same four dominant species again dominate the analysis, with the addition of *Eurycercus lamellatus*. which totally dominated the sample from Lough Egish.

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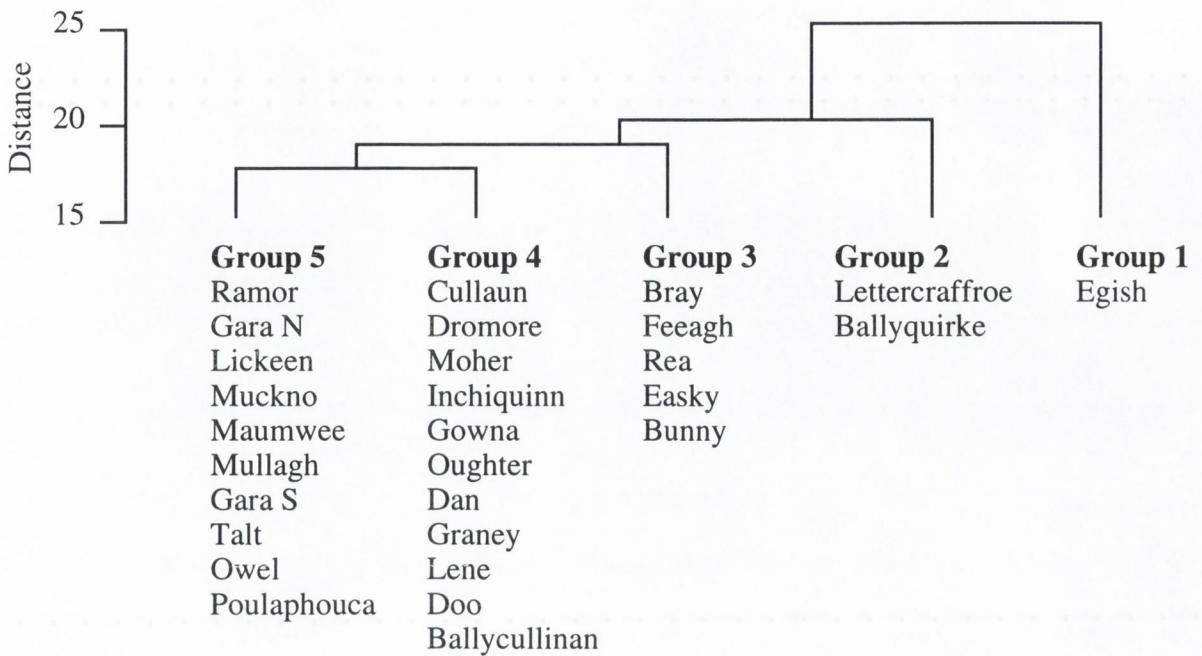
Figure 2.23. Dendogram of clusters produced by using the chydorid data from all samples taken in September 1997. Groups relate to the legend on the MDS plot of the same data (Figure 2.22).

Alona affinis dominated group 5 and *Alonopsis elongata* Group 3 This is consistent with the previous MDS analysis of the 14 month samples and the summer samples. Group 2 had high proportions of *Chydorus sphaericus* as did some of the lakes in Group 4, although the main species in that group was *Pleuroxus truncatus*, which is a species strongly associated with rich vegetation. Lough Egish (Group 1) is totally dominated by *Eurycercus lamellatus*. As with the summer data, the lakes already identified as having low species diversity and one dominant species (Bray, Egish, Poulaphouca, Ramor, Feeagh) were found at the extremities of the plot.

2.4 Discussion

2.4.1 General discussion

In agreement with other studies (Dodson, 1992; Whiteside, 1970; Whiteside & Harmsworth, 1967), species diversity, richness and abundance of chydorids were found to decrease as nutrient enrichment increased. Eutrophic lakes also had significantly higher proportional abundances of *Chydorus sphaericus*. This was also found in Lake le Cruz, Spain (Mezquita & Miracle, 1997), thirteen German lakes (Hofmann, 1996), and a series of lakes studied in Denmark and the USA (Whiteside & Harmsworth, 1967). Although the ubiquitous nature of *Chydorus sphaericus* means that it will probably be found in every lake in Ireland, it has high value as an indicator of eutrophication. The dynamics of the chydorid community are controlled or influenced by many factors including predation, competition, macrophyte diversity and availability of substrata and these will all be affected themselves by increased nutrient enrichment. The effect that nutrient enrichment has on the phytoplankton, and hence the littoral macrophytes and periphyton of a lake, is probably the most important factor affecting the way that chydorids respond to enrichment, as this has implications for so many other factors including food availability, plant refuges and predation (Miskimmin *et al..*, 1995, Rundle & Ormerod, 1991, Rasmussen, 1988, Whiteside, 1970). The effect of low alkalinity on the chydorid community is more noticeable on species rather than on community structure. Marked decreases in species diversity and species richness were not significant in the low alkalinity lakes, but there are several species such as *Alona rustica* and *Chydorus piger* that show preferences for oligotrophic, soft water lakes. *Alonopsis elongata* was found to be particularly dominant in upland, oligotrophic lakes with low pH and low alkalinity.

The multivariate analysis of data collated from 14 sampling trips split the lakes into four groups each of which was dominated by a different species of chydorid (Figures 2.15 and 2.16). Lakes at the extremities of the MDS plot (Lough Bray, Egish and Poulaphouca) were almost totally dominated by *Alonopsis elongata, Chydorus sphaericus* and *Alona affinis* respectively. Towards the centre of the plot, species diversity increased, and the dominance of one particular species became less. These results indicate some environmental stress or perturbation acting on the lakes at the extremities of the MDS plot, as a reduction in community diversity is often associated with environmental perturbation (Hellawell, 1997). Lough Egish was the most productive lake in this study, Bray the most acidic and Poulaphouca had very poor littoral vegetation and an extensive drawdown, as it is used as a reservoir for the Electricity Supply Board. Lakes positioned towards the centre of the plot have less extreme concentrations of TP, pH or littoral disturbance. The lakes of each group share common environmental conditions which probably favours one particular species.

The lakes in Group 4 are all productive (with the exception of Cullaun and Lettercraffroe) which would be classified mesotrophic or eutrophic according to the O.E.C.D. (1982). *Chydorus sphaericus* was the most important species in this group. Cullaun is an outlier in this group and is not solely dominated by *Chydorus sphaericus*. Lettercraffroe is an anomaly of the group and its characteristics are very different from those of the other lakes as it is an oligotrophic, upland lake with low alkalinity. However, the catchment around the lake has been heavily forested, and the land was fertilised to ensure good growing conditions (T. Champ,Central Fisheries Board, *pers. comm*). It did have relatively high amounts of chlorophyll *a* which may be why there was a high proportion of *Chydorus sphaericus*. If the high proportions of *Chydorus sphaericus* in Lettercraffroe are as a direct result of artificial fertilisation, then this is a interesting finding, and one which may strengthen the theory that this group of animals

is useful for assessing the historical changes in a lake. One way of verifying this observation would be to take a core of sediment from Lettercraffroe and see what the proportions of *C. sphaericus* were like before the afforestation.

The lakes in Group 1, which were characterised by high proportions of *Alonopsis elongata* all had very low alkalinities (0.2, 1.86, 2 mg l^{-1}) which is consistent with other reports that this species is tolerant of low alkalinities and pH (Duigan & Kovach, 1994; Duigan, 1992; Whiteside, 1970; Crisp & Heal, 1958). While the three lakes have low alkalinities and pH levels, they also have low productivity and are situated in upland, peaty areas. As many of these lakes have autocorrelating physicochemical variables, it is difficult to ascertain why this species should thrive in these situations. It may be that it has a physiological tolerance of acidic water which allows it to outcompete other species. Another possibility is that it is able to reproduce quicker than other species at lower water temperatures, which is a common characteristic of these upland lakes (Lough Bray and Lough Easky are relatively cold lakes with average temperatures at the surface of 11.5°C and 11.8°C). Also, the habitat structure of these lakes (wave washed shores, small littoral plants such as *Sphagnum* spp. and *Isoetes* sp.) may favour species such as *Alonopsis elongata* which has an affinity for hard substrata such as rock and sand, and stays away from macrophyte beds. Whatever the reason for its success, it seems likely that acidic conditions favour this species, either directly, or indirectly, and this may be useful as an indicator of acidification. A lake in Co. Wicklow which was not included in this study (Glendalough Upper) has been shown to be affected by acidification and a survey of the zoopankton of the lake did find high levels of *Alonopsis elongata*, in comparison to other chydorid species (Bowman, 1991).

Group 3 comprised lakes with high proportions of *Alona affinis* which is perhaps the most common and widespread chydorid in Ireland. The lakes where *Alona affinis* was particularly dominant (Poulaphouca, Rea and Doo) were characterised by poor littoral vegetation and disturbances of the littoral zone by wave action or drawdown. *Alona affinis* has been noted as one of the "pioneer species" of chydorids which can colonise very new habitats, where perhaps littoral vegetation and periphyton are not yet established as it does not depend on a vegetative habitat for success (Robertson, 1990, Whiteside, 1970). It is possible that the disturbance in the littoral zone produces an environment which is best suited to a successful species such as *Alona affinis* which can colonise new environmental niches effectively.

Group 2 was dominated by *Monospilus dispar*, a species which has a preference for sand or gravel habitats (Chengalath, 1982; Smirnov, 1962). The samples from these lakes (Feeagh, Gowna, Dan, Lene) were taken in areas of gravel or sand (with some plant beds in the case of Dan and Gowna) so it is not surprising that abundances of *Monospilus dispar* would be high. What is interesting is that the other abundant chydorid species in the lake provide clues to other characteristics of the lake. Lough Dan which is an acidic, upland, oligotrophic lake had relatively high proportions of *Alonopsis elongata* (11%) while Gowna which is a productive low-lying lake had quite high proportions of *Chydorus sphaericus* (8%). The other lakes, Feeagh and Lene had smaller proportions of *Alona affinis*. Lough Feeagh has high proportions of *Disparalona rostrata*, which is cited as being a benthic dweller (Duigan, 1992). The high dominance of two benthic species is almost certainly connected with the degree of overgrazing by sheep in the catchment which means that there is excessive peat run off into the littoral zone bringing about about a decrease in the ecological quality of the lake. In 1993, 250 tonnes of peat/km^2 was eroded from an overgrazed hillside in the catchment, in comparison to 5 tonnes/km^2 in a control area. Significant changes in the number of taxa

and abundances of macroinvertebrate fauna of the littoral zone have been noted in the period 1971 – 1994 (Whelan *et al.*, 1998) and it is likely that the dominance of the two benthic species of chydorids is a reflection of the increased peat in the littoral zone.

The approach of looking at presence or absence of certain species brings out the "species richness" element of chydorid communities. Multivariate analysis of the chydorid data collected over 14 months has already shown that species diversity increases towards the centre of the plot (Figure 2.15) and away from an environmental stress of some kind. Therefore, it could be expected that species richness would also be higher in lakes that are not under ecological pressure from factors such as eutrophication or acidification. Multivariate analysis of the presence/absence data shows that even with purely qualitative data on the chydorid community, certain aspects of lake quality can be inferred. From the MDS plot (Figure 2.17), it was apparent that eutrophication (Egish and Ramor), low alkalinities (Bray, Easky) and a poor littoral environment with respect to plant cover (Poulaphouca and Doolough) which is probably a result of drawdown as both lakes are used as water supplies, were important factors associated with chydorid community structure. If these factors can be considered as indicators of environmental stress, then it seems that lakes which are under some kind of environmental stress would have very low species richness. Therefore, a combination of information about species richness, species diversity and which chydorids have high proportional abundances can provide a good indication of the ecological quality of a lake.

Lakes with low chydorid species diversity are apparent in analysis of samples taken over the summer or in one month. It is reassuring that the same lakes are at the extremities of all the MDS plots which shows that even with samples taken from the summer, they show up as having poor species diversity, with one species dominating.

Two species were found to be relatively more important in the September samples (in comparison to the annual populations sampled over 14 months). These were *Eurycercus lamellatus* and *Pleuroxus truncatus*. It is likely that this is a reflection of increased macrophyte habitats in lakes during the summer, as both these species have a preference for vegetated habitats.

2.4.2 Application of results from chydorid study - how to use them to monitor lake ecological quality.

From the results shown, it is concluded that chydorids could be used to infer lake quality, in particular, nutrient enrichment, acidification and degradation of macrophytes. They could also provide a more long term view of the ecological status of the lake than snapshot views obtained from chemical measurements. The benefits of using chydorids is that they are easy and quick to sample. It takes 5 minutes to take a 12 second kick sample with a sweep net and sieve and preserve it. The samples are quick to sort when compared with traditional invertebrate samples, once the identification of species has been mastered. Samples in this study took approximately 30 minutes to an hour to sort, count and identify using a binocular microscope and a perspex counting dish. As there are only 41 species recorded from Ireland, it takes a matter of weeks to become familiar with their identification. Some species are very common and widespread and these dominant species (*Alona affinis, Chydorus sphaericus, Alonopsis elongata, Monospilus dispar* and *Eurycercus lamellatus*) are among the easiest chydorids to identify. These species also form the basis of a monitoring proposal outlined below, which seeks to classify lakes according to the relative dominance of particular species in the chydorid community.

On the negative side, the seasonality of the animals may cause some lakes to be assigned incorrectly along a disturbance or quality scale as the dominance of a species may be attributable to sampling coinciding with a natural peak in abundance, rather than an overall dominance of a species because of lake conditions. Lakes sampled once are more likely to be put in a class indicating poorer ecological quality as a result of seasonal variance, then one of high ecological quality, because the chydorid diversity obtained from one sample is very likely to be less then that of the lake as a whole, and as has been indicated, low diversity is also a characteristic of a lake under environmental stress.

The specific substratum preferences of some species may also cause difficulties in classifying lakes, if samples are only taken from one substratum (and hence possibly produce a large number of one species, as in the case of *Monospilus dispar*). A composite of kick-samples taken over several substrata types (see Duigan, 1992) with careful noting of the sites sampled for future reference may reduce this problem.

2.4.3 Proposed scheme for monitoring ecological quality using chydorid communities

1. If possible several samples over the year should be taken from the littoral region of the lake. If only one sampling trip is possible during the year, the summer months (June, July, August, September) will provide the most information.

2. Samples should be taken with a net with mesh not greater than 240 μm. The suggested sampling method would be to do a kick sample (12 seconds) over as many different substrates as possible. The number of 12 second kick samples should be recorded for future reference. In this study, the best method of kick sampling

was found to be a backward shuffle, disturbing the substrate with the heels while sweeping the net in the water in front of the feet to a depth of approximately 0.3 metres (or wellington height!).

3. Samples can be sorted under a dissecting microscope. Subsampling is advised where samples are very large with a lot of detritus and at least 15% of the sample should be counted, or until 50 of the most common individuals are identified.

4. Convert the species abundances to proportional abundances and also record species richness (how many different species there are in the sample).

The results obtained from all the samples can then be applied to a dichotomous key below, which is based on results obtained during the 14 month study, 1996-1997. lakes are separated into four classes, based on the dominance of chydorid species and the Shannon diversity index of the community. The correlations between species and physicochemical variables were also taken into consideration (Table 2.6). The classification above should not be viewed as having strict divisions between classes, rather as a continuum from one to the next. Table 2.11 shows how this twenty nine lakes in this study were classified according to the dichotomous key.

Key for data obtained from the samples:

1. Is there only one species dominant (>0.4 proportional abundance) and is the Shannon diversity index less than one?   **Yes – 4.**

                                                                                    No – 2.

2. Are there 1 or 2 species with medium proportional abundances (> 0.2 each) and is the

Shannon diversity greater than 1?   **Yes** – 7.

                                                     No – 3.

3. Are there more than 2 species with medium proportional abundances (>0.2)?

                                                     Yes – Class 4.

4. Has the dominant species a proportional abundance of ≥ 0.5 and is the Shannon

diversity index ≤ 0.7.   **Yes** – Class 1.

                                                     No – 5.

5. The proportional abundance of the dominant species is ≤ 0.6. What is the species?

Chydorus sphaericus   **Conclusion:** Class 2.

Alonopsis elongata   **Conclusion:** Class 3.

Monospilus dispar   Go to **6**

Alona affinis   **Conclusion:** Class 3.

Alona costata   **Conclusion:** Class 3.

6. What is the second most dominant species?

Chydorus sphaericus.   **Conclusion:** Class 3.

Alona affinis   **Conclusion:** Class 4.

Alonopsis elongata   **Conclusion:** Class 3.

Alona costata   **Conclusion:** Class 4.

Another species   **Conclusion:** Class 4.

7. What is the most abundant species

Chydorus sphaericus	**Conclusion**: Class 4.		
Alonopsis elongata	**Conclusion**: Class 4.		
Alona affinis	**Conclusion**: Class 4.		
Monospilus dispar	**Conclusion**: Class 4.		
Pleuroxus truncatus	**Conclusion:** Class 4.		

Table 2.11. Classification of the 29 study lakes according to their chydorid communites. See text for discussion of classification.

1	2	3	4
Bray	Ballycullinan	Ballyquirke	Bunny
Doo	Gara north	Inchiquinn	Cullaun
Egish	Lettercraffroe	Easky	Dromore
Gara south	Mullagh	Gowna	Graney
Poulaphouca	Oughter	Maumwee	Talt
Ramor	Feeagh	Moher	Dan
Rea		Owel	Lene
		Lickeen	
		Muckno	

Class 1

The high dominance by one species and the low diversity of the community as a whole, is indicative of an environmental stress which is having a large effect on the chydorid communities, to the extent that only one species is really capable of thriving in the lake (although other species may occur, but in low numbers). Depending on the dominant species, this may be indicative of low ecological quality (i.e. a lake that has been significantly degraded from its natural state), if the source of environmental stress or perturbation is unnatural, or it may simply be a reflection of very harsh, natural conditions. Species which were found to be very dominant included:

- *Chydorus sphaericus*. If this species is found to be dominating the community, it is certainly indicative of eutrophication As lakes are very rarely naturally eutrophic (Moss, 1988), a high proportion of this species indicates that the lake has a low ecological quality, as it is not likely that high proportions of this species will be found in pristine lakes. (This analysis is confined to the study of large waterbodies such as lakes. Small bogpools, which are not eutrophic, may have high proportions of *C. sphaericus* owing to reasons other than nutrient enrichment).

- *Alonopsis elongata.* If this species is found to be dominating the community, it is probably as a result of low pH or alkalinity, and the littoral environment which is associated with these lakes. It can not be presumed, however, that this means the lakes are of low ecological quality (as is the case with *C. sphaericus*), as many lakes in Ireland are naturally quite acidic, and therefore, a high dominance of *A. elongata* may be indicative of a pristine, acidic lake, with high ecological quality (i.e. not degraded beyond its natural state). However, it may be that with increasing acidification, *A. elongata* becomes more dominant, so if over the period of long term monitoring, this trend is noticed, it maybe a sign of decreasing ecological quality. One way of determining whether this is the case would be too examine the proportional abundances of *A. elongata* in a lake which is known to have undergone acidification, using palaeolimnology.

- *Alona affinis* If this species is present in very high proportions, it is indicative of a lake whose littoral zone is quite unstable, probably with poor macrophyte communities. These kinds of lakes will probably fall into two categories: those which have naturally wave washed shores, because of the shape of their catchment and the fetch across the lake. In these cases, high proportions of *A. affinis* may not

necessarily be indicative of low ecological quality, as this is a natural phenomenon. The other category, however, comprises lakes which have a lot of habitat disturbance in the littoral zone as a result of anthropogenic influences, such as the damming of lake, and subsequent level fluctuations. In this case, high proportions of *A. affinis* is indicative of low ecological quality, as it implies that the majority of the biota can not cope with the level of habitat disturbance.

Class 2.

The lakes that fell into this category had one species which has quite high dominance, and the species diversity is relatively low. There is some kind of environmental stress having an affect on the chydorid community, but its impact is not as high as it is on the Class 1 lakes. In the case of the lakes in this study, the majority of the ones that were placed into Class 2 had high proportional abundances of *C. sphaericus*, indicating that the environmental stress in question was nutrient enrichment. It is likely, therefore, that the ecological quality of these lakes is degraded, and unless the eutrophication is reversed, they are likely to progress to class 1 in the future. The other lake in this group was Lough Feeagh, which has very low species diversity, and a dominance of *M. dispar* and *D. rostrata*, which, as already discussed, is probably connected with the degree of overgrazing in the catchment, and a decrease in the ecological quality of the lake.

Class 3.

The majority of lakes are classified in this section, and they are mixture of lake types. They all have one or two relatively dominant species, and the species diversity is not particularly high, which may be indicative of an environmental stress which does not have a very severe impact on the littoral zone (as in Class 1) but is, nonetheless,

having some effect on the chydorid community. As in Class 1 the dominant species can indicate whether this environmental stress is unnatural and hence affecting the ecological quality of the lake. *C. sphaericus* is not a feature of these lakes, so eutrophication is unlikely to be a serious concern. In the cases where *A. affinis* is the dominant chydorid (Lough Ballyquirke, Easky, Moher, Muckno and Owel), this is probably indicative of a wave washed shore rather than any anthropogenic impact. Lough Maumwee and Easky, however, had relatively high proportions of *A. elongata*, which could possibly be an indication of the first stages of acidification.

Class 4

The lakes that are placed in this category can be considered to be of high ecological quality, as their chydorid communites appear to be undisturbed by anthropogenic activites, with high diversity and an equal mix of several species. No environmental stress was identified as impacting on the littoral environment.

This classification system could potentially be used to monitor lakes over a long period of time, such that some trends may be become apparent in the chydorid community:

- Increasing dominance in *Chydorus sphaericus* with a concurrent decrease in species diversity and species richness would indicate increasing eutrophication (towards the eutrophic/hypertrophic status) and a decrease in rich, diverse macrophytes. Chlorophyll *a* is also probably increasing.

- Increasing dominance of *Alonopsis elongata* may be a sign of acidification, especially when there is a concurrent decline in species diversity (species richness may still remain relatively high). It is unlikely that this trend would occur with an

increase in eutrophication, as the species mentioned have a distinct preference for oligotrophic water bodies, so if high proportions of this species are found in hard water lakes, it is a sign of good ecological quality, rather than anything to do with the alkalinity.

- Increasing dominance of *Alona affinis* and a decrease in species diversity may indicate that the littoral region has a lot of habitat disturbance which is affecting the structure of the littoral zone. If this is a result of anthropogenic factors, such as draw down, this can be considered to be a sign of low ecological equality. It is highly likely that if this disturbance is affecting the chydorid community to such a degree, then it will also be impacting on much of the biota of the littoral zone.

- Increasing dominance of benthic species such as *Monospilus dispar* and *Disparalona rostrata* may indicate that there is a lot of material such as peat entering the littoral zone. (This conclusion, however, is only based on one lake, Lough Feeagh, so should be treated with some caution).

One way to be sure whether this classification system is sensitive to change within a lake would be to study some the chydorids from sediment cores of lakes which are known to have undergone environmental change such as eutrophication or acidification and several studies of this kind have been carried out in other countries (Miskimmin *et al.*,1995; Hann *et al.*, 1994; Stansfield *et al.*,1989; Hofmann, 1987; Harmsworth & Whiteside, 1968; Frey, 1960). Chydorids preserve very well in sediments and the remains can be identified to species level, using characteristics such as the patterns and shapes of the carapaces, the shape of the headshields and the number of headpores on the headshield and the shape and number of teeth/denticles on the postabdominal tails. Cores can provide a historical record for the lake, and if chydorids can be used to trace changes in their environment, this should be obvious from the pseudofossil remains of

chydorids over time. The protocol for extracting chydorid remains from lake sediments is well documented and is a relatively simple procedure (Frey, 1986).

While it is clear from this study that chydorids can be used to infer the ecological quality of a lake, it would be misleading to suggest that they should be the only factor included in a monitoring scheme. Lakes are extremely complex and highly variable ecosystems and a combination of several factors in an integrated monitoring program is probably needed to assess the real state of a lake (Moss, Johnes & Phillips, 1997). Chemical analysis of lake water can, undoubtedly, be used to gain insight into the stae of a lake, and is crucial to the long term monitoring of water quality. Chemical monitoring can also be used in conjunction with biological monitoring, to assess whether the state of the biological community in question is a result of a natural environmental stress, or whether the chemistry of the lake is being changed by anthropogenic influences, bringing about changes in the diversity of community structure, and a dominance of tolerant species.

"A reduction in community diversity is often associated with environmental perturbation. The identity of the cause of the perturbation may have to be sought by the application of other methods"(Hellawell, 1997).

The inclusion of a biological element in any monitoring scheme is worthwhile and necessary. While chemical monitoring is a crucial part of lake monitoring work, it only presents a short term view of the state of lake (Hellawell, 1997). Much of the chemistry of a lake is highly variable, and is affected by rapidly changing factors such as the weather in the days leading up to the sampling date (particularly rainfall) or the agricultural activities carried out in the catchment. As result of this variability (often seasonal), samples need to be taken very regularly in order to get a realistic view of the

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state of the lake from purely chemical monitoring. It makes sense, therefore, to include a biological element in a monitoring scheme, the community of which is a result of physicochemical conditions over a relatively long period of time, and how these conditions have shaped the lakes habitat and food webs.

Using the structure of the chydorid community and the relative dominance of particular species as indicators, rather than the presence or absence of particular species seems to give a better picture of the ecological quality of the lake (Hofman, 1987). Although some chydorid species have very particular niches with regard to physicochemical variables, many of the species are found over a broad range of lakes. In this study, the crucial factor was whether one species was dominating the community, and what affect this had on the species diversity and richness. While some conclusions can be drawn from simple presence or absence schemes and the distribution of the species, a lot more information about the extent of environmental disturbance or stress can be gained by studying the community structure of the chydorid populations, and the dominance of certain species over others. The question is whether the ecological quality of the lake can be reliably inferred from the chydorid community? From the results in this study, it seems that this is very possible. As the chydorids are a littoral family, they do seem to be sensitive to changes in the littoral zone, which is where the first impacts of most environmental problems are likely to become apparent. For example, regular monitoring of openwater concentration of toal phosphorus and phytoplankton in Lough Conn, one of the western Irish Lakes, failed to detect any nutrient enrichment, even though shoreline algal accumulations suggested eutrophication (McGarrigle et al., 1993). The role of the littoral zone is important to the natural processes in a lake, and any impacts which cause a change in this zone is likely to have serious implications for the lake as a whole. It makes sense, therefore, to include a group of animals from the littoral zone in any monitoring scheme, especially if it has

been shown that they are likely to reflect possible environmental impacts, such as eutrophication and acidification, the two primary problems affecting Irish lakes. While this study has shown that over a broad range of lakes, the chydorids can be used to identify certain characteristics of lakes, it is envisaged that the trends noted between different lakes could be applied to monitor changes *within* a lake, from either the present day, or from a baseline determined using palaeoliminology.

Chapter 3.

The spatial distribution of chydorids in

two different lakes.

3.1 Introduction

If chydorids are to be used as indicators of ecological quality, and the results from Chapter 2 suggest that there is the potential for this, then several issues have to be addressed to ensure that results obtained are indicative of lake ecological quality rather than an artefact of the sampling site or method used in the survey.

3.1.1 Sampling methods

Many different methods have been employed to sample the littoral crustaceans. The difficulty of doing this in a quantitative manner has been cited as the reason why so little work has been done in this area (Brodersen, Dall & Linegaard, 1998; Harrison & Hildrew, 1998; Chengalath, 1982; Campbell *et al*, 1982). The most frequently used sampling methods include:

1. Sweep nets and kick sampling. This method is probably the most commonly used, as it is quick, cheap and effective. This method is insensitive to microhabitats, and the samples that are obtained usually have a large amount of detritus in them, which makes sorting a little more difficult. Some authors advocate the use of a grid over the mouth of the net to exclude large pieces of detritus (Duigan, 1992). A net sweep is known as a semi-quantitative method, in that the method itself is not quantitative, but if you repeat the method exactly (sweeping over the same distance for the same amount of time) at each sampling site, the samples can be compared statistically.

2. Pattern or funnel samplers. (Örnólfsdóttir, 1998; Whiteside & Williams, 1975). This is a method that is quite widely used to catch and monitor chydorids and works quite like the emergent insect traps. They have an upside down funnel connected to a jar where the animals are collected. These traps depend on the fact that some chydorid

species migrate vertically at night. Any animals that find themselves in the wide mouth of the funnel will travel upwards into the narrow mouth, and then fall into the glass jar at the top, from which they can not exit. This method is reported to sample microhabitats very effectively with a lot of replication, as traps can be laid with several funnels, over a very specific area. It is also considered to be reasonably quantitative, as it samples over an exact area (Wiliams & Whiteside, 1978). The samples are quick to sort, as there is no detritus. However, it is wholly reliant on the behaviour of the animals, and may produce a bias towards species, which have a strong tendency to migrate vertically,

3. Plastic bags or enclosures (Paterson, 1993; Daggett & Davis, 1974; Quade, 1969). These are often used to sample among plant stands. A whole plant is enclosed in either a bag or a perspex box (after Downing & Rigler 1984) (often using SCUBA) which ensures that any animals that are in direct association with the plant also get caught. This sampling method is particular to sampling in plant beds, and therefore does not give any information about the areas without plants, which is why it is usually used in conjunction with other sampling methods.

4. Perspex tubes (Irvine, Moss & Balls, 1989; Pennak,1962). This is a method often used to sample shallow lakes or ponds, and also to sample among tall emergent macrophytes such as reeds and rushes. A perspex tube (1 metre in length) is dropped down from the surface either with a plant inside, or in the immediate vicinity of a plant and a bung is placed at the top to hold the water inside. The tube can then be removed and the water emptied into a bucket. A set amount of water can be collected in this manner, so that the method is quantitative.

A combination of all these sampling methods would undoubtedly give a very comprehensive view of the chydorid community in a lake. However, it would be time consuming, both in terms of fieldwork and sample sorting. Therefore, an important consideration when doing littoral surveys is which sampling method gives the most comprehensive picture of the community in question, while still being efficient and reasonably quantitative.

3.1.2 Heterogeneity in chydorid communities

The preference of many chydorid species for specific habitats in the littoral zone is well documented (Table 3.1) (Duigan & Kovach, 1994; Robertson, 1990; Chengalath, 1982; Campbell, Clarke & Kosinski, 1982; Quade, 1969; Smirnov, 1963; Smirnov, 1962; Crisp & Heal, 1958; Smyly, 1958). A survey of Irish chydorids found that 20 of the 32 recorded taxa had significant preferences for particular substrata (Duigan, 1992). It is generally considered that vegetated areas have the highest species richness and diversity (Rundle & Ormerod, 1991; Rasmussen, 1988; Lemly & Dimmick, 1982; Quade, 1969; Smirnov, 1963; Smyly, 1952). A decrease in chydorid diversity as a result of macrophyte loss and concurrent phytoplankton increase has been attributed to the affects of eutrophication (Stansfield et al, 1989, Whiteside, 1970) and low species diversity in lakes with poorly vegetated littoral zones as a result of impoundment has also been found (Smirnov, 1963). However, the fact that vegetated areas often have high diversity of chydorids may lead to non-vegetated areas being ignored in some surveys, which could mean that certain species are not detected (Chengalath, 1982). As well as having a preference for vegetated habitats, some species also seem to have a preference for a particular type or shape of macrophyte (Table 3.2). Microcrustaceans may even avoid habitats on the basis of growth form, or chemicals

that are released by plants (Smiley & Tessier, 1998). Many authors have shown that specific assemblages of chydorids are found in particular habitats (Duigan & Kovach, 1991; Robertson, 1990; Chengalath, 1982; Smirnov, 1963), and in some cases it is the abundance of a particular substratum that will determine species assemblages in a waterbody, rather than physicochemical variables (Quade, 1969). While it seems likely that chydorid species will distribute themselves according to preferred substratum, the degree to which they do so may differ in varying lake types. The distance between suitable habitats is important in determining whether a species will inhabit it or not (Smiley & Tessier, 1998). Large deep lakes are likely to have a more heterogeneous littoral zone than a smaller shallow lake and this may have implications for the movement of chydorids around the lake, and hence their segregation between habitats. High diversity of invertebrates in the littoral zone has been linked to the high level of heterogeneity of the substrata (Brodersen *et al*, 1998) and it may be that the same is true of chydorid communites.

Table 3.1. Known preferences of chydorid species for certain substrates.

Species	Habitat preference	Source
Alona affinis	Non vegetated substrates	Robertson, 1990; Smirnov, 1963
Alonopsis elongata	Rocky/sandy	Chengalath, 1982; Smyly, 1958
Chydorus piger	Rocky/sandy	Chengalath, 1982; Duigan & Kovach, 1994
Chydorus sphaericus	Vegetation	Crisp & Heal, 1958; Smyly 1958
Disparalona rostrata	Non vegetated substrates	Smirnov, 1963; Robertson 1990
Eurycercus lamellatus	Vegetation	Duigan & Kovach, 1994; Smirnov, 1962;
Graptoleberis testudinaria	Vegetation	Duigan & Kovach, 1994; Quade, 1969
Leydigia leydigi	Mud	Chengalath, 1982; Whiteside & Williams, 1978
Monospilus dispar	Sand	Chengalath, 1982; Smirnov, 1963
Pleuroxus aduncus	Vegetation	Chengalath, 1982
Pleuroxus truncatus	Vegetation	Smirnov, 1963; Smyly, 1958
Rhynchotalona falcata	Rocky/sandy	Chengalath, 1982

Table 3.2. Preferences for some chydorid species for various vegetation.

Species	Type of vegetation	Source
Eurycercus lamellatus	Narrow leaves	Duigan & Kovach, 1994
Graptoleberis testudinaria	Broad leaves	Duigan & Kovach, 1994; Quade, 1969
Alona rustica	Bryophytes	Duigan & Kovach, 1994
Alona costata	Floating leaves	Quade 1969
Acroperus harpae	Fine leaves	Quade 1969; Smirnov, 1963

Very little work has been done on how far down the littoral zone chydorid communities persist, although they are thought to have an irregular vertical distribution (Smirnov, 1974). Pelagic zooplankton is known to have very distinct patterns of vertical distribution (Smiley & Tessier, 1998), and phytophilous invertebrates in general have been found to be negatively related to depth (Cyr & Downing, 1988) but the distribution of littoral crustaceans with depth is relatively unknown. Factors which may determine the vertical distribution of animals include resource segregation and predator distribution as well as oxygen, light and temperature changes with depth (Paterson, 1993). The slope of the littoral zone has a large impact on the amount of biomass that can be supported (Rasmussen, 1988), because the rate at which food will pass from the littoral zone into the profundal zone will increase as the slope becomes steeper. Light attenuation, the growth of macrophytes and the movement of sediments and stones will also be affected by the slope of the littoral zone.

Some Russian studies (cited in Smirnov, 1974) have shown that different species have varying responses to depth: *Alonella excisa* and *Alona affinis* stay close to the bottom of the littoral zone, while *Pleuroxus truncatus* is more usually caught at the surface and the density of *Camptocercus rectirostris* and *Oxyurella tenuicaudis* on plants increases with depth. It seems that chydorids can withstand the pressure associated with great depth as some species such as *Eurycercus lamellatus*,

Camptocercus rectirostris and *Alona affinis* have been found at 150 metres (Smirnov, 1974) and *Monospilus dispar* was found at 24 metres by W.J.P. Smyly (Fryer, 1968). However, it is not stated whether these individuals were alive or dead. One study (Paterson, 1993) found that microcrustacean communites did vary with depth, and in particular, the community in the hypolimnion was different from the ones dominanting the epilimnion. *Chydorus brevilabris* showed a preference for water deeper than 4 metres, while higher numbers of *Alona rustica*, *Chydorus linguilabris* and *Alona affinis* were found in less than 4 metres. This was attributed to the lack of macrophytes in the hypolimnion, in comparison to the epilimnion.

The objects of this part of the study were therefore two fold:

• To test the reliability and usefulness of several different sampling methods that are commonly used in littoral crustacean studies and compare them with the method used for the first part of this study (Chapter 2). In particular, I wanted to test whether the one off sampling done with a sweep net gave a reliable indication of the chydorid community as a whole.

• To examine the heterogeneity of the chydorid community in a lake, with respect to species distribution among several different microhabitats and also down the littoral zone with depth.

3.2 Methods

3.2.1 Study Sites

Two quite different lakes were chosen for this study, in order to make a comparison between distinct lake types (both chemically and physically different) as well as comparisons within a lake. The two lakes were Lough Inchiquin, Co. Clare, and Lough Maumwee, Co. Galway both of which were observed to have high chydorid diversity over the two years of intensive sampling (17 species in Lough Inchiquin, 16 in Lough Maumwee). Lough Inchiquin has a volume of about 12 million m^3, a max depth of 29 m and a mean depth of 10.2 m. In contrast, Lough Maumwee has a volume of 535,000 m^3, a max. depth of 7.9 m and a mean depth of only 2 m. The littoral zone of Lough Inchiquin is steep and has a distinct slope. In contrast, the littoral zone in Lough Maumwee has a very gentle slope and the lake as a whole is shallow with plants growing over a large portion of the bottom of the lake. As such, there is no profundal zone in the lake. The slope of the littoral zones (in the vicinity of the sampling area) was calculated as 14.5° for Lough Inchiquin and 5.8° for Lough Maumwee (see section 3.2.2), so the slope of the littoral region in Lough Inchiquin was almost three times that of Lough Maumwee, a fact which will probably have an effect on the habitat structure of the region (Rasmussen, 1988). The two lakes also differ chemically. Lough Inchiquin lies within the predominantly carboniferous limestone of the Fergus catchment, and Lough Maumwee, located in the Corrib catchment, lies on granite and quartzite. In 1996-97, Lough Inchiquin had an median pH value of 8.35 and Lough Maumwee had an median pH value of 6.60. Lough Inchiquin is classified as mesotrophic and Lough Maumwee as oligotrophic according to the OECD (1982) (mean levels of total phosphorus and chlorophyll a).

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The differing physical and chemical parameters of the lake means that the chydorid species assemblages are also quite different. The two lakes have 9 species in common, with other species typical of the different lake types (Table 3.3).

Table 3.3. Species of chydorids recorded in Loughs Lough Inchiquin and Lough Maumwee, July 1996 – September 1997.

Lough Inchiquin	Lough Maumwee
Acroperus harpae	*Acroperus harpae*
Alona affinis	*Alona affinis*
Alona costata	*Alona costata*
Alona quadrangularis	*Alona guttata*
Alona rectangula	*Alona intermedia*
Alonella excisa	*Alona rustica*
Alonella exigua	*Alonella excisa*
Chydorus sphaericus	*Alonella exigua*
Disparalona rostrata	*Alonella nana*
Eurycercus lamellatus	*Alonopsis elongata*
Graptoleberis testudinaria	*Chydorus piger*
Monospilus dispar	*Chydorus sphaericus*
Pleuroxus laevis	*Eurycercus lamellatus*
Pleuroxus trigonellus	*Monospilus dispar*
Pleuroxus truncatus	*Pleuroxus trigonellus*
Pleuroxus uncinatus	*Rhynchotalona falcata*
Pseudochydorus globosus	

3.2.2 Sampling methods

One sampling trip was made to each lake in September 1998, and a variety of habitats was sampled using four different methods (Table 3.4 and 3.5).

Sweep net: Chydorids were sampled by the kick sampling method using a standard 100 μm net which was swept over approximately 1 metre of the lake bed for 12 seconds. The samples were taken from the littoral zone of each lake in a depth of approximately 30 cm, although in Lough Inchiquin, some of the samples were taken slightly deeper, as the lake water level was high. This is the same sampling method that was used in the intensive sampling of the 29 lakes (see Chapter 2), except that the mesh was slightly finer

Perspex tube: This was used to sample in emergent vegetation. A one metre long perspex tube (diameter 5.5cm, volume 2276cm^2) was dropped into the water as quickly as possible and a bung put in place at the top. The tube was then withdrawn and the water inside put in a bucket. 10 litres of water were collected for each sample.

SCUBA with plastic bags. Using SCUBA equipment, submerged plants were enclosed with a plastic bag, with the minimum possible disturbance. The bag was sealed underwater before cutting the plant below the opening of the bag.

Funnel Traps. A trap consisted of 6 funnels (10cm long, with the wide end measuring 7cm in diameter and the narrow end 0.5cm) which were placed upside down in a mesh basket. A glass jar was fixed upside down to the narrow end of the funnel. The trap was then lowered to the bottom (with the wide mouth of the funnels facing down) and left overnight. Funnel traps were laid at 6.00pm and lifted at 11.00am the next morning.

Table 3.4. Sampling Methods used to sample Lough Inchiquin, September, 1998.

Habitat/substrata sampled	Sampling method	Replicates
Submerged Plants (various species)	SCUBA with plastic bags	10
Emergent Plants (*Scirpus* sp)	Perspex tube, 10 litres	3
Sand	Funnel trap	2
Sand	Sweep net	2
Sand with leaves and detritus	Funnel trap	2
Sand with leaves and detritus	Sweep net	2
Rocks covered in Moss	Funnel trap	2
Rocks covered in Moss	Sweep net	2
Rocks, no moss	Funnel trap	2
Rocks, no moss	Sweep net	2
Base of *Scirpus*	Funnel trap	2
Fine weed and *Juncus* sp.	Funnel trap	2
Vertical transect down littoral zone	SCUBA, small sweep net	2

Table 3.5. Sampling Methods used to sample Lough Maumwee, September, 1998.

Habitat/substrata sampled	Sampling method	Replicates
Submerged Plants (various species)	SCUBA with plastic bags	10
Emergent Plants (*Scirpus* sp)	Perspex tube, 10 litres	5
Bare slabs of rock	Funnel trap	2
Bare slabs of rock	Sweep net	2
Base of *Scirpus*	Funnel trap	2
Base of *Scirpus*	Sweep net	2
Small pebbles and submerged plants	Funnel trap	2
Small pebbles and submerged plants	Sweep net	2
Sand, river delta	Funnel trap	2
Sand, river delta	Sweep net	2
Plant detritus, filamentous algae	Funnel trap	2
Plant detritus, filamentous algae	Sweep net	2
Small bare rocks	Funnel trap	2
Small bare rocks	Sweep net	2
Vertical transect down littoral zone	SCUBA, small sweep net	2

3.2.3 Methods used to study vertical distribution of chydorids.

A plastic box with solid sides and the bottom cut out was used to form a quadrat (32cm x 42cm x 20cm), which was placed on the bottom of the lake. A small sweep net (mesh size 172 µm) was used to sweep the inside of the quadrat, and was then sealed inside a plastic bag. This was rinsed at the surface. Any plants within the quadrat were enclosed in plastic bags. This method was used to sample along a transect in the littoral zone. A leaded line 20 metres long was used as a guide, and it was laid from the shoreline out, perpendicular to the shore. The end of it was marked with a buoy. Samples were taken from the deepest end first, and then at every 0.5 metres depth (measured with an Aladin Pro dive computer) until the shoreline was reached. In Lough Inchiquin, samples were taken from 5 metres to 0.5 metres while in Lough Maumwee, the maximum depth found while doing the transects was 2 metres. As the transect line was 20 metres long, the slopes of the littoral zones was calculated as 14.5° for Lough Inchiquin and 5.8° for Lough Maumwee. Light attenuation was also measured (at the buoy marking the end of the transect) using an Li – Cor light meter. The net downward attenuation coefficient (k) of light was calculated by using the slope of the line generated when log (light units) was plotted against depth. The euphotic depth, Z_{eu}, (the depth at which the energy produced by photosynthesis equals the energy used up by respiration, which is where about 1% of surface light remains) was calculated using the equation, $1/k$ ($\log_e 100$) or $4.6/k$.

All samples which were collected were passed through a 73 µm sieve, and then the remainder of the sample was preserved in 70%alcohol. When samples contained plants, the plants were also preserved unless they did not fit in the sample pot, in which case they were washed thoroughly in a sieve, and any material that was caught was

added to the sample. In the laboratory, chydorids were counted and identified as described in Chapter 2.

3.2.4 Statistical analysis.

Chesson's forage ratio (Chesson, 1978) is used to measure the selectivity of a predator for prey items. In this study, it was applied to the data to see which species were positively or negatively selected in the funnel traps. The forage ratio (FR) = (r_i/p_i) / $(\Sigma(r_i/p_i))$ where r_i is the proportional abundance of species i in the funnel traps and p_i is the proportional abundance of species i in the sweep nets. A maximum positive selection for funnel traps (i.e. the species was only caught in funnel traps) would have a value of 1. Neutral selectivity is calculated as the reciprocal of the number of species, and any species with an FR below this neutral selectivity value is negatively selected by the funnel traps.

Multivariate analysis was carried out on the samples taken from each lake using similar methods to those described in Chapter 2. Analysis of the chydorid community found in different habitats was carried out using Multidimensional Scaling (MDS) and cluster analysis in SPSS. Proportional abundances of chydorid species were calculated and a dissimilarity matrix was generated using the euclidean distances between samples. The cluster analysis used was an agglomerative hierarchical cluster analysis using between group average linkage. The multidimensional scaling was conducted in 2 dimensions and plotted using the graphics package, *Cricket Graph*.

When analysing the data collected along transects down the littoral zone, Spearman rank correlation coefficients were calculated for the relationship between

abundance, species richness and Shannon diversity index of the chydorid community with light, depth, and the presence of plants.

3.3 Results

3.3.1 Results of different sampling methods

Species diversity, richness and abundance of chydorids were calculated for each sampling method (Table 3.6). The numbers of animals caught in individual funnels in the funnel traps were very small (often 1 or 2 animals), so the contents from the 6 funnels in a trap were added together and the results were calculated from each trap. The data from the samples taken down the littoral zone along a transect are presented in section 3.3.5.

Table 3.6. Mean (±standard error) Chydorid abundance, species richness, and diversity (Shannon diversity Index) calculated for each sampling method.

Lake	Sampling Method	n	Abundance	Species richness	Species Diversity
Inchiquin	Funnel traps	12	40.4±7.34	8.3±0.5	1.69±0.06
Inchiquin	Plastic bags	10	44±17.9	3.2±0.7	0.85±0.18
Inchiquin	Sweep nets	8	319±183	5.8±0.9	1.05±0.11
Inchiquin	Tubes	3	3±2.5	1.6±1.2	0.36±0.35
Maumwee	Funnel traps	12	45.5±12.6	6.5±0.4	1.4±0.08
Maumwee	Plastic bags	10	25±3.9	3.5±0.4	0.97±0.14
Maumwee	Sweep nets	12	129±45.5	5.2±0.4	1.4±0.07
Maumwee	Tubes	5	73±23.5	4.6±0.8	1.21±0.13

The sampling method used proved to be a significant source of variation in abundance, species diversity and species richness of chydorids caught in each lake (ANOVA, $p \leq 0.05$, d.f. = 3, F – ratio > 10 for Inchiquin, >3.9 for Maumwee) (Figures 3.1 – 3.3). In both lakes, sweep nets caught significantly more animals (ANOVA, LSD post-hoc tests, $p < 0.05$) than the three other sampling methods. Abundances of chydorids caught by each sampling method can not be compared quanititatively,

however, as the methods are not comparable. However, the more animals that are caught, the more data can be obtained, so the method that catches the most animals does have this advantage over other less successful methods. The funnel traps provided the highest species richness and species diversity of chydorids from both lakes (ANOVA, LSD post-hoc tests, $p < 0.05$). A species list for each sampling method as well as the species list collated over the two years intensive sampling is shown in Tables 3.7 and 3.8.
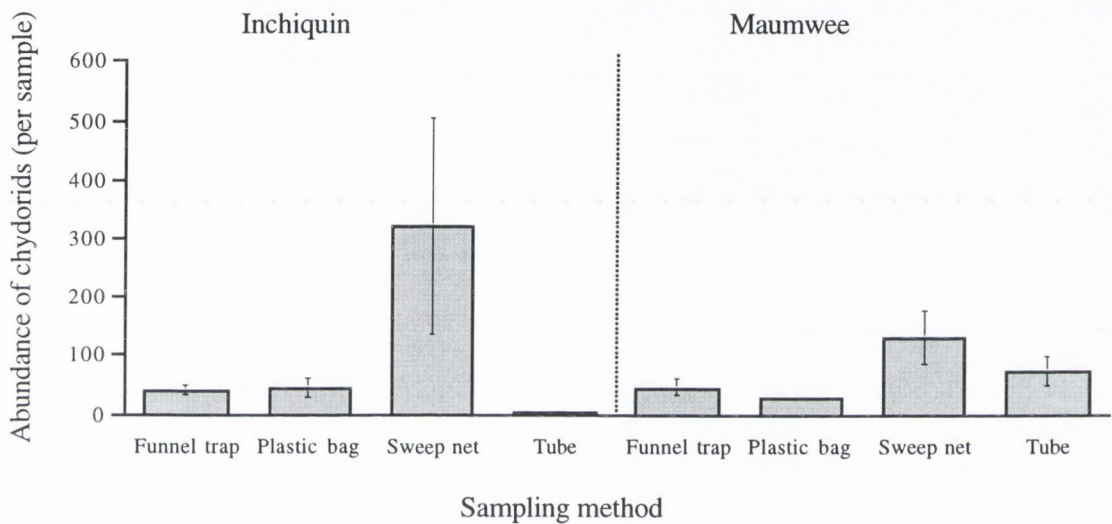
Figure 3.1. Mean abundances (± s.e.) of chydorids caught in Loughs Inchiquin and Maumwee using various sampling methods. See Table 3.6 for values of n.
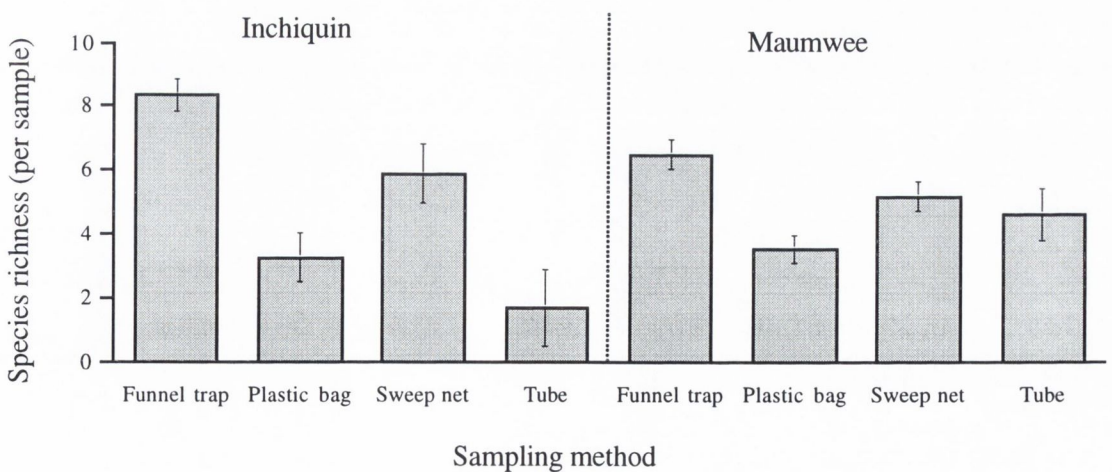
Figure 3.2. Mean species richness (± s.e.) of chydorids caught in Loughs Inchiquin and Maumwee using various sampling methods.

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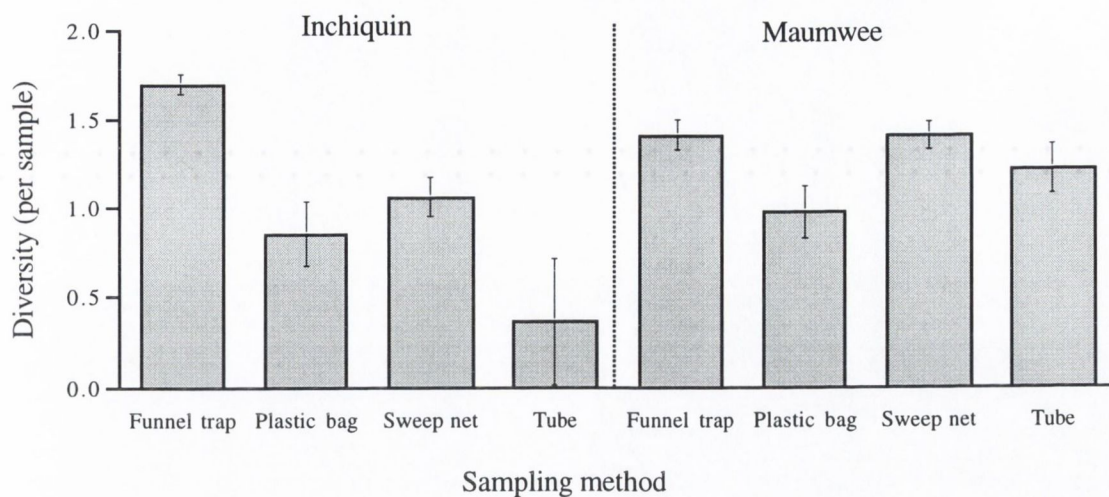
Figure 3.3. Mean shannon diversity (± Standard error) of chydorids caught in Loughs Inchiquin and Maumwee using various sampling methods.

Table 3.7. Species recorded from the 14 months intensive sampling, and from each sampling method in Lough Inchiquin.

Species	14 months sampling	Sweep samples	Funnel traps	Plastic bags (submerged)	Tubes (emergent)
Acroperus harpae	•	•	•	•	
Alona affinis	•	•	•	•	•
Alona costata	•	•	•	•	•
Alona quadrangularis	•				
Alona rectangula	•		•		
Alonella excisa	•			•	
Alonella exigua	•	•	•	•	
Alonella nana			•		
Anchistropus emarginatus		•	•		
Chydorus piger		•			
Chydorus sphaericus	•	•	•	•	
Disparalona rostrata	•				
Eurycercus lamellatus	•	•	•	•	
Graptoleberis testudinaria	•			•	
Monospilus dispar	•				•
Pleuroxus aduncus		•	•	•	
Pleuroxus laevis	•	•	•	•	
Pleuroxus trigonellus	•				
Pleuroxus truncatus	•	•	•		•
Pleuroxus uncinatus	•		•		
Pseudochydorus globosus	•	•	•	•	
Total no. of species	17	12	14	11	4

Table 3.8. Species recorded from the 14 months intensive sampling, and from each sampling method in Lough Maumwee.

Species	14 months sampling	Sweep samples	Funnel traps	Plastic bags (submerged)	Tubes (emergent)
Acroperus harpae	•	•	•	•	•
Alona affinis	•	•	•	•	•
Alona costata	•		•		
Alona guttata	•				
Alona intermedia	•				
Alona rectangula		•	•	•	•
Alona rustica	•	•	•		•
Alonella excisa	•	•	•	•	•
Alonella exigua	•				
Alonella nana	•				
Alonopsis elongata	•	•	•	•	•
Chydorus piger	•	•	•	•	•
Chydorus sphaericus	•	•	•	•	•
Eurycercus lamellatus	•	•	•	•	•
Monospilus dispar	•	•	•		
Pleuroxus trigonellus	•				
Rhynchotalona falcata	•	•	•		
Total	16	11	12	8	9

In both lakes, the number of species identified from the one sampling period in September 1998 was less than the cumulative samples taken over two years. This is to be expected as all chydorids exhibit some degree of seasonality, and it may be that the species not caught in September 1998 were not present at that time of the year.

3.3.2 Comparison of sweep samples and funnel traps

The sweep samples and funnel samples were taken in exactly the same area so that a comparison could be made between their success over specific habitats. Although the total species richness were quite similar between the two sampling methods for both lakes, marked differences were noticed when separate habitats were studied. Habitats sampled in each lake using the two methods are given in Table 3.9.

Table 3.9. Microhabitats samples in Lough Inchiquin and Lough Maumwee using sweep net and funnel trap method in September 1998.

Lough Inchiquin	Lough Maumwee
Rocks covered in moss	Bare slabs of rock
Rocks, no moss	Base of *Scirpus* sp.
Clean sand (no detritus)	Small pebbles and plants (probably *Isoetes* sp.)
Sand and detritus under trees	Sand, river delta
	Plant detritus with lots of algae
	Small bare rocks

In Lough Inchiquin, the differences in chydorid abundance and species diversity between funnel trap samples and sweep samples were significantly different (2 sampled t-test, $p \leq 0.05$) with higher abundances caught in the sweep samples particularly in the samples taken over rock (Figure 3.4). However, the species diversity of chydorids was higher in the funnel trap samples than in the sweep samples (Figure 3.5). In Lough Maumwee, there was a significant difference between the species richness and abundances of chydorids caught with the different sampling methods (2-sampled t-test, $p \leq 0.05$). The funnels had lower abundances (Figure 3.6) but higher species richness (Figure 3.7). The proportion of each species caught with the different sampling method

also differs, which signifies a bias by one or other methods for some species (Figure 3.8 and 3.9).
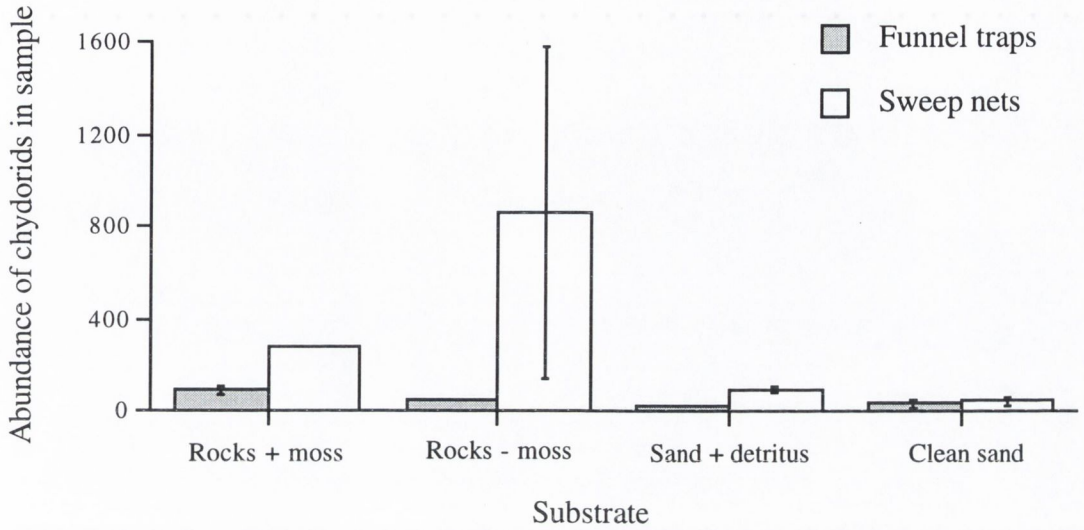
Figure 3.4. Mean abundances (± s.e.) of chydorids found in 4 different habitats in Lough Inchiquin using two sampling methods, funnel traps and sweep nets. $n=2$ for each sampling method.
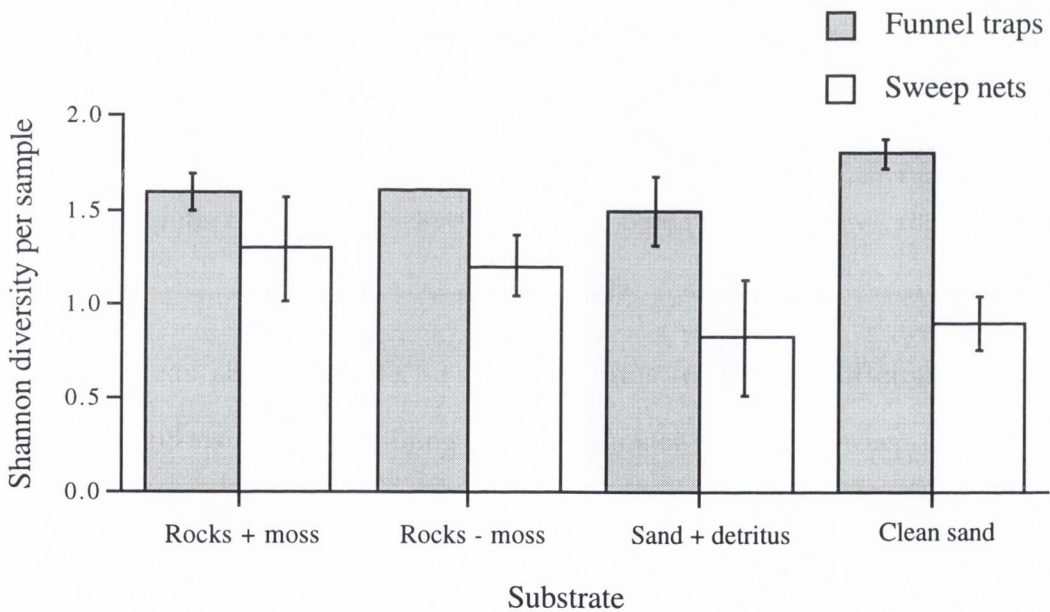
Figure 3.5. Mean species diversity (Shannon Index) (± s.e.) of chydorids found in 4 different habitats in Lough Inchiquin using two sampling methods, funnel traps and sweep nets. $n=2$ for each sampling method.
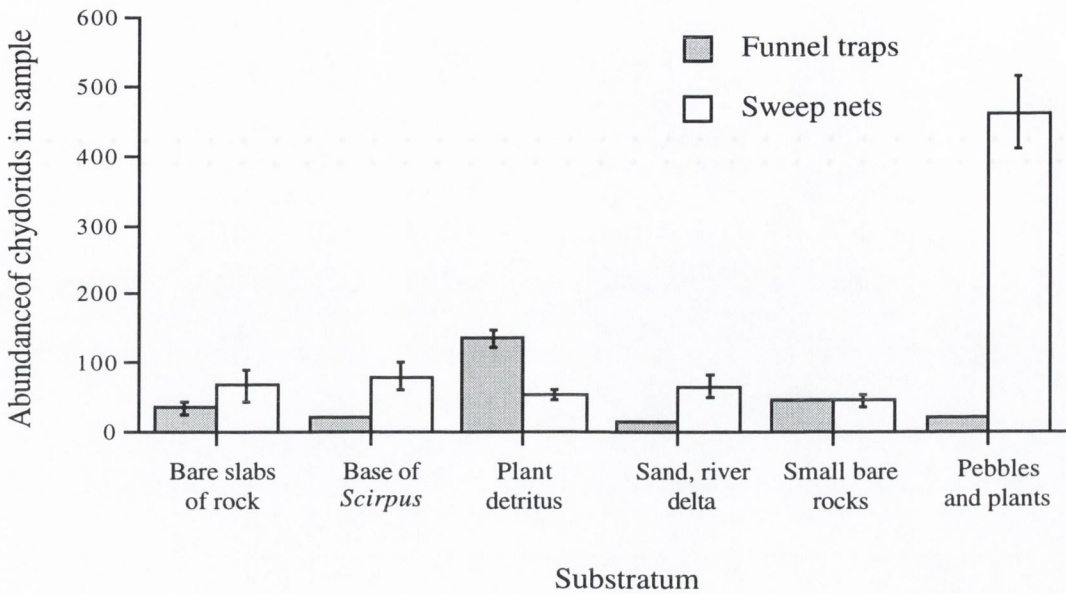
Figure 3.6. Mean abundances of chydorids (± s.e.) found in 6 different habitats in Lough Maumwee using two sampling methods, funnel traps and sweep nets. *n*=2 for each sampling method.
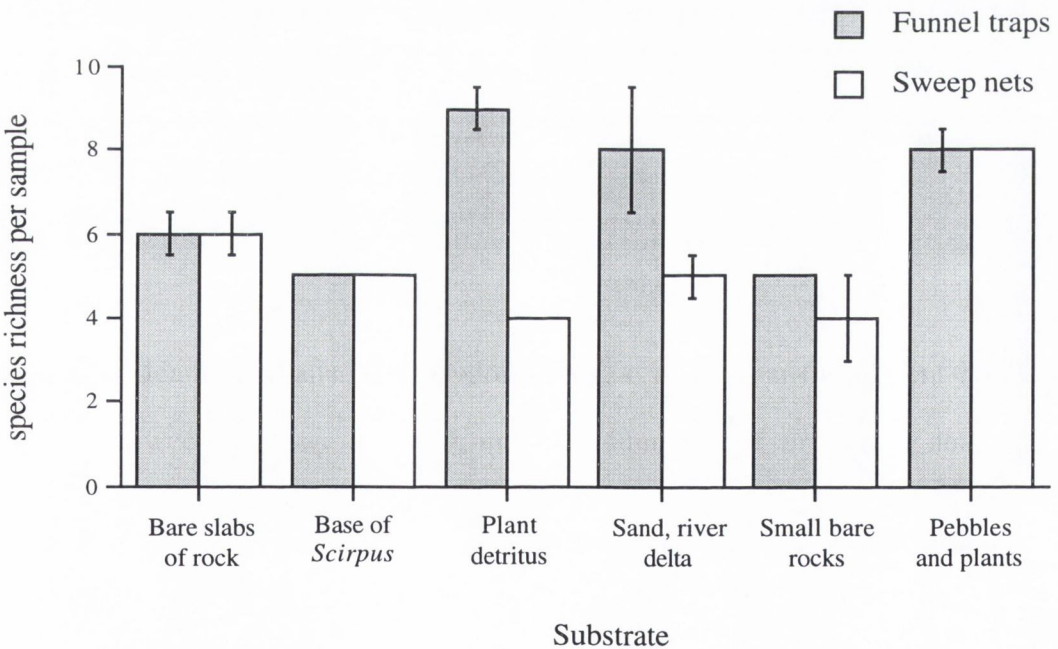
Figure 3.7. Mean species richness (± s.e.) of chydorids found in 6 different habitats in Lough Maumwee using two sampling methods, funnel traps and sweep nets. *n*=2 for each sampling method.
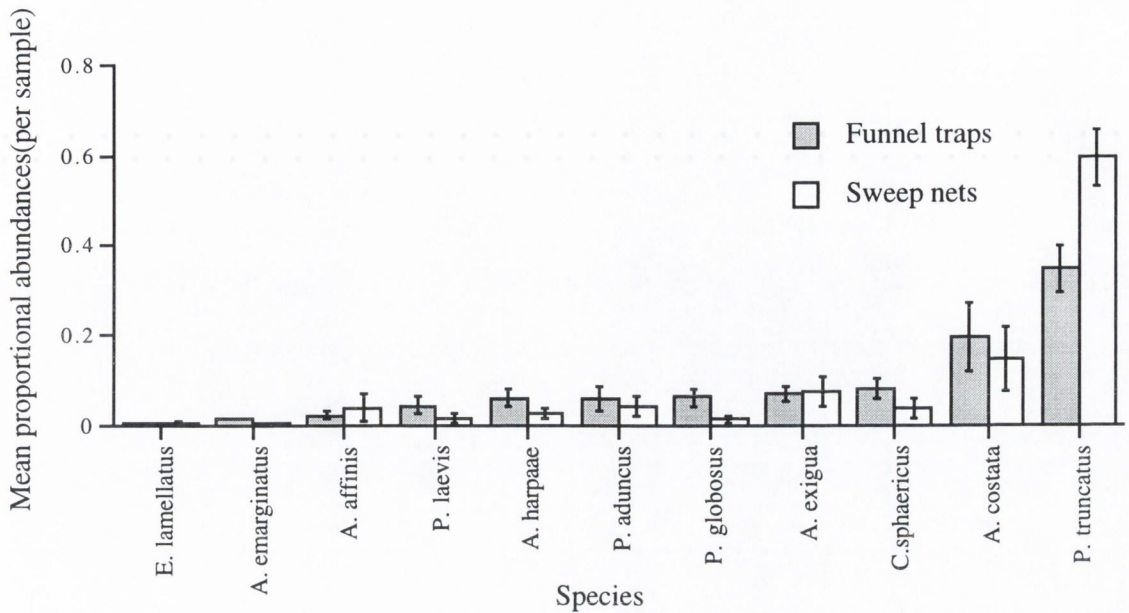
Figure 3.8. Mean proportional abundances (± s.e.) of chydorid species found in Lough Inchiquin, using funnel traps and sweep nets. $n = 8$ for each sampling method.
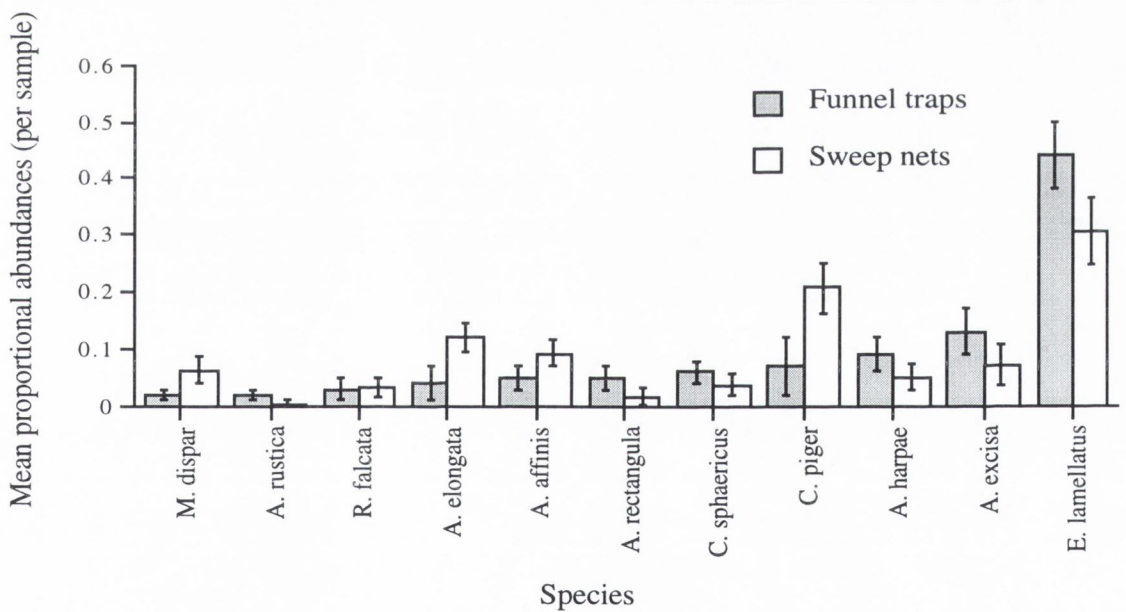
Figure 3.9. Mean proportional abundances (± standard error) of chydorid species found in Lough Maumwee, using funnel traps and sweep nets. $n = 12$ for each sampling method.

There are obvious differences between the proportions of each species caught by the two methods, although a 2 sample t-test showed that the differences were only

significant in Lough Inchiquin ($p \leq 0.05$, 10 d.f.). Chesson's forage ratio was used to see which species were positively or negatively selecting for the funnel traps. Neutral selectivity is indicated by the dotted line in Figures 3.10 and 3.11. Values above the line indicate positive selection by funnel traps for that species and values below the line imply negative selection by funnel traps.
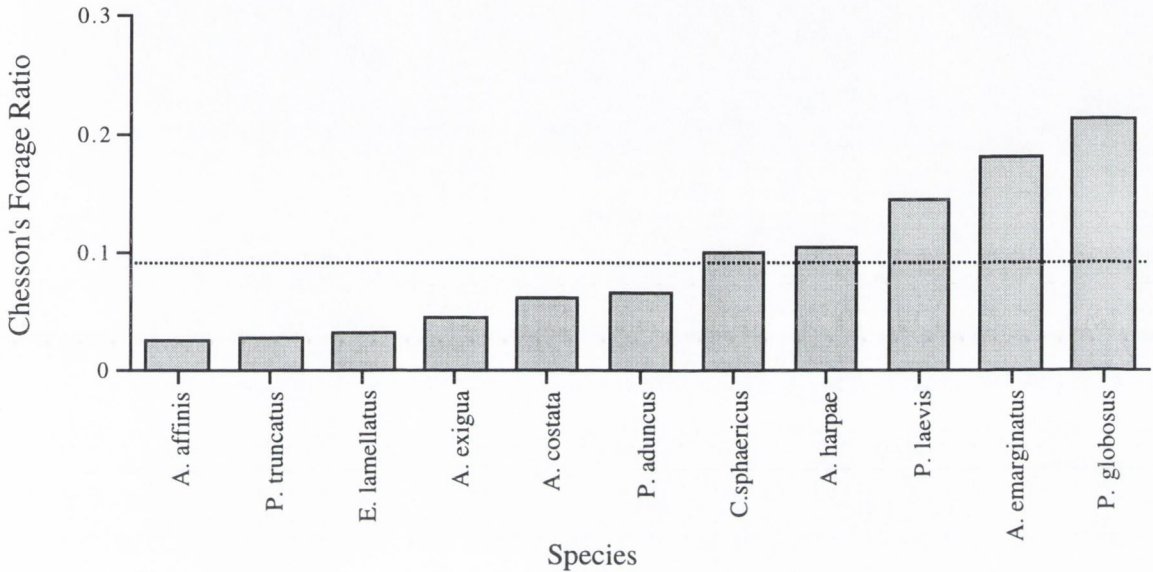
Figure 3.10. Chesson's forage ratio calculated from proportional abundances of chydorids caught in funnel traps or sweep nets in Lough Inchiquin.
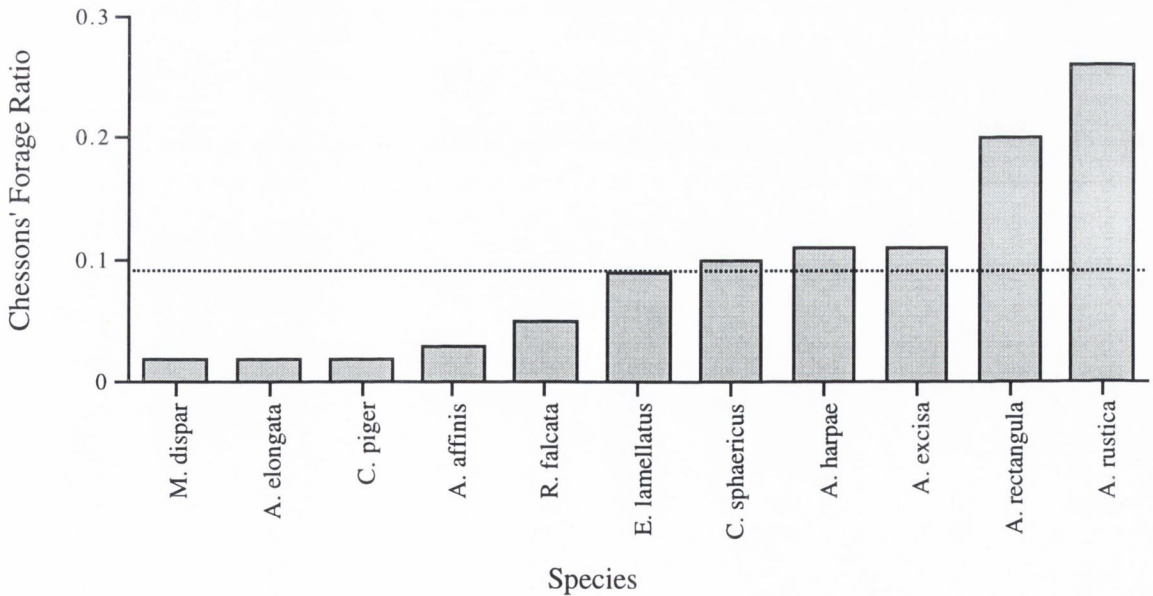
Figure 3.11. Chesson's forage ratio calculated from proportional abundances of chydorids caught in funnel traps or sweep nets in Lough Maumwee.

Some species showed a very definite habit of crawling up vertical surfaces, and hence the funnel traps misrepresent their actual proportion in the community. In Lough Inchiquin, the funnel traps caught a much higher abundance of *Pseudochydorus globosus, Anchistropus emarginatus* and *Pleuroxus laevis* then is present in the area (it is assumed that the sweep nets gives a good estimation of the community composition, as it does not depend on any behavioural aspect of the species), indicating that these species are good climbers. In particular, *P. globosus* showed the highest positive selection by funnel traps, with a Chesson's ratio of 0.214. The most negatively selected species were *Pleuroxus truncatus, Eurycercus lamellatus* and *Alona affinis* which have high proportions in samples taken with other sampling methods. In Lough Maumwee, *Alona rustica* and *Alona rectangula* were found in much higher abundances in the funnel traps, compared with species associated with a burrowing lifestyle (or at least a lifestyle close to the bottom) such as *Monospilus dispar, Alonopsis elongata* and *Chydorus piger* which were found to be negatively selected for by the funnel traps. Two species, *Chydorus sphaericus* and *Acroperus harpae* were found to be close to neutrally selected for by the funnel traps in both lakes (i.e., the funnel traps had no bias, either positive or negative for them). This implies that the behaviour of the species in both lakes is similar, even though the lakes are very different.

3.3.3 The spatial distribution of chydorid communities in different habitats

As the funnel traps in this study did not appear to provide reliable data on the proportions of each species in the sampling area, the analysis of spatial distribution was carried out using the sweep net samples (which came from exactly the same area as the funnel trap samples) and the samples taken from vegetated areas using either the perspex tube (emergent vegetation) or SCUBA and small plastic bags (submerged

vegetation). The aim of this part of the analysis was to assess the differences in chydorid communities both within the different vegetation sampled and between vegetated and non-vegetated habitats. While most of the sweep samples were taken in areas without plants, some areas did have small amounts of submerged vegetation such as clumps of *Isoetes lacustris* in Lough Maumwee.

In both lakes, the sweep samples provided the highest species richness and diversity of the three investigated sampling methods, and the emergent vegetation samples the lowest, with the samples taken from the submerged vegetation in the middle of the range (Table 3.6). The sweep samples also contained the largest number (abundance) of animals, although the methods are not comparable with respect to absolute numbers. This does not support the view from many authors that vegetated areas have the richest chydorid communities. However, a closer look at the specific habitats further assesses the heterogeneity of the areas sampled, as there was a lot of variation within the sampling methods used, depending on the habitat sampled.

Using multivariate analysis, all the data from both lakes were analysed together, in order to see whether the lake (and its associated physicochemical variables) was the main factor for determining the chydorid community. The two lakes had distinctly different communities, and were well separated from each other on the MDS plot (Figure 3.12). This was in agreement with the cluster analysis (Average Linkage between groups) which initially split the samples from the two lakes. This is to be expected as the lakes do have very different characteristics, but does concur with the conclusion from Chapter 2 that a lake can be characterised by its chydorid communities.
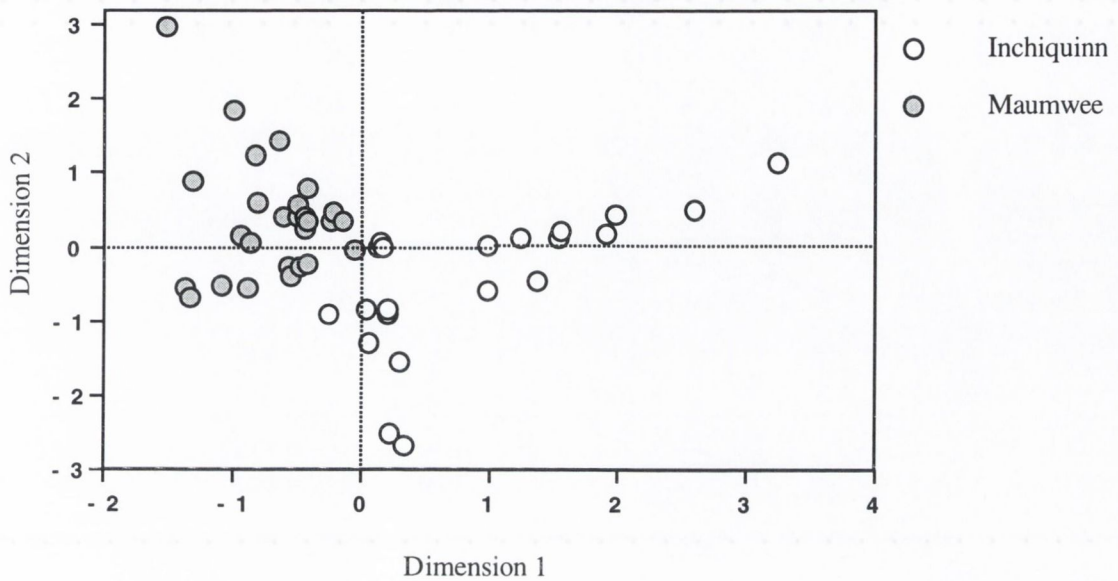
Figure 3.12. MDS plot of the samples taken from Lough Inchiquin and Lough Maumwee, September 1998. Stress = 0.2, R^2=0.85.

From the MDS plot, it can be seen that the samples from Lough Maumwee group together very closely on the left hand side of the ordination, but the samples from Lough Inchiquin are spread over the right hand side of the ordination. The majority of the samples on the right hand side of the graph (with x values >1) are the sweep net samples taken from Lough Inchiquin, while the samples taken from plant habitats are much more similar to the samples in Lough Maumwee, being grouped in the centre of the plot.

In order to assess the variability between sites with a lake, the lakes were analysed separately using multivariate analysis. Each sample was given a number so that it could be identified on the MDS plot (Table 3.10).

Table 3.10. Numbers used to identify the samples taken in Lough Inchiquin, for reference to MDS plots.

Sampling method	Substratum	I.D. Number
plastic bag + scuba	*Ceratophyllum*	1
	Scirpus	2
	Elodea + moss	3
	Elodea + moss	4
	Ceratophyllum	5
	Nuphar	6
	Moss	7
	Scirpus	8
	Potamogeton sp.	9
	Nuphar	10
Sweep net	rock covered in moss	11
	rock covered in moss	12
	rock (no moss)	13
	rock (no moss)	14
	sand (under boats)	15
	sand (under boats)	16
	sand (under trees with detritus)	17
	sand (under trees with detritus)	18
Tube	*Scirpus* (emergent)	19
	Scirpus (emergent)	20
	Scirpus (emergent)	21

An MDS plot of the Lough Inchiquin data produced an ordination with 3 well defined groups (Figure 3.13), which corresponded with the cluster analysis of the same data (Figure 3.14).
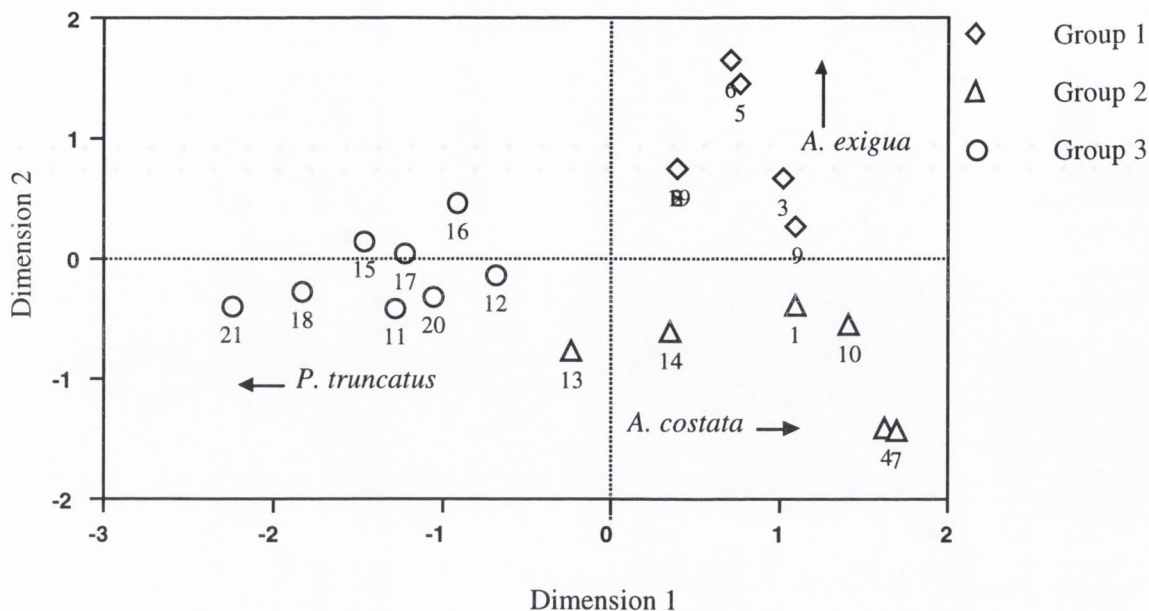
Figure 3.13. MDS plot of samples taken from Lough Inchiquin, using three sampling methods over a variety of substrates. Stress = 0.087, R^2=0.96. See Table 3.10 for identification of samples. The three groups refer to the cluster analysis in Figure 3.14. The arrows indicate increasing dominance by that species.

Group 1	Group 2	Group 3
8. Scirpus	13. Rock, no moss	18. Sand under trees
19. Scirpus (emergent)	14. Rock, no moss	21. Scirpus (emergent)
2. Scirpus	4. Elodea and moss	11. Rock covered in moss
3. Elodea and moss	7. Moss	20. Scirpus (emergent)
9. Potomegeton sp.	1. Ceratophyllum	15. Clean sand
5. Ceratophyllum	10. Nuphar	17. Sand under trees
6. Nuphar		12. Rock covered in moss
		16. Clean sand
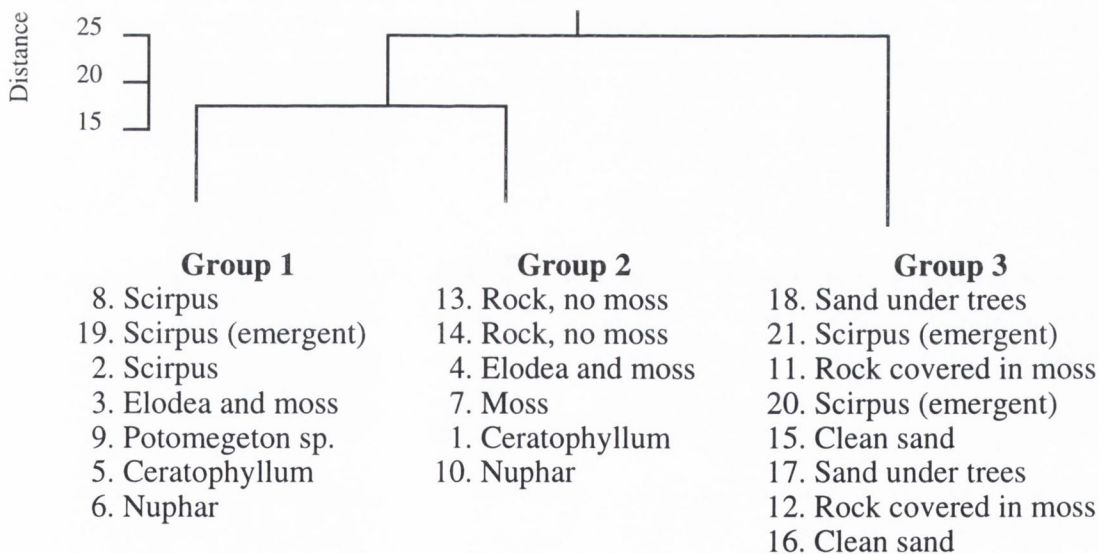
Figure 3.14. Cluster analysis of Lough Inchiquin samples, using Average Linkage (between groups).

The split between samples taken amongst plants and those taken with a sweep net is quite distinct in the MDS plot, with the majority of the plant samples being found on the right hand side of the y axis (Figure 3.13). The only exceptions to this were 2 samples taken from the *Scirpus* beds with the tube sampler (nos. 20 and 21) which had very low abundances, and therefore were not reliable. Three main chydorid species determined the position of the samples on the ordination plot; *Alonella exigua, Alona costata* and *Pleuroxus truncatus* (Figure 3.15). Group 1, which is situated in the top right hand corner of the ordination is composed entirely of samples taken in vegetated areas. The samples grouped together, 2, 19 and 8 had no chydorids in them, but the other four samples were dominated by *Alonella exigua,* with its dominance decreasing towards the centre of the plot. Group 2 is made up of 4 samples from vegetated areas (on the extreme right of the plot) and 2 taken from the benthic area of the littoral zone over a rocky substrate. The group as a whole has *Alona costata* as the dominant species. Group 1 and Group 2 are marked by the absence of *Pleuroxus truncatus*, except in the two sweep samples taken over the rocky substrate (13 and 14), which are ordinated towards the other side of the plot. All the samples in Group 3 are dominated by *Pleuroxus truncatus,* but towards the centre of the plot, the dominance of this species decrease and the proportional abundance of *Acroperus harpae* increases.
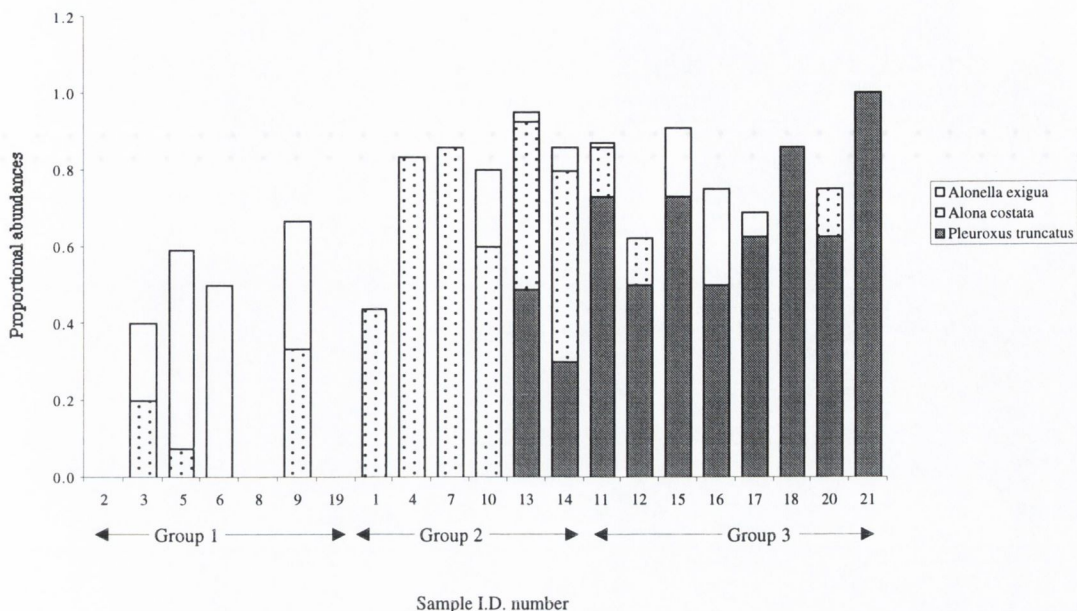
Figure 3.15. Proportional abundances of the three main species identified from the MDS plot in samples taken from Lough Inchiquin, September 1998, from various habitats. Sample identification number refers to Table 3.10. and the group number refers to Figure 3.14.

In Lough Inchiquin, there appeared to be a marked split between plant substrata and benthic substrata such as the sandy and rocky areas. There is also a small distinction between these two benthic substrata, with the sandy areas having lower diversity and abundances of chydorids, and an absence of *Alona costata*. A distinction can also be made at the microhabitat level, with the rocky areas being separated into those covered in moss (almost totally dominated by *Pleuroxus truncatus*) and those without a moss covering (less *P. truncatus* and more *Alona costata*). Two sweep samples were taken over each microhabitat, and these pairs of samples (11 &12, 13 & 14, 15& 16 and 17 & 18) were close together in the MDS plot, which implies that they do have distinctive chydorid communities. It would, however, be difficult to separate each pair from another pair taken in the same area over a different microhabitat, as they were nearly all dominated by *Pleuroxus truncatus*. For example, samples 15, 16 17 and 18 were taken

in the same area, but 15 and 16 were taken over clean sand while 17 and 18 had a lot of detritus in them as the site was overhung by trees. It might be expected that this detritus would influence the chydorid community quite a lot, but this was not found to be the case. Therefore it seems that when using sweep samples as a sampling method, the issue of which microhabitat is being sampled is not as important as recording the kind of substrata in general – i.e. sand or rock or plant. At the smaller level of microhabitat, distinct chydorid communities were hard to differentiate.

In terms of the similarity of these samples with the samples taken during the two years intensive sampling period (described in Chapter 2), the samples on the left hand side of the graph (Figure 3.13) were dominated by *Pleuroxus truncatus*, which was also the species that dominated samples taken in September 1996 and September 1997. When the samples taken in September 1998 over all the substrates are combined to produce an average proportional abundance of species they are most similar to the combined results from 14 months sampling in 1996 and 1997 rather than with either September 1996 or September 1997 (Figure 3.16). These two combined data sets have 7 of the 8 most abundant species in common and they were also found in similar proportions. In contrast, the samples taken in September 1996 and 1997 (over one habitat) have less diversity, and the proportion of species differ considerably from those found in samples taken in 1998 over lots of different substrates.
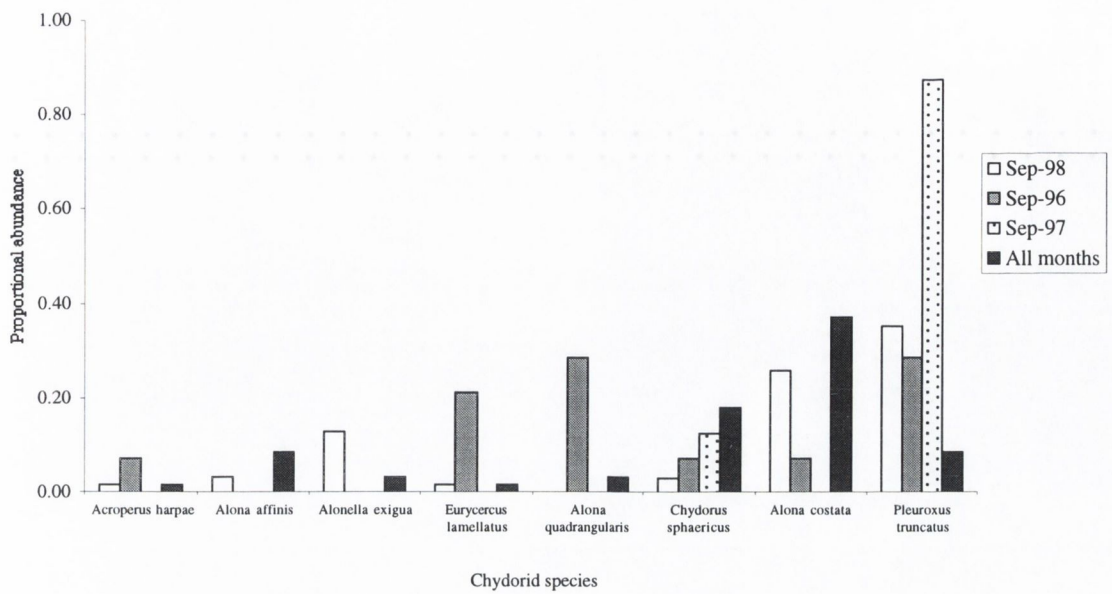
Figure 3.16. Proportional abundances of the common species found in Lough Inchiquin in September 1996, 1997 and 1998 (multiple substrates) and also for the average over the two year intensive sampling.

As in Lough Inchiquin, the samples taken in Lough Maumwee were all given I.D. numbers so that they could be traced in the MDS plot (Table 3.11).

Table 3.11. Numbers used to identify the samples taken in Lough Maumwee, for reference to MDS plots.

Sampling method	Substrate	I.D. Number
plastic bag + scuba	*Potamogeton filiformis*	1
	Eloeocharis	2
	Potamogeton filiformis	3
	Hippuris sp. (Marestail)	4
	Isoetes sp.	5
	Isoetes sp.	6
	Scirpus	7
	Hippuris sp. (Marestails)	8
	fine filaments	9
	fine filaments	10
Sweep net	Bare slabs of rock	11
	Bare slabs of rock	12
	Base of *Scirpus*	13
	Base of *Scirpus*	14
	small pebbles and plants	15
	small pebbles and plants	16
	sand, river delta	17
	sand, river delta	18
	plant detritus with lots of algae	19
	plant detritus with lots of algae	20
	small bare rocks	21
	small bare rocks	22
Tube	*Scirpus* (emergent)	23
	Scirpus (emergent)	24
	Scirpus (emergent)	25
	Scirpus (emergent)	26
	Scirpus (emergent)	27

Unlike Lough Inchiquin, there was not much distinction between the habitats sampled in Lough Maumwee, and in the MDS plot, many of the samples came from dissimilar substrata and habitat structures, clustered together (Figure 3.17). This is mirrored in the cluster analysis which puts the samples into 5 groups at a distance of between 10 and 15, and it is difficult to superimpose these groups on the MDS plot (Figure 3.18).

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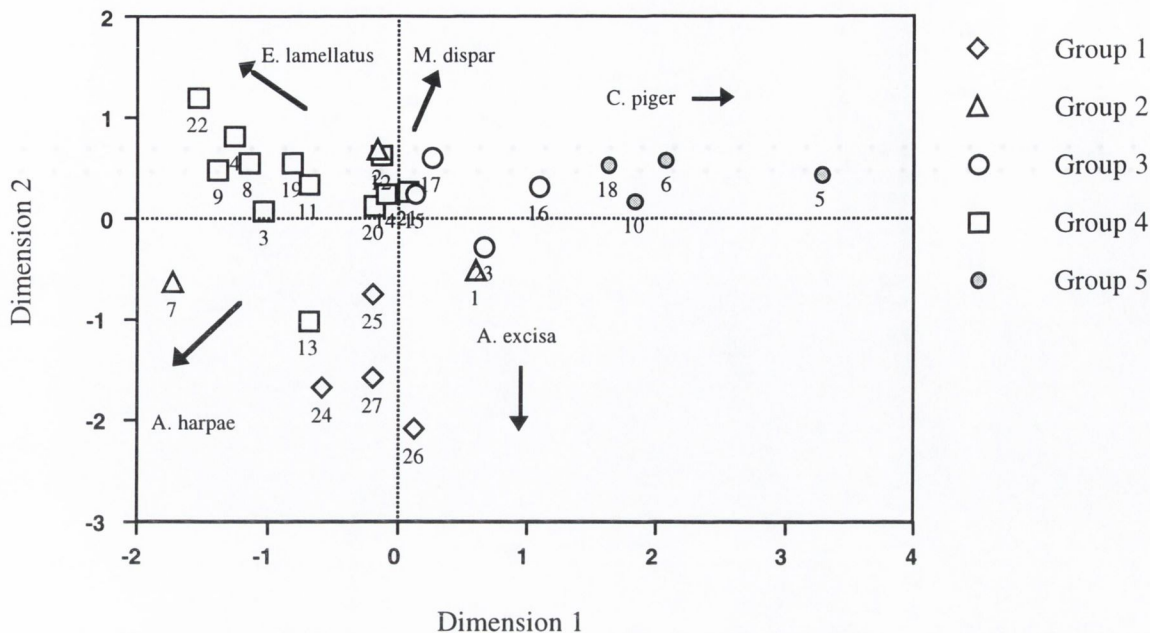
Figure 3.17. MDS plot of samples taken from Lough Maumwee, using three sampling methods over a variety of substrates. Stress = 0.172, R^2=0.87. See Table 3.11 for identification of samples. The five groups refer to the cluster analysis in Figure 3.18. The arrows indicate increasing dominance by that species.

25

20

15

10

Group 5
5. Isoetes
6. Isoetes
18. Sand, river delta
10. Fine filaments

Group 1
24. Scirpus (emergent)
27. Scirpus (emergent)
25. Scirpus (emergent)
26. Scirpus (emergent)

Group 2
1. Potamegeton
2. Eleocharis
7. Scirpus

Group 3
16. Small pebbles + plants
17. Sand, river delta
15. Small pebbles + plants
23. Scirpus (emergent)

Group 4
11. Bare slabs of rock
12. Bare slabs of rock
13. Base of Scirpus
3. Potamegeton
8. Marestails
22. Small bare rocks
14. Base of Scirpus
20. Plant detritus and algae
21. Small bare rocks
19. Plant detritus and algae
9. Fine filaments
4. Marestails

Figure 3.18. Cluster analysis of Lough Maumwee samples, using Average Linkage (between groups).

There are some distinct groups in the Lough Maumwee samples. In particular, Group 1, which comprises 4 of the 5 samples taken in the emergent fringe of *Scirpus* plants. This group had a high proportion of *Alonella excisa* and relatively high species diversity. Group 2 was a small cluster of samples taken in submerged plants, with high proportions of *Acroperus harpae*. This group is hard to pick out on the MDS plot, as it is spread across the centre of the ordination. Group 3 had high species diversity, hence its position at the centre of the plot. The important chydorids in this group were *Chydorus piger, Eurycercus lamellatus* and *Monospilus dispar*, with no species of overall dominance. Group 4 was a mixture of samples taken from submerged plants, and sweep samples over hard rock and areas of plant detritus with lots of filamentous algae. The sweep samples in this group had the highest diversity and are near the centre

of the plot. The plant samples spread towards the left of the plot, and *Eurycercus lamellatus* was more dominant, which is consistent with the observations of many authors that *E. lamellatus* prefers vegetated areas. Group 5 was made up of four samples, three of which were submerged plant samples that were very different from the other plant samples, as they are dominated by *Chydorus piger*, a species almost unanimously associated with hard substrates such as sand or gravel. However, in two cases, the plants in the area were *Isoetes* sp., a species that is small and was found in close association with coarse gravel.

The groups in Lough Maumwee were not as well defined as those in Lough Inchiquin, as most samples had higher diversity, and hence less dominance by a single species (Figure 2.19). Two sweep samples were taken over the same substratum (nos. 11 to 22) but they did not cluster together on the MDS plot, which means that the chydorid communities were different in each sweep sample, even though they were taken over similar substrata. There also seems to be a much higher level of similarity between plant communities and the nearby benthic substrates then in Lough Inchiquin, as demonstrated by the grouping of samples in Group 4 and 5.
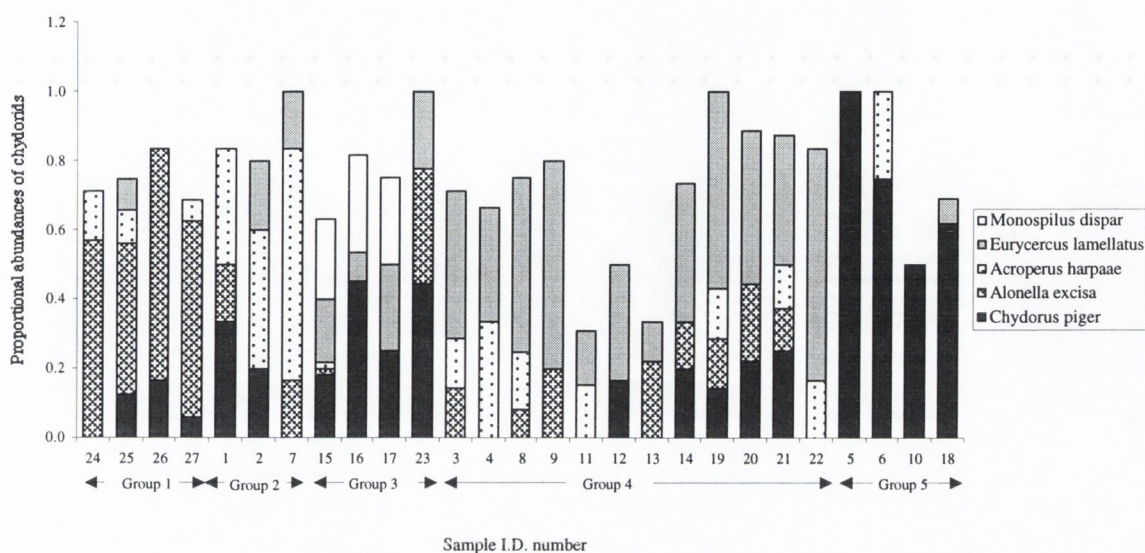
Figure 3.19. Proportional abundances of the five main species identified from the MDS plot in samples taken from Lough Maumwee, September 1998, from various habitats. Sample identification numbers refers to Table 3.11. and the group number refers to Figure 3.18.

In comparison to the samples taken during the two years intensive sampling, the samples from bare slabs of rock, and the small bare rocks (numbers 11, 12, 21 and 22) were taken nearest the sampling site for the two year study. However, these samples did not resemble the samples taken in September 1996 and 1997, when the dominant chydorids were *Alona affinis* and *Chydorus sphaericus*. In contrast, *Eurycercus lamellatus* was an important species in 1998, but was not recorded in high numbers in Lough Maumwee during the two year study. As with Lough Inchiquin, the combined data from all substrata sampled in 1998 was quite similar to the combined data from 14 months sampling in 1996 and 1997. They share 8 of the 9 common species although several of the proportional abundances were quite different (Figure 3.20). For example, the 1998 study had higher proportions of *Acroperus harpae, Chydorus piger* and *Eurycercus lamellatus*, while the 1996-1997 study had a much higher proportion of

Alonopsis elongata. The September 1998 samples had quite different chydorid communities to those sampled in September 1996 and 1997, which reinforces the point that repeated sampling is generally necessary in biological monitoring.
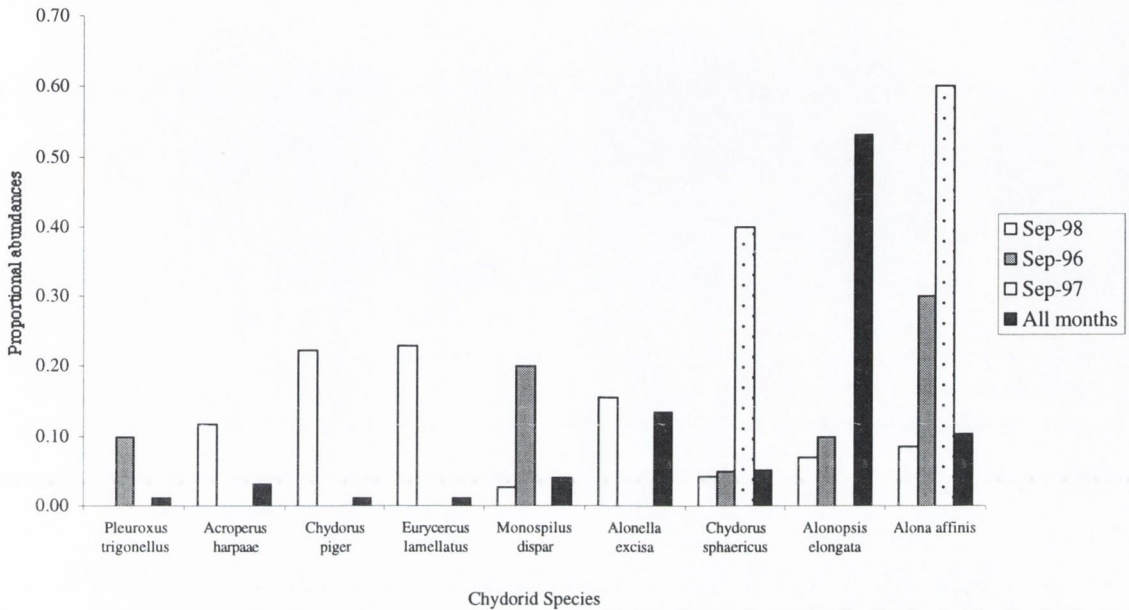
Figure 3.20. Proportional abundances of the common species found in Lough Maumwee in September 1996, 1997 and 1998 (multiple substrates) and also for the average over the two year intensive sampling.

3.3.4 Chydorid communities found amongst submerged vegetation.

The chydorid communities found amongst submerged plants in Lough Inchiquin were quite distinct from the samples taken in non vegetated areas. There was, however, quite a lot of variation within the samples taken in submerged vegetation (Figure 3.13). Even though the submerged plant samples (no. 1-10) were grouped on the right hand side of the plot, they are spread from the top to the bottom, over a broad range of y values. In Lough Maumwee, there was even more variation within the samples taken in submerged macrophytes, with very few of them being grouped together (Figure 3.17 & 3.18). This implies that not all submerged plants have similar chydorid communities, and in fact there was a lot of variation between plant species. Ten samples from various

plants were taken from submerged macrophytes in each lake, and while the degree of replication in specific plants was small, some interesting results were found. The abundance, species richness and diversity of chydorids found in association with submerged plants was analysed for each lake. Where a plant could not be identified, a description of its structure was provided instead.
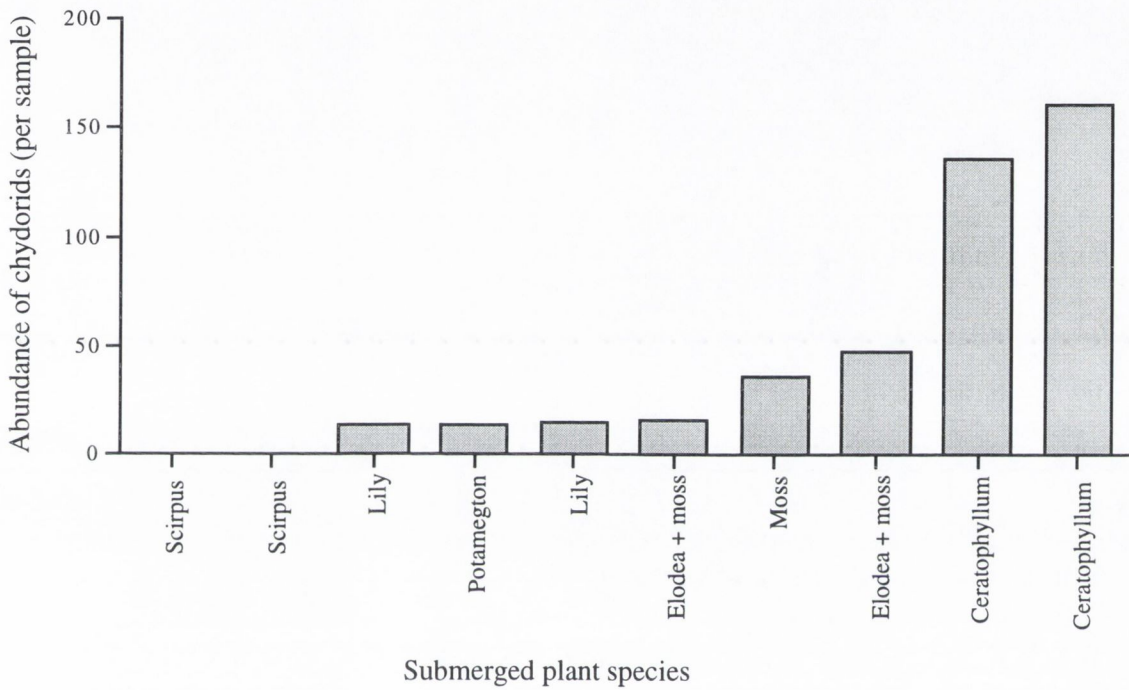
Figure 3.21. Abundance of chydorids (per sample) found amongst submerged plant species taken from Lough Inchiquin.
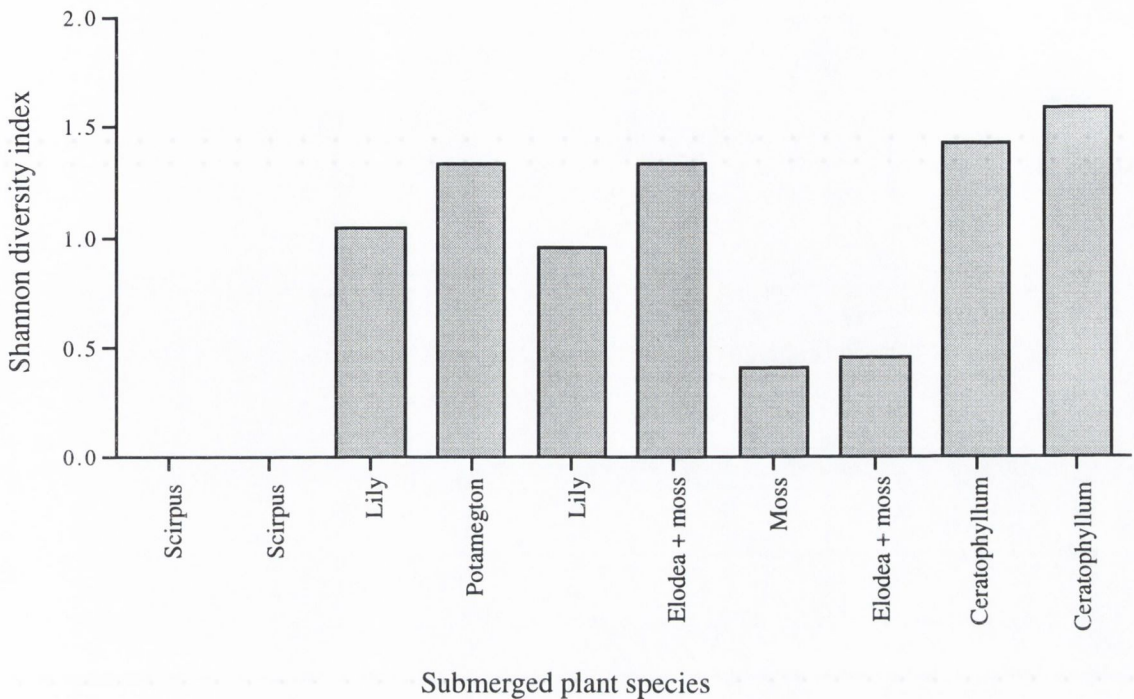
Figure 3.22. Shannon diversity index for the chydorid communities found amongst samples of submerged plant species in Lough Inchiquin.

Ceratophyllum (Hornwort) seems to be a favourable habitat for chydorids as the highest abundance was found amongst this plant, and also the most diverse, with a total of 7 species recorded. While the communities among the Lily, *Nuphar* (underwater leaves) and *Potamogeton* (broad leaved species) had similar species diversity, they had lower abundances and species richness than those among *Ceratophyllum*. The complexity of the *Ceratophyllum* plant probably lends itself well to supporting a large chydorid population, and this is reflected in the lack of chydorids found around the stem of *Scirpus* which has a very simple structure. In fact, it would seem that as the complexity of the plant increases (i.e., the number of branches and leaves) so too does the size of the chydorid community it can support (Figure 3.21). As the abundance of chydorids increased, so too does the complexity of the plant, with *Scirpus* and the underwater leaves of *Nuphar* being relatively simple structures while *Elodea*, moss and *Ceratophyllum* have many branches and leaves in three dimensions. This observation

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was also seen among the samples taken in Lough Maumwee, although the relationship was not as well defined (Figure 3.23).
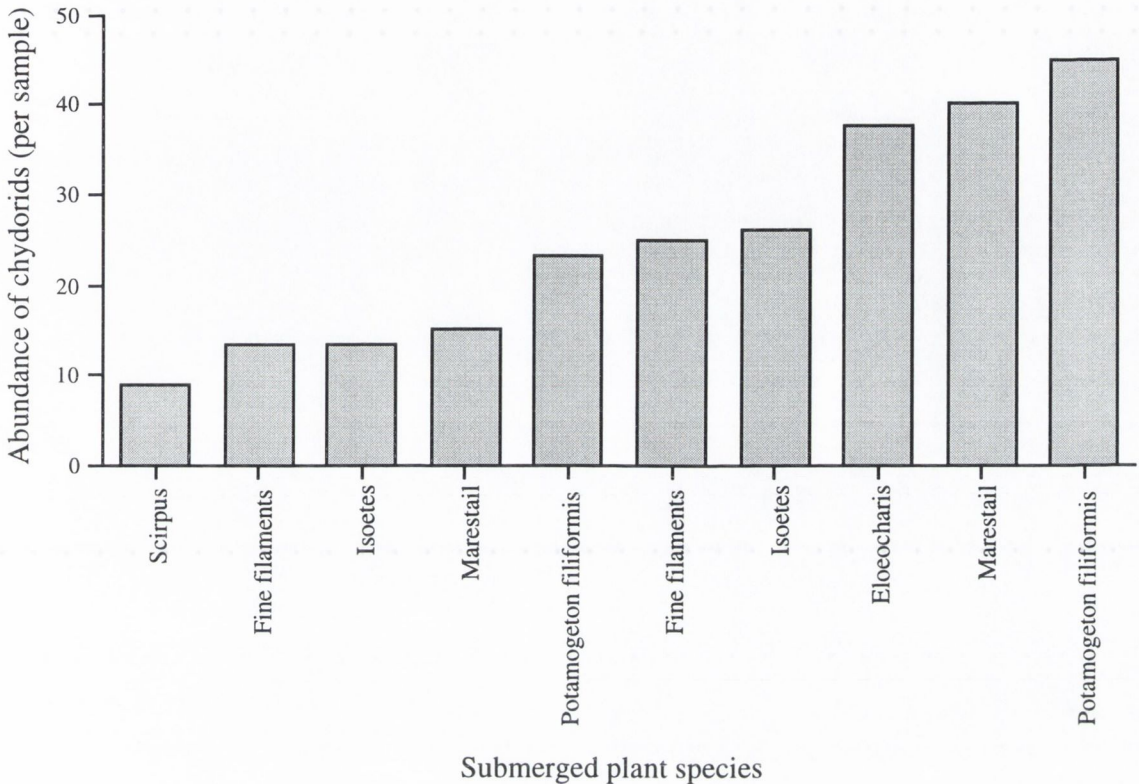
Figure 3.23. Abundance of chydorids found amongst submerged plant species taken from Lough Maumwee.

The plant with the highest abundances of chydorids in Lough Maumwee was *Potamogeton filiformis* which has long thin leaves (less than 1mm in diameter), which in themselves are not complex, but perhaps make a mesh with the other leaves which the chydorids can crawl amongst (Figure 3.23). As in Lough Inchiquin, the base of *Scirpus* was found not to support a rich chydorid community. Overall, the submerged plants in Lough Inchiquin supported a higher abundance of chydorids (44±17.9 chydorids per sample) then the submerged plants in Lough Maumwee (25±3.9 chydorids per sample from Table 3.6).

The species composition of the chydorid communities was different depending on the plant sampled (Figure 3.24). In Lough Inchiquin, four species dominated the plant samples. *Alona costata* and *Alonella exigua* were important species in eight out of the ten samples (the two samples taken at the base of *Scirpus lacustris* did not have any chydorids in them), *Graptoleberis testudinaria* was found in high proportions in the two samples taken in the underwater leaves of *Nuphar* (Lily). *Pleuroxus aduncus* was also found in high proportions in four of the samples.
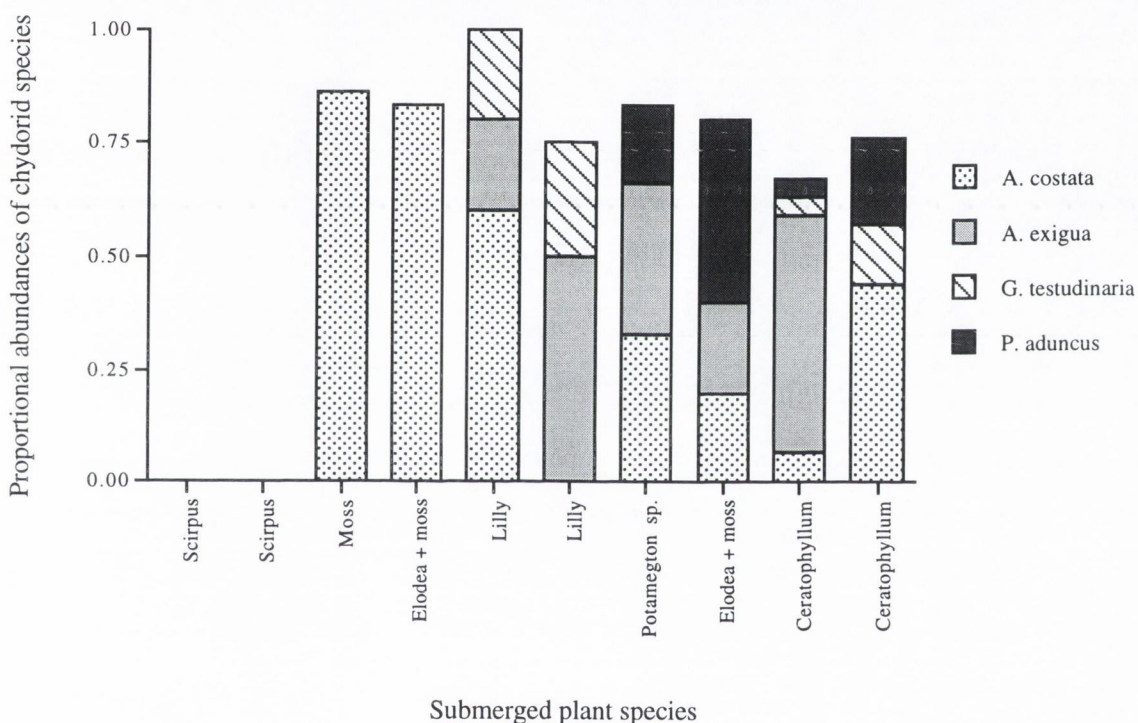
Figure 3.24. Proportional abundances of the four main chydorid species found in association with submerged macrophytes in Lough Inchiquin, September 1998.

In contrast to Lough Inchiquin, the submerged plants sampled in Lough Maumwee had a more diverse chydorid community, with six species found in high proportions (Figure 3.25). The high proportions of *Chydorus piger* and *Alona affinis* were, however, surprising since these species are not generally considered to be associated with plants.

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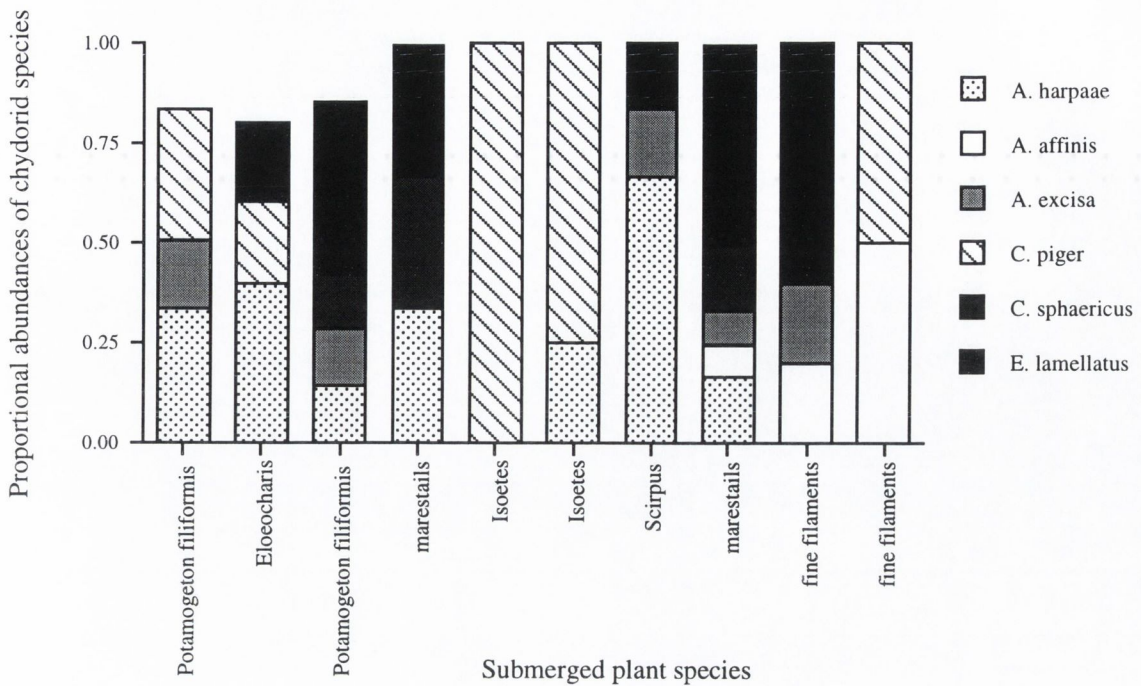
Figure 3.25. Proportional abundances of the four main chydorid species found in association with submerged macrophytes in Lough Maumwee, September 1998.

The emergent vegetation sampled in both lakes was a sedge type, *Scirpus lacustris*, and in Lough Inchiquin, these plants supported a very small mean number of chydorids (3±2.5 s.e., *n*=3), with low mean species richness (1.6±1.2 s.e., *n*=3). In Lough Maumwee, however, a rich and relatively abundant chydorid community was found (mean of 7.3±23.5 chydorids per sample, *n*=5, with a mean shannon diversity index of 1.2±0.13 s.e., *n*=5).

3.3.5 The distribution of chydorids down the littoral zone.

Even though Lough Maumwee is an upland, acid lake with a lot of peat particles, light penetrated a lot deeper than in Lough Inchiquin during the sampling period in September 1998 (Figure 3.26. and 3.27). The euphotic depth of Lough Maumwee is almost twice as deep as that in Lough Inchiquin, and in fact in Lough Maumwee, the majority of the lake's bottom is within the euphotic zone. Littoral

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macrophytes in Lough Inchiquin were found to live from about 4 metres up, although the nature of the plants did change. The plants at the lower depths were tall plants such as Lilies (*Nuphar*), and these gradually gave way to shorter plants such as *Potamogeton, Elodea* and *Chara* in shallower waters. So, although plants were found at 4 metres, they were stretching up several metres to get light. Plants such as *Isoetes* and small *Juncus* sp. were found at all depths sampled (2 metres and upwards) in Lough Maumwee.
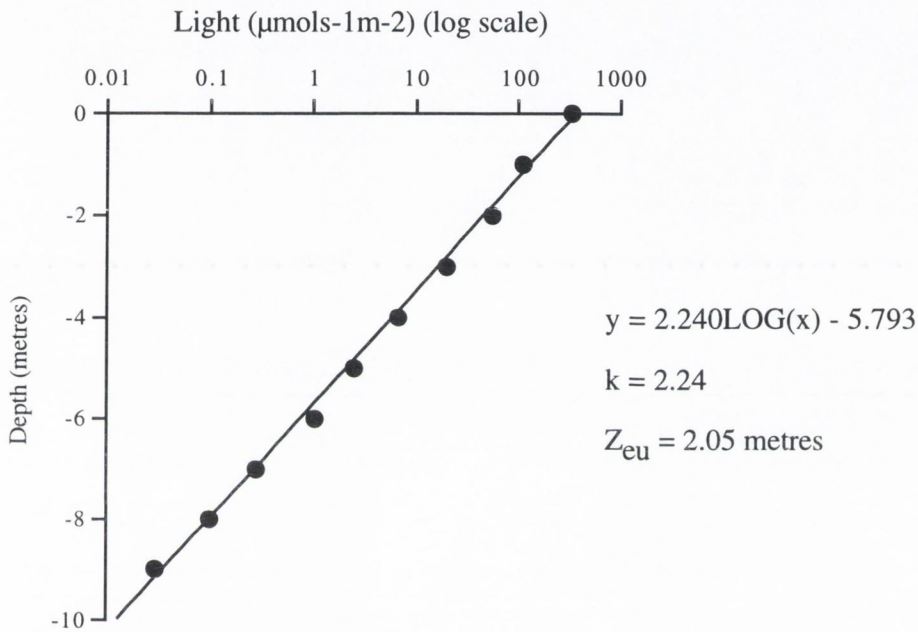
Figure 3.26. Light attenuation in the littoral region of Lough Inchiquin, September 1998. Z_{eu} is the euphotic depth.
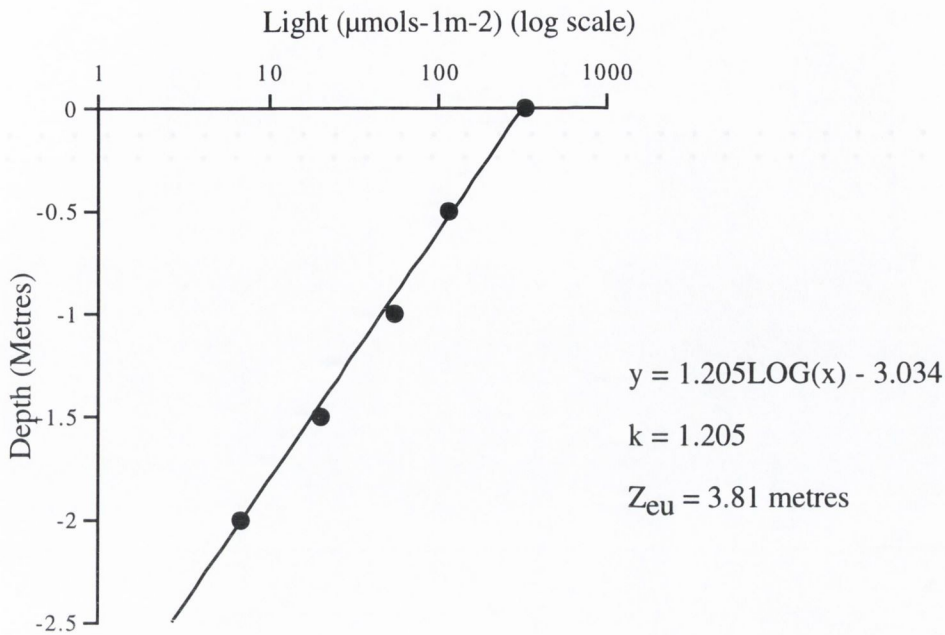
Figure 3.27. Light attenuation in the littoral region of Lough Maumwee, September 1998. Z_{eu} is the euphotic depth.

The pattern of chydorid distribution down the littoral zone was very different in the two lakes. Chydorids were only found above 2 metres in Lough Inchiquin (with the exception of one individual of *Pseudochydorus globosus*). Also, the samples taken at 0.5 metres provided the largest abundance of animals, and deeper than this, the abundance fell off sharply (Figure 3.28). Species richness was also at a maximum in the samples taken at 0.5 metres (5 in transect A, 7 in transect B) and this also dropped considerably with increasing depth (Figure 3.29). In Lough Maumwee, abundant chydorids were found at all depths sampled and there was no pattern of fall off with increasing depth (Figure 3.30). Two or three different species were found at most depths (Figure 3.31).
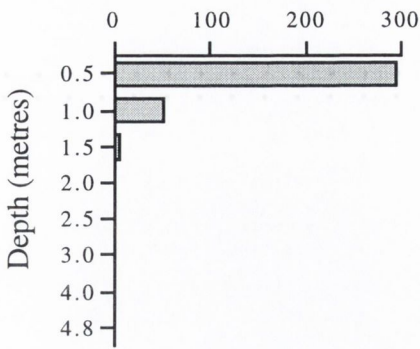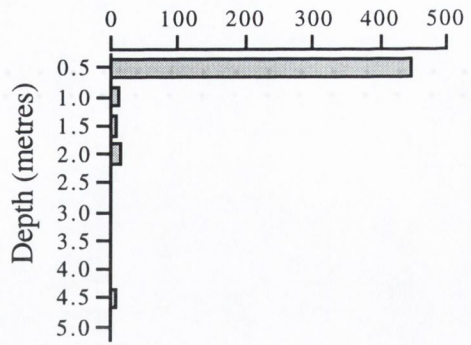
Figure 3.28. Abundance of chydorids found at depths down the littoral zone of Lough Inchiquin, September 1998. Transect A is on the left and Transect B on the right.
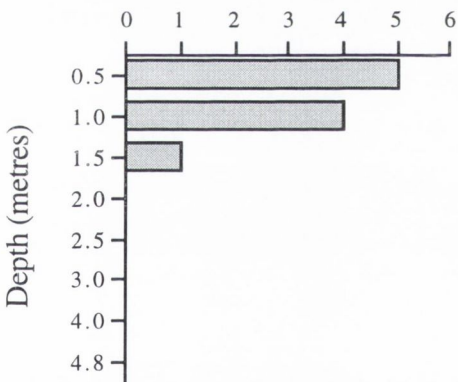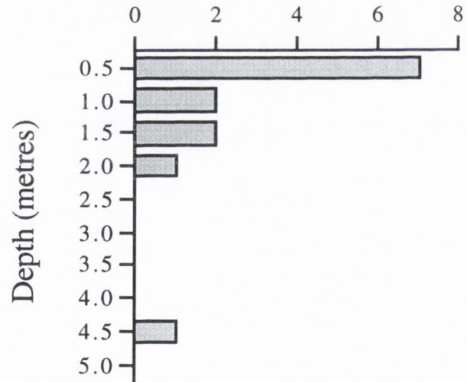
Figure 3.29. Species richness of chydorids found at depths down the littoral zone of Lough Inchiquin, September 1998. Transect A is on the left and Transect B on the right.
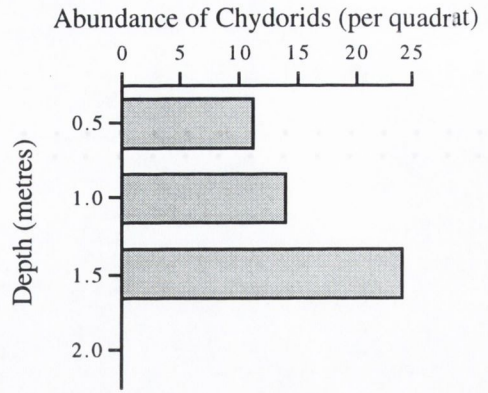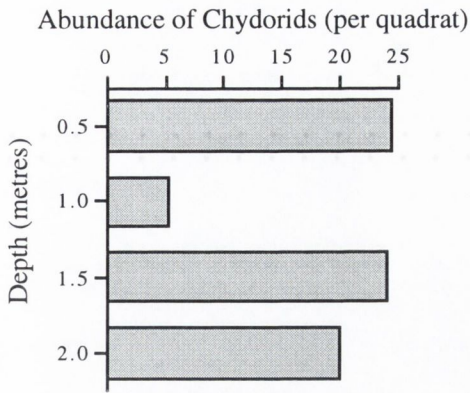
Figure 3.30. Abundance of chydorids found at depths down the littoral zone of Lough Maumwee, September 1998. Transect A is on the left and Transect B on the right.
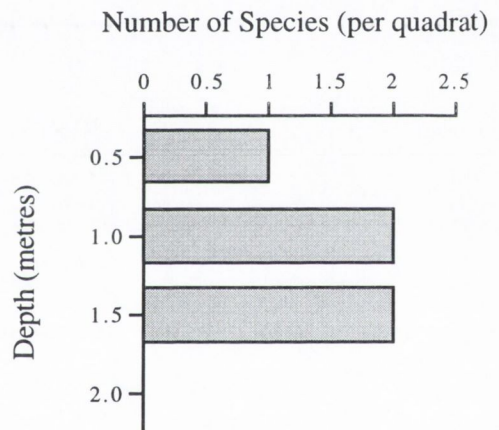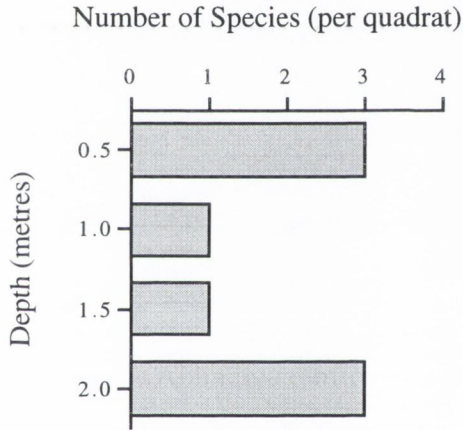
Figure 3.31. Species richness of chydorids found at depths down the littoral zone of Lough Maumwee, September 1998. Transect A is on the left and Transect B on the right.

A high species richness of chydorids was found in the top 0.5 metres of the littoral zone of Lough Inchiquin, but *Alona costata* and *Pleuroxus truncatus* were by far the most dominant. In Lough Maumwee, *Chydorus piger* and *Eurycercus lamellatus* were found to have the highest abundance. *Chydorus piger* and *Monospilus dispar* were found at the lower depths (1.5 m and 2.0 m). Both of these species tend to live close to the substrata at the bottom of the littoral zone and *Monospilus dispar* is probably insensitive to light, as lacks a compound eye, and is adapted for persistent burrowing.

The abundance, species richness and diversity of chydorids in Lough Inchiquin were significantly correlated with depth, light penetration and the presence or absence of plants at the sampling depth (Table 3.12). This was not found to be the case for Lough Maumwee (Table 3.13). As the main difference between the samples taken in Lough Inchiquin and those in Lough Maumwee was that the Lough Maumwee samples stopped at 2 metres, Spearman rank correlations were also calculated for the samples collected only above 2 metres in Inchiquin Significant correlations were also found with depth, light and plants, but the significance level was higher ($p \geq 0.01$).

Table 3.12. Spearman rank correlation coefficients calculated for the relationships between chydorid community variables and depth, light and presence of plants in the littoral zone of Lough Inchiquin. An asterisk denotes a significant relationship at $p \geq 0.05$ (two tailed test).

	Abundance	Species richness	Shannon Diversity
Depth (metres)	-0.761 *	-0.780 *	-0.771 *
Light (µmol s-1m-2)	0.761 *	0.780 *	0.771 *
Plants (presence/absence)	0.525 *	0.527 *	0.378

Table 3.13. Spearman rank correlation coefficients calculated for the relationships between chydorid community variables and depth, light and presence of plants in the littoral zone of Lough Maumwee. An asterisk denotes a significant relationship at $p \geq 0.05$ (two tailed test).

	Abundance	Species richness	Shannon Diversity
Depth (metres)	-0.196	-0.152	0.052
Light (µmol s-1m-2)	0.196	0.152	-0.052
Plants (presence/absence)	-0.253	0.196	0.201

3.4 Discussion

3.4.1 Which method to use for sampling chydorids?

The difficulty in sampling the littoral area in a quantitative manner is an issue which should be addressed before any survey of littoral animals, as the most appropriate method will depend on the questions posed. A variety of different sampling methods have been developed to try to obtain quantitative results. These include grabs, nets, quadrats and funnel traps. The use of funnel traps to quantitatively sample chydorids has become relatively widespread since they were first mentioned in the literature by Whiteside (1974). They have been used for the past several years to monitor chydorid populations in Lake Myvatn (Örnólfsdóttir, 1998), to study the population dynamics of chydorids in the River Thames (Robertson, 1990) and to study spatial distribution of chydorids in Lake Itsaca (Whiteside & Williams, 1975). However, it is acknowledged that this method is dependent on specific behavioural patterns of the animals and that a result of this is that the proportions of animals caught may not be accurate. The funnel traps depend on the fact that most species of chydorids tend to crawl along surfaces (in this case, the inside of a funnel), and that they do so particularly at night-time.

This study has shown that there are several species for which the funnel traps positively select, such as *Psuedochydorus globosus, Anchistropus emarginatus, Pleuroxus laevis, Acroperus harpae, Alona rustica* and *Alona rectangula*. From the fact that these species have a habit of crawling up surfaces, one can infer a lot about their lifestyle and behaviour. *P. globosus* is a scavenger of other crustaceans, and perhaps is used to moving around a lot in order to find food. It has been recorded before that funnel traps catch a lot of *P. globosus* (Whiteside, 1974). *A. emarginatus* has a parasitic lifestyle on *Hydra*, so presumably must be able to climb around plants looking for a host. *Acroperus harpae* has a recorded preference for swimming and crawling amongst

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plants (Fryer, 1968), but the observation that high numbers were caught in these funnel traps is in contrast to Whiteside's (1974) observation that this species was not caught by funnel traps. He also found that *Eurycercus lamellatus* was not caught by funnel traps, although they were in this study. Therefore, it is not safe to presume that a species exhibits consistent vertical migration, based on observations from one lake. Factors such as daylight hours, predation pressure, food availability and macrophyte cover probably combine to produce a littoral environment where vertical migration by a species can be either an advantageous strategy or a waste of energy.

Species which were negatively selected by the funnel traps were *Monospilus dispar, Alonopsis elongata, Chydorus piger, Pleuroxus truncatus* and *Alonella exigua*. The first three of these species have a tendency to frequent non vegetated, benthic substrata such as gravel and sand (Chengalath, 1982; Fryer, 1968; Smirnov, 1963; Whiteside and Williams, 1975), so it was not surprising that these species were not caught in large proportions in the funnel traps. They presumably stay close to the bottom where they are adapted for feeding on the hard substrata. *M. dispar* and *A. elongata* both retain their carapaces, after moulting, and several carapaces can be observed on an individual, all stacked up on top of each other. This is thought to increase their specific gravity and make it easier for them to stick close to the ground (Fryer, 1968). *Monospilus dispar* is very well adapted for burrowing, to the extent that it has lost its compound eye, and relies solely on an ocellus for some degree of light sensitivity (Fryer, 1968). Both *Alonella exigua* and *Pleuroxus truncatus* are very accomplished at crawling, and can stick to the undersides of leaves when foraging for food (Fryer, 1968). They could therefore, easily climb up the insides of a funnel trap if they did vertically migrate, and their tendency not to suggests that vertical migration is not as important for these species as it is for others such as *Pseudochydorus globosus* and *Anchistropus emarginatus*.

While the funnel traps do provide detritus free samples (and hence easy sorting), and are also relatively quantitative, the bias in the species caught was too high to enable reliable useful conclusions about the chydorid community structure to be made. Their use as a monitoring method over a long time period assumes that each species displays the same behaviour of migration all the time. While this may be true, factors such as predation, food availability, oxygen levels, plant cover, wave action and light penetration are likely to affect the degree to which species are migrating, and these factors do vary within a lake depending on the season. One study using funnel traps found no evidence of vertical migration in epiphytic microcrustacea. This was attributed to low edible phytoplankton concentrations and high night time oxygen levels in the plant beds which meant that vertical migration would not be particulalry advantageous (Paterson, 1993). Therefore, if funnel traps are to be used for long term monitoring of cladoceran communities, more study is required into how diel vertical migration of chydorid communities changes over the year, and between different lakes.

3.4.2 One sampling method vs. a combination of several.

In a comparison of sampling methods, there were only two species (*Graptoleberis testudinaria* and *Alonella excisa*) that were restricted to samples taken amongst plants in Lough Inchiquin and. No species were found to be restricted to plant samples from Lough Maumwee. Sweep samples, therefore, do seem to give a good indication of the species present in a lake, especially if sampling is done at different times of the year. One problem which may occur if sweep samples are the only sampling method used in a survey would arise in a lake like Lough Inchiquin, where there was quite a strong distinction between communities in submerged macrophytes and those collected with the sweep net over a benthic substrate. These communities had quite different proportional abundances of species, with the plant communities being

dominated by *Alonella exigua* and *Alona costata*, and the sandy/rocky substrates by *Pleuroxus truncatus*. If only sweep samples had been taken in this case, the importance of *A. costata* and *A. excisa* would have been underestimated and that of *P. truncatus* overestimated.

An interesting result of the spatial sampling in both lakes is that when the samples are combined from all the different habitats, they agree very closely with the data collected on the chydorid community obtained from the 14 months samples in 1996 and 1997. Although the samples in 1996 and 1997 were taken from the same area, perhaps there was a certain amount of shifting of the habitats with the seasons, (e.g., dying back of macrophytes, rising of water levels). Hence, a number of habitats were sampled over the months, even though the sampling site remained the same. It appears, therfore, that to obtain a comprehensive impression of the whole chydorid community of a lake, a study needs to be conducted over either a spatial range that incorporates a number of habitat types or over a large temporal range. What is obvious is that a one-off sampling effort in one sampling site will not provide an accurate record of the chydorid community of the lake. This is consistent with results from Chengalath (1982) and Frey (1960). If one sampling visit is to be made to a lake, a number of habitats should be sampled, perhaps using the composite sampling technique described in Duigan & Kovach, (1994). The other choice is to study samples of surficial sediment which can provide a contemporary cumulative record of the chydorid community, perhaps of the previous few months or a year, depending on the rate of sedimentation of the lake. (Frey, 1960; Whiteside, 1970).

Based on the literature reviewed, it was expected that the vegetated areas sampled using plastic bags and tubes to enclose plants would provide the highest abundances, diversity and species richness of chydorids (Rundle & Ormerod, 1991;

Watkins, Shireman & Haller, 1983; Quade, 1969; Smirnov, 1963; Smyly, 1952). In Chapter 2, it was observed that lakes with a high degree of macrophyte cover had the highest number of species and the most diverse communities, and that lakes with a depauperate community of littoral plants had low chydorid diversity. In this study, the sweep samples (which were not taken in the middle of macrophyte stands) were found overall to have the most diverse communities. In Lough Inchiquin, the highest species richness and diversity of chydorids was found in sweep samples taken over an area of rock covered moss. In Lough Maumwee, the highest species richness and diversity was found in a sweep net sample taken over a mixture of small pebbles and *Isoetes* plants. Individual species of plants in each lake such as *Ceratophyllum, Potamogeton filiformis* and *Hippuris vulgaris* (Marestail) did have a diverse and rich community of chydorids, but other submerged plants had very poor communities. Therefore, it seems that the extra habitats provided by individual plants can not, by itself, account for any observed increase in chydorid diversity. It is more likely that a higher degree of macrophyte cover increases the complexity of the littoral zone and that this complexity has implications for many of the factors controlling chydorid distribution and abundance, including predation, food availability and competition.

3.4.3 The spatial distribution of Chydorids

The results from this section confirm the conclusion from Chapter 2 that lakes have specific communities of chydorids, and that the proportional abundances of the chydorid species can be used to characterise a lake and its littoral environment. Lough Inchiquin and Lough Maumwee had very different communities of chydorids, even though they had several species in common. Some of the habitats sampled in the two lakes were quite similar in terms of structure, such as the beds of emergent *Scirpus*, and the sandy substrate, but even these habitats had distinctly different communities. This

does not agree with Quade (1969) that the plant communities have as much effect on the chydorid assemblages as limnological variables do. It seems likely that the limnological variables such as pH, alkalinity, colour, oxygen and temperature will determine whether a species will initially survive in a newly colonised lake. If it does survive and reproduce effectively, then the success of that species, in relation to other chydorids, will depend on the extent of habitats which suit its behaviour and food requirements.

The main distinction in the chydorid communities in Lough Inchiquin was the difference between samples collected amongst plants, and those taken over the benthic substrata. Secondary to this, there was a split between communities frequenting areas of sand, and those associated with rock. Either *Alonella exigua* or *Alona costata*, both of which are species normally associated with plant habitats (Smirnov, 1963; Smyly, 1958) dominated plant communities. A relationship was observed between increasing complexity of plants (e.g., number of branches and leaves etc.) and abundance of animals. However, the degree of replication was small, so statistical analysis was not possible. The areas with a sandy substrate were dominated by *Pleuroxus truncatus*, which is surprising as this species is cited to be associated with plants (Duigan, 1994; Smirnov, 1963), although it is also associated with areas having a lot of detritus (Duigan, 1992). There was a lot of detritus in this sandy area, as it was overhung by a lot of trees, and separated from the lake body by a fringe of emergent macrophytes. The benthic substratum with the most diverse community was an area of small rocks, some of which were covered with moss. Two samples were taken over clean rocks, and two were taken over rocks with a covering of moss, but it would be hard to differentiate the two chydorid communities at a microhabitat level, except that there was a higher portion of *Pleuroxus truncatus* when moss was present.

In Lough Maumwee, there is no split between communities associated with plants, and those associated with benthic substrates such as sand and rock, as the majority of samples had quite a similar mix of species in various proportions, and so clustered together in the multivariate analysis. The most distinct cluster was a group of four samples taken in the fringe of the emergent *Scirpus* beds, which were dominated more than any other sample by *Alonella excisa*. *Eurycercus lamellatus* dominated a mixture of the samples taken among plants, and over rock substrates. This is in contrast to Smirnov's (1963) observation that this species is restricted to vegetation, and is absent outside vegetated areas. The fact that *Eurycercus lamellatus* was found in such large numbers in many samples in Lough Maumwee suggest a population maxima of this species in September.

The two lakes provided a definite contrast between a littoral zone where the animals are most abundant in the top 0.5 metres and are restricted after 1.5 metres (Lough Inchiquin) and one where the animals are evenly distributed throughout the littoral zone (Lough Maumwee). The distribution of chydorids in Lough Inchiquin is strongly affected by the physical nature of the littoral zone, such as the depth, light penetration and slope, and the biological nature, such as the presence of plants. As these three variables are themselves closely correlated, it is impossible to say which of these variables is the controlling factor, but it is likely that they combine to produce an environment which gets increasingly less suitable for chydorids as depth increases. In contrast to the situation in Lough Inchiquin, the chydorids in Lough Maumwee were not affected by changes in depth, light and presence of plants

The physical nature of the zones provides an insight into why the chydorids are distributed in this way. The littoral zone of Lough Inchiquin is almost three times as steep as that of Lough Maumwee. In sampling the littoral zone in Lough Inchiquin, the

substrata and habitats change visibly when sampling; at five metres there is very fine mud, and as it gets shallower, plants start to become more abundant. The first plants that are noticed are the submerged leaves of tall water lilies (*Nuphar* sp.) and these gradually give way to emergent reeds and rushes, and then smaller submerged plants such as *Ceratophyllum* and broad leafed *Potamogeton* species from about 3 metres upwards. As the plants change, so too do the substrata. Mud and fine silt gradually give way to coarser substrata such as rocks and pebbles, as the water gets shallower. The littoral zone in Lough Inchiquin is therefore very heterogeneous, and it would be expected that the chydorids are more clumped (Daggett & Davis, 1974), and less able to travel between "islands" of suitable habitats (Smiley & Tessier, 1998). In contrast to this, the littoral zone of Lough Maumwee has less distinction between habitats. The lake bottom at 2 metres is very similar to that at 0.5 metres. There is a gentle slope, with predominantly rocks and pebbles, interspersed with small submerged plants such as *Isoetes* or the smaller *Juncus* species. A layer of fine peat overlays most of the littoral zone. It seems likely that the littoral zone does not provide any barriers to the free movement of chydorid species in Lough Maumwee. There are lots of plants covering the bottom of the lake (the average depth of which is 2 metres – well within the euphotic depth of the lake) and although there are distinct microhabitats visible to the human eye, the chydorids did not separate into distinct assemblages according to substratum as they did in Lough Inchiquin.

The fact that the zoobenthos decreases as the slope of a littoral zone increases (Rasmussen, 1988) is mainly because of the effect that the slope has on macrophytes, and the resulting implications for food supply and shading. The algae and bacteria that provide the food supply of the chydorids have been found to have specific preferences for certain areas of the littoral zone and distribute themselves according to depth using flagella or gas vacuoles (Baker, Baker & Tyler, 1985). The slope of the littoral zone in

Lough Inchiquin has probably led to a higher degree of heterogeneity in the littoral zone in comparison to that of Lough Maumwee. The plants are more diverse because there is a distinct change from tall emergent plants reaching from the bottom of the littoral zone, to shorter emergent plants and small submerged plants in the shallower water. The benthos is also affected by the slope, in that there would be more of a tendency for sand and silt to move down the littoral zone, although this would be lessened if there were lots of plants to bind the substrate. The slope of the littoral zone will also mean that detritus (both allochthonous and autochthonous) could fall more quickly down the slope, perhaps before the chydorids get a chance to feed on it. Other factors which might play a role in restricting the chydorids to the upper part of the littoral zone in Lough Inchiquin include the lack of light, as the light attenuates quicker in Lough Inchiquin then it does in Lough Maumwee. This means that photosynthesis, including periiphytic photosynthesis, is restricted to shallower depths resulting in less food production for the chydorids. As quite tall plants grow in the deeper part of the littoral zone in Lough Inchiquin, they will also block light to the benthic plants and animals, thus compounding the problem of food production with increasing depth.

The chydorids from the two lakes surveyed displayed quite different patterns of spatial distribution, both in terms of their distribution among different habitats, and their distribution with depth down the littoral zone. The two of these are almost certainly connected, as the chydorids in Lough Inchiquin had a higher degree of differentiation between habitats and were also restricted to the top metre of the littoral zone. In contrast to this, the chydorid communities of Lough Maumwee did not cluster into specific associations with habitats, and were distributed equally over the depths of the littoral zone. It seems that in Lough Inchiquin, distinct assemblages of chydorids are found in different habitats, because the chydorids have two barriers which prevent them from moving freely between substrata. The first barrier is the slope of the littoral zone, and its

associated factors which means that the chydorids are restricted to the top few metres of the lake. Therefore, to move from one side of the lake to another, they would have to travel horizontally around the lake between different substrata. The second barrier relates to the heterogenous substrata in the littoral zone, some of which may not be suitable for that particular species. The deeper water of the littoral zone acts as a barrier, as does the substratum in front of it. In contrast to this, the distribution and dispersal of chydorids in Lough Maumwee may not be so restricted. As the different substrata do not seem to exclude species it is likely that all species can travel freely between substrata. Even if the littoral zone includes substrata not suitable for one particular species, there is a likelihood that there is, nevertheless, a continuous zone of suitable habitat that circumvents unsuitable habitats. This would be further likely owing to a lack of a deep water barrier to movement.

In conclusion, this study has shown that if only one sampling method for chydorid surveys is to be used, the most informative is a sweep net, preferably over a number of different habitats. If this is done several times during the year, or among a number of contrasting habitats, it will give a good, accurate description of the chydorid community as a whole. Funnel trapping of chydorids did not provide an accurate estimation of the proportions of each species in a community. While it may be useful for ongoing monitoring and behavioural studies, it undoubtedly introduces a bias into qualitative studies. Lough Inchiquin and Lough Maumwee were very different in terms of the chydorid communities. Not only could the lakes be separated initially on the presence and absence of certain species, but the communities were found to have quite different spatial distributions within each lake. Lake morphometry seemed to have an important role in determining the heterogeneity of the chydorid community, and the ease with which the chydorids disperse among different substrates. This is an important conclusion which should be considered in any further work on the spatial distribution of

chydorids, and is probably also applicable to other biota inhabiting the littoral zones of

lakes.

Chapter 4.

Autecology of four chydorid species.

4.1 Introduction

Chapter 2 described how species such as *Alonopsis elongata, Alona affinis, Chydorus sphaericus* and *Monospilus dispar* dominate the chydorid communities in clusters of lakes characterised by certain chemical and physical factors. Why is it that these species become dominant in particular lakes (or at certain times of the year)? Linked with this is how do species which appear to occupy the same position in the food web manage to coexist without excluding each other through competition? This issue has been explored in relation to the open water zooplankton and Hebert & Crease (1980) likened this situation to that described by Hutchinson in 1961 as "The Paradox of the Plankton". Environmental heterogeneity may explain why some species appear to coexist, as several species living together may each occupy different parts of the water body. For example, Leibold & Tessier (1991) found that *Daphnia pulicaria* and *D. galeata mendotae* occupied different areas of the lake owing to the fact that *D.g.mendotae* was not as susceptible to fish predation as *D. pulicaria* and so *D. pulicaria* was excluded from the areas where fish predated actively. Hall (1964) found that *Daphnia pulex* in Base Line Lake, Michigan inhabited the colder, less oxygenated waters in the deeper part of the lake while *D. retrocurva* occupied the warmer epilimnion. While spatial distribution (see Chapter 3) can explain some of the segregation of species of chydorids found in the littoral zone of the Irish study lakes, there are some species which do appear to occupy exactly the same habitat.

Natural cycles of species may also explain how species can coexist without excluding each other. Again, this has been researched for the open water plankton, but not to any great extent in the littoral region. Allan (1977) found *Daphnia ambigua, Daphnia parvula, Bosmina longirostris* and *Ceriodaphnia quadrangula* coexisting in Frains Lake, Michigan. There was a succession of dominant cladocera, with the

Bosmina species appearing first after the ice melt, followed by *D. ambigua*. *C. quadrangular* did not appear until after the water had warmed up to greater than 8°C. Allan attributed these successions purely to temperature, as each species has a different 'Biological Zero' which is the temperature at which the rate of development exceeds zero. Goulden, Henry & Tessier (1982) found that *Bosmina longirostris* could compete with the much larger *D. magna* because *D. magna* populations fluctuated quite considerably as a result of a time lag in responding to lower food levels. The larger *Daphnia* keep on reproducing even after food supplies have dropped too low to sustain an increase in population. *B. longirostris* individuals were then able to exploit the low food levels, and the lack of competition from *D. magna* to build up large populations.. In temporary pools several species may co exist simply because there is not enough time for one species to competitively exclude another (Pajunen, 1986).

If the conclusion from the openwater studies can be applied to the littoral crustaceans, species success would be dependent on many factors such as how fast it can grow and reproduce, the availability of a suitable food and the effects of predation and competition on its mortality. While none of these factors act in isolation, it is useful to assess the contribution that each makes to the population, in order to estimate the importance of each factor to the system as a whole. In particular, information about how each species reacts to changes in temperature, pH and food source could be used to explain some of the mechanisms controlling chydorid communities. Some of this information could also be used to explain the seasonal dynamics of chydorids as most species are known to have one or two peaks of abundance in a year, followed by a population crash (Havens, 1991; Robertson, 1990; Lemly & Dimmick, 1982; Whiteside, Williams & White, 1978; Daggett & Davis, 1974; Keen, 1973).

One measure of success of a species relative to potential competitors is the rate of reproduction. If a species can grow to reproductive age and produce neonates quicker than the other species, it has a better chance of utilising any food resources and building up large populations. If the development time of eggs of species is known, modelling population growth could help to elucidate why certain species become dominant in particular lakes or at different times of the year. Rates of increase of populations have been a subject of discussion for many years, and there is extensive literature on it (e.g. Keen & Nassar, 1981; Paloheimo, 1974; Allan, 1973, Keen, 1973; Caswell, 1972; Edmondson 1972; 1968; Hall, 1964) The instantaneous rate of increase (r) is a function of the instantaneous birth rate (b) and death rate (d):

$$r = b - d$$

r and b can be worked out from the following two equations, and then subtracted to get d.

$$r = (\ln N_{t+1} - \ln N_t)/t \qquad \text{(Keen, 1973)}$$

where t is time, N_{t+1} is the size of the population at time (t +1) and N_t is the size of the population at time (t).

$$b = \frac{\ln[(E/N) + 1]}{D} \qquad \text{(Paloheimo, 1974)}$$

where E is the number of eggs in the population, N is the number of animals in the population and D is the egg development time.

Once r and b, and hence d are known, the potential population increase can be calculated from

$$N_{t+1} = N_t e^{rt} \quad \text{or} \quad N_{t+1} = N_t e^{(b-d)t}$$

At the root of all calculations, however, is a necessity to know the duration of egg development of each species in a particular environment (D), and in itself, the duration of egg development can tell us lot about how well a species is going to do in a particular situation. Three experiments were designed and carried out to test whether varying temperature, pH and food source could account for some of the observed dominance by these species, particularly by influencing egg development time. It was not expected that these three experiments would totally explain the observed dominance of these species as it is likely that many factors (both abiotic and biotic) are important in controlling chydorid dynamics. They may, however, go some way to explaining the mechanisms behind species dominance or lack of it.

4.1.1 The effect of temperature on the duration of egg development

The aim of this experiment was to ascertain the affect of temperature on the duration of egg development time in four different species, *Alonopsis elongata, Alona affinis, Chydorus sphaericus and Acroperus harpae*. The first three of these species were identified as being major components of the chydorid communities in the 29 lakes sampled in Chapter 2. *Acroperus harpae* was included in the experiment as a form of control, as this species was never found to be particularly dominant in any of the study lakes. The success of *A. elongata* in upland, oligotrophic lakes may be connected to an ability to live successfully at colder temperatures. If this is the case, then it would be expected that its reproduction is not slowed by cold temperatures to the same extent as other species. Information about how temperature affects development time in different species can also be used to explain some of the seasonal dynamics of chydorid populations.

Many studies agree that the various stages of asexual reproduction can be affected by environmental conditions such as temperature, predation and food levels. Brambilla (1982) found that changes in temperature affected the volume of eggs and the size at maturity of female *Bosmina longirostris*. They produce large yolky eggs in winter and smaller eggs in summer. While the reason for this is thought to have evolved in relation to predation levels, temperature is the cue which stimulates the change (Kerfoot, 1974). The same phenomenon of producing smaller eggs (in *Daphnia*) in order to avoid predation was observed by Lampert, (1993) although temperature was not implicated as a stimulus. Temperature proved to be a factor in changes in age at maturity, egg development duration and brood size of *Daphnia* by Orcutt & Porter (1984) even though there was considerable interaction with food levels. Korpelainen (1986) found that temperature affected all the reproductive parameters of *Daphnia magna*, including generation time and intrinsic rate of increase and concluded that warmer temperatures brought on early maturation and broods at shorter interval. A decrease in egg development days with increasing temperature was noted by Hebert (1978), Bottrell (1974), George & Edwards (1974) and Hall (1964) in several cladoceran species.

There have been some studies of the effect of temperature on the reproduction of chydorids. Bottrell (1975) found that in six species of chydorids, an increase in temperature significantly decreased the egg development time, and the eggs of epiphytic microcrustaceans took longer to develop than planktonic species. Little variation was found between individuals of the same species at each temperature, but in general, the variability increased at lower temperatures. *Alona affinis* had the slowest development time of three species of chydorids, with *Acroperus harpae* being next and *Chydorus sphaericus* having the fastest development time (Bottrell, 1975). In a study of four species of chydorids, *Chydorus sphaericus, Acroperus harpae, Camptocercus*

rectirostris and *Graptoleberis testudinaria, C. sphaericus* was again found to have the fastest development time at a given temperature, with *G. testudinaria* the slowest (Keen, 1973). The degree to which temperatures fluctuate may also have an effect on the duration of egg development, as constant temperatures are likely to produce longer egg development times. When the egg development time of *Chydorus sphaericus* experiencing fluctuating temperatures was measured, it was found to have a smaller duration of egg development than those in a constant temperature regime, (Meyers, 1984), so laboratory conditions (constant temperatures) probably give an overestimate of natural egg development times, as temperatures in the field are certain to fluctuate diurnally.

From this experiment, regression lines for the egg development time of four species of chydorids will be produced, to see whether the four species have different responses to changing temperature (and hence different shaped regression lines). Bottrell (1975) and Meyers (1984) advocated the use of the curvilinear equation $\log_e D = \log_e a + b \log_e T + c(\log_e T)^2$ to model egg development, where T is the temperature and D is the duration of egg development. This equation can be shortened to $\log_e D = \log_e a + b(\log_e T)^2$ without affecting the predictive value of the model too much. A linear regression line or the use of Krogh's curve or the vant' Hoff-Arrhenius functions were found to produce a significant error (Bottrell, 1975). The Bêlehrádek function, ($\log_e D = \log_e a + b \log_e (T-\alpha)$ where a,b and α are constants) may also be useful for modelling egg development time. Differences in development times for species may vary between sampling sites, so the application of one regression line to a population from a different area may produce a significant error (Bottrell, 1975; Hann, 1984). This underlines the necessity in autecological studies to ensure that the values used from other publications are applicable to the population that is being studied. This is particularly important to Irish chydorid populations, as no record of any autecological studies on Irish chydorids

was found. Given that the geographical distribution of some species in Ireland differs from their distribution in Britain and mainland Europe, it is possible that Irish chydorids have different responses to temperature than members of the same species with a mainland continental distribution. For example, *Alonopsis elongata* is considered as having a northern characteristic in Great Britain (Fryer, 1993), but in Ireland, its distribution is more widespread (Duigan, 1992).

4.1.2 The effect of pH on the duration of egg development

The pH of water has been shown to affect the species diversity and composition of chydorid communities (e.g. Duigan & Kovach, 1994; Berzins & Bertilsson, 1990; Nilssen & Sandøy, 1986; Fryer, 1980; Anderson, Benfield & Buikema, 1977; Carter, 1971). There are some species of chydorids which are able to thrive in acidic waters, such as *Chydorus ovalis, Alonopsis elongata, Alona rustica* and *Alonella excisa* (Duigan & Kovach,1994; Fryer, 1993; Duigan 1992). There are probably several reasons why some species do better at lower pH levels than others. Extreme pH levels may be immediately lethal to some species such as *Daphnia magna* (Fryer, 1980). Low pH values may interfere with respiration, osmoregulation or the permeability of membranes (Havens, 1992; Hellawell, 1986). The resting respiratory rate of *Simocephalus vetulus* at pH 4.0 was found to be only 60% of that at pH 4.5 – 9.5 and filtering rate was found to increase as the pH changed from 4.5 to 9.5 (Ivanova & Klelowski, 1972). The filtering rates of *Diaptomus minutus, Diaphanosoma sp.* and *Holopedium gibberum* were negatively correlated with lake pH in seven Ontario lakes (Bleiwas & Stokes, 1990). Lower pH may also increase the toxic effects of some substances such as ammonia, copper, lead and zinc (Mason, 1981). The lowering of the pH of surface waters owing to acid rain may leach aluminium from some soils, hence raising aluminium in streams and lakes to toxic levels (Hellawell, 1986). At a habitat

level, the littoral regions of acidic lakes are likely to be different to those of alkaline lakes, as the macrophyte communities will be different as well as the type of substrates on the bottom. The upland acidic lakes of Ireland, for example, have a high degree of peat in the littoral region. As they are usually found in mountainous areas, their shorelines are also more exposed and devoid of trees. Changes in predation and competition levels are also likely to occur in lakes with decreasing pH (Stenson, Svensson & Cronberg, 1993; Locke & Sprules, 1993).

The direct effects of pH on the reproductive processes of chydorids is relatively unknown, although Meyers, (1984) suggests that the duration of egg development is independent of water chemistry. However evidence from other animal groups suggests that pH may have an effect on reproductive rates. pH was shown to have a major influence on the reproductive capacity of the rotifer *Brachionus calyciflorus* with the net reproductive rates having two peaks at pH 3.5-4.5 and 8.5-9.5 (Mitchell, 1992). Parthenogenesis in laboratory populations of *Daphnia pulex* was observed only at pH levels of between 7.0 – 8.7, even though it did survive at lower pH levels (Davis & Ozburn, 1969). It seems possible, therefore, that pH may have an effect on chydorid reproductive parameters and hence on the population dynamics of chydorid communities.

4.1.3 Population growth of chydorids in different food sources.

One reason why cladoceran species may be able to coexist without excluding one another could be that the food resources are partitioned among species, each surviving on different parts of the food resource (Allan, 1973). While it is generally thought that chydorids are detritivores, many species have particular adaptations for feeding, and their trunk limbs show much diversity in form and function when it comes

to feeding apparatus (Fryer, 1968). It is likely, therefore, that resource partitioning does play an important role in the dynamics of chydorid communities. The importance of food quality for open water cladocerans has had a lot of study (see Gulati and Demott, 1997 for review). For example, food quality (as opposed to quantity) was found to affect growth and reproduction in *Daphnia hyalina* (Vijverberg, 1976) and *Diaphanosoma excisum* (Jana & Pal, 1984). Differences in growth and reproductive patterns were found between *Daphnia hyalina* and *Daphnia galeata* grown on several different algae (Giani, 1991). A study of population growth rates of three species of cladoceran, (including *Chydorus sphaericus*) found that each species had varying response to food quality. *Chydorus sphaericus* showed the smallest differences in growth among resource type (mono and mixed algal cultures) indicating that it has a generalist feeding habit, while *Bosmina longirostris* appeared to be the most particular (Lundstedt & Brett, 1991).

Food quality seems very likely to be a factor in the dynamics of chydorid communities, and the presence and abundance of a certain food type in a lake may determine the success of a particular species. The degree to which food quality could affect population growth is dependent on how a species can exploit the food. Some species may not be adapted to collecting a food type. *Alonopsis elongata* primarily feeds by scraping materials from substrates. This is also the case for *Alona affinis*, although it may be more adept at collecting larger particles than other species. *Chydorus sphaericus* is particularly adept at scraping or sweeping minute particles from surfaces, which other species may miss (Fryer, 1968). Even if each chydorid species can collect a specific food type, there may then be problems in the assimilation of certain components. Phosphorus and fatty acid have been pinpointed as limiting factors in zooplankton food, and it is thought that the thresholds for these limiting elements differ among species, as the elemental composition of species differ (Gulati & Demott, 1997).

This conclusion was primarily based on *Daphnia* work but it seems likely that the same principle could be true for chydorid species.

4.1.4 Aims of these experiments

The overall aim of these three experiments is to try and isolate the possible factors which lead to the success (or lack of success) of *Alonopsis elongata*, *Alona affinis* and *Chydorus sphaericus* in different lake types. As *A. elongata* was found to dominate in lakes with low pH and alkalinity, low nutrient status and low temperatures, any one of these factors could be the determinant of its success. The response of *A. elongata* to laboratory conditions of varying pH, temperature and food source may provide insight into which is the most important factor. *A. affinis* was found to be dominant in lakes with poorly developed littoral zones, which is probably because it does not depend on macrophytes (and their epiphyton) for survival. If this is the case, *A. affinis* should have a relatively positive response to detritus as a food source, particularly non-living, non-photosynthesising detritus. *C. sphaericus* was found to dominate in nutrient rich waterbodies with high levels of total phosphorus and chlorophyll *a*, indicating that populations of this species should grow well when algae is the food source. Also, if this species is as tolerant as much of the literature suggests, varying degrees of pH and temperature should have less effect on it than on the other three species.

4.2 Methods

4.2.1 Laboratory cultures.

Four species, *Alona affinis*, *Chydorus sphaericus*, *Alonopsis elongata* and *Acroperus harpae* were collected from nearby lakes. The species were seperated into one litre round bottomed flasks filled with filtered pond water and some food. A hay infusion and a soil infusion were prepared by filling 10 litre flasks with distilled water, and adding hay to one and soil to the other. These were autoclaved and left for approximately two months in sunlight. These infusions provided the food source for the laboratory cultures of chydorids.

4.2.2 The effects of temperature on the development time of chydorid eggs.

A 5 litre beaker was filled with 3 litres of pond water filtered through a 30µm sieve. To this, was added 1 litre of the hay infusion and 150 ml of the soil infusion. This culture medium was aerated constantly, and topped up with pond water and the food sources as the experiment progressed. Individuals from each of the four species were separated into glass petri dishes (volume 25ml, diameter 5cm) filled with the culture medium. The medium was changed every three or four days. It was assumed that this provided them with an excess of food, thus negating the effect of food limitation on egg development. (This assumption was based on observations that the same size dishes filled with this culture medium were capable of sustaining large, reproducing populations of each chydorid species). The animals were kept at either 8°C, 12°C, 16°C or 20°C (all temperatures ±1°C). A 12:12, l/d photoperiod was maintained in all cases. The animals used for the experiment were the second generation of animals kept at the relevant temperature. As soon as they were born, they were separated into their own dish, and then monitored for the first signs of ovary swelling. The duration of egg

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development was defined as the time between when the eggs were deposited in the brood chamber, until the time the neonates were born. The animals at 8°C and 12°C were observed at least once every 24 hours, and the ones at 16°C and 20°C were observed twice every 24 hours. The beginning of egg development was taken as half way between the observation when there were no eggs in the brood chamber, and the observation when there were eggs in the brood chamber. Similarly, the time the neonates were born was taken to be half way between the observations when there were embryos in the brood chamber, and when the neonates were swimming freely. A minimum of 10 measurements for each species was collected.

The log transformed data was analysed using a two-way ANOVA (the factors being temperature and species) with interactions (Temperature x species), and Least Squared Difference (LSD) post hoc tests were used to examine which of the species and temperatures, and the interaction between the two were the most significant. The curves that were obtained by graphing development time against temperature for each species were fitted to several models, using least squares regression, and the R^2 for each method determined using the following formula, in order to see which model fitted the curves the best.

$$R^2 = \frac{\sum(\text{Predicted y'} - (\text{mean predicted y'}))^2}{\sum(\text{Observed y'} - (\text{mean observed y'}))^2} = \frac{\text{Model Sum of Squares}}{\text{Total Sum of Squares}}$$

4.2.3 The effects of pH on the development time of chydorid eggs.

Three five litre flasks of culture medium were made up as described in section 4.2.2. with pond water and food, and each was maintained at high pH (8.4 ± 0.1), medium pH (6.6 ±0.1) and low pH (5.0 ±0.1). The high pH culture did not have to be

manipulated at all, as this was the natural pH of the mixture. The medium and low pH cultures were manipulated with 0.1 m HCL and NaOH in order to get the required pH. This was done the night before the culture media was to be used, and the pH was then checked the next morning to see if the pH was correct. Individual animals of the four species were cultured in these three mediums and the egg development was measured according to the method described for Experiment 1. All cultures in the three pH regimes were kept at 16°C with a 12h:12h l/d photoperiod. The culture medium was changed every two days in this experiment. This was because the pH in the medium and low culture media did rise as soon as it was put in the smaller dishes. Changing the water every two days was a compromise between keeping the animals at the relevant pH, while also ensuring minimum disturbance. Ten measurements of egg development at each pH was obtained for analysis.

The untransformed data were analysed using a two factor ANOVA (pH and species) with interactions (pH x species), and Least Squared Difference (LSD) post hoc tests were used to examine which of the species and pH, and the interaction between the two were the most significant.

4.2.4 The effects of different food sources on the population growth of three species of chydorids.

Four food sources were used to test whether the three species (*Alonopsis elongata, Chydorus sphaericus* and *Alona affinis*) were more or less successful in various food types: algae, detritus, sterilised detritus and filtered pond water. Ten adults of each species (obtained from the laboratory culture, explained in 4.2.1) were placed in a 50 ml beaker containing the food source and this was replicated 5 times for each food source. These beakers were then left in the dark at 16°C for 14 days. After 14 days, the

animals in each beaker were removed and counted. The food sources were prepared as follows:

1. **Algae.** *Chlamydomonas reinhardi* was cultured at 15°C in a 12h:12h l/d photoperiod. Some of this culture was then centrifuged twice at 3,000 r/min, at 147° for 20 minutes. The culture medium, and any water was removed in between centrifuging. The algae were counted under a compound microscope to determine the concentration of cells. They were then diluted with pond water (filtered twice through a 30µm sieve), and 50 ml of the mixture was put in each beaker. The end concentration of algal cells was calculated as being 2.88×10^5 cells/ml. The size of these algae was generally between 14 and 22 µm in length.

2. **Detritus.** The culture medium described in section 4.2.2. was used for this part of the experiment. This was made up of a mixture of filtered pond water, hay infusion and soil infusion. 50 ml of this mixture was put in each beaker.

3. **Sterilised detritus.** Some of the culture medium used as the "detritus" food source was autoclaved, and then 50 ml was placed into each beaker. The autoclaving ensured that there were no other animals or micro-organisms in the beakers, and also killed any epiphyton in the mixture, Keeping the beakers in the dark ensured that epiphyton did not have the chance to grow, and so this detritus was of a sterile, non living nature. In contrast, the detritus used in (2.) above, contained other chydorids (*Alona guttata* and *Graptoleberis testudinaria*), oligochaete worms and, presumably, bacteria and photosynthesising periphyton and phytoplankton.

4. **Filtered pond water.** Pond water was filtered twice through a 30µm sieve, and 50 ml was put in each beaker. This was used as the control for the experiment, to assess

whether the chydorid species observed could survive on water and the micro-organisms in it (less than 30μm).

All results were expressed as population change N_t/N_o where N_t and N_o denote the number of individuals present at the end of the experiment and at the beginning of the experiment respectively. The data (which were square root transformed) were analysed using a two-way ANOVA (food source and species) with interactions (food source x species), and Least Squared Difference (LSD) post hoc tests were used to examine which of the species and food source, and the interaction between the two were the most significant.

4.3 Results

4.3.1 The effect of temperature on the duration of egg development

As expected, temperature was found to have a significant effect on the duration of egg development of the four species of chydorids tested. Table 4.1. and Figure 4.1. show the mean (± s.e.) duration of egg development of the four species at the four temperatures tested. An ANOVA showed that temperature, species and the interaction between the two were all very significant sources of variation in egg development time (Table 4.2). The fact that the interaction between temperature and species was a significant source of variation indicates that temperature affected each species differently

Table 4.1. Mean(± s.e.) duration (hours) of egg development of the four species at the four temperatures tested.

| | Temperature | | | | | | | |
| | 8°C | | 12°C | | 16°C | | 20°C | |
Species	Mean ±s.e.	n	Mean ±s.e.	n	Mean ±s.e.	n	Mean ±s.e.	n
C. sphaericus	220.6±6.7	13	114.7±5.4	10	75.2±1.3	35	69.3±1.1	10
A. harpae	294.3±4.9	10	128.2±5.1	10	90.5±1.5	25	75.8±3.3	9
A. affinis	336.0±5.1	10	146.4±3.3	10	103.8±1.5	26	79.4±3.4	10
A. elongata	342.7±4.5	10	207.2±12.6	10	122.2±2.9	21	n.a.	

Table 4.2 ANOVA results for the relationship between temperature, species, the interaction (temperature x species) and the duration of egg development in four species of chydorids.

Source	df	F-ratio	probability
Constant	1	476554	≤0.0001
Temperature	3	1232	≤0.0001
Species	3	130	≤0.0001
Temperature x species	8	6.3	≤0.0001
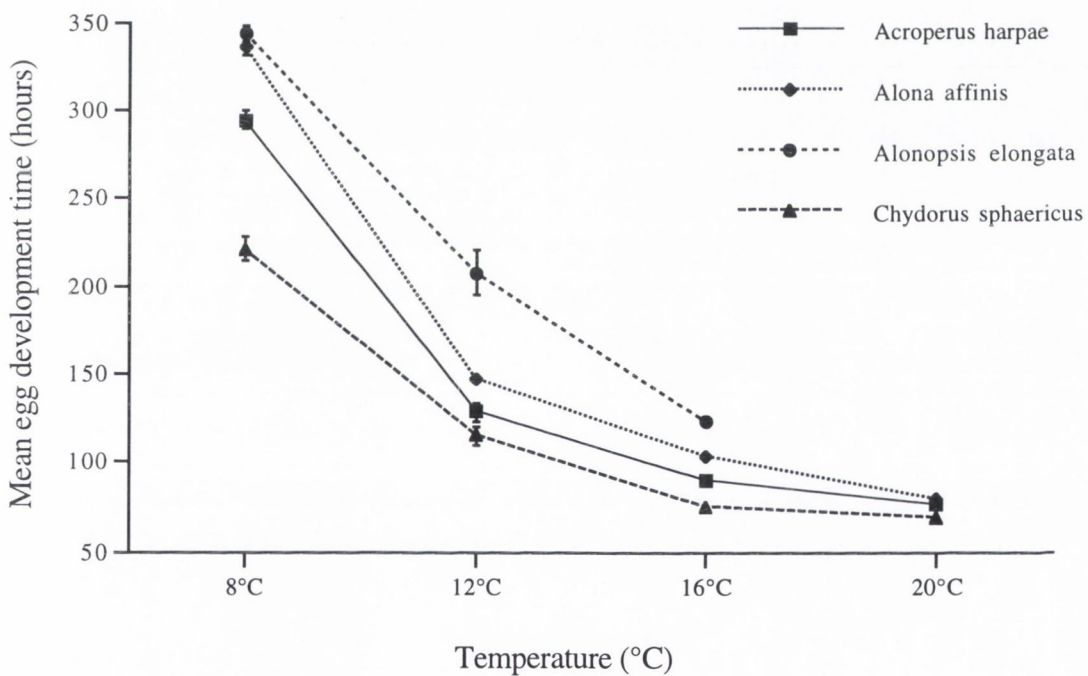
Figure 4.1. Mean egg development times of four chydorid species at 8°C, 12°C, 16°C and 20°C. Error bars indicate standard error.

Alonopsis elongata failed to reproduce successfully at the highest temperature (20°C). Thirty individuals were cultured at 20°C, and none of them produced viable neonates. In thirteen cases, the ovaries of each individual were seen to swell, and eggs

were passed into the brood chamber. However, these eggs were not fully developed and did not have the customary green colour. Within a day of them being laid in the brood chamber, they began to disintegrate. It is, therefore, presumed that a temperature of 20 °C is too warm to allow *Alonopsis elongata* to reproduce successfully.

Three different regression models were fitted to the data for each species (Figures 4.2 – 4.5). In the case of all species, the Bêlehrádek model was found to be the best fitting model for the data, with R^2 values of 0.98-0.99. The two curvilinear models were found to be relatively good fits, although the longer form of the curvilinear equation ($\text{Log}_e D = \log_e a + b \log_e T + c(\log_e T)^2$) was found to overestimate the egg development time at the highest temperature in all cases, and the shorter form ($\text{Log}_e D = \log_e a + b(\log_e T)^2$) was found to underestimate the egg development time at the highest temperature, and at the lowest temperature.
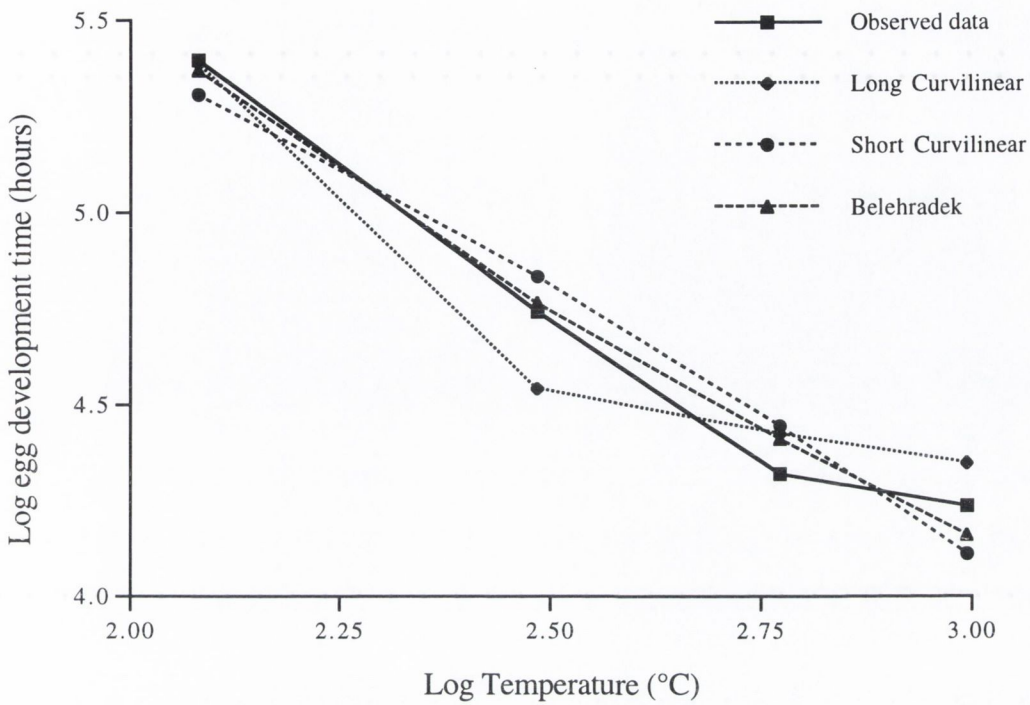
Figure 4.2. Observed values of Log D (egg development time) of *Chydorus sphaericus* plotted against Log T (temperature), with three potential regression models. The long curvilinear model ($Log_e D = log_e a + b log_e T + c(log_e T)^2$) had an R^2 of 0.82, the short curvilinear model ($Log_e D = log_e a + b(log_e T)^2$) had an R^2 of 0.94 and the Bêlehrádek model ($Log_e D = log_e a + b log_e (T-\alpha)$) had an R^2 of 0.98.

Figure 4.3. Observed values of Log D (egg development time) of *Acroperus harpae* plotted against Log T (temperature), with three potential regression models. The long curvilinear model ($\text{Log}_e D = \log_e a + b \log_e T + c(\log_e T)^2$) had an R^2 of 0.86. the short curvilinear model($\text{Log}_e D = \log_e a + b(\log_e T)^2$) had an R^2 of 0.94 and the Bêlehrádek model ($\text{Log}_e D = \log_e a + b \log_e (T-\alpha)$) had an R^2 of 0.98.
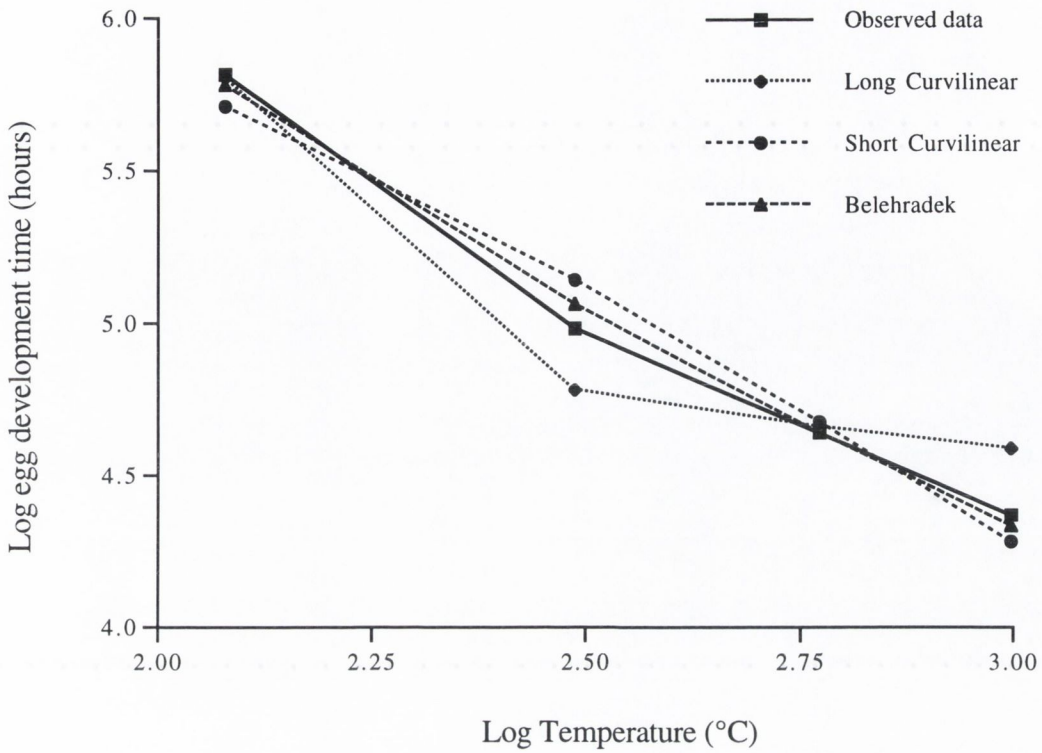
Figure 4.4. Observed values of Log D (egg development time) of *Alona affinis* plotted against Log T (temperature), with three potential regression models. The long curvilinear model ($Log_e D = log_e a + b log_e T + c(log_e T)^2$) had an R^2 of 0.83. the short curvilinear model($Log_e D = log_e a + b(log_e T)^2$) had an R^2 of 0.96 and the Bêlehrádek model ($Log_e D = log_e a + b log_e (T-\alpha)$) had an R^2 of 0.99.
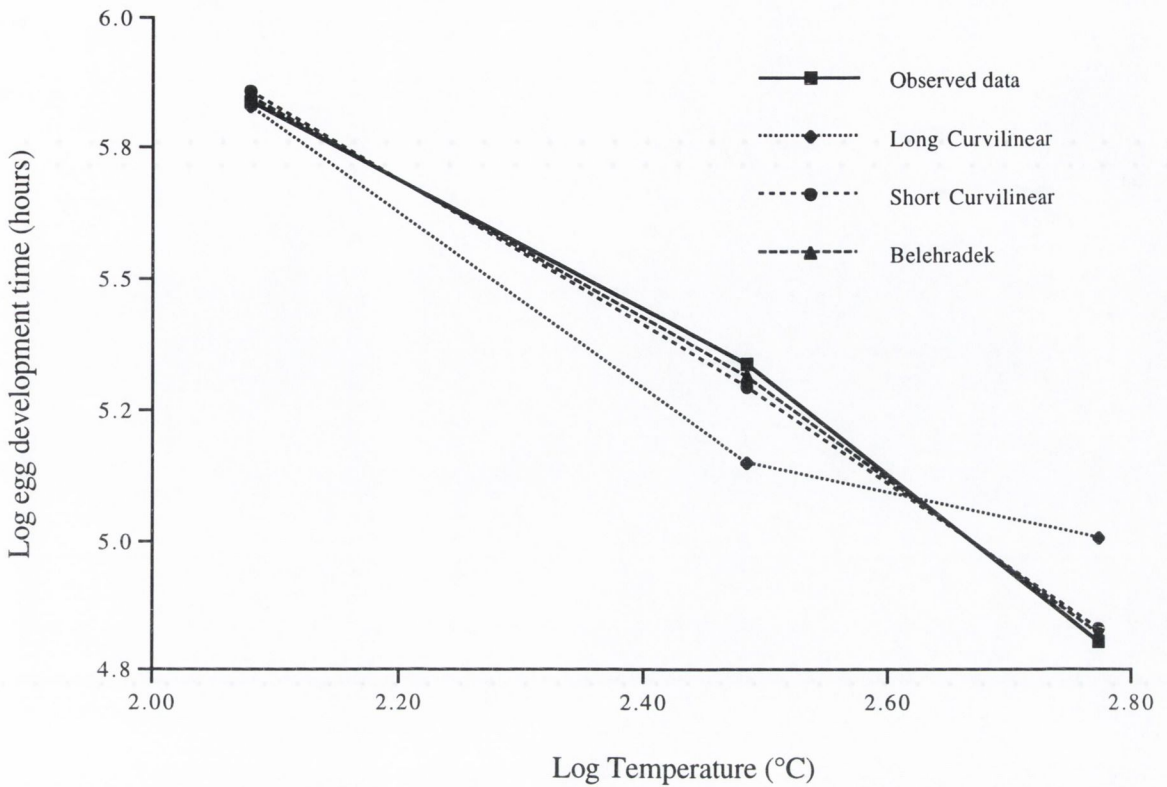
Figure 4.5. Observed values of Log D (egg development time) of *Alonopsis elongata* plotted against Log T (temperature), with three potential regression models. The long curvilinear model ($Log_e D = log_e a + b \, log_e T + c(log_e T)^2$) had an R^2 of 0.78. the short curvilinear model($Log_e D = log_e a + b(log_e T)^2$) had an R^2 of 0.99 and the Bêlehrádek model ($Log_e D = log_e a + b \, log_e (T-\alpha)$) had an R^2 of 0.99.

The curve obtained for *Alonopsis elongata* had quite a different shape from that of the other species, and this is not just attributable to the lack of data from 20°C. As the Bêlehrádek function proved to be the best fitting model for the development curves of these chydorid eggs, this was used to extend the regression lines to cover a range of temperatures from 4°C to 24°C, in order to see whether *Alonopsis elongata* had significantly different egg development times at lower temperatures than other species. This was found to be the case, as *C. sphaericus, A. affinis* and *A. harpae* had very slow egg development times at 4°C, when predicted by the Bêlehrádek model. In contrast, *A. elongata* had a very quick egg development time at 4°C, as the Bêlehrádek model does

not predict a sharp rise in the curve at lower temperatures, as it does for the other three species.
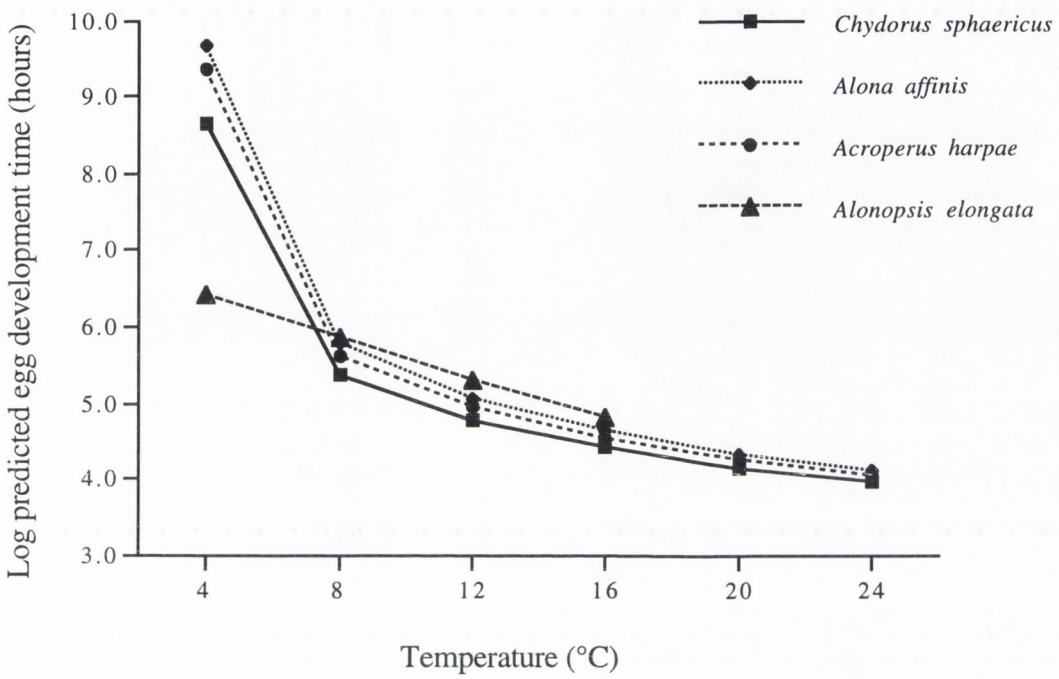
Figure 4.6. Predicted egg development time of four chydorid species using the Bêlehrádek model, $(Log_e D = log_e a + b \log_e (T-\alpha))$, extended to include 4°C and 24°C.

4.3.2 The effect of pH on the duration of egg development

The four species tested were found to have varying reactions to the pH of the culturing medium (Table 4.3 and Figure 4.2).

Table 4.3. Mean (± s.e.) duration (hours) of egg development of the four species cultured in three mediums with different pH.

| Species | pH | | | | | |
| | Low | | Medium | | High | |
	Mean ±s.e.	n	Mean ±s.e.	n	Mean ±s.e.	n
C. sphaericus	79.9±2.6	10	74.5±1.6	13	75.3±1.3	35
A. harpae	98.7±5.6	11	84.12±2.9	10	89.8±1.5	26
A. affinis	96.4±2.3	9	106.6±5.3	10	103.9±1.6	26
A. elongata	n.a.		n.a.		122.3±2.9	21
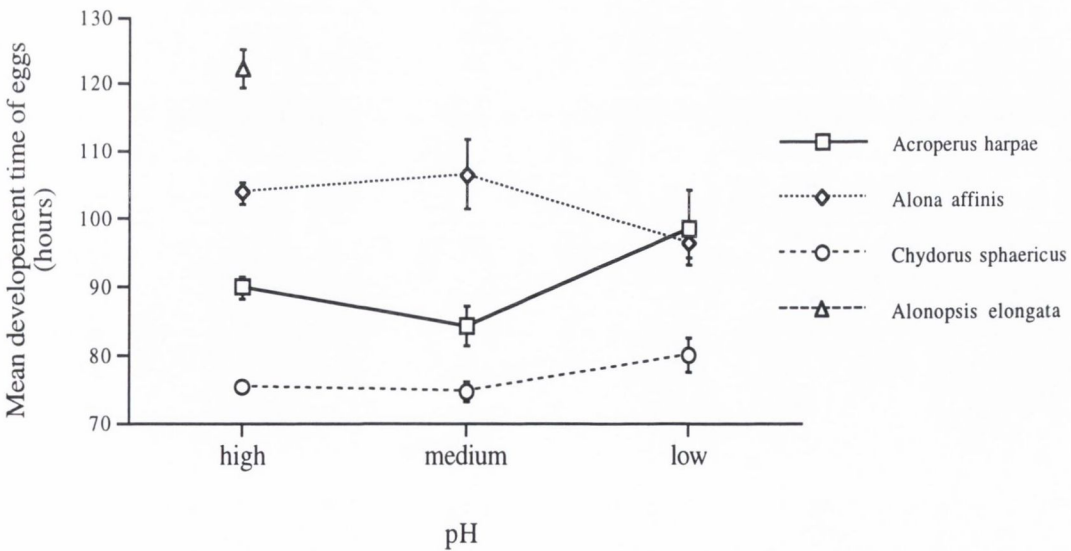
Figure 4.7. Mean egg development times for four chydorid species cultured in three different pH regimes. The bars indicate standard error.

Alonopsis elongata failed to reproduce successfully in the low or medium pH culture mediums. Seventeen individuals were cultured in the low pH and 16 in the medium pH and none of these reproduced successfully. The majority of these individuals died within seven days of being put in either culturing medium. At both low and medium pH, two individuals produced eggs which were passed to the brood chamber, but in both cases, the eggs did not develop fully. Although the culturing medium was changed every two days with new medium adjusted to the required pH, the pH levels did rise in the dishes that the animals were in. It may be that this fluctuation in pH is something which *Alonopsis elongata* is not physiologically adapted to.

An ANOVA of the results show that species, and the interaction between pH and species were significant sources of variation in egg development time (Table 4.4). While pH itself was not a significant source of variation when all species are considered together, LSD post hoc tests show that some of the species have significantly different egg development times in different pH levels, which is why the interaction between pH and species in the ANOVA turns out to be very significant. Egg development of *Acroperus harpae* was quickest at the medium pH level, and slowest at the lowest pH level, and all three pH levels produce significantly different egg development rates ($p \leq$ 0.05). In contrast, at the low pH level, the eggs of *Alona affinis* developed significantly quicker than they did at medium pH ($p \leq 0.05$). At low pH levels, the development time of eggs for the three species are more similar than at other pH levels. In fact, there was no significant difference between the duration of egg development in *Alona affinis* and that of *Acroperus harpae* at low pH, although there was at the other two pH levels. At all pH levels, the eggs of *Chydorus sphaericus* developed the fastest, although the difference was less marked at the lowest pH level.

Table 4.4 ANOVA results for the relationship between pH, species, the interaction (pH x species) and the duration of egg development in four species of chydorids.

Source	df	F-ratio	probability
Constant	1	14353	≤ 0.0001
PH	2	0.97	0.3795
Species	3	87.47	≤ 0.0001
pH x species	4	4.03	≤ 0.005

4.3.3 The number of eggs carried by *Acroperus harpae*

During the course of doing the studies on the effects of temperature and pH on egg development time, it was noticed that *Acroperus harpae* frequently carried only one egg, in contrast to the three other species which almost always carried two eggs. As records were kept of the number of eggs in a brood, temperature and pH, as well as the number of broods of an individual, some analysis of this observation was carried out. Kruskal Wallis tests (rather than ANOVA as the data were not normally distributed) showed that the most significant source of variation in the number of eggs carried by *Acroperus harpae* was the number of times the individual had reproduced ($p < 0.0001$, Chi squared = 29.283, d.f = 3). There were significant differences between the number of eggs carried in the first brood and all succeeding broods, as one egg was very common in the first brood, and two eggs dominated the second, third and fourth broods. The second pregnancy also carried significantly less eggs than the third and fourth pregnancies (Mann Whitney U tests, $p < 0.05$) (Figure 4.8). Temperature also proved to be a significant source of variation($p = 0.047$, Chi squared = 7.96, d.f. = 3), although this was mainly owing to the differences between the number of eggs carried at 16°C

and 20°C. This may be an artefact of an under representation of second or subsequent broods in the 20°C data set. (Figure 4.9). pH was not a significant source of variation in the number of eggs carried by *Acroperus harpae* (Figure 4.10).
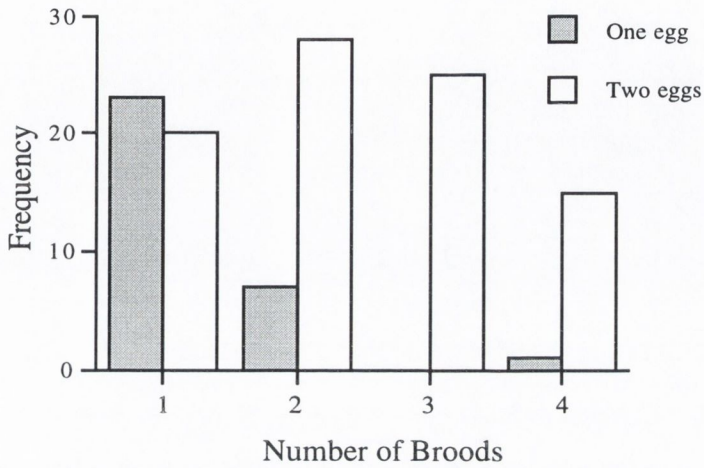
Figure 4.8. The frequency of *Acroperus harpae* broods with one or two eggs in the first, second third and fourth broods. n = 43, 25, 25 and16 for the first, second, third and fourth brood respectively.
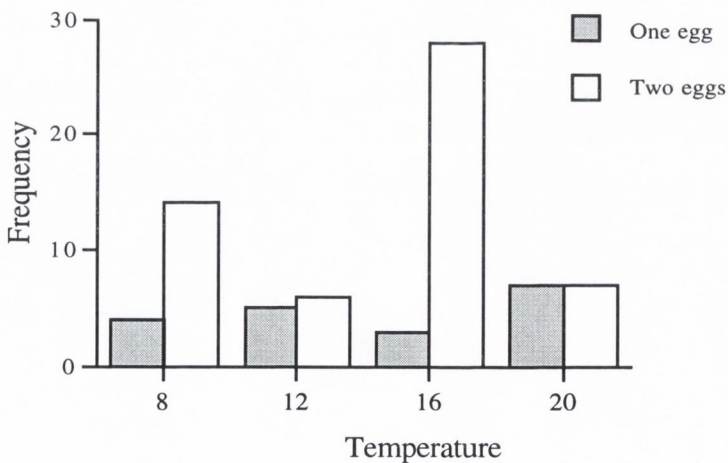
Figure 4.9. The frequency of *Acroperus harpae* broods with one or two eggs, cultured at four different temperatures. n = 18, 11, 31 and 14 for 8°C, 12°C, 16°C and 20°C respectively.
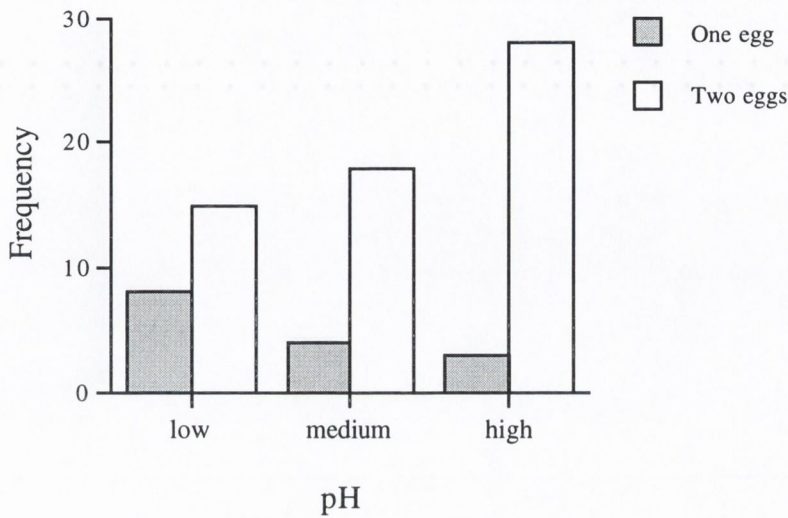
Figure 4.10. The frequency of *Acroperus harpae* broods with one or two eggs, cultured in three different pH levels. Low ph = 5.0, medium pH = 6.6 and high pH = 8.2. n = 23, 22 and 31 for low pH, medium pH and high pH respectively.

4.3.4 The population growth of chydorids in different food sources.

The food type used in each culture proved to have significant effects on the population growths of each of the three chydorid species tested (Table 4.5 and Figure 4.11). Overall, the sterilised detritus proved to be the most successful food source for the three species, with all three species showing positive population growth ($Nt/No \geq 1$). However, all three species had different responses to the food types. An ANOVA on the square root transformed data showed that both food type, species and the interaction between the two were significant sources of variation with respect to population growth (Table 4.6, $p \leq 0.0001$). LSD post hoc tests (at $p \leq 0.05$) showed several interesting interactions between species and food types. *Chydorus sphaericus* did not grow significantly better in any of the food types, and could perhaps, be considered a

generalist feeder. *Chydorus sphaericus* grew significantly better than the other two species in the algae culture. Highest population growth by *Alona affinis* was attained in the sterilised detritus and the detritus treatments, and significantly lower levels were sustained by the algal culture. There was no population growth of *Alona affinis* in filtered pond water, even though both *Chydorus sphaericus* and *Alonopsis elongata* were able to utilise this resource. *Alonopsis elongata* had low population growth in all cultures, in comparison to the other species, and only achieved positive population growth in the sterilised detritus. The growth of *Alonopsis elongata* populations in filtered water and the sterilised detritus was significantly higher than populations grown in detritus or algae.

Table 4.5 Mean population growth, N_t/N_o ± standard error of three chydorid species cultured in four different food types. n in all cases was 5, and N_o was 10 individuals. t = 14 days.

Species	Food Type			
	Algae	Filtered water	Detritus	Sterilised detritus
C. sphaericus	3.5±0.19	3.2±0.26	2.3±0.21	2.9±0.29
A. affinis	2.5±0.23	0.0±0.00	3.4±0.49	3.9±0.54
A. elongata	0.16±0.09	0.5±0.14	0.22±0.09	1.0±0.12

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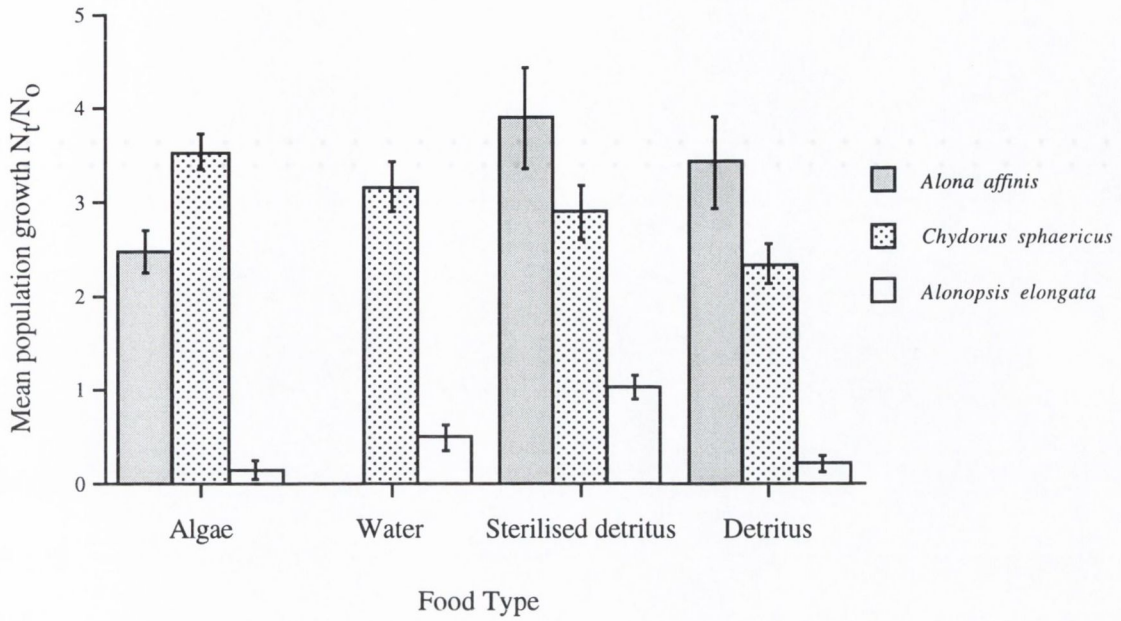
Figure 4.11. Mean population growth, N_t/N_o ± standard error of three chydorid species cultured in four different food types. n in all cases was 5, and N_o was 10 individuals.

Table 4.6. Two way ANOVA to test whether the food type, the species and the interaction between the two were significant sources of variation in population growth.

Source	df	F-ratio	probability
Constant	1	1991	≤0.0001
Food Type	3	30.8	≤0.0001
Species	2	146.3	≤0.0001
Food Type x species	6	37.9	≤0.0001

4.4 Discussion

4.4.1 The effect of temperature on the egg development of chydorids

The role of temperature in controlling egg development time, and hence its relevance to the population dynamics of a species is obviously important. The egg development time of all species decreased as temperature increased. The highest temperature (20 °C) had a strong negative impact on *Alonopsis elongata* which could explain why *Alonopsis elongata* was not found in some of the 29 study lakes with the highest maximum temperatures (Figure 4.12).
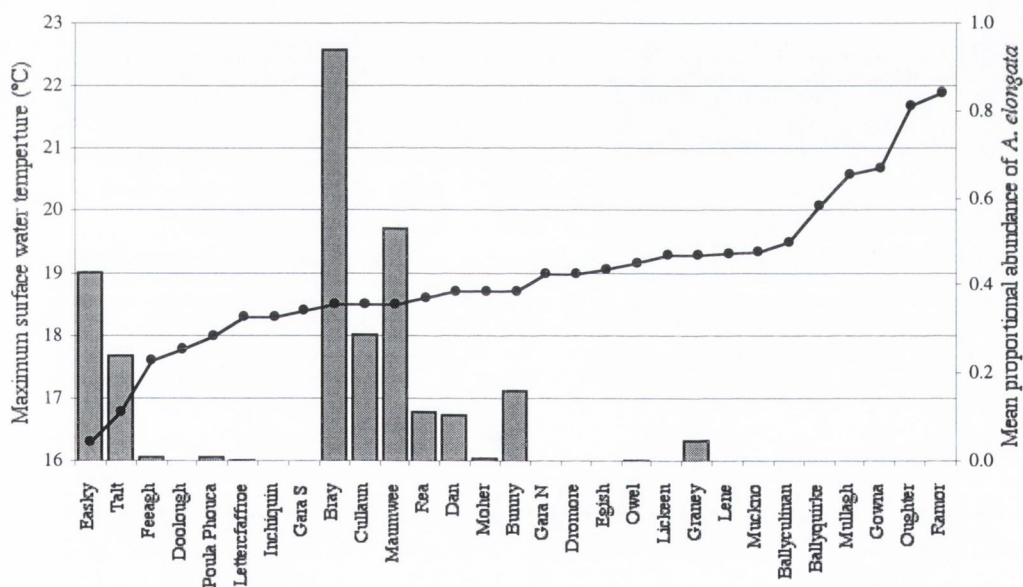
Figure 4.12. Maximum water temperatures (°C) (dotted line) and mean proportional abundances of *Alonopsis elongata* (columns) recorded in 29 study lakes between July 1996 and September 1997.

Although the Bêlehrádek model predicted that *Alonopsis elongata* would have the fastest egg development time at 4°C (which is the average temperature of Irish lakes in

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January), this species was not as abundant over winter as the other species. Of the 29

lakes sampled in January, 1997, the proportion with *A. elongata* populations was very

small (Figure 4.13). At all observed temperatures, *Chydorus sphaericus* had the fastest

egg development time in comparison with the other chydorid species. This is consistent

with other studies (Bottrell, 1974, Keen, 1973) and may at least partially explain the

success of *C. sphaericus* over a wide range of lake types. In some of the 29 lakes

surveyed over two years of the study (Chapter 2), *C. sphaericus* was found to be an

important winter species (Figure 4.13), reproducing by parthenogenesis throughout the

year.
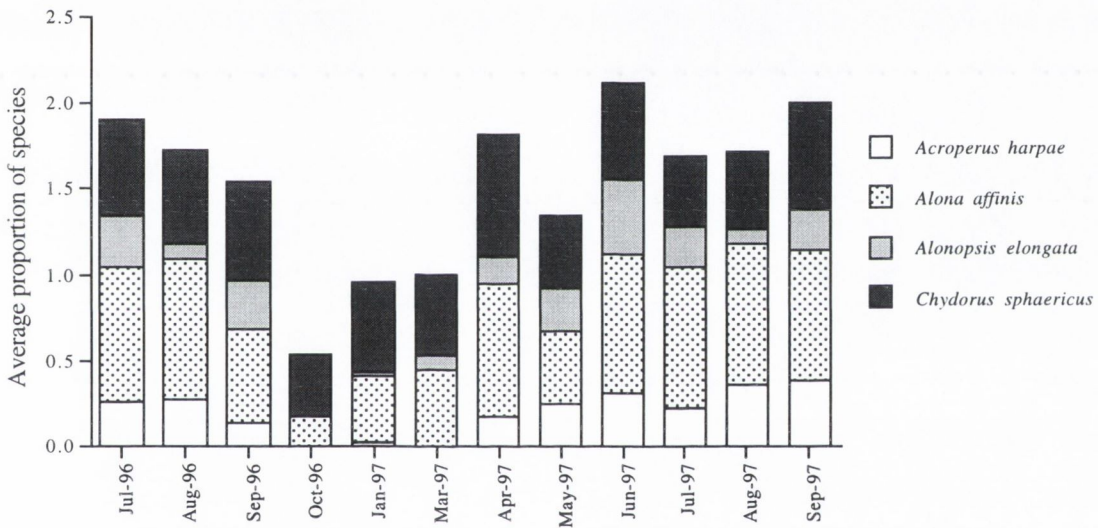
Figure 4.13. The average proportion *Chydorus sphaericus, Alona affinis, Alonopsis elongata* and *Acroperus harpae* in 29 study lakes, sampled between July 1996 and September 1997.

The egg development times of *Chydorus sphaericus* in Bottrell (1974) and

Meyers (1984) were similar to the data from this study (Table 4.7, Figure 4.14). Keen

(1973), however, measured considerably longer egg development times for *C.*

sphaericus than those found in this study, particularly at the lower temperatures (8°C –

16°C). The extent of the difference lessened as the temperature increased, and at 20°C

the egg development times were very similar among all the published studies. Although

only one other publication was found to quote egg development times for *Alona affinis* (Bottrell, 1974), it is also apparent that at high temperatures, the variability in egg development times among different populations is less than that at lower temperatures (Figure 4.15). The egg development times of *Acroperus harpae* were similar to those published by Bottrell (1974), but were quite dissimilar to those published in Keen (1973), which were considerably longer at all temperatures except 20°C (Figure 4.16). The differences between the data from this study, and that published in Keen (1973) highlights the fact that egg development times may vary quite considerably among populations of the same species, and this should be taken into careful consideration if literature derived egg development times are used to estimate population dynamics of different populations. No records of egg development time of *Alonopsis elongata* were found in the literature, so it is impossible to know how the egg development of Irish populations of *A. elongata* compares with populations from elsewhere.

Table 4.7. Egg development times (hours) of chydorid species from four different studies at 8°C, 12°C, 16°C and 20°C.

Species	Temp (°C)	Bottrell, 1974 Thames, U.K.	Keen, 1973 Lawrence Lake, Michigan	Meyers. 1984 Wisconsin	This Study Irish Lakes
Chydorus sphaericus	8	205	350		220
	12	130	220	125	114
	16	93	130	80	75
	20	71	62	58	69
Alona affinis	8	273			336
	12	178			146
	16	127			103
	20	96			79
Acroperus harpae	8	247	400		294
	12	158	260		128
	16	107	150		90
	20	77	75		75
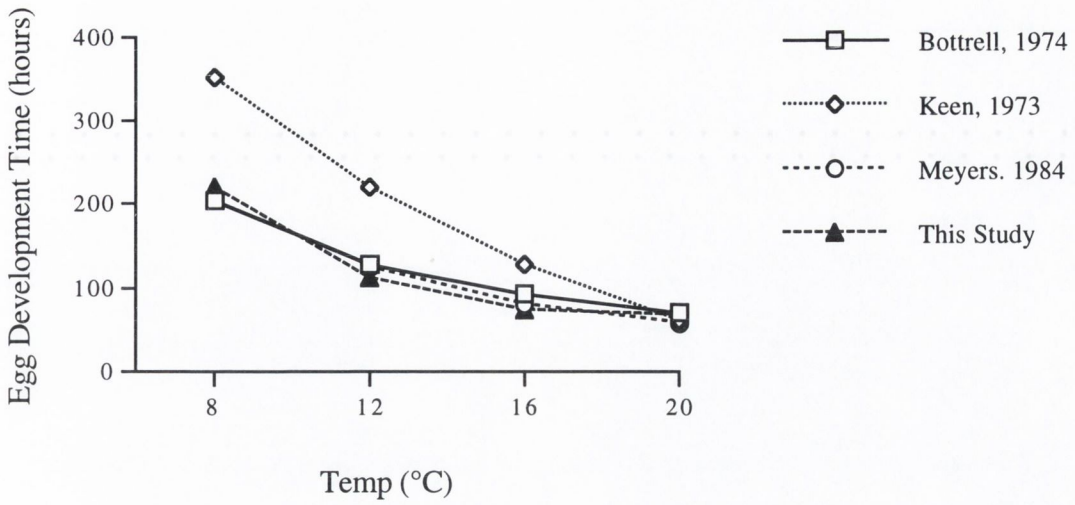
Figure 4.14. Egg development times of *Chydorus sphaericus* taken from four different studies.
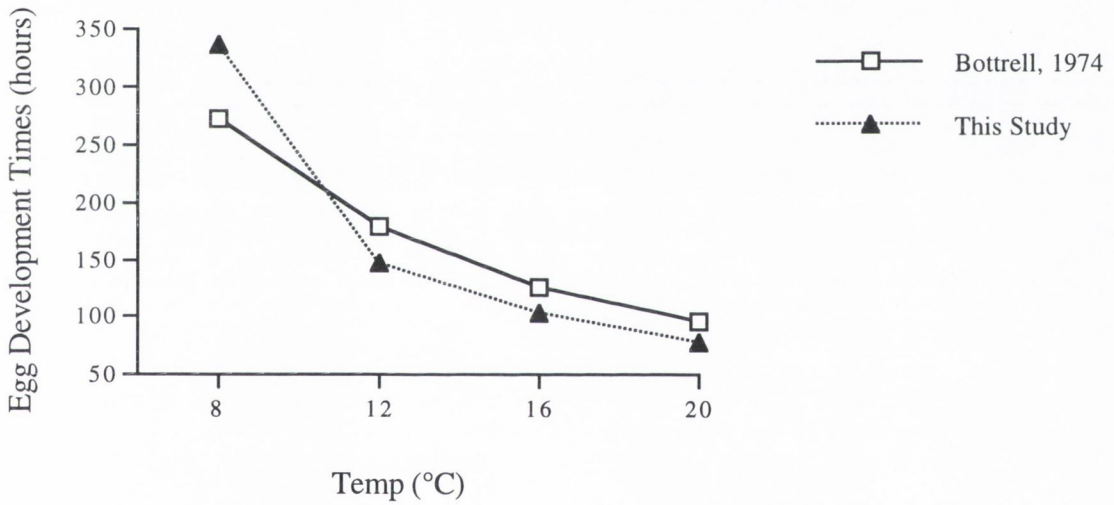
Figure 4.15. Egg development times of *Alona affinis* taken from two different studies.
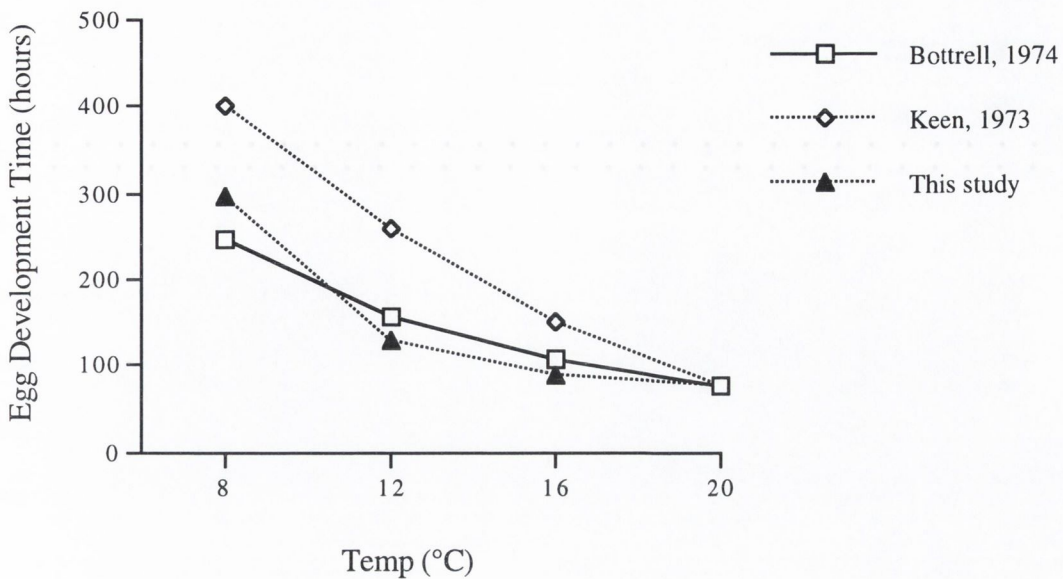
Figure 4.16. Egg development times of *Acroperus harpae* taken from three different studies.

Changes in temperature did not affect all the species to the same degree as can be seen from the slopes of the observed data (Figure 4.1) and that obtained from the predicted Bêlehrádek curves (Figure 4.6). This means that each species has a temperature at which it reproduces favourably in comparison to other species. This is certainly going to have implications for the seasonal dynamics of chydorid species. At 8°C, for example, the egg development times of *Alona affinis* and *Alonopsis elongata* were practically the same, even though at higher temperatures *Alona affinis* had significantly faster development times. If the Bêlehrádek model is used to extend the development curves to colder temperatures, it is predicted that *A. elongata* would have a significantly faster egg development time than the other four species at 4°C. The reliability of the use of this model would be increased if more data points were available. The lack of development of *A. elongata* at 20°C is, however, a valid observation (rather than just a lack of data), and the curve over the other three temperature points is obviously different to those of *A. affinis, A. harpae* and *C. sphaericus*. This indicates that a decrease in temperature affects *A. elongata* to a lesser

degree than the other species. and this may explain its predominance in northern (and hence colder) areas of Britain (Fryer, 1993). It may also explain why it is successful in the colder, upland lakes in Ireland (Figure 4.17). It is, however, apparent that colder temperatures are not the only factor favouring high proportions of *A. elongata*, as high proportional abundances were found in Maumwee, Cullaun and Bunny, none of which have particularly low mean water temperatures. While lower temperatures may mean that *A. elongata* can reproduce faster than other chydorid species, it appears that it can not fully explain the dominance of this species is some lakes.
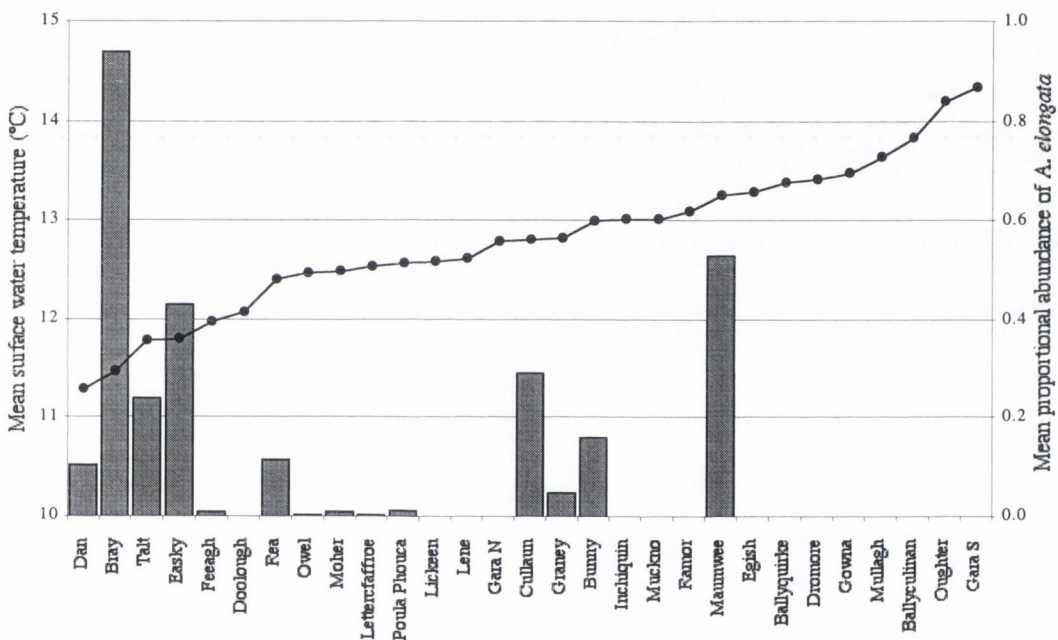
Figure 4.17. Average surface water temperatures (°C) (dotted line) and mean proportional abundances of *Alonopsis elongata* (columns) recorded in 29 study lakes between July 1996 and September 1997.

In order to attempt to see how the different responses to temperature might affect the seasonal dynamics of each species, I attempted to link the egg development times from this chapter with observed seasonal abundances counted for Chapter 2. This, however, proved difficult, as the sampling intervals between July 1996 and September 1997 were generally a minimum of 30 days, which is too long for population modelling.

Keen (1973), for instance, took samples of chydorids for population dynamic studies every two – seven days. The data on egg development times, however, could prove useful for comparisons with future studies on these species. In particular, it would be interesting to compare the data for *A. elongata* with other data from populations outside Ireland.

4.4.2 The effect of pH on the egg development of chydorids

It was found in this study that pH significantly affected the egg development time, which is not in agreement with the opinion of Meyers (1984) that water chemistry does not affect egg development. The pH of the water that the animals were kept in affected each species differently. The eggs of *Alona affinis* developed fastest at low pH, *Acroperus harpae* at medium pH and *Chydorus sphaericus* at medium and high pH. The development of the eggs of *Alonopsis elongata* eggs was totally inhibited by the low and medium pH, although some eggs were passed into the brood chamber. None of them, however, developed fully. It is difficult to know whether the animals were reacting to the pH that the water was adjusted to, or whether they were reacting to fluctuations in the pH over periods of two days. As soon as the animals were put into new containers of water adjusted to the required pH (either 5.0 or 6.6), the pH began to rise, and by the time the water was changed again (2 days later), the pH had, on occasion, risen by up to 2.0 units. As *A. elongata* is frequently found in lakes with very low acidity (lower than 5.0), it is unlikely that the individuals in this experiment were being killed by the lower pH levels. It seems more likely that this species was sensitive to rapid rises in pH, and it was the fluctuations over the two day period which caused the inhibition of egg development. If this is the case, then this in itself, is an interesting result as the other three species were not inhibited to the same extent by the fluctuations. It may be the pH fluctuations caused the observed changes in egg

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development time in the other species, but the animals were still able to produce viable eggs and neonates. It seems likely therefore, that species of chydorids which are very sensitive to fluctuations in pH (such as suggested for *Alonopsis elongata*) will not reproduce very well in lakes where large fluctuations are commonplace. In lakes with large amounts of algae, the pH can often rise considerably during the day, because as the algae photosynthesise, they use up CO_2, and secrete OH- ions. At night time, respiration replaces the CO_2 and the process reverses (Jeffries & Mills, 1990, Wetzel, 1983). Thus, diurnal pH fluctuations in eutrophic lakes with large standing crops of algae are likely to be more severe than in lakes with low concentrations of phytoplankton. This may explain the absence of *Alonopsis elongata* from lakes with high nutrient loads and concentrations of chlorophyll *a*, as diel fluctuation in pH may mean that reproduction in this species is inhibited. Furthermore, lakes with large amounts of diel fluctuations are also likely to have large amounts of seasonal fluctuations in pH, as concentrations of algae increase and decrease. When proportional abundances of *A. elongata* are plotted against fluctuations in lake pH (maximum pH − minimum pH), there is a marked lack of populations in lakes with large differences in seasonal pH (Figure 4.18).
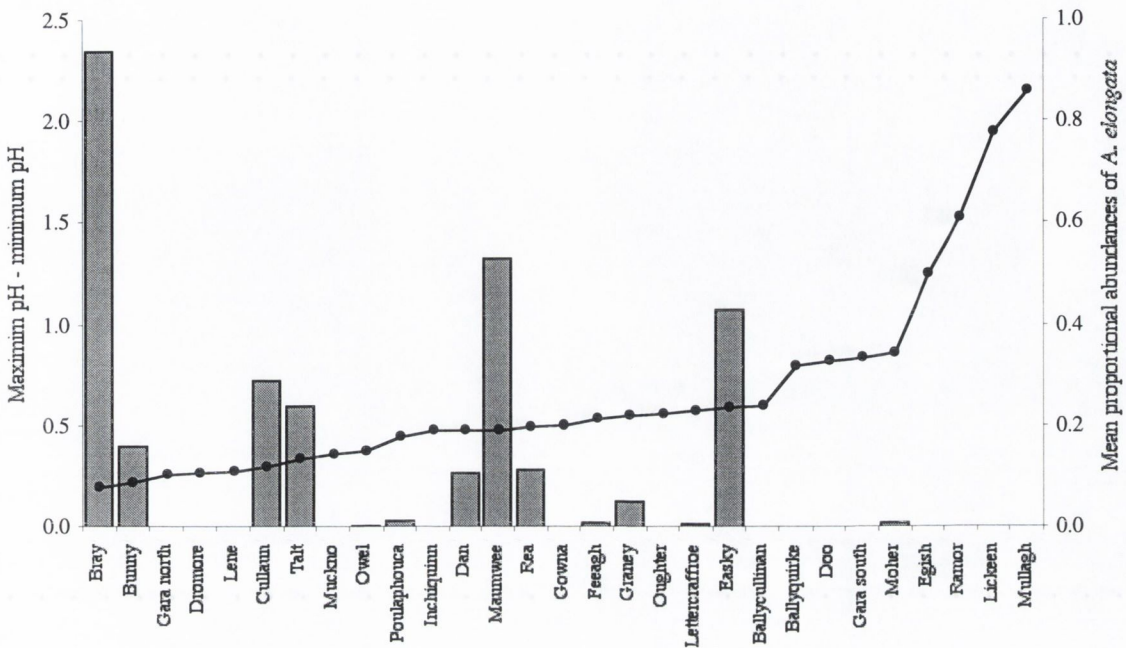
Figure 4.18. Mean proportions of *Alonopsis elongata* in lakes ordered left to right according to the range of pH (maximum pH – minimum pH) measured between July 1996 and September 1997.

4.4.3 The occurrence of one-egged broods in *Acroperus harpae*

Keen (1973) suggested that low food availability, old age or overcrowding may result in chydorids carrying only one egg, rather than the more usual two. In this study, however, it was found that the size of the brood carried by *Acroperus harpae* depended on how many times the individual had reproduced. High proportions of one-egg broods were found to occur during the first reproduction, and two-egg broods during the second, third and fourth reproduction. In *Daphnia* populations, temperature and body size of the mother have an effect on the size of the brood (Orcutt & Porter,1984; Hebert,1978; Kerfoot,1974). Changes in temperature in this study did not adequately explain why some broods had only one egg, but it is possible that at the time of first

reproduction, the carapace length of *A. harpae* individuals was smaller. Whatever the reason for the observed differences in brood sizes, the occurrence of one egg broods in *Acroperus harpae* may have implications for its population growth.

4.4.4 The effect of food type on population growth of chydorids

It has been shown that *C. sphaericus* is tolerant of a wide range of conditions (this chapter), and has a ubiquitous distribution (Chapter 2). The success of *Chydorus sphaericus* in a wide variety of lakes may also be attributable to its generalist habit of feeding. Populations of *C. sphaericus* grew equally well in all the food sources provided in this study: algae (*Chlamydomonas*), detritus, sterilised detritus and water. This generalist nature of *C. sphaericus* was also noticed by Lundstedt (1991), who fed *C. sphaericus* several different types of algae, and found there was very little variation in population growth with varying food sources. The fact that populations of *C. sphaericus* were found to be the most successful (in comparison to the other species) when fed on a culture of algae and on filtered pond water is very interesting, as this species is often found in the pelagic zooplankton. Although some authors observe that this is probably a result of it being able to use algal mats as a substratum on which to live (Fryer 1968, Havens, 1991) it seems that this species can also utilise food sources which are likely to be found in the openwater, and is not constrained to feeding on detritus or among plants. The material in filtered water ($< 30\mu m$) can even support healthy populations of *C. sphaericus*, probably because it is very adept at collecting tiny particles (Fryer, 1968). Its ability to feed on algae may also explain why this species does particularly well in nutrient enriched lakes with high concentrations of chlorophyll *a*. In shallow lakes, a switch from macrophytes to phytoplankton may favour *C. sphaericus* as it does not appear to depend on periphyton or detritus for food, but can survive well on phytoplankton food. A switch from an ecosystem dominated by rooted

macrophytes to a phytoplankton dominance in a lake may, therefore, result in an increase of *C. sphaericus* for two reasons, the use of filaments of algae as a substratum and an ability to utilise an open-water phytoplankton food source. This may explain why Whiteside (1970) observed that in extremely (organically) polluted lakes, species such as *C. sphaericus,* which do not have an affinity for plant beds (perhaps either as a substratum, or as a source of food in the form of periphyton, or more likely, both) are more abundant.

In contrast to *Chydorus sphaericus*, the growth of populations of *Alona affinis* was lowest when the food sources were algae and water filtered through 30μm, and highest when the food source was detritus. The population in filtered water was totally unsuccessful, implying that *Alona affinis* is not adept at collecting very fine particles, and those that it does collect do not provide enough nutrition. Similarly, populations of *Alona affinis* did not grow as well in the algal culture as they did in the detritus treatments which may be a result of the small size of the cells (14-22μm). The *A. affinis* populations, did, however, grow better in the algal cultures than in the filtered water. This implies that while they may be able to collect small particles, they need a large amount of them to survive. This was attained in the algal culture as it contained both small particles from the pond water, and extra algal cells. The use of detritus, rather than algae or water, as a food source indicates that this species is a true littoral inhabitant, and is not restricted to living, photosynthesising material for nutrition. Unlike *Alona affinis*, *Alonopsis elongata* was able to survive in the filtered water, probably because it is capable of extracting small particles from suspension (Fryer, 1968). The algae and the detritus cultures proved to be the least suitable food sources for *Alonopsis elongata*, which may indicate why this species is not successful in nutrient enriched waters, where the most likely food sources would be an abundance of algae, or well developed epiphyton (as simulated by the non – sterilised detritus).

In all three species, the unsterilised detritus proved to be a less successful culturing medium than the sterilised detritus which was used to see whether the animals would survive better with or without well developed epiphyton. The detritus culture did have a lot of other animal life present in it such as other chydorids (*Alona guttata* and *Graptoleberis testudinaria*) and oligochaete worms which may have been competing with the experimental species for resources, and inhibiting their growth and reproduction. However, the success of the sterilised detritus for culturing chydorids indicates that these animals do not need living, photosynthesising material for nutrition, as the beakers, once sterilised, were all kept in the dark for the duration of the experiment. At the temperature that the food experiments were done at (16°C), *Chydorus sphaericus* has the fastest rate of egg development, followed by *Alona affinis* and *Alonopsis elongata* (section 4.3.1). If reproductive rate was the only factor controlling population growth, it would be expected that *C. sphaericus* should have the highest population growth, followed by *A. affinis* and *A. elongata* for all food sources. This was only found to be true for the algal food source. In two of the four food sources tested, *A. affinis* attained higher population growth than *C. sphaericus*. This implies that there is more than just reproductive factors involved in controlling the populations of chydorids, and food type may be an important consideration.

In conclusion, this experimental work has provided some insights into the differences among the four chydorid species used in the study. The results may explain why species can coexist without outcompeting each other. In addition, the information also suggests why some species may become dominant in particular types of lakes. The four species tested all showed varying responses to the three factors investigated – temperature, pH and food source. *Chydorus sphaericus* was found, generally, to be the most tolerant of all conditions which is consistent with its success in a wide variety of

lake conditions. The outcome of the food experiments indicate why this species may be particularly successful in lakes where macrophytes have been replaced by high crops of phytoplankton, and where the littoral environment is not as complex and diverse as it once was. While the egg development time of *Alona affinis* was found to be relatively slow in comparison to *Chydorus sphaericus*, it was able to sustain high population growth in three out of the four food sources tested, and in two cases (the detritus and the sterilised detritus), population growth of *Alona affinis* was slightly higher than that of *Chydorus sphaericus*. This indicates that even though this species may be slow to reproduce, under certain conditions, it can thrive, and probably dominate a chydorid community. *A. affinis* had relatively high population growth when the food source was detritus, particularly sterile detritus (without periphytic growth). This is consistent with observations that this species is a pioneering species (Robertson, 1990, Whiteside, 1970), not reliant on well developed, diverse macrophytes for success. *Alonopsis elongata* proved to be the hardest species to culture and was also relatively unsuccessful in most of the conditions of the three experiments. This was surprising as this species was very common in several of the lakes sampled over the two years field study. The experiments on egg development time under different pH regimes indicated that this species may be sensitive to fluctuations in pH, and this probably indicates that this species will be more successful in lakes where the pH is relatively stable. These kinds of lakes are likely to be oligotrophic, with low nutrient status and small standing crops of algae, and which are not affected by sporadic acidification events. In addition, the lack of population growth of *Alonopsis elongata* when fed on algae alone is consistent with the lack of this species in nutrient enriched waters. The fact that the eggs of *A. elongata* did not develope at 20 °C is also consistent with its absence from the lakes with highest maximum temperatures. The marked contrast in the effect of temperature on *Alonopsis elongata*, in comparison to the other three species will probably have implications for its success in colder water. These conclusions, however, do not explain

why this species is so successful in some of the shallow lakes such as Lough Maumwee, and Lough Easky, with low pH and nutrient status, but which do not have low mean temperatures.

Chapter 5.

General Discussion.

In this chapter, the potential factors influencing the structure of the chydorid community are discussed, in the light of the results from both my own work, presented in Chapters 1-3 and that of the literature. Throughout this thesis, I have used the word 'community' to describe the chydorid species composition and relative abundances in each lake, and as defined by the simple definition of the term community as *"a group of species populations occurring together, as in a pond or woodland"* (Giller, 1984). For some authors, the word 'community' implies a certain level of interaction between the animals. Putman (1994) described the community as *"an interactive assemblage of species occurring together....where ecological function and dynamics are in some way interdependent"*. If, therefore, interactions between different species of chydorids are negligible, the term 'assemblage' may be more appropriate for describing the collection of chydorids in a lake. A quick perusal of the literature concerning chydorids shows that the two terms, community and assemblage, are often used interchangeably, perhaps or perhaps not reflecting the degree of interdependence of the chydorids within each site. This discussion focuses on the processes which structure the chydorid community, which may involve interactions with the wider littoral community (and indeed the lake as a whole) and interactions within the chydorid community.

The structure of any group of organisms in a lake is determined by a number of multi-layered processes which combine to form the characteristic community or assemblage found in the present day (Lawton, 1999; Begon, Harper & Townsend, 1996; Putman, 1994; Holt, 1993; Townsend, 1991; Giller, 1984). Roughgarden and Diamond (1986) combined these processes into a theme which they called "limited membership", a phrase originally coined by Elton (1927), to provide understanding of a wider question, "why is it that what *does* occur together constitutes a limited subset of what *might* occur". The processes that affect the diversity and structure of the community can be summarised as follows:

1. What species are available to colonise a community?

2. What species are taken from the pool of potential candidates?

3. What species can maintain viable populations?

A community can only include species which are able to get to the area to be colonised, and this is mainly reliant on the biogeography and dispersal of chydorids. The two crucial biogeographical factors which appear to affect how many species can colonise a lake are the size of the lake (or 'island' in classical biogeographical terms) and the distance of the lake from other sources. Relationships between species richness and waterbody size have been noted for crustaceans in Yorkshire (Fryer,1985) and in North America (Dodson, 1992), with larger water bodies having more diverse fauna. This was not found to be the case in the 29 study lakes (Chapter 2), although this is probably because all the lakes were relatively big (the smallest was 47,000m^2) and did not represent a large range in lake size. The size of the lake may be important for several reasons. As lake size increases, so too does the potential for colonisation from the catchment, as the area of contact increases between the 'island' and the surrounding area. Also, as a lake increases, it is likely that the number of different habitats will also increase, thus presenting more varying niches for colonisation. The size and extent of the littoral zone of the lake, in comparison to the open water may be of more relevance to the chydorid group than the actual size of the whole lake. Evidence of this is provided in Chapter 3, where it was shown that Lough Maumwee, which has a surface area of 27 hectares, had comparable chydorid species richness (16 species versus 17 species) to Lough Inchiquin which has a surface area of 115 hectares. Lough Maumwee, however, is much shallower than Lough Inchiquin, and the littoral zone extends over the majority of the lake's bottom. This may be why it has high species richness, even though it is a relatively small lake. The number of lakes within a twenty kilometre radius was also a significant factor affecting species richness, with species richness increasing as the

number of lakes close by increased (Dodson, 1992). This is also known as the "species pool affect", with the number of species in the surrounding area being critical to the number of species available to colonise a new area (Zobel, 1997). The dispersal success of chydorids is probably reliant on ephippial eggs which can withstand large fluctuations in environmental conditions, and then hatch in a new environment. Connectance of lakes and ponds by ditches, streams and rivers may also provide a means of dispersal for non ephippial individuals, and indeed diverse chydorid communities have been recorded from several rivers, including the River Thames in England (Robertson, 1990).

Just because a species can reach a new area does not necessarily mean that it will be able to inhabit it. The autecological requirements of each species will determine whether it can initially live in a lake with particular characteristics; notably abiotic but possibly also biotic features of the environment (Holt, 1993). Although many species of chydorids have been shown to tolerate a wide range of the physicochemical variables found in lakes, some do have very definite ecological boundaries which would likely exclude them from some waterbodies. These may include temperature, pH, alkalinity, nutrient concentrations, wave action, turbidity and salinity. Thus, the absence of *Alonopsis elongata* and *Alonella excisa* from lakes with high nutrient status and the preference of *Chydorus piger* for lakes with low alkalinity and pH may be attributable to some chemical boundary which these species cannot overcome physiologically. The autecological work on *Alonopsis elongata* suggests that fluctuations in pH and high temperatures may be a limiting factor for this species. Indeed, the four species tested in Chapter 4 all had differing responses to changes in temperature and pH, which indicates that while their autecological requirements may overlap, they will ultimately have different ranges of tolerance.

If a species has succeeded in reaching an area of potential colonisation, and with suitable physicochemical conditions, it must still develop and maintain a viable population in order to persist in the community. There are many biotic and abiotic factors which influence the success of a species in a community, and depending on how the species copes with each factor will determine its abundance relative to other species. Biotic factors which may influence the success of chydorid species include competition, predation, mutualism and parasitism (Begon, Harper & Townsend, 1996; Putman, 1994; Townsend, 1991; Giller, 1984). Abiotic factors include spatial heterogeneity, water chemistry, sediment structure, environmental fluctuations, seasonal variation and stochastic events such as disturbance. All these factors interact to structure the community which is characteristic of a lake, but some may be of more importance than others.

Many attempts have been made to try and make sense of patterns in community structure. The role of competition has, for a long time been considered fundamental to species diversity and community structure (Stewart, 1996; Townsend, 1991; Giller, 1984) and has been a subject causing divisive debates in ecology (McIntosh, 1995). In the earlier part of this century, the view of a community as an organised, repeated unit, with interspecific competition (and possibly predation) being the main factor determining its structure, was common (McIntosh, 1995). This view was firmly rooted in the views put forward by Clements (1936) who likened communities to superorganisms. Such communities were thought to have attained (or were on their way to reaching) equilibrium, and were resistant to change. An alternative hypothesis was put forward by Gleason (1926) and came to be known as the "individualistic concept". This held that communities were structured more by the dispersal ability of species and abiotic factors such as environmental variation and disturbance, than by biotic interactions (although biotic interactions were important to a certain degree). In a

review of these two concepts by McIntosh (1995), many communities were found to support the Gleasonian, individualistic theory of community structure. Approximately the same amount supported the Clementsian, organismic theory, while many were found to be intermediate between the two. Putman (1994) suggests that equilibrium communities, structured by biotic interactions, are more likely to be composed of vertebrates and K-strategists, while non-equilibrium communities influenced strongly by abiotic factors would probably be made up of r-strategists such as insects and other invertebrates. This seems to be a misleading generalisation, as even among small groups of insects, there is likely to be a large range of reproductive strategies, which, within that group, could be considered r or K strategies. This is probably why McIntosh (1995) found that a wide range of habitats and taxonomic groups supported the Gleasonian or the Clementsian view of community structure, with neither being supported by a particular type of community.

Recognising the fact that a dichotomy between two poles of opinion (biotic versus abiotic factors, equilibrium versus non-equilibrium, interactive versus non-interactive etc) probably did not accurately represent the wide ranging and interacting factors governing community structure, Schoener (1986) devised two sets of axes, along which a wide variety of communities could be spread. The first set of axes comprised organismic characteristics such as body size, generation time and homeostatic ability, while the second set of axes comprised environmental variables such as trophic position, spatial fragmentation and partionability of resources. Depending on the position of the community along these two primitive axes, the community's position along a set of derived axes could be predicted. These ten derived axes encompassed such variables as the relative importance of physical versus biological processes, the relative importance of predation versus competition and the likely outcome of competitive interactions. In such an analysis, Schoener hoped to be able to ascertain

whether attributes of communities tend to be determined by organism characteristics or by environmental characteristics. This scheme is highly complicated but it does serve to highlight the fact that communities with different attributes such as trophic level, body size and homeostatic ability will be affected to a greater or lesser degree by the commonly quoted factors determining community structure.

In seeking general laws in ecology, Lawton (1999) advocated a macroecological approach, which is defined as the search for major, statistical patterns in the types, distributions, abundances and richness of species, from local to global scales, in order to decipher patterns in community ecology. In this respect, the role of wider ecological factors such as regional and historical processes may be equally important to community structure as local interactions such as competition. By plotting local species richness (i.e. of the community) against regional richness (i.e. of the species pool, described above) two types of curves may be produced (Figure 5.1) (Lawton, 1999; Cornell & Lawton, 1992; Decamps & Tabacchi, 1992; Ricklefs, 1987). Type I is a straight line, with local richness directly proportional to, but less than regional richness. This relationship suggests that species interactions such as competition and predation are not as important in structuring the community as are regional factors such as the size of the regional species pool. In contrast, Type II is a curvilinear line which reaches a plateau as the community becomes saturated. In this case, species interactions are very important in structuring communities. Lawton (1999) considered that realistic communities could lie anywhere between a Type I and a Type II system, as species interactions become more important. In addition communities which have a high degree of interspecific competition may conform to a Type I system because environmental disturbance and spatial heterogeneity reduce competition (and hence saturation is rare) (Lawton, 1999; Decamps & Tabacchi, 1992). This approach to studying community structure, therefore, allows communities to be characterised within a continuum,

between interactive and non-interactive and may be useful in determining what the overriding factors affecting the structure of a community are.
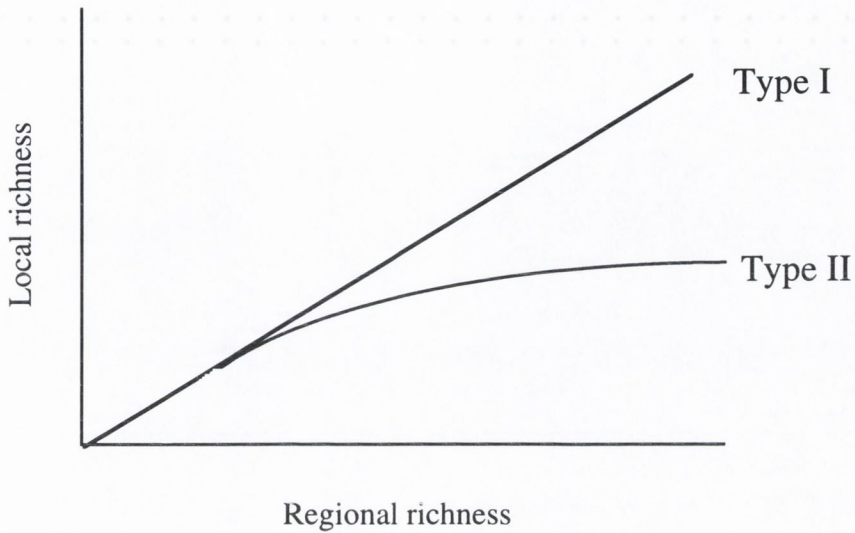
Figure 5.1. Two theoretical curves for the relationship between local and regional species richness in ecological communities (After Cornell & Lawton, 1992).

The preceding discussion of theories regarding community structure seeks to demonstrate how thoughts about the role of competition in community structure have evolved, and how some theories have developed about how all the various factors affecting community structure interact. While competition may be very important in structuring communities, other factors such as regional species richness and environmental disturbance may be of equal, or more importance for some communities. The role which competition plays in the chydorid community structure is unclear. There are, however, some indications that competition may not play an important role in this area. For competition to play an important role in a community, interactions have to take place, by which one organism consumes a resource that would have been available to another (Begon, Harper & Townsend, 1996). Competitive exclusion occurs when this interaction effectively excludes the second organism from the community, and hence changes community composition and diversity. There are many ways in which a group

of animals can minimise the effects of competitive exclusion, including resource partitioning, spatial heterogeneity and temporal variation (all of which interact to a large degree) (Allan, 1973). It is probable that the chydorid group can employ all these techniques in order to avoid competition.

The niche model (Jennions, 1997) explains coexistence owing to resource partitioning and/or spatial and temporal heterogeneity (Jennions, 1997; Giller, 1984; Townsend, 1991; Putman, 1994; Chesson & Case, 1986). The adaptive radiation shown by chydorids in relation to feeding and habitat selection indicates that they can exploit a wide range of ecological niches (Fryer, 1968), and probably decrease the impact of competition within the chydorid community. Chydorids are known to distribute according to habitat preference (Duigan & Kovach, 1994; Robertson, 1990; Chengalath, 1982; Campbell, Clarke & Kosinski, 1982; Quade, 1969; Smirnov, 1963; Smirnov, 1962; Crisp & Heal, 1958; Smyly, 1958). The results from Chapter 3 described the chydorid community of Lough Inchiquin as having quite distinct assemblages, associated with different habitats. Spatial heterogeneity, therefore seems likely to be important for the coexistence of chydorid species within the scale of the whole lake. In addition, Chapter 4 showed that different species had significantly different responses to varying food type, indicating that resource partitioning is also a realistic explanation for coexistence of chydorid species. A final explanation for why so many species of chydorids can coexist in a community may be that food is not limiting. Chydorids are, in general, detritivores, and detritus (and the associated periphyton) is an abundant food source in the littoral zone. Hence competition for food among this group may not be relevant.

If it is true that competition is not very important in structuring chydorid communities, than what is? The role of predation in controlling community structure

has been shown to be important in many communities (Townsend, 1991), including freshwater zooplankton (Allan, 1973) and chydorid communities (Havens, 1991; Williams, 1983). Invertebrate predators were particularly important in controlling the abundances of chydorids in Lake Itsaca, USA (Williams, 1983), where populations protected from invertebrate predation did not crash during the summer, unlike the unprotected populations. While the number of studies on the effects of predation on chydorids is small, it is highly probable that predation is a realistic biotic factor which should be included in any discussion of chydorid community structure. The role that disturbance plays in structuring communities also appears to be an important one, with two fold implications. The first is that disturbance may decrease the importance of competition, as species do not have time to competitively exclude others, before the community is disturbed and effectively reset to a pioneer community. Evidence of this being the case in chydorid communities is suggested in Chapter 2, where lakes with wave washed shores are dominated by *Alona affinis*, a species known for its pioneering abilities, and its tendency to be the first species in newly formed habitats (Robertson, 1990, Whiteside, 1970. The second implication of disturbance is that when it is a feature of a habitat (either frequent large disturbances such as wave action or severe environmental stress), the community becomes *"dominated by opportunistic and rapid colonisers, or species capable of tolerating the form of damage sustained"* (Giller, 1984). Again this has been demonstrated in Chapter 2, where it was noted that lakes under environmental stress, or with wave washed shores were dominated by one species, and as the environmental stress became less, diversity increased. This pattern had been noted in many other communities, and led to the formation of the "Intermediate Disturbance Hypothesis" (Connell 1978), which holds that greatest community diversity will occur at moderate levels of disturbance or environmental stress (Figure 5.2). At low levels of disturbance, high diversity is not found, because competitive exclusion may eliminate some species from the community.
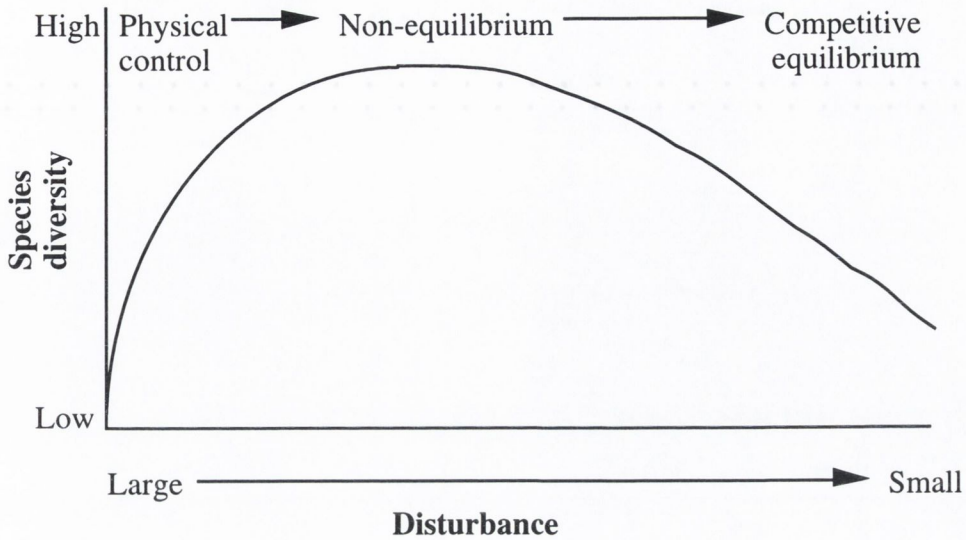
Figure 5.2 The Intermediate Disturbance Theory. (After Connell, 1978).

The roles of competition and disturbance in community structure, therefore, seem to be inextricably linked. In the case of chydorids, however, competitive exclusion may be avoided (or reduced) because relatively abundant food, spatial heterogeneity, temporal variation (seasonal cycles) and resource partitioning reduces the chance that animals will compete for resources. In such communities, species diversity will remain high even when disturbance levels are minimal, and competitive exclusion is probably rare.

Returning to the two types of curves in Figure 5.1, it seems likely that chydorid communities will tend towards Type I curves. While interspecific competition may occur in chydorid communities, they are unlikely to become saturated, or reach equilibrium, owing to the effects of environmental disturbance, heterogeneous spatial distributions, temporal variation, resource partitioning and an abundant food supply. If this is shown to be the case for chydorid communities, further studies of their structure may need to include more macroecological factors such as the size of the regional species pool and the isolation of the lake in question. The use of chydorids as indicators of ecological quality is, I think, strengthened by the conclusions of this discussion as it

seems likely that depauperate communities (such as those highlighted in Chapter 2) are a result of disturbance or environmental stress, rather than biotic interactions. Although predation probably has a large effect on the chydorid communities, it is likely that it is quite seasonal, as the predators themselves (invertebrates rather than fish) will follow seasonal patterns of dominance. In addition, any disturbance or environmental stress which detrimentally effects the chydorid community is also likely to affect their invertebrate predators to some extent. Abiotic factors such as disturbance and the size of the regional species pool seem, therefore, to be the most important factors affecting the *long term* structure of chydorid communities, although biotic interactions, such as predation may be an important factor determining seasonal community structure. This means that chydorid communities may be relatively unstable and inherently sensitive to environmental perturbations, which a community structured more by biotic interactions may not be.

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Appendices

Appendix A. Occurrence of Chydorid species in 29 lakes in Ireland.

Species	Ballycullinan	Ballyquirke	Bray	Bunny	Cullaun	Dan	Doolough	Dromore	Egish	Easky	Feeagh	Gara North	Gara South	Gowna	Graney	Inchiquinn	Lene	Lettercraffroe	Lickeen	Maumwee	Moher	Muckno	Mullagh	Oughter	Owel	Poulaphouca	Ramor	Rea	Talt	No. of occurences
Acroperus harpae	•	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•		•	•	•		•		•		•	•	•	25
Alona affinis	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	29
Alona costata	•	•	•	•	•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	26
Alona guttata				•		•		•				•				•			•		•		•			•				7
Alona intermedia		•							•						•		•	•					•		•					7
Alona quadrangularis		•										•	•			•	•			•	•	•		•					•	10
Alona rectangula		•		•	•			•				•	•	•	•	•	•		•			•		•		•	•	•	•	17
Alona rustica		•	•			•			•	•	•	•		•	•				•							•	•			11
Alonella excisa			•	•	•	•	•			•			•			•			•	•							•	•	•	11
Alonella exigua	•	•		•	•			•				•			•		•		•	•									•	11
Alonella nana		•			•	•	∘		•			•			•		•		•	•	•	•							•	14
Alonopsis elongata	∘		•	•	•	•			•	•				•					•					•	•	•		•	•	15
Anchistropus emarginatus				•				•										•					•							4
Camptocerus rectirostris			•		•	•	•				•	•	•	•	•					•	•	•							•	13
Chydorus ovalis																												•		1
Chydorus piger				•	•					•						•		•				•	•						•	9
Chydorus sphaericus	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	28
Disparalona rostrata	•	•	•					•	•		•	•	•	•	•	•	•		•	•	•	•	•		•	•		•	•	18
Eurycercus lamellatus	•	•			•	•	•			•	•	•	•	•	•	•	•	•	•		•	•		•				•	•	21
Graptoleberis testudinaria	•	•	•	•	•	•	•			•			•		•		•		•	•		•	•		•				•	15
Leydigia leydigi									•														•	•						3
Monospilus dispar		•	•					•	•		•	•	•	•	•	•	•	•	•			•	•		•			•	•	21
Oxyurella tenuicaudis				•			•			•			•																	3
Pleuroxus aduncus							•				•																			2
Pleuroxus laevis	•						•				•			•	•				•	•										7
Pleuroxus denticulatus									•																					1
Pleuroxus trigonellus	•	•	•			•	•				•		•	•	•			•											•	12
Pleuroxus truncatus	•			•	•		•				•			•			•	•			•	•				•			•	11
Pleuroxus uncinatus		•			•		•			•			•	•	•					•	•	•			•				•	11
Pseudochydorus globosus	•			•			•							•	•				•											6
Rhynchotalona falcata		•	•	•	•	•		•			•	•			•			•	•	•				•					•	15
Total no. of species	13	17	12	13	18	17	8	19	6	6	10	13	18	11	15	17	15	15	12	16	20	13	13	12	14	4	10	11	16	

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Appendix B.   Chydorid abundances recorded for 29 study lakes in ireland, between July 1996 and Septemeber 1997.

B.1. Chydorid abundances (per sweep net) in Lough Ballycullinan, Co. Clare.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jun 97	Sep 97
Acroperus harpae	60					16	60
Alona affinis	305			32	7	5	13
Alona costata	5	2					20
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula							
Alona rustica							
Alonella excisa							
Alonella exigua	5	15					
Alonella nana							
Alonopsis elongata							
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	65	24	282	1760		37	147
Disparalona rostrata		2					
Eurycercus lamellatus	10		6	480	156	27	87
Graptoleberis testudinaria	5	4					
Leydigia leydigi							
Monospilus dispar							
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis	10						13
Pleuroxus denticulatus							
Pleuroxus trigonellus						5	413
Pleuroxus truncatus						27	367
Pleuroxus uncinatus							
Pseudochydorus globosus							20
Rhynchotalona falcata							
Total Abundance	465	45	288	2272	163	117	1140
species richness	8	5	2	3	2	6	9
Shannon Diversity Index	1.13	1.16	0.10	0.59	0.17	1.59	1.59

B.2. Chydorid abundances (per sweep net) in Lough Ballyquirke, Co. Galway.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Aug 97	Sep 97
Acroperus harpae	10	16					5			32	
Alona affinis	540	87	280		3	6	243	66	3040		
Alona costata						3		3	20	24	
Alona guttata											
Alona intermedia			120								
Alona quadrangularis	100										
Alona rectangula	10						9	6			
Alona rustica									20		
Alonella excisa											
Alonella exigua											
Alonella nana											
Alonopsis elongata											
Anchistropus emarginatus											
Camptocerus rectirostris											
Chydorus ovalis											
Chydorus piger											
Chydorus sphaericus		47	280	20	1	6	9	6	60	48	60
Disparalona rostrata	100	18	640				5	3	260	8	
Eurycercus lamellatus		3	80			3			20	24	5
Graptoleberis testudinaria	10		40						40		
Leydigia leydigi											
Monospilus dispar		3	1920								5
Oxyurella tenuicaudis											
Pleuroxus aduncus											
Pleuroxus laevis											
Pleuroxus denticulatus											
Pleuroxus trigonellus		13								8	50
Pleuroxus truncatus											
Pleuroxus uncinatus								3	420		
Pseudochydorus globosus											
Rhynchotalona falcata	10		520								
Total Abundance	780	186	3880	20	4	18	271	87	3880	144	120
species richness	7	7	8	1	2	4	5	6	8	6	4
Shannon Diversity Index	1.00	1.45	1.53	0.00	0.56	1.33	0.47	0.93	0.81	1.62	0.98

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B.3. Chydorid abundances (per sweep net) in Lough Bray, Co. Wicklow.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae				11		40	234
Alona affinis				126			26
Alona costata		16					
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula							
Alona rustica			1	6			26
Alonella excisa						80	26
Alonella exigua							
Alonella nana							
Alonopsis elongata	8344	784		137	3200	3520	2470
Anchistropus emarginatus							
Camptocerus rectirostris	28						
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	56		1	1			
Disparalona rostrata							
Eurycercus lamellatus							
Graptoleberis testudinaria	28						
Leydigia leydigi							
Monospilus dispar	168	96	14	51	40		
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus				17			
Pleuroxus truncatus							
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata	56	16					
Total Abundance	**8680**	**912**	**16**	**350**	**3240**	**3640**	**2782**
species richness	**6**	**4**	**3**	**7**	**2**	**3**	**5**
Shannon Diversity Index	**0.22**	**0.51**	**0.46**	**1.36**	**0.07**	**0.17**	**0.44**

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B.4. Chydorid abundances (per sweep net) in Lough Bunny, Co. Clare.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jun 97	Sep 97
Acroperus harpae							
Alona affinis	3		3	20	40	624	440
Alona costata	30	5			10	112	60
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula							80
Alona rustica							
Alonella excisa							27
Alonella exigua							
Alonella nana							
Alonopsis elongata	3						480
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	2	25	16	60	40	24	13
Disparalona rostrata					5	48	153
Eurycercus lamellatus				7			20
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar	47	100		7	5	216	107
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata	2	20				136	27
Total Abundance	87	150	19	93	100	1160	1407
species richness	6	4	2	4	5	6	10
Shannon Diversity Index	1.11	0.95	0.41	0.99	1.26	1.34	1.72

B.5. Chydorid abundances (per sweep net) in Lough Cullaun, Co. Clare.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jun 97	Sep 97
Acroperus harpae			5			20	40
Alona affinis	11	21	125	90	14	300	640
Alona costata	7	5	10	20	21	40	160
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula							
Alona rustica							
Alonella excisa	3						
Alonella exigua							
Alonella nana			5				
Alonopsis elongata	71	71	155	190	343	1180	200
Anchistropus emarginatus		3					40
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	13		265	810	49	80	40
Disparalona rostrata	3	24		10	14		240
Eurycercus lamellatus	1	5				20	40
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar						20	
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							80
Pleuroxus truncatus		3				40	2080
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata		3					
Total Abundance	108	133	565	1120	441	1700	3560
species richness	7	8	6	5	5	8	10
Shannon Diversity Index	1.17	1.42	1.20	0.85	0.80	1.04	1.39

B.6. Chydorid abundances (per sweep net) in Lough Dan, Co. Wicklow.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae												4
Alona affinis	130						3		440	528	56	40
Alona costata		125	20									
Alona guttata	10							4				
Alona intermedia												
Alona quadrangularis												
Alona rectangula												
Alona rustica					5	20	10		7	32	12	36
Alonella excisa												12
Alonella exigua												
Alonella nana												
Alonopsis elongata	330	175	20			5		82	87	8	48	40
Anchistropus emarginatus												
Camptocerus rectirostris	20										8	8
Chydorus ovalis												
Chydorus piger					45							36
Chydorus sphaericus	20	50	20		10	20	3			8	24	
Disparalona rostrata												
Eurycercus lamellatus	80	50							13		16	76
Graptoleberis testudinaria		25						2		32	196	12
Leydigia leydigi												
Monospilus dispar	750	1300	327		315	305	179	63	93	40	48	192
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												
Pleuroxus denticulatus												
Pleuroxus trigonellus												
Pleuroxus truncatus			7									
Pleuroxus uncinatus												
Pseudochydorus globosus												
Rhynchotalona falcata	10	450	73				3	28	53	74	8	36
Total Abundance	**1350**	**2175**	**467**	**0**	**375**	**350**	**198**	**179**	**693**	**722**	**416**	**492**
species richness	**8**	**7**	**6**	**0**	**4**	**4**	**5**	**5**	**6**	**7**	**9**	**11**
Shannon Diversity Index	**1.26**	**1.23**	**1.01**	**0.00**	**0.56**	**0.51**	**0.44**	**1.14**	**1.14**	**1.00**	**1.67**	**1.93**

B.7. Chydorid abundances (per sweep net) in Doolough, Co. Clare.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae									4	41	871	32
Alona affinis	260	343	32			2	3		32	43	676	4
Alona costata		6	12	7					4	2	182	56
Alona guttata												
Alona intermedia												
Alona quadrangularis												
Alona rectangula												
Alona rustica												
Alonella excisa												
Alonella exigua												
Alonella nana												
Alonopsis elongata												
Anchistropus emarginatus												
Camptocerus rectirostris			8									
Chydorus ovalis												
Chydorus piger	70	11	8		4	5	7		16	62	104	16
Chydorus sphaericus												
Disparalona rostrata												
Eurycercus lamellatus												
Graptoleberis testudinaria	5			3						2		
Leydigia leydigi												
Monospilus dispar			4									
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												
Pleuroxus denticulatus												
Pleuroxus trigonellus		6										
Pleuroxus truncatus												
Pleuroxus uncinatus												
Pseudochydorus globosus												
Rhynchotalona falcata												
Total Abundance	335	366	64	10	4	6	10	0	56	151	1833	108
species richness	3	4	5	2	1	2	2	0	4	5	4	4
Shannon Diversity Index	0.59	0.30	1.35	0.64	0.00	0.56	0.64	0.00	1.05	1.21	1.11	1.11

B.8. Chydorid abundances (per sweep net) in Lough Dromore, Co. Clare.

Sampling Date	Sep 96	Jan 97	Apr 97	Jun 97	Jun 97	Sep 97
Acroperus harpae	4				17	
Alona affinis		6	1040	900	167	
Alona costata	15					80
Alona guttata				700		
Alona intermedia						
Alona quadrangularis						
Alona rectangula						
Alona rustica						
Alonella excisa						
Alonella exigua	4					
Alonella nana						
Alonopsis elongata						
Anchistropus emarginatus						
Camptocerus rectirostris	4					
Chydorus ovalis						
Chydorus piger						
Chydorus sphaericus	91	19	440	4900	217	1600
Disparalona rostrata						
Eurycercus lamellatus				300	417	4160
Graptoleberis testudinaria						
Leydigia leydigi						
Monospilus dispar						
Oxyurella tenuicaudis						
Pleuroxus aduncus		6				
Pleuroxus laevis						640
Pleuroxus denticulatus						
Pleuroxus trigonellus			40		133	
Pleuroxus truncatus	29					7520
Pleuroxus uncinatus						80
Pseudochydorus globosus						80
Rhynchotalona falcata					17	
Total Abundance	**145**	**32**	**1520**	**6800**	**967**	**14160**
species richness	**6**	**3**	**3**	**4**	**6**	**7**
Shannon Diversity Index	**1.12**	**0.95**	**0.71**	**0.88**	**1.41**	**1.17**

B.9. Chydorid abundances (per sweep net) in Lough Easky, Co. Sligo.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae							
Alona affinis		37		36	87	20	29
Alona costata	1				7		
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula							
Alona rustica				12			
Alonella excisa		8					
Alonella exigua							
Alonella nana							
Alonopsis elongata	6	19			27	40	105
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus		11	3				7
Disparalona rostrata							
Eurycercus lamellatus							
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar							
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata							
Total Abundance	75	3	7	48	120	60	141
species richness	2	4	1	2	3	2	3
Shannon Diversity Index	1.21	0.00	0.41	0.56	0.73	0.64	0.70

B.10. Chydorid abundances (per sweep net) in Lough Egish, Co. Monaghan.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae	2	30					
Alona affinis				7		16	
Alona costata							
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula							
Alona rustica		26					
Alonella excisa							
Alonella exigua							
Alonella nana							
Alonopsis elongata							
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	19	217	30	327			
Disparalona rostrata							
Eurycercus lamellatus	1			7	18		8
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar							
Oxyurella tenuicaudis		4					
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata							
Total Abundance	22	276	30	340	18	16	8
species richness	3	4	1	3	1	1	1
Shannon Diversity Index	0.49	0.71	0.00	0.19	0.00	0.00	0.00

B.11. Chydorid abundances (per sweep net) in Lough Feeagh, Co. Mayo.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae												
Alona affinis		60							23			
Alona costata						2			5		12	
Alona guttata												
Alona intermedia		20	3									
Alona quadrangularis												
Alona rectangula												
Alona rustica			22					4				
Alonella excisa												
Alonella exigua												
Alonella nana												
Alonopsis elongata							7		5			8
Anchistropus emarginatus												
Camptocerus rectirostris												
Chydorus ovalis												
Chydorus piger		140										
Chydorus sphaericus									5			
Disparalona rostrata		760										
Eurycercus lamellatus												
Graptoleberis testudinaria												
Leydigia leydigi												
Monospilus dispar		1220									5	
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												
Pleuroxus denticulatus												
Pleuroxus trigonellus												
Pleuroxus truncatus												
Pleuroxus uncinatus												
Pseudochydorus globosus												
Rhynchotalona falcata		40	39								139	
Total Abundance	0	2240	64	0	0	2	7	4	37	0	156	8
species richness	0	6	3	0	0	1	1	1	4	0	3	1
Shannon Diversity Index	0.00	1.08	0.81	0.00	0.00	0.00	0.00	0.00	1.07	0.00	0.41	0.00

B.12. Chydorid abundances (per sweep net) in Lough Gara (North), Co. Sligo.

Sampling Date	Jul 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae				56		
Alona affinis	27	19		84	60	941
Alona costata						32
Alona guttata						
Alona intermedia						
Alona quadrangularis						
Alona rectangula						
Alona rustica						
Alonella excisa						
Alonella exigua						
Alonella nana						
Alonopsis elongata						
Anchistropus emarginatus						
Camptocerus rectirostris					7	
Chydorus ovalis						
Chydorus piger						
Chydorus sphaericus	5	13	212	1764	147	176
Disparalona rostrata	10			112	120	128
Eurycercus lamellatus	5					
Graptoleberis testudinaria						
Leydigia leydigi		3				
Monospilus dispar	6		8	252	353	
Oxyurella tenuicaudis						
Pleuroxus aduncus			4			
Pleuroxus laevis						
Pleuroxus denticulatus				28		16
Pleuroxus trigonellus						
Pleuroxus truncatus						
Pleuroxus uncinatus	1			56	20	64
Pseudochydorus globosus						
Rhynchotalona falcata				28	73	
Total Abundance	54	35	224	2380	780	1357
species richness	6	3	3	8	7	6
Shannon Diversity Index	1.42	0.90	0.24	1.00	1.52	1.03

B.13. Chydorid abundances (per sweep net) in Lough Gara (South), Co. Leitrim.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae	5	27					
Alona affinis	15	440		7	20	20	20
Alona costata			3				
Alona guttata							15
Alona intermedia							
Alona quadrangularis							
Alona rectangula						48	15
Alona rustica						12	
Alonella excisa							
Alonella exigua		13					
Alonella nana		40					
Alonopsis elongata							
Anchistropus emarginatus							
Camptocerus rectirostris		13					
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	250	737				300	25
Disparalona rostrata							
Eurycercus lamellatus	70	280				48	
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar							
Oxyurella tenuicaudis			3				
Pleuroxus aduncus							
Pleuroxus laevis		13					
Pleuroxus denticulatus							
Pleuroxus trigonellus						6	
Pleuroxus truncatus		27					
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata							
Total Abundance	340	1590	5	7	20	434	75
species richness	4	9	2	1	1	6	4
Shannon Diversity Index	0.75	1.37	0.69	0.00	0.00	1.04	1.36

B.14. Chydorid abundances (per sweep net) in Lough Gowna, Co. Cavan.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae		7									10	20
Alona affinis	12	54					10		12	51	110	80
Alona costata												20
Alona guttata												
Alona intermedia												
Alona quadrangularis						3						
Alona rectangula												10
Alona rustica												
Alonella excisa												
Alonella exigua												
Alonella nana												
Alonopsis elongata												
Anchistropus emarginatus												
Camptocerus rectirostris											20	10
Chydorus ovalis												
Chydorus piger												
Chydorus sphaericus		14	5						24	21	30	190
Disparalona rostrata	157	320	30	20			50	32	12	39	280	430
Eurycercus lamellatus	15								6			10
Graptoleberis testudinaria												
Leydigia leydigi												
Monospilus dispar	37		10		2			21	102	60	790	260
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												
Pleuroxus denticulatus												
Pleuroxus trigonellus												
Pleuroxus truncatus												
Pleuroxus uncinatus	3	156								9		10
Pseudochydorus globosus												
Rhynchotalona falcata												
Total Abundance	225	551	45	20	2	3	60	53	156	180	1240	1040
species richness	5	5	3	1	1	1	2	2	5	5	6	10
Shannon Diversity Index	0.95	1.05	0.85	0.00	0.00	0.00	0.45	0.67	1.09	1.46	1.03	1.55

B.15. Chydorid abundances (per sweep net) in Lough Graney, Co. Clare.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	May 97	Jun 97	Sep 97
Acroperus harpae					4		
Alona affinis	2				89	40	4
Alona costata		2	2		20	88	
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula					7		
Alona rustica						4	
Alonella excisa							
Alonella exigua							
Alonella nana		2					
Alonopsis elongata					13	8	
Anchistropus emarginatus							
Camptocerus rectirostris				2		4	
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus			3	6	18	12	4
Disparalona rostrata	1				20	4	4
Eurycercus lamellatus	2				4		
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar	2				2	4	12
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus					4		
Pleuroxus truncatus							
Pleuroxus uncinatus	3	2					
Pseudochydorus globosus							
Rhynchotalona falcata						20	
Total Abundance	10	6	5	8	182	184	24
species richness	5	3	2	2	10	9	4
Shannon Diversity Index	1.56	1.10	0.67	0.56	1.70	1.57	1.24

B.16. Chydorid abundances (per sweep net) in Lough Inchiquinn, Co. Clare.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae		13	3							6	6	
Alona affinis		53					7			6	50	
Alona costata	46	380	3	5		5	7		7	48	28	
Alona guttata												
Alona intermedia												
Alona quadrangularis	6	33	13									
Alona rectangula	68											
Alona rustica												
Alonella excisa											22	
Alonella exigua		40									6	
Alonella nana												
Alonopsis elongata												
Anchistropus emarginatus												
Camptocerus rectirostris												
Chydorus ovalis												
Chydorus piger												
Chydorus sphaericus	154	27	3	10				5	13	30		7
Disparalona rostrata	43	13		5							11	
Eurycercus lamellatus		20	10									
Graptoleberis testudinaria		7										
Leydigia leydigi												
Monospilus dispar	25	13								6		
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis	6										6	
Pleuroxus denticulatus												
Pleuroxus trigonellus											17	
Pleuroxus truncatus			13					5		54		47
Pleuroxus uncinatus	3											
Pseudochydorus globosus											6	
Rhynchotalona falcata												
Total Abundance	351	600	45	20	0	5	13	10	20	150	151	53
species richness	8	10	6	3	0	1	2	2	2	6	9	2
Shannon Diversity Index	1.57	1.40	1.61	1.04	0.00	0.00	0.69	0.69	0.64	1.44	1.89	0.38

B.17. Chydorid abundances (per sweep net) in Lough Lene, Co. Westmeath.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae												
Alona affinis	35				8	3			10		30	
Alona costata	4	17	18	110					3	243	530	64
Alona guttata												
Alona intermedia												
Alona quadrangularis							5					
Alona rectangula										18	30	4
Alona rustica												
Alonella excisa												
Alonella exigua												
Alonella nana									9			
Alonopsis elongata												
Anchistropus emarginatus												
Camptocerus rectirostris												
Chydorus ovalis												
Chydorus piger												
Chydorus sphaericus	8						77					
Disparalona rostrata	2								7		160	4
Eurycercus lamellatus									3			
Graptoleberis testudinaria												
Leydigia leydigi												
Monospilus dispar		424	42	150	4		27	5	163	630	310	144
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												8
Pleuroxus denticulatus												
Pleuroxus trigonellus	10											
Pleuroxus truncatus												
Pleuroxus uncinatus												
Pseudochydorus globosus	1											
Rhynchotalona falcata		94	156	510					30	297	10	204
Total Abundance	**60**	**534**	**216**	**770**	**12**	**3**	**108**	**5**	**217**	**1197**	**1070**	**428**
species richness	**6**	**3**	**3**	**3**	**2**	**1**	**3**	**1**	**6**	**5**	**6**	**6**
Shannon Diversity Index	**1.24**	**0.60**	**0.76**	**0.87**	**0.64**	**0.00**	**0.72**	**0.00**	**0.86**	**1.11**	**1.24**	**1.17**

B.18. Chydorid abundances (per sweep net) in Lough Lettercraffroe, Co. Galway.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae	2			480	140	3	
Alona affinis	12	15	174	800	1920	125	
Alona costata	6						
Alona guttata							
Alona intermedia		5					
Alona quadrangularis							
Alona rectangula					20		
Alona rustica							
Alonella excisa							
Alonella exigua							
Alonella nana			3	480			
Alonopsis elongata	12	5			40	8	
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger	114				1820	48	
Chydorus sphaericus		10	141	6400	260		5
Disparalona rostrata							
Eurycercus lamellatus	2						
Graptoleberis testudinaria	28				80		
Leydigia leydigi							
Monospilus dispar		10					
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus	2						
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata		15					
Total Abundance	178	60	318	8160	4280	183	5
species richness	8	6	3	4	7	4	1
Shannon Diversity Index	1.21	1.70	0.73	0.75	1.15	0.80	0.00

B.19. Chydorid abundances (per sweep net) in Lough Lickeen, Co. Clare

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae	7											9
Alona affinis	118	3	4		1	2	48			17	84	474
Alona costata	52	1	80				4		3		67	18
Alona guttata												
Alona intermedia												
Alona quadrangularis												
Alona rectangula							8					9
Alona rustica												
Alonella excisa												
Alonella exigua	45											
Alonella nana												
Alonopsis elongata												
Anchistropus emarginatus												
Camptocerus rectirostris												
Chydorus ovalis												
Chydorus piger												
Chydorus sphaericus	94		88			14	32				4	
Disparalona rostrata		1	28							3	22	72
Eurycercus lamellatus	129	5	4									9
Graptoleberis testudinaria												
Leydigia leydigi												
Monospilus dispar		2										
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												
Pleuroxus denticulatus												
Pleuroxus trigonellus												
Pleuroxus truncatus												
Pleuroxus uncinatus												
Pseudochydorus globosus												
Rhynchotalona falcata			4									9
Total Abundance	445	12	208	0	1	16	92	0	3	20	178	600
species richness	6	5	6	0	1	2	4	0	1	2	4	7
Shannon Diversity Index	1.59	1.42	1.23	0.00	0.00	0.38	1.06	0.00	0.00	0.45	1.07	0.80

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B.20. Chydorid abundances (per sweep net) in Lough Maumwee, Co. Galway.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae	1				20		
Alona affinis	4	30	4			12	17
Alona costata		5				8	
Alona guttata	3						
Alona intermedia		5					
Alona quadrangularis							
Alona rectangula							
Alona rustica		5	2		7		
Alonella excisa	15				13	60	
Alonella exigua							
Alonella nana		5					
Alonopsis elongata	14	10			333		
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger			10				
Chydorus sphaericus	2	5			7	12	11
Disparalona rostrata							
Eurycercus lamellatus						4	
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar		20	1		7		
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus		10					
Pleuroxus truncatus							
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata		5					
Total Abundance	39	100	17	0	387	96	28
species richness	6	10	4	0	6	5	2
Shannon Diversity Index	1.41	2.04	1.07	0.00	0.61	1.15	0.67

B.21. Chydorid abundances (per sweep net) in Lough Moher, Co. Mayo.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae								40			36
Alona affinis	73	41			4	7		460	7	25	23
Alona costata								20			9
Alona guttata											
Alona intermedia		1									
Alona quadrangularis	37	2					18				
Alona rectangula											
Alona rustica											
Alonella excisa		3						40		5	
Alonella exigua											5
Alonella nana											
Alonopsis elongata								10			
Anchistropus emarginatus											
Camptocerus rectirostris											5
Chydorus ovalis											
Chydorus piger		43						90	27		
Chydorus sphaericus	6				8			150		10	41
Disparalona rostrata		3									5
Eurycercus lamellatus	10	7						10			5
Graptoleberis testudinaria										5	
Leydigia leydigi											
Monospilus dispar									7		5
Oxyurella tenuicaudis											
Pleuroxus aduncus											
Pleuroxus laevis										15	
Pleuroxus denticulatus											
Pleuroxus trigonellus											
Pleuroxus truncatus		1									59
Pleuroxus uncinatus											
Pseudochydorus globosus											
Rhynchotalona falcata		1									
Total Abundance	126	102	0	0	12	7	18	820	40	60	189
species richness	4	9	0	0	2	1	1	8	3	5	10
Shannon Diversity Index	1.02	1.33	0.00	0.00	0.64	0.00	0.00	1.37	0.87	1.42	1.85

B.22. Chydorid abundances (per sweep net) in Lough Muckno, Co. Monaghan

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae					32		10
Alona affinis	26	15		100	448	33	70
Alona costata		3		4	8		5
Alona guttata							
Alona intermedia							
Alona quadrangularis	1						
Alona rectangula							
Alona rustica							
Alonella excisa							
Alonella exigua							
Alonella nana							
Alonopsis elongata							
Anchistropus emarginatus							
Camptocerus rectirostris	1	3		8			20
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus		6		108	8		5
Disparalona rostrata							
Eurycercus lamellatus		6		6	240	14	
Graptoleberis testudinaria						5	5
Leydigia leydigi							
Monospilus dispar					8		5
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis		3					
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus		6			8	14	5
Pseudochydorus globosus		6			16		
Rhynchotalona falcata							
Total Abundance	28	48	0	226	768	65	125
species richness	3	8	0	5	8	4	8
Shannon Diversity Index	0.31	1.92	0.00	1.00	1.08	1.20	1.46

B.23. Chydorid abundances (per sweep net) in Lough Mullagh, Co. Cavan.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae							47
Alona affinis	4	3		7	40	107	327
Alona costata			6			13	140
Alona guttata							7
Alona intermedia							
Alona quadrangularis				33			
Alona rectangula							20
Alona rustica							
Alonella excisa							
Alonella exigua							
Alonella nana				7			
Alonopsis elongata							
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	12		366	400			140
Disparalona rostrata		5					
Eurycercus lamellatus							
Graptoleberis testudinaria							13
Leydigia leydigi				7			
Monospilus dispar							
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus					13	87	53
Pseudochydorus globosus							
Rhynchotalona falcata							
Total Abundance	16	8	372	453	53	207	747
species richness	2	2	2	5	2	3	8
Shannon Diversity Index	0.56	0.64	0.08	0.49	0.56	0.88	1.56

B.24. Chydorid abundances (per sweep net) in Lough Oughter, Co. Cavan.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae							
Alona affinis		112		38			28
Alona costata		5					
Alona guttata							
Alona intermedia							
Alona quadrangularis	2		2				
Alona rectangula							
Alona rustica							
Alonella excisa							
Alonella exigua							
Alonella nana							
Alonopsis elongata							
Anchistropus emarginatus	2						
Camptocerus rectirostris		10					12
Chydorus ovalis							
Chydorus piger	2	5					
Chydorus sphaericus				102			208
Disparalona rostrata	4	68		4			150
Eurycercus lamellatus		5					4
Graptoleberis testudinaria							
Leydigia leydigi	2						
Monospilus dispar				4			152
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus							48
Pseudochydorus globosus							
Rhynchotalona falcata							
Total Abundance	12	204	2	149	0	0	602
species richness	5	6	1	4	0	0	7
Shannon Diversity Index	1.56	1.11	0.00	0.81	0.00	0.00	1.52

B.25. Chydorid abundances (per sweep net) in Lough Owel, Co. Westmeath.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae								5				
Alona affinis	270	5	28	9	7		64	32	490	500	3136	640
Alona costata	30	28	413	19			3		300	20		48
Alona guttata												
Alona intermedia											28	
Alona quadrangularis												
Alona rectangula			28						50	60	112	
Alona rustica												
Alonella excisa												
Alonella exigua												
Alonella nana		4					5					
Alonopsis elongata			7				3		20			
Anchistropus emarginatus												
Camptocerus rectirostris												
Chydorus ovalis												
Chydorus piger										80	196	108
Chydorus sphaericus		3		9		12	139	21	50	20		
Disparalona rostrata	115	43	91				3	11	100	270	1400	160
Eurycercus lamellatus												
Graptoleberis testudinaria	5	3	21							10	84	16
Leydigia leydigi												
Monospilus dispar		5	63	14			3		20		28	80
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												
Pleuroxus denticulatus												
Pleuroxus trigonellus												
Pleuroxus truncatus												
Pleuroxus uncinatus												
Pseudochydorus globosus												
Rhynchotalona falcata		1							20			
Total Abundance	420	92	651	51	7	12	219	69	1050	960	4984	203
species richness	4	8	7	4	1	1	7	4	8	7	7	6
Shannon Diversity Index	0.88	1.44	1.22	1.34	0.00	0.00	0.95	1.20	1.45	1.29	0.99	1.15

B.26. Chydorid abundances (per sweep net) in Lough Poulaphouca, Co. Wicklow.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae							
Alona affinis	1400	30		114	20	16	19
Alona costata							
Alona guttata							
Alona intermedia							
Alona quadrangularis							
Alona rectangula							
Alona rustica		3					
Alonella excisa							
Alonella exigua							
Alonella nana							
Alonopsis elongata		3			20		
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis							
Chydorus piger							
Chydorus sphaericus	80	10		2			
Disparalona rostrata							
Eurycercus lamellatus							
Graptoleberis testudinaria							
Leydigia leydigi							
Monospilus dispar							
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata							
Total Abundance	1480	47	0	116	40	16	19
species richness	2	4	0	2	2	1	1
Shannon Diversity Index	0.21	0.99	0.00	0.09	0.69	0.00	0.00

B.27. Chydorid abundances (per sweep net) in Lough Ramor, Co. Cavan.

Sampling Date	Jul 96	Aug 96	Sep 96	Oct 96	Jan 97	Mar 97	Apr 97	May 97	Jun 97	Jul 97	Aug 97	Sep 97
Acroperus harpae										4		
Alona affinis	7	171	42	48				78	7	32	140	5
Alona costata												
Alona guttata												
Alona intermedia				5								
Alona quadrangularis												
Alona rectangula											14	
Alona rustica											7	
Alonella excisa												
Alonella exigua												
Alonella nana												
Alonopsis elongata												
Anchistropus emarginatus												
Camptocerus rectirostris												
Chydorus ovalis												
Chydorus piger												
Chydorus sphaericus		12		14		3	228	1326		20		
Disparalona rostrata	1	6		5						12	441	
Eurycercus lamellatus												
Graptoleberis testudinaria												
Leydigia leydigi												
Monospilus dispar	3	3	3							8	14	
Oxyurella tenuicaudis												
Pleuroxus aduncus												
Pleuroxus laevis												
Pleuroxus denticulatus												
Pleuroxus trigonellus												
Pleuroxus truncatus		6										
Pleuroxus uncinatus										32		
Pseudochydorus globosus												
Rhynchotalona falcata												
Total Abundance	11	198	45	72	0	3	228	1404	7	108	616	5
species richness	3	5	2	4	0	1	1	2	1	6	5	1
Shannon Diversity Index	0.86	0.50	0.24	0.95	0.00	0.00	0.00	0.21	0.00	1.59	0.71	0.01

B.28. Chydorid abundances (per sweep net) in Lough Rea, Co. Galway.

Sampling Date	Sep 96	Jan 97	Apr 97	May 97	Jun 97	Sep 97
Acroperus harpae			2	2	16	
Alona affinis			2	193	2048	56
Alona costata				39	208	108
Alona guttata					32	
Alona intermedia						
Alona quadrangularis						
Alona rectangula				4		4
Alona rustica						
Alonella excisa		1			16	32
Alonella exigua						
Alonella nana						
Alonopsis elongata				4	112	244
Anchistropus emarginatus						
Camptocerus rectirostris						
Chydorus ovalis						
Chydorus piger						
Chydorus sphaericus		2				
Disparalona rostrata						8
Eurycercus lamellatus						
Graptoleberis testudinaria						
Leydigia leydigi						
Monospilus dispar						40
Oxyurella tenuicaudis						
Pleuroxus aduncus						
Pleuroxus laevis						
Pleuroxus denticulatus						
Pleuroxus trigonellus						
Pleuroxus truncatus						
Pleuroxus uncinatus						
Pseudochydorus globosus						
Rhynchotalona falcata						
Total Abundance	0	3	4	240	2432	492
species richness	0	2	2	5	6	7
Shannon Diversity Index	0.00	0.64	0.69	0.63	0.62	1.42

B.29. Chydorid abundances (per sweep net) in Lough Talt, Co. Sligo.

Sampling Date	Jul 96	Sep 96	Jan 97	Apr 97	Jun 97	Jul 97	Sep 97
Acroperus harpae					5		3
Alona affinis	5	4		9	100	306	17
Alona costata	19	1		3	60	270	7
Alona guttata							
Alona intermedia							
Alona quadrangularis	4						
Alona rectangula						6	3
Alona rustica							
Alonella excisa	22	75		6	130	36	17
Alonella exigua							
Alonella nana	2						
Alonopsis elongata	3			45	255	108	
Anchistropus emarginatus							
Camptocerus rectirostris							
Chydorus ovalis		1					
Chydorus piger							
Chydorus sphaericus		1		54	80	12	17
Disparalona rostrata					15	24	3
Eurycercus lamellatus		1					
Graptoleberis testudinaria							3
Leydigia leydigi							
Monospilus dispar							
Oxyurella tenuicaudis							
Pleuroxus aduncus							
Pleuroxus laevis							
Pleuroxus denticulatus							
Pleuroxus trigonellus							
Pleuroxus truncatus							
Pleuroxus uncinatus							
Pseudochydorus globosus							
Rhynchotalona falcata							
Total Abundance	**55**	**84**	**0**	**117**	**645**	**762**	**70**
species richness	**6**	**6**	**0**	**5**	**7**	**7**	**8**
Shannon Diversity Index	**1.42**	**0.51**	**0.00**	**1.17**	**1.58**	**1.37**	**1.83**