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**The relationship between resource elemental
deficiencies and zooplankton community
structure and dynamics**

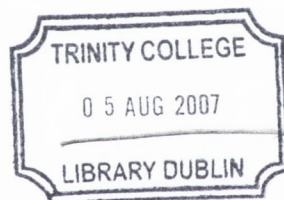
Valerie McCarthy

**A THESIS SUBMITTED TO THE UNIVERSITY OF DUBLIN FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY**

MAY 2007



**SCHOOL OF NATURAL SCIENCES
DEPARTMENT OF ZOOLOGY
UNIVERSITY OF DUBLIN**

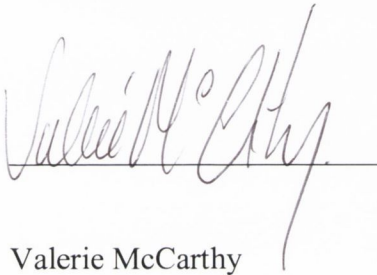


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Declaration

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A handwritten signature in dark ink, appearing to read 'Valerie McCarthy', is written over a horizontal line. The signature is fluid and cursive, with a long, sweeping tail that extends below the line.

Valerie McCarthy

May, 2007

‘There is grandeur in this view of life’

Charles Darwin, *The Origin Of Species*

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Summary

Ecological stoichiometry is the study of the balance of elements in ecological interactions and processes. Recent theoretical and experimental work suggests that consideration of stoichiometric constraints on zooplankton production may substantially improve our understanding of zooplankton community composition and species interactions. This study aimed to examine the role of stoichiometry in influencing zooplankton community structure, species occurrence and seasonal patterns of succession in six lakes in the west of Ireland. Stoichiometric processes were viewed in the context of the overall biotic and abiotic environment which may also potentially influence zooplankton community structure and dynamics.

This research incorporated two field studies involving six sites located in the west of Ireland. These lakes were separated according to alkalinity type, three high-alkalinity and three low-alkalinity lakes. *Daphnia* and calanoids dominated zooplankton biomass throughout the year in the high-alkalinity lakes, whereas cladoceran taxa other than *Daphnia*, such as *Holopedium gibberum* and *Diaphanosoma brachyurum*, dominated at certain times of the year in the low-alkalinity lakes. Overall zooplankton community size structure also differed between the two alkalinity groups, with a greater proportion of larger individuals in the high-alkalinity lakes and smaller individuals dominating the size distribution in the low-alkalinity lakes. Lough Feeagh was found to have the most distinctive taxa composition of the low-alkalinity lakes, with relatively high abundances of *Daphnia* recorded compared with the other low-alkalinity lakes. Lough Talt was also the most distinct high-alkalinity lake, and was quite similar in zooplankton community structure to the low-alkalinity lake, Lough Easky. Both are upland and geographically adjacent lakes. Size distribution analyses and measures of cyclomorphosis in *Daphnia* were used to assess the role of both vertebrate and invertebrate predation in influencing seasonal patterns of species dominance among the lakes. There was strong evidence of fish predation in all three high-alkalinity lakes and in Lough Feeagh, but was weaker in the other two low-alkalinity lakes. There was evidence of invertebrate predation in most lakes; although such evidence was weaker in Lough Carra and Lough Easky. There is, therefore, evidence which suggests that the physical, chemical and biotic environment was fundamental in structuring the zooplankton assemblages of the six lakes of this study.

An intensive two-year study was carried out in Lough Carra, a shallow marl lake in the west of Ireland. This field study investigated whether population fluctuations of the two dominant taxa, *Daphnia* spp. and the calanoid *Eudiaptomus gracilis*, were associated with the

availability of phosphorus and nitrogen. According to stoichiometric theory, zooplankters have a species-specific elemental composition. *Daphnia* have a relatively high phosphorus concentration in their tissues and copepods high nitrogen. *Daphnia* should, therefore, be more sensitive to phosphorus limitation and copepods more sensitive to nitrogen. In accordance with stoichiometric predictions, there was evidence to suggest that *Daphnia* and *Eudiaptomus* reproduction in Lough Carra had contrasting relationships to dietary phosphorus and nitrogen availability. Egg production by *Daphnia* was associated with measures of phosphorus availability, whereas calanoid egg production was associated with measures of nitrogen availability. *Daphnia* biomass was not, however, correlated with phosphorus availability, and neither was calanoid biomass correlated with nitrogen. The ratio of DIN:TP was high when *Daphnia* dominated the zooplankton biomass, and low when calanoids dominated. This pattern is consistent with *Daphnia* acting as a sink for phosphorus and calanoids as a sink for nitrogen and suggests consumer-driven nutrient recycling.

The role of resource quality in influencing zooplankton community structure across all six lakes of this study was then examined. There was a negative relationship between *Daphnia* abundance and the seston C:P and a positive correlation was observed between bulk zooplankton C:P content and bulk seston C:P content. This suggests that in accordance with stoichiometric expectations high-P taxa such as *Daphnia* were replaced by low-P taxa with declining food P content. There were, however, poor associations between seasonal variations in zooplankton dynamics and seasonal fluctuations in nutrient availability in many lakes. This suggests that factors other than resource nutrient limitation, such as fish predation, may have a stronger influence in determining seasonal shifts in taxa dominance. Seston nutrient content, nevertheless, appeared to have some influence in constraining the maximum abundance of high-P taxa such as *Daphnia* across the six study lakes. It is important to consider the role of stoichiometry as only one of several alternative factors influencing zooplankton community structure and dynamics.

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Zooplankton species hold a central location in pelagic food-webs and are typically regulated by a combination of predation and resource limitation. Biotic factors such as predation and interactions between different zooplankton, including inter-specific and interference competition are important in determining community structure and biomass (Gliwicz, 1985). The outcome of biotic interactions such as these will be dependent not only on the tolerance of individual species to their physical and chemical environment but also on their response to food availability. The quality of resources available to aquatic herbivores is often highly variable and depends on ingestibility, digestibility, toxicity and nutritional adequacy (Lampert & Sommer, 1997). Recent studies have highlighted nutrient content as an important determinant of zooplankton food quality (Sterner *et al.*, 1993; Hessen, 1992; Sterner & Elser, 2002). The difference between resource and consumer elemental composition may have an important function in regulating both trophic dynamics and consumer-driven nutrient recycling in plankton food-webs (Sterner & Elser, 2002). This study incorporates two field studies involving six sites located in the west of Ireland. It aims to investigate the role of such nutrient imbalances in influencing zooplankton community structure, species occurrence and seasonal patterns of succession. Additional biotic and abiotic determinants of zooplankton community structure and dynamics will also be considered in order to provide a framework upon which the importance of nutrient limitation in structuring zooplankton communities can be assessed.

1.1 Composition of zooplankton communities

Compared with the multitude of species commonly found in the phytoplankton of freshwaters, the zooplankton of lakes are generally species-poor communities. The main groups comprising the freshwater zooplankton are protozoans, rotifers, copepods and cladocerans. The work presented in this thesis focuses on the final three of these groups.

Rotifera are among the smallest of the metazoan organisms and many have adapted for life in the open water. They are pseudocoelomates with un-segmented, bilateral

symmetry. They are characterised by an apical ciliated region, the corona, which is used for locomotion and food gathering, and secondly by the specialized pharynx (the mastax) which consist of an intricate set of hard jaws called trophus (Ruttner-Kolisko, 1974). Rotifers consume a wide variety of both plant and animal prey, and although some have a highly specialised feeding behaviour, most can be described as generalist filter feeders (Rothhaupt, 1990). Rotifers are small animals which are normally less than 1 mm in length and, owing to their small size, generally constitute only a relatively minor part of zooplankton biomass. They are, however, a considerably important component of the zooplankton, and owing to their rapid turnover and metabolism, often have a major role in the processes of nutrient cycling and energy transfer in lakes (Makarewicz & Likens, 1979).

The class Copepoda are in the subphylum Crustacea. They have a segmented body which is composed of the head, thorax and abdomen. The paired antennules are long and the thoracic limbs are generally used for swimming. The caudal rami is located on the last segment of the abdomen. They possess an exoskeleton, conspicuous first antennae, and a single anterior eye. Currently, ten orders of Copepoda are recognised, only four of which contain primarily free-living freshwater forms, Harpacticoida, Cyclopoida, Calanoida and Gelyelloida (Dole-Olivier *et al.*, 2000). Harpacticoids mostly inhabit the benthos and are only rarely found in the plankton and the Gelyelloida is represented by only two groundwater species. Cyclopoids and calanoids, however, are well represented in the plankton. Most freshwater cyclopoid species are from the family Cyclopoidae (Dole-Olivier *et al.*, 2000). The calanoids are principally represented by the family Diaptomidae which contains about 400 species and over 50 genera (Reddy, 1994). Copepods usually have sexual reproduction and are sexually dimorphic in size. The eggs are held externally in one or two sacs and free-living copepods go through six naupliar and six copepodite life stages, the final copepodite stage being adult (Dussart & Defaye, 1995). Eggs usually develop within 1 – 5 days and development time from egg to adult is generally between one and three weeks. The life-span as adults can be in the order of one to several months although some cyclopoids have periods of diapause that may extend their life-spans for one to two years (Elgmork, 1980). Copepods consist of herbivorous, carnivorous or parasitic forms (Maitland, 1990). Calanoids generally collect their food by filtration, whereas cyclopoids tend to macerate their prey,

however, there are many exceptions and a variable diet is common (Dussart & Defaye, 1995).

Cladocera are members of the sub-class Branchiopoda and are grouped into four orders with eleven families. The term Cladocera, although widely used, has no formal taxonomic status, but is, nevertheless, useful as a descriptive term. It encompasses an eclectic group of organisms, most of which are planktonic, and have branched second antennae that function as swimming appendages. Nevertheless, nearly all members of the Chydoridae and Macrothricidae families and some members of the family Sididae are benthic, and dwell on surfaces such as macrophytes or among sediments and organic detritus (Dole-Olivier *et al.*, 2000). Cladocerans have a single central compound eye and a carapace composed of two valves which enclose the trunk and feeding appendages in nearly all species, although the head remains free. The body ends in a pair of postabdominal claws which can extend beyond the carapace. Cladocerans generally reproduce parthenogenetically and this may be either facultative or obligate. Asexual eggs develop into neonates inside the brood chamber of the female. Neonates are released from the brood chamber just before the mother molts, at which point she extrudes another clutch of eggs into the brood chamber (Hebert, 1980). Neonates in most cladocerans, with the exception of *Leptodora*, resemble adults. Nauplii hatch from a resting egg in *Leptodora*. Males are produced asexually in most species and generally occur during periods of environmental stress, where factors such as food availability, oxygen concentration, photoperiod, temperature and over-crowding can influence their occurrence. During this time females will produce haploid eggs which once fertilised do not develop immediately, but enter diapause (Hebert, 1980). These 'resting eggs' can withstand desiccation and freezing and will eventually give rise to a new generation of genetically distinct parthenogenetic females (Scourfield & Harding, 1966). The protective structure which covers the resting eggs is referred to as an ephippium and is formed from the posterior part of the carapace, which thickens and hardens to form a resilient capsule. When the animal moults this specialised structure separates from the rest of the carapace and closes over the eggs. Some cladoceran species are carnivorous, preying on protozoa, rotifers, and small crustaceans, most, however, are generalist filter feeders. The size of food particles which cladoceran filter feeders can process is often constrained by the size of their filtering apparatus, however, factors other than

morphological restrictions can determine the type of food exploited by a particular species. *Bosmina*, for example, which is a small sized suspension feeder, was found to specialise on large sized particles at certain times and has a dual mode of food collection, large particles can be grasped and small particles filtered (DeMott & Kerfoot, 1982; Bleiwas & Stokes, 1985; Hessen, 1985).

1.2 The role of zooplankton in pelagic ecosystems

Zooplankton is a heterogeneous group of organisms, which occupy a central position in pelagic food webs. They play an important role in lake ecosystems, transferring energy from primary producers to predators and suppressing the abundance of phytoplankton (Havens *et al.*, 1996). When grazing is intense, zooplankton can considerably reduce total phytoplankton biomass and productivity, producing a 'clear-water phase' (Lampert, 1978). The effect of zooplankton on phytoplankton is not only density dependent, but is also influenced by the zooplankton community composition which can vary with productivity and is related to the degree of predation pressure (Jeppesen *et al.*, 2003). The structure of the food-web has strong effects on ecosystem properties and the trophic cascade hypothesis suggests that zooplankton are regulated by zooplanktivorous fish which may, therefore, impact on phytoplankton through reduced grazing by zooplankton (Carpenter & Kitchell, 1993). The central role of zooplankton in biomanipulation efforts to eliminate nuisance algal blooms has long been recognised (Sharpiro & Wright, 1984; Sarnelle, 1992). In many cases, however, changes in zooplankton do not result in the expected changes in phytoplankton (Brett & Goldman, 1996). Jeppesen *et al.* (2003) found that predator regulation of zooplankton biomass was greatest in both nutrient rich and nutrient poor lakes and in shallow lakes, and that trophic cascades were most likely to occur in nutrient rich lakes. Others have postulated, however, the food-web effects decline with increasing nutrient load owing to increased growth of grazing-resistant algae (McQueen *et al.*, 1986). Nevertheless, both hypotheses suggest reciprocal interactions between food-web dynamics and nutrient supply in pelagic ecosystems (Elser *et al.*, 1998). It is not simply the direct method of grazing, however, with which zooplankton affect algae biomass. Zooplankton have at least two counteracting effects on phytoplankton: grazing, which reduces algal standing crop, and nutrient regeneration, which can stimulate growth (Peters and Rigler, 1973). By reducing

algal population density through grazing, zooplankton may also increase the availability of a nutrient resource per algal cell (Elser & Goldman, 1991).

1.3 Factors regulating zooplankton community structure and distribution

Zooplankton populations are characteristically regulated by both bottom-up (resource limitation) and top-down (predation) factors (McQueen *et al.*, 1986), and must be adapted for dealing with pressures in both directions. As zooplankton live in a nutritionally dilute environment, they need to be very proficient in the uptake and utilisation of resources. Their competitive abilities are, therefore, critical and it is essential that they are capable of defending themselves when predation pressure is high (Lampert, 1997). The relative importance of predation or resource limitation varies both between and within lakes and is dependent on fish recruitment and nutrient supply (Jeppesen *et al.*, 2003; Persson *et al.*, 2004).

Size-selective predation by fish can determine zooplankton community structure (Brooks & Dodson, 1965). Heavy predation by visually-foraging planktivorous fish can result in reduced zooplankton biomass, reduced size of individual zooplankton species and a reduction in large taxa such as *Daphnia*. Invertebrate predators such as predaceous cladocerans and copepods as well as some insect larvae, may also affect zooplankton communities. They tend to exert a strong mortality on the smaller zooplankton, as they cannot handle larger prey (Pastorok, 1981) and, therefore, cause a shift in the size spectrum to larger plankton (Wojtal *et al.*, 2004). Invertebrate predators may themselves be preyed upon by planktivorous fish, and in such situations, medium sized zooplankters, which avoid both types of predator, become the most abundant component of the zooplankton (Lynch, 1979; Hanazato & Yasuno, 1989).

Zooplankton can also be strongly influenced by both the quantity and quality of their phytoplankton food supply. Low food quantity causes energy limitation, which occurs because carbon (C) assimilation is reduced owing to the low availability of digestible carbon. Food quantity is one of the most important factors influencing the population dynamics of zooplankton (Muck & Lampert, 1984; Mitchell *et al.*, 1992; Nandini & Sarma, 2003). Low carbon availability may also be caused by digestion

resistant algae. There might be constraints on ingestion owing to the particle size or shape (Webster & Peters, 1978). Structural changes in algae, such as thickened cell walls, can also reduce digestibility (Van Donk *et al.*, 1997; Lürling & Van Donk, 1997), and toxins contained in some cyanobacteria are harmful to zooplankton (Reinikainen *et al.*, 1995; DeMott, 1999). Nevertheless, even when the quantity of digestible carbon is high, growth can be limited by deficiencies in certain biochemical and mineral substances which can not be synthesised within the body. The importance of biochemical compounds such as essential highly unsaturated fatty acids (HUFA) have lately been emphasised (Müller-Navarra, 1995; Brett & Müller-Navarra, 1997). Many recent studies on the food requirements of freshwater zooplankton have also focused on limitation by certain essential elements, particularly phosphorus (P) and nitrogen (N) (Hessen, 1992; Sterner *et al.*, 1993; Weers & Gulati, 1997; Sterner & Elser, 2002; Moe *et al.*, 2005)

Several laboratory studies have shown that deficiencies in N and, particularly in P, reduce the quality of algal food for *Daphnia* (Sterner *et al.*, 1993; Weers & Gulati, 1997; Urabe & Sterner, 2001), *Bosmina* (Schulz & Sterner, 1999) and rotifers (Conde-Porcuna, 2000; Jensen & Verschoor, 2004). Direct addition of phosphorus to P-limited food can stimulate somatic growth of *Daphnia* (Boersma, 2000; DeMott *et al.* 2001; Boersma & Kreutzer, 2002), and isotopic analysis has shown a high assimilation efficiency of P in *Daphnia* grazing on P-deficient food (DeMott *et al.*, 1998). Elemental and biochemical limitation may potentially interact in a complex way and nutrient limited algae have been associated with a reduction in the content of some essential highly unsaturated fatty acids in algal cells (HUFAs; Müller-Navarra *et al.*, 2000; Ferrão-Filho *et al.*, 2003). DeMott (1998) showed, however, that the growth and reproduction of daphniids increased substantially on the addition of *Synechococcus* (high P, low fatty acid content) to *Scenedesmus* (low P, low fatty acid content) food. Consequently, direct mineral limitation is likely to be of substantial importance for the growth of zooplankton herbivores.

1.4 Stoichiometry

‘Ecological stoichiometry is the study of the balance of elements in ecological interactions and processes’ (Sterner & Elser, 2002). Organisms must obey the laws of mass balance and thermodynamics when transferring elements and energy through trophic levels (Lotka, 1925). An important principle in ecological stoichiometry is that the requirements of multiple elements differ both within and among species, and this can cause mismatches between demand and supply at ecological interfaces. For example wide variation in the C:N:P ratios of autotrophs contrasts with the constrained elemental ratios of herbivores and other animals. Consequently, the elemental composition of primary producers frequently do not meet the nutritional requirements of herbivores in aquatic systems (Elser *et al.*, 2000a).

The first studies to deal with zooplankton stoichiometry focused on the overall variability in the chemistry of the zooplankton community (Behrendt, 1990). Subsequent studies, however, revealed distinct patterns in the elemental composition of the major crustacean groups such as cladocerans and calanoids, which were found to demonstrate large interspecific variation in their C:P and C:N ratios (Andersen & Hessen, 1991; Sterner & Hessen, 1994; Elser *et al.*, 2000b; Sterner & Elser, 2002). Cladocerans such as *Daphnia* have low body N:P ratios, whereas calanoids were found to have high N:P contents. Zooplankton were also found to have restricted intraspecific differences in their elemental content and were, therefore, characterised as ‘homeostatic’, meaning that their C:N:P ratios remain relatively constant in spite of wide variation in these ratios in their food resource. Recent studies, however, have examined variation in P-content within single zooplankton species and homeostasis is no longer considered perfect (DeMott *et al.*, 1998; DeMott *et al.*, 2004). The variation in heterotroph stoichiometry is, nevertheless, an order of magnitude less than what is encountered in autotrophs and stoichiometric principals are, therefore, maintained (Sterner & Elser, 2002).

It has been speculated that zooplankton taxa with high P-content such as *Daphnia*, have a greater allocation of P-rich compounds such as nucleic acids (Andersen & Hessen, 1991; Main *et al.*, 1997; Elser *et al.*, 2000b). The ‘growth rate hypothesis’ proposes that variation in the P-content of herbivores reflects increased allocation to

P-rich ribosomal RNA, which is required to meet protein synthesis demands during rapid growth (Elser *et al.*, 1996), and has been supported in a number of studies (Main *et al.*, 1997; Vrede *et al.*, 2002; Elser *et al.*, 2003; Acharya *et al.*, 2004). Moderate declines in P-content with age, were found to be associated with declines in maximal growth rate and RNA content (Main *et al.*, 1997). An organism's requirement for different elements may, therefore, vary throughout its life cycle, and ontogenetic changes in P-content have been shown to be particularly important for copepods (Carrillo *et al.*, 2001; Villar-Argaiz & Sterner, 2002).

In nature herbivores commonly encounter autotroph biomass with a chemical composition very different from their own (Gulati & DeMott, 1997; Brett *et al.*, 2000). *Daphnia* for example, have been found to have a molar C:P ratio of approximately 80 - 90 (Sterner & Hessen, 1994), whereas lake seston can have elemental ratios of between 50 and 1000 (Brett *et al.*, 2000). *Daphnia* production would, therefore, be expected to be particularly sensitive to P-limitation. Organisms that must maintain elevated body nutrient content are considered to be more susceptible to poor food quality as a result of increased C:nutrient ratios (Sterner & Schulz, 1998). Consequently, individual growth and population dynamics may be directly constrained by food quality in terms of nutrient element content.

Thus far, evidence for P-limitation has come largely from laboratory experiments. *Daphnia* have been the main focus of this work, partly because of their central role in lakes and partly because *Daphnia* have high requirements for phosphorus. Early experiments found that *Daphnia* growth was more closely correlated with the P-content of their food resource than the N-content (Sterner *et al.*, 1993). Other studies have found reduced growth of *Daphnia* fed a large amount of P-deficient food (Urabe & Watanabe, 1992; Sterner & Robinson, 1994; Weers & Gulati, 1997; DeMott, 1998; DeMott *et al.*, 1998; DeMott *et al.*, 2001; Boersma & Kreutzer, 2002; Ferrão-Filho *et al.*, 2003), and a mechanistic link between *Daphnia* growth and P availability has been shown in supplementation experiments (Urabe *et al.*, 1997; Boersma & Kreutzer, 2002). Reduced reproduction in *Daphnia* grown on nutrient deficient algae has also been observed (Lürling & Van Donk, 1997; Urabe & Sterner, 2001; Færøvig & Hessen, 2003). Some authors have attempted to expand the work on *Daphnia* to include other taxa such as rotifers (Conde-Porcuna, 2000; Jensen & Verschoor,

2004). The growth response of *Daphnia* to P-limited food has been compared with the growth response of taxa with lower P requirements, such as *Bosmina* (Sterner & Schulz, 1998; Schulz & Sterner, 1999). Consistent with stoichiometry, *Bosmina* were found to be less susceptible to P-limitation. This suggests that there may be a range of lakes with high seston C:P where *Bosmina* have a competitive advantage over *Daphnia* and supports the hypothesis that mineral limitation may also influence zooplankton species distributions (Schulz & Sterner, 1999).

Mineral food-quality limitation has also been suggested under field conditions. Lake surveys have supported the P-limited hypothesis by showing that *Daphnia* abundance was positively correlated with seston particulate P concentration (Hessen, 1992, Hassett *et al.*, 1997; DeMott & Gualti, 1999; Elser *et al.*, 1998; Brett *et al.*, 2000). Other field correlative studies have positively related overall zooplankton community stoichiometry to seston stoichiometry which represents a replacement of P-rich taxa along a gradient of increasing seston P-deficiency (Gulati *et al.*, 1991; Sterner *et al.*, 2000; Villar-Argaiz *et al.*, 2002). Mesocosm experiments have found a positive link between seston nutrient content and *Daphnia* dominated grazer assemblages (Hall *et al.*, 2004), and some have provided a direct mechanistic link between *Daphnia* growth and algal P content (Makino *et al.*, 2002). A limited number of field studies have also examined the link between zooplankton production and seasonal changes in algal quality, and all have supported nutrient limited zooplankton production (DeMott *et al.*, 2001; Scheuerell *et al.*, 2002; Villar-Argaiz *et al.*, 2002).

There is, therefore, much evidence to suggest that autotroph nutritional status strongly affects pelagic community dynamics and organisation, and that stoichiometric processes associated with heterotroph elemental composition are also important in determining the outcome of these effects. For instance, an organism's requirements for different elements may vary throughout its life cycle, and greater sensitivity to a particular nutrient at certain life stages may produce a 'stoichiometric bottleneck' (Villar-Argaiz & Sterner, 2002). Zooplankton community composition may reflect differential mineral nutritional requirements of various zooplankton species. In addition, the responses of plankton communities to variations in food-web structure and predation pressure may be influenced by mineral food-quality effects on zooplankton taxa (Sterner & Hessen, 1994).

1.5 Factors regulating the elemental composition of phytoplankton in nature

Stoichiometric variation in autotrophs is related to autotroph physiology, and because of their ability to store nutrients in excess of their immediate requirements, autotroph nutrient content would be expected to reflect the relative supply of these nutrients in their environment. Autotrophs also exhibit wide inter- and intraspecific variation in elemental composition in response to immediate environmental conditions (Sterner & Elser, 2002). Most variation in autotroph C:N:P ratios can be attributed to a number of factors which alter growth conditions, such as light, CO₂, nutrient supply and temperature. Light intensity can alter autotroph C:N:P because it is directly linked to carbon acquisition through photosynthetic activity (Sterner *et al.*, 1997). As well as this, an increased concentration of CO₂ could increase the rate of photosynthesis by increasing the degree of C fixation (Sterner & Elser, 2002).

Sterner *et al.* (1997) proposed a 'light:nutrient hypothesis', which states that autotroph nutritional status and elemental composition in lakes varies with the ratio of light to nutrient supply. 'Light' in this case, refers to the mean light intensity in the mixed layer and is dependent on both the depth of the mixed layer and the degree of light attenuation. Variations in light attenuation might be associated with differences in water clarity resulting from inorganic substances, dissolved coloured materials, or algal self-shading. Sterner *et al.* (1997) related imbalances in the environmental supply of light in the mixed layer to nutrient supply using TP as an index of P availability. Moreover, positive correlations between the light:TP ratio and particulate C:P under field conditions have been reported (Sterner *et al.*, 1997; Elser *et al.*, 2002). While light may influence the acquisition of C by phytoplankton, differences in the nutrient content of algae are often a function of the ratio of nutrients supplied from the surrounding catchment by way of diffuse and point-sources, or from internal supplies such as diffusion of nutrients across the thermocline from nutrient-rich bottom sediments. Nutrient recycling by heterotrophs may also be an important internal source of nutrients (Elser & Urabe, 1999; Sterner & Elser, 2002). Zooplankton can cause the release of nutrients from algae damaged during the feeding process, from faeces or directly from excretion (Lampert & Sommer, 1997).

1.6 Consumer Driven Nutrient Recycling

Organisms are not fully efficient in the utilization of their food as not all ingested food is assimilated completely or accumulated into the body. A substantial portion of unused material will, therefore, be recycled back into the system. Consequently animals will function as both a source and sink of nutrients (Andersen, 1997). Stoichiometric theory predicts that nutrient recycling should be tightly coupled with resource nutrient ratios (Sterner & Hessen, 1994). Elser *et al.* (1988) found that following a whole-lake experiment algal growth was P-limited when *Daphnia* dominated zooplankton biomass, whereas algae were N-limited when copepods dominated. Andersen & Hessen (1991) later suggested that this was owing to the differential stoichiometric content of the two taxa. Since *Daphnia* have a low N:P content, they likely retained P in their biomass at a high efficiency, while recycling N at a relatively high rate, and as a result adjusted phytoplankton growth toward P-limitation.

Sterner (1990) attempted to theoretically elucidate nutrient flux in homeostatic organisms. In this model, the ratio of N to P released by zooplankton is related tightly to the N:P ratios of food and predicts that the ratio of N to P released decreases with decreasing N:P ratio of the food. The N or P limitation of algal growth may therefore be accelerated by repeated ingestion. Hessen & Andersen (1992) expanded this to include the N:P balance in grazers and hypothesised that algal growth is likely to be limited by P when the zooplankton body composition has a low N:P ratio, but by N when the zooplankton has a high N:P ratio. These are, nevertheless, static models and do not include the response of grazer populations to changes in the quantity and quality of their food. These models suggest that the stoichiometry of nutrient recycling generates an indefinite progression of deteriorating nutrient limitation in algae. Andersen (1997) developed a fully stoichiometrically explicit model which took into account reciprocal feedbacks between algae and grazers. He showed that consumer driven nutrient recycling does not cause a continuous spiral of worsening food quality and slower nutrient recycling. As an alternative, the system may achieve an internal equilibrium, or experience indefinite limit cycles, or even grazer extinction may occur. The specific outcome will be strongly dependent on initial

conditions. Grazer extinction is more likely, for example, in situations where algae have a high C:P content or when grazers have low body C:P.

The predictions of these models were tested by Elser & Urabe (1999). They compiled data from a number of different studies (Le Borgne, 1982; Olsen *et al.*, 1986; Urabe, 1993; Urabe *et al.*, 1995), and found that, as expected, the stoichiometry of released nutrients by grazing zooplankton is not constant but is related to food elemental composition. They also confirmed that consumer N:P content also affects nutrient cycling patterns and that zooplankton communities with low overall N:P recycle nutrients at higher N:P ratios than communities of higher N:P. They also suggested that the food N:P is the primary determinant of consumer driven nutrient recycling and that grazer body N:P is secondary (Elser & Urabe, 1999).

1.7 Thesis layout

This project consisted of two field studies spread over three years. Chapter 2 provides a detailed description of the six study sites involved in this project and outlines the methodology applied to collecting and analysing both biotic and physico-chemical variables. Chapter 4 describes the initial two-year intensive study of Lough Carra, which was carried out between April 2001 and June 2003 as part of an EU project (BUFFER EVK1-CT-1999-00019). Water and zooplankton samples were collected from the lake on a fortnightly basis until October 2002, after which samples were taken once a month. These data provided an insight into seasonal patterns in zooplankton community structure and fecundity and allowed exploration of the potential relationships between zooplankton and the corresponding limnological properties of the water. The initial aim of this work was to investigate the relationship of various zooplankton taxa to the nutrients available to their phytoplankton food supply. Using stoichiometric principals as a basis for this investigation, it was expected that taxa with high elemental P contents would be more sensitive to P-limitation, whereas high N-taxa would be more sensitive to N-limitation. Lough Carra provided an excellent study site for such an analysis, as throughout the year the zooplankton population fluctuated between dominance by *Daphnia*, which have high P requirements, and the calanoid *Eudiaptomus gracilis*, which have high N requirements. The relationship between ambient nutrient availability and zooplankton

abundance was also analysed from the point of view of consumer driven nutrient recycling. The work presented in Chapter 4 forms a large part of an already published manuscript (McCarthy *et al.*, 2006).

Questions arose following the work on Lough Carra as to whether the observed relationships between zooplankton and nutrient availability in this lake were applicable to other lakes with similar water chemistry and zooplankton community structure. The field study was, therefore, expanded to include five other lakes, two of which, Lough Rea and Lough Talt, were similar to Lough Carra in that they had high alkalinity and high pH, with relatively low overall nutrient concentrations. In contrast, the other three lakes, Lough Feeagh, Lough Maumwee and Lough Easky, had low alkalinity concentrations and pH values, but had similarly low nutrient loads to those recorded in Lough Carra. Water and zooplankton samples were taken from each lake on a monthly basis between April 2003 and April 2004. Chapter 3 describes the species composition of the zooplankton community of each lake with the aim of investigating the role of alkalinity in influencing zooplankton community structure and distribution. Seasonal patterns in taxa dominance within each zooplankton assemblage was examined for similarity among lakes within each alkalinity class. Zooplankton size distributions in high- and low-alkalinity lakes were compared to assess the differing role that fish and invertebrate predation may have in influencing seasonal oscillations in zooplankton populations.

Community structure is determined by both physical and chemical parameters such as pH and alkalinity as well as biotic factors such as predation. The availability and quality of resources will, nevertheless, be of fundamental importance. Zooplankton and seston samples were collected from each lake in 2005 and analysed for their nutrient content. In Chapter 5 these data were used to assess the role of resource stoichiometry in influencing zooplankton distribution across the six lakes of this study. In addition, the nutrient content of individuals from the most abundant taxa in each lake was analysed and compared. Furthermore the work presented in this chapter investigated if seasonal zooplankton dynamics could be related to ambient nutrient concentrations using similar methodology to that employed for Lough Carra. Samples were taken on a monthly basis between April 2003 and 2004 for this purpose. The observed patterns were examined and compared with the relationships obtained in

Lough Carra. Chapter 6 is a general discussion of the interplay between the different factors affecting community structure and seasonal dynamics in the six study lakes and combines results from the three preceding chapters.

2.1 Study Sites

2.1.1 Introduction to study sites

Field monitoring of six lakes occurred in two separate stages. The first stage involved an intensive two-year study (April 2001 to June 2003) of Lough Carra, a shallow marl lake situated in Co. Mayo. The second stage involved a broader comparative study incorporating Lough Carra and five other lakes representing two distinct groups; three high-alkalinity and three low-alkalinity (Table 2.1), which were monitored between April 2003 and April 2004.

Table 2.1 Lakes monitored between April 2003 and April 2004.

Low-alkalinity ($< 8 \text{ mg CaCO}_3 \text{ L}^{-1}$)	High-alkalinity ($> 70 \text{ mg CaCO}_3 \text{ L}^{-1}$)
Easky, Co. Sligo	Talt, Co. Sligo
Feeagh, Co. Mayo	Carra, Co. Mayo
Maumwee, Co. Galway	Rea, Co. Galway

All lakes, have been monitored previously on a seasonal basis (Irvine *et al.*, 2001; McGarrigle & Champ 1999; Toner *et al.*, 2005; de Eyto & Irvine, 2005). Baseline information for a number of physico-chemical and biotic variables as well as catchment and land-use data were, therefore, available and were used to establish suitable sites for the study. All lakes have low mean total phosphorus (TP) ($\leq 12 \text{ } \mu\text{g L}^{-1}$) and chlorophyll *a* ($\leq 3.5 \text{ } \mu\text{g L}^{-1}$). Water body characteristics for each lake are given in Table 2.2. According to the OECD (1982) classification scheme, which assigns trophic status based on maximum chlorophyll *a* and mean TP, all of the lakes were classified as oligotrophic, apart from Easky and Carra, which were classified as mesotrophic (Irvine *et al.*, 2001). Recent examination of the geochemical composition of surface sediments in Carra, indicate increased P loads over time and is suggestive of nutrient enrichment (Hobbs *et al.*, 2005).

Table 2.2 Lake catchment area and water body characteristics from Irvine *et al.* (2001).

Lake	Catchment area (km ²)	Surface area (km ²)	Mean depth (m)	Max. depth (m)	Volume (m ³)
Carra	114	16.1	1.75	18	25.2 x 10 ⁶
Talt	4.8	0.95	8.87	41.35	8.46 x 10 ⁶
Rea	135	3.07	3.99	20.93	12.3 x 10 ⁶
Easky	11	1.23	2.38	10.8	2.91 x 10 ⁶
Feeagh	100	4.06	14.53	45.25	58.9 x 10 ⁶
Maumwee	4.3	0.27	1.97	7.9	5.34 x 10 ⁵

2.1.2 Lough Carra

Lough Carra (Fig. 2.1; Fig. 2.2) is a marl lake in the west of Ireland (53 ° 42' N, 09 ° 15' W), with a catchment underlain by carboniferous limestone. It is a well-mixed lake with no evidence of thermal stratification during summer. The lake consists of three well-defined basins; to the north the Castleburke Basin and to the south the Twin Island Basin. Between these lies the Castlecarra Basin. The lake is thought to include spring fed hydrological inputs (Duchas, 2002a). The only basin in Lough Carra which does not have a fluvial input is the Castlecarra basin. The southern basin contains the two most important lotic inputs; the Mullingar and Clooneen rivers. The Keel river is the only surface outflow and enters Lough Mask at its north-eastern shoreline.

The catchment is dominated by grassland used for grazing both sheep and cattle. There are no major centres of population in the Lough Carra catchment, but water is abstracted from the lake for the surrounding rural inhabitants (McGarrigle *et al.*, 2002). The lake is managed as a brown trout (*Salmo trutta* L.) fishery, and other important fish include pike (*Esox lucius* L.), perch (*Perca fluviatilis* L.), eels (*Anguilla anguilla* L.), minnows (*Phoxinus phoxinus* L.), three-spined sticklebacks (*Gasterosteus aculeatus* L.) and ten-spined sticklebacks (*Pygosteus pungitius* L.) (McGarrigle & Champ 1999). In addition to its importance as a natural recreational fishery, Carra is recognised internationally for its wildfowl and rare shoreline vegetation (McGarrigle & Champ 1999). The emergent macrophyte fauna in Lough Carra is dominated by *Phragmites spp.* (Cav. Trin.ex Steud.) and the submerged vegetation by three different species of *Chara spp.* The phytoplankton biomass is

dominated by diatoms which are most prominent from autumn to spring (McGarrigle & Champ 1999; McCarthy *et al.*, 2006).

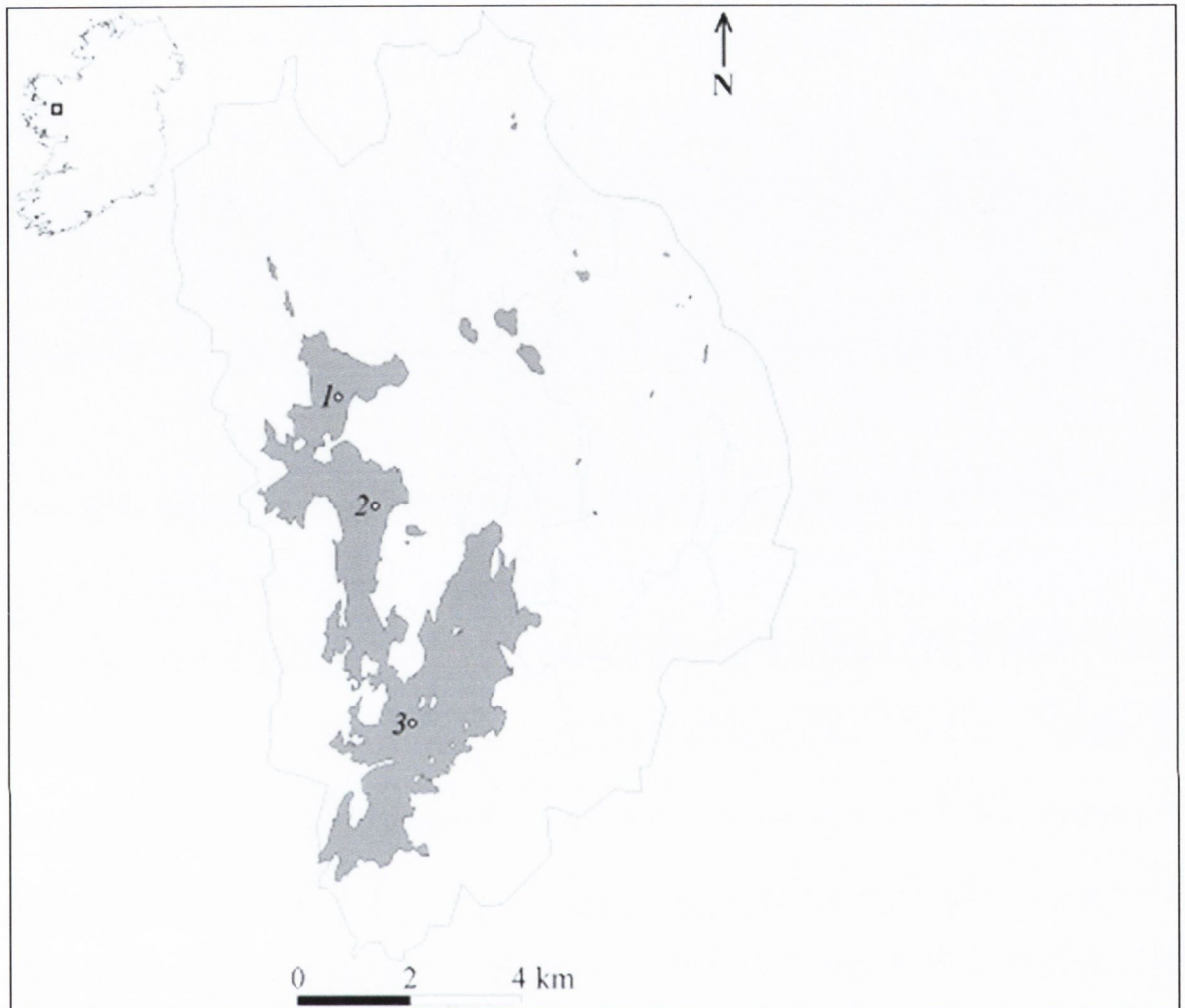


Fig. 2.1 Lough Carra and surrounding catchment in Co. Mayo, showing the three sampling sites; Castleburke = North (1), Castlecarra = Mid (2), Twin Island basin = South (3).



Fig. 2.2 Lough Carra, Co. Mayo.

2.1.3 Lough Talt

Lough Talt (Fig. 2.3; Fig. 2.4) is a deep alkaline lake which is situated in the eastern section of the Moy catchment ($54^{\circ} 05' \text{ N}$, $08^{\circ} 56' \text{ W}$). Lough Talt has surprisingly hard water given that the underlying geology of the catchment is of granite, schist and gneiss. Its only outflow joins the Eignagh river and eventually flows into the Moy river (McGarrigle *et al.*, 1998).

The southern section of the Lough Talt catchment is composed mainly of unexploited peat bogs, with the remaining catchment dominated by relatively low production grassland used principally for grazing sheep and a small number of cattle. There are no major centres of population within the Talt catchment, however, water abstraction from the lake supplies approximately 9,000 people (Sligo County Council, www.sligococo.ie/). Lough Talt supports a population of the rare and threatened Arctic charr (*Salvelinus alpinus* L.). Arctic charr in Lough Conn, the largest lake in the Moy catchment, are extinct, and eutrophication has been identified as the most likely cause (Igoe *et al.*, 2003). Recent surveys, however, suggest that Arctic charr are

also under pressure in Lough Talt, owing to substantial algal growth on the gravel beds used for spawning (Igoe & Hammar, 2004). The lake also contains brown trout, perch and sticklebacks as well as the piscivorous brown trout (ferox trout) (Igoe & Hammar, 2004). Lough Talt is noted for the presence of the semi-aquatic snail *Vertigo geyeri* (Lindholm) and the white-clawed crayfish (*Austropotamobius pallipes* Lereboullet) both of which are listed under the EU Habitats Directive (Duchas, 2002b). The phytoplankton assemblage in June and July 1996 was dominated by cryptophytes such as *Rhodomonas spp.* and *Cryptomonas spp.* The cyanophyte taxa *Aphanothece spp.* was also prevalent during these months (Irvine *et al.*, 2001). *Chara hispida* (L.) is the most widespread species of submerged macrophyte in the lake, and the floating species *Potamogeton natans* (L.) is also common (Irvine *et al.*, 2001).

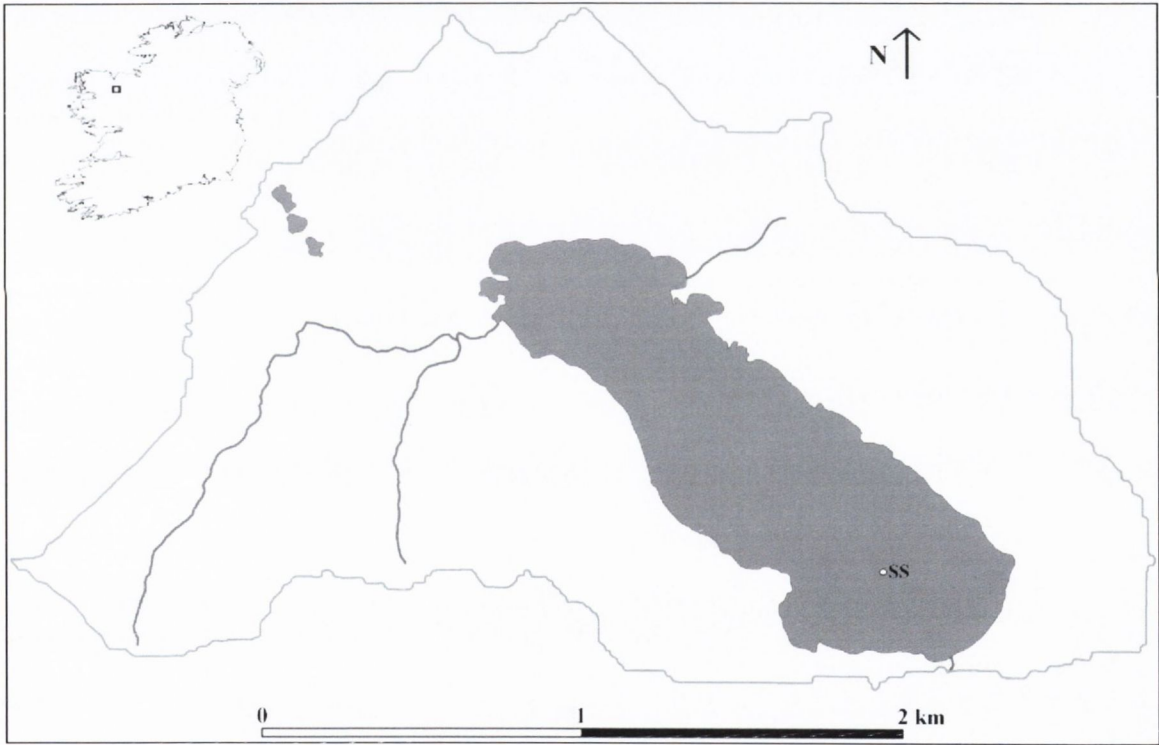


Fig. 2.3 Lough Talt and surrounding catchment in Co. Sligo, showing the sampling site (SS).



Fig. 2.4 Lough Talt, Co. Sligo.

2.1.4 Lough Rea

Lough Rea (Fig. 2.5; Fig. 2.6) is a calcareous limestone lake located at the edge of Loughrea town in Co. Galway (53 ° 11' N, 08 ° 34' W). It was most likely formed by glacial erosion and has a catchment underlain by carboniferous limestone. It has one inflow at its southern end and two outflows from its northern shore.

The lake provides the town's water supply, but it is also an important recreational area and is one of the few inland lakes in Ireland with European Blue Flag status. Approximately 90 % of the catchment area is composed of pasture land which is used principally for grazing sheep and some cattle. The lake is noted internationally for its wildfowl, particularly for shoveler (*Anas clypeata* L.). It is stocked annually with brown trout by the Loughrea Angling Association. There is also a good quantity of coarse fish, namely perch and pike as well as sticklebacks, eels, rudd (*Scardinius erythrophthalmus* L.) and brook lamprey (*Lampetra planeri* Bloch). During June and July the phytoplankton population was found by Irvine *et al.* (2001) to be dominated by cyanophytes particularly *Aphanothece* sp; diatoms such as *Cyclotella* sp. were also prevalent (Irvine *et al.*, 2001). A macrophyte survey of Lough Rea carried out in

August 2004 showed the assemblage to be dominated by *Chara spp.*, with *Phragmites australis* and *Eleocharis palustris* (L.) also common.

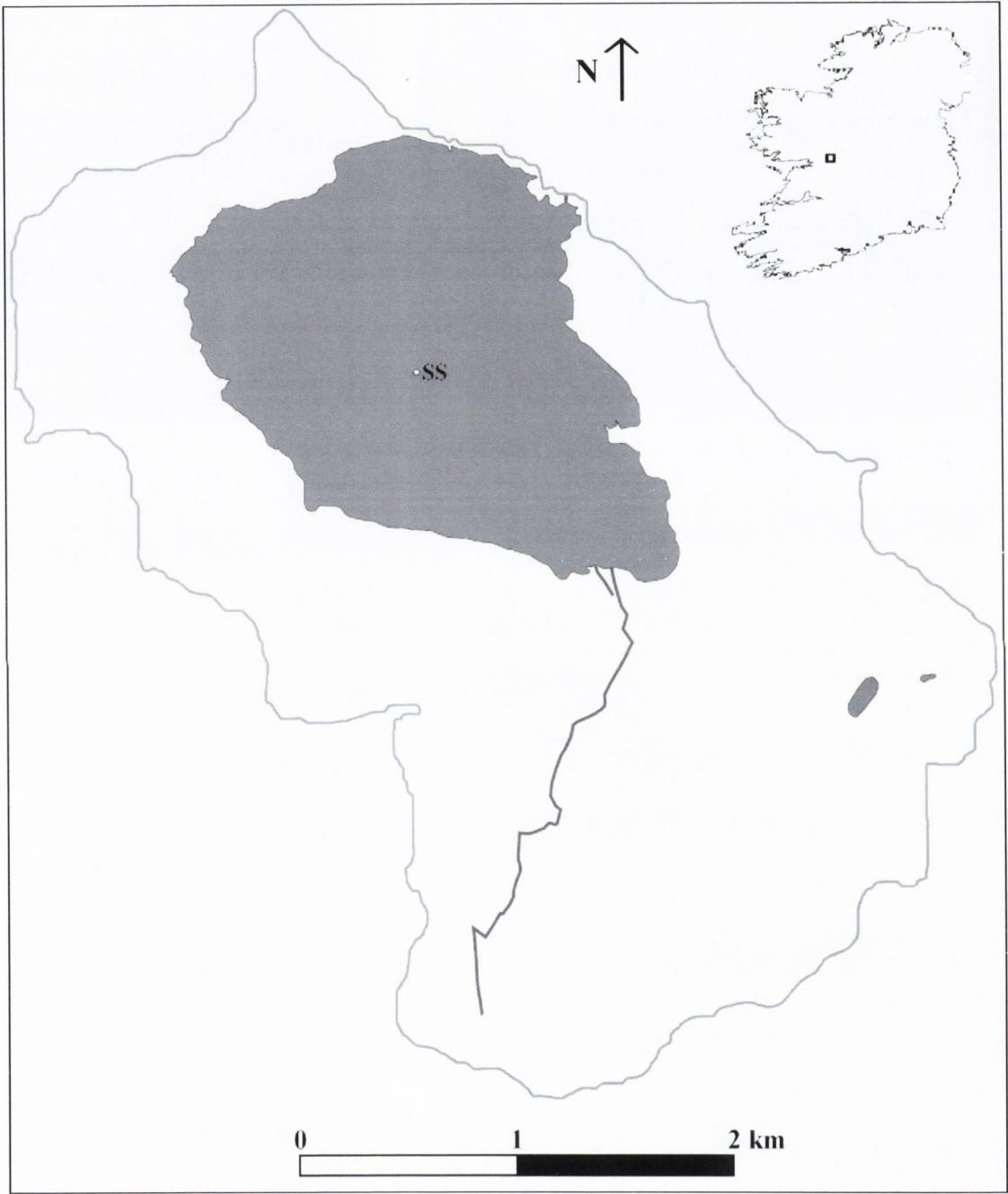


Fig. 2.5 Lough Rea and surrounding catchment in Co. Galway, showing the sampling site (SS).



Fig. 2.6 Lough Rea, Co. Galway.

Photo by Marilyn Phibes (www.Flickr.com)

2.1.5 Lough Feeagh

Lough Feeagh (Fig. 2.7; Fig 2.8) is a low-alkalinity lake situated in the Burrishoole catchment, north of Clew Bay ($53^{\circ} 57' \text{ N}$, $09^{\circ} 35' \text{ W}$). The lake is of glacial origin and is located in the Nephin Beg mountain range. The bed rock is composed largely of Dalradian schists and quartzites, or quartzite gneiss and schist mixes with some outcropping of sandstone and limestone (Long *et al.*, 1992). There are three principal lakes in the Burrishoole system; the freshwater Lough Feeagh and Bunaveela, and the brackish Lough Furnace which is tidal and meromictic. The catchment is drained by approximately 45 km of poorly buffered small shallow rivers (Byrne *et al.*, 2003). Lough Feeagh is linked by two short outflows to Lough Furnace.

Approximately 30 % of the catchment is under active coniferous forestry management (Byrne *et al.*, 2003) and thinning and clear-felling are ongoing. Agriculture is predominantly hillside farming of mountain sheep with a small number of cattle. In large parts of the catchment overgrazing by sheep has contributed to severe hillside erosion which has led to the acidification and peat siltation of the

streams and lakes (Poole *et al.*, 2003). The catchment contains important spawning grounds for Atlantic salmon (*Salmo salar* L.). Other fish in the lake include brown trout, eels and three-spined sticklebacks (Byrne *et al.*, 2003). The phytoplankton community was dominated by chlorophytes between June and July 1996 (Irvine *et al.*, 2001). The submerged macrophyte assemblage includes *Chara globularis* (Thuillier) and *Potamogeton crispus* (L.). *Sparganium emersum* (Rehmann) is the most prominent emergent macrophyte present in the lake (Irvine *et al.*, 2001).



Fig. 2.7 Lough Feeagh and surrounding catchment in Co. Mayo, showing the sampling site (SS).



Fig. 2.8 Lough Feeagh, Co. Mayo.

2.1.6 Lough Easky

Lough Easky (Fig. 2.9; Fig. 2.10) is a low-alkalinity lake located in the Ox mountains, north of Lough Talt ($54^{\circ} 09' \text{ N}$, $08^{\circ} 51' \text{ W}$) at an altitude of 190 m, and is underlain by granite and a mixture of schist and gneiss. Its outflow is into the Easky river, which enters the Atlantic ocean at Easky town.

The catchment area consists of unexploited peat bogs and the coarse vegetation is used as commonage for grazing sheep. Similar to Lough Talt, Easky is also used as a regional water supply for the nearby inhabitants and serves approximately 6,000 people (Sligo County Council, www.sligococo.ie/). Lough Easky contains brown trout and sea trout (*Salmo trutta trutta* L.). Past surveys reported the presence of Arctic charr in the lake (Igoe *et al.*, 2003), but these have not been found in recent surveys and the population is now believed to be extinct (Fran Igoe, *personal communication*). The phytoplankton community was found to be dominated by cyanophytes between June and July 1996, with taxa such as *Aphanothece* spp. and *Merismopedia* spp. prevalent, although *Anabaena flos-aquae* was also widespread (Irvine *et al.*, 2001).

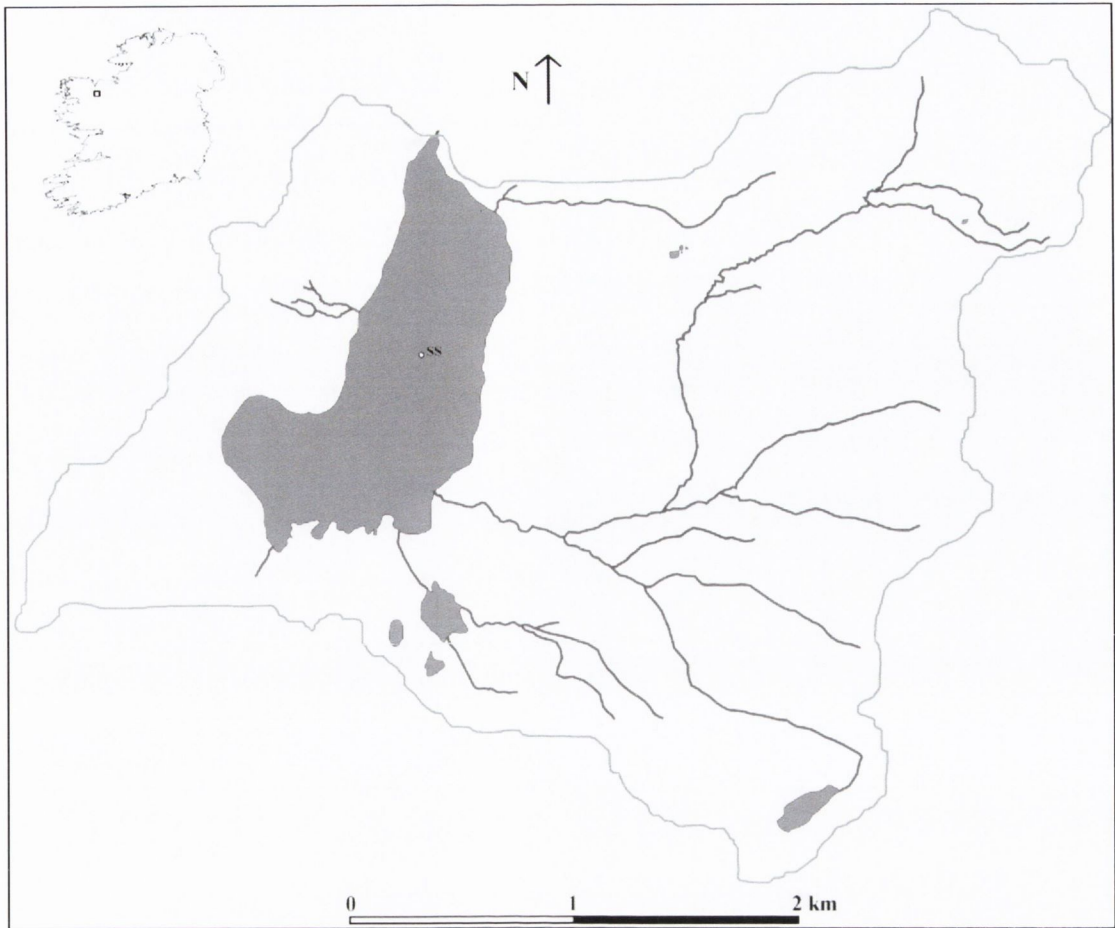


Fig. 2.9 Lough Easky and surrounding catchment in Co. Sligo, showing the sampling site (SS).



Fig. 2.10 Lough Easky, Co. Sligo.

2.1.7 Lough Maumwee

Lough Maumwee (Fig. 2.11; Fig. 2.12) is a low-alkalinity lake located in the Corrib catchment ($53^{\circ} 28' \text{ N}$, $09^{\circ} 32' \text{ W}$). It is a shallow lake which does not stratify. The catchment lies on Devonian granites and quartzite. The lake has two fluvial inputs, and its only output flows into Loughanillaun, located to the south of Maumwee, which itself joins Lough Corrib to the east by means of the Folore river.

Low relief blanket peatland characterises the landscapes around Lough Maumwee and the coarse vegetation is used as commonage for grazing sheep. Peat cutting is on going around Lough Maumwee (Flower *et al.*, 1994). Brown trout fry and salmon fry are found in the lake, along with eels and minnow (Bowman, 1987). Chlorophytes and dinophytes have been found to be the main contributors to phytoplankton biomass in Maumwee, with cryptophytes also found in large numbers (Irvine *et al.*, 2001). The submerged macrophyte assemblage consists of *Eriocaulon septangulare* (Withering) and the emergent flora is dominated by *Eleocharis acicularis* (L.) (Irvine *et al.*, 2001).

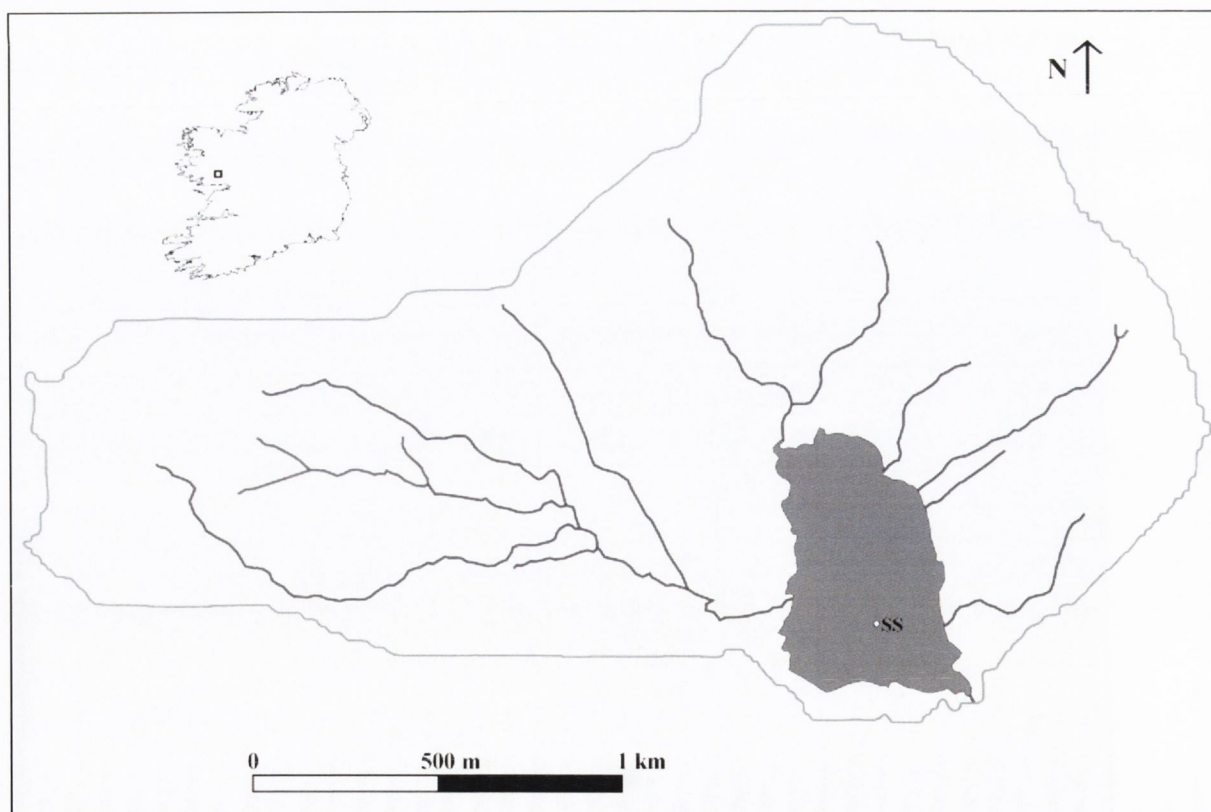


Fig. 2.11 Lough Maumwee and surrounding catchment in Co. Galway, showing the sampling site (SS).



Fig. 2.12 Lough Maumwee, Co. Galway.

2.2. General Methods

2.2.1 Sampling Procedure

Lough, Easky, Talt, Feeagh and Maumwee were sampled from a 3.5 m Avon inflatable boat and Lough Carra and Rea were sampled from a hired anglers boat. A GPS (Garmin® GPS 12) and an Echo Sounder (Scubapro® PDS-2) were used to locate sampling sites and estimate the depth from which a zooplankton vertical haul was taken. Zooplankton was collected using a 53 μm mesh net (diameter 0.25 m) with a flow meter attached. The net was lowered to a depth of 10 m in all lakes, apart from Maumwee, from which a 2 m haul was taken owing to its shallow depth. The net was drawn vertically through the water column at an approximate speed of 1 m s^{-1} . The standard 10 m haul taken in most of the lakes, may have resulted in an under-estimation of zooplankton abundances in deep lakes such as Feeagh and Talt, which had maximum recorded depths of approximately 45 m and 41 m, respectively. Zooplankton often employ day-time vertical migration from surface waters to deep-water refuges, moving back to shallower depths at night to feed under the cover of

darkness (Lampert & Sommer, 1997; Jeppesen *et al.*, 1997). As a result, zooplankton biomass and abundances calculated for these two lakes may not entirely reflect the numbers of zooplankton present throughout the entire water column. After collection zooplankton was transferred to a 500 ml storage jar and narcotised with chloroform water, to prevent ejection of eggs, prior to being stored in industrial methylated spirits. An estimate of the distance towed through the water (D) was obtained using a pre-calibrated flow meter, and the volume of water (V) filtered was calculated from $V = D\pi r^2$, where r is the radius of the opening of the net. Vertically integrated samples of the water column were taken using a plastic tube 5 cm in diameter and 6 m in length. Conductivity, pH and temperature were measured using WTW® meters. Secchi depth was also recorded. In Lough Carra, there were three sampling sites, one located in each of the three basins. There was only one sampling site in all other lakes, and this was generally located in an area with a depth greater than 10 m to facilitate the zooplankton vertical haul, except in the very shallow Lough Maumwee from which the vertical haul was taken at a depth greater than 2 m. With the exception of Lough Carra, sampling took place once a month between April 2003 and April 2004. Sampling on Lough Carra began in April 2001 and was carried out fortnightly until October 2002, and then monthly until April 2004. Until April 2002 only a single haul was taken from each of the three sampling sites in Lough Carra and, thereafter, four hauls were taken at each site. In all other lakes four zooplankton hauls were taken at each site.

2.2.2 *Limnological laboratory techniques*

Dissolved nutrient analyses (soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP) and dissolved inorganic nitrogen (DIN)) were made on water filtered through 0.45 µm Whatman® membrane filters. Total phosphorus (TP), TDP and total nitrogen (TN) were analysed after digestion under pressure with potassium peroxide sulphate ($K_2S_2O_8$). Phosphorus concentrations were determined using spectrophotometer absorbance at 882 nm following Eisenreich *et al.* (1975). Nitrogen analyses were carried out using a continuous flow auto-analyser (AutoAnalyzer 3®, Bran + Luebbe) following Grasshoff *et al.* (1999). Particulate phosphorus (PP) and particulate nitrogen (PN) were estimated as the difference between total P or N and the dissolved fractions of P or N.

Chlorophyll *a* analyses were carried out on 1 L triplicate samples from each integrated water sample, filtered through Whatman® GF/C filters and extracted with methanol (Standing Committee of Analysts, 1980) with absorbance read in a spectrophotometer at 665 and 750 nm in a 5 cm cell. Alkalinity was analysed on a 50 ml unfiltered sample of lake water by Gram titration according to Mackereth *et al.* (1978). Dissolved organic carbon (DOC) was analysed in Whatman® GF/C filtered water, using a TOC analyser (Schimadzu® TOC 5000A). Suspended solids and suspended particulate organic matter were obtained following Allen (1989). True colour (measured after filtration through Whatman® GF/C filters) and turbidity were measured using a Hach® DR2000 spectrometer.

2.2.3. Quality control

For all phosphorus and nitrogen analyses, quality control (QC) samples of known concentration were used to assess the performance of the analytical methods employed. Standard solutions for use as QC samples in N and P analyses were prepared with reagents which were independent to those used for the construction of standards, and therefore provided a degree of quality assurance as well as QC. For nitrogen analyses a QC with a concentration of 1 mg L⁻¹ NO₃-N was prepared and for phosphorus analyses a QC concentration of 0.025 mg L⁻¹ PO₄-P was used. The QC analyses for TN and DIN had a mean value (±SD) of 1.04 ± 0.07 mg L⁻¹ NO₃-N and 0.98 ± 0.06 mg L⁻¹ NO₃-N, respectively. Total phosphorus and SRP quality assurance values had a mean (± SD) of 0.026 ± 0.003 mg L⁻¹ PO₄-P and 0.024 ± 0.001 mg L⁻¹ PO₄-P, respectively, and all quality assurance values were within acceptable ranges (± 3 %).

2.2.4 Zooplankton laboratory techniques

Zooplankton species were identified following Scourfield & Harding (1966); Harding & Smith (1974); Ruttner-Kolisko (1974); Pontin (1978); Reddy (1994); Dussart & Defaye (1995) and Einsle (1996), and counted in a 5 ml grooved circular perspex disc (Jones, 1979). In developing their key to copepod identification, Harding & Smith (1974) found that a dichotomous guide was not a feasible method of identification

owing to the fact that copepods are not only taxonomically close to one another, but also phenotypically quite variable, so much so that a single character difference is often insufficient for taxonomic separation. A 'tabular' type key was, therefore, designed in which taxonomically useful characters are compared in all the species. The degree of variation in copepods, particularly, cyclopoid copepods, however, often made it difficult to identify an individual to species. Certain key features allowed the separation of an individual down to one of a small group of species. It was often difficult, thereafter, to separate the individual out further, with the formula of characteristics frequently matching a number of possible species. For the cyclopoids, the key was suitable only for females and, as recommended by Harding & Smith (1974), only egg-bearing females were identified to species level. Egg bearing females were not present in a number of samples, and when present could be quite rare. As a result, copepod species identification was patchy and irregular and unsuitable for abundance estimation. Copepod identification was, therefore, principally used to indicate the presence of certain species in a particular lake. For biomass calculations, all species of copepod were grouped either as calanoids or cyclopoids.

The mean of four well-mixed 5 ml sub-samples taken from a known volume using a wide-bore pipette (Bottrell *et al.*, 1976) was used to estimate zooplankton abundance. For biomass and fecundity analyses a further sub-sample, of sufficient volume to obtain a suitable count size, was removed from each of the four replicates and pooled. A minimum of 50 individuals from each of the taxa scored for fecundity (Table 2.4) was required to obtain a suitable count size. For zooplankton biomass calculations the lengths of the first 50 rotifers encountered in the pooled samples and the lengths of crustaceans including copepod nauplii, up to a minimum of 100 post-naupliar individuals of the most abundant taxa in the sample were measured using a calibrated ocular micrometer. Prior to July 2003, the lengths of crustaceans including copepod nauplii up to a minimum of 50 post-naupliar individuals were measured in Lough Carra.

Copepod total body-length (TL) was measured from the top of the head to the base of the furci rami. Cladoceran total body-length (TL) was measured from the top of the head to the tip of the abdomen, not including spines or projections. Sizes quoted

throughout this thesis refer to the total body-length. Taxa abundance was converted to biomass using regression formulae relating length to weight calculated for individuals from the most abundant taxa in each lake (Table 2.3). For other crustacean taxa, formulae were taken from Bottrell *et al.* (1976), Rosen (1981) and Dumont *et al.* (1975). Rotifer abundance was converted to biomass by converting volume to fresh weight assuming a specific gravity of 1, following Ruttner-Kolisko (1977). Fresh weight was converted to dry-weight using values calculated by Pauli (1989). If the specific value was unavailable a ratio of 0.10 was assumed.

Table 2.3 Linear regression relating length (mm) with dry weight (µg) in freshwater crustaceans from the six lakes using the equation $\text{Ln}W = \text{Ln}a + b\text{Ln}L$, n = number of observations; $c.i$ = confidence interval; P = level of significance; r^2 = coefficient of determination; * From de Eyto & Irvine (2005).

	Date	Species	Range in length (mm)	n	$\text{Ln}a$	$b \pm 95\% c.i$	r^2	P
Maumwee *	Oct. 2000	Cyclopoid	0.49 – 1.09	34	1.71	1.45 ± 0.7	0.41	< 0.01
		<i>Holopedium gibberum</i>	0.60 – 1.09	30	2.16	2.41 ± 0.5	0.76	< 0.01
		<i>Bosmina coregoni</i>	0.32 – 0.60	16	2.33	1.96 ± 0.8	0.55	< 0.01
Carra *	May 2001	<i>Daphnia hyalina</i>	0.81 – 1.72	43	2.55	1.21 ± 0.3	0.46	< 0.01
		<i>Eudiaptomus gracilis</i>	0.70 – 1.30	35	2.60	2.33 ± 0.8	0.43	< 0.01
Easky	June 2004	Calanoid	0.83 – 1.65	64	1.53	3.24 ± 0.2	0.54	< 0.001
		<i>Ceriodaphnia spp.</i>	0.38 – 0.9	43	2.73	3.69 ± 0.3	0.76	< 0.001
		Cyclopoid	0.63 – 1.43	41	1.90	3.75 ± 0.3	0.34	< 0.001
Feeagh	June 2004	<i>Eudiaptomus gracilis</i>	0.68 – 1.70	52	1.38	3.58 ± 0.3	0.38	< 0.001
		Cyclopoid	0.63 – 1.65	50	1.92	2.94 ± 0.1	0.78	< 0.001
		<i>Daphnia spp.</i>	0.83 – 1.83	44	1.63	2.52 ± 0.1	0.86	< 0.001
Rea	June 2004	<i>Eudiaptomus gracilis</i>	0.55 – 1.38	48	1.45	3.63 ± 0.1	0.85	< 0.001
		Cyclopoid	0.53 – 1.18	44	1.18	2.10 ± 0.4	0.34	< 0.001
		<i>Daphnia spp.</i>	0.53 – 2.05	56	1.40	2.74 ± 0.2	0.75	< 0.001
Talt	June 2004	Calanoid.	0.98 – 1.63	22	1.66	2.97 ± 0.4	0.52	< 0.001
		Cyclopoid	0.65 – 1.45	38	1.33	3.53 ± 0.2	0.62	< 0.001
		<i>Daphnia spp.</i>	0.73 – 1.75	37	1.22	3.02 ± 0.2	0.69	< 0.001

On each sampling date a minimum of 50 individuals of the most abundant taxa in each lake were scored for length and number of eggs (Table 2.4). On rare occasions

during the sampling period some taxa were present in such low abundances that it was not possible to count 50 individuals. In these situations fecundity counts were terminated when half the volume of the original samples had been analysed. The length of the smallest egg-bearing female was used as an estimate of the minimum size at maturity and all individuals of an equal or greater size were assumed to be mature. The number of eggs per mature female was then calculated.

Table 2.4 Taxa analysed for fecundity parameters in each of the six lakes, April 2003 – April 2004.

Carra	Talt	Rea	Easky	Feeagh	Maumwee
<i>Daphnia spp.</i>	<i>Daphnia spp.</i>	<i>Daphnia spp.</i>	Calanoid	<i>Daphnia spp.</i>	<i>Daphnia spp.</i>
Calanoid	Calanoid	Calanoid	Cyclopoid	Calanoid	Cyclopoid
	Cyclopoid		<i>Ceriodaphnia spp.</i>	Cyclopoid	<i>Bosmina spp.</i>
			<i>Bosmina spp.</i>	<i>Diaphanosoma sp.</i>	<i>Diaphanosoma sp.</i>
					<i>Holopedium sp.</i>

3.1 Introduction

The occurrence of zooplankton species in lake communities depends on water temperature and chemistry, food availability and biotic interactions such as competition or predation (Gliwicz, 1990). In addition, the dispersal abilities of different taxa and the historical sequence and rate of colonisation (Jenkins & Buikema, 1998) contribute to the structure of zooplankton communities. Early limnological research focused on the effect of physical factors on zooplankton community structure (Hutchinson, 1967). Factors such as morphology, lake depth (O'Brien *et al.*, 2004) and turbidity (Cuker & Hudson, 1992) have all been implicated in determining species distribution. Some taxa have been found to be particularly tolerant to factors such as low levels of oxygen (Hutchinson, 1967), or pH (Hamilton, 1958; Stenson, 1973).

A number of chemical elements could also limit zooplankton production (Sterner & Elser, 2002). Ionic calcium (Ca) in the water is the principal source of Ca for zooplankton (Cowgill *et al.*, 1986). In crustaceans most of the Ca within their body is associated with carbonate and phosphate minerals in the carapace, and thus at least some proportion of this body-Ca must be regenerated after each molt (Stevenson, 1985). Calcium is, therefore, vital for growth in crustacean taxa with a calcified exoskeleton, and its availability may be a major constraint to their distribution (Økland & Økland, 1985; Meyran, 1998). Zooplankton species have variable Ca content, ranging from 0.1 to 4.4 % of dry weight (Wærvågen *et al.*, 2002). The body content of Ca in some *Daphnia* species has been found, at least partly, to reflect ambient Ca concentrations (Cowgill *et al.*, 1986). Calcium may, therefore, be of particular importance in soft-water lakes, limiting the distribution of certain heavily calcified zooplankton. Hessen *et al.* (1995a) found that there was a lower occurrence of *Daphnia* in soft-water lakes. Tessier and Horwitz (1990) observed an increased prevalence of large bodied crustaceans, replacing small bodied rotifers with increasing Ca concentration. Water-hardness can also influence the distribution of *Daphnia* species (Wærvågen *et al.*, 2002), and experimental studies on the calcification and Ca content of *Daphnia magna* suggest a competitive disadvantage of

the species in Ca-poor waters (Alstad *et al.*, 1999). However, the distribution and abundance of zooplankton is influenced by such a wide array of interconnected factors, that often it is difficult, and indeed meaningless, to relate community structure to any solitary abiotic or biotic variable. Calcification in crustaceans, for example, is related not only to bicarbonate concentration (Mezquita *et al.*, 1999), but also to pH levels (Malley, 1980; France, 1987). In addition, specific Ca content in *Daphnia* can change depending on moulting status or animal size (Alstad *et al.*, 1999). Consequently, factors such as age, the availability of food and fish predation, may all have an effect on the Ca content of an individual.

Many descriptive field studies have implicated both predation and competition as factors which may regulate zooplankton species occurrence and seasonal dynamics and their relative importance in determining community structure has been debated (Sih *et al.*, 1985). The size-selective foraging behaviour of fish is considered to be critical in determining plankton community structure (Brooks & Dodson, 1965). Large-bodied zooplankters, such as *Daphnia*, are the favoured prey of visually foraging planktivorous fish, and are therefore rare or absent when such fish are abundant (O' Brien, 1979; Zaret, 1980; Vanni & Findlay, 1990). When high densities of planktivorous fish are present, the size distribution of the zooplankton community shifts from large to smaller zooplankton such as *Bosmina* (Post & McQueen, 1987; Black & Hairston, 1988; Wahlström *et al.*, 2000).

Invertebrate predation may also have an important role to play in determining the outcome of zooplankton interactions. Predacious invertebrates detect their prey by mechano- or chemoreception (Herzig & Auer, 1990). Food selection by invertebrates will depend on their ability to capture and handle prey and they, therefore, generally select for small to intermediate sized prey (Pastorok, 1981; Zaret, 1980; Hanazato & Yasuno, 1989). Yan *et al.* (1991) found that when fish predation was absent, predation from larval *Chaoborus* reduced the abundance of *Bosmina* and was responsible for maintaining the unusually small crustacean zooplankton biomass in their study lake. Predacious invertebrates are themselves preyed upon by fish but also compete with fish for prey, resulting in a more complex food-web composition known as intraguild predation (Wissel *et al.*, 2003). In a Minnesota pond, both fish and *Chaoborus* reduced the densities of the competitively superior *Ceriodaphnia*

spp., which were replaced by *Daphnia pulex*, a much larger species. When fish numbers were very high, however, the community was dominated by *Bosmina* and rotifers, which also dominated when both fish and *Chaoborus* were rare (Lynch, 1979).

Predation is a strong selective factor and as a result prey have evolved many defence mechanisms that help to lower their mortality. Cyclomorphosis involves recurrent, seasonal, or induced changes in body form. Examples of cyclomorphosis are found in several taxa: *Daphnia* (Grant & Bayly, 1981; Tollrian, 1995), *Ceriodaphnia* (Zaret, 1972), *Bosmina* (Black, 1980) and rotifers (Gilbert, 1966). The morphological changes affect very different aspects of the phenotype such as helmet size, helmet shape, tail spine length, antennae length and ‘neck-teeth’ (small protuberances in the dorsal mid-line). Induction of cyclomorphosis has been attributed to triggers such as increased temperature (Yurista, 2000) or turbulence (Hazelwood, 1966). Several authors, however, have shown that cyclomorphosis can be induced by the presence of predators. Jacobs (1967) found that excuberant forms of a species of *Daphnia* were better able to avoid predation by guppy (*Poecilia reticulata*) than the non-excuberant forms. This proposal was extended by Dodson (1974a), who suggested that cyclomorphosis may be an adaptation for avoiding invertebrate predators. He proposed that the various morphological changes make capture by invertebrate predators difficult, as they are dependent on tactile manipulation of prey. The protrusions also function in reducing the visible parts of the bodies of larger zooplankters, thus reducing the impact of visual predators. This hypothesis was supported by a study of Alaskan lakes, in which it was found that the helmeted form of a cyclomorphotic *Daphnia* was less vulnerable to both trout and copepod predation than the ‘normal type’ *Daphnia* (O’ Brien *et al.*, 1979).

While the effects of fish predation in determining the outcome of zooplankton species interactions have been clearly documented in freshwater systems (Threlkeld, 1979; Zaret, 1980; Turner & Mittelbach, 1990; De Robertis, 2002; Persson, *et al.*, 2004), the role of exploitative competition in natural populations is less apparent (DeMott & Kerfoot, 1982; Càceres, 1998), particularly in systems where fish predation is absent or unimportant. Fishless lakes are characteristically dominated by large zooplankton species, sometimes to the exclusion of small species (Brooks & Dodson, 1965; Zaret,

1980; Shapiro & Wright, 1984). It is not clear why large plankton suppress small species in the absence of fish (Lampert & Sommer, 1997). The size-efficiency hypothesis provides an explanation (Brooks & Dodson, 1965; Hall *et al.*, 1976), and suggests that all planktonic herbivores are in competition for the fine particulate matter of the open water. The larger sized species were assumed to be more efficient grazers and it was found that the threshold food concentration necessary to ensure that assimilation equals respiration declines with increasing body size (Gliwicz, 1990). It was, therefore, suggested that as a result of competition for food, larger-bodied zooplankton species will be favoured, while fish predation shifted communities towards smaller-bodied species (Vanni, 1987). Nevertheless, patterns in seasonal succession have been observed, whereby small species out-compete larger species and was related to the greater vulnerability of juvenile *Daphnia* to co-exploitative interactions with *Ceriodaphnia*. This resulted in the seasonal succession of *Daphnia* by *Ceriodaphnia* in the natural population (Neill, 1975; Lynch, 1978). Small- and large-body species have also been found to co-exist owing to the ability of smaller species such as *Bosmina* to forage more effectively on high quality food, such as highly edible flagellates (DeMott & Kerfoot, 1982), or their ability to successfully reproduce following oscillations in *Daphnia* populations as a result of over exploitation of food resources (Goulden *et al.*, 1982).

An alternative hypothesis to the size-efficiency hypothesis postulates that invertebrate predation is greater in fishless lakes or where fish predation is reduced, and that the invertebrates decrease the abundance of smaller zooplankton species (Dodson, 1974b; Hanazato & Yasuno, 1989). It may be that the combined effects of competitive suppression of small species by large herbivores and predation by invertebrates is the most important factor in reducing the abundance of small species, when fish predation is weak (Neill, 1981; Vanni, 1986; Mumm, 1997; Ślusarczyk, 1997)

The overall outcome of these biotic interactions will, nevertheless, be affected by the physical and chemical condition of the system in which they exist. Abiotic factors may influence the physiology and behaviour of organisms, and species interactions could, therefore, be affected by abiotic factors such as pH and temperature. These factors may directly affect zooplankton community structure owing to physiological intolerance or they may affect zooplankton indirectly by influencing biotic

interactions. Variables such as oxygen and pH often regulate fish occurrences in some areas, thereby affecting zooplankton species structure (Rahel, 1984). It was also found that with increasing water colour invertebrate predators such as *Chaoborus* would become more important than vertebrate predators, thus shifting the zooplankton assemblage towards larger species (Wissel *et al.*, 2003). Consequently, the most appropriate approach may be to consider how the relative importance of predation and exploitative competition may vary along gradients of abiotic change (Arnott & Vanni, 1993).

In this chapter the zooplankton community structure of three hard-water and three soft-water lakes was examined in order to test for variation in species occurrence, abundance and dominance between the two alkalinity groups. Differences in the seasonal dynamics of individual taxa across lakes were investigated, and size-distribution analyses used to estimate the influence that fish and invertebrate predation may have in structuring seasonal patterns in species dominance between the high- and low alkalinity lakes. The *a priori* premise was that communities would differ between high- and low- alkalinity lakes owing the contrasting abiotic conditions (eg. alkalinity, pH) and that these abiotic factors would have some influence on the outcome of seasonal biotic interactions such as predation and competition.

3.2 Methodology

Zooplankton and water were collected and analysed using methodology outlined in Chapter 2 (section 2.2). In addition, phenotypic variation in *Daphnia* was observed on a number of sampling dates. To describe this cyclomorphosis, the body length and helmet length of a minimum of 50 *Daphnia* per sample were measured in all lakes, apart from Lough Easky. The ratio of helmet length to body length (HL:BL) was then calculated and used as an indicator of predation pressure.

The biomass ratio of zooplankton to phytoplankton has previously been found to be closely correlated with the number of planktivorous fish caught in multi-mesh sized gill-nets in Danish and New Zealand lakes (Jeppesen *et al.*, 2000). The zooplankton:phytoplankton biomass ratio might, therefore, be an approximate indicator of the level of fish predation. A low zooplankton:phytoplankton ratio could indicate high predation pressure on zooplankton by fish, whereas a high zooplankton:phytoplankton ratio could indicate a higher grazing pressure on phytoplankton. The zooplankton:phytoplankton biomass ratio (DW:DW) was, therefore, calculated assuming a conversion factor of 66 between chlorophyll *a* and phytoplankton dry weight.

3.2.1 Statistical analyses

Non-metric multidimensional scaling (MDS) was used to discriminate sites on the basis of their biotic composition using Primer® Version 5. Multivariate approaches such as MDS ordination are more appropriate for the analyses of biological data than standard univariate statistical techniques, owing to the complex nature of such data where species distribution and abundances may be influenced by a wide array of inter-correlated factors. Multivariate techniques retain and incorporate the multidimensionality of ecological data sets and reduce them to a few interpretable dimensions. The available data is, therefore, exploited in a much more complete way than is possible with univariate techniques, in which it is required to collapse the full set of species counts for a sample into a single coefficient (e.g. diversity index, total abundance). Multivariate methods compare samples based on the extent to which they share particular species. Although the algorithm involved in calculating an MDS

ordination is itself complex, the rationale behind it is straightforward. Very few model assumptions about the data or the inter-relationships between samples are made. An MDS ordination is a non-parametric analysis based on a (dis)similarity matrix which is constructed among all the samples. A 'map' is created which aims to represent the data as points in a specified number of dimensions (usually 2-d) such that the relative distances apart of all points are in the same rank order as the corresponding dissimilarities among samples (Clarke & Warwick, 1997). The ordination is thus very easy to interpret, with points which are close together representing values of the variable set which are very similar. The MDS algorithm is an iterative procedure which aims to reduce stress. Stress can be thought of as a measure of the difficulty involved in compressing the sample relationships into a small number of dimensions (Clarke & Warwick, 1997). A stress value < 0.05 indicates that the ordination is an excellent representation of the high-dimensional assemblage structure and there is a very low probability of misinterpretation. A stress value > 0.3 indicates that samples were almost arbitrarily placed on the ordination plot, their locations being more or less random (Clarke & Warwick, 1997).

Similarity matrices were calculated using the Bray-Curtis coefficient of similarity, which was originally applied to studies of terrestrial communities (Bray & Curtis, 1957) and is generally recommended for analyses of community structure (Clarke & Warwick, 1997). The similarity matrices were applied to both zooplankton abundance in numbers m^{-2} and biomass in $\mu g\ DW\ m^{-2}$, having firstly been manipulated using fourth-root transformation, which downweights the effect of common taxa. Fourth-root transformation is intermediate between two extremes: that of no transformation, for which only the common species contribute to the similarity matrix and presence/absence which allocates equal importance to both rare and common species. Multidimensional scaling was also used to differentiate lakes based on their physical and chemical properties. These data are different from the biological data in that zeros no longer dominate, and it is possible to approximate normality using a simple logarithmic transformation. The data was firstly standardised into a common dimensionless measurement prior to transformation. Principal component analyses is generally considered appropriate for plotting abiotic variables, however, when the number of variables is small, an MDS plot will be similar in practice to PCA (Clarke & Warwick, 1997).

Pairwise ANOSIM (Analysis of Similarities) tests were carried out to test for differences in zooplankton community structure among lakes. ANOSIM is a non-parametric permutation procedure, applied to the rank similarity matrix underlying the MDS ordination of samples. It generates an R statistic which falls between 0 and 1, where $R = 0$ represents a situation where the null hypothesis is true, and there is no difference between sites. A one-way ANOSIM was carried out to test for differences between high- and low-alkalinity lakes. All ANOSIM tests were calculated with 999 permutations based on Bray-Curtis similarity matrices using Primer® Version 5. Since the physical and chemical variables could be transformed to approximate normality, differences between high and low-alkalinity lakes were tested using a one-way MANOVA (Multivariate Analyses of Variance) in which the F -test is replaced by a test known as *Wilks' λ* . It is analogous to the univariate ANOVA test, but is used when there are multiple response variables. The procedure was carried out using Data Desk® Version 6. Dissimilarities between zooplankton community structure were related to physical and chemical variables using the BIO-ENV procedure in Primer® Version 5. This measures any correlation between the rank-orders of the (dis)similarity matrix calculated for species composition and the (dis)similarity matrix between sampling units based on environmental variables using the weighted Spearman rank correlation coefficient (p_w). The BIO-ENV procedure selects a subset of the physical and chemical variables which maximise the rank correlation (p_w) between biotic and environmental (dis)similarity matrices. To avoid the confounding effects of collinearity, sets of variables which had mutual correlations were reduced to a single representative to be included in both the MANOVA and BIO-ENV analyses.

The effects of alkalinity on various univariate measures of zooplankton community structure were tested using Repeated Measures Analysis of Variance (ANOVA) calculated with Data Desk® Version 6. The repeated measures ANOVA allows for the analysis of the effects of many factors over time. Three factors were included in the model. These were alkalinity and lake while sampling trip provided for the repeated measure. A standard split-plot, univariate model was employed and the interaction between alkalinity and sampling trip was analysed to test if changes in measures of zooplankton community structure over time were different for the two alkalinity groups. Highly skewed data were normalised using logarithmic

transformations. Where appropriate Mann-Whitney *U*-Tests were used to test the difference between two groups of non-parametric data using SPSS® Version 12.

3.3 Results

3.3.1 Abiotic parameters

A high pH and Secchi depth was recorded in Lough Carra over the three-year sampling period (April 2001 – April 2004) of this study (Table 3.1). There was also a high pH and Secchi depth recorded in Talt and Rea between April 2003 and April 2004 (Table 3.1). Both Lough Carra and Rea had low mean colour and turbidity with no consistent seasonal fluctuations. Lough Talt had a higher mean colour and turbidity compared with the other high-alkalinity lakes, colour in particular was relatively high and ranged from 17 – 57 mg L⁻¹ PtCo. Alkalinity and conductivity values were high in all three lakes (Table 3.1), and followed similar seasonal patterns in Carra and Rea, with minima in late summer and autumn, most likely a result of CaCO₃ precipitation associated with summer photosynthesis. In contrast, alkalinity and conductivity values in Talt varied little throughout the year with no seasonal pattern evident.

A low pH and Secchi depth was recorded in Easky, Feeagh and Maumwee between April 2003 and April 2004 (Table 3.1). In Maumwee, however, the Secchi disc was often still visible by the time it reached the lake bed. These lakes had low mean alkalinity and conductivity (Table 3.1), with no consistent seasonal fluctuations. Colour and turbidity values were high in all three lakes (Table 3.1), and reflected their location in peaty catchments. The greatest turbidity values were recorded in Feeagh in August 2003. A large peak in turbidity values also occurred in Easky in January 2004, during which time a substantial quantity of detritus was evident in the water column, which affected zooplankton sampling.

The lowest TP concentrations were recorded in Maumwee and the lowest TN concentrations in Talt (Table 3.1). Nutrient dynamics of the six study lakes will be discussed in detail in Chapters 4 and 5.

Table 3.1 Physical and chemical characteristics mean $\pm$ SE, range and sample size (*n*) for Lough Carra (April 2001 – April 2004) and Lough Talt, Rea, Easky, Feeagh and Maumwee (April 2003 – April 2004).

	Alkalinity (mg L ⁻¹ CaCO ₃)	Conductivity (μ S cm ⁻¹)	pH	Colour (mg L ⁻¹ PtCo)	Turbidity (FTU Turb Units)	Secchi (m)	TP (μ g L ⁻¹)	TN (mg L ⁻¹)
Carra								
Mean $\pm$ SE	138 $\pm$ 3.4	321 $\pm$ 5.7	8.4 $\pm$ 0.02	13.5 $\pm$ 1.5	4.9 $\pm$ 0.7	4.4 $\pm$ 0.1	11.6 $\pm$ 0.8	0.75 $\pm$ 0. 03
Range	99 - 177	238 - 389	8.0 – 8.6	1 - 28	0 - 18	2.8 – 6.9	5.1– 34.8	0.4 – 1.4
<i>N</i>	(49)	(44)	(51)	(26)	(26)	(55)	(55)	(50)
Talt								
Mean $\pm$ SE	77 $\pm$ 2.3	186 $\pm$ 2.0	8.0 $\pm$ 0.1	26.3 $\pm$ 3	5.0 $\pm$ 0.3	4.4 $\pm$ 0.2	9.6 $\pm$ 0.9	0.33 $\pm$ 0.06
Range	69 - 99	166 - 191	7.5 – 8.4	17 - 57	3 - 9	3.5 – 5.3	4.5 – 16.7	0.12 – 0.82
<i>N</i>	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)
Rea								
Mean $\pm$ SE	110 $\pm$ 5.1	269 $\pm$ 8.1	8.4 $\pm$ 0.1	14.6 $\pm$ 4	2.8 $\pm$ 0.5	6.1 $\pm$ 0.4	12.0 $\pm$ 0.8	0.62 $\pm$ 0.05
Range	85 - 143	228 - 307	8.1 – 8.7	1 - 39	0 - 6	4.4 – 8.7	7.8 – 17.4	0.41 – 1.00
<i>N</i>	(12)	(12)	(12)	(12)	(12)	(11)	(12)	(12)
Easky								
Mean $\pm$ SE	4.3 $\pm$ 0.46	51 $\pm$ 2.6	6.2 $\pm$ 0.2	55.9 $\pm$ 4	12.8 $\pm$ 0.8	2.2 $\pm$ 0.2	9.6 $\pm$ 1.0	0.42 $\pm$ 0.06
Range	1.4 – 7.0	24 - 60	5.5 – 7.6	36 - 79	8 - 17	1.5 – 4.3	5.1 – 18.9	0.16 – 0.95
<i>N</i>	(12)	(12)	(12)	(12)	(12)	(11)	(12)	(12)
Feeagh								
Mean $\pm$ SE	7.9 $\pm$ 0.31	82 $\pm$ 5.1	7.4 $\pm$ 0.1	82.5 $\pm$ 6	15.7 $\pm$ 0.7	2.4 $\pm$ 0.3	9.4 $\pm$ 0.8	0.56 $\pm$ 0.11
Range	5.7 – 9.2	34 - 96	6.7 – 8.4	61 - 139	12 - 20	1.5 – 5.0	6.4 – 16.7	0.32 – 1.74
<i>N</i>	(12)	(12)	(12)	(12)	(12)	(11)	(12)	(12)
Maumwee								
Mean $\pm$ SE	4.0 $\pm$ 0.26	56 $\pm$ 3.2	7.1 $\pm$ 0.2	37.9 $\pm$ 5	7.3 $\pm$ 0.8	3.0 $\pm$ 0.1	4.8 $\pm$ 0.6	0.47 $\pm$ 0.11
Range	2.8 – 5.2	46 - 76	6.3 – 8.9	18 - 72	4 - 15	2.4 – 3.8	2.4 – 8.9	0.12 – 1.18
<i>N</i>	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)

3.3.2 Zooplankton taxa occurrence and distribution

The number of taxa identified per lake ranged from forty-four to seventy-five. Lough Carra was found to be the most species rich lake. This high species diversity was an artefact of the longer sampling period, with seventeen taxa recorded exclusively in the samples taken before April 2003. If Lough Carra had only been sampled between April 2003 and April 2004, as were the five other lakes, its taxonomic list of fifty-eight, would have been more similar in number to theirs.

A total of fifteen cladoceran, twelve copepod and sixty-one rotifer taxa were identified. Rotifers were consistently the most abundant and species rich component of the zooplankton community in all lakes, of which two species, *Keratella cochlearis* and *Kellicottia longispina*, were particularly common, with an occurrence > 50 % recorded in each lake (Table 3.2). Other important rotifer taxa included

Polyarthra spp., *Synchaeta* spp., *Gastropus stylifer*, *Filinia* spp. and the predatory *Asplanchna* spp. Some littoral, periphytic or benthic genera, which are rare in the plankton such as *Macrochaetus* and *Trichotria* were recorded in the shallow lakes only.

Only two species of *Daphnia* were identified, *Daphnia hyalina* and *D. cucullata*. Both were recorded in all lakes, but in very low numbers in Lough Easky (Table 3.2), which was the only lake in which *Daphnia* formed only a trivial component of overall biomass. *Ceriodaphnia* were more important in Easky, with two species recorded, *Ceriodaphnia setosa* and *C. quadrangula*. *Ceriodaphnia* were absent from only one lake, Lough Rea, but occurred very sporadically and in low numbers in Lough Carra. *Sida crystallina* was recorded in all lakes apart from Lough Rea from which *Polyphemus* spp. and *Simocephalus* spp. were also absent. Both of these species were rare, however, with *Polyphemus* only occurring in high numbers in Maumwee and *Simocephalus* only in Easky. Both were present in very low numbers on rare occasions in Lough Carra. Two species of *Bosmina* were recorded, with only one species, *Bosmina longispina*, ubiquitous to all lakes. This was the only species of *Bosmina* found in Talt, Easky and Maumwee, with *Bosmina longirostris* co-occurring in the other three lakes. *Diaphanosoma brachyurum* and *Holopedium gibberum* were both more prevalent in the low-alkalinity lakes, and had a particularly high occurrence in Maumwee.

Table 3.2 Mean percentage occurrence of each taxa (percentage occurrence = $n_a/N \times 100$ where n = number of individuals recorded for taxa a and N = the total number of individuals recorded on each sample date) of for each of the six lakes, April 2001 – April 2004, $n = 55$ (Lough Carra) and April 2003 – April 2004, $n = 12$ (all other lakes). * Taxa recorded in Lough Carra exclusively between April 2001 and April 2003.

	Carra	Talt	Rea	Easky	Feeagh	Maumwee
Cladocera						
<i>Bosmina longirostris</i> (Leydig)	0.2	0	0.09	0	0.8	0
<i>Bosmina longispina</i> (Leydig)	0.2	0.4	1.4	3.4	2.7	11.3
<i>Bosmina</i> sp.	0.3	0	4.2	0	3.3	0
<i>Bythotrephes longimanus</i> * (Leydig)	0.05	0.02	0	0.07	0.01	0.08
<i>Ceriodaphnia quadrangula</i> (Müller)	0	0.03	0	0.7	0	0
<i>Ceriodaphnia setosa</i> (Matile)	0	0.09	0	2.5	0	0
<i>Ceriodaphnia</i> spp.	<0.001	0.04	0	3.4	0.01	0.01
Chydorid	0.03	0.01	0.02	0.04	0.05	0
<i>Daphnia cucullata</i> (Sars)	1.6	0.5	2.0	<0.01	1.7	0.8
<i>Daphnia hyalina</i> (Sars)	4.7	4.6	9.3	0.01	8.5	1.7
<i>Diaphanosoma brachyurum</i> (Liéven)	0.03	0.03	0.01	0.2	2.7	6.1
<i>Holopedium gibberum</i> (Zaddach)	<0.001	0.03	<0.01	0.5	0.2	3.1
<i>Leptodora kindtii</i> (Focke)	0.09	0.09	0.08	0.01	0.03	0.02
<i>Polyphemus pediculus</i> * (Leydig)	<0.01	0	0	0	0	0.04
<i>Sida crystallina</i> (Müller)	0.03	<0.01	0	0.04	0.03	0.02
<i>Simocephalus vetulus</i> * (Müller)	<0.001	0	0	0.01	0	0
Copepoda						
Calanoid	11.6	5.9	17.3	9.5	25.9	1.5
Cyclopoid	1.5	11.3	0.5	5.8	6.5	12.5
Harpacticoid Copepod *	<0.01	0	<0.01	0	0.02	0.01
Rotifera						
<i>Anuraeopsis fissa</i> (Gosse)	0.2	0.01	0.06	0.02	0.01	0.06
<i>Argonotholca foliacea</i> * (Ehrb.)	0.01	0.02	0	<0.01	0	0
<i>Ascomorpha ecaudis</i> (Perty)	0	0	0	0.05	0	0
<i>Ascomorpha ovalis</i> (Carlin)	<0.01	<0.01	0.1	0.2	0	0.04
<i>Ascomorpha</i> spp. (Perty)	1.0	0.02	0.06	0.04	0	0.01
<i>Asplanchna</i> spp. (Gosse)	0.7	0.01	7.1	0.3	4.8	0.2
<i>Asplanchnopus</i> spp. * (de Guerne)	0.02	<0.01	0	0	0	0
<i>Brachionus angularis</i> (Gosse)	0	0.01	0	0	0	0
<i>Brachionus calyciflorus</i> (Pallas)	0	0	0	0	0	0.02
<i>Brachionus quadridentatus</i> (Hermann)	<0.01	0	<0.01	0	<0.01	0
<i>Brachionus rubens</i> (Ehrb.)	<0.01	0	0	0	0	0
<i>Brachionus</i> spp. (Pallas)	<0.01	0.4	0	0.3	0.04	0.01
<i>Cephalodella gibba</i> (Bory de St Vincent)	<0.07	0	0	0	0	0
<i>Collotheca mutabilis</i> (Hudson)	0.03	0.05	0.23	0.3	0.03	0.5
<i>Collotheca pelagica</i> (Rousselet)	0.01	0.02	0.1	0.05	0.04	0.09
<i>Collotheca</i> spp. (Harring)	<0.01	0	0	0	0	<0.01
<i>Colurella</i> spp. * (Bory de St Vincent)	0.02	0	0	0	0	0
<i>Conochiloides dossuarius</i> (Hudson)	1.6	3.0	1.3	7.7	4.7	15.5
<i>Conochilus hippocrepis</i> (Schränk)	0.09	11.1	0.04	4.7	0.04	2.6
<i>Conochilus unicornis</i> (Rousselet)	0.03	0.4	0.3	0.2	0.2	0.8
<i>Epiphanes brachionus</i> (Ehrb.)	<0.01	0.07	0.02	0	0	0

Table 3.2 Continued

	Carra	Talt	Rea	Easky	Feeagh	Maumwee
<i>Epiphanes senta</i> (Müller)	0.01	0.07	0.2	0.2	0	0.01
<i>Epiphanes spp.</i> (Ehrb.)	0.02	0.02	<0.01	0	<0.01	0.01
<i>Euchlanis dilatata</i> (Ehrb.)	<0.01	0	0.01	0	0.06	0
<i>Euchlanis spp.</i> (Ehrb.)	0.08	0.01	0.02	<0.01	0.02	0
<i>Filinia spp.</i> (Bory de St Vincent)	2.7	0.3	0.7	0.07	2.3	0.3
<i>Gastropus hyptopus</i> (Ehrb.)	0.09	0.09	0.20	0.27	0.04	0.05
<i>Gastropus spp.</i> (Imhof)	0.02	0.01	0	0	0	<0.01
<i>Gastropus styliifer</i> (Imhof)	1.5	1.8	2.6	0.03	0.3	0.5
<i>Graptolebris testudinaria</i> *	<0.01	0	0	0	0	0
<i>Kellicottia longispina</i> (Kellicott)	11.5	29.9	24.5	29.9	9.8	12.6
<i>Keratella cochlearis</i> (Gosse)	29.1	20.4	22.5	25.06	15.3	7.02
<i>Keratella quadrata</i> (Müller)	0.4	0.5	0.02	0.4	0.5	0.05
<i>Keratella serrulata</i> * (Ehrb.)	<0.01	0	0	0	0	<0.01
<i>Keratella spp.</i> (Bory de St Vincent)	12.4	0	0	0	0	0
<i>Lecane lunaris</i> (Nitzsch)	0	0	0	0.01	0	0.02
<i>Lecane spp.</i> * (Nitzsch)	0.02	0	0.01	0.02	0.01	0.06
<i>Lepadella ovalis</i> * (Bory de St Vincent)	<0.01	0	0	0	0	0
<i>Macrochaetus spp.</i> * (Perty)	<0.01	0	0	0	0	0
<i>Mytilina spp.</i> * (Bory de St Vincent)	<0.01	0	0	0	0	0
<i>Notholca labis</i> (Gosse)	<0.01	0.01	0	0	0	0
<i>Platyas spp.</i> * (Harring)	<0.01	0	0	0	0.3	0
<i>Ploesoma hudsoni</i> * (Imhof)	0.1	0	<0.01	0	0	0
<i>Ploesoma spp.</i> (Herrick)	1.5	0	0	0	0	0
<i>Ploesoma truncatum</i> (Levander)	0.1	0	<0.01	0	0.7	0.1
<i>Polyarthra spp.</i> (Ehrb.)	10.4	6.0	2.7	3.7	6.4	2.9
<i>Pompholyx spp.</i> (Gosse)	2.2	0.01	0	0.2	0	0
<i>Rhinoglena frontalis</i>	<0.01	0	<0.01	0	0	<0.01
<i>Rotaria spp.</i> (Scopoli)	0.03	0.02	0	0.02	0.06	0
<i>Scaridium longicaudum</i> (Müller)	<0.01	0	0	0	0	0
<i>Squatinella rostrum</i> (Schmarda)	<0.01	0	0	0	0	0
<i>Squatinella sp.</i> * (Bory de St Vincent)	<0.01	0	0	<0.01	0	0
<i>Synchaeta grandis</i> * (Zacharias)	<0.01	0	0	0	0	0.03
<i>Synchaeta longipes</i> (Gosse)	0.03	1.5	0.2	0.01	0.2	0.7
<i>Synchaeta oblonga</i> (Ehrb.)	0.8	0.6	0.3	0.08	0.7	16.1
<i>Synchaeta pectinata</i> (Ehrb.)	<0.01	0	0	0	0	0
<i>Synchaeta spp.</i> (Ehrb.)	2.8	0.6	1.5	0.04	0.5	2.1
<i>Synchaeta tremula</i> (Müller)	<0.01	0.05	0	0	0.05	0
<i>Testudinella spp.</i> (Bory de St Vincent)	<0.01	0	0	0	0	0
<i>Trichocerca spp.</i> (Lamarck)	0.1	0.03	0.4	0.1	0.9	0.5
<i>Trichotria pocillum</i> (Müller)	<0.01	0	0.02	0	0	0.01

Three species of calanoid copepod were recorded, of which *Eudiaptomus gracilis* was the most common. The other two species were quite rare, and recorded only in Talt and Easky, two upland and geographically adjacent lakes. One of these species, *Mixodiaptomus laciniatus*, occurred solely in Lough Easky (Table 3.3). Nearly all of the seven species of cyclopoid copepod successfully identified to species were in the genus *Cyclops*, apart from *Macrocylops distinctus* which was recorded in Easky, and *Eucyclops macruioides* and *Mesocyclops leuckarti* which were found in Lough Rea. These were the only two species of cyclopoid recorded in Lough Rea, which is, therefore, considered to have the most distinctive cyclopoid community of all the lakes.

Table 3.3 Checklist of copepod species identified in the six lakes, April 2001 – April 2004 (Lough Carra) and April 2003 – April 2004 (all other lakes).

	Carra	Talt	Rea	Easky	Feeagh	Maumwee
Calanoid						
<i>Eudiaptomus gracilis</i> (Sars)	+	-	+	+	+	+
<i>Mixodiaptomus laciniatus</i> (Lilljeborg)	-	-	-	+	-	-
<i>Arctodiaptomus laticeps</i> (Sars)	-	+	-	+	-	-
Cyclopoid						
<i>Macrocylops distinctus</i> (Richard)	-	-	-	+	-	-
<i>Eucyclops macruioides</i> (Lilljeborg)	-	-	+	-	-	-
<i>Mesocyclops leuckarti</i> (Claus)	-	-	+	-	-	-
<i>Cyclops furcifer</i> (Claus)	+	+	-	-	-	+
<i>Cyclops vicinus</i> (Ulianine)	-	-	-	-	+	+
<i>Cyclops strenuus</i> (Fischer)	-	+	-	+	+	-
<i>Cyclops abyssorum</i> (Sars)	-	+	-	+	-	-
<i>Megacyclops gigas</i> (Claus)	-	+	-	-	-	-
<i>Megacyclops viridis</i> (Jurine)	+	+	-	-	-	+

Rotifers were the most abundant component of the zooplankton assemblage in all lakes, although they had greater mean abundance in the high-alkalinity lakes (Table 3.4). The greatest abundances of *Daphnia* were generally recorded in the high-alkalinity lakes, but Feeagh also had relatively high abundances of *Daphnia* which were comparable to those of Talt (Table 3.4). The lowest abundance of calanoid copepods was recorded in Maumwee. The low-alkalinity lakes generally had lower maximum abundances of calanoids, compared with the high-alkalinity lakes, but the abundance of calanoids in Talt was low compared with the other high-alkalinity lakes (Table 3.4). The highest mean abundance of *Bosmina* was recorded in Rea, although

generally *Bosmina* abundance was lower in the high-alkalinity lakes when compared with the low-alkalinity lakes. The highest abundances of both *Diaphanosoma* and *Holopedium* were recorded in the low-alkalinity lakes (Table 3.4).

Table 3.4 Abundance of major zooplankton taxa (ind. x 10³ m⁻²), mean ± SE, range and sample size (*n*), in Lough Carra (April 2001 – April 2004) and Lough Talt, Rea, Easky, Feeagh and Maumwee (April 2003 – April 2004).

	Rotifers	<i>Daphnia</i>	<i>Bosmina</i>	<i>Ceriodaphnia</i>	<i>Diaphanosoma</i>	<i>Holopedium</i>	Post-naupliar Calanoids	Post-naupliar Cyclopoids
Carra								
Mean ± SE	1355 ± 137	101 ± 26	9.9 ± 4		0.5 ± 0.2	0.003 ± 0.003	199 ± 30	15 ± 4
Range	181 – 4571	0 – 1197	0 – 229		0 – 12	0 – 0.2	22 – 1595	0 – 167
<i>N</i>	(55)	(55)	(55)		(55)	(55)	(55)	(55)
Talt								
Mean ± SE	1067 ± 363	70 ± 27	6 ± 2	2 ± 1	0.5 ± 0.4	0.5 ± 0.4	82 ± 17	157 ± 53
Range	79 – 4564	7 – 321	0 – 18	0 – 15	0 – 5	0 – 5	12 – 177	29 – 692
<i>N</i>	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)
Rea								
Mean ± SE	1760 ± 370	304 ± 123	154 ± 104		0.3 ± 0.3	0.1 ± 0.1	467 ± 126	480 ± 102
Range	491 – 4241	0 – 1419	0 – 1162		0 – 3	0 – 1	137 – 1607	15 – 1051
<i>N</i>	(11)	(11)	(11)		(11)	(11)	(11)	(11)
Easky								
Mean ± SE	818 ± 296	0.2 ± 0.1	38 ± 10	73 ± 28	2 ± 1	6 ± 2	104 ± 27	63 ± 16
Range	32 – 3657	0 – 1	0 – 107	0 – 288	0 – 16	0 – 20	14 – 361	5 – 186
<i>N</i>	(12)	(12)	(12)	(12)	(12)	(12)	(12)	(12)
Feeagh								
Mean ± SE	347 ± 90	74 ± 25	49 ± 20	0.04 ± 0.04	19 ± 9	1 ± 1	188 ± 81	47 ± 23
Range	65 – 1057	5 – 249	0 – 224	0 – 0.4	0 – 84	0 – 12	0.4 – 850	2 – 264
<i>N</i>	(11)	(11)	(11)	(11)	(11)	(11)	(11)	(11)
Maumwee								
Mean ± SE	124 ± 43	5 ± 2	21 ± 8		12 ± 8	6 ± 2	3 ± 1	25 ± 13
Range	21 – 528	0.1 – 25	0 – 87		0 – 89	0 – 21	0 – 12	0.2 – 156
<i>N</i>	(12)	(12)	(12)		(12)	(12)	(12)	(12)

3.3.3 Among lake comparison of zooplankton community structure

There was a significant difference in zooplankton community structure between the high-alkalinity and low-alkalinity lakes (One-way ANOSIM, $R = 0.47$, $P \leq 0.001$), based on a similarity matrix calculated from the abundance of zooplankton in numbers per m². Pairwise tests (Table 3.5) revealed that there was no significant difference between the three basins of Lough Carra and that the community structure of Lough Rea and Lough Carra were barely distinguishable from one another (pairwise R -values < 0.25 between Lough Rea and both the North and Mid basins of Lough Carra). Lough Talt was the most distinct of the three high-alkalinity lakes with

R-values between it, Lough Rea and the three basins of Lough Carra > 0.70 . These *R*-values were higher than those between Talt and some of the low-alkalinity lakes. This separation between Talt and the other high-alkalinity sites can be seen in the MDS ordination of zooplankton community abundances shown in Fig. 3.1, in which Talt is positioned very close to Easky. Lough Feeagh, a low-alkalinity lake, is positioned close to the high-alkalinity lakes, and pairwise *R*-values between it and both Carra and Rea in particular, are quite low.

The differences between Lough Talt and the other high-alkalinity lakes were less marked, however, when comparisons in community structure were carried out based on zooplankton biomass and not abundances. To calculate the similarity matrix from the biomass data, rotifer, calanoid and cyclopoid species were pooled into their respective groups. This was considered appropriate owing to the methodology used for calculating biomass, in which copepods were not identified to species level because of time constraints, and representation of rotifer species diversity was reduced because only the first fifty individuals (and consequently the most numerically abundant species) were included in the analyses. Some studies of marine macrobenthos and meiobenthos have found that very little information is lost in the aggregation of species level data to family or even higher taxonomic levels (Gray *et al.*, 1998; Clarke & Warwick, 1997), although there is still some debate on this subject (Mauer, 2000). There was, nevertheless, a significant difference between high- and low-alkalinity lakes (One-way ANOSIM, $R = 0.53$, $P \leq 0.001$). The similarity between Lough Rea and the three basins of Lough Carra became more pronounced, and there was no longer a statistically significant difference between the two lakes (Table 3.5). Similar to the MDS ordination based on zooplankton abundance, Lough Feeagh was positioned adjacent to the high-alkalinity lakes in the ordination derived from zooplankton biomass (Fig. 3.2).

Table 3.5 *R*-values (Pairwise ANOSIM) and statistical significance (*P*) of differences in zooplankton community structure between six lakes, April 2003 – April 2004.

Lake Comparison	Abundance (Individuals m ⁻²)		Biomass (µg DW m ⁻²)	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Talt – Rea	0.82	≤0.001	0.48	≤0.001
Talt – Maumwee	0.73	≤0.001	0.67	≤0.001
Talt – Feeagh	0.61	≤0.001	0.22	≤0.05
Talt – Easky	0.57	≤0.001	0.56	≤0.001
Talt – Carra South	0.73	≤0.001	0.40	≤0.001
Talt – Carra North	0.73	≤0.001	0.56	≤0.001
Talt – Carra Mid	0.73	≤0.001	0.40	≤0.001
Rea – Maumwee	0.83	≤0.001	0.81	≤0.001
Rea – Feeagh	0.38	≤0.001	0.29	≤0.001
Rea – Easky	0.80	≤0.001	0.78	≤0.001
Rea – Carra South	0.39	≤0.001	-0.01	0.51
Rea – Carra North	0.18	≤0.05	0.06	0.13
Rea – Carra Mid	0.12	≤0.05	-0.07	0.93
Maumwee – Feeagh	0.34	≤0.001	0.40	≤0.001
Maumwee – Easky	0.61	≤0.001	0.58	≤0.05
Maumwee – Carra South	0.71	≤0.001	0.76	≤0.001
Maumwee – Carra North	0.74	≤0.001	0.86	≤0.001
Maumwee – Carra Mid	0.77	≤0.001	0.86	≤0.001
Feeagh – Easky	0.68	≤0.001	0.59	≤0.001
Feeagh – Carra South	0.30	≤0.001	0.28	≤0.001
Feeagh – Carra North	0.21	≤0.001	0.44	≤0.001
Feeagh – Carra Mid	0.29	≤0.001	0.35	≤0.001
Easky – Carra South	0.76	≤0.001	0.70	≤0.001
Easky – Carra North	0.82	≤0.001	0.84	≤0.001
Easky – Carra Mid	0.81	≤0.001	0.85	≤0.001
Carra South – Carra North	0.02	0.29	0.12	0.53
Carra South – Carra Mid	-0.03	0.62	-0.03	0.65
Carra North – Carra Mid	-0.05	0.78	0.01	0.34

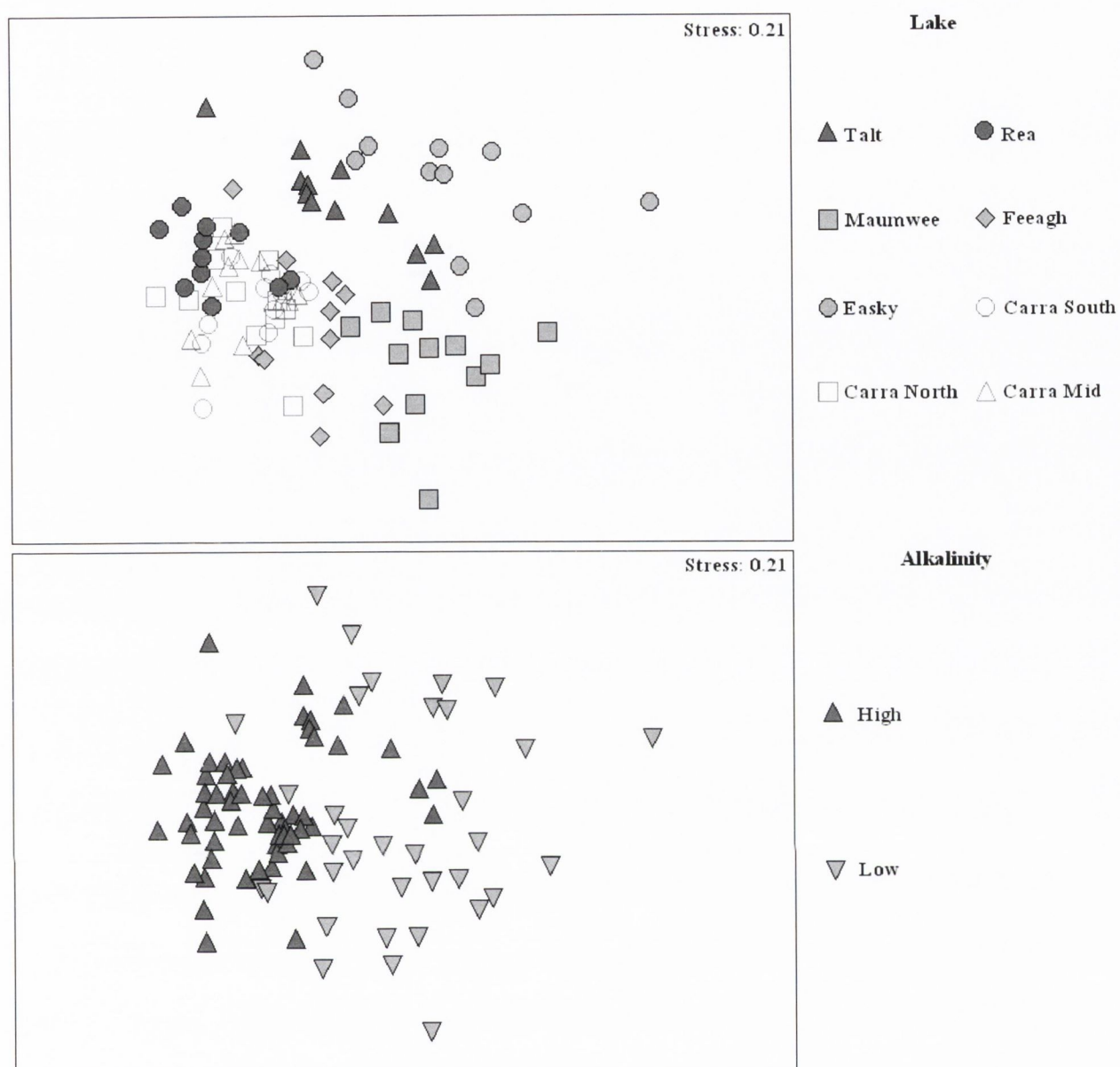


Fig. 3.1 Two-dimensional MDS ordination of zooplankton community structure based on abundances (individuals m^{-2}) of the six study lakes, April 2003 – April 2004. Two plots are shown; divided according to lake and alkalinity class.

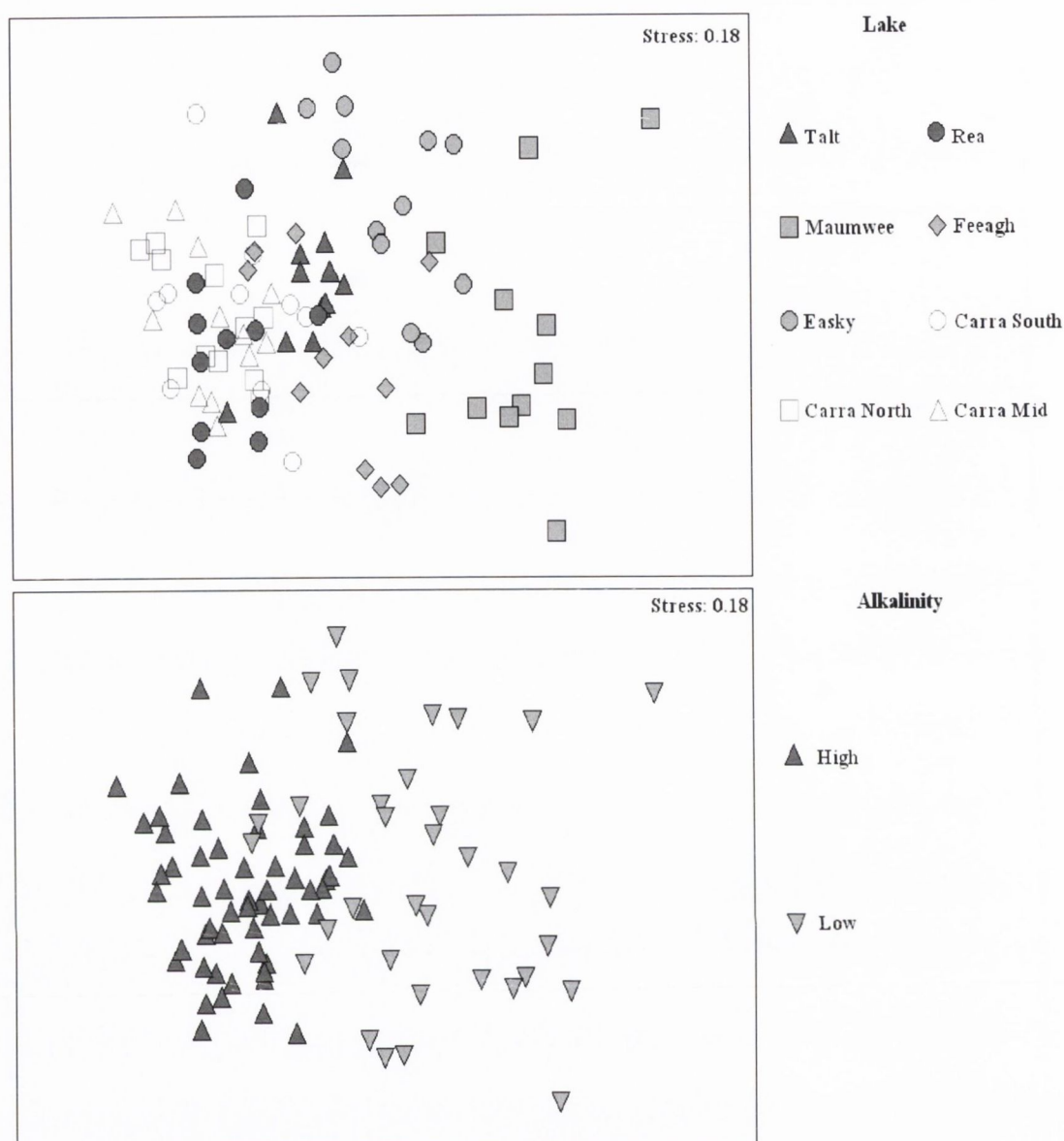


Fig. 3.2 Two-dimensional MDS ordination of zooplankton community structure based on biomass ($\mu\text{g DW m}^{-2}$) of the six study lakes, April 2003 – April 2004. Two plots are shown; divided according to lake and alkalinity class.

A similar distribution of lakes to that observed for the zooplankton data is evident in the MDS ordination of physical chemical variables (Fig. 3.3). Alkalinity, conductivity and pH were excluded from this analyses as the lakes were selected and grouped on the basis of these variables. Rea and Carra are positioned close together, with Talt a little further apart and close to the low-alkalinity lakes. There is a significant difference between high-alkalinity and low-alkalinity lakes (One-way MANOVA, *Wilks' λ* = 0.20, approximate $F_{9,72}$ = 32.4, $P \leq 0.001$). When the results for the

dependent variables were considered separately using a Bonferroni adjusted alpha level, four variables showed a significant difference between high- and low-alkalinity lakes and included TN, TP, colour and turbidity. In order to discover which abiotic variables best explain the pattern in zooplankton community structure, patterns in biotic variables were matched to the patterns in the distribution of the physical and chemical variables using the BIO-ENV procedure in Primer® Version 5. As expected the set of parameters which best groups the sites, in a manner consistent with the patterns in zooplankton abundance contained only one variable, alkalinity ($p_w = 0.49$). The next best combination contained four variables and also incorporated alkalinity but in addition included temperature, TP, particulate suspended organic matter and TN ($p_w = 0.48$).

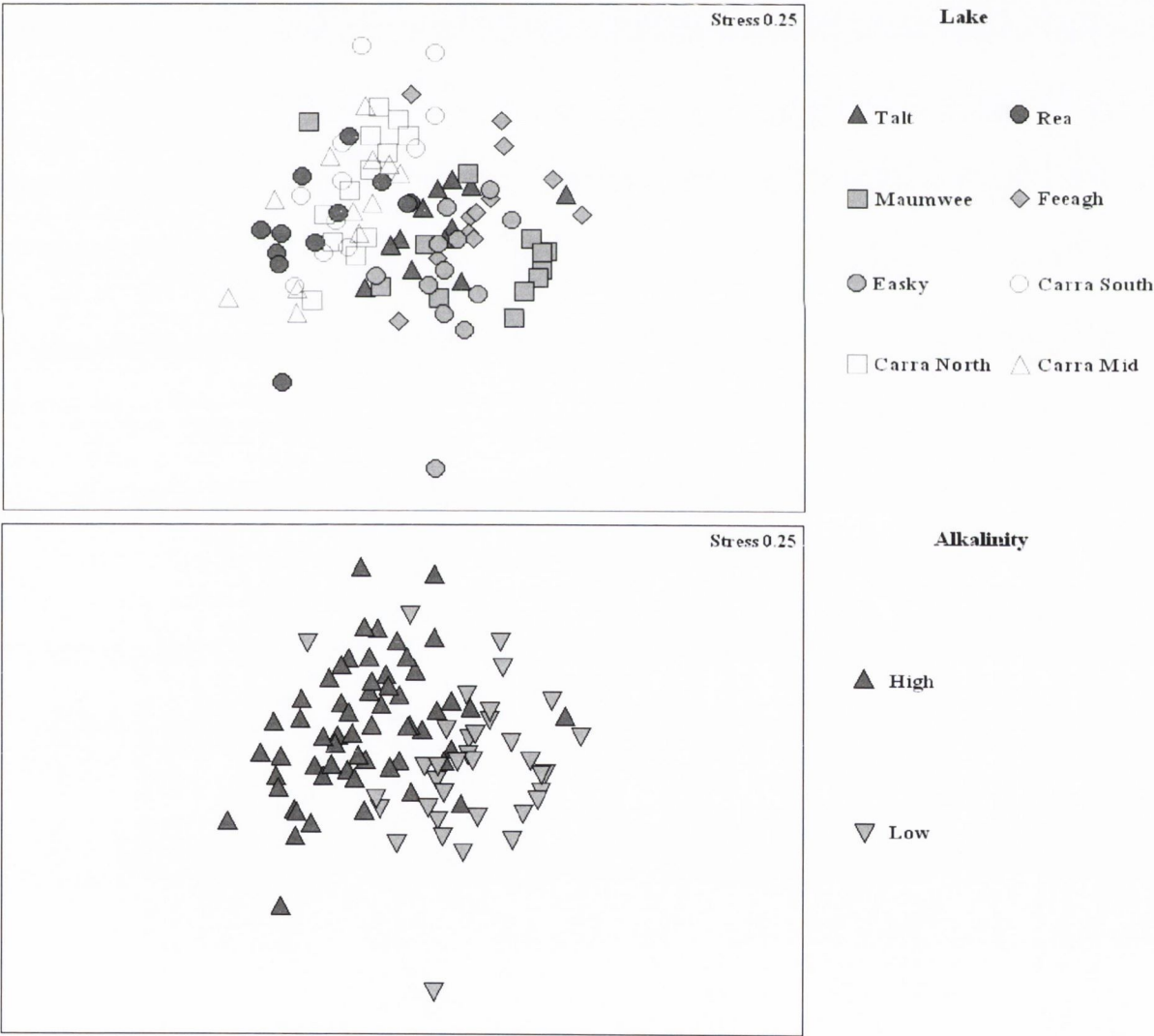


Fig. 3.3 Two-dimensional MDS ordination of physical and chemical variables (excluding alkalinity, conductivity and pH) of the six study lakes, April 2003 – April 2004. Two plots are shown; divided according to lake and alkalinity class.

Alkalinity was also the most important factor explaining patterns in zooplankton biomass ($p_w = 0.53$). The next best combination of variables which accounted for patterns in biomass also included alkalinity, but added TP ($p_w = 0.51$).

3.3.4 Zooplankton taxa dominance

Although rotifers were the most numerically important component of the zooplankton community in each lake, their contribution in terms of biomass was minor. The biomass of each lake was dominated by only a small number of taxa. This was particularly evident in the high-alkalinity lakes in which both *Daphnia* and calanoids accounted for more than 80 % of total biomass, apart from Talt where cyclopoids were also a substantial constituent of the community (Fig. 3.4). In Carra and Rea cyclopoids comprised a very low, often negligible part of the zooplankton taxa. Patterns of dominance were more diverse in the low-alkalinity lakes. In Lough Feeagh *Daphnia*, calanoids and cyclopoids also dominated zooplankton, but in addition *Bosmina* and *Holopedium* collectively accounted for 20 % of total biomass. Both *Daphnia* and *Holopedium* made a small contribution to the zooplankton community of Maumwee, which was dominated by calanoids, *Bosmina* and *Diaphanosoma*. *Holopedium*, calanoids, cyclopoids and *Ceriodaphnia* all formed a significant component of the zooplankton community of Lough Easky with *Bosmina* also accounting for approximately 13 % of total biomass. *Daphnia*, however, did not contribute much to the overall biomass of Easky (Fig. 3.4).

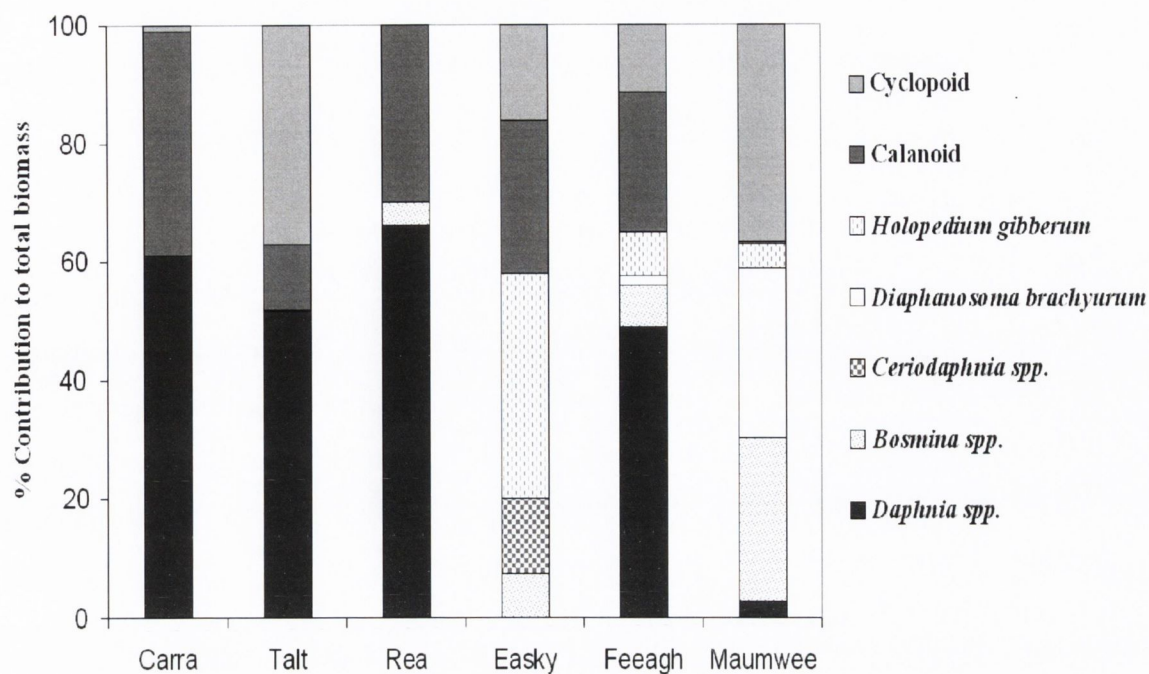


Fig. 3.4 Mean percentage contribution to total biomass between April 2001 – April 2002, n = 55 (Lough Carra) and April 2003 – April 2004, n = 12 (all other lakes).

3.3.5 Zooplankton seasonal dynamics

Zooplankton biomass varied considerably over time both within and among the six lakes from April 2003 to April 2004 (Fig. 3.5). Mean zooplankton biomass ($\pm$ SE) ranged from $8 \times 10^4 \pm 2 \times 10^4 \mu\text{g DW m}^{-2}$ (n = 12) in Maumwee to $9 \times 10^5 \pm 3 \times 10^5 \mu\text{g DW m}^{-2}$ (n = 11) in Rea. There was a tendency toward greater biomass in the high-alkalinity lakes, with the highest values reaching $35 \times 10^5 \mu\text{g DW m}^{-2}$ in Lough Carra in April 2004. There was a common pattern of low zooplankton biomass from late autumn through winter to early spring in the low-alkalinity lakes. This was particularly evident in Maumwee. A similar reduction in zooplankton during the winter was not apparent in most of the high-alkalinity lakes, apart from Talt, in which biomass declined steadily from November onwards, and was very similar to Easky in this respect. Peaks in biomass occurred during spring and early summer in both Feeagh and Maumwee. Biomass remained very low during this period in Easky and only increased between August and November.

The zooplankton community of the high-alkalinity lakes was dominated at all times of the year by either copepods or *Daphnia* (Fig. 3.6). In Carra and Rea biomass fluctuated between dominance by *Daphnia* and dominance by the calanoid *Eudiaptomus gracilis*. In Carra this was marked by long periods of dominance by each taxa. In the summer and autumn, more than 90 % of the community biomass was composed of calanoids, whereas *Daphnia* dominated in winter and spring. In contrast, there were sharp oscillations between a community dominated by *Eudiaptomus* and one by *Daphnia* throughout the entire year in Rea. These periods of dominance were brief, usually lasting one to two months. Cyclopoid copepods formed a major component of the zooplankton community of Talt and dominated for much of the year, particularly in summer and autumn. In Talt *Daphnia* accounted for more than 90 % of the community biomass in June 2003, and again became important between November and January. Cyclopoids and calanoids were also important at this time, during which all three taxa together accounted for more than 98 % of zooplankton biomass. Calanoid copepods dominated during the spring of both 2003 and 2004.

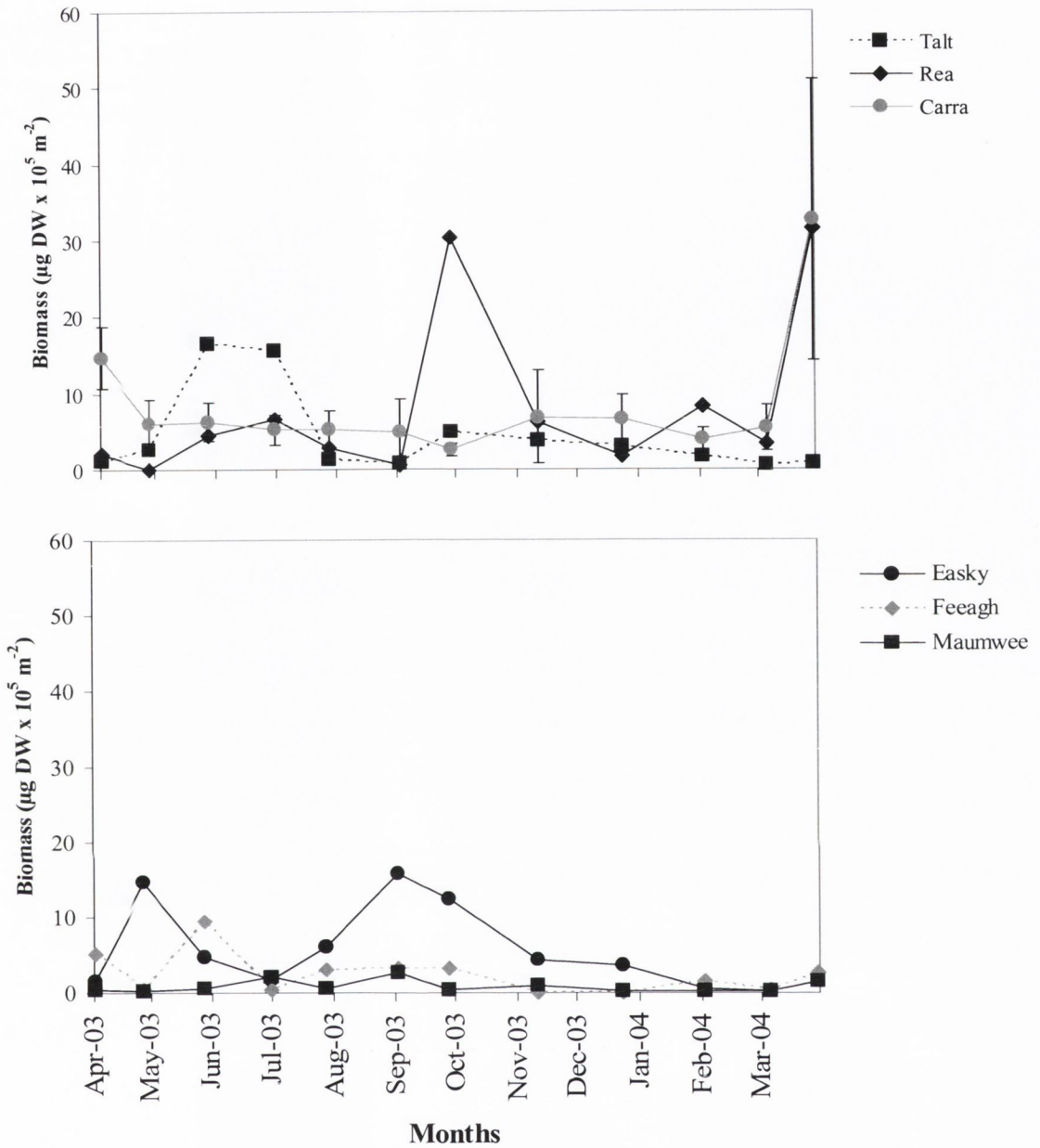


Fig. 3.5 Total zooplankton biomass for high- and low-alkalinity lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n = 3$) of the three basins in Lough Carra are shown.

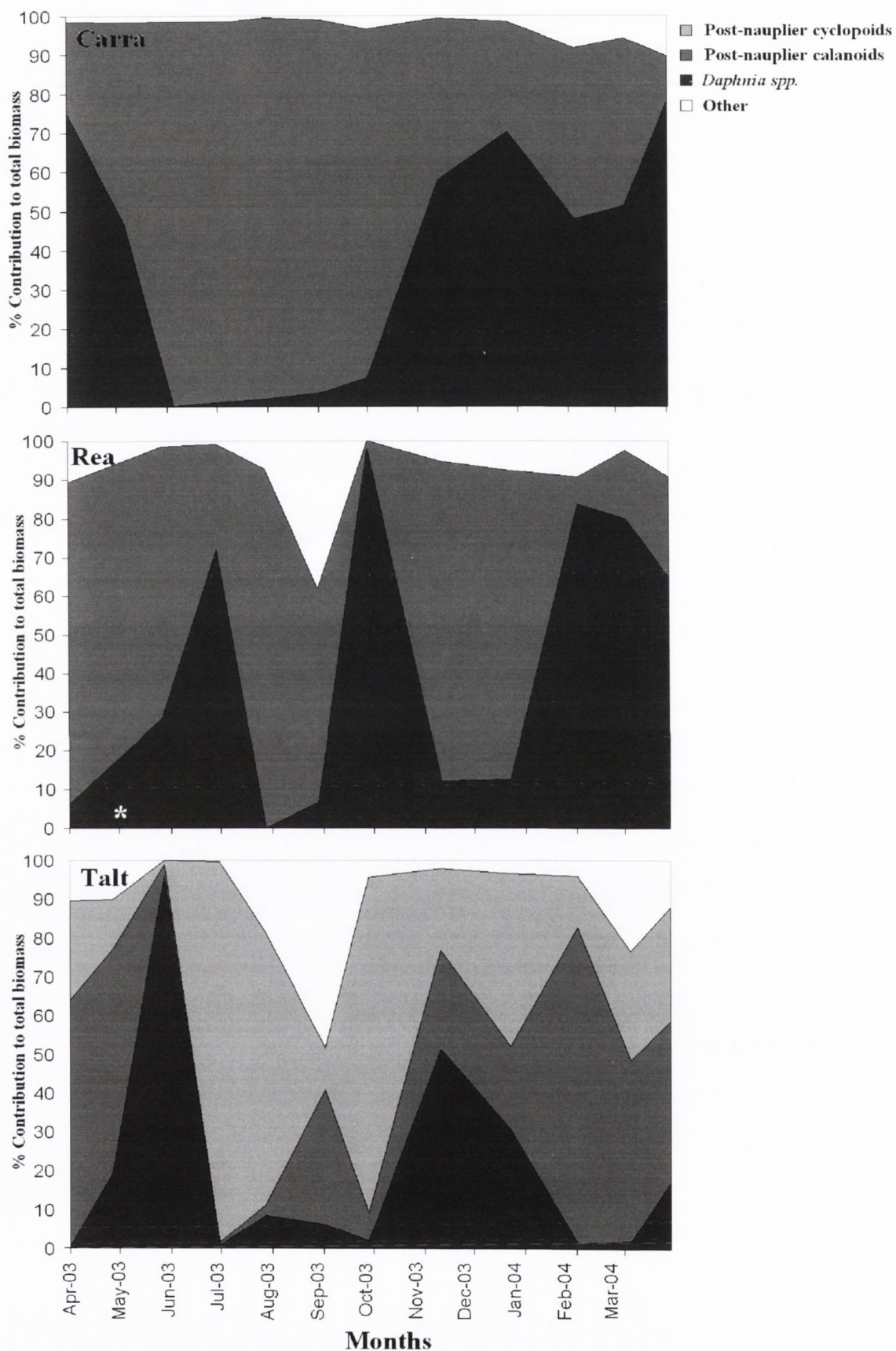


Fig. 3.6 Percentage contribution to total biomass of the most dominant taxa in the high-alkalinity lakes, April 2003 – April 2004. * = Missing sample.

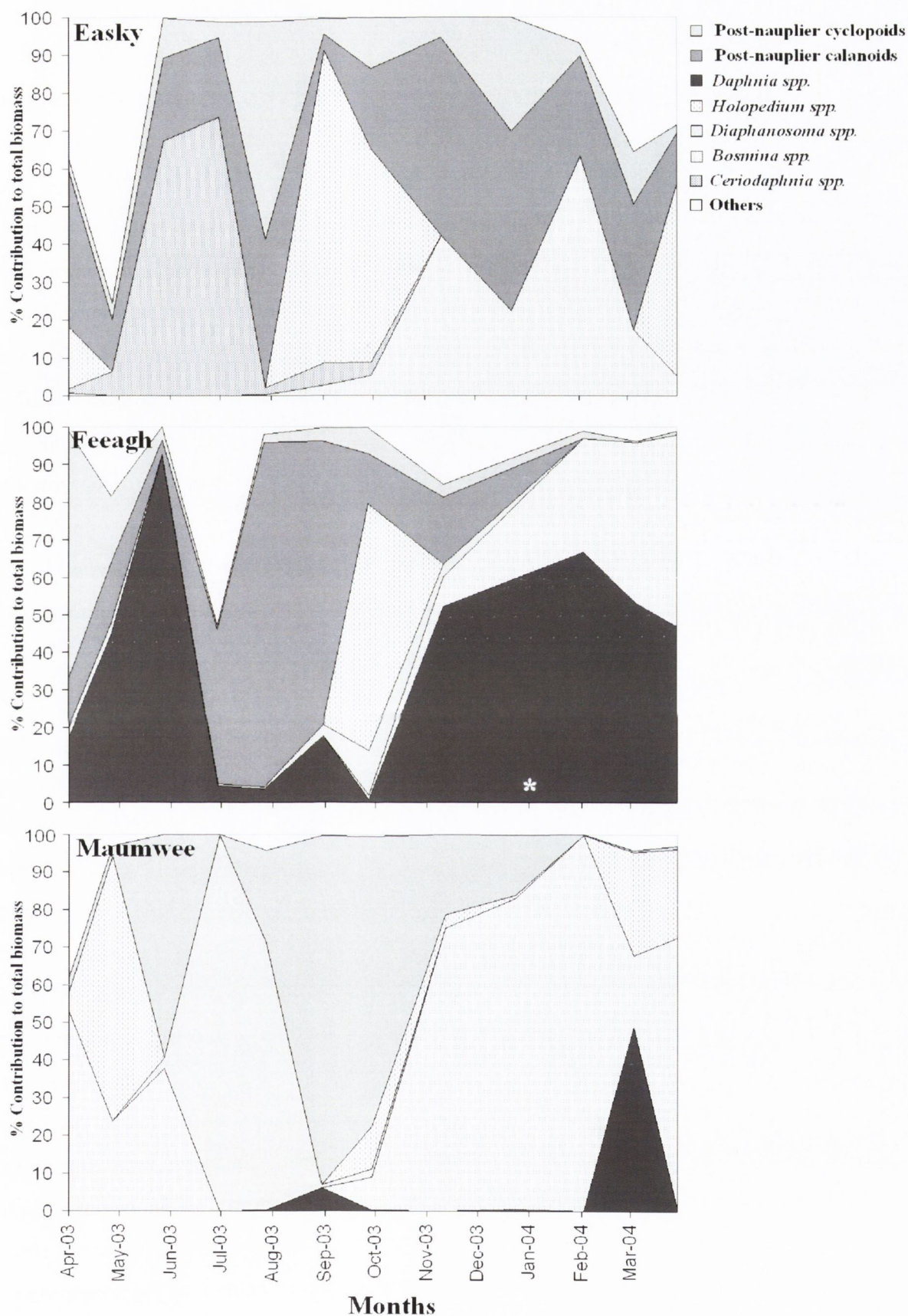


Fig. 3.7 Percentage contribution to total biomass of the most dominant taxa in the low-alkalinity lakes, April 2003 – April 2004. * = Missing sample.

Several other cladoceran taxa, as well as copepods and *Daphnia* formed an important component of the zooplankton biomass in the low-alkalinity lakes (Fig. 3.7). *Daphnia* were particularly important in Feeagh, and dominated the biomass for much of the year, apart from late summer and early autumn, where the biomass was mostly dominated by the calanoid *Eudiaptomus gracilis*. *Holopedium gibberum* was important for a brief period in autumn, and during winter *Bosmina* spp. also formed a major component of the zooplankton community. In Maumwee, *Bosmina* were particularly important, and dominated for a long period between late autumn and early spring. Between July and August more than 70 % of the zooplankton biomass consisted of *Diaphanosoma brachyurum*, and between September and October, cyclopoids accounted for more than 70 % of the community biomass. In Maumwee, *Holopedium gibberum* was also a principal component of the zooplankton community in May 2003 and *Daphnia* in March 2004. Lough Easky was dominated by *Ceriodaphnia* spp. in the summer of 2003 and by *Holopedium gibberum* in the autumn, with calanoids, cyclopoids and *Bosmina* all forming substantial fractions of the biomass throughout the rest of the year.

A significant effect of alkalinity on *Daphnia* abundance was recorded (Repeated measure ANOVA, $F_{1,59} = 5.94$, $P \leq 0.05$). There was, however, a significant negative effect of alkalinity on the abundance of other cladocerans such as *Diaphanosoma* and *Holopedium* (Repeated measure ANOVA, $F_{1,68} = 12.19$, $P \leq 0.01$) (Fig. 3.8). There was also a relatively consistent seasonal trend in rotifer and cyclopoid abundance within each alkalinity group. In the case of cyclopoids this is reflected in the significant interaction between sampling trip and alkalinity (Repeated measure ANOVA, $F_{11,69} = 2.22$, $P \leq 0.05$). For both cyclopoids and rotifers, abundances decreased to very low levels in the winter months in the low-alkalinity lakes, but remained relatively high during this period in the high-alkalinity lakes, with the notable exception of the rotifer population in Lough Talt, which was more similar to patterns of abundance in Lough Easky. Patterns in cyclopoid abundances in Lough Carra were also different from those of the other two high-alkalinity lakes, but their numbers were very low and they formed only a trivial component of the zooplankton community of Carra.

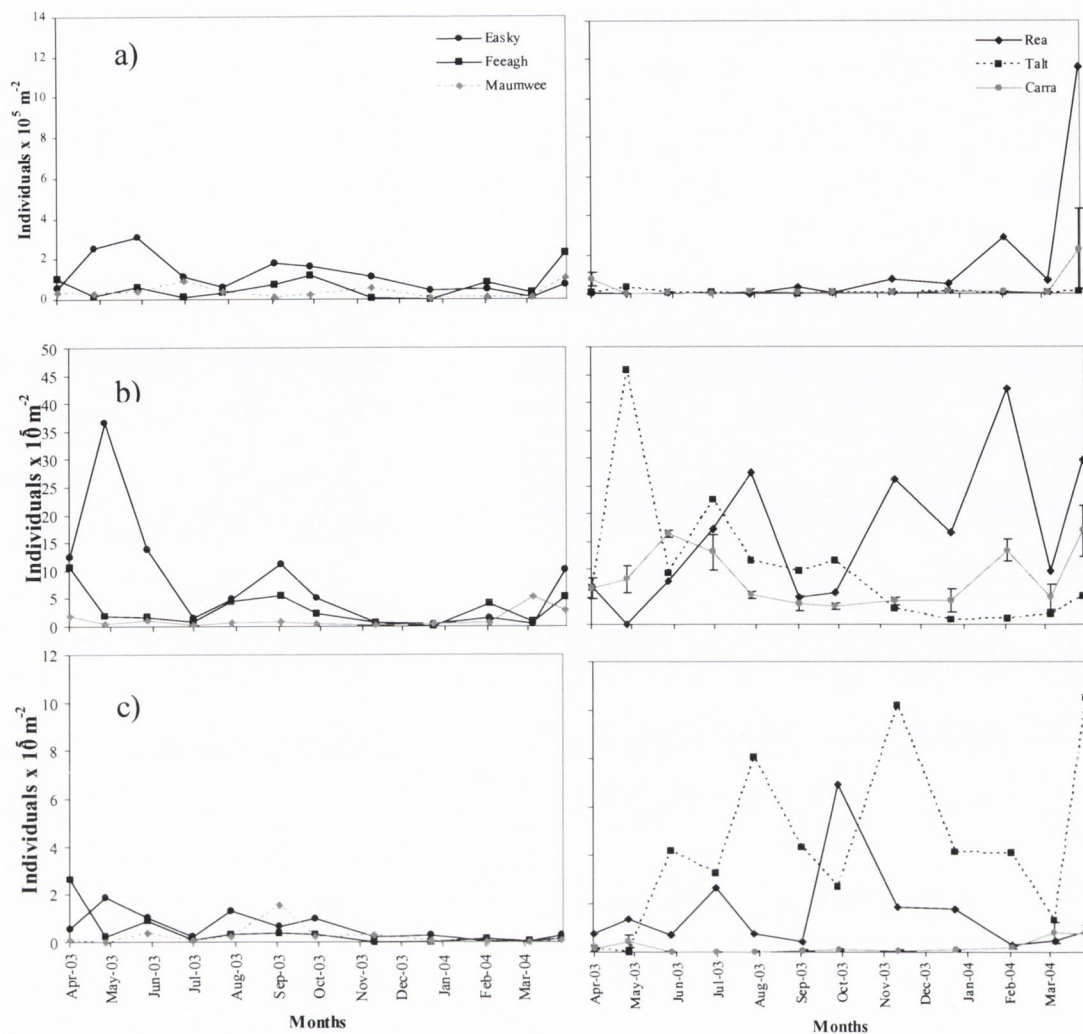


Fig. 3.8 Abundances of (a) cladoceran taxa (excluding *Daphnia*), (b) rotifers and (c) post-naupliar cyclopoids in three low-alkalinity and three high-alkalinity lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n = 3$) of the three basins in Lough Carra are shown.

3.3.6 Predatory cladoceran dynamics

As a result of the sampling methodology used throughout the course of this study, it is probable that there is an overall underestimation of predatory cladocerans abundances in all lakes. This is owing to the ability of many predatory cladocerans such as *Leptodora* and *Bythotrephes* to avoid capture in a zooplankton net by active swimming and avoidance behaviour. Consequently, predatory cladocerans only occurred sporadically in the zooplankton samples and the calculated abundances are almost certainly an underestimation of the actual population.

Three either partly or wholly carnivorous species of cladoceran were identified in the six lakes. *Polyphemus* was the rarest of the three species, and only occurred in two lakes, Carra and Maumwee; the latter of which was the only lake that contained a sizeable population reaching a maximum of 509 ind. m⁻² in August 2003. *Bythotrephes longimanus* was more prevalent, and apart from Rea, was found in all lakes and was more widespread in the low-alkalinity lakes (Mann-Whitney U, $P \leq 0.01$) (Fig. 3.9). It was generally present between May and October, but was not recorded from November to April in any lake. *Bythotrephes* was not identified in Carra between April 2003 and April 2004, however, it was recorded in relatively large numbers between May and September 2002. *Leptodora* had higher abundances in the high-alkalinity lakes (Mann-Whitney U, $P \leq 0.001$) (Fig. 3.9), and was consistently present between April and October, attaining a maximum of 14900 ind. m⁻² in Lough Rea in June 2003. In the low-alkalinity lakes *Leptodora* was only present in low numbers between June and September reaching a maximum of 2500 ind. m⁻² in Lough Feeagh in August 2002.

Larvae of the phantom midge *Chaoborus* (Diptera, Chaoboridae) were recorded in Feeagh in August and September 2003 with abundances, respectively, of 1035 ind. m⁻² and 560 ind. m⁻². They were not observed in any other lake between April 2003 and April 2004. They were found, however, on a number of occasions prior to April 2003 in Lough Carra.

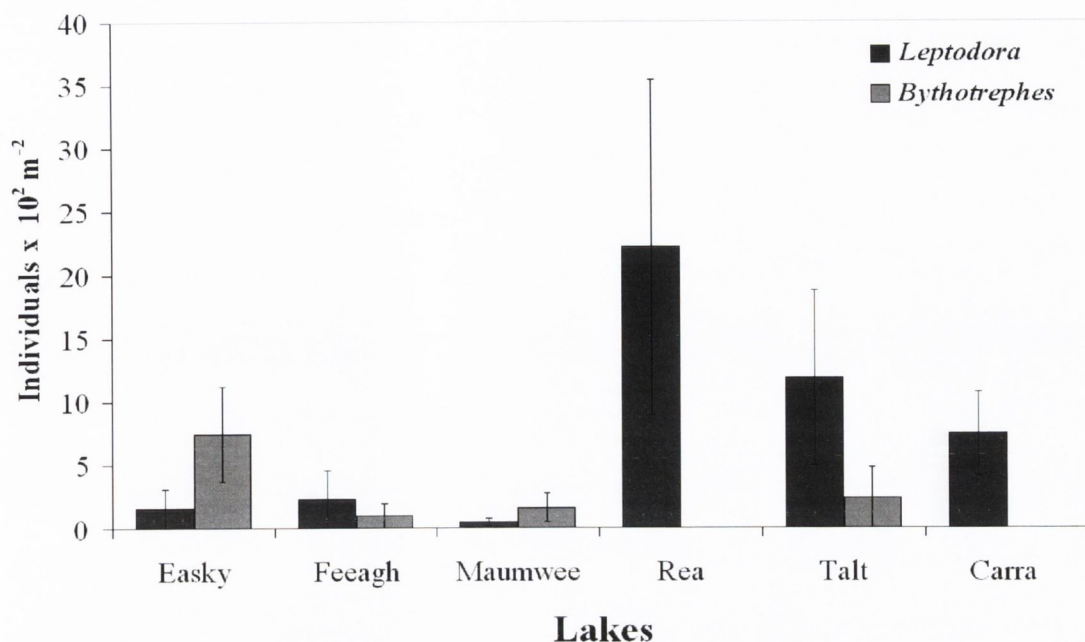


Fig. 3.9 Mean abundances ($\pm$ SE, $n = 12$) of *Leptodora kindtii* and *Bythotrephes longimanus* in all lakes, April 2003 – April 2004.

3.3.7 Zooplankton community size distribution

In the low-alkalinity lakes, the size structure of the crustacean community showed a greater frequency of individuals in the small size classes (0 – 0.5 mm) compared with larger ones, and in Feeagh and Maumwee there were very low numbers in the largest size ranges (1.31 – 1.80 mm) (Fig. 3.10). In Easky there was a reduced number of individuals in the mid-range size classes (0.81 – 1.10 mm), composed mostly of copepod copepodites. The small size classes of the low-alkalinity lakes were dominated by *Bosmina*, as well as copepod copepodites in Feeagh, and *Ceriodaphnia* in Easky. The larger size ranges were dominated by cyclopoids in all three low alkalinity lakes; occurring with *Daphnia* in Maumwee and calanoids in Easky.

In the high-alkalinity lakes there was a more even distribution of individuals across all size classes compared with the low-alkalinity lakes (Fig. 3.10). The smaller size classes in the high-alkalinity lakes (0 – 0.6 mm) were dominated by calanoid and cyclopoid nauplii, although in Talt there were fewer individuals in these size classes. The larger size classes (1.31 – 2.00 mm) were dominated by *Daphnia* in all lakes, although in Talt calanoids and cyclopoids also contributed a sizeable proportion to

these size ranges. The largest size classes (2.01 – 8.00 mm) were mostly composed of *Leptodora* or *Bythotrephes*.

There was an effect of alkalinity on mean crustacean size (Repeated measure ANOVA, $F_{1,69} = 23.99$, $P \leq 0.001$). The mean crustacean size was highest in Lough Talt at all times of the year and with the exception of July, was lowest in Maumwee.

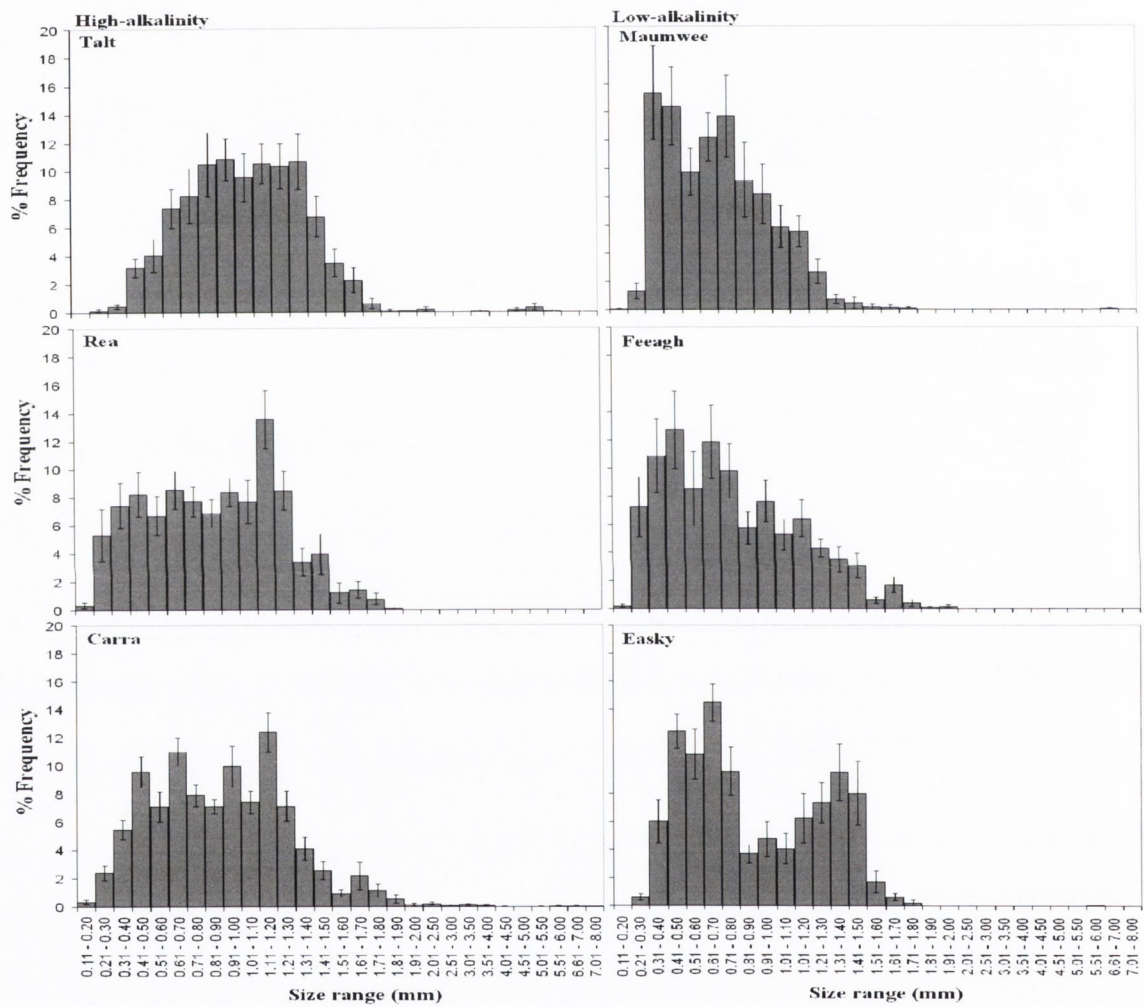


Fig. 3.10 Mean size distributions ($\pm$ SE, $n = 12$) of post-naupliar crustaceans for each of the six lakes, April 2003 – April 2004.

3.3.8 Evidence for fish Predation

3.3.8.1 Size distributions

There was no consistent seasonal pattern within each alkalinity group in the size distributions of the post-naupliar crustacean community. Examination of the size

distributions of each lake over the twelve month sampling period, suggests that both fish and invertebrate predation may influence zooplankton community structure in a number of lakes.

In Lough Carra, the number of larger *Daphnia* (1.41- 2.00 mm) was lowest between June and October (Fig. 3.11), but there was no increase in smaller sized genera such as *Bosmina* between June and August. *Bosmina* numbers did increase in September, but this increase was maintained throughout subsequent months and coincided with a rise in large sized *Daphnia* in November.

In Lough Rea there was also a reduction in large sized *Daphnia* between August and September (Fig. 3.12). In August this represented a decrease in *Daphnia* of all sizes. Although the proportion of *Daphnia hyalina* continued to decline in September, there was an associated increase in smaller *Daphnia cucullata* (0.11 – 0.50 mm) abundance. *Bosmina* also increased in September. Reduction in large sized *Daphnia* and the subsequent rise in small sized *Bosmina* was also observed in November and January, suggesting that factors other than size-selective fish predation may be responsible for the observed reduction in large sized *Daphnia* in Lough Rea.

There was no shift from larger to smaller size classes during the summer in Lough Talt (Fig. 3.13), but the larger size classes were dominated by cyclopoid copepods. During this time there was, nevertheless, a decline in the number of *Daphnia* of all sizes, particularly between July and October, but no increase in *Bosmina* or other small Cladocera. There was another decrease in *Daphnia* numbers from February to April 2004.

In Lough Feeagh there was an overall reduction in the number of *Daphnia* of all sizes between July and October (Fig. 3.14). There was also a corresponding increase in the number of other smaller zooplankton, particularly between 0.31 mm and 0.80 mm in length owing to increasing calanoid copepodite numbers.

In Maumwee the seasonal changes in crustacean size distribution reflected the seasonal changes in the zooplankton community structure (Fig. 3.15). *Bosmina* and *Holopedium* dominated in spring, and were replaced by *Diaphanosoma* during the

summer and cyclopoid copepodites in the autumn, all of which have overlapping sizes. There was no indication of a reduction in larger sized individuals during summer and the maximum size remained small relative to other lakes throughout the year. There was, however, a decline in the number of individuals in the smallest size classes (0 – 0.6 mm) between July and September.

In Easky temporal changes in the size distributions of the crustacean community was determined by seasonal fluctuations in the abundance of copepods, particularly calanoid copepodites. In spring there was a large number of copepodites and *Ceriodaphnia*, and as a result the size frequency was skewed towards the smaller size classes below 1.00 mm in length (Fig. 3.16). The larger size classes (1.10 – 1.70 mm) were dominated by both cyclopoids and calanoids, which were most prevalent between October and March. Between September and March a reduction in the number of calanoid copepodites was evident from the decrease in the number of individuals in the medium size classes (0.81 - 1.20 mm).

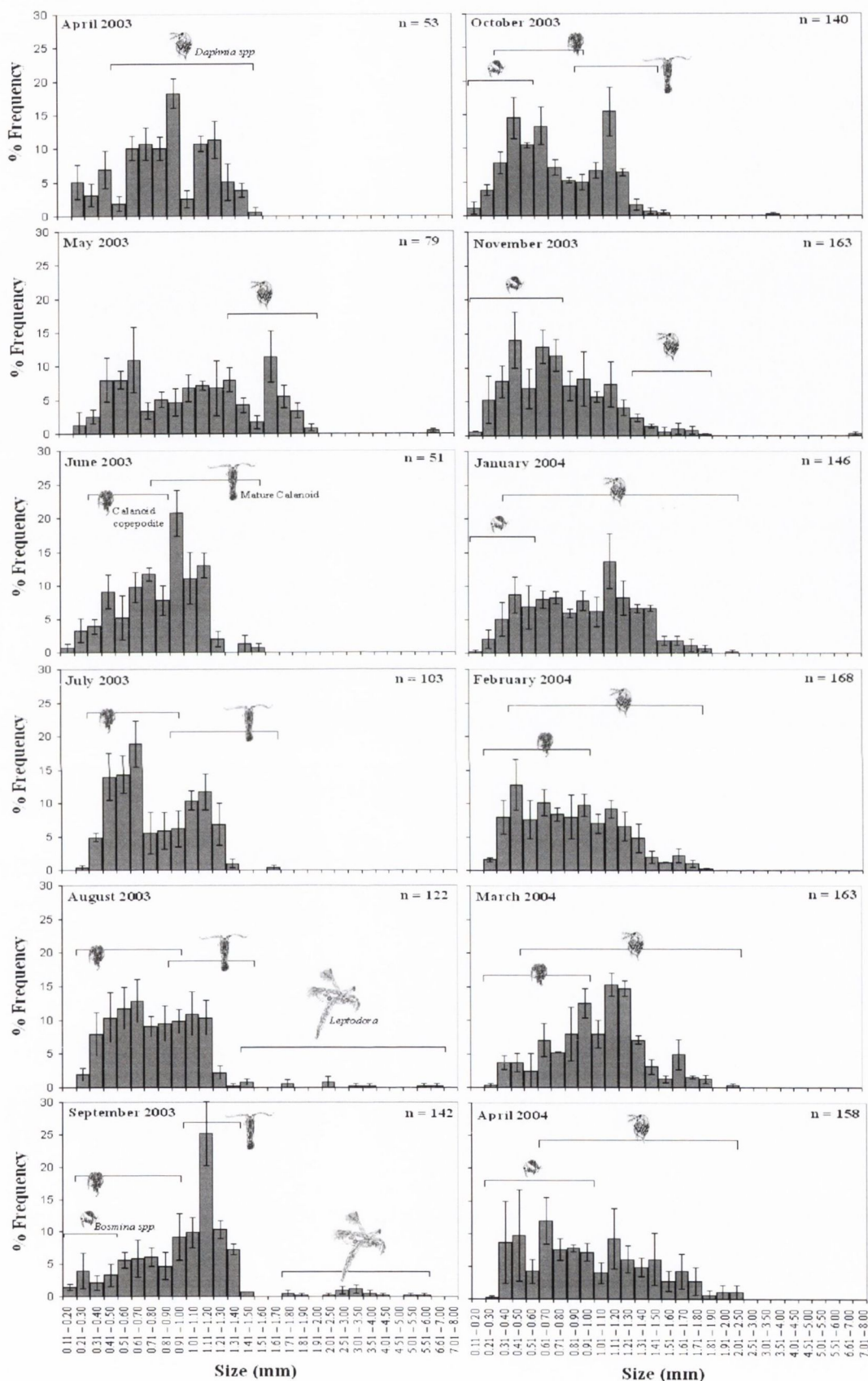


Fig. 3.11 Size distribution (mm) (mean $\pm$ SE, $n = 3$) of post-naupliar crustaceans for the three basins of Lough Carra, April 2003 – April 2004. Demarcations identify the most dominant zooplankton taxa occupying the specified ranges.

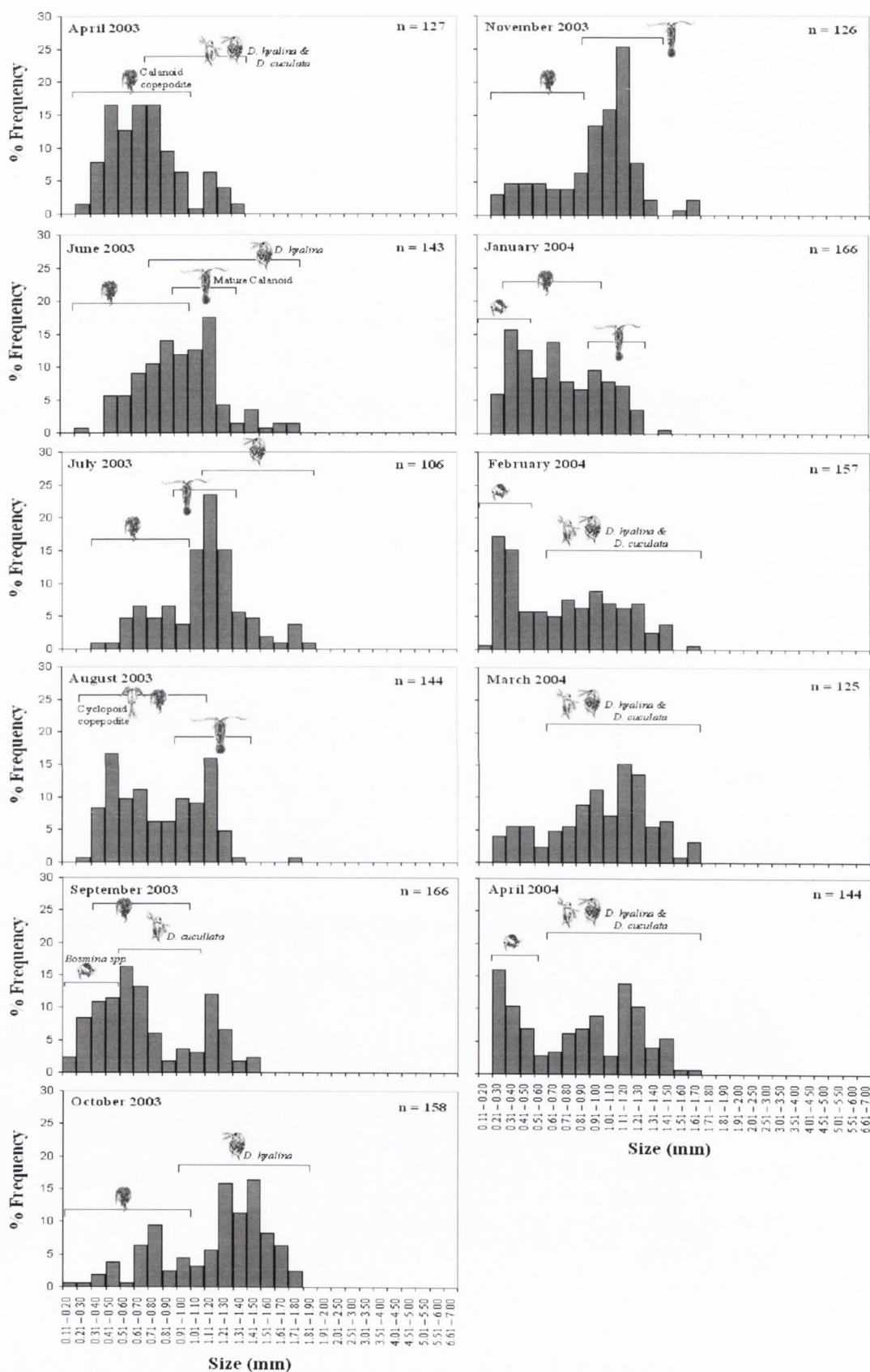


Fig. 3.12 Size distribution (mm) of post-naupliar crustaceans in Lough Rea, April 2003 – April 2004. Demarcations identify the most dominant zooplankton taxa occupying the specified ranges.

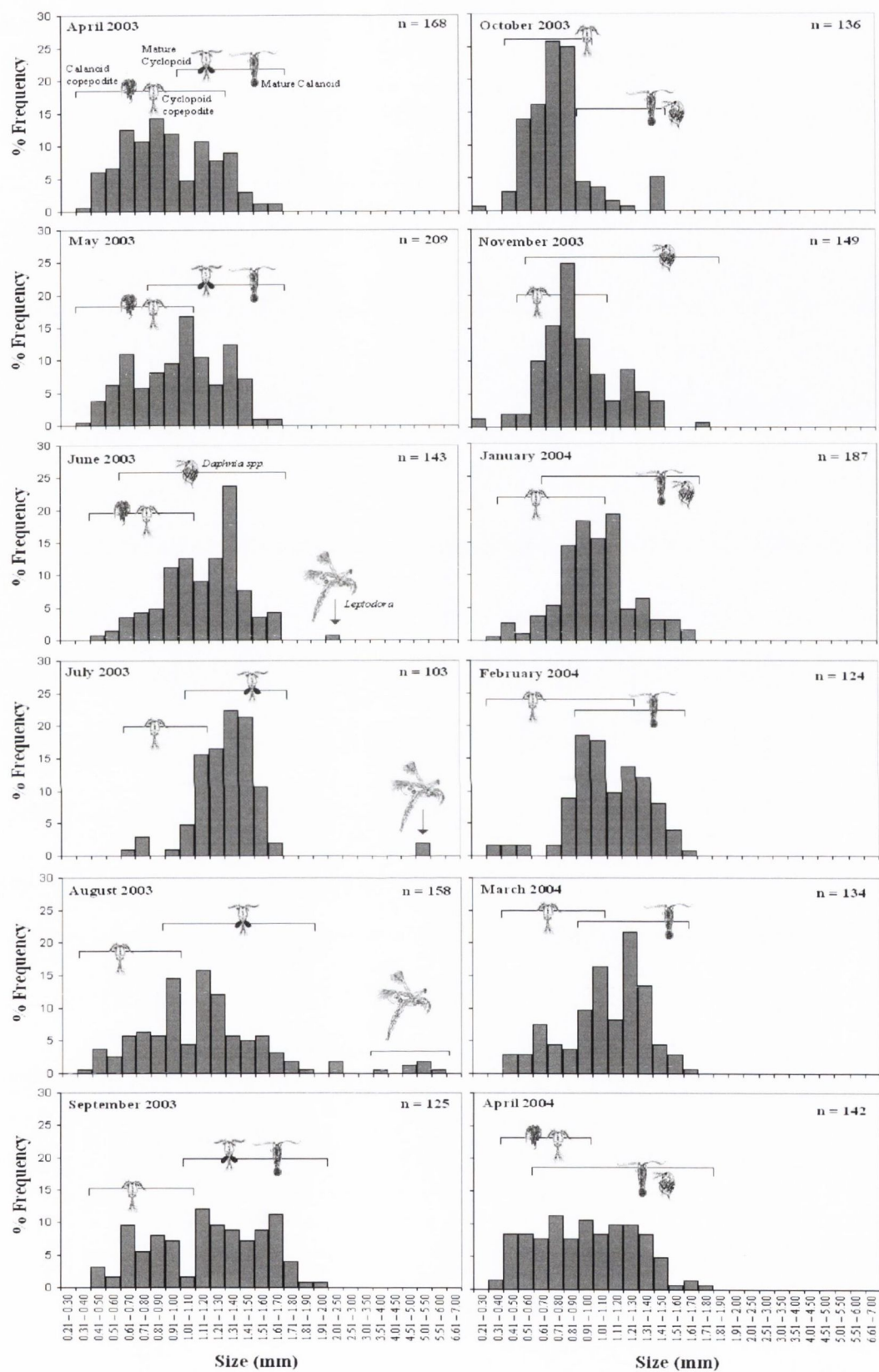


Fig. 3.13 Size distribution (mm) of post-naupliar crustaceans in Lough Talt, April 2003 – April 2004. Demarcations identify the most dominant zooplankton taxa occupying the specified ranges.

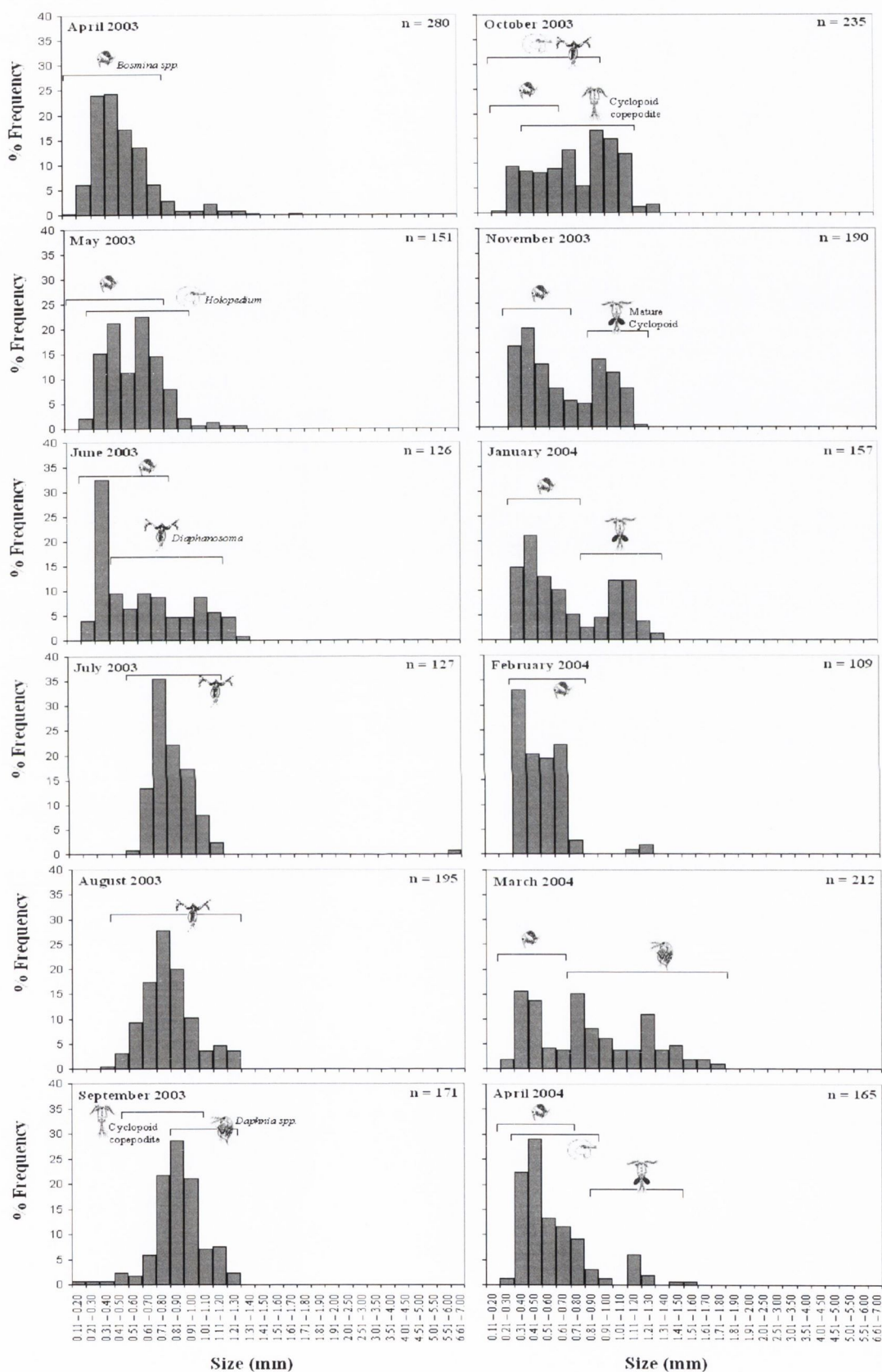


Fig. 3.15 Size distribution (mm) of post-naupliar crustaceans in Lough Maumwee, April 2003 – April 2004. Demarcations identify the most dominant zooplankton taxa occupying the specified ranges.

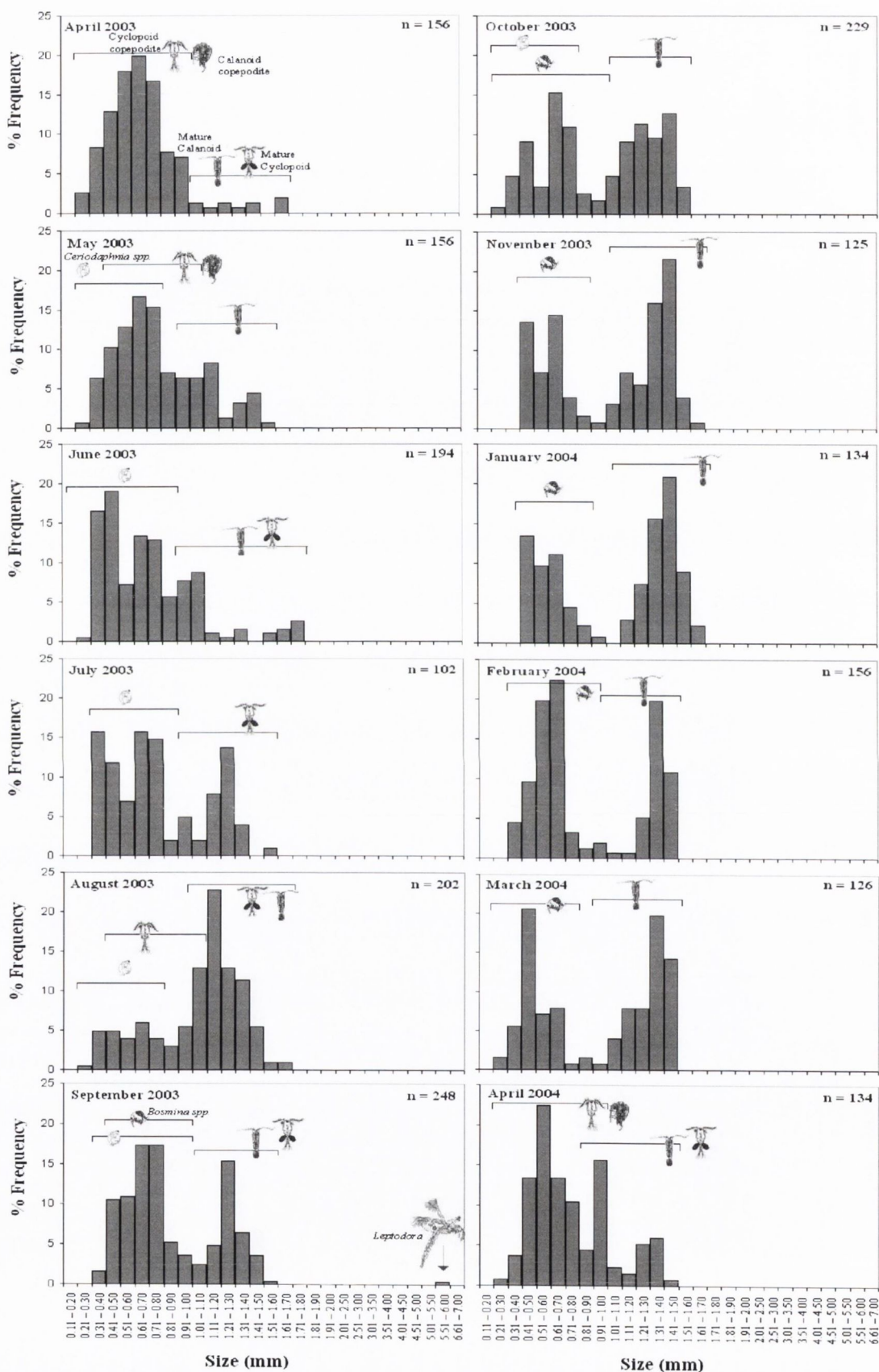


Fig. 3.16 Size distribution (mm) of post-naupliar crustaceans in Lough Easky, April 2003 – April 2004. Demarcations identify the most dominant zooplankton taxa occupying the specified ranges.

3.3.8.2 *Zooplankton:phytoplankton biomass ratio*

The highest zooplankton:phytoplankton biomass ratios were recorded in Carra, during March and April of both 2003 and 2004, reaching 2.1 and 2.9, respectively. However, values were lower during the rest of the year, ranging from 0.07 to 0.7. These were, nevertheless, generally higher than the zooplankton:phytoplankton ratios recorded in the other two high-alkalinity lakes, particularly during the summer and early autumn and again during winter (Fig. 3.17). There was a peak in the zooplankton:phytoplankton ratio in Talt in July, but the ratio remained below 0.2 for the rest of the year. In Rea, there was also a peak in the zooplankton:phytoplankton ratio in October 2003 and again in April 2004, but the ratio was generally less than 0.3 throughout the rest of the year.

Among the low-alkalinity lakes the lowest zooplankton:phytoplankton ratios were generally recorded in Feeagh, with values ranging from 0.01 to 0.4. In Easky the ratio remained low in spring and early summer, increasing between August and October, reaching a maximum of 0.6 and declining again over the winter. In Maumwee, a maximum zooplankton:phytoplankton ratio of 0.8 occurred in September 2003, with a smaller peak of 0.5 occurring in November. However, the ratio was generally much lower throughout late winter and spring (Fig. 3.17).

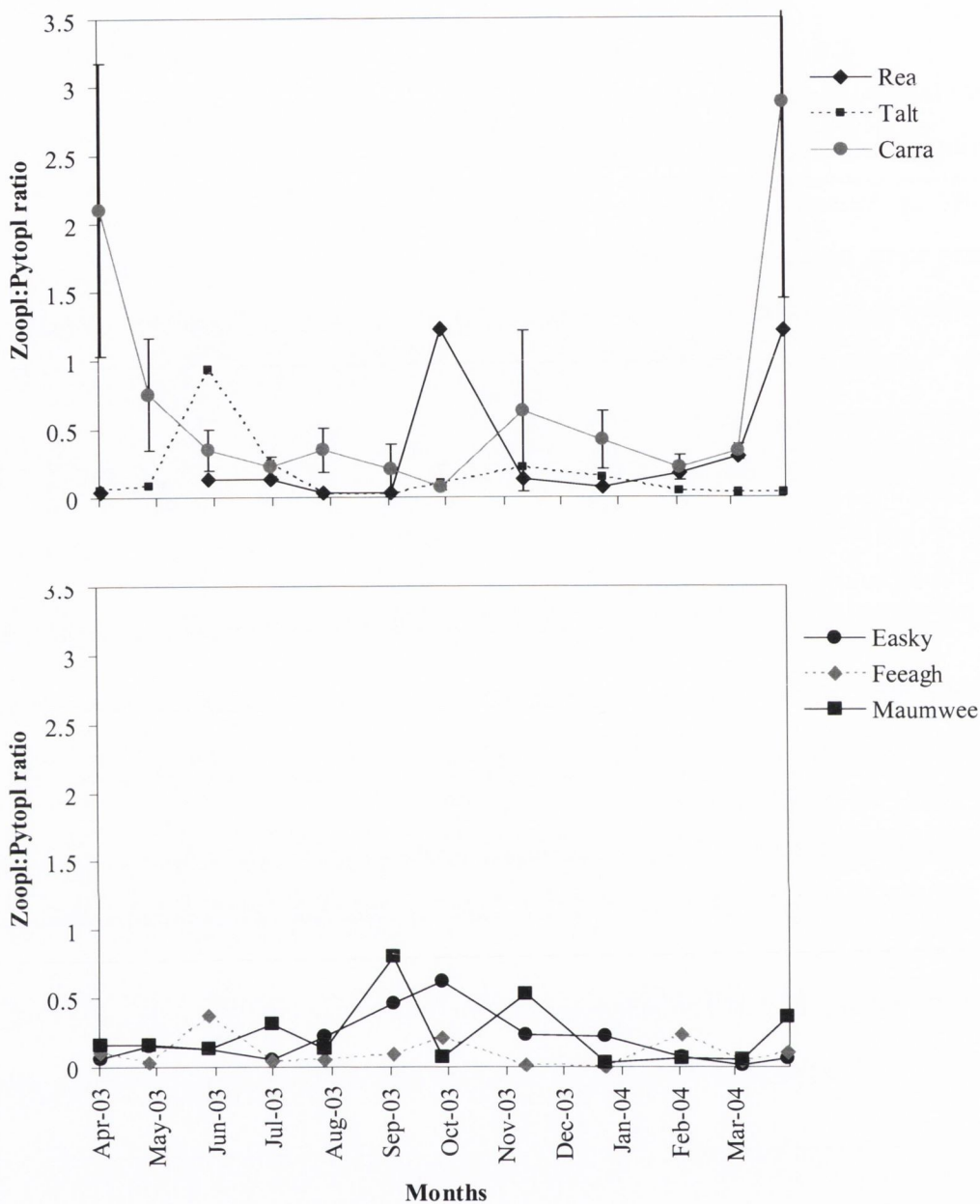


Fig. 3.17 The zooplankton:phytoplankton biomass ratio (DW:DW) assuming a conversion factor of 66 between chlorophyll *a* and dry weight (Jeppesen *et al.*, 2000) for each of the six lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n = 3$) of the three basins of Lough Carra are shown.

3.3.8.3 Cyclomorphosis

Daphnia individuals from the high-alkalinity lakes had larger helmets than individuals from the low-alkalinity lakes and were present over a longer time period in the high- compared with the low-alkalinity lakes. This is reflected in the significant interaction between sampling trip and alkalinity (Repeated measures ANOVA, $F_{8,48} =$

3.13, $P \leq 0.05$). The greatest helmet length compared with body length (HL:BL) was recorded consistently in Lough Talt (Fig. 3.18). Both Talt and Rea had pronounced seasonal patterns, with HL:BL increasing over the summer months and declining in autumn. In Carra, however, there was no increase in HL:BL over the summer, as the HL:BL ratio was very similar over the entire period from May to November. In the low-alkalinity lakes, Maumwee and Feeagh, HL:BL ratios remained low for much of the year only increasing briefly between July and August.

In Maumwee, helmets were almost undetectable on the larger sized individuals, although in Lough Feeagh, helmets became quite prevalent in the largest *Daphnia* (i.e. those greater than 1.71 mm), but absent from those individuals between 1.21 and 1.70 mm in length (Fig.3.19). In Lough Carra, the HL:BL ratio was similar for *Daphnia* in all size classes. In Lough Talt, the largest HL:BL ratios were recorded on smaller individuals between 0.71 and 1.30 mm. In Lough Rea, the HL:BL ratio was lower in the 0.71 to 1.30 mm size categories than in either the preceding or subsequent size categories.

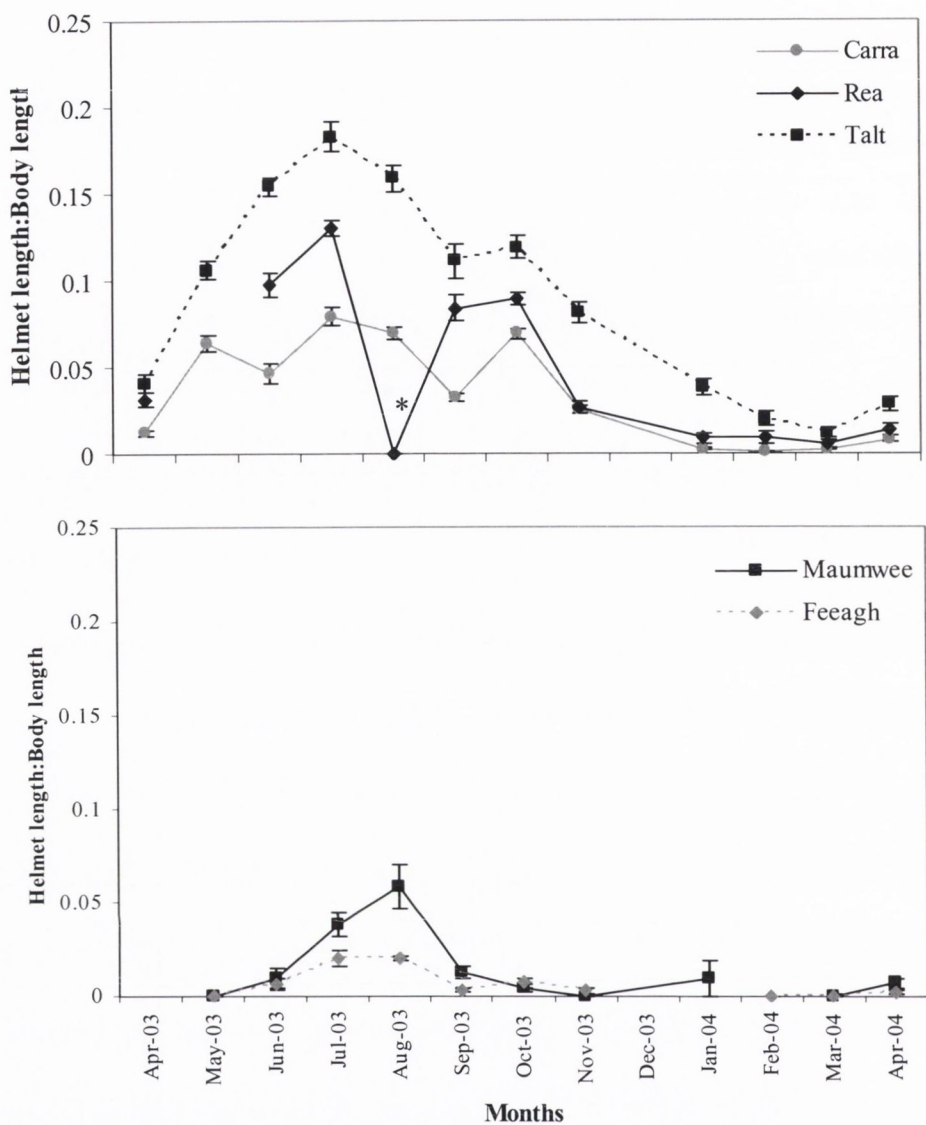


Fig. 3.18 The ratio of helmet length to body length (HL:BL) of *Daphnia* (mean $\pm$ SE) from five lakes, April 2003 – April 2004. * *Daphnia* abundances were very low in this sample and only three individuals were recorded, none of which carried helmets.

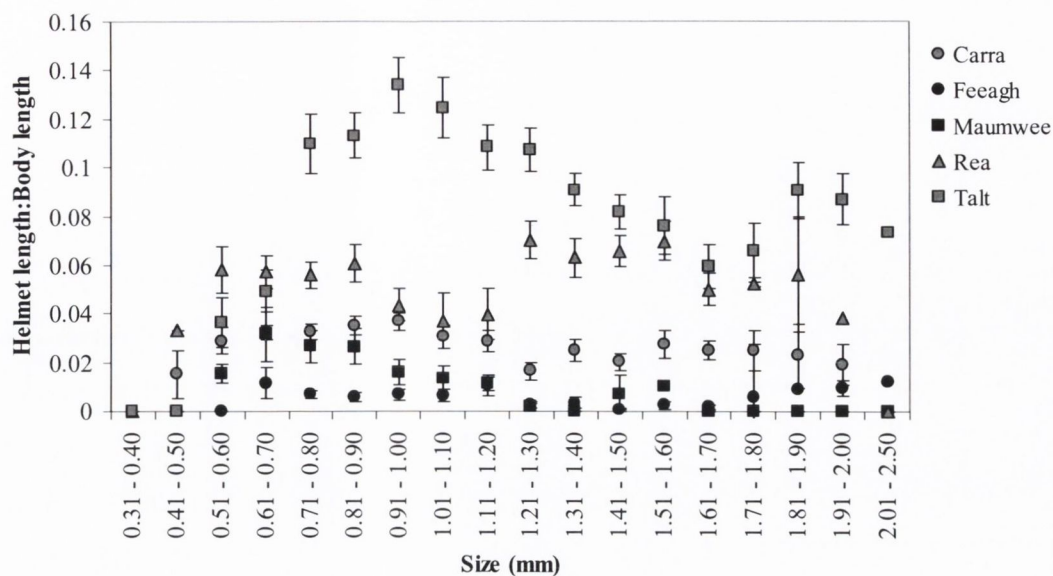


Fig. 3.19 Relationship between the body length and the helmet length to body length ratio (HL:BL) of *Daphnia* from five lakes (mean $\pm$ SE), April 2003 – April 2004.

3.4 Discussion

3.4.1 Alkalinity and zooplankton community structure

Daphnia and copepods dominated zooplankton biomass throughout the year in the high-alkalinity lakes, whereas in the low-alkalinity lakes cladoceran species other than *Daphnia* dominated at certain times of the year. This supports previous studies which reported low numbers of large, calcium dependent species, such as *Daphnia*, in soft-water lakes (Tessier & Horwitz, 1990; Hessen *et al.*, 1995a; Hessen *et al.*, 1995b; Wærvågen *et al.*, 2002). Reduced growth and reproduction for *Daphnia* has also been recorded under low ambient Ca concentrations (Alstad *et al.*, 1999; Hessen *et al.*, 2000). The particularly low occurrence of *Daphnia* in Easky may be the result of a direct physiological effect of low pH. Values of pH below 6.0 have been found to adversely affect *Daphnia* survival and reproduction (Walton *et al.*, 1982; Havens, 1992), and pH measurements in Easky were below 6 on seven of the twelve sampling dates of this study. There was also a positive relationship between rotifer abundance and alkalinity, which is contrary to previous studies showing increases in small rotifers with decreasing water hardness (Tessier & Horwitz, 1990) and pH (Yan & Geiling, 1985). Nevertheless, increased rotifer abundance with increasing pH has been observed (see review: Brett, 1989), but these relationships were rarely statistically significant. There was no pattern in individual species occurrence and no difference in rotifer standing biomass between high- and low-alkalinity lakes.

Holopedium gibberum and *Diaphanosoma brachyurum* were more prevalent in the low-alkalinity compared with high-alkalinity lakes. *Holopedium gibberum* is a species that occurs predominantly in low-alkalinity lakes (Hamilton, 1958). They do not have a calcified carapace, but are instead covered by a polysaccharide mantle, affording an advantage in calcium poor waters. *Diaphanosoma* have also been found to contain low levels of calcium in their bodies (Wærvågen *et al.*, 2002). Furthermore, high pH may prevent formation of the muco-polysaccharide mantle in *Holopedium* (Hessen *et al.*, 1995b) and *Diaphanosoma* is considered to be particularly tolerant to low pH (Kappes & Sinsch, 2005).

Lough Feeagh had the most distinctive taxa composition of the low-alkalinity lakes, largely because of the high *Daphnia* abundances. The *Bosmina* community in Lough Feeagh was also marked by co-occurrence of two species within the genus, *B. longispina* and *B. longirostris*, and was the only low-alkalinity lake to contain both species. *Bosmina longispina* is an acidophilic species (Fryer, 1993) and was recorded in all study lakes, but only tended to co-occur with *B. longirostris* in the high-alkalinity lakes. *Bosmina longirostris* requires alkaline water of relatively high ionic content with a plentiful supply of calcium (Fryer, 1993), and was found to be confined to alkaline or near-neutral waters in Britain (Fryer, 1993). These differences in Feeagh may be accounted for by the relatively high alkalinity concentrations, which reached a maximum of $9.3 \text{ mg L}^{-1} \text{ CaCO}_3$, compared with the other low-alkalinity lakes in this study.

Nevertheless, the large numbers of *Daphnia* recorded in Feeagh could also be attributed to lake depth. Lough Feeagh is the deepest of the low-alkalinity lakes with a maximum depth of approximately 45 m compared with 10 and 8 m in Easky and Maumwee, respectively. An important regulating factor for zooplankton in lakes is predation, and previous studies have suggested that top-down control from fish predation is more important in shallow lakes than in deep lakes, apart from lakes with a high abundance of submerged macrophytes (Jeppesen *et al.*, 1997). This is because at a given epilimnion TP concentration, the biomass of fish per m^3 is higher in shallow lakes. In addition the biomass of benthic invertebrates is higher in shallow lakes, and fish are, therefore, less dependent on zooplankton prey than in deep lakes. Consequently, their density can remain relatively high even during periods when zooplankton is scarce, thus maintaining a continuously high predation pressure on zooplankton populations than would be possible in deep lakes. The opportunity for zooplankton to escape predation by vertical migration is also reduced in shallow lakes. There is, therefore, a possibility that predation pressure from fish was more severe in Easky and Maumwee, which could account for the low numbers of *Daphnia* recorded in these lakes compared with Feeagh. Nevertheless, the large coverage of submerged macrophytes in Maumwee, which had a mean depth of less than 2 m, is also a potential mechanism by which zooplankton can avoid fish predation. Submerged macrophytes provide a refuge against fish predation for pelagic and plant associated cladocerans (Jeppesen *et al.*, 1997). Macrophyte refuges are the shallow

lake alternative to vertical migration, which is generally not available as a method of predator avoidance in shallow lakes (Jeppesen *et al.*, 1997). There is also very little evidence to suggest that predation pressure in either Easky or Maumwee was more severe than in Feeagh. Seasonal patterns in crustacean size distributions in Feeagh show a reduction in larger sized *Daphnia* during the summer and early autumn, which may be the result of fish predation. Similar reductions were not, however, evident in the other two low-alkalinity lakes. The ratio of zooplankton:phytoplankton biomass was also lower in Feeagh than in either Easky or Maumwee and remained relatively low throughout the year, which could indicate higher predation pressure compared with the other low-alkalinity lakes. Nevertheless, in the absence of quantitative data on fish numbers, the extent of fish predation in each of the lakes remains speculative. Nonetheless, the deep waters in Feeagh allows for the possibility that *Daphnia* escaped predation by vertical migration through the water column, a method of predator avoidance which is not available to zooplankton populations in either Easky or Maumwee.

Overall, total zooplankton biomass was generally greatest in the high-alkalinity lakes and the size distribution analyses showed that the zooplankton communities of the low-alkalinity lakes were skewed toward smaller sized individuals. Field surveys have reported that large bodied zooplankton species were replaced by smaller ones in soft-water localities (Tessier & Horwitz, 1990; Hessen *et al.*, 1995a). A positive correlation has been found between *Daphnia* body size and their specific Ca contents (Wærvågen *et al.*, 2002). It was suggested that calcium availability could offer an auxiliary explanation to fish predation in accounting for the size structure of zooplankton communities, although it is probably less important than fish predation (Wærvågen *et al.*, 2002).

3.4.2 *The effect of geographical proximity and altitude on species occurrence*

Lough Talt did not conform well to patterns of zooplankton structure observed in the other two high-alkalinity lakes and in some respects was quite similar in zooplankton community structure to Easky. Several taxa in particular mark Talt as separate from Carra and Rea. These include the presence of *Ceriodaphnia*, the high abundance of

cyclopoid copepods and the low abundance and unique species composition of calanoid copepods.

Ceriodaphnia were extremely rare or absent in all lakes apart from Talt and Easky, with a population comprising two species, *C. setosa* and *C. quadrangula*, the latter of which is considered to be the most acid tolerant (Fryer, 1993; Ribiero *et al.*, 2000), although a survey of Irish lakes found *C. setosa* over a broad range of pH (Caroni, 2000). It is possible that the low standing biomass of *Daphnia* in Easky allowed some competitive release for *Ceriodaphnia*. The nearby Talt, however, had a very large population of *Daphnia* co-existing with *Ceriodaphnia* over a large part of the year. It has been postulated that *Ceriodaphnia* are more successful under conditions of low food availability (Neill, 1975; Tessier & Goulden, 1987). Nevertheless, compared with the other lakes Talt did not have particularly low chlorophyll *a* concentrations.

Calanoid copepods often have distinct and restricted distributions (Fryer & Joyce, 1981). *Eudiaptomus gracilis* was found in nearly all lakes apart from Talt, but was recorded previously in Talt by Caroni (2000). *Eudiaptomus gracilis* is amongst the most common calanoid copepods in Europe (Jiménez-Melero *et al.*, 2005), occurring across a wide range of conditions from the smallest pool to the largest lake, and across a broad range of altitudes, depths and pH (Nilssen & Wærvågen, 2003). Although it is frequently associated with other calanoid species (Harding & Smith, 1974), it was, nonetheless, the only calanoid recorded in the majority of the study lakes, with the exception of Easky and Talt. This corresponds to the findings of Caroni (2000). *Mixodiaptomus laciniatus* was also recorded in Easky and *Arctodiaptomus laticeps* was recorded in both Talt and Easky. *Mixodiaptomus laciniatus* is typical of cold high altitude oligotrophic water bodies (Dussart, 1967) and has been recorded in high altitude subarctic ponds (Rautio, 2001), in deep subalpine lakes in Italy (Premazzi *et al.* 2003) and in oligotrophic high mountain lakes in Spain (Villar-Argaiz *et al.*, 2000). Lough Easky is a relatively high altitude, low productivity lake and is, therefore, a typical habitat for *M. laciniatus*. Alternatively, *Arctodiaptomus laticeps* has an extraordinarily discontinuous distribution with patterns of occurrence which are often difficult to explain (Reddy, 1994). Some of the similarities between Easky and Talt may be the result of historical

patterns of distribution and colonization particularly because of the geographical proximity of the two lakes.

Other factors which differentiated Lough Talt from the other high-alkalinity lakes in this study included the lower percentage occurrence and biomass of calanoids, and the greater biomass and percentage occurrence of cyclopoids. It may be that this large population of cyclopoids reduced calanoid biomass through predation of calanoid nauplii and copepodites, which are common prey of cyclopoid copepods (Soto & Hurlbert, 1991). *Cyclops abyssorum*, in particular, has been found to favour calanoid prey, even when other food such as rotifers or cladocerans are available in high numbers (Fryer, 1957).

3.4.3 Evidence for fish predation

There was good evidence for fish predation in the high-alkalinity lakes. In accordance with expectations of size-selective predation (Brooks & Dodson, 1965), body-size of the crustacean community in Carra decreased from spring to late autumn, including fewer large *Daphnia* in summer and autumn compared with spring (Fig. 3.11), although there was no overall shift towards dominance of smaller genera such as *Bosmina*. A similar reduction in crustacean body-size with a decrease in large sized *Daphnia* was also evident in Rea between August and September (Fig. 3.12), a lake which is annually stocked with trout. In addition the zooplankton:phytoplankton biomass ratio was low between April and August 2003 (Fig. 3.17), which could indicate considerable predation pressure during this period. There was a brief increase in the zooplankton:phytoplankton ratio between September and November which suggests strong grazing pressure of zooplankton on phytoplankton, facilitated perhaps by a reduction in fish predation. This was followed by a decline in *Daphnia* numbers as well as a decline in the zooplankton:phytoplankton ratio between November and January and suggests a further increase in predation pressure by fish. Rea is a shallow lake and it may be that benthic-planktivorous fish could substitute their diets with benthic invertebrates, thus maintaining a strong overall predation pressure on zooplankton throughout the winter (Jeppesen *et al.*, 1997). In Talt, there was a decline in *Daphnia* abundance between July and October and again between February and April 2004 (Fig. 3.13). The principal fish in the lake is trout, but Arctic charr are also

present, which often employ a zooplanktivorous feeding habit (Frost, 1977; Langeland *et al.*, 1991). When charr and trout are found together, trout often exclude charr from the littoral areas, particularly during the summer, but this habitat segregation is not maintained during winter and charr then move to a benthic diet (Langeland *et al.*, 1991). This pattern has been observed in Irish lakes (Igoe & Hammer, 2004). A gill net survey of Talt carried out in February 2004, however, found more Arctic charr in pelagic nets compared with benthic nets, but the opposite was observed for trout (Igoe *et al.*, 2004). This suggests that in Talt, charr do not switch back to a benthic diet in winter. It is, therefore, probable that the decline in *Daphnia* numbers between February and April is the result of charr predation.

Among the low-alkalinity lakes, Feeagh had the strongest evidence for fish predation based on size-distribution analyses. Fish predation by YOY brown trout was likely responsible for the reduction of larger sized *Daphnia* in Feeagh during the summer and early autumn (Fig. 3.14). The zooplankton:phytoplankton ratio was also low throughout the year in Feeagh, which is consistent with the premise of heavy fish predation on zooplankton. In Easky and Maumwee, however, there was little evidence of fish predation based on changes in crustacean size distribution throughout the year (Fig. 3.15 & 3.16, respectively). However, the overall small zooplankton size in the low-alkalinity lakes, compared with the high-alkalinity lakes (Fig. 3.11) may indicate a high degree of fish predation all year round. This in conjunction with a continuously low ratio of zooplankton:phytoplankton biomass could provide additional evidence for fish predation. The maximum recorded values of the zooplankton:phytoplankton ratio in Maumwee and Easky were lower than the maximum values recorded in the three-high alkalinity lakes, although higher than in Feeagh, and may suggest that Maumwee and Easky were experiencing greater fish predation pressure than the high-alkalinity lakes. The zooplankton:phytoplankton ratio in Easky was relatively low between April and July 2003, only increasing between August and October before declining again during winter. The higher values during autumn might suggest reduced fish predation throughout this period relative to other times of the year and corresponded to a period in which *Holopedium* dominated zooplankton biomass. In Maumwee, however, evidence for fish predation based on seasonal variation in the zooplankton:phytoplankton ratio was less explicit. This ratio in Maumwee was more variable than that observed in Easky. It remained low

between the spring and late summer of 2003 but was relatively high in September, which corresponded to an increase in *Daphnia* biomass. The ratio of zooplankton:phytoplankton also increased between November and December, declining to low levels for the remainder of the winter and early spring. Nonetheless, the species composition in the lake changed very little over the entire period between October 2003 and April 2004, being largely dominated by *Bosmina*. High *Daphnia* biomass recorded in March 2004 corresponded to a period of relatively low zooplankton:phytoplankton ratio. This is contrary to expectations based on the supposition of increased fish predation during this period, as *Daphnia* would be expected to decline, not increase, if as the zooplankton:phytoplankton ratio suggested, there was high predation pressure from fish.

Overall, there is more consistent evidence for fish predation in Feeagh and in the three high-alkalinity lakes than in either Maumwee or Easky. All of the low-alkalinity lakes in this study have high colour and turbidity, owing to their location in peaty catchments. Consequently, it could be postulated that fish predation is reduced in these lakes, owing to the effects of turbidity and colour on light attenuation and scattering. This may be the reason for the poor evidence for fish predation in Easky and Maumwee. Nevertheless, Feeagh had the highest concentrations of colour and turbidity but, nevertheless, there was relatively good evidence for fish predation in this lake.

3.4.4 Evidence for invertebrate predation

There was good evidence for invertebrate predation in Talt and Rea, based on size-distribution analyses and measures of cyclomorphosis as well as abundance measurements of predatory invertebrates. Evidence of predation by invertebrates was less apparent in Carra. Rea had a much higher mean abundance of *Leptodora* (Fig. 3.10) than any of the other lakes, maximal numbers of which were recorded in June and corresponded to a peak in the ratio of HL:BL in *Daphnia* (3.18). This is suggestive of increased predation pressure. The increase in *Bosmina* and *D. cucullata* in Rea during September could be a response to reduced predation pressure from invertebrates, particularly from *Leptodora*, which declined in numbers during this time. *Bosmina* densities continued to increase thereafter reaching a maximum

abundance in April 2004. In Talt the larger HL:BL ratio of *Daphnia* in the smaller size ranges (Fig. 3.19) indicates that invertebrate predation may also be particularly high in this lake. Cyclopoid copepods and *Leptodora* were the most notable invertebrate predators in the lake, both of which experienced maxima in abundance during July. Size distribution analyses revealed that smaller sized crustaceans were almost eliminated from the lake during this period. There was also a decline in calanoids, particularly copepodites, which are also likely to be heavily predated upon by cyclopoids. Although *Leptodora* were present in Carra between May and October, they occurred in much lower numbers than in the other high-alkalinity lakes. Their greatest abundance was recorded in September. This peak was much later than the June and July peaks in *Leptodora* abundance observed, respectively, in Rea and Talt. The low numbers of *Leptodora* during the summer in Carra is consistent with the premise of fish predation and it is, therefore, unlikely that predation by *Leptodora* can account for the low summer and autumn abundances of *Bosmina*. On the contrary, *Bosmina* numbers actually began to increase in September, thus coinciding with the increase in *Leptodora* during this period. Observed patterns of cyclomorphosis in the *Daphnia* population of Lough Carra provide further evidence of a low influence of predacious invertebrates in structuring the zooplankton community. The helmet sizes of *Daphnia* in Lough Carra were smaller than those recorded in the other high alkalinity lakes. There was also very little change in helmet size between May and October and the ratio of HL:BL was relatively constant among *Daphnia* of all sizes.

There was some evidence for invertebrate predation across all low-alkalinity lakes, although weaker for Easky than for either Feeagh or Maumwee. Although *Daphnia* in Feeagh had the smallest helmet size of all lakes, peaks in the ratio of HL:BL, nevertheless, occurred in July and August and corresponded to peaks in predacious invertebrates. *Leptodora* and *Bythotrephes* were recorded in the August samples and Feeagh was the only lake in which *Chaoborus* was found, which was recorded in August and September. While high abundances of *Bosmina* were observed in June, numbers were almost undetectable between July and September. There is much evidence to suggest that invertebrate predation had an important role in influencing zooplankton community structure in Maumwee. The ratio of HL:BL of *Daphnia* were larger than in Feeagh. The helmets were most evident between June and September and most pronounced in smaller sized *Daphnia* suggesting induction by invertebrate

predators. Predacious invertebrates in the lake included *Leptodora*, *Bythotrephes*, *Polyphemus pediculus* and cyclopoid copepods, all of which were prevalent between June and October. *Bythotrephes* was the most abundant of the predacious cladocerans and reached maximum numbers in August. *Bosmina* dominated biomass for much of the year, but appeared to be the most vulnerable cladoceran species to these predators, with declines in abundance occurring between July and October. Cyclopoid copepods were also likely to be an important predator in Maumwee. Large numbers of cyclopoids, particularly in September, coincided with major declines in the abundances of nearly all cladocerans except *Daphnia*, whose numbers increased during this period. In Easky both *Leptodora* and *Bythotrephes* were present, and the latter reached relatively high abundances compared with that observed in the other lakes. Both species were present between April and October. There is also a relatively large population of cyclopoid copepods in the lake, and large numbers of mature cyclopoids were present between August and October. Low numbers of *Bosmina* between May and August suggest that the *Bosmina* population may have experienced predation pressure. Nevertheless, *Bosmina* began to increase in abundance from September, when invertebrate density was high.

3.4.5 Competitive biotic interactions

In Carra there was no increase in the abundance or biomass of calanoids during the summer, despite the large decline in *Daphnia*. Their dominance of zooplankton biomass at this time was simply a consequence of reduced *Daphnia* abundance and biomass during summer and autumn. The fluctuating patterns of dominance between *Eudiaptomus* and *Daphnia* in Rea, however, follow a different pattern to those observed in Carra. There was no large scale decline in *Daphnia* abundance during the summer and autumn and unlike Carra, there was an increase in calanoid abundance during periods of decline in *Daphnia* abundance. This would suggest a possible competitive interaction between the two species. Both *Daphnia* and calanoid copepods are probably best characterised as grazers with somewhat different feeding strategies. *Daphnia* are exclusively filter-feeders, whereas copepods such as *Eudiaptomus* also have a raptorial feeding strategy and can select food particles individually based on size, motility or quality (DeMott & Moxter, 1991). Although calanoids have been found to preferentially graze larger sized food particles than filter

feeders such as *Daphnia* (Yoshida *et al.*, 2001) there is, nevertheless, much overlap in their food size spectra (Adrian & Schneider-Olt, 1999; Sommer *et al.*, 2003). It is, therefore, plausible that observed variations in the abundance of *Daphnia* and *Eudiaptomus* in Rea was the result of exploitive competition between the two genera.

According to the size-efficiency hypothesis (Hall *et al.*, 1976), small cladocerans such as *Bosmina* should be inferior competitors to larger sized *Daphnia*. Large species such as *Daphnia* have been shown to competitively reduce the density of small zooplankton such as *Bosmina* (Goulden & Hornig, 1980; Vanni, 1986; Kerfoot *et al.*, 1988). In Carra and Rea, *Daphnia* and *Bosmina* co-existed throughout the year and had very similar seasonal patterns of abundance, mutually increasing to maximum densities in both lakes during April. It may be that *Bosmina* in these lakes forage differentially on a subset of edible algae thus facilitating co-existence with larger competitors such as *Daphnia*. The greater effectiveness of *Bosmina* at selecting certain categories of food within the available range of resources has been recorded previously (DeMott & Kerfoot, 1982; DeMott, 1982; Bleiwas & Stokes, 1985) and suggests that single factor hypotheses such as the size-efficiency model may not be sufficient for predicting the outcome of competitive interactions. Other factors such as resource composition or abiotic environment must also be taken into account.

3.4.6 Conclusion

Differences in zooplankton community structure were observed between the high- and low-alkalinity lakes of this study. The high-alkalinity lakes were dominated by either *Daphnia* or copepods, whereas other cladoceran taxa such as *Bosmina*, *Ceriodaphnia*, *Holopedium* and *Diaphanosoma* dominated low-alkalinity lakes at certain times of the year.

Overall zooplankton community size structure also differed between the two alkalinity groups, with larger individuals dominating in the high-alkalinity lakes and smaller individuals dominating the size spectrum in the low-alkalinity lakes. This was not, however, reflective of the degree of fish predation, as size distribution analyses provided a strong case for large influences of fish predation on the zooplankton assemblage of Lough Feeagh. Most invertebrates are tactile predators, and unlike

fish, they do not depend on light to detect prey. Higher invertebrate predation would, therefore, be expected in the low-alkalinity lakes. There was, however, evidence to suggest that invertebrate predators were important in the high-alkalinity lakes, Rea and Talt. Nevertheless, helmet size of *Daphnia* in the low-alkalinity lakes were much smaller than those in the high-alkalinity lakes, and could be interpreted to imply that invertebrate predation is less important in these lakes. It is more likely, however, that the smaller helmet sizes are a consequence of the dual effect of cyclomorphosis proposed by Dodson (1974a). Large protrusions such as helmets were considered important, not only for interfering with the handling ability of grasping invertebrate predators, but also in decreasing the reactive distances of fish to their prey. In the low-alkalinity lakes where visibility is reduced, *Daphnia* may only require a helmet size large enough to defend against invertebrate predators, without needing combined protection from visual planktivores such as fish. This is advantageous as there may be some costs associated with large helmets (Dodson, 1974a; Spaak & Boersma, 1997). The observation that helmeted *Daphnia* in the low-alkalinity lakes were almost all confined to the smaller size classes provides further support for this hypothesis.

While the presence and abundances of particular species within a water body was related to the abiotic environment, nevertheless, the relative importance of such factors as predation and competition varied considerably; even among lakes with very similar communities and water chemistry. Fluctuations in dominance between *Daphnia* and calanoids in Carra and Rea, for example, can to some extent be attributed to fish predation. In Talt invertebrate predation, particularly from cyclopoids appeared to affect abundances of calanoids. In Rea a competitive interaction between *Daphnia* and calanoids was also evident with an increase in calanoid abundance during periods of decline in *Daphnia* abundance. Differences in resource availability between these lakes may account for this, as the concentration and quality of food can determine the degree to which predators influence the dynamics and abundance of herbivores (DeMott & Kerfoot, 1982; Vanni, 1987).

This field study suggests that the physical, chemical and biotic environment is important in structuring zooplankton assemblages. However, the availability and quality of resources is also an important determinant of zooplankton community structure and biomass (Lampert, 1977; DeMott & Kerfoot, 1982; DeMott, 1989;

Gliwicz & Lampert, 1993) and should also be considered. Recent studies on the food requirements of freshwater zooplankton have focused attention on elemental and biochemical limitation of food (Hessen, 1992; Sterner *et al.*, 1993; Sterner & Elser, 2002). Resource nutrient limitation might be an important factor influencing zooplankton community structure and distribution, and consideration of such issues may provide further clarification in accounting for zooplankton occurrence across the six lakes of this study. Such interactions are explained further in Chapters 4 and 5.

4.1 Introduction

Stoichiometric theory predicts contrasting response among zooplankton species to nutrient limitation, because there are large inter-species differences in cellular C:N:P ratio (Sterner & Hessen, 1994). These differences affect competition among species (Schulz & Sterner, 1999; Conde-Porcuna, 2000) and relative rates of nutrient regeneration (Olsen *et al.*, 1986; Elser *et al.*, 1988). Some taxa, such as daphniids (Andersen & Hessen, 1991) and rotifers (Conde-Porcuna, 2000; Jensen & Verschoor, 2004), are more susceptible to phosphorus limitation, owing to their high cellular P content, than taxa with lower cellular P contents, such as *Bosmina* (Urabe & Watanabe, 1992; Schulz & Sterner, 1999). Copepods, which have high cellular N:P ratio (Sterner & Hessen, 1994; Sterner, 1998), are more likely to be sensitive to deficiencies in dietary nitrogen (N) (Hessen, 1992; Kiørboe, 1989; Van Nieuwerburgh *et al.*, 2004).

Frequently, the elemental and biochemical composition of the primary producers do not meet the nutritional requirements of herbivores in aquatic systems (Elser *et al.*, 2000b). Seasonal patterns in the quantity and quality of phytoplankton affect fecundity and growth of zooplankton (Brett *et al.*, 2000), with at least some zooplankton (e.g. *Daphnia*) capable of rapid responses to fluctuating food supply (George & Reynolds, 1997). Temporal variations in the supply of nutrients, as well as alterations in the physical environment such as temperature and day length (Sterner *et al.*, 1997), alter nutrient ratios in algae, while top-down effects of predation (Brooks & Dodson, 1965) operate concurrently to influence the overall structure and composition of the zooplankton.

Previous work on nutrient limitation of the zooplankton has focussed on individual growth, with fewer investigations of the relationship between nutrient limitation of resources and zooplankton community composition and population dynamics (Gulati & DeMott, 1997). Most field investigations that have analysed the effects of nutrient ratios on zooplankton populations (Hessen, 1992; Hassett *et al.*, 1997; Sterner *et al.*,

1997; Brett *et al.*, 2000) have provided evidence for nutrient limitation, particularly of P, in natural zooplankton communities. A threshold of food C:P ratio calculated for *Daphnia* growth and reproduction (Urabe & Watanabe, 1992; Sterner & Hessen, 1994; Brett *et al.*, 2000; Anderson & Hessen, 2005) is usually considered to occur in the region of 200 - 350 (molar); above which daphniid production is believed to be P-limited, provided that other limiting factors are not involved. Nevertheless, the interplay between individual growth and seasonal trends in zooplankton community structure is unclear. Investigations examining the relationship between seasonal nutrient availability and zooplankton community structure and fecundity are scarce (DeMott *et al.*, 2001; Conde-Porcuna *et al.*, 2002; Scheuerell *et al.*, 2002).

Population models of stoichiometric consumer-resource interactions have shown that food elemental composition may have profound effects on population dynamics (Sterner & Elser, 2002; Elser & Urabe, 1999). The importance of consumers in regulating ecosystem processes such as nutrient recycling have recently been recognised. Both zooplankton and algal elemental composition influence the rate and ratios of nutrient release. The release of N:P by a grazer will be dependent not only on the elemental composition of its food supply but also on the elemental requirements of the grazer itself. Thus, the stoichiometry of nutrient recycling is a feedback mechanism linking grazer dynamics and the nutritional status of the algae (Elser & Urabe, 1999). Elser *et al.* (1988) showed that when *Daphnia* dominated biomass there was a shift to P-limited phytoplankton growth, whereas dominance by copepods was associated with N-limited growth. Since then, however, relatively few studies have examined stoichiometric recycling interactions (Sommer & Sommer, 2006) and little evidence exists, apart from that provided by Elser *et al.* (1988), which shows that the differential nutrient recycling of various zooplankton taxa affects phytoplankton nutritional status in natural environments (Elser & Urabe, 1999).

In this chapter it was investigated whether, in accordance with stoichiometric theory, *Daphnia* is more sensitive than the calanoid copepod *Eudiaptomus gracilis* to fluctuations in dietary P, and their role in consumer-driven nutrient recycling was examined. Correlation and stepwise regression analyses were used to examine the relationship between seasonal fluctuations in the chemical and biotic environment and zooplankton community structure, biomass and fecundity.

4.2 Methodology

Zooplankton and water were collected and analysed between April 2001 and June 2003 using methodology outlined in Chapter 2 (section 2.2). The following section provides an explanation of additional methodology to those previously discussed in Chapter 2.

4.2.1 Estimation of C:N:P in the seston and zooplankton

Phosphorus availability for zooplankton in the lake was assessed using an estimation of the seston C:P ratio, obtained by approximating the ratio of light:total phosphorus in the water column. Changes in the ratio of the availability of light to nutrient supply is thought to control nutrient use efficiency in autotrophs. Increased light results in greater C fixation, thereby increasing the amount of C relative to P in algae (Sterner *et al.*, 1997). The ratio of light:TP, as an index for the C:P ratio, has previously been applied to the prediction of zooplankton dynamics by Scheuerell *et al.* (2002), and involved estimating the mean light intensity in the mixed layer as a fraction of the surface light. Since Lough Carra is a shallow lake that rarely if ever stratifies, the mixed layer was estimated as the depth of the water column at the time of sampling. On four occasions between April and September 2005, the C, N and P content of seston and plankton from the North basin of Lough Carra was analysed. The samples for seston nutrient content determination were collected using the 6 m integrated tube and passed through a 53 μm mesh to remove zooplankton. Sub-samples of approximately 2000 – 4000 ml were then filtered through precombusted (550 °C) acid-washed Whatman® GF/C filters. Filters were dried at 60 °C and weighed. Carbon and nitrogen were measured in triplicate using a LECO® – CNS analyser. Phosphorus analyses was carried out in triplicate and determined spectrophotometrically by the ascorbate-reduced molybdenum-blue method following combustion at 550 °C for 2 h and digested with potassium peroxide sulphate ($\text{K}_2\text{S}_2\text{O}_8$) under pressure (Eisenreich *et al.*, 1975). Zooplankton was collected using a zooplankton net with a 53 μm mesh size and placed in a 2 L bottles containing surface water. On return to the laboratory, the zooplankton were again passed through a 53 μm mesh and rinsed with distilled water and then added to 500 ml of distilled

water. Aliquots of 30 to 500 ml were removed and filtered through precombusted (550 °C) acid-washed Whatman® GF/C filters, dried at 60 °C, weighed and analysed for C, N and P content following the same procedures as those described above for seston. All measurements for C, N and P were carried out using controls lacking zooplankton or seston.

4.2.2. *Phytoplankton analyses*

Single 120-ml sub-samples of the well-mixed integrated water samples were taken and preserved with Lugol's Iodine for phytoplankton analysis. Phytoplankton samples from the North and South basins, collected from July 2002 to July 2003, were counted and identified across a transect of a circular chamber (25 ml) using an inverted microscope.

4.2.3 *Zooplankton fecundity analyses*

On each sampling date from January 2002 to January 2003, a minimum of 50 individuals of both *Daphnia* and *Eudiaptomus* were scored for length and number of eggs. The length of the smallest egg-bearing female was used as an estimate of the minimum size at maturity and all individuals of an equal or greater size were assumed to be mature. The number of eggs per mature female was calculated for both taxa. As this parameter in *Daphnia* depends directly on carapace length, on each sampling date a regression line was calculated to define the relationship between the number of eggs and the body length of egg bearing females according to Vijverberg *et al.* (2005). The resulting regression equations were used to calculate the standard egg number (SEN) on each sample date, defined as the clutch size for a female of standard length (1.5 mm).

4.2.4 *Statistical analyses*

Pearson's product-moment and Spearman's rank correlations and multiple regression analyses were carried out using SPSS® Version 11. Pearson's product moment correlation analysis was carried out on parametric data. Highly skewed data were normalised using logarithmic transformations. Spearman's rank correlation analysis

was performed when at least one non-parametric variable was involved. Multiple regression was performed using a forward stepwise procedure to compensate for covariance (Quinn & Keough, 2002). Variables with a P -value > 0.05 were selected and only those independent variables which were correlated significantly with the dependent variable were included in the model. Separate analyses carried out for each basin indicated, in most cases, similar relationships among variables. For clarity only the results of the correlation analyses for the entire lake are presented.

4.3 Results

4.3.1 Nutrient dynamics

Total nitrogen and DIN concentrations were strongly seasonal, with higher concentrations in winter (December – February) and spring (March – May), declining through summer (June – August) to an autumn minimum (September – November) (Fig. 4.1). DIN, in particular, was very low in autumn, ranging from 0.004 – 0.36 mg L⁻¹, which is close to the threshold suggested as an indicator of N-limitation (Hochstädter, 2000). Maximum values of DIN were recorded in all basins during spring 2002, reaching highest concentrations of 0.88 mg L⁻¹ in the South basin. There was no distinct seasonal pattern in either soluble reactive phosphorus or total phosphorus concentrations over the study period, apart from large peaks of TP, reaching approximately 35 µg L⁻¹, in all basins during winter. TP concentrations fluctuated throughout the rest of the year, with a mean (± SE) for the entire lake of 11.6 ± 0.59 µg L⁻¹ (n = 135) (Fig. 4.1). SRP concentrations increased between November 2001 and April 2002 in all basins; otherwise the concentrations remained low, with a mean (± SE) of 2.4 ± 0.16 µg L⁻¹ (n = 135).

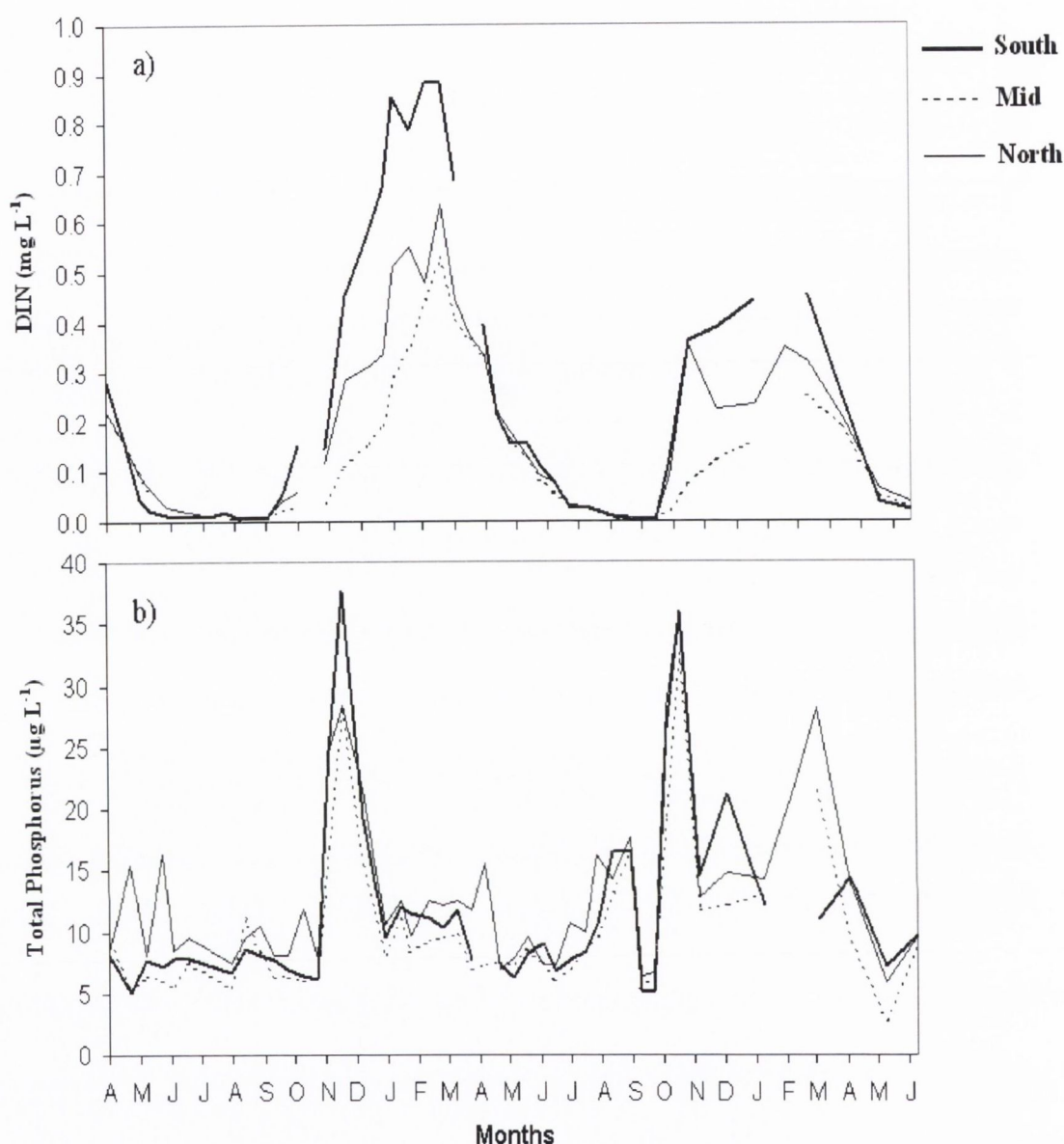


Fig. 4.1 (a) Dissolved inorganic nitrogen (DIN) concentration (mg L^{-1}) and (b) Total phosphorus (TP) concentration ($\mu\text{g L}^{-1}$) in each of three Lough Carra basins, April 2001 – June 2003.

The DIN:TP ratio was calculated to provide an estimate of the limiting nutrient for phytoplankton as recommended by Morris & Lewis (1988). They considered these fractions of N and P representative of the bulk of available N and P to phytoplankton. Values greater than 27 (molar) were taken as an indicator of P-limitation, and values below 2 (molar) an approximate indicator of N-limitation. In Lough Carra, the ratio of DIN:TP indicated probable N-limitation for most of the period between August and October and ranged from 0.32 – 23 (52 % of the values within this range were $\leq$

2) and mostly P-limitation throughout the rest of the year with values ranging from 12 – 197 (88 % of the values within this range were ≥ 27). In June, July and November the DIN:TP ratio was generally between the two thresholds of limitation (ranging from 3 – 61). Approximations of the mean seston C:P (Light:TP) ratio ($\pm$ SE) in Lough Carra, estimated from Sterner *et al.* (1997), was 308 ± 2.6 ($n = 132$) and varied between 252 and 420. There was no significant association between the ratio of DIN:TP and the predicted C:P ratio (Pearson's $r = 0.09$, $P \geq 0.05$, $n = 125$). The mean C:P ratio ($\pm$ SE) measured from samples taken between April and September 2005 was 223 ± 84 ($n = 4$). There was generally good agreement between these values and the estimated C:P (Light:TP) ratio, with the exception of a low value of 75 recorded in July 2005 (Table 4.1). This was also the only date in which the C:P ratio of the zooplankton was higher than that of the seston and was coincident with calanoid dominated zooplankton biomass. The N:P ratios of seston and zooplankton measured in 2005 indicate that P was the most deficient element in the seston relative to the elemental contents of the zooplankton, apart from July where the seston N:P was only 9 compared with a N:P ratio of 77 recorded for plankton. In July nitrogen was, therefore, the most deficient nutrient in the seston relative to the nutrient content of the zooplankton and indicates severe nitrogen limitation for the zooplankton (Table 4.1).

Table 4.1 Ratio of C:P and N:P in zooplankton and seston in the North basin of Lough Carra.

		April 2005	May 2005	July 2005	September 2005
C:P	Zooplankton	101	95	420	308
	Seston	157	249	75	412
N:P	Zooplankton	19	15	77	30
	Seston	24	31	9	43

A similar seasonal trend in chlorophyll *a* concentration occurred in each of the three basins, with lowest values in spring. The mean chlorophyll *a* concentration ($\pm$ SE) for all three basins of Lough Carra was $2.5 \pm 0.1 \mu\text{g L}^{-1}$ ($n = 141$) and ranged from $0.3 - 8.5 \mu\text{g L}^{-1}$. While there were no significant associations between chlorophyll *a* and either TP or TN, there was a negative correlation between chlorophyll *a* and DIN (Pearson's $r = -0.31$, $P \leq 0.001$, $n = 128$), and a significant positive association

between chlorophyll *a* and soluble reactive phosphorus (Pearson's $r = 0.28$, $P \leq 0.001$, $n = 135$).

4.3.2 *Phytoplankton community structure*

Diatoms dominated the phytoplankton community in Lough Carra, comprising about 50 % of cells throughout much of the year. Chlorophytes were the second most abundant taxon, followed closely by cryptophytes. In both the South and North basins, cyanophytes usually comprised only about 8 % of the total community. In the North basin they dominated briefly during late July 2002, however, accounting for approximately 69 % of phytoplankton cells and again from March - June 2003, comprising between 10 – 40 % of the phytoplankton (Fig. 4.2).

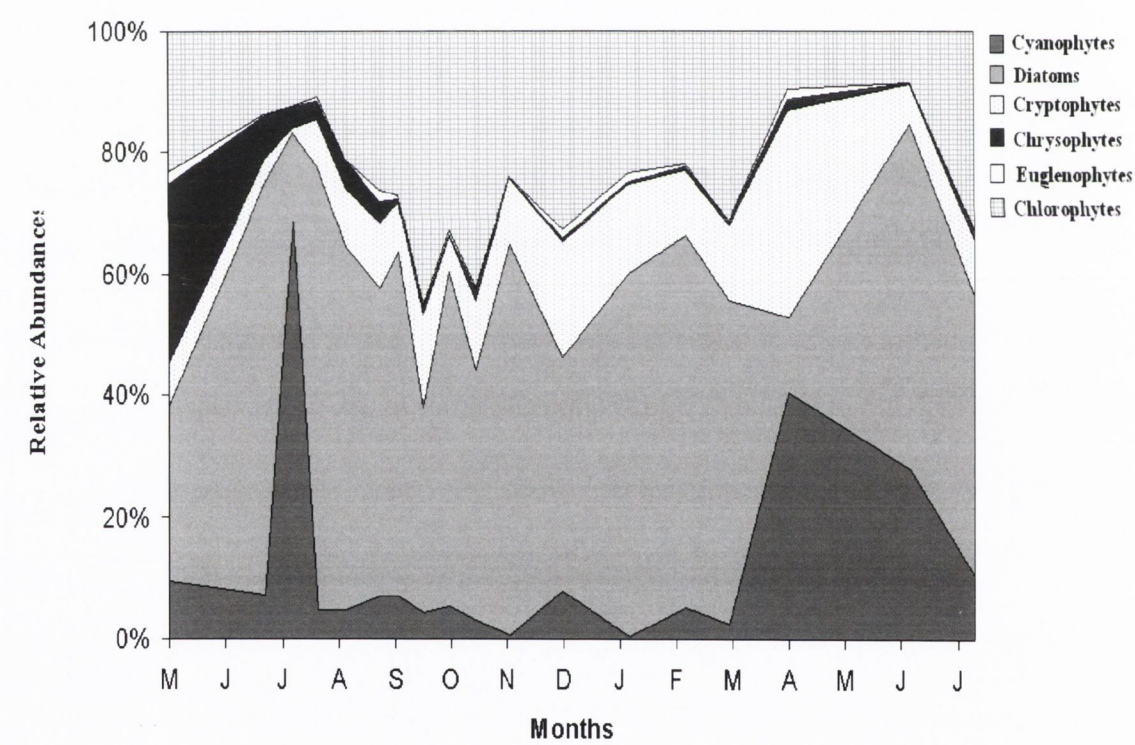


Fig. 4.2 Relative abundances of phytoplankton in the North basin, Lough Carra, May 2002 – July 2003.

4.3.3 Zooplankton community structure

Seventeen species of Cladocera were recorded in Lough Carra over the sampling period. Copepods comprised principally *Eudiaptomus gracilis* and cyclopoid copepods, mainly *Cyclops spp.* Rotifers, dominated by *Keratella cochlearis* and *Kellicottia longispina*, were the most diverse and abundant component of the community. Three species of predatory cladoceran, *Bythotrephes longimanus*, *Leptodora kindtii* and *Polyphemus pediculus*, were present, and most abundant between June and November of both 2001 and 2002. The total estimated biomass of zooplankton in Lough Carra ranged from 0.4 $\mu\text{g DW L}^{-1}$ to 5455 $\mu\text{g DW L}^{-1}$. Maximum biomass occurred in the South basin in spring 2002. Zooplankton biomass was dominated by *Daphnia hyalina*, *Daphnia cucullata* and the calanoid copepod, *Eudiaptomus gracilis*. The mean biomass of *Daphnia* and *Eudiaptomus* ($\pm$ SE) was, respectively, $73 \pm 43 \mu\text{g DW L}^{-1}$ and $44 \pm 7 \mu\text{g DW L}^{-1}$ ($n = 129$). Together, these two genera accounted for approximately 98 % of mean zooplankton biomass, with seasonally fluctuating dominance by *Daphnia* and *Eudiaptomus* (Fig. 4.3).

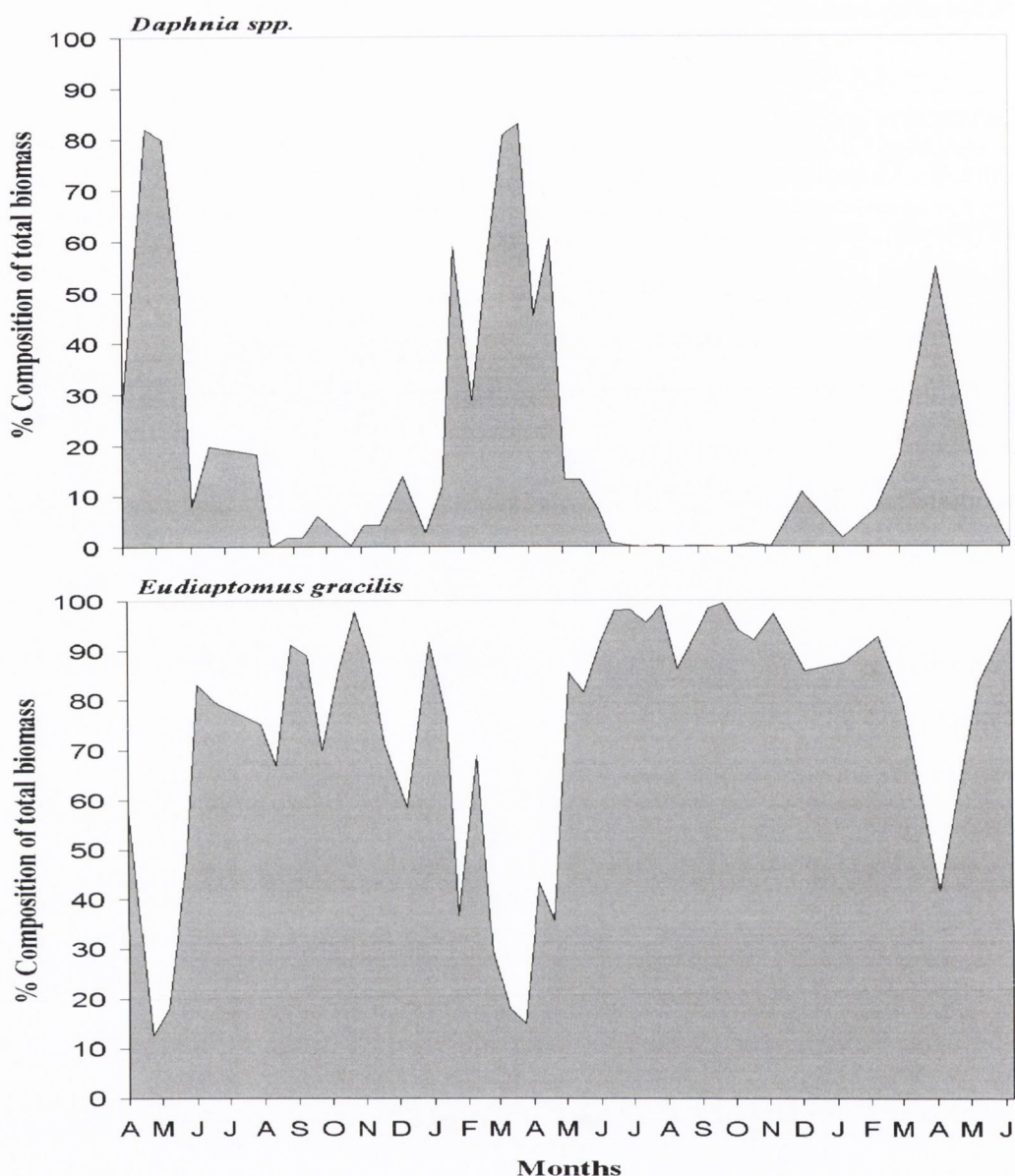


Fig. 4.3 Mean percentage contribution of *Daphnia spp.* and post-naupliar *Eudiaptomus gracilis* to total zooplankton biomass for the three basins of Lough Carra, April 2001 – June 2003.

Maximum *Daphnia* biomass occurred in the spring of both years, declining to low values in summer and autumn. In both 2001 and 2002, *Daphnia* biomass was very low during autumn, ranging between 0 and 0.012 $\mu\text{g DW L}^{-1}$. *Eudiaptomus* biomass ranged from 0.10 - 671 $\mu\text{g L}^{-1}$, and was greatest during spring of 2002 in the North basin, but no consistent seasonal pattern of calanoid biomass was evident.

4.3.4 Relationships of the zooplankton assemblage to nutrient availability

There was evidence that zooplankton herbivores suppressed algal biomass (Table 4.2), with maximum *Daphnia* biomass during spring 2001, 2002 and 2003 associated with minimum chlorophyll *a* concentrations (Fig. 4.4). Peaks of other cladoceran herbivores also occurred in spring in all three basins. Additionally, chlorophyll *a* correlated negatively with calanoid biomass (Table 4.2), and this relationship was particularly evident during periods of low *Daphnia* biomass (Fig. 4.4).

Table 4.2 Pearson's product-moment correlation coefficients (and sample size) for in-lake physical and chemical variables and various zooplankton biomass ($\mu\text{g DW L}^{-1}$) categories for Lough Carra, April 2001 – June 2003. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; SRP, soluble reactive phosphorus; TP, total phosphorus; PP, particulate phosphorus; TDP, total dissolved phosphorus; DIN, dissolved inorganic nitrogen; TN, total nitrogen; PN, particulate nitrogen. Significant relationships in bold.

	Total Zooplankton	Rotifers	<i>Daphnia</i> spp.	Other Cladoceran Herbivores	<i>Eudiaptomus gracilis</i>	Calanoid nauplii	<i>Cyclops</i> spp.	Cyclopoid nauplii
SRP	-0.03 (126)	-0.12 (126)	-0.04 (99)	-0.10 (39)	-0.07 (126)	0.08 (124)	-0.12 (49)	0.15 (115)
TP	-0.01 (126)	-0.12 (126)	-0.17 (99)	0.10 (39)	-0.06 (126)	0.19 * (124)	-0.46 *** (49)	-0.08 (115)
PP	-0.09 (125)	0.00 (98)	-0.01 (98)	0.07 (39)	-0.12 (125)	-0.04 (123)	-0.39 ** (49)	0.02 (114)
TDP	-0.05 (111)	-0.08 (111)	-0.16 (85)	-0.03 (34)	-0.05 (111)	0.17 (109)	-0.18 (37)	0.04 (100)
DIN	0.31*** (119)	0.22 * (119)	0.66 *** (93)	0.31 * (38)	0.13 (119)	0.15 (117)	0.28 (43)	0.61*** (108)
TN	0.24 ** (112)	-0.02 (112)	0.40 *** (86)	0.20 (34)	0.13 (112)	0.07 (105)	-0.40 (37)	0.40*** (101)
PN	-0.07 (112)	-0.23 * (112)	-0.28 * (86)	0.02 (34)	0.07 (112)	-0.07 (110)	-0.38 * (37)	-0.24 * (101)
Suspended Particulate Organic Matter	-0.24 ** (122)	0.09 (122)	-0.21 * (95)	-0.53 *** (39)	-0.17 (122)	-0.15 (120)	-0.07 (48)	-0.15 (111)
Chlorophyll <i>a</i>	-0.36 *** (126)	-0.17 (126)	-0.37 *** (99)	-0.26 (39)	-0.27 ** (126)	-0.07 (124)	-0.32 * (49)	-0.10 (115)

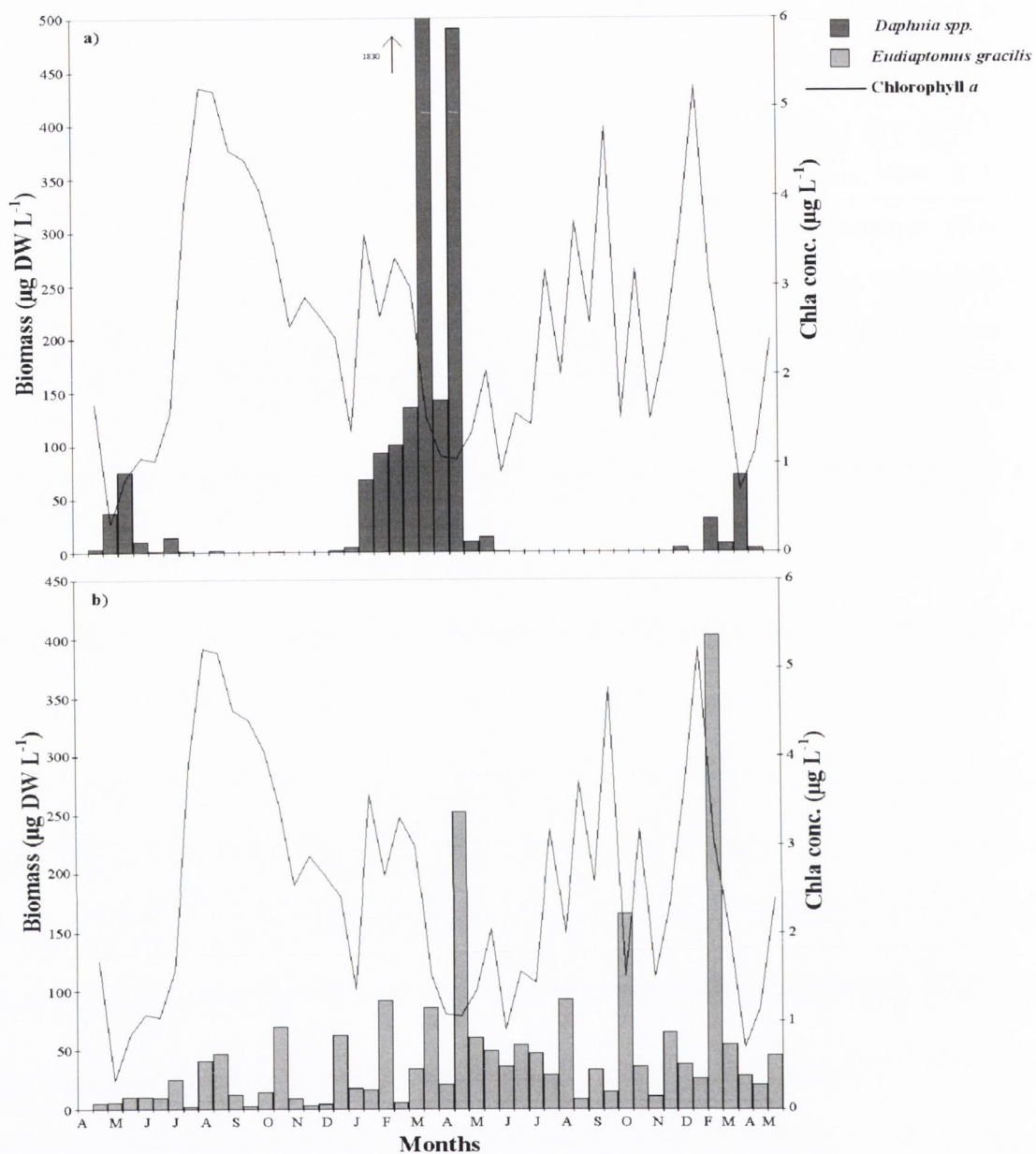


Fig. 4.4 (a) Mean biomass of *Daphnia* spp. ($\mu\text{g DW L}^{-1}$) and chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) and (b) mean biomass of post-naupliar *Eudiaptomus gracilis* ($\mu\text{g DW L}^{-1}$) and mean chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) for the three basins of Lough Carra from April 2001 to June 2003.

The zooplankton:phytoplankton biomass ratios calculated for each basin over the two-year sampling were generally high, particularly during late winter and spring, with a ratio as high as 43 recorded in the South basin in April 2002 (Fig. 4.5). The zooplankton:phytoplankton ratios tended to be lower during summer and autumn, but were, nevertheless, relatively high and fluctuated throughout late summer and autumn. In the North and Mid basins, for example, the zooplankton:phytoplankton

ratio was 1.5 during August, and in October a ratio of 2.7 was recorded in the Mid basin.

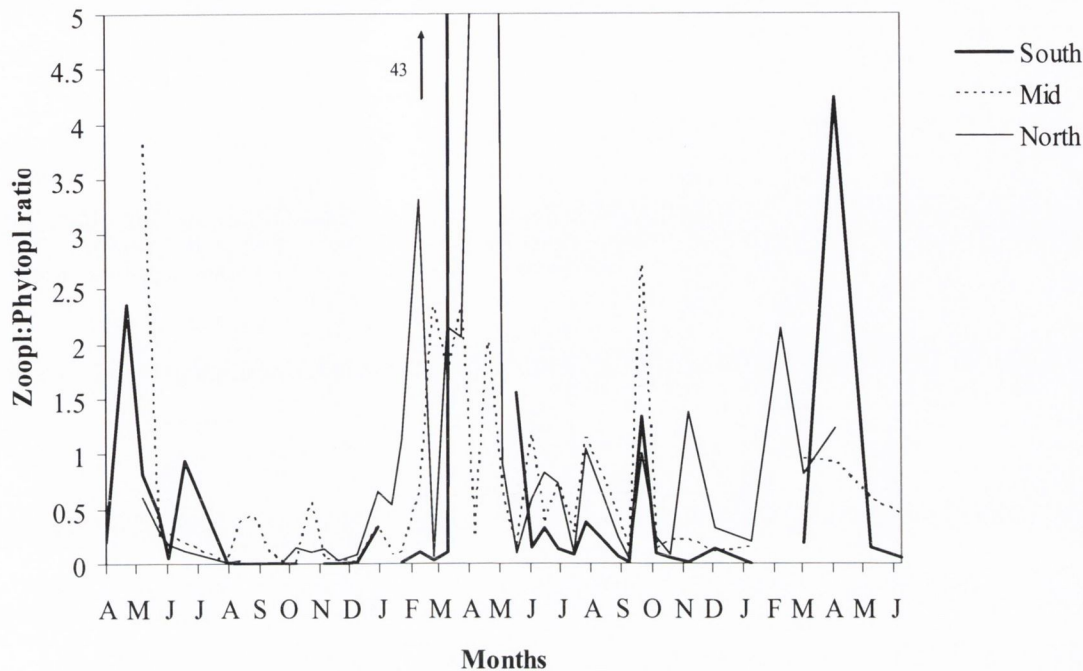


Fig. 4.5 The zooplankton:phytoplankton biomass ratio (DW:DW) assuming a conversion factor of 66 between chlorophyll *a* and dry weight (Jeppesen *et al.*, 2000) for the three basins of Lough Carra, April 2001 – June 2003.

Zooplankton biomass (Table 4.2) correlated positively with DIN and TN, but not with TP or SRP, and these relationships were particularly strong for *Daphnia*. The very low autumn concentrations of DIN and total nitrogen corresponded with low *Daphnia* biomass in the autumn of both 2001 and 2002. Maximum recorded DIN concentration occurred in March 2002 in all basins (South: 0.88 mg L⁻¹, Mid: 0.64 mg L⁻¹ and North: 0.53 mg L⁻¹) and concurred with large increases in *Daphnia* biomass. Stepwise multiple regression suggested DIN as the most significant variable (highest partial correlation) associated with *Daphnia* biomass ($r = 0.72$, Adj. $r^2 = 0.55$, $P \leq 0.001$). *Daphnia* biomass, however, correlated negatively with particulate nitrogen. There was no significant relationship between *Daphnia* biomass and any of TP, SRP or PP. Where there was a significant relationship between phosphorus and other zooplankton taxa, this relationship tended to be negative, apart from calanoid nauplii biomass, which correlated positively with TP (Table 4.2).

The ratio of DIN:TP correlated positively with zooplankton biomass (Table 4.3), and particularly with *Daphnia*. The calanoids were the only zooplankton group which did not show a significant relationship with DIN:TP. There was also a positive association between *Daphnia* and the predicted ratio of C:P (Light:TP), but no significant relationship with calanoid biomass.

Table 4.3. Spearman-rank correlation coefficients (and sample size) for; DIN:TP and predicted C:P ratios and various zooplankton biomass ($\mu\text{g DW L}^{-1}$) categories, for Lough Carra, April 2001 – June 2003. * $P \leq 0.05$, *** $P \leq 0.001$; DIN, dissolved inorganic nitrogen; TP, total phosphorus; C, carbon; P, phosphorus. Significant relationships in bold.

	Total Zooplankton	Rotifers	<i>Daphnia</i> spp.	Other Cladoceran Herbivores	<i>Eudiaptomus</i> <i>gracilis</i>	Calanoid nauplii	<i>Cyclops</i> spp.	Cyclopoid nauplii
DIN:TP	0.34 *** (119)	0.25 *** (119)	0.63 *** (119)	0.37 *** (119)	0.11 (119)	0.10 (119)	0.44 *** (119)	0.58 *** (123)
Predicted C:P (Light:TP)	0.11 (124)	0.29 *** (124)	0.21 * (124)	0.13 (124)	0.07 (124)	-0.12 (124)	0.06 (124)	-0.11 (127)

4.3.5 Zooplankton community size structure

The size structure of the mature crustacean community in each of the three basins tended towards smaller size between early and late summer of both 2001 and 2002, with decreases in the number of individuals in the larger size classes (excluding those size ranges that were composed only of the predator *Leptodora kindtii*, 3.0 – 7.0 mm) (Fig. 4.6).

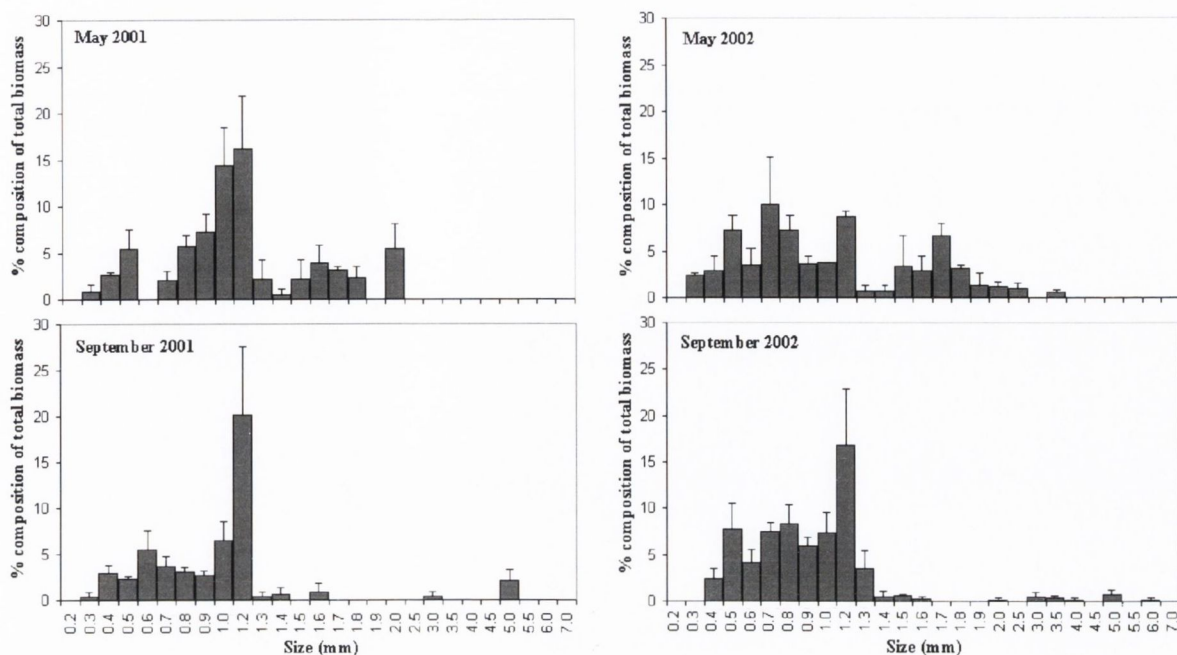


Fig. 4.6 Mean size distribution ($\pm$ SE, $n = 3$) of post-naupliar crustaceans for the three basins of Lough Carra for May and September 2001 and 2002.

4.3.6 Zooplankton fecundity

The fecundity of *Daphnia* spp. followed similar patterns in all three basins. The mean number of eggs per female was lowest between mid April and May in each of the three basins, with the greatest increase occurring between July and August (Fig. 4.7). A similar seasonal trend in *Daphnia* SEN was evident, which ranged from 0 – 1.7 eggs per female of standard size. There was a tendency towards greater calanoid egg production over the winter and spring months, declining through summer and autumn. A particularly evident reduction in clutch size occurred between June and September, increasing again in late October (Fig. 4.7).

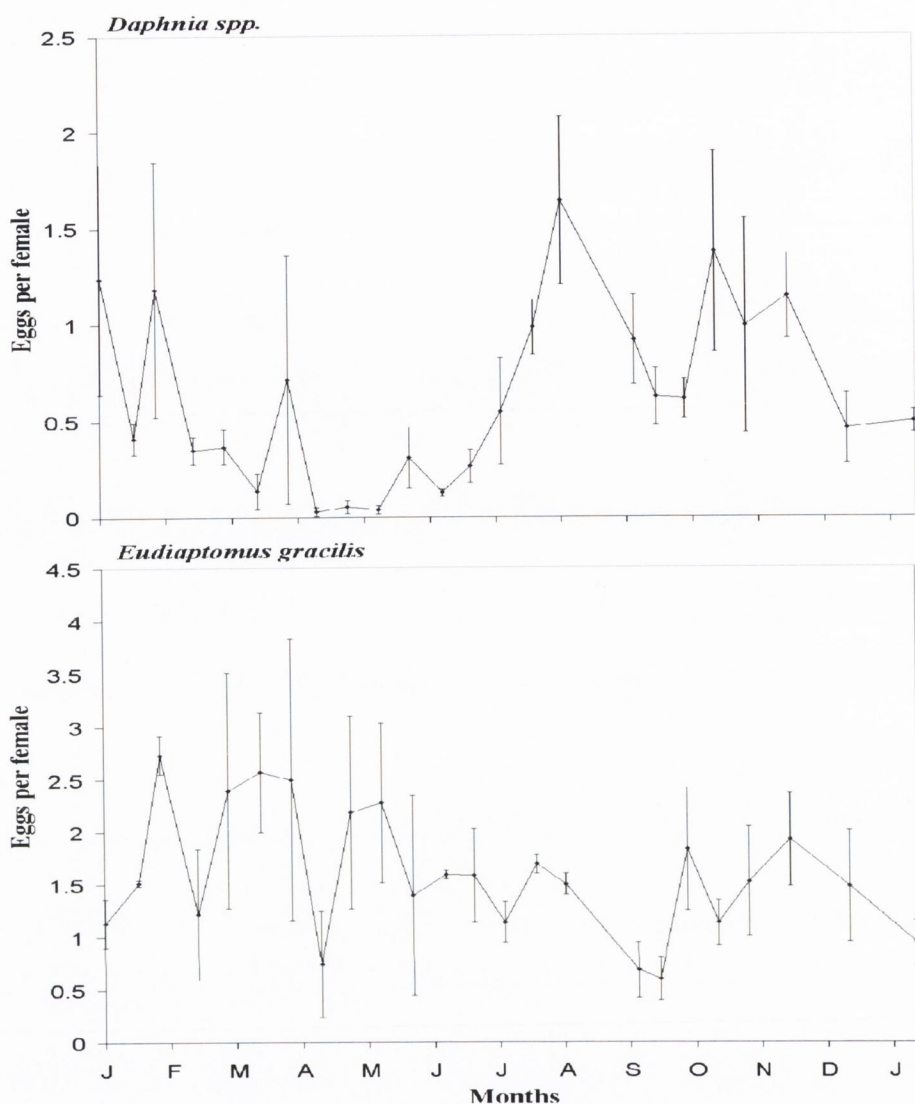


Fig. 4.7 Mean number of eggs per *Daphnia* spp. and *Eudiaptomus gracilis* female ($\pm$ SE, $n = 3$) for the three basins of Lough Carra, Jan 2002 – Jan 2003.

Both the number of eggs per female and the SEN of *Daphnia* correlated positively with both TP and chlorophyll *a*, but the number of eggs per female was negatively related to DIN (Table 4.4). There was a positive relationship between DIN and the number of eggs per calanoid female (Table 4.4). The ratio of DIN:TP was correlated negatively with both measures of *Daphnia* fecundity and positively with calanoid egg production. There was also a negative relationship between the predicted ratio of C:P and the number of eggs per *Daphnia* female, but no significant relationship with calanoid fecundity (Table 4.5; Fig. 4.8). The lowest number of eggs per *Daphnia* female was recorded between March and May 2002. This coincided with increasing *Daphnia* biomass and declining chlorophyll *a* concentration. Nevertheless, during

periods of very low *Daphnia* biomass with relatively high chlorophyll *a* concentration, particularly from mid June onwards, the negative relationship between the number of eggs per *Daphnia* female and the estimated seston C:P ratio (Spearman rank $r = -0.37$, $P \leq 0.05$, $n = 39$) and DIN:TP ratio (Spearman rank $r = -0.38$, $P \leq 0.05$, $n = 39$) persisted, whereas the correlation between *Daphnia* egg production and chlorophyll *a* was not significant (Pearson's $r = 0.23$, $P \geq 0.05$, $n = 38$). To compare the relative reproductive output between calanoid and *Daphnia*, the difference between the mean number of eggs per calanoid female and the mean number of eggs per *Daphnia* female for the three basins of Lough Carra was calculated. Increases in calanoid egg production relative to *Daphnia* egg production showed a positive association with both the mean approximated ratio of C:P (Spearman rank $r = 0.45$, $P \leq 0.05$, $n = 24$) and the mean DIN:TP ratio (Spearman rank $r = 0.66$, $P \leq 0.001$, $n = 24$) (Fig. 4.9).

Table 4.4 Pearson's product-moment correlation coefficients (and sample size) for in-lake physical and chemical variables and measures of *Daphnia spp.* and *Eudiaptomus gracilis* fecundity for Lough Carra, Jan 2002 – Jan 2003. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; SRP, soluble reactive phosphorus; TP, total phosphorus; PP, particulate phosphorus; TDP, total dissolved phosphorus; DIN, dissolved inorganic nitrogen; TN, total nitrogen; PN, particulate nitrogen. Significant relationships in bold.

	<i>Daphnia spp.</i> eggs:females	<i>Daphnia spp.</i> SEN	<i>Eudiaptomus gracilis</i> eggs:females
SRP	0.22 (65)	0.02 (51)	0.08 (69)
TP	0.35 ** (65)	0.29 * (51)	-0.05 (69)
TDP	0.23 * (62)	0.21 (48)	-0.10 (68)
PP	0.23 (64)	0.17 (50)	0.05 (68)
DIN	-0.36 * (65)	-0.25 (51)	0.28 * (69)
TN	-0.05 (65)	-0.03 (51)	0.17 (69)
PN	0.29 * (64)	0.24 (51)	-0.10 (69)
Chlorophyll <i>a</i>	0.41 *** (65)	0.35 * (51)	-0.12 (69)

Table 4.5 Spearman-rank correlation coefficients (and sample size) for DIN:TP and predicted C:P ratios and measures of *Daphnia* spp. and *Eudiaptomus gracilis* fecundity for Lough Carra, Jan 2002 – Jan 2003 * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; DIN, dissolved inorganic nitrogen; TP, total phosphorus; C, carbon; P, phosphorus. Significant relationships in bold.

	<i>Daphnia</i> spp. eggs: females	<i>Daphnia</i> spp. SEN	<i>Eudiaptomus gracilis</i> eggs: females
DIN:TP	-0.45 *** (70)	-0.42*** (55)	0.31 *** (70)
Predicted C:P (Light:TP)	-0.30 * (70)	-0.27 (55)	0.04 (70)

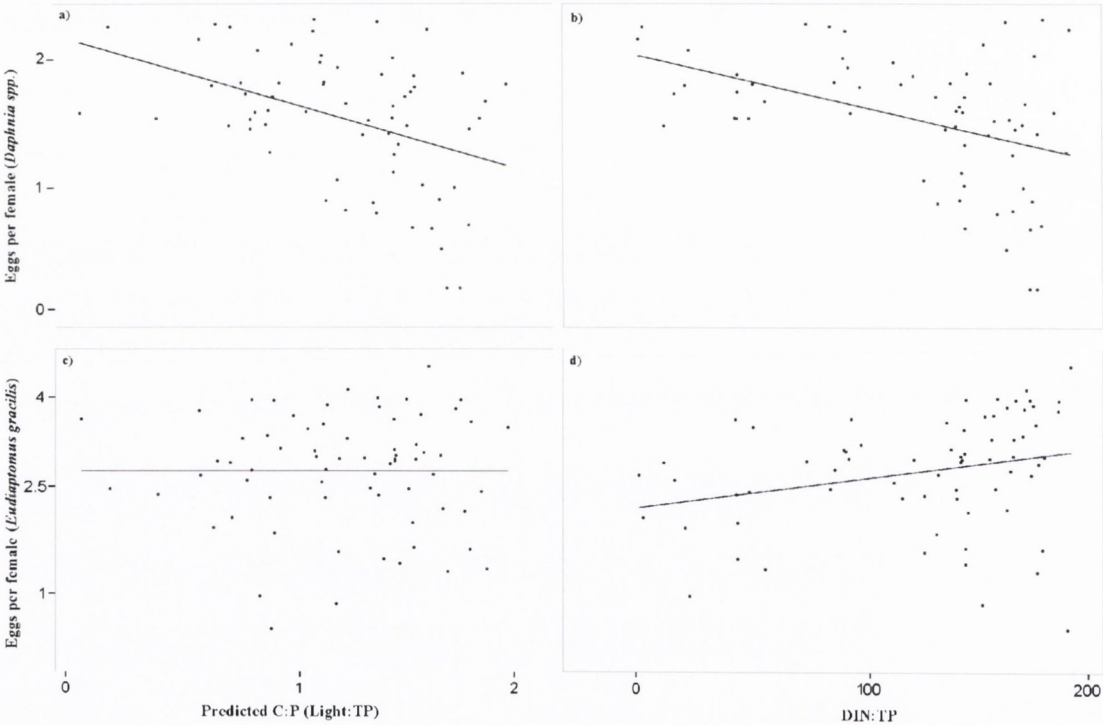


Fig. 4.8 (a) The relationship between the number of eggs per *Daphnia* female and the predicted ratio of C:P (Light:TP) ($r^2 = 0.17$, $P \leq 0.001$, $n = 65$), b) the relationship between the number of eggs per *Daphnia* female and the ratio of DIN:TP ($r^2 = 0.18$, $P \leq 0.001$, $n = 65$), c) the relationship between the number of eggs per *Eudiaptomus gracilis* female and the predicted ratio of C:P (Light:TP) ($r^2 = 0$, $P \geq 0.05$, $n = 69$) and d) the relationship between the number of eggs per *Eudiaptomus gracilis* female and the ratio of DIN:TP ($r^2 = 0.08$, $P \leq 0.05$, $n = 69$) in Lough Carra, Jan 2002 – Jan 2003. All variables were logarithmically transformed.

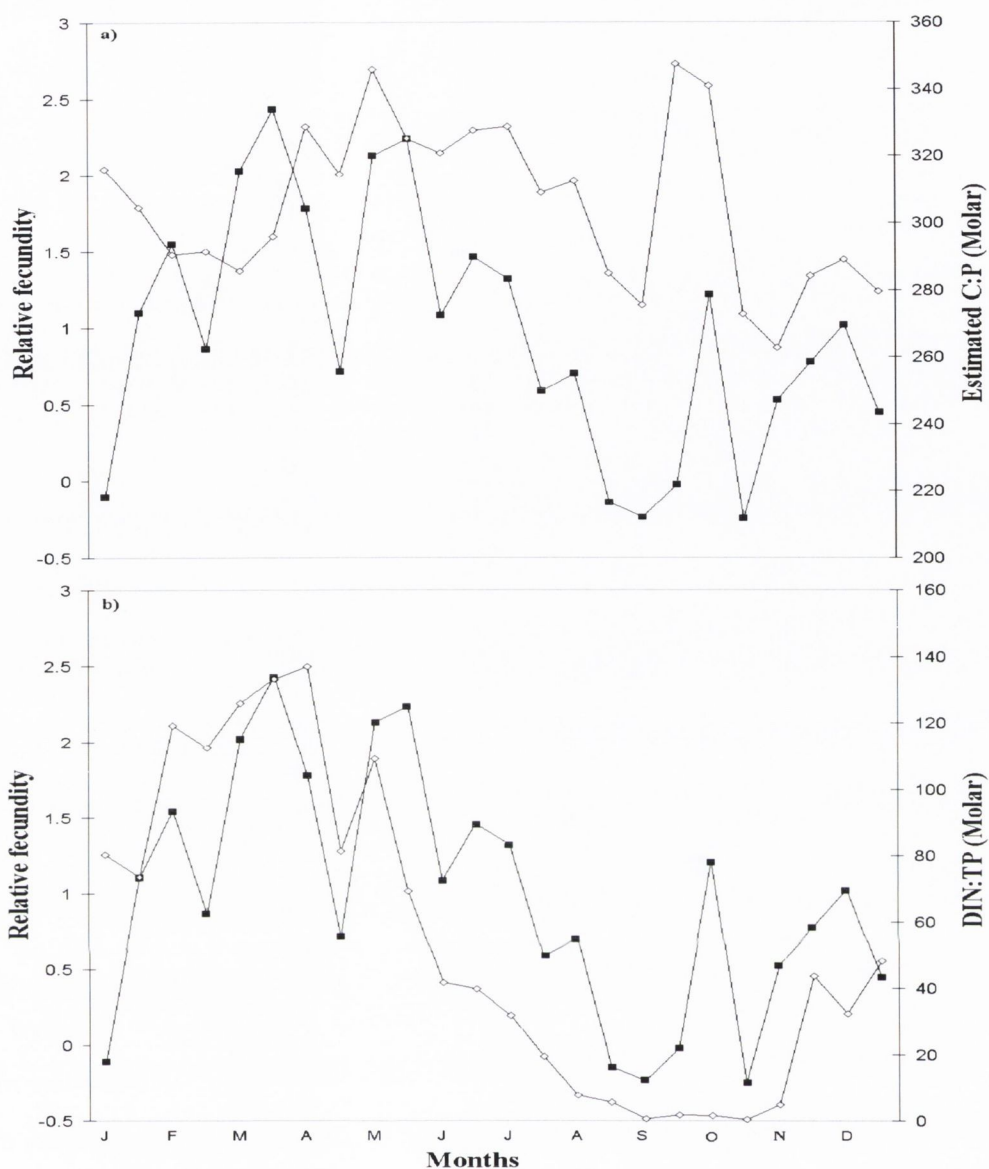


Fig. 4.9 (a) Relative fecundities of *Eudiaptomus gracilis* compared with *Daphnia* (the mean number of eggs per *Eudiaptomus gracilis* female minus the mean number of eggs per *Daphnia* female) and the estimated C:P ratio of the seston and (b) relative fecundities of *Eudiaptomus gracilis* compared with *Daphnia* and the ratio of DIN:TP of the seston in Lough Carra, Jan 2002 – Jan 2003.

4.4 Discussion

4.4.1 Zooplankton community structure

The work in Lough Carra suggests that there is no relationship between P availability and *Daphnia* biomass. This is contrary to other field studies that report a positive relationship between the abundance of *Daphnia* and seston phosphorus (Hessen, 1992; Hassett *et al.* 1997; DeMott & Gulati, 1999; Brett *et al.*, 2000). In our study, whenever a significant relationship between zooplankton biomass and phosphorus occurred, this was negative, even for *Daphnia*; and irrespective of high DIN:TP ratios recorded that indicated P-limitation throughout much of the year. Conde-Porcuna *et al.* (2002) also did not find a significant correlation between phosphorus and daphniid biomass in a P-limited reservoir and Sterner (1998) failed to relate mean *Daphnia* birth rate and seston C:P in a lake expected to be P-limited. It may be that a clear demonstration of P-limitation on *Daphnia* is only likely across large ranges of C:P ratio, such as in the study of Makino *et al.* (2002) who found effects of P-limitation on a *Daphnia* population when C:P ranged from 100 to 600.

The greatest increase in biomass of both *Daphnia* and calanoids occurred in the spring of 2002, which coincided with a dramatic increase in DIN concentrations. Conversely, extremely low *Daphnia* biomass during summer and autumn corresponded to almost undetectable levels of DIN. Although nitrogen is required for protein synthesis, it is unlikely that *Daphnia* would be affected more than *Eudiaptomus* by nitrogen limitation, given the latter's low C:N content. Consequently, it is difficult to account for the apparent relationship between nitrogen and *Daphnia* in Lough Carra. It is unlikely that this relationship is causal. The seasonal reduction in DIN during the summer growing period is probably the result of increased autotroph growth and utilisation. Seasonal fluctuations in *Daphnia* biomass, however, are more difficult to explain. A combination of size-selective fish predation and density dependent resource limitation is the most likely explanation for the decline of *Daphnia* in early spring. The zooplankton:phytoplankton biomass ratios were extremely high during spring (Fig. 4.5), particularly in comparison with the zooplankton:phytoplankton ratios recorded in the other high-alkalinity lakes in this study, such as Rea in Co. Galway and Talt in Co. Sligo (see section 3.3.8.2), and

suggest very high zooplankton grazing pressure on phytoplankton during this period. The invertebrate predators *Bythotrephes* and *Leptodora* are in the lake, but were not sufficiently numerous to have a major impact on *Daphnia* (Barbiero *et al.*, 2004; Wojtal *et al.*, 2004), although *Bythotrephes* abundance was highly patchy. There was also evidence of adequate phytoplankton for pelagic herbivores during summer and autumn. Phytoplankton chlorophyll *a* increased during this period, and was associated with relatively high *Daphnia* egg production, despite low *Daphnia* biomass, suggesting sufficient availability of food.

Low nitrogen availability, which can result in dominance by cyanophytes which may be inedible to *Daphnia* (Van Donk *et al.*, 1997; Ghadouani *et al.*, 2003), might also be of some importance in explaining the reduction in *Daphnia* biomass during the summer and autumn. In the North basin cyanophytes (comprising mainly *Anabaena* spp., *Synechococcus* spp. and *Mycrocystis* spp.) dominated briefly in July 2002, but nevertheless accounted for < 8 % of the phytoplankton community in the South basin, and diatoms and chlorophytes were prevalent throughout summer and autumn in both basins. Other food quality factors may be involved which were not measured here, such as deficiencies in essential fatty acids (Müller-Navarra *et al.*, 2000; Ferrão-Filho *et al.*, 2003), which may become particularly important at low algal C:P ratio when P is not limiting (Boersma, 2000), or digestion resistance such as chemical deterrents, or restrictions on ingestion owing to particle size or shape (Van Donk *et al.*, 1997). Large colonial chlorophyte cells which are imbedded in a gelatinous sheath might be consumed by zooplankton, but they are poorly digested, resulting in reduced zooplankton growth rates (Porter, 1976). DeMott & Tessier (2002) and DeMott *et al.* (2004) found evidence for only weak and sporadic *Daphnia* P-limitation in lakes, despite a negative correlation between *Daphnia* growth and seston C:P. Growth assays and assimilation experiments revealed that food limitation was, in fact, more strongly associated with an increase in the percentage of digestion-resistant algae.

4.4.2 Stoichiometric retention of nutrients in zooplankton biomass

If a nutrient is in short supply in the food relative to demand, the animal should discriminately accumulate that element into the body tissue to maximise growth and reproduction, while eliminating nutrients in excess (Urabe *et al.*, 1995). During

summer and autumn calanoids dominated the total zooplankton biomass in Lough Carra. While *Eudiaptomus* abundance did not show marked summer increases in response to the declines of *Daphnia*, however, it is plausible that nitrogen limitation for primary production was accentuated by persistence of the calanoids in the DIN limited environment, facilitated by the ability of calanoids to feed discriminately based on food nutrient status (Butler *et al.*, 1989). Owing to their high N content, calanoids could differentially accumulate N in their biomass and recycle P at a relatively high rate. Elser *et al.* (1988) found that, under conditions of *Daphnia* dominance, phytoplankton growth was P-limited while, in situations where calanoids dominated, the phytoplankton were N-limited. Brett *et al.* (1994) found that *Diaptomus* markedly increased SRP relative to DIN, resulting in a low DIN:SRP ratio. In contrast, *Daphnia* increased the DIN:SRP ratio. Similar patterns were evident in Lough Carra. The vast difference between zooplankton and seston N:P contents in July 2005 further demonstrates that, during the summer, a considerable quantity of N relative to P was retained in the calanoid dominated zooplankton. At the same time the high zooplankton C:P ratio relative to the seston suggests a disproportionate excretion of P relative to N. Andersen (1997) suggested that the differential recycling of nutrients by zooplankton grazers is most likely to influence phytoplankton nutrient limitation in lakes where the N:P ratio of external nutrient loading is $< 40:1$. Using TN and TP as indices of nutrient loading, Elser & Urabe (1999) suggested that $\sim 25\%$ of lakes had $TN:TP < 40$. The $TN:TP$ ratio in Lough Carra was < 40 during the summer months, consistent with calanoid mediated N-limitation to the plankton. Variable release ratios are produced when consumers retain the element in least supply and discard elements that are in excess (Elser & Urabe, 1999). When *Daphnia* act as a significant sink for P, a positive correlation should be expected between *Daphnia* abundance and the seston C:P ratio (DeMott & Gulati, 1999). In Lough Carra, during spring, *Daphnia* may have acted as a sink of P, but a source of N, accounting, therefore, for the substantial increase in the ratio of DIN:TP during this period. The extremely high numbers of *Daphnia* during the spring of 2002 compared with the same period in 2001 and 2002 and the corresponding high concentrations of DIN in spring 2002 compared with 2001 and 2002, provides further support that *Daphnia* may have been accentuating the already high concentrations of DIN at this time of the year.

4.4.3 Zooplankton fecundity

According to stoichiometric theory, the relative requirements for C, N and P differ among zooplankton taxa because of interspecific variation in the elemental content of their cells. Relative to copepods, the cellular ratio of N:P in *Daphnia* is lower, and as a result they are considered to have comparatively high requirements for P relative to N in their diets. Our results suggest that, in accordance with stoichiometric predictions, *Daphnia* and calanoid reproduction had opposite relationships to the availability of dietary phosphorus. In Lough Carra, there was a greater number of calanoid eggs per female relative to the number of *Daphnia* eggs per female during periods of high DIN:TP and estimated C:P (Light:TP) ratios (Fig. 4.8). This suggests that *Daphnia* egg production in Lough Carra was sensitive to P-limitation, whereas calanoid egg production increased with the availability of N. Although correlations must be interpreted with caution, especially under complex field conditions, the opposite fecundity responses of the two taxa is further supported by the negative associations between the number of eggs per *Daphnia* female and the ratios of DIN:TP and approximated C:P; and the lack of a significant relationship between the estimated ratio of C:P and calanoid fecundity, coupled with a weak but positive relationship with the DIN:TP ratio (Fig.4.7). Both *in-situ* and *ex-situ* experimental tests, although not within the framework of this particular study, would, however, be necessary in order to provide categorical evidence for the potential relationship between P-availability and *Daphnia* fecundity, and N-availability and calanoid fecundity in Carra.

Reduction in the number of females carrying eggs can be symptomatic of low quantity, as well as quality, of food supply (Sterner & Schulz, 1998). Although the greatest reduction in *Daphnia* egg production in Lough Carra occurred during a period of low phytoplankton biomass and high *Daphnia* biomass between April and June 2002, which is consistent with other work (e.g. Tessier & Consolatti, 1991; Lampert, 1993; Boersma, 1995), the importance of phosphorus limitation is suggested by the negative relationships between *Daphnia* fecundity and the ratios of both DIN:TP and predicted C:P that were maintained even after spring and early summer sampling dates were eliminated from correlation analysis. Between July 2002 and January 2003, *Daphnia* biomass was very low, chlorophyll *a* concentration high and

estimations of the ratio of C:P often above a frequently suggested C:P-limitation threshold of between 200 and 300 (Urabe & Watanabe, 1992; Brett *et al.* 2000; Anderson & Hessen, 2005). These periods of high C:P ratio and chlorophyll *a* concentration indicate low quality food, although quantitatively sufficient, and generally corresponded to periods of low *Daphnia* fecundity. In contrast, increased *Daphnia* egg production was associated with decreased modelled C:P ratio. This provides evidence that *Daphnia* fecundity was positively associated with the availability of dietary P and supports previous laboratory studies which have observed reduced clutch size in *Daphnia* fed P-deficient food (Sterner *et al.*, 1993; Lürling & Van Donk, 1997; Schulz & Sterner, 1999; DeMott *et al.*, 2001; Ferrão-Filho *et al.*, 2003).

Higher P content, relative to that of the adult, has been recorded in *Daphnia* neonates (DeMott *et al.*, 1998; DeMott, 2003; Færøvig & Hessen, 2003). Phosphorus content decreases rapidly at specific life stages and its reduction is particularly apparent with the development of ovaries (DeMott, 2003). Juveniles assign all available P to somatic growth but, once ovary development begins, an increasing proportion of P is invested in egg production (Færøvig & Hessen, 2003). A constant allocation of P to eggs, regardless of the availability of dietary P, was also observed by Becker & Boersma (2005). Consequently, egg production in *Daphnia* could certainly be sensitive to low P.

The reduced calanoid egg production associated with lower N availability concurs with observations by Kiørboe (1989) of copepod egg production declining with algal C:N ratio. Carrillo *et al.* (1996) found a high portion of N in copepod nauplii, declining rapidly with age and at a greater rate than P. This suggests a high allocation of nitrogen by gravid female calanoids to eggs and a reduction in clutch size under low nitrogen availability. This also provides an explanation for the observations that calanoids in food-limited environments invest in larger, but fewer, eggs that provide reserves for naupliar development (Hart *et al.*, 1995).

4.4.4 Conclusion

This study provides a field test of the effect of the availability of dietary N and P on patterns of dominance between high P *Daphnia* and low P calanoids. The ratio of DIN:TP was high when *Daphnia* dominated zooplankton biomass and low when calanoids dominated. The direct effect of elemental composition of algae on zooplankton communities can be confounded by interactions between herbivore and resource, through grazing effects and nutrient regeneration (Urabe, 1995; Urabe *et al.*, 2002). Suppression of P through stoichiometric retention in *Daphnia* during spring may account for the positive associations between the ratios of DIN:TP and estimated C:P and *Daphnia* biomass. Conversely, retention of N in calanoids during the summer may have accentuated N-limitation of the phytoplankton. There was also some suggestion that phosphorus availability was positively associated with *Daphnia* egg production, but was not related to calanoid fecundity, this would be consistent with stoichiometric expectations, but requires further experimental studies to verify the correlative observations of this study.

5.1 Introduction

One method of predicting which nutrient will limit phytoplankton growth involves comparing the relative quantities of available nutrients with the average requirements of phytoplankton cells and then using this to identify the nutrient in shortest supply. Pelagic autotrophs are multispecies assemblages with overlapping sizes, which are varyingly mixed with detritus, bacteria, Protozoa and small metazoan zooplankton. Consequently, the elemental composition at the base of pelagic food webs is generally measured on bulk samples of particles or seston. The composition of marine seston is relatively uniform and the C:N:P ratio is accepted to be close to 106:16:1, which is referred to as the Redfield ratio (Redfield, 1958). Seston composition ratios close to the Redfield ratio suggest a balanced flow of nutrients between the organisms and their environment, and are consistent with nutrient-saturated growth rate (Sterner & Elser, 2002). Seston stoichiometry that diverges from the Redfield ratio is considered to be evidence for nutrient limited growth. The generally nutrient-rich organic matter in oceanic systems contrasts with the generally nutrient-poor seston of lakes. Lake seston elemental ratios often deviate from the Redfield ratio and are highly variable (Hessen, 1992; Sterner & Elser, 2002). Values of seston C:P ranging from 55 – 1630 and N:P ratios ranging from 6.5 – 125 have been recorded in many lakes (Elser *et al.*, 2000b).

Stoichiometry is essentially concerned with proportions and consequently nutrient ratios are characteristically used to assess nutrient limitation in aquatic systems (Sterner & Elser, 2002). Indices of external nutrient supply, such as the ratio of TN:TP, are used extensively, and have been shown to be reliable predictors of nutrient limitation in chemostat studies (Rhee, 1978). In natural assemblages, however, assessment of nutrient limitation using these ratios is more difficult. This is because N and P are present in lakes in a variety of forms, some of which are not readily available to phytoplankton. The ratio of TN:TP combines seston composition and nutrient supply and is widely used for the assessment of nutrient limitation in

natural assemblages (Elser *et al.*, 1990). Other indices such as the ratio of DIN:TP and DIN:SRP have been used as indicators of N or P limitation (Morris & Lewis, 1988; Morales-Baquero *et al.*, 1999). The ratio of DIN:TP was considered to be a particularly good indicator of nutrient limitation by Morris & Lewis (1988), because both DIN and TP were regarded as the most readily available forms of nitrogen and phosphorus, respectively.

As zooplankton demonstrate an interspecific variation in their C:P and C:N ratios (Andersen & Hessen 1991), their stoichiometric requirements for these elements will consequently differ. Resource stoichiometry may, therefore, have an important role to play in determining zooplankton community structure. Taxa such as *Daphnia*, for example, have been found to experience growth penalties owing to P-limitation when their seston food source had a high C:P ratio (MacKay & Elser, 1998; Elser *et al.*, 2001; Makino *et al.*, 2002). A pattern of species replacements in zooplankton communities would, therefore, be predicted as high-P taxa are replaced by low-P taxa with declining food P content. In such situations a positive correlation should be evident between bulk zooplankton P content and bulk seston P content (Gulati *et al.*, 1991; Sterner, *et al.*, 2000; Sterner & Elser, 2002). The role of food elemental composition in structuring zooplankton communities can also be assessed by relating seston stoichiometry directly to the abundance of individual taxa which comprise the zooplankton assemblage. Field studies, for example, have found that the abundance of *Daphnia* is positively correlated with seston particulate P concentration (Hessen, 1992) and negatively correlated with the seston C:P ratio (Hassett *et al.*, 1997; DeMott & Gulati, 1999).

Zooplankton have long been assumed to maintain strict elemental homeostasis. This supposition is largely based on early work which found distinctive differences in elemental composition among zooplankton taxa, but no detectable intraspecific variation in elemental content (Andersen & Hessen, 1991; Hessen & Lyche, 1991). This was despite relatively strong seasonal and between-lake variation in the abundance and elemental content of their food (Sterner & Hessen, 1994). Recently, however, variation in the P content of individual zooplankton species have been examined, and some of these studies have shown ontogenetic changes in P content, which are particularly discernable in copepods (Carrillo *et al.*, 2001). In addition,

declines in *Daphnia* P content with age can be associated with declines in maximal growth and RNA content (Main *et al.*, 1997). Others have recorded declines in *Daphnia* P content when feeding on P-deficient diets in the laboratory (DeMott *et al.*, 1998; Plath & Boersma, 2001; DeMott, 2003), and field studies provide some evidence that natural populations of *Daphnia* experience P deficits in their tissues (DeMott *et al.* 2001; DeMott *et al.*, 2004). Nevertheless, this intraspecific variability in nutrient content was found to be much less than in algae, and the foundation of stoichiometric models are, therefore, still supported. DeMott *et al.* (2004) suggested, that previous studies (reviewed by Sterner & Hessen, 1994) failed to find evidence of variation in *Daphnia* P content because of the low seston C:P ratios in their study lakes, where P-limited *Daphnia* growth would not be expected.

This chapter aims to expand on the work carried out in Lough Carra between April 2001 and 2002 (Chapter 4). Two additional lakes, with similar water chemistry and zooplankton community structure to that found in Carra (i.e. high-alkalinity lakes with a zooplankton assemblage which fluctuates between dominance by either *Daphnia* or copepods) were examined, in conjunction with three lakes with low alkalinity concentrations and variable zooplankton community structure. Two approaches were used to investigate nutrient limitation and recycling in these six study lakes. First, zooplankton and water were sampled between April 2003 and April 2004, with two objectives: (1) To examine whether there was any evidence for a relationship between species with contrasting stoichiometry and the availability of either nitrogen or phosphorus. Taxa with a low elemental ratio of N:P were expected to be more sensitive to phosphorus availability and those with a high specific N:P ratio to be more sensitive to nitrogen; and (2) To establish whether a similar pattern of consumer driven nutrient recycling to that observed in Carra was evident in the other high-alkalinity lakes, and to investigate whether these observations differed from those patterns evident in the low-alkalinity lakes.

Second, seston and zooplankton elemental contents were measured on three occasions between April and September 2005. The objectives of this part of the study were fourfold: (1) To compare bulk seston and zooplankton stoichiometry in each lake to look for evidence of nutrient limitation and consumer driven nutrient recycling; (2) To relate seston elemental ratio to the zooplankton community composition in order

to investigate if there is a reduction in the abundance of P-rich taxa at higher seston C:P ratios; (3) To test the accuracy of estimations of phytoplankton nutrient deficiencies (e.g. DIN:TP ratio), by relating them to the elemental content of the seston; and (4) To test for intraspecific variation in the elemental content of dominant taxa among lakes and to relate such variation to seston nutrient content.

5.2 Methodology

Water samples and zooplankton were collected and analysed between April 2003 and April 2004 according to the methodology outlined in Chapter 2 (section 2.2). Seston and zooplankton samples were collected in May and September 2005 from each lake and in July 2005 from Carra. Samples collected in April 2005 from Carra, Talt and Easky, were intended as a trial run to test methodology, but are, nevertheless, included in the analyses and discussion. The C, N and P content of the seston and zooplankton was analysed according to the methodology described in Chapter 4 (section 4.2.1). In May and September, a single zooplankton vertical haul was taken in each lake, from which zooplankton community structure and abundances were estimated. Water samples were also taken on these dates and analysed for phosphorus and nitrogen. The following section provides an explanation of additional methodology to those discussed in preceding chapters.

5.2.1 Analyses of the C:N:P content of individual zooplankton taxa

During April and September 2005 animals were collected with vertical hauls, using a zooplankton net with a 53 μm mesh size, and placed in 25 L containers with surface water. The most abundant taxa at the time of sampling were analysed for nutrient content (Table 5.1). Live animals were sorted under a dissecting microscope, and placed in groups on pre-weighed tinfoil cups. Each group contained from 6 to 12 individuals for P analyses and between 80 and 100 individuals for C and N analyses. Where possible, only non-egg bearing female cladocerans were used, and eggs were removed from copepods. Samples were dried at 60 °C and weighed to the nearest μg on a micro balance (Sartorius® SC2 Micro Balance). For P analyses the zooplankton were transferred to 25 ml pyrex® bottles, combusted at 550 °C for 2 h and digested with potassium peroxide sulphate ($\text{K}_2\text{S}_2\text{O}_8$) under pressure. P was determined spectrophotometrically using the ascorbate-reduced molybdenum-blue method (Eisenreich *et al.*, 1975). Phosphorus analyses was carried out in triplicate and controls lacking zooplankton were carried through the entire analyses procedure. Carbon and nitrogen content was determined using a Thermo Delta^{plus}® CF-IRMS (Isotopic ratio mass spectrometer).

Table 5.1 Taxa analysed for C, N and P content, May and September 2005.

	Carra	Talt	Rea	Easky	Feeagh	Maumwee
May 2005	<i>Daphnia</i>	<i>Daphnia</i>	<i>Daphnia</i>	<i>Ceriodaphnia</i>	<i>Daphnia</i>	<i>Bosmina</i>
	Calanoid	Calanoid	Calanoid	Calanoid	Calanoid	<i>Holopedium</i>
	<i>Bosmina</i>	Cyclopoid	<i>Bosmina</i>	<i>Holopedium</i>		Cyclopoid
September 2005	<i>Daphnia</i>	<i>Daphnia</i>	<i>Daphnia</i>	Calanoid	<i>Daphnia</i>	<i>Holopedium</i>
	Calanoid	Calanoid	Calanoid	<i>Holopedium</i>	Calanoid	Cyclopoid
	Cyclopoid	Cyclopoid		Cyclopoid	Cyclopoid	<i>Diaphanosoma</i>

5.2.2 Statistical analyses

Differences in elemental composition for zooplankton taxa and differences among lakes in the elemental content of both *Daphnia* and calanoids were examined using a one-way ANOVA with the elemental composition (% C, % N and % P) as the dependent variable and either taxa or lake as the independent variable. A one-way ANOVA was also used to examine differences in fecundity parameters among lakes, with the number of eggs per female as the dependent variable and lake as the independent variable. ANOVAs were carried out using Data Desk® Version 6. LSD *Post-hoc* tests were applied for individual pairwise comparisons. All % N, % P, % C and fecundity data were log transformed before statistical analysis to stabilise variances. Pearson's product-moment and Spearman's rank correlations were used to test the linear association between two variables and were carried out using SPSS® Version 12. Pearson's product moment correlation analysis was carried out on parametric data. Highly skewed data were normalised using logarithmic transformations. Spearman's rank correlation analysis was preformed when at least one non-parametric variable was involved.

5.3 Results

5.3.1 Nutrient dynamics

Similar fluctuations in TP concentration were observed in all low-alkalinity lakes, although the lowest TP values were, consistently, recorded in Maumwee (Table 5.2). The greatest disparity in TP concentration among low-alkalinity lakes occurred in January, when a very large peak of $18.9 \mu\text{g L}^{-1}$ was recorded in Easky (Fig. 5.1). Total phosphorus concentrations in the high-alkalinity lakes were generally higher than those recorded in the low-alkalinity lakes. There was little seasonal variation within lakes and very little difference among the three high-alkalinity lakes, with Talt showing the greatest divergence, particularly in summer and autumn. In Lough Carra, there was no winter peaks in TP between April 2003 and April 2004, which contrasted with the large winter maxima of approximately $35 \mu\text{g L}^{-1}$ which were evident in Lough Carra during the previous two years (see section 4.3.1).

Table 5.2 Mean ($\pm$ SE), range and sample size (n) of measures of nitrogen and phosphorus for the six lakes (April 03 – April 04). SRP, soluble reactive phosphorus; TP, total phosphorus; PP, particulate phosphorus; PP, particulate phosphorus; DIN, dissolved inorganic nitrogen; TN, total nitrogen, * = below detection limit.

	SRP ($\mu\text{g L}^{-1}$)	TP ($\mu\text{g L}^{-1}$)	PP ($\mu\text{g L}^{-1}$)	DIN (mg L^{-1})	TN (mg L^{-1})
Carra					
Mean $\pm$ SE	2.2 ± 0.2	10.4 ± 0.6	6.1 ± 0.6	0.17 ± 0.03	0.88 ± 0.04
Range	0.6 – 5.4	2.8 – 18.2	0.1 – 11.6	0 – 0.68	0.47 – 1.48
N	(35)	(35)	(35)	(35)	(12)
Talt					
Mean $\pm$ SE	2.2 ± 0.3	9.6 ± 0.9	5.4 ± 0.9	0.03 ± 0.01	0.33 ± 0.06
Range	0.9 – 3.7	4.5 – 16.7	1.5 – 12.6	0.001 – 0.05	0.12 – 0.82
N	(12)	(12)	(12)	(12)	(12)
Rea					
Mean $\pm$ SE	2.6 ± 0.3	12.0 ± 0.8	6.1 ± 0.9	0.03 ± 0.01	0.62 ± 0.05
Range	0.9 – 5.5	7.8 – 17.4	1.3 – 10.0	* – 0.11	0.41 – 1.00
N	(12)	(12)	(12)	(12)	(12)
Easky					
Mean $\pm$ SE	1.5 ± 0.2	9.6 ± 1.0	6.3 ± 1.0	0.04 ± 0.01	0.42 ± 0.06
Range	0.5 – 3.9	5.1 – 18.9	2.0 – 15.4	0.01 – 0.09	0.16 – 0.95
N	(12)	(12)	(12)	(12)	(12)
Feeagh					
Mean $\pm$ SE	2.3 ± 0.3	9.4 ± 0.8	3.8 ± 0.8	0.11 ± 0.01	0.56 ± 0.11
Range	1.2 – 4.1	6.4 – 16.7	0.4 – 10.1	0.03 – 0.14	0.32 – 1.74
N	(12)	(12)	(12)	(12)	(12)
Maumwee					
Mean $\pm$ SE	0.9 ± 0.2	4.8 ± 0.6	2.3 ± 0.5	0.01 ± 0.004	0.47 ± 0.11
Range	* – 2.8	2.4 – 8.9	0.5 – 6.8	* – 0.05	0.12 – 1.18
N	(12)	(12)	(12)	(12)	(12)

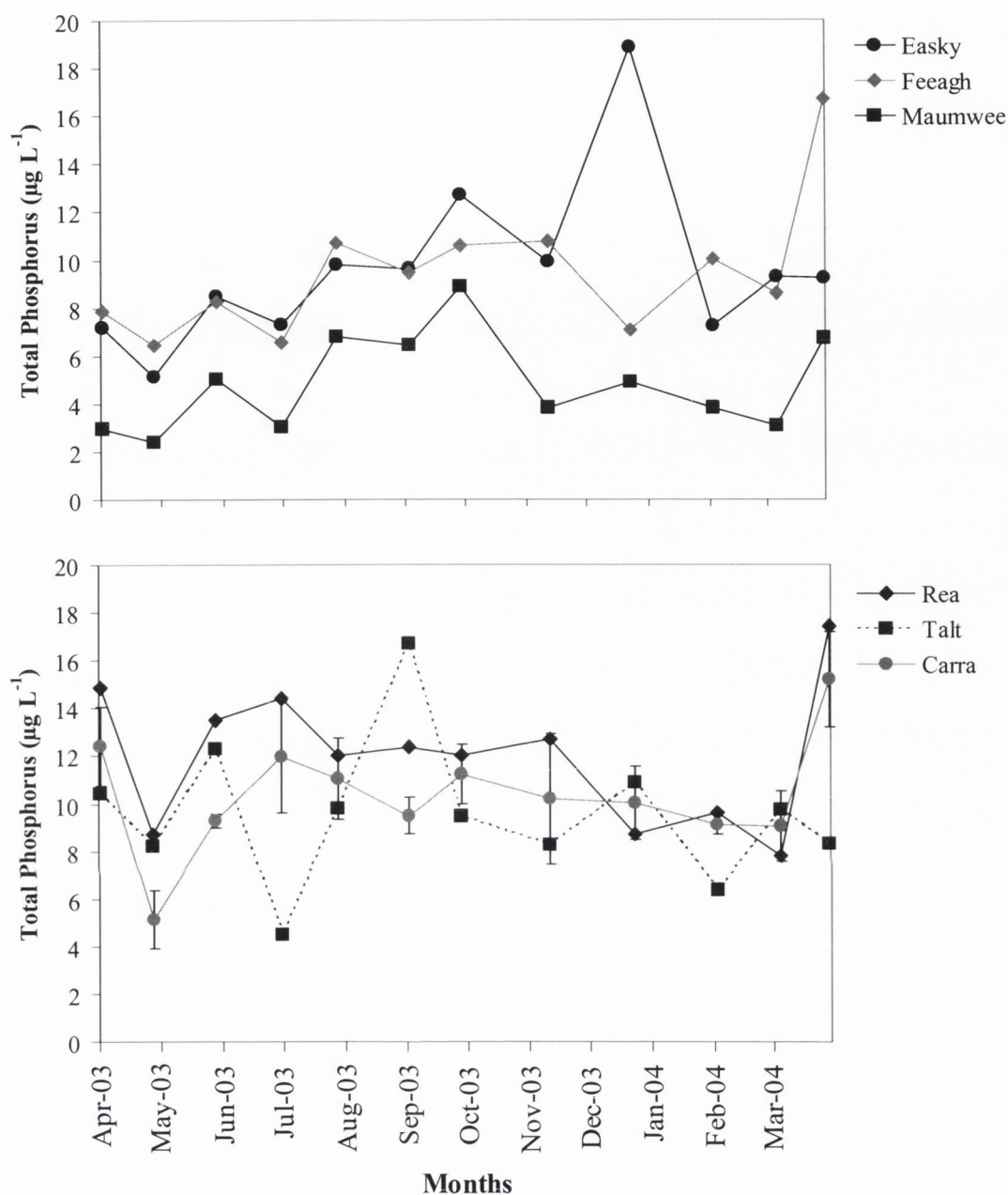


Fig. 5.1 Total phosphorus (TP) concentrations ($\mu\text{g L}^{-1}$) for all lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n=3$) of the three basins of Lough Carra are shown.

Seasonal fluctuations in SRP concentrations followed remarkably similar patterns in all six lakes, with Maumwee showing the lowest values at all times of the year (Fig. 5.2). There was a tendency for the low-alkalinity lakes to have lower SRP concentrations (Table 5.2).

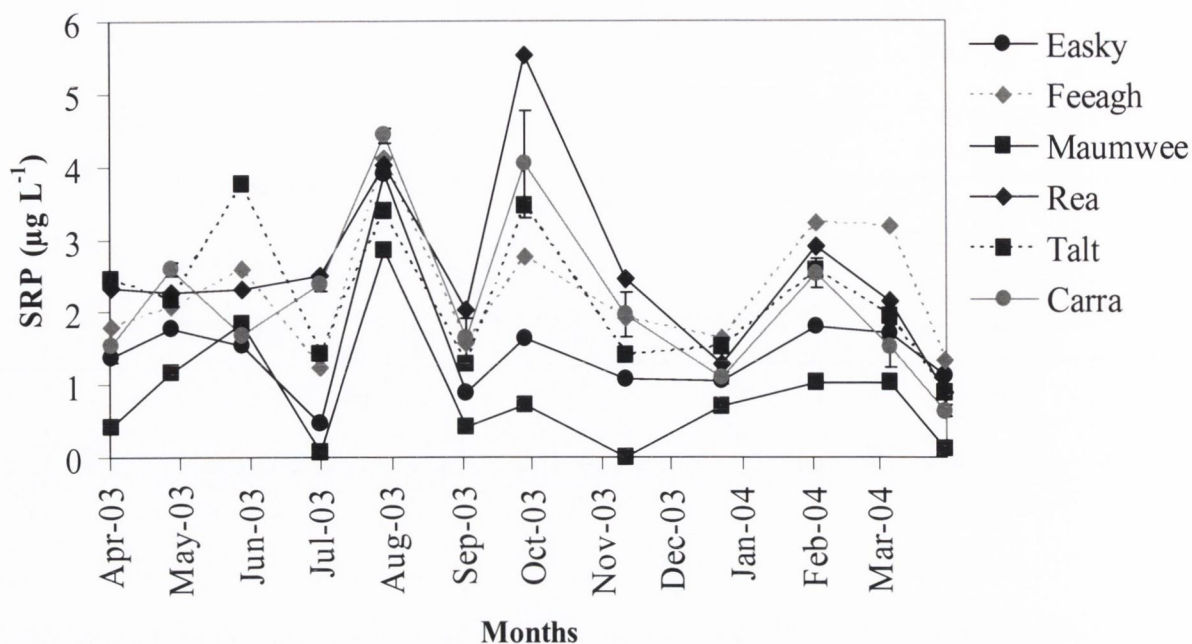


Fig. 5.2 Soluble reactive phosphorus (SRP) concentrations ($\mu\text{g L}^{-1}$) for all lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n=3$) of the three basins of Lough Carra are shown.

Reasonably similar fluctuations in TN concentration occurred in the low-alkalinity lakes. There was a small peak in concentration in all lakes between August and September and another larger peak during spring in both Maumwee and Feeagh, although no spring peak was evident in Easky (Fig. 5.3). There was no consistent seasonal pattern of TN concentration in the high-alkalinity lakes. For most of the year, Carra had the highest TN concentration and had the greatest mean TN of all lakes (Table 5.2). There were TN maxima in both Talt and Rea between August and September, which was not as evident in Lough Carra (Fig. 5.3). There were also very similar patterns and concentrations of TN in Easky and Talt throughout the year, only diverging during winter.

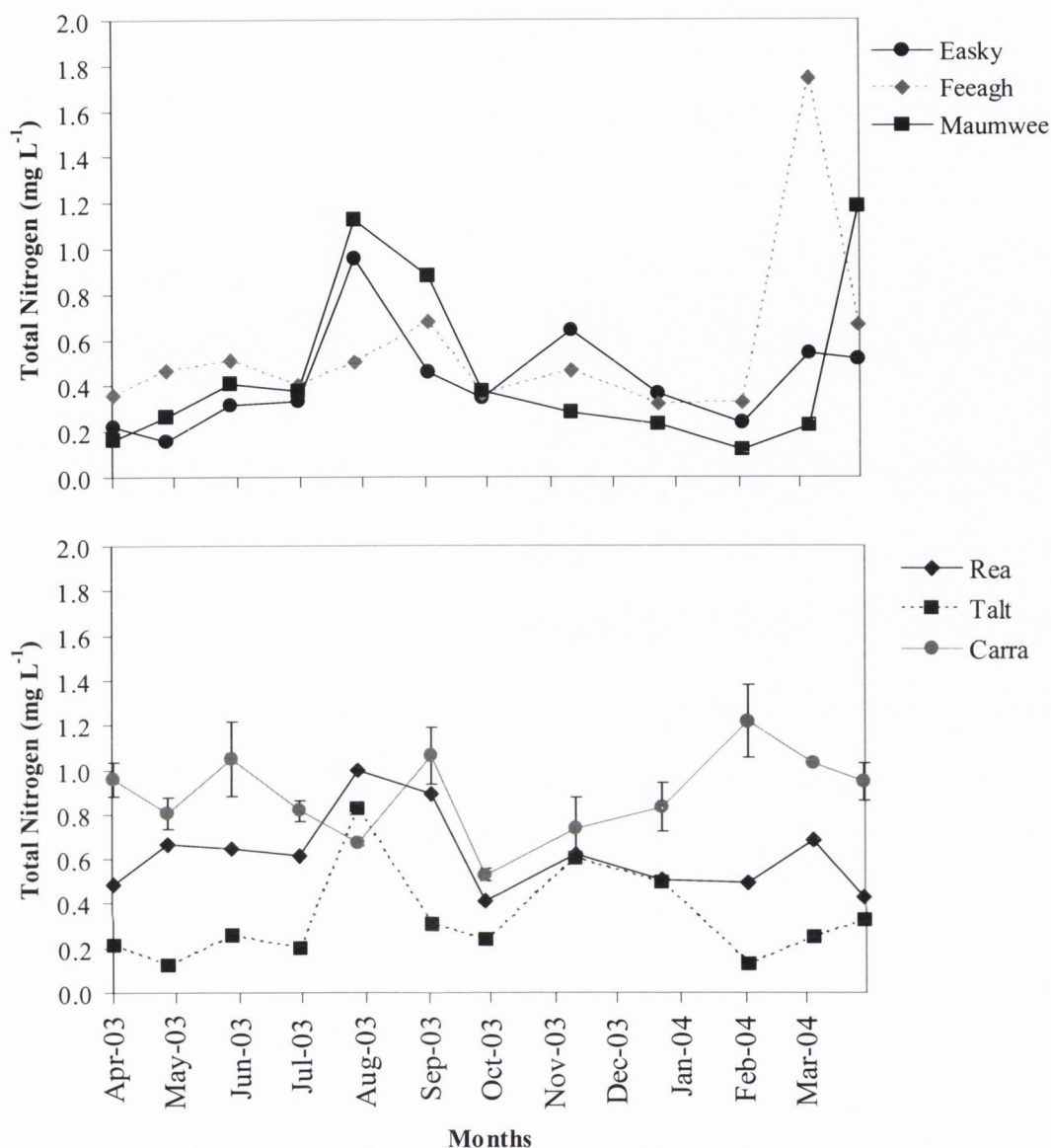


Fig. 5.3 Total nitrogen (TN) concentrations (mg L^{-1}) for all lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n=3$) of the three basins of Lough Carra are shown.

Variability in DIN concentrations in Carra between April 2003 and April 2004 were consistent with the strongly seasonal patterns observed in this lake during the previous two years (see section 4.3.1) This pattern of winter and spring maxima, followed by extremely low, and often undetectable, levels of DIN during the summer and autumn was also observed in the other high-alkalinity lakes, but was not evident in the low-alkalinity lakes (Fig. 5.4). Nevertheless, the concentrations of DIN in Carra reached much higher concentrations during winter and spring than was observed in either of the other two high-alkalinity lakes. Analogous to preceding

years, the highest values were recorded in the South basin, with a maximum of 0.68 mg L⁻¹ recorded in February 2004 (Table 5.2). Summer and autumn values in Carra ranged from 0 – 0.24 mg L⁻¹, which is below 0.3 mg L⁻¹ and, therefore, within ranges thought to indicate N-limitation (Hochstädter, 2000). DIN concentrations were, however, outside this range during winter and spring in Carra. In contrast, DIN values in all of the other lakes were well within this threshold at all times of the year.

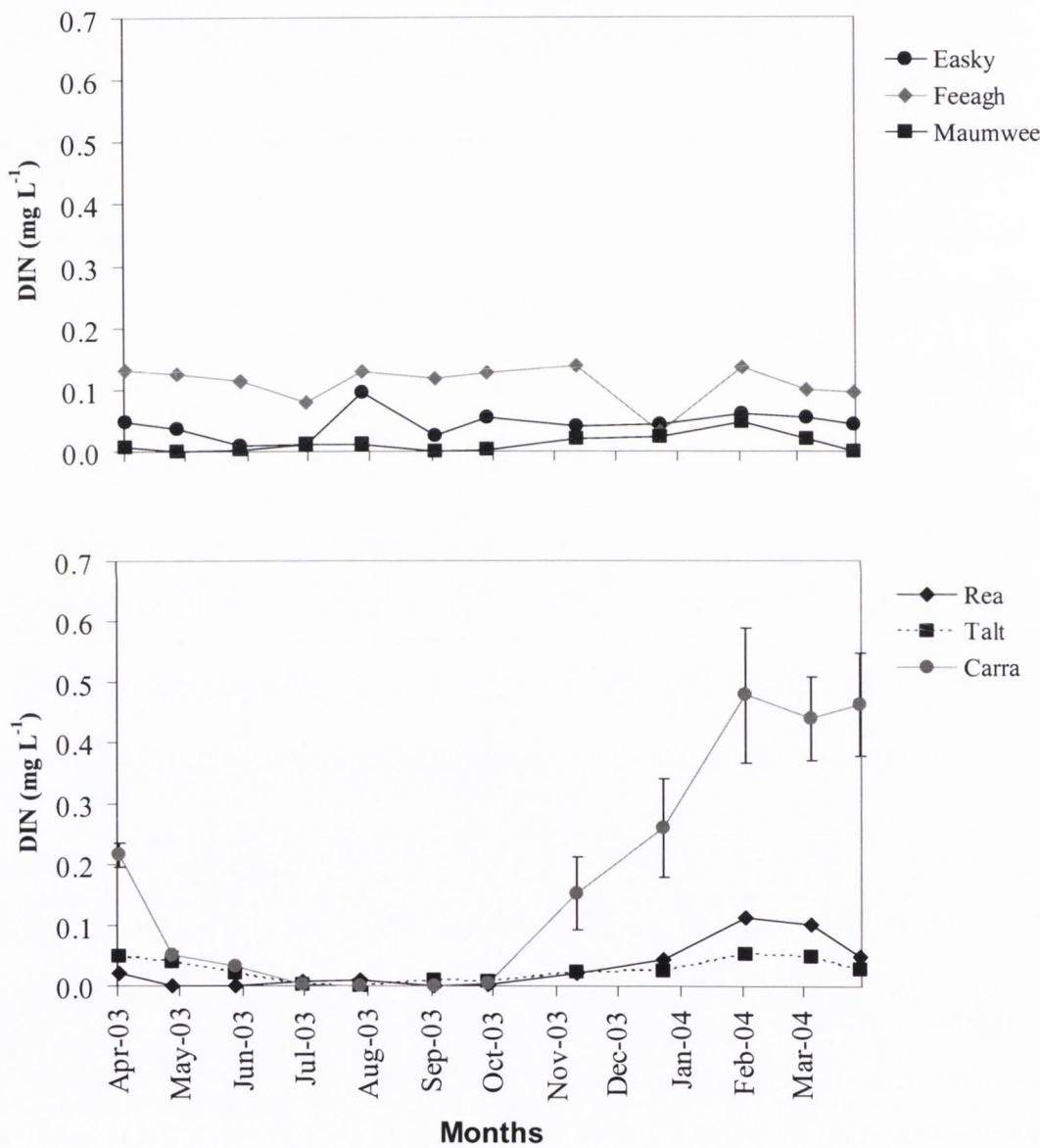


Fig. 5.4 Dissolved inorganic nitrogen (DIN) concentrations (mg L⁻¹) for all lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n=3$) of the three basins of Lough Carra are shown.

The highest DOC values were generally recorded in Talt (Table 5.3). The highest mean SS concentration was recorded in Rea (Table 5.3), but this was an artefact of

the two particularly high values recorded in June and November. Peaks in SS in June were also recorded in Talt, Feeagh and Maumwee, but were much smaller than those observed in Rea. Suspended solid values fluctuated throughout the year in Carra, with no large peaks evident at any stage. There was no June peak in SS concentration in Easky, but a very large maximum of 6.6 mg L⁻¹ was recorded in January, which corresponded to a peak in TP, and was conspicuous by a large quantity of visible detritus in the water column at the time of sampling. This large amount of detrital material clogged the zooplankton net and made their collection extremely difficult. There was also a large peak in particulate suspended organic matter evident in Easky during January (Fig. 5.5). The lowest organic matter values were recorded consistently in Talt, with concentrations never exceeding 0.50 mg L⁻¹. Concentrations of organic matter fluctuated throughout the year in most lakes, with no sizeable peaks, apart from that observed in Easky. There was a relatively large peak in Rea during May, but this sample was taken from the shoreline, owing to unfavourable weather conditions.

Table 5.3 Mean ($\pm$ SE), range and sample size (*n*) of dissolved organic carbon (DOC), particulate suspended organic matter, suspended solids (SS) and chlorophyll *a* for the six lakes (April 03 – April 04).

	DOC (mg L ⁻¹)	Particulate suspended organic matter (mg L ⁻¹)	SS (mg L ⁻¹)	Chlorophyll <i>a</i> (µg L ⁻¹)
Carra				
Mean $\pm$ SE	9.0 $\pm$ 1.2	0.67 $\pm$ 0.08	1.34 $\pm$ 0.15	2.3 $\pm$ 0.2
Range	3.5 – 28.9	0.10 – 2.00	0.20 – 4.88	0.7 – 5.0
<i>n</i>	(32)	(35)	(35)	(35)
Talt				
Mean $\pm$ SE	29.5 $\pm$ 8.5	0.22 $\pm$ 0.05	0.57 $\pm$ 0.08	2.3 $\pm$ 0.3
Range	3.2 – 101.3	0 – 0.50	0.10 – 1.15	1.1 – 3.7
<i>n</i>	(11)	(11)	(11)	(12)
Rea				
Mean $\pm$ SE	12.0 $\pm$ 5.8	0.63 $\pm$ 0.12	1.55 $\pm$ 0.55	3.6 $\pm$ 0.4
Range	3.9 – 69.3	0.20 – 1.75	0.25 – 6.40	1.3 – 5.8
<i>n</i>	(11)	(12)	(12)	(12)
Easky				
Mean $\pm$ SE	10.7 $\pm$ 1.9	1.13 $\pm$ 0.28	1.73 $\pm$ 0.51	3.2 $\pm$ 0.3
Range	4.3 – 22.7	0.33 – 3.80	0.70 – 6.60	1.3 – 5.1
<i>n</i>	(11)	(11)	(11)	(12)
Feeagh				
Mean $\pm$ SE	17.2 $\pm$ 4.3	0.46 $\pm$ 0.06	1.11 $\pm$ 0.23	1.8 $\pm$ 0.3
Range	5.9 – 46.5	0.20 – 1.00	0.40 – 3.29	0.4 – 3.9
<i>n</i>	(11)	(12)	(12)	(12)
Maumwee				
Mean $\pm$ SE	8.7 $\pm$ 2.2	0.54 $\pm$ 0.07	1.03 $\pm$ 0.28	1.9 $\pm$ 0.2
Range	2.8 – 26.6	0.25 – 1.00	0.13 – 3.79	0.8 – 3.7
<i>n</i>	(11)	(11)	(12)	(12)

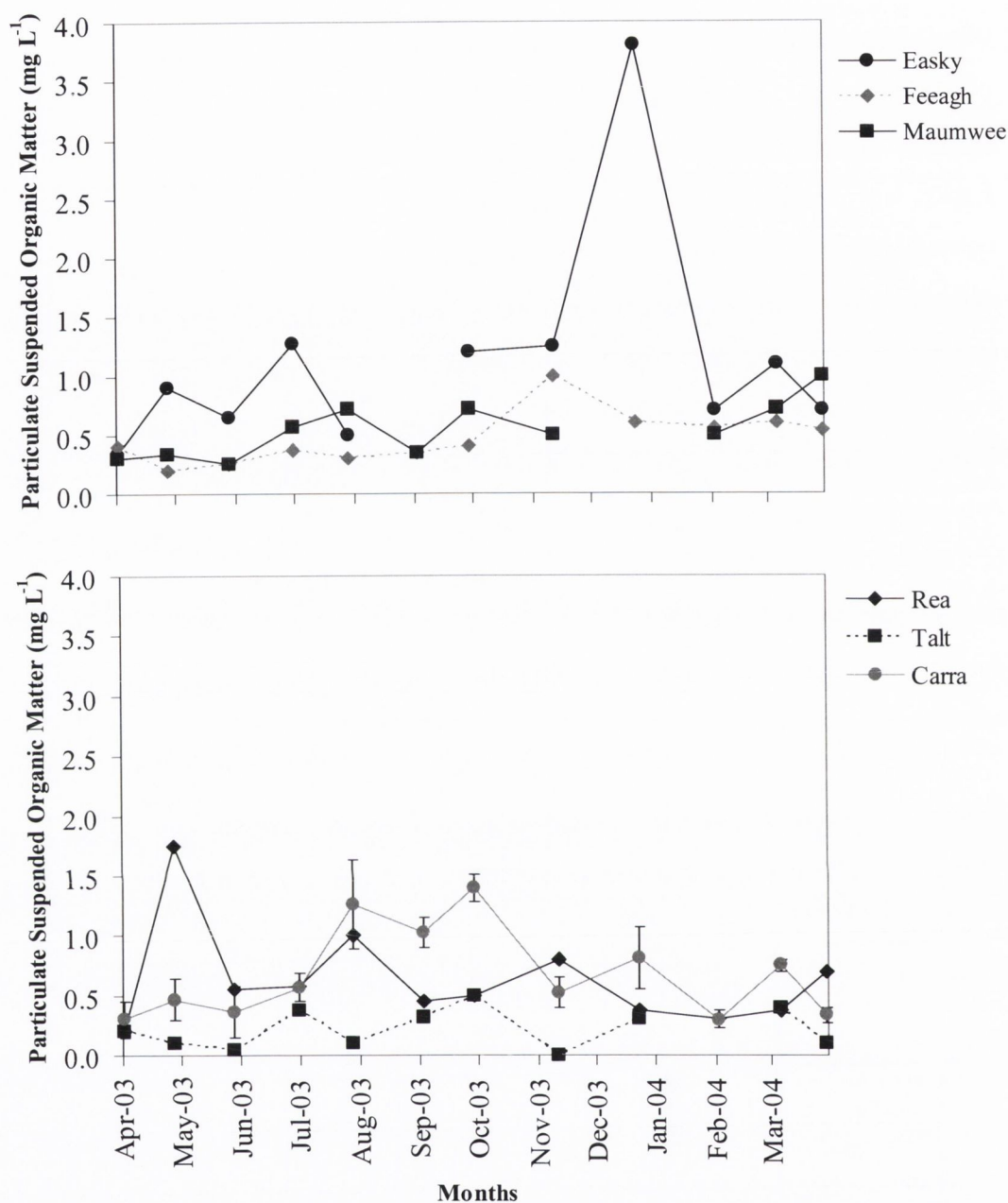


Fig. 5.5 Particulate suspended organic matter concentrations (mg L^{-1}) for all lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n=3$) of the three basins of Lough Carra are shown.

There was tendency towards declining chlorophyll *a* concentrations during late autumn and winter in Easky and Talt, both of which had very similar patterns in chlorophyll *a* throughout the year, although there were generally higher concentrations in Easky (Fig. 5.6). There was also low chlorophyll *a* concentrations in Feeagh during winter, which increased slightly in spring but reached greatest concentrations between August and September. There was an increase in chlorophyll

a in Lough Carra during September, reaching maximum values in October and declining to relatively low concentrations in spring. Overall, Lough Rea had the highest concentrations of chlorophyll *a* over much of the year (Table 5.3), but there was a sharp decline between September and October.

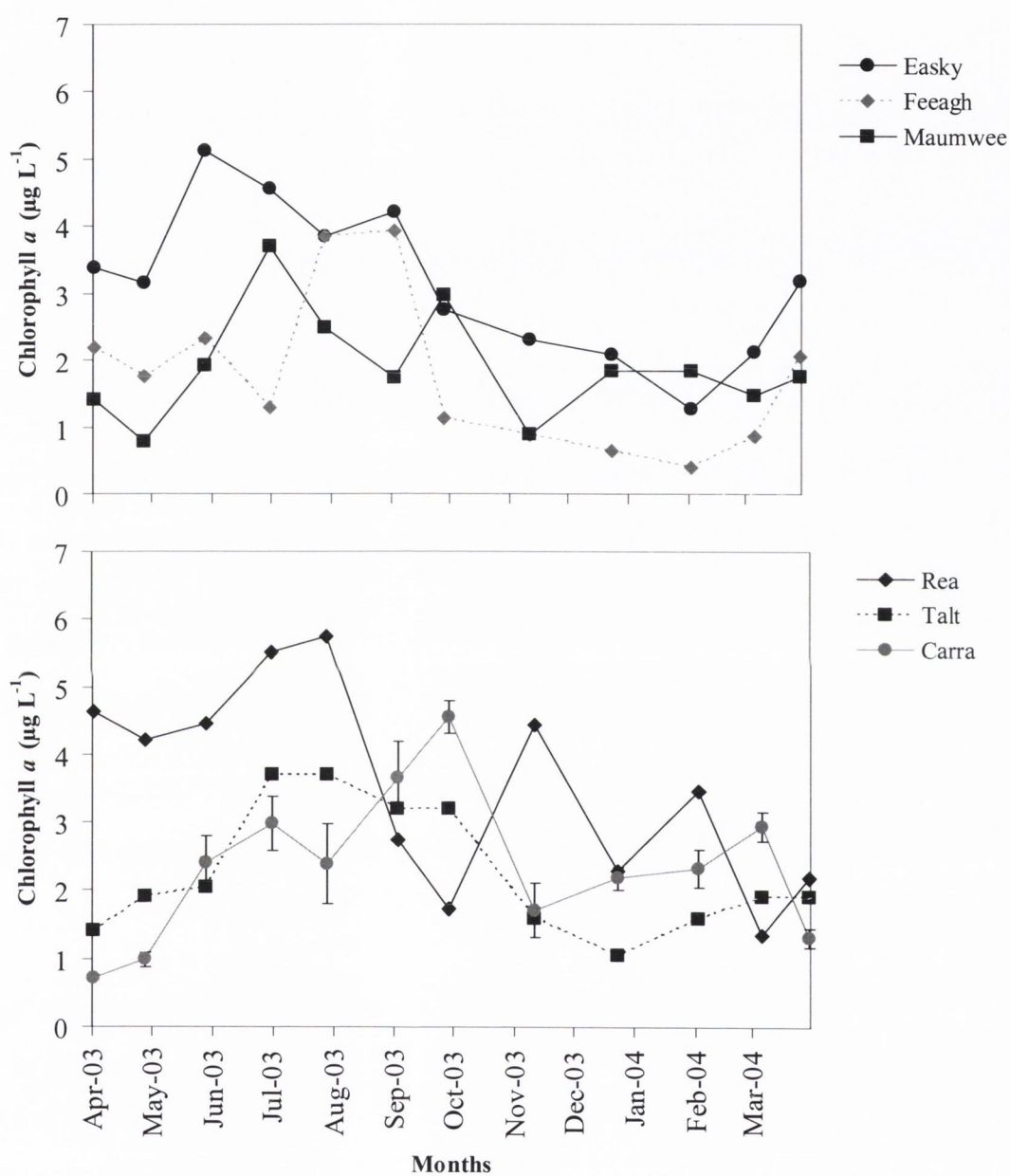


Fig. 5.6 Chlorophyll *a* concentrations ($\mu\text{g L}^{-1}$) for all lakes, April 2003 – April 2004. Mean values ($\pm$ SE, $n=3$) of the three basins of Lough Carra are shown.

The ratio of DIN:TP was calculated and used to estimate the extent of N- or P-limitation for phytoplankton growth over the course of the year in each of the six sampling lakes. The DIN:TP ratio was recommended by Morris & Lewis (1988) as a

suitable index of N and P availability to phytoplankton because it represents the bulk of N and P available to phytoplankton and was used in Chapter 4 (section 4.3.1) to predict nutrient limitation in Carra. According to this ratio all three high-alkalinity lakes showed N-limitation during most of summer and autumn months. Values of DIN:TP below 2 (molar) (indicating N-limitation) occurred in Rea between May and October and in Talt and Carra between July and October. There was no evidence of P-limitation in either Talt or Rea according to the DIN:TP ratio, although values did reach 29 during March 2004 in Rea, but were generally below the threshold of 27, which is suggested to be indicative of P-limitation. The highest DIN:TP ratio recorded in Talt was only 18. Phosphorus limitation was, however, apparent in Carra between February and May based on the ratio of DIN:TP, with values reaching a maximum of 171 in the South basin in February 2004. There was no evidence of either P- or N-limitation in Lough Easky. The ratio of DIN:TP was, nevertheless, very low in Easky over the course of the year with values ranging from 2 to 21. There were only brief periods when the DIN:TP ratio fell below 2 in Maumwee. This occurred between May and June and again between September and October. There was no suggestion of P-limitation from the DIN:TP ratio in Maumwee. Although the maximum ratio was 27, the ratio was usually much lower than this, with a mean ($\pm$ SE) of 7 ± 2.3 ($n = 12$). There was evidence for P-limitation in Feeagh between April and June and again between November and February with a maximum DIN:TP ratio of 43 recorded in May 2003. There was no indication of N-limitation in Feeagh at any stage during the year based on the ratio of DIN:TP.

The ratio of C:P in the seston was estimated for Carra and Maumwee between April 2003 and April 2004 using the ratio of light to total phosphorus (light:TP) as an indirect index for seston C:P following Sterner *et al.* (1997). This method was used previously for Carra in Chapter 4 and was deemed appropriate for Maumwee, as it is also a shallow lake which does not stratify, and the depth of the mixed layer could, therefore, be related to the depth of the water column at the time of sampling. Estimated values of C:P in Maumwee were high throughout the year ranging from 344 to 732, and were, therefore, always greater than the predicted threshold value of 200 - 350 (molar) above which *Daphnia* are considered to become P-limited (Urabe & Watanabe, 1992; Sterner & Hessen, 1994; Anderson & Hessen, 2005). Values in

Carra varied little throughout the year, but were generally lower than those observed in Maumwee and ranged between 263 and 301.

5.3.2 C:N:P content of seston and zooplankton

5.3.2.1 Comparison between the ratio of DIN:TP and seston elemental content

The C:P, C:N and N:P ratios of the seston in May and September 2005 generally indicated simultaneous moderate P and N deficiencies for phytoplankton (Table 5.4). High C:P seston ratios > 129 and N:P ratios > 22 are indicative of P-deficiency, whereas C:N ratios > 8.3 is suggestive of N-limitation (Healey & Hendzel, 1980). In May there was no indication of nutrient deficiency in Talt. In Rea and Easky, however, C:P and C:N ratios suggest co-limitation by P and N, while the N:P ratios of these lakes implied a reasonably balanced supply of N and P. The C:P and C:N ratios of Maumwee, also suggested co-limitation by P and N but the N:P ratio indicated P-limitation. Elemental ratios in Feeagh and Carra implied P-limitation with no suggestion of N-limitation. During May the DIN:TP ratios were in the main within ranges which indicate either co-limitation, reciprocal limitation or nutrient sufficiency (Morris & Lewis, 1988), and were, therefore, in accordance with seston elemental ratios. In Maumwee, however, the ratio of DIN:TP was suggestive of N-limitation, although both seston C:P and N:P ratios suggested P-limitation, but was, nevertheless, in agreement with the C:N ratio, which also indicated N-limitation.

Co-limitation of N and P in all lakes during September was suggested by ratios of C:P and C:N (Table 5.4). Ratios of N:P, however, generally suggested P deficiency, apart from Talt in which N:P ratios implied a relatively sufficient availability of both nutrients. The DIN:TP ratios were generally in agreement with observations of nutrient deficiencies based on seston nutrient contents. In Rea and Maumwee, however, the DIN:TP ratio implied nitrogen limitation, which despite being in agreement with the seston C:N ratio, did not concur with C:P and N:P ratios, both of which indicated P-limitation.

Table 5.4 Seston elemental composition ratios of C:N, C:P and N:P and the ratio of DIN:TP in the water column for each of the six lakes. Identification of nutrient deficiency for phytoplankton, based on the nutrient ratios of seston, after Healey & Hendzel (1980), and based on the ratio of DIN:TP, after Morris & Lewis (1988). **N**, nitrogen deficiency; **P**, phosphorus deficiency; **PP**, severe phosphorus deficiency; **NN**, severe nitrogen deficiency.

	C:N	C:P	N:P	DIN:TP
May 2005				
Carra	8.1	249 ^P	31 ^P	88 ^P
Talt	6.0	130	22	20
Rea	17.8 ^{NN}	170 ^P	10	2
Easky	21.1 ^{NN}	269 ^{PP}	13	10
Feeagh	6.7	202 ^P	30 ^P	38 ^P
Maumwee	10.4 ^N	257 ^P	25 ^P	1 ^N
September 2005				
Carra	9.5 ^N	412 ^{PP}	43 ^P	3
Talt	8.9 ^N	164 ^P	19	2
Rea	8.4 ^N	209 ^P	25 ^P	0.2 ^N
Easky	9.1 ^N	261 ^P	29 ^P	2
Feeagh	10.8 ^N	256 ^P	24 ^P	13
Maumwee	10.6 ^N	546 ^{PP}	52 ^P	1 ^N

5.3.2.2 Relationship between seston and zooplankton elemental content

High seston C:P ratios were recorded in Maumwee and Carra in September 2005 (Table 5.5) and were above the proposed threshold value of 200 - 350 at which *Daphnia* is believed to become P-limited (Urabe & Watanabe, 1992; Anderson & Hessen, 2005). The remaining seston C:P values were generally < 250. In most lakes, the C:P ratio was higher in September than in May, in Easky, however, the C:P ratio varied little between the two sampling dates. Zooplankton C:P ratios also increased from May to September in all lakes. The C:P of the seston was normally greater than that of the zooplankton, except during September in Feeagh when the seston C:P ratio was less than that of the zooplankton (Table 5.5.).

The N:P ratios recorded in Carra were higher in the seston than the zooplankton, indicating P deficiency of the zooplankton. Phosphorus deficiencies, however, were only evident during September in Maumwee and during May in Feeagh. In contrast, the N:P ratios for Feeagh in September suggested seston was deficient in N. At this time cyclopoid and calanoid copepods, as well as *Diaphanosoma*, dominated the zooplankton community. There is also a suggestion of N-limitation for zooplankton in Rea, particularly in May at which time over 90 % of the zooplankton community was composed of calanoids. In September, however, values of seston N:P in Rea,

were very close to the N:P ratio of the zooplankton. This was also the case for the remaining lakes, although in general the N:P ratio of seston was slightly greater than that of the zooplankton (Table 5.5).

With the exception of a single outlier (from Carra in July 2005) there was a general positive association between bulk zooplankton C:P ratios and seston C:P ratios (Fig. 5.7). In Carra during July the zooplankton C:P ratio was high relative to the seston C:P ratio and corresponded to a period of low *Daphnia* abundance and dominance of zooplankton biomass by calanoids; consistent with calanoids suppressing availability of P to phytoplankton (see Chapter 4). Removal of the outlying datum from the analyses resulted in a significant positive correlation between zooplankton C:P and seston C:P (Spearman rank, $r = 0.58$, $P \leq 0.05$, $n = 15$). Scatter with the relationship between zooplankton C:P and seston C:P was most apparent at ratios of seston C:P between 250 and 270 which is within the predicted threshold of P-limitation for *Daphnia* (Urabe & Watanabe, 1992; Anderson & Hessen, 2005). There was no significant relationship between zooplankton C:N and the corresponding elemental ratio in seston (Spearman rank, $r = 0.44$, $P = 0.09$, $n = 16$).

Table 5.5 Ratio of C:P and N:P in zooplankton and seston for each of the six lakes.

C:P	May 2005		September 2005	
	Seston	Zooplankton	Seston	Zooplankton
Carra	249	95	412	308
Talt	130	101	164	122
Rea	170	107	209	141
Easky	269	70	261	248
Feeagh	202	140	256	306
Maumwee	257	145	546	277
N:P	May 2005		September 2005	
	Seston	Zooplankton	Seston	Zooplankton
Carra	31	15	43	30
Talt	22	18	19	17
Rea	10	18	25	27
Easky	13	12	29	26
Feeagh	30	21	24	38
Maumwee	25	24	52	40

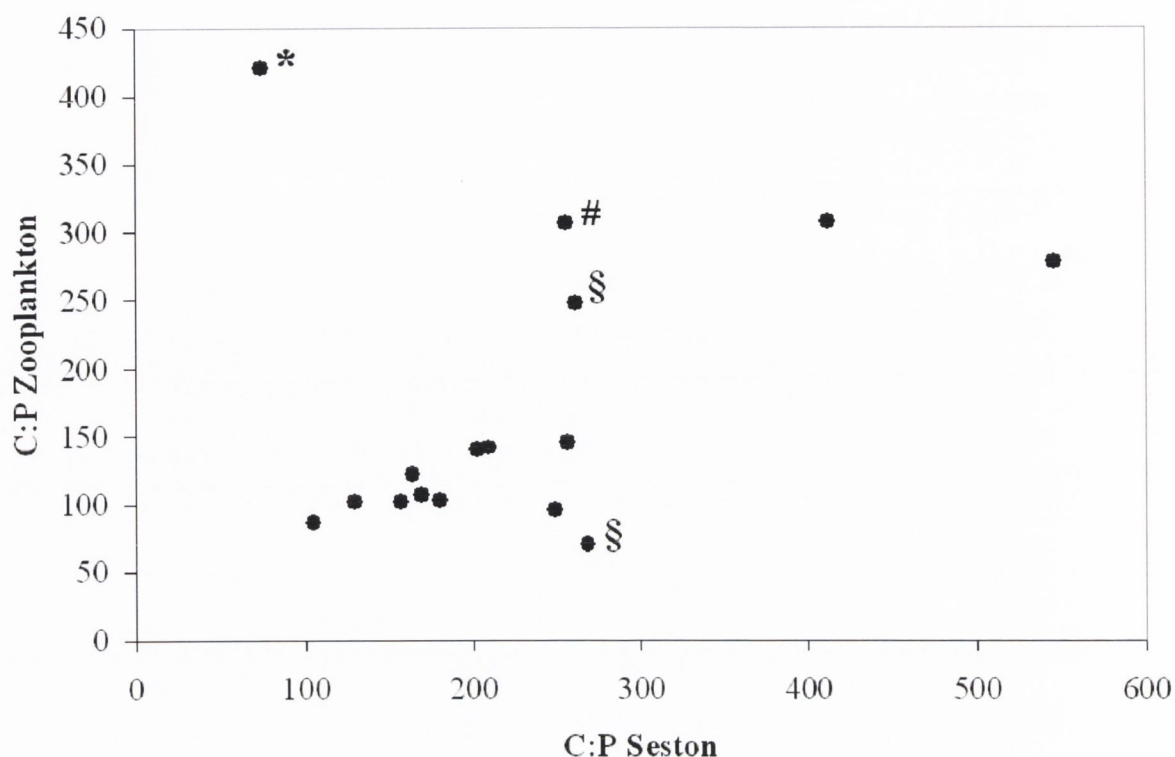


Fig. 5.7 Zooplankton C:P plotted against seston C:P of the six study lakes, samples were collected between April and September 2005. * This data point represents the samples collected from Carra in July 2005; # sample collected from Feeagh in September; § samples collected in Easky.

5.3.2.3 Zooplankton elemental content

There was a significant variation in P, C and N content among taxa (One-way ANOVA, $F_{4,30} = 8.15$, $P \leq 0.001$, $F_{4,30} = 4.94$, $P \leq 0.01$ and $F_{4,30} = 4.63$, $P \leq 0.01$, respectively). LSD *Post-hoc* tests revealed that the difference in % P content among taxa could be attributed predominantly to *Daphnia*, which showed a statistically significant difference in % P with all taxa ($P \leq 0.01$ in each case). In contrast, no significant difference in P content was found between any other taxa. Interspecific variation in C and N could be attributed to differences between *Daphnia* and calanoids ($P \leq 0.01$ and $P \leq 0.001$, respectively), and *Daphnia* and cyclopoids ($P \leq 0.001$ and $P \leq 0.01$, respectively). There was also a difference in both C and N content between *Bosmina* and calanoids ($P \leq 0.05$ in each case) and a difference in C content between *Bosmina* and cyclopoids ($P \leq 0.01$). *Daphnia* were, therefore, responsible for the greatest amount of variation in nutrient content among taxa, and had the greatest % P content of all species ranging from 1.32 % to 1.73 % (Table 5.7).

Alternatively, cyclopoids, and particularly calanoids, had the highest specific N contents of all the taxa examined (Fig. 5.8), which ranged from 8.20 % to 13.80 % in calanoids and 10.38 % to 12.92 % in cyclopoids.

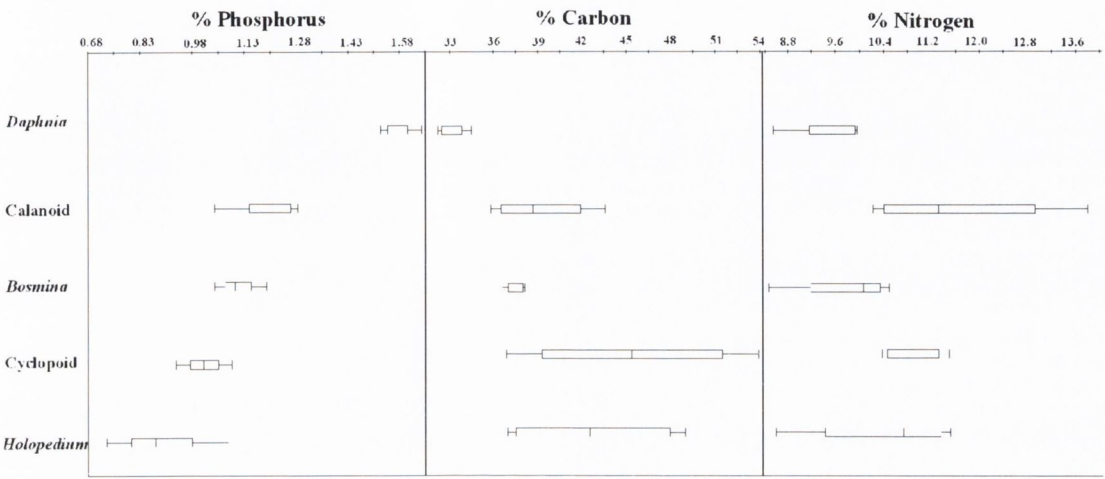


Fig. 5.8 Box-and-whisker displays of distributions of all field samples by zooplankton taxa and element (C, N and P as percent of dry weight). Boxes indicate medians and the 25th and 75th quartiles; whiskers indicate the extent of the main body of data. Samples were collected between May and September 2005 (*Daphnia* n = 7, Cyclopoid n = 6, *Bosmina* n = 5, Calanoid n = 11, *Holopedium* n = 3).

There was no significant difference among lakes in the percentage P, C or N content of *Daphnia* (One-way ANOVA, $F_{3,4} = 1.41$, $P = 0.39$, $F_{3,4} = 0.09$, $P = 0.96$ and $F_{3,4} = 0.22$, $P = 0.88$, respectively), or P or C content of calanoids (One-way ANOVA, $F_{4,6} = 0.92$, $P = 0.51$ and $F_{4,7} = 0.10$, $P = 0.98$, respectively). There was, however, a difference in the N content of calanoids among lakes (One-way ANOVA, $F_{4,7} = 9.06$, $P \leq 0.01$). LSD *Post-hoc* tests revealed that calanoids in both Easky and Talt had a lower N content than calanoids from the other lakes ($P \leq 0.05$ for Talt - Feeagh, $P \leq 0.01$, in all other cases), but there was no difference in calanoid N content between Easky and Talt ($P = 0.42$). There was also no other significant difference in the N content of calanoids among any of the other lakes (Fig. 5.9).

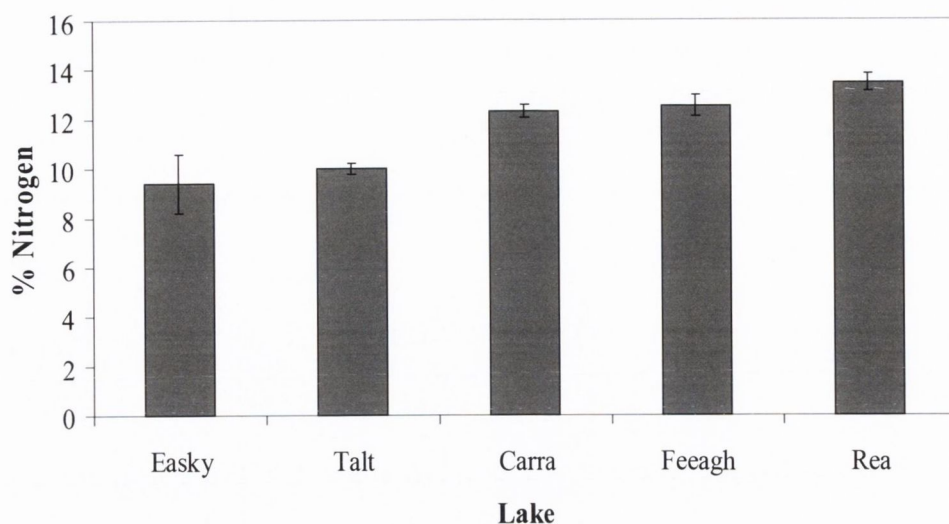


Fig. 5.9 Mean ($\pm$ SE, $n = 2$) % nitrogen (N) of calanoids from May 2005 and September 2005.

Daphnia had the lowest N:P and C:P ratios and calanoids and cyclopoids relatively high N:P and C:P ratios (Fig. 5.10). Highest nutrient ratios were found in *Diaphanosoma* and *Holopedium*, although the measurement for *Diaphanosoma* was based on only one sample. *Bosmina* and calanoid copepods had very similar elemental contents.

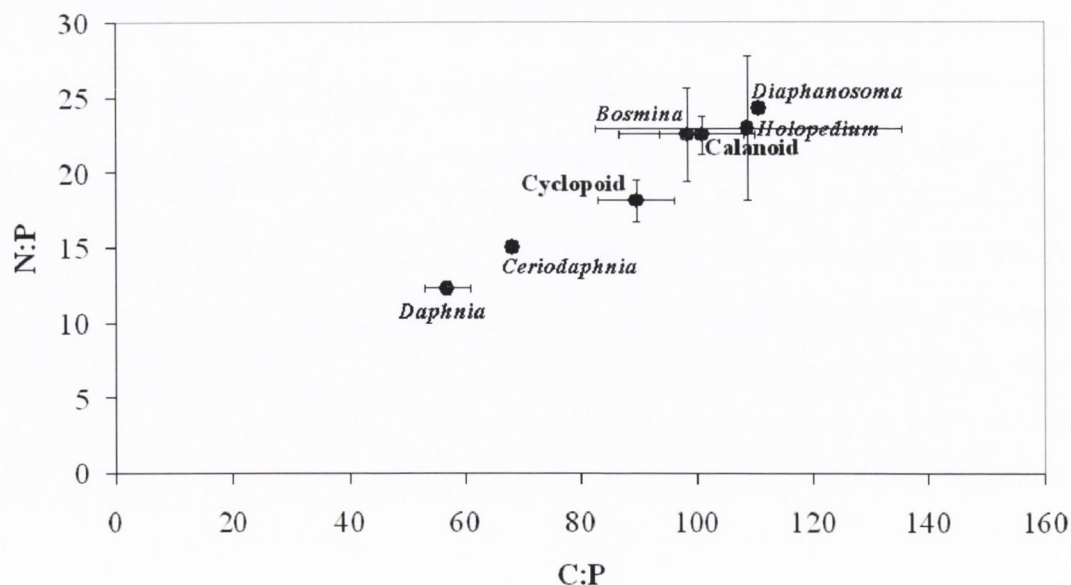


Fig. 5.10 Interspecific variation in the mean elemental composition of various taxa of zooplankton. Horizontal and vertical bars represent SEs. Samples were collected between May and September 2005 (*Daphnia* $n = 7$, *Ceriodaphnia* $n = 1$, *Cyclopoid* $n = 6$, *Bosmina* $n = 5$, *Calanoid* $n = 11$, *Holopedium* $n = 3$, *Diaphanosoma* $n = 1$).

5.3.2.4 Relationship between zooplankton and seston elemental content

There was a negative relationship between *Daphnia* abundance and seston C:P ratio, (Pearson's, $r = -0.89$, $P \leq 0.01$, $n = 9$; samples in which no *Daphnia* were recorded were not included in the correlation analyses) (Fig. 5.11). There was also a negative correlation between the abundance of *Daphnia* and the ratio of N:P (Pearson's, $r = -0.78$, $P \leq 0.05$, $n = 9$; samples in which no *Daphnia* were recorded were not included in the correlation analyses) (Fig. 5.12), but no relationship with the ratio of C:N (Pearson's, $r = -0.05$, $P = 0.90$, $n = 9$; samples in which no *Daphnia* were recorded were not included in the correlation analyses). Although there was no significant relationship between seston elemental content and either calanoid or cyclopoid abundances, there was, nevertheless, a negative correlation between seston C:P and the abundance of calanoid nauplii (Pearson's, $r = -0.56$, $P \leq 0.05$, $n = 13$), but no relationship with cyclopoid nauplii (Pearson's, $r = -0.19$, $P = 0.56$, $n = 12$). There were no other significant relationships between seston elemental content and any of the other zooplankton taxa.

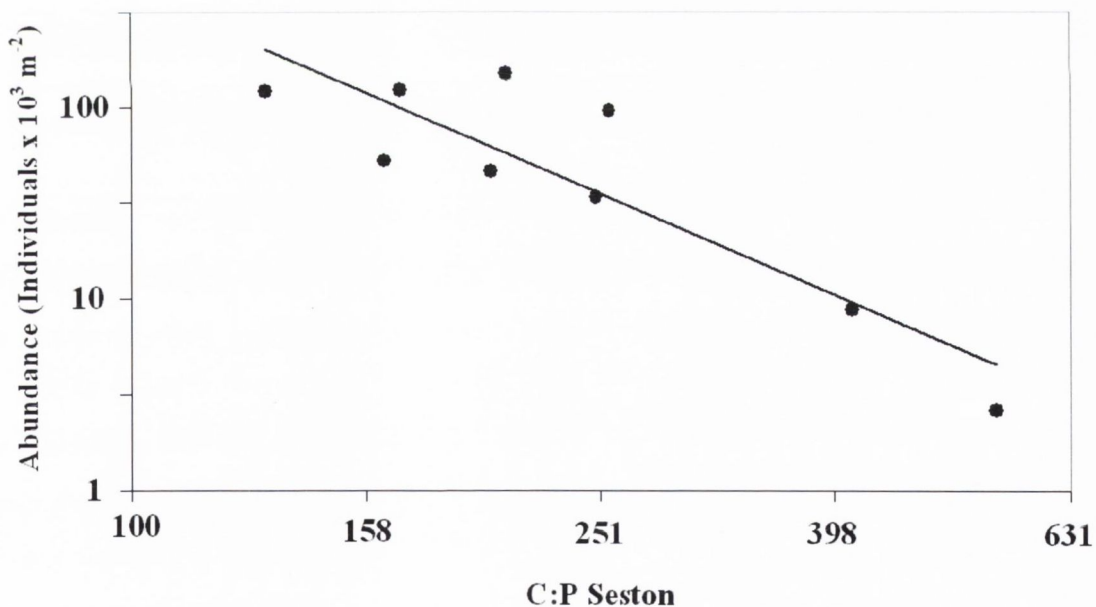


Fig. 5.11 Relationship between *Daphnia* abundance and seston C:P ratio. The curve is the least squares regression line ($r^2 = 0.78$, $P \leq 0.01$, $n = 9$). Linear regressions are: $y = 10.9 - 2.6x$. All variables were logarithmically transformed. Samples were collected between May and September 2005.

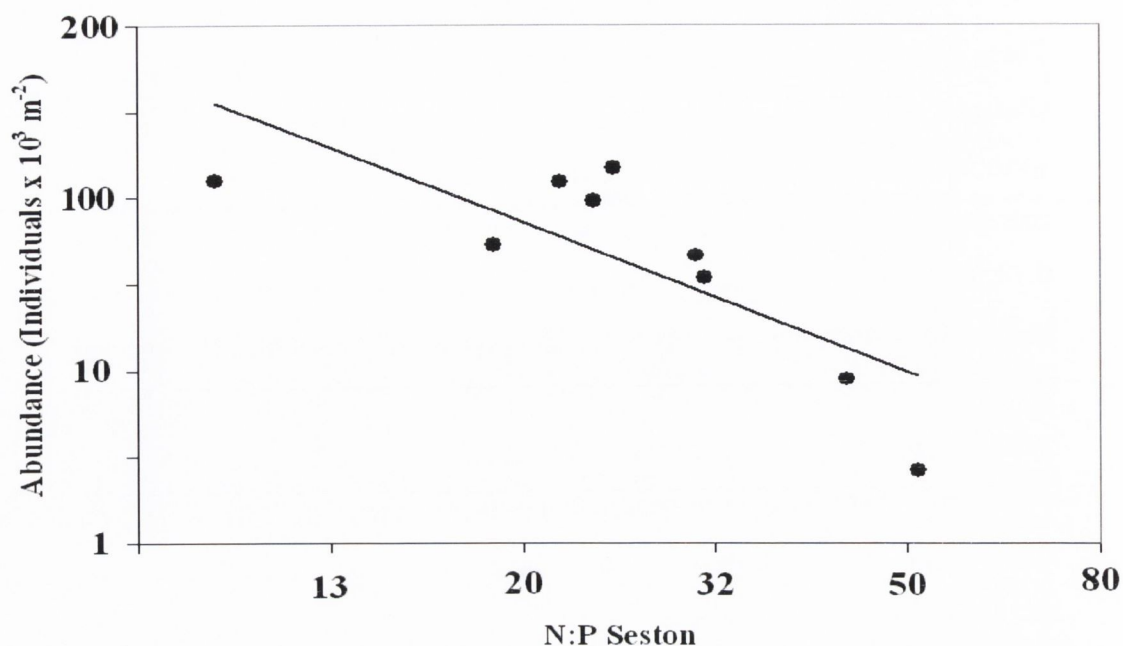


Fig. 5.12 Relationship between *Daphnia* abundance and seston N:P ratio. The curve is the least squares regression line ($r^2 = 0.62$, $P \leq 0.05$, $n = 9$). Linear regressions are: $y = 7.7 - 2.2x$. All variables were logarithmically transformed. Samples were collected between May and September 2005.

5.3.3 Relationship of the zooplankton assemblage to nutrient availability

In Talt increased biomass of *Bosmina* and calanoids in spring and early summer and again during winter corresponded to decreases in chlorophyll *a* concentration, and there was a negative correlation between chlorophyll *a* and both *Bosmina* and calanoid biomass (Pearson's, $r = -0.79$, $P \leq 0.01$, $n = 12$ and $r = -0.76$, $P \leq 0.01$, $n = 12$, respectively). There was also a negative relationship between *Bosmina* and chlorophyll *a* in Maumwee (Pearson's, $r = -0.69$, $P \leq 0.01$, $n = 12$) and Easky (Pearson's, $r = -0.58$, $P \leq 0.05$, $n = 12$). The only other indication of possible grazing pressure by herbivorous zooplankton on phytoplankton was observed in Carra, where as previously observed, *Daphnia* were correlated negatively with chlorophyll *a* (Pearson's, $r = -0.63$, $P \leq 0.05$, $n = 12$). In Easky, *Ceriodaphnia* biomass tended to increase with increasing chlorophyll *a* concentration (Pearson's, $r = 0.83$, $P \leq 0.01$, $n = 12$), and a similar pattern was also observed between calanoid biomass and phytoplankton in Feeagh (Pearson's, $r = 0.79$, $P \leq 0.01$, $n = 11$).

Total zooplankton in Rea was negatively associated with both TN and PN concentration (Pearson's, $r = -0.63$, $P \leq 0.05$, $n = 11$ and $r = -0.61$, $P \leq 0.05$, $n = 11$, respectively). In Maumwee, however, total zooplankton biomass was correlated positively with concentrations of TN and PN (Pearson's, $r = 0.64$, $P \leq 0.05$, $n = 12$, in both cases), and positively with the ratio of TN:TP (Spearman rank, $r = 0.67$, $P \leq 0.05$, $n = 12$). In addition, there was a negative relationship between zooplankton biomass in Maumwee and estimates of the C:P ratio (Light:TP) (Spearman rank, $r = -0.58$, $P \leq 0.05$, $n = 12$).

As previously observed, *Daphnia* biomass in Carra was correlated positively with DIN concentration (Table 5.6). There were, however, no other significant relationships recorded between these two variables in any other lake. The only significant relationship between *Daphnia* and any measurement of phosphorus availability was observed in Rea, in which *Daphnia* was correlated positively with particulate phosphorus (Table 5.6). In this lake, peaks in *Daphnia* biomass corresponded to periods of *Daphnia* dominated zooplankton biomass (see section 3.3.5), and were associated with peaks in particulate phosphorus concentration (Fig. 5.13). There was also a negative relationship between *Daphnia* biomass in Rea and both TN and PN concentrations (Table 5.6). A negative relationship between *Daphnia* and PN was also observed in Carra, and is consistent with what was found in previous years in this lake (see section 4.3.4). As expected, *Daphnia* biomass in Carra was correlated positively with the ratio of DIN:TP (Table 5.6), but this relationship was not observed elsewhere.

Table 5.6 (A) Pearson's product-moment correlation coefficients and (B) Spearman rank correlation coefficients (and sample size) for in-lake measures of phosphorus and nitrogen and *Daphnia* biomass ($\mu\text{g DW m}^{-2}$) for the six study lakes, April 2003 – 2004. * $P \leq 0.05$, ** $P \leq 0.01$; DIN, dissolved inorganic nitrogen; TN, total nitrogen; PN, particulate nitrogen; PP, particulate phosphorus. Significant relationships in bold.

	A	DIN	TN	PN	PP	B	DIN:TP
Carra		0.73 ** (12)	0.13 (12)	-0.62 * (12)	0.07 (12)		0.65 * (12)
Talt		-0.35 (12)	0.26 (12)	0.29 (12)	0.26 (12)		-0.19 (12)
Rea		0.31 (11)	-0.79 ** (11)	-0.79 ** (11)	0.79 ** (11)		0.18 (11)
Easky		0.16 (12)	0.19 (12)	0.18 (12)	0.20 (12)		0.13 (12)
Feeagh		0.11 (11)	0.10 (11)	-0.03 (11)	-0.09 (11)		0.32 (11)
Maumwee		-0.34 (12)	0.49 (12)	0.49 (12)	0.40 (12)		-0.36 (12)

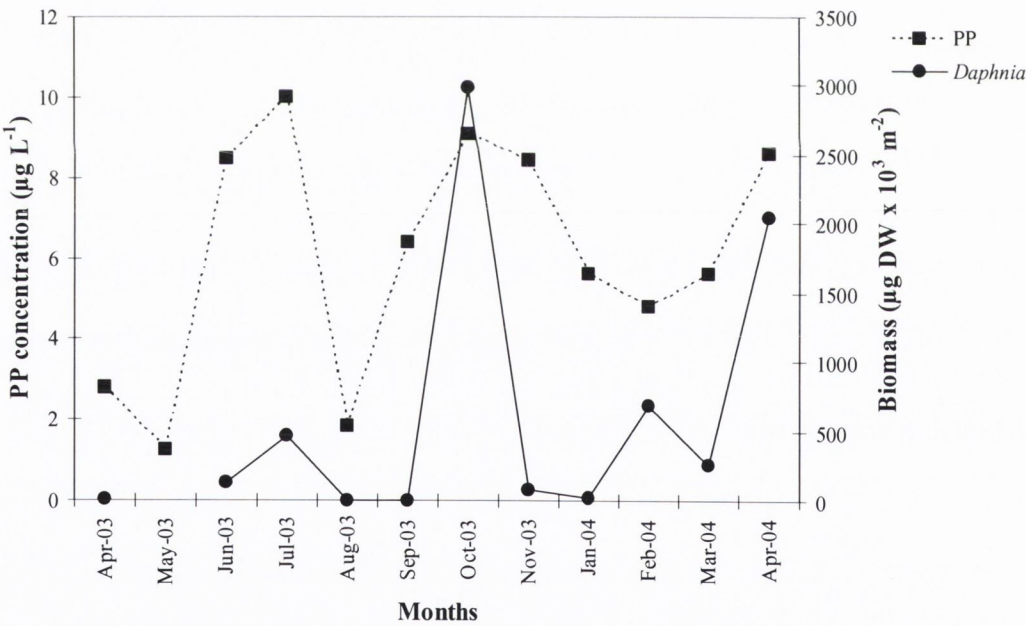


Fig. 5.13 Relationship between particulate phosphorus (PP) concentration ($\mu\text{g L}^{-1}$) and *Daphnia* biomass ($\mu\text{g DW m}^{-2}$) in Lough Rea, April 2003 – April 2004.

Post-nauplier calanoid biomass in Carra was correlated negatively with DIN concentrations and with the ratio of DIN:TP (Table 5.7). A negative relationship was also evident between post-nauplier calanoid biomass and DIN concentration in Maumwee (Fig. 5.14), but was not statistically significant. There was, nevertheless, a

significant negative correlation between post-naupliar calanoid abundance in Maumwee and DIN concentration (Pearson's, $r = -0.70$, $P \leq 0.05$, $n = 12$). In contrast, there was a positive relationship between calanoids in Talt and both DIN concentration and the ratio of DIN:TP (Table 5.7), with fluctuations in calanoid biomass corresponding closely to fluctuations in DIN concentration (Fig. 5.15). In Carra, there was a positive association between post-naupliar calanoid biomass and PN, a relationship which was also observed in Maumwee. In addition, however, there was a positive association between post-naupliar calanoids and PP concentration in Maumwee (Table 5.7). A comparison of these two variables over time, however, revealed a poor association, with calanoid maxima actually corresponding to decreased PP concentration, and there was no relationship when copepodites were removed from the analyses (Pearson's, $r = 0.27$, $P = 0.40$, $n = 12$). A positive association with TP concentration was found in Rea (Table 5.7), but again this relationship was not significant when only mature calanoids were taken into account (Pearson's, $r = 0.46$, $P = 0.16$, $n = 11$). There was also a positive association between calanoid nauplii abundance in Rea and TP (Pearson's, $r = 0.69$, $P \leq 0.05$, $n = 11$).

Table 5.7 (A) Pearson's product-moment correlation coefficients and (B) Spearman rank correlation coefficients (and sample size) for in-lake measures of phosphorus and nitrogen and post-naupliar calanoid biomass ($\mu\text{g DW m}^{-2}$) for the six study lakes, April 2003 – 2004. * $P \leq 0.05$; DIN, dissolved inorganic nitrogen; TN, total nitrogen; PN, particulate nitrogen; TP, total phosphorus; PP, particulate phosphorus. Significant relationships in bold.

	A	DIN	PN	TP	PP	B	DIN:TP
Carra		-0.60 * (12)	0.59 * (12)	-0.26 (12)	-0.28 (12)		-0.66 * (12)
Talt		0.68 * (12)	-0.53 (12)	0.02 (12)	-0.23 (12)		0.70 * (12)
Rea		-0.23 (11)	-0.11 (11)	0.61 * (11)	0.10 (11)		0.01 (11)
Easky		0.08 (12)	0.11 (12)	0.26 (12)	0.34 (12)		-0.03 (12)
Feeagh		0.11 (11)	0.52 (11)	-0.25 (11)	-0.20 (11)		0.18 (11)
Maumwee		-0.36 (12)	0.59 * (12)	0.56 (12)	0.58 * (12)		-0.41 (12)

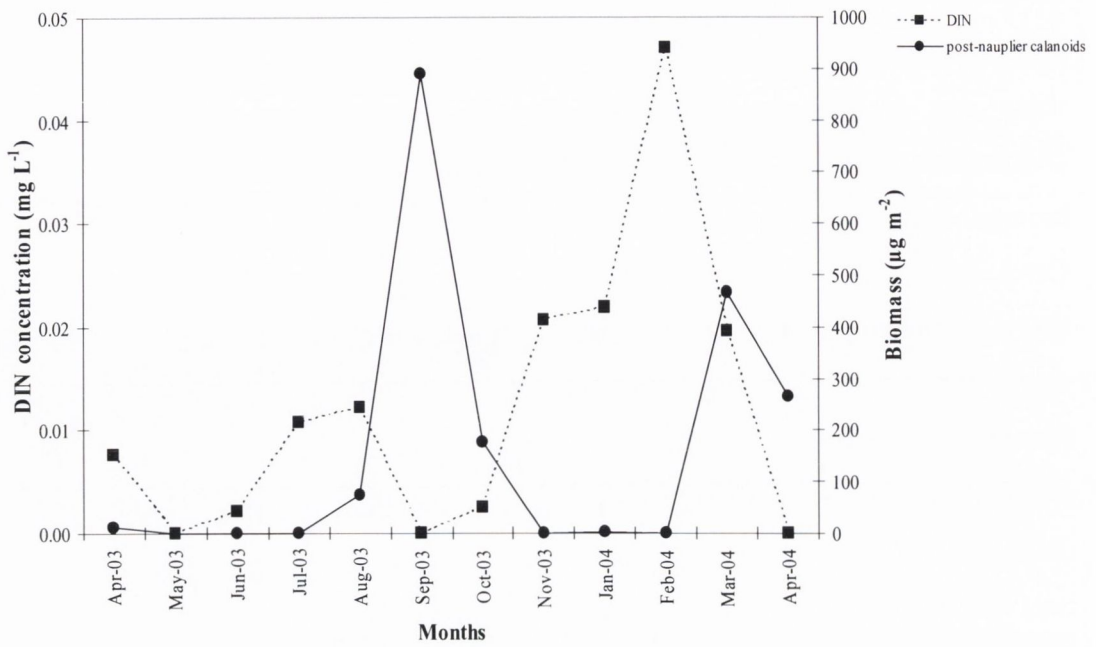


Fig. 5.14 Relationship between dissolved inorganic nitrogen (DIN) concentration (mg L^{-1}) and post-naupliar calanoid biomass ($\mu\text{g DW m}^{-2}$) in Lough Maumwee, April 2003 – April 2004.

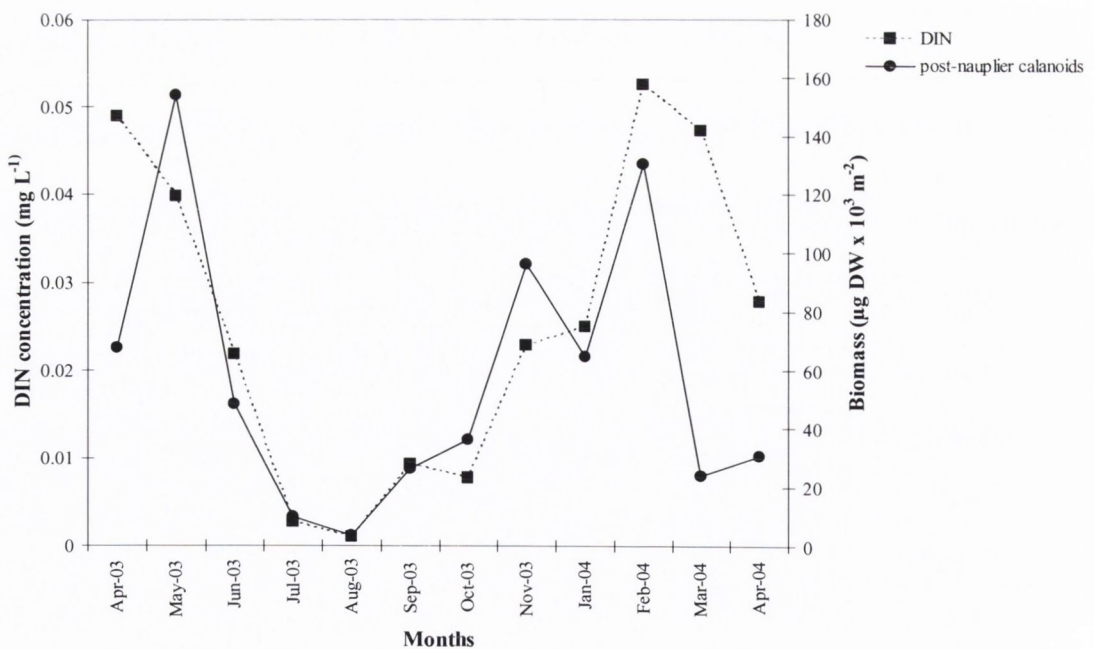


Fig. 5.15 Relationship between dissolved inorganic nitrogen (DIN) concentration (mg L^{-1}) and post-naupliar calanoid biomass ($\mu\text{g DW m}^{-2}$) in Lough Talt, April 2003 – April 2004.

Increased post-naupliar cyclopoid biomass corresponded to decreased DIN concentration in both Maumwee and Rea (Pearson's, $r = -0.62$, $P \leq 0.05$, $n = 12$ and $r = -0.61$, $P \leq 0.05$, $n = 11$, respectively) with analogous relationships with the ratio of DIN:TP (Spearman rank, $r = -0.58$, $P \leq 0.05$, $n = 12$ and $r = -0.80$, $P \leq 0.01$, $n = 11$, respectively). In contrast, cyclopoids were correlated positively with DIN and the ratio of DIN:TP in Carra (Spearman rank, $r = 0.62$, $P \leq 0.05$, $n = 12$), nevertheless, seasonal fluctuations in cyclopoid biomass were not closely coupled to the concentration of DIN in this lake. Among other taxa there were very few relationships of note with ambient nutrient concentrations.

5.3.4 Zooplankton fecundity

Egg production of all taxonomic groups fluctuated throughout the year, and was generally highly variable among lakes, with the exception of cyclopoids, *Bosmina* and *Diaphanosoma* which had similar seasonal oscillations in clutch size, in all the lakes for which their fecundity was measured. Egg production in all taxa followed similar seasonal fluctuations in both Easky and Talt.

Cyclopoid fecundity was examined in four lakes, only one of which, Talt, was in the high alkalinity group. There was a similar reduction in the number of cyclopoid eggs per female between late autumn and early winter in all four lakes (Fig. 5.16). Cyclopoid clutch size ranged from 0 – 7.2 eggs per female. Maximum cyclopoid egg production occurred between March and April in all lakes apart from Feeagh, where greatest fecundity occurred in September. Cyclopoid fecundity was generally lower in Feeagh compared with the other lakes, with a mean ($\pm$ SE) of 0.6 ± 0.4 eggs per female ($n = 11$), however there was no statistically significant difference in cyclopoid fecundity among lakes (One-way ANOVA, $F_{3,26} = 0.35$, $P = 0.79$).

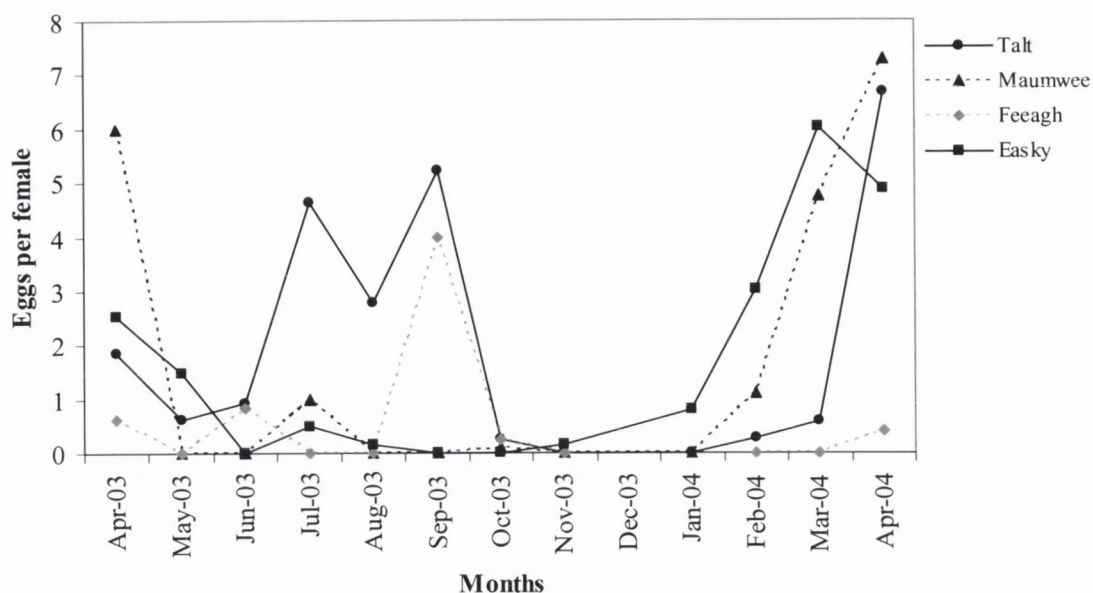


Fig. 5.16 Cyclopoid eggs per female for Lough Talt, Lough Maumwee, Lough Feeagh and Lough Easky, April 2003 – April 2004.

The pattern of reduced egg production between late autumn and winter was ubiquitous to all three taxa analysed for fecundity parameters in Talt. *Daphnia*, calanoid and cyclopoid clutch sizes all declined to very low levels between October and January. This was followed by a large peak in egg production by both calanoids and cyclopoids between February and April (Fig. 5.17).

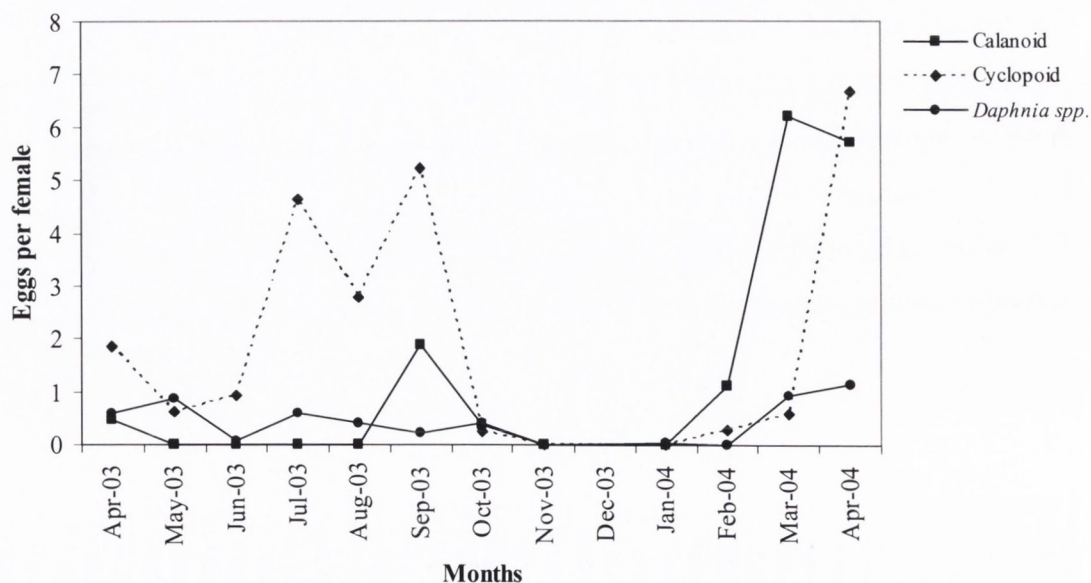


Fig. 5.17 Calanoid, Cyclopoid and *Daphnia* spp. eggs per mature female, Lough Talt, April 2003 – April 2004.

All taxa in Easky also showed a similar reduction in fecundity during winter, although it was not as manifest for *Ceriodaphnia* as it was for the cyclopoids, calanoids and *Bosmina* (Fig. 5.18). There were peaks in *Ceriodaphnia* egg production in the spring of both 2003 and 2004, with the highest value of 1.8 eggs per female recorded in April 2003. Maximum cyclopoid, calanoid and *Bosmina* fecundity was also evident in Easky between spring and early summer. Egg numbers began to decline for all taxa in September, apart from *Ceriodaphnia*, which continued to have relatively high clutch sizes between September and November, ranging from 0.3 – 0.6 eggs per female. Mean *Ceriodaphnia* fecundity ($\pm$ SE) in Easky was 0.5 ± 0.1 eggs per female ($n = 12$).

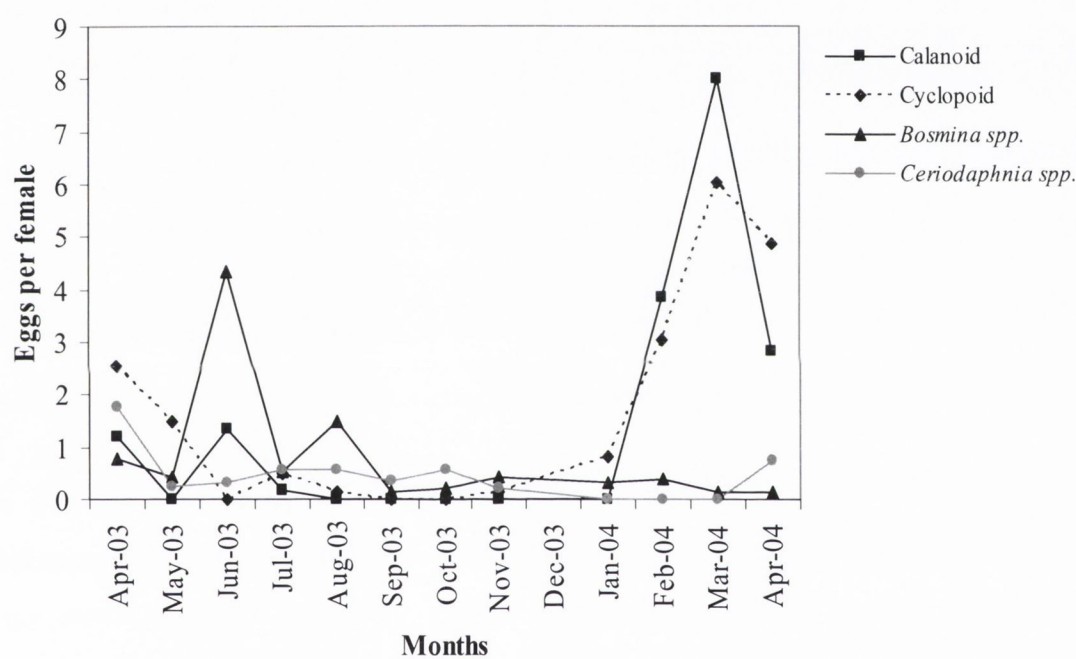


Fig. 5.18 Calanoid, Cyclopoid, *Bosmina* spp. and *Ceriodaphnia* spp. eggs per mature female, Lough Easky, April 2003 – April 2004.

Diaphanosoma and *Bosmina* egg production was low in all of the lakes, in which their fecundity was measured, much of the year. Declines in both the number of eggs per female *Daphnia* and *Bosmina* began in September and continued in all cases until April of the following year. Peaks in *Bosmina* egg production occurred between May and August in both Maumwee and Easky with maximum values of 3.0 and 4.3 eggs, respectively. Maximum *Diaphanosoma* fecundity also occurred between May and August reaching highest values of 0.2 eggs per female in both Feeagh and Maumwee.

There was no common seasonal trend in calanoid or *Daphnia* fecundity among lakes. In Easky, Talt and Carra, calanoid egg production was greatest during spring, with a maximum of 8.0 eggs per female recorded in Easky during March, and 6.2 eggs per female in Talt, with a lower value of only 3.4 eggs per female in Carra. Calanoid fecundity generally remained low in these lakes throughout the rest of the year, apart from a small peak in Easky during June, of 1.3 eggs per female, and in Talt during September, of 1.9 eggs per female. In Carra, calanoid clutch sizes remained relatively stable during the rest of the year, with no major fluctuations, apart from a slight increase between September and October. In both Rea and Feeagh, calanoid egg production was quite variable throughout the year, with no sustained periods of increase or decrease. There was no difference in mean calanoid fecundity among lakes (One-way ANOVA, $F_{4,38} = 0.43$, $P = 0.79$). There was also no difference in the mean number of *Daphnia* eggs per female among lakes (One-way ANOVA, $F_{4,39} = 2.20$, $P = 0.09$), although in general Talt had the highest clutch sizes, reaching a maximum of 1.6 eggs per female in April 2004. There was also a very large peak in *Daphnia* clutch size in Carra during the spring of 2004 with a maximum mean clutch size ($\pm$ SE) for the three basins of 1.1 ± 0.4 eggs per female ($n = 3$), which was recorded in March. There was also a much smaller peak in *Daphnia* fecundity in Carra between June and July, declining to low levels in August and remaining low until March of the following year. *Daphnia* fecundity in Maumwee followed a very similar pattern to this, but clutch sizes were generally smaller, with maximum numbers only reaching 0.2 eggs per female. *Daphnia* egg production varied considerably in both Feeagh and Rea, and more or less followed alternative seasonal patterns, with increases in clutch sizes in Feeagh occurring during periods of decline in Rea.

5.3.5 Presence of ephippia

Daphnia ephippia were most frequently observed in Carra, and were very prevalent in April 2004. During this time ephippia were recorded on approximately 10 % of the female population in the Mid basin, and on 1 % of the females in the South basin, but were not recorded at all in the North basin. This was much greater than in April 2003, in which only 1 % of females in the South basin were carrying ephippia, with no ephippia recorded in either of the other two basins. In September 2003 and February

2004 ehippia were detected on almost 2 % of females in the Mid basin of Carra. Approximately 6 % of *Daphnia* were carrying ehippium in Feeagh during September 2003.

Holopedium ehippia were recorded in Maumwee in November 2003 on almost 2 % of the individuals scored for fecundity. In addition about 9 % of *Ceriodaphnia* carried ehippia during November 2003 in Easky. In January 2004 a large number of both *Bosmina* and *Daphnia* ehippia were observed free in the water column of Easky. A considerable amount of detritus was present in the lake at this time, which made zooplankton collection difficult. The free ehippia formed a notable portion of this material, although their numbers were not recorded. At this time there was also an ehippium observed free in the water column in the Mid basin of Carra.

5.3.6 Presence of males

Male *Daphnia* were observed in all lakes apart from Easky and Feeagh (Fig. 5.19). Nevertheless, since *Daphnia* ehippia were recorded in both of these lakes, it is almost certain that males were present at some stage during the sampling period, but were rare. Male *Daphnia* were most frequently observed in Carra, and were most common during winter and spring, with maximum numbers recorded in April 2004. Maximum male *Daphnia* abundance in Rea was also recorded in April 2004. The lowest observed male *Daphnia* abundance was in Maumwee, with an abundance of 317 ind. m⁻² recorded in September. Male *Daphnia* were also observed in Maumwee in the October sample, but they were not scored during calculation of taxa abundance, but noted during fecundity analyses. They are therefore omitted from Fig. 3.21. In a similar way, male *Daphnia* were also recorded in Carra during April, May and September 2003 and in Talt during March 2004. A single male *Ceriodaphnia* and a male *Bosmina* were observed in Easky in January 2004, but no other males of any species were recorded in any other lake.

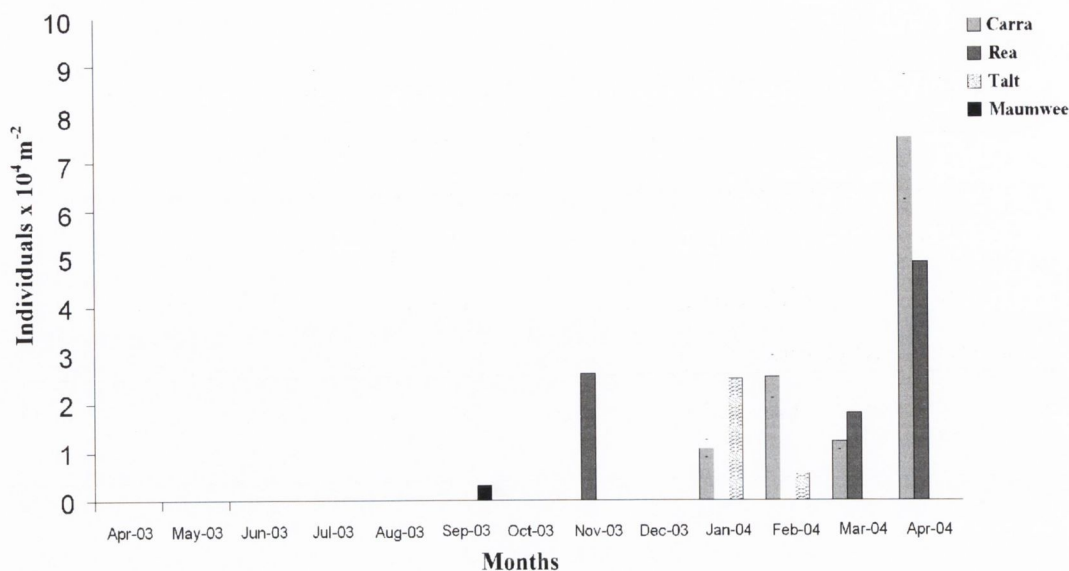


Fig. 5.19 Abundance of male *Daphnia*, April 2003 – April 2004. Mean values ($\pm$ SE, $n = 3$) of the three basins in Lough Carra are shown.

5.3.7 Relationships of zooplankton fecundity with nutrient availability

There were few significant relationships between the number of eggs per female of any taxa and measures of nutrient availability. Unlike what was previously observed there was no significant relationship between *Daphnia* fecundity and phosphorus concentrations in Carra; although the relative reproductive output between calanoids and *Daphnia* (the difference between the mean number of eggs per calanoid female and the mean number of eggs per *Daphnia* female), showed a positive association with the concentration of DIN (Pearson's, $r = 0.60$, $P \leq 0.05$, $n = 12$) and with both the ratios of DIN:MRP and DIN:TP (Spearman rank, $r = 0.59$, $P \leq 0.05$, $n = 12$ and Pearson's, $r = 0.65$, $P \leq 0.05$, $n = 12$, respectively) and although not significant (Pearson's, $r = 0.55$, $P = 0.06$, $n = 12$), there was a relatively close relationship between the number of eggs per female calanoid and the concentration of TN (Fig. 5.20). In Maunwee, there was also a significant relationship between the number of eggs per female *Bosmina* and TN concentration (Pearson's, $r = 0.63$, $P \leq 0.05$, $n = 12$) (Fig. 5.21). Apart from these two examples there was no evidence to suggest that zooplankton fecundity was associated with nutrient availability in any other lake.

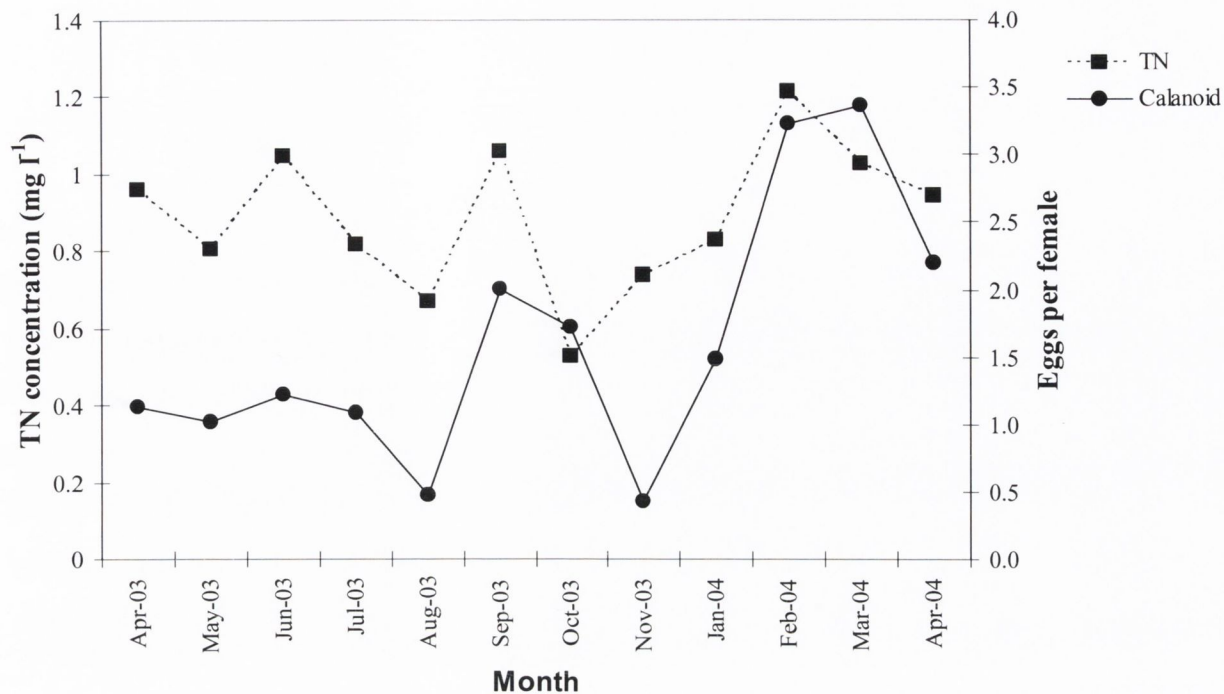


Fig. 5.20 Relationship between total nitrogen (TN) concentration (mg L⁻¹) and the number of eggs per female calanoids in Carra, April 2003 – 2004.

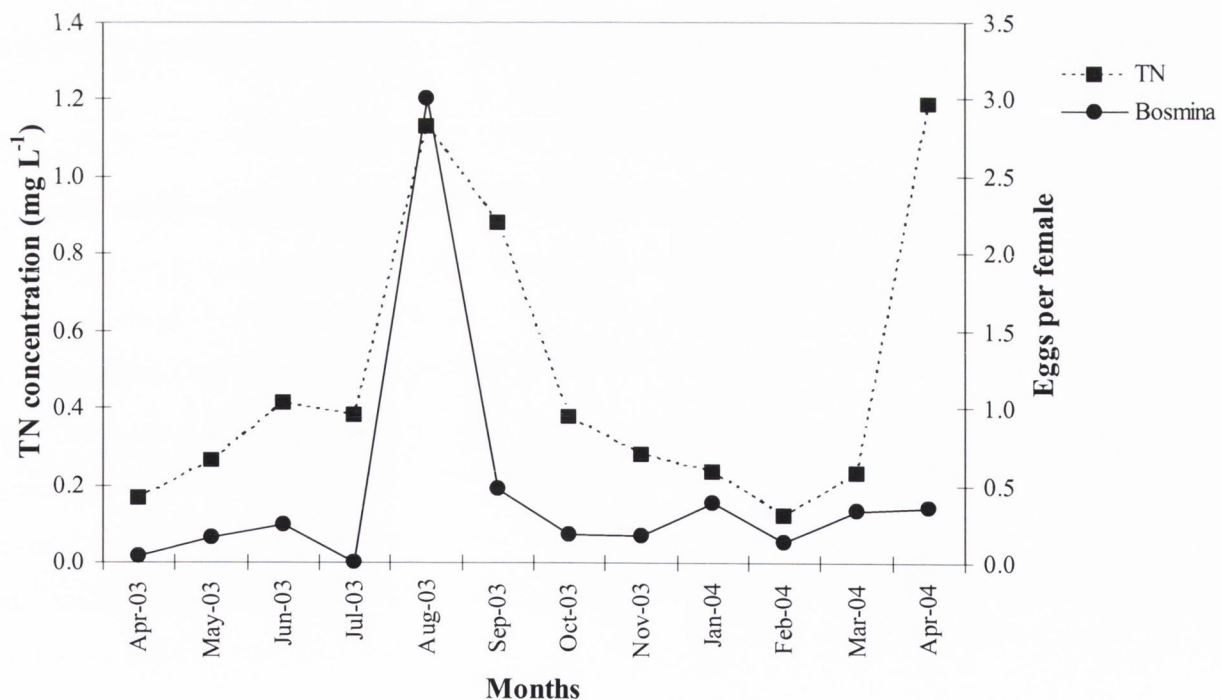


Fig. 5.21 Relationship between total nitrogen (TN) concentration (mg L⁻¹) and the number of eggs per female *Bosmina* in Maumwee, April 2003 – 2004.

5.4 Discussion

5.4.1 Relationship between zooplankton composition and seston stoichiometry

Both dissolved nutrients and seston stoichiometry suggest that in the majority of lakes there was no severe single P- or N-limitation of phytoplankton. On the contrary, seston elemental content generally indicated simultaneous moderate P and N deficiency or implied a balanced supply of the two nutrients. Morris & Lewis (1988) tested nine indices for accuracy in predicting nutrient limitation. Index values between the N- and P-limitation boundary lines were considered to be indicative of combined limitation, which was also considered inseparable from the category of nutrient sufficiency. Hansen *et al.* (1997) recorded a seston N:P ratio less than 22 following nutrient enrichment bioassays, however, a strong phytoplankton growth response was recorded in response to nutrient additions and was greatest upon addition of both N and P, which suggests co-limitation of phytoplankton by both nutrients. Co-limitation of phytoplankton by both N and P has often been recorded (Morris & Lewis, 1988; Elser *et al.*, 1990). The seston N:P ratios which were less than 22 in this study of six lakes are, therefore, just as likely to suggest co-limitation by both nutrients as they are to suggest nutrient sufficiency.

Correlation analyses revealed that there was a negative relationship between *Daphnia* abundance and both seston C:P and N:P ratios, indicating that the occurrence of *Daphnia* in the six study lakes was related to the availability of phosphorus. The abundance of *Daphnia* has previously been found to be positively correlated with seston particulate P concentration across 47 Norwegian lakes (Hessen, 1992) and negatively correlated with the seston C:P ratio of a set of temperate North American lakes (Hassett *et al.*, 1997). Total zooplankton biomass was also found to be correlated negatively with the seston C:P ratio in a whole lake experiment, and *Daphnia* were almost entirely absent from sites with a C:P ratio greater than 1000 (Elser *et al.*, 1998). DeMott & Gulati (1999) also found an inverse relationship between *Daphnia* abundance and the seston C:P ratio of three Dutch lakes, but no relationship between seston C:P and the abundances of zooplankton with low P requirements. This is similar to what was observed in the six lakes of this study, in which taxa such as *Bosmina* and copepods, which have relatively high cellular N:P

ratios, were not associated with the ratio of seston C:P. The only other zooplankter to show a significant relationship with seston elemental content were calanoid nauplii, which are now known to have a higher specific P-content than either copepodites or adults (Villar-Argaiz *et al.*, 2000; Carrillo *et al.*, 2001). They were found to be the most phosphorus rich component of the zooplankton community of Lake Michigan (Sternner & Schulz, 1998).

It may be that the abundance of zooplankton with high P requirements in the six lakes of this study were constrained to some extent by the seston C:P ratio. This is despite the fact that P-limitation for zooplankton was only apparent in a small number of lakes at the time of sampling. In 2005, three lakes, Maumwee, Carra and Feeagh, showed evidence of P-limitation based on seston N:P ratios, although seston C:P ratios were generally below threshold values which indicate possible P-limitation to *Daphnia* (Urabe & Watanabe, 1992; Brett *et al.*, 2000; Anderson & Hessen, 2005). In September 2005, however, high seston C:P ratios in Carra, and particularly Maumwee, were above resource thresholds for *Daphnia*. Estimations of seston C:P ratios in both of these lake, calculated from the ratio of Light:TP, were high between April 2003 and 2004, and in Maumwee was generally above the resource threshold. Both Maumwee and Carra, therefore, showed the most consistent evidence for P-limitation to zooplankton, although in Carra, such P-limitation was only evident during winter and spring.

Correlations, nevertheless, do not provide direct evidence for underlying mechanisms. Many other factors may possibly influence the occurrence of *Daphnia* such as predation, phytoplankton composition and abiotic conditions. Nonetheless, further support that community structure is influenced by seston stoichiometry is provided by the positive association between seston C:P and bulk zooplankton C:P, and indicates that high-P herbivores were generally not favoured at high C:P ratios. A similar relationship was also observed in a survey of 13 Dutch lakes (Gulati *et al.*, 1991; Sternner & Elser, 2002). Although the overall stoichiometry of the zooplankton community of the six study lakes was positively related to seston stoichiometry, there was, nevertheless, one apparently unusual observation and a certain degree of scatter, particularly at a seston C:P ratio of approximately 250. The outlier corresponded to a sample collected from Carra in July 2005, during which time calanoids dominated

biomass and the ratio of DIN:TP was low. The high zooplankton C:P ratio relative to the seston C:P at this time suggests a disproportionate excretion of P relative to N, as high-N calanoids accumulated a comparatively higher amount of N and released a greater proportion of P. A similar situation to this was also observed in Feeagh during September 2005, when bulk zooplankton C:P was greater than seston C:P. At this time the zooplankton community of Feeagh was dominated by both cyclopoid and calanoid copepods as well as *Diaphanosoma*, all of which were found to have high N requirements. In September, the high ratio of N:P measured in the zooplankton compared with that of the seston, suggested that N was the most deficient element in the lake for zooplankton at this time. This September sample from Feeagh corresponds to one of the points causing the scatter observed in Fig. 5.7. In addition, two of the other points located within this scatter correspond to samples taken in Easky, a lake with a low *Daphnia* biomass, which is almost certainly a consequence of its low pH and alkalinity conditions. Sterner *et al.* (2000) reported a statistically significant, although generally weak, correlation between bulk zooplankton P content and the P content of seston in a set of Canadian lakes. Their sample lakes did not include many *Daphnia* dominated systems, and they considered this to be the most likely reason for the weak relationship observed. It is, therefore, possible to account for much of the scatter in Fig. 5.7, which further supports the suggested relationship between bulk zooplankton C:P ratios and the same ratio in the seston food resource.

5.4.2 Relationship between zooplankton dynamics and the availability of nutrients

Despite the positive associations between the occurrence of P-rich taxa, such as *Daphnia*, and seston P availability across the six lakes of this study, there were no strong and consistent seasonal relationships observed between zooplankton and the availability of nutrients such as phosphorus and nitrogen in the water column. There was some evidence for resource P-limitation for zooplankton in Maumwee, Carra and Feeagh, which is supported not only by direct measures of seston elemental content but also for Carra and Feeagh by the high winter and spring ratios of DIN:TP and in Carra and Maumwee high estimated C:P (Light:TP) ratios for much of the year in Maumwee and during winter and spring in Carra. Nonetheless, between July and October very low DIN:TP ratios recorded in Carra suggest N-limitation during this period, a pattern also observed in the other two high-alkalinity, although in Rea a

reduction in DIN:TP was evident from May onwards. The suggestion of N-limitation in the high-alkalinity lakes during the summer is corroborated to some extent by measures of seston stoichiometry in both Rea and Carra, where high sestonic C:N and low N:P values were recorded in 2005 during May and July, respectively. At these times bulk zooplankton N:P ratios were also higher than those of the seston, indicating that N was the most deficient nutrient relative to zooplankton requirements. In Rea the bulk zooplankton N:P ratio was also higher than the seston N:P during September, but the difference between the two ratios was much less than that observed in May. Seston elemental content indicated that Feeagh may also have experienced deficits in N relative to zooplankton needs during September, but the ratio of DIN:TP indicated that Feeagh may experience P-limitation throughout much of winter and spring. This is supported by the high seston C:P and N:P ratios recorded in May 2005.

The zooplankton and nutrient dynamics observed in Carra between April 2003 and 2004 corresponded to observations made in the lake during the previous two years. High *Daphnia* biomass during spring and low biomass during summer was coincident with high and low concentrations of DIN respectively. This is similar to what was observed in Chapter 4 and is consistent with the premise of consumer driven nutrient recycling. Comparable patterns in consumer driven nutrient recycling were not, however, observed in the other high-alkalinity lakes, despite similar patterns in nutrient availability among all three lakes. There was a suggestion for such a relationship in Rea, where maximum cyclopoid biomass during the summer corresponded to reduced DIN concentration. This summer peak in cyclopoid biomass, however, was only evident for a brief period in August 2003 and is unlikely to have accounted for the consistently low values of DIN over the late spring and summer. Overall, evidence for the presence of consumer driven nutrient recycling in lakes other than Carra is poor.

There was also a positive association between fractions of N and calanoid fecundity in Lough Carra, but unlike the previous two years there was no relationship between P and *Daphnia* egg production. Fecundity patterns in the other lakes failed to show significant relationships with measures of in-lake P and N availability, although in Maumwee, there was a positive association between the number of eggs per *Bosmina*

female and the concentration of TN. Between April 2001 and 2003, evidence for nutrient limitation for zooplankton in Carra was principally provided by patterns in fecundity, whereas fluctuations in community biomass were more suggestive of nutrient recycling by herbivores. Such evidence based on fecundity patterns was absent from the other lakes in the study and the weaker evidence in Carra compared with previous years further emphasises the need for experimental verification of the field based evidence in Chapter 4.

Although most of the correlations between zooplankton and nutrient availability in the six study lakes were in agreement with stoichiometric expectations, there were, nevertheless, no consistent relationships evident across all lakes. The only lake to show a positive, but weak, relationship between *Daphnia* biomass and phosphorus was Rea, and no associations were found between other P-rich taxa such as *Ceriodaphnia*, even in lakes such as Easky where they dominate biomass at certain stages during the year. Hall *et al.* (2004) also failed to find a relationship between sestonic C:P ratios and species, other than *Daphnia*, with high specific P content. They provided two potential explanations for this. The first suggests that these species were capable of differentially using a high-P resource such as bacteria. The second suggests that body nutrient composition might not always directly correlate with the nutrient demands of grazers, as other traits such as respiration rate and conversion efficiency may also determine nutrient demands.

There are a number of possible explanations for the poor association between zooplankton seasonal dynamics and nutrient concentrations in the present study. For example, there was no evidence of large seasonal shifts in nutrient limitation in any of the study lakes, and at least two lakes showed little or no evidence for nutrient limitation at all. Previous investigations showing relationships between seasonal nutrient availability and zooplankton community structure and fecundity were carried out in conditions where large variations in food quality occurred (DeMott *et al.*, 2001; Makino *et al.*, 2002; Scheuerell *et al.*, 2002; Park *et al.*, 2003). It may also be possible that the zooplankton community in some of the lakes are food quantity and not quality limited. It has been suggested that the relative importance of algal quality for zooplankton production may decline with decreasing algal quantity (Sterner & Robinson, 1994; Rothhaupt, 1995; Sterner, 1997). At very low food concentration

when production is close to zero, metabolic requirements for C are understood to become more important than growth requirements for nutrient elements. Contrary to these findings, however, Boersma & Kreutzer (2002) found that even at low food levels not only was energy important, but so too was the mineral content of the food. Despite these two conflicting results, it will, nevertheless, be difficult to separate food quantity and quality effects in natural situations. Confounding effects of food quantity may influence attempts to directly associate zooplankton biomass and reproduction to ambient nutrient conditions. In Lough Feeagh for example, chlorophyll *a* concentrations fell below $1 \mu\text{g L}^{-1}$ for much of autumn and winter. Assuming that all particulate matter is edible, this would be well below the threshold food concentration (which approximates $1.8 \mu\text{g}$ of chlorophyll *a* L^{-1}) which is required by herbivores to balance metabolic losses (Lampert, 1977; Sterner & Schulz, 1998). This may account for the dearth of significant relationships between zooplankton egg production and biomass and measures of nutrient availability in Feeagh. In many of the other lakes chlorophyll *a* fell below the threshold concentration at various stages throughout the year. The presence of cladoceran males and ehippia in many of the lakes also suggest some deterioration of the environment, such as a change in food concentration or over-crowding. In Carra for example, ehippia and males were most frequently observed during periods of maximum *Daphnia* abundance. The production of males in this case was most likely owing to density dependent resource limitation. Male *Daphnia* in Talt were most evident during the winter as was *Ceriodaphnia* and *Bosmina* males and ehippia in Easky. Reduced chlorophyll *a* concentrations during this period in both of these lakes is suggestive of food quantity limitation. In addition, other food quality factors, which were not measured in this study, may be determining the nutritional quality of the phytoplankton. For example, algae size and shape, digestion resistance, secondary metabolites and biochemical composition have all been used to explain food quality for zooplankton (Van Donk *et al.*, 1997; Brett & Müller-Navarra, 1997; Lampert & Sommer, 1997; DeMott, 1999; DeMott *et al.*, 2001; Ferrão-Filho *et al.*, 2005).

There is some evidence to suggest that both fish and invertebrate predation in the six study lakes influenced seasonal patterns in community structure (Chapter 3). Predation and nutrient supply are both considered important in influencing food-web dynamics and their relative importance is still a matter of discussion (McQueen *et al.*,

1986; Jeppesen *et al.*, 1997). As discussed in Chapter 3, declines in *Daphnia* biomass in lakes such as Feeagh, Carra and Talt and Rea can to some extent be attributed to fish predation. Predation may, therefore, have a greater role to play than nutrients in influencing the seasonal dynamics of the zooplankton populations of these lakes.

5.4.3 Elemental content of individual zooplankton taxa

Overall, the elemental contents of all the analysed zooplankton taxa were in agreement with previous reports for freshwater taxa (Andersen & Hessen, 1991; Sterner & Hessen, 1994; Elser *et al.*, 2000b; Carrillo *et al.*, 2001; Sterner & Elser, 2002). Cladocerans such as *Daphnia* have been found to have N:P ratios between 12 and 18, whereas the N:P ratios in calanoids copepods generally exceed 30. Most of this stoichiometric variation has been related to variation in P content which has been found to range from 0.5 % to over 2.5 % of dry weight (Main *et al.*, 1997; Elser *et al.*, 2000b; Sterner & Elser, 2002). In contrast, % N in zooplankton varies over a relatively narrow range, from approximately 8 – 12 % (Walve & Larson, 1999). Measures of zooplankton stoichiometry in this study were in full accord with these observations. In conjunction, *Daphnia* were found to be responsible for the greatest amount of variation in elemental content among taxa. These differences, however, were not entirely owing to differences in % P. *Daphnia* had lower N than calanoids, and there was also statistically significant difference in the C and N content of *Bosmina* and calanoids.

When taxa were ordered along a gradient of increasing N:P and C:P ratios, however, a number of discrepancies with published data became apparent. Firstly, in contrast to previous studies (Andersen & Hessen, 1991), *Ceriodaphnia* were found to have a lower specific P content than *Daphnia*. In addition, *Diaphanosoma* and *Holopedium* were found to have higher N:P contents than copepods, which is at variance with previously reported values (Andersen & Hessen, 1991; Sterner & Schulz, 1998; Sterner & Elser, 2002). The stoichiometric ratios calculated for *Diaphanosoma* and *Ceriodaphnia* in this study, however, were based on only one observation. Additionally, there was a methodological issue relating to stoichiometric measurements for *Holopedium*. It was often difficult to remove algae and detritus found clinging to the surface of the muco-polysaccharide mantle of individuals from

this taxa, which may account not only for the inconsistency with published data, but also for the large variations around the mean stoichiometric ratios calculated for this cladoceran.

There was no observed difference in elemental content of *Daphnia* among lakes and no relationship between the % P content of *Daphnia* and the seston C:P ratio of the lakes. *Daphnia*, therefore, maintained a relatively constant elemental content despite differences in seston stoichiometry. Contrary to these findings, DeMott *et al.* (2004) found that declines in the P-content of natural populations of *Daphnia* were associated with declines in dietary P. The results presented here, however, are consistent with the earlier studies of Andersen & Hessen (1991) and Hessen & Lyche (1991), which found no evidence for variation in *Daphnia* P-content between lakes and seasons. Their study sites showed signs of only weak or sporadic resource P-deficiency and were analogous to the lakes in this study in that seston C:P ratios were often less than 250. Nevertheless, mesocosm experiments carried out by DeMott *et al.* (2004) over a range of sestonic C:P from 100 to 300 found a decline in *Daphnia* P-content with increasing seston C:P ratio. There was, nevertheless, a difference among lakes in the % N content of calanoids, and this difference implicitly arose from Easky and Talt, which were the only lakes which had calanoid populations comprising more than just *Eudiaptomus gracilis*. In Easky *Mixodiaptomus laciniatus* and *Arctodiaptomus laticeps* were also recorded, and *Arctodiaptomus laticeps* was the only species of calanoid recorded in Talt. Variation in calanoid N-content among lakes was, therefore, the result of inter-specific differences in the specific N-content of calanoids. In addition, there was a large variation around the mean % N content calculated for calanoids in Easky, which is probably owing to the larger number of calanoid species observed in this lake compared with the other lakes, which all had calanoid communities comprising only one species.

5.4.4 Conclusion

This field study provides some evidence which suggests that the occurrence of *Daphnia* across six lakes may be related to dietary P availability and, moreover, as predicted by stoichiometric theory other coexisting zooplankton species were found to be less sensitive to P-limitation. The bulk zooplankton C:P ratios of the six lakes

were also found to be positively associated with sestonic C:P ratios and this linear pattern was evident even at low seston C:P values.

There were, however, very weak associations between seasonal variations in zooplankton dynamics and seasonal fluctuations in nutrient availability in many of the lakes. This suggests that factors other than elemental resource limitation, such as fish predation or food quantity limitation, may have a greater influence on the seasonal patterns in the zooplankton community structure of these lakes. Nevertheless, the data also suggest that at any given time the maximum abundance of high-P taxa such as *Daphnia* may be somewhat constrained by the seston C:P values.

There was also inconsistent evidence between support for consumer driven recycling in Carra compared with the other high-alkalinity lakes, despite comparable zooplankton community structures and water chemistry in all three lakes. This emphasises a high degree of variability in the potential for zooplankton to regulate the identity of the growth limiting nutrient in a lake. Lough Carra, represented a relatively unique situation among these lakes, in which fluctuations between high-N calanoid dominated biomass and high-P *Daphnia* dominated biomass corresponded to periods of reduced nitrogen and phosphorus loading, respectively. Increased biomass of both taxa, therefore, helped to accentuate the already N-limited and P-limited environments.

The majority of published material on lake seston nutrient ratios originates from data collected in Canada (Brett *et al.*, 2000). Generalisations about ‘typical’ lake seston may, therefore, be biased, but for now it is difficult to say to what degree or in what direction such bias may occur (Brett *et al.*, 2000). The elemental ratios of seston in the six lakes of this study are, therefore, an important addition to the current knowledge base, and provide data which suggests that some of these lakes are nutrient limited at certain times of the year. When combined with indices that represent N and P availability to phytoplankton (eg. DIN:TP and Light:TP), there was evidence to suggest that Carra and Rea were N-limited during the summer. There was also evidence of P-limitation in Carra during the winter and spring, and in Maumwee throughout much of the year.

Analyses of the nutrient content of seston and zooplankton in the six lakes of this study revealed an association between zooplankton community structure and seston elemental composition. A positive correlation was observed between bulk zooplankton C:P content and bulk seston C:P content, which suggests that with declining food P content, high-P taxa are replaced by low-P taxa. A similar relationship was also recorded in a group of thirteen Dutch lakes (Gulati *et al.*, 1991). The occurrence of *Daphnia* in the six lakes was also negatively correlated with the ratio of seston C:P and is in agreement with studies which also positively related the abundance of high-P taxa such as *Daphnia* to seston P (Hessen, 1992; Hassett *et al.*, 1997; DeMott & Gulati, 1999). The patterns observed in this study are, therefore, in accordance with the hypothesis that stoichiometry may be involved in determining zooplankton community structure in natural populations, as seston C:P appeared to have some influence in constraining the maximum abundance of high-P taxa such as *Daphnia* across the six study lakes. There was also a negative relationship between P-rich calanoid nauplii abundance and seston C:P, providing additional evidence for the importance of resource elemental content for zooplankton communities.

Other factors were, nevertheless, also responsible for the observed distribution of zooplankton. Alkalinity and pH were found to have a role to play in influencing

zooplankton community structure in the six study lakes. *Daphnia* and copepods, for example, dominated zooplankton biomass in the high-alkalinity lakes at all times of the year and generally had a lower abundance and biomass in the low-alkalinity lakes compared with the high-alkalinity. *Daphnia* had a particularly reduced occurrence in Lough Easky, which had the lowest recorded pH values of all lakes. In contrast, cladoceran taxa such as *Holopedium* and *Diaphanosoma* were more widespread in the low-alkalinity lakes compared with the high-alkalinity lakes, which is in accordance with previous studies which found an association between these species and low-alkalinity environments (Hamilton, 1958; Hessen *et al.*, 1995b; Kappes & Sinsch, 2005). The size structure of the crustacean community in the low-alkalinity lakes showed a greater frequency of individuals in the smaller size classes, whereas there was a more even distribution of individuals across all size classes in the high-alkalinity lakes and supports previous field surveys which found a replacement of large bodied zooplankton by smaller taxa along a gradient of decreasing alkalinity (Tessier & Horwitz, 1990; Hessen *et al.*, 1995a). The abiotic environment was, therefore, involved in influencing the overall distribution of taxa across the six lakes of this study.

Although there was some evidence to suggest a relationship between the occurrence of zooplankton taxa such as *Daphnia* and seston elemental content in the six lakes of this study, in many of the lakes there was a poor association between ambient nutrient availability and seasonal variation in zooplankton population dynamics. With the exception of Carra, evidence for resource nutrient limitation based on zooplankton fecundity patterns was absent and there is a need to support the apparent relationship in Carra with experimental verification.

A disproportionate amount of research on food quality has focused on *Daphnia* (Sternner & Schulz, 1998; Brett *et al.*, 2000). To fully understand the resource elemental limitation of zooplankton, research on taxa other than *Daphnia* is required (Sternner & Schulz, 1998). In this field study, three of the study lakes were dominated by cladoceran species other than *Daphnia*. There was, nevertheless, no seasonal stoichiometric associations observed for these taxa. If the hypothesis of mineral limitation is indeed universal, other zooplankton with high P contents would be expected to respond similarly to seston C:P ratios. Hall *et al.* (2004) also failed to find

a relationship between P-rich *Ceriodaphnia* and the availability of dietary P, and suggested that *Ceriodaphnia* may be better than *Daphnia* at exploiting high-P resources such as bacteria, and are consequently less affected by P-limitation than *Daphnia*. In fact, *Daphnia* have been found to be effective grazers on bacteria (Geller & Müller, 1981; Hart & Jarvis, 1993) and should be capable of utilising this P resource more effectively than most other cladoceran taxa (Sterner & Schulz, 1998). The alternative explanation provided by Hall *et al.* (2004) for the poor response of P-rich taxa other than *Daphnia*, suggests that traits in addition to elemental composition may influence grazer nutrient requirements. Further work which combines body nutrient composition with other physiological and ecological factors is, therefore, necessary. An integrated approach such as this should provide clarification on the role of zooplankton stoichiometry in determining the outcome of zooplankton competitive interactions in different food-quality environments (Hall, 2004; Hall *et al.*, 2004).

In field populations it is often difficult to assess the degree of nutritional stress, largely owing to the myriad of interacting factors which may influence zooplankton communities. Declines in populations may be the result insufficient food quantity or quality, predation, competition, or disadvantageous abiotic factors. In my study lakes, size distribution analyses provided evidence to suggest that both invertebrate and vertebrate predation influenced seasonal patterns of zooplankton. Inference of fish predation was particularly evident in Feeagh, Carra and Talt and Rea and invertebrate predation in Feeagh, Maumwee, Talt and Rea. It is also not possible to rule out the effect of other factors such as low food quantity or other food quality parameters, such as algal digestion resistance or toxicity or insufficient biochemical content, which were not investigated in this study.

Nevertheless, stoichiometry may provide further clarification on some of the observed interactions between zooplankton taxa recorded in Chapter 3. Differences in the alternating patterns of dominance between *Daphnia* and *Eudiaptomus* in both Rea and Carra could not be entirely attributed to differences in fish predation pressure between the two lakes. In Rea, fluctuations between the two taxa may be the result of competitive interaction between the two consumers, and ecological stoichiometry provides a possible mechanism for such competition. Lough Rea was the only lake in which a positive correlation was observed between *Daphnia* biomass and TP

concentration as well as a negative relationship with TN and PN. Although these relationships were relatively weak, the correlations were nevertheless supported by the fact that *Daphnia* dominated zooplankton standing biomass in Rea when TP concentrations were high. There was also a positive association between post-naupliar calanoids in Rea and TP concentration, but this relationship was entirely a consequence of the relationship between copepodites and TP. There was also a positive relationship between calanoid nauplii and TP. This is consistent with studies which have identified strong ontogenetic shifts in the phosphorus content of copepods, and suggests a life-history bottleneck, wherein the calanoid population was constrained by the availability of phosphorus during early life stages (Carrillo *et al.*, 1996; Villar-Argaiz & Sterner, 2002). A specific P content of 1.2 % P as DW was recorded for early stage (CII) copepodites by Villar-Argaiz *et al.* (2000) which would make them as sensitive to P-limitation as some species of *Daphnia*. It is, therefore, likely that at certain stages of their life-history, calanoids are in competition for phosphorus with *Daphnia*. Declines in *Daphnia* abundance in Rea may consequently have resulted in a competitive release, allowing for increased post-naupliar calanoid biomass. Consideration of the role of P-limitation of copepods at early copepodite stages would, therefore, be an important development in our understanding of crustacean competition and copepod success (Villar-Argaiz *et al.*, 2000).

Species specific variation in the stoichiometry of grazers has the potential to influence competition and may also promote herbivore co-occurrence in homogenous environments (Sterner & Hessen, 1994; Andersen *et al.*, 2004; Loladze *et al.*, 2004). Taxa such as *Bosmina*, which have been found to be less sensitive to P-limitation than *Daphnia* (Schulz & Sterner, 1999), may be considered to occupy different 'stoichiometric niches'. Using a stoichiometrically explicit model, Hall (2004) predicted coexistence at intermediate nutrient supply when each grazer is limited by the resource for which it is the lesser competitor. In such a scenario resource quantity limits the P-poor consumer and resource quality the P-rich consumer. Models such as this, which have not yet been confirmed experimentally, may provide further elucidation on the observed patterns of co-existence between *Bosmina* and *Daphnia* in lakes such as Rea, Carra and Feeagh.

The importance of ‘bottom-up’ stoichiometric effects on consumer dynamics will also be dependant on the relative impact of ‘top-down’ forces (Andersen *et al.*, 2004). Elser *et al.* (1998) hypothesized that *Daphnia* is regulated equally by both predation and stoichiometric food quality. They suggested that *Daphnia* can endure substantial predation pressure in a lake with a high quality food resource. Alternatively, food resource quality can be insufficient to allow *Daphnia* growth and reproduction, even in a lake where planktivores are absent and low-quality food has been found to dampen cascading trophic interactions (Elser *et al.*, 1998). In the lakes of this study, there was some evidence to suggest that seston nutrient content influenced zooplankton community structure, and particularly the distribution of P-rich taxa such as *Daphnia*. Nevertheless, there was no consistent evidence across all six lakes that seasonal fluctuations in zooplankton biomass and community structure were influenced by seston nutrient content. It is, therefore, important to consider the role of stoichiometry as only one of several alternative factors influencing zooplankton community structure and dynamics.

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