ZOOPLANKTON IN THE NEWLY FORMED CARDIFF BAY

A thesis submitted for the higher degree of Doctorate of Philosophiae

by

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V Summary

1. Despite their wider importance in freshwaters, the ecology of zooplankton has been neglected in artificial lakes. Seasonal, spatial and community dynamics were therefore examined in Cardiff Bay, a recently formed, artificial, freshwater lake of 200 ha in urban south Wales.

2. Global meta-analysis illustrated that zooplankton composition probably differs systematically between artificial and natural lakes, with natural lakes appearing to create more conditions for specialist taxa.

3. Fortnightly surveys over two years show that Cardiff Bay has quickly acquired zooplankton composition typical of large, eutrophic lakes. Seasonal dynamics generally follow the Plankton Ecology Group (PEG) succession model, with dominant zooplankton apparently co-existing through variations in population timing linked to variations in the size-range of algal food.

4. Extensive spatial data reveal relatively homogeneous zooplankton composition across the main body of Cardiff Bay, probably reflecting homogeneous water quality, lake mixing and artificial aeration. In contrast, on a smaller spatial scale, zooplankton abundance is structured spatially around food concentrations in warmer water. Spatial-scale could be important in detecting the relative influence of spatial and environmental factors on zooplankton more generally.

5. In one of the first ever investigations of its type in zooplankton, temporal and spatial data from Cardiff Bay were used to assess functional trait composition and nestedness. Environmental dynamics and food-resource seasonality were matched by marked seasonal change in zooplankton trait composition and diversity, implying that seasonality has formed an important template for trait selection. Spatial variations were only important for trait composition locally.

6. These data add fundamentally to the understanding of the ecology of Cardiff Bay as a newly formed, artificial and lowland lake, while also contributing to the understanding zooplankton ecology more generally. The effects of lake management techniques on Cardiff Bay's zooplankton require further investigation. Longer-term surveys are advocated to track planktonic development, while more detailed investigations of the ecological role of zooplankton in Cardiff Bay will provide valuable management information.

Chapter 1: General Introduction

1.1 Abstract

1. Zooplankton are key organisms in the transfer of energy between trophic levels in standing waters. They have been used as model organisms in studies of competition, dispersal, predator-prey interactions and in the development of general ecological theory. However, studies of zooplankton in natural lakes have been far more numerous than those in artificial water bodies.

2. Available literature suggests that several areas of zooplankton community ecology have been relatively neglected in artificial lakes. These include i) direct comparisons between zooplankton assemblages in artificial and natural lakes, despite their differences in age; ii) hydrological and morphological factors that could potentially cause variations within and between lakes; iii) the effects of lake management on seasonal zooplankton dynamics and zooplankton distribution; iv) over-wintering populations; v) zooplankton functional traits, and trait character in relation to possible environmental selection. Zooplankton case studies in lowland, artificial, urban lakes are surprisingly rare given that such lakes are now often developed for amenity, recreation, conservation and flood storage, in addition to their role in water supply.

3. In this thesis, a series of hypotheses were developed in order to address the above gaps in knowledge and tested in Cardiff Bay, a recently formed and highly managed urban freshwater lake in South Wales (UK). Specific questions addressed were: 1) Globally, do artificial water bodies support different zooplankton assemblages from those in natural lakes? 2) Does the zooplankton community of Cardiff Bay vary in ways predicted by ecological theory, and particularly as predicted by the Plankton Ecology Group (PEG) qualitative model of plankton succession? 3) In Cardiff Bay, is there a persisting community of interacting zooplankton species even over less productive periods of the year? 4) Do spatial and temporal dynamics in the zooplankton community of Cardiff Bay reflect local water quality? 5) Do management practices in Cardiff Bay influence the temporal and spatial dynamics of

zooplankton? 6) Do the traits of zooplankton species in Cardiff Bay vary spatio-temporally in ways that might reflect environmental variation?

1.2 Introduction

Zooplanktonic micro-invertebrates live suspended in the open water of water bodies ranging in scale from water-filled ditches to the open oceans (Gurney, 1933a). As primary and secondary consumers, zooplankton are pivotal in the transfer of energy between trophic levels and nutrient cycling in aquatic ecosystems (Hutchinson, 1967). Zooplankton are also ideal model organisms that have been involved centrally in the development of classical ecological theory. The most common freshwater species are arthropod crustaceans and aschelminth rotifers (Thorton *et al.,* 1980) whose small size, relatively short generation time and ease of culture have encouraged studies of wide ecological relevance, such as competitive interactions (e.g. Leibold, 1991; Dawidowicz and Weilanier, 2004; Vijverberg and Vos, 2006), species co-existence (Hutchinson, 1967; Richerson *et al.,* 1970; Grenney *et al.,* 1973; Gaedeke and Sömmer, 1986; Keitel and Chase, 2004), trophic interactions (e.g. Brooks and Dodson, 1965; Dodson, 1974) and succession (Sömmer *et al.,* 1986).

Despite their importance, there is a surprising lack of literature focussing on zooplankton community dynamics in artificial water bodies, where traditionally phytoplankton and microbial ecology have been of primary research interest (e.g. Tadonléke and Sime-Ngando 2000; Jardillier *et al.,* 2004). This gap is unfortunate, because artificial water bodies are increasingly being developed for amenity, recreation, nature conservation, energy generation and flood defence in addition to their long-standing role in water supply. Enhanced knowledge of zooplankton ecology in these systems would not only increase opportunities to examine ecological theory, but also would improve the basis for lake management.

In this opening chapter, available literature is reviewed to inform the development of key questions and hypotheses about spatial and seasonal zooplankton community dynamics in Cardiff Bay, a recently formed urban freshwater lake in South Wales (UK). This introduction also outlines the scope and contents of the rest of the thesis.

1.3 Zooplankton Community Ecology and Artificial Water Bodies

1.3.1 Artificial Water Bodies

Provision of water, renewable energy and flood defence are principal reasons for the construction of artificial water bodies. However, their creation is increasingly aimed also at encouraging economic growth in an area, through attracting businesses, recreation and amenity (Hoyle, 2000). Other opportunities also arise in these cases, for example for ecological restoration and nature conservation. Such waterfront regeneration schemes were popular in the USA in the 1970s (Jones, 2007) and have since been used as models for the regeneration of other maritime cities such as Barcelona, Rotterdam, Amsterdam, London, Cardiff, Liverpool and Bristol.

Artificial water bodies are geologically very young compared with natural lakes formed over millennia, but the rate at which zooplankton communities become established in new water body is poorly known and there are few studies investigating the establishment of zooplankton dynamics in artificial lakes. Regular small-scale disturbances, however, can prevent zooplankton communities reaching equilibrium (Matsumura-Tundisi and Tundisi, 2002; Scheffer *et al.,* 2003; Aubé *et al.,* 2005), implying that only a short time following initial colonisation, there may be no discernible impact of water body age, consistent with observations by Dodson *et al.* (2006).

Such disturbances might include those arising from management activities. Since artificial water bodies are generally created for the provision of services or amenity, human influence commonly continues after construction. Management practices such as artificial destratification are often employed to reduce the undesirable impacts of eutrophication, such as cyanobacterial blooms, reduced oxygen concentration and increased turbidity (Cowell *et al.,* 1987; Hawkins and Griffiths, 1993; Lewis *et al.,* 2003; Antenucci *et al.,* 2005; Becker *et al.,* 2006; Burford and O'Donohue, 2006). Changes in zooplankton composition from large to small bodied cladocera have been observed during aeration (e.g. Cowell *et al.,* 1987) but few studies have documented the effect of this remediation method on whole zooplankton assemblages or the potential disturbance to community dynamics (Sömmer *et al.,* 1986).

Large-scale studies have shown that water-body size, productivity and geographic location all influence zooplankton species richness and community composition in lakes (e.g. Fryer, 1985; Sömmer, 1996; Dodson, 1991; Dodson, 1992; Hessen *et al.,* 2006). Whilst these large-scale studies provide a useful context for understanding influences on zooplankton species diversity among natural lakes on single continents, few studies have considered the extent to which artificial water bodies modify zooplankton richness or composition in relation to key, large-scale influences such as lake size, depth, morphology and continental position. In one large-scale study, Dodson (1992) considered the effect of lake size and depth on zooplankton, but not differences between artificial and natural lakes. This lack of specific assessment is surprising due to differences in age, hydrological regime, morphometric characteristics and degree of human influence between artificial and natural water bodies. All of these may be expected to influence zooplankton communities. Investigations into the potential assemblage differences between artificial and natural water bodies could provide an important insight into ecosystem-wide variations, which in turn is vital to the identification and application of management needs, but are as yet lacking.

1.3.2 Drivers of Seasonal Zooplankton Dynamics

Competitive exclusion theories predict that competing species cannot co-exist, since the most effective resource-exploiting species out-compete and exclude others, ultimately leading to complete dominance by one species (Hardin, 1960). In reality, water bodies rarely reach such stages of equilibrium (Hutchinson, 1961; Matsumura-Tundisi and Tundisi, 2002; Scheffer *et al.,* 2003) and generally contain a greater diversity of species than would be expected from traditional competition models. Periodic fluctuations in selective processes allow the co-existence of competing zooplankton species (Richerson *et al.,* 1970; Grenney *et al.,* 1973; Gaedeke and Sömmer, 1986; Keitel and Chase, 2004) in line with the intermediate disturbance hypothesis (Connell, 1978).

Annual zooplankton community dynamics are driven by factors such as temperature (e.g. Stockwell and Sprules, 1995; Wolfinbarger, 1999; Benndorf *et al.,* 2001; Rettig *et al.,* 2006), primary production and nutrient availability (e.g. Hessen at al 2006), flushing rate (Wolfinbarger, 1999), predator-prey interactions (Boersma *et al.,* 1996) and competition between species (Hu and Tessier, 1995; Cáceres, 1998). Variations in lake morphology, and stratification also have potentially large effects (e.g. Matveev and Matveeva, 2005). However, interactions among the many drivers involved are complex (Brönmark and Hansson, 2005; Schalau *et al.,* 2007).

Despite this complexity, seasonality among freshwater zooplankton is relatively predictable, engendered initially by a bloom of small phytoplankton in early spring which is grazed down by small herbivorous zooplankton. Larger-celled phytoplankton are then exploited by larger herbivores before grazing pressure exceeds primary production, which coupled with nutrient depletion leads to a collapse in algal food resources and a mid-summer decline in zooplankton abundance (Tessier and Welser, 2006). A secondary peak in zooplankton abundance is common, as phytoplankton populations recover in early autumn. These events are expressed in the Plankton Ecology Group's (PEG) qualitative model (Sömmer *et al.,* 1986), conceived for typical stratifying lakes but tested initially using data from 24 lakes, ponds and unmixed reservoirs. The PEG model is considered to provide a basis for eutrophic, temperate, stratifying lakes in general, and emphasises the seasonal effects of temperature, light, nutrients and fish predation as major factors driving plankton development.

While many predictions from the PEG model are well supported, tests and applications have overwhelmingly involved natural rather than artificial lake-systems. As discussed, management practices such as aeration are often designed to disrupt some of the factors that drive plankton dynamics, increasing oxygen concentration and limiting light availability (e.g. Heo and Kim, 2004; Müller and Stadelmann, 2004; Becker *et al.,* 2006). Artificial aeration homogenises lake physico-chemistry (e.g. Heo and Kim, 2004), lowers surface water temperatures, and can lower internal phosphorous loading, altering phytoplankton succession (e.g. Becker *et al.,* 2006). In some cases, previously dominant cyanobacteria are replaced by diatoms that are more easily exploited by zooplankton (e.g. Steinberg, 1983; Wetzel, 2001; Lewis *et al.,* 2003; Heo and Kim 2004; Becker *et al.,* 2006). Alterations in mixing depth and temperature regime might also be expected to affect zooplankton succession (Gerten and Adrian, 2002; Berger *et al.,* 2007). Reduced residence time in artificial lakes and reservoirs might also affect the applicability of PEG predictions by promoting flushing of phytoplankton and zooplankton and disrupting the succession of communities (Sömmer et al. 1986).

In addition to the bias towards natural lake-based studies of seasonal zooplankton dynamics, temporal investigations have tended to concentrate on more productive periods between spring and autumn, when zooplankton abundance is generally highest (e.g. Whiteside *et al.,* 1978; Vanni and Temte, 1990; Müller-Navarra and Lampert, 1996; Talling, 2003; Tessier and Welser, 2006; Horppila *et al.,* 2009). This has resulted in limited information on over-wintering zooplankton populations in temperate freshwater systems. However, terrestrial carbon sources can act as important energy subsidies for freshwater ecosystems (Pace *et al.,* 2004; Carpenter *et al.,* 2005; Maguire and Grey, 2006; Matthews and Mazumder, 2006) suggesting that zooplankton community dynamics can continue over periods of low quality autochthonous production.

1.3.3 Drivers of Spatial Zooplankton Dynamics

Natural animal populations are rarely homogeneously distributed. Neither are their distributions entirely random. According to hierarchy theory, at the whole-lake scale physical abiotic factors, such as lake morphometry (Håkanson, 2005), river inflow (Yacobi *et al.,* 1993; Romare *et al.,* 2005), surrounding land use (George and Winfield, 2000; Dodson *et al.,* 2005; Hoffmann and Dodson, 2005; Dodson *et al.,* 2009) and wind-induced water movement (George and Edwards, 1976; George, 1981; Kalikhman *et al.,* 1992; Jones *et al.,* 1995; Thackeray *et al.,* 2004) are dominant drivers of zooplankton patchiness. However at smaller scales, contagious biotic interactions tend to dominate, with habitat selection theory stating that individuals choose habitats to maximise fitness (Rosenzweig, 1991), so that food-finding (Matthews and Mazumder, 2006), mate-finding or predator avoidance (Shurin, 2001; Castro *et al.,* 2007; Lageren *et al.,* 2008) have important influences on community structure.

The role of spatial heterogeneity in communities is central to most ecological theories (Legendre and Fortin, 1989) and receives considerable interest in the literature. Two important concepts are integral to the spatial structure of a community of organisms: Spatial dependence, which arises from the Environmental Control model of the 1950s (Bray and Curtis, 1957; Whittaker, 1956) and dictates that community structure is driven by the spatial structure of environmental factors (Legendre, 1993; Legendre and Legendre, 1998); and spatial autocorrelation, which occurs when community structure develops due to the contagious biotic process within the community itself (Legendre, 1993). Both concepts show that communities are intrinsically spatial and demand that space is considered in ecological studies, either as a confounding variable that can lead to bias, or as a predictor or covariable in analysis (Dray *et al.,* 2006). The Multiple Driving Force Hypothesis is used to describe the coupling of physical and biological driving forces in this way (Pinel-Alloul, 1995) and knowledge of how these driving forces structure zooplankton communities at different spatial scales is essential to the management and conservation of a particular ecosystem (Legendre *et al.,* 2005) but has rarely been investigated explicitly in zooplankton.

Studies of spatial pattern in zooplankton communities have overwhelmingly involved natural lakes. As discussed, artificial lakes are younger but also, where they are eutrophic, can be characterised by management practices intended to alter natural conditions (e.g. Heo and Kim, 2004; Müller and Stadelmann, 2004; Becker *et al.,* 2006). Such effects may reasonably be expected to homogenise lake zooplankton community abundance and distribution but have seldom been evaluated using spatially-explicit sampling. This is surprising both from the point of view of assessing management effects and consequences for zooplankton structure.

1.3.4 Quantifying Zooplankton Diversity

The theory of island biogeography (MacArthur and Wilson, 1967), while developed with respect to terrestrial ecosystems, is also an important principle in the study of lake zooplankton. Central to its application to zooplankton is the effective dispersal between and colonisation of water bodies. Zooplankton are often assumed to be effective dispersers, due to their cosmopolitan distribution, small size and ability to produce desiccation-resistant propagules (Maguire, 1963; Wetzel, 2001; Charalambidou and Santamaría, 2002; Green *et al.,* 2002), making use of passive vectors such as wind (Cohen and Shurin, 2003) and larger animals (Proctor, 1964).

However the rates and relative importance of each are difficult to determine (Holland and Jenkins, 1998; Cáceres and Soluk, 2002). Moreover, studies designed to detect the existence of such vectors were carried out under artificial conditions and their repetition in more natural situations have been inconclusive (Proctor, 1964; Holland and Jenkins, 1998; Jenkins and Underwood, 1998; Cáceres and Soluk, 2002).

Complex interactions between a number of factors drive zooplankton community dynamics. The relative importance of regional processes, such as colonisation and dispersal, and local processes, such as competition and predation, influences community composition (Havel *et al.,* 2002; Havel and Shurin, 2004). Colonisation of a habitat by species within the regional pool can increase local species richness by supplying new species or new individuals of existing species, while local abiotic processes can increase mortality and reduce local species richness. If sites are readily supplied with regionally available species, local processes are expected to shape the local community structure but when dispersal is limited, biotic and abiotic factors determine community composition (Holland and Jenkins, 1998; Naeslund and Norberg, 2006).

Biodiversity is an important measure of ecosystem structure and function, often expressed as species richness or diversity (e.g. Naeem *et al.,* 1994; Tilman *et al.,* 1996; McGrady-Steed *et al.,* 1997; Naeem and Li, 1997; Mulder *et al.,* 2001). However an increasing number of authors are reporting that functional trait composition and diversity gives a more accurate representation of ecosystem structure and function, and greater trait diversity is more likely to provide protection against ecosystem perturbations than the number of species alone (e.g. Tilman *et al.,* 1996; Hooper and Vitousek, 1997; Tilman *et al.,* 1997; Tessier *et al.,* 2000; Tilman, 2001; Flynn *et al.,* 2009). A diverse range of functional traits can be used to investigate mechanisms involved in assemblage organisation, diversity dynamics (Erős *et al.,* 2009), ecosystem resilience (Petchey and Gaston, 2009) and evolutionary processes (e.g. Ackerley *et al.,* 2006) in ways that might be limited using taxonomic groups alone.

Many studies, particularly initial developmental work, on functional diversity have focussed on plant and aquatic macro-invertebrate communities (Charvet *et al.,* 2000;

Henry *et al.,* 2001; Statzner *et al.,* 2001; Mason *et al.,* 2003; Heemsbergen *et al.,* 2004; Bady et al, 2005) and while the range of organisms included in trait-based work is increasing (Zak *et al.,* 1994; Stevens *et al.,* 2003), very few have considered functional diversity in freshwater zooplankton (but see Barnett *et al.,* 2007). Consequently, the majority of zooplankton studies continue to focus on taxonomic diversity and there is a limited amount of information available on the functional traits of freshwater zooplankton.

Processes that promote the co-existence of different taxa tend to produce nested communities (Worthen *et al.,* 1998; Fleishman and Murphy, 1999; Fernández-Juricic, 2002; Facelli et al, 2005; Elmendorf and Harrison, 2009), whereby species-poor assemblages are non-random subsets of species-rich ones (Patterson and Atmar, 1986). Spatially and temporally heterogeneous habitats ensure that each taxon can exploit a portion of the habitat but none can exclusively exploit the entire habitat range (Tilman, 2001). Studies of nestedness have overwhelmingly focussed on the spatial structure of nested communities (e.g. Paterson and Atmar, 1986; Wright *et al.,* 1998; Cook and Quinn, 1998; Driscoll, 2008) with only a small number investigating nestedness of temporal assemblages (e.g. Norton *et al.,* 2004; Bloch *et al.,* 2007; Elmendorf and Harrison, 2009; Heino *et al.,* 2009). Moreover, studies investigating nestedness almost exclusively use taxonomic- rather than trait-based approaches, and concentrate on organisms other than zooplankton.

1.3.5 Implications

This review has highlighted several areas of zooplankton ecology that have been relatively neglected in the literature, particularly with respect to artificially formed water bodies. Very few studies have made direct comparisons of zooplankton assemblages between artificial and natural water bodies despite differences in age, morphology, hydrology and degree of human influence that are potentially important in shaping temporal and spatial zooplankton dynamics. The PEG model (Sömmer *et al.,* 1986) is a highly-cited qualitative prediction of plankton succession, yet many empirical studies of temporal zooplankton dynamics focus on more productive periods of the year and the model's applicability to artificial systems has yet to be thoroughly tested. Winter periods continue to be overlooked, limiting information on over-wintering communities. In general community ecology, recent studies have identified limitations in using taxonomic approaches to quantify biodiversity and ecosystem characteristics. While increasing attention is being paid to trait diversity in other organisms, information on zooplankton functional traits is severely limited.

1.4 Aims

Stemming from the foregoing review, the broad aim of this PhD is to address some of the gaps in the literature, which include both issues specific to artificial water bodies and those applicable to more general ecological concepts. Assessments of spatial and temporal trends in the zooplankton community of the newly formed, and highly managed, Cardiff Bay will be used to address these gaps through a series of testable hypotheses to answer the following questions:

1. Globally, do artificially formed water bodies support different zooplankton assemblages to those found in natural lakes?
2. Does the zooplankton community of Cardiff Bay vary in ways predicted by ecological theory, and particularly by predictions based on the Plankton Ecology Group (PEG) qualitative model of plankton succession?
3. In Cardiff Bay, is there a persisting community of interacting zooplankton species even over less productive periods of the year?
4. Do spatial and temporal dynamics in the zooplankton community of Cardiff Bay reflect local water quality variables?
5. Do management practices employed in Cardiff Bay influence the temporal and spatial dynamics of zooplankton?
6. Do the traits of zooplankton species in Cardiff Bay vary spatio-temporally in ways that might reflect environmental variation?

Each of the following chapters in this thesis is intended to stand alone for future publication as a separate journal article: Chapter 2 of this thesis addresses the first of these key questions; Chapter 3 addresses question 2, 3 and the temporal elements of questions 4 and 5; Chapter 4 addresses the spatial elements of the latter two questions; and the final question is addressed in Chapter 5.

1.5 Study Area

With the exception of the global meta-analysis in Chapter 2, all the work for this thesis was focussed on Cardiff Bay (51°29'07"N 3°11'12"W; 200ha area; mean depth 4.03m; maximum depth 13.39m) (Fig. 1.1). Located in temperate south Wales (UK), the Bay was formed when the rivers Taff and Ely were impounded by a 1.1km long barrage in April 2001, as part of an urban regeneration scheme devised in the 1980s to inundate 190ha of tidal mudflats with a freshwater lake. The lake is eutrophic, with mean total phosphorous concentration 88.3μgl^{-1}, mean chlorophyll *a* concentration 6.7μgl^{-1}, and maximum chlorophyll *a* concentration 450.6μgl^{-1} and as such is designated a sensitive area under the Urban Wastewater Treatment Directive (Council of the European Communities, 1991). Diatom assemblages in the Bay have been used to indicate poor water quality in the main body of the Bay, with higher water quality occurring in the Rivers Taff and Ely (Jüttner et al, 2009). In order to maintain water quality, the Cardiff Bay Barrage Bill (1991) and Cardiff Bay Barrage Act (1993) obliged Cardiff Harbour Authority (CHA) to carry out continuous monitoring and management of the lake and its surroundings. Because dissolved oxygen could fall to concentrations detrimental to salmonids, especially in summer, a statutory target to maintain >5mg O_2 l^{-1}, is delivered by an aeration system over the entire lake bed that pumps air into the lake and promotes mixing throughout the summer. During extended periods of hot dry weather, the aeration system can be supplemented with a mobile, oxygenation barge, which was employed several times during the study period (Table 1.1).

The lake is connected to the adjacent saline estuary of the River Severn (Appendix 1) by navigable locks, but saline sumps on the landward side of the barrage collect the small amount of salt water entering the Bay to prevent stagnation at the lake bed. Regular surface-water skimming is carried out to remove allochthonous debris, algal scum and surface vegetation that have a potential oxygen demand. The lake bed is dominantly soft sediment, occupied by large densities of larval Chironomidae with few macrophyte stands. Fish are relatively abundant and dominated by roach (*Rutilus rutilus* (Linnaeus, 1758)), dace (*Leuciscus leuciscus* (Linnaeus, 1758)) and chub (*Leuciscus cephalus* (Linnaeus, 1758)). Soon after formation, the lake was invaded by zebra mussels *Driessena polymorpha* (Pallas, 1771) which now form large densities on hard surfaces. There have also been ongoing attempts to manage chironomid numbers using *Bacillus thuringiensis* (*Bti*) (Vaughan *et al*., 2008).

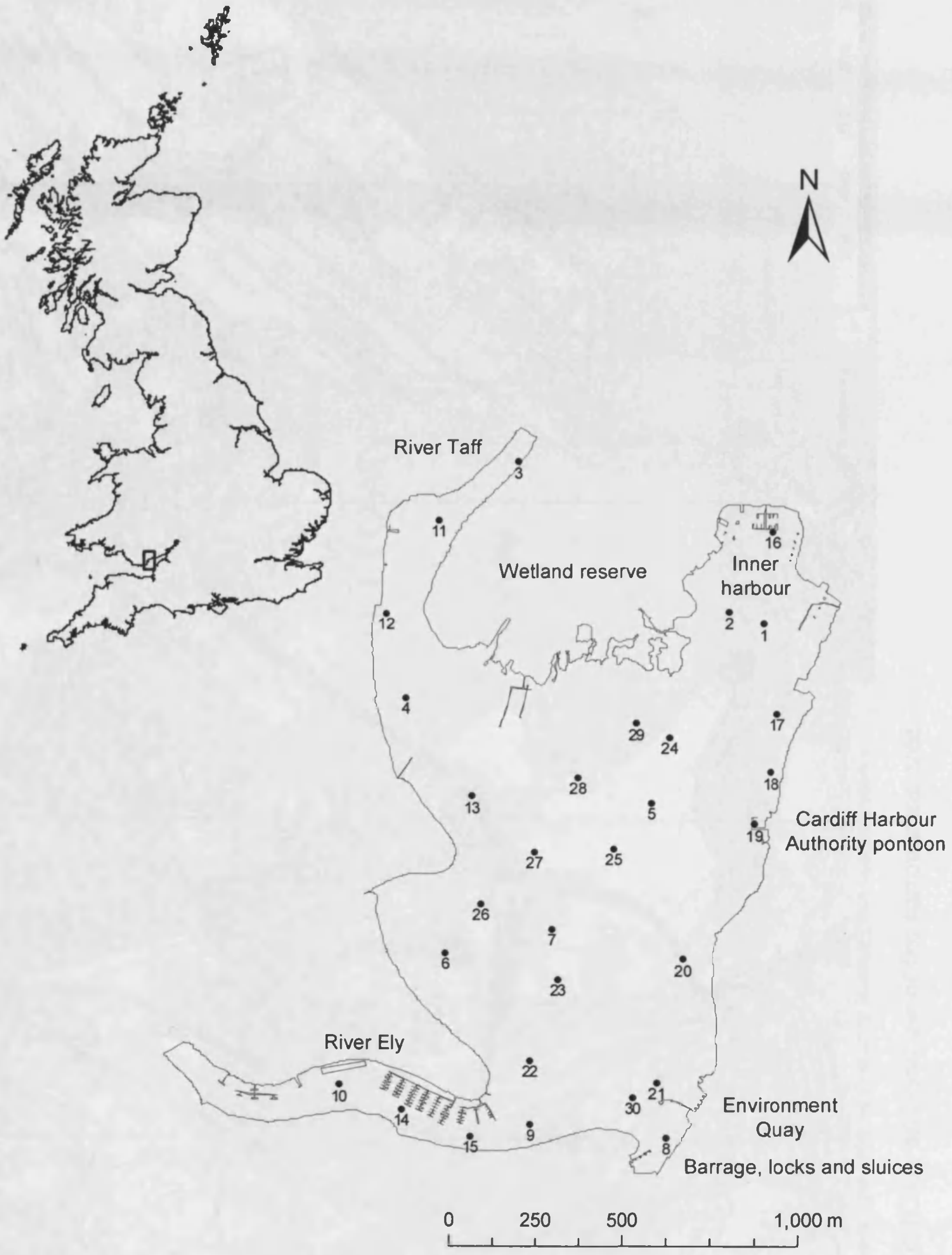

Figure 1.1: The Cardiff Bay study area showing the positions of 30 sampling sites. Seasonal surveys included sites 1-10, while spatial surveys included all 30 sites plus eight grid sampling positions at sites 3, 10, 16 and 19.

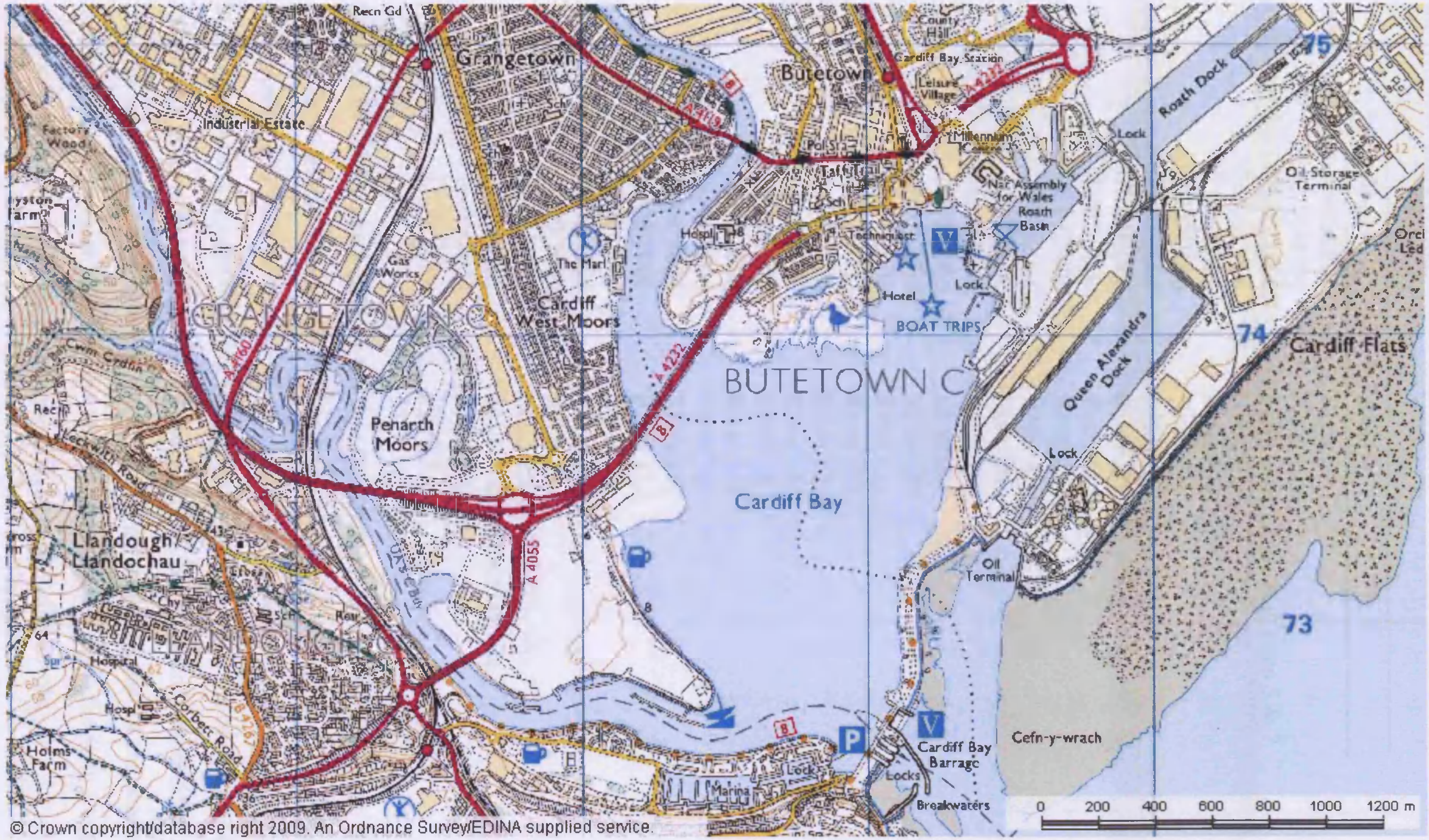

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Figure 1.2: Cardiff Bay and land use of the surrounding area

Table 1.1: Dates and areas of deployment for mobile oxygenation of Cardiff Bay, over the two year study period.

Date	Area
14/05/2006	River Ely
15/05/2006	River Ely
05/06/2006	Main body of the Bay sites 5 & 7
26/06/2006	River Ely
27/06/2006	River Ely
01/07/2006	River Ely
06/07/2006	River Ely
07/07/2006	River Ely
08/07/2006	River Ely
09/07/2006	River Ely
10/07/2006	River Ely
12/07/2006	River Ely
14/07/2006	River Ely
23/07/2006	River Ely
27/07/2006	River Ely
29/07/2006	River Ely
30/07/2006	River Ely
01/08/2006	River Ely
02/08/2006	River Ely
03/08/2006	River Ely
06/08/2006	River Ely
11/08/2006	River Ely
20/08/2006	River Ely
23/08/2006	River Ely
26/08/2006	River Ely
28/08/2006	River Ely
10/09/2006	River Ely
09/06/2007	Main body of the Bay site 7
10/06/2007	Main body of the Bay site 7
16/06/2007	River Ely
17/06/2007	River Ely

Situated in the Northern area of the Bay between the River Taff and Inner Harbour, Cardiff Bay wetland was opened as a wildlife reserve in 2002 (Fig. 1.3). It is an area of approximately 10ha consisting of a series of shallow vegetated lagoons. A reservoir in the north of the reserve contains surface water run-off and is the only water body in the reserve accessible to the public. A narrow ditch (reen) extends around the reserve and was constructed to prevent public access to the southern part of the reserve. The mean depth of the water bodies in the reserve is approximately 0.6m with a maximum depth of approximately 2.5m, depending on Bay-wide water levels.

Vegetation on the wetland reserve includes species of the *Salix*, *Phragmites* and *Alnus* genera, tall herb fen and grasses. It is heavily managed, with ongoing coppicing and control and removal of invasive species, such as Japanese Knotweed (*Fallopia japonica*) and species of *Typha*. Vegetation species composition shows evidence of a disturbed ecosystem, with a temporal shift from saline- to freshwater-tolerant (Banks, 2008; Banks, 2009).

In combination, this array of management pressures and attributes makes Cardiff Bay an extremely interesting location in which to examine the key questions raised in the thesis.

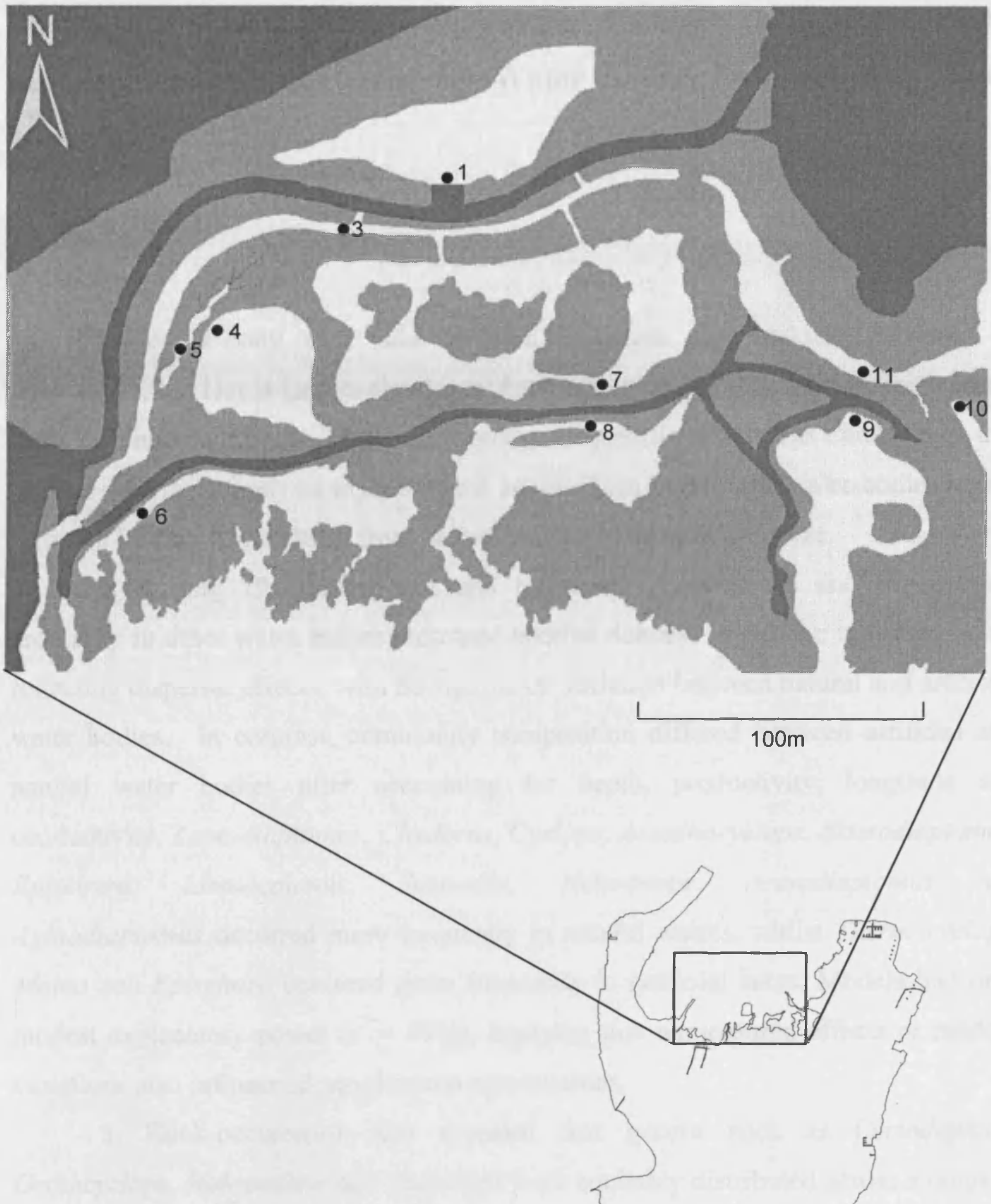

Figure 1.3: Sampling sites in the Cardiff Bay wetland reserve. Unshaded areas represent water; light grey areas vegetation; and dark areas paths and roads.

Chapter 2: Contrasting Zooplankton Richness and Composition between Natural and Artificial Water Bodies Using Global Meta-analysis

2.1 Abstract

1. Water-body size and location influence zooplankton diversity in freshwaters, but less is known about how these effects are modified in artificial waters or on different continents. To provide context for specific research in Cardiff Bay, this chapter uses meta-analysis to assess how zooplankton in artificial water-bodies across different biomes might differ from natural water bodies of similar size.

2. Among 79 lakes, ponds and reservoirs (11 artificial and 68 natural), proximity to other water bodies increased species richness in all lake types, probably reflecting dispersal effects, with no significant variation between natural and artificial water bodies. In contrast, community composition differed between artificial and natural water bodies after accounting for depth, productivity, longitude and conductivity. *Leptodiaptomus*, *Chydorus*, *Cyclops*, *Acanthocyclops*, *Skistodiaptomus*, *Epischura*, *Limnocalanus*, *Senecella*, *Heterocope*, *Arctodiaptomus* and *Aglaodiaptomus* occurred more frequently in natural waters, whilst *Thermocyclops*, *Moina* and *Epischura* occurred more frequently in artificial lakes. Models had only modest explanatory power (r^2 = 48%), implying that unmeasured effects or random variations also influenced zooplankton communities.

3. Rank-occurrence data revealed that genera such as *Ceriodaphnia*, *Orthocyclops*, *Holopedium* and *Eucyclops* were equitably distributed across a range of water body sizes, depths and climates. Other genera were more exclusive to specific conditions, typically those also associated with natural lakes (e.g. *Limnocalanus*, *Senecella*, *Heterocope*, *Arctodiaptomus* and *Aglaodiaptomus*).

4. Although restricted by the low number of artificial water bodies available for analysis, these results are among the first to illustrate potentially systematic global differences in zooplankton communities between natural and artificial lakes despite their similar richness. Local factors appear to create specialist conditions in natural lakes, possibly due to a lack of specific niches in artificial water bodies. Potential explanations require investigation, but the most likely hypothesis is that management

or disturbance restrict species composition in artificial lakes, while lake age, stability, habitat 'naturalness' and complexity combine to enhance species persistence in natural lakes.

2.2 Introduction

Large-scale studies have shown that water-body size, productivity and geographic location all influence zooplankton species richness and community composition in lakes (e.g. Fryer, 1985; Sömmer, 1986; Dodson, 1991; Dodson, 1992; Hessen *et al.*, 2006). Island biogeography theory predicts a strong positive relationship between area and species richness, with larger habitats generally supporting a larger number of niches and increased immigration (MacArthur and Wilson, 1967). Both increased zooplankton richness and compositional change, therefore, are expected with increasing lake area (Dodson, 1992; Shaw and Kelso, 1992; O'Brien *et al.*, 2004; Karatayev *et al.*, 2005; Tavernini *et al.*, 2009; Dodson *et al.*, 2009). Similarly, deeper water bodies support vertical segregation in a greater number of depth-related niches (Strøm, 1946), with several authors reporting changes in zooplankton diversity and composition with lake depth (Green and Vascotto, 1978; Dodson, 1992; Korhola, 1999; Korhola *et al.*, 2000; O'Brien *et al.*, 2004; Amsinck *et al.*, 2006; Tavernini *et al.*, 2009).

Changes in food resource availability associated with primary productivity also affect zooplankton species richness and community structure (Dodson, 1992; Dodson *et al.*, 2009). Although the precise nature of these effects is debated, the generally accepted models are that richness and composition change unimodally (e.g. Dodson *et al.*, 2000; Barnett and Beisner, 2007) or linearly with productivity (Chase and Ryberg, 2004; Hoffmann and Dodson, 2005), depending on the scale of observation (Chase and Ryberg, 2004) and the metric used to measure productivity (Thackeray, 2007).

In terrestrial habitats, geographic location is a further important determinant of species richness, with environmental predictability, increased solar energy, climatic variation and land area all expected to increase richness as latitude and/or altitude decrease (Gaston and Spicer, 2004). These patterns are reflected among freshwater zooplankton (Hobæk *et al.*, 2002; Shurin *et al.*, 2007; Tavernini *et al.*, 2009).

Community composition is highly dependent on geographic location (Keller and Pitbalo, 1989; Shaw and Kelso, 1992; Dodson, 2009), and specialist species are more likely to occur under more extreme climatic conditions (Halvorsen and Gullestad, 1976).

Whilst these large-scale studies provide a useful context for understanding influences on zooplankton species diversity among natural lakes on single continents, few studies have considered the extent to which zooplankton in artificial lakes follow the same trends. Though Dodson (1992) considered the effect of lake size and depth on zooplankton species richness, differences between artificial and natural lakes were not resolved. This lack of specific assessment is surprising, since artificial water bodies differ from natural water bodies not only in their age, but also hydrological regimes, morphometric character and degree of stability caused by human influence and management. All of these may be expected to influence pelagic zooplankton communities strongly.

Although it is difficult to predict accurately the ultimate biological character of new water bodies (Baxter and Glaude, 1980), long-term fluctuations in zooplankton communities following an water body's construction have been documented (Holland and Jenkins, 1998; De Mérona *et al.,* 2001). Investigation into the potential differences in zooplankton communities between natural and artificial lakes could provide an important insight into ecosystem-wide variations, which in turn could inform management needs.

In this chapter, a meta-analytical approach (Osenberg *et al.,* 1999) was used to make quantitative comparisons of well-studied lakes, using existing published data to obtain a global perspective of zooplankton communities in natural and artificial water bodies. Such analysis is useful in overcoming the challenges involved in collecting first-hand data from lakes over a wide geographical range and can increase statistical power by considering a larger number of lakes and studies, reducing the impact of any uncertainties associated with individual studies. This meta-analysis provides a global context with which to compare the zooplankton community of the newly formed Cardiff Bay.

2.3 Aims and Hypotheses

The broad aim of this chapter was to identify potential influences on zooplankton community composition and richness among world lakes, and assess whether artificial and natural water bodies support different zooplankton communities. Two hypotheses were tested:

Hypothesis 1: Zooplankton taxon richness and community composition reflect water body morphometric variables. Specifically, characteristics related to lake size and geographical location are expected to predict taxon richness and community structure.

Hypothesis 2: Artificial water bodies, such as man-made reservoirs and impoundments exhibit different morphometric characteristics to naturally formed lakes. They are also more heavily managed. As such, zooplankton taxon richness and community composition are also expected to differ.

2.4 Methods

2.4.1 Data Sources

This work was based on a literature search of studies on freshwater zooplankton in world lakes, reservoirs and ponds using the online database ISI Web of Science with the initial key words: "zooplankton"; "species"; "freshwater"; and either "lake", "pond" or "reservoir". Data were obtained from either the primary literature or associated supplementary material. Where possible, information was gathered for each water body on the number of pelagic crustacean zooplankton species; surface area (m^2); residence time (days); maximum and mean depth (m); conductivity (µS); primary production ($mgCm^{-2}day^{-1}$); surface elevation (m); latitude (^oN); longitude (^oW); distance to nearest standing water body, visible on a 1:250,000 scale map (km); and the number of lentic freshwater bodies in a 20km radius. Other ecological factors, such as the presence or absence of fish and specific lake chemistry, are recognised as being important, but data were not available for all of the water bodies included in analysis.

2.4.2 Study Selection

Data from natural and artificial water bodies, of various size, morphology and hydrological regime, from a range of latitudes and longitudes, were considered provided that zooplankton species lists were recorded over at least two years and in different seasons to minimise inter annual and inter seasonal variations in community composition (Dodson, 1992). Only pelagic zooplankton was considered in species lists, excluding all littoral species. This is consistent with an earlier study by Dodson (1992), who excluded all scapholeberidae, all sididae except *Diaphanosoma*, all chydoridae except *Chydorus sphaericus*, all macrothricidae, and all species of *Simocephalus*, *Polyphemus*, *Macrocyclops*, *Ectocyclops*, *Megacyclops*, *Paracyclops*, *Microcyclops* and *Ergasilus*.

Since zooplankton species were identified by numerous researchers, lists of genera were used for community analysis in an attempt to reduce the impact of inconsistencies or local variations in taxonomy. The genus data took the form of presence-absence.

2.4.3 Statistical Analysis

To examine correlates with community composition, data on zooplankton genera from water bodies with full genus listings were first ordinated using Detrended Correspondence Analysis (DCA), chosen because of the large number of zero values in presence-absence data, the unimodal nature of the data, and the need to generate ordination axes unconstrained by environmental variables (Speckman *et al.,* 2005). No weighting was applied to individual genera. Regression analysis of DCA scores, as well as species richness, was carried out against all environmental variables (log(n+1) transformed) in order to identify correlates with zooplankton species richness and community composition, along with 95% confidence and prediction intervals. Maximum depth was chosen as a representative depth variable, since mean and maximum depth were highly correlated.

Typically in ecological studies, multicollinearity occurs among potential explanatory variables making it difficult to partition the effects of single factors on species richness and community composition. To overcome this, general linear model analysis of covariance (ANCOVA) was used to determine whether zooplankton communities differed significantly between artificial and natural water bodies whilst controlling for variance in the data due to other correlates. Potential covariates were first identified from results of the regression analysis and gradients of each were compared for parallelism and transformed where necessary (Riggs *et al.*, 2008).

To investigate zooplankton community composition further among different groups of water bodies, Two-way Indication Species Analysis (TWINSPAN) (Hill and Šmilauer, 2005), using five equally cut levels, was carried out on percentage occurrence data in order to classify zooplankton genera into those that commonly co-occurred in the different water bodies. Zooplankton genus rank-occurrence plots were constructed using mean occurrence to account for differences in number of water bodies between groups and chi-squared tests were carried out to test whether their distributions differed significantly from random among artificial and natural water bodies.

2.5 Results

A total of 106 lakes, reservoirs and ponds was identified from the literature for which sufficiently comprehensive data existed on pelagic crustacean species richness (Appendix 1). Data on 65 of these were obtained from Dodson's (1992) study on North American lakes. Full species lists were available for 79 of the 106 water bodies and of these 79 water bodies, 11 were artificial.

2.5.1 Correlates of Zooplankton Species Richness and Composition

As expected, species richness increased with increasing surface area, depth and number of lentic water bodies in a 20km radius but decreased with increasing distance to the nearest water body (Fig. 2.1a). Ordination using DCA showed that DCA axis 1 score decreased with increasing depth, elevation and primary productivity (Fig. 2.1b) but increased with latitude and longitude, consistent with the low scores of the predominantly tropical *Thermocyclops* genus and high scores of *Limnocalanus* and *Diaptomus*, tolerant of low temperatures (Gurney, 1933b) (Fig. 2.2b). Other genera scoring highly on DCA1 included *Heterocope*, *Chydorus* and *Eurytemora*, with *Eudiaptomus*, *Moina*, *Diaphanosoma*, *Arctodiaptomus* and *Tropocyclops* having low scores. DCA axis 2 scores declined with depth and primary productivity (Fig. 2.1c), consistent with high scoring *Moina* species often reported in small ponds and puddles (Fig. 2.2b). DCA2 score increased with increasing isolation and conductivity, consistent with species of the low scoring *Holopedium* genus (Fig. 2.2b), which includes species with a preference for soft waters (Scourfield and Harding, 1994). Other high scoring genera on DCA2 included *Arctodiaptomus*, *Eucyclops* and *Acanthocyclops*, while low scoring taxa included *Orthocyclops*, *Leptodiaptomus*, *Skistodiaptomus*, *Senecella* and *Epischura*.

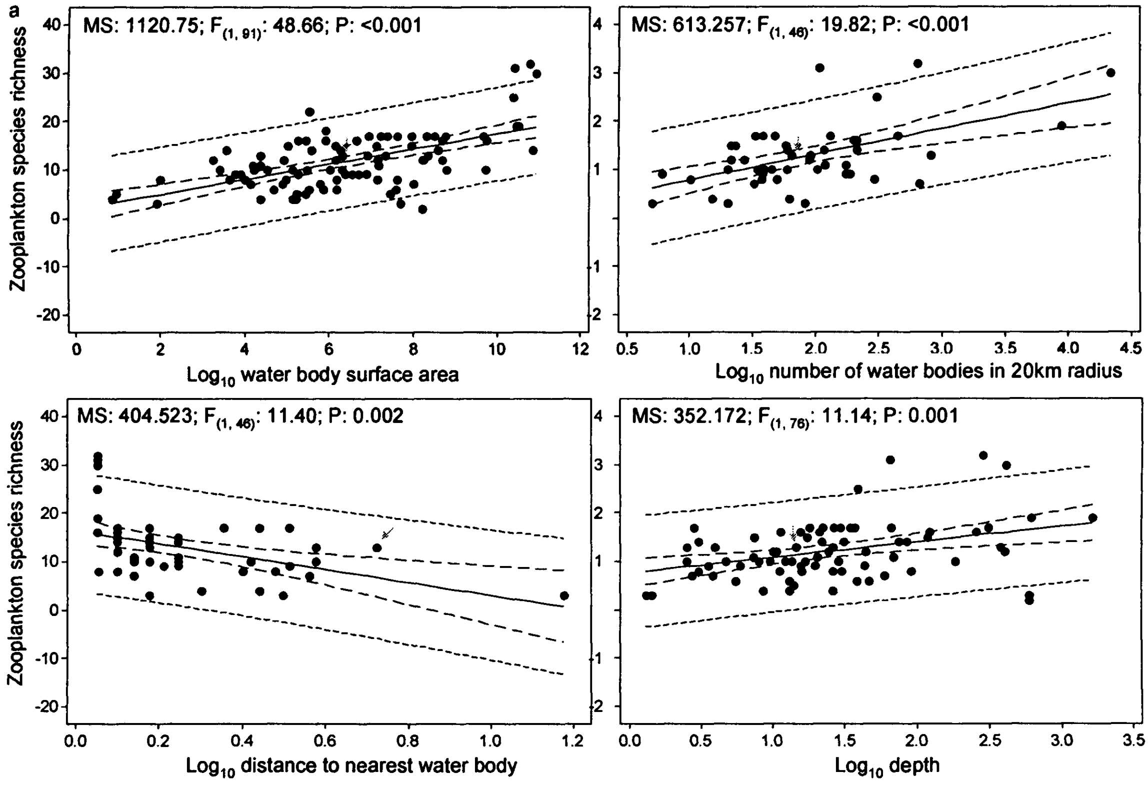

Figure 2.1a: Regression plots zooplankton species richness with characteristics of water bodies, showing 95% confidence intervals (– – –) and 95% prediction intervals (----). MS: mean sum of squares; F: test value with associated degrees of freedom; P: probability value, not corrected for multiple testing. Grey arrows indicate the position of Cardiff Bay where applicable.

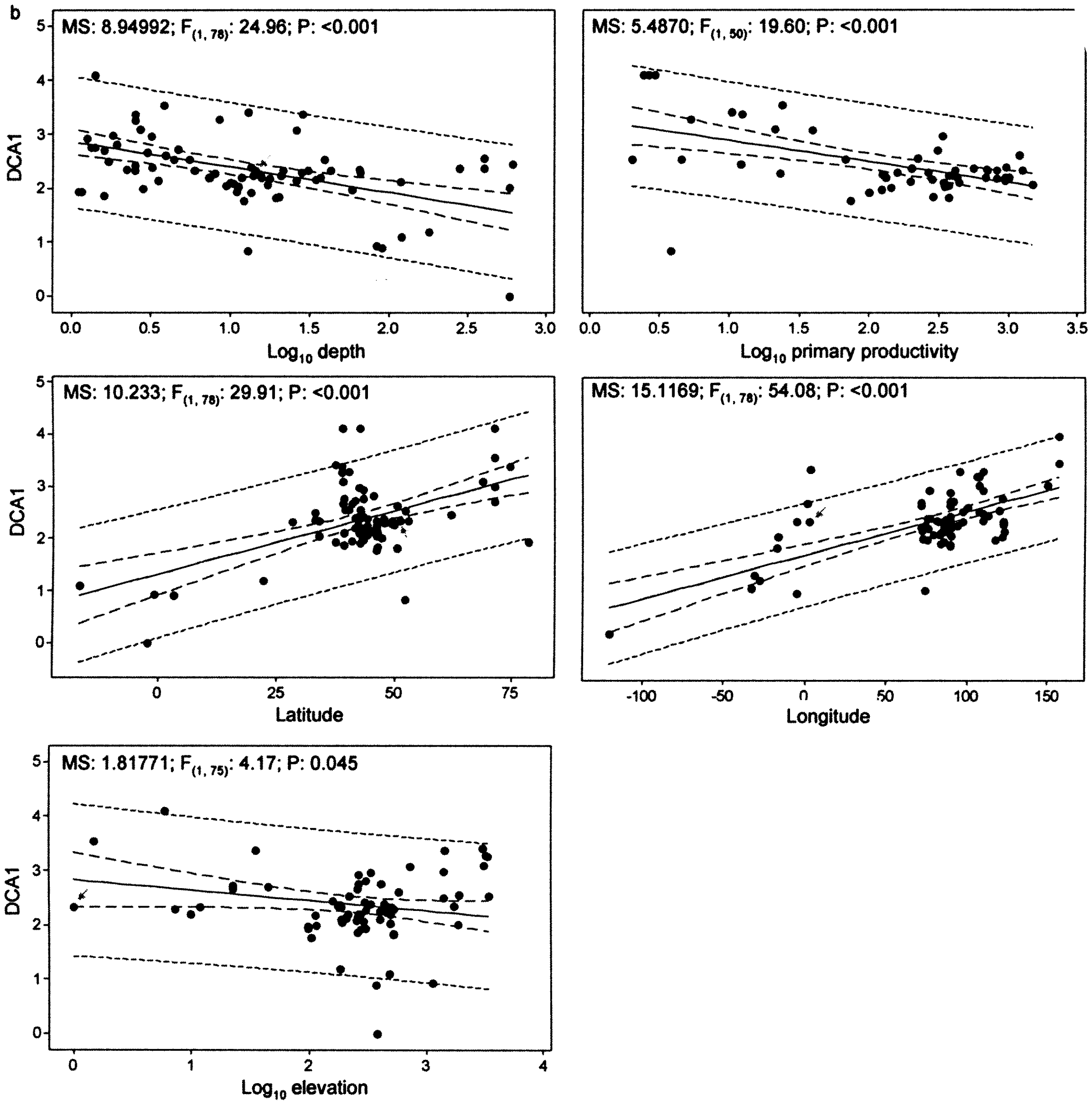

Figure 2.1b: Regression plots of DCA axis 1 scores with characteristics of water bodies, showing 95% confidence intervals (– – –) and 95% prediction intervals (----). DCA axes scores were obtained from ordination of zooplankton genera data from 79 lakes. MS: mean sum of squares; F: test value with associated degrees of freedom; P: probability value, not corrected for multiple testing. Grey arrows indicate the position of Cardiff Bay where applicable

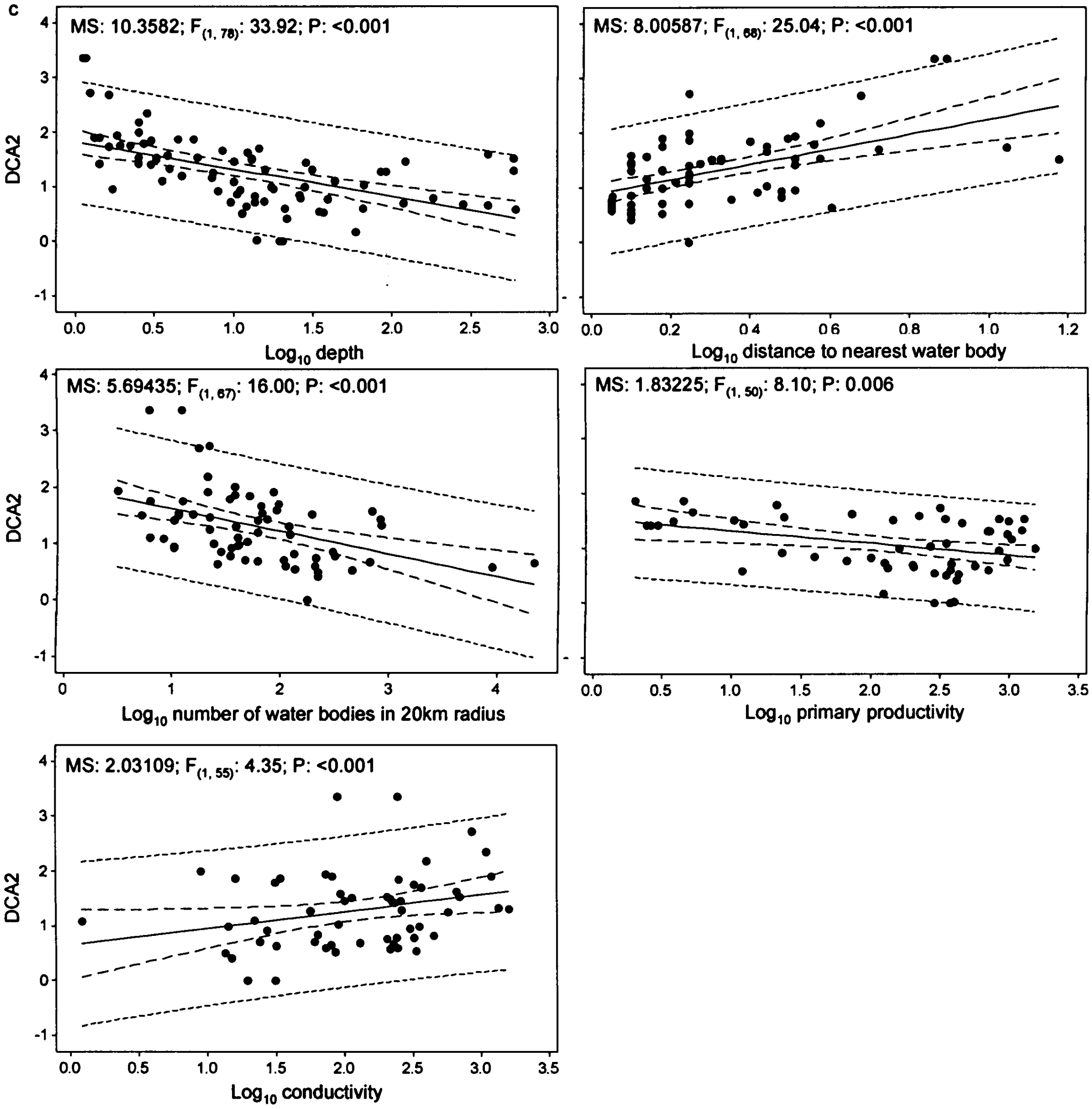

Figure 2.1c: Regression plots DCA axis 2 scores with characteristics of water bodies, showing 95% confidence intervals (– – –) and 95% prediction intervals (----). DCA axes scores were obtained from ordination of zooplankton genera data from 79 lakes. MS: mean sum of squares; F: test value with associated degrees of freedom; P: probability value, not corrected for multiple testing. Grey arrows indicate the position of Cardiff Bay where applicable

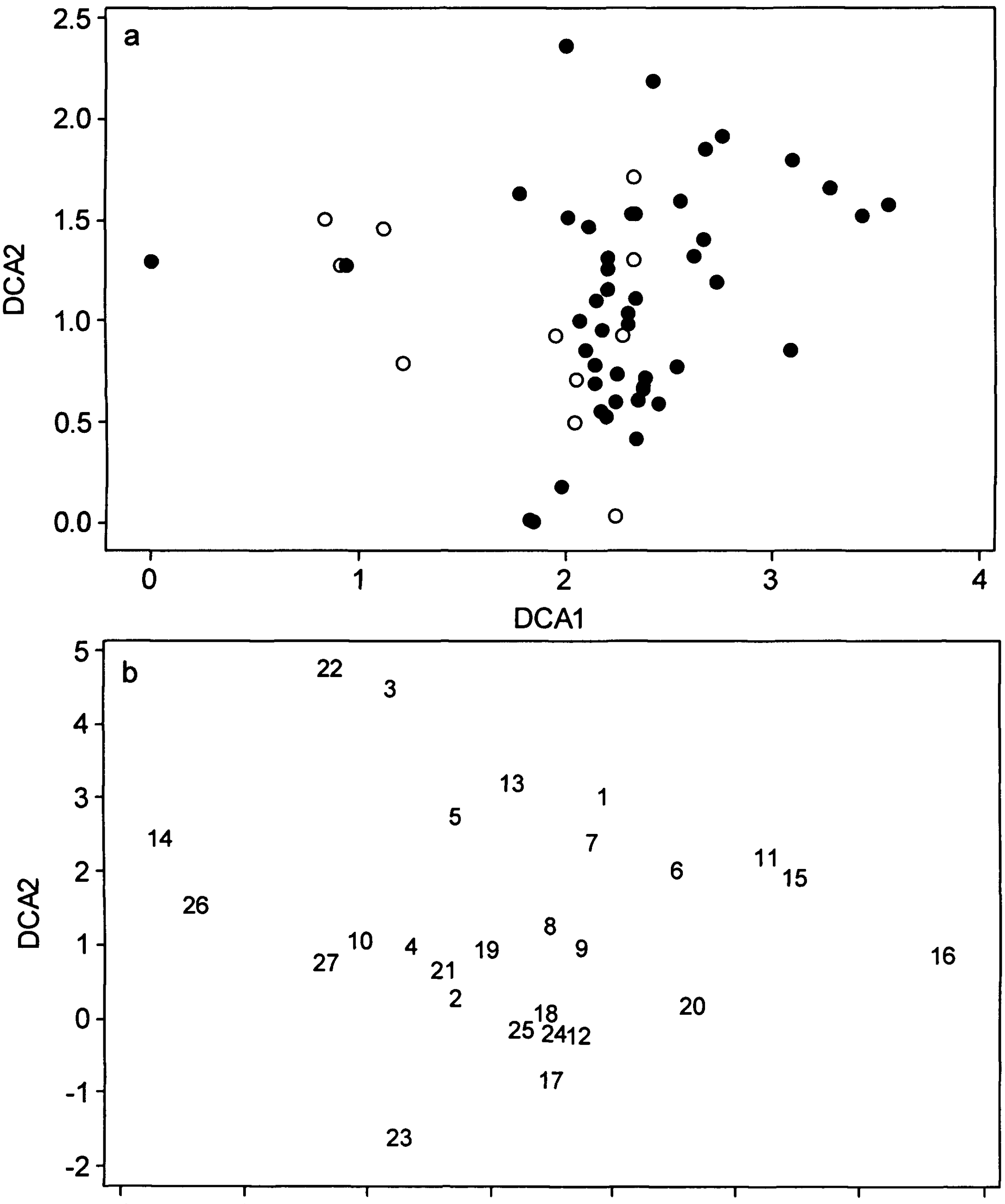

Figure 2.2: Water body (a) and genera (b) axes scores from DCA ordination of zooplankton genera recorded in 79 world lakes. DCA axis 1 scores differ significantly between artificial (○) and natural (●) water bodies (ANCOVA, $F_{(1, 35)}=6.62$; P=0.017). Genera are labelled as follows: 1: *Acanthocyclops*; 2: *Aglaodiaptomus*; 3: *Arctodiaptomus*; 4: *Bosmina*; 5: *Ceriodaphnia*; 6: *Chydorus*; 7:*Cyclops*; 8: *Daphnia*; 9: *Diacyclops*; 10: *Diaphanosoma*; 11: *Diaptomus*; 12: *Epischura*; 13: *Eucyclops*; 14: *Eudiaptomus*; 15: *Eurytemora*; 16: *Heterocope*; 17: *Holopedium*; 18: *Leptodiaptomus*; 19: *Leptodora*; 20: *Limnocalanus*; 21: *Mesocyclops*; 22: *Moina*; 23: *Orthocyclops*; 24: *Senecella*; 25: *Skistodiaptomus*; 26: *Thermocyclops*; 27: *Tropocyclops*

TWINSPAN identified four groups of water bodies, differing in physical and chemical characteristics (Fig. 2.3). Group 1 generally contained large, deep, tropical water bodies, while group 4 water bodies were smallest and most isolated. Groups 2 and 3 were made up of mainly intermediate sized water bodies and contrasted in primary production, with group 2 water bodies being more eutrophic than those in group 3 and supporting greater species richness (Fig. 2.4). In addition, zooplankton community composition, indicated by DCA axes scores also differed between TWINSPAN groups (Fig. 2.4).

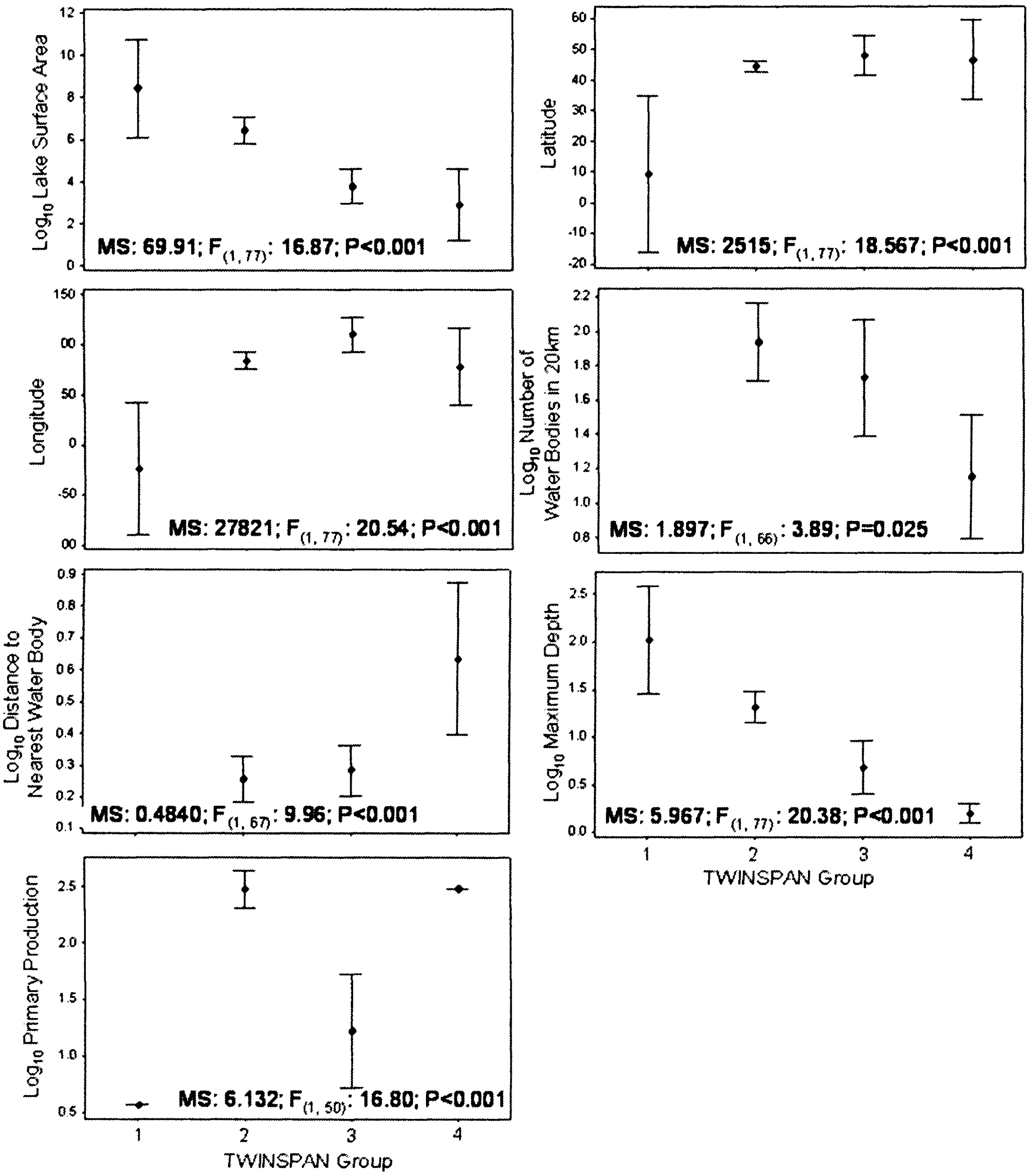

Figure 2.3: Groups identified using TWINSPAN of 79 well-studied world lakes, with variations in lake characteristics among groups, identified using ANOVA. MS: mean sum of squares; F: test value with associated degrees of freedom; P: probability value, not corrected for multiple testing.

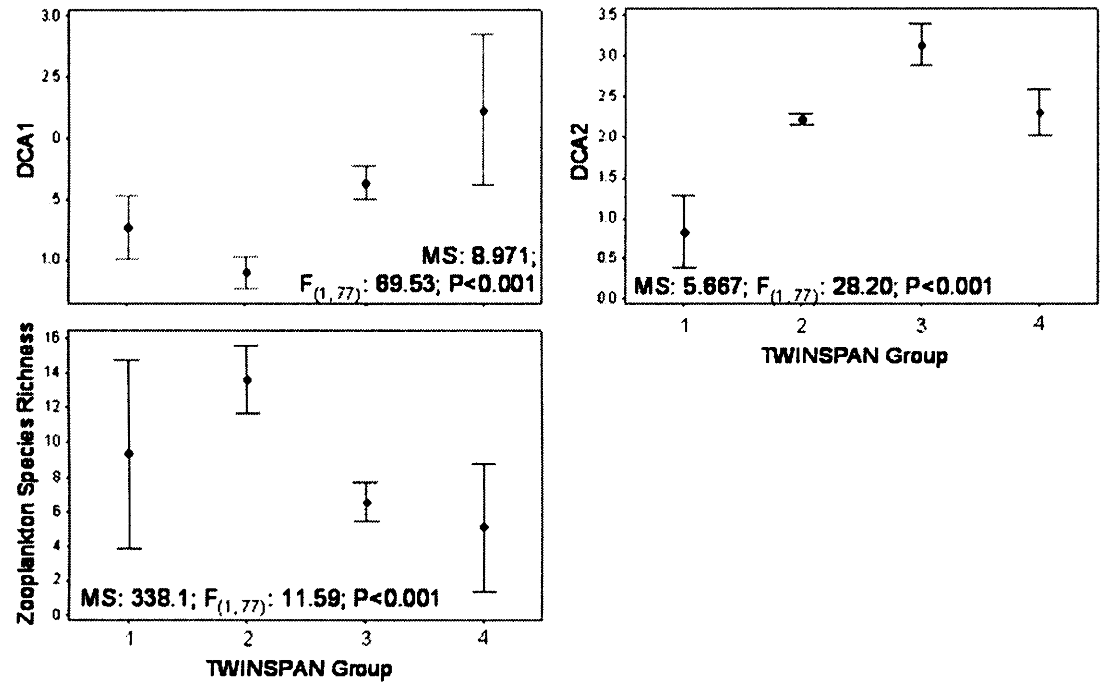

Figure 2.4: Groups identified using TWINSPAN of 79 well-studied world lakes, with variations in zooplankton community composition, represented by DCA axes, and species richness, identified using ANOVA. MS: mean sum of squares; F: test value with associated degrees of freedom; P: probability value, not corrected for multiple testing.

2.5.2 Natural vs. Artificial Water Bodies

General linear model ANCOVA revealed that the number of water bodies in a 20km radius was a more important covariate of species richness than whether a water body was artificial or natural, explaining 33.21% of the variance in species richness (Fig. 2.5). Similarly, there was no difference in DCA axis 2 scores between artificial and natural water bodies. Conductivity was the only significant covariate, explaining 59.78% of the variance in DCA2. Conversely, DCA axis 1 scores differed significantly between artificial and natural water bodies when accounting for variance caused by differences in depth, primary productivity and longitude (Fig. 2.2a). Together, these variables explained 47.7% of the variation in DCA1.

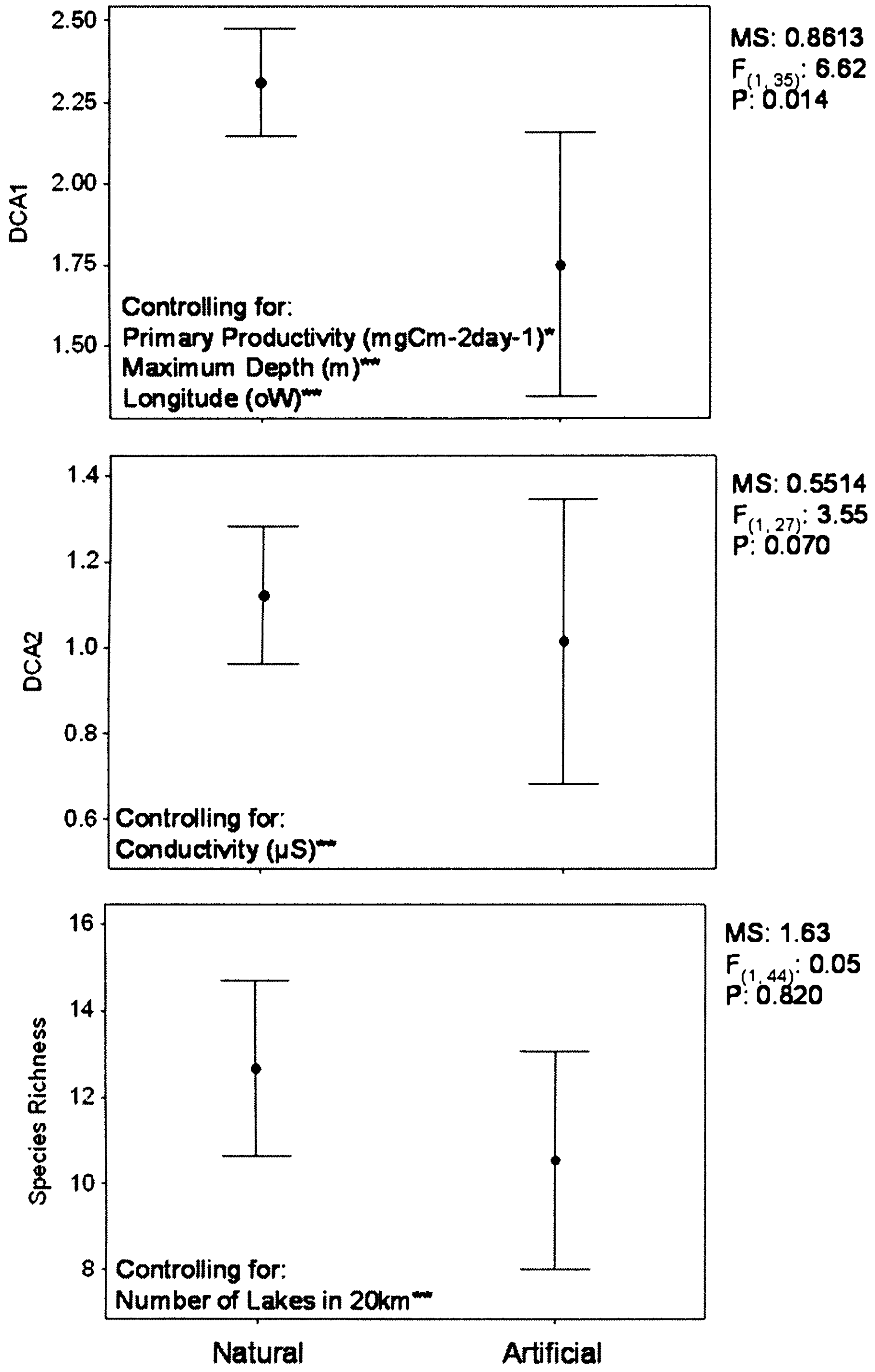

Figure 2.5: Results of ANCOVA testing the hypothesis that zooplankton species richness and community composition differ between artificial and natural water bodies, whilst controlling for variation due to significant covariates. Only significant covariates were included in models. ** indicates that covariate P values are significant at ≤ 0.01; * indicates that P values are significant at ≤ 0.05. MS: mean sum of squares; df: degrees of freedom; F: test value; P: probability value.

]

Rank-occurrence plots revealed that several zooplankton taxa occurred relatively equitably among the four TWINPSAN groups and among natural and artificial water bodies. *Ceriodaphnia* showed a particularly equitable occurrence among groups of water bodies, with a 26:27:25:22 split between TWINSPAN groups 1, 2, 3, and 4 and a 51:49 split between natural and artificial water bodies. *Orthocyclops*, *Holopedium* and *Eucyclops* showed similar patterns of occurrence between artificial and natural water bodies. However, some genera appeared to be more specialised. *Thermocyclops*, occurred only in the tropical water bodies of group 1, whilst *Leptodora*, *Skistodiaptomus*, *Orthocyclops*, *Senecella* and *Aglaodiaptomus* were only recorded in the more productive group 2 water bodies. *Heterocope* only occurred in group 3 water bodies and *Arctodiaptomus* was present only in the smaller, more isolated water bodies of group 4 (Fig. 2.6b). *Limnocalanus*, *Senecella*, *Heterocope*, *Arctodiaptomus* and *Aglaodiaptomus* appeared to be the most specialised genera among artificial and natural water bodies, occurring exclusively in natural lakes (Fig. 2.6c). As well as these five genera, *Leptodiaptomus*, *Chydorus*, *Cyclops*, *Acanthocyclops*, *Skistodiaptomus* and *Epischura* species also had significantly higher occurrence in natural lakes, as revealed with chi squared tests (Table 2.1). Conversely, *Thermocyclops*, *Moina* and *Eudiaptomus* species occurred significantly more often in artificial water bodies.

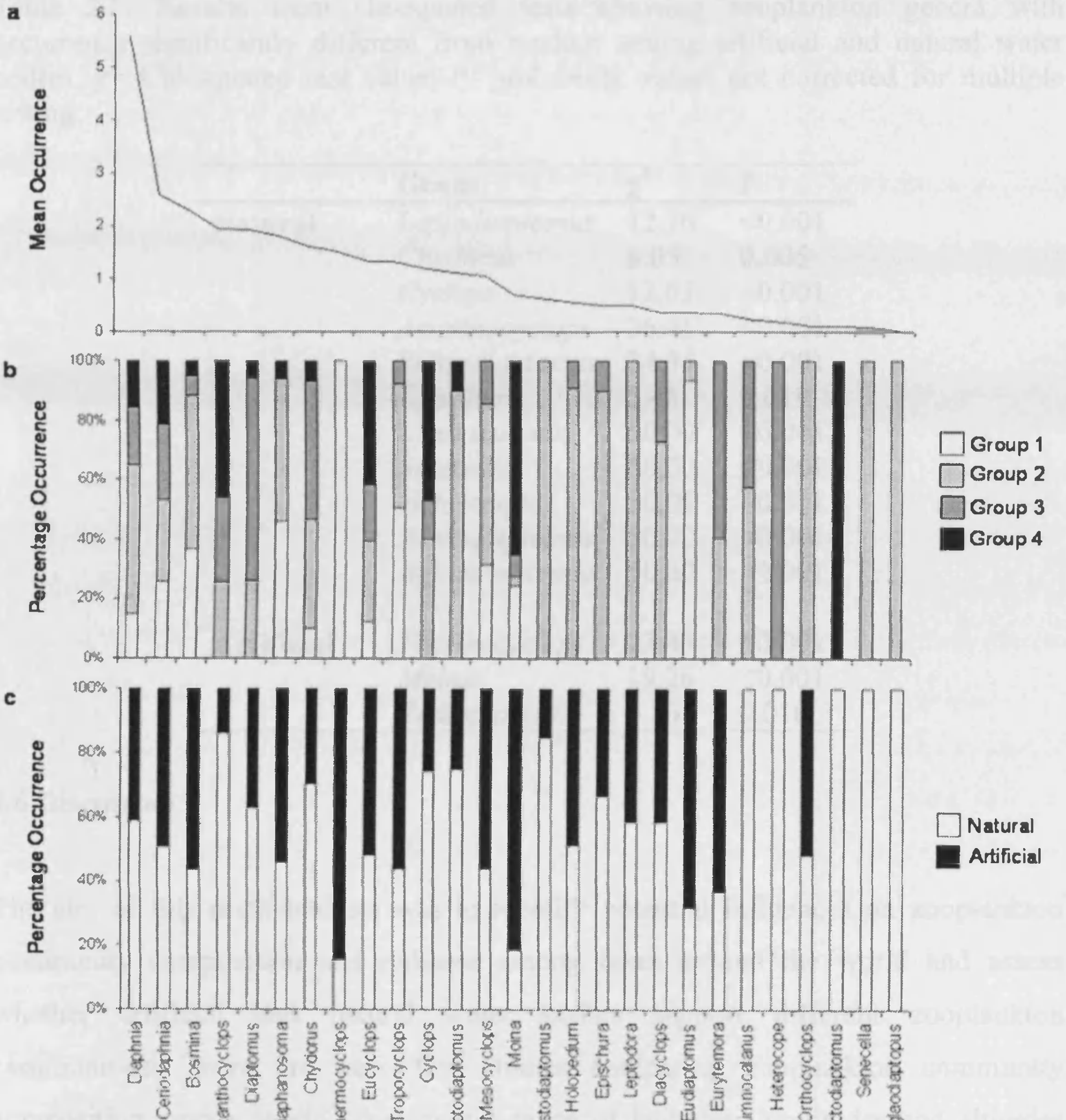

Figure 2.6: Occurrence of 29 zooplankton genera recorded in 79 lakes: a) shows mean total occurrence of each genera among all water bodies; b) identifies percentage occurrence of genera in each TWINSPAN group of water bodies; c) shows percentage occurrence of genera in natural and artificial water bodies.

Table 2.1: Results from chi-squared tests showing zooplankton genera with occurrence significantly different from random among artificial and natural water bodies. χ^2: Chi-squared test value; P: probability value, not corrected for multiple testing.

	Genus	χ^2	**P**
Natural	*Leptodiaptomus*	12.76	<0.001
	Chydorus	8.05	0.005
	Cyclops	12.03	<0.001
	Acanthocyclops	26.41	<0.001
	Skistodiaptomus	24.34	<0.001
	Epischura	5.48	0.019
	Limnocalanus	50.00	<0.001
	Senecella	50.00	<0.001
	Heterocope	50.00	<0.001
	Arctodiaptomus	50.00	<0.001
	Aglaodiaptomus	50.00	<0.001
Artificial	*Thermocyclops*	23.43	<0.001
	Moina	19.26	<0.001
	Eudiaptomus	6.56	0.010

2.6 Discussion

The aim of this meta-analysis was to identify potential influences on zooplankton community composition and richness among lakes around the world and assess whether artificial and natural water bodies support different zooplankton communities. There are very few studies comparing zooplankton community composition among world lakes over a range of latitudes, longitudes and altitudes simultaneously. A major problem encountered in undertaking such analysis is the risk of inconsistencies in the taxonomic identification of zooplankton species. In the present study, the slight reduction in resolution incurred when grouping zooplankton by genera was considered an appropriate trade-off to account for these inconsistencies.

Two hypotheses were tested. Firstly that zooplankton richness and community composition reflect water body morphometric variables and secondly that differences in these variables between natural and artificial water bodies lead to differences in zooplankton richness and community composition. The first hypothesis was supported, with several variables correlating with both richness and composition. This did not lead to differences in species richness between water body types, but as expected community composition, quantified using DCA axes scores, differed between artificial and natural water bodies after accounting for depth, productivity, longitude or conductivity.

2.6.1 Correlates of Zooplankton Species Richness and Composition

Previous studies have shown that factors related to water body size and geographic location are important influences on zooplankton species richness and community composition (Table 2.2). Central to these postulated effects is the theory of island biogeography and the importance of habitat size, dispersal and species interactions in shaping lentic zooplankton communities (Hobæk *et al.,* 2002). In the present study, and in agreement with Dodson (1992), the number of water bodies in a 20km radius was found to be a significant predictor of zooplankton species richness (Fig. 2.1a). This agreement is unsurprising, since a large number of the water bodies for which this information was available were included in Dodson's (1992) study and is probably due the increased likelihood of immigration from regional source populations. More interesting in the present context is how the natural or artificial nature of water bodies affected richness or community composition (see below).

Among the water bodies studied, zooplankton community composition was linked with water body depth, productivity and conductivity, in concurrence with previous studies (Table 2.2). It is generally accepted that deeper lakes support a larger number of vertical niches, allowing greater niche separation of competing species (Strøm, 1946). Dodson *et al* (2009) documented a shift in community composition from small to large zooplankton species with increasing productivity and conductivity of temperate lakes in Northern Wisconsin (USA). The unimodal productivity-zooplankton diversity model (e.g. Dodson *et al.,* 2000; Barnett and Beisner, 2007) suggests that there is an optimum productivity at which zooplankton communities are most diverse. Above this, changes in phytoplankton composition associated with eutrophication lead to the development of zooplankton communities better adapted for dominance by blue-green algae species (Richman and Dodson, 1983; Smith, 1983; Gliwicz and Lampert, 1990; Watson *et al.,* 1997). The present study revealed no such relationship with species richness but a linear relationship was apparent between productivity and community composition represented by DCA axes (Fig. 2.1b and Fig 2.1c).

Whilst zooplankton species richness was correlated with water body surface area, surprisingly there appeared to be no effect on community composition. Even more surprisingly, when controlling for covariates, surface area did not significantly explain any variation in species richness (Figure 2.5). This result is in contrast with numerous other studies, which have identified positive relationships between surface area and both richness and composition (Table 2.2). Furthermore, it is in contrast to the predictions of the island biogeography theory that as area increases, there is a higher probability of immigration and a larger number of available niches allowing more species to coexist (MacArthur and Wilson, 1967). In a study of Norwegian lakes, however, Hessen *et al* (2006) also found that water body size had no significant positive effect on zooplankton species richness and in fact showed a weakly negative relationship. Instead these authors found intrinsic factors such as primary productivity, linked with zooplankton community composition in the present study, and fish community structure were most important, exerting bottom-up and top-down control of the zooplankton community respectively.

Table 2.2: Drivers of zooplankton species richness and community composition identified from previous large-scale studies of zooplankton in freshwater lakes.

Driver	Species Richness	Community Composition
Conductivity		Dodson *et al.*, 2009 Present Study
Depth	Dodson, 1992 O'Brien *et al.*, 2004 Tavernini *et al.*, 2009 Present Study	Green and Vascotto, 1978 Korhola, 1999 Korhola *et al.*, 2000 Amsinck *et al.*, 2006 Present Study
Productivity	Dodson, 1992	Dodson *et al.*, 2009 Present Study
Geographic Location	Dodson, 1992 Present Study	Shaw and Kelso, 1992 Dodson *et al.*, 2009 Present Study
Surface Area	Dodson, 1992 O'Brien *et al.*, 2004 Karatayev *et al.*, 2005 Tavernini *et al.*, 2009 Dodson *et al.*, 2009 Present Study	Shaw and Kelso, 1992 Dodson *et al.*, 2009

Rank occurrence data revealed that among the water bodies studied, the genus *Ceriodaphnia* showed a cosmopolitan distribution among TWINSPAN groups of water bodies, characteristic of generalist taxa. This suggests that *Ceriodaphnia* species are found in a range of water bodies of different sizes, depths, climates and degrees of isolation. Conversely, a number of genera appeared to be specialists, each occurring in only one TWINSPAN group. *Thermocyclops* was only recorded in the tropical water bodies of group 1; *Leptodora*, *Skistodiaptomus*, *Orthocyclops*, *Senecella* and *Aglaodiaptomus* only in the more productive water bodies of group 2; *Heterocope* only in group 3; and *Arctodiaptomus* only in the more isolated water bodies of group 4.

2.6.2 Natural vs. Artificial Water Bodies

Analysis of covariance revealed that longitude was linked with zooplankton community composition regardless of whether the water bodies were artificial or naturally formed. While this may be an artefact of the larger representation of North American lakes in the study, among which Dodson (1992) reported that changes in species richness were independent of longitude, there are very few studies that have investigated inter-continental longitudinal gradients in zooplankton communities.

Zooplankton community composition, represented by the first DCA ordination axis, differed between artificial and natural water bodies, as well as with within-lake characteristics depth, primary productivity and longitude. Artificial water bodies are geologically very young, compared with natural lakes formed over thousands of years. Whilst this difference in age may be expected to produce markedly different zooplankton communities, there is no evidence of this being the case. Dodson *et al.* (2006), for example found that water body age had no effect on zooplankton species richness in a study of lakes between 3 and 9500 years old. How rapidly zooplankton communities become established in a water body is unknown and there are few studies investigating the acquisition of zooplankton communities in artificial water bodies. Zooplankton communities, however, may never reach equilibrium due to regular small-scale disturbances (Matsumura-Tundisi and Tundisi, 2002; Scheffer *et al.,* 2003), suggesting that only a short time following initial colonisation, there may be no discernible impact of water body age.

The nature of water body construction, often for the provision of human services or amenity, commonly necessitates maintenance of good water quality in artificial water bodies. Management practices such as artificial destratification and biomanipulation of fish communities are often employed to reduce the undesirable impacts of eutrophication, such as cyanobacterial blooms, reduced oxygen concentration and increased turbidity (Cowell *et al.,* 1987; Hawkins and Griffiths, 1993; Lewis *et al.,* 2003; Antenucci *et al.,* 2005; Becker *et al.,* 2006; Burford and O'Donohue, 2006). Changes in zooplankton composition from large to small bodied cladocera have been observed during aeration (e.g. Cowell *et al.,* 1987) but there are few other studies documenting the effect of this remediation method on zooplankton communities. Biomanipulation relies on the alteration of zooplankton community structure for the control of algae. Such management practices are a probable cause of variation in zooplankton communities between artificial and natural water bodies (e.g. Brooks and Dodson, 1965; Cowell *et al.,* 1987; Hessen *et al*, 1995; Shurin, 2001; Shurin and

Allen, 2001) and therefore likely to produce the observed differences in the present study.

The variance in DCA axis 1 explained by productivity, depth, longitude and water body type was a relatively modest 47.7%, suggesting the importance of some unmeasured factors or stochasticity in structuring zooplankton communities among the studied water bodies. Similarly, the variance explained in species richness by significant factors was only 33.2%. Previous studies have shown biotic interactions such as predation, competition and dispersal to be important drivers of zooplankton community structure (Hobæk *et al.,* 2002), none of which could be quantified in the present study. The importance of fish predation in structuring zooplankton communities was examined by Brooks and Dodson (1965), who proposed the Size Efficiency Hypothesis to explain the mechanism behind observed changes to zooplankton communities under different predation regimes. This hypothesis states that when free of predation pressure, larger herbivorous zooplankton will dominate, due to the competitive advantage of being able to more efficiently exploit fine particulate matter. Conversely, under intense predation by planktivorous fish, larger bodied zooplankton are selected against, allowing smaller species to dominate, whilst under moderate predation, populations of larger zooplankton are low enough to allow the co-existence of large and small species. Various studies since have corroborated this hypothesis at least qualitatively (e.g. Hessen *et al*, 1995; Shurin, 2001; Shurin and Allen, 2001; Vakkileinen *et al.*, 2004; Hülsmann *et al.,* 2005) with Shurin (2001) highlighting the importance of a diverse regional species pool in determining the impact of predation on zooplankton communities. In potential agreement with this, the present study showed that proximity to other water bodies - potential sources of immigrant taxa - was linked with zooplankton species richness.

The occurrences of *Ceriodaphnia, Orthocyclops*, *Holopedium* and *Eucyclops* species were relatively equitable among natural and artificial water bodies, suggesting that these are tolerant of the range of conditions responsible for variation in zooplankton communities between the two types of water body. However, among the water bodies included in the present analysis, five genera were only observed in natural water bodies: *Limnocalanus*, *Senecella*, *Heterocope*, *Arctodiaptomus* and *Aglaodiaptomus*. Information on the ecological preferences of these genera is limited due to species-specific variations. However *Heterocope*, *Limnocalanus* and *Senecella*, along with *Leptodiaptomus*, which occurred significantly more often in natural water bodies, all contain at least some species which show a preference for deep water (Table 2.3), consistent with relatively low scores of each on at least one of the DCA axes. *Acanthocyclops* and *Cyclops* also occurred more frequently in natural water bodies and are relatively cool water species (Table 2.3). Conversely, species of the genus *Thermocyclops*, which occurred more often in artificial water bodies, tend to show a tolerance to a range of water temperatures, with some exclusively warm water species. Although the representation of artificial lakes was limited, these observations could suggest that the natural lakes in this study provided conditions favourable to deeper and cooler water species. This would be consistent with the use of artificial mixing in artificial water bodies, which destratifies the water column, likely removing deep, cool refugia.

In contrast to natural water bodies, none of the genera occurred exclusively in artificial water bodies. In other words, while all taxa found in artificial water bodies are also found in natural lakes, the opposite is not true, suggesting that certain niches are lacking in the artificial lakes tested. These results should be considered with caution and require further investigation due to the limited representation of artificial water bodies in the present meta-analysis, but could suggest that management practices in artificial water bodies reduce the number of specific niches available for more specialist taxa.

In conclusion, while there was an effect of longitude on zooplankton community composition among the water bodies studied here, there also appear to be differences in the scale at which the processes linked with changes in species richness and composition acted. Proximity to a larger number of lakes was found to be important in maintaining species richness, likely through increased immigration from regional source populations. Community composition however, was linked with intrinsic factors such as depth, productivity and conductivity, acting at the local scale, and depended on whether a water body was man-made or naturally formed. These results are among the first to suggest that zooplankton communities in artificial water bodies may be structured significantly differently from those in naturally formed lakes. Intrinsic local factors appear to create conditions favourable to more specialist taxa in natural water bodies. Whether these observations are the result of variations in bottom-up or top-down influences between artificial and natural lakes is unknown and undoubtedly complex to determine. Nevertheless, they highlight the potential for variations at higher trophic levels, as well as bottom-up effects such as water chemistry, that require future investigation.

Cardiff Bay is a shallow freshwater lake, at low elevation in a temperate climate. Within the context of this meta-analysis, the Bay appears to support a zooplankton assemblage typical of other water bodies of similar characteristics. Intrinsic local factors are likely to be important in structuring the zooplankton community, which due to the artificial nature of the Bay, is expected to consist of species adapted to a range of environmental conditions.

Table 2.3: Zooplankton genera that occurred significantly more frequently (or exclusively) in either artificial or natural water bodies in a meta-analysis of global water bodies, with notes on their ecology.

Genus	**Water body preference**	**Ecology**	**References**
Acanthocyclops	Natural	Cyclopoid copepod Relatively cool water genus Large-bodied Widely distributed across north America and Europe	Thorp and Covich, 2001 Wissinger *et al.*, 1999
Aglaodiaptomus	Natural (exclusively)	Calanoid copepod Mostly herbivorous Relatively large-bodied Absent from man-made impoundments in Carolina (USA)	Taylor *et al.*, 1999
Arctodiaptomus	Natural (exclusively)	Calanoid copepod Salinity tolerance Tolerance of a range of temperatures	Jiménez-Melero *et al.*, 2007
Chydorus	Natural	Cladoceran Herbivorous Small-bodied	Dodson, 1992
Cyclops	Natural	Cyclopoid copepod Zooplanktivorous Large-bodied Relatively cool-water species	Thorp and Covich, 2001
Epischura	Natural	Calanoid copepod	Chow-Fraser and Maly, 1988

		Zooplanktivorous/omnivorous Large-bodied Multiple clutches from single mating	Thorp and Covich, 2001 Lampert and Sömmer, 2007
Eudiaptomus	Artificial	Calanoid copepod Herbivorous	Lampert and Sömmer, 2007
Heterocope	Natural (exclusively)	Calanoid copepod Zooplanktivorous At least some deep water species Absent from very shallow water bodies	Lueke and O'Brien, 1981
Leptodiaptomus	Natural	Calanoid copepod Some saline tolerance Some preference for deeper habitats	Montiel-Martínez *et al.*, 2008
Limnocalanus	Natural (exclusively)	Calanoid copepod Carnivorous Tolerant of low temperatures Preference for deeper habitats	Scourfield and Harding, 1994 Thorp and Covich, 2001 Gurney, 1933b
Moina	Artificial	Cladoceran Produce both males and females from ephippial eggs Relatively high salinity tolerance Produce swarms Common in temporary ponds and pools	Thorp and Covich, 2001
Senecella	Natural (exclusively)	Calanoid copepod Herbivorous Some saline tolerant species	Vyshkvartzeva, 1994

		Some preference for deeper habitats	
Skistodiaptomus	Natural	Calanoid copepod Omnivorous	Balcer *et al.*, 1984
Thermocyclops	Artificial	Cyclopoid copepod Tolerant of higher temperatures	Maier, 1989 Maier, 1993

Chapter 3: Testing the PEG Model of Plankton Succession in a Newly Formed Urban Lake

3.1 Abstract

1. Zooplankton seasonality in temperate lakes is expected to reflect a predictable sequence of interactions among grazing zooplankton and phytoplankton of contrasting size. However, available models focus mostly on natural rather than artificial water bodies. Intensive zooplankton counts over two contrasting years were therefore used to investigate whether zooplankton dynamics in the newly-formed, eutrophic and highly managed Cardiff Bay (Wales) conformed to natural patterns. Interactions among species were investigated indirectly from zooplankton abundance, algal counts and stable isotope composition.

2. Despite some variations between years in species richness, composition and timing, seasonal variations in abundance were clear. Zooplankton numbers peaked initially in spring then declined within one month before reaching a smaller subsequent peak in late summer.

3. There was large species turnover within years, but most seasonal variations in abundance were generated by the cladocerans *Bosmina longirostris* (Müller, 1758) and *Daphnia hyalina* (Leydig, 1860). Variations in their $\delta^{15}N$ and $\delta^{13}C$ signatures suggested resource overlap within years, but the species never peaked simultaneously, and as expected were linked with smaller and larger phytoplankton respectively.

4. These data show that Cardiff Bay has rapidly acquired zooplankton composition typical of large, eutrophic lakes, while dynamics generally follow the Plankton Ecology Group (PEG) qualitative model despite intensive management. Dominant zooplankton appear to co-exist through variations in timing of abundance linked to variations in the size-range of algal prey. Variations in zooplankton composition continued into winter with only minor departures from PEG predictions.

3.2 Introduction

Zooplankton community dynamics are driven by complex interactions between a number of factors (Brönmark and Hansson, 2005; Schalau *et al.,* 2007). The principal drivers, however include temperature (e.g. Stockwell and Sprules, 1995; Wolfinbarger, 1999; Benndorf *et al.,* 2001; Rettig *et al.,* 2006), primary production, nutrient availability (e.g. Hessen at al 2006), flushing rate (Wolfinbarger, 1999), predator-prey interactions (Boersma *et al.,* 1996) and competition between species (Hu and Tessier, 1995; Cáceres, 1998). Variations in lake morphology, character, and stratification also have potentially large effects (e.g. Matveev and Matveeva, 2005).

Despite the complexity, seasonality among freshwater zooplankton is relatively predictable, engendered initially by a bloom of small phytoplankton in early spring grazed down by small herbivorous zooplankton. Larger-celled phytoplankton are then exploited by larger herbivores before grazing pressure exceeds primary production, which coupled with nutrient depletion leads to a collapse in algal food resources (clear water phase) and a mid-summer decline in zooplankton abundance (Tessier and Welser, 2006). A secondary peak in zooplankton abundance often follows as phytoplankton populations recover in early autumn. These events are expressed in the Plankton Ecology Group's (PEG) qualitative model (Sömmer *et al.,* 1986), conceived for typical stratifying lakes but tested initially using data from 24 lakes, ponds and unmixed reservoirs. The PEG model is considered to provide a basis for eutrophic, temperate, stratifying lakes in general, and emphasises the seasonal effects of temperature, light, nutrients and fish predation as major factors driving plankton development.

While many predictions from the PEG model are well supported, tests and applications have overwhelmingly involved natural rather than artificial lake-systems. Not only do the latter contrast with natural lakes in age, but their management is often designed to disrupt some of the factors that drive plankton dynamics. For example, artificial aeration and mixing are used to prevent stratification and associated cyanobacterial blooms while increasing oxygen concentration and limiting light availability (e.g. Heo and Kim, 2004; Müller and Stadelmann, 2004; Becker *et al.,* 2006). Such effects homogenise lake physico-chemistry (e.g. Heo and Kim, 2004) lower surface water temperatures and can lower internal phosphorous loading to alter phytoplankton succession (e.g. Becker *et al.,* 2006). In some cases, previously dominant cyanobacteria are replaced by diatoms that are more easily exploited by zooplankton (e.g. Steinberg, 1983; Wetzel, 2001; Lewis *et al.,* 2003; Heo and Kim 2004; Becker *et al.,* 2006). Alterations in mixing depth and temperature regime might also be expected to affect zooplankton succession (Gerten and Adrian, 2002; Berger *et al.,* 2007). Reduced residence time in artificial lakes and reservoirs could affect the applicability of PEG predictions by promoting flushing of phytoplankton and zooplankton and disrupting the succession of communities (Sömmer *et al*., 1986). Tests under artificial-lake conditions allow an assessment of the robustness of the PEG model under novel circumstances, and indicate how rapidly typical planktonic dynamics emerge in newly formed lake systems.

Cardiff Bay represents an ideal opportunity to test the central predictions of the PEG model on a highly managed, new, artificial lake. The lake was formed in 2001 by the construction of a barrage across the combined estuaries of two eutrophic rivers to permanently inundate under freshwater almost 200 hectares of former inter-tidal mud-flats. The Bay is intensively managed to maintain oxygen concentrations and disrupt stratification by an extensive aeration system. Other *ad-hoc* management activities take place, for example to control benthic chironomids (Vaughan *et al.* 2008). In all these respects, Cardiff Bay represents an extreme test of how widely the PEG predictions might be generalised.

3.3 Aims and Hypotheses

The temporal dynamics of the zooplankton community in Cardiff Bay were appraised through continuous fortnightly surveys over two contrasting years to examine whether zooplankton dynamics followed PEG predictions. In particular, three specific hypotheses were tested about the emergent properties of zooplankton dynamics observable at the whole-lake scale:

Hypothesis 1: Variations in the zooplankton community of Cardiff Bay track proximate environmental factors with seasonality that conforms to PEG predictions, i.e. an initial spring peak in zooplankton, with smaller herbivores preceding larger herbivores (see Fig. 6 in Sömmer *et al.,* 1986).

Hypothesis 2: Co-existing herbivorous zooplankton in Cardiff Bay partition resources through temporal separation of their population peaks, linked in turn with algal resources of contrasting size. Evolutionary explanations for temporal succession among zooplankton was more implicit than explicit in PEG predictions, but must provide the ultimate basis for species sequences.

Hypothesis 3: A zooplankton community persists over less productive periods of the year and involves a combination of different taxa. Although a minor feature of the PEG model, year-round sampling in Cardiff Bay provided an opportunity to test the prediction that adult zooplankton persist into winter as well as resting stages.

3.4 Methods

3.4.1 Zooplankton Collection

Ten sites were chosen for zooplankton collection throughout Cardiff Bay over a range of potential habitats with each adjacent to existing points for water quality sampling (see Fig. 1.1). Zooplankton at each was sampled fortnightly between March 2006 and February 2008 using a fine mesh (60μm) conical plankton net of mouth diameter 0.20m, on a steel mouth-reducing frame to minimise water disturbance (De Bernardi, 1984). The net was lowered to the lake-bed using the on-board depth meter and metre-markers on the rope as a guide, and then hauled vertically through the water column while zooplankton was collected on a piece of 60μm nylon mesh (approximately 8cm x 8cm) screwed to the net base. After rinsing, this square of mesh was removed and fixed in 70% methylated ethanol. The net was rinsed thoroughly between samples.

During the summer, the net was hauled at each site on each sampling occasion, but double hauls were used during winter when zooplankton density was particularly low to increase the number of individuals in the sample and to reduce the risk of under-representing rare species. Zooplankton abundances were expressed as the number of individuals per m^3.

In the laboratory, zooplankters in each sample were counted and identified to species (Gurney, 1933a; Gurney, 1993b; Harding and Smith, 1974; Scourfield and Harding, 1994). Particularly dense samples were re-suspended and 10% sub-samples were taken following McCauley (1984), provided that the total number of individuals in a sample exceeded 150 (Chimey and Bowers, 2006). For this study, abundance data were combined from the 10 sites for each sampling occasion, but inter-site differences are explored elsewhere (see Chapter 4).

3.4.2 Water Quality

On each sampling occasion and at each site, temperature, pH, dissolved oxygen, turbidity, conductivity and salinity were recorded using a portable sonde (model 6920, YSI Inc., USA) and data logger (model 650MDS, YSI Inc., USA). Water samples were collected and analysed using a fluorimeter (bbe Moldaenke, Germany) to determine the total concentration (μgl^{-1}) and activity of chlorophyll *a* associated with green algae, blue-green algae, diatoms and cryptophytes at each site. Algal cell counts were made through approximately fortnightly collection between March and October of surface water samples. From these data, algal genera were classified into more readily ingested (<30μm) and less readily ingested (>30μm) groups (Nadin-Hurley and Duncan, 1976; Fergusson *et al.,* 1982), and more readily ingestible genera further classified into five size-classes: <10μm; 10-15μm; 15-20μm; 20-25μm; and 25-30μm, based on the maximum linear length (see Agasild and Nõges, 2005). Suspended solids, heavy metal and nutrient concentrations were measured approximately monthly year-round, through surface water sample collection. Meteorological readings were recorded automatically every 15 minutes by fixed telemetry at Environment Quay (see Fig. 1.1). River flow rates were also measured every 15 minutes at Enivronment Agency (EA) gauging stations at St Fagans for the River Ely and at Pontypridd for the River Taff. Records of these data were available from the time of impoundment in 2001. Mean values of the environmental variables from the 10 sites were used in subsequent analysis to maintain compatibility with the zooplankton data.

3.4.3 Stable Isotope Analysis

Stable isotope analysis was carried out on all zooplankton species collected in sufficient density over the sampling period. This was to assess inter- or intra-specific variations in likely carbon sources and trophic position and test the hypothesis that co-existing herbivorous zooplankton in Cardiff Bay partition resources through temporal separation of population peaks linked with algal food resources. For the most abundant species, *Daphnia hyalina* (Leydig, 1860) and *Bosmina longirostris* (Müller, 1785), samples were separated by year of collection in order to assess any changes in $\delta^{13}C$ and $\delta^{15}N$ between years. Where numbers were too low for monthly separation, individuals were combined over the entire sampling period to give a pooled $\delta^{13}C$ and $\delta^{15}N$ signature. Isotopic signatures were also assessed in *Dreissena polymorpha* larvae after decalcification to prevent bias towards calcium carbonate enrichment. Decalcification followed Pennington and Hadfield (1989), and involved exposure in hydrochloric acid diluted at pH5 for 3 hours followed by rinsing in distilled water.

All samples were freeze-dried for 24 hours before weighing (10mg ± 2mg) directly into 6x4mm tin capsules (Elemental Microanalysis Ltd, Cambridgeshire, UK) to be combusted at 1020°C. Analysis of ^{13}C and ^{15}N was conducted at the University of California, Davis Stable Isotope Facility, USA, using a Europa Hydra 20/20 continuous-flow isotope mass spectrometer (CF-IRMS) (Sercon Ltd, Cheshire, UK). Results are reported using standard isotope ratio notation (parts per thousand, ‰) as the relative difference to standards Pee Dee Belemnite for ^{13}C, and N_2 in air for ^{15}N according to the equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where δX is $\delta^{13}C$ or $\delta^{15}N$ and R is the $^{13}C/^{12}C$ or $^{15}N/\,^{14}N$ ratio, respectively.

Replicate laboratory reference standards were run every 12 samples and measurement errors (standard deviation) of the analysis were ± 0.03 ‰ for ^{13}C and ± 0.2 ‰ for ^{15}N.

All Cardiff Bay isotopic signatures were derived retrospectively on samples that had been preserved in 70% methylated ethanol which might affect isotopic values, but

Feuchtmayr and Grey (2003) justify this approach provided results are interpreted with care. Since the greatest preservation effects occur with six days of preservation (Salonen and Sarvala, 1980), consistency is achieved by treating all samples similarly and using samples that have been preserved for longer, in this case up to two years. Moreover, the effects of preservation in 70% methylated ethanol on isotopic signatures were assessed directly during this study using a culture of *Daphnia magna* (Straus, 1820) filtered through 1mm mesh to sort individuals into large (>1mm) and small (<1mm) body sizes. Five replicate samples from each size category were either frozen from live at -20°C until analysis or preserved in 70% methylated ethanol for two weeks prior to isotope analysis. Gut content was not removed from any individuals (see Feuchtmayr and Grey, 2003), and all other steps followed identical procedures to the Cardiff Bay samples. Preservation method had no effect on $\delta^{15}N$ in either large or small *D. magna*, with changes imperceptible (Table 3.1). Effects on $\delta^{13}C$ were significant, with a mean difference of 0.92‰ between live-frozen and ethanol-preserved samples, with consequences also for C:N ratios, but the absolute effects were small relative to variations within and between species (see Results). Body-size effects were also small.

Table 3.1: Variations in 13C and 15N signatures between *Daphnia magna* of different body size and subject to different preservation technique (live-frozen or preserved in methylated ethanol (IMS)) according to ANOVA. SS: Sum of squares; MS: mean square; F: test value with associated degrees of freedom; P: probability value (not corrected for multiple testing).

Body size	Small	Large		ANOVA			
	Mean	**Mean**		**SS**	**MS**	**$F_{(1,18)}$**	**P**
C:N ratio	6.63	7.34	Size	2.51	2.51	1.64	0.217
			Error	27.59	1.53		
δC	-24.14	-24.70	Size	1.305	1.305	4.92	0.04
			Error	4.770	0.265		
δN	14.83	15.14	Size	0.472	0.472	1.22	0.283
			Error	6.941	0.386		
Preservation technique	Frozen **Mean**	IMS **Mean**		**SS**	**MS**	**$F_{(1,18)}$**	**P**
C:N ratio	5.84	8.12	Preservation	25.918	25.918	111.42	<0.001
			Error	4.187	0.233		
δC	-23.99	-24.91	Preservation	4.189	4.189	39.94	<0.001
			Error	1.886	0.105		
δN	14.88	15.10	Preservation	0.242	0.242	0.61	0.446
			Error	7.171	0.398		

3.4.4 Statistical Analysis

All early stage juvenile zooplankton including all stage I, II and III copepodites, were excluded from analyses, since individuals smaller than 60μm were unlikely to be representatively sampled using the collection technique. Dominant species were defined as those contributing >10% of the total zooplankton abundance in any sampling period.

To test hypotheses 1 and 3, species data from all samples were first ordinated using Detrended Correspondence Analysis (DCA), chosen because of the large number of zero values in the zooplankton species abundance data, the unimodal nature of the data, and the need to generate ordination axes unconstrained by environmental variables (Speckman *et al.,* 2005). Abundance data were log (n+1) transformed prior to analysis, with no weighting applied to individual species. Ordination data permitted the visualisation of species changes through time, but DCA axes scores were also related to environmental variables using correlation. In addition, Two-way Indication Species Analysis (TWINSPAN) (Hill and Šmilauer, 2005), using five equal cut levels, was carried out on percentage abundance data in order to classify zooplankton species into those that commonly co-occurred through time (Hill and Šmilauer, 2005). The species-groups identified then acted as a further basis for appraising seasonal variations in numbers.

To test hypothesis 2, in addition to assessing overlap between abundant species on isotopic measurements and species-separation through time, zooplankton species' abundances were correlated against the abundances of algae of contrasting size, in both cases after log (n+1) transformation to homogenise variances.

3.5 Results

3.5.1 Environmental Conditions

In addition to typical seasonal variations in climatic conditions, the two study years differed (Fig. 3.1). For example, peak temperature in July 2006 was 3.8°C higher than in July 2007 and 4°C above the long-term July average for Cardiff (Met Office, 2008) (Fig. 3.1a). Mean residence time was shorter in the summer of 2007 than in 2006 due to increased rainfall over that period (Fig. 3.1f). There was also among year variation in seasonal patterns of dissolved oxygen concentration (DO) (Fig. 3.1b), salinity (Fig. 3.1c), nutrients (Fig. 3.1h) and chlorophyll *a* (Fig. 3.1g). For example, in both 2006 and 2007, chlorophyll *a* concentration showed two peaks, one in the spring and the next in the summer. Whilst this suggests that phytoplankton dynamics followed predictions made by the PEG model, the initial peak occurs earlier in 2007 than in 2006 and the subsequent peak is much greater. In combination, these variations provided the potential for zooplankton community composition to vary both within and between years.

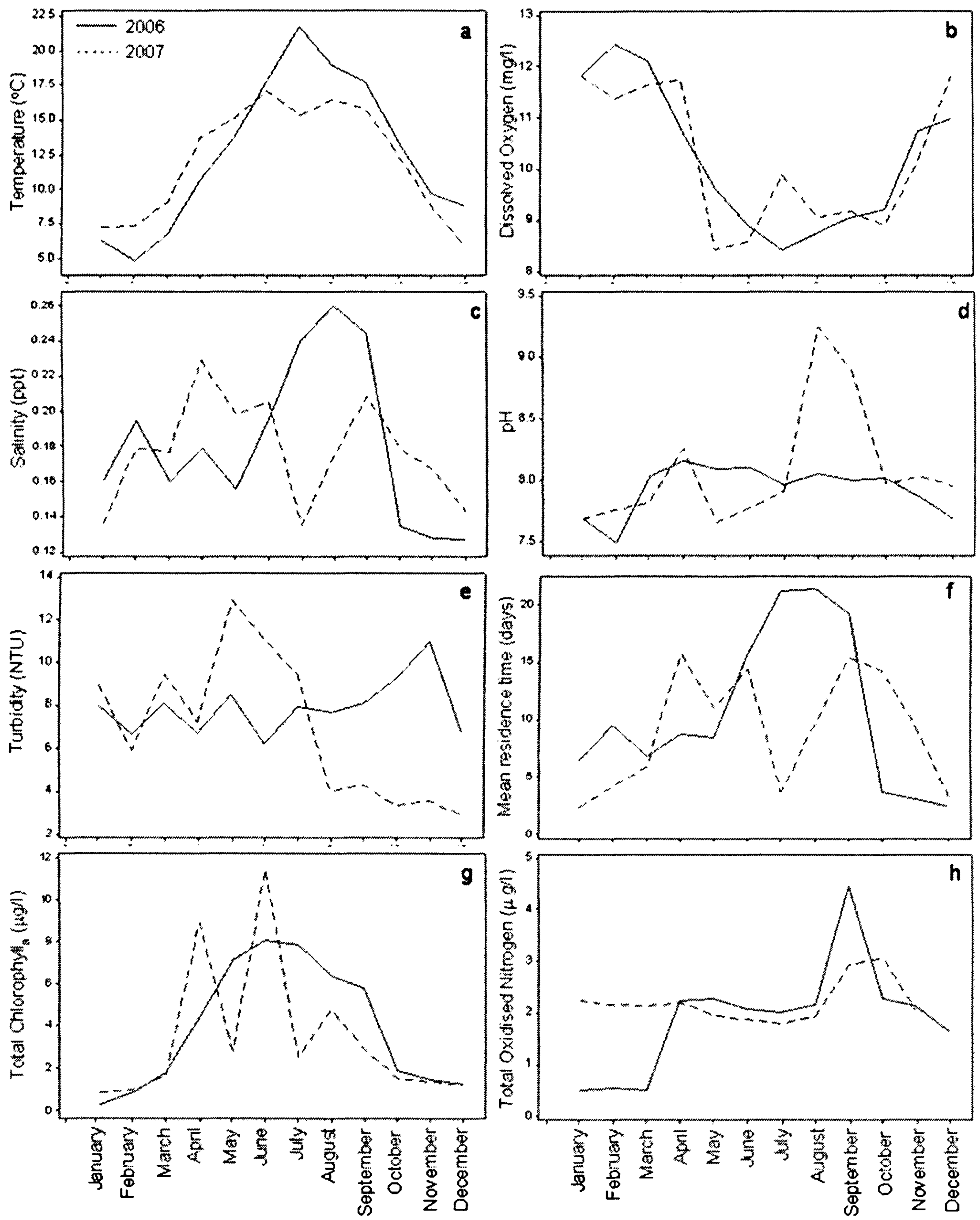

Figure 3.1: Variations in environmental variables in Cardiff Bay over the two-year study period.

3.5.2 Zooplankton Community Composition

Ordination using DCA captured major variations in composition among the zooplankton community recorded in Cardiff Bay (Fig. 3.2). The most marked were seasonal trends in composition on axis 1, with a second axis suggesting some tendency for composition to vary slightly between the two years of the study (Fig. 3.3). In turn, seasonal variations in composition were reflected in strong correlations between axis 1 ordination scores and variables such as day length, water temperature, dissolved oxygen concentration, pH, total oxidised nitrogen concentration and river discharge (Table 3.2). DCA axis 2 was less specifically related to day length but also inversely correlated with salinity and chlorophyll *a*, and hence apparent environmental variations between 2006 and 2007. Other subtle inter-annual variations in composition included a reduction in mean number of species and mean alpha diversity between years 1 and 2 (Table 3.3).

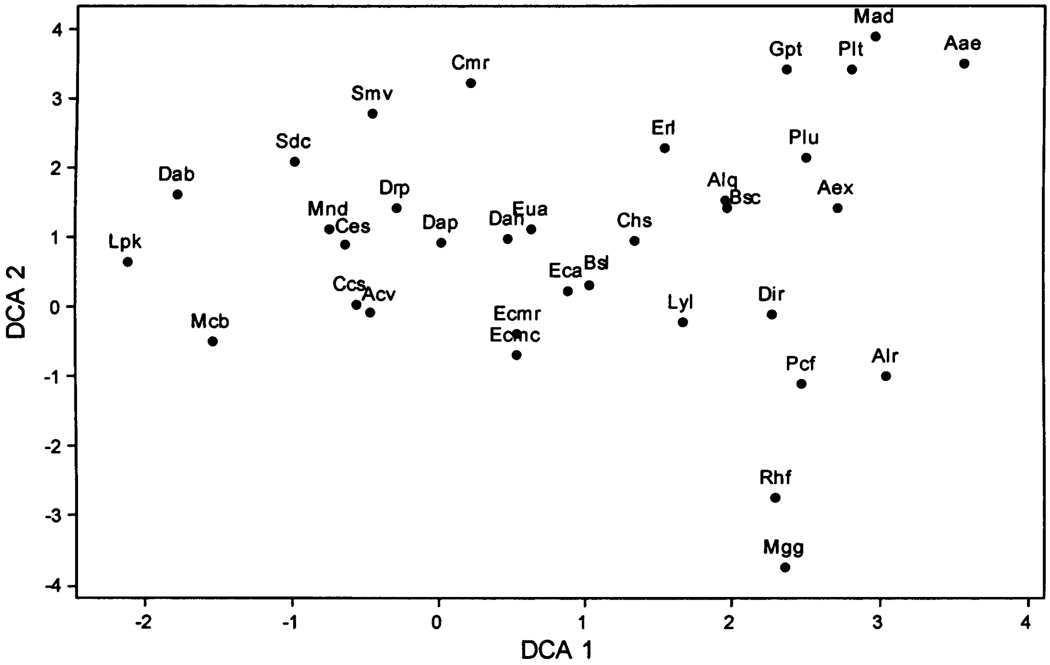

Figure 3.2: Species ordination axes scores from DCA of zooplankton species in Cardiff Bay over the two-year study period. Aae: *Alonopsis elongata*; Acv: *Acanthocyclops vernalis*; Aex: *Alonella excisa*; Alr: *Alona rectangula*; Alq : *Alona quadrangularis*; Bsc: *Bosmina corregoni*; Bsl: *Bosmina longirostris*; Ccs: *Cyclops strenuus*; Ces: *Ceriodaphnia setosa*; Chs: *Chydorus sphaericus*; Cmr: *Camptocercus rectirostris*; Dab: *Diaphanomsoma brachyurum*; Dah: *Daphnia hyalina*; Dap: *Daphnia pulex*; Dir: *Disparolona rostrata*; Drp: *Dreissena polymorpha* larvae; Eca: *Eucyclops agilis*; Ecmc: *Eucyclops macruroides*; Ecmr: *Eucyclops macrurus*; Erl: *Eurycercus lamellatus*; Eua: *Eurytemora affinis*; Gpt: *Graptoleberis testudinaria*; Lpk: *Leptodora kindtii*; Lyl: *Leydigia leydigi*; Mad: *Macrocyclops distinctus*; Mcb: *Microcyclops bicolor*; Mgg: *Megacyclops gigas*; Mnd: *Monospillus dispar*; Pcf: *Paracyclops fimbriatus*; Plu: *Pleuroxus uncinatus*; Plt: *Pleuroxus trigonellus*; Rhf: *Rhyncotalona falcata*; Sdc: *Sida crystallina*; Smv: *Simocephalus vetulus*.

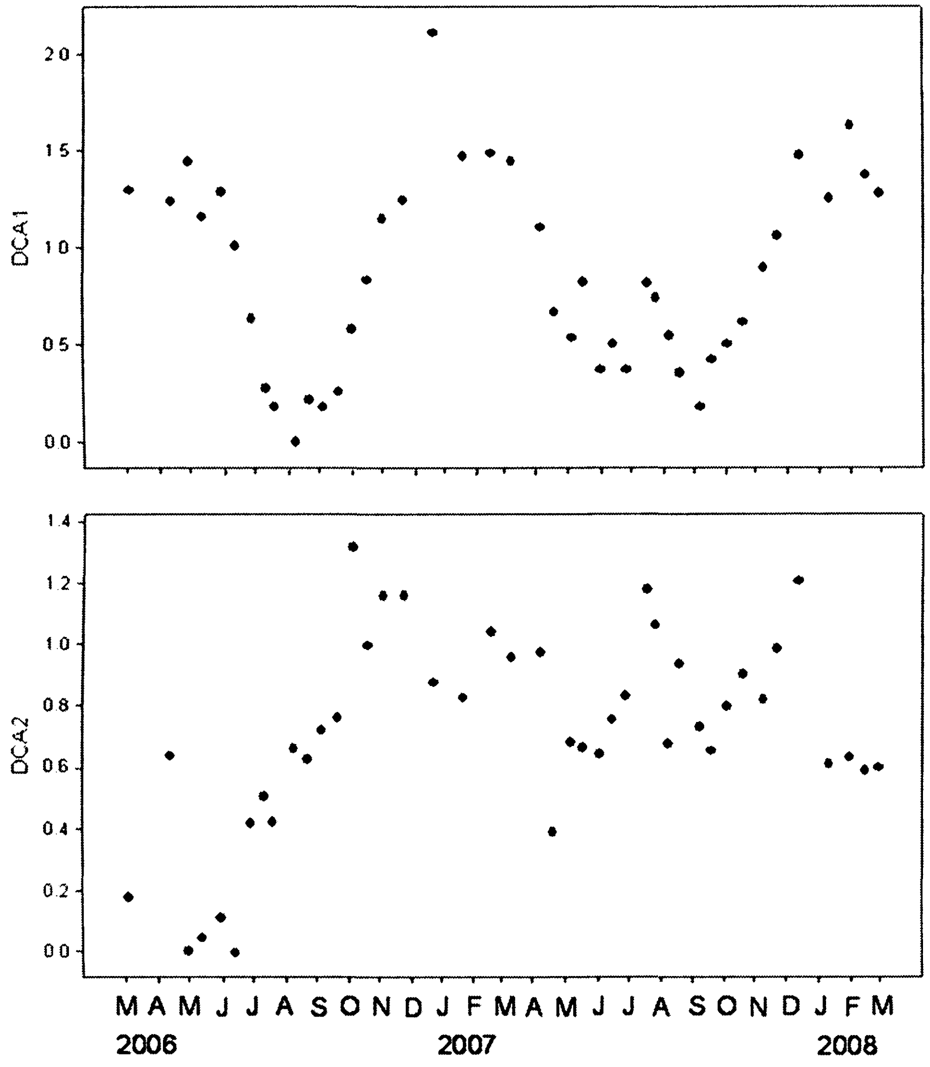

Figure 3.3: Sampling date ordination axes scores from DCA, plotted by date, over the two-year study period.

Table 3.2: Environmental correlates with DCA axes 1 and 2, resulting from an ordination of zooplankton species in Cardiff Bay over the two year sampling period (N=42 sampling occasions). Bold typeface indicates statistically significant Pearson's correlation co-efficient. Probability values not corrected for multiple testing.

	DCA 1	DCA 2
Temperature (^{0}C)	**-0.818** **P <0.001**	-0.238 P = 0.129
Hours of daylight	**-0.601** **P <0.001**	**-0.433** **P = 0.004**
Dissolved oxygen concentration (mgl^{-1})	**0.541** **P <0.001**	-0.069 P = 0.666
Salinity (‰)	**-0.638** **P <0.001**	**-0384** **P = 0.012**
pH	**-0.401** **P = 0.009**	-0.215 P = 0.171
Turbidity (NTU)	-0.156 P = 0.324	0.148 P = 0.349
Total chlorophyll$_a$ concentration (μgl^{-1})	-0.147 P = 0.353	**-0.315** **P = 0.042**
Total Nitrogen concentration (μgl^{-1})	**-0.459** **P = 0.032**	0.172 P = 0.445
Combined river flow rate (m^{3}sec^{-1})	**0.469** **P = 0.002**	0.178 P = 0.253

Table 3.3: Between-year variation in species diversity and number of zooplankton species in Cardiff Bay, according to ANOVA (N=42 sampling occasions). SS: sum of squares; MS: mean square; F: test value, with associated degrees of freedom; P: probability value, not corrected for multiple testing.

	Year 1 mean	Year 2 mean		ANOVA			
				SS	MS	$F_{(1,41)}$	P
Number of species	18	14	Year	190.9	190.9	15.77	<0.001
			Error	496.3	12.1		
Shannon Index (α)	1.47	1.28	Year	1.2705	1.2705	14.34	<0.001
			Error	3.6331	0.0886		

In numerical terms, the cladocerans *Bosmina longirostris* and *Daphnia hyalina* dominated the zooplankton community over both sampling years in summer along with the cyclopoid copepod *Eucyclops agilis* (Koch, 1838) (Fig. 3.4). Winter communities differed more between years, with the latter species numerically dominant over the autumn/winter period of 2006/2007 along with the small-bodied detritivorous cladocerans *Alona quadrangularis* (Müller, 1776) and *Pleuroxus uncinatus* (Baird, 1850). By contrast, *B. longirostris* and *D. hyalina* remained dominant throughout the autumn and winter of 2007/2008 with the large herbivorous calanoid copepod *Eurytemora affinis* (Poppe, 1880) (Fig. 3.4).

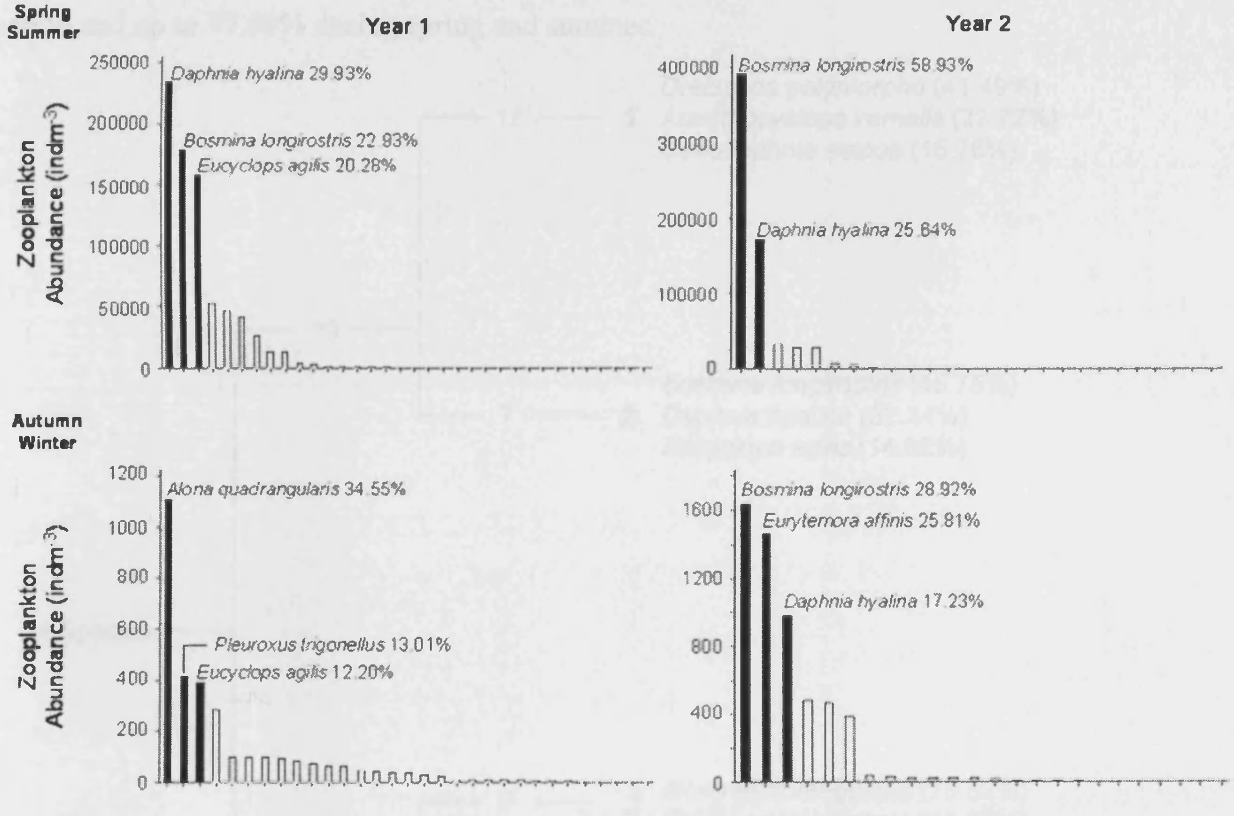

Figure 3.4: Species rank-abundance plots for spring/summer and autumn/winter of each sampling year, showing percentage abundance of dominant species (shaded) within each period.

TWINSPAN captured these patterns effectively, grouping four sets of co-occurring species respectively dominated by 1) the larvae of the invasive Zebra Mussel, *Dreissena polymorpha*, the cyclopoid copepod *Acanthocyclops vernalis* (Müller, 1776) and the small cladoceran *Ceriodaphnia setosa* (Matile, 1890); 2) the widespread dominants, *B. longirostris*, *D. hyalina* and *E. agilis*; 3) *A. quadrangularis* and another small cladoceran *Chydorus sphaericus* (Müller, 1785) and 4) The cyclopoid *Eucyclops macrurus* (Sars, 1863), which accounted for 82.17% of the total abundance of group 4 throughout the sampling period (Fig. 3.5). In turn, Group 1) species were important for a relatively short period during each summer, Group 2) species were present year-round but comprised up to 97.89% of the zooplankton during the spring and summer, and dominated the major zooplankton peaks, Group 3) was important late in the zooplankton year, during late winter, and Group 4) had one major peak in abundance during August of the first sampling year (Fig. 3.6). In numerical terms, TWINSPAN Group 2 species were the most dominant zooplankton species, accounting for 86.14% of zooplankton abundance over the whole sampling period and up to 97.89% during spring and summer.

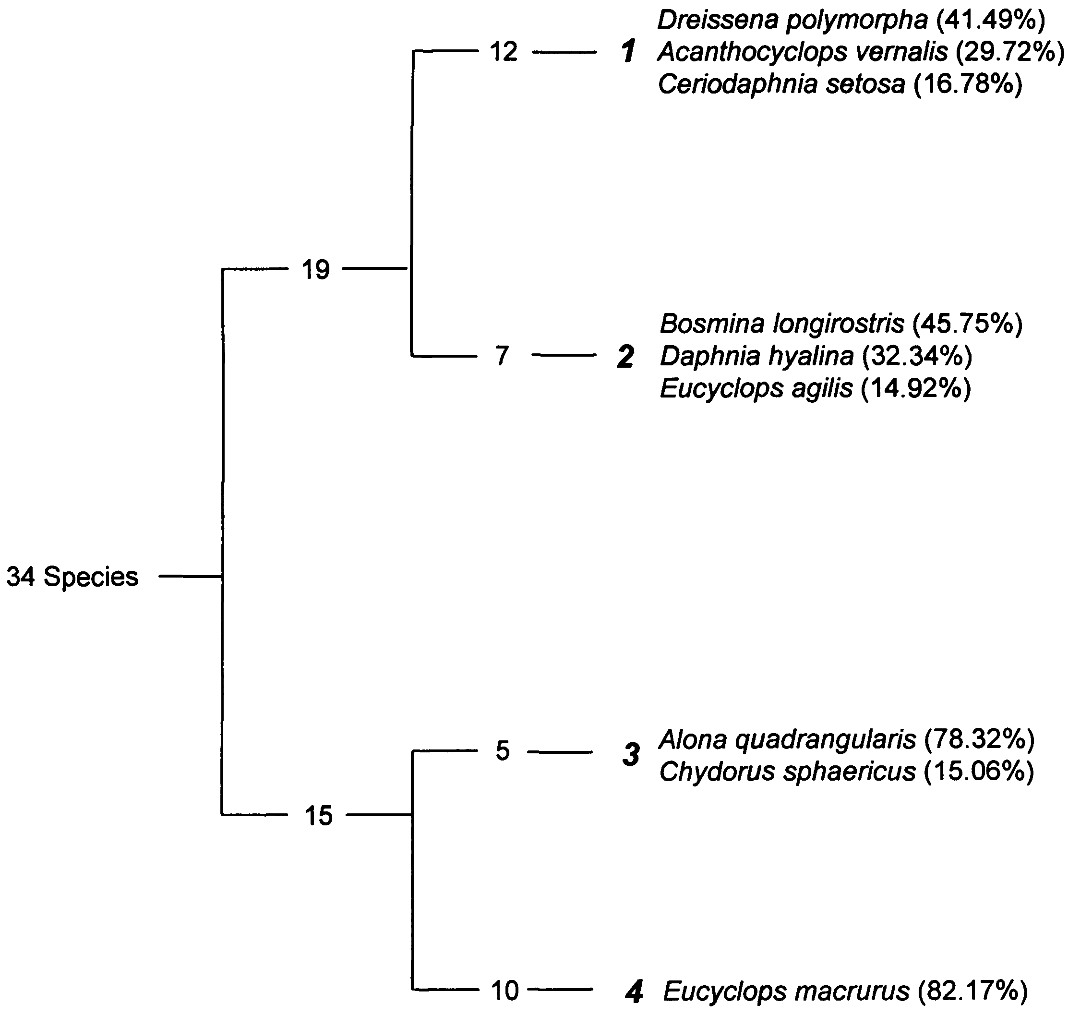

Figure 3.5: Dendrogram identifying species groups from a TWINSPAN analysis of zooplankton species in Cardiff Bay over the two-year study period. The number of species at each split level is indicated and dominant species in each group are listed with percentage abundance in parentheses.

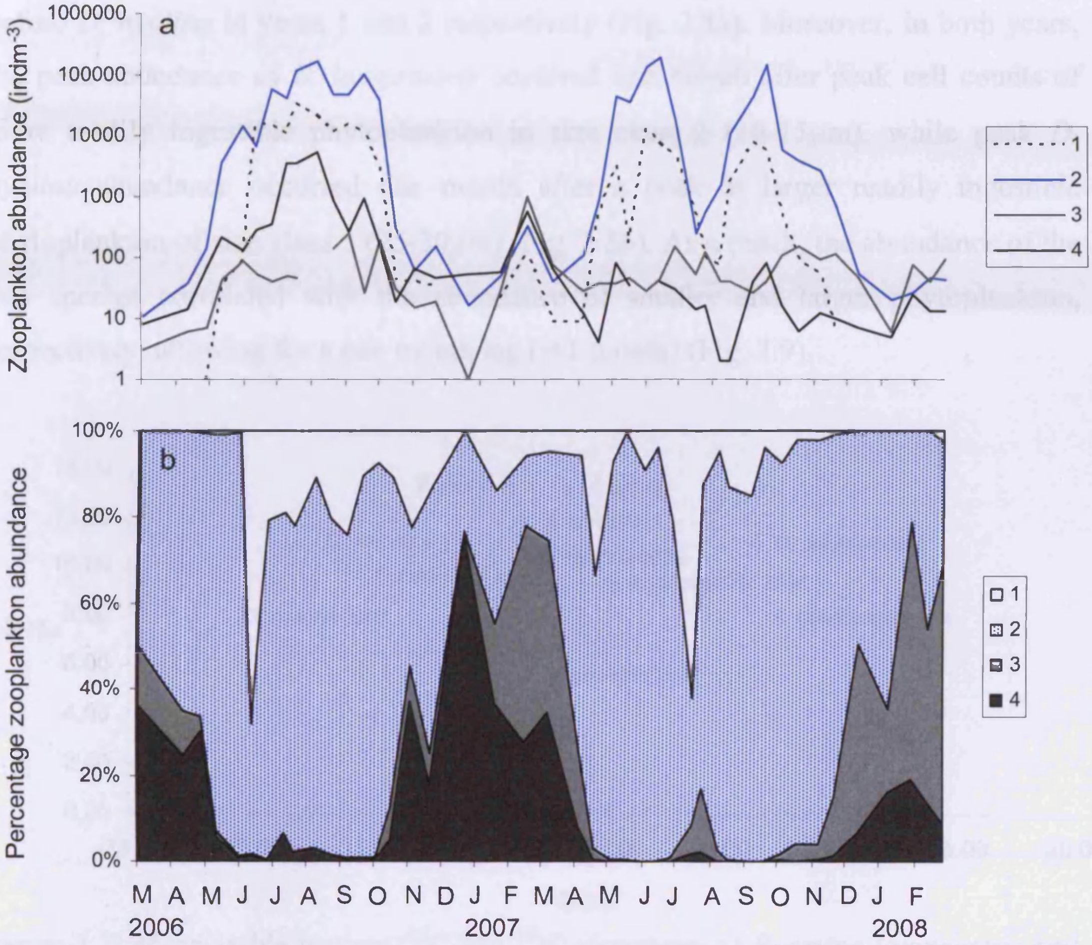

Figure 3.6: Temporal variations in a) absolute and b) relative abundance of species groups identified from TWINSPAN analysis of zooplankton species in Cardiff Bay over the two-year sampling period.

3.5.3 Potential Interactions Between Dominant Species

Although the peak abundances of *E. agilis* coincided with those of *B. longirostris* and *D. hyalina*, values of $\delta^{15}N$ for *E. agilis* were higher than those for either of the two cladocerans, and suggested feeding at a higher trophic level (Fig. 3.7). Conversely, isotopic signatures for both $\delta^{13}C$ and $\delta\ ^{15}N$ overlapped markedly between *B. longirostris* and *D. hyalina* in both sampling years (Fig. 3.7). Moreover, isotopic signatures of these two cladocerans changed near-identically between 2006 and 2007, with both species showing more carbon-depleted signatures in 2007, indicating a shift to more terrestrial carbon sources. This near-identical change suggests similar responses to changing conditions and hence overlapping resource requirements.

However, the peak abundances of *B. longirostris* and *D. hyalina* never coincided throughout the sampling period, with *B. longirostris* peaking two and four months before *D. hyalina* in years 1 and 2 respectively (Fig. 3.8a). Moreover, in both years, the peak abundance of *B. longirostris* occurred one month after peak cell counts of more readily ingestible phytoplankton in size class 2 (10-15μm), while peak *D. hyalina* abundance occurred one month after a peak in larger readily ingestible phytoplankton of size class 5 (25-30μm) (Fig. 3.8b). As a result, the abundance of the two species correlated with the abundance of smaller and larger phytoplankton, respectively, allowing for a one month lag (t+1 month) (Fig. 3.9).

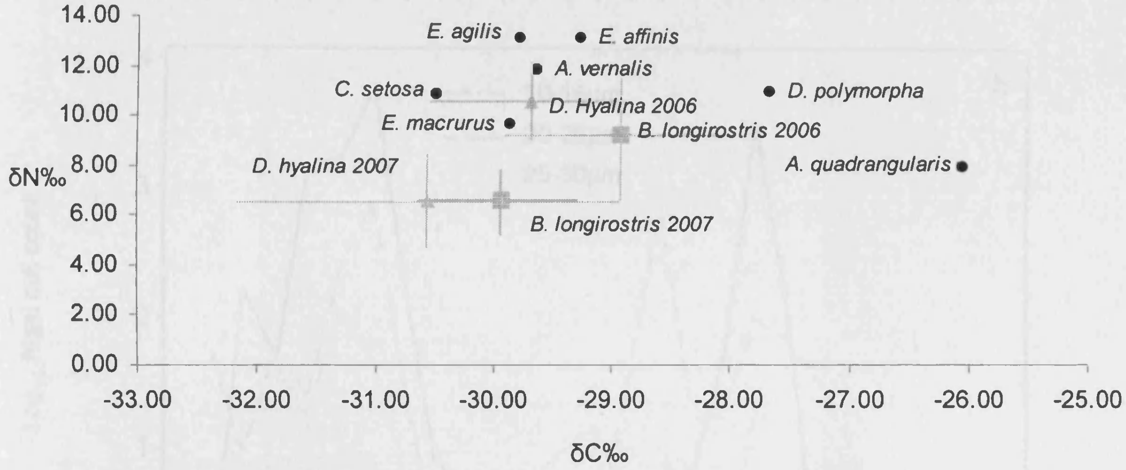

Figure 3.7: Mean stable isotope (^{13}C and ^{15}N) signatures of *Bosmina longirostris* and *Daphnia hyalina* in 2006 and 2007, showing standard deviation from the mean. δC and δN for other less abundant zooplankton species are mean values from combined samples over the two-year sampling period.

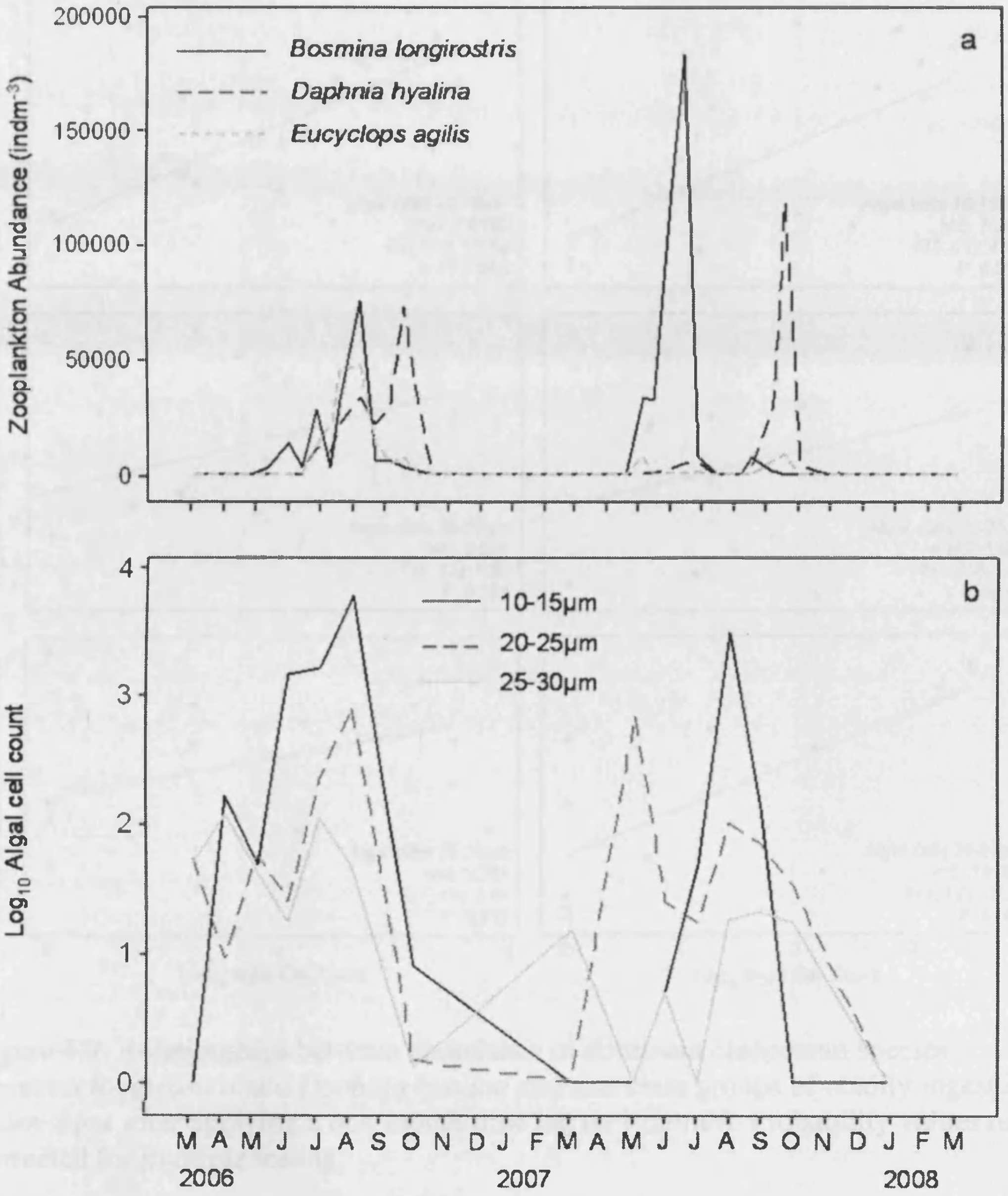

Figure 3.8: Temporal variations in a) abundance of the three numerically dominant zooplankton species and b) cell counts of groups of readily ingestible algae in Cardiff Bay over the two-year sampling period.

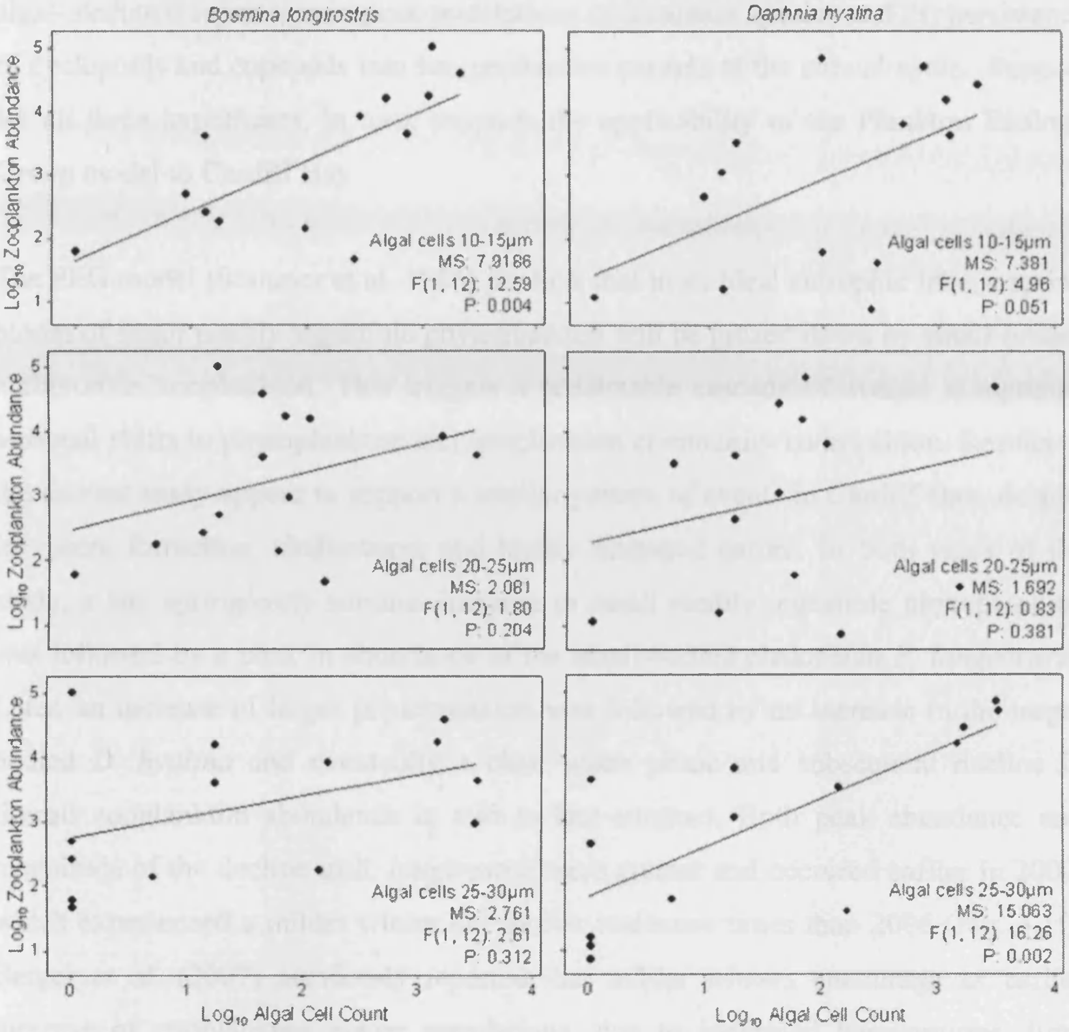

Figure 3.9: Relationships between abundance of dominant cladoceran species *Bosmina longirostris* and *Daphnia hyalina* and size class groups of readily ingestible green algae after applying a one-month time lag (t+1 month). Probability values not corrected for multiple testing.

3.6 Discussion

The aim of this study was to investigate whether the artificial and highly managed nature of Cardiff Bay led to deviations from traditional conceptual models of seasonal plankton dynamics. At the whole-lake scale, the relative role of temperature, limiting nutrients, light and fish predation in structuring zooplankton could not be isolated experimentally. Nevertheless, time series data on zooplankton, supported by extensive environmental measurements over a two-year period along with stable isotope data, allowed three central hypotheses to be tested. All were supported, with data showing i) clear and expected seasonality among zooplankton; ii) evidence of temporal and algal-mediated separation in peak populations of dominant species and iii) persistence of cyclopoids and copepods into less productive periods of the annual cycle. Support for all three hypotheses, in turn, supports the applicability of the Plankton Ecology Group model to Cardiff Bay.

The PEG model (Sömmer et al. 1986) predicts that in an ideal eutrophic lake, a spring bloom of small readily ingestible phytoplankton will be grazed down by small-bodied herbivorous zooplankton. This triggers a predictable cascade of events, comprising seasonal shifts in phytoplankton and zooplankton community composition. Results of the current study appear to support a similar pattern of events in Cardiff Bay, despite its recent formation, shallowness and highly managed nature. In both years of the study, a late spring/early summer increase in small readily ingestible phytoplankton was followed by a peak in abundance of the small-bodied cladoceran *B. longirostris*. Later, an increase in larger phytoplankton was followed by an increase in the large-bodied *D. hyalina* and eventually a clear water phase and subsequent decline in overall zooplankton abundance in mid to late summer. Both peak abundance and magnitude of the decline in *B. longirostris* were greater and occurred earlier in 2007, which experienced a milder winter but shorter residence times than 2006 (Fig. 3.1f). Berger *et al.* (2007) previously reported that milder winters encourage an earlier increase of zooplankton grazer populations, due to increased temperatures, light penetration and algal production, causing an earlier and more severe clear-water phase. The elevated flow and shortened residence time in July 2007 also coincides with the *B. longirostris* population crash. The resultant reduction in mean residence time, from 21 days in July 2006 to 4 days in July 2007, may have been great enough to remove large numbers of zooplankton, since populations did not begin to recover until residence time increased. This recovery appears to include a small increase in *B. longirostris* followed by an increase in *D. hyalina*, which may suggest that high flushing in summer has an important impact on zooplankton community dynamics. As predicted in the first hypothesis, results from Cardiff Bay suggest that the dynamics of the zooplankton community were highly seasonal, tracking environmental variables such as day length, water temperature, dissolved oxygen, pH, total oxidised nitrogen concentration and river discharge.

The competitive exclusion principle predicts that species with identical requirements for a limiting resource are unable to co-exist in a particular ecosystem, leading to dominance by one species (Hardin, 1960). However, this is rarely the case in natural plankton communities, which tend to exist in a state of intermediate disturbance, never reaching equilibrium due to temporal fluctuations in biotic and abiotic processes, such as selective predation, flushing rates and nutrient supply (Hutchinson, 1961; Richerson *et al.,* 1970; Grenney *et al.,* 1973; Matsumura-Tundisi and Tundisi, 2002; Keitel and Chase, 2004). If the frequency of disturbances to a planktonic community exceeds one generation time, an ecosystem is likely to support a greater number of species than would be expected in an ecosystem at complete equilibrium (Gaedeke and Sömmer, 1986).

Stable isotope analysis revealed an overlap in trophic level between *B. longirostris* and *D. hyalina.* Despite differences in body size *Bosmina* and *Daphnia* species are able to exploit similar resources, making them potential competitors (DeMott and Kerfoot, 1982; Kurmayer, 2001). Competition theories have recognised that the presence of two different food sources is vital for the co-existence of competitive zooplankton species (Rothaupt, 1988 and Ciros-Pérez *et al.,* 2001). Algal cell count data from Cardiff Bay reveal that a range of genera are potentially ingestible to *B. longirostris* and *D. hyalina* (<30μm) and that there appears to be a temporal separation in the peak abundance of different algal size classes. Coexisting zooplankton species with similar environmental requirements are often able to partition resources by exhibiting different behaviour or life history responses to food resource availability (DeMott, 1982; DeMott and Kerfoot, 1982; Børsheim and Andersen, 1987; Repka *et al.,* 1999), suggesting that bottom-up processes are important in regulating zooplankton community structure (McQueen *et al.,* 1986; Sarvala *et al.,* 1998). The correlation between populations of *B. longirostris* and *D. hyalina* and different size classes of readily ingestible phytoplankton, suggests that the coexistence of these two potential competitors could be mediated by the timing of blooms of different algal taxa, as predicted in hypothesis 2. These findings are supported by those of Matveev and Balseiro (1990), who showed that seasonal dynamics of the phytoplankton are important in zooplankton co-existence and may in part explain how two potentially competing species can successfully co-exist and dominate the zooplankton community of Cardiff Bay.

Zooplankton abundance tends to be much higher between spring and autumn, the main reproductive period for many species, when phytoplankton is generally abundant. As such, many studies investigating zooplankton seasonal dynamics, concentrate solely on this period (e.g. Whiteside *et al.,* 1978; Vanni and Temte, 1990; Müller-Navarra and Lampert, 1996; Talling, 2003; Tessier and Welser, 2006; Horppila *et al.,* 2009). However, terrestrial carbon sources can act as important energy subsidies for freshwater ecosystems (Pace *et al.,* 2004; Carpenter *et al.,* 2005; Maguire and Grey, 2006; Matthews and Mazumder, 2006), with terrestrial detritus entering freshwater food webs through processing by microorganisms (Hessen *et al.*, 1990). These subsidies may be particularly important in the maintenance of zooplankton communities over periods of low quality autochthonous production. Observations from Cardiff Bay suggest that an over-wintering population of cladocera and copepoda zooplankton species exists throughout less productive periods of the year, as predicted by the PEG model and hypothesis 3. This is supported by the results of the stable isotope analysis, which show that terrestrial carbon was probably more important in the diets of both *B. longirostris* and *D. hyalina* during the summer of 2007 than 2006. The shorter residence times observed in the Bay in the summer of 2007 could have reduced autochthonous production through increased flushing of phytoplankton, resulting in an increased importance of allochthonous carbon sources to the zooplankton population.

Overall, data from Cardiff Bay appear to support the PEG model and imply the rapid acquisition of species assemblages and interactions seen in large eutrophic natural lakes. Evidence from the present study suggests that there are variations in zooplankton species composition even over less productive periods of the year. The implication is that seasonal studies restricted to more productive periods may detect only a limited proportion of the zooplankton community and that year-round studies provide a more accurate assessment of zooplankton community dynamics.

Chapter 4: Resolving Variation in Spatial Structure in the Zooplankton of a Newly Formed Urban Lake

4.1 Abstract

1. Spatial heterogeneity in populations and communities arises due to aggregation and variations along environmental gradients. Detecting the resulting structure depends on appropriately-scaled sampling, but scale-dependence among zooplankton has seldom been investigated. Here, spatial structure at scales ranging from 1m to 2700m was investigated for zooplankton in the newly-formed Cardiff Bay in relation to environmental variation. Particular attention was given to the possible effects of i) variations in water quality between major tributaries; ii) homogenising effects caused by lake mixing and artificial aeration and iii) variations in current velocity created by the Bay's flowpaths.

2. Despite minor variations between its two major tributaries, water quality across Cardiff Bay was relatively homogeneous. In contrast, the numerically dominant zooplankton species (*Daphnia hyalina* (Leydig, 1860), *Eurytemora affinis* (Poppe, 1880) and *Eucyclops agilis* (Koch, 1838)) had highly contagious distributions that reflected increased abundance in warmer locations with increased chlorophyll *a*. These factors explained a substantial proportion of spatial variance in abundance, while spatial autocorrelation, indicative of unmeasured drivers and intrinsic community processes, appeared to be less important.

3. Variations in zooplankton community composition across Cardiff Bay were weaker, and reflected subtle shifts caused by small numbers of species in relation to temperature, oxygen and chlorophyll *a* concentration as well as salinity. The largest proportion of variance in community composition explained by environmental factors was at 1900-1999m, while inferred biotic factors explained a greater proportion of variance at the finest sampling scale.

4. These data appear to suggest that relatively homogeneous water quality in the main body of Cardiff Bay, probably reflecting lake mixing and artificial aeration, has given rise also to relatively homogeneous zooplankton species composition. In contrast, patterns of zooplankton abundance in the dominant species are more structured spatially around algal food concentrations located in warmer waters. These

data, particularly on abundance, suggest that spatial-scale could be important in the detection of the relative influence of spatial and environmental factors on zooplankton more generally.

4.2 Introduction

Natural animal populations are rarely distributed either evenly or completely randomly. According to hierarchy theory, processes acting at different scales interact to affect distributions such that finer-scale processes act within coarser-scaled pattern. For example, physical processes such as wind and water currents are important structuring forces for plankton communities at broad scales, within which finer-scaled biotic effects, such as reproduction, predator-prey interactions, competition and food availability operate to form gradients, aggregations, swarms or layers of organisms (Pinel-Alloul, 1995).

The role of spatial heterogeneity in populations and communities is central to many ecological theories (Legendre and Fortin, 1989), but two important concepts are central. Firstly, spatial dependence, which arises from the Environmental Control model of the 1950s (Bray and Curtis, 1957; Whittaker, 1956), dictates that community structure is driven by spatial structure in environmental factors (Legendre, 1993; Legendre and Legendre, 1998). Second, spatial autocorrelation, occurs when organisms develop pattern due to contagious physico-chemical forcing of environmental conditions or from community interactions such as predation or competition (Legendre, 1993). Both concepts explain why communities are intrinsically spatial and demand that space is considered in ecological studies explicitly, either as a confounding variable that can lead to bias, or as a predictor or covariable in analysis (Dray *et al.,* 2006).

That certain physical and biological factors influence animal distribution is well understood, but knowledge of how structure develops over different spatial scales is essential to the management and conservation of particular ecosystems (Legendre *et al.,* 2005). Moreover, the degree of spatial heterogeneity, relative importance of environmental drivers and ability to detect aggregations and gradients is highly dependent on sampling resolution (Pinel-Alloul, 1995; Fahd *et al.,* 2007). It is therefore imperative that sampling and experimental design reflect this spatial-dependence.

In the case of lake zooplankton, neither physical nor biological processes alone explain spatial heterogeneity. Rather they interact, with the relative contribution of each changing over different spatial scales (Richerson *et al.,* 1978; Malone and McQueen, 1983; Pinel-Alloul and Pont, 1991; Shurin and Allen, 2001). At the whole-lake scale, physical abiotic processes, such as lake morphometry (Håkanson, 2005), river inflow (Yacobi *et al.,* 1993; Romare *et al.,* 2005), surrounding land use (George and Winfield, 2000; Dodson *et al.,* 2005; Hoffmann and Dodson, 2005; Dodson *et al.,* 2007) and wind-induced water movement (George and Edwards, 1976; George, 1981; Kalikhman *et al.,* 1992; Jones *et al.,* 1995; Thackeray *et al.,* 2004) are dominant drivers of zooplankton patchiness. However, towards smaller scales biotic driving forces are expected to dominate. At these finer scales, habitat selection theory states that individuals choose habitats to maximise fitness (Rosenzweig, 1991), so that food-finding (Matthews and Mazumder, 2006), mate-finding or predator avoidance (Shurin, 2001; Castro *et al.,* 2007; Lageren *et al.,* 2008) have important influences. The Multiple Driving Force Hypothesis is used to describe the coupling of physical and biological driving forces in this way (Pinel-Alloul, 1995).

Overwhelmingly, spatial pattern among zooplankton has been investigated in natural lakes. Artificial lakes are not only younger and characterised by more generalist zooplankton species (see Chapter 2) but also, where they are eutrophic, can be characterised by management practices intended to alter natural conditions. For example, artificial aeration and mixing are sometimes used to prevent stratification and associated cyanobacterial blooms while increasing oxygen concentration and limiting light availability to phytoplankton (e.g. Heo and Kim, 2004; Müller and Stadelmann, 2004; Becker *et al.,* 2006). Such effects homogenise lake physico-chemistry (e.g. Heo and Kim, 2004) and may be reasonably expected to homogenise lake zooplankton community abundance and distribution. Lakes characterised by such effects have seldom been evaluated using spatially-explicit sampling, which is surprising both from the point of view of assessing management effects and also appraising the consequences for zooplankton structure.

In Cardiff Bay, artificial aeration is undertaken to prevent oxygen depletion and disrupt stratification, and, along with internal circulation from the Bay's two major tributaries, is likely to enhance lake mixing. Elsewhere, seasonal dynamics of the zooplankton community have been assessed (see Chapter 3) but the Bay also provides an opportunity to test the importance of sampling scale and spatial heterogeneity for zooplankton distribution in a system maintained in a state of physical disturbance.

4.3 Aims and Hypotheses

The broad aim of this study was to assess the spatial distribution of zooplankton in Cardiff Bay, with particular emphasis on the environmental factors potentially responsible for structuring populations and communities over different spatial extents and how the artificial nature of the Bay influences zooplankton distribution. This was achieved by addressing the following hypotheses, tested through observations of zooplankton community composition from extensive surveys.

Hypothesis 1: Spatial variation in zooplankton abundance in Cardiff Bay is linked with proximate environmental factors. In the main body of the Bay, for example, some aspects of environmental quality are expected to be homogenised by the aeration techniques employed in maintaining Bay water quality, leading to a relatively homogeneous distribution of zooplankton. However, the rivers Taff and Ely are expected to support lower abundances than sites in the main body of the Bay due to shorter residence times in these quasi-riverine locations.

Hypothesis 2: Spatial variation in zooplankton community structure in Cardiff Bay is also linked with proximate environmental factors. The zooplankton community in the main body of the Bay is predicted to reflect the expected homogeneous nature of the water quality, while the rivers Taff and Ely are expected to support different zooplankton communities adapted to their more riverine nature. Dominant zooplankton species are expected to co-exist through exploitation of different environments that reflect favourable conditions for the different taxa.

Hypothesis 3: Environmental factors explain a higher proportion of observed variation in zooplankton abundance and community composition at larger sampling scales, while biotic processes are expected to dominate at smaller scales. While these biotic processes relating to zooplankton behaviour were not tested directly, spatial autocorrelation was assessed at different sampling scales using ordinations of distance matrices to represent spatial pattern among explanatory variables.

4.4 Methods

4.4.1 Zooplankton Collection

Sampling was conducted using a hierarchic survey design. To assess broad scale spatial variability, samples were collected from thirty sites without replicates, encompassing the main body of the Bay and the lower reaches of the River Taff and River Ely (see Fig. 1.1) in September 2007. This period was chosen because zooplankters were expected to be relatively abundant and species-rich at this time. Zooplankton at each site were sampled by boat using a fine mesh (60μm) conical plankton net of mouth diameter 0.20m, on a steel mouth-reducing frame to minimise water disturbance (De Bernardi, 1984). The net was lowered to the lake-bed using the on-board depth meter and metre-markers on the rope as a guide, and then hauled vertically through the water column while zooplankton collected on a piece of 60μm nylon mesh (approximately 8cm x 8cm) screwed to the net base. After rinsing, this square of mesh was removed and fixed in 70% methylated ethanol. The net was then rinsed thoroughly between samples.

Sampling was conducted at a finer spatial scale at four of the 30 survey sites, where the original sample point was incorporated into a three-site by three-site grid with 1m spacing. For this finer scale sampling, only sites at which the boat could be moored were used to prevent movement of the boat during sampling. Each fine-scale site was accessed by attaching the plankton net to a length of scaffold marked at 1m intervals from the net mouth, extended from the side of the boat, marked at 1m intervals from the original sampling point. A pulley at the end of the scaffold was used to lower the net into the water. Samples were collected and preserved using the same method as previously described.

In the laboratory, zooplankters in each sample were counted and identified to species level, using identification keys (Gurney, 1933a; Gurney, 1993b; Harding and Smith, 1974; Scourfield and Harding, 1994). Due to the high density of zooplankton, 10% sub-samples were taken following McCauley (1984), provided the total number of individuals in a sample exceeded 150 (Chimney and Bowers, 2006).

4.4.2 Water Quality

On each sampling occasion and at each site, temperature, pH, dissolved oxygen, turbidity, conductivity and salinity were recorded using a portable sonde (model 6920, YSI Inc., USA) and data logger (model 650MDS, YSI Inc., USA). Water samples were collected and analysed using a fluorimeter (bbe Moldaenke, Germany) to identify the total concentration (μgl^{-1}) and activity of chlorophyll *a* associated with green algae, blue-green algae, diatoms and cryptophytes at each site. River discharge was measured every 15 minutes at Environment Agency (EA) gauging stations at St Fagans for the River Ely and Pontypridd for the River Taff. These data were available from the time of impoundment in 2001. Current velocity is rarely measured in the main body of the Bay and was not available for the present sampling occasion. Therefore, data from a previous survey undertaken by Cardiff Harbour Authority (CHA) on 12/02/2008 under similar flow conditions was used and interpolated using ArcGIS (ESRI, 2004) so that current velocity could be estimated for each sampling site in main body of the Bay. Velocity was measured every five seconds across a series of transects using a 1500kHz frequency Acoustic Doppler Current Profiler (Sontek, USA) linked into a laptop running Coastal Surveyor software (Sontek, USA).

4.4.3 Statistical Analysis

All early stage juvenile zooplankton including all stage I, II and III copepodites, were excluded from analyses, since those individuals smaller than 60μm were unlikely to be representatively sampled using the chosen technique.

To test hypotheses 1 and 2, species data from all samples were first ordinated using Detrended Correspondence Analysis (DCA), chosen because of the large number of zero values in the zooplankton species abundance data, the unimodal nature of the data, and the need to generate ordination axes unconstrained by environmental variables (Speckman *et al.,* 2005). Abundance data were log-transformed prior to analysis, with no weighting applied to individual species. Principal Components Analysis (PCA) was carried out on environmental data due to the large amount of multicollinearity between variables. DCA axes scores were related to PCA axes scores using Pearson's correlation coefficient. Results from the DCA as well as environmental variables from the 62 sites (Fig. 1.1, page 14) and zooplankton abundance across the Bay were mapped using interpolation in ArcGIS (ESRI, 2004).

In order to examine the importance of spatial variables on the zooplankton community, principal coordinates of neighbourhood matrix (PCNM) analysis was carried out, following the procedure outlined in Borcard *et al.* (2004). This procedure involves creating a matrix of Euclidean distances between all pairs of sampling points. However, due to the physical structure of the Bay, the Euclidean distance between certain sample points would have represented a distance over land and would have been inappropriate for use in analysis of the zooplankton community. Instead, ArcGIS (ESRI, 2004) was used to measure the shortest path distance between points where Euclidean distances would have included land. A threshold distance was then computed that was equal to the smallest distance linking all sites in a single network, using single linkage cluster analysis. This threshold value was used to truncate the original distance matrix, with all values greater than the threshold replaced with an arbitrarily large value (four times the threshold). This produced a matrix representing the nearest sites, with all other pairings considered far apart. Principal coordinates of the truncated matrix were obtained for the new matrix and positive eigenvalues retained. A stepwise regression was used to obtain the principal coordinates that significantly explained any variation in the DCA axes and hence zooplankton community composition. The significant principal coordinates could then be treated as spatial explanatory variables (PCNM axes).

Zooplankton species distributions were examined using variance:mean ratios. To test hypothesis 3, the importance of environmental and spatial variables on zooplankton abundance and community composition at different sampling scales was examined. To do this, mean values of zooplankton abundance, DCA, PCA and PCNM axes scores were calculated for each possible site pairing. Regressions of mean abundance and DCA axes scores were then carried out against mean PCA and PCNM scores for groups of pairings in each of 28 distance classes.

4.5 Results

4.5.1 Environmental Conditions

Variations in environmental conditions in the main body of Cardiff Bay were relatively small between sites (Fig. 4.1), although there were some moderate differences in water quality between the mouths of the two main tributaries, the Taff and Ely. The Ely had temperatures slightly greater than the River Taff by c1.5°C, and also the lowest dissolved oxygen concentration at c8.0 mg/l. Chlorophyll$_a$ concentration was highest in the inner harbour and other shallower areas in the main body of the Bay, with site 5 (Fig. 1.1) showing a lower concentration, probably due to the location of an aeration bubbler. The rivers and near-barrage sites also had lower chlorophyll *a* concentrations. pH in the Bay was circumneutral to mildly alkaline throughout, varying by no more than 0.4 units between the lowest pH in the River Ely and highest in the Taff. Salinity varied only by 0.4‰ but was highest near the barrage, where the saline sumps are located, and lowest in the River Taff. Turbidity was lowest in both rivers and highest at the shallow site 6 (Fig. 1.1). In the main body of the Bay, flow was highest in the area around the mouth of the Taff. There were also areas of faster flow near the shallower sites to the south west of the Bay and near the barrage.

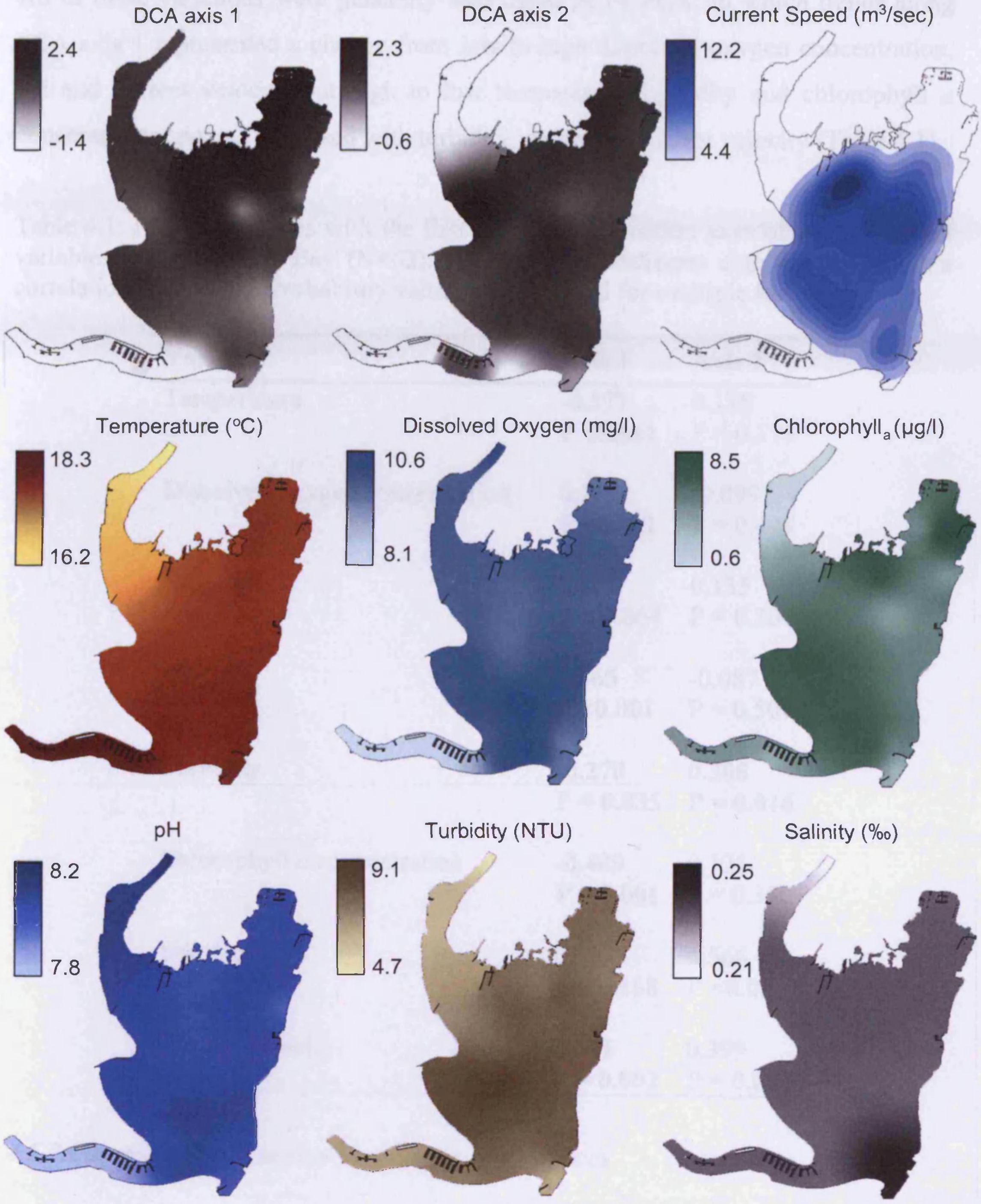

Figure 4.1: Variations in zooplankton community composition (represented by DCA axes scores) and environmental conditions across Cardiff Bay as interpolated from data taken at 62 sampling points in September 2007.

All of these variations were generally well captured by PCA, in which trends along PCA axis 1 represented a change from low to high dissolved oxygen concentration, pH and current velocity but high to low temperature, turbidity and chlorophyll *a* concentration. Axis 2 increased with turbidity, depth and current velocity (Table 4.1).

Table 4.1: Major correlates with the first two PCA ordination axes of environmental variables across Cardiff Bay (N=62). Bold typeface indicates significant Pearson's correlation coefficient. Probability values not corrected for multiple testing.

Variable	**Axis 1**	**Axis 2**
Temperature	**-0.577** **P <0.001**	0.178 P = 0.171
Dissolved oxygen concentration	**0.709** **P <0.001**	-0.099 P = 0.449
Salinity	0.021 P = 0.864	0.135 P = 0.300
pH	**0.665** **P <0.001**	-0.087 P = 0.507
Turbidity	**-0.270** **P = 0.035**	**0.308** **P = 0.016**
Chlorophyll *a* concentration	**-0.409** **P = 0.001**	0.121 P = 0.350
Site depth	0.169 P = 0.188	**0.566** **P <0.001**
Current velocity	**0.381** **P = 0.002**	**0.399** **P = 0.001**

4.5.2 Community Composition and Species Abundances

A total of 17 species of zooplankton was identified during the spatially intensive surveys reported here. Overall zooplankton abundance varied by 6405ind/m^3 between the least and most dense samples, with numbers concentrated at sites in the inner harbour or near the barrage, but lowest in the rivers mouths, particularly the Taff (Fig. 4.2). Zooplankton abundance declined moderately with dissolved oxygen concentration and salinity, but increased with turbidity, chlorophyll *a* concentration and, interestingly current velocity, as reflected in positive correlation with PCA axis 2 (Table 4.2). All three numerically dominant species (*Daphnia hyalina*, *Eurytemora affinis* and *Eucylops agilis)* followed similar trends with respect to temperature, dissolved oxygen and chlorophyll *a*, but there were also some contrasts that reflected variations among these species in the conditions occupied (Table 4.3). With high variance:mean ratios, each of these three species was highly aggregated either near the barrage, in the inner harbour and near the centre of the Bay (*D. hyalina*, variance:mean = 1191.59 and *E. agilis*, variance:mean = 204.26); or in the inner harbour and at the mouth of the Ely *(E. affinis*, variance:mean = 297.55) (Fig. 4.2). Interestingly, in no case was there a strongly negative effect of current velocity. *D. hyalina* differed from *E. affinis* and *E. agilis* in being independent of pH and turbidity, whilst the saline-tolerant *E. affinis* was apparently independent of salinity.

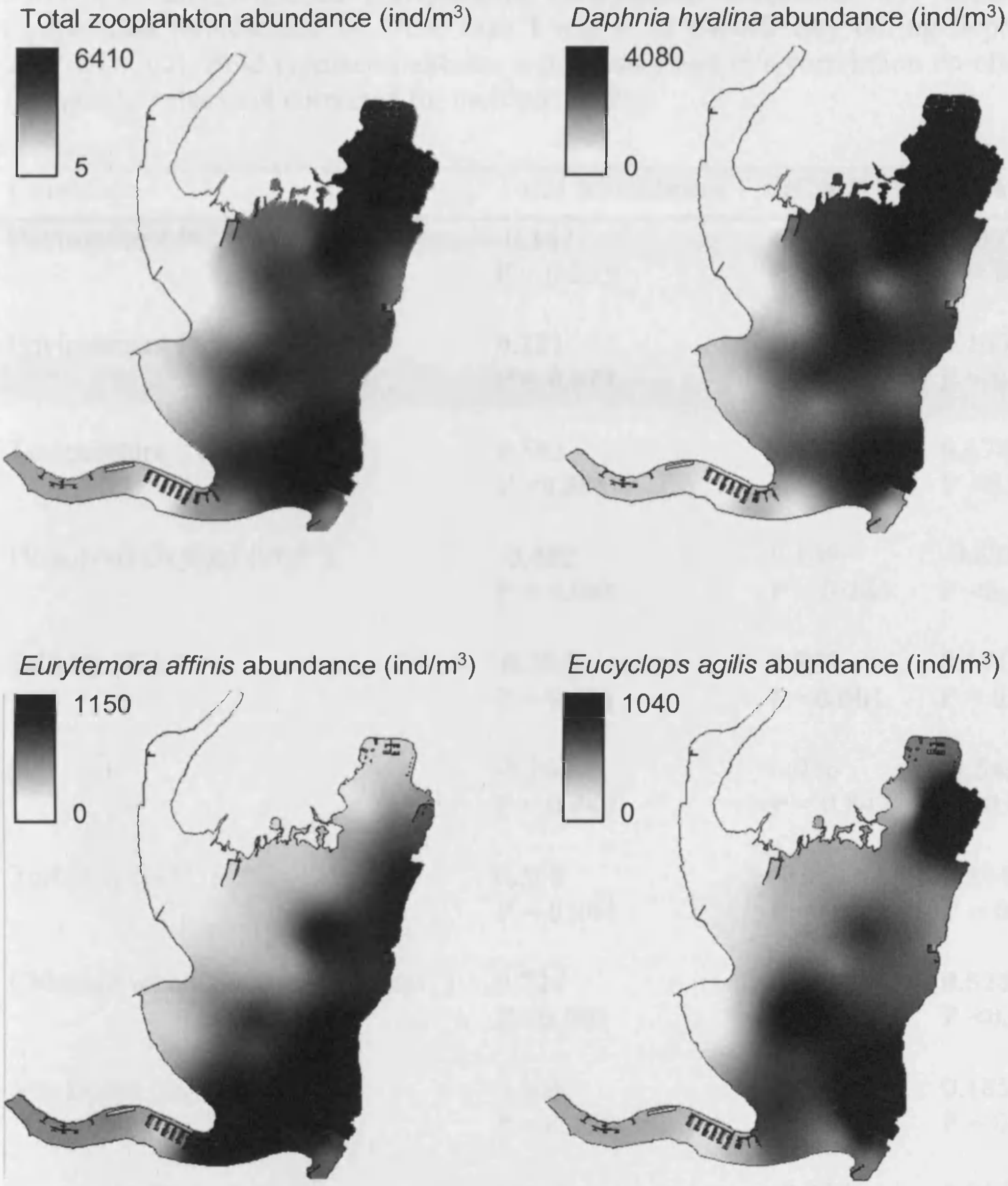

Figure 4.2: Distribution of total zooplankton abundance and abundance of the three numerically dominant species in Cardiff Bay during September 2007.

Table 4.2: Environmental correlates of zooplankton abundance and community composition (represented by DCA axes 1 and 2) in Cardiff Bay during September 2007 (N = 62). Bold typeface indicates significant Pearson's correlation co-efficient. Probability values not corrected for multiple testing.

Correlate	**Total Abundance**	**DCA 1**	**DCA 2**
Environment PCA 1	-0.147 P = 0.253	-0.016 P = 0.902	**-0.397** **P = 0.001**
Environment PCA 2	**0.281** **P = 0.027**	-0.127 P = 0.327	0.165 P = 0.201
Temperature (°C)	**0.582** **P <0.001**	**-0.255** **P = 0.047**	**0.670** **P <0.001**
Dissolved Oxygen (mgl^{-1})	**-0.432** **P = 0.001**	0.139 P = 0.284	**-0.638** **P <0.001**
Salinity (‰)	**-0.303** **P = 0.018**	**0.538** **P <0.001**	0.171 P = 0.181
pH	**-0.264** **P = 0.040**	0.026 P = 0.842	**-0.543** **P <0.001**
Turbidity (NTU)	**0.360** **P = 0.004**	-0.251 P = 0.051	**0.304** **P = 0.017**
Chlorophyll *a* Concentration (μgl^{-1})	**0.724** **P <0.001**	**-0.559** **P <0.001**	**0.528** **P <0.001**
Site Depth (m)	0.165 P = 0.199	**0.283** **P = 0.026**	0.185 P = 0.150
Current Velocity ($msec^{-1}$)	**0.263** **P = 0.039**	-0.324 P = 0.080	0.063 P = 0.742

Table 4.3: Environmental correlates with the abundance of dominant zooplankton species across 62 sampling sites in Cardiff Bay in September 2007 (N=62). Bold typeface indicates significant Pearson's correlation co-efficient. Probability values not corrected for multiple testing.

Variable	*Daphnia hyalina*	*Eurytemora affinis*	*Eucyclops agilis*
Temperature (^{o}C)	**0.459** **P <0.001**	**0.490** **P <0.001**	**0.461** **P <0.001**
Dissolved Oxygen (mgl^{-1})	**-0.317** **P = 0.013**	**-0.422** **P = 0.001**	**-0.365** **P = 0.004**
Salinity (‰)	**-0.394** **P = 0.002**	-0.031 P = 0.815	**-0.346** **P = 0.006**
pH	-0.123 P = 0.347	**-0.459** **P <0.001**	**-0.285** **P = 0.026**
Turbidity (NTU)	0.236 P = 0.068	**0.571** **P <0.001**	**0.467** **P <0.001**
Chlorophyll *a* Concentration (µgl^{-1})	**0.690** **P <0.001**	**0.353** **P = 0.005**	**0.586** **P <0.001**
Site Depth (m)	0.021 P = 0.872	**0.291** **P = 0.019**	0.157 P = 0.224
Current Velocity (m^{3}sec^{-1})	**0.289** **P = 0.023**	0.062 P = 0.630	0.173 P = 0.180

Ordination of individual species' abundances using DCA revealed that much of the variation in axis 1 reflected a trend from samples characterised by *Eucylops macrurus* and *Cyclops strenuus* to those characterised by *Bosmina longirostris, Diaphanosoma brachyurum, Ceriodaphnia setosa* and *Sida crystallina* (Fig. 4.3). In turn, these changes tracked increasing salinity and declining chlorophyll *a* (Table 4.2). On axis 2, assemblages shifted from samples characterised by *Alona quadrangularis, Pleuroxus uncinatus* and *Chydorus sphaericus* to those typified by *Disparolona rostrata* (Fig. 4.3) as temperature increased, oxygen concentrations fell and chlorophyll *a* concentration increased. This was reflected in the negative correlation between DCA axis 2 and PCA axis 1 (Table 4.2). Of the three numerically dominant species, only *D. hyalina* varied strongly along DCA axis 1 (r = 0.49; P <0.001; N = 62) but interestingly, none of the three dominant species varied strongly along DCA axis 2 (r

= 0.09; P = 0.130; N = 62). Spatial structure in community composition reflected all of these effects. For example, in general, both axes scores were relatively homogeneous in the main body of the Bay but low values on DCA axis 1 occurred in the River Ely and near site 5 in the main body of the Bay, while low values on DCA axis 2 occurred in both rivers and site 5 (Fig. 4.1).

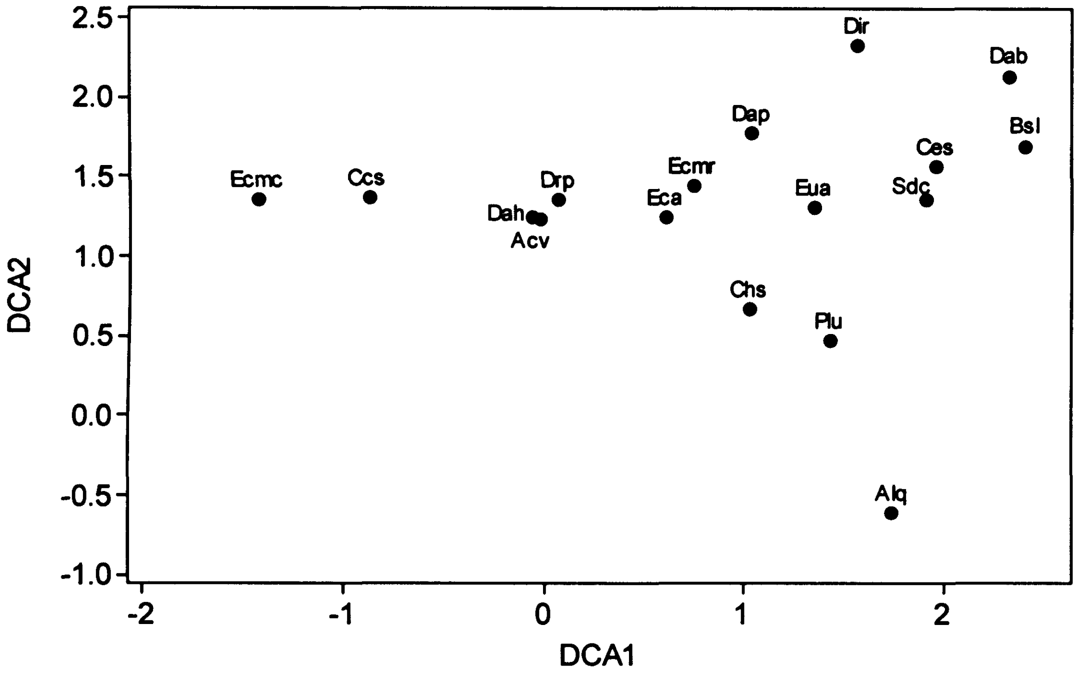

Figure 4.3: Species ordination axes scores from DCA of zooplankton species in Cardiff Bay. Acv: *Acanthocyclops vernalis*; Alq: *Alona quadrangularis*; Bsl: *Bosmina longirostris*; Ccs: *Cyclops strenuus*; Ces: *Ceriodaphnia setosa*; Chs: *Chydorus sphaericus*; Dab: *Diaphanomsoma brachyurum*; Dah: *Daphnia hyalina*; Dap: *Daphnia pulex*; Dir: *Disparolona rostrata*; Drp: *Dreissena polymorpha* larvae; Eca: *Eucyclops agilis*; Ecmc: *Eucyclops macruroides*; Ecmr: *Eucyclops macrurus*; Eua: *Eurytemora affinis*; Plu: *Pleuroxus uncinatus*; Sdc: *Sida crystallina.*

4.5.3 Sampling Scale Effects

Stepwise regressions at each sampling scale revealed that spatial and environmental factors, represented by PCNM and PCA respectively, explained substantially more variance in zooplankton abundance than in community composition, as represented by DCA axes 1 and 2 (Fig. 4.4). Spatial factors generally explained most variation in abundance at scales between 300m and 2099m between sites, implying that similar environmental conditions occurred over these distances. Environmental factors appeared to be most important in explaining abundance both at the finest and largest sampling scales (Fig. 4.4).

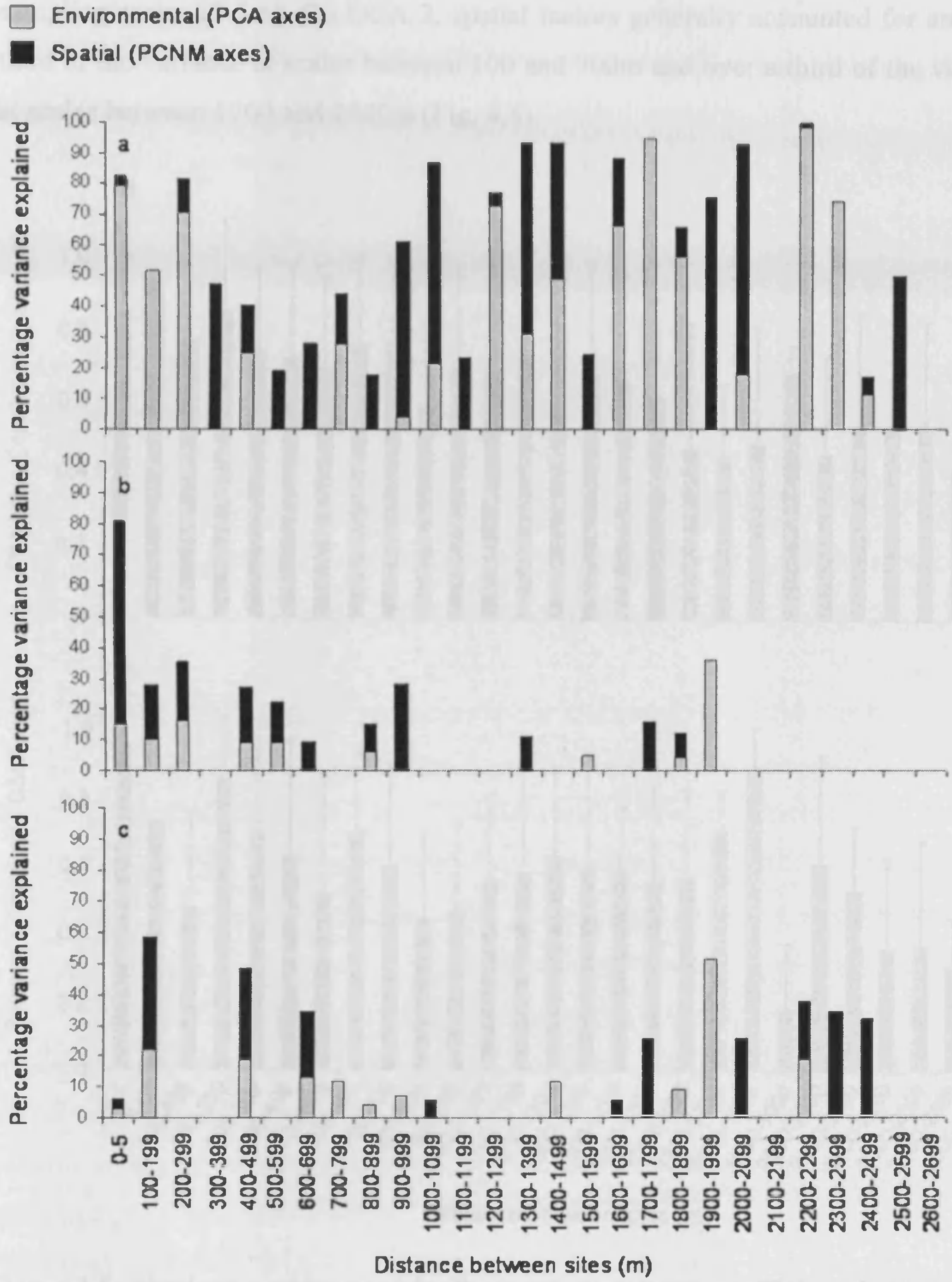

Figure 4.4: Percentage variance in a) total zooplankton abundance, b) DCA axis 1 and c) DCA axis 2 explained by PCA and PCNM axes representing environmental and spatial factors respectively, with increasing distance between pairs of sites.

Community composition, represented by DCA axes scores, was more similar at finer spatial scales with similarity decreasing as distance between sites increased (Fig. 4.5). Spatial factors explained the majority of variance (65.5%) in DCA axis 1 at the finest sampling scales (0-5m). On DCA 2, spatial factors generally accounted for around a third of the variance at scales between 100 and 700m and over a third of the variance at scales between 1700 and 2500m (Fig. 4.4).

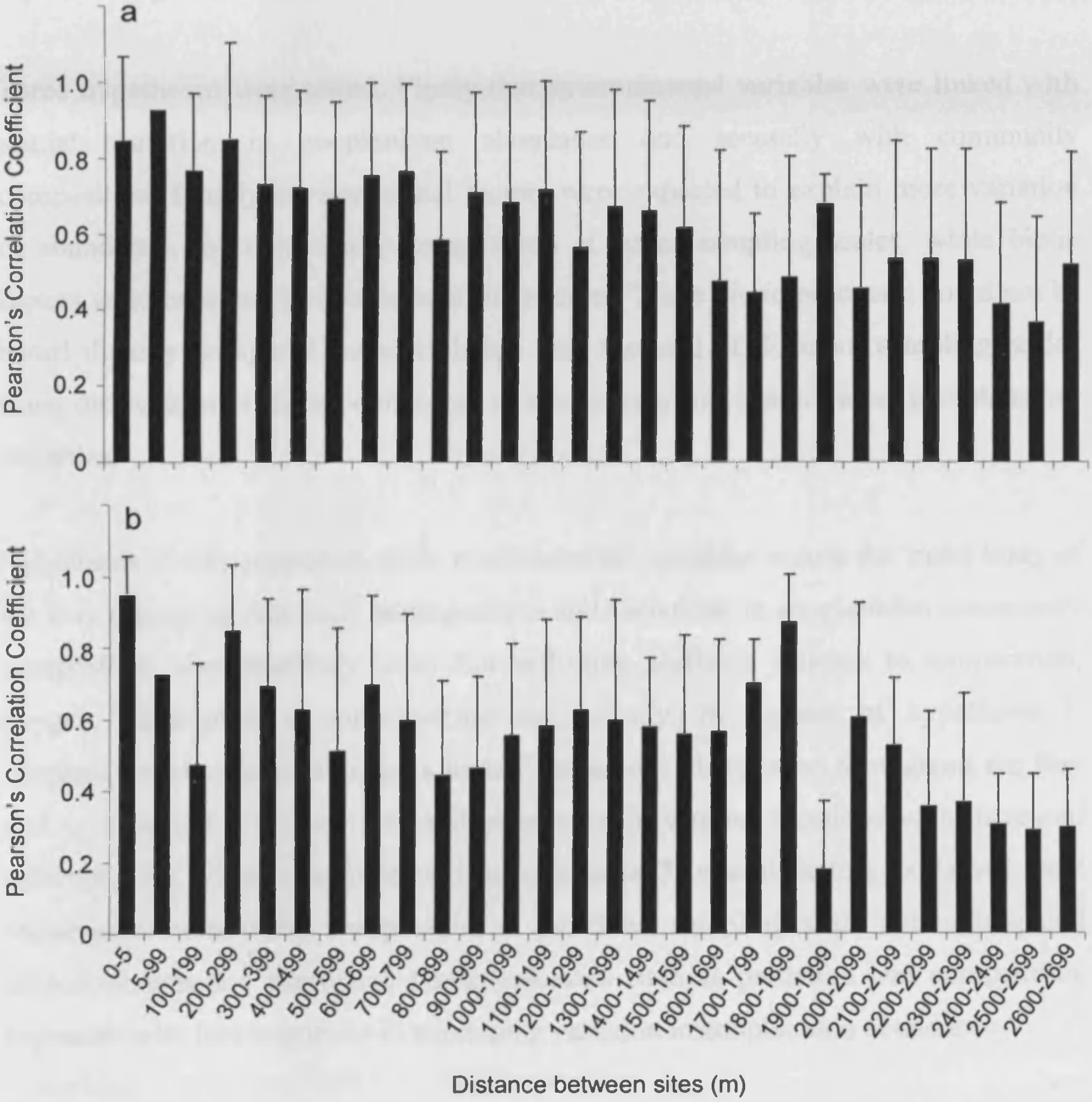

Figure 4.5: Similarity, represented by Pearson's correlation coefficient, between sites in a) DCA axes scores from an ordination of zooplankton species in Cardiff Bay and b) PCA axes scores from an ordination of environmental variables, with increasing distance between pairs of sites, showing standard deviation from the mean.

4.6 Discussion

The aim of this study was to assess the spatial dynamics of the zooplankton community in Cardiff Bay. Particular emphasis was given to the environmental factors responsible for structuring the community at different spatial scales and whether the artificial nature of the Bay influenced zooplankton distribution in this highly managed system.

Three hypotheses were tested. Firstly that environmental variables were linked with spatial variation in zooplankton abundance and secondly with community composition. Finally environmental factors were expected to explain more variation in abundance and community composition at larger sampling scales, while biotic factors were expected to dominate at finer scales. These biotic processes could not be tested directly so spatial autocorrelation was assessed at different sampling scales using ordinations of distance matrices to represent spatial pattern among explanatory variables.

Hypothesis 2 was supported, with environmental variables across the main body of the Bay appearing relatively homogeneous and variations in zooplankton community composition also relatively weak but reflecting shifts in relation to temperature, oxygen, chlorophyll *a* concentration and salinity. In support of hypothesis 1, zooplankton abundance showed a highly contagious distribution throughout the Bay and as expected reflected increased abundance in warmer locations with increased chlorophyll *a*. Finally, as predicted in hypothesis 3, spatial factors explained most variation in community composition at the finest sampling scale although spatial autocorrelation and associated biotic processes such as predation and competition, appeared to be less important in explaining variation in zooplankton abundance.

Artificial aeration can be used as a restorative technique in eutrophic water bodies, preventing stratification and associated cyanobacterial blooms, maintaining oxygen concentration and limiting light availability to phytoplankton (e.g. Heo and Kim, 2004; Müller and Stadelmann, 2004; Becker *et al.,* 2006). The nature of aeration techniques leads to homogenisation of lake physico-chemistry (e.g. Heo and Kim, 2004) and may be expected to homogenise zooplankton abundance and community structure. However, to date, studies concerned with the impacts of aeration on zooplankton have concentrated more on comparisons of communities before and after restoration (e.g. Cowell *et al.,* 1987; Oberholster *et al.,* 2007) and less on the impact on whole-lake spatial distribution. Water quality variables in the present study varied little in the main lake body, with the largest variations occurring between the main body of the Bay and the Rivers Taff and Ely. Although it was not possible to test the impact directly, the homogeneity of water quality and zooplankton community composition probably reflected lake mixing. This implies that the artificial aeration, employed in the Bay to maintain water quality, is successful in promoting water column mixing, but an experimental study would be required to conclude this with certainty.

Despite relatively weak variation in both, environmental variables were linked with changes in community composition and appeared to be reflected in the contrasting communities observed in the main body of the Bay, Taff and Ely. At sites in the main body, large-bodied zooplankton species accounted for 80% of the community but made up 57% of the community in the River Ely and only one third of the community in the River Taff. Generally faster flow rates in the rivers than in the main body might have been expected to drive these differences in body size. Richardson (1992) reported faster washout times in larger-bodied cladocera, but surprisingly community composition in the present study was independent of current velocity. To fully investigate the influence of hydrological regime, community composition would ideally be considered over a range of flow rates. River flow rates in the present study were relatively low and their influence on community composition may be greater at higher flow rates (Richardson, 1992).

In contrast to community composition, patterns of abundance in the dominant zooplankton species are more structured spatially around food concentrations located in warmer conditions, as expected. The mapping of zooplankton occurrence, as in the present study, could potentially be used to infer the distribution of planktivorous fish in the Bay. Planktivorous fish, and in particular their larvae, tend to aggregate both spatially and temporally at higher zooplankton density (Chick and Van Den Avyle, 1999). With particularly dense patches of zooplankton occurring in the inner harbour and near the barrage, these areas could be important feeding areas for species such as roach (*Rutilus rutilus*), dace (*Leuciscus leuciscus*) and chub (*Leuciscus cephalus*) that have been recorded in the Bay.

The heterogeneity of zooplankton abundance was reflected in the high variance:mean ratios and therefore clustered distributions of the three dominant species: *Daphnia hyalina* was most dense near the barrage, inner harbour and near the centre of the Bay; *Eurytemora affinis* was aggregated in the inner harbour, while *Eucyclops agilis* was aggregated at the mouth of the Ely. Of the three dominant species *D. hyalina* showed the greatest abundance, as reflected by total zooplankton abundance and the large variation on the first DCA axis. Unlike *E. agilis and E. affinis,* and contrary to expectations, *D. hyalina* abundance increased with current velocity, implying that under low flow conditions *D. hyalina* were concentrated in areas of faster flow. The copepods *E. affinis* and *E. agilis* abundances were independent of velocity but copepods are generally stronger swimmers than cladocerans (Richardson, 1992) and are therefore less likely to be influenced by current velocity at low flow rates. These results, however, should be interpreted with caution, since current velocity was not available for the sampling occasion and was used from a previous occasion under similar flow conditions. *D. hyalina* distribution was independent of turbidity, while *E. affinis* and *E. agilis* abundances tended to be higher in areas of slightly higher turbidity. This could reflect the competitive advantage gained by copepods due to their generally higher turbidity tolerance than cladoceran zooplankton (e.g. Hart, 1990; Hann and Zrum, 1997). *E. affinis* was independent of salinity, which reflects its relatively high salinity-tolerance, while *D. hyalina* and *E. agilis* were both less abundant in areas of higher salinity, despite only small changes in salinity levels.

As well as the importance of environmental variables, variance in Cardiff Bay's zooplankton abundance and community composition was also explained by inferred biotic drivers. Knowledge of how different drivers structure zooplankton communities at different spatial scales is essential in accurately representing community structure. Moreover, the degree of spatial heterogeneity detected, relative importance of driving forces and ability to detect aggregations are highly dependent on sampling resolution (Pinel-Alloul, 1995). At the finest scales, spatial autocorrelation, which occurs when organisms develop pattern due to contagious physico-chemical forcing of environmental conditions or community interactions such as predation or competition

(Legendre, 1993) is expected to dominate. At the largest scales, the physical characteristics of the lake environment, such as lake hydrology and morphometry become more important (Richerson *et al.,* 1978; Malone and McQueen, 1983; Pinel-Alloul and Pont, 1991; Shurin and Allen, 2001). In Cardiff Bay, as predicted in hypothesis 3, spatial factors explained most variance at the smallest distance between sites (0-5m) in the first DCA axis. This suggests that inferred biotic factors are important in shaping Cardiff Bay's zooplankton community at the finest sampling scale, in line with the Multiple Driving Force Hypothesis (Pinel-Alloul, 1995). However, in zooplankton abundance, environmental factors explained a substantial proportion of variance, particularly at smaller sampling scales, and inferred biotic factors appeared to be less important. This was not predicted in hypothesis 3, but probably reflected the similarity of water quality conditions between sites of close proximity.

In summary, these data appear to suggest that relatively homogeneous water quality in the main body of Cardiff Bay, probably reflecting lake mixing and artificial aeration, has given rise also to relatively homogeneous zooplankton composition. In contrast, patterns of zooplankton abundance in the dominant species are more structured spatially around food concentrations located in warmer conditions. Despite this apparent homogeneity, spatial scale remains important in the detection of the relative influence of environmental and inferred biotic factors on zooplankton community composition. This is particularly the case with respect to zooplankton abundance, implying that scale-dependent effects should be a more prominent consideration in zooplankton sampling.

Chapter 5: Zooplankton Trait Structure and Diversity in a Newly Formed Urban Lake

5.1 Abstract

1. Species' traits can illustrate evolutionary aspects of habitat selection more than traditional taxonomy while also revealing species' functions. So far, however, trait-based approaches have been neglected in studies of the seasonal and spatial dynamics of freshwater zooplankton communities.

2. Data from the newly-formed Cardiff Bay were used to assess temporal patterns among zooplankton traits over a two-year period and across a range of lake habitats during an extensive late-summer survey. Patterns of trait nestedness were appraised to assess how more specialised traits were restricted to specific conditions.

3. Trait composition was well captured by two major ordination axes along which variations were dominantly seasonal and spatial, respectively. Trait representation changed progressively between early spring and late summer as slower growing, omnivorous or zooplanktivorous species with low C:N ratio and high assimilation efficiency gave way to more asexually or rapidly-reproducing filter-feeders or detritivores with high C:N ratios. This inter-annually consistent trend then reversed between September and February/March.

4. By contrast, spatial pattern in trait composition reflected variations among herbivorous, swimming species that mostly occupied the inner harbour and other shallow pockets of Cardiff Bay with elevated temperature.

5. Trait diversity varied seasonally more than spatially, and peaked near-continuously throughout each summer period. Conditions in the two river tributaries (Taff and Ely), and in Cardiff Bay's associated wetlands, contributed to most of the variation in trait diversity while also supporting some specific trait features.

6. Trait structure was nested in both space and time, illustrating how some traits, drawn from a more widespread pool, occurred only under some specific conditions.

7. As one of the first to assess the trait composition and nestedness in lake zooplankton, this study illustrates how dynamic changes in environmental conditions and food resources over the annual cycle have formed an important template for trait

selection in this group. At least in the newly-formed Cardiff Bay, spatial variations are less important for trait composition than are seasonal variations, though local conditions nevertheless support zooplankton with specific features.

5.2 Introduction

Although traditional taxonomy has been central to studies of assemblage composition (e.g. Naeem *et al.,* 1994; Tilman *et al.,* 1997; McGrady-Steed *et al.,* 1997; Naeem and Li, 1997; Mulder *et al.,* 2001), some authors are now reporting how the functional traits of organisms provide important additional insights into ecosystem structure and function. Functional measures, in turn, are more likely than species lists to indicate how ecosystem processes are affected by modification (e.g. Tilman *et al.,* 1996; Hooper and Vitousek, 1997; Tilman *et al.,* 1997; Tessier *et al.,* 2000; Tilman, 2001; Flynn *et al.,* 2009; Pollard and Yuan, 2009); traits with the greatest effects on ecosystem functioning are those that influence the dynamics of limiting resources, trophic interactions and responses to disturbance (Chapin *et al.,* 1997). Functional traits can be used to investigate the mechanisms influencing assemblage organisation, trait-based diversity (Erős *et al.,* 2009) and ecosystem resilience (Petchey and Gaston, 2009) in ways that might be limited using taxonomy alone.

Traits also provide an insight into evolutionary processes. Habitat template theory (Southwood 1977), applied to freshwaters for example by Townsend & Hildrew (1994), Poff (1997) and Reynolds (2001), postulates how variations in the physico-chemical and biological character of ecosystems, in time and space, are key agents that have selected those organism traits most likely to succeed under given conditions. Although they cannot reveal evolutionary dynamics directly, species traits represent those features of organisms that might be at selective advantage, particularly where traits are shared across several co-occurring species. As with ecosystem functions, such selective effects are revealed by traits far better than by conventional taxonomy.

Many of the initial studies on functional diversity have focussed on plant and insect communities (Charvet *et al.,* 2000; Henry *et al.,* 2001; Statzner *et al.,* 2001; Mason *et al.,* 2003; Heemsbergen *et al.,* 2004; Bady *et al.,* 2005). While the range of organisms included in trait-based work is increasing (Zak *et al.,* 1994; Stevens *et al.,* 2003), very few have considered freshwater zooplankton (but see Barnett *et al.*, 2007). This is also true of evolutionary trait analysis despite other ecological theory being applied to zooplankton (see Chapter 3 on the PEG model). This gap is surprising in view of the diverse trait characteristics demonstrated by zooplankton and the clear sensitivity of their community composition to seasonal and spatial environmental variation (see Chapters 3, 4 and 5).

As a complement to trait analysis, the nested subset hypothesis was proposed to describe the extent to which species-poor assemblages are non-random subsets of species-rich ones (Patterson and Atmar, 1986). In nested communities, generalist taxa tend to be more frequent across sites and samples, while specialists are restricted to specific environmental conditions. Traits and mechanisms that promote the co-existence of different taxa are particularly important in producing nested communities (Wright and Reeves, 1992; Facelli et al, 2005; Elmendorf and Harrison, 2009). In other words, in spatially and temporally heterogeneous habitats each taxon successfully exploits a portion of the habitat but no taxa are able to exploit fully the entire habitat range (Tilman, 2001). Some mechanisms that allow this coexistence of potentially competing species, such as resource partitioning (e.g. Leibold, 1991) and frequency dependent predation (Levin and Segel, 1982; Gendron, 1987) are independent of abiotic environmental fluctuations, while others depend on variations in environmental conditions to provide the heterogeneity needed to support species coexistence (Chesson 2000).

Most studies of nestedness have focussed on how communities are structured spatially (e.g. Paterson and Atmar, 1986; Driscoll, 2008) with only a small number investigating changes in nestedness over time (e.g. Norton *et al.*, 2004; Bloch *et al.*, 2007; Heino *et al.*, 2009). Even fewer have investigated temporal nestedness (e.g. Elmendorf and Harrison, 2009), despite evidence that environmental variation could generate the conditions for nesting by causing a sequence of community assembly or disassembly through time (Taylor and Warren, 2001; Elmendorf and Harrison, 2009). Moreover, despite obvious links with the evolutionary dimensions of trait selection, studies investigating nestedness almost exclusively use taxonomic- rather than trait-based approaches. Such trait-based approaches should be able to detect whether trait-poor assemblages are non-random subsets of trait-rich ones. If this was the case, an assemblage of generalist traits would be expected to occur over a range of conditions, with a subset of specialist traits restricted to a specific set of environmental conditions. Since a range of studies have highlighted the importance of considering traits in evolutionary ecology (Southwood 1977), biodiversity assessment (Erős *et al.*, 2009) and ecosystem function (Tilman *et al.*, 1996; Hooper and Vitousek, 1997; Tilman *et al.*, 1997; Tessier *et al.*, 2000; Tilman, 2001; Flynn *et al.*, 2009; Pollard and Yuan, 2009), it is logical to assume the importance of these traits in community nestedness.

In this chapter, data from temporal and spatial surveys of zooplankton in Cardiff Bay were used to analyse trait diversity and nestedness. The species data have been used previously to assess temporal (Chapter 3) and spatial patterns (Chapter 4) across Cardiff Bay, but here they provide one of the first assessments of trait patterns in lake zooplankton. Cardiff Bay is particularly well suited to such an investigation because environmental conditions vary substantially over time (Chapter 3), while local variations in the main Bay or associated wetlands create conditions that could favour distinct trait expression (see below and Chapter 4). As a newly formed lake, trait assessment in Cardiff Bay will also provide an interesting example for comparison in future studies of zooplankton in lakes elsewhere.

5.3 Aims and Hypotheses

This study was aimed primarily at developing an understanding of the temporal and spatial dynamics of Cardiff Bay zooplankton using basic information on the functional traits of zooplankton species. Three hypotheses were tested:

Hypothesis 1: Zooplankton trait diversity and composition in Cardiff Bay vary seasonally, linked with environmental conditions that also affect wider zooplankton development under the PEG model (see Chapter 3). Changes among primary producers and other food sources under this model are likely to have had substantially selective effects on trait character. Specifically, smaller sized herbivores were expected to be more important during early spring, followed later in the season by larger zooplanktivores in line with existing qualitative models of plankton succession (e.g. Sömmer *et al.*, 1986). Taxa with lower C:N ratios were expected to be more important over winter periods, when autochthonous food quality is likely to be lower (i.e. lower in essential fatty acids) and terrestrial subsidies are likely to be poorer in essential nutrients.

Hypothesis 2: Zooplankton trait diversity and composition vary between sites in Cardiff Bay linked with proximate environmental factors. Recent investigations (Chapter 4) show that conditions are relatively homogeneous in the main body of the Bay, probably reflecting whole-lake mixing. However, local variations in the mouths of the two main rivers were expected to produce conditions differing from the main Bay, while sites in the wetland reserve are expected to support a higher proportion of littoral species, adapted to shallow, macrophyte-rich habitats.

Hypothesis 3: The zooplankton community is nested over space and time, with a generalist trait assemblage present throughout the sampling period and at all sites, and a subset of specialist taxa adapted to certain environmental criteria at favourable times of the year and at favourable sites.

5.4 Methods

5.4.1 Zooplankton Collection

Ten sites for zooplankton collection were chosen throughout Cardiff Bay over a range of habitats with each adjacent to existing locations used for water-quality sampling. Zooplankton at each site were sampled fortnightly between March 2006 and February 2008 using a fine mesh (60μm) conical plankton net of mouth diameter 0.20m, on a steel mouth-reducing frame to minimise water disturbance (De Bernardi, 1984). The net was lowered to the lake-bed using the on-board depth meter and metre-markers on the rope as a guide, and then hauled vertically through the water column while zooplankton collected on a piece (approximately 8cm x 8cm) of 60μm nylon mesh screwed to the net base. After rinsing, this square of mesh was removed and fixed in 70% methylated ethanol. The net was rinsed thoroughly between samples.

Additionally, one extensive spatial survey was undertaken during September 2007, encompassing 62 sites throughout the Bay using the same collection method, and 10 sites in the adjacent wetland. Each wetland site was accessed by foot and at each a pump was used to pass 2l of water through the plankton net. When in the water, the pump was raised and lowered to ensure the whole water column was sampled. As with the sampling method used in the main body of the Bay, a 60µm nylon mesh was screwed to the base of the net in order to collect the zooplankton, which were immediately fixed in 70% methylated ethanol.

During the summer, the net was hauled once at each site on each sampling occasion, but double hauls were used at low plankton density during winter to increase the number of individuals in the sample and to reduce the risk of under-representing rare species. Zooplankton abundances were expressed as the number of individuals per m^3 sampled.

In the laboratory, zooplankton in each sample were counted and identified to species (Gurney, 1933a; Gurney, 1993b; Harding and Smith, 1974; Scourfield and Harding, 1994). Particularly dense samples were mixed and 10% sub-samples were taken following McCauley (1984); provided that the total number of individuals in a sample exceeded 150.

5.4.2 Water Quality

On each sampling occasion and at each site, temperature, pH, dissolved oxygen concentration, turbidity, conductivity and salinity were recorded using a portable sonde (model 6920, YSI Inc., USA) and data logger (model 650MDS, YSI Inc., USA). Water samples were collected and analysed using a fluorimeter (bbe Moldaenke, Germany) to identify the total concentration ($\mu g l^{-1}$) and activity of chlorophyll *a* associated with green algae, blue-green algae, diatoms and cryptophytes at each site. River discharge was measured every 15 minutes at Environment Agency (EA) gauging stations at St Fagans for the River Ely and Pontypridd for the River Taff. These data were available from the time of impoundment in 2001. Current velocity is rarely measured in the main body of the Bay and was not available for the present sampling occasions. Therefore data from a previous survey undertaken by CHA on 12/02/2008 under similar flow conditions was used and interpolated using ArcGIS (ESRI, 2004) so that current velocity could be estimated for each sampling site in main body of the Bay. Velocity was measured every five seconds across a series of transects using a 1500kHz frequency Acoustic Doppler Current Profiler (Sontek, USA) linked into a laptop running Coastal Surveyor software (Sontek, USA).

5.4.3 Trait Data

Information on a total of 42 categories of 14 functional traits (Table 5.1) was collected for a total of 39 zooplankton species found in spatial, temporal and wetland surveys in Cardiff Bay using information from a range of literature (Appendix 2). Much of the information on species body size and general ecology, such as habitat preference and locomotion, was available from Gurney (1933a and b) and Scourfield and Harding (1994). For filter-feeding cladoceran species, body size information was used to estimate the maximum food particle size (Burns, 1968) and studies directly examining mesh sizes of filter feeders were also used to estimate food particle size categories (e.g. Geller and Müller, 1981; Brendelberger and Geller, 1985; Hessen, 1985; Mangalo, 1987; Brendelberger, 1991). Life history experimental studies were important sources of information on reproduction, generation times, population increase (e.g. Bottrell, 1975; Guisande and Gliwicz, 1992; Burns, 2000; Ferrao-Filho *et al.,* 2000) and feeding ecology traits such as grazing rates, C:N ratios and assimilation efficiencies (e.g. Peterston Holm *et al.,* 1983; Porter *et al.,* 1983). However, since the nature of such experiments is to assess the impact of a range of conditions, such as predation, crowding and temperature, on zooplankton life history traits, only data quoted for species experiencing control conditions, rather than experimental treatments, were included in this study.

Table 5.1: Zooplankton traits used in analyses of trait diversity in Cardiff Bay, showing classification categories and label codes.

Category	Trait	Classification	Code
Body Structure	Maximum adult body length (mm)	< 0.5	1
		0.5 - 1.0	2
		1.0 - 2.0	3
		2.0 - 3.0	4
		3.0 - 4.0	5
		> 4.0	6
Reproduction	Reproductive mode	Asexual	7
		Sexual	8
	Generation time (days)	Low (<10)	9
		Medium (10-25)	10
		High (>25)	11
	Maximum clutch size (individuals per clutch)	Low (<5)	12
		Medium (5-20)	13
		High (>20)	14
	Maximum rate of population increase, r (day^{-1})	Fast (>0.3)	15
		Slow (<0.3)	16
Feeding Ecology	Food Source	Detritus	17
		Phytoplankton	18
		Phytoplankton + Zooplankton	19
		Zooplankton	20
	Feeding mechanism	Filter	21
		Suspension	22
		Raptorial	23
	Maximum size of particle ingested (µm)	<20	24
		20-100	25
		100-300	26
		300-500	27
		>500	28
	Maximum clearance rate (µL per individual per hour)	Low (<100)	29
		High (>100)	30
	Assimilation efficiency (%)	High (>50)	31
		Low (<50)	32
	C:N ratio	High (>5)	33
		Low (<5)	34
Habitat	Preferred adult habitat	Pelagic	35
		Benthic	36
		Littoral	37
	Salinity tolerance	High	38
		Low	39
	Primary locomotion method	Swimming	40
		Scrambling	41
		Attached	42

Trait information for freshwater zooplankton is sparse and consequently precise values were not available for some traits. To overcome this, species were assigned to broad categorical values (e.g. high versus low; fast versus slow, etc.) either directly, or by extrapolation from other species of the same genera.

Log (n+1) abundance-weighted presence-absence species x trait matrices generated from spatial and temporal surveys were converted to site x trait and date x trait matrices.

5.4.4 Statistical Analysis

Trait diversity was calculated using Simpson's index based on all traits present in each sample, i.e. at each site for spatial surveys and each sampling occasion for temporal surveys:

$$\text{Simpson's diversity, } D = \frac{\Sigma n(n-1)}{N(N-1)}$$

where n is the relative abundance of individuals present in a particular trait category; and N is the total number of organisms across all traits. Species diversity was also calculated using the same formula, where n is the relative abundance of individuals of a particular species and N is the total number of organisms across all species.

Functional redundancy was assessed by plotting species diversity by trait diversity (Béche and Resh, 2007); where trait diversity increases at rates equal to species diversity, new species are assumed to add new functions, while increase at rates slower than species diversity implies that functions are replicated across species (i.e. there is redundancy in functional traits between species).

Ordination using principal component analysis (PCA) was carried out on the log(n+1) abundance-weighted presence-absence sample x trait matrix of all traits found over the spatial and temporal surveys, and linear correlations between each trait and each respective PCA axis assessed. Pearson's correlation coefficients (r) were also assessed between the trait PCA axes and environmental variables across sites on each sampling occasion and for each site. The spatial distributions of trait diversity and PCA axes representing trait composition scores were mapped using interpolation in ArcGIS (ESRIS, 2004).

The binary-matrix nestedness temperature calculator (BINMATNEST) (Rodrgíuez-Girones and Santamaría, 2006) was used to quantify the nestedness of the zooplankton communities with respect to the spatial and temporal distribution of functional traits. BINMATNEST re-orders presence-absence matrices to produce maximally nested matrices and calculates the matrix temperature, ranging from 0-100° (0° indicating a perfectly nested matrix, whereby each trait is present in all assemblages richer than the most depauperate one in which that trait occurs, and 100° indicating a completely random matrix). Significance was determined through comparison to temperatures of 100 matrices generated randomly from the observed data using the conservative null model III, which is less sensitive to species richness and occurrences. Null model III assumes that the probability of a cell being occupied is equal to the average probabilities of occupancy of its row and column and is less likely than null model I (which assumes occurrence of each trait is equally likely at all sites) to generate type I errors (Rodriguez-Girones and Santamaria, 2006). Correlates of nestedness were identified using Spearman's rank correlation (ρ) between environmental variables and the rank order of sites or sampling dates in maximally nested matrices.

5.5 Results

PCA from the ordination of the sample x trait matrix (Table 5.2; Fig. 5.1) gave two clear trait axes respectively explaining 45.7% and 10.8% of the trait variance. Positively scoring taxa on PCA axis 1 were swimming species characterised by slow-rates of population increase, long generation times and large clutch size coupled with high assimilation efficiency, high clearance rates, low C:N ratios and a tendency toward large food particles. At the other extreme were more rapidly growing species with asexual reproduction and intermediate clutch-size that were often filter feeders characterised by small food particles, low clearance rates, low assimilation efficiency, high C:N ratio, and sometimes detritivory with benthic or scrambling habits. PCA axis 2 represented a simpler trend from pelagic herbivores with short generation time to benthic or scrambling taxa with intermediate generation time.

Table 5.2: Significant trait correlates, identified using Pearson's correlation coefficient, of PCA axes scores resulting from an ordination of zooplankton functional traits in Cardiff Bay. * indicates significance at $P \leq 0.05$; ** indicates significance at $P \leq 0.01$; *** indicates significance at $P \leq 0.001$. Probability values not corrected for multiple testing.

Trait	PC1	Trait	PC2
Slow rate of population increase	0.94***	Herbivore	0.74***
Large clutch size	0.92***	Pelagic	0.72***
High assimilation efficiency	0.90***	Short generation time	0.47**
High clearance rate	0.83***	Food particles 20-100μm	0.44**
Raptorial	0.78***	Swimming	0.42**
Swimming	0.76***	High C:N ratio	0.39*
Food particles >500μm	0.56***	High clearance rate	0.39*
Low C:N ratio	0.56***	Body length 1.0-2.0mm	-0.33*
Long generation time	0.55***	Low clearance rate	-0.39*
Littoral	0.53***	Food particles >500μm	-0.39*
Body length 1.0-2.0mm	0.49**	Low C:N ratio	-0.39*
Omnivore	0.45**	Intermediate generation time	-0.41**
Zooplanktivore	0.44**	Benthic	-0.42**
Food particles 300-500μm	0.38*	Scrambling	-0.45**
Food particles 20-100μm	-0.37*		
Body length 0.5-1.0mm	-0.41**		
Food particles <20μm	-0.46**		
Intermediate generation time	-0.49**		
High C:N ratio	-0.56***		
Benthic	-0.63***		
Scrambling	-0.70***		
Detritivore	-0.79***		
Low clearance rate	-0.83***		
Intermediate clutch size	-0.86***		
Low assimilation efficiency	-0.90***		
Asexual reproduction	-0.92***		
Fast rate of population increase	-0.94***		
Filter feeder	-0.95***		

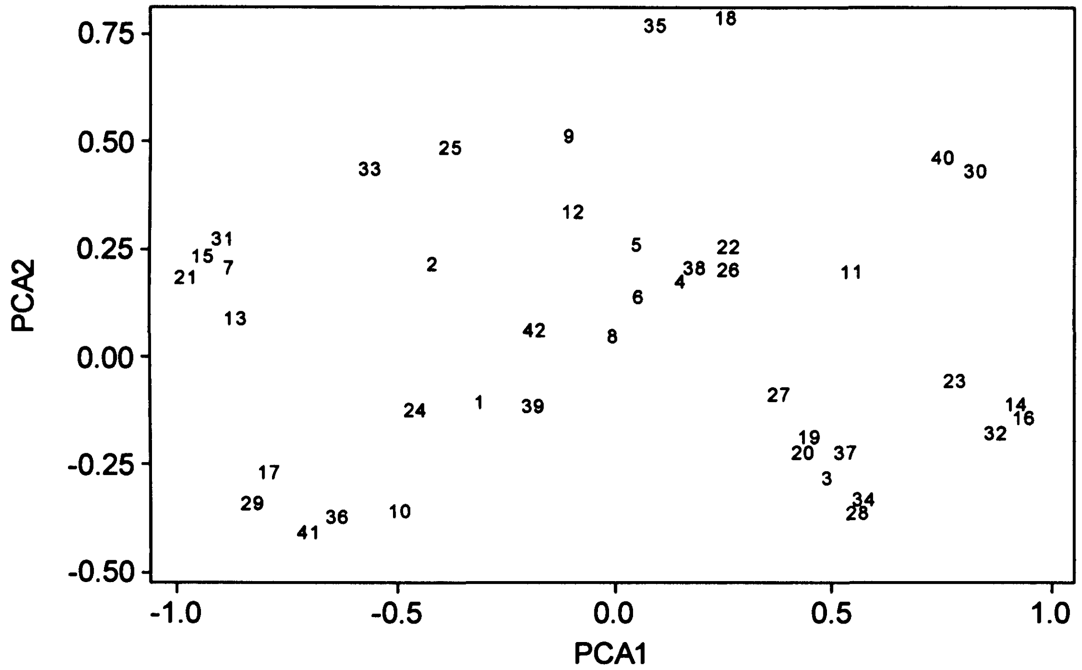

Figure 5.1: Position of zooplankton traits resulting from a presence-absence ordination of traits of all zooplankton species present in Cardiff Bay. For trait codes refer to Table 5.1.

5.5.1 Seasonal Variation in Trait Composition

Seasonal variations in trait PCA 1 were pronounced in both study years (Fig. 5.2), and reflected in strong correlation with temperature, day length and dissolved oxygen (Table 5.3). PCA 1 scores declined progressively between late winter/early spring to late summer, implying a steady shift from slower growing, omnivorous or zooplanktivorous swimming species with low C:N ratio and high assimilation efficiency to more rapidly or asexually reproducing filter feeders or detritivores with high C:N ratios. This trend then reversed from September to February/March.

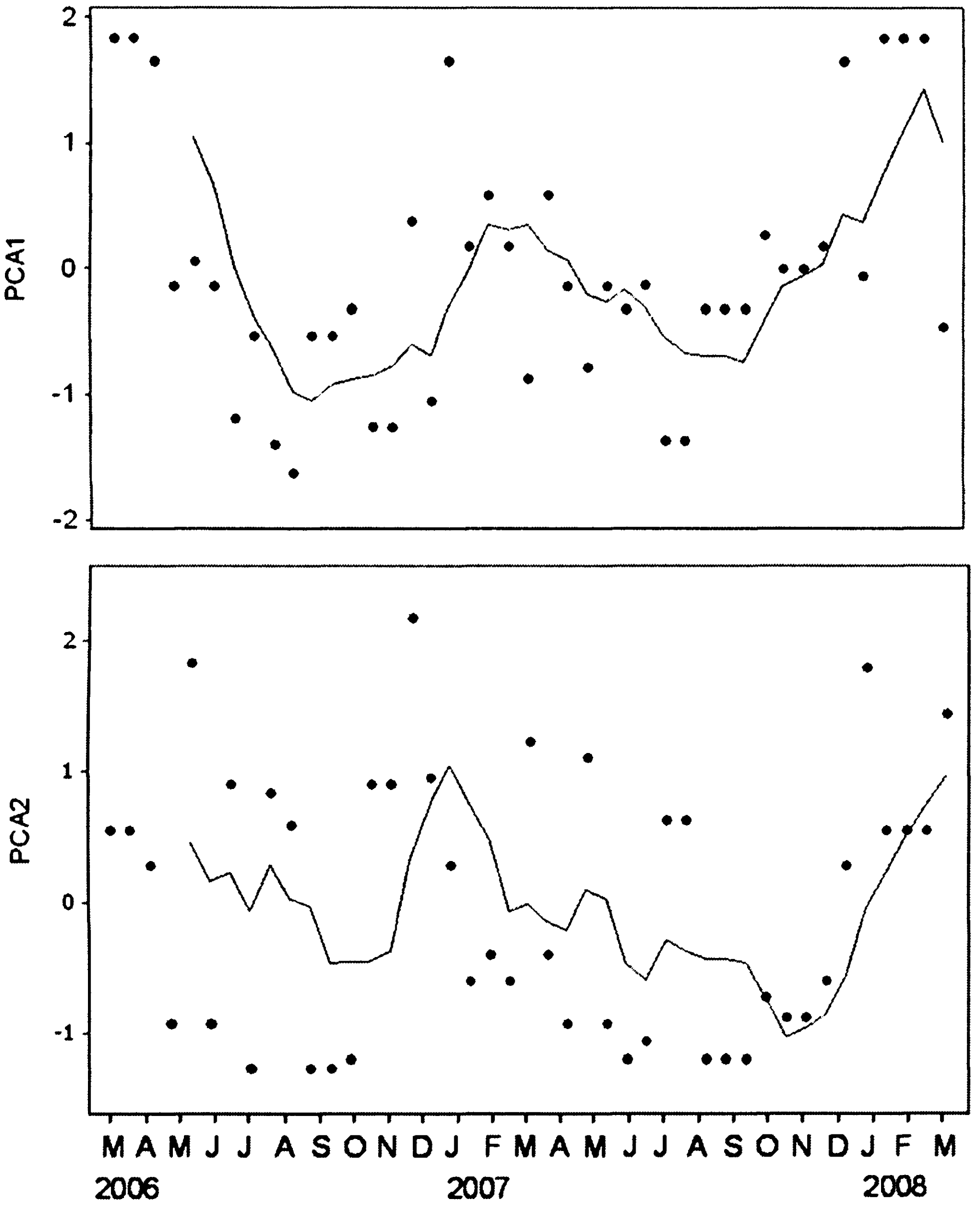

Figure 5.2: PCA axis 1 and 2 scores resulting from an ordination of zooplankton functional traits in Cardiff Bay over the two year sampling period, showing the 5 data-point moving average trend line.

Table 5.3: Environmental correlates of trait diversity and composition (i.e. trait PCA scores) of all zooplankton species present in Cardiff Bay, identified using Pearson's correlation coefficient. Bold typeface indicates a significant probability vaule (not corrected for multiple testing).

Survey	**Variable**	**PCA1**	**PCA2**	**Trait Diversity**
Temporal	Temperature	**-0.635** **P<0.001**	**-0.427** **P = 0.005**	**0.803** **P<0.001**
	Dissolved oxygen concentration	**0.454** **P = 0.003**	0.225 P = 0.151	**-0.643** **P<0.001**
	Salinity	-0.200 P = 0.204	**-0.427** **P = 0.005**	**0.495** **P = 0.001**
	pH	-0.060 P = 0.707	**-0.374** **P = 0.015**	0.250 P = 0.111
	Chlorophyll *a* concentration	-0.005 P = 0.973	-0.224 P = 0.154	0.106 P = 0.503
	Total Oxidised Nitrogen concentration	-0.391 P = 0.072	**-0.525** **P = 0.012**	**0.608** **P = 0.016**
	Day length	**-0.476** **P = 0.001**	**-0.282** **P = 0.012**	**0.638** **P<0.001**
Spatial	Temperature	**-0.297** **P = 0.012**	**0.237** **P = 0.047**	**0.336** **P = 0.004**
	Dissolved oxygen concentration	**0.505** **P<0.001**	-0.211 P = 0.078	**-0.480** **P <0.001**
	Salinity	0.007 P = 0.952	-0.078 P = 0.080	-0.169 P = 0.159
	pH	0.067 P = 0.578	**-0.393** **P = 0.001**	0.014 P = 0.905
	Chlorophyll *a* concentration	0.030 P = 0.804	0.081 P = 0.499	-0.036 P = 0.763
	Current velocity	**-0.330** **P = 0.005**	-0.165 P = 0.166	**0.390** **P = 0.001**
	Depth	**0.273** **P = 0.020**	-0.207 P = 0.080	**0.382** **P = 0.001**

Trait PCA axis 2 was less clearly seasonal, though nevertheless some variation through time was reflected by increases among herbivorous and swimming taxa during cooler periods with low salinity tolerance and low nitrate concentration, for example in early spring (Table 5.3; Fig. 5.2).

Multiple regression analysis indicated that PCA axes 1 and 2 explained respectively 25.8% (MS = 1.5153; $F_{(1, 41)} = 14.25$; P = 0.001) and 28.4% (MS = 1.6658; $F_{(1, 41)} = 16.23$; P <0.001) of the variation in trait diversity, and this also varied seasonally. Diversity values increased strongly with day length, temperature and other seasonal variables to peak near-continuously throughout the summer period in both study years, despite a reduction in diversity which occurred following a high-flow event in July 2007 (Table 5.3; Fig. 5.3).

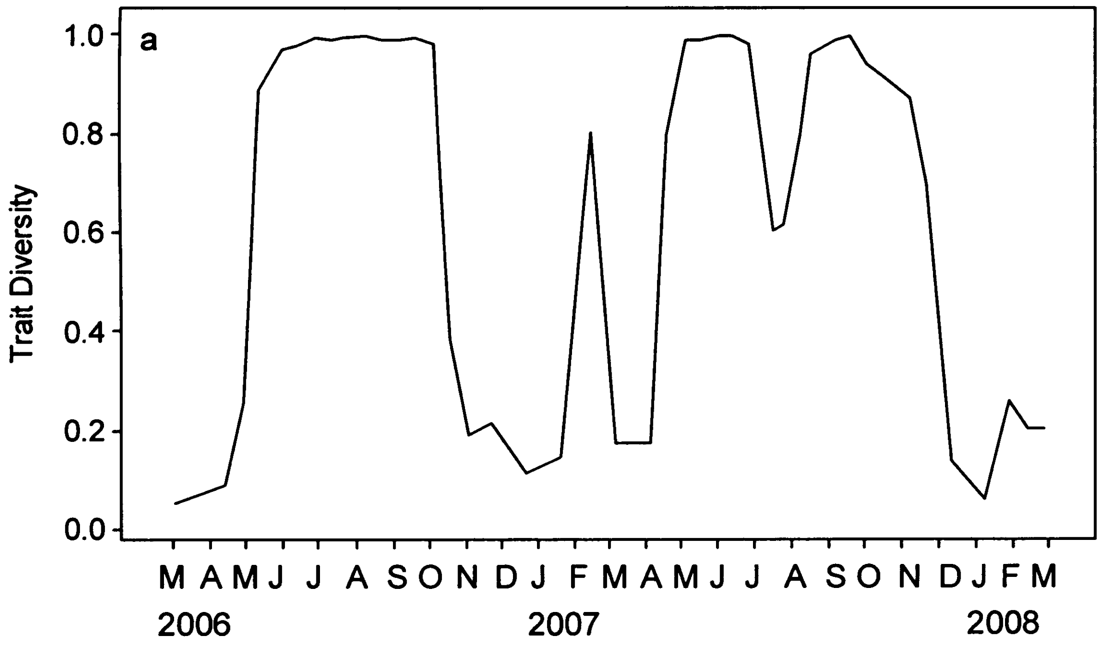

Figure 5.3: Temporal changes in trait diversity over a two-year sampling period of zooplankton in Cardiff Bay.

According to BINMATNEST based on functional traits, the zooplankton community of Cardiff Bay showed a marginally significantly nested sub-structure over time (T = 10.758°; P = 0.050), with the ranking of sampling occasion in the maximally packed matrix showing correlation with temperature (Spearman's rank correlation, ρ = 0.625; d.f..= 42) and dissolved oxygen (ρ = 0.460; d.f. = 42). These data suggest that a core of functional traits persisted throughout the sampling period, while other traits only occurred seasonally. These included zooplanktivory during spring and summer, while larger bodied taxa appeared least frequently in winter. Taxa attached to vegetation were only ever present in early summer.

5.5.2 Spatial Variation in Trait Composition

The extensive spatial survey was undertaken in September 2007, when overall trait diversity was high (Fig. 5.3), overall values of trait PCA 1 were close to average when judged over the entire sampling period and trait PCA 2 scores were relatively low (Figs 5.2 and 5.4).

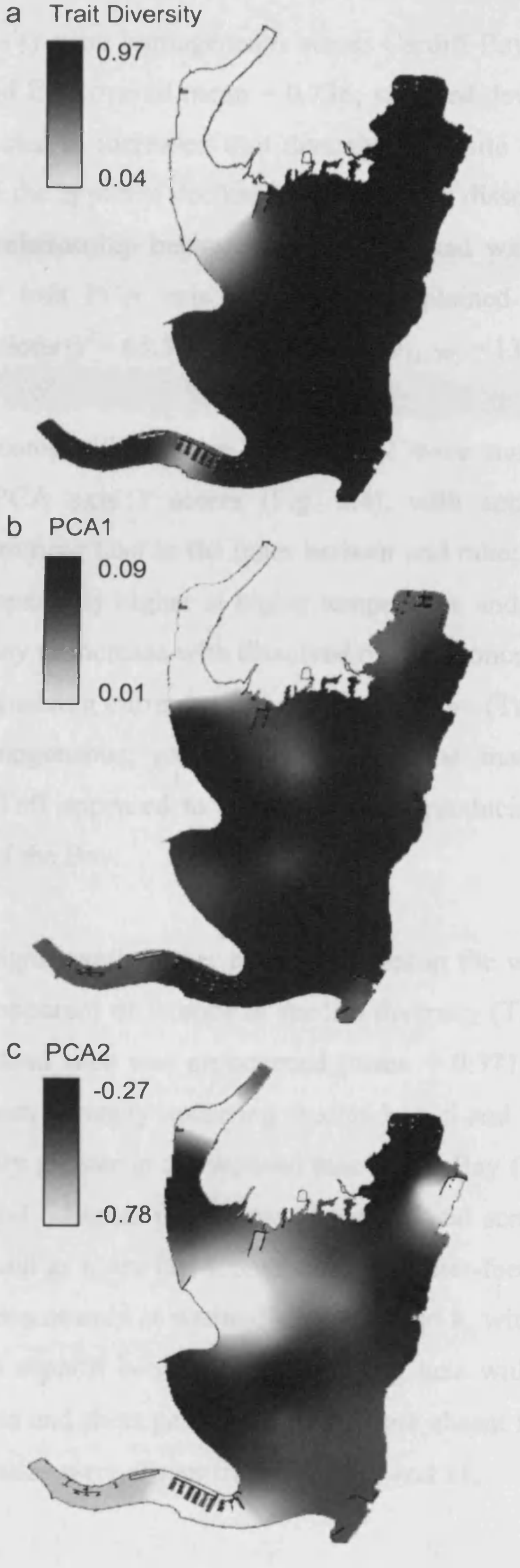

Figure 5.4: Spatial distribution of a) zooplankton trait diversity; b) PCA axis 1; and c) PCA axis 2 scores resulting from an ordination of zooplankton trait composition in September 2007 Cardiff Bay.

Values of trait diversity were homogeneous across Cardiff Bay but with lower values in the River Taff and Ely (overall mean = 0.736; standard deviation = 0.330) (Table 5.4). This was reflected in increased trait diversity with site depth, current velocity and temperature and the apparent decline with increasing dissolved oxygen, probably due to the inverse relationship between this variable and water temperature (Table 5.3). Only the first trait PCA axis significantly explained any variation in trait diversity across locations (r^2= 65.5%; MS = 5.8100; $F_{(1, 70)} = 132.92$; $P < 0.001$).

Variations in trait composition along PCA axis 2 were more pronounced across Cardiff Bay than PCA axis 1 scores (Fig. 5.4), with apparent aggregations of herbivorous and swimming taxa in the inner harbour and other shallower areas of the Bay. Values were apparently higher at higher temperature and lower pH (Table 5.3). Despite some tendency to increase with dissolved oxygen concentration and site depth but decrease with increasing current speed and temperature (Table 5.3), PCA1 scores were relatively homogeneous, particularly through the main body of the Bay. However, the river Taff appeared to support faster reproducing, smaller herbivores than the main body of the Bay.

Trait diversity was significantly lower across the sites in the wetland reserve than in the Bay, despite no apparent difference in species diversity (Table 5.4). Variation in diversity among wetland sites was pronounced (mean = 0.371; standard deviation = 0.349), with the highest diversity occurring at sites 3, 4, 5 and 7. Scores on both trait axes were significantly greater in the wetland than in the Bay (Table 5.4), suggesting that the Bay supported a higher proportion of benthic and scrambling taxa than the wetland reserve, as well as more fast-reproducing and filter-feeding taxa. Vegetation-attached taxa were present only at wetland sites 3, 4, and 8, with the former two sites also the only sites to support benthic and scrambling taxa within the wetland. Taxa with small clutch sizes and short generation times were absent from sites 7 and 9 and those with low C:N ratios were absent from sites 6, 9 and 11.

Table 5.4: A comparison using ANOVA of diversity and composition (i.e. trait PCA scores) of all zooplankton species present between the Bay and associated wetland reserve. Probability values not corrected for multiple testing.

	Cardiff Bay		**Wetland reserve**		**ANOVA**
Dependent variable	Mean	SD	Mean	SD	
Species diversity	0.391	0.137	0.486	0.301	MS: 0.0772 $F_{(1,70)}$: 2.76 P: 0.101
Trait diversity	0.736	0.330	0.371	0.349	MS: 1.144 $F_{(1,70)}$: 10.37 P: 0.002**
PCA 1	0.050	0.011	0.064	0.017	MS: 5.779 $F_{(1,70)}$: 6.11 P: 0.016*
PCA 2	-0.710	0.103	-0.604	0.165	MS: 5.040 $F_{(1,70)}$: 5.27 P: 0.025*

As with temporal pattern, trait composition among zooplankton in Cardiff Bay and its associated wetlands had a significantly nested sub-structure ($T = 4.06563^{\circ}$; $P < 0.001$) with the ranking of sites in the maximally packed matrix correlating most strongly with dissolved oxygen concentration ($\rho = 0.496$; d.f. = 71). Most traits were present throughout the Bay, making up the core of generalists, with a subset of apparently more specialised traits being more localised. For example, vegetation-attached taxa occurred at the fewest sites and only in the River Ely and at some wetland sites; benthic and scrambling taxa were only present at sites in the River Taff and near to the pontoon to the east of the Bay; taxa with small clutch sizes and short generation times were absent from the River Taff and one site in the inner harbour; and taxa with low C:N ratios were absent from both rivers.

5.5.3 Trait Diversity and Species Diversity

Species diversity and trait diversity were not linearly related among either temporal or spatial samples (Fig. 5.5a and b). Quadratic regression provided a good fit with the temporal data (Fig. 5.5a), implying the existence of functional redundancy when trait diversity was high (Bêche and Resh, 2007) but was a poor fit with the spatial data (Fig. 5.5b). Both temporal and spatial trait diversity increased non-linearly with total zooplankton abundance (Fig. 5.6a and 5.6b), indicating that at the greater abundances recorded, further increases in abundance led to smaller increases in trait diversity.

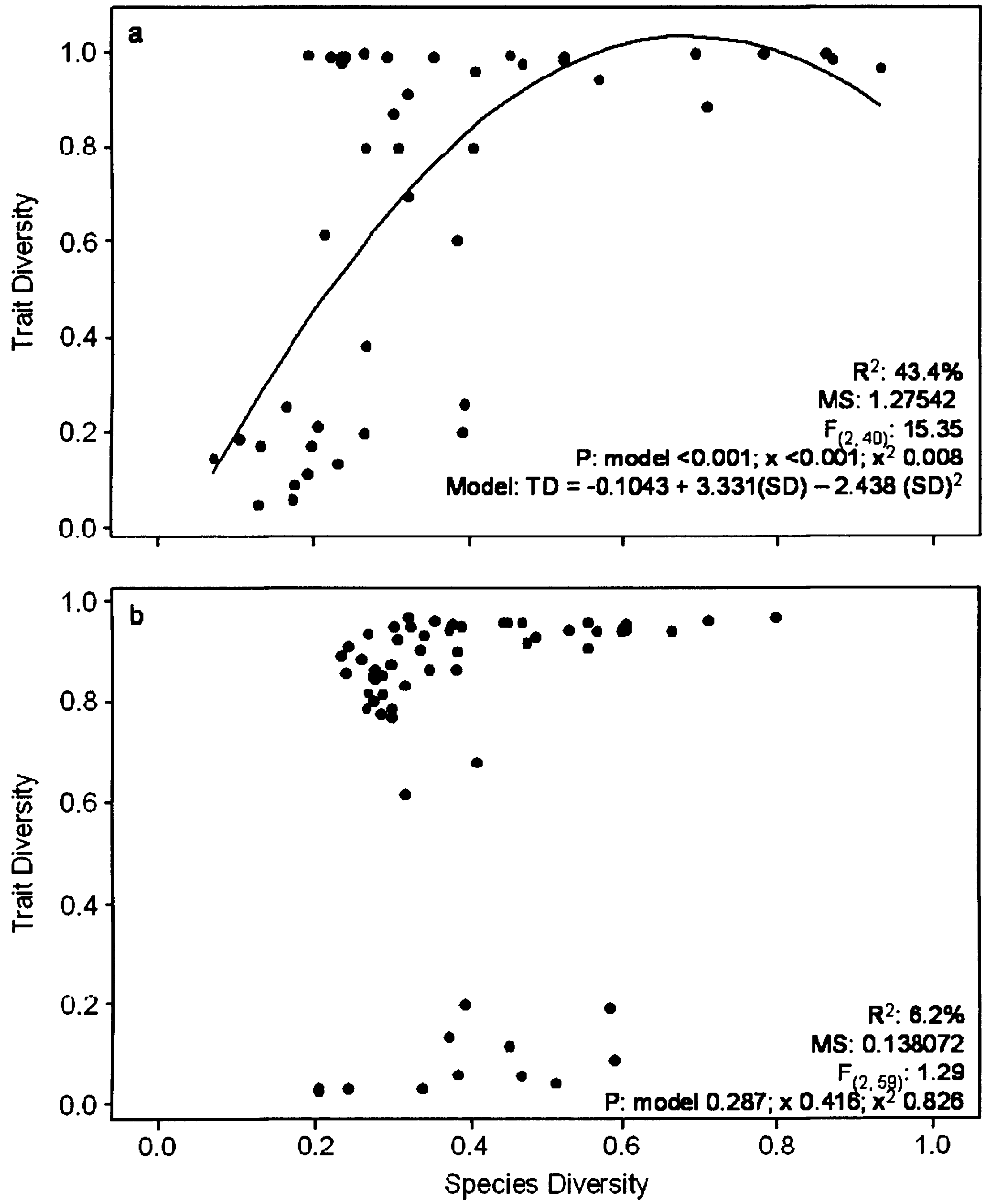

Figure 5.5: The relationship between trait diversity (TD) and species diversity (SD) in a) temporal surveys and b) spatial surveys, showing the results of quadratic regression

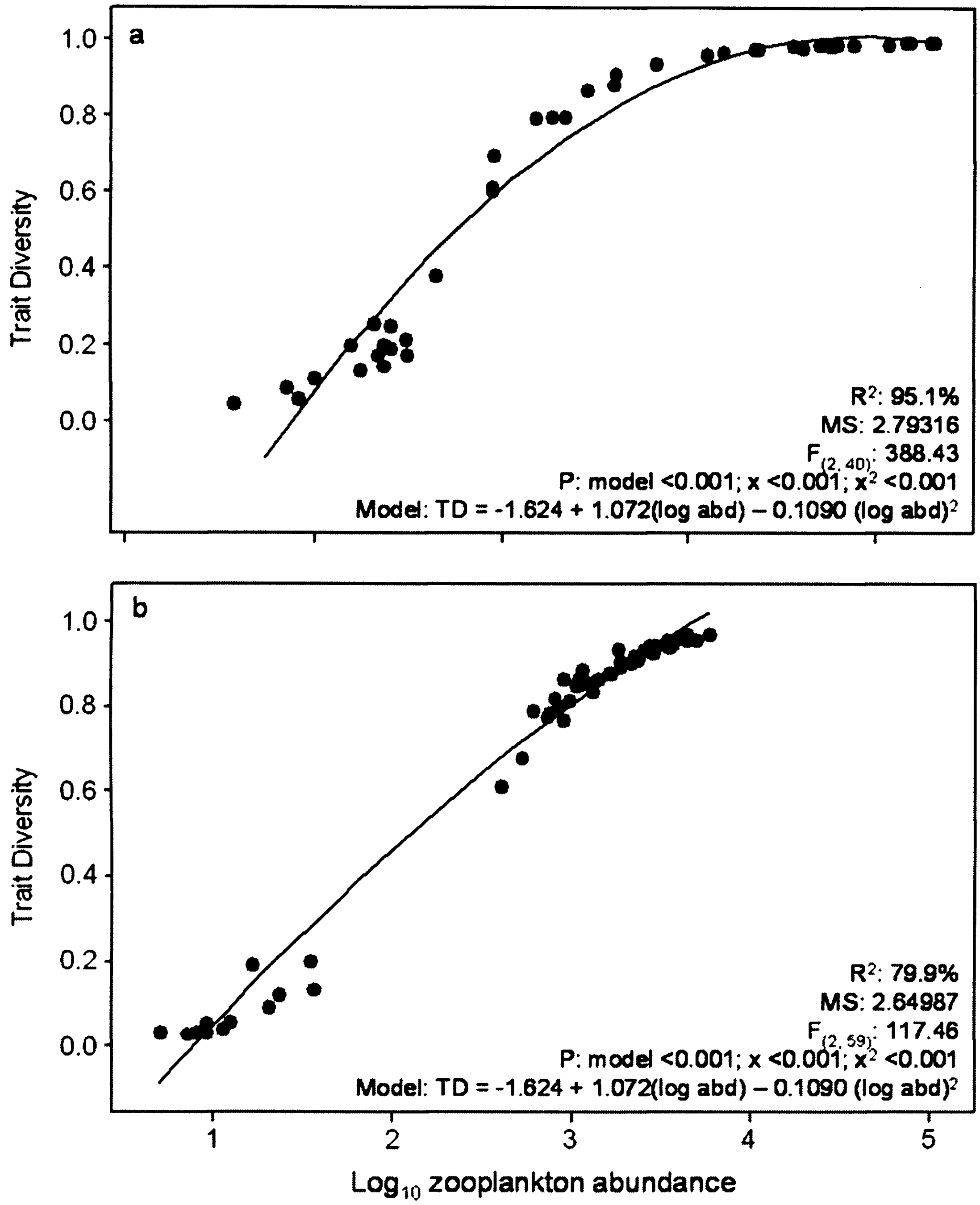

Figure 5.6: The relationship between trait diversity (TD) and log(n+1) transformed zooplankton abundance (log abd) in a) temporal surveys and b) spatial surveys, showing the results of quadratic regression

5.6 Discussion

While recent calls for studies to place greater emphasis on trait-based analysis have resulted in an increasing number of trait-based studies, trait analyses of freshwater zooplankton assemblages remain relatively few, with even fewer attempts to quantify nestedness using functional traits. The present study was aimed primarily at developing an understanding of the temporal and spatial dynamics of Cardiff Bay zooplankton using basic information on the functional traits of zooplankton species.

Three simple hypotheses were tested: that environmental variation in time (1) and space (2) should engender variations in zooplankton trait diversity and composition, and that differences in zooplankton trait composition would produce a nested community over space and time (3). All three hypotheses were supported. Seasonal changes occurred in community composition between slower growing, omnivorous or zooplanktivorous species with low C:N ratio and high assimilation efficiency in early spring and asexually or rapidly-reproducing filter-feeders or detritivores with high C:N ratios in late summer. Spatial pattern in trait composition revealed that herbivorous swimming species dominated the inner harbour and other shallow pockets of Cardiff Bay. Data revealed a nested structure among community traits both in space and time, illustrating how a subset of specialist traits occurred only under certain conditions. While there are caveats about the specificity and limited amount of zooplankton functional trait information available, relatively broad trait categories were nevertheless considered to provide appropriate resolution in testing the three hypotheses.

5.6.1 Seasonal Variation in Trait Composition

There have been no previous studies of temporal changes in zooplankton community composition specifically focussing on functional traits. However the PEG model of plankton succession (Sömmer *et al.,* 1986) provides qualitative predictions of broad groups of zooplankton that would be expected throughout the year. Small herbivores are expected to exploit a spring phytoplankton bloom, with larger taxa following later in the year as larger-celled phytoplankton increase. Under low food conditions experienced in winter, overall zooplankton abundance falls to very low levels but there is evidence that terrestrial carbon sources can act as important energy subsidies over less productive periods (Grey *et al.,* 2001; Pace *et al.,* 2004; Carpenter *et al.,* 2005; Maguire and Grey, 2006; Matthews and Mazumder, 2006), with microbially-processed terrestrial detritus entering freshwater food webs. Indeed, surveys have found that variations in the zooplankton of Cardiff Bay continue into winter (see Chapter 3).

As predicted, marked seasonal patterns in trait diversity and trait-based community composition were observed, which was reflected in strong correlations with temperature, day length, total oxidised nitrogen concentration and dissolved oxygen, although multicolinearity between these variables complicates the determination of causal effects on assemblage dynamics. The presence of taxa with low C:N ratios in late winter/early spring and high C:N ratios in later in summer, could suggest that food quality was limited over the winter period (Perhar and Arhonditis, 2009). The results suggest that zooplankton occurring in winter/early spring could be adapted to periods of low quality or quantity food resources through low reproductive output to reduce energy expenditure and high assimilation efficiencies to maximise nutrient intake. In contrast, taxa present in summer are more able to rapidly reproduce (e.g. Schalau *et al.,* 2008) and can afford lower assimilation efficiencies due to an abundant food supply.

The nested nature of the zooplankton community suggested that an overall assemblage comprising generalist zooplankton traits was present throughout the temporal sampling period, within which a subset of traits occurred only at favourable times of the year. Over the two-year sampling period, most functional traits were present all year, making up the core group of generalists. However, several traits appeared and disappeared throughout the two years: zooplanktivory, during late winter/early spring and summer; vegetation-attached taxa, which were only ever present in summer; and larger body sizes, which occurred least frequently in winter, consistent with predictions of the PEG model, which expect that larger zooplankton increase following an increase in larger-celled phytoplankton in the summer (Sömmer *et al.,* 1986).

5.6.2 Spatial Variation in Trait Composition

A previous spatial survey of the zooplankton in Cardiff Bay (see Chapter 4) had shown that species composition in the main body of the Bay was relatively homogeneous but that the quasi-riverine areas showed greater variation. It was therefore expected that the distribution and diversity of zooplankton functional traits would show homogeneity in the main body of the Bay but that variations in the rivers, as well as the wetland reserve, would produce a nested community structure.

As expected, sites in the main body of the Bay appeared homogeneous in terms of trait diversity, distribution of specific traits and water quality, and contained most of the core of generalist traits. The quasi-riverine areas showed lower diversity and appeared to support different assemblages to the main body of the Bay. These variations produced a nested community structure, indicating that certain sites supported conditions favourable to specific trait groups. Specifically, the River Ely was the only area to support vegetation-attached taxa; benthic and scrambling taxa were only found at sites in the River Taff and near to the pontoon to the east of the Bay; and taxa with small clutch sizes and short generation times were absent from the Taff. These differences from the main body of the Bay show that conditions in the rivers support specific trait features and could indicate that taxa in the rivers are adapted to the variable flow conditions experienced over time (see Chapter 3). Here, benthic, scrambling and vegetation-attached taxa could be more likely to persist than pelagic taxa under high flow conditions, consistent with the decline in PCA axis 1 with increased current velocity. To investigate this fully, however a series of extensive spatial surveys would be needed over a range of flow conditions and as discussed in Chapter 4, the flow data available for the Bay was limited.

Despite similar species diversity between the two areas, trait diversity in the wetland reserve was lower than in the Bay. Benthic and scrambling taxa were less likely to occur in the wetland reserve. All sites in the wetland supported some swimming taxa but vegetation-attached taxa were surprisingly only present at sites 3, 4, and 8. This could be a consequence of the restriction of placing sampling sites only in areas safely accessible by foot, which tended to be away from large stands of vegetation and could have resulted in under-representation of vegetation-attached taxa in samples. The wetland survey was limited by accessibility of sites and ideally would have involved a more extensive range of sites and sampling dates. Nevertheless, this one-off survey implies that the wetland area supports a trait assemblage different to that in the main body of the Bay.

5.6.3 Conclusion

Overall, results from Cardiff Bay highlight non-random patterns in the zooplankton community both spatially and over time. Functional redundancy in the Bay was generally high, implying the existence of a large number of shared traits among species and that the loss of species would not necessarily lead to a loss in functional diversity (Petchey and Gaston, 2009). This would be particularly true during the summer and in the main body of the Bay where diversity was highest. Here, the co-existence of a large number of species could be due to the lack of competitive exclusion through intermediate levels of disturbance (Richerson *et al.,* 1970; Grenney *et al.,* 1973; Connell, 1978; Gaedeke and Sömmer, 1986; Keitel and Chase, 2004), which may help to maintain ecosystem resilience through numerous taxa sharing the same functional niche (Naeem and Li, 1997). At lower diversity, however, as recorded in the Taff and wetlands and throughout the Bay over winter periods, the removal of species would more likely lead to the loss of ecosystem function. Here, the maintenance of conditions that support specific zooplankton traits would be important in the maintenance of diversity.

This is one of the first studies to have investigated zooplankton community composition and nestedness using functional traits and suggested how dynamic changes in environmental conditions and food resources over the annual cycle have formed an important template for trait selection. At least in Cardiff Bay, site-to-site variations are less important for trait composition, though local conditions nevertheless support zooplankton with specific features.

Chapter 6: Discussion

6.1 Background

Despite the importance of zooplankton in aquatic ecosystems, and their value as model organisms in ecological investigations, there are several areas of zooplankton ecology that have been relatively overlooked in the literature. Specifically, at the outset of this thesis, three important gaps were identified:

1. Very few studies have directly compared zooplankton assemblages between artificial and natural water bodies, or investigated how the managed and artificial character of man-made water bodies affects seasonal and spatial community dynamics.
2. Many studies of zooplankton dynamics focus on more productive periods of the year, overlooking winter assemblages.
3. Recent studies have identified limitations in using taxonomic approaches to quantify biodiversity and ecosystem characteristics in a range of systems, yet information on zooplankton functional traits is limited and trait-based investigations of zooplankton community dynamics so far do not exist.

The broad aim of this PhD was to address these gaps through spatial and temporal surveys of the zooplankton community in the newly formed, and highly managed, Cardiff Bay. Six key questions were devised and introduced in Chapter 1, which informed a series of testable hypotheses.

1. Globally, do artificially formed water bodies support different zooplankton assemblages to those found in natural lakes?
2. Does the zooplankton community of Cardiff Bay vary in ways predicted by ecological theory, and particularly by predictions based on the Plankton Ecology Group (PEG) qualitative model of plankton succession?
3. In Cardiff Bay, is there a persisting community of interacting zooplankton species even over less productive periods of the year?
4. Do spatial and temporal dynamics in the zooplankton community of Cardiff Bay reflect local water quality variables?

5. Do management practices employed in Cardiff Bay influence the temporal and spatial dynamics of zooplankton?
6. Do the traits of zooplankton species in Cardiff Bay vary spatio-temporally in ways that might reflect environmental variation?

Cardiff Bay's attributes and management procedures provided an ideal context in which to examine the key questions. A meta-analysis of zooplankton data from a range of global water bodies was carried out in Chapter 2 of this thesis to address the first of these key questions. Chapter 3 addressed question 2, 3 and the temporal elements of questions 4 and 5, through analysis of the temporal dynamics of zooplankton in Cardiff Bay, while Chapter 4 addressed the spatial elements of the latter two questions. The final question was addressed in Chapter 5, where a trait-based approach was used to analyse spatio-temporal dynamics of the Bay's zooplankton community.

6.2 Synthesis

Overall, the studies involved in this thesis were not experimental and relied on ecological surveys and statistical approaches to form conclusions. Consequently, the results tended to be focussed at the whole-lake level, since more detailed investigation into individual drivers of zooplankton dynamics was not possible. This was primarily due to the challenges of creating the large-scale experiments that would be otherwise necessary to test such hypotheses.

Additionally, where statistical tests were performed separately on a number of variables, probability values were not corrected for multiple testing. It is recognised that this approach increases the risk of producing false positive results.

Despite these short-comings, this thesis included some novel approaches to address a number of areas of zooplankton ecology that have been relatively neglected in the literature. The resultant data add fundamentally to the understanding of the ecology of Cardiff Bay, while also contributing to zooplankton ecology more generally.

6.2.1 Zooplankton Assemblages in Natural and Artificial Water Bodies

A meta-analysis of zooplankton assemblages was carried out using data from previous studies of a range of water bodies around the world (Chapter 2). The number of artificial water bodies was low compared with natural lakes, consistent with the relative bias in the literature. While ideally the analysis would have involved a large and equal number of both, the results were among the first to indicate that zooplankton communities may indeed differ between artificial and natural water bodies, despite apparent similarities in richness.

Most taxa were present across both natural and artifical water bodies, while local factors, such as lake depth, productivity and conductivity, appeared to create conditions favourable to specialist taxa in natural lakes. It was not possible to investigate the precise causes of these apparent differences. However, possible mechanisms could include differences in age between newly formed water bodies and lakes formed over millennia, although to date there is been no evidence of this being an important factor (Dodson *et al.,* 2006), and management techniques, such as artificial aeration, which alter water quality (Cowell *et al.,* 1987; Hawkins and Griffiths, 1993; Lewis *et al.,* 2003; Antenucci *et al.,* 2005; Becker *et al.,* 2006; Burford and O'Donohue, 2006).

The differences observed in zooplankton assemblages present the possibility that differences occur at other trophic levels between artificial and natural water bodies. If true, such variations could necessitate different management and conservation considerations between natural and artificial water bodies. Further research would ideally encompass a larger number of water bodies, particularly artificial ones, from a wider range of latitude and longitudes, and include measures of dispersal and local conditions, as well as data on the abundance of predator taxa, in order to partition out the drivers of these potential variations.

Within the context of this meta-analysis, Cardiff Bay appears to support a zooplankton assemblage typical of other water bodies of similar morphometric characteristics and trophic status. Intrinsic local factors are likely important in structuring the zooplankton community, which due to the artificial nature of the Bay, was expected to consist of mainly generalist species, adapted to a range of environmental conditions.

6.2.2 Temporal Dynamics of the Cardiff Bay Zooplankton Community

Fortnightly surveys over two years (Chapter 3) revealed that Cardiff Bay had already acquired a zooplankton community typical of large eutrophic lakes. There was large species turnover over the sampling period but two of the dominant species (*Daphnia hyalina* and *Bosmina longirostris*) appeared to coexist through variation in seasonal timing linked to variations in the size-range of their algal resources. Community dynamics generally followed the PEG model (Sömmer *et al.,* 1986), despite intensive management in the Bay, and broadly indicated succession from cyclopoid copepods in autumn/winter to small-bodied cladocera in late winter/early spring, dominant cladocera later in spring and larger cladocera and cyclopoids in mid-summer. However, a period of high flow in the second sampling year resulted in a population crash in *B. longirostris* and suggested that shorter retention times could have an important impact on successional dynamics of the plankton. The temporal nature of both the taxonomic- and trait- classified (see *6.2.4*) zooplankton community was reflected in correlations with seasonally changing environmental variables.

Temporal surveys also revealed that variations in over-wintering assemblages of zooplankton continued into winter periods, despite apparent low productivity. Allochthonous carbon sources (Grey *et al.,* 2001; Pace *et al.,* 2004; Carpenter *et al.,* 2005; Maguire and Grey, 2006; Matthews and Mazumder, 2006) and benthic algae (Karlsson and Säwström, 2009) can be important energy subsidies in freshwater ecosystems when autochthonous production is limited but these could not be quantified during the present study. Nevertheless, the presence of a diverse zooplankton community over winter implies that seasonal studies restricted to more productive periods (e.g. Whiteside *et al.,* 1978; Vanni and Temte, 1990; Müller-Navarra and Lampert, 1996; Talling, 2003; Tessier and Welser, 2006; Horppila *et al.,* 2009) may detect only a limited proportion of the zooplankton community and that year-round studies provide a more accurate assessment of zooplankton community dynamics.

A more thorough examination of temporal changes in stable isotopes, as well as fatty acid composition, in Cardiff Bay's planktonic communities could reveal more precisely: a) the importance of alternative carbon sources over periods of low autochthonous production, through testing the hypothesis that the relative importance of allochthonous carbon sources increases during winter or during periods of shortened residence time; and b) the mechanisms behind coexistence of the dominant zooplankton species, by testing the hypothesis that *Daphnia hyalina* and *Bosmina longirostris* coexist through temporal partitioning of food resources.

6.2.3 Spatial Dynamics of the Cardiff Bay Zooplankton Community

An extensive spatial survey (Chapter 4) appeared to suggest that relatively homogeneous water quality in the main body of Cardiff Bay, probably reflecting lake mixing and artificial aeration, has given rise also to relatively homogeneous zooplankton species composition. In contrast, patterns of zooplankton abundance in the dominant species are more structured spatially around food concentrations located in warmer waters. Planktivorous fish, and in particular their larvae, tend to aggregate both spatially and temporally at higher zooplankton density (Chick and Van Den Avyle, 1999). With particularly dense patches of zooplankton occurring in the inner harbour and near the barrage, these areas were identified as potentially important feeding areas for species such as roach (*Rutilus rutilus*), dace (*Leuciscus leuciscus*) and chub (*Leuciscus cephalus*) that have been recorded in the Bay.

The data, particularly on abundance, suggest that spatial-scale could be important in the detection of the relative influence of spatial and environmental factors on zooplankton more generally. Biotic factors are also important in community spatial structure (Legendre, 1993): Behavioural factors such as predator avoidance, competitive interactions and mate-finding in zooplankton can all produce small-scale contagious distributions (Pinel-Alloul *et al.*, 1988). Additionally, the Bay's flow paths and aeration system undoubtedly influence zooplankton distribution, particularly at high flow. Ideally any future surveys would include quantification of these potentially important biotic and physical effects for a complete assessment of the spatial distribution of zooplankton and the importance of sampling scale.

6.2.4 Zooplankton Trait Structure and Diversity in Cardiff Bay

A trait-based analysis of the spatial and temporal survey data (Chapter 5) was one of the first to assess trait composition and nestedness in lake zooplankton. Although traditional taxonomy has been central to studies of assemblage composition (e.g. Naeem *et al.,* 1994; Tilman *et al.,* 1997; McGrady-Steed *et al.,* 1997; Naeem and Li, 1997; Mulder *et al.,* 2001), some authors report that functional measures are more likely than species lists to indicate how ecosystem processes are affected by modification (e.g. Tilman *et al.,* 1996; Hooper and Vitousek, 1997; Tilman *et al.,* 1997; Tessier *et al.,* 2000; Tilman, 2001; Flynn *et al.,* 2009; Pollard and Yuan, 2009). Traits can also provide an insight into evolutionary processes, e.g. habitat template theory (Southwood 1977), postulates how variations in the physico-chemical and biological character of ecosystems, in time and space, are key agents that have selected those organism traits most likely to succeed under given conditions.

Functional trait information for freshwater zooplankton is limited, so traits were categorised into relatively broad categories. Nevertheless, results suggested that dynamic changes in environmental conditions and food resources over the annual cycle have formed an important template for trait selection. Site-to-site variations were less important for trait composition, although local conditions in the Taff, Ely and the Bay's associated wetland reserve contributed to most of the variation in trait diversity while also supporting some specific trait features.

As a shallow artificial freshwater lake, at low elevation in a temperate climate, Cardiff Bay was expected to support a community of generalist taxa adapted to a range of conditions (see *6.2.1*). In support of this, trait structure was nested in both space and time. This illustrates that a core of generalist traits existed over a range of conditions found in the Bay over time and among sites, but also that some traits, drawn from this widespread core, occurred only under some specific conditions. The maintenance of these specific conditions is likely to be important in maintaining diversity in the Cardiff Bay system (Petchey and Gaston, 2009). Further investigation into the specific conditions under which each trait is selected for could be used for projecting the response of trait composition and ecosystem functioning to longer-term environmental change. An accurate measurement of the functional traits for the specific zooplankton found in Cardiff Bay would provide a better understanding of their spatial and temporal dynamics. However, the data obtained from this literature review revealed that overcoming the limited amount of trait information that exists on freshwater zooplankton by using relatively broad trait categories can nevertheless provide an important insight into community dynamics and ecosystem function.

6.3 Conclusion and Future Research Needs

Together, these data suggest that Cardiff Bay supports a zooplankton community typical of natural lakes of similar morphometric characteristics and trophic status, despite its recent formation and highly managed nature. The role of management techniques *per se* in producing such a typical zooplankton community remains unclear. However, several areas are highlighted that should be of particular interest for future investigation and a better understanding of zooplankton ecology in general and the role of zooplankton in the Cardiff Bay ecosystem:

i. General Zooplankton Research

The potential differences identified between zooplankton in natural and artificial lakes are extremely interesting and accurately partitioning out the mechanisms behind these differences is imperative for understanding the importance of conservation and management in different water body types. Seasonal surveys identified the potential role of residence time in plankton succession, as well as the need for future temporal work to include winter assemblages for accurate descriptions of community composition. The spatial survey revealed the importance of scale in detecting environmental and spatial drivers of zooplankton abundance and composition, but further investigation into the role of biotic and abiotic factors would be particularly interesting to assess accordance with the Multiple Driving Force Hypothesis. Trait-based analysis highlighted the lack of functional trait information available for freshwater zooplankton but also the role of functional diversity in quantifying community dynamics. Further work is needed to expand the data base of zooplankton functional traits, ideally to bring it in line with other groups of organisms, such as freshwater macroinvertebrates, for which more comprehensive data collections are available. Future studies of zooplankton communities should include assessments of trait structure and diversity to illustrate evolutionary aspects of habitat selection and ecosystem resilience, rather than rely on taxonomic approaches alone.

ii. The Effects of Lake Management Techniques on Cardiff Bay's Zooplankton

Zooplankton likely hold a pivotal role in Cardiff Bay's aquatic ecosystem in the transfer of energy between trophic levels and control of algal development. As such, a precise understanding of the impact of management techniques on zooplankton composition, abundance and distribution could be extremely beneficial. In particular, several areas of Cardiff Bay's management are likely to have direct effects on the zooplankton community, the quantification of which would be useful in inferring their influence at other trophic levels. These include the artificial aeration system and resultant impacts on flow paths and oxygen dynamics; nutrient and water quality management; fisheries management policy; operation of the barrage and the resultant small variations in salinity in and around the navigable locks.

iii. Long-term Planktonic Development in Cardiff Bay

The development of the zooplankton community over time will be pivotal to the long-term ecology of Cardiff Bay as a whole, and could be affected by natural lake aging; nutrient management and dynamics; fish population development; climate change; macrophyte management and development. Using the two years of data in the present study, it is not possible to conclude how the zooplankton community in Cardiff Bay is likely to change in the long term or whether an equilibrium community has been reached. However, previous studies have shown that periodic disturbances and fluctuations in environmental conditions generally prevent zooplankton communities ever reaching equilibria (Hutchinson, 1961; Matsumura-Tundisi and Tundisi, 2002; Scheffer *et al.*, 2003). For this reason it is unlikely that the zooplankton community of Cardiff Bay has reached a successional climax, rather continual development is likely across years in the long term. Tracking this development could be key to understanding the impacts of long-term environmental change and for informing projections for long-term management programs.

iv. The Ecological Role of Zooplankton in Cardiff Bay

Several processes are critical for a comprehensive understanding of the Cardiff Bay ecosystem and the role of zooplankton therein, raising a number of questions that require further investigation and are also critical to zooplankton ecology in general: a) What is the role of zooplankton in the transfer and fate of pollutants through trophic levels? b) How does the presence of invasive zebra mussels (*Dreissena polymorpha*), and the potential competitive pressure they exert affect zooplankton community dynamics? c) How does fish predation influence zooplankton abundance, community composition and seasonal population timing? d) How does the zooplankton community respond to changes in river discharge and whole-lake retention time? e) What impacts do changes in algal quality and quantity have on zooplankton community dynamics?

Such longer-term surveys and assessments at higher trophic levels could provide an insight into the Bay's ecosystem as a whole, its dynamics over space and time and could be a valuable tool for informing future management of this and other artificial water bodies.

References

Ackerley, D. D., Schwilk, D. W. and C. O. Webb, 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology* 87 (suppl.): 50-61

Agasild, H. and T. Nõges, 2005. Cladoceran and rotifer grazing on bacteria and phytoplankton in two shallow eutrophic lakes: *in situ* measurement with fluorescent microspheres. *Journal of Plankton Research* 27: 1155-1174

Amsinck, S. L., Strzelczak, A., Bjerring, R., Landkildehus, F., Lauridsen, T., Christoffersen, K. and E. Jeppesen, 2006. Lake depth rather than fish planktivory determines cladoceran community structure in Faroese lakes – evidence from contemporary data and sediments. *Freshwater Biology* 51: 2124-2142

Antenucci, J. P., Ghagouani, A., Burford, M. A. and J. R. Romero, 2005. The long-term effect of artificial destratification on phytoplankton species composition in a subtropical reservoir. *Freshwater Biology* 50: 1081-1093

Aubé, C. I., Locke, A. and G. J. Klassen, 2005. Zooplankton communities of a dammed estuary in the Bay of Fundy, Canada. *Hydrobiologia* 548: 127-139

Bady, P., Dolédec, S., Fesl, C., Gayraud, S., Bacchi, M. and F. Schöll, 2005. Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. *Freshwater Biology* 50: 159-173

Balcer, M. D., Korda, N. L. and S. I. Dodson, 1984. *Zooplankton of Great Lakes: a guide to the identification and ecology of the common crustacean species.* London: The University of Wiscon Press

Banks, Z., 2008. *Flora and Fauna Monitoring 2007.* Cardiff Harbour Authority Monitoring Report

Banks, Z., 2009. *Flora and Fauna Monitoring 2008.* Cardiff Harbour Authority Monitoring Report

Barnett, A. J. and B. E. Beisner, 2007. Zooplankton biodiversity and lake trophic state: explanations invoking resource abundance and distribution. *Ecology* 88: 1675-1686

Barnett, A. J., Finlay, K. and B. E. Beisner, 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology* 52: 796-813

Baxter, R. M. and P. G. Glaude, 1980. Environmental effects of dams and impoundments in Canada: experience and prospects. *Canadian Bulletin of Fisheries and Aquatic Science* 205: 34

Béche, L. A. and V. H. Resh, 2007. Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Archiv für Hydrobiologie* 169: 1-23

Becker, A., Herschel, A. and C. Wilhelm, 2006. Biological effects of incomplete stratification of hypertrophic freshwater reservoir. *Hydrobiologia* 559: 85-100

Benndorf, J., Kranich, J., Mehner, T. and A. Wagner, 2001. Temperature impact on the midsummer decline of Daphnia galeata: An analysis of long-term data from the biomanipulated Bautzen Reservoir (Germany). *Freshwater Biology* 46: 199-211

Berger, S. A., Diehl, S., Stibor, H., Trommer, G., Ruhenstroth, M., Wild, A., Weigert, A., Jäger, C.G. and M. Streibel, 2007. Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton. *Oecologia* 150: 634-654

Bloch, C. P., Higgins, C. L. and M. R. Willig, 2007. Effects of large-scale disturbance on metacommunity structure of terrestrial gastropods: temporal trends in nestedness. *Oikos* 116: 395-406

Boersma, M., van Tongeren, O. F. R. and W. M. Mooij, 1996. Seasonal patterns in the mortality of *Daphnia* species in a shallow lake. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 18-28

Borcard, D., Legendre, P., Avois-Jacquet, C. and H. Tuomisto, 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85: 1826-1832

Børsheim, K. Y. and S. Andersen, 1987. Grazing and food size selection by crustacean zooplankton compared to production of bacteria and phytoplankton in a shallow Norwegian mountain lake. *Journal of Plankton Research* 9: 367-379

Bottrell, H. H., 1975. Generation time, length of life, instar development and frequency of moulting, and their relationship to temperature in eight species of Cladocera from the River Thames, Reading. *Oecologia* 19: 129-140

Bray, J. R. and J. T. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325-349

Brendelberger, H., 1991. Filter mesh size of cladocerans predicts retention efficiency for bacteria. *Limnology and Oceanography* 36: 884-894

Brendelberger, H. and W. Geller, 1985. Variability of filter structures in eight Daphnia species: mesh sizes and filtering areas. *Journal of Plankton Research* 7: 473-486

Brönmark, C. and L. Hansson, 2005. *The biology of lakes and ponds*. 2nd ed. Oxford: Oxford University Press

Brooks, J. L. and S. I. Dodson, 1965. Predation, body size, and composition of plankton. *Science* 150: 28-35

Burford, M. A. and M. J. O'Donohue, 2006. A comparison of phytoplankton community assemblages in artificially and naturally mixed subtropical water reservoir. *Freshwater Biology* 51: 973-982

Burns, C. W., 1968. The relationship between body size of filter-feeding cladocera and the maximum size of particle ingested. *Limnology and Oceanography* 13: 675-678

Burns, C. W., 2000. Crowding-induced changes in growth, reproduction and morphology of *Daphnia*. *Freshwater Biology* 43: 19-29

Cáceres, C. E., 1998. Seasonal dynamics and interspecific competition in Oneida Lake *Daphnia*. *Oecologia* 115: 233-244

Cáceres, C. E. and D. A. Soluk, 2002. Blowing in the wind: A field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* 131: 402-408

Cardiff Bay Barrage Act 1993. (c42), London: HMSO

Cardiff Bay Barrage Bill: Environmental Statement 1991. London: HMSO

Carpenter, S. R., Cole, J. J., Pace, M. L., Van de Bogert, M., Bade, D. L., Bastviken, D., Gille, C. M., Hodgson, J. R., Kitchell, J. F. and E. S. Kritzberg, 2005. Ecosystem subsidies: Terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. *Ecology* 86: 2737-2750

Castro, B. B., Marques, S. M. and F Conçalves, 2007. Habitat selection and diel distribution of the crustacean zooplankton from a shallow Mediterranean lake during the turbid and clear water phases. *Freshwater Biology* 52: 421-433

Chalambidou, I., Santamaría, L., 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. *Acta Oecologia* 23: 165-176

Chapin, F. S., III, Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E. and D. Tilman, 1997. Biotic control over the functioning of ecosystems. *Science* 277: 500-504

Charvet, S., Statzner, B., Usseglio-Polatera, P. and B. Dumont, 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology* 43: 277-296

Chase, J. M. and W. A. Ryberg, 2004. Connectivity, scale dependence, and the productivity-diversity relationship. *Ecology Letters* 7: 676-683

Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366

Chick, J. H. and Van Den Avyle, M. J., 1999. Zooplankton variability and larval striped bass foraging: Evaluating potential match/mismatch regulation. *Ecological Applications* 9: 320-334

Chimney, M.J. and J.A. Bowers, 2006. The influence of subsample size in a study of freshwater zooplankton. *Journal of Freshwater Ecology* 21: 349-351

Chow-Fraser, P. and E. J. Maly, 1988. Aspects of mating, reproduction, and co-occurrence in three freshwater calanoid copepods. *Freshwater Biology* 19: 95-108

Ciros-Pérez, J., Carmona, M. J. and M. Serra, 2001. Resource competition between sympatric sibling rotifer species. *Limnology and Oceanography* 46: 1511-1523

Cohen, G. M. and J. B. Shurin, 2003. Scale-dependence and mechanisms of dispersal in freshwater zooplankton. *Oikos* 103: 603-617

Connell, J. H., 1978. Diversity in tropical rainforests and coral reefs: High diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199: 1302-1310

Cook, R. R. and J. F. Quinn, 1998. An evaluation of randomization models for nested species subsets analysis. *Oecologia* 113: 584-592

Council of the European Communities, 1991. Directive 1991/91/271/EEC of the Eurpoean parliament and of the council of 21 May 1991 concerning urban waste-water treatment. *Official Journal of the European Communities* 135: 40-52

Cowell, B. C., Dawes, C. J., Gardiner, W. E. and S. M. Scheda, 1987. The influence of whole lake aeration on the limnology of a hypereutrophic lake in central Florida. *Hydrobiologia* 148: 3-24

Dawidowicz, P. and M. Wielanier, 2004. Costs of predator avoidance reduce competitive ability of *Daphnia. Hydrobiologia* 526: 165-169

De Bernardi, R., 1984. Methods for the estimation of zooplankton abundance. In: Downing, J.A. and F.H. Rigler, eds. *A manual on methods for the assessment of secondary productivity in fresh waters.* Oxford: Blackwell Scientific Publications, 1984, pp. 59-83

De Mérona, B., Medes Dos Santos, G. and R. Gonçalves De Almeida, 2001. Short-term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. *Environmental Biology of Fishes* 60: 375-392

De Mott, W. R., 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina. Limnology and Oceanography* 27: 518-527

De Mott, W. R. and W. C. Kerfoot, 1982. Competition among cladocerans: Nature of the interaction between *Bosmina* and *Daphnia. Ecology* 63: 1949-1966

Dodson, S. I., 1974. Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. *Ecology* 55: 605-613

Dodson, S. I, 1991. Supplementary Material: Data Base and Literature for Dodson, S., 1992. Predicting crustacean zooplankton species richness. *Limnology and Oceanography* 37: 848-856

Dodson, S. I, 1992. Predicting crustacean zooplankton species richness. *Limnology and Oceanography* 37: 848-856

Dodson, S. I., Arnott, S. E. and K. L. Cottingham, 2000. The relationship in lake communities between primary productivity and species richness. *Ecology* 81: 2662-2679

Dodson, S. I., Lillie, R. A. and S. Will-Wolf, 2005. Land use, water chemistry, aquatic vegetation, and zooplankton community structure of shallow lakes. *Ecological Applications* 15: 1191-1198

Dodson, S. I., Everhart, W. R., Jandl, A. K. and S. J. Krauskopf, 2006. Effects of watershed land use and lake age on zooplankton species richness. *Hydrobiologia* 579: 393-399

Dodson, S. I., Newman, A. L., Will-Wolf, S., Alexander, M. L., Woodford, W. P. and S. Van Egeren, 2009. The relationship between zooplankton community structure and lake characteristics in temperate lakes (Northern Wisconsin, USA). *Journal of Plankton Research* 31: 93-100

Dray, S., Legendre, P. and P. R. Peres-Neto, 2006. Spatial modelling: A comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483-493

Driscoll, D. A., 2008. The frequency of metapopulations, metacommunities and nestedness in a fragmented landscape. *Oikos* 117: 297-309

Elmendorf, S. C. and S. P. Harrison, 2009. Temporal variability and nestedness in California grassland species composition. *Ecology* 90: 1492-1497

Erős, T., Heino, J., Schmera, D. and M. Rask, 2009. Characterising functional trait diversity and trait-environment relationships in fish assemblages of boreal lakes. *Freshwater Biology* 54: 1788-1803

ESRI, 2004. *ArcGIS 9.0.* Environmental Systems Research Institute Inc., Redlands

Facelli, J. M., Chesson, P. and N. Barnes, 2005. Differences in seed biology of annual plants in arid lands: A key ingredient to the storage effect. *Ecology* 86: 2998-3006

Fahd, K., Florencio, M., Keller, C. and L. Serrano, 2007. The effect of sampling scale on zooplankton community assessment and its implications for the conservation of temporary ponds in south-west Spain. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17: 175-193

Ferguson, A. J. D., Thompson, J. M. and C. S. Reynolds, 1982. Structure and dynamics of zooplankton communities maintained in closed systems, with special reference to the algal food supply. *Journal of Plankton Research* 4: 523-543

Ferrao-Filho, A. S., Azevedo, S. M. F. O. and W. R. DeMott, 2000. Effects of toxic and non-toxic cyanobacteria on the life history of tropical and temperate cladocerans. *Freshwater Biology* 45: 1-19

Feuchtmayr, H. and J. Grey, 2003. Effect of preparation and preservation procedures on carbon and nitrogen stable isotope determinations from zooplankton. *Rapid Communications in Mass Spectrometry* 17: 2605-2610

Fleishman, E. and D. D. Murphy, 1999. Patterns of nestedness in a Great Basin butterfly community. *Oecologia* 119: 133-139

Flynn, D. F. B. Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., Simpson, N., Mayfield, M. M. and F. DeClerk, 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12: 22-23

Fryer, G., 1985. Crustacean diversity in relation to the size of water bodies: Some facts and problems. *Freshwater Biology* 15: 347-361

Gaedeke, A. and U. Sömmer, 1986. The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. *Oecologia* 71: 25-28

Gaston, K. J. and J. I. Spicer, 2004. *Biodiversity: An Introduction.* 2nd ed. Oxford: Blackwell Science

Geller, W. and H. Müller, 1981. The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. *Oecologia* 49: 316-321

Gendron, R. P., 1987. Models and mechanisms of frequency-dependent predation. *The American Naturalist* 130: 603-623

George, D. G., 1981. Wind-induced water movements in the south basin of Windermere. *Freshwater Biology* 11: 37-60

George, D. G. and R. W. Edwards, 1976. Effect of wind on distribution of chlorophyll *a* and crustacean plankton in a shallow eutrophic reservoir. *Journal of Applied Ecology* 13: 667-690

George, D. G. and I. J. Winfield, 2000. Factors influencing the spatial distribution of zooplankton and fish in Loch Ness, UK. *Freshwater Biology* 43: 557-570

Gerten, D. and R. Adrian, 2002. Species-specific changes in the phenology and peak abundance of freshwater copepods in response to warm summers. *Freshwater Biology* 47: 2163-2173

Gliwicz, Z. M. and W. Lampert, 1990. Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. *Ecology* 71: 691-702

Green, A., J., Figuerola, J., Sánchez, M. I., 2002. Implications of waterbird ecology for the dispersal of aquatic organisms. *Acta Oecologia* 23: 177-189

Green, R. H. and G. L. Vascotto, 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. *Water Research* 12: 583-590

Grenney, W. J., Bella, D. A. and H. C. Curl, 1973. A theoretical approach to interspecific competition in phytoplankton communities. *The American Naturalist* 107: 405-425

Grey, J., Jones, I. and D. Sleep, 2001. Seasonal changes in the source of organic matter in the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. *Limnology and Oceanography* 46: 505-513

Guisande, C. and Z. M. Gliwicz, 1992. Egg size and clutch size in two *Daphnia* species grown at different food levels. *Journal of Plankton Research* 14: 997-1007

Gurney, R., 1933a. *British Freshwater Copepoda Volume I.* London

Gurney, R., 1933b. *British Freshwater Copepoda Volume III.* London

Håkanson, L., 2005. The importance of lake morphometry for the structure and function of lakes. *International Review of Hydrobiology* 90: 433-461

Halvorsen, G. and N. Gullestad, 1976. Freshwater Crustacea from some areas of Svalbard. *Archiv für Hydrobiologie* 78: 383-395

Hann, B. J. and L. Zrum, 1997. Littoral microcrustaceans (Cladocera, Copepoda) in a prairie coastal wetland: Seasonal abundance and community structure. *Hydrobiologia* 357: 37-52

Hardin, G., 1960. The competitive exclusion principle. *Science* 131: 1292-1297

Harding, J. P. and W. A. Smith, 1974. *A Key to the British Freshwater Cyclopoid and Calanoid Copepods.* 2 ed. Freshwater Biological Association, publication no. 18

Hart, R. C., 1990. Zooplankton distribution in relation to turbidity and related environmental gradients in a large subtropical reservoir: patterns and implications. *Freshwater Biology* 24: 241-263

Havel, J. E., Shurin, J. B. and J. R. Jones, 2002. Estimating dispersal from patterns of spread: spatial and local control of lake invasions. *Ecology* 83: 3306-3318

Havel, J. E. and J. B. Shurin, 2004. Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnology and Oceanography* 49: 1229-1238

Hawkins, P. R. and D. J. Griffiths, 1993. Artificial destratification of a small tropical reservoir – effects upon the phytoplankton. *Hydrobiologia* 254: 169-181

Heemsbergen, D. A., Berg, M. P., Loreau, M., Van Hal, J. R., Faber, J. H. and H. A. Verhoef, 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* 306: 1019-1020

Heino, J., Mykrä, H. and T. Muotka, 2009. Temporal variability of nestedness and idiosyncratic species in stream insect assemblages. *Diversity and Distributions* 15: 198-206

Henry, M., Stevens, H. and W. P. Carson, 2001. Phenological complementarity, species diversity, and ecosystem function. *Oikos* 92: 291-296

Heo, W. –M. and B. Kim, 2004. The effect of artificial destratification on phytoplankton in a reservoir. *Hydrobiologia* 524: 229-239

Hessen, D. O., 1985. Filtering structures and particle size selection in coexisting cladocera. Oecologia 66: 368-372

Hessen, D. O., Andersen, T. and A. Lyche, 1990. Carbon metabolism in a humic lake: Pool sizes and cycling through zooplankton. *Limnology and Oceanography* 35: 84-99

Hessen, D. O., Faafeng, B. A. and T. Andersen, 1995. Replacement of herbivore zooplankton species along gradients of ecosystem productivity and fish predation pressure. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 733-742

Hessen, D. O., Faafeng, B. A., Smoth, V. H., Bakkestuen, V. and B. Walseng, 2006. Extrinsic and intrinsic controls of zooplankton diversity in lakes. *Ecology* 87: 433-443

Hill, M. O. and O. Šmilauer, 2005. *TWINSPAN for Windows version 2.3*. Centre for Ecology and Hydrology and University of South Bohemia, Huntingdon and Ceské Budejovice.

Hobæk, A., Manca, M. and T. Andersen, 2002. Factors influencing species richness in lacustrine zooplankton. *Acta Oecologia* 23: 155-163

Hoffmann, M. D. and S. I. Dodson, 2005. Land use, primary productivity and lake areas as descriptors of zooplankton diversity. *Ecology* 86: 255-261

Holland, T. A. and D. G. Jenkins, 1998. Comparison of processes regulating zooplankton assemblages in new freshwater pools. *Hydrobiologia* 387-388: 207-214

Hooper, D. U. and P. M. Vitousek, 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277: 1302-1305

Horpila, J., Eloranta, P., Liljendahl-Nurminen, A., Niemistö, J. and Z. Pekcan-Hekim, 2009. Refuge availability and sequence of predators determine the seasonal succession of crustacean zooplankton in a clay-turbid lake. *Aquatic Ecology* 43: 91-103

Hoyle, B., 2000. Global and local change on the port-city waterfront. *Geographical Review* 90: 395-417

Hu, S.S. and A.J. Tessier 1995. Seasonal succession and the strength of intra- and interspecific competition in a *Daphnia* population. *Ecology* 76: 2278-2294

Hülsman, S., 2001. Reproductive potential of *Daphnia galeata* in relation to food conditions: implications of a changing size-structure of the population. *Hydrobiologia* 442: 241-252

Hutchinson, G. E., 1961. The paradox of the plankton. *The American Naturalist* 95: 137-145

Hutchinson, G. E., 1967. *A Treatise on Limnology*. New York: Wiley and Sons

Jardillier, L., Basset, M., Domaizon, I., Belan, A., Amblard, C., Richardot, M., and D. Debroas, 2004. Bottom-up and top-down control of bacterial community composition in the euphotic zone of a reservoir. *Aquatic Microbial Ecology* 35: 259-273

Jenkins, D. G. and M. D. Underwood, 1998. Zooplankton may not disperse readily in wind, rain, or waterfowl. *Hydrobiologia* 387-388: 15-21

Jiménez-Melero, R., Parra, G., Souissi, S. and F. Guerrero, 2007. Post-embryonic developmental plasticity of *Arctodiaptomus salinus* (Copepoda: Calanoida) at different temperatures. *Journal of Plankton Research* 29: 553-567

Jones, A. L., 2007. On the water's edge: developing cultural regeneration paradigms for urban waterfronts. In: Smith, M. K., ed. *Tourism, Culture and Regeneration*. Wallingford: CABI, 2007, pp143-150

Jones, R. I., Fulcher, A. S., Jayakody, J. K. U., Laybourn-Parry, J., Shine, A. J., Walton, M. C. and J. M. Young, 1995. The horizontal distribution of plankton in a deep, oligotrophic lake – Loch Ness, Scotland. *Freshwater Biology* 33: 161-170

Jüttner, I., Chimonides, P. J. and S. J. Ormerod, 2009. Using diatoms as quality indicators for a newly-formed urban lake and its catchment. *Ecological Monitoring and Assessment* In press

Kalikhman, I., Walline, P. and M. Gophen, 1992. Simultaneous patterns of temperature, oxygen, zooplankton and fish distribution in Lake Kinneret, Israel. *Freshwater Biology* 28: 337-347

Karatayev, A. Y., Burlakova, L. E. and S. I. Dodson, 2005. Community analysis of Belarusian lakes: relationship of species diversity to morphology, hydrology and land use. *Journal of Plankton Research* 27: 1045-1053

Karlsson, J. and C. Säwström, 2009. Benthic algae support zooplankton growth during winter in a clear-water lake. *Oikos* 118: 539-544

Keitel, J. M. and J. M. Chase, 2004. Disturbance, predator and resource interactions alter container community composition. *Ecology* 85: 2085-2093

Korhola, A., 1999. Distribution patterns of Cladocera in subarctic Fennoscanadian lakes and their potential in environmental reconstruction. *Ecography* 22: 357-373

Korhola, A., Orlander, H. and T. Blom, 2000. Cladoceran and chironomid assemblages as quantitative indicators of water depth in subarctic Fennoscanadian lakes. *Journal of Paleolimnology* 24: 43-54

Kurmayer, R., 2001. Competitive ability of *Daphnia* under dominance of non-toxic filamentous cyanobactera. *Hydrobiologia* 442: 279-289

Lageren, R., leberfinger, K. and J. A. E. Stenson, 2008. Seasonal autogenic variation in diel vertical migration of *Chaoborus flavicans* and its effect on depth-selection behaviour of other zooplankton. *Limnology and Oceanography* 53: 1083-1092

Lampert, W. and U. Sömmer, 2007. *Limnoecology*. Oxford: Oxford University Press

Legendre, P., 1993. Spatial autocorrelation: Trouble or new paradigm? *Ecology* 74: 1659-1673

Legendre, P and L. Legendre, 1998. *Numerical Ecology*. Elsevier, Amsterdam, The Netherlands

Legendre, P. and M-J. Fortin, 1989. Spatial and ecological analysis. *Vegetatio* 80: 107-138

Legendre, P., Borcard, D. and P. R. Peres-Neto, 2005. Analysing beta diversity: Partitioning the spatial variation of community composition data. *Ecological Monographs* 75: 435-450

Leibold, M. A., 1991. Trophic interactions and habitat segregation between competing *Daphnia* species. *Oecologia* 86: 510-520

Levin, S. A. and L. A. Segel, 1982. Models of influence of predation on aspect diversity in prey populations. *Journal of Mathematical Biology* 14: 253-284

Lewis, D. M., Elliott, A., Brookes, J. D., Irish, A. E., Lambert, M. F. and C. S. Reynolds, 2003. Modelling the effects of artificial mixing and copper sulphate dosing on phytoplankton in an Australian reservoir. *Lakes and Reservoirs: Research and Management* 8: 31-40

Lueke, C. and W. J. O'Brien, 1981. Phototoxicity and fish predation: selective factors in color morphs in *Heterocope*. *Limnology and Oceanography* 26: 454-460

MacArthur, R. H. and E. O. Wilson, 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press

Maier, G., 1989. The seasonal cycle of *Thermocyclops crassus* (Fischer 1853) (Copepoda: Cyclopoida) in a shallow, eutrophic lake. *Hydrobiologia* 178: 43-58

Maier, G., 1993. An example of niche partitioning in three coexisting freshwater cyclopoid copepods. *Journal of Plankton Research* 15: 1097-1102

Maguire, B., 1963. The passive dispersal of small aquatic organisms and their colonisation of isolated bodies of water. *Ecological Monographs* 33: 161-185

Maguire, C. M., and J. Grey, 2006. Determination of zooplankton dietary shift following a zebra mussel invasions, as indicated by stable isotope analysis. *Freshwater Biology* 51: 1310-1319

Malone, B. J. and D. J. McQueen, 1983. Horizontal patchiness in zooplankton populations in two Ontario kettle lakes. *Hyrdobiologia* 99: 101-124

Mangalo, H., 1987. Variation in the intersetular distance on filter setae of *Simocephalus vetulus* (O. F. Muller) (Crustacea: Cladocera). *Freshwater Biology* 17: 169-176

Mason, N. W. H., MacGillivray, K., Steel, J. B. and W. J. Barstow, 2003. An index of functional diversity. *Journal of Vegetation Science* 14: 571-578

Matsumura-Tundisi, T. and J. G. Tundisi. eds, 2002. *Zooplankton Diversity Change in Man-Made Lakes. Case Study of the Bara Bonita Reservoir, Sp, Brazil.* 4th International Conference on Reservoir Limnology of Water

Matthews, B. and A. Mazumder, 2006. Habitat specialisation and the exploitation of allochthonous carbon by zooplankton. *Ecology* 87: 2800-2812

Matveev, V. F. and E. G. Balseiro, 1990. Contrasting responses of two cladocerans to changes in the nutritional value of nannoplankton. *Freshwater Biology* 23: 197-204

Matveev, V. F. and L. K. Matveeva, 2005. Seasonal succession and long-term stability of pelagic community in a productive reservoir. *Marine and Freshwater Research* 58: 1137-1149

Met. Office, 2008. *Cardiff 1971-2000 Climate Averages.* [online]. Available at: http://www.metoffice.gov.uk/climate/uk/averages/19712000/sites/cardiff.html. [Accessed 15 October 2008]

McCauley, E., 1984. The estimation of the abundance and biomass of zooplankton in samples. In: Downing, J.A. and F.H. Rigler, eds. *A manual on methods for the assessment of secondary productivity in fresh waters.* Oxford: Blackwell Scientific Publications, 1984, pp. 228-261

McGrady-Steed, J., Harris, P. M. and P. J. Morin, 1997. Biodiversity regulates ecosystem predictability. *Nature* 390: 162-165

McQueen, D. J., Post, J. R. and E. J. Mills, 1986. Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fish and Aquatic Sciences* 43: 1571-1581

Montiel-Martínez, A., Ciros-Pérez, J., Ortega-Mayagoita, E. and M. Elías-Gutiérrez, 2008. Morphological, ecological, reproductive and molecular evidence for *Leptodiaptomus garciai* (Osorio-Tafall 1942) as a valid endemic species. *Journal of Plankton Research* 30: 1079-1093

Mulder, C. P. H., Uliassi, D. D. and D. F. Doak, 2001. Physical stress and diversity-productivity relationships: The role of positive interactions. *Proceedings of the National Academy of Science USA* 98: 6704-6708

Müller, R. and P. Stadelmann, 2004. Fish habitat requirements as the basis for rehabilitation of eutrophic lakes by oxygenation. *Fisheries Management and Ecology* 11: 251-260

Müller-Navarra, D. and W. Lampert, 1996. Seasonal patterns of food limitation in *Daphnia galeata*: separating food quantity and food quality effects. *Journal of Plankton Research* 18: 1137-1157

Nadin-Hurley, C. M. and A. Duncan, 1976. Comparison of daphnid gut particles with sestonic particles present in two Thames Valley reservoirs throughout 1970 and 1971. *Freshwater Biology* 6: 109-123

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H. and R. M. Woodfin, 1994. Declining biodiversity can alter performance of ecosystems. *Nature* 368: 734-737

Naeem, S., and S. Li, 1997. Biodiversity enhances ecosystem stability. *Nature* 390: 507-509

Naeslund, B. and J. Norberg, 2006. Ecosystem consequences of the regional species pool. *Oikos* 115: 504-512

Norton, J., Lewis, J. W. and D. Rollinson, 2004. Temporal and spatial patterns of nestedness in eel macroparasite communities. *Parasitology* 129: 203-211

Oberholster, P. J., Botha, A. –M. and T. E. Cloete, 2007. Ecological implications of artificial mixing and bottom-sediment removal for a shallow urban lake, Lake Sheldon, Colorado. *Lakes and Reservoirs Research and Management* 12: 73-86

O'Brien, W. J., Barfield, M., Bettez, N. D., Gettel, G. M., Hershey, A. E., McDonald, M. E., Miller, M. C., Mooers, H., Pastor, J., Richards, C. and J. Schuldt, 2004. Physical, chemical, and biotic effects on arctic zooplankton communities and diversity. *Limnology and Oceanography* 49: 1250-1261

Osenberg, C. W., Sarnelle, O., Cooper, S. D. and R. D. Holt, 1999. Resolving ecological questions through meta-analysis: Goals, metrics, and models. *Ecology* 80: 1105-1117

Pace, M. L., Cole, J. J., Carpenter, s. R., Kitchell, J. F., Hodgson, J. R., Van de Bogert, M. C., Bade, D. L., Kritzberg, E. S. and D. Bastviken, 2004. Whole-lake carbon-13 additions reveal terrestrial support for aquatic food webs. *Nature* 427: 240-243

Paterson, B. D. and W. Atmar, 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* 28: 65-82

Pennington, J. T. and M. G. Hadfield, 1989. A simple nontoxic method for the decalcification of living invertebrate larvae. *Journal of Experimental Marine Biology and Ecology* 130: 1-7

Perhar, G. and G. B. Arhonditis, 2009. The effects of seston food quality on planktonic food web patterns. *Ecological Modelling* 220: 805-820

Petchey, O. L. and K. J. Gaston, 2009. Effects on ecosystem resilience of biodiversity, extinction, and the structure of regional species pools. *Theoretical Ecology* 2: 177-187

Peterston Holm, N., Ganf, G. G. and J. Shapiro, 1983. Feeding and assimilation rates in *Daphnia pulex* fed *Aphanizomenon flos-aquae. Limnology and Oceanography* 28: 677-687

Pinel-Alloul, B., 1995. Spatial heterogeneity as a multiscale characteristic of zooplankton community. *Hydrobiologia* 300/301: 17-42

Pinel-Alloul, B. and D. Pont, 1991. Spatial distribution patterns in freshwater macrozooplankton. *Canadian Journal of Zoology* 69: 1557-1570

Poff, N. L., 1997. Landscape filters and species traits: Towards mechanistic understanding and predation in stream ecology. *Journal of the North American Benthological Society* 16: 391-409

Pollard, A. I. and L. L. Yuan, 2009. Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity- based measures. *Freshwater Biology* In press

Porter, K. G., Feig, Y. S. and E. S. Vetter, 1983. Morphology, flow regimes, and filtering rates of *Daphnia*, *Ceriodaphnia*, and *Bosmina* fed natural bacteria. *Oecologia* 58: 156-163

Proctor, V. W., 1964. Viability of crustacean eggs recovered from ducks. *Ecology* 45: 656-658

Repka, S., Veselá, S., Weber, A. and K. Schwenk, 1999. Plasticity in filtering screens of *Daphnia* cucullata x galeata hybrids and parental species at two food concentrations. *Oecologia* 120: 485-491

Rettig, J.E., Schuman, L.S. and J.K. McCloskey, 2006. Seasonal patterns of abundance: do zooplankton in small ponds do the same thing every spring-summer? *Hydrobiologia* 556: 193-207

Reynolds, C. S., 2001. Emergence in pelagic communities. *Scientia Marina* 65 (supplement 2): 5-30

Richman, S. and S. I. Dodson, 1983. The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus. Limnology and Oceanography* 28: 948-956

Richardson, W. B., 1992. Microcrustacea in flowing water – experimental analysis of washout times and a field-test. *Freshwater Biology* 28: 217-230

Richerson, P. J., Armstrong, R. and C. R. Goldman, 1970. Contemperaneous Disequilibrium: a new hypothesis to explain the 'Paradox of the Plankton'. *Proceedings of the National Academy of Sciences* 67: 1710-1714

Richerson, P. J., Powell, T. M., Leigh-Abbott, M. R. and J. A. Coil, 1978. Spatial heterogeneity in a closed basin. In *Spatial Pattern in Plankton Communities*. Steele, J. H. (ed.). *Mar Sci.* (Plenum) 3: 239-276

Riggs, M. R., Haroldson, K. J. and M. A. Hanson, 2008. Analysis of covariance modles for data from observational field studies. *Journal of Wildlife Management* 72: 34-43

Rodrgíuez-Girones, M. A. and L. Santamaría, 2006. A new algorithm to calculate the nestedness temperature of presence-absence matrices. *Journal of Biogeography* 33: 924-935

Romare, P., Schindler, D. E., Scheuerell, M. D., Scheuerell, J. M., Litt, A. H. and J. H. Shephard, 2005. Variation in spatial and temporal gradients in zooplankton spring development: The effect of climatic factors. *Freshwater Biology* 50: 1007-1021

Rosenzweig, M. L., 1991. Habitat selection and population interactions: The search for mechanism. *The American Naturalist* 137 (suppl.): 5-28

Rothaupt, K. O., 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. *Nature* 333: 660-662

Salonen, K. and J. Sarvala, 1980. The effects of different preservation methods on the carbon content of *Megacyclops gigas*. *Hydrobiologia* 72: 281-285

Sarvala, J., Helminen, H., Saarikari, V., Salonen, S. and V. Kristiina, 1998. Relations between planktivorous fish abundance, zooplankton and phytoplankton in three lakes of differing productivity. *Hydrobiologia* 363: 81-95

Schalau, K., Rinke, K., Straile, D. and F. Peeters, 2007. Temperature is a key factor explaining interannual variability of *Daphnia* development in spring: a modelling study. *Oecologia* 157: 531-543

Scheffer, M., Rinaldi, S., Huisman, J. and F. J. Weissing, 2003. Why plankton communities have no equilibrium: solutions to the paradox. *Hydrobiologia* 419: 9-18

Scourfield, D. J. and J. P. Harding, 1994. *A key to the species of freshwater cladocera*. Freshwater Biological Association

Shaw, M. A. and J. R. M. Kelso, 1992. Environmental factors influencing zooplankton species composition of lakes in north-central Ontario, Canada. *Hydrobiologia* 241: 141-154

Shurin, J. B., 2001. Interactive effects of predation and dispersal on zooplankton communities. *Ecology* 82: 3404-3416

Shurin, J. B. and E. G. Allen, 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. *The American Naturalist* 158: 624-637

Shurin, J. B., Arnott, S. E., Hillebrand, H., Langmuir, A., Pinel-Alloul, B., Winder, M. and N. D. Yan, 2007. Diversity-stability relationship varies with latitude in zooplankton. *Ecology Letters* 10: 127-134

Smith, V. H., 1983. Low nitrogen to phosphorous ratios favour dominance by blue-green algae in lake phytoplankton. *Science* 221: 669-671

Sömmer, U. Z., Gliwicz, M., Lampert, W. and A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh water. *Archiv für Hydrobiologie* 106: 433-471

Sömmer, U., 1996. Plankton ecology: The past two decades of progress. Naturwissenschaften 83: 293-301

Southwood, T. R. E., 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337-365

Speckman, S. G., Piatt, J. F., Minte-Vera, C. V. and J. K. Parrish, 2005. Parallel structure among environmental gradients and three trophic levels in a subarctic estuary. *Progress in Oceanography* 66: 25-65

Statzner, B., Hildrew, A. H. and V. H. Resh, 2001. Species traits and environmental constraints: Entomological research and the history of ecological theory. *Annual Review of Entomology* 46: 291-316

Steinberg, C., 1983. Effects of artificial destratification on the phytoplankton populations in a small lake. *Journal of Plankton Research* 5: 855-864

Stevens, R. D., Cox, S. B., Strauss, R. E. and M. R. Willig, 2003. Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal gradients. *Ecology Letters* 6: 1099-1108

Stockwell, J.D. and W.G. Sprules, 1995. Spatial and temporal patterns of zooplankton biomass in Lake Erie. *ICES Journal of Marine Science* 52: 557-564

Strøm, K. M., 1946. The ecological niche. *Nature* 157: 375

Tadonléke, R. D. and T. Sime-Ngando, 2000. Rates of growth and microbial grazing mortality of phytoplankton in a recent artificial lake. *Aquatic Microbial Ecology* 22: 301-313

Talling, J. F., 2003. Phytoplankton-zooplankton seasonal timing and the 'clear-water phase' in some English lakes. *Freshwater Biology* 48: 39-52

Tavernini, S., Primicerio, R. and G. Rossetti, 2009. Zooplankton assembly in mountain lentic waters is primarily driven by local processes. *Acta Oecologica* 35: 22-31

Taylor, B. E., Leeper, D. A., McClure, M. A. and A. E. DeBiase, 1999. Carolina Bays: Ecology of aquatic invertebrates and perspectives on conservation. In: Batzer, D. P., rader, R. B. and S. A. Wissinger (eds). *Invertebrates in Freshwater Wetlands of North America: Ecology and Management.* New York: John Wiley and Sons, 1991, pp. 167-196

Taylor, C. M. and M. L. Warren Jr., 2001. Dynamics in species composition of stream fish assemblages: Environmental variability and nested subsets. *Ecology* 82: 23-30

Tessier, A. J., Leibold, M. A. and J. Tsao, 2000. A fundamental trade-off in resource exploitation and consequences to plankton communities. *Ecology* 81: 826-841

Tessier, A. J. and J. Welser, 2006. Cladoceran assemblages, seasonal succession and the importance of a hypolimnetic refuge. *Freshwater Biology* 25: 85-93

Thackeray, S. J., 2007. Crustacean zooplankton species richness and productivity: to what extent do the conclusions depend on the choice of metrics used? *Oikos* 116: 614-628

Thackeray, S. J., George, D. G., Jones, R. I. and I. J. Winfield, 2004. Quantitative analysis of the importance of wind-induced circulation for the spatial structuring of planktonic populations. *Freshwater Biology* 49: 1091-1102

Thornton, K. W., Kimmel, B. and F. E. Payne, 1980. *Reservoir Limnology: Ecological Perspectives.* New York: Wiley

Thorp, J. H. and A. P. Covich (eds), 2001. *Ecology and Classification of North American Freshwater Invertebrates.* London: Academic Press

Tilman, D., Wedin, D. and J. Knops, 1996. Productivity and sustainability influence by biodiversity in grassland ecosystems. *Nature* 379: 718-720

Tilman, D., Naeem, S., Knops, J., Reich, P., Seiman, E., Wedin, D., Ritchie, M. and J. Lawton, 1997. Biodiversity and ecosystem properties. *Science* 278: 1866-1867

Tilman, D., 2001. Functional Diversity. In: *Encyclopedia of Biodiversity* (ed. Levin, S. A.). San Diego: Academic Press, pp 109-120

Townsend, C. R. and A. G. Hildrew, 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology* 31: 265-275

Vakkilainen, K., Kairesalo, T., Heitala, J., Balaya, D. M., Bécares, E., Van de Bund, W. J., Van Donk, E., Fernández-Aláez, M., Gyllström, M., Hansson, L. –A., Miracle, M. R., Moss, B., Romo, S., Rueda, J. and D. Stephen, 2004. Response of zooplankton to nutrient enrichment and fish in shallow lakes: a pan-European mesocosm experiment. *Freshwater Biology* 49: 1619-1632

Vanni, M. and J. Tempte, 1990. Seasonal patterns of grazing and nutrient limitations of phytoplankton in a eutrophic lake. *Limnology and Oceanography* 35: 697-709

Vaughan, I. P., Newberry, C., Hall, D. J., Liggett, J. S. and S. J. Ormerod, 2008. Evaluating large-scale effects of *Bacillus thuringiensis* var. *israelensis* on non-biting midges (Chironomidae) in a eutrophic urban lake. *Freshwater Biology* 53: 2117-2128

Vijverberg, J. and M. Vos, 2006. Predator-released compounds, ambient temperature and competitive exclusion among differently sized *Daphnia* species. *Freshwater Biology* 51: 756-767

Vyshkvartzeva, N. V., 1994. *Senecella siberica* n. sp. and the position of the genus *Senecella* in Calanoida classification. *Hydrobiologia* 292/293: 113-121

Watson, S. B., McCauley, E. and J. A. Downing, 1997. Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. *Limnology and Oceanography* 42: 487-495

Wetzel 2001. *Limnology. Lake and river ecosystems.* 3 ed. San Diego: Elsevier Science, p. 1006

Whiteside, M.C., Williams, J.B. and C.P. White, 1978. Seasonal abundance and pattern of Chydorid Cladocera in mud and vegetative habitats. *Ecology* 59: 1177-1188

Whittaker, R. H., 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1-80

Wissinger, S. A., Bohonak, A. J., Whiteman, H. H. and W. S. Brown, 1999. Subalpine wetlands in Colorado: Habitat permanence, salamander predation, and invertebrate communities. In: Batzer, D. P., rader, R. B. and S. A. Wissinger (eds). *Invertebrates in Freshwater Wetlands of North America: Ecology and Management*. New York: John Wiley and Sons, 1991, pp. 757-790

Wolfinbarger, W.C., 1999. Influences of biotic and abiotic factors on seasonal succession of zooplankton in Hugo Reservoir, Oklahoma, U.S.A. *Hydrobiologia* 400:13-31

Worthen, W. B., Jones, M. T. and R. M. Jetton, 1998. Community structure and environmental stress: Dessication promotes nestedness in mycophagous fly communities. *Oikos* 81: 45-54

Wright, D. H. and J. H. Reeves, 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia* 92: 416-428

Wright, D. H., Patterson, B. D., Mikkelson, G. M., Cutler, A. and W. Atmar, 1998. A comparative analysis of nested subset patterns of species composition. *Oecologia* 113: 1-20

Yacobi, Y. Z., Kalikhman, I., Gophen, M. and P. Walline, 1993. The spatial distribution of temperature, oxygen, plankton and fish determined simultaneously in Lake Kinneret, Israel. *Journal of Plankton Research* 15: 589-601

Zak., J. C., Willig, M. R., Moorhead, D. L. and H. G. Wildman, 1994. Functional diversity of microbial communities. *Soil Biology and Biochemistry* 26: 1101-1108

Appendices

Appendix 1

Water bodies included in the meta-analysis (Chapter 2) listed in order of lake surface area

Lake	Lake area (m2)	Natural/Artificial	Residence time (days)	Pelagic crustacean species	Maximum depth (m)	Mean depth (m)	Conductivity (uS)	Primary productivity (mgC/m2/day)	Elevation (m)	Latitude (degrees N)	Longitude (degrees W)	Distance to nearest water body (km)	Waterbodies within 20km	References
Superior, USA/Canada	82400000000	N	69715	30	406	148	79	200	185	47.5	88	0.12	21863	2
Victoria, Tanzania/Uganda/Kenya	68000000000	N	8395	14	83	40			1133	-1	-33			40
Michigan, USA	58000000000	N	36135	32	281	84	226	550	180	44	87	0.12	633	2, 30
Baikal, Russia	31500000000	N	120450	19	1637	758		75	456	53	-108.2			11, 62
Great Slave, Canada	28600000000	N	2920	19	613	73	215	11	159	62	113	0.12	8805	11
Erie, USA/Canada	25800000000	N	949	31	64	17	242	696	178	42	81	0.12	105	2
Winnipeg, Canada	23700000000	N	1277.5	25	38	12	205	66	219	52	97	0.12	301	11
Kariba, Zambia/Zimbabwe	5500000000	A	1095	16	120	29.2	100		485	-17	-28			36
Nasser, Egypt	5237000000	A		10	180	25.2	239		183	22	-31			16, 33
Rybinsk, Russia	4550000000	A		17	28	5.6		242	102.4	58	-38			11, 28
Balaton, Hungary	596000000	N	730	10	11.2	3.2	660	72.29	104.8	46	-17			11, 45, 54, 63
Leman, Switzerland	582000000	N	4161	17	310	154.4			372	46	-6			11
Tahoe, USA	488000000	N	237250	12	404	313	92	219	1914	39.1	120.1	0.25	87	21
Constance, Germany	475000000	N	1569.5	16	254	90			395	47	-9			11
Texoma, USA	380000000	A		14	30	9.7	1600	700	187	33.8	96.7	0.5	113	9
Neusiedlersee, Austria/Hungary	315000000	N	1569.5	17	1.8	1.3	1100		115.4	47	-16			17, 52
Maggiore, Italy	212000000	N	1460	13	372	177.4			193	45	-8			11
Oneida, USA	207000000	N		17	16.8	6.8	298	822	112	43.2	75.9	2.25	37	11
Kinneret, Israel	168000000	N	1825	12	43	25.6			-209	32	-35			11
Matano, Indonesia	164000000	N	36500	2	590		260		382	-2.28	-121.19			50
Clear, USA	162000000	N		12	9	6.5	256	440	404	39	122.8	0.25	20	20, 60
George, USA	100000000	N		7	58	8		120	98	43	73			30
Memphremagog, USA/Canada	90000000	N	620.5	15	117	17.2	130	197	208	45.1	72.3	0.25	57	44
Washington, USA	87600000	N	876	17	65.2	32.9	90	263	6.3	47.6	122.4	1.75	46	14, 15
Crater, USA	48000000	N		3	589	325	113	142	1882	42.9	122.1	14	4	11, 32
Prado Reservoir, Columbia	40000000	A	53.3	8	90	45	55.8		370	3	74			22
Mendota, USA	39400000	N		17	25.3	12.4	320	938	259	43.1	88.4	1.25	32	11
Bielersee, Switzerland	39000000	N	55		74	30			429	47	-7			51
Myvatn, Iceland	37300000	N		6	4.5	2.5			288	65	17.4			11
Cranberry, USA	28000000	A		5	13	5		391.2	460	44	74			30
Erken, Sweden	22900000	N		17	21	9				59	18			11
Tjeukemeer, Netherlands	21000000	N	62.05	13	1.5	1	700	822	-1	52.8	-5	2.75	63	29, 42
Ersom, USA	17300000			12										11
Trout, USA	16100000	N		17	35.7	14.6	85	419	496	46	89.7	0.5	441	11
Windermere, UK	14800000	N	142.5	11	67				40	54	2			11, 18, 19
Itans Reservoir, Brazil	13400000	A		12	23	5.1	500							52
Boquerao de Parelhas, Brazil	13300000	A		8	29	5.8	800							52
Suwa, Japan	13000000	N	48		6.4	4.1			759	36	-138			51
Steinsfjorden, Norway	12800000	N		15						60	-10			11
Gull, USA	8270000	N		17	33.5	12.4	335	280	270	42.4	85.4	0.25	128	30, 31, 39
Gargalheiras Reservoir, Brazil	7800000	A		13	25	4.7	800			-6	36			52
Cruzeta Reservoir, Brazil	7490000	A	273	9	14.5	2.7	600			-6	38			52
Mikolajskie, Poland	4990000	N		9										11
Stechlin, Germany	4250000	N		16										11
Thonotosassa, USA	3450000	N		9	4.9	3.5		1250	11	28	82.1	2.25	184	8, 61
D'Endine, Italy	2340000	N		9										11
Cardiff Bay, UK	2000000	A	5	13	13.4	4	364			51	3	4.25	89	37
Mergozzo, Italy	1820000	N		14	73	45			195	45	-8			11
Toolik, USA	1490000	N		8	25	7	63	38	725	68.6	149.6	0.125	285	11, 38
Saidenbach, Germany	1460000	A	220	6	45	15			439	50	-13			24, 25
Wingra, USA	1400000			15	6.4	2.7	574	945	263	43.1	89.4	0.75	20	11
Haussee, Germany	1360000	N		12										11
Esthwaite, UK	1000000	N		10	15.5	6.4			65.3	54	2			11

Appendix 1 continued

Lake	Lake area (m2)	Natural/Artificial	Residence time (days)	Pelagic crustacean species	Maximum depth (m)	Mean depth (m)	Conductivity (uS)	Primary productivity (mgC/m2/day)	Elevation (m)	Latitude (degrees N)	Longitude (degrees W)	Distance to nearest water body (km)	Waterbodies within 20km	References
Schohsee, Germany	830000	N		18										11
Sparkling, USA	815000	N		16	20	10.9	72	367	499	46	89.7	0.25	195	11
Latnjajaure, Sweden	730000	N		6										11
Imikpuk, USA	610000	N		7	2.8	2.1		23	0.5	71.3	156.7	0.375	660	6
Char, USA	526000			3	27.5	10.2	222	11.2	34	74.7	94.8	0.875	70	48
Pavin, France	440000	N			98	52			1197	45	-2			51
Crystal, USA	367000	N		14	20.47	10.4	14	408	506	46	89.6	0.25	208	11
Reservoir de la Sep, France	330000	A		6	37	14		1320.76	500	46	-3			53, 56, 57
Heiligensee, Germany	320000	N		22										11
Ogelthorpe, USA	300000	A		10	8.5	2.5	60	370	190	33.8	83.2	0.5	44	43
Lake 223, Canada	273000	N		16	14.4	7.2		124	405	49.7	93.7	0.12	199	11
Monterosi, Italy	271000	N		5										11
Eunice, USA	182000	N		9	42	15.8	21.1		480	49.3	122.6	0.62	37	11
Little Rock, USA	182000	A		16	10.3	3.5	12.6	343	500	46	89.7	0.25	208	11
Port-Bielh, France	165000	N		5										11
V.Finstertaler, Austria	157000	A		4										11
Long, USA	158000	N		4	7.5	1.89		4.24	3209	40.1	105.6	1.75	61	11
Mirror, USA	150000			10	10.9	5.6	31	129	214	43.9	71.7	3	24	34
Piburger See, Austria	134000	N	1000	4	25	14			913	47	-10			46
Marion, USA	133000	A		10	7	2.4	26	22	305	49.3	122.6	1.62	33	11
Gwendoline, Canada	130000	N		10	27	13.4	13.2	157	522	49.3	122.6	0.37	38	41
St George, Canada	103000	N		15	16.2	6.04	350	1500	295	44	79.4	0.5	22	35, 47
Linsley Pond, USA	94000	N		8	14.8	6.7		685	8.9	41.3	72.7	0.25	36	4
Frain's, USA	83000	N		12	9.5	3.4			253	42.3	83.6	0.25	26	1, 26, 49
Santo Parmense, Italy	80000	N		7										11
Holon, USA	60000			6										11
Lawrence, Usa	49600			14	12.5	5.9	450	99	276	42.4	85.4	2	127	59
Vechten, Netherlands	47100	A		6	12	6		2.76		52	-5			23
Peter, USA	24000	N		11	19.3	8.3	30	284	522	46.2	89.2	0.75	169	5, 27
La Caldera, Spain	23000	N		4	12	4.7		9.4	3040	37.1	3.3	1	14	11
Bavarian Sausage Pond, USA	16000	N		10	1.5	0.7	400		301	43	89.5	2.75	19	7
Wintergreen, USA	15000	N		11	6.3	3.5		1011	274	42.4	85.4	0.37	116	55
Leechmere, UK	14000	N		7	1.7	0.97	30	20	3097	38.8	107.1	2.62	31	12
Miller Woods No. (new) 22, USA	9830			3	9	2	0.21	339	187	46.2	87.1	0.75	7	11
Tuesday Bog, USA	7900	N		9	18.5	10	18.5	368	522	50.3	89.2	0.75	169	5
Dynamite, USA	6000	N		9	2.5	2			209	43	87.9	0.75	5	58
Mexican Cut L1	4980			7	4.5	2.1	33	3.5	3433	42.4	107.1	0.75	35	11
Little Bullhead Pond, USA	3720			14	2	1.31			21.5	40.6	71.6	0.75	58	3
Pantano Pallone, Italy	2480	N		10										11
Poltruba, Czech Republic	1800	N		12										11
Mexican Cut L12	1700			7	3.4	1.4	15	1	3432	40	107.1	0.75	35	11
NARL IBP Pond A+B, USA	714			8	0.4	0.3		1.6	5	42.5	156.7	0.25	793	10, 11
Kendal II, USA	707			3	0.6	0.3		307	44.1	71.3	1.5	10		11
Tu-Vu 11, USA	617			3	0.1	0.04	245		307	78.5	117.2	6.75	5	13
NARL IBP Pond D, USA	500			8	0.4	0.3		1.9	5	38.7	156.7	0.25	793	10, 11
Velka Arazim	382			10										11
NARL IBP Pond C, USA	332			8	0.4	0.3		1.4	5	71.3	156.7	0.25	793	10, 11
Sughereto, Italy	99.4	N		8										11
Riessen Pond	35			4	0.9	0.4			307	45.3	122	0.5	11	11
Miramar 1	20			3	0.15	0.06	88		307	37.2	117.2	6.25	11	13
Pargrunden, Finland	8	N		5										11
Furuskar, Finland	6	N		4										11
Martin Pond	4			1	0.23	0.18	850		264	43	89.4	0.75	20	11

References

1. Allan, J. D., 1977. An analysis of seasonal dynamics of a mixed population of *Daphnia* and the associated cladoceran community. *Freshwater Biology* 7: 505-512
2. Beeton, A. M., 1965. Eutrophication of the St. Lawrence Great Lakes. *Limnology and Oceanography* 10: 240-254
3. Black, R. W. II and N. G. Hairston Jr., 1988. Predator driven changes in community structure. *Oecologia* 77: 468-479
4. Brugham, R. B., 1978. Human disturbance and the historical development of Linsley Pond. *Ecology* 59: 19-36
5. Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Cochran, P. A., Elser, J. J., Elser, M. M., Lodge, D. M., Kretchmer, K. and X. He, 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68: 1863-1876
6. Comita, G. W., 1956. A study of a calanoid copepod populaton in an arctic lake. *Ecology* 37: 576-591
7. Cooper, S. D. and D. W. Smith, 1982. Competition, predation and the relative abundances of two species of *Daphnia*. *Journal of Plankton Research* 4: 859-879
8. Cowell, B. C., Dye, C. W. and R. C. Adams, 1975. A synoptic study of the limnology of Lake Thonotosassa, Florida. Part I. Effects of primary sewage and citrus wastes. *Hydrobiologia* 46: 301-345
9. Dirnberger, J. M. and S. T. Threlkeld, 1986. Advective effects of a reservoir flood on zooplankton abundance and dispersion. *Freshwater Biology* 16: 387-396
10. Dodson, S. I., 1979. Body size patterns in arctic and temperate zooplankton. *Limnology and Oceanography* 24: 940-949
11. Dodson, S. I, 1991. Supplementary Material: Data Base and Literature for Dodson, S., 1992. Predicting crustacean zooplankton species richness. *Limnology and Oceanography* 37: 848-856
12. Dodson, S. I, 1992. Predicting crustacean zooplankton species richness. *Limnology and Oceanography* 37: 848-856

13. Ebert, T. A. and M. L. Balko, 1987. Temporary pools as islands in space and time: the biota of vernal pools in San Diego, Southern California, USA. *Archiv für Hydrobiolgie* 110: 101-123

14. Edmonson, W. T. and J. T. Lehman, 1981. The effect of changes in the nutrient income on the condition of Lake Washington. *Limnology and Oceanography* 26: 1-29

15. Edmonson, W. T. and A. H. Litt, 1982. *Daphnia* in Lake Washington. *Limnology and Oceanography* 27: 272-293

16. El-Shabrawy, G. M. and H. J. Dumont, 2003. Spatial and seasonal variation of the zooplankton in the coastal zone and main khors of Lake Nasser (Egypt). *Hydrobiologia* 491: 119-132

17. Forro, L. and H. Metz, 1987. Observations on the zooplankton in the reed belt area of Neusiedlersee. *Hydrobiologia* 145: 299-307

18. George, D. G., Talling, J. F. and E. Rigg, 2000. Factors influencing the temporal coherence of five lakes in the English Lake District. *Freshwater Biology* 43: 449-461

19. George, D. G., Maberly, S. C. and D. P. Hewitt, 2004. The influence of the North Atlantic Oscillation on the physical, chemical and biological characteristics of four lakes in the English Lake District. *Freshwater Biology* 49: 760-774

20. Goldman, C. R. and R. G. Wetzel, 1963. A study of the primary productivity of Clear Lake, Lake County, California. *Ecology* 44: 283-294

21. Goldman, C. R., 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. *Limnology and Oceanography* 33: 1321-1333

22. Guevera, G., Lozano, P., Reinoso, G. and F. Villa, 2008. Horizontal and seasonal patterns of tropical zooplankton from the eutrophic Prado Reservoir (Colombia). *Limnologica* 39: 128-139

23. Gulati, R. D., Siewertsen, K. and G. Postma, 1982. The zooplankton: its community structure, food and feeding, and role in the ecosystem of Lake Vechten. *Hydrobiologia* 95: 127-163

24. Horn, W. and H. Horn, 1995. Interrelationships between crustacean zooplankton and phytoplankton: Results from 15 years of field observations at the

mesotrophic Saidenbach Reservoir (Germany). *Hydrobiologia* 307: 231-238

25. Horn, W., 2003. Long-term development of the crustacean plankton in the Saidenbach Reservoir (Germany) – changes, causes, consequence. *Hydrobiologia* 504: 185-192
26. Kerfoot, W. C., 1981. Long-term replacement cycles in cladoceran communities: A history of predation. *Ecology* 62: 216-233
27. Kitchell, J. A. and J. F. Kitchell, 1980. Size-selective predation, light transmission, and oxygen stratification: Evidence from the recent sediments of manipulated lakes. *Limnology and Oceanography* 25: 389-402
28. Kopylov, A. I., Kosolapov, D. B. and E. A. Zabotkina, 2007. Viruses in the plankton of the Rybinsk Reservoir. *Microbiology* 76: 782-790
29. Lammens, E. H. R. R., Boesewinkel-De Bruyn, N., Hoogveld, H. and E. Van Donk, 1992. P-load, phytoplankton, zooplankton and fish stock in Loosdrecht Lake and Tjeukemeer: confounding effects of predation and food availability. *Hydrobiologia* 233: 87-94
30. Lane, P. A., 1975. The dynamics of aquatic systems: A comparative study of the structure of four zooplankton communities. *Ecological Monographs* 45: 307-336
31. Lane, P. A., 1979. Vertebrate and invertebrate predation intensity on freshwater zooplankton communities. *Nature* 280: 391-393
32. Larson, D. W., Dahm, C. N. and N. S. Geiger, 1987. Vertical partitioning of the phytoplankton assemblages in ultra-oligotrophic Crater Lake, Oregon, USA. *Freshwater Biology* 18: 429-442
33. Mageed, A. A. A. and M. T. Heikal, 2006. Factors affecting seasonal patterns in epilimnon zooplankton community in one of the largest man-made lakes in Africa (Lake Nasser, Egypt). *Limnologica* 36: 91-97
34. Makarewicz, J. C. and G. E. Likens, 1979. Structure and function of the zooplankton community of Mirror Lake, New Hampshire. *Ecological Monographs* 49: 109-127
35. Malone, B. J. and D. J. McQueen, 1983. Horizontal patchiness in zooplankton populations in two Ontario kettle lakes. *Hyrdobiologia* 99: 101-124

36. Masundire, H. M., 1997. Spatial and temporal variations in the composition and density of crustacean plankton in the five basins of Lake Kariba, Zambia-Zimbabwe. *Journal of Plankton Research* 19: 43-62

37. Merrix, F. L., Thackeray, S. J. and S. J. Ormerod, unpubl. data

38. Miller, M. C., Hater, G. R., Spatt, P., Westlake, P. and D. Yeakel, 1986. Primary production and its control in Toolik Lake, Alaska, USA. *Archiv für Hydrobiologie* 74 (suppl): 97-132

39. Moss, B., Wetzel, R and G. H. Lauff, 1980. Annual productivity and phytoplankton changes between 1969 and 1974 in Gull Lake, Michigan. *Freshwater Biology* 10: 113-121

40. Mwebaza-Ndawula, L., 1994. Change in relative abundance of zooplankton in northern Lake Victoria, East Africa. *Hydrobiologia* 272: 259-264

41. Neil, W. E. and A. Peacock, 1980. Breaking the Bottleneck: Interactions of invertebrate predators and nutrients in oligotrophic lakes. In: Kerfoot, W. C., ed. *Evolution and Ecology of Zooplankton Communities.* CITY, University Press, DATE, pp. 715-724

42. Nie, H. W., Bromley, H. J. and J. Vijverberg, 1980. Distribution patterns of zooplankton in Tjeukemeer, the Netherlands. *Journal of Plankton Research* 24: 317-334

43. Orcutt, J. D., Jr. and M. L. Pace, 1984. Seasonal dynamics of rotifer and crustacean zooplankton populations in a eutrophic, monomictic lake with a note on rotifer sampling techniques. *Hydrobiologia* 119: 73-80

44. Pace, M. L., 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnology and Oceanography* 31: 45-55

45. Pálffy, K. and L. Vörös, 2003. Effect of ultraviolet radiation on phytoplankton primary production in Lake Balaton. *Hydrobiologia* 506: 289-295

46. Pernthaler, J., Šmek, K., Sattler, B., Schwarzenbacher, A., Bobkova, J. and R. Psenner, 1996. Short-term changes of protozoan control of autotrophic picoplankton in an oligo-mesotrophic lake. *Journal of Plankton Research* 18: 443-462

47. Post, J. R. and D. J. McQueen, 1987. The impact of planktivorous fish on the structure of a plankton community. *Freshwater Biology* 17: 79-89

48. Roth, J. C. and J. C. H. Carter, 1972. Life cycle and seasonal abundance of the copepod *Limnocalanus macrurus* Sars in a high Arctic lake. *Limnology and Oceanography* 17: 363-370

49. Roth, J. C., 1968. Benthic and limnetic distribution of three *Chaoborus* species in a southern Michigan lake (Diptera, Chaoboridae). *Limnology and Oceanography* 13: 242-249

50. Sabo, E., Roy, D., Hamilton, P. B., Hehanussa, P. E., Mcneely and G. D. Haffner, 2008. The plankton community of Lake Matano: Factors regulating plankton composition and relative abundance in an ancient tropical lake of Indonesia. *Hydrobiologia* 615: 225-235

51. Sömmer, U. Z., Gliwicz, M., Lampert, W. and A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh water. *Archiv für Hydrobiologie* 106: 433-471

52. Sousa, W., Attayde, J. L., Da Silva-Rocha, E. and E. M. Eskinazi-Sant'anna, 2008. The response of zooplankton assemblages to variations in the water quality of four man-made lakes in semi-arid north eastern Brazil. *Journal of Plankton Research* 30: 699-708

53. Tadonleke, R. D., Sime-Ngado, T., Amblard, C., Sargos, O. and J. Devaux, 2008. Primary productivity in the recently flooded 'Sep Reservoir' (Puy-de-Dôme, France). *Journal of Plankton Research* 22: 1355-1375

54. Tatrai, I., Istvánovics, V., Tóth, L. -G. and I. Kóbor, 2008. Management measures and long-term water quality changes in Lake Balaton (Hungary). *Archiv für Hydrobiologie* 172/1: 1-11

55. Threkeld, S. T., 1979. The midsummer dynamics of two *Daphnia* species in Wintergreen Lake, Michigan. *Ecology* 60: 165-179

56. Thouvenot, A., Debroas, D., Richardot, M. and J. Devaux, 1999a. Impact of natural metazooplankton assemblage on planktonic microbial communities in a newly flooded reservoir. *Journal of Plankton Research* 21: 179-199

57. Thouvenot, A., Richardot, M., Debroas, D. and J. Devaux, 1999b. bacterivory of metazooplankton, ciliates and flagellates in a newly flooded reservoir. *Journal of Plankton Research* 21: 1659-1679

58. Vanni, M. J., 1986. Fish predation and zooplankton demography: Indirect effects. *Ecology* 67: 337-354

59. Wetzel, R. G., 2001. *Limnology: Lake and River Ecosystems*. 3 ed. San Diego: Elsevier Science

60. Wurtsbaugh, W. and H. Li, 1985. Diel migrations of a zooplanktivorous fish (*Meidia beryllina*) in relation to the distribution of its prey in a large eutrophic lake. *Limnology and Oceanography* 30: 565-576

61. Wygaard, G. A., Elmore, J. L. and B. C. Cowell, 1982. Dynamics of a subtropical plankton community, with emphasis on *Mesocyclops edax*. *Hydrobiologia* 89: 39-48

62. Yoshida, T., Sekino, T., Genkai-Kato, M., Logacheia, N., Bondarenko, N. A., Kawabata, Z., Khodzher, T., Melnik, H. G., Hino, S., Nozaki, K., Nishimura, Y., Nagata, T., Higashi, M. and M. Nakanishi, 2003. Seasonal dynamics of primary production in the pelagic zone of southern Lake Baikal. *Limnology* 4: 53-62

63. Zánkai, P. N. and J. E. Ponyi, 1986. Composition, density and feeding of crustacean zooplankton community in a shallow temperate lake (Lake Balaton, Hungary). *Hydrobiologia* 135: 131-147

Appendix 2

Zooplankton species showing assigned traits used in analysis (Chapter 5). For trait codes see Table 5.1

Species	References	Trait Code																																							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Acanthocyclops bicuspidatus	27, 4			●					●		●				●		●			●				●					●		●	●			●			●		●	●		
Acanthocyclops venustus	27			●					●		●				●		●				●			●					●		●	●			●			●		●	●		
Acanthocyclops vernalis	27, 3, 36, 29, 8, 42			●					●		●				●		●				●			●					●		●	●			●	●				●	●		
Acroperus harpae	50, 12, 9		●					●	●			●		●		●		●				●				●				●			●	●			●			●		●	
Alona quadrangularis	50, 12, 42		●					●	●		●			●		●		●				●				●				●			●	●			●			●	●		
Alona rectangula	50, 12		●					●	●		●			●		●		●				●				●				●			●	●			●			●		●	
Alonella excisa	50, 12	●						●	●		●			●		●		●				●			●					●			●	●				●		●		●	
Alonopsis elongata	50, 12		●					●	●		●			●		●		●				●				●				●			●	●			●			●	●	●	
Bosmina corregoni	23, 50, 12, 31		●					●	●	●			●			●		●				●		●		●					●		●	●		●				●	●		
Bosmina longirostris	7, 49, 50, 54, 24, 56, 12, 31, 34, 47, 25, 14, 3, 32, 40, 42		●					●	●	●			●			●		●				●		●	●					●			●	●		●				●	●		
Camptocercus rectirostris	50, 12			●				●	●		●			●		●		●				●				●				●			●	●		●	●			●		●	
Ceriodaphnia setosa	50, 12, 42		●					●	●		●			●		●		●				●				●				●			●		●	●		●		●	●		
Chydorus sphaericus	50, 23, 24, 12, 3, 34, 9, 42	●						●	●		●			●			●		●			●			●						●		●	●		●				●	●		
Cyclops strenuus	27, 19				●				●			●			●		●				●			●					●		●	●			●			●		●	●		
Daphnia hyalina	23, 11, 50, 24, 56, 12, 22, 52, 5, 42				●			●	●			●		●		●			●			●				●					●		●	●		●				●	●		
Daphnia pulex	11, 50, 24, 56, 12, 45,11, 21, 37, 20, 38, 32, 44, 3,					●		●	●	●				●		●			●			●				●					●		●	●		●				●	●		
Diaphanosoma brachyurum	50, 12, 23, 24, 3, 31, 35, 44		●					●	●		●			●		●			●			●				●					●		●	●		●				●	●		
Diaptomus castor	28				●				●			●			●		●		●				●				●				●	●		●				●		●	●		
Disparalona rostrata	50, 12	●						●	●		●			●		●		●				●			●					●			●	●			●			●		●	
Dreissena polymorpha	42, 39, 46, 48			●					●			●			●	●		●				●			●					●			●	●		●				●	●		
Eucyclops agilis	27, 42			●					●			●			●		●			●				●				●			●	●		●				●		●	●		
Eucyclops macruroides	27			●					●			●			●		●			●				●				●			●	●		●				●		●	●		
Eucyclops macrurus	27, 42			●					●			●			●		●			●				●				●			●	●		●				●		●	●		
Eurycercus lamellatus	50, 12, 9			●				●	●			●		●		●		●				●				●				●			●	●			●			●		●	
Eurytemora affinis	28, 52, 4, 42			●					●			●			●		●		●				●				●				●	●		●		●			●		●		
Graptoleberis testudinaria	50, 12, 9		●					●	●		●			●		●		●				●				●				●			●	●			●			●		●	
Halicyclops aqueoreus	27		●						●			●			●		●		●					●		●					●	●		●				●		●	●		
Leptodora kindti	50, 16, 29, 15						●	●	●			●		●		●					●			●					●		●		●		●	●				●	●		
Leydigia leydigi	50, 12		●					●	●		●			●		●		●				●				●				●			●	●			●			●		●	
Macrocyclops distinctus	27			●					●			●			●		●	●						●					●		●	●			●			●		●	●		
Megacyclops gigas	27, 33					●			●			●			●		●				●			●					●		●	●			●		●			●	●		
Microcyclops bicolor	27		●						●			●			●		●		●					●		●					●	●		●				●		●	●		
Monospillus dispar	50, 12	●						●	●		●			●		●		●				●			●					●			●	●			●			●		●	
Paracyclops fimbriatus	27		●						●			●			●		●		●					●		●					●	●		●				●		●	●		
Pleuroxus trigonellus	50, 12		●					●	●			●		●		●		●				●			●					●			●	●			●			●		●	
Pleuroxus uncinatus	50, 12, 9		●					●	●			●		●		●		●				●			●					●			●	●			●			●		●	
Rhyncotalona falcata	50, 12		●					●	●		●			●		●		●				●			●					●			●	●			●			●		●	
Sida crystallina	50, 12, 23					●		●	●			●		●		●		●				●				●					●		●	●				●		●			●
Simocephalus vetulus	11, 50, 56, 12, 51, 41, 9, 43, 17				●			●	●		●			●		●		●				●				●				●		●		●				●		●			●
Tropocyclops prasinus	27, 4, 18		●						●			●			●		●		●					●		●					●	●		●		●				●	●		

* *Bosmina* species display a dual feeding mechanism, whereby smaller particles are captured through filter-feeding and larger particles through grasping

** Temperate cladoceran reproductive cycles include periods of asexual and sexual reproduction

References

1. Abdullahi, B. A., 1990. The effect of temperature on reproduction in three species of cyclopoid copepods. *Hydrobiologia* 196: 101-109
2. Ask, J., Reinikaihnen, M. and U. Barnstedt, 2006. Variation in hatching success and egg production of *Eurytemora affinis* (Calanoida, Copepoda) from the Gulf of Bothnia, Baltic Sea, in relation to abundance and clonal differences of diatoms. *Journal of Plankton Research* 28: 683-694
3. Barnett, A. J., Finlay, K. and B. E. Beisner, 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology* 52: 796-813
4. Barthel, K. G., 1983. Food uptake and growth efficiency of *Eurytemora affinis* (Copepoda, Calanoida). *Marine Biology* 74: 269-274
5. Berberovic, R., 1990. Elemental composition of two co-existing Daphnia species during the seasonal course of population development in Lake Constance. *Oecologia* 84: 340-350
6. Beyrend-Dur, D., Souissi, S., Devreker, D., Winkler, G. and J. -S. Hwang, 2009. Life cycle traits of two transatlantic populations of *Eurytemora affinis* (Copepoda: Calanoida): salinity effects. *Journal of Plankton Research* 31: 713-728
7. Bogden, K. and J. J. Gilbert, 1984. Body size and food size in freshwater zooplankton. *Proceedings of the National Academy of Sciences* 81: 6427-6431
8. Borsheim, K. Y., 1987. Grazing and food size selection by crustacean zooplankton compared to production of bacteria and phytoplankton in a shallow Norweigian mountain lake. *Journal of Plankton Research* 9: 367-379
9. Bottrell, H. H., 1975. Generation time, length of life, instar development and frequency of moulting, and their relationship to temperature in eight species of Cladocera from the River Thames, Reading. *Oecologia* 19: 129-140
10. Brendelberger, H., 1991. Filter mesh size of cladocerans predicts retention efficiency for bacteria. *Limnology and Oceanography* 36: 884-894

11. Brendelberger, H. and W. Geller, 1985. Variability of filter structures in eight Daphnia species: mesh sizes and filtering areas. *Journal of Plankton Research* 7: 473-486

12. Burns, C. W., 1968. The relationship between body sixe of filter-feeding cladocera and the maximum size of particle ingested. *Limnology and Oceanography* 13: 675-678

13. Burns, C. W., 2000. Crowding-induced changes in growth, reproduction and morphology of *Daphnia. Freshwater Biology* 43: 19-29

14. Byron, E. R., Folt, C. L. and C. R. Goldman, 1984. Copepod and cladoceran success in an oligotrophic lake. *Journal of Plankton Research* 6: 45-66

15. Cummins, K. W., Costa, R. R., Rowe, R. E., Moshiri, G. A., Scanlon, R. M. and R. A. Zajdel, 1969. Ecological energetics of a natural population of the predaceous zooplankter *Leptodora kindtii* Focke (Cladocera). *Oikos* 20: 189-223

16. De Eyto, E and K. Irvine, 2005. Variation in the biomass of functional groups comprising the open-water plankton of shallow lakes in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* 105B: 53-58

17. DeMott, W. R., 1998. Utilisation of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by Daphnids. *Ecology* 79: 2463-2481

18. DeMott, W. R. and M. D. Watson, 1991. Remote detection of algae by copepods: responses to algal size, odours and motility. *Journal of Plankton Research* 13: 1203-1222

19. Elbourn, C. A., 1966. The life cycle of *Cyclops strenuus strenuus* Fischer in a small pond. *Journal of Animal Ecology* 35: 333-347

20. Ferrao-Filho, A. S., Azevedo, S. M. F. O. and W. R. DeMott, 2000. Effects of toxic and non-toxic cyanobacteria on the life history of tropical and temperate cladocerans. *Freshwater Biology* 45: 1-19

21. Ferrao-Filho, A. S. and S. M. F. O. Azevedo, 2003. Effects of unicellular and colonial forms of toxic Microcystis aeruginosa from laboratory cultures and natural populations on tropical cladocerans. *Aquatic Ecology* 37: 23-35

22. Geller, W., 1989. The energy budget of two sympatric *Daphnia* species in Lake Constance: productivity and energy residence times. *Oecologia* 78: 242-250
23. Geller, W. and H. Müller, 1981. The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. *Oecologia* 49: 316-321
24. Gillooly, J. F. and S. I. Dodson, 2000. Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater cladocera. *Limnology and Oceanography* 45: 22-30
25. Goulden, C. E., Henry, L. L. and A. J. Tessier, 1982. Body size, energy reserves, and competative ability in three species of cladocera. *Ecology* 63: 1780-1789
26. Guisande, C. and Z. M. Gliwicz, 1992. Egg size and clutch size in two *Daphnia* species grown at different food levels. *Journal of Plankton Research* 14: 997-1007
27. Gurney, R, 1933a. *British Fresh-water Copepoda.* London: Ray Society
28. Gurney, R, 1933b. *British Fresh-water Copepoda.* London: Ray Society
29. Havel, J. E., 1985. Predation of common invertebrate predators on long- and short- featured *Daphnia retrocurva. Hydrobiologia* 124: 141-149
30. Hessen, D. O., 1985. Filtering structures and particle size selection in coexisting cladocera. Oecologia 66: 368-372
31. Hessen, D. O., Andersen, T. and A. Lyche, 1989. Differential grazing and resource utilisation of zooplankton in a humic acid lake. *Archiv für Hydrobiologie* 114: 321-347
32. Kirk, K. L. and J. J. Gilbert, 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. *Ecology* 71: 1741-1755
33. Krylov, P. I., 1988. Predation of the freshwater cyclopdoid copepod Mega*cyclops gigas* on lake zooplankton: functional response and prey selection. *Archiv für Hydrobiologie* 113: 231-250
34. Lair, N., 1991. Grazing and assimilation rates of natural populations of planktonic cladocerans in a eutrophic lake. *Hydrobiologia* 251: 51-61
35. Lemke, A. M. and A. C. Benke, 2003. Growth and reproduction of three cladoceran species from a small wetland in the south-eastern USA. *Freshwater Biology* 48: 589-603

36. Li, J. L. and W. L. Hiram, 1979. Species-specific factors affecting predator-prey interactions of the copepod *Acanthocyclops vernalis* with its prey. *Limnology and Oceanography* 24: 613-626

37. Lürling, M. and E. Van Donk, 1997. Life history consequences for *Daphnia pulex* feeding on nutrient-limited phytoplankton. *Freshwater Biology* 38: 693-709

38. Lürling, M., Roozen, F., Van Donk E. and B. Goser, 2003. Response of *Daphnia* to substances released from crowded congeners and conspecifics. *Journal of Plankton Research* 25: 967-978

39. MacIsaac, H. J., Sprules, W. G., Johannsson, O. E. and J. H. Leach, 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Oecologia* 92: 30-39

40. Main, T. M., Dobberfuhl, D. R. and J. J. Elser, 1997. N:P stoichiometry and ontogeny of crustacean zooplankton: A test of the growth rate hypothesis. *Limnology and Oceanography* 42: 1474-1478

41. Mangalo, H., 1987. Variation in the intersetular distance on filter setae of *Simocephalus vetulus* (O. F. Muller) (Crustacea: Cladocera). *Freshwater Biology* 17: 169-176

42. Merrix, F. L., Thackeray, S. J. and S. J. Ormerod, unpubl data

43. Nandini, S. and S. S. S. Sarma, 2000. Lifetable demography of four cladoceran species in relation to algal food (*Chlorella vulgaris*) density. *Hydrobiologia* 435: 117-126

44. Nandini, S. and S. S. S. Sarma, 2003. Population growth of som genera of cladocerans (Cladocera) in relation to algal food (*Chlorella vulgaris*) levels. *Hydrobiologia* 491: 211-219

45. Peterston Holm, N., Ganf, G. G. and J. Shapiro, 1983. Feeding and assimilation rates in *Daphnia pulex* fed *Aphanizomenon flos-aquae*. *Limnology and Oceanography* 28: 677-687

46. Pires, L. M. D., Jonker, R. R., Van Donk, E., and H. J. Laanbroek, 2004. Selective grazing by adults and larvae of the zebra mussel (*Dreissena polymorpha*): application of flow cytometry to natural seston. *Freshwater Biology* 49: 116-126

47. Porter, K. G., Feig, Y. S. and E. S. Vetter, 1983. Morphology, flow regimes, and filtering rates of *Daphnia*, *Ceriodaphnia*, and *Bosmina* fed natural bacteria. *Oecologia* 58: 156-163

48. Sprung, M., 1989. Field and laboratory observations of *Dreissena polymorpha* larvae: abundance, growth, mortality and food demands. *Archiv für Hydrobiologie* 115: 537-561

49. Schoeberg, S. A., 1989. Effects of algal concentration, bacterial size, and water chemistry on the injestion of natural bacteria by cladocerans. *Journal of Plankton Research* 11: 1273-1295

50. Scourfield, D. J. and J. P. Harding, 1994. *A key to the British species of freshwater cladocera, with notes on their ecology*. Freshwater Biological Association

51. Sharma, P. C. and M. C. Plant, 1984. An energy budget for *Simocephalus vetulus* (O. F. Mulller) (Crustacea: Cladocera). *Hydrobiologia* 111: 37-42

52. Smyly, W. J. P., 1979. Population dynamics of *Daphnia hyalina* Leydig (Crustacea: Cladocera) in a productive and an unproductive lake in the English Lake District. *Hydrobiologia* 64: 269-278

53. Tackx, M. L. M., Herman, P. J. M., Gasparini, S., Irigoien, X., Billiones, R. and M. H. Daro., 2003. Selective feeding of *Eurytemora affinis* (Copepoda, Calanoida) in temperate estuaries: model and field observations. *Estuarine, Coastal and Shelf Sciences* 56: 305-311

54. Toth, L., G. and K. Kato, 1997. Size-selective grazing of bacteria by *Bosmina longirostris* - and image-analysis study. *Journal of Plankton Research* 19: 1477-1493

55. Webster, K. E. and R. H. Peters, 1978. Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. *Limnology and Oceanography* 23: 1238-1248

56. Wu, Y. G., Lin, C. X. and L. Yuan, L., 2007. Characteristics of six cladocerans in relation to ecotoxicity testing. *Ecological Indicators* 7: 768-