PHYTOPLANKTON - ZOOPLANKTON INTERACTIONS IN MT BOLD RESERVOIR, SOUTH AUSTRALIA.

Volume One

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A thesis submitted to the University of Adelaide
for the degree of Doctor of Philosophy.

March 1990

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SUMMARY

The thesis is an investigation of the interactions between phytoplankton and zooplankton in Mt Bold Reservoir, South Australia (35° 07' S., 138° 43' E.). The dynamics of the reservoir plankton were examined over two annual cycles which had different physical and chemical environments. In the first year the reservoir water was derived mainly from the catchment; in the second year the reservoir water was mainly pumped from the Murray River. The river water was more transparent, more saline and had lower nutrient concentrations than the catchment water. In the first year the reservoir was stratified throughout the summer although the mixed depth fluctuated with changes in daily solar radiation. During the second year there were large fluctations in mixed depth and the reservoir was intermittently mixed throughout summer. As a consequence of the different conditions the plankton communities differed between the two seasons. *Microcystis aeruginosa* dominated the phytoplankton in the first year but was greatly reduced in the second year. In the second year several cladocerans and rotifers were either completely absent or were greatly reduced in the reservoir. Discrete plankton communities were defined using classification and ordination analyses. Communities so defined did not consistently agree with those described by the SD index of Lewis (1978a). During the study period the changes in the phytoplankton communities followed the categories of Reynolds (1980) i.e. autogenic succession, allogenic shifts and reversions. The latter two categories were associated with changes in the physical environment and occasionally with changes in the zooplankton communities. Due to the potential time lags between cause and effect, the specific influence of zooplankton on phytoplankton composition could not be isolated in Mt Bold Reservoir. In the first year there was a critical mean irradiance above which light no longer limited phytoplankton biomass accumulation, thus initiating the spring bloom. During the second year there was no significant spring phytoplankton bloom despite an improved light climate. This was most likely due to the high flushing rate and the low nutrient levels during that spring.

During the monitoring of Mt Bold Reservoir there were occasions when the plankton communities changed over a short time period as a result of the rapid increase or decrease of component populations. The extent to which these changes were a result of horizontal heterogeneity or patchiness was examined through an intensive sampling program during a summer growing season. There was little patchiness evident for the phytoplankton and zooplankton taxa examined at the spatial and temporal scales sampled. During this study, rapid declines in population density were documented for some of the phytoplankton taxa. The potential contributions of washout, sedimentation and grazing to these losses were

assessed. Although sedimentation could account for the losses of a diatom, losses of other taxa were most likely due to grazing by zooplankton.

The influence of zooplankton on the composition of Mt Bold Reservoir phytoplankton was examined through a series of enclosure experiments done over a summer growth season. Phytoplankton biomass as chlorophyll *a* and the chlorophyll *a* : phaeophytin *a* ratio did not change in the enclosures in response to zooplankton grazing. Phytoplankton species richness and diversity did not change but the frequencies of many individual phytoplankton taxa differed in response to zooplankton grazing. Neither taxonomic identity nor size as measured by GALD (Lewis 1976) and volume determined phytoplankton susceptibility to grazing. This suggested that other criteria were important in food selection, criteria which differed between experiments. Classification and ordination successfully differentiated the grazed from the ungrazed phytoplankton communities based on the different frequencies of component taxa. There was an indication that within the enclosures, zooplankton grazing advanced the phytoplankton community composition in time. Microzooplankton grazing was not examined in the enclosure experiments but there was evidence that it was significant.

Mt Bold zooplankton communities were dominated by calanoid copepods although cladocerans were usually present and occasionally dominant. *In situ* grazing measurements using natural food tracers demonstrated that in Mt Bold Reservoir calanoid copepods had comparable grazing rates to cladocerans, both on an individual basis and on a biomass basis. The calanoid copepods utilized a wider range of natural food sizes than the cladocerans. There was a substantial amount of variation in grazing rates on natural food so that the use of specific rates to predict zooplankton grazing in other natural situations was not valid. However the grazing rates of specific zooplankton taxa on specific food tracers were consistent. The influence of suspended particulates on the grazing rates of Mt Bold Reservoir zooplankton was investigated. Field experiments showed that grazing rates of both calanoid copepods and cladocerans were reduced although there was no change in food selectivity. Laboratory experiments showed that grazing rates were reduced across a wide range of suspended particulate concentrations. Comparisons between grazing rates in suspensions of algae and of clay showed that the reductions were not only due to the increased particle concentrations in the clay suspensions. The absolute reduction in grazing rate per unit of clay suspension was the same for the copepod and the cladoceran however the relative reduction for the cladoceran was greater than for the copepod which implied that the relative reduction in food consumption was greater. The dominance of calanoid copepods in the turbid water of Mt Bold Reservoir may be due to these grazing advantages.

DECLARATION

To the best of my knowledge and belief, this thesis contains no material previously submitted for a degree or any other award, in any university by any person, or any material previously published or written by another person, except where due reference is made in the text. I consent to the thesis being made available for copying and loan if accepted for the award of the degree.

Chester Merrick

ACKNOWLEDGEMENTS

"All is flux, nothing is stationary."

Heracleitus 513 BC

CHAPTER ONE: INTRODUCTION

1.1 Study Background and Aims.

Periodic changes in the quantity and composition of plankton are well known phenomena in many water bodies. When these changes are a seasonal or an annual occurrence they are termed a succession, although they do not exactly match the terrestrial concept (Reynolds 1980; Sommer 1987).

The main environmental factors that influence phytoplankton periodicity have been identified for a long time (Hutchinson 1967). Despite this early recognition and an extensive literature documenting the periodic changes in phytoplankton (see reviews by Lund 1965; Hutchinson 1967; Round 1971; Kalff and Knoechel 1978; Margalef 1978; Smayda 1980; Reynolds 1980, 1984a; Harris 1986; Sommer *et al.* 1986), a complete understanding of the processes involved has yet to be achieved. The environmental factors that influence phytoplankton may be broadly split into growth factors, which generally result in population increase, and loss factors, which generally result in population decrease (Kalff and Knoechel 1978). The major growth factors are light, temperature and nutrients while the major loss factors are sedimentation, predation (grazing and parasitism), hydraulic washout and death (Reynolds 1984a). An outline of the roles of these factors gives the background to the present study.

Solar radiation provides the light energy necessary for phytoplankton carbon fixation and hence phytoplankton growth. In addition, the absorption of solar energy and its dissipation as heat influences the temperature and the stability of the water column (Wetzel 1975). The initiation of spring phytoplankton growth due to an increase in available light is well known in many lakes (Hutchinson 1967), resulting in a wide appreciation of the importance of light availability in controlling phytoplankton production (Talling 1971). Light availability to phytoplankton is a function of three interacting components: (1) the intensity and duration of surface radiation, (2) radiation attenuation with depth and (3) the stability of the water column (Talling 1971; Reynolds 1984a). Although the form of the relationship between photosynthetic rate and light intensity is consistent, there are marked differences in photosynthetic efficiency between phytoplankton taxa (Harris 1978, 1980a). Consequently different light climates will influence phytoplankton composition as well as abundance.

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Many cellular processes are temperature dependent, with optimal rates occurring between 25 and 40 °C (Reynolds 1984a). Although early reports of different thermal optima for phytoplankton growth allowed some explanation of the occurrence of specific phytoplankton taxa, the variability of these apparent temperature responses in different geographical locations cast doubt on these interpretations (Hutchinson 1967). Because temperature and light both influence photosynthesis, it is difficult to separate their effects on phytoplankton growth in nature (Lund 1965). A more important consequence of temperature fluctuation is the associated influence on the stability of the water column, thereby controlling access to light and nutrients.

Chemical control of phytoplankton abundance and composition through essential nutrients was extensively investigated by Pearsall (1932). Although a wide range of nutrients may potentially influence phytoplankton growth (see Lund 1965; Likens 1972; Morris 1980), phosphorus, nitrogen and silicon are the major limiting elements (Lund 1965). The dominant role of phosphorus has been well established through the development of chlorophyll-phosphorus models to describe algal biomass levels in lakes (e.g. Dillon and Rigler 1974; Smith 1982). Because phytoplankton consume and deplete nutrients which then limit phytoplankton growth, a potential for nutrient based competition exists between phytoplankton species (Sommer 1987). Tilman (Titman 1976; Tilman 1977) established that such competition resulted in different phytoplankton species dominating in response to various nutrient ratios maintained in steady state culture experiments. Application of these results to natural phytoplankton communities in culture (Sommer 1983) or in the field (Kilham and Kilham 1980, 1984) demonstrated the potential influence of nutrients on phytoplankton periodic change. This approach has been criticized (e.g. Harris 1980b, 1986) on the basis that steady state conditions do not apply in nature. This debate is not over the importance of nutrients to phytoplankton but rather over the mechanism of influence.

Because of the potential variation with depth of the major growth factors, the growth of phytoplankton is greatly influenced by its distribution in the water column (Walsby and Reynolds 1980). However since most phytoplankton are more dense than water and therefore sink (Hutchinson 1967), a fundamental requirement for phytoplankton growth is suspension in the water column (Reynolds 1984a). Sedimentation may thus control the abundance and composition of the phytoplankton community. Hutchinson (1967) considered that much of the seasonal succession of phytoplankton could be due to the interrelation

between turbulence of the water column and sinking speed of the phytoplankton. Examples of this are the sedimentation of diatoms with the onset of thermal stratification reported by Lund (1971), Knoechel and Kalff (1975) and Reynolds (1976). One potential advantage of sedimentation is the increased rate of nutrient uptake by the phytoplankton cell (Munk and Riley 1952). The nutritional benefits of mobility have been established for cyanobacteria (e.g. Ganf and Oliver 1982), however the nutritional benefits of sinking to phytoplankton populations have yet to be demonstrated (Walsby and Reynolds 1980).

The potential loss of phytoplankton from hydraulic washout is dependent on the retention time of the water body. This may range from a very short time for a river to a very long time for a closed basin with no outlet. River phytoplankton, which represent an extreme case, are reviewed by Hynes (1970). Dickman (1969) and Reynolds and Lund (1988) describe more intermediate examples where hydraulic washout has a substantial seasonal impact on phytoplankton abundance and, through differential growth rates and reproductive strategies, on phytoplankton composition.

Causes of death in phytoplankton cells may be divided into three groups: physiological death; toxicity and allelopathy; and pathogenic organisms (Reynolds 1984a). These are briefly considered below:

1. Physiological death may result from light or nutrient deficiency. Examples are the decline in diatom populations upon the exhaustion of silicon in the water column (Lund 1965) and the demise of cyanobacteria through excessive solar radiation after bloom formation (Reynolds 1987a).

2. Phytoplankton secrete a variety of chemical substances into their surroundings (Fogg 1977). Although many are metabolic by-products, there is evidence that some are detrimental to other organisms including algae. The toxicity of some cyanobacteria is well known (Fogg et al. 1973).

3. Pathogens of phytoplankton include viruses, bacteria and fungi (Reynolds 1984a). The latter have been extensively studied (Canter and Lund 1953) and may cause substantial losses to phytoplankton populations (Canter and Lund 1948; Reynolds 1973). Considered to be parasites, they are host specific and thus have a marked influence on phytoplankton composition.

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The zooplankton community includes protozoa (ciliates and amoebae), rotifers, and crustaceans (copepods and cladocerans). These animals feed on phytoplankton in both marine (Raymont 1983) and freshwater (Hutchinson 1967) systems, thereby removing algal biomass. In addition the selection of preferred food results in an altered phytoplankton composition. Although the herbivorous nature of many zooplankton has been known for a long time (Hutchinson 1967), only relatively recently has there been acceptance of their potential to control phytoplankton populations (Canter and Lund 1968; Porter 1977; Frost 1980). Zooplankton recycle nutrients through excretion and egestion of incompletely digested algal food (Lehman 1980b). Ganf and Blazka (1974) and Lehman (1980a) both demonstrated that substantial proportions of the nutrient requirements of natural phytoplankton communities may be supplied through zooplankton recycling. Since these nutrients are potentially available to ungrazed as well as grazed algae, changes in phytoplankton composition may be accelerated (Lehman 1980b).

It should be made clear that the various environmental factors that influence phytoplankton periodicity do not do so in isolation from each other. There is a great deal of interaction such that the specific effect of any one factor is difficult to isolate and assess. Growth factors have received more attention in the literature than loss factors despite wide acceptance of the importance of the latter (Kalff and Knoechel 1978). One distinction between growth and loss factors is the time scale of action. The replacement of one phytoplankton species by another due to differential resource utilization generally takes place over a longer time scale than the changes in abundance or composition resulting from differential losses (Kalff and Knoechel 1978). When the phytoplankton community experiences rapid change, loss factors are likely to be more important than growth factors.

Australian inland waters have many distinctive features not shared by water bodies of the northern temperate regions where most limnological research has been done (Williams 1980b, 1982). These include chemical (Buckney 1980), physical (Kirk 1979, 1985; Imberger 1985) and biological (Williams 1980b) characteristics. Of particular interest to phytoplankton growth and periodicity is the low light penetration in many Australian inland waters due to dissolved colour (Kirk 1976, 1977) and suspended particulates (Kirk 1985). The influence of this light climate on phytoplankton has been investigated in a typical turbid water body (Mt Bold Reservoir, South Australia) by Oliver (1981), Ganf and Oliver (1982) and Oliver and Ganf (1988). The influence of nutrients and water column stability on

Mt Bold Reservoir phytoplankton was also examined by Ganf (1980), Oliver (1981) and Ganf (1982), however none of these studies considered the effect of zooplankton grazing on the phytoplankton community.

Australian zooplankton communities have a high degree of endemism (Williams 1980b, 1982). Zooplankton community diversity in Australian lakes was considered to be low based on average momentary species composition (Bayly and Williams 1973), however a recent review by Mitchell (1986) found that while cladocerans and cyclopoid copepods are less diverse, calanoid copepods are more diverse. Mitchell (1986) concluded that Australian zooplankton communities differed from those elsewhere in the world. Of particular relevance to zooplankton community grazing is that copepods are generally more abundant than cladocerans in Australian lakes (Mitchell 1986). Mitchell (1986) reported that little information was available on the feeding behaviour of Australian zooplankton, calanoid copepods in particular.

Considering the potential for zooplankton to influence the phytoplankton community, the lack of information on this interaction represents a substantial gap in our understanding of plankton dyanamics in Australian water bodies. This thesis addresses this gap in a typical Australian turbid water body; Mt Bold Reservoir, South Australia.

The specific aims of this study were as follows:

1. Describe the physical and chemical environment of the reservoir.

2. Describe the patterns of abundance and compositional change in both phytoplankton and zooplankton communities.

3. Examine the interactions between the plankton communities and the environment.

4. Examine the spatial distribution of the plankton and investigate the phytoplankton population changes during a rapid community transition.

5. Investigate the influence of zooplankton grazing on phytoplankton abundance and composition and examine the influence of phytoplankton size on susceptibility to grazing.

6. Measure *in situ* grazing rates of the zooplankton and investigate food selection between copepods and cladocerans.

7. Investigate the influence of suspended particulates on the grazing behaviour of copepods and cladocerans.

The first three aims were investigated through a two year intensive sampling program while the fourth aim was addressed in a separate intensive sampling program during a growing season. Mt Bold Reservoir was used as the study site since there was extensive background information available on factors controlling phytoplankton populations (Ganf 1980; Oliver 1981; Ganf 1982; Ganf and Oliver 1982; Oliver and Ganf 1988). Mt Bold is a storage reservoir that does not feed directly into the water distribution system. Consequently control of plankton blooms by copper sulphate or artificial destratification is not part of routine management. This allows an uninterrupted sequence of events to be followed in the plankton populations. The fifth aim was examined in a series of *in situ* enclosure experiments across a growing season. The sixth and seventh aims were met using a combination of field and laboratory measurements. Inherent in the above aims is a requirement for the delineation of plankton communities. The background and procedures used are outlined below. As this study concentrates on the influence of zooplankton grazing, a general outline of zooplankton grazing research and a brief account of zooplankton feeding processes follows this.

1.2 Plankton Community Definition

The periodic changes in plankton communities may be either discrete steps or gradual transitions. Objective definition of the boundaries in time of planktonic communities is an ongoing problem. Reynolds (1980) used the summed difference (SD) index of Lewis (1978a), itself a modification of the succession rate index of Jassby and Goldman (1974a), to identify periods of change in the phytoplankton communities of five British lake systems. Reynolds (1980) defined the phytoplankton communities of these lake systems as those periods with an SD rate of change of less than $0.1 \ d^{-1}$, while rates exceeding $0.1 \ d^{-1}$ indicated periods of significant change in composition. The choice of $0.1 \ d^{-1}$ as a critical SD value seemed to be a retrospective result of agreement between the communities so defined and a subjective grouping of the species assemblages recorded.

Multivariate statistical techniques have been extensively used in terrestial community

ecology (Greig-Smith 1983; Gauch 1984). The application of multivariate analyses to aquatic systems is less common (Allen and Koonce 1973; Bartell *et al.* 1978; Harris and Piccinin 1980). The diversity of applications has resulted in extensive methodology, however comparative tests have demonstrated the superiority of relatively few techniques (Gauch 1984), thus making the choice of technique easier. The aim of multivariate analysis is to objectively summarize the data and to expose inherent structure. The two broad approaches used here were classification and ordination.

Classification involves grouping similar entities (e.g. samples) into clusters which may subsequently be arranged into a hierarchy indicating relationships among them. There are two steps in classification. Firstly the similarity or dissimilarity of all entities with each other is calculated. The Bray-Curtis index which was used is an intermediate measure which does not emphasize either dominant or rare components (Greig-Smith 1983). Secondly, a fusion procedure is applied to build up a hierarchy of clusters. The unweighted pair groups method with arithmetic averages (UPGMA) which was used is also an intermediate fusion strategy recommended for general use (Greig-Smith 1983).

Ordination endeavours to represent the relationships between entities in a low dimension space. Conceptually ordination has two stages. Initially all of the entities are located in a many dimensioned space in terms of their components. For example each sample may be located in a species space comprised of all its component species. These located positions are then projected onto a series of axes which best fit their distributions in space. The projected positions are defined in terms of vectors from the origin of the axes. Ideally a limited number of axes explains the projected distribution and these are used to summarize the relationships between the entities. Detrended correspondence analysis (DCA) was the ordination technique used. It is regarded as an appropriate general method (Gauch 1984), with both disadvantages (Wartenberg *et al.* 1987) and advantages (Peet *et al.* 1988).

1.3 Zooplankton Grazing

Interest in zooplankton feeding was stimulated by the early observations of an inverse relationship between the quantities of phytoplankton and of zooplankton in the sea. Alternative hypotheses were put forward by Hardy (1935) and Harvey *et al.* (1935) to explain these observations. Hardy (1935) proposed that zooplankton were excluded from

high concentrations of phytoplankton while Harvey *et al.* (1935) proposed that grazing by zooplankton accounted for the observed phytoplankton distributions. Several early studies (e.g. Anderson *et al.* 1955; Wright 1958; Martin 1965) attributed seasonal changes in phytoplankton abundance to the influence of zooplankton grazing based on this reciprocal relationship, however these studies did not directly measure zooplankton feeding.

The first measurement of zooplankton grazing rates by Fuller and Clarke (1936) was to determine if marine copepods obtained adequate particulate food for their needs without nourishment from dissolved organic substances. Grazing measurements were continued in order to resolve the above issues (e.g. Gauld 1951; Bainbridge 1953; Ryther 1954).

Similar questions arose with the food sources of freshwater zooplankton. In a detailed study of the plankton of Lake Erken, Nauwerck (1963) concluded that phytoplankton were not of primary importance to the zooplankton and suggested that bacteria and detritus were the most important food sources. These results were reanalysed and refuted by Cushing (1976), however aspects of this re-analysis were subsequently questioned by Lewis (1977c) and Knoechel (1977). Irrespective of this, the ability of zooplankton to feed on bacteria was demonstrated by Gliwicz (1969) and Haney (1973). Gulati (1975) subsequently established the importance of bacteria as a food source for zooplankton in Lake Vechten.

Much of the early research on zooplankton grazing was directed towards understanding the feeding response to different food concentrations (Ryther 1954; Rigler 1961; Mullin 1963; McMahon and Rigler 1963, 1965; Burns and Rigler 1967; Schindler 1968; Frost 1972, 1975; Mullin *et al.* 1975); different animal and food sizes (McMahon and Rigler 1963; McMahon 1965; Schindler 1968; Burns 1968a, 1969a, 1969b; Richman and Rogers 1969; Frost 1972, 1977); and environmental factors that influenced grazing rates (McMahon 1965; Schindler 1968; Burns 1968b, 1969b). The basis of this work was the expectation that the consequences of zooplankton grazing in nature could be predicted if all these relationships were quantified. Application of laboratory derived grazing rates to field populations was attempted by Enright (1969), Gliwicz (1970), Hargrave and Geen (1970), Jassby and Goldman (1974b), Coveney *et al.* (1977), Lewis (1978b) and Horn (1981) with contrasting results. Thus Gliwicz (1970), Jassby and Goldman (1974b), Coveney *et al.* (1977) and Lewis (1978b) all reported that zooplankton grazing had a minimal effect on the phytoplankton populations they examined. Enright (1969), Hargrave and Geen (1970) and Horn (1981) all

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reported substantial effects. Uncertainty over the validity of applying laboratory based measurements in the field lead to direct measurements. Direct investigations of the influence of zooplankton grazing on the phytoplankton community were through *in situ* grazing measurements and *in situ* enclosure experiments.

Early examples of *in situ* grazing measurements are the extensive studies of Gliwicz (1968, 1969, 1977) and Haney (1971, 1973). Gliwicz (1968), using an *in situ* feeding chamber, estimated that the zooplankton community ingested 48-162% of their biomass on a daily basis. Gliwicz (1969) used the same methodology to show that the feeding selectivity of zooplankton taxa in the community differed and Gliwicz (1977) demonstrated a relationship between this selectivity and the seasonal changes in both zooplankton and phytoplankton communities. Haney (1971, 1973) used a modified feeding chamber with radioisotope labelled food tracers to measure the *in situ* grazing of zooplankton communities through two growth seasons. Daily community grazing rates ranged from less than 10% to in excess of 100% of the volume the zooplankton occupied, thus demonstrating the potential for zooplankton to influence phytoplankton abundance.

Early examples of the use of enclosures are the studies of Anderson (1958) and Porter (1972, 1973a, 1973b). Anderson (1958) reported an increase in the chlorophyll concentration in bottles of Soap Lake water from which zooplankton had been removed. Porter (1972, 1973a, 1973b) used a series of enclosures with and without zooplankton to demonstrate the effects of grazing on phytoplankton composition throughout a growth season. The phytoplankton taxa showed three distinct responses to zooplankton grazing. There was a suppressed group of greens, diatoms, nanoflagellates and cryptomonads; an unaffected group of large desmids, dinoflagellates, filamentous diatoms and colonial cyanobacteria; and finally a group of colonial green algae that increased in the presence of grazing through nutrient uptake during gut passage.

Interest in the influence of zooplankton grazing on freshwater phytoplankton was stimulated by observations that changes at higher trophic levels (e.g. fish) may be felt down the food chain through zooplankton to phytoplankton (Hrbacek *et al.* 1961; Brooks and Dodson 1965). The size-efficiency hypothesis proposed by Brooks and Dodson (1965) to explain these changes in community structure was the subject of much research (see review by Hall *et al.* 1976). The potential utilization of the coupling between consumers and producers to

control the latter has since been extensively examined (Shapiro *et al.* 1975; Shapiro 1980; Lynch and Shapiro 1981; Elliot *et al.* 1983; Benndorf *et al.* 1984; Goad 1984; Olrik *et al.* 1984; Reinertsen and Olsen 1984; Shapiro and Wright 1984; Spencer and King 1984; Uehlinger and Bloesch 1987; Vanni 1987a, 1987b). It has lead to the present debate over 'bottom-up' versus 'top-down' control of lake ecosystems (Harris 1986; McQueen *et al.* 1986; Dorazio *et al.* 1987; Kitchell and Carpenter 1988; McQueen and Post 1988).

1.4 Zooplankton Feeding Processes

Early accounts of the mechanisms of food collection by macrozooplankton are those by Cannon (1933) for cladocerans, Lowndes (1935) for calanoid copepods, and Fryer (1957a) for cyclopoid copepods. Cladocerans and calanoid copepods were considered to be filter feeders while cyclopoid copepods were considered to be raptorial or grasping feeders. The traditional view of filter feeding was that water passed through a mesh of setae and setules which sieved out food particles. Cladocerans used their thoracic limbs to draw a current of water through a feeding chamber formed from their carapace. The food particles were filtered out using these same limbs, collected in a food groove and then passed to the mandibles and mouth. In calanoid copepods the feeding current was derived from the locomotory activity of the antennules. Setae on the maxillae filtered out food particles which were then passed to the mouth. Filtering was considered a passive process with particle retention a sole function of the sieving properties of the mesh (Boyd 1976; Nival and Nival 1976, 1979; Frost 1977; Geller and Muller 1981). An alternative raptorial mode of feeding was proposed for calanoid copepods to explain their feeding behaviour on large food particles (Conover 1966, 1968; Richman and Rogers 1969).

Recent appreciation of the viscous environment in which zooplankton exist (Purcell 1977; Zaret 1980a) has resulted in a re-examination of the traditional view of filter feeding (Rubenstein and Koehl 1977; Alcaraz *et al.* 1980; Koehl and Strickler 1981; Gerritsen and Porter 1982; Paffenhoffer *et al.* 1982; Vanderploeg and Ondricek-Fallscheer 1982; Porter *ct al.* 1983). Contemporary interpretation (e.g. Koehl 1984; Paffenhofer 1984a; Strickler 1984) of calanoid copepod filtering considers that large food particles are individually detected and captured or rejected from within a feeding envelope (Friedman 1980) which is scanned by chemoreceptors and mechanoreceptors on the appendages (Friedman and Strickler 1975; Poulet and Marsot 1978; Friedman 1980; Strickler 1982; Andrews 1983; Legier-Visser et al.

1986). Small food particles are directed towards the mouthparts without contacting the maxillae setae (Price *et al.* 1983; Vanderploeg and Paffenhofer 1985; Price and Paffenhofer 1986). Cladocerean filtering is still open to much debate (Fryer 1987). At issue is whether water passes through the mesh on the thoracic limbs (Brendelberger *et al.* 1986) or if these act like solid paddles which guide food particles towards the collecting area (Gerritsen *et al.* 1988). A feature of the current filter feeding model is an acceptance of an extensive behavioural component in food particle selection compared with the previous mechanistic model.

CHAPTER TWO: MATERIALS AND METHODS

2.1 Study Area

Mt Bold Reservoir (35°07'S., 138°43'E.) is located on the Onkaparinga River in the Mt Lofty Ranges, 35 km from Adelaide, South Australia (Figure 2.1). The reservoir is 247 m above sea level and has a dendritic morphology characteristic of a flooded river valley (Figure 2.2). At full storage capacity the reservoir has a surface area of 308 hectares, an average depth of 25.4 m with the maximum depth of 41.4 m at the dam wall, and a volume of 45,900 Ml. There is a fixed outlet 15 m from the bottom at the wall. Figure 2.2 shows the morphology and bathymetry of the reservoir.

Mt Bold Reservoir has two major water sources; its catchment in the Mt Lofty Ranges and the Murray River. The catchment which covers an area of 388 km^2 is extensively used for agriculture with some urban development. Consequences of this multiple land use on water quality have been examined by Ganf (1982). The Adelaide region has a Mediterranean climate with 70% of the annual rainfall occuring in the six month winter-spring period (Schwerdtfeger 1976). This concentration of rain initiates erosional problems in the catchment which contribute to the suspended sediment load of the reservoir water.

Increased water consumption during the dry summer and the lack of sufficient storage means that water is pumped from the Murray River (Figure 2.1) to augment the natural supply throughout the dry period. The Murray-Darling river system is the major drainage system for south-eastern Australia (Figure 2.2); features of this system are given in Bayly and Williams (1973) and Walker (1979, 1986).

2.2 Physical and Chemical Measurements

Water temperature was measured to ±0.1 °C using a thermister probe (TPS Pty. Ltd. Brisbane, Australia), which was calibrated against a National Standards Laboratory certified mercury in glass thermometer. Dissolved oxygen was measured using a permeable membrane electrode (YSI Model 51B; Yellow Springs Instruments, Yellow Springs, Ohio, USA) with manual temperature correction. Before use the electrode was calibrated against saturated air.

Upwelling and downwelling irradiance was measured simultaneously using two quantum sensors (LI192) mounted in opposite directions. These quantum sensors coupled to quantum meters (LI185S; Lambda Instruments, Lincoln, Nebraska, USA) measured the waveband 400-700 nm which is equivalent to photosynthetically active radiation or PAR (Kirk 1983). Irradiance depth profiles were done one metre away from the side of the boat, under constant sky conditions.

Water depth was measured on the dam wall. Daily inflow and outflow was recorded by the Engineering and Water Supply Department of South Australia (E. & W.S.) using Leupold and Stevens Type A71 recorders at gauging stations above and below the reservoir.

Chemical analyses were done fortnightly by the E. & W. S. as part of routine water quality monitoring. Analyses were based on the automated Technicon procedures as outlined in Ganf (1982). Conductivity was measured fortnightly by the E. & W.S. using a conductivity meter with automatic temperature compensation (Model CDM83; Radiometer, Copenhagen, Denmark). Conductivity was reported corrected to 25 °C.

2.3 Biological Measurements

Water samples were collected from discrete depths with a 1 litre Friedinger bottle. Integrated euphotic zone samples were obtained using a 4m PVC tube sampler (Lund and Talling 1957). Water samples were stored in acid washed polythene bottles which were kept cool and dark in polystyrene boxes until in the laboratory.

The vertical distribution of chlorophyll *a* was determined using a submersible Otter pump (Beresford, Birmingham, UK) connected to a hose which was lowered down the water column. *In situ* fluorescence measurements were made with a Turner Model III fluorometer (Turner Associates, Palo Alto, California), fitted with a flow through door. Continuous output was recorded on a chart recorder (Rikadenki, Kogyo Co. Ltd., Tokyo). Fluorescence units were converted to chlorophyll *a* concentrations by analysis of samples from the outflow.

Water samples for chlorophyll *a* analysis were concentrated onto Whatman GF/C filters, homogenized, and the pigment extracted cold (12 h) in 90% (v/v) acetone. Chlorophyll *a* concentration was estimated spectrophotometrically using the formula of Talling and Driver

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(1963). Chlorophyll a : phaeophytin a or the acid ratio (Golterman *et al.* 1978) was obained after acidification of the 10 ml chlorophyll a extracts with 100 μl 4N HCl and remeasuring the 665 nm absorbance after 10 minutes.

Phytoplankton in water samples were preserved in 1% Lugols iodine solution (Vollenweider 1974) and concentrated by sedimentation. Samples were allowed a minimum of 3 h per cm of water column height to allow complete sedimentation of small cells (Furnet and Benson-Evans 1982). Phytoplankton cells in the concentrate were counted in settling tubes with an inverted microscope (Nikon Diaphot) by the technique of Lund *et al.* (1958). Silicone 781 glass sealant (Dow Corning) was used to glue the coverslips to the glass tubing to make settling tubes. This was found to be more durable than the Araldite (Ciba-Geigy) recommended by Lund *et al.* (1958). To allow the counting of individual cells; *Microcystis* colonies were broken by sonication using an MSE ultrasonic disintegrator (Measuring and Scientific Equipment, Crawley, UK) as described by Reynolds and Jaworski (1978). Average cell surface areas and volumes were computed from microscopic measurements of cell dimensions using formulae of equivalent geometric shapes (Reynolds 1984a; Bartsch 1974). Phytoplankton were identified using the keys of Prescott (1978).

Zooplankton were collected from discrete depths using a modified Schindler (1969) trap with a volume of 13 litres. Zooplankton were concentrated onto a 40 μm stainless steel mesh, back washed into a constant volume funnel and preserved in 4% (v/v) formalin. Integrated vertical samples of zooplankton were collected from vertical hauls (1 m s^{-1}) of a conical net. The net had a mouth diameter of 0.25 m, mesh width of 64 μm, porosity of 29% and an open area of 2.22 (Tranter and Smith 1968). Zooplankton numbers were estimated by counting subsamples taken with a wide bore pipette, using counting trays and a stereomicroscope (Zeiss SR). For identification, individual animals were disected with electrolytically sharpened tungsten needles and mounted in polyvinyl-alcohol-lactophenol. Zooplankton were identified from the keys of Bayly (1961, 1964) and Williams (1980a) (Copepoda); Bayly *et al.* (1967) and Smirnov and Timms (1982) (Cladocera); and Koste (1978) (Rotifera). Zooplankton biomass was computed from microscopic length measurements using established length-dry weight regressions.

Dry weight was measured by concentrating the plankton onto pre-washed and pre-weighed Whatman GF/C filters, drying at 105 °C, cooling in a desiccator, and re-weighing on a

Cahn Model G ratio electrobalance (Ventron Instruments, Paramount, California). The filters were then combusted at 550 °C in a muffle furnace and re-weighed to give the proportion of inorganic to organic material. Dry weights of individual zooplankton species were obtained by placing several similar sized individuals onto pre-weighed metal gauzes and following the above dry weight procedure.

Particle concentrations were measured with a Coulter Counter (Model TAII; Coulter Electronics, Hertfordshire, UK) fitted with either 140, 70 or 30 μm apertures. Sodium chloride (0.5 or 2% w/v AR) was used as the electrolyte with 0.5-2 ml of the particle suspension added to 40 ml of electrolyte. Distilled water freshly double-filtered through 0.22 μm membrane filters was used for the electrolyte solvent. This was necessary to ensure low background counts. Latex beads (Coulter Electronics) were used to calibrate the instrument.

2.4 Zooplankton Grazing Measurement

Zooplankton grazing was measured through measurement of the amount of radioactivity the animals accumulate from a suspension of radioactively labeled cells. ^{14}C was the radionuclide used to label the algal cells due to its ease of incorporation and low energy radiation. Grazing measurements were made on board a boat on the reservoir and in the laboratory.

Algal culture

Both pure cultures and natural phytoplankton assemblages from Mt Bold were used as food and labeled as food tracers. The pure cultures were obtained from the University of Texas Starr collection (Starr 1978). The algae were grown in either ASM1 (Gorham et al. 1964) or WC (Guillard and Lorenzen 1972) media. Cultures were maintained in constant environment growth chambers (Warren Sherer, Melbourne, Australia) at 20-25 °C, at a photon irradiance of c. 50 μE m^{-2} s^{-1} (400-700 nm) under Sylvania cool white fluorescent tubes with a 14:10 h light-dark cycle. Mt Bold water was filtered through 100 μm and 40 μm stainless steel screens to remove zooplankton and large algae. The remaining natural seston was then filtered onto membrane filters and resuspended in ASM1 or WC media to give a culture of natural phytoplankton.

*Allowance was not made for the potential loss of radioactivity during preservation which may have been significant (Thompson et al. 1982).

^{14}C labelling

One to five mCi (37-185 MBq) of NaH^{14}CO$_3$ (Amersham Australia) was diluted with autoclaved distilled water to make a stock solution of 50-100 μCi ml^{-1} (1.85-3.70 MBq ml^{-1}) which was stored in a ground glass stoppered bottle at 2 °C. Fifty μCi (1.85 MBq) of this stock solution was inoculated into 100 ml of a freshly subcultured pure algal culture and incubated as above for at least a week before use. When natural Mt Bold phytoplankton was used a minimum incubation time was required so the inoculated cultures (50 μCi per 100 ml) were kept in continuous low light (c. 30 μE m^{-2} s^{-1}) at the collection temperature of the water sample. Continuous light allows photosynthetic uptake of ^{14}C but inhibits cell division thereby maintaining initial composition. Incubation times were also shortened by reducing the amount of carrier (non-radioactive medium) in the culture media. A time series experiment was done to determine the minimum incubation time necessary to obtain adequately labeled food. Prior to use the labeled cultures were gently filtered onto membrane filters, rinsed, and resuspended in non-radioactive media (ASM1 or filtered reservoir water).

Zooplankton feeding

Feeding experiments were done in 2 or 13 litre containers which are relatively large for these measurements (Rigler 1971). Animals were allowed to acclimatize in these containers for 10 minutes (field) or 60 minutes (laboratory) in subdued light before measurement. Labeled algal tracer was injected into and gently but thoroughly mixed throughout the container. The feeding period was measured from the completion of mixing to the middle of the removal of animals from the food suspension. Time series experiments were done to establish the gut passage times of the zooplankton present and the feeding period used was shorter than these. After mixing the tracer in, the animals were not disturbed until the end of the feeding period. The animals were then removed by rapidly pouring the feeding suspension through a 100 μm screen and immediately anaesthetized by immersion in carbonated water (commercial soda water) to prevent gut evacuation. After 2 minutes the animals were thoroughly rinsed in deionized water to remove adhering algae and preserved in Lugols iodine to minimize loss of radioactivity[*](Holtby and Knoechel 1981; Persson 1982). Duplicate volumes of feeding suspension were filtered onto Whatman GF/C filters to determine the activity per volume. Filters were stored dry with algae uppermost in glass scintillation vials in the dark. Samples of the feeding suspension were preserved in Lugols

iodine or 4% (v/v) formalin for cell concentration measurement which was done either microscopically or using a Coulter Counter. When using the Coulter Counter samples were preserved with 0.22 μm membrane filtered formalin as the Lugols iodine reacted with the electrodes causing erratic counts.

Measurement of ingested radioactivity

In the laboratory, for zooplankton community grazing rates the whole zooplankton sample was filtered onto Whatman GF/C paper which was then placed into a glass scintillation vial with the animals uppermost. For zooplankton species grazing rates, groups of individuals were picked out of the sample using fine forceps under a stereomicroscope and placed onto Whatman GF/C paper which then went into a scintillation vial, animals uppermost. After 1 ml of tissue solubilizer (NCS, Amersham) was added to all scintillation vials they were then digested for 12 h at 50 °C in a waterbath. The glass fibre filter paper did not dissolve but always lay flat on the bottom of the vial. After cooling, 10 ml of scintillation fluor (6 g PPO and 75 mg POPOP per litre toluene) was added to the vials which were then dark adapted for 3-12 h to minimize chemiluminescence. Radioactivity in the samples was measured using a liquid scintillation spectrometer (Model 3330, Packard Tri-Carb). Due to the low radioactivity of small groups of animals, samples were counted for 20 minutes each which meant up to 48 h between the first and the last samples. This is insignificant with respect to the half life of ^{14}C (5700 y) but chemiluminescence and background counts may change during this period. Consequently background counts were determined at the beginning and at the end of such periods before exposure to light for vials containing GF/C paper, NCS and scintillation fluor. Filtering and feeding rates were calculated using standard equations (e.g. Peters 1984).

Quenching

Correction for self-absorption was not necessary for the zooplankton since tissue solubilizer was used. Solubilizer was also used to break down the phytoplankton cells since the radioactivity of the animals and that of the feeding suspension must be counted at the same efficiency. However solubilization of phytoplankton results in coloured solutions which can cause severe quenching. Where high concentrations of algae were used in experiments, quenching was checked and minimum amounts of feeding suspension filtered for radioactivity

determinations. Quenching was also checked when high concentrations of inorganic sediments were used in experiments.

2.5 Data Analysis

Statistical analysis was done based on Sokal and Rohlf (1981), utilizing the BIOM package supplied by these authors. Multivariate analyses were done using a numerical taxonomy package NTP (Belbin *et al.* 1984) and the SPSS (Nie *et al.* 1975) and SPSS^X (SPSS 1986) statistical packages. Specific experimental design, methodology and analysis are given in the relevant sections. Levels of significance are indicated as follows:

ns = not significant; $*$ = $0.01 < P < 0.05$; $**$ = $0.001 < P < 0.01$; $***$ = $P < 0.001$.

CHAPTER THREE: MT BOLD RESERVOIR LIMNOLOGY 1981-1983

3.1 PHYSICAL AND CHEMICAL ENVIRONMENT

3.1.1 Hydrology

Rainfall in the catchment of Mt Bold Reservoir varied seasonally and between the years of the study. Table 3.1 shows the monthly rainfall recorded in the Mt Lofty Ranges catchment from 1981 to 1983 inclusive, and the annual totals for each year. The annual average is 736 mm (Schwerdtfeger 1976) so 1981 and 1983 had above average, while 1982 had below average rainfall. Most of the rain falls during the southern winter (Table 3.1).

The seasonal differences in rainfall combined with variable consumption outflows, result in large fluctuations in water storage in the reservoir. Figures 3.1a-b show the water depth (measured at the reservoir wall) and the volume of water stored in Mt Bold Reservoir from September 1981 to September 1983. Water is pumped from the Murray River during periods of low rainfall. Figures 3.2a-b show the total daily inflow into Mt Bold during the study, with the contribution from the Murray River indicated.

In September 1981 the reservoir was full with a wall depth of 41.40 m and a volume of 45,900 Ml. Throughout the summer of 1981/1982 there was little inflow, resulting in a reduction in storage until August 1982 when the reservoir had a depth of 16.45 m and a volume of 3875 Ml. Pumping was initially commenced in April 1982 but stopped in anticipation of rain by June 1982. Insufficient rainfall during the 1982 winter resulted in pumping beginning again in August 1982 and continuing throughout the 1982/1983 summer until April 1983. During this period the depth of the reservoir increased to around 30 m where it was maintained by pumping. The 1983 winter rainfall resulted in catchment run off which rapidly filled the reservoir by September 1983.

A consequence of the different annual rainfall was that during the 1981/1982 summer growth season the water in the reservoir was from the catchment, while in the 1982/1983 summer growth season it was primarily Murray River water.

The ratio of daily inflow volume to stored water volume varies as a result of fluctuations in

both variables. Figures 3.4a-b show this ratio expressed as a percentage; it ranges from 0 to 11% d^{-1}. The latter represents a theoretical complete*dilution time of 9 days. The theoretical complete*dilution time was short during much of the 1982/1983 pumping from the Murray River. Catchment run off during winter 1983 briefly resulted in short theoretical *dilution times.   (*dilution = replacement)

Mt Bold is a storage reservoir, providing water to a supply reservoir downstream. Outflow from Mt Bold is controlled and varies on an operational as well as a seasonal basis. Figures 3.3a-b show the daily outflow from Mt Bold during the study. Gaps in the record are due to gauge malfunction. The ratio of daily outflow volume to stored water volume is shown as a percentage in Figures 3.4a-b; it ranges from 0.005 to 7% d^{-1}. The latter represents a supply duration of 14 days.

3.1.2 Wind

Surface wind provides the main external force to mix the water column (Green *et al.* 1987). Figures 3.5a-b show the daily wind run recorded at Mt Bold during the study. The daily wind run ranged from 24 to 352 km d^{-1}. There was no marked seasonality of wind run during the study although monthly averages (Figure 3.6) suggest higher wind runs during summer compared to winter and a higher wind run throughout the 1982/1983 summer compared to the 1981/1982 summer.

3.1.3 Solar Radiation

Figures 3.7a-b show the daily total solar radiation recorded in Adelaide during the study period. There is a distinct annual cycle due to the 35 °S. latitude of Adelaide, with a range from 2.0 to 33.4 MJ m^{-2} d^{-1}. Intermittent cloud cover reduces the daily solar radiation markedly during summer, less so in winter.

Both photosynthetically active radiation (PAR) and heat energy input into the reservoir vary over the year. Variation in PAR directly influences the growth potential of phytoplankton. Heat energy absorption changes the temperature of the reservoir water which again directly influences the growth rate of plankton. In addition the surface layers are differentially heated, creating a vertical gradient of water density which stabilizes the

water column and reduces vertical water movements.

3.1.4 Temperature

Mt Bold Reservoir is a warm monomictic lake according to the classification of Hutchinson and Loffler (1956). The mean water column temperature in Mt Bold varied from 9.2 to 22.2 °C during the study period. The maximum temperature recorded was 28.0 °C at the surface and the minimum was 9.0 °C at the bottom. Figure 3.8 shows the seasonal variation of water temperature with depth from September 1981 to September 1983, recorded at the southern site (Ganf 1982).

After isothermal conditions through winter 1981, the reservoir started to stratify during September 1981. The water column was strongly stratified throughout the summer of 1981/1982, breaking down to isothermy in March 1982. During September 1982 a temperature gradient was initiated, however the water column was only weakly stratified over the 1982/1983 summer, and was isothermal by April 1983. The lack of a strong temperature gradient over the 1982/1983 summer was likely due to the proportionally large flow through during this period (Figure 3.4) and the increased amount of wind (Figure 3.6).

3.1.5 Water Column Stability

Numerical estimates of water column stability due to temperature induced density gradients were obtained by calculating the Brunt-Vaisala frequency (N^2) for the water column. N^2 has units of frequency as it is the natural frequency of vertical oscillation for a given displacement from an equilibrium (Mortimer 1974; Harris 1983). The greater the stability, the more spatially constrained is the amplitude of oscillation, hence the greater the frequency (Viner 1985).

Water temperatures were converted to densities using the 5th degree polynomial expression of Kell (1967). The Brunt-Vaisala frequency was calculated from $N^2 = (g/\rho_0)(d\rho/dz)$ where g is the acceleration due to gravity, ρ_0 is the density of surface water, and $d\rho/dz$ is the density gradient throughout the water column. The density term used as the denominator (ρ_0) may be the density of the surface water (Phillips 1966), the average density of the water column (Reynolds *et al.* 1984; Imberger 1985), or the density of pure water at 4 °C (Trimbee

and Harris 1984a). Mt Bold N^2 calculated using the average density of the water column was less than 1% smaller than N^2 calculated using the surface density.

The Brunt-Vaisala frequency of the whole water column is shown in Figures 3.9a-b for September 1981 to September 1983. Sampling dates are numbered from the start of the study period. N^2 values ranged from 10.7×10^{-6} to 843.6×10^{-6} s^{-2}, which represented the gradient from complete vertical mixing to stratification in Mt Bold Reservoir. The water column was more stable during the 1981/1982 summer than the 1982/1983 summer (Figure 3.9). The Brunt-Vaisala frequency for the whole water column is less sensitive to partial column mixing than if a shorter column length is considered. For this reason Trimbee and Harris (1984a) and Reynolds $et\ al.$ (1984) used the top 6 m of 10 m and 12 m water columns respectively. If the vertical depth range in Mt Bold was restricted to 6 m from the surface, then N^2 values ranged from 0 to 2102.8×10^{-6} s^{-2}. With this restriction the N^2 stability of Mt Bold Reservoir was comparable to values obtained in Northern Hemisphere lakes. Trimbee and Harris (1984a) recorded a maximum of c. 1900×10^{-6} s^{-2} in Guelph Lake, Canada; Reynolds $et\ al.$ (1984) recorded a maximum of 2280×10^{-6} s^{-2} in Lund Tube C, England; while Harris (1983) reported a range from 0 to c. 3700×10^{-6} s^{-2} for a 6 m column in Esthwaite Water, England. The N^2 stability found in Mt Bold Reservoir does not support the generalization of Imberger (1985) that Southern Hemisphere lakes are characterized by extremely strong buoyancy stabilization of the water column.

3.1.6 Vertical Mixing

One consequence of the increased stability due to thermal stratification is a reduction of vertical mixing in the water column. Definition of the extent of vertical mixing is not exact. Harris $et\ al.$ (1980a) used the depth to the maximum temperature change; Reynolds (1980) used the depth where the temperature gradient first exceeds 1 °C m^{-1}; while Lewis (1978b) defined the mixed depth as that over which nutrients and gases were freely redistributed within a 24 hour period.

The depth of maximum temperature change was determined from the individual temperature-depth profiles, as well as the depths at which the temperature gradient exceeded 1 °C m^{-1}. The latter was only present during the 1981/1982 summer; throughout the 1982/1983 summer the temperature gradient was less than 1 °C m^{-1}. Where there were

two or more depth intervals with equal maximum temperature changes, this definition of the mixed depth could not be applied. To resolve these difficulties the temperature-depth profiles were examined from the bottom up, and the depth where the temperature gradient deviated from an exponential form, was used as the mixed depth. This estimate was based on the understanding that if a water body was heated by radiation alone and no water movements occurred in it, then the temperature would decrease exponentially from the surface (Hutchinson 1957). This was an overestimation for those profiles where there were multiple steps although many of these were considered to be diurnal events.[*] Green *et al.* (1987) reported that New Zealand lakes also have relatively low gradients of temperature in the metalimnion.

Figures 3.10a-b show the estimated mixed depth (z_{mix}) as well as the maximum depth of the reservoir throughout the study period. During the 1981/1982 summer the mixed depth fluctuated between 5 and 10 m with several distinct oscillations. These fluctuations coincided with changes in daily solar radiation; increases in mixed depth followed days with reduced solar radiation input (Figure 3.11a). The fluctuations in mixed depth did not coincide with changes in the daily wind run. Wind induced turbulence at the water surface may have contributed to the mixed depth deepening since the daily wind run does not record wind gusts which may be sufficient to cause major mixing events (Green *et al.* 1987).

Thermal stratification was broken down in February 1982 when the whole water column was mixed following several days of reduced solar radiation. There was no major increase in the daily wind run across this period. The lack of importance of wind in the breakdown of thermal stratification in Southern Hemisphere lakes was noted by Imberger (1985) who reported that the elimination of the temperature gradient by penetrative convective cooling at night was often the cause of overturn in Southern Hemisphere lakes.

Throughout the 1982/1983 spring and summer the mixed depth fluctuated between 8 and 16 m, again with distinct oscillations. The increases in mixed depth were again associated with reduced solar radiation (Figure 3.11b). On two occasions the entire water column was mixed; both coincided with reduced solar radiation. There was also an increased wind run on the second occasion.

During the 1982/1983 summer there were periodic maintainance shutdowns in pumping

from the Murray River (Figure 3.2). These resulted in variations in the flow of water into the reservoir which may have contributed to the fluctuations in the mixed depth.

In March 1983 the water column was completely mixed following several days of reduced solar radiation and increased wind run.

Comparison of the vertical mixing estimates (Figure 3.10) with the calculated water column stability (Figure 3.9) shows that generally these two variables were negatively correlated. Thus decreases in N^2 coincided with increases in mixed depth. However a direct relationship between N^2 and z_{mix} could not be derived because the increases in mixed depth followed reduced solar radiation input just prior to the change (Figures 3.11a-b). The stability of the water column at the time of the change was not known. It would seem though that the relationship is not linear. N^2 generally increases through the 1981/1982 summer yet the mixed depth does not generally decrease. It is of note here that in 1981/1982 the water column mixed completely soon after maximum stability. In contrast N^2 was generally decreasing when the water column mixed in 1982/1983.

3.1.7 Underwater Light Climate

Solar radiation provides light for photosynthesis. The extent to which light penetrates water and is available to phytoplankton depends on absorption and scattering in the water column and the optical characteristics of the phytoplankton.

Ideally, the intensity of monochromatic light decreases exponentially with depth as described by the Beer-Lambert law; $I_z = I_0 e^{-Kz}$ where I_z is the light intensity at depth z metres, I_0 the surface intensity, and K the vertical attenuation coefficient (ln units m^{-1}). In practice, the attenuation of 400-700 nm photosynthetically active radiation (PAR) follows this relationship (Kirk 1977) and K for natural waters may be determined from a plot of ln I_z against z. Linear regression analysis was used to obtain the line of best fit on these plots, including any sub-surface deviations.

Estimates of the average vertical attenuation ceofficient of the downwelling irradiance (K_dave) in Mt Bold Reservoir during the study period are shown in Figures 3.12a-b and Appendix 3.1 with the associated standard error. Values ranged from 0.336 ± 0.006 to 3.558

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$\pm$ 0.051 ln m^{-1}. These limits and this range are within those reported for other Australian inland water bodies by Kirk (1983), however the lower limit is exceptionally low for Mt Bold Reservoir (Oliver and Ganf 1988). Initially in September 1981 K_dave peaked at 3.56 ln m^{-1} following catchment run-off. Throughout summer 1981 K_dave decreased to a minimum of 1.78 ln m^{-1} with several minor oscillations coinciding with chlorophyll a maxima (Figure 3.25), finally resulting in a large increase in K_dave which accompanied a large chlorophyll a peak following the breakdown of thermal stratification in March 1982. In the spring of 1982 the vertical attenuation coefficient decreased to exceptionally low levels, for Mt Bold Reservoir, after pumping from the Murray River commenced (Figure 3.2). Throughout the summer of 1982/1983 the vertical attenuation coefficient remained at these exceptionally low levels, reaching a minimum of 0.34 ln m^{-1}. K_dave rapidly increased with the inflow of catchment water in the winter of 1983.

Figures 3.13a-b show the euphotic depth (z_{eu}) which is defined as that depth to which 1% of sub-surface irradiance penetrates (Talling 1971). The euphotic depth was estimated from the regression equation between ln I_z and z. This depth approximates the photosynthetic limit and ranged from 1.29 to 13.70 m during the study period. Because Figure 3.13 is essentially a reciprocal plot of Figure 3.12; when the vertical attenuation coefficient is small, a small change has a large effect on the euphotic depth. Similarly a large change in a large attenuation coefficient has a small effect on the euphotic depth. Thus the euphotic depth was around 2 m from September 1981 to August 1982. From September 1982 until May 1983 it fluctuated between 8 and 13 m.

The ratio of upwelling to downwelling irradiance at any depth is termed the reflectance (R) at that depth. Reflectance increases with increasing depth until it becomes a constant, termed the asymptotic reflectance (R_a) (Kirk 1977). The asymptotic reflectance R_a was estimated on each sampling date from a plot of the reflectance at each depth against depth. When estimating R_a, changes in R when the upwelling irradiance was less than 1 μE m^{-2} s^{-1} were ignored. These changes were not considered reliable due to meter insensitivity. Estimates of R_a in Mt Bold during the study period are shown in Figures 3.14a-b and Appendix 3.1; values ranged from 0.024 to 0.141. These values are within the range reported by Kirk (1977) who attributed high values of R_a to high turbidity. There was an overall increase in R_a i.e. the maximum proportion of light scattered, until October 1982 after which it decreased rapidly to starting levels. The water column depth at which R_a was

reached, i.e. where the light field became completely uniform, is shown in Figures 3.15a-b. This depth ranged from 0.2 to 8.0 m, within the range reported by Kirk (1985) for turbid to clear inland waters. During the 1982/1983 season this depth was substantially deeper than during the 1981/1982 season.

An estimate of the ability of natural water to scatter light, the asymptotic backscattering coeficient (b_b'), was derived by Kirk (1977) who showed that $b_b' = 2KR_a$. Figures 3.16a-b and Appendix 3.1 show b_b' during the study period; values ranged from 0.024 to 0.730 ln m^{-1}, similar to those reported by Kirk (1980) who demonstrated a linear relationship between b_b' and nephelometric turbidity. Recently Ganf et $al.$ (1989) showed that 3.6 may be a more appropriate constant in the above relationship.

Kirk (1981a) used a Monte Carlo simulation procedure to derive relationships between the vertical attenuation coefficient (K), the irradiance reflectance (R), the absorption coefficient of the medium (a), and the scattering coefficient of the medium (b). Estimation of a and b from these relationships enables comparison of the separate contributions of absorption and scattering to the attenuation of light in the water column.

For the Mt Bold data the estimate of R_a was used as the reflectance at the euphotic depth, from which the estimates of a and b were then calculated using Figure 2 of Kirk (1981b) and the relationships described therein. Corrections were made for the changing solar altitude throughout the year. Adelaide midday solar angle varies from 12° to 58° away from the zenith (Spencer 1982). Estimates of a and b are plotted in Figures 3.17a-b on the same scale and listed in Appendix 3.1. Values for a ranged from 0.19 to 2.03 m^{-1}, and for b from 0.91 to 19.47 m^{-1}. These ranges are similar to those reported by Kirk (1981b) for other Australian inland waters.

The reduction in K during the 1982/1983 season coincided with a reduction in light scattering by suspended particulates although absorption was also reduced during this period. Scattering increases the probability of absorption due to an increase in the pathlength travelled by the photon. There were only minor increases in the absorption coefficient a during the major chlorophyll a peaks in the 1981/1982 season (Days 81, 114, 190; Figures 3.17 and 3.25). This implied that most light absorption was due to dissolved coloured substances in the water or gilvin (Kirk 1976) which is characteristic of Australian

inland waters. Direct measurements of gilvin concentrations were not made. Gilvin is formed during the decomposition of plant material (Kirk 1983) so catchment runoff would be expected to have higher concentrations than the Murray River water. This is supported by the variation in a during the study period (Figure 3.17).

The scattering coefficient b increased to a maximum during the chlorophyll a peak around Day 190 (Figures 3.17 and 3.25). This implies that the large increase in light attenuation during this bloom was due to scattering induced absorption. The dominant alga during this bloom was *Microcystis aeruginosa* (Section 3.2.4). Light scattering by the gas vesicles in *Microcystis aeruginosa* was documented by Walsby (1972). Other peaks in the scattering coefficient were associated with water inflow; either from the catchment (Days 11 and 701), or from the Murray River (Day 345). Scattering would be due to suspended sediments; either carried by the inflowing water or resuspended by them from the reservoir bottom. The rapid reduction in the scattering coefficient after the initial inflow of Murray River water (Day 352) was likely a reflection of the large flow through at that time (Figure 3.4), rather than sedimentation of the sediment load.

The attenuation coefficient K can be partitioned into the extinction due to phytoplankton ($K_s B$, where B is the biomass in terms of chlorophyll a and K_s is the specific extinction coefficient per unit biomass) and a background extinction coefficient (K_q, which is due to water, dissolved coloured compounds and suspended particulate matter) (Reynolds 1984a). When K_s and K_q are constant, they may be estimated from the linear relationship between the extinction coefficient K and the phytoplankton biomass B. During periods of rapid phytoplankton growth, K_q may remain constant. Table 3.2 shows K_s and K_q estimated by linear regression between K and chlorophyll a concentration on four occasions of rapid phytoplankton growth in 1981/1982. K_s values ranged from 0.012 to 0.033 ln (mg chl a)$^{-1}$ m^2 while K_q ranged from 1.64 to 2.46 ln m^{-1}. These estimates are within the ranges reported in the literature using this technique (Reynolds 1984a; Oliver and Ganf 1988). There was no change in K with increasing phytoplankton biomass during the 1982/1983 growth season. It should be noted here that because increases in K are a result of both absorption and scattering, the values obtained for K_s by this method are overestimates since scattering is not considered. Figure 3.17 demonstrates that phytoplankton may cause substantial light scattering.

The ratio of the euphotic depth to the mixed depth (z_{eu}/z_{mix}) is an indicator of the proportion of time spent in a favourable light climate. Figures 3.18a-b show this ratio; it varied from 0.061 to 3.003 during the study period. Typically this ratio was around 0.1 in winter. During the 1981/1982 summer it increased to around 0.3 with a peak of 0.85. Despite the lack of strong stratification during the 1982/1983 summer, the exceptional transparency of the water column resulted in this ratio oscillating between 0.7 and 1.5, with a peak of 3.0.

Coincident with the changes in both euphotic and mixed depths, there is seasonal variation in solar irradiance (Figure 3.7). Riley (1957) estimated the average irradiance within the mixed zone ($\overline{I}$) as; $\overline{I} = I_0(1 - e^{-Kz_{mix}})/Kz_{mix}$ where I_0 is the average daily solar irradiance for the prior week, z_{mix} the mixed depth, and K the vertical attenuation coefficient. Appendix 3.1 lists the calculated estimates of $\overline{I}$ on each sampling date during the study period. Generally the pattern of variation in $\overline{I}$ in Mt Bold Reservoir was the same as that for the ratio of the euphotic depth to the mixed depth (Figure 3.18).

3.1.8 Dissolved Oxygen

The distribution of dissolved oxygen (DO) in a water body is a function of supply (atmospheric exchange and photosynthesis), consumption (respiration) and water movement (Wetzel 1975). The solubility of oxygen in water is inversely dependent on the temperature (Hutchinson 1957), thus a changing thermal structure will influence the distribution of dissolved oxygen in the water column. Changing temperatures may influence the dissolved oxygen concentration or the percent saturation.

Figure 3.19 shows the depth-time distribution of dissolved oxygen in Mt Bold Reservoir during the study period. The pattern of DO distribution throughout the water column reflected water movement as indicated by the thermal structure, however the absolute concentrations of DO deviated substantially from those expected based on temperature only. When the reservoir was isothermal in September 1981 there was a uniform DO concentration throughout the water column. With the onset of thermal stratification DO concentrations decreased with increasing depth giving the characteristic clinograde profile of a eutrophic water body (Wetzel 1975). Throughout December 1981 there was a negative heterocline DO profile with the minimum immediately below the thermocline. By late summer the profile

was again clinograde with a very strong DO gradient associated with the thermocline. Dissolved oxygen concentrations in the hypolimnion during this period were less than 0.5 mg l^{-1}. This strong gradient persisted, despite the gradual breakdown of thermal stratification, until March 1982.

During the 1982/1983 summer the dissolved oxygen profile was $\underset{\wedge}{\text{orthograde}}$ although the lack of a strong thermocline meant there was no persistent reduction of dissolved oxygen in the hypolimnion.

The solubility of oxygen in water was determined, for the temperatures of Mt Bold Reservoir, from the formula of Montgomery *et al.* (1964). The influence of both atmospheric and hydrostatic pressure on oxygen solubility in the water column were not considered. The actual concentrations measured were compared with the calculated saturation values. Generally the measured concentrations were lower than the saturation values even during winter when water circulation and atmospheric exchange would promote equilibrium. This actual deficit (Hutchinson 1957) results from the uptake of oxygen in the free water or at the sediment-water interface, due to biological respiration and chemical oxidation of organic matter. Note that the salinity (Figure 3.23) of Mt. Bold Reservoir water would reduce the saturation DO concentration (Wetzel 1975) however this reduction would not account for the observed deficit.

Brief periods of supersaturation occurred in the upper layers of the water column, as shown in Figure 3.19. During summer these coincided with phytoplankton blooms (Figure 3.25), and so were the result of photosynthetic activity. The winter 1983 periods of supersaturation did not coincide with phytoplankton blooms or catchment run off, but may have resulted from recent upwelling or surface heating where the DO-temperature equilibrium had not yet been regained (Hutchinson 1957).

3.1.9 Nutrients

The importance of the chemical composition of natural waters in regulating phytoplankton abundance and composition has long been recognized (Reynolds 1984a). Phosphorus and/or nitrogen concentrations are commonly limiting (Lund 1965; Hutchinson 1967), and the consequences to the plankton of increased loadings of these nutrients through eutrophication

are well documented (Likens 1972). The importance of phosphorus to phytoplankton is its role in cellular metabolism, while nitrogen is a major constituent of cellular protoplasm (Wetzel 1975).

Routine analyses for phosphorus and nitrogen were done by the Engineering and Water Supply Department of South Australia. Surface water was sampled at fortnightly intervals while bottom samples were taken intermittently.

Figures 3.20.1a-b and 3.20.2a-b show total phosphorus (TP) and soluble reactive phosphate (SRP) concentrations of surface water and 30 m water respectively during the study period. Soluble reactive phosphate is considered to be available to phytoplankton. In September 1981 SRP concentrations throughout the water column were around 100 μg l^{-1}. SRP then decreased with the onset of phytoplankton growth, until surface concentrations of c. 15 μg l^{-1} were reached after the second major peak in chlorophyll a during the 1981/1982 summer (Day 114; Figure 3.25). Surface water SRP concentrations increased with the breakdown of thermal stratification (Day 161; Figure 3.10) then decreased again during the subsequent phytoplankton bloom (Day 190; Figure 3.25). Concentrations remained low during the 1982 winter when there was no catchment inflow and then decreased further with the inflow of Murray River water. During the summer of 1982/1983 SRP concentrations in the water column were <5 μg l^{-1}. When the water column mixed in March 1983 (Day 547; Figure 3.10) surface SRP concentrations briefly increased, with major increases following the first inflow from the catchment. At this time (Day 679) the phosphorus was almost entirely SRP, probably from super-phosphate fertilizer application on the catchment. Following further large inflows from the catchment, surface SRP concentration briefly decreased, however by September 1983 SRP concentrations had increased to September 1981 levels. Particulate phosphorus makes up the difference between TP and SRP. This particulate phosphorus includes soluble organically bound phosphorus which may be available to phytoplankton through phosphatase activity (Nalewajko and Lean 1980).

Figures 3.21.1a-b and 3.21.2a-b show the total Kjeldahl nitrogen (TKN) (organic nitrogen and ammonia) and inorganic nitrogen (IN) (nitrate and nitrite) concentrations in surface and 30 m water respectively during the study period. In September 1981 IN concentrations throughout the water column were about 500 μg l^{-1}. Concentrations were reduced to c. 100 μg l^{-1} following the two phytoplankton blooms of the 1981/1982 summer (Day 114; Figure

3.25), and then increased with the breakdown of thermal stratification (Day 161; Figure 3.10). Inorganic nitrogen concentrations increased with the initial inflow of Murray River water until August 1982, thereafter they decreased. During the 1982/1983 summer, IN concentrations decreased to <10 μg l^{-1} in the surface waters, with a small increase during mixing (Day 547; Figure 3.10). Large increases in IN concentration accompanied catchment inflow during the 1983 winter.

The absolute values and seasonal changes in nutrient concentrations described above for the 1981/1983 study period generally agree with those documented by Ganf (1982) for Mt Bold Reservoir during 1978/1979. However the minimum concentrations of both SRP (<5 μg l^{-1}) and IN (<10 μg l^{-1}) during this study were substantially lower than those recorded by Ganf (1982), i.e. >20 μg l^{-1} and >200 μg l^{-1} respectively. Ganf (1982) used bioassay experiments to examine the algal growth potential in the euphotic zone throughout a typical annual cycle and related the results to the nutrient concentrations in the water column. Ganf (1982) found that the major nutrient input to Mt Bold Reservoir occurred during winter run off from the catchment. Murray River water had a significantly lower nutrient load than water derived from the catchment. Furthermore, using bioassay experiments, algal growth potential was undetectable in the euphotic zone during summer stratification. Upon mixing, nutrients from hypolimnion water enabled algal growth in the euphotic zone. Ganf (1982) also demonstrated a lack of correspondance between the chemically determined nutrient concentrations and the algal growth potential on several occasions, suggesting that the measured nutrients were not necessarily available to the phytoplankton and that there was another (unknown) limiting nutrient.

The relative proportion of nitrogen to phosphorus indicates which nutrient may be limiting and also influences phytoplankton biomass and composition (Smith 1982). Forsberg *et al.* (1978) set a critical level for nitrogen limitation as TN/TP $<$ 10 by weight and for phosphorus limitation as TN/TP $>$17. When TN/TP was between 10 and 17, either or both nutrients could be limiting. Figures 3.22.1a-b and 3.22.2a-b show the TN/TP ratio by weight in the surface and 30 m water respectively during the study period. In the surface water TN/TP ranged from 7 to 69, although it was less than 10 on one occasion only (Day 21). This range represents nitrogen limitation through to severe phosphorus limitation. Surface TN/TP was greater than 17 from January 1982 until the breakdown of thermal stratification in early March 1982 and again throughout most of the period of pumping i.e.

for most of the 1982/1983 growth season (Figure 3.22.1). During February 1983 the TN/TP ratio was greater than 40, implying severe phosphorus limitation. Apart from the above periods, the surface TN/TP ratio was between 10 and c. 17 during the study.

3.1.10 Salinity

Figures 3.23.1a-b and 3.23.2a-b show the 25 °C conductivity (K) of surface and 30 m water respectively, in Mt Bold Reservoir during the study period. Conductivity values ranged from 318 to 1390 μS cm^{-1}. Water from the catchment had a low conductivity while Murray River water had a high conductivity. Thus the changes shown in Figure 3.23 result from the changing contribution of water from these two sources. Because Australian inland waters are dominated by sodium and chloride (Bayly and Williams 1973), conductivity may be converted to total dissolved solids (TDS) using the relationship of Williams (1966) as follows; TDS = $(3.4\times10^{-6} K_{18} + 0.666) K_{18}$ where TDS is in ppm and K_{18} is the conductivity in μsiemens or μmho at 18 °C. Conductivity increases with increasing temperature and may be corrected to a standard temperature of 18 °C using the following formula from Bayly and Williams (1973); $K_{18} = K_t / [1+0.025(t-18)]$ where K_t is the measured conductivity at t °C. Using the two equations above, TDS was estimated to range from 181 to 793 ppm in Mt Bold Reservoir during the study period.

3.2 MT BOLD PHYTOPLANKTON

3.2.1 Phytoplankton Biomass Concentration

Chlorophyll a Vertical Distribution

Figure 3.24 shows the depth distribution of chlorophyll a in the upper 15 m of the water column on a series of dates through the 1981/1982 growth season. Chlorophyll a profiles were obtained from *in situ* fluorescence measurements taken within one hour of midday. Fluorescence units were converted to chlorophyll a concentrations by regression of fluorescence readings on extracted chlorophyll a from calibration samples. Conversion of fluorescence measurements to chlorophyll a concentrations must be done with care as background fluorescence may change considerably.

Throughout the 1981/1982 growth season there were no major chlorophyll a maxima below 4 m depth. The integrated 0-4m tube samples taken at the same time are marked on Figure 3.24; these adequately sampled the chlorophyll a distribution in the water column. The estimated vertical mixing depths based on temperature distributions (Figure 3.10) are indicated in Figure 3.24. The vertical distribution of chlorophyll a coincides with the mixed depth on some occasions but on others, phytoplankton buoyancy and motility overcome the apparent influence of water movement.

Chlorophyll a Integrated Samples

Figures 3.25a-b show the chlorophyll a concentration of Mt Bold Reservoir from an integrated 0-4 m tube sample, during the study period. Integrated sample chlorophyll a concentrations ranged from 0.30 to 70.75 μg l^{-1}. The patterns of chlorophyll a change in Mt Bold were similar for the two growing seasons studied, although chlorophyll a concentrations during phytoplankton maxima in 1982/1983 were 15 to 40% of the 1981/1982 levels (Figure 3.25).

Generally chlorophyll a concentrations were low throughout winter. Phytoplankton concentration started to increase in September, resulting in the first chlorophyll a peak in November (Days 81 and 429 or 27.XI.81 and 10.XI.82 respectively). After a decrease to low concentrations a second chlorophyll a peak followed 30-40 days later (Days 114 and 469 or 30.XII.81 and 20.XII.82). A longer period of c. 70 days with lower but fluctuating concentrations was followed by a third chlorophyll a peak (Days 190 and 547 or 16.III.82 and 08.III.83) around the breakdown of thermal stratification (Figure 3.10).

Chlorophyll a : Phaeophytin a

The acid ratio of the integrated samples is shown in Figures 3.26a-b. The ratio ranged from 1.10 to 1.79. A ratio of 1.0 indicates that all of the absorption is due to phaeophytin a while a ratio of 1.7 indicates that it is all due to chlorophyll a (Golterman et $al.$ 1978). Ratios in excess of 1.7 may be due to incomplete conversion of the chlorophyll a to phaeophytin a upon acidification (Bailey-Watts 1982).

During most of the sampling period the ratio oscillated between 1.4 and 1.7, but on two

occasions (Days 95 and 473) the ratio indicated substantial degradation of the chlorophyll a (Figure 3.26). Both of these occasions were during or immediately after a major phytoplankton bloom (Figure 3.25).

Phytoplankton Volume Concentration

Figures 3.27a-b show the estimated total cell volume concentration of the phytoplankton in Mt Bold Reservoir during the study period, plotted on a log scale for convenience. Slopes on this figure give estimates of the rate of change in terms of $\log_{10}$ units per day. Total phytoplankton volume concentration estimates ranged from 1.06×10^4 to 3.63×10^7 μm^3 ml^{-1}. A comparison of Figures 3.25 and 3.27 indicates that the maximum chlorophyll a did not coincide with the maximum total phytoplankton volume. The general lack of correlation between these two measures of phytoplankton biomass is shown in Figures 3.28a-b for the 1981/1982 and 1982/1983 seasons respectively. Note that chlorophyll a concentrations >25 μg l^{-1} and phytoplankton volume concentrations $>10^7$ μm^3 ml^{-1} are excluded from Figure 3.28. However, if the major algal blooms were considered individually, then there were linear relationships between chlorophyll a and phytoplankton volume when one or two taxa dominated. Table 3.3 lists the regressions obtained during these periods, as well as the major phytoplankton components. Despite the small numbers of data points and the errors involved in estimating total volumes, it is apparent that the different phytoplankton taxa contain different chlorophyll a concentrations per unit cell volume. Consequently a general relationship between total phytoplankton volume and chlorophyll a concentration could not be used to directly compare phytoplankton biomass in Mt Bold Reservoir during the study period.

Of note here are the changes in chlorophyll a and phytoplankton volume on one particular occasion. From Day 81 to Day 88 chlorophyll a concentration was reduced (Figure 3.25) but the total phytoplankton volume increased (Figure 3.27). The chlorophyll : phaeophytin ratio decreased across this period (Figure 3.26) suggesting that some of the absorbance attributed to chlorophyll was in fact due to phaeophytin.

3.2.2 Phytoplankton Species Composition

Table 3.4 lists the phytoplankton taxa recorded in Mt Bold Reservoir during the study

period, with estimates of cell size [Greatest Axial Linear Dimension or GALD (Lewis 1976), Second Greatest Axial Linear Dimension or SGALD (Lewis 1979) and volume] and/or colony size [GALD, SGALD and volume] where appropriate. Colony sizes of the chain forming phytoplankton (*Melosira* spp. and *Anabaena* sp.) and of *Microcystis aeruginosa* were not estimated. Estimates of the surface area : volume ratio are also listed in Table 3.4.

Figures 3.29.1a-b to 3.29.5a-b show the estimated densities of the phytoplankton taxa during the study period, plotted on a log scale for convenience. Note the change of scale for the larger *Staurastrum, Volvox* and *Ceratium* taxa. Figure 3.30 summarizes the occurrences of the phytoplankton taxa throughout the study period. Figures 3.29 and 3.30 show that some phytoplankton taxa were present for long periods of time during the study while others occurred only briefly. Similarily some taxa reached high abundances while others remained low. The frequency distributions of phytoplankton taxa abundance were used to describe these differences. Lewis (1977a) used the coefficient of variation (CV) and the skewness of the abundance frequency distributions to characterize the growth of phytoplankton species. Species with a high CV and skewness were considered opportunistic or r-selected while species with a low CV and skewness were considered conservative or K-selected (Lewis 1977a).

Tables 3.5a-b list these statistics for the phytoplankton taxa recorded during each of the seasons studied. The coefficients of variation (Table 3.5a) were between 88% and 655% which represented a considerable range of growth response between phytoplankton taxa. All but one taxon had a CV >100% indicating that within most taxa there was high variability in abundance. The phytoplankton taxa are ordered in Table 3.5a with respect to increasing CV in 1981/1982. Several taxa showed substantial differences in CV between the two seasons. *Microcystis, Sphaerocystis, Cyclotella 2, Ankistrodesmus, Chlamydomonas, Ochromonas* and *Cryptomonas 2* all decreased while *Melosira 3, Closteriopsis, Carteria* and *Volvox* all increased in the 1982/1983 season relative to 1981/1982.

Similar results as described above for the CV were obtained for the skewness statistic (Table 3.5b). Skewness ranged from 1.06 to 7.76, the positive values indicate a skew or tail to the right of the frequency distribution. This is from growth pulses which result in abundances above the modal level. Skewness for many taxa also varied between the seasons. *Microcystis, Sphaerocystis, Cyclotella 2, Ankistrodesmus, Chlamydomonas, Ochromonas, Cryptomonas 1,*

Cryptomonas 2 and *Cyanarcus* all decreased substantially while *Melosira 3, Closteriopsis, Carteria, Schroederia* and *Oocystis* all increased in 1982/1983 relative to 1981/1982.

Comparison of Tables 3.4 and 3.5 indicates there was no consistent relationship between either the specific morphology of the phytoplankton taxa (as described by the surface area to volume ratio) or the taxonomic position and either the CV or the skewness during both of the seasons. However some phytoplankton taxa of similar general morphology have similar statistics on occasion e.g. *Volvox* and *Coelastrum*; *Microcystis* and *Sphaerocystis*. Furthermore there were no morphological characteristics shared by those taxa whose CV or skewness either increased or decreased between the two seasons.

3.2.3 Phytoplankton Species Change

The degree to which phytoplankton taxa co-occur is a measure of the ecological similarity between the taxa (Lewis 1977b). Phytoplankton abundance represents the response of taxa to both past and present environmental conditions. However the change in abundance represents the response to environmental conditions during the period of change with less influence of previous history (Lewis 1977b).

From the abundance estimates of each phytoplankton taxon, the rate of change in abundance between sampling dates, in ln units per day, was calculated. This calculation of net growth rate between the sampling dates did not include any error associated with the abundance estimates. The net growth rates between sampling dates were compared for pairs of taxa across each season using Pearson's correlation coefficient. Sampling dates on which either of the taxa were absent were not included in the correlation, thus reducing the bias caused by periods with no change.

The significant correlations between the net growth rates of the respective phytoplankton taxa are shown in Table 3.6 for the 1981/1982 and 1982/1983 seasons, above and below the diagonal respectively. The sign and level of significance of the correlations are indicated in Table 3.6. Identification letters are assigned to the taxa for convenience; these are listed in Table 3.4. Figures 3.31.1a-b show the positive correlations between taxa during the study period while Figures 3.31.2a-b show the negative correlations.

There were 65 significant correlations between 19 phytoplankton taxa during the 1981/1982 season; 51 were positive and 14 were negative. Of the 51 positive correlations, 27 were within a tight group of 8 taxa (*Anabaena, Cyclotella 2, Melosira 1, Melosira 3, Chlamydomonas, Oocystis, Ochromonas* and *Cryptomonas 1*) which all had very similar net growth responses (Figure 3.31.1a). Examination of Table 3.4 indicates that this group cut across taxonomic, size and morphological categories. Of the 14 negative correlations, 8 involved *Cyanarcus* (Figure 3.31.2a). This phytoplankton taxa had strong negative correlations with all members of the group above, implying that its net growth response was completely out of phase with those of the group. *Cyanarcus* does not appear to have any outstanding difference in taxonomic position or morphology from this group (Table 3.4).

There were 76 significant correlations between 26 phytoplankton taxa in the 1982/1983 season; 56 were positive, 20 negative. Within the positive correlations several taxa (eg *Microcystis, Cryptomonas 1, Cyclotella 1, LSC, LGS, SMS and UBG*) grouped together with similar net growth responses (Figure 3.31.1b), yet again this grouping did not follow taxonomic or morphological categories. Negative correlations in net growth response were more widespread during the 1982/1983 season compared with the 1981/1982 season (Figure 3.31.2b).

Comparison of Figures 3.31.1 and 3.31.2 indicates that those phytoplankton taxa that were tightly grouped in 1981/1982, were not grouped together in 1982/1983. This implies that the ecological similarity of the phytoplankton taxa as measured by correlated net growth rates may change seasonally. Although there were both positive and negative correlations between the net growth rate of taxa, this approach did not result in any separation of these taxa into discrete communities.

3.2.4 Phytoplankton Community Composition

Although many phytoplankton taxa occur in Mt Bold Reservoir, at any one time only a few dominate the community either numerically or in terms of biomass. A brief description of the dominant changes in phytoplankton community composition follows. Initially densities are considered, then contributions to volume, where these differ from the former. Figures 3.32.1a-b to 3.32.5a-b show the percentage composition, based on density, of the Mt Bold phytoplankton community during the study period. The phytoplankton community is

separated into broad taxonomic categories for ease of interpretation. In the 1982/1983 period a group of unidentified algae contributed substantially to the community composition.

Figures 3.32.1a-3.32.5a show that throughout September and October 1981 *Ochromonas* and *Cryptomonas 1* numerically dominated the phytoplankton with *Ankistrodesmus*, *Cryptomonas 2*, *Chlamydomonas* and *Schroederia* present as subdominants. By mid November both *Cryptomonas* species and *Ochromonas* had decreased and by the end of November *Cyclotella 2*, *Melosira 1* and *Carteria* were dominant. The increase in these three taxa coincided with the first peak in chlorophyll *a* concentration for the 1981/1982 growth season (Figure 3.25). These three algae all decreased rapidly in the first week of December to be replaced by *Microcystis* and *Ankistrodesmus*.

Microcystis increased from mid November until it dominated completely throughout December, coinciding with the second chlorophyll *a* peak (Figure 3.25). In early January *Microcystis* decreased and *Schroederia* briefly dominated. By mid January *Microcystis* and *Carteria* were co-dominant followed by *Ankistrodesmus*, *Cyclotella 2* and *Melosira 3*. All algae except *Microcystis* decreased by early February leaving *Microcystis* in total dominance throughout February, March and April. The third peak in chlorophyll *a* concentration occurred in mid March (Figure 3.25).

At the end of April there was an increase in *Cyclotella 2* some two months after the breakdown of thermal stratification (Figure 3.10), as well as a brief pulse of *Coelastrum*. *Microcystis* densities fluctuated throughout May, June and July, occasionally dominating before disappearing completely by August. *Anabaena*, *Cyanarcus*, *Melosira 3*, *Cyclotella 2* and *Trachelomonas* also fluctuated as subdominants throughout May, June and July. During July and August *Cyanarcus* dominated; with *Ochromonas* subdominant in July and *Sphaerocystis* in August.

The composition of the phytoplankton during the 1982/1983 growth season (Figures 3.32.1b to 3.32.5b) differed from the 1981/1982 season. In September and October 1982 *Cyanarcus* dominated, with *Cyclotella 2* subdominant in September and *Ochromonas*, *Oocystis* and *Schroederia* subdominants in October. In November *Cyanarcus* was replaced by *Schroederia* and there was a brief mid month pulse of *Carteria* coinciding with the first peak in chlorophyll *a* of the 1982/1983 season (Figure 3.25). In late November an unidentified small

spherical alga (*SMS*) increased but by early December *Schroederia* was again dominant. In mid December it was replaced by an unidentified cyanobacteria (*UBG*) and then by *Oocystis* which dominated from the end of December to mid January after which *Schroederia* was co-dominant once again.

At the end of January *Microcystis* appeared and was briefly dominant. Although *Microcystis* was present until August it did not completely dominate the phytoplankton as in the 1981/1982 season. For most of February and March *Oocystis* dominated until replaced by *Microcystis* in late March. There were peaks of *Sphaerocystis* in early February and mid March and *Ceratium* appeared briefly in mid March. *Cyclotella 2* increased at the end of March and throughout April, May, June and July was co-dominant with *Microcystis*. *Cryptomonas 1* and *UBG* were subdominants. *Sphaerocystis* and the unidentified algae *LSC* and *SMS* were all present in July. *Microcystis* and *Cyclotella 2* were replaced by *Ochromonas* in August and in September *Ochromonas* and *Cryptomonas 2* co-dominated.

The composition of the phytoplankton community based on biomass often differs from that based on densities. When small celled phytoplankton taxa dominate numerically, they do not always contribute greatly to the total biomass. Figures 3.33.1a-b to 3.33.5a-b show the percentage composition based on biomass for the study period.

In September and October 1981 *Chlamydomonas*, *Mallomonas* and *Cryptomonas* spp. made up most of the community biomass (Figures 3.33.1a-3.33.5a) rather than the numerically dominant *Ochromonas*. In November *Cyclotella 2* and *Carteria* contributed the most biomass; in December *Microcystis* and *Cyclotella 2* alternated as the major contributors. From late December through January 1982 *Cyclotella 2*, *Carteria* and *Melosira 3* had a greater biomass than the numerically dominant *Microcystis*, however *Microcystis* did completely dominate the phytoplankton from mid February through March. *Cyclotella 2*, *Melosira 3* and *Trachelomonas* dominated the biomass from April through to August 1982.

Cyclotella 2 again dominated the phytoplankton biomass during September and October 1982 with *Oocystis* subdominant (Figures 3.33.1b-3.33.5b). In mid November *Carteria* was dominant until replaced by *Oocystis* in late November. An increase in *Volvox* from early to late December coincided with the second chlorophyll *a* peak of the 1982/1983 period (Figure 3.25). *Volvox*, which was completely dominant in late December, was completely replaced by

Oocystis in early January 1983. *Oocystis* dominated throughout January and February. In early March 1983 there was an increase in *Ceratium* biomass which coincided with the third chlorophyll *a* peak of 1982/1983 (Figure 3.25). From late March through to early August 1983 *Cyclotella 2* completely dominated the phytoplankton biomass, being replaced in late August by *Cryptomonas 2* with *Chlamydomonas* as a subdominant.

3.2.5 Phytoplankton Community Definition

Two independent multivariate analyses; Bray-Curtis with UPGMA classification and DCA ordination (Section 1.2), were used to define the phytoplankton communities and to examine the relationships between them. Phytoplankton taxa densities were ln transformed prior to analysis to reduce the influence of very high densities (Section 3.3.5). Figures 3.34a and 3.34b show the results of separate DCA ordinations for the 1981/1982 and 1982/1983 periods respectively. These figures have the first vector on the X axis and the second vector on the Y axis. Sampling dates are identified by the day number from the start of sampling; these are joined sequentially for ease of interpretation. Figures 3.35a and 3.35b show the Bray-Curtis with UPGMA classification results superimposed onto the DCA plots of vectors 1 and 2. Sample dates which have an average similarity of 0.4 are grouped by dashed lines. Groups of sampling dates which are related at a lower similarity of 0.28 have the same identification letter.

These analyses indicate that there were four major groups of sampling dates in 1981/1982 (A-D) which could be subdivided into eleven minor groups as follows; A1-3, B1-2, C1-4 and D1-2 (Figure 3.35a). There were five major groups of sampling dates in 1982/1983 (E-I) which could be subdivided into twelve minor groups as follows; E1-4, F, G1-2, H1-3 and I1-2 (Figure 3.35b). Definition of these groups is subjective, however the close agreement of the two independent multivariate analyses supports the delineation shown. Table 3.7 lists the sequential periods (in terms of day number) of the sampling date groups or phytoplankton communities, and indicates the relationships between them by an identification code. Major and minor communities are indicated by a letter and a number respectively in the identification code. Figures 3.34 and 3.35 and Table 3.7 show that on several occasions during both years the phytoplankton community returned to previous communities; either those immediately prior or even previous to this. Thus the changes that occurred either resulted in new communities or a return to previous communities. Table 3.7 also lists the

transition periods between communities, in terms of day number.

3.2.6 Phytoplankton Community Change

From the previous descriptions and analyses it is clear that the composition of the
phytoplankton community changed during the study period. These changes were not
continuous nor were they always of the same magnitude. One measure of the rate of
community change is the summed difference index (SD) proposed by Lewis (1978a). This
was estimated over a short time interval as;

$$SD = \sum_i \{|[b_i(t_1)/B(t_1)] - [b_i(t_2)/B(t_2)]|\}/(t_2 - t_1)$$

where $b_i(t)$ is the abundance of the ith taxa, and $B(t)$ the community size at time t.
Abundance and size may be expressed in terms of numbers or biomass (Lewis 1978a).
Figures 3.36a-b show the SD index based on phytoplankton numbers in Mt Bold during the
study period. Values of SD ranged from 1.0×10^{-3} to 0.57 d^{-1}. It should be noted from the
equation that the summed difference index is dependent on the sampling interval, thus
artificially low values may result from long sampling intervals. Rates of change less than 0.1
d^{-1} were used by Reynolds (1980) to define stable periods in the phytoplankton community
while rates exceeding 0.1 d^{-1} indicated periods of significant change. The periods of change
indicated by the SD index were compared with the transition periods between communities
defined by the multivariate analyses of the previous section, termed MVA communities.
Because the SD index is dependent on the sampling interval, it reflects the rate of change
rather than the absolute change. The absolute summed difference change is given by the
numerator in the equation prior to division by the sampling interval.

Figure 3.37a shows the position of each sampling interval of the 1981/1982 season on a plot
with the SD index (as a rate) on the X axis and the absolute SD change on the Y axis.
Symbols indicate if the sampling intervals correspond to major, minor or no change between
the MVA communities. Sampling intervals of interest are identified by the day number at
the end of the interval. Figure 3.37b is the corresponding plot for the 1982/1983 season. The
linear relationships on these plots are reflections of the most common (uniform) sampling
intervals.

During the 1981/1982 season almost all the major and minor MVA community changes had
associated SD rates >0.1 d^{-1} (Figure 3.37a). An exception was interval 123 which

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corresponded to a major MVA community change. The long sampling interval (18 days) reduced the SD rate to below 0.1 d^{-1}; the absolute SD change (1.47) was higher than that for most other sampling intervals and therefore reflected a community change. The other exception was interval 39 which corresponded to a minor MVA community change. Again the sampling interval may have been the cause although it was only 12 days. If it was the more common 7 days, interval 39 would be moved to the right on the plot until the SD rate was >0.1 d^{-1}. Figure 3.37a initially suggests that an absolute SD change in excess of 0.7 corresponds to an MVA community change, irrespective of the sampling time interval. However there were several sampling intervals (140, 240, 310, 345, 366) which had SD rates >0.1 d^{-1} and absolute SD changes >0.7 but which did not reflect any changes in the MVA communities (Figure 3.37a).

During the 1982/1983 season most of the major MVA community changes had SD rates >0.1 d^{-1} but the majority of the minor MVA changes had SD rates <0.1 d^{-1} (Figure 3.37b). Three of these minor MVA changes (intervals 562, 701, 737) and the one major change exception (interval 716) were over long sampling intervals (15-21 days) which disproportionately reduced the SD rates since the absolute SD changes were high. The other minor MVA changes (intervals 436, 491, 497, 529) all had absolute SD changes <0.7 so the sampling interval was not implicated. Once again there were several sampling intervals (469, 479, 501, 512, 515, 533) which had SD rates >0.1 d^{-1} and absolute SD changes >0.7 yet did not reflect changes in the MVA communities.

It would seem from Figures 3.37a-b that neither the SD rate of change nor the absolute SD change consistently agreed with community changes as defined by the multivariate analyses. Harris (1986) describes the dependence of SD on the time interval of sampling as a fundamental problem of the index. Using both daily and weekly samples Harris (1986) found that there was little similarity between the calculated rates of change; both in magnitude and in temporal sequence of change.

3.2.7 Phytoplankton Community Comparison 1981/1982 vs. 1982/1983

To compare the phytoplankton communities between the two years of the study period, the multivariate analyses were repeated using the complete data set. Because the results of such analyses depend on the data used, the relationships between sampling date groups may

differ between the individual years and the combined years. Figure 3.38 shows the Bray-Curtis with UPGMA classification results superimposed onto the DCA ordination plot of vectors 1 and 2. Sampling dates are grouped at the same average similarity (0.4) as for the individual year analyses; dates within a group have the same numbered symbol, groups of dates which are related at 0.28 similarity have the same symbol.

These analyses resulted in four major communities (A-D) across the study period which could be divided into twenty minor communities at 0.4 average similarity as follows; A1-3, B1-4, C1-7 and D1-6. Major communities B, C and D were separated in the ordination by vectors 1 and 2 but separation of communities A and C required other ordination axes (Figure 3.38). Figure 3.39 indicates the particular year a sample date belonged to, with open symbols for 1981/1982 and closed symbols for 1982/1983. Comparison of Figures 3.38 and 3.39 shows that most (17 out of 20) of the minor communities were specific to one or other year. The three exceptions each had single overlapping dates, two of which covered the beginning and the end of the study period. The major community B was only present in the first year (1981/1982), while major community A was mainly present in the first year with minor overlap into the second year. Major community D was mainly present in the second year (1982/1983) with a single overlap into the first year. Major community C was present in both of the study years.

Table 3.8 lists the sequential periods (in terms of day numbers) of the phytoplankton communities across the study period and indicates the relationships between them. The community intervals and transition periods for the two year combined data (Table 3.8) were the same as those for the separate years (Table 3.7), however the affinities of some sample date groups changed between the individual years and when both years were combined. For example, the seven community intervals between Days 415 and 505 represented three major communities (E, F and G) in the individual analysis but were all placed into the same major community (D) in the combined analysis. Table 3.8 shows that the phytoplankton communities differed between most of the two years. They were similar at the beginning and the end of the study period.

The composition of each phytoplankton community was determined by ranking the dominant taxa present. For each taxon the maximum ln transformed density was divided into six equal intervals and the density on each sampling date was given a score from 0 to 5

corresponding to the appropriate density interval. Scores for each taxon were then averaged across all sampling dates in the community and the average scores of all taxa present in the community were ranked. Table 3.9 lists the taxa in order of dominance within each phytoplankton community. Taxa of equal rank are enclosed by brackets. The major communities were characterised by one or more taxa although these taxa were not necessarily dominant in all minor communities therein, and were also present in other major communities. Major community A was characterised by *Ochromonas* and *Cryptomonas 1*; community B by *Microcystis*; community C had either *Cyanarcus* or *Cyclotella 2* and community D had *Schroederia*.

3.3 MT BOLD ZOOPLANKTON

3.3.1 Zooplankton Sampling

Zooplankton were sampled at intervals between 3 and 21 days from the southern site (Ganf 1982) of the reservoir. A single profile was taken on each occasion with trap samples at 1 m, then 2 m intervals until 10 m, then 5 m intervals to the bottom. Routinely a single subsample of between 10 and 20% of the trap sample was counted. The rational for this sampling procedure was based on the following investigations:

1. Prior analysis of surface samples taken fortnightly during 1977/1978 (E. & W.S. unpublished data) suggested that there was no consistent difference in total zooplankton densities between the southern and northern sites (Ganf 1982) of the reservoir throughout the year (t_{25} 0.45, ns).

2. On 14.XII.81 two duplicate profiles were taken about 100 m apart to compare horizontal with vertical variation in zooplankton density. ANOVA showed that five of the eight major zooplankton taxa present had significantly different densities at different depths while none of the taxa differed in density between the two sites.

3. A series of five consecutive trap samples was taken at the same location and depth on 28.IX.81. Total zooplankton numbers were determined by counting whole samples. Analysis of this series indicated that a single trap sample gave an estimate of the mean zooplankton number with 15% error at a 95% confidence level.

4. The variation between subsamples was examined by repeated subsampling of a single

trap sample. Assuming a random distribution of organisms within the trap sample, the mean to variance ratio of the subsamples can be compared to that expected from a Poisson distribution (Elliot 1971). The densities of all ten zooplankton taxa scored were randomly distributed across the subsamples.

3.3.2 Zooplankton Species Composition

The dominant zooplankton taxa in Mt Bold Reservoir during the study period were; the calanoid copepods *Boeckella triarticulata* Thompson, *Calamoecia ampulla* (Searle), their copepodites and nauplii; the cladocerans *Daphnia carinata* King, *Ceriodaphnia quadrangula* (Muller), *Ceriodaphnia cornuta* Sars, *Diaphanosoma unguiculatum* Gurney and *Bosmina meridionalis* Sars; and the rotifers *Hexarthra mira* (Hudson), *Synchaeta pectinata* Ehrenberg, *S. stylata* Wierzejski, *S. oblonga* Ehrenberg, *Keratella australis* (Berzins), *K. cochlearis* (Gosse), *K. procurva* (Thorpe), *K. quadrata* (Muller), *K. slacki* (Berzins), *K. tropica* (Apstein), *K.valga* (Ehrenberg), *Polyarthra dolichoptera* (Idelson), *P. vulgaris* Carlin, *Conochilus dossarius* (Hudson), *Asplanchna priodonta* Gosse and *A. brightwelli* Gosse. The parasitic rotifer *Ascomorphella volvocicola* (Plate) was present during blooms of its *Volvox* host. The close relationship between this parasite and its host is described in Ganf *et al.* (1983). Due to the lack of published keys on the Australian cyclopoid copepods, taxa were only identified to genus. The dominant genera were *Microcyclops*, *Mesocyclops* and *Australocyclops*.

Figures 3.40.1a-b to 3.40.16a-b show the depth distribution of the density estimates for the Mt Bold zooplankton taxa during the study period. Density estimates are grouped into six ranks of abundance, represented by different circle sizes. For all taxa the abundance classes are; <0.1, 0.1-1.0, 1.0-10, 10-100, 100-1000 and >1000 individuals per litre. Superimposed on Figures 3.40.1 to 3.40.16 is the reservoir depth recorded at the dam wall. Samples were taken between Days 415 and 443 however these were combined before counting thus depth distributions are not plotted. Density estimates of each zooplankton taxa at each depth sampled were averaged. Figures 3.41.1a-b to 3.41.3a-b show the mean (±se) density estimates for Mt Bold zooplankton taxa during the study period.

The calanoid copepod *Boeckella triarticulata* is common and widely distributed throughout Australasia (Bayly 1964). It is ubiquitous across the Murray-Darling basin, occurring

perennially in most reservoirs (Shiel 1981). *Boeckella triarticulata* was present in Mt Bold Reservoir during most of the study period (Figures 3.40.1a-b) although its abundance varied (Figures 3.41.1a-b). The average density of *Boeckella* in the water column during spring 1981 was around 1 animal per litre. Densities increased in December 1981 to a maximum of 46 ± 16 (mean $\pm$ se) animals per litre and remained high ($>5\ l^{-1}$) throughout the 1981/1982 summer. *Boeckella* density declined in March 1982 and after a brief absence in April 1982, fluctuated around 1 animal per litre through winter 1982. In spring 1982 densities increased to $9 \pm 3\ l^{-1}$, and then declined to around 1 animal per litre during the 1982/1983 summer. A brief absence in March 1983 was followed by densities which fluctuated around 1 animal per litre throughout winter 1983.

The smaller calanoid copepod *Calamoecia ampulla* is found across south-eastern and south-western Australia, often in association with the larger *Boeckella triarticulata* (Bayly and Williams 1973). *Calamoecia ampulla* is widely distributed in the Murray-Darling basin, being the dominant copepod in many reservoirs therein (Shiel 1981). *Calamoecia ampulla* was present in Mt Bold Reservoir throughout the study period (Figures 3.40.2a-b); it varied in abundance in a similar manner to *B. triarticulata* (Figures 3.41.1a-b). The average density of *Calamoecia* was less than 1 animal per litre in early spring 1981. *Calamoecia* density increased in October 1981 and reached 103 ± 37 animals per litre in mid December 1981. Densities remained high ($>10\ l^{-1}$) throughout the 1981/1982 summer, declined in March 1982 but then increased to high levels ($>10\ l^{-1}$) by July 1982, and reached a maximum of 154 ± 38 animals per litre in October 1982. *Calamoecia* densities remained high ($>10\ l^{-1}$) throughout the 1982/1983 summer but in late April 1983 declined and fluctuated around 1 animal per litre during winter 1983.

The cyclopoid copepod genera; *Microcyclops, Mesocyclops* and *Australocyclops* all occur widely in the Murray-Darling basin (Shiel 1981). The densities of these three genera are combined in Figures 3.40.3 and 3.41.1. Cyclopoid copepods were present in Mt Bold Reservoir throughout the study period (Figures 3.40.3a-b). Cyclopoid densities were between 1 and 5 animals per litre in spring and early summer 1981/1982 and increased to between 20 and 30 animals per litre in late summer/autumn 1982, with a maximum density of $38 \pm 9\ l^{-1}$ in late March 1982 (Figures 3.41.1a-b). In winter 1982 cyclopoid densities declined and remained around 1 animal per litre throughout spring and summer 1982/1983. After a brief increase to $17 \pm 3\ l^{-1}$ in May 1983, cyclopoid densities decreased and remained

around 1 animal per litre throughout winter 1983.

The copepodite stages of both calanoid copepods are not differentiated in Figures 3.40.4 and 3.41.1. Calanoid copepodites were present in Mt Bold Reservoir throughout the study period (Figures 3.40.4a-b). Patterns of abundance reflected those of the adult copepods, with summer maxima and winter minima (Figures 3.41.1a-b). Maximum densities of 64 $\pm$ 16 and 60 $\pm$ 24 copepodites per litre occurred in late November 1981 and late September 1982 respectively, preceding the adult maxima. Another maxima of 46 $\pm$ 19 copepodites per litre was recorded in late August 1983 just proir to the end of the study period.

The naupliar stages of all copepods are combined in Figures 3.40.5 and 3.41.1. Nauplii were present in Mt Bold Reservoir throughout the study period (Figures 3.40.5a-b); mean densities ranged from 4 $\pm$ 1 to 212 $\pm$ 74 nauplii per litre (Figures 3.41.1a-b). Naupliar patterns of abundance reflect those of adult copepods although naupliar densities were less variable.

The five dominant cladocerans recorded from Mt Bold Reservoir are all common and widely distributed throughout Australian inland waters; the Murray-Darling basin in particular (Smirnov and Timms 1983; Shiel 1981).

Daphnia carinata was seasonal in Mt Bold Reservoir (Figures 3.40.6a-b). *Daphnia* densities were between 0.1 and 1 animal per litre for most of spring and early summer 1981/1982 (Figures 3.41.2a-b). Densities increased rapidly in early February 1982 to 25 $\pm$ 8 animals per litre, then decreased equally rapidly in late February 1982. *Daphnia* was absent or remained at low densities (0.1-$1.0\ l^{-1}$) throughout autumn and winter 1982. During the summer of 1982/1983 there were three peaks in *Daphnia* density at 3-4 week intervals. On one occasion a maximum of 43 $\pm$ 13 animals per litre was recorded. *Daphnia* densities decreased to <1 animal per litre throughout autumn and winter 1983.

Ceriodaphnia quadrangula was present in Mt Bold Reservoir throughout the study period (Figures 3.40.7a-b) although it had seasonal variations in abundance (Figures 3.41.2a-b). *Ceriodaphnia quadrangula* densities were initially high ($>10\ l^{-1}$) in spring 1981 and increased to 50 $\pm$ 11 animals per litre in early November 1981. After an abrupt decrease to around $1\ l^{-1}$ in late November 1981, *C. quadrangula* densities increased in early January

1982 to a maximum of 72 $\pm$ 20 animals per litre. Densities remained around 10 animals per litre until early April 1982 when there was a brief increase to 37 $\pm$ 17 l^{-1}. *C. quadrangula* densities then declined to <1 l^{-1} until August 1982 when they increased to 39 $\pm$ 15 animals per litre in September 1982. In December 1982 densities declined to <1 animal per litre and remained low for the rest of the study period.

Ceriodaphnia cornuta was only recorded in Mt Bold reservoir during the autumn and winter of 1982 (Figures 3.40.8a-b). Densities were usually between 0.1 and 1.0 animals per litre but reached a maximum of 9 $\pm$ 1 l^{-1} in mid April 1982 (Figures 3.41.2a-b).

Diaphanosoma unguiculatum was seasonal in Mt Bold Reservoir during the study period (Figures 3.40.9a-b). *Diaphanosoma* densities were between 0.1 and 1.0 animal per litre during spring 1981, with a brief absence around the end of November 1981 (Figures 3.41.2a-b). Densities increased in early January 1982 and fluctuated between 1 and 10 animals per litre until mid April 1982. During this period a maximum density of 16 $\pm$ 12 l^{-1} was reached in mid March 1982. *Diaphanosoma* densities decreased in April 1982 and remained <1 animal per litre throughout winter 1982. After a brief increase in September 1982 which reached 9 $\pm$ 5 animals per litre, *Diaphanosoma* densities decreased and remained between 0.1 and 1.0 l^{-1} for the rest of the study period, with occasional periods of absence.

Bosmina meridionalis was only recorded in Mt Bold Reservoir during the 1981/1982 year of the study period (Figures 3.40.10a-b). *Bosmina* increased rapidly in mid December 1981 to 30 $\pm$ 11 animals per litre and then remained at densities >10 l^{-1} until the end of January 1982 (Figures 3.41.2a-b). Densities then decreased until mid April when there was a rapid increase, to a maximum of 33 $\pm$ 19 animals per litre, followed by an equally rapid decline. There were only occasional traces of *Bosmina* in the reservoir for the rest of the study period.

All of the rotifer species recorded in Mt Bold Reservoir during the study period are widely distributed throughout the Murray-Darling basin (Shiel 1981) and the genera recorded are the main ones in the reservoirs therein (Shiel and Koste 1986). Figures 3.40.11a-b to 3.40.16a-b show the depth distribution of each rotifer genus; where there was more than one species, densities have been combined.

Hexarthra mira was the most common rotifer in Mt Bold Reservoir although it was not perennial (Figures 3.40.11a-b). *Hexarthra* was present from October 1981 until July 1982 at densities between 1 and 10 animals per litre, with a density of 26 ± 14 l^{-1} in early December 1981 (Figures 3.41.3a-b). It was then absent or at low densities (<0.1 l^{-1}) until December 1982 after which densities increased to around 10 animals per litre until April 1983. A maximum density of 56 ± 17 animals per litre occurred in late December 1982. After April 1983 densities decreased to <1 l^{-1} and by June 1983 *Hexarthra* was absent from the reservoir.

Syncheata spp. presence in Mt Bold reservoir was sporadic (Figures 3.40.12a-b) and usually at low densities (<1 l^{-1}) (Figures 3.41.3a-b). On two occasions however *Syncheata* densities were very high; 216 ± 48 and 4700 ± 2103 animals per litre in early and late November 1981 respectively. On both occasions the increases were rapid and were followed by equally rapid decreases.

Keratella spp., *Polyarthra* spp. and *Conochilus* sp. were only present in Mt Bold Reservoir during the first year (1981/1982) of the study period (Figures 3.40.13a-b to 3.40.15a-b). *Keratella* spp. and *Polyarthra* spp. both increased rapidly at the end of November 1981, with maxima of 387 ± 167 and 127 ± 41 animals per litre respectively (Figures 3.41.3a-b). *Conochilus* sp. also showed a small increase at this time. Densities of all three genera decreased just as rapidly in early December 1981. *Keratella* spp. were then present at low densities (<1 l^{-1}) until July 1982 while *Polyarthra* spp. were absent until April 1982 when densities increased to about 1 animal per litre until June 1982. *Conochilus* sp. was absent until late January 1982 when densities rapidly increased to 100 ± 35 animals per litre, then declined equally as rapidly. All three of these rotifer genera showed minor density increases in mid April 1982 (Figures 3.41.3a-b).

Asplanchna spp. were present on two occasions during the study period (Figures 3.40.16a-b). Densities reached 12 ± 5 animals per litre in early December 1981 and a maximum of 122 ± 7 l^{-1} in late March 1983 (Figures 3.41.3a-b).

The zooplankton taxa present in Mt Bold Reservoir during the study period represent a small fraction of the total recorded by Shiel (1981) for the Murray-Darling basin. However the Mt Bold taxa were the same as those found in other reservoirs and lakes in this basin

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(Croome 1980; Hillman 1980; Powling 1980; Shiel 1981; Geddes 1984b).

Figure 3.42 summarises the incidence of the zooplankton taxa throughout the study period. Solid lines on this figure indicate a substantial presence, dots indicate low densities. The perennial, seasonal or sporadic occurrence of the zooplankton taxa found in Mt Bold is in general agreement with the results from other reservoirs and lakes in the Murray-Darling basin (Walker and Hillman 1977; Shiel 1981; Geddes 1984b). However there were notable differences between the 1981/1982 and the 1982/1983 seasons in Mt Bold. The cladocerans *Bosmina meridionalis* and *Ceriodaphnia cornuta* and the rotifers *Polyarthra* spp., *Keratella* spp. and *Conochilus* sp. were either completely absent or greatly reduced in 1982/1983. Shiel *et al.* (1987) noted that the lack of rotifers in Mt Bold Reservoir during the 1982/1983 season was the reverse of the rotifer response in other pumped water storages and suggested that it was due to the chlorination of River Murray water in the pipeline prior to release into the reservoir.

The maximum densities of individual zooplankton taxa in Mt Bold Reservoir (Figure 3.41) were high compared to other Murray-Darling basin reservoirs and lakes, however the variation in density across the study period was similar to that reported in the literature (Walker and Hillman 1977; Shiel 1981; Geddes 1984b).

The depth distribution of zooplankton shown in Figures 3.40.1a-b to 3.40.16a-b indicates that the stratified sampling with respect to depth was appropriate. Thus for all taxa there was a higher density of animals in the upper 10 m of the water column in which there was a greater sampling effort. At the same time most taxa were present throughout the water column at the time of sampling. There were however, notable reductions in animal density coinciding with depth distributions of dissolved oxygen (Figure 3.19). Zooplankton often avoid anoxic hypolimnion water during vertical migration (Hutchinson 1957). The densities of all Mt Bold zooplankton taxa except *Bosmina meridionalis, Keratella* spp. and the copepod nauplii were substantially reduced when dissolved oxygen concentrations were less than 1 mg per litre. Heaney *et al.* (1986) frequently found *Ceriodaphnia quadrangula* in Esthwaite Water at dissolved oxygen concentrations <1 mg l^{-1} but all other zooplankton recorded, including *Bosmina longirostris,* avoided near-anoxic conditions.

3.3.3 Zooplankton Biomass

Areal abundance of each zooplankton taxon in the water column of Mt Bold Reservoir was calculated by using an appropriate weighting factor on the density estimate from each depth. The weighting factors reflected the volume of the water column represented by each sample; the depth interval between successive samples was halved. The areal abundance estimates for each zooplankton taxon are given in Appendix 3.2 using the taxa codes of Figure 3.40. The areal abundance estimates were used to estimate total areal biomass and to examine the composition of the zooplankton community in terms of both numbers and biomass.

Total zooplankton areal biomass in the water column was estimated by conversion of the abundance of each zooplankton taxon to a biomass, using dry weight estimates for each taxon, and then summation of the biomass of all taxa. Figures 3.43a-b show the estimated total zooplankton areal biomass in Mt Bold Reservoir during the study period; areal biomass estimates ranged from 0.3 to 64.5 g dry wt m^{-2}. Total zooplankton areal biomass varied on a seasonal basis with summer maxima and winter minima. During spring 1981 zooplankton areal biomass increased slowly until late November 1981 when there was a rapid increase, reaching the maximum of 65 g dry wt m^{-2} in mid December 1981. There was a major reduction in phytoplankton biomass (Figures 3.25 and 3.27) and an increase in phaeophytin (Figure 3.26) coinciding with this zooplankton increase. Zooplankton areal biomass decreased abruptly after the mid December maximum with no change in composition (Figure 3.44). In early January 1982 zooplankton areal biomass increased to 38 g dry wt m^{-2} followed by an abrupt decrease. This increase coincided with another reduction in phytoplankton biomass (Figures 3.25 and 3.27). Zooplankton areal biomass then fluctuated between 10 and 30 g dry wt m^{-2} until February 1982 when it decreased and remained at less than 5 g dry wt m^{-2} throughout winter 1982.

Total zooplankton areal biomass increased in spring 1982 and fluctuated between 5 and 35 g dry wt m^{-2} throughout the 1982/1983 summer (Figure 3.43). Zooplankton areal biomass increases in early November and late December 1982 coincided with decreases in phytoplankton biomass and increased phaeophytin in the latter instance (Figure 3.26), however a major zooplankton increase to 35 g dry wt m^{-2} in late January 1983 was not reflected in the phytoplankton biomass (Figures 3.25 and 3.27). By early March 1983 zooplankton biomass decreased to less than 10 g dry wt m^{-2} where it remained throughout

winter 1983.

3.3.4 Zooplankton Community Composition

Figures 3.44.1a-b to 3.44.3a-b show the percentage composition of the zooplankton community, based on numbers, during the study period. The zooplankton community is separated into copepods, cladocerans and rotifers for ease of interpretation.

Copepod taxa numerically dominated the zooplankton community in Mt Bold Reservoir during most of the study period (Figures 3.44.1a-b). Within this category copepod nauplii were the most abundant taxa, representing up to 84% of the total zooplankton numbers. *Calamoecia* was the dominant adult copepod with up to 50% of the total numbers while *Boeckella* made up to 20%. Calanoid copepodite numbers made up to 52% of the total numbers, but were usually less than the combined adult calanoid copepod numbers. Cyclopoid copepods made up to 40% of total numbers.

Cladocerans were a major numerical component of the zooplankton community on three occasions during the study period (Figures 3.44.2a-b). In spring 1981 *Ceriodaphnia quadrangula* made up 20-50% of the community numbers; from February to April 1982 *C. quadrangula*, *C. cornuta*, *Diaphanosoma* and *Bosmina* together made up 10-45%; and finally from mid August to November 1982 *C. quadrangula* was 10-35% of the total zooplankton numbers.

Rotifers dominated the Mt Bold zooplankton community on several brief occasions between November 1981 and January 1982 and also in March 1983. The dominant genera on these occasions are shown in Figures 3.44.3a-b. Besides these pulses, *Hexarthra* sp. made up 10-15% of the community from late March to late April 1982 and 10-40% from mid December 1982 to February 1983 (Figures 3.44.3a-b).

The relative abundance of crustacean groups in the Mt Bold zooplankton is in agreement with the general findings of Mitchell (1986) for low altitude Australian lakes. Mitchell (1986) noted the dominance of copepods, in particular calanoids, over cladocerans in the limnetic zone of these lakes. Mitchell (1986) concludes that the zooplankton communities of Australian lakes differ from those of comparable environments in other regions of the world.

However Mitchell (1986) rejects the view that Australian zooplankton communities are simple in terms of species composition and argues that the differences are not adequately described by the commonly used 'mean momentary species composition' (cf. Bayly and Williams 1973).

Figures 3.45.1a-b to 3.45.3a-b show the percentage composition of Mt Bold zooplankton, based on biomass, during the study period. Copepod taxa still dominated the zooplankton community in terms of biomass (Figures 3.45.1a-b). The contribution of the larger adult copepods to the total community biomass was increased; *Boeckella* and *Calamoecia* adults represented up to 80% and 70% respectively of the total biomass at different times, although copepod nauplii still made up to 52% at other times. Cyclopoid copepods were 25-50% of total biomass between late March and mid June 1982.

Cladocerans often represented a greater proportion of total community biomass than of total numbers (Figures 3.45.2a-b). In spring 1981 cladocerans made up about 80% of the community biomass with *Daphnia* representing up to 65%. In mid February 1982 *Daphnia* contributed 57% while in mid March 1982 cladocerans made up 53% of total biomass. From mid September 1982 until mid March 1983 *Daphnia* represented from 8 to 80%, while from August to September 1983 it made up about 50% of the total biomass.

The contribution by rotifers to the total zooplankton biomass was reduced overall with one exception when *Syncheata* represented 70% of the total (Figures 3.45.3a-b).

3.3.5 Zooplankton Community Definition

Both classification and ordination (Section 1.2), were used to define discrete zooplankton communities during the study period. Initial analyses, using raw total column density scores, resulted in little agreement between the two approaches except that both differentiated sampling dates with very high rotifer densities (Days 56, 81, 88, 114, 562) from the rest. There was little differentiation of sampling date groups beyond this. The zooplankton density scores were ln transformed to reduce the influence of the very high densities and subsequent analyses resulted in good differentiation of sampling date groups. There was also good agreement between groups defined by the two analyses.

Figures 3.46a and 3.46b show the results of separate DCA ordinations for the 1981/1982 and 1982/1983 periods respectively. Sampling day numbers are joined sequentially with the first vector plotted on the X axis and the second vector on the Y axis. Figures 3.47a and 3.47b show the Bray-Curtis with UPGMA classification results, superimposed onto the DCA plots of vectors 1 and 2, for the 1981/1982 and 1982/1983 periods respectively. Sample dates which have an average similarity of 0.8 are grouped by dashed lines. Groups of dates which are related at an average similarity of 0.75 have the same identification number.

These analyses resulted in five major groups of sampling dates in 1981/1982 (1-5; Figure 3.47a) and two major groups in 1982/1983 (6-7; Figure 3.47b). The former could be divided into eight minor groups (1, 2A-C, 3, 4 and 5A-B) and the latter into six minor groups (6A-D, 7A-B). Table 3.10 lists the sequential periods (in terms of day number) of the sampling date groups or zooplankton communities and of the transition intervals between them. Major and minor communities are indicated by a number and a letter respectively in the identification code. Table 3.10 shows that during both years the changes in zooplankton communities involved both new communities and returns to previous communities.

3.3.6 Zooplankton Community Change

The rate of change in zooplankton community composition was determined using the summed difference index as was done for the phytoplankton community (Section 3.2.6). Figures 3.48a-b show the SD index based on zooplankton numbers in Mt Bold Reservoir during the study period; values ranged from 0.005 to 0.610 per day. Because of the differences in generation times, the critical SD rate of 0.1 d^{-1} used for phytoplankton communities by Reynolds (1980) would not necessarily be appropriate for zooplankton communities. It was expected that a comparison of the transition periods between the zooplankton communities defined by the multivariate analyses (MVA communities) and the corresponding SD values would indicate a more appropriate critical SD value.

Figure 3.49a shows the position of each sampling interval of the 1981/1982 season on a plot with the SD rate on the X axis and the absolute SD change on the Y axis. Symbols indicate if the intervals correspond to changes between the MVA communities, intervals of interest are identified by the day number at the end of the interval. Figure 3.49b is the corresponding plot for the 1982/1983 season.

Figure 3.49a indicates that during the 1981/1982 period there was little agreement between the MVA community changes and either the SD rate or the absolute SD change. Thus major and minor changes in the MVA communities had SD rates ranging from 0.012 to 0.482 d^{-1} and absolute SD changes ranging from 0.144 to 1.928. There were also sampling intervals (60, 84, 88, 114, 123) which had high SD values (both rates and absolute changes) yet did not correspond to changes in the MVA communities. During the 1982/1983 season all the MVA community changes had low SD rates and most had low absolute SD changes (Figure 3.49b). Sampling interval 569 had the highest SD values yet did not correspond to an MVA change. It was not possible to use the MVA communities to indicate an appropriate SD value for change in the zooplankton community, since there was no consistent agreement between the SD values and the MVA transition periods.

3.3.7 Zooplankton Community Comparison 1981/1982 vs. 1982/1983

To compare the zooplankton communities between the two years of the study period, the multivariate analyses were repeated using the combined data. Figure 3.50 shows the Bray-Curtis with UPGMA classification results superimposed onto the DCA ordination plot of vectors 1 and 2. Sampling dates are grouped at the same average similarity (0.8) as for the individual years, dates within groups have the same lettered symbols, groups related at 0.75 average similarity have the same symbol.

These analyses resulted in five major communities (1-5) at 0.75 average similarity across the study period which split into fourteen minor communities at 0.8 average similarity as follows; 1A-G, 2A-B, 3, 4A-B and 5A-B. Major communities 1, 2, 3 and 4 were separated in the ordination by vectors 1 and 2 but the separation of community 5 required other ordination axes. Figure 3.51 indicates the year each sampling date belonged to, with open symbols for 1981/1982 and closed symbols for 1982/1983. Comparison of Figures 3.50 and 3.51 indicates that all but one of the minor communities were specific to one or other year. Three of the major communities (2, 3 and 4) were only present in the first year (1981/1982). The major community 5 was only present in the second year (1982/1983) while the major community 1 was present in both years.

Table 3.11 lists the sequential periods (in terms of day numbers) of the zooplankon communities across the study period and indicates the relationships between them. The

community intervals and transition periods for the combined two year data (Table 3.11) were essentially the same as for the separate years (Table 3.10), although the affinities of some sample date groups changed between the individual years and when both years were considered together. For example the zooplankton community 1 in the individual 1981/1982 analysis was joined into the larger community 1 when both years were analysed together. Table 3.11 shows that the zooplankton communities differed between most of the two years, although they were similar at the beginning and end of both years.

The composition of the zooplankton communities was determined in the same manner as was done for the phytoplankton communities (Section 3.2.7). Table 3.12 lists the taxa in order of dominance within each zooplankton community. The zooplankton communities were not characterised by different taxa, but rather by differing proportions of the same taxa. This was a reflection of the high overall similarity of the zooplankton communities.

3.4 DISCUSSION

3.4.1 Comparison of the 1981/1982 and 1982/1983 Seasons

There were many physical and chemical differences in Mt Bold Reservoir between the two seasons studied. The lack of winter rainfall in 1982 resulted in the reservoir containing water pumped from the Murray River during the 1982/1983 growth season. The river water was more transparent, more saline and had lower nutrient levels than water derived from the catchment in the previous year. The pumping itself altered the residence time, thermal structure and mixing regime of the reservoir. The plankton communities also differed, both quantitatively and qualitatively, between the two seasons. Figure 3.52 summarizes the changes and the relationships between the plankton communities during the study period. Periods of persistent and intermittent thermal stratification and pumping are marked on Figure 3.52.

The general sequence of events in Mt Bold Reservoir during the 1981/1982 season was comparable to those described for many temperate, stratifying water bodies by Hutchinson (1957, 1967), Reynolds (1980, 1984a, 1984b) and Sommer et al. (1986). The spring onset and autumn breakdown of thermal stratification, the increased euphotic to mixing depth ratio and the depletion of nutrients in the epilimnion over summer are well documented

characteristics of these waters. The patterns of plankton biomass, i.e. spring, early summer and autumn phytoplankton maxima and a summer zooplankton maximium are also characteristic responses to these environmental changes.

Reviews by Round (1971), Margalef (1978) and Reynolds (1980) all contend that the major environmental factors controlling phytoplankton community change are nutrients and water column stability. Round (1971) stressed the importance of the onset and breakdown of thermal stratification on phytoplankton change, describing these periods as cardinal or shock points. Other cardinal points recognised by Round (1971) occur in mid-winter and mid-summer, corresponding to the periods of extremes in resource levels.

During the 1981/1982 season in Mt Bold the phytoplankton community rapidly changed several times in late spring and early summer (Figure 3.52). These changes commenced about one month after the establishment of persistent thermal stratification. On several occasions a single sampling date represented a different community during this period. The phytoplankton community did not change after the breakdown of thermal stratification, remaining constant for two months afterwards. Phytoplankton community changes followed the starting, stopping and restarting of pumping from the Murray River in April, June and August 1982 respectively.

The changes in Mt Bold phytoplankton composition during the 1981/1982 season were similar at the phyla or class level to those frequently observed in temperate lakes (Hutchinson 1967; Fogg 1975). The general sequence was from cryptomonads in spring, through diatoms, greens and cyanobacteria in early summer to cyanobacteria in late summer and autumn and then to diatoms and cyanobacteria in winter.

Reynolds (1980) examined the seasonal periodicity of phytoplankton communities in five stratifying English lake systems over several annual cycles and classified these changes into three categories:

1. Autogenic succession, under relatively constant physical conditions.

2. Allogenic shifts, arising from more permanent perturbations in physical structure.

3. Reversions, arising from temporary structural perturbations followed by renewed

physical stability.

Reynolds (1984b) extended this analysis to include stratifing temperate lakes in both Europe and North America. Although the specific sequence recorded in Mt Bold during 1981/1982 did not exactly match any outlined by Reynolds (1980, 1984b), the community changes in Mt Bold fit the categories he proposed. Thus there were reversions and shifts as well as autogenic changes that occurred when the physical structure of the reservoir was constant.

During the 1982/1983 season, the combination of pumping, solar radiation and surface wind resulted in repeated large fluctuations of the mixed depth (Figure 3.10) throughout the spring-summer period. Harris *et al.* (1980a) described a similar situation during a three year study of Hamilton Harbour (Lake Ontario) where there were periods of partial mixing throughout summer. In this extensive study, Harris and Piccinin (1980) showed that in the absence of nutrient limitation (the prevailing situation in Hamilton Harbour), physical variability in the water column strongly influenced phytoplankton community composition. Harris and Piccinin (1980) showed that there were critical z_{eu}/z_{mix} ratios for the presence or absence of particular groups of phytoplankton species. Trimbee and Harris (1984) compared two seasons in Guelph Lake, one of which was characterised by intermittent mixing throughout the summer, and attributed the differences in phytoplankton composition and dynamics to the mixing differences. The mixing in Mt Bold during the 1982/1983 season is also similar to the intermittent mixing regimes artificially imposed in studies using the Lund Tubes, the results of which are summarized by Reynolds *et al.* (1983, 1984) and Reynolds (1986). In these experiments normal (unmanipulated) seasonal periodicity of the phytoplankton was suppressed. During the periods of artificial mixing, phytoplankton typical of well mixed water columns such as diatoms and desmids were promoted. Upon subsequent restratification the normal summer sequence from colonizing r-species (flagellates) to conservative K-species (colonial greens and blue-greens) developed. The artificial mixing regime resulted in a higher frequency of phytoplankton community change and lower mean phytoplankton biomass.

During the 1982/1983 season the Mt Bold phytoplankton community changed at regular intervals throughout spring and summer (Figure 3.52). There were several reversions and shifts (*sensu* Reynolds 1980) during this period which were associated with the partial mixing and subsequent stabilization of the water column. Phytoplankton community

changes followed the complete breakdown of thermal stratification and also the stopping of pumping; both occurred in March 1983. From mid autumn to mid winter the phytoplankton community was constant, coinciding with a period of constant physical structure.

In Mt Bold Reservoir the average chlorophyll *a* concentration was lower during 1982/1983 compared with 1981/1982 despite the improved light climate. This was most likely due to the reduced nutrient loading during 1982/1983. Total phytoplankton volume did not reflect this due to the dominant contribution of *Volvox* in both seasons.

There was little overlap of phytoplankton communities between the 1981/1982 and the 1982/1983 seasons (Figure 3.52), however the differences were usually due to changed combinations and proportions of the dominant phytoplankton taxa rather than completely new taxa (Table 3.9). It was not possible to attribute these differences only to the different mixing regimes of the two seasons since both chemical and optical characteristics of the reservoir water also differed substantially.

During 1981/1982 the zooplankton community rapidly changed in late spring and early summer then remained constant for the rest of summer (Figure 3.52). During autumn and winter the zooplankton community changed at intervals of one to two months; the final communities were similar to those of the previous spring. During the 1982/1983 season the zooplankton community was constant throughout spring, changed once, and then was constant for most of summer. There were several changes in late summer/early autumn and winter. The 1982/1983 zooplankton communities were very similar until the changes in early winter, after which the communities were again similar to those occurring previously.

There was little specific overlap of zooplankton communities between the 1981/1982 and 1982/1983 seasons (Figure 3.52), although once again the differences between the communities were mainly due to different combinations of the different taxa (Table 3.12). Most of the 1982/1983 communities were similar to those at the beginning and end of the 1981/1982 season. Figure 3.52 indicates that there was little correlation between phytoplankton community changes and zooplankton community changes except during the late spring/early summer period of 1981/1982. The zooplankton community did not appear to respond to the intermittent mixing during 1982/1983 nor to the concurrent phytoplankton changes.

3.4.2 Causes of Change in Phytoplankton Community Composition

Examination of the periods of major compositional change in the Mt Bold phytoplankton community may give some indication of the forces behind these changes. Because of the short duration of many communities and transitional periods (Figure 3.52), attention was focussed on loss factors rather than resource-based growth factors although the latter were considered where appropriate.

Table 3.13 summarizes the major changes in phytoplankton community composition and biomass during the study period as well as changes in water column mixing, z_{eu}/z_{mix} and zooplankton community biomass and composition. For the mixed depth and zooplankton areal biomass estimates, both coincident and seven day lagged changes are shown. These will be briefly discussed below.

The first three transitions (numbers one to three between minor communities A1-A2-A3-A2; Table 3.13) reflect changing proportions between *Ochromonas* and *Cryptomonas* species. The mixed depth decreased, resulting in a small increase in z_{eu}/z_{mix} from 0.17 to 0.26, and zooplankton biomass (hence grazing pressure) slowly increased across this period. Cryptomonads occur across a wide range of nutrient and mixing conditions in nature (Reynolds 1980) however under the experimental conditions of the Lund Tubes *Cryptomonas* coincided with a z_{eu}/z_{mix} <0.67 and reduced grazing pressure (Reynolds *et al.* 1984). *Cryptomonas* was reported to be readily grazed by natural zooplankton communities by Thompson *et al.* (1982). The fourth transition (A2-B1) represents the replacement of these flagellates by diatoms. This transition coincided with a change in the zooplankton community composition although total zooplankton biomass decreased at the same time. The mixed depth did not change. This transition also coincided with the end of the light limited spring growth period (Section 3.4.3) and the phytoplankton biomass increased substantially. The vernal increase in phytoplankton biomass in stratifying systems is traditionally composed of diatoms (Reynolds 1980). The fifth transition (B1-B2), in which the green flagellate *Carteria* briefly increased, coincided with a large increase in zooplankton biomass and a small decrease in the mixed depth. Diatoms were still present and there was a further large increase in phytoplankton biomass.

The sixth transition (B2-B3) resulted in the replacement of the diatoms by *Microcystis*. The

mixed depth continued to decrease, resulting in a large increase in z_{eu}/z_{mix} to 0.85. There was also a large increase in zooplankton biomass during this transition. Diatoms traditionally decrease with the onset of stable stratification from increased sedimentation losses while *Microcystis* prefers the establishment of stable conditions (Reynolds 1980). The very large decrease in phytoplankton biomass indicated that large losses of diatoms occurred through sedimentation and/or grazing during this change. Thompson *et al.* (1982) reported that *Melosira* was partly edible to zooplankton. Dominance of *Microcystis* was by default since the absolute biomass was very low. The seventh transition (B3-C1) was a brief replacement of *Microcystis* by diatoms, representing a reversal of the previous change. The mixed depth increased during this change, reducing z_{eu}/z_{mix} to 0.32, and the zooplankton biomass remained high. The eighth transition (C1-B4) again reversed the sequence, with *Microcystis* replacing the diatoms. The mixed depth further increased, reducing z_{eu}/z_{mix} to 0.22, and there was a large increase in zooplankton biomass. The increased mixed depth would increase diatom suspension rather than loss, indicating that this replacement may be due primarily to zooplankton grazing. Zooplankton generally prefer to feed on diatoms to *Microcystis* (Reynolds 1984a). The decline in diatoms may also be due to Si limitation, the concentrations of which were not measured.

The ninth (B4-D1) and tenth (D1-B4) transitions represented the replacement of *Microcystis* by the attenuate green *Schroederia* and vice versa. During both of these transitions the mixed depth remained constant (z_{eu}/z_{mix} c. 0.35) and zooplankton biomass was high. The ninth transition is difficult to interpret because *Schroederia* is a fast growing r-selected colonist while *Microcystis* is a slow growing K-selected competitor (Reynolds 1984a). Although the sampling interval was long, there was no indication from the daily solar radiation record (Figure 3.11a) of a physical perturbation happening within it. There is a suspicion that this change was due to an unofficial cosmetic application of copper sulphate during this period. Copper sulphate treatments of algal blooms were routine in Mt Bold prior to 1980 (Oliver 1981) but were officially stopped thereafter. The eleventh transition (B1-B4) resulted in complete dominance by *Microcystis*. The mixing depth increased, giving a z_{eu}/z_{mix} of 0.2, and the zooplankton biomass decreased.

The next five transitions (numbers twelve to sixteen) represent a cycling between one community dominated by *Microcystis* (B4) and another with contributions from diatoms, greens and cyanobacteria (C2). The water column was completely mixed throughout this

period and the z_{eu}/z_{mix} ratio fluctuated between 0.11 and 0.15. The zooplankton biomass was low throughout this period with only one minor change in composition. It would seem that neither of these two factors was responsible for the alternating changes between the two phytoplankton communities. Examination of Figure 3.52 indicates that the twelfth change followed the initial start of pumping from the River Murray, and the thirteenth occurred when this pumping stopped. The fourteenth, fifteenth and sixteenth changes all occurred during an extended break in pumping, the former two represented a pulse of *Anabaena* and the latter resulted in a *Microcystis-Melosira-Sphaerocystis* association. The seventeenth transition (C2-C3) coincided with the restarting of pumping. There was little change in either mixed depth or zooplankton biomass. There was no immediate change in phytoplankton community composition with the onset of temporary thermal stratification in spring 1982/1983. The eighteenth transition (C3-C4) resulted when the water column was completely mixed to the bottom following the initial onset of thermal stratification. There was also a large increase in zooplankton biomass during this change.

The next five changes (numbers nineteen to twenty three) each coincided with a fluctuating mixed depth. Zooplankton biomass was high to medium throughout this period. The nineteenth transition resulted in *Schroederia*. The mixed depth decreased from 16 to 3 m during this change. Due to the exceptionally high transparency of the water at this time (Figure 3.12) the latter mixed depth gave a z_{eu}/z_{mix} of 3.0. Transition numbers twenty (D1-D2) and twenty one (D2-D3) reflect a rapid pulse of *Carteria*. The mixed depth continued to fluctuate wildly and the zooplankton biomass increased during these changes. Transition numbers twenty two (D3-D4) and twenty three (D4-D5) reflect a similar pulse in a small cyanobacterium (*UBG*). Both zooplankton biomass and the mixed depth decreased during this change.

The next six transitions (numbers twenty four to twenty nine) represent a cycling between three communities (D5, D6 and C5) which have different proportions of *Oocystis, Schroederia, Microcystis, Sphaerocystis* and *UBG*. Although not completely consistent, there was a repeated trend from D6 (*Oocystis*) through D5 (*Schroederia*) to C5 (*Microcystis-Sphaerocystis*) with decreasing mixed depth. Reynolds *et al.* (1984) reported prolific increases in *Sphaerocystis* during stable periods and declines with mixing in the Lund Tube experiment. In the same experiment *Microcystis* did not decrease during mixing but increased during stable periods, eventually dominating the phytoplankton (Reynolds *et*

al. 1984).

During the thirtieth transition (C5-C6) the reservoir was mixed to the bottom, resulting in a decrease in z_{eu}/z_{mix} to 0.2. Phytoplankton biomass decreased partly due to dilution (concentration decrease $>>$ areal decrease) however the immediate compositional change from *Oocystis* to *Microcystis* was probably not associated with this mixing. The final four transitions of the study period (numbers thirty one to thirty four) involved the replacement of *Cyclotella* and *Microcystis* by *Ochromonas*. The thirty first change (C6-C7) followed the end of pumping from the Murray River. The reservoir was starting to stratify during the last two changes (C6-A2) and (A2-A1) and there was an increase in zooplankton biomass. At the end of the study period the conditions in the reservoir and the phytoplankton community composition were the same as at the beginning of the study.

It is clear from the above discussion that it is difficult to attribute any particular change in the Mt Bold phytoplankton community composition solely to zooplankton although there is no doubt that zooplankton contributed substantially to the phytoplankton changes on several occasions. Changes in zooplankton biomass seemed to have a greater influence than changes in zooplankton composition. This is indicated by examining the periods of change in the zooplankton community (Figure 3.52); changes in zooplankton composition are often not reflected in the phytoplankton community. It is also clear that there were changes in the phytoplankton community composition which were independent of zooplankton, mixing depth and pumping.

This inability to isolate the specific effect of zooplankton on the phytoplankton compositional changes in Mt Bold Reservoir is because:

1. Phytoplankton compositional changes are often due to a combination of several factors (Lund 1965).

2. There are time lags between cause and effect which are specific to each factor and target taxon (Harris 1986, 1987).

It is the opinion of Harris (1986, 1987) that these time lags between the environmental change and the algal response negate any attempt to correlate algal composition with ecological conditions at any point in time. In an extensive study Harris and co-workers

(Harris *et al.* 1980a, 1980b, 1983; Haffner *et al.* 1980; Harris and Piccinin 1980; Sephton and Harris 1984) investigated the relationship between the physical variability of Hamilton Harbour (Lake Ontario) and its phytoplankton. They found that weekly data did not allow the full description of the physical and biological dynamics of this system. Through time series analysis of a daily data set, Sephton and Harris (1984) determined that while changes in phytoplankton community structure were driven by changes in z_{eu}/z_{mix}, the response was not immediate and different phytoplankton species exhibited different responses and lags. A similar time series analysis of a daily data set from Guelph Lake, Ontario, by Harris and Trimbee (1986) showed that the daily sampling was necessary to document the mechanisms driving the phytoplankton community changes. In the present study, uneven sampling intervals did not allow time series analysis.

3.4.3 Spring Initiation of Phytoplankton Growth

In northern temperate lakes both temperature and light control phytoplankton growth in winter (Lund 1965; Hutchinson 1967). The initiation of growth in spring results when these factors are no longer limiting.

During the 1981/1982 season in Mt Bold Reservoir, the average temperature of the water column was 10.8 °C at the start of the first chlorophyll *a* increase (Day 21). In the three weeks prior to this the average temperature had increased by 0.9 °C. Just prior to the first algal bloom (Day 74) of the 1981/1982 season, the average temterature was 13.0 °C. In the previous week the average temperature was 13.1 °C and three days into this algal bloom (Day 77) the average temperature was 13.3 °C. Increased water column temperatures did not seem responsible for either the onset of phytoplankton growth or in particular the initiation of the first algal bloom of the 1981/1982 season. Low temperature limitation of phytoplankton growth in Mt Bold is unlikely if northern hemisphere results are considered. Thus Rodhe (1948) demonstrated that several diatoms have thermal optima below 10 °C and diatoms regularly bloom in northern temperate lakes at temperatures lower than the minimum recorded in Mt Bold (Ruttner 1963; Macan 1970). A specific example of this is the well studied growth of *Asterionella* in Windermere which starts to increase at water temperatures of 4 °C (Lund *et al.* 1963).

Spring phytoplankton growth has been attributed to improving irradiance (Riley 1942; Lund

1965; Talling 1971). The average irradiance within the mixed zone ($\overline{I}$) was used as a measure of the mean irradiance received by a phytoplankton cell (Riley 1957). The relationship between $\overline{I}$ and phytoplankton biomass during the spring growth period is shown in Figure 3.53a for the 1981/1982 season. There was a linear relationship between $\overline{I}$ and chlorophyll a concentration (Chl$a$); [Chl$a$ = 3.88 $\overline{I}$ − 0.03, r^2 = 0.97, n = 5] between Days 21 and 49 (Figure 3.53a). The increase in $\overline{I}$ during this period was due to a reduction in the mixed depth (Figure 3.10), increased solar irradiance (Figure 3.11a), and a reduced vertical attenuation coefficient (Figure 3.12). An increase in the mixed depth (Figure 3.10) resulted in decreased $\overline{I}$ and chlorophyll a (Days 60 to 70) however by Day 74 both had recovered although the mixed depth had not changed. The recovery seemed to be due to increased solar irradiance (Figure 3.11a) and a reduced attenuation coefficient (Figure 3.12). By Day 77 phytoplankton biomass appeared independent of $\overline{I}$ at a value of 1.57 MJ m^{-2} d^{-1}. This critical mean irradiance at which light no longer limits phytoplankton biomass accumulation has been reported in both marine (Hitchcock and Smayda 1977) and freshwater studies (Geddes 1984a) including Mt Bold Reservoir (Oliver and Ganf 1988).

During the initiation of phytoplankton growth, zooplankton areal biomass slowly increased though with marked oscillations (Figure 3.43). Between Days 74 and 77 when the phytoplankton bloom started there was a minimal change in zooplankton biomass and by implication grazing pressure. Thus the non-linear response of phytoplankton biomass above the critical mean irradiance value was not due to a release from zooplankton grazing pressure.

The 1981/1982 vernal phytoplankton increase was significantly delayed relative to the onset of thermal stratification, due to the high attenuation coefficient. From the 1981/1982 season, an improved light climate should lead to an earlier initiation of phytoplankton growth. During the 1982/1983 season the vertical attenuation coefficient for PAR decreased to exceptionally low levels (Figure 3.12). Figure 3.53b shows the relationship between $\overline{I}$ and phytoplankton biomass during the start of the 1982/1983 growth season. There was a rapid initial increase in chlorophyll a with increasing $\overline{I}$ (Days 324 to 352) but then $\overline{I}$ continued to increase with no consistent response in chlorophyll a concentration (Figure 3.53b). The increases in $\overline{I}$ were due to decreases in mixed depth (Figure 3.10) and decreases in the vertical attenuation coefficient (Figure 3.12). On Days 387 and 408 the decreases in $\overline{I}$ were due to increases in the mixed depth.

Between Days 339 and 352 there was a decrease in zooplankton areal biomass (Figure 3.43) which may have contributed to the initial phytoplankton increase. However the zooplankton areal biomass remained low (3-5 g dry wt m^{-2}) between Days 352 and 373 when the phytoplankton biomass did not increase with increasing $\overline{I}$, implying that the lack of phytoplankton growth was not due to increasing grazing pressure.

The average temperature of the water column increased 2.1 °C, from 9.2 °C to 11.3 °C, during the initial chlorophyll a increase (Days 324 to 352) of the 1982/1983 season. Average temperatures increased by another 2 °C, from 11.3 °C to 13.3 °C, between Days 352 and 380 indicating that the lack of phytoplankton growth was not due to reduced temperatures.

Throughout the 1982/1983 season the water in Mt Bold Reservoir was derived from the Murray River, with the commencement of major pumping on Day 331 (Figure 3.2). At the start of pumping the volume of water stored in Mt Bold Reservoir was very low (Figure 3.1), consequently the volume of incoming water was a large proportion of that stored (Figure 3.4). The outflow of water from the reservoir was reasonably high (Figure 3.3) and was thus a large proportion of storage (Figure 3.4). Consequently there was considerable 'flow through' at the start of the 1982/1983 season which decreased as the stored volume slowly increased (Figure 3.1). This hydraulic washout would substantially inhibit phytoplankton biomass accumulation as Reynolds (1984a) described for Grasmere, in the English Lake District. The flushing rate of Grasmere is up to 11% d^{-1}, which results in a severe depletion of the suspended stock (Reynolds 1984a). Recently Reynolds and Lund (1988) attributed the lack of typical eutrophic phytoplankton in Grasmere, despite increased nutrient loading, to this high flushing rate. However a close examination of the inflow and outflow rates of Mt Bold shows that the combined effect of these two was greater during the early period of chlorophyll a increase (Days 331 to 352) than during the period when the phytoplankton biomass did not increase (Days 352 to 380). It would seem that initially phytoplankton growth overcame the washout losses but was then inhibited.

The incoming water from the Murray River was more saline (Figure 3.23) and lower in nutrients (Figures 3.20 and 3.21) than the water in the reservoir at the start of the 1981/1982 season which was derived from the catchment. Salinity can control phytoplankton distribution and succession (Smayda 1980; Reynolds 1984a). Summer salinities of 30 ppt cause the collapse of the annual *Nodularia* bloom in the Peel-Harvey estuary system

(Lukatelich and McComb 1986). Although the maximum salinity in Mt Bold Reservoir was only 0.8 ppt, there was a rapid increase to this level with the commencement of pumping which could inhibit phytoplankton growth. The absolute concentrations of SRP and IN were exceptionally low during the 1982/1983 season (E. & W.S. 1987) and the TN:TP ratio was very high, implying severe phosphorus limitation of phytoplankton growth. Thus the chemical status of the water in the reservoir would have contributed substantially to the lack of phytoplankton growth despite a favourable light climate at the start of the 1982/1983 season.

3.4.4 Dominance of *Microcystis aeruginosa*

The most marked difference in the phytoplankton composition between the two seasons was the reduction in importance of the cyanobacterium *Microcystis aeruginosa* during the second year. *Microcystis* dominated from mid December 1981 until July 1982 (Figure 3.32.4a). It was present from late January 1983 until August 1983 but substantial populations only occurred between March 1983 and mid June 1983 (Figure 3.32.4b). The water column was completely mixed from mid March 1983 (Day 562; Figure 3.10) and pumping from the Murray River stopped in late March 1983 (Day 567; Figure 3.2). It would initially seem that full development of *Microcystis* during 1982/1983 only took place when the reservoir was no longer intermittently mixed, but was completely mixed. *Microcystis* also reached maximum population levels when the water column was completely mixed in the 1981/1982 season (Day 190). Close examination of the vertical distribution of *Microcystis* during the 1981/1982 bloom (Day 190; Figure 3.24) shows that it was concentrated in the upper layers of the isothermal water column. This results from it ability to regulate its buoyancy (Walsby and Reynolds 1980) and overcome the effects of water circulation. Oliver (1981) documented a similar situation for *Microcystis* in Mt Bold Reservoir during autumn 1980. During the period of intermittent mixing in the 1982/1983 season, *Microcystis* tended to occur when the mixed depth was shallow i.e. when the water column was restratified (section 3.4.2). This was the preference reported for *Microcystis* by Reynolds (1980). Trimbee and Harris (1984) also reported that the growth of *Microcystis* was inhibited by naturally occurring intermittent mixing of the water column during the summer growth period.

Another physical influence on the growth of *Microcystis* during the 1982/1983 season was the high flushing rate. *Microcystis* perennation is by the maintenance of vegetative propagules

which sediment to the lake bottom and overwinter in a dormant state (Reynolds *et al.* 1981). Summer populations originate from this overwintering stock and although there is no mass re-infection, their extent would be dependent on the viability of the stock (Reynolds *et al.* 1981). The substantial flow-through during the very low water levels that occurred in Mt Bold Reservoir at the beginning of the 1982/1983 season would have reduced the stock from which inocula could be recruited. A similar reason was proposed by Reynolds and Lund (1988) for the absence of *Microcystis* from Grasmere, which also has a high flushing rate.

The chemical characteristics of the water potentially contributed to the lack of *Microcystis* dominance in the 1982/1983 season. One such characteristic was the salinity of the pumped river water. Increasing salinity has been shown to limit the growth and field distribution of *Microcystis aeruginosa* (Sellner *et al.* 1988). In field sampling by these authors along a salinity gradient, *Microcystis* was not found when the salinity increased to 1-2 ppt, while laboratory experiments suggested that salinities above 0.5 ppt could limit *Microcystis* distribution. The salinity of Mt Bold Reservoir water ranged between 1010 and 1390 μS cm^{-1} from September 1982 to July 1983 (Figure 3.23). Using the conversion of Williams (1966) for Australian inland waters, these salinities are equivalent to a total dissolved solids (TDS) range of 0.5 to 0.8 ppt. Thus the salinity in Mt Bold was high enough to limit *Microcystis* growth. There was however, substantial growth within this period; from March to June 1983.

Other chemical factors possibly limiting *Microcystis* growth during the 1982/1983 season were the very low absolute SRP and inorganic N concentrations as well as the high TN/TP ratio. The absolute N and P requirements of cyanobacteria are no higher than for other algal groups (Reynolds and Walsby 1975). Cyanobacteria frequently become dominant in lakes when nutrient concentrations are at their seasonal minima (Hutchinson 1967; Lund 1965), achieving bloom-forming populations through utilization of nutrients previously stored (Reynolds 1987a) and also through their ability to utilize hypolimnetic nutrients by controlled vertical migrations (Ganf and Oliver 1982). The association of cyanobacteria with low N/P ratios (Rhee 1978) does not apply to *Microcystis* which does not fix atmospheric nitrogen (Reynolds and Walsby 1975).

3.4.5 Zooplankton Seasonality

Despite the accumulation of extensive information on the biology of freshwater zooplankton, Hutchinson (1967) considered that it was inadequate to support a convincing model of zooplankton seasonal succession. Hutchinson (1967) identified three categories of characteristics which influence zooplankton seasonality; life history timing, food and interactions such as predation and competition.

The importance of fish predation in structuring zooplankton communities was established by Hrbacek *et al.* (1961) and later Brooks and Dodson (1965) used a balance between predation and competition in their 'size-efficiency hypothesis' to explain the co-existance of large and small zooplankton. The emphasis on vertebrate and invertebrate predation (Hall *et al.* 1976; Zaret 1980b) continued until it became clear that some zooplankton communities are governed only by competitive interactions between the zooplankton constituents (Lynch 1978; DeMott and Kerfoot 1982; DeMott 1983). Competitive interactions have also been used to explain the observed transition from copepods to cladocerans during eutrophication (McNaught 1975; Muck and Lampert 1984). Changes in zooplankton community composition with changes in lake trophic status may mimic the seasonal changes observed annually in a eutrophic lake (Gliwicz 1977). The competitive interactions are often based on differences in food utilization by the competitors. The selection of different food by copepods and cladocerans, resulting from their different feeding modes, is well documented (Bogdan and McNaught 1975; Gliwicz 1977; Okamoto 1984a), although the results are quite variable (Peters 1984). Mechanisms proposed for the differences in food utilization by succeeding cladocerans include variations in the carapace gap width (Gliwicz 1977, 1980) and differences in the dimensions of the filtering apparatus (Geller and Muller 1981; Brendelberger and Geller 1985).

In a review of the seasonality of aquatic invertebrates within Southern Hemisphere inland waters, Hart (1985) listed thermal, nutritional and predation influences on zooplankton seasonality. Hart (1985) distinguished two limnetic situations; water bodies with seasonal thermal stratification or with continuous circulation, however, was unable to draw consistent conclusions about the pattern and magnitude of zooplankton seasonality in either of these situations. The seasonal responses of zooplankton principally reflect system-specific events and interactions (Hart 1985).

Although many zooplankton taxa occurred throughout the study and the communities defined by multivariate analyses had a high overall similarity, there was a marked sequence of peaks in numerical abundance for certain Mt Bold zooplankton (Figure 3.41). During the 1981/1982 season the cladoceran *Ceriodaphnia quadrangula* was followed by both calanoid copepods, *Boeckella* and *Calamoecia*, which were then followed by the cladocerans *Bosmina, Diaphanosoma* and *C. quadrangula*, and then *Daphnia* in that order. During the 1982/1983 season the peaks in abundance occurred earlier and were not as distinct as in 1981/1982. There was a transition from *Diaphanosoma* and *C. quadrangula* to *Calamoecia* and then later to *Daphnia* in 1982/1983.

Brief consideration of other turbid water bodies shows some similarities and contrasts in zooplankton seasonality. Hart (1986b) reported a consistent annual sequence from calanoid copepods to cladocerans in a seven year study of Lake le Roux, a turbid reservoir in South Africa. The onset of the annual increase of each taxon was closely correlated with the average water temperature although there was no causal link implied (Hart 1986b). Water column transparency and chlorophyll *a* concentration were significant co-variates with temperature however Hart (1986b) was not able to explain the observed seasonality using these factors. In the hypertrophic Hartbeespoort Dam (South Africa) cladocerans dominated the zooplankton (Jarvis 1986). Concomitant with the dominance of the phytoplankton by *Microcystis*, there was a replacement of *Daphnia* by *Ceriodaphnia*. Jarvis (1986) proposed that the large *Microcystis* colonies hindered *Daphnia* feeding while *Ceriodaphnia* was less inhibited, however fish predation was not excluded. In Mt Bold Reservoir *Daphnia* decreased prior to major increases in *Microcystis* but was not replaced by *Ceriodaphnia*. In Lake Alexandrina (South Australia), a shallow turbid impoundment on the Murray River, Geddes (1984b) reported a summer sequence in density peaks from *Daphnia, Calamoecia* and *Diaphanosoma* to *Bosmina* and *Moina* and then to *Boeckella*. Although zooplankton composition was attributed to a combination of turbidity and fish predation, the specific causes of replacements were not examined (Geddes 1984b). In the absence of data on fish populations, the separate influences of predation and competition on the zooplankton seasonality observed in Mt Bold Reservoir was not known.

3.4.6 Zooplankton Biomass vs. Phytoplankton Biomass

There are two opposing hypotheses about the control of biomass in pelagic food webs (McQueen *et al.* 1986; Dorazio *et al.* 1987). One hypothesis is that pelagic trophic level biomass is controlled from below by producers, the 'bottom-up' model, and the other hypothesis is that it is controlled from above by consumers, the 'top-down' model. These two models are both supported by measured relationships between nutrients, phytoplankton, zooplankton, planktivores and piscivores (McQueen *et al.* 1986); each trophic level being in turn a consumer and a producer. The derivation of these relationships determines which model is supported. The bottom-up model is supported by measurements of consumer biomass at different but stable levels of producer biomass; while the top-down model is supported by manipulations of consumer biomass at equal producer growth potential. Uncontrolled field data cannot be used to test either model however an examination of the general relationship between two of these trophic levels i.e. phytoplankton and zooplankton, gives some insight into the control of biomass.

Phytoplankton biomass concentrations were converted to areal biomass estimations by assuming that the integrated sample concentration was distributed throughout the mixed layer as defined by the mixed depth estimate. Figure 3.24 indicates that this assumption will both overestimate and underestimate the total phytoplankton biomass in the water column at different times, however in the absence of profiles throughout the study period it is a reasonable approximation.

Phytoplankton areal biomass estimates in Mt Bold Reservoir ranged from 3.0 to 1627.3 mg chlorophyll *a* m^{-2} and from 92.0 to 2.54×10^5 mm^3 cell volume m^{-2}. Areal biomass varied during the study period in a similar manner to biomass concentrations, although peaks in biomass when the water column was stratified were reduced relative to when the water column was mixed. Figures 3.54a-b show the relationship between zooplankton areal biomass and the phytoplankton areal biomass (in terms of cell volume) in Mt Bold Reservoir throughout the study period. Initially there was a strong positive correlation between these two variables. The spring 1981 phytoplankton increase was followed by a zooplankton increase with a lag of between 7 and 10 days. Both phytoplankton and zooplankton decreased abruptly in December 1981, again with a lag of 10 days. The direction of control during the increase seemed to be from the bottom up, given the time lag between prey and

predator densities.

In March 1982 zooplankton biomass decreased to low levels (<5 g dry wt m^{-2}) while phytoplankton biomass increased and remained at relatively high levels ($> 5.0 \times 10^4$ mm^3 m^{-2}) until mid May. The dominant taxon contributing to the initial phytoplankton biomass increase was *Volvox* which was not available to the zooplankton but was eliminated by a parasitic rotifer (Ganf *et al.* 1983). Numerically the phytoplankton was dominated by *Microcystis* at the time of the decrease in zooplankton biomass. Zooplankton biomass remained low throughout autumn and winter 1982 and yet the phytoplankton biomass was relatively high until mid July 1982. This implied that either the phytoplankton were still unavailable to the zooplankton or that the zooplankton were limited by some other factor during this period. The dominant phytoplankton taxon throughout winter 1982 was *Cyclotella 2* which should have been readily grazed by the zooplankton present. This suggests that neither bottom-up nor top-down control was operating between these two trophic levels during this period. An uncoupling at the zooplankton-phytoplankton link was experimentally demonstrated by McQueen and Post (1988) and attributed to increased planktivore predation.

The responses described above for the 1981/1982 season were repeated in the 1982/1983 season. In spring 1982 zooplankton biomass increases followed phytoplankton biomass increases with lags of 7 days. At the end of November 1982 zooplankton biomass decreased while phytoplankton biomass increased to a maximum. *Volvox* again dominated the phytoplankton biomass on this occasion. A substantial increase in zooplankton biomass due to *Daphnia carinata* in late January 1983 did not coincide with any major change in phytoplankton biomass. In March 1983 zooplankton biomass again decreased to low levels while the phytoplankton biomass increased mainly due to *Ceratium*. Once again zooplankton biomass remained low (<5 g dry wt m^{-2}) throughout autumn and winter 1983 with a relatively high phytoplankton biomass ($> 3.0 \times 10^4$ mm^3 m^{-2}). An increase in zooplankton biomass in August 1983 followed a decrease in phytoplankton biomass.

It is clear that the relationship between zooplankton and phytoplankton biomass varied in Mt Bold Reservoir during the study period. It ranged from a tight linkage in spring to an apparent uncoupling during winter. The extent of biomass control between these two trophic levels was not constant.

CHAPTER FOUR: PLANKTON DISTRIBUTION

4.1 INTRODUCTION

Spatial heterogeneity is widely recognized in both phytoplankton (Platt and Denman 1980; Reynolds 1984a) and zooplankton (Hutchinson 1967; George 1981). Distributions of zooplankton resulting from vertical migration have been extensively investigated (Hutchinson 1967) although the mechanisms are not fully understood (Bayly 1986). The distribution of phytoplankton has been examined in response to the large vertical environmental changes in water bodies in order to understand the suspension mechanisms of phytoplankton (Reynolds 1984a, 1987a). The early assumption that plankton were homogeneously distributed in the horizontal plane was shown to be incorrect with the advent of continuous sampling techniques (Harris 1980b). Much effort has since been directed at understanding the causes and consequences of plankton patchiness (Steele 1976; Platt and Denman 1980; Reynolds 1984a). This understanding has depended on an acceptance of the influence and importance of scale (both spatial and temporal) in plankton ecology (Allen 1977; Harris 1980b; Reynolds 1984a). With specific regard to phytoplankton horizontal patchiness, Reynolds (1984a) recognizes three scales or types; small scale, large scale and advective patchiness. These are briefly described below. Small scale patchiness is on the scale of millimeters or seconds and results from the displacement of parcels of water by other parcels within which the plankton particle may or may not be present. The individual plankton particle does not remain in any one position for long enough for this patchiness to be influenced by differential growth as a result of its position. Large scale patchiness is on the scale of kilometers or days and occurs in open water where horizontal diffusion is the dominant dissipating force. The maintenance of large scale patchiness is dependent on patch growth exceeding patch losses. Advective patchiness is intermediate in scale between the above two. It occurs when closed basins limit horizontal diffusion resulting in compensatory return flows. Advective patchiness is enhanced by characteristics of the plankton such as regulation in the vertical plane. George (1981) recognizes the above three scales or types of patchiness with regard to zooplankton distribution patterns, however he attributes small scale patchiness to behavioural responses of the animals.

During the two year monitoring of Mt Bold Reservoir (Chapter 3) there were many occasions when the plankton communities changed over a short time period, as a result of

the rapid increase or decrease of component populations. Because of the limited horizontal sampling during the monitoring, these changes could be a result of the horizontal heterogeneity or patchiness of the plankton populations. Thus although the sampling was relatively frequent, on successive dates a different patch of water with its component plankton could have been sampled resulting in the appearance of rapid community change.

The aim of the present study was to demonstrate that these rapid plankton population changes were not simply due to horizontal patchiness. To achieve this aim, it was necessary to sample several sites within a short time period to record simultaneous changes in populations. It was also necessary to sample at a frequency such that any rapid fluctuations in density would be recorded. Although both phytoplankton and zooplankton show horizontal patchiness, in this study, interest was primarily on phytoplankton population changes. Not all phytoplankton taxa changed rapidly during the monitoring so in this study target taxa were choosen and their density changes followed, rather than counting all taxa. There was an element of risk here because the occurrence of any particular taxa could not be predicted. Consequently any member of any of several morphological groups which appeared and which was considered likely to have rapid density changes was followed.

4.2 EXPERIMENTAL METHODS

4.2.1 Field and Laboratory Procedure

Samples were taken twice a week, at intervals of three or four days, from the southern site (Ganf 1982) and from four other sites within the bay immediately upstream of the southern site (Figure 2.2). All sites were marked by mooring points and were at least 100 m apart. Sampling was localized in this manner since the aim was to validate the occurrence of extensive rapid phytoplankton changes rather than characterize the whole reservoir. Duplicate 0-4 m integrated-tube water samples were taken at each site for phytoplankton. A single vertical 0-20 m net tow was taken at each site for zooplankton. Temperature, dissolved oxygen and light (PAR) attenuation profiles were taken weekly at the southern site.

A 500 ml subsample of the water sample was allowed to sediment (at 3 h cm^{-1}), concentrated to 100 ml, again allowed to sediment and concentrated to 10 ml. Using standard measuring cylinders complete sedimentation took 6 days. Between 0.5 and 3% of

the initial 500 ml was settled and duplicate perpendicular transects, which averaged 50 fields of view each at ×400 were scored. Dominant zooplankton were scored from duplicate subsamples ranging from 0.3 to 2% of each net sample.

Although samples were taken every three or four days, it was not necessary to count every sample in anticipation of a population change. Consequently samples from all sites were counted at two week intervals until mid December when all sampling dates were counted thereafter. All zooplankton samples from the southern site were counted to check for rapid changes.

4.2.2 Phytoplankton Counting

Non-random distribution of phytoplankton cells in inverted microscope settling chambers is a potential source of error when only part of the chamber floor is counted (Lund *et al.* 1958). Sandgren and Robinson (1984) recently demonstrated an 'edge effect' where there was increased settling in the peripheral regions of the settling chamber compared with the central regions. Sandgren and Robinson (1984) warned against the assumption that counting replicate transects across the chamber would overcome the sampling bias caused by such a non-random distribution of cells. These transects sample the central region more than the periphery, and thus may give biased density estimates with non-random distributions (Sandgren and Robinson 1984). It was therefore necessary to check for a biased density estimate due to non-random distribution of the target phytoplankton taxa on the floor of the settling chamber.

The tube of the settling chamber had an internal diameter (13.3 mm) such that a transect through the centre represented 50 adjacent fields of view (FOV) at ×400. The floor of the settling chamber was divided into three concentric regions as follows; (1) a central circle with a radius of 5 FOV; (2) an annulus around this central circle with a width of 10 FOV; and (3) the remaining annulus around the periphery of the tube with a width of 10 FOV. The areas of these three regions were 5.6, 44.4 and 88.9 mm² respectively, which gave a weighting factor on one field of view within each region of 1, 8 and 16 respectively. Phytoplankton taxa scores within each region were weighted by the appropriate factor and then summed to give a weighted transect score. For each of the target phytoplankton taxa, the unweighted score for the complete transect of 50 fields of view was compared with the

*This assumption resulted in an overestimate of the volume filtered given the characteristics of the net (Section 2.3) (Tranter and Smith 1968).

weighted score. This comparison was done on one sampling date (16.XI.84) for duplicate transects from each water sample. Table 4.1 lists the unweighted and weighted densities (numbers ml^{-1}) of five target phytoplankton taxa in the water samples from this date. Paired t comparisons showed there was no significant difference between the unweighted and weighted density estimates for any of the taxa tested. As there was no evidence of an 'edge effect' for these taxa, perpendicular transects through the centre were used.

4.2.3 Net Calibration

It is well documented in the literature that net samplers generally collect less zooplankton than trap samplers per unit volume (Schindler 1969; Duncan 1975; Bottrell *et al.* 1976). Potential underestimation of zooplankton densities by net avoidance and clogging was examined on the first sampling date (2.XI.84) of the study period. At each of the five sites, trap samples were taken from 1, 5, 10, 15 and 20 m depths at the same time as the vertical net tow from 20 m to the surface. In the absence of a flow meter, the amount of water filtered during the net tow was*assumed to be equal to the cross-sectional area of the net opening multiplied by the tow length. The density estimates from the five trap samples of each profile were averaged to give an unweighted density estimate for the water column from 20 m depth to the surface. The zooplankton density estimates at each depth were also weighted using a factor reflecting the volume of water represented by each sample; the depth intervals between successive intervals were halved.

Table 4.2 lists the mean densities of the dominant zooplankton taxa from the net, unweighted trap and weighted trap samples. Differences in densities of each taxa between net and unweighted trap samples were tested using a paired t test on the means across the five sites. ANOVA was not used since the trap samples had an inherent density variation with depth, not present in the integrated net samples. Table 4.3 summarizes these analyses. There were significantly lower densities in the net samples for all zooplankton taxa except *Diaphanosoma*. The mean ratio of net density to unweighted trap density for each taxon, is also shown in Table 4.3 expressed as a percentage. Mean net densities ranged from 19% of the trap density for *Boeckella*, up to 55% of the trap density for *Diaphanosoma*. The densities of copepod adults and juvenile stages were proportionally lower in the net samples compared to the densities of the cladoceran taxa (Table 4.3). This is in general agreement with literature findings that copepods effectively avoid net samplers (Fleminger and Clutter

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1965; Clutter and Anraku 1968; De Bernardi 1984), however these differences were not significant when tested by ANOVA ($F_{6,28}$ 2.40, ns) due to considerable inter-site variation in the ratio for each taxon. Duncan (1975) reported a net-loss factor of 2.7 or 37% with no significant differences between zooplankton taxa. Studies cited in Bottrell *et al.* (1976) found net densities reduced by up to eight times (13%), while Schindler (1969) reported a mean of 64% with a range from 49 to 86% for different taxa.

The weighted trap density estimate at each site was compared with the mean unweighted trap density estimate using a *t* test. The variance of the weighted estimate could not be calculated because of the lack of replicate samples at each depth. Although in most instances the weighted density estimate was lower than the mean unweighted estimate (Table 4.3), the difference was not significant at any site for any taxa.

4.3 RESULTS

4.3.1 Physical and Chemical Environment

During the study period there was a steady reduction in water depth, from a wall depth of 40.2 to 34.0 m (Figure 4.2), and in storage volume, from 42300 to 26500 Ml. Inflow from the catchment was low; maximum daily inflow volume was 55 Ml d^{-1} which represented 0.13% d^{-1} of the stored volume at the time. Pumping from the Murray River commenced on 5.I.85 with daily inflow volumes up to 159 Ml d^{-1}, or 0.59% d^{-1} of stored volume, during the final week of the study period. The recorded daily outflow volume ranged from 161 to 320 Ml d^{-1}, representing 0.43 to 1.0% d^{-1} of total storage. There were gaps in the outflow record due to gauge malfunction.

Figure 4.1a shows the daily wind run recorded at Mt Bold during the study; it ranged from 61 to 299 km d^{-1}. The monthly average for November and December was 125 and 142 km d^{-1} respectively, while the average for the period in January was 106 km d^{-1}.

The daily total solar radiation recorded in Adelaide during the study period is shown in Figure 4.1b; it ranged from 9.3 to 33.6 MJ m^{-2} d^{-1}.

Figure 4.2 shows the variation of water temperature with depth during the study period.

There was a distinct thermocline present throughout the study period which slowly sank down the water column from about 8 m to about 12 m. A secondary thermocline at about 6 m was evident from late December. The persistent thermal stratification indicated that mixing was restricted across the thermocline. The mixed depth was estimated as the depth of the maximum temperature change (Harris *et al.* 1980a). Table 4.4 lists the mixed depth (z_{mix}) estimates on each sampling date, with two estimates when a secondary thermocline was present. Water column stability within the epilimnion was estimated by calculating the Brunt-Vaisala frequency (N^2) for the 0-10 m layer. N^2 values for this depth interval are listed in Table 4.4; values ranged from 461×10^{-6} to 1430×10^{-6} s^{-2} during the study period. The highest stability was in early December (Table 4.4).

Figure 4.3 shows the depth-time distribution of dissolved oxygen during the study period. The pattern of dissolved oxygen distribution supports the previous general interpretation of water movement based on the thermal structure.

Estimates of the average vertical attenuation coefficient (K_dave) of downwelling irradiance were obtained by linear regression analysis of PAR intensity against depth. Estimates with associated standard error are listed in Table 4.4. Values of K_dave ranged from 1.55 to 2.32 ln m^{-1} with a marked decrease in early January, indicating an increase in water column transparency.

Routine nutrient analyses were done by the E. & W.S. during the study period. Monthly samples were taken at 10 m depth intervals. Table 4.5 lists the concentrations of total phosphorus, soluble reactive phosphorus, inorganic nitrogen (nitrate and nitrite), and total Kjeldahl nitrogen (organic nitrogen and ammonia) in these samples.

Soluble reactive phosphorus concentrations, which ranged from 37 to 101 μg l^{-1}, decreased in the surface waters towards the end of the study period. Inorganic nitrogen concentrations, which ranged from 0.29 to 0.76 mg l^{-1}, also decreased in surface waters in early January. The ratio of total nitrogen to total phosphorus is listed in Table 4.5. TN:TP ranged from 5 to 15, indicating some potential nitrogen limitation, however the absolute concentrations of phosphorus and nitrogen were not likely to limit phytoplankton growth during the study period.

The conductivity of the water samples is also listed in Table 4.5; it ranged from 451 to 524 μS cm^{-1}, with a slight increase towards the end of the study period.

4.3.2 Phytoplankton

Figures 4.4a-f show the mean ($\pm$se) density estimates across the five sites for the six target phytoplankton taxa during the study period. Density (numbers ml^{-1}) is plotted on a log scale to illustrate agreement with exponential growth. On each sampling date the density estimates of each taxon were compared between the five sites by two level nested ANOVA. Table 4.6 summarizes the ANOVA results and Table 4.7a-b shows the results of unplanned comparisons between means by the T method (Sokal and Rohlf 1981) for density differences, between sites and between duplicate tubes within sites, that were significant by ANOVA.

There were significant density differences between sites on eleven occasions and between duplicate tube samples within sites on ten occasions out of a possible fifty seven for each (Table 4.6). Of the latter, only three were significant by the unplanned comparison. These three all involved different taxa and different sites (Table 4.7b). Nine of the inter-site differences were significant by unplanned comparison. On several occasions the sites at the ends of a density gradient were significantly different from each other, while on other occasions single or pairs of sites were significantly different from the rest (Table 4.7a). No one site was consistently different from the others. The large *Cryptomonas A* species showed the most frequent inter-site differences although overall four of the six taxa were involved.

Table 4.8 gives a breakdown of the variance components due to the various sampling levels, expressed as a percentage of their sum. This shows the relative importance of each of the sampling levels in the variance of a single observation (Sokal and Rohlf 1981). During this study the contribution of any one sampling level to the total variance ranged from 0 to 100% (Table 4.8). There was no consistent pattern across all taxa or within a taxa throughout the study period, however in 56% of cases the duplicate counting transects accounted for the majority of the variance.

A brief description of the density changes of the six target phytoplankton taxa follows. The *Melosira* scored during this study was recorded as *Melosira 2* in the 1981-1983 monitoring (Table 3.4). Cell densities increased throughout November at an average rate of 0.191 $\pm$

0.004 ln units per day (Figure 4.4a). The rate of increase then slowed to 0.100 ± 0.004 ln d^{-1} during December, until a mean maximum cell density of 10200 ± 580 cells ml^{-1} was reached on 24.XII.84. Then there was a rapid decline in density at an average rate of -0.532 ± 0.018 ln d^{-1} until after 11 days the mean density was 45 ± 7 cells ml^{-1}. After this decrease there was no significant change in cell density until the end of the study period.

Figure 4.4b shows the density changes of the *Carteria* species. This taxon was not recorded until the second week of December. Cell densities increased rapidly at an average rate of 0.353 ± 0.027 ln d^{-1} until a mean maximum cell density of 7600 ± 830 cells ml^{-1} was reached on 28.XII.84. Then there was a rapid decrease in density at an average rate of -0.562 ± 0.022 ln d^{-1} until a mean density of 10 ± 3 cells ml^{-1} was reached after 14 days (Figure 4.4b)

The *Ankistrodesmus* species was not recorded until mid November (Figure 4.4c). The density of this taxon slowly increased at an average rate of 0.026 ± 0.002 ln d^{-1} until 21.XII.84. There was then a rapid density increase which levelled off and a maximum cell density of 600 ± 30 cells ml^{-1} was reached on 31.XII.84. A rapid decline followed at an average rate of -0.486 ± 0.040 ln d^{-1} until a mean density of 27 ± 4 cells ml^{-1} was reached after 7 days. Cell densities were at this level until the end of the study period.

The large *Cryptomonas A* species scored during this study was reported as *Cryptomonas 2* in the 1981-1983 monitoring (Table 3.4). The density of this taxon slowly increased until the end of November, then slowly decreased until 21.XII.84 (Figure 4.4d). Cell densities then rapidly increased at an average rate of 0.326 ± 0.057 ln d^{-1} to a maximum cell density of 95 ± 18 cells ml^{-1} on 28.XII.84. The density then decreased at an average rate of -0.382 ± 0.050 ln d^{-1} until a mean density of 5 ± 2 cells ml^{-1} was reached after 10 days.

Figure 4.4e shows the density changes of the smaller *Cryptomonas B* species. This taxon steadily decreased from a maximum mean density of 35 ± 7 cells ml^{-1} at the start of the study until it was not recorded at the end of December. Just prior to its absence there was a small increase in density which coincided with the rapid increase noted for *Cryptomonas A*.

The *Schroederia* species did not show a rapid decrease in density at the end of December (Figure 4.4f). This taxon increased until it reached a maximum of 510 ± 14 cells ml^{-1} at

the end of November, then it slowly decreased until it reached a density of 98 ± 6 cells ml^{-1} on 21.XII.84. From 21.XII.84 the density of *Schroederia* steadily increased at an average rate of 0.074 ± 0.003 ln d^{-1} until it reached a mean density of 470 ± 20 cells ml^{-1} at the end of the study period (Figure 4.4f).

Where appropriate, linear regression analysis was used to obtain estimates of the rate of change in density. Regression analysis was done at each sampling site for each taxon separately. The regression analysis tested differences between mean densities across the sampling dates in question, as well as testing for linear relationships between ln density and time. Table 4.9 summarizes the regression analysis results. The group F ratio tests differences between the means, the linear F ratio tests the variation explained by a linear relationship, and the deviation F ratio tests variation unexplained by the linear relationship.

Most of the phytoplankton taxa showed significant changes in density at all sites during the periods of increase and decrease (Table 4.8). The exception was *Cryptomonas A*, where on three occasions there was no significant change in density. During the periods of change there were significant linear relationships between ln density and time at most sites for *Melosira*, *Carteria* and *Schroederia*. The change in density of *Ankistrodesmus* and *Cryptomonas A* did not always fit an exponential relationship. There were also significant deviations from linearity at all sites during the increase period for *Carteria*; these are evident in Figure 4.4b.

Regression coefficients were compared by ANOVA (Sokal and Rohlf 1981). During the period of density decline, there was no significant difference in the rate of decrease of any of the individual taxa, between the five sites. Similarly there was no significant difference in the rate of increase of *Schroederia* across the same period, between the five sites. Where significant linear relationships were present, the rates of decrease of *Melosira*, *Carteria*, *Ankistrodesmus* and *Cryptomonas A* were not significantly different at any of the five sites.

4.3.3 Zooplankton

Figures 4.5a-h show the mean ($\pm$se) net density estimates across the five sites for the dominant zooplankton taxa present during the study period. The dominant taxa were; the calanoid copepods *Boeckella triarticulata*, *Calamoecia ampulla*, their copepodites and nauplii; the cladocerans *Daphnia carinata*, *Ceriodaphnia quadrangula*, *Diaphanosoma*

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unguiculatum and *Bosmina meridionalis*. Rotifers were present at low densities throughout the study period. There were no large increases in rotifer density recorded although these could have been missed, given the potential for rapid increase and decrease (Chapter 3).

Most of the zooplankton taxa showed a similar pattern of density change during the study period. Initial densities of most taxa were low ($<$1-2 individuals l^{-1}) and most remained low throughout November. There were some small density increases in the first half of December however most taxa increased substantially during the second half of December (Figure 4.5). Densities of most taxa then decreased in early January. Exceptions to this general pattern were the calanoid copepodites and *Ceriodaphnia*. Both of these taxa showed decreases in density in December and increases in early January (Figures 4.5c and 4.5f).

The density estimates of each zooplankton taxon at each of the five sampling sites were compared across the study period using a factorial ANOVA. A mixed model was used, with the sampling dates a random factor and the sites a fixed factor. Table 4.10 summarizes the results of these analyses. As was evident from Figures 4.5a-h, there were significant changes in density for all taxa during the study period. There were no consistent differences in density between the five sampling sites for any taxa except *Ceriodaphnia*. Inter-site density differences for this taxon were marginally significant. *Diaphanosoma* and *Bosmina* had significant interaction terms; these imply that although there were significant differences in density between the sampling dates, these were dependent on the site considered. Table 4.11 shows the percentage contribution of each variance component to the total density variance for each zooplankton taxa across the study period. For all taxa the largest source of variance was the sampling date followed by the replicate counts. The variance contributed by the sites was negligible for all taxa.

The grazing pressure of the zooplankton community was estimated using biomass since the zooplankton taxa present differed in size. Biomass was calculated using average dry weights for each taxon. Figure 4.6 shows the mean ($\pm$se) total biomass (μg dry wt l^{-1}) of the zooplankton community across the five sites during the study period, with the separate contributions of copepod and cladoceran taxa marked. Total zooplankton community biomass ranged from 48 ± 6 to 740 ± 39 μg dry wt l^{-1} and the contribution of calanoid copepods ranged from 44 to 86% of the total biomass. Zooplankton biomass generally follows the same pattern as density. There was little change throughout November until mid

December, then there was a large and rapid increase until early January, followed by a decrease at the end of the study (Figure 4.6).

4.4 DISCUSSION

4.4.1 Phytoplankton Spatial Homogeneity

The variation in density of the target phytoplankton populations between the sampling sites was small throughout the study period (Figures 4.4a-f). A large amount of the variance in this study was associated with the counting procedure (Table 4.8), which is in contrast to the results of Irish and Clarke (1984) on the distribution of several phytoplankton taxa within the Lund tubes in Blelham Tarn. Using comparable methods these authors had a consistently small variance between counts, with the largest variance between field samples. In the present study there was little horizontal heterogeneity evident in the target phytoplankton at the spatial and temporal scales sampled. These results were initially unexpected given the reports of phytoplankton patchiness at equivalent (George and Edwards 1976; Heaney 1976) and smaller (Irish and Clarke 1984) spatial scales. However the former studies involved phytoplankton capable of regulating their position in the water column; *Microcystis* and *Ceratium* respectively. George and Edwards (1976) and George and Heaney (1978) both found that diatoms and green algae were homogeneously distributed when *Microcystis* and *Ceratium* were patchy.

The dominant factor influencing horizontal distribution patterns of phytoplankton in lakes is wind induced circulation (George and Edwards 1976). During the Mt Bold study the average daily wind run was equivalent to a steady wind speed of 1.5 m s^{-1}. This appeared sufficient to maintain a homogeneous distribution of the target phytoplankton populations. George and Edwards (1976) showed that *Microcystis* patchiness in Eglwys Nynydd Reservoir was dissipated at wind speeds above 4 m s^{-1} and Heaney and Talling (1980) reported a similar critical wind speed for *Ceratium* patchiness in Esthwaite Water. Because the morphometry of Mt Bold Reservoir differs from the above water bodies, it is likely that a different critical wind speed controls the occurrence of phytoplankton patchiness.

4.4.2 Zooplankton Spatial Homogeneity

Although the net tow integrated any vertical discontinuities, there was little evidence of horizontal patchiness among the zooplankton taxa in Mt Bold Reservoir at the scales sampled. The variation in density of the zooplankton taxa between the sampling sites was small throughout the study period (Figure 4.5a-h). Most variance was between the sampling dates with the remainder due to the counting procedure; there was little variance associated with the sampling sites (Table 4.11). The dominant contribution by the sampling dates agrees with the results of Lewis (1978c) in Lake Lanao and of Evans and Sell (1983) in Lake Michigan. Both of these authors found that more variation was associated with sampling date than with sampling site, although the interactions between date and site were also significant in their studies. The absence of horizontal patchiness in zooplankton distributions was unexpected, given the results of George and Edwards (1976), Malone and McQueen (1983) (and references therein) and Teraguchi *et al.* (1983). These authors all reported patchy horizontal distributions for zooplankton populations.

Comparison of the spatial distributions of different zooplankton taxa must be done with care since the variance of replicate samples varies with population density (Downing *et al.* 1987; Pinel-Alloul *et al.* 1988). With this consideration, Pinel-Aloul *et al.* (1988) found that the spatial distributions of smaller zooplankton were more heterogeneous than those of larger animals.

4.4.3 Phytoplankton Population Declines

During the 1984/1985 summer there were similar changes (in both direction and magnitude) in the density of the target phytoplankton taxa at all of the sampling sites in Mt Bold Reservoir. There is no doubt that widespread and rapid declines in density occurred between 24.XII.84 and 11.I.85 for four of the target taxa. The declines in density were not all simultaneous, but overlapped each other, starting with *Melosira* and progressing through *Carteria*, *Cryptomonas A* and *Ankistrodesmus* (Figure 4.4a-d). Another of the target taxa, *Schroederia*, did not decline in density during this period (Figure 4.4f).

The main factors causing phytoplankton loss in lakes and reservoirs are hydraulic washout, sedimentation, grazing (including parasitism) and death through cellular breakdown and

decomposition (Jassby and Goldman 1974b; Jewson *et al.* 1981; Crumpton and Wetzel 1982; Reynolds 1984a). The potential contribution of each of these factors to the phytoplankton losses recorded during this study is considered below.

Hydraulic Washout

The daily inflow and outflow was a small proportion of storage in Mt Bold Reservoir during the study period. It is unlikely that there was any significant loss of phytoplankton due to hydraulic washout during this period. The maintenance of thermal and dissolved oxygen stratification throughout the period of decline (Figures 4.2 and 4.3) would suggest that there was little bulk transfer of epilimnetic water into the hypolimnion at this time. Mt Bold Reservoir has a fixed outlet 15 m from the wall bottom, so there was no offtake of epilimnetic water.

Rapid phytoplankton losses due to hydraulic washout would not be selective i.e. all taxa would decline simultaneously at the same rate unless either of the following two conditions prevailed: (1) the extent of the flow through was essentially that of a river such that sequential population pulses passed the sampling points; or (2) there were very significant differences between the intrinsic growth rates of the taxa. Although the rates of decline of the target taxa in Mt Bold were the same, these taxa did not decline simultaneously. During the period of decline there was not extensive flow through. If there was extensive flow through and if washout was considered responsible for the phytoplankton losses, then the actual growth rate of Schroederia (whose density increased across this period) was about 0.6 $\ln d^{-1}$ or 0.9 doublings d^{-1}. This growth rate is high but possible for such an alga (Reynolds *et al.* 1984). A decline in density of those zooplankton taxa not able to avoid the washout current would be expected. This was not evident for any taxa at the start of the phytoplankton decline, however several zooplankton taxa decreased in density at the end of the phytoplankton decline (Figures 4.5a-h).

Cellular Death

The contribution of cellular death to natural phytoplankton losses is often quoted but rarely quantified (Reynolds 1984a), consequently there is little agreement over its importance. Part of the difficulty is the recognition of dying cells; there is no clear boundary between

physiologically stressed and moribund cells. Estimates of cellular death rates in diatom populations by Knoechel and Kalff (1978) and Reynolds *et al.* (1982) were a small proportion of total losses however Jassby and Goldman (1974b) considered cell mortality to be the major cause of phytoplankton loss in their study. The latter result may have been due to the authors extrapolation from carbon fixation rates to cell production rates.

Cellular death was not determined in the present study although the integrity of cellular contents was visually checked during the microscope counting. Reynolds (1984a) commented on the arbitrary nature of such visual examination. Nevertheless there were few instances of cells with disrupted contents present in the samples during the period of phytoplankton decline.

Sedimentation

With the exception of some cyanobacteria, phytoplankton are normally denser than water and tend to sink (Hutchinson 1967). Sinking rates are dependent on both morphological and physiological factors (Oliver *et al.* 1981; Reynolds 1984a). Losses due to sinking were not directly estimated in this study. However potential sinking rates that would account for the observed losses were calculated and compared to literature values.

Reynolds and Wiseman (1982) and Gibson (1984) estimated the intrinsic (still water) sinking rate (v') of the phytoplankton *in situ* from the sinking loss rate (k_s) and the mixed depth (z_{mix}), by considering that phytoplankton loss from a turbulent water mass followed an exponential function. Assuming that the phytoplankton populations were not growing, that population losses were entirely due to sinking and that there was no resuspension of sedimented cells, these authors derived the following relationship: $v'/z_{mix} = (1 - 1/e^{k_s})$. Table 4.12 shows the intrinsic sinking rates (v') calculated using this relationship for four of the target phytoplankton taxa. Separate sinking rates were calculated using the mean depths of both primary and secondary thermoclines which were present during the period of phytoplankton loss (Figure 4.2). The latter value assumed that the density decrease observed using the 4 m tube sampler only extended to the depth of the upper thermocline while the former value assumed that the decrease went to the lower thermocline. In the absence of sampling a vertical profile, the true situation was not known. The calculated intrinsic sinking rates ranged from 1.8 to 4.9 m d^{-1} or 21 to 58 μm s^{-1} (Table 4.12).

Reynolds (1984a) reported an intrinsic sinking rate of 0.6 m d^{-1} for chains of *Melosira italica* 1-2 cells long. These chains of *Melosira italica* had similar dimensions (cell diameter 6.3 μm, cell length 19 μm) to the *Melosira 2* in the present study (cell diameter 8 μm, cell length 8 μm) whose chains were usually 2-4 cells long. It is clear that the calculated intrinsic sinking rate for *Melosira 2* in Mt Bold (Table 4.12) is 4-7 times greater than that reported for *Melosira italica*. It is unlikely that this calculated sinking rate is very accurate; it is more likely that the recorded losses were not all entirely due to sinking. Gibson (1984) reported a disagreement between the intrinsic sinking rate of *Melosira italica* measured in the laboratory and a higher rate calculated from declining field populations in Lough Neagh, however he considered that neither washout nor grazing would account for the discrepancy. Most published measurements of sinking rates in freshwater phytoplankton are for diatoms so direct comparisons could not be made for the other target taxa.

Reynolds and Wiseman (1982) examined the sinking losses of several phytoplankton taxa as part of an intensive study of phytoplankton loss processes in the experimental Lund Tubes. These authors did not record any *Cryptomonas* spp. (mainly *C. ovata*) in their sediment traps although this taxon reached a maximum density of 1526 cells ml^{-1} in the upper 5 m of the water column and rapidly decreased to 9 cells ml^{-1} at a rate of -0.48 ln units d^{-1}. Reynolds and Wiseman (1982) concluded that a minimal proportion (<4%) of the standing crops of *Cryptomonas* spp. and *Ankyra* (which has a similar morphology to both *Schroederia* and *Ankistrodesmus*) was lost through sinking.

Sedimentation could account for part of the density decline of *Melosira* during this study however this is unlikely for the other taxa.

Grazing

Literature reports on the effect of zooplankton grazing on phytoplankton range from no impact to being the major cause of algal mortality (see Chapter 1). Estimates of the impact of zooplankton grazing involve measurements of three components: (1) zooplankton abundance; (2) individual or community grazing rates; and (3) food selection (Thompson *et al.* 1982). During the present study only the zooplankton abundance was directly measured. In the absence of direct grazing rate and selection measurements, for the purpose of this discussion, a general value from the literature was utilized. In a recent review of

zooplankton grazing literature, Peters (1984) obtained a median filtering rate of 0.35 ml (μg dry wt)$^{-1}$ d^{-1} for both calanoid copepods and cladocerans. This is a very general value and it was used here in preference to more specific values for Mt Bold zooplankton which resulted from measurements made under different conditions (Chapter 6).

Using this value the total community biomass was converted to a community filtering rate (CFR) which is indicated on Figure 4.6. The estimated community filtering rate ranged from 17 to 260 ml l^{-1} d^{-1} which was equivalent to the zooplankton processing 1.7 to 26% of the volume they occupied each day. The total zooplankton biomass values used in the calculation of the community filtration rate were underestimates due to net avoidance (section 4.2.4). Since the ratio of net density to trap density did not differ significantly between taxa, a mean value for all taxa (37%) was used to correct for net avoidance. With this correction, the zooplankton community potentially processed between 5 and 70% of the volume they occupied per day.

This calculated range for the zooplankton community filtration rate is comparable with measured *in situ* rates reported for a variety of different lakes. Thus Haney (1973) measured maximum CFR of >300% d^{-1} during summer in eutrophic Heart Lake while Gulati *et al.* (1982) reported CFR of up to 73% d^{-1} in mesotrophic Lake Vechten. Thompson *et al.* (1982) found that the CFR in the Lund Tubes ranged from 0.2 to 200% d^{-1} through a seasonal cycle while Hart (1986a) reported a CFR range of 0.1 to 75% in the oligotrophic and turbid Lake le Roux. Although there are many measurements of zooplankton CFR reported in recent literature, few consider (and quantify) the consequences to the phytoplankton populations. The intensive studies by Reynolds and co-workers on phytoplankton losses within the Lund Tubes are an exception. Reynolds *et al.* (1982) demonstrated that the almost complete elimination of populations of *Ankyra judayi* and *Chromulina* sp., the control of populations of *Cryptomonas* spp. and some of the losses of *Asterionella* could all be attributed to the observed CFR. Within the limitations of the present study, similar conclusions could not be drawn, however it seems highly likely that zooplankton grazing was responsible for most of the decrease in density of the target phytoplankton populations in Mt Bold Reservoir during this study.

It cannot be assumed that the volume of water processed by the zooplankton community is necessarily cleared of suspended phytoplankton. It is well known that zooplankton feed

selectively (Peters 1984) and any consideration of the impact of zooplankton grazing on phytoplankton should take this into account. A selectivity factor based on gut analyses by Ferguson *et al.* (1982) was incorporated into the conclusions of Reynolds *et al.* (1982). There were indications that the selection of the target phytoplankton taxa by the Mt Bold zooplankton community was not uniform. It is apparent that *Schroederia* was not grazed to the same extent as the other taxa since it is unlikely that *Schroederia* would maintain the positive net growth observed if it was subject to the same grazing losses as the other taxa. While such a gross growth rate ($0.6 \ln d^{-1}$) is not impossible, it is unlikely that *Schroederia* would maintain it while the morphologically similar *Ankistrodesmus* declined at the same rate as the other taxa. A more subtle selectivity may be evident between the four taxa which decreased. Thus between 31.XII.84 and 4.I.85, *Cryptomonas A* decreased from 63 to 9 cells ml^{-1}; *Melosira* decreased from 240 to 45 cells ml^{-1}; *Ankistrodesmus* decreased from 598 to 86 cells ml^{-1}; and *Carteria* decreased from 3695 to 440 cells ml^{-1} (Figures 4.4a-d). This implies different preferences for these taxa by the zooplankton community (or its component taxa). Measurement of Mt Bold zooplankton grazing rates, and the selection of phytoplankton is considered in a later chapter.

It is of note that in this study the transparency of the water column increased during the decline of the target phytoplankton populations (Table 4.4 and Figures 4.4a-d). This 'clear-water phase' can be attributed to zooplankton grazing since this appears to be the main cause of phytoplankton losses. A distinct spring clear-water phase has been observed in many temperate lakes (Sommer *et al.* 1986). It often coincides with a peak of zooplankton abundance and Lampert *et al.* (1986) demonstrated experimentally that the clear-water phase in Schohsee was caused by zooplankton grazing. There was no clear-water phase associated with zooplankton abundance peaks evident during the 1981-1983 study of Mt Bold Reservoir (Chapter 3).

CHAPTER FIVE

5.1 INTRODUCTION

Physical, chemical and biological factors all contribute to changes in the composition of natural phytoplankton communities (Lund 1965; Round 1971; Smayda 1980; Reynolds 1984a). The specific contribution of one of these factors such as zooplankton grazing is difficult to isolate against a background of change in the other factors. One solution is to isolate part of the natural system in an enclosure such that the factor of interest can be manipulated while other variables are held constant.

The use of enclosures in aquatic ecosystems has been stimulated by the recent necessity to test the effects of polluting compounds on natural communities as well as for the understanding of natural processes (Boyd 1981). Aquatic enclosures are termed microcosms, mesocosms or limnocorrals in the literature; inconsistent distinction being made based on size and position in the water body. Historical and general methodological reviews of enclosure research are given by Boyd (1981), Banse (1982) and Lundgren (1985). Extensive but specific accounts of large scale enclosure experiments are those of Grice and Reeve (1982), Lund and Reynolds (1982) and Brockman *et al.* (1983). Because of their lower cost and labour requirements, small scale enclosures have been widely used since the development of plastic films, resulting in an extensive literature. The enclosure of a volume of water by definition isolates it from its immediate environment such that water movement by currents, nutrient transfers and exchanges of organisms (e.g. recruitment from resting stages and migration) are inhibited. Artificial nutrient enrichment, flow through and mixing systems within the enclosures have all been used in attempts to overcome this isolation. Nevertheless these often influence the experimental outcome as much as the imposed treatments. An inherent advantage of aquatic enclosures is the ability to make repeated measurements on the same body of water. It is also possible to determine the precision of these measurements through replication of the enclosures.

Zooplankton grazing has long been recognized as a cause of losses in phytoplankton production (Hutchinson 1967). Despite this recognition there is still much debate over the importance of grazing (Reynolds 1984a). The influence of zooplankton grazing on phytoplankton populations may be both quantitative and qualitative. The former is simply

because zooplankton grazing reduces the amount or biomass of phytoplankton present. The qualitative effect is due to both selective feeding and nutrient recycling by the zooplankton. Because zooplankton feed selectively, specific phytoplankton taxa will be reduced while others are not. Similarly the recycling of nutrients by zooplankton will stimulate growth in phytoplankton that are not grazed. Overall the composition of the phytoplankton community changes in response to zooplankton grazing.

Factors controlling phytoplankton growth and succession in Mt Bold Reservoir have been investigated by Ganf (1980) and Oliver (1981). Neither of these studies considered the influence of zooplankton grazing on the phytoplankton community of Mt Bold Reservoir, which is a turbid water body, a characteristic shared with many Australian inland waters (Kirk 1979). The aim of this research was to examine the extent to which the herbivorous zooplankton altered the phytoplankton composition in Mt Bold Reservoir.

The general approach taken was to remove the zooplankton grazers from an enclosed volume of water which was then incubated *in situ* in the reservoir. Predator exclusion is a technique used in both terrestial and aquatic ecosystems to establish the effects of predation on a prey community. Through enclosure, the effects of changes in major factors that influence phytoplankton composition such as thermal stability, light intensity and nutrient availability (Reynolds 1984a) can be minimized. At the same time care must be taken that the results of enclosures are relevant to the reservoir at the time; that is that the effect of enclosure itself does not induce changes in the composition of the phytoplankton community which are not applicable to the reservoir. This meant that the most appropriate time to use enclosures was during a period when the reservoir was thermally stratified. At this time immobilization of a volume of water in an enclosure reflects conditions in the epilimnion. Coincident with this, light will not limit algal growth since the vernal increase in solar irradiance has usually occurred in Mt Bold Reservoir by this time and algal growth is independent of light availability (Oliver 1981). Furthermore the enclosures can be maintained in the euphotic zone. Nutrients are usually depleted in the epilimnion of Mt Bold Reservoir during stratification (Ganf 1982) which means that the elimination of nutrient exchange through enclosure is not critical. Enclosure at this time also prevents pulsed nutrient enrichment from temporary breakdown of thermal stratification.

The specific experimental design is outlined below. Because enclosure itself can alter the

phytoplankton community, controls with grazers added were used. These bag effects were also minimized by having a short incubation time. This was also necessary because the changes specifically due to the removal of grazers may be transient within the enclosures. Despite the short incubation time there was no intention to measure zooplankton feeding rates in these experiments, since the changes in phytoplankton recorded were net changes over this time. Because both zooplankton and phytoplankton communities change in Mt Bold Reservoir the impact of zooplankton grazing on the phytoplankton community may vary in time. To investigate this a series of enclosure experiments was done, with overlapping incubation times. Both treatments (zooplankton removal) and controls (zooplankton addition) were replicated adequately in each experiment to enable reliable statistical analyses (Lynch and Shapiro 1981). This replication allowed univariate data to be analysed using standard ANOVA techniques. Comparisons of the phytoplankton communities as a whole required multivariate statistical techniques. Details of the methods used are given in the introductory chapter.

5.2 EXPERIMENTAL METHODS

Eleven separate enclosure experiments were done during the summer of 1982/1983. Ten of the experiments were consecutive while the eleventh was done five weeks after the tenth, during an algal bloom. The experiments ran for ten to fourteen days and overlapped in time from three to seven days. Each experiment consisted of five control enclosures and five treatment enclosures, except for the first and fourth experiments, which only had two of each.

Enclosures were plastic bags made from tubular, 150 μm thick, pallet wrap (Poly Products, Adelaide, Australia) which had a*flat diameter of 91 cm and a*flat length of 1 metre. The first experiment used bags with a*flat length of 2 metres. These lengths allowed the enclosures to be contained within the anticipated euphotic zone. The tops of the bags were gathered and clamped around a 15 cm length of 10 cm diameter PVC pipe with a screw thread cap, which also served as an anchoring point. The bottoms of the bags were sealed using waterproof adhesive tape. Bag volumes were calculated by comparing the filling time of a container of known volume to the bag filling time. The mean bag volume of the 1 m*flat length bags was 156.8 $\pm$ 0.8 l, and that of the 2 m*flat length bags double this. (*flat = unfilled).

All bags were filled *in situ* with reservoir water pumped from 3 m which was above the thermocline throughout the experimental period. The water was filtered through a 40 μm stainless steel screen which effectively removed all hatched stages of the zooplankton present including rotifers. Large phytoplankton were also removed or broken up by this screen. Experiments 1 and 4 had reduced numbers of enclosures due to slow filtering and filling times. Samples of the filtrate were taken at the start and finish of filling each bag to determine the initial (<40 μm) phytoplankton composition. Every alternate bag was inoculated with zooplankton caught using a modified 13 l Schindler trap. The animals were gently concentrated onto a 40 μm screen and resuspended in filtered water from the same depth as they had been caught. It was not possible to stock the bags with the same density of zooplankton as in the reservoir, because the zooplankton abundance at any one depth is not representative of the whole water column and may change on a diurnal basis. Consequently the same catching effort was used for all grazed bags within an experiment and the catching effort was maintained between experiments, so that the zooplankton density in the bags changed in the same relative fashion as in the reservoir. Thus 4-5 traps were used to inoculate each alternate bag with zooplankton, while 2 traps were preserved at random each time, in 4% formalin, to estimate species composition. Once filled, the bags were closed and anchored by a 0.5 m cord to a buoy. The twenty bags of two overlapping experiments were all attached at 5 m intervals to a long mooring line running in a N.-S. direction. This allowed each bag considerable movement in response to wind driven currents which facilitated suspension of phytoplankton within the enclosures. In the initial experiments small air bubbles in the bags kept them constantly at the reservoir surface. Due to the exceptional transparency of the water column during this summer (Figure 3.12), the high light intensity may have inhibited both phytoplankton growth and zooplankton grazing in the bags. Consequently in later experiments small sand weights were added to the bags to position them below the surface.

At the end of each experiment, duplicate water samples were removed from the bags using an integrating tube sampler. The contents of all the bags were then filtered through a 50 μm conical net, the zooplankton caught were checked for visible signs of life and then preserved in 4% formalin. The loss of zooplankton between the 40 μm initial and 50 μm final screen size was minimal. Chlorophyll *a* concentration and the phytoplankton species composition of the bags was determined. The frequency of occurence of the individual phytoplankton species was scored rather than the density. This required that a constant volume (500 ml)

be initially sedimented; a constant subsample (2%) of this settled and a constant number of fields of view (50) scored. It was also necessary to establish that the phytoplankton cells were randomly distributed on the floor of the settling tube. Random distribution of the phytoplankton was established by scoring the numbers of biomass units of each species per field of view for a transect across the floor of the settling chamber. The ratio of the variance to the mean for each species was then tested against a Poisson distribution expectation of equality using a χ^2 test (Elliott 1971). There was agreement ($P < 0.05$) with the Poisson series for all the taxa scored indicating a random distribution.

5.3 RESULTS

5.3.1 Initial Zooplankton

The density and composition of zooplankton both influence the effect of grazing on phytoplankton communities. It was necessary to establish that the zooplankton communities were sufficiently uniform within the grazed bags of each experiment, so that they could be analysed as one treatment.

The mean densities of the initial zooplankton inoculations for all enclosure experiments are shown in Table 5.1. The dominant taxa were; the calanoid copepods *Boeckella triarticulata*, *Calamoecia ampulla*, their copepodites and nauplii; the cladocerans *Daphnia carinata*, *Ceriodaphnia quadrangula*, *Diaphanosoma unguiculatum*, and *Moina micura* Kurz; and the rotifer *Hexarthra mira*. The uniformity of the inoculations into the grazed bags within each experiment was tested by a mixed model factorial ANOVA with replication where zooplankton taxa was a fixed factor and bag a random factor. In this analysis the zooplankton taxa were essentially dummy variables since it was expected that within each experiment there would be differences between the densities of different taxa. The analysis was done this way to avoid the type I error associated with repeated low level ANOVA. The results of these analyses are given in Table 5.2. As well as the expected differences in density between the taxa for all experiments, there were also significant differences between the bags within experiments 2, 3, 5, 6, 8, 9 and 11. This meant that within these experiments zooplankton taxa initially differed in density between the grazed bags. A significant interaction term (experiments 2, 6, 9 and 11) meant that a particular bag or taxa could not be isolated as different from the others in these experiments. The differences between the

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grazed bags as shown by the ANOVA may refer to one or more taxa which may differ in density between one or more bags within each experiment. The extent of these differences in zooplankton density can be examined using an unplanned comparison among the means such as the T-method (Sokal and Rohlf 1981). Table 5.3 lists the results of such comparisons. The T-method does not discriminate between bags which are marginally different using ANOVA (experiments 3, 5 and 6) as it is a more conservative test (Sokal and Rohlf 1981). Three of the dominant nine zooplankton taxa showed density differences between bags within experiments (Table 5.3). Despite these differences the initial zooplankton densities were all high enough to allow the replicate grazed bags to be considered as one treatment.

5.3.2 Final Zooplankton

The density and composition of the zooplankton in the grazed bags may change during the experiment. Similarly zooplankton may develop in the ungrazed bags from eggs or accidental contamination during the filling procedure. To determine the extent of either of these possibilities, it was necessary to examine the final zooplankton communities at the end of the experiment. The mean final densities of the dominant zooplankton taxa for all enclosure experiments are shown in Tables 5.4 and 5.5 for grazed and ungrazed treatments respectively. By the end of the experiments both *Moina* and *Hexarthra* were rare in the bags while substantial numbers of juvenile cladocerans and the chydorid *Chydorus sphaericus* (Muller) had developed. The final densities of the dominant zooplankton taxa were compared between the bags within each treatment of each experiment, as was done for the initial zooplankton inoculations. The results of these analyses are in Tables 5.6 to 5.9. In the grazed bags (Table 5.6) there were significant differences between the bags within experiments 2, 3, 5, 7 and 11 as well as the expected differences in density between the zooplankton taxa. This meant that within the grazed treatments of these experiments the final zooplankton densities differed. Table 5.7 shows details of these differences. Seven of the nine zooplankton taxa differed in final density between the bags of the grazed treatments. This within experiment variation in the final zooplankton composition of the grazed bags combined with the variation in initial zooplankton composition meant that the bags did not all experience the same grazing pressure. The implications of this will be discussed in later sections. In the ungrazed treatments (Table 5.5) there were low final densities of zooplankton taxa so that for some experiments (4, 6, 10 and 11) there were insufficient numbers for analysis. In those experiments where there were sufficient numbers, there were

significant differences between taxa in experiment 3 and between bags in experiments 2, 3, 5, 7 and 9 (Table 5.8). The lack of significant differences between taxa in the ungrazed bags was due to the low numbers of all animals in these bags. Table 5.9 shows that the bag differences were due to single bags. Both initial and final zooplankton densities in the grazed bags were over an order of magnitude greater than those in the ungrazed bags so that regardless of the variation within the grazed treatments, they could be considered distinct from the ungrazed treatment in all experiments.

5.3.3 Zooplankton Biomass

The zooplankton taxa in the bags vary considerably in size so the differences in density shown above do not enable comparisons of the total grazing pressure in the bags. For such comparisons the densities of each taxa in each bag were converted to biomass using a dry weight estimate for each taxa. The estimates of total zooplankton biomass (μg dry wt l^{-1}) for each bag are listed in Tables 5.10, 5.11 and 5.12 for initial grazed, final grazed and final ungrazed treatments respectively. The within and between experiment variation in grazing pressure as measured by zooplankton biomass was examined for each of these treatments separately, using a two level nested ANOVA. With respect to the initial inoculations into the grazed treatments there were significant differences in zooplankton biomass between the experiments ($F_{10,38}$ 20.28, $P < 0.001$) and between the bags within the experiments ($F_{38,49}$ 2.95, $P < 0.001$). In the grazed treatments there were significant differences in final zooplankton biomass between the experiments ($F_{9,37}$ 9.06, $P < 0.001$) and between the bags within the experiments ($F_{37,47}$ 8.98, $P < 0.001$). This was also the case for the final zooplankton biomass in the ungrazed treatments; between experiments ($F_{9,35}$ 5.03, $P < 0.001$) and between bags ($F_{35,45}$ 10.19, $P < 0.001$). The between bag differences are shown in Tables 5.13a, 5.13b and 5.13c for initial grazed, final grazed and final ungrazed treatments respectively. There are fewer differences between bags based on biomass compared with density, nevertheless there is close agreement with different bags in each case. Both initial and final estimates of zooplankton biomass in the grazed bags were about two orders of magnitude greater than those in the ungrazed bags.

When all bags are combined within each experiment the changes in zooplankton biomass across all eleven experiments can be examined. The initial zooplankton inoculations split into two groups; a lower biomass group (experiments 4, 3, 7, 11, 5, 10, 6, 1, 2) and a higher

biomass group (experiments 9, 8). The final grazed treatments also fall into two groups but the order is quite different; a lower biomass group (experiments 9, 8, 10) and a higher group (experiments 2, 3, 5, 7, 11, 6, 4). In the ungrazed treatments there is also two groups of final zooplankton biomass; a lower group (experiments 11, 10, 6, 8, 4) and a higher group (experiments 3, 9, 2, 7, 5).

The substantial changes in zooplankton biomass within the bags during the experiments precludes comparison of this measure of grazing pressure with the phytoplankton response within the individual bags. In addition to the biomass changes, the composition of the zooplankton community also changes during the experiments. This is illustrated by comparing Tables 5.14 and 5.15 which show the copepod biomass : cladoceran biomass ratio for the initial and final zooplankton respectively. Not only is there variation within some experiments but this ratio may change substantially during the experiments. Once again correlation of zooplankton composition and phytoplankton response within individual bags is difficult.

5.3.4 Zooplankton Survival

The change in zooplankton composition during the experiments can be examined in terms of the individual zooplankton taxa. Table 5.16 shows the mean change in density of the dominant zooplankton taxa in the grazed treatments during each experiment, in both absolute and relative terms. *Boeckella* and *Daphnia* densities increased during the experiments from experiment 3 until experiment 7, thereafter decreasing in experiments 8 to 10. The final experiment 11 showed a marked increase for these two taxa. Copepod nauplii decreased in density during all experiments probably by development into copepodite stages. *Moina* decreased in those experiments in which it was present while *Calamoecia* decreased in the majority of the experiments. Other taxa were less consistent in their responses during the experiments (Table 5.16).

5.3.5 Phytoplankton Biomass

Mean initial chlorophyll *a* concentration ranged from 1.05 ± 0.07 to 3.72 ± 0.21 μg l^{-1} for the ten overlapping experiments, then increased to 6.23 ± 0.19 μg l^{-1} for the final eleventh experiment (Tables 5.17a-b). The equality of the initial chlorophyll *a* concentrations within

each experiment was tested by a two level nested ANOVA. Table 5.18 shows that there were no significant differences in initial chlorophyll a concentration between the grazed and the ungrazed treatments. Experiments 5, 6, 7, 8 and 11 did have significant differences in chlorophyll concentration between bags within treatments. Table 5.19 shows the results of unplanned comparisons among these chlorophyll concentrations. The significant differences between bags were not confined to either of the grazed or ungrazed treatments nor were they due to an individual bag being different from all the others. In general where there were significantly different bags within treatments, they were along a gradient of initial chlorophyll a concentration.

Mean final chlorophyll a concentration ranged from 0.56 ± 0.02 to 2.02 ± 0.26 μg l^{-1} for the overlapping experiments, increasing to 7.37 ± 0.69 μg l^{-1} for experiment 11 (Tables 5.17a-b). Two level nested ANOVA within each experiment (Table 5.18) showed there were significant differences in final chlorophyll a concentrations between the grazed and ungrazed treatments for experiments 1, 10 and 11 only. Experiment 1 showed an increase in chlorophyll a in the ungrazed treatment (2.16 vs. 1.05 μg l^{-1}) while this was reversed in experiment 10 which showed a decrease in the ungrazed treatment (0.48 vs. 0.63 μg l^{-1}). Experiment 11 showed an increase in the ungrazed treatment (9.68 vs. 5.07 μg l^{-1}). There were significant differences in final chlorophyll a concentrations between bags within treatments for experiments 2 through to 9 and 11 (Table 5.18). Unplanned comparisons (Table 5.20) showed that these differences were not confined to either of the two treatments nor were they only due to an individual bag being different from the rest. Experiments 2, 5, 7, 8 and 11 did have individual bags which were significantly different from all the others within a treatment (Table 5.20). Removal of these bags from the analysis was not justifiable in terms of different zooplankton biomass levels (Section 5.3.3). If all eleven experiments were combined, the final chlorophyll a concentrations in the grazed treatments were lower than those in the ungrazed treatments.

It is apparent there was considerable variation in both initial and final chlorophyll a concentrations in the bags. Because of this it was not adequate to compare the grazed and ungrazed treatments using only the final chlorophyll a concentrations. It was more appropriate to consider the change in chlorophyll a concentrations within the individual bags. This is expressed in ln units per day in Table 5.21. Mean chlorophyll a net growth rates ranged from -0.142 to 0.077 ln d^{-1} for bags from either treatment across all

experiments. One level ANOVA (Table 5.22) showed there was no significant difference in chlorophyll a net growth rates between the grazed and the ungrazed treatments in any of the ten overlapping experiments. Experiment 11 showed a significant increase in growth rate in the ungrazed treatment (0.033 vs. -0.018 ln d^{-1}). Some of the loss of significance is due to the reduction in degrees of freedom since there is no measure of error for growth within each bag. If combined across all experiments, the mean net growth rates in the ungrazed treatments were greater than those in the grazed treatments.

One level ANOVA, with the treatments within each experiment combined, showed that net growth rates did vary significantly across the ten overlapping experiments ($F_{9,77}$ 19.95, P < 0.001). Unplanned comparisons among the means divided the experiments into two groups; experiments 5, 6, 7 and 10 with lower net growth rates and experiments 1, 2, 3, 4, 8 and 9 with higher net growth rates. This grouping corresponds with the development of low levels of nutrients in the epilimnion. Thus initially higher net growth rates (1, 2, 3, 4) are followed by lower net growth rates (5, 6, 7) during extended stratification and nutrient deficiency. A final increase in net growth rate (8, 9) coincides with a small mixing event (Figure 3.10). These proposed changes are not supported by the measurements of nutrient concentrations in the surface water of Mt. Bold Reservoir across this period (Figures 3.20.1 and 3.21.1). Total phosphorus and nitrogen levels are low throughout the summer however the long time intervals between nutrient measurements means that short term fluctuations may be missed.

5.3.6 Chlorophyll a : Phaeophytin a

The mean chlorophyll a : phaeophytin a ratio of the treatments varies from 1.09 to 1.63 across all experiments (Tables 5.23a-b). Two level nested ANOVA established that initially there was no significant difference in this ratio between the treatments in any experiment (Table 5.24). Similar ANOVA showed that the final ratio differed significantly between the grazed and ungrazed treatments only in experiments 10 and 11 (Table 5.24). In experiment 10 the ungrazed treatment had an unexpected lower mean ratio than the grazed treatment (1.47 vs. 1.56) whereas in experiment 11 the ungrazed treatment had a higher mean ratio than the grazed treatment (1.46 vs. 1.32). There were significant differences between bags within treatments in experiments 8, 9 and 11 (Table 5.24) which were identified using unplanned comparisons (Table 5.25). Even within these treatments a comparison of the chlorophyll a : phaeophytin a ratio in the bags with the final zooplankton biomass they

contain (Section 5.3.3) is contradictory. Thus the bag with the highest ratio may have the highest zooplankton biomass (experiment 8; bag 10) or the lowest (experiment 9; bag 6). This lack of any direct relationship between final zooplankton biomass and the chlorophyll a : phaeophytin a ratio is further illustrated in Figures 5.1a and 5.1b for low (ungrazed) and high (grazed) final zooplankton biomass respectively.

5.3.7 Phytoplankton Composition

Although the phytoplankton biomass in most of the enclosures was not significantly influenced by zooplankton grazing, the composition of the phytoplankton community was expected to differ between the grazed and the ungrazed treatments. A general measure of community composition is the richness or number of taxa present. Table 5.26 shows the numbers of phytoplankton taxa scored in each treatment as well as the numbers which are shared between the treatments for all experiments. During all experiments the number of taxa present increased in both grazed and ungrazed treatments from the initial score. Most of the initial taxa remained in the bags at the end of the experiments although experiments 3 and 4 had up to 30% losses (Table 5.26). The numbers of taxa in the grazed and ungrazed treatments were similar although in seven out of eleven experiments the ungrazed treatments had slightly more taxa present. Most of the taxa in the grazed treatments were present in the ungrazed treatments; the differences were due to new taxa. Changes in community composition can be examined through diversity indices which measure both species richness and evenness.

The Shannon Wiener diversity index (Pielou 1977) was calculated for the phytoplankton in each bag using the frequency data (Fott 1975). Mean diversities for the initials and the two treatments in each experiment are listed in Table 5.27. Diversity values range from 2.6033 to 4.0166 with the initial generally lower than the grazed treatment which is itself lower than the ungrazed treatment. This range in diversity (Table 5.27) is greater than that reported by either Porter (1973a) or Peer (1986). A three level nested ANOVA done on all the data showed that there were significant differences in phytoplankton diversity between the experiments ($F_{10,22}$ 3.61, P < 0.01), between the treatments ($F_{22,85}$ 5.53, P < 0.001), and between the bags ($F_{85,107}$ 2.27, P < 0.001). Two level nested ANOVA and pairwise comparisons were done to examine these differences. Table 5.28 lists the ANOVA results for each experiment separately. Experiments 1, 2, 5, 6, 7 and 8 have significant differences

between the treatments, while experiments 2, 4, 5 and 8 have significant differences between bags within treatments. Pairwise comparisons listed in Table 5.29 show that in all the former experiments the diversity of the initial sample is significantly lower than that of the ungrazed treatment, while neither the initial sample nor the ungrazed treatment are different from the grazed treatment. Table 5.29 also shows that bag differences are mainly within the grazed treatments. Separate one level ANOVA's were done on each treatment with the bags for each experiment combined. There were significant differences in phytoplankton diversity between the experiments for the initials ($F_{10,35}$ 3.186, P < 0.01), the ungrazed treatments ($F_{10,79}$ 23.74, P < 0.001), and the grazed treatments ($F_{10,78}$ 7.81, P < 0.001). However pairwise comparisons show no consistent change in phytoplankton diversity with time i.e. across the experiments, for any treatment.

Species richness of the grazed treatments increased compared to the initial samples, but this was not supported by differences in the Shannon Weiner diversity index despite this index being sensitive to changes in richness (Peet 1974). This suggested that the evenness of the taxa in the grazed treatments was reduced relative to the initial samples. Table 5.30 shows the evenness calculated from the mean Shannon Weiner diversity index and the number of taxa scored in each treatment (Krebs 1972). There was no difference in evenness between the initial samples and the grazed treatments across all experiments (t_{10} 0.21, n.s.). Differences in phytoplankton composition between the grazed and the ungrazed treatments must be at the level of the individual taxon.

5.3.8 Phytoplankton Specific Composition

The main phytoplankton taxa scored in the enclosure experiments are listed in Table 5.31. As discussed in Chapter 2 the phytoplankton were not always completely identified however the taxa were scored consistently within and across the experiments so this does not affect the results. The mean frequencies of the phytoplankton taxa in all experiments are tabled in Appendices 5.1, 5.2 and 5.3 for the initials, final ungrazed and final grazed treatments respectively.

The initial species composition of all enclosures in two experiments (1 and 8) was determined and the uniformity of individual taxa tested by two level nested ANOVA. There were no significant differences in initial phytoplankton frequencies between the bags destined

for either of the two treatments. For these two experiments (1 and 8) there were three instances of significant differences between bags within treatments involving 2 taxa out of 20. This was an adequate demonstration of within experiment homogeneity and consequently for the remainder of the experiments only the first and last samples were counted to examine compositional change with time. Due to the potential variation in response to the enclosure and treatments, the final phytoplankton frequencies were counted in full. Unfortunately some samples were lost before counting so not all experiments have all replicates. The theoretical detection limit based on the proportion of the sample counted and assuming a uniform distribution for this estimation only, was 4 cells per ml, so there were taxa which were not initially recorded but developed populations during the experiments. There were also taxa which only occurred in one or two fields of view in one experiment; these were considered rare and excluded from the analyses. One phytoplankton taxon, the large desmid *Staurastrum*, was rarely scored in the fields of view but was present in the sedimented samples of several experiments. The whole sedimented sample was scored and used to compare the two treatments for this taxon, but these scores were not used with the frequency scores of the other taxa.

In each experiment the response of individual phytoplankton taxa to the removal of grazers was examined using a two level nested ANOVA. In those experiments where there were only two bags per treatment (1 and 4) a one level ANOVA was used to test for differences. Because the data was a proportion it was normalized using an arcsin square root transformation (Sokal and Rohlf 1981). Figure 5.2 summarizes the results of these analyses. In all experiments there were significant differences in the frequency of individual phytoplankton taxa between the grazed and the ungrazed treatments. The same taxa were not always responsible for these differences although some taxa were consistently different in a majority of experiments. There were also significant differences between bags within treatments. These were not investigated since correlations between individual phytoplankton taxa and individual zooplankton taxa within the bags would not be reliable due to the changes in zooplankton during the experiments (Section 5.3.3). The directions of the ungrazed differences are also shown in Figure 5.2. These were generally consistent across the experiments for most taxa but some taxa did differ e.g. *Sphaerocystis* (SP), *Melosira* (MV) and the pennate diatoms (P1, P2 and P3).

The differences in frequency are broadly summarized below:

1. The colonial green *Oocystis* (OO) did not differ between the treatments while the other colonial green *Sphaerocystis* (SP) decreased in two ungrazed treatments but increased in a third.

2. The attenuate unicellular green *Schroederia* (SS) increased in two ungrazed treatments as did the similar *Ankistrodesmus* (AN), but a similar form without a bifurcate spine (TS) decreased in one ungrazed treatment. The larger *Closteriopsis* (CL) showed no difference between treatments.

3. Unidentified flagellates, (F0, F1, F2, F3 and CS; in order of increasing size), all increased in the ungrazed treatments. The other flagellate *Cryptomonas ovata* (CO) also increased in four ungrazed treatments.

4. The crysophyte *Ochromonas* (OM) did not differ between the ungrazed and the grazed treatments.

5. The cyanobacteria *Cyanarcus* (CN) did not differ between the treatments but single cells and small colonies of *Microcystis aeruginosa* (MA) increased in the ungrazed treatments.

6. The centric diatoms *Cyclotella meneghiniana* (CM) and *Cyclotella* sp. (CY) increased in the ungrazed treatments. The latter, a small cell, was rarely recorded in the initial samples but numerically dominated the ungrazed treatments while being almost absent from the grazed treatments. A third large unidentified centric diatom (DS) also increased in the ungrazed treatments while *Melosira* (MV) decreased in one and increased in another ungrazed treatment.

7. The pennate diatoms, (P1, P2, P3, P4, P5, L1, L2, DB and PT), all increased in ungrazed treatments except for experiments 9 and 10, where some decreased. P1 to P5 cover a five fold increase in length but did not show a different response to grazing.

8. The large desmid *Staurastrum* decreased in the ungrazed treatments but this may be an artifact since this large cell was likely included with the zooplankton inoculations.

9. Finally, a larger unidentified spherical cell (LS) did not differ between the treatments but a smaller one (SM) increased in the ungrazed treatments.

5.3.9 Phytoplankton Size Structure

The phytoplankton taxa scored in the enclosures covered a wide range of sizes and shapes. The greatest axial linear dimension or GALD (Lewis 1976) was measured for each taxon and the biomass unit volume was calculated in order to quantify these differences. The GALD measurements which ranged from 4 to 125 μm were divided into 13 equal size classes of 10 μm intervals. Four of these size classes were not represented, leaving nine into which the phytoplankton taxa were allocated. The mean frequencies of all taxa within each size class were summed and compared between the grazed and the ungrazed treatments for all experiments. Table 5.32 which lists the summed frequencies shows that the majority of the plankton scored fall into the first three size classes. Examination of Table 5.32 shows that the summed frequencies differ between the two treatments in several GALD size classes which change across the experiments. These size frequency distributions were compared in each experiment using a Kolmogorov-Smirnov two sample test, the results of which are also in Table 5.32. This shows there are significant differences between the GALD frequency distributions of the grazed and ungrazed treatments in five experiments.

A similar analysis was done using the biomass unit volume of each taxon since GALD by itself does not completely describe the size of the taxon. The biomass unit volume which ranged from 16 to 9595 μm^3 was also divided into nine size classes each of which was roughly double the volume of the previous one. Table 5.33 shows the volume frequency distributions and the results of comparison between treatments in each experiment. The phytoplankton are more widely distributed across the range of volume size classes compared to GALD. The summed frequencies differ between the two treatments in several volume size classes but not consistently across the experiments. There are significant differences between the volume frequency distributions of the grazed and ungrazed treatments in six experiments, five of which are also different in the GALD analysis (Tables 5.32 and 5.33). While these analyses indicate that the response of the phytoplankton taxa to zooplankton grazing can depend on size and shape, they do not indicate which individual size classes differ between the treatments.

A more specific approach to determine any general pattern in the size and shape of the taxa which responded to grazing, was to locate each taxon on a plot of GALD vs. biomass unit volume. Figure 5.3 shows the location of each phytoplankton taxon on the GALD vs.

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volume axes with volume on a logarithmic scale for convenience. *Microcystis aeruginosa* was not included as reliable measurements of the colonies were not made. The bifurcation on this figure reflects the two dominant shapes; spheres and attenuate cylinders. For each experiment the response of each taxon to grazing was expressed as a ratio of the mean ungrazed frequency divided by the mean grazed frequency. Table 5.34 shows the mean ungrazed over grazed ratio for each taxon across all experiments, with those which are significant by ANOVA marked. These values were then superimposed onto the GALD vs. volume figure and examined for patterns.

The plots for all experiments are shown in Figures 5.4a-k. Examination of these figures shows that GALD did not consistently restrict whether or not a phytoplankton taxon was reduced by grazing. Taxa with a GALD >60 μm were not reduced in four experiments (2, 6, 8 and 9) but were reduced in the other seven, although in only four of these (1, 4, 5 and 11) were the grazing reductions significant. These between experiment differences may be explained in terms of zooplankton composition or biomass but a comparison with either the initial or final zooplankton communities did not support this. In most experiments there was an upper limit on the biomass unit volume which was reduced by grazing. *Sphaerocystis* with a mean unit volume of 9542 μm^3 was reduced in experiment 3 only, while *Oocystis* with a mean unit volume of 9595 μm^3 was not reduced in any experiment.There was no lower limit of either GALD or the biomass unit volume for taxa reduced by grazing in the enclosure experiments.

5.3.10 Phytoplankton Community Composition

It was apparent that there were differences in the frequencies of many individual phytoplankton taxa between the grazed and the ungrazed treatments yet there was no consistent separation of the treatments based on the incidence or size or shape of their component phytoplankton taxa. Multivariate statistical methods were used to integrate the frequency data, allowing comparison of the phytoplankton communities as a whole in each bag of each treatment. The specific analytical methods used for the enclosure experiment data were introduced in earlier chapters.

The results of a hierarchical classification using the Bray-Curtis dissimilarity measure and the UPGMA fusion procedure for each experiment are presented as a series of dendrograms

in Figures 5.5a-k. In all experiments except 1 and 8; sample numbers 1 and 2 are initial samples, sample numbers between 3 and 12 are from ungrazed enclosures, and sample numbers between 13 and 22 are from grazed enclosures. Duplicate samples from each enclosure are indicated by number pairs i.e. (3, 4) to (21, 22). Missing sample numbers imply either the enclosure did not exist (experiment 4) or the samples were lost before counting. In experiment 1; sample numbers 1 to 8 are the initials, sample numbers 9 to 12 are from the ungrazed enclosures, and sample numbers 13 to 16 are from the grazed enclosures. In experiment 8; sample numbers 1 to 20 are the initials, sample numbers 21 to 30 are from the ungrazed enclosures, and sample numbers 31 to 40 are from the grazed enclosures.

Experiment 1 (Figure 5.5a) which is representative, is examined in detail. Samples 1 to 8 which correspond to two samples from each of the four initial bags, group together under a highest common dissimilarity of 0.23. Within this group of eight samples the two replicates from each bag (1, 2), (3, 4) etc. do not necessarily pair off together, which implies that the initial phytoplankton community composition is homogeneous. Samples 9 to 12 represent the ungrazed treatments. Here the two replicates from each bag are more similar to each other than to those of the other bag. The two ungrazed bags are joined at a common dissimilarity of 0.25. The grazed samples (13 to 16) show more dissimilarity as a group, being joined at 0.44, but again the two replicates from each bag pair off. Thus in experiment 1 there are three distinct phytoplankton communities which are more than 0.50 dissimilar from each other. The initial group joins the grazed group at 0.57 dissimilarity, slightly before the ungrazed group at 0.61. This implies that the grazed treatment is slightly closer in composition to the initial reservoir treatment than the ungrazed treatment.

The characteristics detailed above for experiment 1 are listed for all experiments in Table 5.35. This shows that for experiment 8, the other experiment with complete initials scored, the initial replicates do not pair up with each other, indicating homogeneity. For all other experiments except 9 the two initial replicates pair with each other before joining another treatment. For experiment 9 the two initials group with an ungrazed bag. Generally, the initial replicates are more similar to each other than either of the treatment groups are (Table 5.35). Table 5.35 also shows that the ungrazed replicates pair together more often than the grazed and there tends to be more dissimilarity among the grazed treatments.

In experiments 1, 2, 3, 4, 6, 7 and 10 there are always three distinct phytoplankton

communities; initial, ungrazed and grazed (Figure 5.5). In experiment 11 the ungrazed bags group together as do the grazed bags except bag 8 which joins the ungrazed group. Experiment 8 also had distinct groups except for one ungrazed replicate from bag 5 which joins the grazed group. The grazed and ungrazed bags each split into two groups in experiment 9. One of the ungrazed bags (5) joins the initials while the other ungrazed bags (1 and 3) join one of the grazed groups (bags 4, 6, 8 and 10). Experiment 5 has one grazed bag (4) and one ungrazed bag (9) in the opposite group as well as the grazed group split into two. The ungrazed group joins one grazed group (bags 8 and 10) before together they join first the other grazed group (bags 2 and 6) and then the final ungrazed bag (9).

The order in which these three phytoplankton communities relate to each other is also listed in Table 5.35. In six experiments the grazed community is more similar to the ungrazed community than to the initial community, in three experiments the grazed community is closer to the initial community while in two experiments there is no preference. Since both treatments are subject to short term enclosure effects, this should differentiate them both from the initial samples.

Similar hierarchical classification was done using frequency scores from all of the experiments together, in order to examine the relationships between the treatments of all the experiments. The UPGMA fusion procedure showed a temporal gradient of dissimilarity rather than any tight grouping. Furthest neighbour fusion was done to emphasize any grouping present but did not simplify the relationships. The dendrograms from these analyses are not presented as they add little to the overall picture. More interpretable results are achieved after ordination using detrended correspondance analysis (DCA).

Figures 5.6a-d show the results of an ordination using the complete data. These figures are plots of the first and second vectors as the X and Y axes respectively. In this ordination of the complete data set the first and second vectors between them describe over 50% of the variation. Figures 5.6a-d are all to the same scale and may be superimposed to give a complete picture, but are easier to interpret separately. Figure 5.6a shows the plot for experiments 1, 2 and 3. Each experiment in isolation confirms the classification results i.e. the initial, final ungrazed and final grazed phytoplankton are distinctly different communities. Further to this each treatment is grouped separately on this plot; there is no overlap of treatments. The treatments within all the other experiments are distinct (Figures

5.6b, 5.6c, 5.6d), although there is some overlap of grazed and ungrazed treatments in experiments 5 and 9 as was found in the classification. Between experiments there is considerable overlap both within and between treatments e.g. experiments 2 vs.6 ungrazed treatments or experiments 5 grazed vs. 2 initial. Separation of these communities may require other ordination axes. Nevertheless different treatments do not overlap in sequential experiments. The trajectories of the different experiments can be examined by plotting the mean vectors for each treatment and joining sequential experiments. Figure 5.7 shows the trajectories of the three treatments for all of the experiments. There is a substantial time interval between experiments 10 and 11 hence they have not been joined. Figure 5.7 suggests that the second vector (Y axis) is differentiating the ungrazed and the grazed treatments; the latter treatment always has larger second vector values. The first vector (X axis) seems to differentiate the effects of enclosure i.e. the initials have larger first vector values than either the grazed or the ungrazed treatments. There are also temporal changes along the X axis which may reverse in direction e.g. between experiments 5, 6 and 7.

The configuration produced by an ordination is completely dependent on the data used so the groups and paths described above are only applicable to the complete data. Figures 5.8a-d show the results of an ordination using only the grazed and the ungrazed data without the influence of the initial samples. These two treatments are still distinct communities within each experiment (Figures 5.8a-d). Here the first vector (X axis) differentiates the two treatments with a greater vector value for the grazed treatment, although again there is overlap in experiments 5 and 9. There are also temporal changes along this axis with larger vector values for the later experiments. These two trends suggest that within the enclosures the grazed treatments can speed up a temporally changing phytoplankton composition. When these two treatments are ordinated separately neither of them are aligned temporally along an axis.

5.4 DISCUSSION

5.4.1 Initial Conditions

Throughout the experiments the initial starting conditions allowed the planned analysis to be done. Thus the initial chlorophyll a concentrations did not differ between the two treatments and initially the phytoplankton composition was homogeneous across the

treatments within each experiment. The grazed and ungrazed treatments imposed were successful. Bags that were inoculated with zooplankton retained viable populations and bags from which the zooplankton were filtered did not develop consequential populations during the experiments. However the variation in zooplankton biomass and composition in the grazed bags during the experiments did restrict the interpretation of the changes in phytoplankton composition in these bags. This is a consequence of working with natural populations *in situ* although zooplankton survival within the bags was comparable to other enclosure experiments of this size reported in the literature e.g. Porter (1972).

5.4.2 Phytoplankton Biomass

There were no significant differences in phytoplankton biomass, as measured by chlorophyll *a*, between the grazed and the ungrazed treatments in the majority of the experiments. This result was surprising since it was expected that zooplankton grazing would reduce the overall amount of phytoplankton present. It was also contrary to much of the enclosure literature (Porter 1973a; Shapiro *et al.* 1975; Lynch 1978; Andersson *et al.* 1978; Lynch and Shapiro 1981; Elliot *et al.* 1983; Shapiro and Wright 1984; Hessen and Nilssen 1986) so is examined further. It is first necessary to examine the methodology before any explanations are proposed.

There was no evidence that the measurements of chlorophyll *a* concentrations were invalid. The duplicate extractions from each bag consistently show good precision (Tables 5.17a-b). Accompanying the inoculation of zooplankton, large phytoplankton which were retained on the 40 μm screen were also added to the bags. These additions may have overshadowed reductions in chlorophyll *a* due to grazing but this was unlikely here as the majority of the phytoplankton cells present were <40 μm (Figure 5.3). An exception was the large desmid *Staurastrum*; present in experiments 8 to 11 and usually more frequent in the grazed bags, which was likely seeded into these bags with the zooplankton. Another possible source of chlorophyll *a* is the periphyton which developed on the enclosure walls. This was not included through the use of a tube to sample only the planktonic algae. It was possible that differential extraction of chlorophyll *a* from the different taxonomic groups of phytoplankton may have biased the comparison since compositional changes did occur. For example acetone extraction is known to underestimate chlorophyll *a* in cyanobacteria (Rai and Marker 1982). However the compositional changes recorded involved fluctuations in several

taxonomic groups of algae (Table 5.31 and Figure 5.2) and in particular cyanobacteria did not dominate. Overall, the chlorophyll a measurements did not appear to be wrong.

Significant changes in phytoplankton biomass will not occur if the grazing pressure is insufficient. The final zooplankton biomass within the grazed bags ranged from 98.8 to 730.5 μg dry wt l^{-1} across all the experiments and was an order of magnitude higher than that within the ungrazed bags (Tables 5.11 and 5.12). The mean zooplankton biomass throughout the whole water column of Mt Bold Reservoir during the same period ranged from 176.1 to 1087.2 μg dry wt l^{-1} (Section 3.3.3) so the grazed bag zooplankton concentrations were comparable and not insignificant. The mean zooplankton biomass in the two experiments (1 and 11), where the phytoplankton biomass did decrease in the grazed bags, was not the highest for the experiments with means of 461.0 and 457.9 μg dry wt l^{-1} respectively. Note this estimate for experiment 1 is the initial biomass only as the final was not saved. The inoculation time should be considered along with grazing pressure. Thus ten to fourteen days may not have been long enough for the imposed grazing pressure to reduce the phytoplankton biomass although it was long enough for the phytoplankton composition to change. The incubation time was intentionally kept short to minimize enclosure effects. Close examination of the results of Vanni (1986a, 1986b) and Ganf (1983) shows that in the first 8 to 15 days of their experiments phytoplankton biomass may increase in the grazed enclosures before the grazers eventually reduce it.

Finally, nutrient limitation of phytoplankton growth must be examined. The concentrations of soluble phosphorus and nitrogen (nitrate and nitrite) in the surface water of Mt Bold Reservoir were very low throughout the period of the overlapping experiments; <5 μg l^{-1} and <0.01-0.03 mg l^{-1} respectively (Figures 3.20.1 and 3.21.1).The changes in chlorophyll a concentrations in the ungrazed enclosures were usually negative (Table 5.21) indicating sub-optimal growth conditions during the experiments. The rapid recycling of nutrients by grazing zooplankton may enable nutrient limited algae within the grazed bags to maintain biomass levels. The net changes in chlorophyll a in Mt Bold Reservoir during this period were also small and often negative (Figure 3.25 and Table 5.21). The magnitude and direction of the changes in chlorophyll a concentration in the enclosure experiments were reflected in the reservoir. Experiment 11 was done after the breakdown of thermal stratification (Figure 3.10) and the surface water had increased nutrient concentrations; 22 μg l^{-1} and 0.07 mg l^{-1} soluble phosphorus and nitrogen respectively (Figures 3.20.1 and

3.21.1). This experiment had a positive change in chlorophyll *a* concentration in the ungrazed bags and a negative change in the grazed bags. Strong nutrient limitation is advantageous in discriminating between grazing effects and differential nutrient uptake and growth in the short term. Enclosure experiments with artificial nutrient enrichment often result in phytoplankton compositional changes which must be separated from the other treatment effects (Lynch and Shapiro 1981; Vyhnalek 1983; Uehlinger *et al.* 1984; Vanni 1986b).

A combination of nutrient limitation, zooplankton grazing intensity and short incubation time have enabled a balance between the reduction of phytoplankton biomass by grazing and the stimulation of phytoplankton growth by nutrient recycling. At the same time there is a redistribution of the available resources into those taxa which are not subject to grazing, thus the specific composition changes. Enclosure experiments by DeCosta *et al.* (1983) showed no difference in phytoplankton biomass between natural plankton controls and zooplankton enriched treatments. Both chlorophyll *a* and total phosphorus concentrations were low.

5.4.3 Chlorophyll *a* : Phaeophytin *a*

Phaeopigments are found in the gut and faecal pellets of many species of zooplankton (Currie 1962; Daley 1973) and ambient concentrations have been used as measures of herbivorous zooplankton grazing activity (Welschmeyer *et al.* 1984; Downs and Lorenzen 1985). Consequently higher concentrations of phaeopigments were expected in the grazed bags. These may contribute substantially to the chlorophyll *a* absorption measured in these bags. There were no significant differences in the final chlorophyll *a* : phaeophytin *a* ratio between the grazed and the ungrazed treatments for the majority of the experiments. The range of the ratio recorded implied that 0 to 100% of the absorbance was due to chlorophyll *a* . Although there were a few individual values outside of this range (1.0 to 1.7), the precision of the duplicate determinations from each bag was equivalent to that for the chlorophyll *a* determinations (Tables 5.17 vs. 5.23). A potential source of bias in these measurements may be interference from the breakdown of chlorophylls *b* and *c* (Helling and Baars 1985). Breakdown products of chlorophylls *a*, *b* and *c* do not all absorb in the same manner. Arguments against this here are as for the previous discussion on chlorophyll extraction.

Helling and Baars (1985) found in their grazing experiments, of 14 to 21 h duration, that phaeopigments both increased and decreased in dark controls relative to the initial concentrations, although the process causing this was unknown. These authors also found that while phaeopigments increased in the grazed bottles, the results were more variable with low grazing pressure. In the results reported here there was no systematic change in the chlorophyll a : phaeophytin a ratio between the initials and either grazed or ungrazed treatments (Table 5.23). There was also no reduction in variation with increasing final zooplankton biomass (Figures 5.1a vs. 5.1b). The lack of interpretable response may be due to the low concentrations of chlorophyll present for most of the experiments. This was supported by experiment 11 in which there was a significant decrease in the grazed treatment ratio and where the chlorophyll a concentrations were the highest for all experiments.

5.4.4 Phytoplankton Composition

There were no significant differences in either species richness or diversity between the grazed and the ungrazed treatments. This does not agree with the results of either McCauley and Briand (1979) or Peer (1986). Both of these studies found that a reduction in grazing resulted in reduced phytoplankton diversity. Here the grazed treatment diversity is usually lower than the ungrazed (Table 5.27) but there is greater variation within the grazed treatments and consequently this difference is not significant. Porter (1973a) also found no consistent effect of increased grazing intensity on phytoplankton diversity using the Shannon Weiner index.

All experiments had significant differences in specific phytoplankton taxa between the grazed and ungrazed treatments. This parallels the majority of enclosure experiments reported where grazing pressure has been manipulated. Several taxa which changed in these experiments show similar responses in other published work. Just as here the responses were not always consistent, so too do they vary in the literature. Some specific comparisons are made with the literature:

1. Flagellates have a mixed response to grazing in the enclosure literature. Porter (1973a, 1973b), Lynch (1978), McCauley and Briand (1979), Vyhnalek (1983) and Vanni (1986b) all reported that they were suppressed by grazing as was found in these experiments. Schoenberg and Carlson (1984) found that most flagellates declined in

the presence of grazers but occasionally *Cryptomonas* became dominant. Similar variable responses for *Cryptomonas* were shown by Andersson *et al.* (1978) and Vanni (1986a) while Lynch and Shapiro (1981) and Fott (1975) both found *Cryptomonas* dominated the grazed situations.

2. *Ankistrodesmus* and *Schroederia* were both suppressed by grazing in two experiments here. McCauley and Briand (1979), Lynch and Shapiro (1981) and Peer (1986) all found *Ankistrodesmus* decreased in grazed enclosures yet Porter (1973a) reported no change. Lynch (1978) showed *Schroederia* increased with grazing while Vyhnalek (1983) found that the larger *Schroederia robusta* decreased and the smaller *Schroederia setigeria* increased with grazing.

3. The colonial green *Sphaerocystis* increased in the grazed bags of Porter (1973a, 1973b) and Vanni (1986a) but decreased in those of Lynch and Shapiro (1981) and Lynch (1978). In the work reported here *Sphaerocystis* increased in the grazed bags of experiments 1 and 2 but was suppressed in those of experiment 3. Small colonies of the cyanobacteria *Microcystis* were suppressed by grazing in the Mt Bold enclosures. Similar results were found by both Schoenberg and Carlson (1984) and Andersson *et al.* (1978), while Porter (1973a) found *Microcystis* was not affected.

4. Centric diatoms were suppressed by grazers here as was also reported by Porter (1973a), Andersson *et al.* (1978), McCauley and Briand (1979), and Vyhnalek (1983). Pennate diatoms were also suppressed in most experiments here, irrespective of their length which reached 125 μm. Porter (1973a), Andersson *et al.* (1978), Lynch (1978), McCauley and Briand (1979), Vyhnalek (1983) and Vanni (1986a) all reported pennate diatoms decreased with increased grazing but particular species also increased e.g. *Nitzschia* (Vyhnalek 1983) and *Synedra* (Vanni 1986a).

5. The colonial green *Oocystis* was common throughout the experiments but showed no significant response to grazing. Porter (1973a) also reported it not affected but Lynch (1978), Lynch and Shapiro (1981) and Vyhnalek (1983) all found it was suppressed by grazing.

The phytoplankton taxa that responded to grazing did not fall into any taxonomic groupings. In particular the cyanobacteria *Microcystis aeruginosa* appeared to be grazed by zooplankton in these enclosure experiments. The lack of importance of taxonomic boundaries has been noted by other authors (Porter 1973b; Vyhnalek 1983; Vanni 1986a).

Figures 5.4a-k show that there was no consistent relationship between phytoplankton size and response to zooplankton grazing. In these experiments there was no upper limit of GALD above which the phytoplankton were not grazed. Biomass unit volume did show an upper boundary around 9000 μm^3 above which taxa were rarely grazed, but below this there was no consistency. These results as well as an examination of the literature show that size is not a consistent predictor of phytoplankton susceptibility to grazing. The data in the enclosure literature is often not from specific measurements of the size limits but results from fractionation of the food supply. For example, although Lampert *et al.* (1986) found that a <35 μm fraction was suppressed by grazing and a 35-250 μm fraction was enhanced, this did not imply that all taxa in the larger fraction were not grazed, and vice versa. For instance Porter (1973a) reported that phytoplankton with a longest dimension >30 μm were unaffected by grazing as a group while small (2-30 μm) phytoplankton were suppressed as a group. However within both groups there were subgroups with opposite responses. Thus large diatoms were suppressed and small greens, blue-greens and diatoms were unaffected (Porter 1973b). Similarily Vyhnalek (1983) found that phytoplankton which passed through a 40 μm screen were suppressed by grazing while those which were retained by the screen were enhanced. Exceptions to this were *Schroederia* from the small fraction which increased and *Aphanizomenon* and *Melosira* from the large fraction which both decreased.

These examples are from enclosure experiments where size limitations were inferred from changes in the phytoplankton populations, as was done in the present experiments. More direct measurements of food size limitations were reported by Porter (1973a), Nadin-Hurley and Duncan (1976) and Ferguson *et al.* (1982) all of whom examined the gut contents of individual zooplankton. Porter (1973a) found that phytoplankton taxa >40 μm were rarely ingested but the maximum length of an ingested cell was 80 μm. A sharply defined upper limit to the size of ingested algae was not found (Porter 1973a). Nadin-Hurley and Duncan (1976) concluded that width was the limiting factor for ingestion rather than length. This supports the finding in the present work that volume rather than GALD may place an upper limit on zooplankton food size. Ferguson *et al.* (1982) found that phytoplankton taxa whose dimensions exceeded 60 μm in any plane were rarely ingested by even the largest zooplankton. Irrespective of the upper size limit it is apparent from Figures 5.4a-k that within the size range of grazed phytoplankton, zooplankton selected food on criteria other than size. Furthermore these criteria seem to vary between the experiments. The between experiment variation may be due to changes in individual zooplankton feeding behaviour as

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well as a changing zooplankton community structure.

Both the classification and the ordination procedures separated the phytoplankton taxa of each experiment into three distinct communities; initial, grazed and ungrazed. The use of multivariate techniques to analyse phytoplankton community changes has concentrated on temporal changes e.g. Allen *et al.* (1977), Bartell *et al.* (1978), Harris and Piccinin (1980) and Maddock and Taylor (1984). An example of its use to interpret experimental manipulations of phytoplankton communities is the work of Oviatt *et al.* (1977) in land based tanks. These authors found that three sewage enrichment treatments were easily separated by multivariate analysis using broad phytoplankton biomass measurements. Unexpectedly, when these authors used detailed phytoplankton species abundance in the analysis there was no clear separation (Oviatt *et al.* 1977).

The ordination of treatments from all experiments together showed there was a temporal change in the ungrazed phytoplankton community composition and there was an indication that at times zooplankton grazing shifted the community composition along this temporal path. Intuitively this is attractive because an ungrazed community in one experiment has been subject to zooplankton grazing in the reservoir since the ungrazed community of the previous experiment. However care must be taken with this interpretation as the initial samples did not show similar temporal changes to the ungrazed and grazed communities.

The influence of microzooplankton (<40 μm) grazing on the phytoplankton community was not addressed in these experiments although there was some evidence to suggest that it could be significant. It was initially assumed that both grazed and ungrazed enclosures would have equivalent concentrations of heterotrophic organisms that passed through the 40 μm screen. However by the end of experiment 5 there was a high concentration of a heterotrophic ciliate (R.J.Shiel, pers. comm.) in the ungrazed bag 9 of this experiment. This ciliate was also present in the other ungrazed bags but at low concentrations. The frequencies of small phytoplankton such as *Cyclotella* sp. and small flagellates were substantially reduced in bag 9 compared with the other ungrazed bags in this experiment. The protozoon may have increased in the absence of larger predators and grazed on the smaller algae, thereby altering the phytoplankton composition. This may explain the dissimilarity of bag 9 from all other bags in experiment 5 in the classification of the phytoplankton community (Figure 5.5e). The subtlety of this grazing influence may be

shown through the grazed bag 4 in experiment 5 which also had a low concentration of the ciliate. The phytoplankton composition of this grazed bag 4 was more similar to that of the ungrazed bags than to the other grazed bags in which the ciliate was absent (Figure 5.5e). This ciliate did not attain similar high concentrations in any of the other experiments.

CHAPTER SIX: ZOOPLANKTON GRAZING

6.1 A REVIEW OF TERMS AND METHODS

[*]In terms of energy or mass transfer, ingestion is the most significant interaction between an animal and its environment (Spomer 1973). Consequently, the measurement of zooplankton grazing rates is fundamental to an understanding of the interactions between zooplankton and phytoplankton.

Several terms are used in the literature to quantitatively describe the energy or mass flow between phytoplankton and zooplankton, however there is no consistency in usage. In this study the following terms and definitions are used:

- Feeding rate - a measure of mass or energy flow into the animal expressed in terms of cell number or cell biomass per animal per unit time. A synonym in the literature is ingestion rate.

- Filtering rate - the volume of food suspension from which a zooplankter would have to remove all cells in the unit of time to provide its measured food intake. Synonyms in the literature include grazing rate and clearance rate.

In this study grazing rate is used as a general term when neither of the above two measures are specified.

There are two basic approaches to the measurement of zooplankton grazing: the animals are in a suspension of food and either the rate of accumulation of food by the animals or its rate of loss from the suspension is measured. The former method usually involves marking the food while the latter involves sequential estimates of food biomass (Peters 1984).

The oldest technique is to measure the change in the number of suspended food particles, before and after exposure to feeding animals, by direct microscopic counting (Gauld 1951; Mullin 1963; McQueen 1970; Hargrave and Geen 1970; Borsheim and Olsen 1984; Havens and DeCosta 1985; Horn 1985a; Knisely and Geller 1986). The change in food concentration is a measure of the amount of food eaten, however since grazing rates are dependent on food concentration, this can be too simplistic. Problems with using cell counts are that long

exposures are required for measurable concentration changes during which food sedimentation and growth can occur. Sedimentation, which results in a variable food concentration on offer to the zooplankton as well as an artificial reduction in food concentration, may be alleviated by mixing the food suspension. Growth may be corrected for through an ungrazed control but in the grazed situation food growth may be enhanced by recycling of nutrients via zooplankton excretion (Gliwicz 1975; Porter 1976; Roman and Rublee 1980). Long exposures can be overcome by increasing animal concentrations but feeding interference through crowding may result (Hayward and Gallup 1976; Helgen 1987). The necessity for concentration changes to be statistically significant may result in excessive counting requirements especially in natural phytoplankton communities (Peters 1984).

A more recent method of measuring food concentration changes is by electronic particle analysis (Sheldon and Parsons 1967; McQueen 1970; Kersting and Holterman 1973; Richman et al. 1980; Vanderploeg 1981; Richman and Dodson 1983; Ganf and Shiel 1985a). The basis of these methods is that the particles in suspension interrupt an electric or light field and their number and size can be determined from this. These methods overcome some of the problems of direct microscope counts but introduce others. The main advantage is that large numbers of particles may be counted and measured in a short time thus statistically significant concentration differences may be determined without long exposure times or animal crowding. The disadvantage is the ambiguity of the measurements; living, non living, intact and broken phytoplankton cells are not discriminated and the physical characteristics of size and shape may be interpreted differently electronically (Harbison and McAlister 1980). Electronic counters have been used to examine the selection of foods of different size by zooplankton (Berman and Richman 1974; Poulet 1978). Selective feeding on the most abundant size class of food particles (peak tracking) has been demonstrated (Wilson 1973; Berman and Richman 1974) but may be an artifact of both particle modification during feeding (O'Connors et al. 1976; Deason 1980) and the associated statistical analysis (Peters 1984). Vanderploeg et al. (1984) found little agreement between the selection of food indicated by the Coulter counter and that determined by microscopic counting.

Other measures of biomass such as dry weight, carbon content and chlorophyll concentration (Hargis 1977; Bowers 1980; Nizan et al. 1986) are used to estimate the removal of food from suspension. These enable comparisons between studies but require long exposure times and have the same problems.

The simplest method for investigating the accumulation of food by the animals is to directly examine the gut contents (Porter 1973a; Nadin-Hurley and Duncan 1976; Infante 1978a, 1978b; Turner 1984, 1987). However quantitative estimates of ingestion are usually not possible because of differential digestion of food particles; the gut contents are usually unrepresentative samples of what has been ingested.

One way of overcoming this is to use inert beads or non food particles as a marker in the food (Burns 1968a; Wilson 1973; Gliwicz 1969, 1977). These have the added advantage of having standard characteristics (e.g. size, shape, taste) any one of which may be varied for experimental purposes. Since these particles may be resuspended after gut passage, the feeding period should be related to gut passage time. Beads are usually used as an index of selective feeding rather than a measure of absolute grazing rates. It is apparent that artificial foods such as hard, usually spherical beads are poor substitutes for natural phytoplankton, with obvious consequences to the relevance of these measurements.

The most appropriate way of marking natural food is to use radiotracers (Nauwerck 1959; Richman 1964; Sorokin 1968; Lampert 1974; Daro 1978; Roman and Rublee 1981). Grazing rates are measured by allowing the animals to feed in a suspension of radioactively labelled food. Radionuclides commonly used are ^{14}C, ^{3}H and ^{32}P which are all easily incorporated into the food cell and emit low energy radiation for safety. The feeding period is less than the gut passage time, which means no change in food concentration, but may result in artificial grazing rates due to disturbed animal behaviour (Peters 1984). Disturbance to the animals may be reduced by introducing low concentrations of radioactive food into a non radioactive food suspension (Burns and Rigler 1967; Haney 1971, 1973; Gulati *et al.* 1982; Hart and Christmas 1984; Hart 1986). This assumes that the ingestion of the labelled food indicates the ingestion of the unlabelled food which is only valid when the same food is used.

Another *in situ* technique is to estimate grazing rates from the gut contents of the animals and the turnover time of these contents or gut evacuation time (Mackas and Bohrer 1976; Dagg 1983; Kiorbe *et al.* 1985). Chlorophyll and its derivatives are the usual index used to estimate gut fullness. The advantage of this method is that food ingestion occurs prior to animal capture and therefore grazing is not disturbed by experimental manipulation (Christoffersen and Jespersen 1986). However gut evacuation time is influenced by many environmental factors (Baars and Helling 1985) and since it is usually estimated independently of animal

collection, it may not be applicable to collection conditions. Furthermore, the basic assumption that chlorophyll and its derivatives are not destroyed or absorbed in the gut has been shown to be invalid (Conover *et al.* 1986; Lopez *et al.* 1988; Head 1988) and it cannot be considered a conservative measure of gut fullness.

Zooplankton grazing rates are influenced by both inherent and environmental factors. Factors such as temperature (Burns and Rigler 1967; Kibby 1971a) and dissolved oxygen concentration (Kring and O'Brien 1976) which influence metabolic rates thereby influence grazing rates. Both the quantity and quality of food has a marked influence on zooplankton rates (Porter 1977; Frost 1980). These environmental factors are of particular importance when measuring grazing rates in the laboratory. While laboratory conditions may be controlled, they may still be quite artificial with obvious consequences for the results. Laboratory grazing measurements must be applicable to the field to be of ecological significance. The methods of measuring zooplankton grazing rates described in the previous paragraphs can be used in the field as well as in the laboratory. Given the potentially artificial conditions of the latter, the former approach results in more realistic measurements. No particular method of measuring zooplankton grazing rates is optimal. Different methods provide different information with varying degrees of efficiency. In the present study, a modification of the *in situ* radiotracer technique of Haney (1971) was used in the field and a modification of the radiotracer technique of Burns and Rigler (1967) was used in the laboratory. Details of these methods are given in Chapter 2 and in each specific section.

6.2 VERIFICATION OF TECHNIQUE

6.2.1 Labelling Natural Phytoplankton Assemblages

One requirement of the radiotracer technique is for the radioactivity of the food tracer to be high enough such that the small amounts ingested by the animal during the short feeding times are measurable above the background. To obtain a high specific activity in the food tracer the amount of carrier (non radioactive isotope) in the growth medium is reduced and the incubation period with the radioisotope is prolonged. If natural phytoplankton assemblages are labelled then the incubation period should be kept to a minimum so that the size frequency distribution of the natural assemblage is not altered. A time series experiment was done to establish the minimum incubation period required to adequately

label the natural assemblage. An assumption here was that all of the assemblage was labelled at the same rate. This is not necessarily valid since the photosynthetic capacity of phytoplankton varies between species (Reynolds 1984). However the time series indicated the uptake of label across the incubated assemblage. When different fractions of the natural assemblage were labelled (Section 6.3), separate specific activities were measured.

Mt Bold Reservoir water was collected with a 4 m integrated tube sampler, filtered through 100 μm and 40 μm screens and then onto a 0.45 μm membrane filter. The concentrate was washed and resuspended in ASM1, an artificial culture medium with no carbon. Four duplicated treatments were set up, each using 300 ml of this stock. Treatments were as follows: (1) original stock; (2) stock + 3 mM NaH^{12}CO$_3$; (3) stock + 22.5 μM NaH^{14}CO$_3$; and (4) stock + 3 mM NaH^{12}CO$_3$ + 22.5 μM NaH^{14}CO$_3$. The hot (+^{14}C) treatments were used to measure the accumulation of ^{14}C in the presence or absence of carrier, while the cold treatments ($-^{14}$C) were used to monitor the size frequency distribution of the natural assemblage during incubation. All treatments were incubated at 16 °C under continuous low light (30 μE m^{-2} s^{-1}). At around 12 h intervals, duplicate 10 ml samples were removed from the hot treatments and the accumulated radioactivity in the phytoplankton was measured using liquid scintillation techniques. After 26 and 76 h of incubation, 3 ml samples were removed from the cold treatments and added to 40 ml of 0.22 μm membrane filtered 0.5% NaCl. The size frequency distribution of particles was determined across 14 Coulter Counter channels using a 140 μm aperature (ESD range 2.4 to 49 μm).

Figure 6.1 shows the radioactivity (mean $\pm$se cpm) accumulated in the natural phytoplankton during the incubation. Radioactivity, which is plotted on a log scale for convenience, was accumulated more rapidly in the absence of carrier. In the carrier-free cultures, there was a rapid accumulation of radioactivity in the first 15 h then the rate of accumulation slowed until there was little change after 48 h. In contrast, in the cultures with added carrier, radioactivity accumulated throughout the incubation.

Figure 6.2 shows the particle size frequency distribution in each treatment after 26 and 76 h. Frequency is plotted on a log scale for convenience. The size frequency distributions were compared using the Kolmogorov-Smirnov two sample test. There were significant differences within each treatment between the sampling times and between the treatments at each sampling time. Generally an increased incubation period and the addition of carbon resulted

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in higher frequencies across the size spectrum.

As a consequence of these results, the natural phytoplankton assemblages were labelled in a carrier-free medium with an incubation period of 36 h.

6.2.2 Zooplankton Gut Passage Times

When using radioisotopes for grazing measurements, the feeding time must be less than the gut passage time of the animals, otherwise ingested radioactivity will be lost in the faeces. A general gut passage time for the Mt Bold Reservoir zooplankton community and gut passage times for individual zooplankton taxa were determined by measuring the amount of radioactivity accumulated after feeding for different lengths of time. The gut passage time was inferred from the change in the rate of accumulation of radioactivity when defecation begins.

These time series experiments were done in a boat on the reservoir, using previously labelled natural phytoplankton as a food tracer. The feeding vessel was a 20 litre bucket into which 13 litres of whole Mt Bold water, collected using a modified Schindler trap, was gently released and allowed to stand for 10 minutes before the addition of tracer. Feeding periods were 4, 8, 12, 16 and 20 minutes. Grazing measurement procedure was as described in Chapter 2. For gut passage times of specific taxa, groups of 50 individuals were measured together so that the radioactivity accumulated during short feeding periods was measurable above the background.

Figure 6.3 shows the accumulation of radioactivity in the whole (>100 μm) zooplankton community during three separate experiments done over a three week period. The mean ($\pm$se) accumulated radioactivity of triplicate samples of the zooplankton community after each feeding period is expressed as a percentage of the maximum mean value in each experiment. On two occasions (25.XI.83 and 2.XII.83) the accumulation of radioactivity reached a maximum after 12 minutes. On 25.XI.83 there was a substantial accumulation of radioactivity by 4 minutes while on 2.XII.83 this rapid accumulation took 8 minutes. On the third occasion (15.XII.83) radioactivity accumulated at a constant rate until 16 minutes, after which there was no change.

There was considerable variation in the accumulation of radioactivity both within and between experiments. Part of the within experiment variation was due to the unequal quantities of animals in the different feeding samples. Because the liquid scintillation technique used (Chapter 2) was destructive, feeding sample biomass was not determined. Between experiment differences in the accumulation of radioactivity were due in part to different zooplankton compositions. For example, the zooplankton community was dominated by *Boeckella* on 15.XII.83 and on this date the community accumulation of radioactivity paralleled that of *Boeckella*. Other factors which influence gut passage time are temperature (Dam and Peterson 1988) and food concentration (Peters 1984).

Figure 6.4 shows the accumulation of radioactivity by *Boeckella* on 15.XII.83 and by *Boeckella*, *Calamoecia* and *Ceriodaphnia* on 12.I.84. The mean ($\pm$se) accumulated radioactivity of single samples from duplicate experiments (15.XII.83) or duplicate samples from duplicate experiments (12.I.84) is expressed as a percentage of the maximum mean value in each experiment. In both these experiments the accumulation of radioactivity by *Boeckella* was constant for 20 minutes, although on 15.XII.83 the variation at 12 and 16 minutes was large. This variation was reduced with increased replication on 12.I.84. Both *Calamoecia* and *Ceriodaphnia* showed a reduced rate of accumulation between 12 and 16 minutes.

The gut passage times inferred from these experiments are comparable with literature values for related taxa (Peters 1984). Although there was considerable variation in the accumulation of radioactivity, the results of these experiments indicated that a feeding period of 10 minutes was less than the gut passage times of the dominant zooplankton taxa in Mt Bold and of the zooplankton community generally.

6.2.3 Effect of Tracer Concentration

A prerequisite of the *in situ* technique for zooplankton grazing measurement is that the addition of the radioactive tracer should not significantly increase the concentration of food particles in the grazing chamber. A further consideration is that the ingestion of the radioactive tracer should not be influenced by the quantity present. The latter condition was tested in two separate experiments which indirectly addressed the former condition.

The filtering rate of *Daphnia carinata* was measured in the laboratory, using ^{14}C labelled *Ankistrodesmus* (10.VIII.84) and *Cyclotella* (28.IX.84). Tracer volumes ranged from 5 to 25 ml, in 5 ml increments, injected into a 2 litre volume of Mt Bold water. Grazing measurement procedures were as described in Chapter 2. In the first experiment (10.VIII.84) two replicates of each tracer volume were done with 5 samples, each of 5 animals, removed from each replicate. In the second experiment (28.IX.84) three replicates of each tracer volume were done with 5 samples, each of three animals, removed from each replicate. The number of animals in each sample was reduced when the number of replicates was increased since there was still sufficient radioactivity to be reliably measured.

The mean ($\pm$se) filtering rates of *Daphnia carinata* ranged from 0.42 ± 0.03 to 0.56 ± 0.04 and 0.37 ± 0.04 to 0.47 ± 0.04 ml animal^{-1} h^{-1} in the 10.VIII.84 and 28.IX.84 experiments respectively. Nested ANOVA showed that there was no significant difference in filtering rate across the range of tracer volumes in either experiment. This implied that the ingestion of the tracer was independent of the amount present. The lack of a reduction in filtering rate with increased tracer volume indicated that, in these experiments, the addition of the tracer did not substantially increase the food particle concentration. Since this condition would not necessarily be met in all experiments and given that the ingestion of tracer was independent of the amount present; the general approach was to use the minimum quantity of tracer which still enabled reliable measurement of radioactivity ingested during the short feeding period.

6.3 *IN SITU* GRAZING RATES OF MT BOLD ZOOPLANKTON ON WHOLE AND SIZE-FRACTIONATED NATURAL PHYTOPLANKTON

6.3.1 INTRODUCTION

Reviews by Lund (1965), Hutchinson (1967), Fogg (1975), and Wetzel (1975) all diminished the importance of zooplankton grazing on the growth and abundance of phytoplankton in freshwater systems (Frost 1980). These conclusions were a likely consequence of the estimates of zooplankton grazing rates available to these authors. These tended to be low, for copepods in particular, and quite variable e.g. Tables 16-6 and 16-8 in Wetzel (1975), resulting in the early belief that calanoid copepod filtering rates were much lower than cladocerans (Wetzel 1975). Considering the dominance of calanoid copepods in the

zooplankton of Mt Bold Reservoir (Chapter 3) it was of particular interest to compare calanoid copepod grazing rates with cladoceran grazing rates in Mt Bold Reservoir. This comparison would indicate if the potential grazing pressure exerted by the zooplankton community was sufficient to influence the abundance and composition of the phytoplankton. Since the feeding mechanisms of calanoid copepods differ from those of cladocerans (Peters 1984 and references therein), it was expected that the grazing pressure exerted by these two zooplankton types would differ across the phytoplankton community. In particular the size of food particle most effectively grazed upon may differ, which would potentially influence the composition of the phytoplankton community.

The aims of these experiments were: (1) to measure *in situ* grazing rates of Mt Bold zooplankton on the whole natural phytoplankton community; and (2) to compare the grazing rates of these zooplankton on two different size fractions of the natural phytoplankton community.

6.3.2 METHODS

Mt Bold Reservoir water was collected with a 4 m integrated tube sampler and filtered through screens and onto membrane filters so the following size ranges were obtained: 0.45-100 μm (TOTAL), 5-40 μm (NANNO) and 40-100 μm (NET). The size range 0.45-5 μm (ULTRA) was also used in the 10.II.84 experiment. Each fraction was labelled with ^{14}C and used as a food tracer to measure zooplankton grazing rates by the procedures already described. Three separate experiments were done over a two week period with the grazing measurements done between 1100 and 1500 h. Animals were collected from the depth of maximum density (5 or 10 m).

Table 6.1 shows the numbers of food types and replicates used in each experiment. The numbers of separate groups of animals measured from each replicate feeding session and the numbers of individual animals making up the groups are also shown in Table 6.1. These varied when there were insufficient numbers present to make up a constant total. When this occurred the exact number used was recorded and the individual grazing rate adjusted accordingly. Because tissue solubilizer was used, there was no differential self-absorption of radiation due to the different numbers of animals in the scintillation vials. However this variation in animal numbers was a disadvantage on occasions when a particular category

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(taxa or size) could not be found in the feeding sample. This was a consequence of working with natural populations *in situ*. Because of the absence of *Daphnia* from the reservoir on 10.II.84, *Daphnia* from a laboratory culture previously isolated from Mt Bold Reservoir were added to the feeding vessels in order to measure *in situ* grazing rates for a range of sizes of this taxa.

During each experiment the composition and density of the zooplankton in the water column was determined. Duplicate trap samples were taken at 5, 10, 15, 20 and 25 m, subsamples counted, and the total densities of each taxa in the water column calculated. Densities were converted to biomass using literature values. The composition and density of the phytoplankton community was determined from a 0-4 m integrated water sample. Established volumes of individual phytoplankton taxa were used to convert densities to biomass.

6.3.3 RESULTS

Table 6.2 lists the mean ($\pm$se) filtering rates (ml animal^{-1} h^{-1}) of the dominant zooplankton present during each experiment, on the food types offered. Filtering rates were compared within each experiment by ANOVA. Filtering rates were log transformed prior to the analyses because the variance increased with the mean in most instances. The results of pairwise comparisons between the means are also shown in Table 6.2 using letter superscripts between taxa within the complete food and number subscripts between the food types within each taxa.

6.3.3.1 Whole Food

Mean ($\pm$se) filtering rates on the TOTAL food ranged from 0.02 ± 0.01 to 3.77 ± 0.30 ml animal^{-1} h^{-1} across the three experiments. Within the 25.I.84 and 3.II.84 experiments, the filtering rates of *Boeckella* were significantly higher ($P < 0.05$) than the filtering rates of all other taxa in these experiments. Within the 25.I.84 experiment, *Calamoecia*, *Ceriodaphnia* and *Daphnia* (1 mm) had similar filtering rates as did *Diaphanosoma* and *Bosmina* with the latter group lower than the former. *Calamoecia*, *Ceriodaphnia*, *Diaphanosoma* and *Daphnia* (1 mm) all had similar filtering rates within the 3.II.84 experiment. Four groups of taxa had similar filtering rates within the 10.II.84 experiment with some overlap between the groups.

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Daphnia (2, 2.5 and 3 mm) had the highest filtering rates followed by *Boeckella* and *Diaphanosoma* and then *Daphnia* (1 mm) and then *Calamoecia* and *Ceriodaphnia*. Cyclopoid copepods had the lowest filtering rates across all three experiments.

6.3.3.2 Size-Fractionated Food

The filtering rates of each taxa on the NANNO and NET food fractions were not significantly different from each other within the 25.I.84 experiment, nor from the TOTAL food with the exception of *Calamoecia*. Within the 3.II.84 experiment the filtering rates of the cladoceran taxa on the NET fraction were significantly lower (P < 0.05) than on the NANNO fraction which did not differ from the TOTAL food. The filtering rate of *Calamoecia* did not differ between the two size fractions nor from the total food. The filtering rate of *Boeckella* on the NET fraction was significantly lower than on the NANNO fraction, however neither differed from the TOTAL fraction. Within the 10.II.84 experiment, the filtering rates of the calanoid copepods, *Daphnia* (1-3 mm) and *Ceriodaphnia* did not differ between the TOTAL food, NANNO and NET fractions. The filtering rate of *Diaphanosoma* on the NET fraction was significantly (P < 0.05) less than on the NANNO fraction which did not differ from the TOTAL food. Within the 1, 2.5 and 3 mm *Daphnia* the filtering rates on the ULTRA fraction did not differ from the other size fractions, however for the 2 mm *Daphnia* the filtering rate on the ULTRA fraction was significantly (P < 0.05) higher than that on the other fractions.

6.3.3.3 Body Size

In the 10.II.84 experiment, grazing measurements were made on four size classes of *Daphnia*; 1, 2, 2.5 and 3 mm carapace length measured from the eye to the base of the tail spine. Figure 6.5 shows the mean (±se) filtering rates of these size classes of *Daphnia* on each food type plotted against body size. Filtering rate increased with body size for the TOTAL, NANNO and NET food types. Filtering rates on the ULTRA food type initially increased with body size between 1 and 2 mm but then remained constant from 2 to 3 mm. Table 6.3 shows the results of power regression analysis between filtering rate and body size for each food type. The power exponents range from 1.567 to 2.078 (Table 6.3). The power functions were significant for the TOTAL, NANNO and NET food types but not for the ULTRA food type.

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6.3.3.4 Filtering Rate Variation

To enable comparison between the different sized taxa, filtering rates on an individual basis were converted to a biomass basis. Table 6.4 lists the mean ($\pm$se) filtering rates (ml (μg dry wt)$^{-1}$ h^{-1}) of the dominant zooplankton on the TOTAL food in each of the three experiments. Mean ($\pm$se) weight specific filtering rates ranged from 0.009 ± 0.002 to 0.071 ± 0.038 ml (μg dry wt)$^{-1}$ h^{-1} across the experiments. Weight specific filtering rates were compared within each experiment by ANOVA and the results of pairwise comparisons are shown in Table 6.4 using superscripts. *Ceriodaphnia* had the highest and *Diaphanosoma* had the lowest weight specific filtering rates in the 25.I.84 experiment. In both the 3.II.84 and 10.II.84 experiments, *Diaphanosoma* had the highest and *Calamoecia* had the lowest weight specific filtering rates (Table 6.4)

6.3.3.5 Feeding Rates

Because filtering rate is dependent on the food concentration, mean filtering rates on the TOTAL food were converted to feeding rates (expressed on a volume basis) to enable comparison within taxa between experiments. Table 6.5 lists the mean ($\pm$se) feeding rates ($10^6 \mu$m^3 animal^{-1} h^{-1}) of the dominant zooplankton in each of the three experiments. Mean ($\pm$se) feeding rates ranged from 0.057 ± 0.005 to 3.182 ± 0.167 $10^6 \mu$m^3 animal^{-1} h^{-1} across the experiments. Feeding rates were compared within each taxa between experiments by ANOVA and the results of pairwise comparisons are shown in Table 6.5 using superscripts. There were significant differences in the feeding rates between the three experiments for all zooplankton taxa except *Diaphanosoma*.

To enable comparison between the different sized taxa, feeding rates on an individual basis were converted to a biomass basis. Table 6.6 lists the mean ($\pm$se) weight specific feeding rates ($10^6 \mu$m^3 (μg dry wt)$^{-1}$ h^{-1}) of the dominant zooplankton on the TOTAL food, in each of the three experiments. Mean ($\pm$se) weight specific feeding rates ranged from 0.009 ± 0.002 to 0.145 ± 0.008 $10^6 \mu$m^3 (μg dry wt)$^{-1}$ h^{-1} across the experiments. Weight specific feeding rates were compared across the experiments by ANOVA and the results of pairwise comparisons are shown in Table 6.6 using superscripts. *Ceriodaphnia* had the highest and *Calamoecia* had the lowest weight specific feeding rates across the experiments. Between these extremes there was no distinct separation of taxa or experiments (Table 6.6).

Conversion to biomass did not result in uniform feeding rate measurements between the taxa across the three experiments.

6.3.3.6 Community Filtration Rate Contributions

The consequences of the variable individual grazing rates were examined further by relating them back to the field conditions. Table 6.7 lists the proportional composition of the zooplankton community during each of the experiments, based on numbers and on biomass, and the relative filtering rates of the individual taxa. The relative contribution of each taxon to the total community filtration rate is also listed. Figure 6.6 shows the relationship between the contribution to biomass and the contribution to filtering for the dominant taxa on each food type in the three experiments. Each taxon ∧ in each experiment is identified by a key number listed in Table 6.7. The contributions of *Diaphanosoma* and *Daphnia* (1 mm) were minimal so were not plotted. Figure 6.6 shows that there was no tight relationship between the contribution to filtering and the contribution to biomass for any food type.

6.3.4 DISCUSSION

There are no published grazing rates for the Australasian zooplankton taxa; *Boeckella triarticulata*, *Calamoecia ampulla* and *Diaphanosoma unguiculatum*. For the more widely distributed taxa; *Daphnia carinata*, *Ceriodaphnia quadrangula* and *Bosmina meridionalis*, Haney (1973) reported filtering rates for *C. quadrangula* and Ganf and Shiel (1985a) reported filtering and feeding rates for *D. carinata* and *C. quadrangula*. The former study was *in situ* with natural phytoplankton but used labelled cultures of yeast as food tracers while the latter study was in the laboratory using pure algal cultures as food and a Coulter counter for grazing measurement. Consequently, the results from the present study were not directly comparable with any literature report since the experimental conditions with regard to both animals and food were not equivalent. However the relative magnitudes and directions of preference were comparable within the experiments and are discussed with reference to the literature.

6.3.4.1 Filtering Rates

Two points of note are the high absolute filtering rate of *Boeckella*, only exceeded by that of

>2 mm *Daphnia*, and the generally high *in situ* filtering rates recorded for all zooplankton except the cyclopoid copepods. Calanoid copepod filtering rates measured in this study were an order of magnitude higher than those reported earlier e.g. Nauwerck (1959), Comita (1964), Richman (1966), McQueen (1970), Kibby (1971b), Kibby and Rigler (1973), and Bogdan and McNaught (1975), despite similar techniques in some instances. The present results contradict the early belief that calanoid copepod filtering rates were much lower than cladocerans (Wetzel 1975). An extensive compilation of published filtering rates for both copepods and cladocerans by Peters (1984; Figure 9.11) shows that although calanoid copepods may filter at higher weight specific rates than cladocerans, the median values for these two groups of zooplankton were the same. Peters (1984) considered the previous findings that copepods filter at lower rates than cladocerans to be artifacts of the experimental methods used, which were more appropriate for cladocerans and underestimated copepod filtering. The size of the experimental feeding chamber used seems to be of particular importance, with reduced copepod grazing rates in small volumes (Anraku 1964; Paffenhofer 1971, 1976). High copepod grazing rates are associated with the use of large (>2.5 l) experimental volumes (Peters 1984).

Inappropriate experimental methodology may also be the cause of the lower grazing rates recorded earlier for zooplankton e.g. Tables 16-6 and 16-8 in Wetzel (1975). Although some grazing measurement techniques are more recent than others, Peters (1984; Figure 9.10) found that weight specific filtering rates measured by the three common techniques (cell counting, Coulter counting and radioisotope labelling) were all quite variable and rates from the different techniques could not be reliably separated. In addition to the volume of the feeding container considered above; crowding (Hargrave and Geen 1970; Hayward and Gallup 1976) and pre-experimental nutritional status (McAllister 1970; Frost 1972) are both major influences on grazing rate measurements (Peters 1984). More recent measurements of zooplankton grazing rates e.g. Thompson *et al.* (1982), Osgood (1982), Richman and Dodson (1983), Zankai (1983), Janicki and DeCosta (1984), and Fulton (1988) are substantially higher than earlier measurements, probably as a result of more appropriate experimental conditions.

The low filtering rates recorded for the cyclopoid copepod taxa in this study indicated that these taxa did not ingest significant amounts of phytoplankton. Fryer (1957b) and Bayly and Williams (1973) considered the larger *Mesocyclops* to be mainly carnivorous and the

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smaller *Microcyclops* to be mainly herbivorous.

6.3.4.2 Size Selection

The filtering rates of both calanoid copepods (*Boeckella triarticulata* and *Calamoecia ampulla*) were not significantly different between the NANNO and NET fractions (Table 6.2), with one exception (*Boeckella*; 3.II.84), despite the large difference in body size. Most literature on food size selection by copepods indicates that large food is preferred over small, with the exception of small species which may prefer small food. Thus *Diaptomus ashlandi* (Bowers 1980) and *Diaptomus minutus* (Bogdan and McNaught 1975) with body lengths about 1 mm, preferred food <10 μm and <22 μm respectively, although Richman *et al.* (1980) reported a preference for >12 μm food by *Diaptomus ashlandi*. The larger congeners; *Diaptomus oregonensis* (McQueen 1970; Richman *et al.* 1980), *D. pallidus* (Janicki and DeCosta 1984), *D. siciloides* (Richman *et al.* 1980) and *D. sicilis* (Vanderpleog 1981; Vanderploeg *et al.* 1984) all prefer larger food, although Bowers (1980) reported a seasonal switch from small food to large food by *D. sicilis*. Similar preferences for larger food were reported for the related *Eudiaptomus gracilis* (Muck and Lampert 1984; Lampert and Taylor 1985; Horn 1985a, 1985b) and *Eudiaptomus graciloides* (Gliwicz 1969; Lampert and Taylor 1985), however Okamoto (1984b) found a preference for small food by *Eodiaptomus japonicus* and Okamoto (1984a) reported a seasonal switch from small food to large food by *E. japonicus*. Chow-Fraser and Wong (1985) found that *Limnocalanus macrurus, Senecella calanoides* and *Epischura lacustris* all preferred larger food, while Forsyth and James (1984) reported that *Calamoecia lucasi* preferred algae over bacteria.

Similar preferences for larger food were reported for the marine copepods; *Calanus pacificus* (Parsons *et al.* 1967), *Pseuodcalanus minutus* (Parsons *et al.* 1967; Hargrave and Geen 1970), *Paracalanus parvus* (Bartram 1980), *Paracalanus* sp. (Paffenhoffer 1984a, 1984b), *Eucalanus pileatus* (Paffenhoffer 1984a), *Acartia tonsa* (Hargrave and Geen 1970; Bartram 1980), *Acartia clausi* (O'Connors *et al.* 1976; Donaghay and Small 1979), *Temora longicornis* (Hargrave and Geen 1970; O'Connors *et al.* 1980), *Eurytemora affinis* (Richman *et al.* 1980) and *Oithona similis* (Hargrave and Geen 1970).

The filtering rate of *Daphnia carinata* on the NANNO fraction was greater than that on the NET fraction in all experiments and for all size classes of *D. carinata*, although this

difference was not significant in the 25.I.84 experiment (Table 6.2). There are many different preferences reported for *Daphnia* spp. in the literature, covering a broad size spectrum. Thus no selection was reported between algae and bacteria for *Daphnia pulex* (Lampert 1974; Borsheim and Olsen 1984), *D. magna* (Gophen 1977) and *D. rosea* (DeMott 1982). Similarly no selection was found between different sized algae for *D. magna* (McMahon and Rigler 1965; Kersting and Holterman 1973), *D. galeata* (Bogdan and McNuaght 1975), *D. longispina* (Muck and Lampert 1984) and *D. parvula* (Janicki and DeCosta 1984). A preference for bacteria over algae was reported for *D. pulex* (Lampert 1974) and *D. magna* (Hadas *et al.* 1982) and small algae were preferred to large algae by *D. pulex* (Berman and Richman 1974; Meise *et al.* 1985); *D. cucullata* (Irvine 1986) and *D. longispina hyalina* (Okamoto 1984a, 1984b). A preference for algae over bacteria was reported for *D. longispina* (Borsheim and Andersen 1987; Kankaala 1988), *D. rosea* (DeMott and Kerfoot 1982; DeMott 1983) and *D. pulicaria* (DeMott and Kerfoot 1982; DeMott 1983). Large algae were preferred to small algae by *D. pulex* (Osgood 1982), *D. hyalina* (Horn 1985a, 1985b; Lampert and Taylor 1985), *D. cucullata* (Lampert and Taylor 1985) and *D. galeata* (Lampert and Taylor 1985). Gliwicz (1969, 1977) found a preference for 10 μm inorganic particles over 5 μm by *D. cucullata* and *D. longispina* while Hesson (1985) found that *D. longispina* preferred 5 μm beads over both 0.5 μm and 1 μm beads.

The filtering rate of *Ceriodaphnia quadrangula* on the NANNO fraction was greater than that on the NET fraction in all experiments, although this difference was only significant in the 3.II.84 experiment (Table 6.2). Gophen *et al.* (1974) reported that *Ceriodaphnia reticulata* preferred bacteria over algae and Lampert and Taylor (1985) found that *C. reticulata* preferred small algae over large algae. In contrast Forsyth and James (1984) reported that *C. dubia* filtered at similar rates on natural phytoplankton and bacteria and Hesson (1985) found that *C. quadrangula* preferred 5 μm beads over 0.5 μm and 1 μm beads.

The filtering rate of *Diaphanosoma unguiculatum* on the NANNO fraction was greater than that on the NET fraction in all experiments, although this difference was not significant in the 25.I.84 experiment (Table 6.2). Geller and Muller (1981) considered *Diaphanosoma brachyurum* a bacteria feeder, based on its fine mesh size and preference for <5 μm beads reported by Gliwicz (1977). Hesson (1985) also found *D. brachyurum* ingested <5 μm beads with no selection below this size. In contrast, Gliwicz (1969) found that *D. brachyurum* ingested 10-15 μm sand in preference to 3-5 μm sand and DeMott and Kerfoot (1982)

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reported that *D. brachyurum* preferred algae to bacteria. Janicki and DeCosta (1984) reported a higher filtering rate on >20 μm natural phytoplankton by *D. leuchtenbergianum*.

In the only experiment (25.I.84) where *Bosmina meridionalis* was present in sufficient numbers to be measurable, the filtering rate on the NET fraction was greater than that on the NANNO fraction, although this difference was not significant (Table 6.2). Most recent literature reports a preference for larger food by *Bosmina* (DeMott 1982; Bogdan and Gilbert 1982; Janicki and DeCosta 1984; Bleiwas and Stokes 1985; Johnsen and Borsheim 1988) in contrast to earlier results with inorganic particles (Burns 1968a; Gliwicz 1969, 1977) and some recent studies using natural food (Ross and Munawar 1981; Borsheim and Andersen 1987). DeMott and Kerfoot (1982) found that the grazing preference of *Bosmina longirostris* shifted between bacteria and different sized algae and proposed two distinct modes of feeding to explain this; small-particle filtering and large particle grasping. The results of Bleiwas and Stokes (1985) were consistent with this proposal and Hesson (1985) also reported a seasonal switch in preference between different sizes of inorganic bead. Johnsen and Borsheim (1988) found that the selection of large particles over small by *Bosmina* increased with increasing filtering rates through an adjustment in the filtration apparatus to allow for greater water flow.

It is clear from the above discussion that many zooplankton do not show consistent food size preferences. Even where cladocerans were directly compared to calanoid copepods, there was no consistent pattern in selectivity. In the present study cladocerans preferred a narrower range of food particles than calanoid copepods (Table 6.2). This contrasted with the results of Bogdan and McNaught (1975), Janicki and DeCosta (1984) and Okamoto (1984a, 1984b).

6.3.4.3 Body Size, Grazing and Selection

Filtering rates of *Daphnia carinata* increased with body size with all food except for the smallest fraction (Figure 6.5). It is well established that zooplankton grazing rates increase with body size (Peters and Downing 1984; Peters 1984 and references therein). Studies by Chow-Fraser and Knoechel (1985), Haney (1985) and Knoechel and Holtby (1986a, 1986b) have all indicated that body size is a dominant factor regulating cladoceran grazing rates. Typically for *Daphnia* the relationship between body length and filtering rate is described by a power function with an exponent range between 1 and 3 (Ganf and Shiel 1985a; Table

7). The power exponents reported in the present study are within this range.

There was an increased selection of the ULTRA size fraction by the 2 mm *Daphnia* relative to both smaller and larger sized *Daphnia* (Figure 6.5). Increased selection for bacteria over algae by juvenile animals compared to adult animals was reported for *Daphnia pulex* (Lampert 1974), *D. rosea* and *D. pulicaria* (DeMott and Kerfoot 1982), *D. parvula* (Porter *et al.* 1983) and *D. longispina* (Borsheim and Andersen 1987). Okamoto (1984a) found that different size fractions of natural phytoplankton were ingested at different rates by different sized *Daphnia longispina hyalina* and furthermore this selection varied seasonally. Hartmann (1985) reported that small *Daphnia pulicaria* appeared to select the filamentous alga *Oscillatoria* over the smaller unicellular *Ankistrodesmus* in contrast to the preference of large *D. pulicaria*. However this result was shown to be due to an accumulation of the filaments in the food groove of the smaller animal which was unable to reject them (Hartmann 1985). Chow-Fraser and Wong (1986) reported decreased ingestion of small algae (<10 μm) by *Epischura lacustris* during its development. Across a range of different zooplankton taxa, Bogdan and Gilbert (1984) found no general relationship between zooplankton body length and ability to ingest small food.

6.3.4.4 Grazing Rate Variation

Across the three experiments there was considerable variation in the filtering rates of zooplankton taxa on the complete food (Table 6.2). On an individual basis, the highest mean filtering rate was 30 times the lowest mean filtering rate. Both animal size and food concentration are major influences on filtering rate measurements (Peters 1984). Conversion to biomass reduced the variation in mean filtering rate, however there was still an 8-fold range across the experiments (Table 6.4). On an individual basis, the highest mean feeding rate was 56 times the lowest rate (Table 6.5). Conversion to biomass still resulted in a 16-fold range across the experiments (Table 6.6).

Another source of variation in grazing rate measurement is food quality. One simple measure of quality is size. When the complete food was partitioned into the NANNO and NET fractions there was still considerable variation in filtering rate measurements within these fractions across the three experiments (Table 6.2). On an individual basis there was a 19-fold range in mean filtering rates on the NANNO food type and a 92-fold range on the

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NET food type. Conversion to biomass resulted in an 8-fold range in mean filtering rates on the NANNO food type and a 16-fold range on the NET food type. Feeding rates on each food fraction could not be estimated as the contribution of each fraction to the total food biomass was not known.

Variability in zooplankton grazing rate measurements is of great concern when trying to predict the impact of zooplankton on the phytoplankton community within a water body. In particular the general use of single value grazing rates (Section 4.4.3.4) would appear to have limited validity.

6.4 INGESTION OF SPECIFIC ALGAL TRACERS BY ZOOPLANKTON.

6.4.1 INTRODUCTION

Many studies report *in situ* grazing measurements made using pure cultures of algae or bacteria as feeding tracers (Haney 1973; Thompson *et al.* 1982; Lampert and Taylor 1985; Chow-Fraser 1986a; Hart 1986; Jarvis 1986; Kankaala 1988). The assumption of the *in situ* technique that the ingestion of the labelled tracer reflects the ingestion of unlabelled food is only valid when they are identical. Although this limitation is often acknowledged when using pure tracers, it has not been widely examined. Given the variation in size and shape present in phytoplankton, a wide range of grazing rates would be expected using different algal tracers in a common food suspension.

Taxonomic identity is a composite determinant of food quality. From the variable results of the previous section, it was of interest to determine if the grazing rate of specific zooplankton taxa on specific food types was consistent.

The purpose of these experiments was: (1) to examine the selection of specific algal tracers by zooplankton taxa; and (2) to determine if filtering rates on specific algal tracers were consistent between the zooplankton taxa.

6.4.2 METHODS

The labelled tracers used were; *Ankistrodesmus falcatus* (UTEX 101), *Staurastrum gracile*

(UTEX LB562), *Cyclotella* sp. (UTEX 1269), *Microcystis aeruginosa* (UTEX LB2063), *Selanastrum capricornutum* (UTEX 1648), *Chlorella vulgaris* (UTEX 29), *Carteria* sp. (UTEX 2), and *Chlamydomonas reinhardtii* (UTEX 89).

Zooplankton were collected from Mt Bold Reservoir and maintained in lake water overnight. Feeding experiments were done in the laboratory in 2 litre polythene bottles of lake water. Prior to the experiments animals were allowed to acclimatize for 1 hour in these containers. After addition of the tracer the bottles were gently inverted twice to ensure complete mixing. Zooplankton grazing rates were determined as previously described. Particle concentrations in the feeding suspensions were determined using a Coulter Counter, for the latter three experiments. Table 6.8 shows the numbers of tracer types and replicates, the numbers of separate groups of animals measured, and the numbers of individual animals in the groups, for each of the experiments done.

6.4.3 RESULTS

Table 6.9 lists the mean (±se) filtering rates of *Boeckella triarticulata* and two sizes of *Daphnia carinata* (1 mm and 2 mm carapace length) with five food tracers. Table 6.10 lists the mean (±se) filtering rates of *Calamoecia ampulla* and *Ceriodaphnia quadrangula*, in three separate experiments, with seven food tracers. Mean filtering rates of the animals were compared within each experiment by factorial ANOVA, with both animal and tracer type fixed factors, the results of which are shown in Table 6.11. There were significant differences in filtering rates between the animals and between the food tracers in all experiments (Table 6.11). The results of pairwise comparisons between the means, within each experiment, are shown in Tables 6.9 and 6.10 using superscripts.

Table 6.12 shows the mean (±se) particle concentrations (numbers ml^{-1}) of the food suspensions in the 1985, 1986 and 1987 experiments. Particle concentrations were compared within each experiment by ANOVA and pairwise comparisons were made between the means; these are shown in Table 6.12 using superscripts. There were significant differences in particle concentration between the food suspensions within each experiment. Since filtering rate is dependent on food concentration, comparison of the filtering rates between the algal tracers within each experiment would appear to be invalid, although comparison between the zooplankton taxa for any specific algal tracer would still be valid. However, the

size frequency distributions of the food suspensions differed between tracer types. Table 6.13 shows the mean ($\pm$se) particle concentrations of the food suspensions in the 1985 and 1986 experiments, expressed on a volume basis ($mm^3\ l^{-1}$). The size frequency distribution for the 1987 experiment was not available. There were no significant differences by ANOVA between the food suspensions, on a volume basis, in either experiment and thus comparison within these experiments was valid. The results of pairwise comparisons between the means across the experiments are shown in Table 6.13 using superscripts. Neither filtering nor feeding rates were directly comparable between experiments as the food concentrations differed.

Table 6.14 shows the filtering rates on the tracers ranked for convenient comparison within each experiment, according to the pairwise comparison results. In the 1984 experiment the large *Daphnia carinata* (2 mm) filtered *Ankistrodesmus, Staurastrum, Cyclotella* and *Selenastrum* at equal rates but filtered *Microcystis* at a reduced rate. The smaller *Daphnia carinata* (1 mm) filtered both *Microcystis* and *Staurastrum* at a reduced rate but had equal filtering rates on the other three tracers. *Boeckella triarticulata* had equal filtering rates on *Selenastrum* and *Staurastrum*, equal but reduced filtering rates on *Ankistrodesmus* and *Cyclotella* and a greatly reduced filtering rate on *Microcystis*.

In the 1985 experiment the tracer types were ranked in the same order for both *Calamoecia ampulla* and *Ceriodaphnia quadrangula* with the exception of *Microcystis*. *Ceriodaphnia* had a reduced filtering rate on *Microcystis* relative to *Calamoecia*. In the 1986 experiment the rankings were again similar for both animals except that *Calamoecia* had reduced filtering rates on *Cyclotella, Carteria* and *Microcystis* relative to *Ceriodaphnia*. In the 1987 experiment, the rankings were similar for both animals except that *Ceriodaphnia* had reduced filtering rates on *Staurastrum* and *Microcystis* relative to *Calamoeica*.

Generally, in the three experiments with *Calamoecia* and *Ceriodaphnia*, the filtering rates on *Ankistrodesmus, Cyclotella* and either *Chlorella, Carteria* or *Chlamydomonas* were all similar, while those on *Staurastrum* and *Microcystis* were also similar but were reduced relative to the above.

6.4.4 DISCUSSION

The zooplankton filtering rates obtained using pure algal tracers (Tables 6.9 and 6.10) were

the same order of magnitude as those obtained using natural algal tracers (Table 6.2) despite a reduced feeding suspension volume and greater animal disturbance due to handling.

6.4.4.1 Tracer Selection

Studies by Lampert and Taylor (1985) and Chow-Fraser (1986a) both report the results of *in situ* grazing measurements using more than one algal tracer. In the former study the selection of a green alga tracer *Scenedesmus acutus* and a smaller cyanobacterium tracer *Synechococcus elongatus* by a calanoid copepod *Eudiaptomus* and the cladocerans *Daphnia* and *Ceriodaphnia* was examined. Lampert and Taylor (1985) found that *Eudiaptomus* had a strong preference for *Scenedesmus*, *Daphnia* had a slight preference for *Scenedesmus* and *Ceriodaphnia* preferred *Synechococcus*. In the present study there was good agreement between the tracer preferences of *Calamoecia* and *Ceriodaphnia* and between *Boeckella* and *Daphnia*. Chow-Fraser (1986a) measured the grazing rate of the calanoid copepod *Diaptomus minutus* using *Scenedesmus ovalis*, *Chlorella vulgaris*, *Chlamydomonas* sp., *Pediastrum* sp. and *Anabaena* sp. tracers. She found that there was no significant difference between the grazing rates using *Scenedesmus* and *Chlorella* but both the larger tracers *Pediastrum* and *Chlamydomonas* gave higher grazing rates while the filamentous cyanobacterium *Anabaena* gave a lower grazing rate than *Scenedesmus*. In the present study the filtering rates of both copepods were reduced using the cyanobacterium *Microcystis* tracer. The largest tracer *Staurastrum* was filtered at a reduced rate by *Calamoecia* but not by *Boeckella*.

Further comparison can be made with studies of specific algal preferences by Mt Bold zooplankton. Ganf and Shiel (1985a) examined the grazing rates of *Daphnia carinata* and *Ceriodaphnia quadrangula* on pure suspensions (10^4 cells ml^{-1}) of *Ankistrodesmus falcatus*, *Dictyosphaerium pulchellum*, *Scenedesmus quadricaudata*, and *Staurastrum gracile* using a Coulter Counter. Ganf and Shiel (1985a) found that for both of these cladocerans there was a reduction in individual grazing rates as the algal size increased i.e. in the order of the above list. In a similar study Ellis (1984) measured the grazing rates of *Boeckella symmetrica* (1.1 mm) and *Daphnia carinata* (2 mm) on pure suspensions (10^4 cells ml^{-1}) of *Ankistrodesmus falcatus*, *Chlorella vulgaris*, *Chlamydomonas reinhardtii*, *Cyclotella meneghiniana*, *Microcystis aeruginosa* and *Staurastrum gracile* using a Coulter Counter. For *B. symmetrica* there was no significant difference between the feeding rates on *Staurastrum*,

Chlorella, Ankistrodesmus and *Microcystis* although feeding rates increased in this order. The feeding rate on *Cyclotella* was significantly higher than on *Chlamydomonas* which was significantly higher than the above group. For *D. carinata* the lowest feeding rate was on *Staurastrum* and then on *Microcystis*. There was no significant difference between the feeding rates on *Ankistrodesmus, Chlorella* and *Cyclotella* but *Chlamydomonas* was fed on at a significantly higher rate. Ellis (1984) found that neither *D. carinata* nor *B. symmetrica* fed at reduced rates with increased particle size. In the present study the selection of the different tracers by either the cladocerans or the calanoid copepods was not on a basis of size alone. In contrast to the above results for *B. symmetrica, B. triarticulata* fed on the *Staurastrum* tracer at the highest rate. The feeding responses of *B. symmetrica* on pure cultures of *Microcystis* and *Cyclotella* also differed from those of *B. triarticulata* on these tracers. There was good agreement between *Daphnia carinata* (2 mm) feeding on pure cultures and *D. carinata* (1 mm) feeding on tracers but not with *D. carinata* (2 mm) feeding on tracers. Although these comparisons differ in measurement technique, they indicate that results obtained using tracers do not necessarily represent results with pure cultures.

6.4.4.2 *Microcystis* Selection

In the present study the filtering rates of the dominant Mt Bold zooplankton were reduced using the cyanobacterium *Microcystis aeruginosa* tracer. This was in agreement with most literature on the response of zooplankton to cyanobacteria food. Negative influences were reported for cladocerans (Arnold 1971; Schindler 1971; Crowley 1973; Hayward and Gallup 1976; Webster and Peters 1978; Gliwicz and Siedlar 1980; Porter and Orcutt 1980; Lampert 1981b; Holm *et al.* 1983; Porter and McDonough 1984; Infante and Abella 1985; Chow-Fraser and Sprules 1986; Fulton 1988), for copepods (Schindler 1971; McNaught *et al.* 1980; Hartmann 1985; Fulton 1988), and for rotifers (Pourriot 1977; Snell 1980). Cyanobacteria food may also have neutral or positive influences on cladocerans and copepods (McNaught *et al.* 1980), rotifers (Starkweather 1981), ostracods (Grant *et al.* 1983), and ciliates (Brabrand *et al.* 1983).

Literature reports specifically on the influence of *Microcystis aeruginosa* food also vary although most are negative. Cladocerans seem to be most studied with *Daphnia* spp. (Schindler 1971; Lampert 1981a, 1982; Nizan *et al.* 1986; Jarvis *et al.* 1987), *Ceriodaphnia* spp. (Lampert 1982; Jarvis *et al.* 1987), *Diaphanosoma* spp. (Lampert 1982; Jarvis *et al.*

1987), *Moina* spp. (Hanazato and Yasuno 1987; Jarvis *et al.* 1987), and *Bosmina* spp. (Lampert 1982; Jarvis *et al.* 1987) all showing negative influences. Positive or neutral responses were also found for *Daphnia* spp. (DeBernardi *et al.* 1981) and *Ceriodaphnia* sp. (O'Brien and deNoyelles 1974). Copepods usually avoid or have a low consumption of *Microcystis* (Schindler 1971; Jarvis *et al.* 1987) with a notable exception in *Thermocyclops hyalinus* which extensively grazes the dominant *Microcystis* in Lake George, Uganda (Moriarty *et al.* 1973). Jarvis *et al.* (1987) found that the rotifer *Brachionus calyciflorus* preferred *Microcystis* to *Chlorella*.

Haney (1987) and Lampert (1987) consider that there are three broad mechanisms by which cyanobacteria may influence zooplankton:

1. Cyanobacterial colonies or filaments may be too large to handle, or may interfere with the grazing process, or may cause rejection responses.

2. Ingested cyanobacteria may be poorly digested and assimilated, or may lack essential nutirents.

3. Cyanobacteria may be toxic to zooplankton.

Since the *Microcystis aeruginosa* culture used in the present study was unicellular or at most had small aggregates of cells, it would seem that the third mechanism was responsible for the reduced short term grazing rates observed in both cladocerans and copepods.

6.4.4.3 Selection Consistency

Although the filtering rates of both *Calamoecia* and *Ceriodaphnia* were not directly comparable between the experiments, the order of preference for the tracers was consistent. This result supports the invariant specific selection of food concept as established for calanoid copepods by Bartram (1980), Vanderploeg (1981), Vanderploeg *et al.* (1984), and Knisely and Geller (1986). These authors found that zooplankton grazing on particular phytoplankton was consistent throughout the year and furthermore selection was an invariant function of particle size. Similar results were reported for cladocerans by Geller and Muller (1981), Gophen and Geller (1984), and Hessen (1985). These authors all related the invariant size selection to the morphology of the food collecting limbs on the

zooplankton. They assumed that the setae and setule arrangements on the thoracic limbs of the cladocerans act as sieves; an assumption that is still widely debated e.g. Porter *et al.* (1983), Ganf and Shiel (1985a, 1985b), Brendelberger *et al.* (1986), Fryer (1987), and Gerritsen *et al.* (1988). It should be noted that an invariant selection of food does not necessitate acceptance of a mechanistic model of food collection; specific feeding behaviours may achieve the same result.

6.5 THE INFLUENCE OF SUSPENDED PARTICULATES ON MT BOLD ZOOPLANKTON GRAZING

6.5.1 INTRODUCTION

A feature of many mainland Australian waters is their high turbidity due to inorganic suspended particulates (Kirk 1985). This is shared by water bodies in other arid or semi arid regions in Africa (Davies and Walmsley 1985) and America (Marzolf and Arruda 1980). Inorganic particles enter the water column via riverine inputs or sediment resuspension within the water body or may be formed by chemical precipitation or flocculation (Melack 1985). In Australia the riverine inputs result from soil erosion due to a combination of; the aridity of the climate and consequent variable rainfall, the high clay content and low permeability of the soil, and the sparse or disturbed vegetative cover (Olive and Walker 1982). The inorganic suspended sediments are predominantly very fine clay particles with the majority less than 0.2 μm in diameter (Olive and Walker 1982). Examples of the turbidity range recorded for southern Australian inland waters are 80-350 NTU for the Darling River (Shiel 1985) and 25-155 NTU for Lake Alexandrina (Geddes 1984a). The turbidity of Mt. Bold Reservoir ranged from 1-220 JTU or NTU between 1940 and 1986 (E. & W.S. 1987).

Suspended particulates may modify both the physical and the chemical environment within a water body. Penetration of heat energy is reduced (Ellis 1936; Schiebe *et al.* 1975) with consequences for internal water movements (Imberger 1985). Suspended particulates influence light attenuation and modify spectral quality (Ellis 1936; Kirk 1983). The chemical environment may be altered through nutrient stripping or release by suspended particulates (Nalewajko and Lean 1980) or the uptake of trace metals (Hart 1982). Combinations of the above factors may in turn influence primary production (Marzolf and Osborne 1972; Selkirk

1982; Kirk 1983, 1985; Grobbelaar 1985) and phytoplankton composition (Avnimelech *et al.* 1982; Cuker 1987).

Suspended particulates have both positive and negative influences on zooplankton populations. The visibility and susceptibility of zooplankton to visual predators decreases as turbidity increases (Vinyard and O'Brien 1976; Confer *et al.* 1978; Gardner 1981), so suspended particulates may provide a refuge from predation for large zooplankton. At the same time however, zooplankton ingest considerable amounts of the suspended inorganic material (Paffenhofer 1972; Marzolf and Arruda 1980; Arruda *et al.* 1983; G-Toth 1984; G-Toth *et al.* 1986; Gliwicz 1986; Hart 1987; Vanderploeg *et al.* 1987) and particulate organic food intake and assimilation is reduced (Marzolf and Arruda 1980; Arruda *et al.* 1983; McCabe and O'Brien 1983; Vanderploeg *et al.* 1987; Hart 1988). Nevertheless dissolved organic matter (Stumm and Morgan 1970) and bacteria (Pedros-Alio and Brock 1983) may be adsorbed onto the inorganic particulates and subsequently utilized upon ingestion by the zooplankton (Arruda *et al.* 1983). Various combinations of these factors have been used to explain the spatial and/or temporal distributions of zooplankton observed in the field. Some examples are considered below.

During a comparison of two lakes with different turbities in western USA, McCabe and O'Brien (1983) found a higher relative abundance of larger zooplankton in the more turbid lake, which they attributed to reduced predation by planktivorous fish. Similarly Geddes (1984b) considered that the co-occurence of large and small zooplankton in turbid Lake Alexandrina, South Australia, was primarily due to reduced fish predation and later supported this with the observation that the density of the large zooplankton decreased during an unusually clear period (Geddes 1988). Carvalho (1984) reported that *Daphnia gessneri* was absent from an Amazon floodplain lake during periods of low water and high turbidity. This absence was explained by high fish predation prior to the low water period followed by an unspecified turbidity effect based on literature evidence. Zettler and Carter (1986) found that the structure of the zooplankton community was closely related to a spatial and temporal turbidity gradient in Lake Temiskaming, Canada, with different responses for different zooplankton taxa. Mean body size increased and the density of smaller zooplankton decreased with increasing turbidity. Zettler and Carter (1986) proposed a combination of predation and impaired feeding to account for these observations. An earlier study of Patalas and Salki (1984) also examined the effects of turbidity on

zooplankton community structure in Southern Indian Lake, a newly created Canadian reservoir, but these were not isolated from other factors such as water temperature (Zettler and Carter 1986). In a seven year study on the zooplankton of Lake le Roux, South Africa, Hart (1986b) found that zooplankton biomass was reduced at both low and high turbidities. The former was attributed to fish predation and the latter to feeding interference. Large cladocerans (*Daphnia* spp.) were absent during two periods of very high turbidity while copepods were not reduced as severely. In a later study Hart (1988) attributed the observed field abundances of different zooplankton taxa to differential feeding capabilities with increased turbidity, although other influences were not excluded.

Threlkeld (1986) considered that most field studies of the influence of turbidity on zooplankton dynamics have not distinguished between the effects of the suspended particulates and the advective influence (Dirnberger and Threlkeld 1986) of large amounts of inflowing flood water that often accompanies the increase in suspended particulate concentration. Threlkeld (1986) examined the life history parameters of four cladocerans in flood water with increased silt concentration from Lake Texoma, USA. There was good agreement between the field population dynamics and the life table responses in the flood waters. These results disagreed with a study by Scholtz *et al.* (1988) on the effects of turbidity on the life history parameters of two *Daphnia* species. In contrast to expectations based on seasonal occurrence, the clear water *Daphnia pulex* had a more optimal rate of increase than the turbid water *Daphnia barbarta* across the range of turbidities where the latter dominated. Scholtz *et al.* (1988) concluded that fish predation rather than turbidity *per se* influenced the seasonality of these species. A recent study by Threlkeld and Sorballe (1988) reported few effects of mineral turbidities up to 100 mg l-1 on either phytoplankton or zooplankton populations, however this interpretation was limited by the unreplicated experimental design.

Daytime vertical distributions of zooplankton were found to be closer to the surface with increased turbidity in the studies of Zettler and Carter (1986) and Cuker (1987). These were attributed to reduced predation by fish in the surface waters, giving the zooplankton access to greater algal food resources.

Although some of these field studies report different distributions for different zooplankton taxa in response to turbidity, few specifically examined the influence of turbidity on

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zooplankton grazing. Laboratory experiments by Marzolf and Arruda (1980), McCabe and O'Brien (1983), Arruda *et al.* (1983), G-Toth *et al.* (1986), Vanderploeg *et al.* (1987) and Hart (1988) all examined the influence of suspended particulates on the grazing rates of *Daphnia* spp. The recent studies of Vanderploeg *et al.* (1987) and Hart (1988) examined the influence of suspended particulates on copepods and compared copepods with cladocerans. Given the dominance of copepods in the zooplankton of Mt Bold Reservoir (Chapter 3) and in many other turbid Australian water bodies (Mitchell 1986), it was anticipated that the grazing response of the local copepods in suspended particulates would differ from that of the local cladocerans.

Using representative copepods and cladocerans from Mt Bold Reservoir, the aims of these experiments were: (1) to determine the influence of suspended particulates on zooplankton *in situ* grazing rates and on the selection of food tracers; and (2) to investigate the relationship between suspended particulate concentration and zooplankton grazing rates.

6.5.2 FIELD DETERMINATIONS

6.5.2.1 METHODS

Two field experiments were done at a time when the suspended particulate concentration in in Mt Bold Reservoir was high as a result of pumping from the Murray River. Due to the low chlorophyll *a* concentration present in the reservoir at this time, laboratory cultures of phytoplankton (*Chlorella, Ankistrodesmus* and *Staurastrum*) were labelled with ^{14}C and used as food tracers. *Boeckella triarticulata* Thompson and *Daphnia carinata* King grazing rates in the turbid Mt Bold water were compared to grazing rates in clear water from an adjacent farm dam. Grazing measurements were done in buckets as previously described. Table 6.15 shows the structure of each experiment, listing water types, food types with numbers of replicates, the numbers of separate groups of animals measured and the numbers of individual animals making up the groups. Water samples were taken from which organic and inorganic seston and chlorophyll *a* concentrations were determined. Suspended particle concentrations were also measured using a Coulter Counter.

6.5.2.2 RESULTS

Table 6.16 lists the mean ($\pm$se) filtering rates (ml animal^{-1} h^{-1}) of *Boeckella* and three size classes of *Daphnia* (1, 2 and 2.5 mm) on the two food tracers in clear and in turbid water for the two experiments. Filtering rates were compared within each experiment by ANOVA; the results of specific comparisons are shown in Table 6.17a-b for the 21.III.84 and 4.IV.84 experiments, respectively.

In the 21.III.84 experiment, the Mt Bold water had a total (mean $\pm$ se) seston concentration of 21.41 ± 0.28 mg l^{-1} with 16.04 ± 0.27 mg l^{-1} (75%) inorganic and 5.37 ± 0.02 mg l^{-1} (25%) organic and a chlorophyll *a* concentration of 5.74 ± 0.12 μg l^{-1}. In contrast, the farm dam water had a total seston concentration of 3.39 ± 0.14 mg l^{-1} with 0.14 ± 0.09 mg l^{-1} (4%) inorganic and 3.25 ± 0.09 mg l^{-1} (96%) organic and a chlorophyll *a* concentration of 3.56 ± 0.61 μg l^{-1}. The Mt Bold water had a total particle (ESD range 1.5-49 μm) concentration of $4.7 \times 10^5 \pm 1.9 \times 10^4$ particles ml^{-1} while the farm dam water had $1.3 \times 10^5 \pm 3.0 \times 10^3$ particles ml^{-1}.

Within the 21.III.84 experiment, the filtering rates of *Boeckella* and of the three size classes of *Daphnia* were reduced in the turbid Mt Bold water relative to the clear farm dam water (Table 6.12), however this reduction was only significant ($P < 0.05$) in the case of *Daphnia* (2 mm) feeding on *Chlorella* (Table 6.13a). In the clear water there was a tendency for *Daphnia* of all size classes to filter at higher rates on *Chlorella* relative to *Staurastrum* and this trend was maintained in the turbid water, although it was not significant in either case. In clear water *Boeckella* filtered at significantly ($P < 0.01$) higher rates on *Staurastrum* relative to *Chlorella* but this was not significant in turbid water.

In the 4.IV.84 experiment, the Mt Bold water had a total seston concentration of 38.24 ± 0.63 mg l^{-1} with 28.97 ± 0.42 mg l^{-1} (76%) inorganic and 9.27 ± 0.35 mg l^{-1} (24%) organic and a chlorophyll *a* concentration of 8.07 ± 0.10 μg l^{-1}. In contrast the farm dam water had a total seston concentration of 3.91 ± 0.12 mg l^{-1} with 0.99 ± 0.05 mg l^{-1} (25%) inorganic and 2.92 ± 0.08 mg l^{-1} (75%) organic and a chlorophyll *a* concentration of 1.71 ± 0.13 μg l^{-1}. The Mt Bold water had a total particle (ESD range 1.5-49 μm) concentration of $3.8 \times 10^5 \pm 1.6 \times 10^4$ particles ml^{-1} while the farm dam water had $1.8 \times 10^5 \pm 1.0 \times 10^4$ particles ml^{-1}.

As a result of increased replication within the 4.IV.84 experiment (Table 6.11), the filtering rates of *Boeckella* and all size classes of *Daphnia* were significantly ($P < 0.01$ or $P < 0.001$) reduced in the turbid Mt Bold water relative to the clear farm dam water (Tables 6.12 and 6.13b). These reductions ranged from 26 to 82%. In both clear and turbid water *Boeckella* filtered at significantly ($P < 0.01$ or $P < 0.001$) lower rates on *Ankistrodesmus* relative to *Staurastrum*. In both clear and turbid water *Daphnia* (1 mm) filtered at significantly ($P < 0.01$ or $P < 0.001$) higher rates on *Ankistrodesmus* relative to *Staurastrum*. For *Daphnia* (2 and 2.5 mm) there was no significant difference between the filtering rates on *Ankistrodesmus* relative to *Staurastrum* in either clear or turbid water.

Figure 6.7 shows the mean ($\pm$se) filtering rates of the three size classes of *Daphnia*, in clear or in turbid water, using *Ankistrodesmus* or *Staurastrum* as food tracers. Filtering rate increased with body size in both clear and turbid water using both tracer types. Table 6.18a-b shows the results of linear and power regression analysis respectively, between filtering rate and body size for each combination of water and tracer type. There was a linear relationship between filtering rate and body size in clear water for both tracer types (Figure 6.7 and Table 6.18a) while in turbid water a power relationship best described the relationship for both tracer types (Figure 6.7 and Table 6.18b).

Table 6.19 lists the absolute reductions in filtering rates with increased seston concentration (assuming a linear relationship), for the 4.IV.84 experiment, expressed on an individual animal basis and on a biomass basis, for both tracer types.

6.5.2.3 DISCUSSION

6.5.2.3.1 Reduction of filtering rate by suspended particulates.

The reduced filtering rate of *Daphnia carinata* in the presence of suspended particulates found in this study agrees with the results obtained for *Daphnia pulex* (Marzolf and Arruda 1980; Arruda *et al.* 1983; McCabe and O'Brien 1983; Vanderploeg *et al.* 1987), *Daphnia parvula* (Arruda *et al.* 1983), *Daphnia galeata* (G-Toth *et al.* 1986), *Daphnia gibba*, *Daphnia barbata*, *Daphnia longispina* and *Moina brachiata* (Hart 1988). In contrast, Gaddy and Parker (1986) reported that the ingestion rate of *Daphnia pulex* was unaffected by an increased concentration of suspended volcanic ash, however Vanderploeg *et al.* (1987)

questioned these results because the animals were starved prior to the feeding measurement. The relationship between *Daphnia carinata* filtering rate and body length seemed to be altered in the presence of suspended sediment (Figure 6.7). Ganf and Shiel (1985a) reported a power relationship with an exponent of 2.03 for *Daphnia carinata* grazing on pure *Ankistrodesmus*, using a Coulter Counter for filtering rate measurement, which was within the exponent range of 1 to 3 reported for *Daphnia* (Ganf and Shiel 1985a). In the present study the turbid water power exponent averaged 1.6 while the clear water filtering rates were directly proportional to body length. Porter *et al.* (1983) found that *Daphnia parvula* filtering rates on algae (*Chlamydomonas reinhardi*) increased more rapidly with body size than filtering rates on bacteria and suggested that different processes were involved in the capture of these two particle types. The different slopes or exponents in turbid water relative to clear water, observed in the present study (Table 6.14a-b) may indicate a similar situation, i.e. the presence of suspended particulates alters the capture process.

At the time of these experiments there were no reports (known to this author) on the influence of suspended particulates on the grazing rates of freshwater copepods, although Paffenhofer (1972) found that the ingestion rate of the marine copepod *Calanus helgolandicus* was reduced by a suspension of 'red mud', a mixture of aluminium and iron oxides remaining after the extraction of aluminium from bauxite. The reduced filtering rate of *Boeckella* found in the present study supports this result. More recently Hart (1988) reported that the feeding rate of *Metadiaptomas meridianus* was reduced in the presence of suspended silt in Lake le Roux, South Africa, while Vanderploeg *et al.* (1987) found that the feeding rate of *Diaptomus sicilis* was not reduced at the average concentrations of suspended calcite present in Lake Michigan, USA.

6.5.2.3.2 Selection of different food tracers.

In clear water the filtering rate of *Boeckella* using *Ankistrodesmus* was 63% of that using *Staurastum*; in turbid water this ratio was 51%. The presence of suspended particulates did not appear to greatly alter the copepods selection for *Staurastrum* (or selection against *Ankistrodesmus*). For *Daphnia* (1 mm) these ratios were 151% and 433% in clear and turbid water respectively, which indicated that for this cladoceran, the selection for *Ankistrodesmus* (or against *Staurastrum*) was substantially increased in the presence of suspended particles. It is of interest to note that this selection was not maintained by the larger cladocerans

(Daphnia 2 and 2.5 mm) in either clear or turbid water in this experiment. Hart (1988) reported large differences in the filtering rates of several zooplankton on different food tracers (*Scenedesmus, Selenastrum* and *Chlorella*) in the turbid water of Lake le Roux, suggesting strong selectivity. Furthermore the slopes of the linear relationships between filtering rate and turbidity differed for the different food tracers (Hart 1988; Table 4) which indicated that selection could be influenced by the turbidity level.

6.5.2.3.3 Filtering versus feeding reduction.

The reduced filtering rate measured in the turbid water may have been simply due to the increased particle concentration. Thus although the filtering rate decreased, the feeding rate may have remained constant. Feeding rates were not directly measured in these experiments. In the 4.IV.84 experiment, the turbid water had about double the particle concentration of the clear water, so the filtering rate should have been halved for a constant particle intake. Although the measured reduction with *Ankistrodesmus* was around 50% for *Boeckella* and *Daphnia* (1 mm), for *Daphnia* (2 and 2.5 mm) it was less than this. This implied that the longer animals were able to overcome the filtering rate reduction due to increased particle concentration. The filtering rate reduction with *Staurastrum* ranged from 26% to 82% which indicated there was some inhibition of zooplankton grazing in excess of the reduction due to increased particle concentration, as well as some avoidance of this reduction.

6.5.2.3.4 Comparisons between size and taxa.

In absolute terms, on an individual basis, the smallest animal (*Daphnia* 1 mm) had the smallest reduction in filtering rate per unit increase in seston concentration (Table 6.19). This implies that the food intake of this animal would be least affected by the seston increase. However on a biomass basis the smallest animal had the highest reduction in filtering rate per unit increase in seston concentration (Table 6.19). Since on a weight basis metabolic activity (e.g. respiration rate) increases with decreasing animal body size (Lampert 1984), this indicates that the smallest animal would be most disadvantaged in terms of energy requirements.

Due to the different grazing modes of calanoid copepods and cladocerans (Peters 1984), it was anticipated that these two types of animal would differ in their grazing response to

suspended particulates. A comparison of equivalent sized *Boeckella* (25 μg dry wt) and *Daphnia* (2 mm or 29 μg dry wt) within the 4.IV.84 experiment did not show any consistent difference. With *Ankistrodesmus* as a food tracer, *Boeckella* showed a 51% reduction and *Daphnia* a 41% reduction, however with *Staurastrum*, *Boeckella* had a 40% reduction and *Daphnia* a 42% reduction. When compared on a biomass basis, the filtering rate reductions of these two animals were equivalent (Table 6.19). These results contrast with those of Hart (1988) who found that, on a biomass basis, copepod filtering rates were reduced less than cladoceran filtering rates with increased turbidity.

The results obtained in the field experiment discussed above were between two levels of turbidity only. For a more extensive examination of the relationship between zooplankton grazing rates and suspended particulates, it was necessary to do more controlled experiments in the laboratory.

6.5.3 LABORATORY INVESTIGATIONS

6.5.3.1 METHODS

Boeckella triarticulata Thompson, *Calamoecia ampulla* (Searle) and *Ceriodaphnia quadrangula* (O.F. Muller) were collected from Mt Bold Reservoir and maintained in lake water in the laboratory until required. *Ankistrodesmus falcatus* var. *acicularis* (UTEX 101) was used as both a food and a feeding tracer during the experiments. The alga was cultured in WC medium and appropriate experimental cell concentrations were prepared by dilution with WC medium. Exponentially growing *Ankistrodesmus* was uniformly labelled by incubating with $NaH^{14}CO_3$ in CO_3-free WC medium for 3-5 days.

Artificial clay suspensions were made using kaolinite ball clay in deionized water. Suspensions were sonicated before use to reduce aggregation of clay particles. Particle concentrations and size frequency distributions were measured using a Coulter Counter with either a 30 or a 70 μm aperature. A linear regression between clay dry weight and particle concentration, for the range 10 to 200 mg l^{-1}, was determined:
particles ml^{-1} = 87988 + 27638 mg l^{-1} (r^2 0.998)
This facilitated preparation of clay suspensions of known particle concentration. Nephelometric turbidity of the clay suspensions were measured using a Hach 2100A

turbidimeter. A linear regression between clay dry weight and nephelometric turbidity, for the range 10 to 200 mg l^{-1}, was determined:

$$NTU = 0.1431 + 0.5134 \ mg \ l^{-1} \ (r^2 \ 1.00)$$

This enabled comparison with literature results reported in NTU. The clay dry weight range of 10 to 200 mg l^{-1} was equivalent to 6 to 100 NTU.

Feeding experiments were done in 2 litre polythene bottles in which animals were allowed to acclimatize for 1 hour prior to the experiment. After addition of the tracer the bottles were gently inverted twice to ensure complete mixing and resuspension of the feeding suspension. Zooplankton grazing rates were determined as previously described. Quenching by either clay or the algal food was checked by comparing the radioactivity of the feeding suspension across the range of clay or algal concentrations. Feeding rates were not calculated for animals grazing in the clay suspensions since there was no direct measurement of the clay ingested with the algal tracer. It was assumed that there was no discrimination between ^{14}C labelled and unlabelled *Ankistrodesmus* when the two were offered at the same time. During each experiment the body lengths of 30 *Ceriodaphnia* (eye to base of caudal spine), 20 *Boeckella* (metasomal) and where appropriate 30 *Calamoecia* (metasomal) individuals were measured to enable biomass estimation.

A preliminary experiment (4.IV.86) measured the filtering rates of the animals in Mt Bold water, under laboratory light and under dark conditions, to check on the effect of reduced light levels within the more turbid clay suspensions. Another experiment (2.V.86) measured the filtering and feeding rates of the animals in pure *Ankistrodesmus* food to establish the feeding responses with increasing food concentration. Two experiments (10.IV.86 and 16.IV.86) measured the filtering rates of the animals across a range of clay concentrations. The final two experiments measured filtering rates in both clay and algae in various mixtures (24.IV.86) and separately (2.V.86) to compare feeding responses in equivalent particle suspensions. Table 6.20 lists the feeding media, the numbers of replicates, the numbers of separate groups of animals measured and the numbers of individual animals making up the groups for each of the experiments done.

6.5.3.2 RESULTS

6.5.3.2.1 Light versus Dark Filtering

Boeckella had a mean (±se) filtering rate of 1.30 ± 0.06 ml animal^{-1} h^{-1} in the light and 1.04 ± 0.04 ml animal^{-1} h^{-1} in the dark, while *Ceriodaphnia* had filtering rates of 0.14 ± 0.02 and 0.12 ± 0.01 ml animal^{-1} h^{-1} in light and dark respectively. ANOVA showed there was no significant difference between the light and dark filtering rates for either animal. A reduction in light levels (associated with increased suspended particulates) did not appear to influence the filtering rates of these animals and subsequent experiments were done in laboratory light.

6.5.3.2.2 Effect of Food Concentration on Filtering and Feeding Rates

Figures 6.8a-c show the mean (±se) filtering and feeding rates of *Boeckella*, *Calamoecia* and *Ceriodaphnia* respectively, on *Ankistrodesmus* concentrations ranging approximately from 10^3 to 10^5 cells ml^{-1}. All animals showed initial increases followed by decreases in filtering rate with increasing food concentrations (Figures 6.8a-c). The corresponding feeding rate, showed initial increases followed by a levelling off to a more or less constant rate with increased food concentration. Table 6.21 lists the mean (±se) filtering and feeding rates in each of the *Ankistrodesmus* concentrations; these were compared by ANOVA and the results of pairwise comparisons between algal concentrations for each animal are shown in Table 6.21 using superscripts. *Boeckella* had a maximum mean filtering rate of 0.825 ± 0.051 ml animal^{-1} h^{-1} at a food concentration of $4.8 \times 10^3 \pm 0.3 \times 10^3$ cells ml^{-1} (Figure 6.8a). The maximum mean feeding rate for *Boeckella* was $1.14 \times 10^4 \pm 1.18 \times 10^3$ cells animal^{-1} h^{-1} at a food concentration of $1.1 \times 10^5 \pm 2.7 \times 10^3$ cells ml^{-1}. *Calamoecia* had a maximum mean filtering rate of 0.107 ± 0.010 ml animal^{-1} h^{-1} and a maximum mean feeding rate of $1.81 \times 10^3 \pm 1.82 \times 10^2$ cells animal^{-1} h^{-1} at the same food concentrations as for *Boeckella* (Figure 6.8b). *Ceriodaphnia* had maximum mean filtering and feeding rates of 0.201 ± 0.009 ml animal^{-1} h^{-1} and $3.59 \times 10^3 \pm 1.81 \times 10^2$ cells animal^{-1} h^{-1} respectively, again at the same food concentrations as for *Boeckella* (Figure 6.8c). The incipient limiting food concentration was between 10^4 and 5×10^4 cells ml^{-1} for all animals.

The specific activities (cpm ml^{-1}) of the feeding suspensions were significantly different by

ANOVA. Pairwise comparisons indicated that the specific activity of the 5×10^3 cells ml^{-1} *Ankistrodesmus* suspension was significantly (P < 0.05) lower than the others, which were not significantly different from each other. This low specific activity did not correspond to the highest algal concentration so quenching by the algae was not indicated.

In the course of this experiment there was evidence of microzooplankton in the initial specific activity samples. The possible contribution of these animals to the specific activity estimations was not known. To investigate this, the microzooplankton were filtered out from the remaining filtrate and the specific activity of the feeding suspension remeasured using samples of two volumes (50 and 75 ml). There was a considerable time delay (3 h) between the initial and the second specific activity sampling. Specific activities were reduced in the second samples, probably as a result of microzooplankton grazing since the largest reductions were in the lowest algal concentrations. It was realized that the inclusion of the microzooplankton in the initial specific activity samples was acceptable since the radioactivity they contained came from the original food suspension. Nevertheless it was considered prudent to sample for specific activity immediately after the feeding session. A comparison of the samples of different volumes from the second sampling showed that there was a higher specific activity in the smaller volume sample and that the difference between the samples was larger at higher algal concentrations. This indicated some cell breakage was occurring which increased at higher cell concentrations. The reduction at the highest algal concentration was 6% so the influence on the filtering rates was small.

6.5.3.2.3 Effect of Suspended Particulates on Filtering Rates

Two experiments were done to cover a range of suspended sediment concentrations from 10 to 160 mg l^{-1} (6 to 86 NTU). Both experiments had controls with no clay. The results for both experiments are shown in Figures 6.9a-b for *Boeckella* and *Ceriodaphnia* respectively. For both animals the filtering rates decreased with increasing suspended sediment concentration. *Boeckella* showed a steady decrease across the range of clay concentrations investigated (Figure 6.9a) while *Ceriodaphnia* showed a rapid reduction initially which then leveled off at higher clay concentrations (Figure 6.9b).

The control filtering rates were not the same for both experiments. Uniform *Ankistrodesmus* food tracer concentrations were used within each experiment, however there was a difference

between the two experiments; 1.07×10^4 cells ml^{-1} on 10.IV.86 vs. 5.8×10^3 cells ml^{-1} on 16.IV.86. This concentration difference accounted for the difference between the control filtering rates for *Boeckella*. There was good agreement between these control filtering rates and the rate predicted from the grazing response in Figure 6.8a; 0.62 vs. 0.64 ml animal^{-1} h^{-1} on 10.IV.86 and 2.V.86 respectively and 0.75 vs. 0.79 ml animal^{-1} h^{-1} on 16.IV.86 and 2.V.86 respectively. The tracer concentration difference did not account for the large difference between the control filtering rates of *Ceriodaphnia*. For *Ceriodaphnia* the control rates were much lower than the predicted rates; 0.04 vs. 0.17 ml animal^{-1} h^{-1} on 10.IV.86 and 2.V.86 respectively and 0.10 vs. 0.20 ml animal^{-1} h^{-1} on 16.IV.86 and 2.V.86 respectively. Part of the difference between the control filtering rates of *Ceriodaphnia* was due to the significantly (t_{58} 6.64, P $<$ 0.001) smaller animals used in the 10.IV.84 experiment (mean $\pm$se; 605 $\pm$ 5 μm) compared with the 16.IV.84 experiment (690 $\pm$ 12 μm). Zooplankton filtering rates increase with body size (Peters 1984 and references therein). However, using the relationship between filtering rate and body size of *Ceriodaphnia quadrangula* feeding on *Ankistrodesmus* reported by Ganf and Shiel (1985a), the above size difference would only result in a filtering rate difference of 0.006 ml animal^{-1} h^{-1} or a 27% reduction. Furthermore the body size of the animals used in the 2.V.84 experiment (628 $\pm$ 11 μm) was not larger than those in the above two experiments. There was no significant (t_{38} 1.19, ns) difference in body length of *Boeckella* between the 10.IV.84 experiment (1153 $\pm$ 21 μm) and the 16.IV.84 experiment (1185 $\pm$ 17 μm).

Within both experiments the specific activities of the food suspensions were compared by ANOVA; there were no significant differences in specific activity between the treatments in either experiment. Because a constant amount of tracer was added to each experimental container and equal volumes of the food suspensions were measured, this implied that there was no quenching of radiation due to the increased clay concentrations in these two experiments.

Regression analysis was used to examine the relationship between animal filtering rate and clay concentration within each experiment. Table 6.22a-b summarizes the linear and power regression analysis results respectively. There were significant differences between the mean filtering rates for both animals in both experiments. For both animals there were significant linear relationships between filtering rate and clay concentration for the low range (0-40 mg l^{-1}) of clay concentration (Table 6.22a). The regression slope for *Boeckella* was marginally

significantly more negative than the regression slope for *Ceriodaphnia*. There was no significant linear relationship between filtering rate and the high range (80-160 mg l^{-1}) of clay concentration for either animal. *Ceriodaphnia* had significant deviations from a linear relationship but *Boeckella* did not. The lack of a significant linear relationship for *Boeckella* was likely due to the small number of data points (3) in the regression. The only significant power relationship was between *Ceriodaphnia* filtering rate and the low range of clay concentration (Table 6.22b).

The results of the two separate experiments are combined in Figure 6.10 which shows the filtering rate relative to the control, expressed as a percentage, plotted against clay concentration. The different consequences of increased clay concentration on the two animals is illustrated in Figure 6.10. Thus although increased clay concentrations reduced the filtering rates of both animals at about the same rate, the proportional decrease was much greater for the cladoceran compared with the calanoid copepod. For example, the addition of 40 mg l^{-1} clay reduced the filtering rate of *Ceriodaphnia* to 36% of its control rate while the filtering rate of *Boeckella* was reduced to 76% of its control rate. At the highest clay concentration used (160 mg l^{-1}), the *Ceriodaphnia* filtering rate was reduced to 15% of the control rate while that for *Boeckella* was 56% of the control.

6.5.3.2.4 Effect of Increased Clay Proportion on Filtering Rates

The reductions in filtering rate with increased clay concentration (Figure 6.10) may have been due entirely to the increased particle concentration, analagous to the effect of increased *Ankistrodesmus* concentrations (Figures 6.8a-c). To investigate this, the proportion of clay in the feeding suspension was increased while the total particle volume was kept constant. Volume was used rather than particle numbers since an *Ankistrodesmus* cell has a much larger volume than the clay particle.

Table 6.23 shows the mixtures of clay and *Ankistrodesmus*, in terms of particle numbers and volume concentration, in which the zooplankton filtering rates were measured. Mixtures 1 and 4 were complemented by mixtures 2 and 5 respectively; where the proportions of clay to algae in the former (1:10) were reversed in the latter (10:1), while the total particle concentration on a volume basis remained constant for each pair. Using the Coulter Counter it was estimated that one average *Ankistrodesmus* cell had a volume equivalent to fifty

average clay particles with an ESD >1 μm. The mean ($\pm$se) filtering rates of *Boeckella*, *Ceriodaphnia* and *Calamoecia* in these mixtures are listed in Table 6.23; these were compared between the mixtures for each animal by ANOVA. The results of pairwise comparisons between mixtures are shown in Table 6.19 using superscripts. There were significant ($P < 0.05$) differences between the filtering rates in both of the complementary mixtures (1 vs. 2 and 4 vs. 5) for *Boeckella* and *Ceriodaphnia*, and in one only (1 vs. 2) for *Calamoecia*. At the low particle concentration (mixtures 1 and 2) there was a significant increase in filtering rate with an increase in clay proportion for all three animals (Table 6.23). At the high particle concentration (mixtures 4 and 5) there was a decrease in filtering rate with an increase in clay proportion which was significant ($P < 0.05$) for *Boeckella* and *Ceriodaphnia* but not significant for *Calamoecia*. The increased filtering rate in mixture 1 versus mixture 2 was unexpected and was likely a consequence of the lower algal concentration rather than the higher clay concentration in mixture 1.

The specific activities of the food suspensions were significantly different by ANOVA. Pairwise comparisons indicated that the specific activities of mixtures number 5 and 4 were significantly lower than the others, with the former also lower than the latter. These differences indicated that quenching or cell breakage was occurring at the highest algal and clay concentrations. The consequence of this was that the animal filtering rates were potentially overestimated. However since the maximum reduction in specific activity was 10%, the influence on the filtering rates was small.

All filtering rates in this experiment were substantially lower than was expected from previous results. Despite this, the response of the two animal types to increasing particle concentration could be examined. Table 6.24 lists the rates of change in filtering rate (assuming a linear response) in mixtures with either constant algae and increasing clay or constant clay and increasing algae. Comparison of the results in mixtures 2, 3 and 4 which had a constant *Ankistrodesmus* concentration (10^4 cells ml^{-1}) with increasing clay concentrations (1.7, 17.4 and 203.6 mg l^{-1} respectively) showed that the filtering rate of *Ceriodaphnia* between mixtures 2 and 3 decreased at a more rapid rate compared to *Boeckella*. The rate of decrease between mixtures 3 and 4 was the same for both animals. Comparison of the results in mixtures 1, 3 and 5 which had a constant clay concentration (17.4 mg l^{-1}) with increasing *Ankistrodesmus* concentration (10^3, 10^4 and 10^5 cells ml^{-1} respectively) showed that the filtering rate of *Boeckella* decreased at a more rapid rate

compared to *Ceriodaphnia* on both occasions. For both animals the initial reduction was greater with increased algae than with increased clay but the second reduction was greater with clay than with algae. The rate of change in filtering rate of *Calamoecia* was always smaller than those of *Boeckella* or *Ceriodaphnia* (Table 6.24) however the absolute filtering rates of *Calamoecia* in this experiment were unreliably low (Table 6.23).

It was evident that filtering rates varied between experiments in apparently comparable situations. To verify the results of the previous experiment, filtering rates were measured in pure *Ankistrodesmus* suspensions (10^4 and 10^5 cells ml^{-1}) as well as in the equivalent clay concentration. Table 6.25 shows the mean ($\pm$se) filtering rates of *Boeckella*, *Calamoecia* and *Ceriodaphnia* in low and high concentrations of both *Ankistrodesmus* and clay which had the same total volume. Filtering rates of each animal were compared between the paired food suspensions by ANOVA. Filtering rates of *Boeckella* and *Ceriodaphnia* were significantly reduced in clay relative to algae at the low concentrations. The reduced filtering rate of *Calamoecia* in clay was not significant. At high concentrations the filtering rates of *Calamoecia* and *Ceriodaphnia* were significantly reduced in clay relative to algae but there was a significant increase in the filtering rate of *Boeckella* in clay relative to in algae. The specific activity of the food suspensions were significantly different by ANOVA but pairwise comparisons did not support this.

6.5.3.3 DISCUSSION

6.5.3.3.1 Light versus dark grazing

Although many zooplankton increase their grazing activity at night (Haney and Hall 1975; Starkweather 1975; Baars and Oosterhuis 1984; Stearns 1986; Roman *et al.* 1988), the effect of the intensity and quality of light on grazing rates is not clear (Peters 1984). McMahon (1965) reported no effect on the feeding rate of *Daphnia magna* when the light intensity ranged from darkness to 500 foot-candles, however above this the feeding rate increased in high food concentrations but was relatively constant in low food concentrations. McMahon (1965) covered a wide range of light intensities (0 to 10000 foot-candles) with large intervals between the experimental intensities. Schindler (1968) found no significant difference in the feeding rate of *Daphnia magna* between darkness and 1000 ft candles. On a much finer scale, Buikema (1973) obtained differences in *Daphnia pulex* filtering rates across a light intensity

range of 0 to 110 foot-candles; the significance of which depended on the animal size and degree of acclimatization to the light levels. Horn (1981) found that the grazing rate of *Daphnia hyalina* increased at light intensities below 50 lux. Between 50 and 9000 lux, grazing rate was constant. More recently Stearns (1986) reported a significant negative correlation between *Acartia tonsa* grazing and light intensity across the range 0 to 20 μE m^{-2} s^{-1}. Using the conversion factors in Strickland (1958) and Morel and Smith (1974) the light intensities used by McMahon (1965), Schindler (1968), Buikema (1973) and Horn (1981) were equivalent to 0-2000, 0-200, 0-22 and 1-170 μE m^{-2} s^{-1} respectively. In the present study, the lack of significant differences in filtering rates of *Boeckella* and *Ceriodaphnia* between light intensities of 0 and c. 20 μE m^{-2} s^{-1} contrasted with the results of Buikema (1973) and Stearns (1986), but agreed with those of Horn (1981).

Work by Watts and Young (1980) and Young *et al.* (1984) suggested that *Daphnia magna* grazing rates were influenced by changes in light field distribution rather than changes in light intensity. Because the presence of suspended particles alters the light field distribution (Kirk 1983), if correct, this would invalidate the application of these light versus dark results to the later experiments with clay suspensions.

6.5.3.3.2 Filtering and feeding rates on *Ankistrodesmus*

The general shape of the filtering and feeding curves of *Boeckella, Calamoecia* and *Ceriodaphnia* with increasing *Ankistrodesmus* concentrations (Figures 6.8a-c) agreed with literature reports for zooplankton grazing on many different algal foods (Peters 1984 and references therein). The slow increase in feeding rate above the incipient limiting food concentration, evident for all animals in this study, was not statistically significant. The incipient limiting concentration of between 10^4 and 5×10^4 cells ml^{-1} or 2.4 to 12 ppm (vol/vol) found for these animals is within the range reported for freshwater zooplankton by Peters (1984; Figure 9.4). Ganf and Shiel (1985a) reported an incipient limiting concentration of 4×10^4 cells ml^{-1} for *Ceriodaphnia quadrangula* feeding on *Ankistrodesmus*.

The relationship between food concentration and feeding rate has been described using several different mathematical models (Frost 1972; Mullin *et al.* 1975; Lam and Frost 1976; Lehman 1976; Porter *et al.* 1982), however no particular model has been identified as superior to the others (Peters 1984). One area of distinction between some of these models

involves different predictions about filtering rates at low food concentrations and several studies have examined this 'threshhold' grazing behaviour (Frost 1975; Muck and Lampert 1980; Porter *et al.* 1982). Within this study there was a reduction in filtering rates at the lowest food concentration relative to the second lowest concentration for all animals, although this reduction was only significant for *Boeckella*. There were however, insufficient measurements made at low food concentrations to warrant investigation of this relationship.

Specific comparisons may be made with the results of Ganf and Shiel (1985a) for *Ceriodaphnia quadrangula* feeding on *Ankistrodesmus*. Using a Coulter counter to measure grazing rates, these authors reported a maximum mean filtering rate of 0.06 ml animal^{-1} h^{-1} at a food concentration of 1.9×10^4 cells ml^{-1} and a maximum mean feeding rate of 2.5×10^3 cells animal^{-1} h^{-1}, for 0.7 mm individuals. These maximum grazing rates were substantially lower than those obtained in the present study despite a smaller average animal size (0.63 mm) in the present study. The different techniques (radioisotope vs. Coulter counter) used to measure grazing rates means that these results are not directly comparable, however, comparisons of these techniques have not revealed systematic differences of the magnitude found here (Hargis 1977; Peters 1984). These were more likely due to artifacts of the experimental conditions such as previous feeding history of the experimental animals and size of feeding container used. With respect to the former, the animals of Ganf and Shiel (1985a) were starved "for at least 3 hours but usually overnight" while in the present study they were maintained in lake water overnight and acclimated to the feeding conditions prior to measurement. Starvation alters zooplankton grazing rates (McMahon and Rigler 1963; McAllister 1970; Frost 1972). The size of the grazing chamber or volume of food suspension used (30 ml by Ganf and Shiel (1985a) vs. 2000 ml in this study) has also been shown to influence grazing rates (Anraku 1964; Paffenhofer 1971, 1976). O'Brien (1988) suggested that the marked decrease in feeding rate of a predatory copepod *Heterocope septentrionalis* with decreasing container size was due to an 'edge effect' where the animal did not feed within a certain fixed distance from the container edge. A similar inhibition may occur with herbivorous zooplankton although Elmore (1982) reported that container volume did not directly influence life history parameters of *Diaptomus dorsalis*, which would depend partly on grazing rate.

There are no published grazing rates for *Boeckella triarticulata* on *Ankistrodesmus*, however, Ellis (1984) measured a mean ±se filtering rate of 0.25 ± 0.02 ml animal^{-1} h^{-1} at a food

concentration of 10^4 cells ml^{-1}, for *Boeckella symmetrica* Sars with a metasomal length of 1.1 mm, using a Coulter Counter and an experimental procedure similar to Ganf and Shiel (1985a). Again this result is substantially lower than that obtained in the present study at a similar food concentration with similar sized animals (mean ±se metasomal length; 1165 ± 16 μm) and is likely due to the different experimental conditions at the time of measurement.

6.5.3.3.3 Variation in filtering rates between experiments

Between the experiments there was considerable variation in filtering rates within each zooplankton taxon, in apparently comparable experimental conditions. Some of these differences were partially explained in terms of different food concentrations or body sizes, however a large amount of variation could not be accounted for in this manner. This was a consequence of using field populations since although the pre-experimental protocol was uniform, there was no control over the physiological (e.g. nutritional) status of the animals used. This status can have a marked influence on zooplankton grazing rates (Peters 1984 and references therein). Chow-Fraser (1986b) showed that zooplankton grazing rates were significantly influenced by collection and by the acclimation period, with different responses for a cladoceran (*Daphnia* sp.) and a copepod (*Diaptomus oregonensis*).

6.5.3.3.4 Relationship between filtering rate and clay concentration

The reduced filtering rates of *Boeckella* and *Ceriodaphnia* with increased clay concentration found in this laboratory study agreed with the field results, and with the literature for other copepods and cladocerans. In the present study, the relationship between filtering rate and clay concentration was a linear function, for both animal types, in the range 0-40 mg l^{-1}. Neither linear nor power functions explained a significant amount of the variation in filtering rate across the 80-160 mg l^{-1} range (Table 6.22a-b), however a linear function was used for comparative purposes with the literature. Table 6.26 lists the relationships for this study as well as those reported by other authors. Although McCabe and O'Brien (1983) reported a power function (Table 6.26), they considered that there was no reduction in filtering rate at turbidities less than 10 NTU. Arruda *et al.* (1983) did not fit any mathematical functions to their data for *Daphnia pulex* and *Daphnia parvula*, however a log-log plot of feeding rate versus sediment concentration (Arruda *et al.* 1983; Figure 2) showed a similar situation; no change until 10 mg l^{-1} followed by a rapid decrease. In the present study, filtering rates of

both animal types at 10 mg l^{-1} were significantly reduced from the rates at 0 mg l^{-1}.

Direct comparison of the relationships in Table 6.26 was not always immediately possible due to differing functions and units. Comparison of Tables 6.22b and 6.26 shows that the exponents for both *Boeckella* and *Ceriodaphnia* in this study were much lower than those reported for *Daphnia galeata* by G-Toth *et al.* (1986) and for *Daphnia pulex* by McCabe and O'Brien (1983). The latter direct comparison was made because there was a linear relationship between mg l^{-1} clay and NTU in the present study. These comparisons indicate that the filtering rate of the animals in the present study was less influenced by clay than the *Daphnia* spp. were influenced by suspended particulates in the above two studies.

Using the mean filtering rates at each clay concentration and the concentration of *Ankistrodesmus* food tracer; feeding rates on *Ankistrodesmus* were calculated as a proportion of animal body weight per day (without considering the accompanying clay ingestion). Dry weights of 7.2×10^{-5} μg per *Ankistrodesmus* cell (Holm *et al.* 1983), 25 μg for *Boeckella*, and 3.3 and 4.5 μg for *Ceriodaphnia* on 10.IV.86 and 16.IV.86 respectively, were used. Linear functions were established between the consumption rate (%body dry wt. d^{-1}) and the nephelometric turbidity (NTU) for both animal types; these are listed in Table 6.27.

Comparison of the relationships for the calanoid copepods *Metadiaptomus* (Table 6.26) and *Boeckella* (Table 6.27) indicated that the rate of change in consumption for *Metadiaptomus* across 0-225 NTU was in between the rates of change for *Boeckella* for the 0-40 mg l^{-1} and 80-160 mg l^{-1} ranges. A similar comparison between *Ceriodaphnia* in this study and the cladocerans in Hart (1988) showed that the rate of change in consumption for *Ceriodaphnia* from 0-40 mg l^{-1} was larger than those for the *Daphnia* spp. but smaller than for *Moina brachiata*. For the 80-160 mg l^{-1} range, the *Ceriodaphnia* rate was smaller than all but *Daphnia longispina*. Comparison of the rates of change in consumption between the Mt Bold Reservoir animals indicated that, on a biomass basis, *Ceriodaphnia* was more influenced by increases at low clay concentration than *Boeckella*, but less influenced by increases at high clay concentration.

6.5.3.3.5 Turbidity tolerance

Using the same procedure as Hart (1988), a turbity tolerance was estimated for each of the

two animals in this study. A general respiration-biomass relationship was used to estimate the daily respiratory demands of the animals in terms of body dry weight. This relationship was determined by Hart (1988) from data of Lampert (1984) as follows:

Respiratory demand = 37.15 (Body dry wt)$^{-0.172}$

where respiratory demand is %body carbon respired d^{-1} and body dry wt is in μg. Note the negative exponent here which is missing in equation (2) of Hart (1988). This relationship assumed a constant respiration rate independent of the substrate. Body carbon was assumed to account for 50% of zooplankton dry weight (Waters 1977). Using the relationships between consumption and turbidity in Table 6.27, the critical turbidity levels (T_c) at which ingestion rate balanced respiratory costs were calculated and are listed in Table 6.27. This calculation assumed that respiration rate and assimilation efficiency were independent of turbidity, and that assimilation efficiency was 100%. While these assumptions regarding assimilation efficiency are not necessarily valid (McCabe and O'Brien 1983, Arruda *et al.* 1983) they were made to enable comparisons with the literature. Negative values of T_c imply that ingestion rates were too low to balance respiration requirements at the measured or projected control levels of zero turbidity. Although artificial, they still proportionally reflect the energetic burden on the animal in those conditions (Hart 1988). The T_c values for *Boeckella* and for *Ceriodaphnia* in this study were lower than the corresponding values for *Metadiaptomus* and for all cladocerans except *Daphnia longispina* (Table 6.26) in Hart (1988). This implied that these two Mt Bold Reservoir animals were not tolerant of high levels of turbidity compared with the Lake le Roux animals. If however, the Mt Bold animals were compared with each other, then the copepod had the higher T_c value and thus a higher turbidity tolerance than the cladoceran.

It is of note that the slopes of the consumption rate-turbidity responses for *Boeckella* and *Ceriodaphnia* agree with the turbidity tolerance T_c ranking for the 0-40 mg l^{-1} range but not for the 80-160 mg l^{-1} range. Hart (1988) found a reverse order between consumption rate slope and turbidity tolerance T_c (Table 6.26), and concluded that turbidity tolerance was due more to the magnitude of feeding rates at low turbidity levels rather than the slope of the feeding-turbidity response. Hart (1988) reported complete agreement between the calculated turbidity tolerance T_c and the observed tolerance based on field abundances.

During the 1981/1983 monitoring of Mt Bold Reservoir (Chapter 3) the suspended sediment concentration ranged from 2 to 20 NTU (E. & W.S. 1987). This was an unusually low range

and did not allow an assessment of the influence of suspended sediment on the abundance of specific zooplankton during this period. It was apparent however that the composition of the zooplankton community in Mt Bold Reservoir changed substantially during the monitoring period (Chapter 3) in the absence of large changes in suspended sediment concentration.

It should be noted that zooplankton may directly influence suspended sediment concentrations. Gliwicz (1986) documented periodic decreases in the concentration of suspended clay in Cahora Bassa, Mozambique, and demonstrated that they were due to zooplankton grazing. Sedimentation of the suspended clay was substantially increased through incorporation into zooplankton faeces.

It was clear from the experiments using complementary mixtures of clay and algae, with equivalent total particle volumes, that suspended particulates usually reduced filtering rates more than what was due to the increase in particle volume. The mechanism of this reduction was not determined, however some aspects were brought out. Despite their different grazing modes, both *Boeckella* and *Ceriodaphnia* had the same absolute reduction in filtering rate per unit increase in clay concentration across the low range. The different consequences of suspended particulates to these two animal types were a result of the relative reduction in filtering rate and the resulting relative reduction in consumption.

CHAPTER SEVEN: CONCLUSIONS

The two year monitoring study of Mt Bold Reservoir (Chapter 3) was done to provide background data from which specific questions would be investigated. This study demonstrated that the physical and chemical environment of Mt Bold Reservoir changed as a result of the different origins of the stored water. Water turnover times, temperatures, nutrients and salinity all fluctuated across the study and exceptional ranges of light attenuation were recorded. The physical and chemical environment appeared stable for some extended periods and yet during summer the mixed depth responded rapidly to reduced solar radiation resulting in an unstable environment.

It was shown that the plankton communities varied during the study and were also capable of rapid changes in abundance and composition. Multivariate analyses resulted in a consistent definition of the plankton communities across the study although this definition was still subjective. The plankton communities defined by multivariate analyses did not consistently agree with those defined using the summed difference index and this comparison did not suggest more appropriate critical values for the SD index for either phytoplankton or zooplankton. The changes in the phytoplankton communities could be allocated to the categories proposed by Reynolds (1980, 1984b) for phytoplankton periodicity. The phytoplankton communities did not follow a unidirectional sequence of successional changes but often reverted to previous communities and repeated cycles through several communities. Although the zooplankton communities had a higher similarity than the phytoplankton communities, there were fewer changes and less reversions during this study.

The frequency of sampling in this study during the growing season was higher than that often reported for similar studies in the literature. This was in response to a growing appreciation of the potentially dynamic character of the planktonic environment. Although a short sampling interval resulted in more reliable data on plankton changes, interpretation of these changes with respect to the changing environment was not necessarily enhanced. The problem of time lags here has already been discussed. It should be noted that the time scales of change are a continuum and natural sampling intervals to adequately describe several different events do not necessarily exist. Limited spatial sampling showed that the changes in plankton communities recorded were not fluctuations in local populations.

The enclosure experiments were done to examine the specific effect of zooplankton on Mt Bold Reservoir phytoplankton composition. A series of experiments was done in order to record the changing influence over a summer growing season. It was clearly demonstrated that phytoplankton community composition differed between the zooplankton grazed and ungrazed treatments. There were however no consistent criteria in terms of taxonomic identity or size which differentiated these communities. No clear selection pattern was evident across the summer period despite overlapping experiments, although the effect of grazing was always shown. This may of been partly due to the unusual environmental conditions present in Mt Bold Reservoir during these experiments. One problem of the enclosures was that the natural zooplankton community in the grazed enclosures was both heterogeneous and variable during the incubation. Each grazed enclosure had a unique grazing regime which meant that the final outcome was unpredictable. Establishment of the individual grazing responses of each zooplankton taxon on each phytoplankton taxon, while possible, were beyond the means of this study.

Mt Bold Reservoir zooplankton were dominated by calanoid copepods although cladocerans and rotifers were often present and occasionally dominant. *In situ* grazing experiments using natural food tracers showed that in Mt Bold Reservoir calanoid copepods had comparable grazing rates to cladocerans, both on an individual basis and on a biomass basis. Furthermore the calanoid copepods utilized a wider range of natural food sizes than the cladocerans. It was intended to combine the *in situ* grazing rates on natural food, measured for each of the dominant zooplankton taxa, with the densities of these zooplankton taxa measured in Mt Bold Reservoir, to estimate the potential grazing losses during the monitoring study. However the variability of the *in situ* grazing rates made it clear that any such estimate would be quite unreliable. It was apparent that zooplankton grazing rates should be measured at the same time as the plankton populations are monitored if valid estimates of the losses due to grazing are desired. The variable grazing rates were partly due to the range of food types available since grazing rates of specific zooplankton taxa on specific food tracers were consistent.

Suspended particulates reduced the grazing rates of both calanoid copepods and cladocerans although there was no change in food selectivity. These reductions were above that due to the increased particle concentration of the particulate suspensions. The absolute reduction in grazing rate per unit of particulate suspension was the same for both copepod and

cladoceran but the relative reduction for the cladoceran was greater than for the copepod. This implied that the relative reduction in food consumption was greater for the cladoceran which may contribute to the dominance of calanoid copepods in the turbid water of Mt Bold Reservoir.

BIBLIOGRAPHY

Alcaraz, M., Paffenhöfer, G.A. & Strickler, J.R. (1980) Catching the algae: a first account of visual observations on filter-feeding calanoids. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 241-248.

Allen, T.F.H. (1977) Scale in microscopic algal ecology: a neglected dimension. *Phycologia* 16, 253-257.

Allen, T.F.H., Bartell, S.M. & Koonce, J.F. (1977) Multiple stable configurations in ordination of phytoplankton community change rates. *Ecology* 58, 1076-1084.

Allen, T.F.H. & Koonce, J.F. (1973) Multivariate approaches to algal stratagems and tactics in systems analysis of phytoplankton. *Ecology* 54, 1234-1246.

Anderson, G.C., Comita, G.W. & Engstrom-Heg, V. (1955) A note on the phytoplankton - zooplankton relationship in two lakes in Washington. *Ecology* 36, 757-759.

Anderson, G.C. (1958) Seasonal characteristics of two saline lakes in Washington. *Limnol. Oceanogr.* 3, 51-68.

Andersson, G., Berggren, H., Cronberg, G. & Gelin, C. (1978) Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia* 59, 9-15.

Andrews, J.C. (1983) Deformation of the active space in the low Reynolds number feeding current of calanoid copepods. *Can. J. Fish. Aquat. Sci.* 40, 1293-1302.

Anraku, M. (1964) Some technical problems encountered in quantitative studies of grazing and predation of marine planktonic copepods. *J. Oceanogr. Soc. Jap.* 20, 19-29.

Arnold, D.E. (1971) Ingestion, assimilation, survival and reproduction by *Daphnia pulex* fed seven species of blue-green algae. *Limnol. Oceanogr.* 16, 906-920.

Arruda, J.A., Marzolf, G.R. & Faulk, R.T. (1983) The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. *Ecology* 64, 1225-1235.

Avnimelech, Y., Troeger, B.W. & Reed, L.W. (1982) Mutual flocculation of algae and clay: evidence and implications. *Science* 216, 63-65.

Baars, M.A. & Helling, G.R. (1985) Methodical problems in the measurement of phytoplankton ingestion rate by gut fluorescence. *Hydrobiol. Bull.* 19, 81-88.

Baars, M.A. & Oosterhuis, S.S. (1984) Diurnal feeding rhythms in North Sea copepods measured by gut fluorescence, digestive enzyme activity and grazing on labelled food. *Netherlands Journal of Sea Research* 18, 97-119.

Bailey-Watts, A. (1982) The composition and abundance of phytoplankton in Loch Leven (Scotland) 1977-1979 and a comparison with the succession in earlier years. *Intern. Rev. Gesam. Hydrobiol.* 67, 1-25.

Bainbridge, R. (1953) Studies on the interrelationships of zooplankton and phytoplankton. *J. Mar. Biol. Assoc. U.K.* 32, 385-447.

Banse, K. (1982) Experimental marine ecosystem enclosures in a historical perspective. In Grice, G.D. & Reeve, M.R. (eds.) "Marine Mesocosms. Biological and Chemical Research in Experimental Ecosystems". Springer-Verlag, Berlin. pp. 11-24.

Bartell, S.M., Allen, T.F.H. & Koonce, J.F. (1978) An assessment of principal component analysis for description of phytoplankton periodicity in Lake Wingra. *Phycologia* 17, 1-11.

Bartram, W.C. (1980) Experimental development of a model for the feeding of neritic copepods on phytoplankton. *J. Plankton Res.* 3, 25-51.

Bartsch, H.J. (1974) "Handbook of Mathematical Formulas". Academic Press, New York. 525pp.

Bayly, I.A.E. (1961) A revision of the inland water genus *Calamoecia* (Copepoda: Calanoida). *Aust. J. Mar. Freshwater Res.* 12, 54-91.

Bayly, I.A.E. (1964) A revision of the Australian species of the freshwater genera *Boeckella* and *Hemiboeckella*. *Aust. J. Mar. Freshwater Res.* 15, 180-233.

Bayly, I.A.E. (1986) Aspects of diel vertical migration in zooplankton, and its enigma variations. In DeDeckker, P. & Williams, W.D. (eds.) "Limnology in Australia". C.S.I.R.O., Australia and Junk, Dordrecht. pp. 349-368.

Bayly, I.A.E., Bishop, J.A. & Hiscock, I.D. (eds.) (1967) "An Illustrated Key to the Genera of the Crustacea of Australian Inland Waters". Australian Society for Limnology. 37pp.

Bayly, I.A.E. & Williams, W.D. (1973) "Inland Waters and Their Ecology". Longman, Melbourne. 316pp.

Belbin, L., Faith, D.P. & Minchin, P.R. (1984) "Some algorithms contained in the Numerical Taxonomy Package NTP". C.S.I.R.O. Technical Memorandum 84/23. C.S.I.R.O. Institute of Biological Resources, Division of Water and Land Resources, Canberra.

Benndorf, J., Kneschke, H., Kossatz, K. & Penz, E. (1984) Manipulation of the pelagic food web by stocking with predacious fishes. *Int. Rev. Gesamten. Hydrobiol.* 69, 407-428.

Berman, M.S. & Richman, S. (1974) The feeding behaviour of *Daphnia pulex* from Lake Winnebago, Wisconsin. *Limnol. Oceanogr.* 19, 105-109.

Bleiwas, A.H. & Stokes, P.M. (1985) Collection of large and small food particles by *Bosmina*. *Limnol. Oceanogr.* 30, 1090-1092.

Bogdan, K.G. & Gilbert, J.J. (1982) Seasonal patterns of feeding by natural populations of *Keratella, Polyarthra*, and *Bosmina*: clearance rates, selectivities, and contributions to community grazing. *Limnol. Oceanogr.* 27, 918-934.

Bogdan, K.G. & Gilbert, J.J. (1984) Body size and food size in freshwater zooplankton. *Proc. Natl. Acad. Sci. U.S.A.* 81, 6427-6431.

Bogdan, K.G. & McNaught, D.C. (1975) Selective feeding by *Diaptomus* and *Daphnia*. *Verh. Int. Verein. Limnol.* 19, 2935-2942.

Borsheim, K.Y. & Andersen, S. (1987) Grazing and food size selection by crustacean zooplankton compared to production of bacteria and phytoplankton in a shallow Norwegian mountain lake. *J. Plankton Res.* 9, 367-379.

Borsheim, K.Y. & Olsen, Y. (1984) Grazing activities by *Daphnia pulex* on natural populations of bacteria and algae. *Verh. Int. Verein. Limnol.* 22, 644-648.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. & Weglenska, T. (1976) A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24, 419-456.

Bowers, J.A. (1980) Feeding habit of *Diaptomus ashlandi* and *Diaptomus sicilis* in Lake Michigan. *Int. Rev. Gesamten. Hydrobiol.* 65, 259-267.

Boyd, C.M. (1976) Selection of particle sizes by filter-feeding copepods: a plea for reason. *Limnol. Oceanogr.* 21, 175-180.

Boyd, C.M. (1981) Microcosms and experimental planktonic food chains. In Longhurst, A.R. (ed.) "Analysis of Marine Ecosystems". Academic Press, London. pp. 627-649.

Brabrand, A., Faafeng, B.A., Kallqvist, T. & Nilssen, J.P. (1983) Biological control of undesirable cyanobacteria in culturally eutrophic lakes. *Oecologia (Berlin)* 60, 1-5.

Brendelberger, H. & Geller, W. (1985) Variability of filter structures in eight *Daphnia* species: mesh sizes and filtering areas. *J. Plankton Res.* 7, 473-486.

Brendelberger, H., Herbeck, M., Lang, H. & Lampert, W. (1986) *Daphnia*'s filters are not solid walls. *Arch. Hydrobiol.* 107, 197-202.

Brockmann, U.H., Dahl, E., Kuiper, J. & Kattner, G. (1983) The concept of POSER (Plankton Observation with Simultaneous Enclosures in Rosfjorden). *Mar. Ecol.*

Prog. Ser. 14, 1-8.

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

Buckney, R.T. (1980) Chemistry of Australian waters: the basic pattern, with with comments on some ecological implications. In Williams, W.D. (ed.) "An Ecological Basis for Water Resource Management". A.N.U. Press, Canberra. pp. 12-22.

Buikema, A.L. Jr. (1973) Filtering rate of the cladoceran *Daphnia pulex* as function of body size, light, and light acclimation. *Hydrobiologia* 41, 515-527.

Burns, C.W. (1968a) The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.* 13, 675-678.

Burns, C.W. (1968b) Direct observations of mechanisms regulating feeding behaviour of *Daphnia,* in lakewater. *Int. Rev. Gesamten. Hydrobiol.* 53, 83-100.

Burns, C.W. (1969a) Particle size and sedimentation in the feeding behaviour of two species of *Daphnia. Limnol. Oceanogr.* 14, 392-402.

Burns, C.W. (1969b) Relation between filtering rate, temperature and body size in four species of *Daphnia. Limnol. Oceanogr.* 14, 693-700.

Burns, C.W. & Rigler, F.H. (1967) Comparison of filtering rates of *Daphnia rosea* in lake water and in suspensions of yeast. *Limnol. Oceanogr.* 12, 492-502.

Cannon, H.G. (1933) On the feeding mechanism of the Brachiopoda. *Phil. Trans. R. Soc. Ser. B.* 222, 267-352.

Canter, H.M. & Lund, J.W.G. (1948) Studies on plankton parasites. I. Fluctuations in numbers of *Asterionella formosa* Hass. in relation to fungal epidemics. *New Phytol.* 47, 238-261.

Canter, H.M. & Lund, J.W.G. (1953) Studies on plankton parasites. II. The parasitism of diatoms with special reference to lakes in the English Lake District. *Trans. Br. Mycol. Soc.* 36, 13-37.

Canter, H.M. & Lund, J.W.G. (1968) The importance of Protozoa in controlling the abundance of planktonic algae in lakes. *Proc. Linn. Soc. Lond.* 179, 203-219.

Carvalho, M.L. (1984) Influence of predation by fish and water turbidity on a *Daphnia gessneri* population in an Amazonian floodplain lake, Brazil. *Hydrobiologia* 113, 243-247.

Chow-Fraser, P. (1986a) An empirical model to predict *in situ* grazing rates of *Diaptomus minutus* Lilljeborg on small algal particles. *Can. J. Fish. Aquat. Sci.* 43, 1065-1070.

Chow-Fraser, P. (1986b) Effect of collection and acclimation period on grazing rates of limnetic zooplankton. *Hydrobiologia* 137, 203-210.

Chow-Fraser, P. & Knoechel, R. (1985) Factors regulating *in situ* filtering rates of Cladocera. *Can. J. Fish. Aquat. Sci.* 42, 567-576.

Chow-Fraser, P. & Sprules, W.G. (1986) Inhibitory effect of *Anabaena* sp. on *in situ* filtering rate of *Daphnia. Can. J. Zool.* 64, 1831-1834.

Chow-Fraser, P. & Wong, C.K. (1985) Herbivorous feeding of three large freshwater calanoid copepods, *Limnocalanus macrurus* Sars, *Senecella calanoides* Juday, and *Epischura lacustris* Forbes. *Verh. Int. Verein. Limnol.* 22, 3195-3198.

Christoffersen, K. & Jespersen, A-M. (1986) Gut evacuation rates and ingestion rates of *Eudiaptomus graciloides* measured by means of the gut fluorescence method. *J. Plankton Res.* 8, 973-983.

Clutter, R.I. & Anraku, M. (1968) Avoidance of samplers. In Tranter, D.J. & Fraser, J.H. (eds.) "Zooplankton Sampling. Monographs on Oceanographic Methodology 2". U.N.E.S.C.O. Press, Paris. pp. 57-76.

Comita, G.W. (1964) The energy budget of *Diaptomus siciloides,* Lilljeborg. *Verh. Int. Verein. Limnol.* 15, 646-653.

Confer, J.L., Howwick, G.L., Corzette, M.H., Kramer, S.L., Fitzgibbon, S. & Landesburg, R. (1978) Visual predation by planktivores. *Oikos* 31, 27-37.

Conover, R.J. (1966) Feeding on large particles by *Calanus hyperboreus* (Kröyer). In Barnes, H. (ed.) "Some Contemporary Studies in Marine Science". George Allen and Unwin, London. pp. 187-194.

Conover, R.J. (1968) Zooplankton - life in a nutritionally dilute environment. *Am. Zool.* 8, 107-118.

Conover, R.J., Durvasula, R., Roy, S. & Wang, R. (1986) Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton, and some of the consequences. *Limnol. Oceanogr.* 31, 878-887.

Coveney, M.F., Cronberg, G., Enell, M., Larsson, K. & Olofsson, L. (1977) Phytoplankton, zooplankton and bacteria - standing crop and production relations in a eutrophic lake. *Oikos* 29, 5-21.

Croome, R.L. (1980) Lake Hume. In Williams, W.D. (ed.) "An Ecological Basis for Water Resource Management". A.N.U. Press, Canberra. pp. 305-310.

Crowley, P.H. (1973) Filtering rate inhibition of *Daphnia pulex* in Wintergreen Lake water. *Limnol. Oceanogr.* 18, 394-402.

Crumpton, W.G. & Wetzel, R.G. (1982) Effects of differential growth and mortality in the seasonal succession of phytoplankton populations in Lawrence Lake, Michigan. *Ecology* 63, 1729-1739.

Cuker, B.E. (1987) Field experiment on the influences of suspended clay and P on the plankton of a small lake. *Limnol. Oceanogr.* 32, 840-847.

Currie, R.I. (1962) Pigments in zooplankton faeces. *Nature* 193, 956-957.

Cushing, D.H. (1976) Grazing in Lake Erken. *Limnol. Oceanogr.* 21, 349-356.

Dagg, M.J. (1983) A method for the determination of copepod feeding rates during short time intervals. *Mar. Biol.* 75, 63-67.

Daley, R.J. (1973) Experimental characterization of lacustrine chlorophyll diagenesis. II. Bacterial, viral and herbivore grazing effects. *Arch. Hydrobiol.* 72, 409-439.

Dam, H.G. & Peterson, W.T. (1988) The effect of temperature on the gut clearance rate constant of planktonic copepods. *J. Exp. Marine Biol. Ecol.* 123, 1-14.

Daro, M.H. (1978) A simplified ^{14}C method for grazing measurements on natural planktonic populations. *Helgolander wiss Meeresunters* 31, 241-248.

Davies, B.R. & Walmsley, R.D. (eds.) (1985) Perspectives in Southern Hemisphere limnology. *Developments in Hydrobiology* 28, 1-263.

Deason, E.E. (1980) Potential effect of phytoplankton colony breakage on the calculation of zooplankton filtration rates. *Mar. Biol.* 57, 279-286.

De Bernardi, R. (1984) Methods for the estimation of zooplankton abundance. In Downing, J.A. & Rigler, F.H. (eds.) "A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters". Blackwell, Oxford. pp. 59-86.

De Bernardi, R., Guissani, G. & Pedretti, E.L. (1981) The significance of blue-green algae as food for filter-feeding zooplankton: experimental studies on *Daphnia* spp. fed by *Microcystis aeruginosa. Verh. Int. Verein. Limnol.* 21, 477-483.

Decosta, J., Janicki, A., Shellito, G. & Wilcox, G. (1983) The effect of phosphorus additions in enclosures on the phytoplankton and zooplankton of an acid lake. *Oikos* 40, 283-294.

De Mott, W.R. (1982) Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina. Limnol. Oceanogr.* 27, 518-527.

De Mott, W.R. (1983) Seasonal succession in a natural *Daphnia* assemblage. *Ecol. Monogr.* 53, 321-340.

De Mott, W.R. & Kerfoot, W.C. (1982) Competition amongst cladocerans: nature of the interaction between *Bosmina* and *Daphnia. Ecology* 63, 1949-1966.

Dickman, M. (1969) Some effects of lake renewal on phytoplankton productivity and species composition. *Limnol. Oceanogr.* 14, 660-666.

Dillon, P.J. & Rigler, F.H. (1974) The phosphorus-chlorophyll relationship in lakes. *Limnol. Oceanogr.* 19, 767-773.

Dirnberger, J.M. & Threlkeld, S.T. (1986) Advective control of reservoir zooplankton abundance and dispersion. *Freshwater Biol.* 16, 387-396.

Donaghay, P.L. & Small, L.F. (1979) Food selection capabilities of the estuarine copepod *Acartia tonsa. Mar. Biol.* 52, 137-156.

Dorazio, R.M., Bowers, J.A. & Lehman, J.T. (1987) Food-web manipulations influence grazer control of phytoplankton growth rates in Lake Michigan. *J. Plankton Res.* 9, 891-899.

Downing, J.A., Perusse, M. & Frenette, Y. (1987) Effect of interreplicate variance on zooplankton sampling design and data analysis. *Limnol. Oceanogr.* 32, 673-680.

Downs, J.N. & Lorenzen, C.J. (1985) Carbon : pheopigment ratios of zooplankton fecal pellets as an index of herbivorous feeding. *Limnol. Oceanogr.* 30, 1024-1036.

Duncan, A. (1975) Production and biomass of three species of *Daphnia* coexisting in London reservoirs. *Verh. Int. Verein. Limnol.* 19, 2858-2867.

Elliott, E.T., Castañares, L.G., Perlmutter, D. & Porter, K.G. (1983) Trophic-level control of production and nutrient dynamics in an experimental planktonic community *Oikos* 41, 7-16.

Elliott, J.M. (1971) "Some methods for the statistical analysis of samples of benthic invertebrates". Freshwater Biological Association Scientific Publication No. 25. 144pp.

Ellis, M.M. (1936) Erosion silt as a factor in aquatic environments. *Ecology* 17, 29-42.

Ellis, M. (1984) "The influence of phytoplankton food quality and abundance on feeding behaviour and survival of zooplankton". B.Sc. Honours Thesis, University of Adelaide, Australia.

Elmore, J.L. (1982) The influence of food concentration and container volume on life history parameters of *Diaptomus dorsalis* Marsh from subtropical Florida. *Hydrobiologia* 89, 215-223.

Enright, J.T. (1969) Zooplankton grazing rates estimated under field conditions. *Ecology* 50, 1070-1075.

Evans, M.S. & Sell, D.W. (1983) Zooplankton sampling strategies for environmental studies. *Hydrobiologia* 99, 215-223.

E. & W.S. (1987) "A compilation of water quality data for reservoirs in the Mt Lofty Ranges 1940-1986". Report 87/10, Engineering and Water Supply Department, South Australia.

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

Fleminger, A. & Clutter, R.I. (1965) Avoidance of towed nets by zooplankton. *Limnol. Oceanogr.* 10, 96-104.

Fogg, G.E. (1975) "Algal Cultures and Phytoplankton Ecology". (2nd Edn). The University of Wisconsin Press, Wisconsin. 175pp.

Fogg, G.E. (1977) Excretion of organic matter by phytoplankton. *Limnol. Oceanogr.* 22, 576-577.

Fogg, G.E., Stewart, W.D.P., Fay, P. & Walsby, A.E. (1973) "The Blue-Green Algae". Academic Press, London. 459pp.

Forsberg, C., Ryding, S.O., Claesson, A. & Forsberg, A. (1978) Water chemical analyses and/or algal assay? Sewage effluent and polluted lake water studies. *Mitt. Internat. Verein. Limnol.* 21, 352-363.

Forsyth, D.J. & James, M.R. (1984) Zooplankton grazing on lake bacterioplankton and phytoplankton. *J. Plankton Res.* 6, 803-810.

Fott, J. (1975) Seasonal succession of phytoplankton in the fish pond Smyslov near Blatna, Czechoslovakia. *Arch. Hydrobiol. Suppl.* 46, 259-279.

Friedman, M.M. (1980) Comparative morphology and functional significance of copepod receptors and oral structures. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 185-197.

Friedman, M.M. & Strickler, J.R. (1975) Chemoreceptors and feeding in calanoid copepods (Arthropoda: Crustacea). *Proc. Natl. Acad. Sci. USA* 72, 4185-4188.

Frost, B.W. (1972) Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr.* 17, 805-815.

Frost, B.W. (1975) The threshold feeding behaviour in *Calanus pacificus*. *Limnol. Oceanogr.* 20, 263-266.

Frost, B.W. (1977) Feeding behaviour of *Calanus pacificus* in mixtures of food particles. *Limnol. Oceanogr.* 22, 472-491.

Frost, B.W. (1980) Grazing. In Morris, I. (ed.) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. pp. 465-491.

Fryer, G.S. (1957a) The feeding mechanism of some freshwater cyclopoid copepods. *Proc. Zool. Soc. Lond.* 129, 1-25.

Fryer, G.S. (1957b) The food of some freshwater cyclopoid copepods and its ecological significance. *J. Anim. Ecol.* 26, 263-286.

Fryer, G. (1987) The feeding mechanisms of the Daphniidae (Crustacea: Cladocera): recent suggestions and neglected considerations. *J. Plankton Res.* 9, 419-432.

Fuller, J.L. & Clarke, G.L. (1936) Further experiments on the feeding of *Calanus finmarchicus*. *Biol. Bull. Woods Hole* 70, 308-320.

Fulton, R.S. III (1988) Grazing on filamentous algae by herbivorous zooplankton. *Freshwater Biol.* 20, 263-271.

Furnet, J.E. & Benson-Evans, K. (1982) An evaluation of the time required to obtain complete sedimentation of fixed algal particles prior to enumeration. *Br. Phycol. J.* 17, 253-258.

Gaddy, A.J. & Parker, R.A. (1986) Zooplankton grazing activity and assimilation in the presence of Mount St. Helen's ash. *Northwest Sci.* 60, 47-51.

Ganf, G.G. (1980) "Factors controlling the growth of phytoplankton in Mount Bold Reservoir, South Australia". Australian Water Resources Council Technical Paper No. 48. Australian Government Publishing Service, Canberra. 109pp.

Ganf, G.G. (1982) Influence of added nutrient on the seasonal variation of algal growth potential of Mt. Bold Reservoir, South Australia. *Aust. J. Mar. Freshwater Res.* 33, 475-490.

Ganf, G.G. (1983) An ecological relationship between *Aphanizomenon* and *Daphnia pulex*. *Aust. J. Mar. Freshwater Res.* 34, 755-773.

Ganf, G.G. & Blazka, P. (1974) Oxygen uptake, ammonia and phosphate excretion by zooplankton of a shallow equatorial lake (Lake George, Uganda). *Limnol. Oceanogr.* 19, 313-325.

Ganf, G.G. & Oliver, R.L. (1982) Vertical separation of light and available nutrients as a factor causing replacement of green algae by blue-green algae in the plankton of a stratified lake. *J. Ecol.* 70, 829-844.

Ganf, G.G., Oliver, R.L. & Walsby, A.E. (1989) Optical properties of gas-vacuolate cells and colonies of *Microcystis* in relation to light attenuation in a turbid, stratified reservoir

(Mt Bold Reservoir, South Australia). *Aust. J. Mar. Freshwater Res.* 40, 595-611.

Ganf, G.G. & Shiel, R.J. (1985a) Feeding behaviour and limb morphology of two cladocerans with small intersetular distances. *Aust. J. Mar. Freshwater Res.* 36, 69-86.

Ganf, G.G. & Shiel, R.J. (1985b) Particle capture by *Daphnia carinata*. *Aust. J. Mar. Freshwater Res.* 36, 371-381.

Ganf, G.G., Shiel, R.J. & Merrick, C.J. (1983) Parasitism: the possible cause of the collapse of a *Volvox* population in Mount Bold Reservoir, South Australia. *Aust. J. Mar. Freshwater Res.* 34, 489-494.

Gardner, M.B. (1981) Mechanisms of size selectivity by planktivorous fish: a test of a hypothesis. *Ecology* 62, 571-578.

Gauch, H.G. Jr. (1984) "Multivariate Analysis in Community Ecology". Cambridge University Press, Cambridge. 298pp.

Gauld, D.T. (1951) The grazing rate of planktonic copepods. *J. Mar. Biol. Ass. U.K.* 29, 695-706.

Geddes, M.C. (1984a) Limnology of Lake Alexandrina, River Murray, South Australia, and the effects of nutrients and light on the phytoplankton. *Aust. J. Mar. Freshwater Res.* 35, 399-415.

Geddes, M.C. (1984b) Seasonal studies on the zooplankton community of Lake Alexandrina, River Murray, South Australia, and the role of turbidity in determining zooplankton community structure. *Aust. J. Mar. Freshwater Res.* 35, 417-426.

Geddes, M.C. (1988) The role of turbidity in the limnology of Lake Alexandrina, River Murray, South Australia; comparisons between clear and turbid phases. *Aust. J. Mar. Freshwater Res.* 39, 201-209.

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

George, D.G. (1981) Zooplankton patchiness. *Rep. Freshwater Biol. Ass.* 49, 32-44.

George, D.G. & Edwards, R.W. (1976) The effect of wind on the distribution of chlorophyll *a* and crustacean plankton in a shallow eutrophic reservoir. *J. App. Ecol.* 13, 667-690.

George, D.G. & Heaney, S.I. (1978) Factors influencing the spatial distribution of phytoplankton in a small productive lake. *J. Ecol.* 66, 133-155.

Gerritsen, J. & Porter, K.G. (1982) The role of surface chemistry in filter feeding by zooplankton. *Science* 216, 1225-1227.

Gerritsen, J., Porter, K.G. & Strickler, J.R. (1988) Not by sieving alone: observations of suspension feeding in *Daphnia*. *Bull. Mar. Sci.* 43, 366-376.

Gibson, C.E. (1984) Sinking rates of planktonic diatoms in an unstratified lake: a comparison of field and laboratory observations. *Freshwater Biol.* 14, 631-638.

Gliwicz, Z.M. (1968) The use of anaesthetizing substrates in studies on the food habits of zooplankton communities. *Ekol Pol. A* 16, 279-295.

Gliwicz, Z.M. (1969) Studies on the feeding of pelagic zooplankton in lakes with varying trophy. *Ekol. Pol. A* 17, 663-708.

Gliwicz, Z.M. (1970) Calculation of food ration of zooplankton community as an example of using laboratory data for field conditions. *Pol. Arch. Hydrobiol.* 17, 169-175.

Gliwicz, Z.M. (1975) Effect of zooplankton grazing on photosynthetic activity and compsition of phytoplankton. *Verh. Int. Verein. Limnol.* 19, 1490-1497.

Gliwicz, Z.M. (1977) Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake. *Ekol. Pol.* 25, 179-225.

Gliwicz, Z.M. (1980) Filtering rates, food size selection, and feeding rates in cladocerans. Another aspect of interspecific competition in filter-feeding zooplankton. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 282-291.

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Gliwicz, M.Z. (1986) Suspended clay concentration controlled by filter-feeding zooplankton in a tropical reservoir. *Nature* 323, 330-332.

Gliwicz, Z.M. & Siedlar, E. (1980) Food size limitation and algae interfering with food collection in *Daphnia*. *Arch. Hydrobiol.* 88, 155-177.

Goad, J.A. (1984) A biomanipulation experiment in Green Lake, Seattle, Washington. *Arch. Hydrobiol.* 102, 137-153.

Golterman, H.L., Clymo, R.S. & Ohnstad, M.A.M. (1978) "Methods for Physical and Chemical Analysis of Fresh Waters". Blackwell, Oxford. 213pp.

Gophen, M. (1977) Feeding of *Daphnia* on *Chlamydomonas* and *Chlorobium*. *Nature* 265, 271-273.

Gophen, M., Cavari, B.Z. & Berman, T. (1974) Zooplankton feeding on differentially labelled algae and bacteria. *Nature* 247, 393-394.

Gophen, M. & Geller, W. (1984) Filter mesh size and food particle uptake by *Daphnia*. *Oecologia (Berlin)* 64, 408-412.

Gorham, P.R., McLachlan, J., Hammer, U.T. & Kim, W.K. (1964) Isolation and culture of toxic strains of *Anabaena flos-aquae* Lyngb. de Breb. *Verh. Int. Verein. Limnol.* 15, 796-804.

Grant, I.F., Egan, E.A. & Alexander, M. (1983) Measurement of rates of grazing of the ostracod *Cyprinotus carolinensis* on blue-green algae. *Hydrobiologia* 106, 199-208.

Green, J.D., Viner, A.B. & Lowe, D.J. (1987) The effect of climate on lake mixing patterns and temperatures. In Viner, A.B. (ed.) "Inland Waters of New Zealand". D.S.I.R. Bulletin 241, Wellington. pp. 65-95.

Greig-Smith, P. (1983) "Quantitative Plant Ecology". Blackwell, Oxford. 359pp.

Grice, G.D. & Reeve, M.R. (eds.) (1982) "Marine Mecocosms. Biological and Chemical Research in Experimental Ecosystems". Springer-Verlag, Berlin. 430pp.

Grobbelaar, J.U. (1985) Phytoplankton productivity in turbid waters. *J. Plankton Res.* 7, 653-663.

G-Tóth, L. (1984) Feeding behaviour of *Daphnia cucullata* Sars in the easily stirred up Lake Balaton as established on the basis of gut content analysis. *Arch. Hydrobiol.* 101, 531-553.

G-Tóth, L., V-Balogh, K. & Zankai, N.P. (1986) Significance and degree of abioseston consumption in the filter-feeder *Daphnia galeata* Sars am. Richard (Cladocera) in Lake Balaton. *Arch. Hydrobiol.* 106, 45-60.

Guillard, R.R. & Lorenzen, C.J. (1972) Yellow-green algae with chlorophyllide *c*. *J. Phycol.* 8, 10-14.

Gulati, R.D. (1975) A study on the role of herbivorous zooplankton community as primary consumers of phytoplankton in Dutch lakes. *Verh. Int. Verein. Limnol.* 19, 1202-1210.

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

Hadas, O., Cavari, B.Z., Kott, Y. & Bachrach, U. (1982) Preferential feeding behaviour of *Daphnia magna*. *Hydrobiologia* 89, 49-52.

Haffner, G.D., Harris, G.P. & Jarai, M.K. (1980) Physical variability and phytoplankton communities. III. Vertical structure in phytoplankton populations. *Arch. Hydrobiol.* 89, 363-381.

Hall, D.J., Threlkeld, S.T., Burns, C.W. & Crowley, P.H. (1976) The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. Syst.* 7, 177-208.

Hanazato, T. & Yasuno, M. (1987) Evaluation of *Microcystis* as food for zooplankton in a eutrophic lake. *Hydrobiologia* 144, 251-259.

Haney, J.F. (1971) An *in situ* method for the measurement of zooplankton grazing rates. *Limnol. Oceanogr.* 16, 970-977.

Haney, J.F. (1973) An *in situ* examination of the grazing activities of natural zooplankton communities. *Arch. Hydrobiol.* 72, 87-132.

Haney, J.F. (1985) Regulation of cladoceran filtering rates in nature by body size, food concentration, and diel feeding patterns. *Limnol. Oceanogr.* 30, 397-411.

Haney, J.F. (1987) Field studies on zooplankton-cyanobacteria interactions. *N.Z. J. Mar. Freshwater Res.* 21, 467-475.

Haney, J.F. & Hall, D.J. (1975) Diel vertical migration and filter-feeding activities of *Daphnia. Arch. Hydrobiol.* 75, 413-441.

Harbison, G.R. & McAlister, V.L. (1980) Fact and artifact in copepod feeding experiments. *Limnol. Oceanogr.* 25, 971-981.

Hardy, A.C. (1935) Phytoplankton ecology and the hypothesis of animal exclusion. *Proc. Linn. Soc. Lond.* 148, 64-70.

Hargis, J.R. (1977) Comparison of techniques for the measurement of zooplankton filtration rates. *Limnol. Oceanogr.* 22, 942-945.

Hargrave, B.T. & Geen, G.H. (1970) Effects of copepod grazing on two natural phytoplankton populations. *J. Fish. Res. Bd. Can.* 27, 1395-1403.

Harris, G.P. (1978) Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 10, 1-163.

Harris, G.P. (1980a) The measurement of photosynthesis in natural populations of phytoplankton. In Morris, I. (ed.) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. 625pp.

Harris, G.P. (1980b) Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. *Can. J. Fish. Aquat. Sci.* 37, 877-900.

Harris, G.P. (1983) Mixed layer physics and phytoplankton populations: studies in equilibrium and non-equilibrium ecology. In Round, F.E. & Chapman, D.J. (eds.) "Progress in Phycological Research. Volume 2". Elsevier Biomedical Press. pp. 1-52.

Harris, G.P. (1986) "Phytoplankton Ecology: Structure, Function and Fluctuation". Chapman & Hall, London. 384pp.

Harris, G.P. (1987) Time series analysis of water quality data from Lake Ontario: implications for the measurement of water quality in large and small lakes. *Freshwater Biol.* 18, 389-403.

Harris, G.P., Haffner, G.D. & Piccinin, B.B. (1980b) Physical variability and phytoplankton communities. II. Primary productivity by phytoplankton in a physically variable environment. *Arch. Hydrobiol.* 88, 393-425.

Harris, G.P. & Piccinin, B.B. (1980) Physical variability and phytoplankton communities. IV. Temporal changes in the phytoplankton community of a physically variable lake. *Arch. Hydrobiol.* 89, 447-473.

Harris, G.P., Piccinin, B.B., Haffner, G.D., Snodgrass, W. & Polak, J. (1980a) Physical variability and phytoplankton communities. I. The descriptive limnology of Hamilton Harbour. *Arch. Hydrobiol.* 88, 303-327.

Harris, G.P., Piccinin, B.B. & Van Ryn, J. (1983) Physical variability and phytoplankton communities. V. Cell size, niche diversification and the role of competition. *Arch. Hydrobiol.* 98, 215-239.

Harris, G.P. & Trimbee, A.M. (1986) Phytoplankton population dynamics of a small reservoir: physical/biological coupling and the time scales of community change. *J. Plankton Res.* 8, 1011-1025.

Hart, B.T. (1982) Uptake of trace metals by sediments and suspended particulates: a review. *Hydrobiologia* 91, 299-313.

Hart, R.C. (1985) Seasonality of aquatic invertebrates in low-latitude and Southern Hemisphere inland waters. *Hydrobiologia* 125, 151-178.

Hart, R.C. (1986a) Aspects of the feeding ecology of turbid water zooplankton. *In situ* studies of community filtration rates in silt-laden Lake le Roux, Orange River, South Africa. *J. Plankton Res.* 8, 401-426.

Hart, R.C. (1986b) Zooplankton abundance, community structure and dynamics in relation to inorganic turbidity, and their implications for a potential fishery in subtropical Lake le Roux, South Africa. *Freshwater Biol.* 16, 351-371.

Hart, R.C. (1987) Observations on calanoid diet, seston, phytoplankton - zooplankton relationships, and inferences on calanoid food limitation in a silt-laden reservoir. *Arch. Hydrobiol.* 111, 67-82.

Hart, R.C. (1988) Zooplankton feeding rates in relation to suspended sediment content: potential influences on community structure in a turbid reservoir. *Freshwater Biol.* 19, 123-139.

Hart, R.C. & Christmas, G.L. (1984) A twin Gliwicz-Haney *in situ* zooplankton grazing chamber: design, operation and potential applications. *J. Plankton Res.* 6, 715-719.

Hartmann, H.J. (1985) Feeding of *Daphnia pulicaria* and *Diaptomus ashlandi* on mixtures of unicellular and filamentous algae. *Verh. Int. Verein. Limnol.* 22, 3178-3183.

Harvey, H.W., Cooper, L.H.N., Lebour, M.V. & Russell, F.S. (1935) Planktonic production and its control. *J. Mar. Biol. Ass. U.K.* 20, 407-441.

Havens, K. & DeCosta, J. (1985) An analysis of selective herbivory in an acid lake and its importance in controlling phytoplankton community structure. *J. Plankton Res.* 7, 207-222.

Hayward, R.S. & Gallup, D.N. (1976) Feeding, filtering and assimilation in *Daphnia schoedleri* Sars as affected by environmental conditions. *Arch. Hydrobiol.* 77, 139-163.

Head, E.J.H. (1988) Copepod feeding behaviour and the measurement of grazing rates *in vivo* and *in vitro*. *Hydrobiologia* 167/168, 31-41.

Heaney, S.I. (1976) Temporal and spatial distribution of the dinoflagellate *Ceratium hirudinella* O.F. Muller within a small productive lake. *Freshwater Biol.* 6, 531-542.

Heaney, S.I., Smyly, W.J.P. & Talling, J.F. (1986) Interactions of physical, chemical and biological processes in depth and time within a productive English lake during summer stratification. *Int. Rev. Gesamten. Hydrobiol.* 71, 441-494.

Heaney, S.I. & Talling, J.F. (1980) Dynamic aspects of dinoflagellate distribution patterns in a small productive lake. *J. Ecol.* 68, 75-94.

Helgen, J.C. (1987) Feeding rate inhibition in crowded *Daphnia pulex*. *Hydrobiologia* 154, 113-119.

Helling, G.R. & Baars, M.A. (1985) Changes in the concentrations of chlorophyll and phaeopigment in grazing experiments. *Hydrobiol. Bull.* 19, 41-48.

Hessen, D.O. (1985) Filtering structures and particle size selection in coexisting Cladocera. *Oecologia (Berlin)* 66, 368-372.

Hessen, D.O. & Nilssen, J.P. (1986) From phytoplankton to detritus and bacteria: effects of short-term nutrient and fish perturbations in a eutrophic lake. *Arch. Hydrobiol.* 105, 273-284.

Hillman, T.J. (1980) Lake Burley Griffin. In Williams, W.D. (ed.) "An Ecological Basis for Water Resource Management". A.N.U. Press, Canberra. pp. 317-323.

Hitchcock, G.L. & Smayda, T.J. (1977) The importance of light in the irradiation of the 1972-1973 winter-spring diatom bloom in Narragansett Bay. *Limnol. Oceanogr.* 22, 126-131.

Holm, N.P., Ganf, G.G. & Shapiro, J. (1983) Feeding and assimilation rates of *Daphnia pulex* fed *Aphanizomenon flos-aquae*. *Limnol. Oceanogr.* 28, 677-687.

Holtby, L.B. & Knoechel, R. (1981) Zooplankton filtering rates: error due to loss of radioisotopic label in chemically preserved samples. *Limnol. Oceanogr.* 26, 774-780.

Horn, W. (1981) Phytoplankton losses due to zooplankton grazing in a drinking water reservoir. *Int. Rev. Gesamten. Hydrobiol.* 66, 787-810.

Horn, W. (1985a) Investigations into the food selectivity of the planktonic crustaceans *Daphnia hyalina, Eudiaptomus gracilis* and *Cyclops vicinus. Int. Rev. Gesamten. Hydrobiol.* 70, 603-612.

Horn, W. (1985b) Results regarding the food of the planktonic crustaceans *Daphnia hyalina* and *Eudiaptomus gracilis. Int. Rev. Gesamten. Hydrobiol.* 70, 703-709.

Hrabcek, J., Dvorakova, M., Korinek, M. & Prochazkova, L. (1961) Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verh. Int. Verein. Limnol.* 14, 192-195.

Hutchinson, G.E. (1957) "A Treatise on Limnology. Volume I. Geography, Physics and Chemistry." Wiley, New York. 1015pp.

Hutchinson, G.E. (1967) "A Treatise on Limnology. Volume II. Introduction to Lake Biology and the Limnoplankton." Wiley, New York. 1115pp.

Hutchinson, G.E. & Loffler, H. (1956) The thermal classification of lakes. *Proc. Natl. Acad. Sci. USA* 42, 84-86.

Hynes, H.B.N. (1970) "The Ecology of Running Waters". Liverpool University Press, Liverpool. 555pp.

Imberger, J. (1985) Thermal characteristics of standing waters: an illustration of dynamic processes. *Hydrobiologia* 125, 7-29.

Infante, A. (1978a) A method for the study of foods of herbivorous zooplankton. *Trans. Amer. Micros. Soc.* 97, 256-258.

Infante, A. (1978b) Natural food of herbivorous zooplankton of Lake Valencia (Venezuela). *Arch. Hydrobiol.* 82, 347-358.

Infante, A. & Abella, S.E.B. (1985) Inhibition of *Daphnia* by *Oscillatoria* in Lake Washington. *Limnol. Oceanogr.* 30, 1046-1052.

Irish, A.E. & Clarke, R.T. (1984) Sampling designs for the estimation of phytoplankton abundance in limnetic environments. *Br. Phycol. J.* 19, 57-66.

Irvine, K. (1986) Differential feeding behaviour between the dominant cladocera as an explanation of zooplankton community structure in the Loosdrecht Lakes. *Hydrobiol. Bull.* 20, 121-134.

Janicki, A. & DeCosta, J. (1984) The filtering rates of four herbivorous crustaceans on nannoplankton and net plankton fractions in an acid lake in West Virginia. *Int. Rev. Gesamten. Hydrobiol.* 69, 643-652.

Jarvis, A.C. (1986) Zooplankton community grazing in a hypertrophic lake (Hartbeespoort Dam, South Africa). *J. Plankton Res.* 8, 1065-1078.

Jarvis, A.C., Hart, R.C. & Combrink, S. (1987) Zooplankton feeding on size fractionated *Microcystis* colonies and *Chlorella* in a hypertrophic lake (Hartbeespoort Dam, South Africa): implications to resource utilization and zooplankton succession. *J. Plankton Res.* 9, 1231-1249.

Jassby, A.D. & Goldman, G.R. (1974a) A quantitative measure of succession rate and its application to the phytoplankton of lakes. *Am. Nat.* 108, 688-693.

Jassby, A.D. & Goldman, C.R. (1974b) Loss rates from a lake phytoplankton community. *Limnol. Oceanogr.* 19, 618-627.

Jewson, D.H., Rippey, B.H. & Gilmore, W.K. (1981) Loss rates from sedimentation, parasitism, and grazing during the growth, nutrient limitation, and dormancy of a diatom crop. *Limnol. Oceanogr.* 26, 1045-1056.

Johnsen, G.H. & Borsheim, K.Y. (1988) Functional response and food selection of the water flea, *Bosmina longispina*. *J. Plankton Res.* 10, 319-325.

Kalff, J. & Knoechel, R. (1978) Phytoplankton and their dynamics in oligotrophic and eutrophic lakes. *Ann. Rev. Ecol. Syst.* 9, 475-495.

Kell, G.S. (1967) Precise representation of volume properties of water at one atmosphere. *J. Chem. Eng. Data* 12, 66-69.

Kankaala, P. (1988) The relative importance of algae and bacteria as food for *Daphnia longispina* (Cladocera) in a polyhumic lake. *Freshwater Biol.* 19, 285-296.

Kersting, K. & Holterman, W. (1973) The feeding behaviour of *Daphnia magna* studied with the coulter counter. *Verh. Int. Verein. Limnol.* 18, 1434-1440.

Kibby, H.V. (1971a) Effect of temperature on the feeding behaviour of *Daphnia rosea*. *Limnol. Oceanogr.* 16, 580-581.

Kibby, H.V. (1971b) Energetics and population dynamics of *Diaptomus gracilis*. *Ecol. Monogr.* 41, 311-327.

Kibby, H.V. & Rigler, F.H. (1973) Filtering rates in *Limnocalanus*. *Verh. Int. Verein. Limnol.* 18, 1457-1461.

Kilham, P. & Kilham, S.S. (1980) The evolutionary ecology of phytoplankton. In Morris, I. (ed.) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. pp. 571-597.

Kilham, S.S. & Kilham, P. (1984) The importance of resource supply rates in determining phytoplankton community structure. In Meyers, D.G. & Strickler, J.R. (eds.) "Trophic Interactions Within Aquatic Ecosystems". Westview Press. pp. 7-27.

Kiorboe, T., Mohlenberg, F. & Riisgard, H.U. (1985) *In situ* feeding rates of planktonic copepods: a comparison of four methods. *J. Exp. Mar. Biol. Ecol.* 88, 67-81.

Kirk, J.T.O. (1976) Yellow substance (gelbstoff) and its contribution to the attenuation of photosynthetically active radiation in some inland and coastal south-eastern Australian waters. *Aust. J. Mar. Freshwater Res.* 27, 61-71.

Kirk, J.T.O. (1977) Use of a quanta meter to measure attenuation and underwater reflectance of photosynthetically active radiation in some inland and coastal south-eastern Australian waters. *Aust. J. Mar. Freshwater Res.* 28, 9-21.

Kirk, J.T.O. (1979) Spectral distribution of photosynthetically active radiation in some south-eastern Australian waters. *Aust. J. Mar. Freshwater Res.* 30, 81-91.

Kirk, J.T.O. (1980) Relationship between nephelometric turbidity and scattering coefficients in certain Australian waters. *Aust. J. Mar. Freshwater Res.* 31, 1-12.

Kirk, J.T.O. (1981a) Monte Carlo study of the nature of the underwater light field in, and the relationships between optical properties of, turbid yellow waters. *Aust. J. Mar. Freshwater Res.* 32, 517-532.

Kirk, J.T.O. (1981b) Estimation of the scattering coefficient of natural waters using underwater irradiance measurements. *Aust. J. Mar. Freshwater Res.* 32, 533-539.

Kirk, J.T.O. (1983) "Light and Photosynthesis in Aquatic Ecosystems". Cambridge University Press, Cambridge. 401pp.

Kirk, J.T.O. (1985) Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. *Hydrobiologia* 125, 195-208.

Kitchell, J.F. & Carpenter, S.R. (1988) Food web manipulation in experimental lakes. *Verh. Int. Verein. Limnol.* 23, 351-358.

Knisely, K. & Geller, W. (1986) Selective feeding of four zooplankton species on natural lake phytoplankton. *Oecologia (Berlin)* 69, 86-94.

Knoechel, R. (1977) Analyzing the significance of grazing in Lake Erken. *Limnol. Oceanogr.* 22, 967-969.

Knoechel, R. & Holtby, L.B. (1986a) Construction and validation of a body-length-based model for the prediction of cladoceran community filtering rates. *Limnol. Oceanogr.*

31, 1-16.

Knoechel, R. & Holtby, L.B. (1986b) Cladoceran filtering rate : body length relationships for bacterial and large algal particles. *Limnol. Oceanogr.* 31, 195-200.

Knoechel, R. & Kalff, J. (1975) Algal sedimentation: the cause of a diatom - blue-green succession. *Verh. Int. Verein. Limnol.* 19, 745-754.

Knoechel, R. & Kalff, J. (1978) An *in situ* study of the species productivity and population dynamics of five planktonic diatoms. *Limnol. Oceanogr.* 23, 195-218.

Koehl, M.A.R. (1984) Mechanisms of particle capture by copepods at low Reynolds numbers: possible modes of selective feeding. In Meyers, D.G. & Strickler, J.R. (eds.) "Trophic Interactions Within Aquatic Ecosystems". Westview Press. pp. 135-166.

Koehl, M.A.R. & Strickler, J.R. (1981) Copepod feeding currents: food capture at low Reynolds number. *Limnol. Oceanogr.* 26, 1062-1073.

Koste, W. (1978) "Rotaria: Die Radertiere Mitteleuropas (Uberordnung Monogononta)" Revision after M. Voigt (1956/57). Borntraeger: Stuttgart-Berlin.

Krebs, C.J. (1972) "Ecology: The Experimental Analysis of Distribution and Abundance". Harper & Row, New York. 694pp.

Kring, R.L. & O'Brien, W.J. (1976) Effects of varying oxygen concentrations on the filtering rate of *Daphnia pulex. Ecology* 57, 808-814.

Lam, R.K. & Frost, B.W. (1976) Model of copepod filtering response to changes in size and concentration of food. *Limnol. Oceanogr.* 21, 490-500.

Lampert, W. (1974) A method for determining food selection by zooplankton. *Limnol. Oceanogr.* 19, 995-998.

Lampert, W. (1981a) Toxicity of the blue-green *Microcystis aeruginosa*: effective defence mechanism against grazing pressure by *Daphnia. Verh. Int. Verein. Limnol.* 21, 1436-1440.

Lampert, W. (1981b) Inhibitory and toxic effects of blue-green algae on *Daphnia. Int. Rev. Gesamten. Hydrobiol.* 66, 285-298.

Lampert, W. (1982) Further studies on the inhibitory effect of the toxic blue-green *Microcystis aeruginosa* on the filtering rate of zooplankton. *Arch. Hydrobiol.* 95, 207-220.

Lampert, W. (1984) The measurement of respiration. In Downing, J.A. & Rigler, F.H. (eds.) "A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters". Blackwell, Oxford. pp. 413-468.

Lampert, W. (1987) Laboratory studies on zooplankton - cyanobacteria interactions. *N.Z. J. Mar. Freshwater Res.* 21, 483-490.

Lampert, W., Fleckner, W., Rai, H. & Taylor, B.E. (1986) Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase. *Limnol. Oceanogr.* 31, 478-490.

Lampert, W. & Taylor, B.E. (1985) Zooplankton grazing in a eutrophic lake: implications for diel vertical migration. *Ecology* 66, 68-82.

Legier-Visser, M.F., Mitchell, J.G., Okubu, A. & Fuhrman, J.A. (1986) Mechanoreception in calanoid copepods. A mechanism for prey detection. *Mar. Biol.* 90, 529-535.

Lehman, J.T. (1976) The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. *Limnol. Oceanogr.* 21, 501-516.

Lehman, J.T. (1980a) Nutrient recycling as an interface between algae and grazers in freshwater communities. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 251-263.

Lehman, J.T. (1980b) Release and cycling of nutrients between planktonic algae and herbivores. *Limnol. Oceanogr.* 25, 620-632.

Lewis, W.M. Jr. (1976) Surface/volume ratio: implications for phytoplankton morphology. *Science* 192, 885-887.

Lewis, W.M. Jr. (1977a) Ecological significance of the shapes of abundance frequency distributions for coexisting phytoplankton species. *Ecology* 58, 850-859.

Lewis, W.M. Jr. (1977b) Net growth rate through time as an indication of ecological similarity among phytoplankton species. *Ecology* 58, 149-157.

Lewis, W.M. Jr. (1977c) Comments on the analysis of grazing in Lake Erken. *Limnol. Oceanogr.* 22, 966-967.

Lewis, W.M. Jr. (1978a) Analysis of succession in a tropical phytoplankton community and a new measure of succession rate. *Am. Nat.* 112, 401-414.

Lewis, W.M. Jr. (1978b) Dynamics and succession of the phytoplankton in a tropical lake: Lake Lanao, Philippines. *J. Ecol.* 66, 849-880.

Lewis, W.M. Jr. (1978c) Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. *Ecology* 59, 666-671.

Lewis, W.M. Jr. (1979) "Zooplankton Community Analysis". Springer, New York. 163pp.

Likens, G.E. (ed.) (1972) "Nutrients and Eutrophication: the Limiting Nutrient Controversy". Special Symposia, Volume 1. Am. Soc. Limnol. Oceanogr. Allen Press, Lawrence, Kansas.

Lopez, M.D.G., Huntley, M.E. & Sykes, P.F. (1988) Pigment destruction by *Calanus pacificus*: impact on the estimation of water column fluxes. *J. Plankton Res.* 10, 715-734.

Lowndes, A.G. (1935) The swimming and feeding of certain calanoid copepods. *Proc. Zool. Soc. Lond.* 107, 687-715.

Lukatelich, R.J. & McComb, A.J. (1986) Nutrient levels and the development of diatom and blue-green algal blooms in a shallow Australian estuary. *J. Plankton Res.* 8, 597-618.

Lund, J.W.G. (1965) The ecology of the freshwater phytoplankton. *Biol. Rev.* 40, 231-293.

Lund, J.W.G. (1971) An artificial alteration of the seasonal cycle of the plankton diatom *Melosira italica* ssp. *subarctica* in an English lake. *J. Ecol.* 59, 521-533.

Lund, J.W.G., Kipling, C. & LeCren, E.D. (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia* 11, 143-170.

Lund, J.W.G., MacKereth, F.J.H. & Mortimer, C.H. (1963) Changes in depth and time of certain chemical and physical conditions and of the standing crop of *Asterionella formosa* Hass. in the north basin of Windermere in 1947. *Phil. Trans. R. Soc. Lond. (B)* 246, 255-290.

Lund, J.W.G. & Reynolds, C.S. (1982) The development and operation of large limnetic enclosures in Blelham Tarn, English Lake District, and their contribution to phytoplankton ecology. *Prog. Phycol. Res.* 1, 1-65.

Lund, J.W.G. & Talling, J.F. (1957) Botanical limnological methods with special reference to the algae. *Bot. Rev.* 23, 489-583.

Lundgren, A. (1985) Model ecosystems as a tool in freshwater and marine research. *Arch. Hydrobiol. Suppl.* 70, 157-196.

Lynch, M. (1978) Complex interactions between natural coexploiters - *Daphnia* and *Ceriodaphnia*. *Ecology* 59, 552-564.

Lynch, M. & Shapiro, J. (1981) Predation, enrichment, and phytoplankton community structure. *Limnol. Oceanogr.* 26, 86-102.

Macan, T.T. (1970) "Biological Studies of the English Lakes". Longman, London. 260pp.

Mackas, D.L. & Bohrer, R. (1976) Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *J. Exp. Mar. Biol. Ecol.* 25, 77-85.

Maddock, L. & Taylor, F.J. (1984) The application of multivariate statistical methods to phytoplankton counts from the Hauraki Gulf, New Zealand. *N.Z. J. Mar. Freshwater Res.* 18, 309-322.

Malone, B.J. & McQueen, D.J. (1983) Horizontal patchiness in zooplankton populations in two Ontario kettle lakes. *Hydrobiologia* 99, 101-124.

Margalef, R. (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1, 493-510.

Martin, J.H. (1965) Phytoplankton - zooplankton relationships in Narragansett Bay. *Limnol. Oceanogr.* 10, 185-191.

Marzolf, G.R. & Arruda, J.A. (1980) Roles of materials exported by rivers into reservoirs in the nutrition of cladoceran zooplankton. In "Restoration of Lakes and Inland Waters". U.S. Environmental Protection Agency, Washington, D.C. pp. 53-55.

Marzolf, G.R. & Osborne, J.A. (1972) Primary production in a Great Plains reservoir. *Verh. Int. Verein. Limnol.* 18, 126-133.

McAllister, L.D. (1970) Zooplankton rations, phytoplankton mortality and the estimation of marine production. In Steele, J.H. (ed.) "Marine Food Chains". University of California Press. pp. 419-457.

McCabe, G.D. & O'Brien, W.J. (1983) The effects of suspended silt on feeding and reproduction of *Daphnia pulex*. *Am. Midl. Nat.* 110, 324-337.

McCauley, E. & Briand, F. (1979) Zooplankton grazing and phytoplankton species richness: field tests of the predation hypothesis. *Limnol. Oceanogr.* 24, 243-252.

McMahon, J.W. (1965) Some physical factors influencing the feeding behaviour of *Daphnia magna* Straus. *Can. J. Zool.* 43, 603-611.

McMahon, J.W. & Rigler, F.H. (1963) Mechanisms regulating the feeding rate of *Daphnia magna* Straus. *Can. J. Zool.* 41, 321-332.

McMahon, J.W. & Rigler, F.H. (1965) Feeding rate of *Daphnia magna* Straus in different foods labeled with radioactive phosphorus. *Limnol. Oceanogr.* 10, 105-113.

McNaught, D.C. (1975) A hypothesis to explain the succession from calanoids to cladocerans during eutrophication. *Verh. Int. Verein. Limnol.* 19, 724-731.

McNaught, D.C., Greismer, D. & Kennedy, M. (1980) Resource characteristics modifying selective grazing by copepods. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 292-298.

McQueen, J.D. (1970) Grazing rates and food selection in *Diaptomus oregonensis* (Copepoda) from Marion lake, British Columbia. *J. Fish. Res. Bd. Can.* 27, 13-20.

McQueen, D.J. & Post, J.R. (1988) Cascading trophic interactions: uncoupling at the zooplankton - phytoplankton link. *Hydrobiologia* 159, 277-296.

McQueen, D.J., Post, J.R. & Mills, E.L. (1986) Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* 43, 1571-1581.

Meise, C.J., Munns, W.R. Jr. & Hairston, N.G. Jr. (1985) An analysis of the feeding behaviour of *Daphnia pulex*. *Limnol. Oceanogr.* 30, 862-870.

Melack, J.M. (1985) Interactions of detrital particulates and plankton. *Hydrobiologia* 125, 209-220.

Mitchell, B.D. (1986) Entomostracan zooplankton communities of Australian freshwater lakes and ponds. In DeDeckker, P. & Williams, W.D. (eds.) "Limnology in Australia". C.S.I.R.O., Australia and Junk, Dordrecht. pp. 369-386.

Morel, A. & Smith, R.C. (1974) Relation between total quanta and total energy for aquatic photosynthesis. *Limnol. Oceanogr.* 19, 591-600.

Montgomery, H.A.C., Thom, N.S. & Cockburn, A. (1964) Determination of dissolved oxygen by the Winkler method and the solubility of oxygen in pure water and sea water. *J.*

Appl. Chem. 14, 280-296.

Moriarty, D.J.W., Darlington, J.P.E.C., Dunn, E.G., Moriarty, C.M. & Tevlin, M.P. (1973) Feeding and grazing in Lake George, Uganda. *Proc. R. Soc. Lond. B.* 184, 299-319.

Morris, I. (ed.) (1980) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. 625pp.

Mortimer, C.H. (1974) Lake hydrodynamics. *Mitt. Internat. Verein. Limnol.* 20, 124-197.

Muck, P. & Lampert, W. (1980) Feeding of freshwater filter-feeders at very low food concentrations: poor evidence for 'threshold feeding' and 'optimal foraging' in *Daphnia longispina* and *Eudiaptomus gracilis. J. Plankton Res.* 2, 367-379.

Muck, P. & Lampert, W. (1984) An experimental study on the importance of food conditions for the relative abundance of calanoid copepods and cladocerans. 1. Comparative feeding studies with *Eudiaptomus gracilis* and *Daphnia longispina. Arch. Hydrobiol. Suppl.* 66, 157-179.

Mullin, M.M. (1963) Some factors affecting the feeding of marine copepods of the genus *Calanus. Limnol. Oceanogr.* 8, 239-250.

Mullin, M.M., Fuglister-Stewart, E. & Fuglister, F.J. (1975) Ingestion by planktonic grazers as a function of concentration of food. *Limnol. Oceanogr.* 20, 259-262.

Munk, W.H. & Riley, G.A. (1952) Absorption of nutrients by aquatic plants. *J. Mar. Res.* 11, 215-240.

Nadin-Hurley, C.M. & Duncan, A. (1976) A comparison of daphnid gut particles with the sestronic particles present in two Thames Valley reservoirs throughout 1970 and 1971. *Freshwater Biol.* 6, 109-123.

Nalewajko, C. & Lean, D.R.S. (1980) Phosphorus. In Morris, I. (ed.) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. pp. 235-258.

Nauwerck, A. (1959) Zur Bestimmung der Filterierrate limnischer Planktontiere. *Arch. Hydrobiol. Suppl.* 25, 83-101.

Nauwerck, A. (1963) Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symbol. Bot. Upsal.* 17, 1-163.

Nie, N.H., Hull, C.H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. (1975) "Statistical Package for the Social Sciences". McGraw-Hill, New York. 675pp.

Nival, P. & Nival, S. (1976) Particle retention efficiencies of an herbivorous copepod, *Acartia clausi* (adult and copepodite stages): effects on grazing. *Limnol. Oceanogr.* 21, 24-38.

Nival, P. & Nival, S. (1979) Calculations of particle retention efficiency. *Limnol. Oceanogr.* 24, 995-998.

Nizan, S., Dimentman, C. & Shilo, M. (1986) Acute toxic effects of the cyanobacterium *Microcystis aeruginosa* on *Daphnia magna. Limnol. Oceanogr.* 31, 497-502.

O'Brien, W.J. (1988) The effect of container size on the feeding rate of *Heterocope septentrionalis*, a freshwater predaceous copepod. *J. Plankton Res.* 10, 313-317.

O'Brien, W.J. & de Noyelles, F. Jr (1974) Filtering rate of *Ceriodaphnia reticulata* in pond waters of varying phytoplankton concentrations. *Am. Midl. Nat.* 91, 509-512.

O'Connors, H.B. Jr., Biggs, D.C. & Ninivaggi, D.V. (1980) Particle size dependent maximum grazing rates for *Temora longicornis* fed natural particle assemblages. *Mar. Biol.* 56, 65-70.

O'Connors, H.B., Small, L.F. & Donaghay, P.L. (1976) Particle size modification by two classes of the estuarine copepod *Acartia clausi. Limnol. Oceanogr.* 21, 300-308.

Okamoto, K. (1984a) Size-selective feeding of *Daphnia longispina hyalina* and *Eodiaptomus japonicus* on a natural phytoplankton assemblage with the fractionizing method. *Mem. Fac. Sci. Kyoto Uni. Biol. Ser.* 9, 23-40.

Okamoto, K. (1984b) Diurnal changing patterns in the *in situ* size-selective feeding activities of *Daphnia longispina hyalina* and *Eodiaptomus japonicus* in a pelagic area of Lake

Biwa. *Mem. Fac. Sci. Kyoto Uni. Biol. Ser.* 9, 107-132.

Olive, L.J. & Walker, P.H. (1982) Processes in overland flow erosion and production of suspended material. In O'Loughlin, E.M. & Cullen, P. (eds.) "Prediction in Water Quality". Aust. Acad. Sci., Canberra. pp. 87-119.

Oliver, R.L. (1981) Factors controlling phytoplankton seasonal succession in Mt. Bold Reservoir, South Australia. Ph.D. Thesis. University of Adelaide. 207pp.

Oliver, R.L. & Ganf, G.G. (1988) The optical properties of a turbid reservoir and its phytoplankton in relation to photosynthesis and growth (Mount Bold Reservoir, South Australia). *J. Plankton Res.* 10, 1155-1177.

Oliver, R.L., Kinnear, A.J. & Ganf, G.G. (1981) Measurements of cell density of three freshwater phytoplankters by density gradient centrifugation. *Limnol. Oceanogr.* 26, 285-294.

Olrik, K., Lundoer, S. & Rasmussen, K. (1984) Interactions between phytoplankton, zooplankton, and fish in the nutrient rich shallow lake Hjarbaek Fjord, Denmark. *Int. Rev. Gesamten. Hydrobiol.* 69, 389-405.

Osgood, R.A. (1982) Differential filtration efficiencies of *Daphnia pulex*. *Can. J. Zool.* 60, 2129-2133.

Oviatt, C.A., Perez, K.T. & Nixon, S.W. (1977) Multivariate analyses of experimental marine ecosystems. *Helgolander Wiss. Meersunters* 30, 30-46.

Paffenhöfer, G.A. (1971) Grazing and ingestion rates of nauplii, copepodids, and adults of the marine planktonic copepod *Calanus heloglondicus*. *Mar. Biol.* 11, 286-298.

Paffenhöfer, G.A. (1972) The effects of suspended 'red mud' on mortality, body weight, and growth of the marine planktonic copepod, *Calanus helgolandicus*. *Water Air Soil Pollution* 1, 314-321.

Paffenhöfer, G.A. (1976) Feeding, growth, and food conversion of the marine planktonic copepod *Calanus helgolandicus*. *Limnol. Oceanogr.* 21, 39-50.

Paffenhöfer, G.A. (1984a) Calanoid copepod feeding: grazing on small and large particles. In Meyers, D.G. & Strickler, J.R. (eds.) "Trophic Interactions Within Aquatic Ecosystems". Westview Press. pp. 75-95.

Paffenhöfer, G.A. (1984b) Food ingestion by the marine planktonic copepod *Paracalanus* in relation to abundance and size distribution of food. *Mar. Biol.* 80, 323-333.

Paffenhöfer, G.A., Strickler, J.R. & Alcaraz, M. (1982) Suspension feeding by herbivorous calanoid copepods: a cinematographic study. *Mar. Biol.* 67, 193-199.

Parsons, T.R., Le Brasseur, R.J. & Fulton, J.D. (1967) Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton. *J. Oceanogr. Soc. Japan* 23, 10-17.

Patalas, K. & Salki, A. (1984) Effects of impoundment and diversion on the crustacean plankton of Southern Indian Lake. *Can. J. Fish. Aquat. Sci.* 41, 613-637.

Pearsall, W.H. (1932) Phytoplankton in the English lakes. II. The composition of phytoplankton in relation to dissolved substances. *J. Ecol.* 20, 241-262.

Pedrós-Alió, C. & Brock, T.D. (1983) The importance of attachment to particles for planktonic bacteria. *Arch. Hydrobiol.* 98, 354-379.

Peer, R.L. (1986) The effects of microcrustaceans on succession and diversity of an algal microcosm community. *Oecologia (Berlin)* 68, 308-314.

Peet, R.K. (1974) The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5, 285-307.

Peet, R.K., Knox, R.G., Case, J.S. & Allen, R.B. (1988) Putting things in order: the advantages of detrended correspondence analysis. *Am. Nat.* 131, 924-934.

Persson, G. (1982) Losses of isotopic label upon liquid preservation of zooplankton in feeding and assimilation studies. *Arch. Hydrobiol.* 94, 502-519.

Peters, R.H. (1984) Methods for the study of feeding, grazing and assimilation by zooplankton. In Downing, J.A. & Rigler, F.H. (eds.) "A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters". Blackwell, Oxford. pp. 336-412.

Peters, R.H. & Downing, J.A. (1984) Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* 29, 763-784.

Phillips, O.M. (1966) "The Dynamics of the Upper Ocean". Cambridge University Press, Cambridge.

Pielou, E.C. (1977) "Mathematical Ecology". Wiley, New York. 385pp.

Pinel-Alloul, B., Downing, J.A., Pérusse, M. & Codin-Blumer, G. (1988) Spatial heterogeneity in freshwater zooplankton: variation with body size, depth, and scale. *Ecology* 69, 1393-1400.

Platt, T. & Denman, K. (1980) Patchiness in phytoplankton distribution. In Morris, I. (ed.) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. pp. 413-431.

Porter, K.G. (1972) A method for the *in situ* study of zooplankton grazing effects on algal species composition and standing crop. *Limnol. Oceanogr.* 17, 913-917.

Porter, K.G. (1973a) The selective effects of grazing by zooplankton on the phytoplankton of Fuller Pond, Kent, Conneticut. Ph.D. Thesis. Yale University. 192pp.

Porter, K.G. (1973b) Selective grazing and differential digestion of algae by zooplankton. *Nature* 244, 179-180.

Porter, K.G. (1976) Enhancement of algal growth and productivity by grazing zooplankton. *Science* 192, 1332-1334.

Porter, K.G. (1977) The plant-animal interface in freshwater ecosystems. *Am. Sci.* 65, 159-170.

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

Porter, K.G., Gerritsen, J. & Orcutt, J.D. Jr. (1982) The effect of food concentration on swimming patterns, feeding behaviour, ingestion, assimilation, and respiration by *Daphnia. Limnol. Oceanogr.* 27, 935-949.

Porter, K.G. & McDonough, R. (1984) The energetic cost of response to blue-green algal filaments by cladocerans. *Limnol. Oceanogr.* 29, 365-369.

Porter, K.G. & Orcutt, J.D. Jr (1980) Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae for *Daphnia*. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 268-281.

Poulet, S.A. (1978) Comparison between five coexisting species of marine copepods feeding on naturally occurring particulate matter. *Limnol. Oceanogr.* 23, 1126-1143.

Poulet, S.A. & Marsot, P. (1978) Chemosensory grazing by marine calanoid copepods. *Science* 200, 1403-1405.

Pourriot, R. (1977) Food and feeding habits of Rotifera. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 8, 243-260.

Powling, I.J. (1980) Limnological features of some Victorian reservoirs. In Williams, W.D. (ed.) "An Ecological Basis for Water Resource Management". A.N.U. Press, Canberra. pp. 332-344.

Prescott, G.W. (1978) "How to Know the Freshwater Algae" (3rd Edn.). Wm. C. Brown, Iowa. 293pp.

Price, H.J. & Paffenhöfer, G.A. (1986) Capture of small cells by the copepod *Eucalanus elongatus. Limnol. Oceanogr.* 31, 189-194.

Price, H.J., Paffenhöfer, G.A. & Strickler, J.R. (1983) Modes of cell capture in calanoid copepods. *Limnol. Oceanogr.* 28, 116-123.

Purcell, E.M. (1977) Life at low Reynolds number. *Am. J. Physics* 45, 3-11.

Rai, H. & Marker, A.F.H. (eds.) (1982) The measurement of photosynthetic pigments in freshwaters and standardization of methods. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 16, 1-130.

Raymont, J.E.G. (1983) "Plankton and Productivity in the Oceans. Vol. 2. Zooplankton". Pergamon Press, New York. 824pp.

Reinertsen, H. & Olsen, Y. (1984) Effects of fish elimination on the phytoplankton community of a eutrophic lake. *Verh. Int. Verein. Limnol.* 22, 649-657.

Reynolds, C.S. (1973) The seasonal periodicity of planktonic diatoms in a shallow eutrophic lake. *Freshwater Biol.* 3, 89-110.

Reynolds, C.S. (1976) Succession and vertical distribution of phytoplankton in response to thermal stratification in a lowland mere, with special reference to nutrient availability. *J. Ecol.* 64, 529-550.

Reynolds, C.S. (1980) Phytoplankton assemblages and their periodicity in stratifying lake systems. *Holarctic Ecology* 3, 141-159.

Reynolds, C.S. (1984a) "The Ecology of Freshwater Phytoplankton". Cambridge University Press, Cambridge. 384pp.

Reynolds, C.S. (1984b) Phytoplankton periodicity: the interactions of form, function and environmental variability. *Freshwater Biol.* 14, 111-142.

Reynolds, C.S. (1986) Experimental manipulations of phytoplankton periodicity in large limnetic enclosures in Blelham Tarn, English Lake District. *Hydrobiologia* 138, 43-64.

Reynolds, C.S. (1987a) Cyanobacterial water-blooms. In Callow, J.A. (ed.) "Advances in Botanical Research" Vol. 13. Academic Press, London. pp. 67-143.

Reynolds, C.S. & Jaworski, G.H.M. (1978) Enumeration of natural *Microcystis* populations. *British Phycol. J.* 13, 269-277.

Reynolds, C.S., Jaworski, G.H.M., Cmiech, M.A. & Leedale, G.F. (1981) On the annual cycle of the blue-green alga *Microcystis aeruginosa* Kutz. emend. Elenkin. *Phil. Trans. R. Soc. Lond. B* 293, 419-477.

Reynolds, C.S. & Lund, J.W.G. (1988) The phytoplankton of an enriched soft-water lake subject to intermittent hydraulic flushing (Grasmere, English lake District). *Freshwater Biol.* 19, 379-404.

Reynolds, C.S., Thompson, J.M., Ferguson, A.J.D. & Wiseman, S.W. (1982) Loss processes in the population dynamics of phytoplankton maintained in closed systems. *J. Plankton Res.* 4, 561-600.

Reynolds, C.S. & Walsby, A.E. (1975) Water-Blooms. *Biol. Rev.* 50, 437-481.

Reynolds, C.S. & Wiseman, S.W. (1982) Sinking losses of phytoplankton in closed limnetic systems. *J. Plankton Res.* 4, 489-522.

Reynolds, C.S., Wiseman, S.W. & Clarke, M.J.O. (1984) Growth and loss-rate responses of phytoplankton to intermittent artificial mixing and their potential application to the control of planktonic algal biomass. *J. App. Ecol.* 21, 11-39.

Reynolds, C.S., Wiseman, S.W., Godfrey, B.M. & Butterwick, C. (1983) Some effects of artificial mixing on the dynamics of phytoplankton populations in large limnetic enclosures. *J. Plankton Res.* 5, 203-234.

Rhee, G.Y. (1978) Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition and nitrate uptake. *Limnol. Oceanogr.* 23, 10-25.

Richman, S. (1964) Energy transformation studies on *Diaptomus oregonensis*. *Verh. Int. Verein. Limnol.* 15, 654-659.

Richman, S. (1966) The effect of phytoplankton concentration on the feeding rate of *Diaptomus oregonensis. Verh. Int. Verein. Limnol.* 16, 392-398.

Richman, S., Bohon, S.A. & Robbins, S.E. (1980) Grazing interactions among freshwater calanoid copepods. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 219-233.

Richman, S. & Dodson, S.I. (1983) The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus. Limnol. Oceanogr.* 28, 948-956.

Richman, S. & Rogers, J.N. (1969) The feeding of *Calanus helgolandicus* on synchronously growing populations of the marine diatom *Ditylum brightwellii. Limnol. Oceanogr.* 14, 701-709.

Rigler, F.H. (1961) The relation between concentration of food and feeding rate of *Daphnia magna* Straus. *Can. J. Zool.* 39, 857-868.

Rigler, F.H. (1971) Feeding rates: zooplankton. In Edmondson, W.T. & Winberg, G.G. (eds.) "A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters". Blackwell, Oxford. pp. 228-255.

Riley, G.A. (1942) The relationship of vertical turbulence and spring diatom flowerings. *J. Mar. Res.* 5, 67-87.

Riley, G.A. (1957) Phytoplankton of the north central Sargasso Sea. *Limnol. Oceanogr.* 2, 252-270.

Rodhe, W. (1948) Environmental requirements of fresh-water plankton algae. Experimental studies in the ecology of phytoplankton. *Symb. Bot. Upasaliens.* 10, 1-149.

Roman, M.R., Ashton, K.A. & Gauzens, A.L. (1988) Day/night differences in the grazing impact of marine copepods. *Hydrobiologia* 167/168, 21-30.

Roman, M.R. & Rublee, P.A. (1980) Containment effects in copepod grazing experiments: a plea to end the black box approach. *Limnol. Oceanogr.* 25, 982-990.

Roman, M.R. & Rublee, P.A. (1981) A method to determine *in situ* zooplankton grazing rates on natural particle assemblages. *Mar. Biol.* 65, 303-309.

Ross, P.E. & Munawar, M. (1981) Preference for nannoplankton size fractions in Lake Ontario zooplankton grazing. *J. Great Lakes Res.* 7, 65-67.

Round, F.E. (1971) The growth and succession of algal populations in freshwaters. *Mitt. Internat. Verein. Limnol.* 19, 70-99.

Rubenstein, D.I. & Koehl, M.A.R. (1977) The mechanisms of filter feeding: some theoretical considerations. *Am. Nat.* 111, 981-994.

Ruttner, F. (1963) "Fundamentals of Limnology". University of Toronto Press, Toronto. 307pp.

Ryther, J.H. (1954) Inhibitory effects of phytoplankton upon the feeding of *Daphnia magna* with reference to growth, reproduction, and survival. *Ecology* 35, 522-523.

Sandgren, C.D. & Robinson, J.V. (1984) A stratified sampling approach to compensating for non-random sedimentation of phytoplankton cells in inverted microscope settling chambers. *Br. Phycol. J.* 19, 67-72.

Sellner, K.G., Lacouture, R.V. & Parrish, C.R. (1988) Effects of increasing salinity on a cyanobacteria bloom in the Potomac River estuary. *J. Plankton Res.* 10, 49-61.

Schiebe, F.R., Ritchie, J.C. & McHenyy, J.R. (1975) Influence of suspended sediment on the temperature of surface waters of reservoirs. *Verh. Int. Verein. Limnol.* 19, 133-136.

Schindler, D.W. (1968) Feeding, assimilation and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. *J. Anim. Ecol.* 37, 369-385.

Schindler, D.W. (1969) Two useful devices for vertical plankton and water sampling. *J. Fish. Res. Bd. Can.* 26, 1948-1955.

Schindler, J.E. (1971) Food quality and zooplankton nutrition. *J. Anim. Ecol.* 40, 589-595.

Schoenberg, S.A. & Carlson, R.E. (1984) Direct and indirect effects of zooplankton grazing on phytoplankton in a hypereutrophic lake. *Oikos* 42, 291-302.

Scholtz, S., Seaman, M.T. & Pieterse, A.J.H. (1988) Effects of turbidity on life history parameters of two species of *Daphia. Freshwater Biol.* 20, 177-184.

Schwerdtfeger, P. (1976) Climate. In Twidale, C.R., Tyler, M.J. & Webb, B.P. (eds.) "Natural History of the Adelaide Region". Royal Society of South Australia. pp. 75-86.

Selkirk, W.T. (1982) An analysis, by bioassay, of factors which limit algal growth in the P.K. le Roux impoundment, Orange River, South Africa. *Hydrobiologia* 97, 151-156.

Sephton, D.H. & Harris, G.P. (1984) Physical variability and phytoplankton communities. VI. Day to day changes in primary productivity and species abundance. *Arch. Hydrobiol.* 102, 155-175.

Shapiro, J. (1980) The importance of trophic-level interactions to the abundance and species composition of algae in lakes. *Developments in Hydrobiology* 2, 105-116.

Shapiro, J., Lamarra, V. & Lynch, M. (1975) Biomanipulation: an ecosystem approach to lake restoration. In Brezonik, P.L. (ed.) "Symposium on Water Quality Management through Biological Control (Proceedings)". University of Florida, Gainesville. 164pp.

Shapiro, J. & Wright, D.I. (1984) Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biol.* 14, 371-383.

Sheldon, R.W. & Parsons, T.R. (1967) "A Practical Manual on the Use of the Coulter Counter in Marine Science". Coulter Electronics of Canada. Oakville, Ontario.

Shiel, R.J. (1981) Plankton of the Murray-Darling river system. Ph.D. Thesis, University of Adelaide. 287pp.

Shiel, R.J. (1985) Zooplankton of the Darling River system, Australia. *Verh. Int. Verein. Limnol.* 22, 2136-2140.

Shiel, R.J. & Koste, W. (1986) Australian Rotifera: ecology and biogeography. In DeDeckker, P & Williams, W.D. (eds.) "Limnology in Australia". C.S.I.R.O., Australia and Junk, Dordrecht. pp. 141-150.

Shiel, R.J., Merrick, C.J. & Ganf, G.G. (1987) The Rotifera of impoundments in Southeastern Australia. *Hydrobiologia* 147, 23-29.

Smayda, T.J. (1980) Phytoplankton species succession. In Morris, I. (ed.) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. pp. 493-570.

Smirnov, N.N. & Timms, B.V. (1983) A revision of the Australian Cladocera (Crustacea). *Records of the Australian Museum Suppl.* 1, 1-132.

Smith, V.H. (1982) Predicting the effects of eutrophication: responses in the phytoplankton. In O'Loughlin, E.M. and Cullen, P. (eds.) "Prediction in Water Quality". Australian Academy of Science, Canberra. pp. 249-264.

Snell, T.W. (1980) Blue-green algae and selection in rotifer populations. *Oecologia (Berlin)* 46, 343-346.

Sokal, R.R. & Rohlf, F.J. (1981) "Biometry". 2nd edn. W.H.Freeman & Co., San Francisco. 859pp.

Sommer, U. (1983) Nutrient competition between phytoplankton species in multispecies chemostat experiments. *Arch. Hydrobiol.* 96, 399-416.

Sommer, U. (1987) Factors controlling the seasonal variation on phytoplankton species composition - a case study for a deep, nutrient rich lake. In Round, F.E. & Chapman, D.J. (eds.) "Progress in Phycological Research". Vol. 5. Elsevier Biomedical Press. pp. 123-178.

Sommer, U., Gliwicz, Z.M., Lampert, W. & Duncan, A. (1986) The PEG model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* 106, 433-471.

Sorokin, J.I. (1968) The use of ^{14}C in the study of nutrition of aquatic animals. *Mitt. Internat. Verein. Limnol.* 16, 1-41.

Spencer, C.N. & King, D.L. (1984) Role of fish in regulation of plant and animal communities in eutrophic ponds. *Can. J. Fish. Aquat. Sci.* 41, 1851-1855.

Spencer, J.W. (1982) "Adelaide Solar Tables". C.S.I.R.O. Div. Bldg. Res. Technical Paper. 2nd Series 47. pp. 8-11.

Spomer, G.G. (1973) The concept of interaction and operational environment in environmental analyses. *Ecology* 54, 200-204.

SPSS (1986) "SPSS^X User's Guide". (2nd edn.) SPSS Inc. McGraw-Hill, New York. 988pp.

Starkweather, P.L. (1975) Diel patterns of grazing in *Daphnia pulex* Leydig. *Verh. Int. Verein. Limnol.* 19, 2851-2857.

Starkweather, P.L. (1981) Trophic relationships between the rotifer *Brachionus calyciflorus* and the blue-green alga *Anabaena flos-aquae. Verh. Int. Verein. Limnol.* 21, 1507-1514.

Starr, R.C. (1978) The culture collection of algae at the University of Texas at Austin. *J. Phycol. Suppl.* 14, 47-100.

Stearns, D.E. (1986) Copepod grazing behaviour in simulated natural light and its relation to noctural feeding. *Mar. Ecol. Prog. Ser.* 30, 65-76.

Steele, J.H. (1976) Patchiness. In Cushing, D.H. & Walsh, J.J. (eds.) "The Ecology of the Seas". W.B.Saunders, Philadelphia. pp. 98-115.

Strickland, J.D.H. (1958) Solar radiation penetrating the ocean. A review of requirements, data and methods of measurement, with particular reference to photosynthetic productivity. *J. Fish. Res. Bd. Can.* 15, 453-493.

Strickler, J.R. (1982) Calanoid copepods, feeding currents, and the role of gravity. *Science* 218, 158-160.

Strickler, J.R. (1984) Sticky water: a selective force in copepod evolution. In Meyers, D.G. & Strickler, J.R. (eds.) "Trophic Interactions within Aquatic Ecosystems". Westview Press. pp. 187-239.

Stumm, W. & Morgan, J.F. (1970) "Aquatic Chemistry. An Introduction Emphasizing Chemical Equilibria in Natural Waters". Wiley-Interscience, New York. 583pp.

Talling, J.F. (1971) The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. *Mitt. Internat. Verein. Limnol.* 19, 214-243.

Talling, J.F. & Driver, D. (1963) Some problems in the estimation of chlorophyll *a* in phytoplankton. Proceedings of the Conference on Primary Productivity Measurement, Marine and Freshwater. U.S. Atomic Energy Commission, Division of Technical Information. TID-7633. pp. 142-146.

Teraguchi, M., Stucke, D.E. & Noga, M.M. (1983) Spatial dynamics of *Mesocyclops edax* (S.A.Forbes), *Tropocyclops prasinus mexicanus* Kiefer, *Diaptomus pallidus* Herrick, *Ceriodaphnia lacustris* (Birge), *Bosmina longirostris* (O.F.Muller), *Daphnia parvula* (Fordyce) and nauplii in a northeastern Ohio pond. *Int. Rev. Gesamten. Hydrobiol.* 68, 863-883.

Thompson, J.M., Ferguson, A.J.D. & Reynolds, C.S. (1982) Natural filtration rates of zooplankton in a closed system: the derivation of a community grazing index. *J. Plankton Res.* 4, 545-560.

Threlkeld, S.T. (1986) Life table responses and population dynamics of four cladoceran zooplankton during a reservoir flood. *J. Plankton Res.* 8, 639-647.

Threlkeld, S.T. & Soballe, D.M. (1988) Effects of mineral turbidity on freshwater plankton communities: three exploratory tank experiments of factorial design. *Hydrobiologia* 159, 223-236.

Tilman, D. (1977) Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58, 338-348.

Titman, D. (1976) Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science* 192, 463-465.

Tranter, D.J. & Smith, P.E. (1968) Filtration Performance. In Tranter, D.J. & Fraser, J.H. (eds.) "Zooplankton Sampling. Monographs on Oceanographic Methodology No. 2". U.N.E.S.C.O., Paris. pp. 27-56.

Trimbee, A.M. & Harris, G.P. (1984) Phytoplankton population dynamics of a small reservoir: effect of intermittent mixing on phytoplankton succession and the growth of blue-green algae. *J. Plankton Res.* 6, 699-713.

Turner, J.T. (1984) Zooplankton feeding ecology: contents of fecal pellets of the copepods *Temora turbinata* and *T. stylifera* from continental shelf and slope waters near the mouth of the Mississippi River. *Mar. Biol.* 82, 73-83.

Turner, J.T. (1987) Zooplankton feeding ecology: contents of fecal pellets of the copepod *Centropages velificatus* from waters near the mouth of the Mississippi river. *Biol. Bull.* 173, 377-386.

Uehlinger, U. & Bloesch, J. (1987) The influence of crustacean zooplankton on the size structure of algal biomass and suspended and settling seston (Biomanipulation in limnocorrals II). *Int. Rev. Gesamten. Hydrobiol.* 72, 473-486.

Uehlinger, U., Bossard, P., Bloesch, J., Burgi, H.R. & Buhrer, H. (1984) Ecological experiments in limnocorrals: methodological problems and quantification of the epilimnetic phosphorus and carbon cycles. *Verh. Int. Verein. Limnol.* 22, 163-171.

Vanderploeg, H.A. (1981) Seasonal particle-size selection by *Diaptomus sicilis* in off-shore Lake Michigan. *Can. J. Fish. Aquat. Sci.* 38, 504-517.

Vanderploeg, H.A., Eadie, B.J., Liebig, J.R., Tarapchak, S.J. & Glover, R.M. (1987) Contribution of calcite to the particle-size spectrum of Lake Michigan seston and its interactions with the plankton. *Can. J. Fish. Aquat. Sci.* 44, 1898-1914.

Vanderploeg, H.A. & Ondricek-Fallscheer, R.L. (1982) Intersetule distances are a poor predictor of particle-retention efficiency in *Diaptomus sicilis*. *J. Plankton Res.* 4, 237-244.

Vanderploeg, H.A. & Paffenhöfer, G-A. (1985) Modes of algal capture by the freshwater copepod *Diaptomus sicilis* and their relation to food-size selection. *Limnol. Oceanogr.* 30, 871-885.

Vanderploeg, H.A., Scavia, D. & Liebig, J.R. (1984) Feeding rate of *Diaptomus sicilis* and its relation to selectivity and effective food concentration in algal mixtures and in Lake Michigan. *J. Plankton Res.* 6, 919-941.

Vanni, M.J. (1986a) Fish predation and zooplankton demography: indirect effects. *Ecology* 67, 337-354.

Vanni, M.J. (1986b) Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. *Limnol. Oceanogr.* 31, 1039-1056.

Vanni, M.J. (1987a) Effects of nutrients and zooplankton size on the structure of a phytoplankton community. *Ecology* 68, 624-635.

Vanni, M.J. (1987b) Effects of food availability and fish predation on a zooplankton community. *Ecol. Monogr.* 57, 61-88.

Viner, A.B. (1985) Thermal stability and phytoplankton distribution. *Hydrobiologia* 125, 47-69.

Vinyard, G.L. & O'Brien, W.J. (1976) Effects of light and turbidity on the reactive distance of bluegill (*Lepomis machrochirus*). *J. Fish. Res. Bd. Can.* 33, 2845-2849.

Vollenweider, R.A. (ed.) (1974) "A Manual on Methods for Measuring Primary Production in Aquatic Environments". Blackwell, Oxford. 225pp.

Vyhnálek, V. (1983) Effect of filter-feeding zooplankton on phytoplankton in fish ponds. *Int. Rev. Gesamten. Hydrobiol.* 68, 397-410.

Walker, K.F. (1979) Regulated streams in Australia: the Murray-Darling river system. In Ward, J.V. & Stanford, J.A. (eds.) "The Ecology of Regulated Streams". Plenum, New York. pp. 143-163.

Walker, K.F. (1986) The Murray-Darling river system. In Davies, B.R. & Walker, K.F. (eds.) "The Ecology of River Systems". Junk, Dordrecht. pp. 631-659.

Walker, K.F. & Hillman, T.J. (1977) "Limnological survey of the River Murray in relation to Albury-Wodonga, 1973-1976". Albury-Wodonga Development Corporation. 256pp.

Walsby, A.E. (1972) Structure and function of gas-vacuoles. *Bact. Rev.* 36, 1-32.

Walsby, A.E. & Reynolds, C.S. (1980) Sinking and floating. In Morris, I. (ed.) "The Physiological Ecology of Phytoplankton". Blackwell, Oxford. pp. 371-412.

Wartenberg, D., Ferson, S. & Rohlf, F.J. (1987) Putting things in order: a critique of detrended correspondence analysis. *Am. Nat.* 129, 434-448.

Waters, T.F. (1977) Secondary production in inland waters. *Adv. Ecol. Res.* 10, 91-164.

Watts, E. & Young, S. (1980) Components of *Daphnia* feeding behaviour. *J. Plankton Res.* 2, 203-212.

Webster, K.E. & Peters, R.H. (1978) Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. *Limnol. Oceanogr.* 23, 1238-1245.

Welschmeyer, N.A., Copping, A.E., Vernet, M. & Lorenzen, C.J. (1984) Diel fluctuation in zooplankton grazing rate as determined from the downward vertical flux of pheopigments. *Mar. Biol.* 83, 263-270.

Wetzel, R.G. (1975) "Limnology". Saunders, Philadelphia. 743pp.

Williams, W.D. (1966) Conductivity and the concentration of total dissolved solids in Australian lakes. *Aust. J. Mar. Freshwater Res.* 17, 169-176.

Williams, W.D. (1980a) "Australian Freshwater Life. The Invertebrates of Australian Inland Waters". (2nd edn.) Macmillan, Melbourne. 321pp.

Williams, W.D. (1980b) Distinctive features of Australian water resources. In Williams, W.D. (ed.) "An Ecological Basis for Water Resource Management". A.N.U. Press, Canberra. pp. 6-11.

Williams, W.D. (1982) Australian conditions and their implications. In O'Loughlin, E.M. & Cullen, P. (eds.) "Prediction in Water Quality". Australian Academy of Science, Canberra. pp. 1-10.

Wilson, D.S. (1973) Food size selection among copepods. *Ecology* 54, 909-914.

Wright, J.C. (1958) The limnology of Canyon Ferry Reservoir. I. Phytoplankton - zooplankton relationships in the euphotic zone during September and October, 1956. *Limnol. Oceanogr.* 3, 150-159.

Young, S., Taylor, V.A. & Watts, E. (1984) Visual factors in *Daphnia* feeding. *Limnol. Oceanogr.* 29, 1300-1308.

Zankai, N.P. (1983) Ingestion rates of some *Daphnia* species in a shallow lake (Lake Balaton, Hungary). *Int. Rev. Gesamten. Hydrobiol.* 68, 227-237.

Zaret, R.E. (1980a) The animal and its viscous environment. In Kerfoot, W.C. (ed.) "Evolution and Ecology of Zooplankton Communities". University Press of New England, New Hampshire. pp. 3-9.

Zaret, T.M. (1980b) "Predation and Freshwater Communities". Yale University Press, New Haven, Connecticut. 187pp.

Zettler, E.R. & Carter, J.C.H. (1986) Zooplankton communuity and species responses to a natural turbidity gradient in Lake Temiskaming, Ontario - Quebec. *Can. J. Fish. Aquat. Sci.* 43, 665-673.