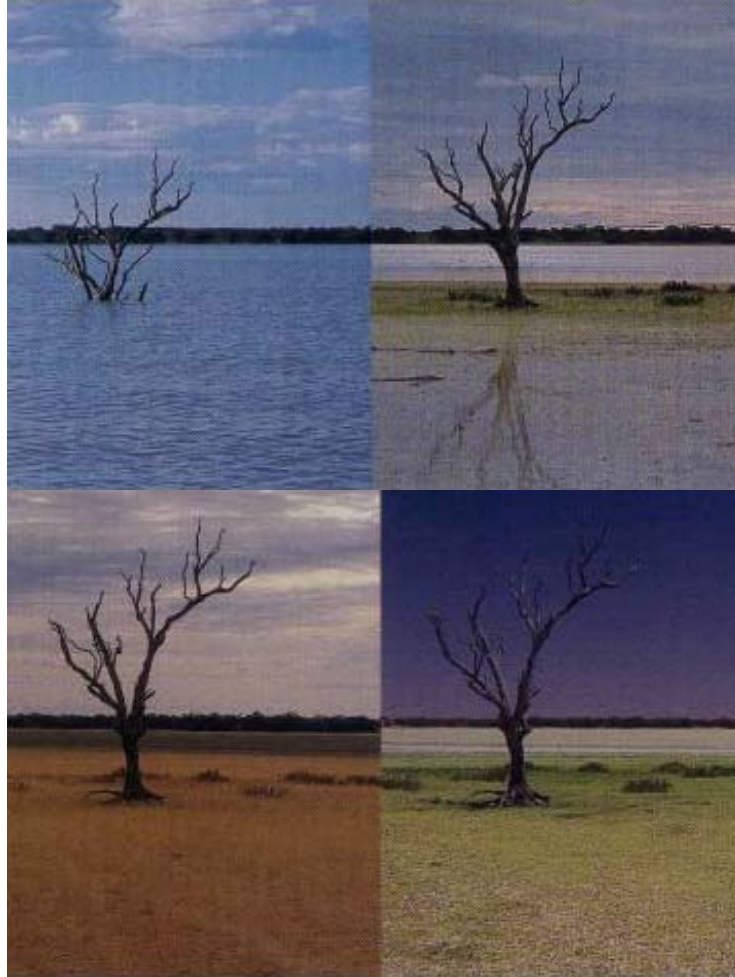


Ecology and management of Ephemeral Deflation Basin Lakes

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Cover photo: Lake.Malta throughout a wet/dry cycle (B.Gawne).

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SUMMARY

Ephemeral Deflation Basin Lakes (EDBL) are a critical component of lowland river floodplain ecosystems that provide habitat for large numbers of animals and plants and provide a number of environmental services, including water purification and flood mitigation. EDBL also represent a valuable resource for human activities with many being used as water storages to supply domestic and agricultural needs.

Water resource development has altered the hydrological cycles of many EDBL, such as the Menindee Lakes in western New South Wales. The Menindee Lakes is an integral part of the Murray-Darling Basin's water supply infrastructure. Flow regulation since the late 1960s has altered the periodicity of flooding and complete drying events experienced by each of the Menindee lakes. The lakes are now wetter for longer and the dry periods much shorter. Such changes of the hydrological cycle are considered a key threat to wetland ecosystem integrity and have been associated with declines in wetland water quality, diversity and productivity. The cycle of wetting and drying is believed to be key to the rehabilitation of these systems within the current supply regimes. At present, however, our conceptual understanding of how hydrological change impacts on EDBL ecosystem integrity is fragmented, and much of the available information is derived from non-arid zone systems.

This study sought to provide information linking hydraulic regime and ecological processes within the Lakes, which can be used to support the development of environmentally sensitive management processes. The specific objectives of the project were to develop an understanding of the ecological responses of EDBL water quality and biota to flooding and drying through a mixture of field surveys, targeted experiments and modelling, and to produce management guidelines for water regime management of these systems. This report addresses the first of these aims. Guidelines for the management of EDBL are presented as a separate document (Scholz and Gawne 2004¹).

Monitoring

During the 1996-2003 study-period, the Menindee Lakes experienced two major drying episodes: August 1997 - August 1998 and November 2001 – February 2004. These coincided with El Niño Southern Oscillation (ENSO) events, during which Darling River inflows to Lake Wetherell were reduced. ENSO events occur at frequencies ranging from 2-8 years and impact more on summer than winter precipitation within the Darling River catchment. Prediction of the ENSO index offers a mechanism for assessing probabilities of annual river discharge into the Menindee Lakes, and for adjusting management actions accordingly.

EDBL ecosystem processes are driven by a range of factors, such as season, trophic interactions and cycles of flooding and drying, that operate over different temporal scales. Despite potentially complex interactions between these factors, generalized responses to flooding and drying were identified, especially during the initial post-flood and late drying phases when hydrological influences are likely to be greatest. Responses of water quality, phytoplankton, zooplankton and fish communities to episodes of lake drying and re-flooding identified through the current study period (1996-2003) are summarised below.

¹ Scholz O. and Gawne B. (2004). Guidelines for the management of ephemeral deflation basin lakes. Report to the Murray-Darling Basin Commission, Canberra. Project R1011). Murray-Darling Freshwater Research Centre, Lower Basin Laboratory, Mildura.

As lakes dried, salinity, total nitrogen and phosphorus concentrations and TN:TP ratios increased. There was no overall response of turbidity to changes in water level. Rates of change in water quality increased as water levels fell. In the larger storages this effect was most marked once water levels fell below 56.16-57.03 mAHD (0.89-1.76 m depth) in Lake Pamamaroo, 55.99-56.57 mAHD (1.64-2.22 m depth) in Lake Menindee, and 56.12-56.75 mAHD (3.44-4.07 m depth) in Lake Cawndilla. Changes in water quality as lakes dried were driven primarily by evaporation once lakes became hydraulically isolated. However, little information currently exists regarding the role of groundwater interactions.

Changes in water quality in response to re-flooding generally reflected the quality of the inflowing waters. Post-inundation increases in turbidity were short lived. Flooding stimulated a pulse of inorganic nitrogen and phosphorus that declined to low concentrations within 3 months after flooding. Relatively more inorganic nitrogen than phosphorus was made available following flooding to support biotic production. Flooding inflows appeared to be more important than autochthonous releases from the sediments in determining post-inundation nutrient status, and hence of productive potential. However, significant releases of nutrients from the sediments were observed in Lake Menindee after flooding in 1998.

Increases in the frequency and duration of river flood pulses increase allochthonous inputs to floodplain wetlands. It also reduces the severity of drying events and thus also the potential for sediment nutrient transformations. Under these circumstances, organic matter may be expected to accumulate in EDBL causing them to function as net nutrient sinks. Indeed, this appears to be the case in lakes Malta, Balaka and Bijiji.

Hydraulic regulation has also modified the nature of connections between each of the lakes below the Menindee Main Weir and their primary source of water, the Darling River. Instead of being directly connected to the Darling River, the lakes are now connected in series, with riverine inflows directed through only one lake, Lake Pamamaroo. The current hydraulic regime has increased the potential for sediment, salt and nutrient loading in these lakes. There is thus a real need to address the connectivity of these lakes and the potential for hydraulic management to address the issue of loading.

Phytoplankton assemblages (with the exception of cyanobacteria) varied more in response to flooding and drying than they did to season. Lake drying stimulated increases in phytoplankton abundance through population growth and/or evaporative concentration. Lake drying also led to predictable changes in phytoplankton community composition, involving amongst others, increases in potentially toxic cyanobacterial species, especially where drying coincided with warmer summer temperatures. Lake flooding stimulated increases in phytoplankton abundance through both external loading and population growth. Whilst temporal changes in phytoplankton community structure through cycles of lake flooding and drying could be attributed to processes such as external loading and evaporative concentration, respectively, and to growth, mediated by changes in nutrient availability and turbidity, we suggest that 'top-down' trophic cascading may play an equally important role in regulating the development of potentially nuisance algal blooms, especially as lakes dried.

Phytoplankton community structure in the larger lakes was also affected by the passage of water from Lake Pamamaroo to Lake Cawndilla. Changes in community structure evident through these serially connected lakes were characterised by increases in median cell density, increases in Chlorophyceae, and decreases in Cryptophyceae and Bacillariophyceae. These changes corresponded with progressive reductions in median turbidity and increases in median total phosphorus concentrations.

Temporal variations in zooplankton communities were related to both season and drying. Rotifer communities were generally more diverse and abundant than were crustaceans. Rotifer assemblages varied more in response to season than did microcrustacea. Stronger

positive correlations of rotifers with phytoplankton biomass suggested that seasonal changes in community structure were related to food preference and availability. Lake drying accounted for as much of the observed temporal variation of rotifers as did season, with lower temperatures and lake drying leading to reductions in both diversity and concentration. More of the variation encountered in microcrustacean assemblages was explained by lake drying than by season, and involved increases in both diversity and abundance. Changes in zooplankton community structure driven by both season and lake drying may thus modify food web interactions through changes in availability to fish and grazing pressure on lower trophic levels. Post-inundation responses of zooplankton were not examined from field data, but were from mesocosm investigations. These are discussed below.

Eleven species of fish were recorded from the Menindee Lakes between 1997 and 2002. As lakes dried, fish abundances declined and the fish community became simplified. This led to the loss of the only piscivore (golden perch) and to the numerical dominance of smaller planktivorous fish species (mosquitofish and smelt). Lake flooding re-established a more diverse fish fauna that was dominated numerically by carp, goldfish, bony herring and golden perch. Golden perch were amongst the first to re-invade filling lakes and appeared to move sequentially through the Menindee system as each of the lakes filled. Whilst the extent of lake drying influenced the within-lake persistence of fish species and their contribution to post-flood assemblages, the composition of post-flood fish assemblages depended largely on the duration of lake connection with the main stream and on the momentary structure of the riverine fish community.

Flooding during 1998 coincided with recruitment in golden perch and carp populations. Ageing of golden perch larvae caught within the Menindee Lakes late in 1997 indicated that spawning had occurred over an extended period between May and September, much earlier and for longer and at lower temperatures than previously reported from elsewhere in the Basin. The responses to flow/water level and temperature reported here and from throughout the Murray-Darling Basin clearly indicate that spawning activity in golden perch is quite variable and not exclusively dependent on either flooding or season.

Targeted investigations

In addition to the monitoring program discussed above, which identified responses to flooding and drying, a series of targeted investigations helped identify more specifically ecosystem responses to differences in hydraulic regime. These investigations included an examination of plant seed banks through the Menindee system and a series of mesocosm-scale studies that allowed us to examine post inundation responses of aquatic processes to experimental manipulations that would otherwise not have been possible at the whole-lake scale.

Hydrology is considered to be an important structuring agent of wetland seed banks and plant communities. The plant seed bank of the smaller and more ephemeral Lake Malta was much larger, more diverse, contained more species with persistent seed banks, and was more evenly distributed throughout the elevation range than that recorded in the much larger and relatively more permanent lakes Tandure, Menindee and Cawndilla. These differences were consistent with hypothesised hydraulic structuring processes. In the larger lakes, greater wave energy and steeper littoral gradients impacted negatively on the establishment of lakeshore plants, reducing the potential for plant regeneration, seed production, and seed deposition to a narrow littoral zone. Further, regulation has decreased the connectivity of these larger lakes with other elements of the river system thereby reducing the potential for external seed contributions, especially during floods when seed loads are likely to be highest.

In the first of four mesocosm-scale experiments we examined how the duration of the drying phase impacts on post-inundation responses. More terrestrial vegetation was present prior to inundation of experimental ponds that had been dry for longer (6½ vs 3½ months). Ponds that had been drier for longer developed more algae and supported a greater diversity of zooplankton. These data suggested that the development of lakebed vegetation during periods of lake exposure plays a potentially important role in structuring post-inundation aquatic function.

In the second experiment, in which we examined the effects of vegetation and grazing on post inundation responses, the presence of lakebed vegetation had little impact on aquatic production (measured indirectly as algal biomass), or zooplankton densities, but did lead to greater zooplankton diversity. The absence of a treatment effect on aquatic production we believed was due to the indirect nature of its measurement, which did not include the epiphytic algae attached to submerged vegetation or the impact of grazing.

In the third mesocosm experiment, in which we examined the effects of organic matter and habitat structure provided by vegetation on post-inundation responses, the presence of lakebed vegetation stimulated primary production, but had little impact on zooplankton density or diversity. Habitat structure did not affect zooplankton abundance or diversity but multivariate analysis did reveal an effect on community structure.

In the fourth experiment we examined the role of bottom-up and top-down effects in determining post-flood productivity in ephemeral lakes. We manipulated hydrological regime (keeping some sediments wet and allowing others to dry completely) and predator presence (the addition or exclusion of predators). Our results indicated that both predator presence and nutrient releases from dried sediments did indeed impact on lake response to flooding after a drying event. Whilst there were no differences in net primary production between treatments, drying did stimulate secondary production. Although net primary production did not differ between experimental treatments, the partitioning of production between planktonic and benthic phases did, modifying the availability of food to plankton grazers and altering metabolic pathways (*e.g.* microbial loop).

Our experiments demonstrate the potentially important role of lake drying on post-inundation aquatic ecosystem function. Firstly, drying facilitates the mineralisation of sediment nutrients and the establishment of lakebed vegetation, both of which contribute organic matter and nutrients following inundation, thereby stimulating system productivity. Secondly, the presence of inundated vegetation plays an important role in providing the habitat diversity necessary to support greater biodiversity. Finally, drying has the potential to modify metabolic pathways, and that biotic responses to such changes depend on the suite of organisms present in the system. Developing a better understanding of the factors and the interactions that influence an ephemeral wetland's response to flooding and drying will help explain variable responses to flooding observed in natural systems.

Conceptual model of EDBL function

Whilst the pressure placed on managers to achieve both environmental and water resource objectives has increased, the knowledge required to achieve these objectives is not readily available. Although there is an increasing body of knowledge concerning various aspects of the ecology of these systems, such knowledge is fragmented and is not integrated within a conceptual framework appropriate to EDBL that encompasses aspects of both wet and dry lake phases. We reviewed the effects of flooding and drying on lakes and used this to propose a conceptual model that identifies 5 stages in the cycle of flooding and drying.

- 1 The first phase occurs as a dry or partially dried lake floods. This initial flooding phase is characterised by high habitat abundance and diversity provided primarily by inundated terrestrial vegetation, such as grasses, and by high productivity fuelled by the inflow of nutrients and organic matter with the floodwaters and by releases from the sediments and the decomposition of inundated terrestrial vegetation. Changes in primary and secondary production following wetland inundation tend to follow a predictable successional sequence.
- 2 During the late flood phase, fish populations increase due to both immigration and local recruitment, and provide increasing top-down pressure on secondary production. As water levels continue to increase, the inundation of littoral fringe vegetation, such as lignum, black box and red gum provides additional aquatic habitat, although at this time also much of the habitat structure and complexity across the lakebed provided by inundated grasses and herbs begins to decline as they decompose.
- 3 During the late wet phase, fish populations are established, the productive pulse fuelled by nutrient releases from the sediments and decomposing vegetation subsides, and habitat structure/complexity is restricted to the littoral fringe.
- 4 During the drying phase the lake contracts, littoral habitat is exposed, water quality changes (elevated salt, nitrogen and phosphorus concentrations) and becomes less buffered to diel fluctuations in temperature. During this period aquatic organisms become concentrated and once the lake becomes too shallow to offer fish refuge, avian predation of fish increases. These processes impact on trophic interactions. This process continues until physical conditions become too harsh and the lake ultimately dries.
- 5 Finally, once the lakebed has been exposed it becomes an important terrestrial habitat for a range of plants and animals.

This conceptual model incorporates aspects of the Flood Pulse Concept (FPC), Trophic Cascade/Food Web and Geomorphic Trophic models. Whilst floods have the potential to stimulate productivity through bottom-up forcing, as suggested by the FPC, and to create aquatic habitat, these ecological benefits are to a large extent reliant on the occurrence of dry phases that allow lakebed vegetation to develop, organic matter to accumulate and sediment nutrients to be mineralised. Our model also indicates that lake wetting and drying influences the significance of top-down forcing on food webs by key predators as suggested by the trophic cascade model. The Geomorphic-Trophic model also plays a role in our model in so far as some of the observed changes appear to be driven by the changes in lake shape and size that occur as the lake dries.

Although data from other ephemeral systems were used to validate several of the key concepts presented in our model, we recognise that the knowledge base on which our model is founded is far from complete and that there may be areas where the model is inappropriate. We believe, however, that this synthesis of the available information will prove a useful guide to identifying management targets and likely outcomes of management actions.

Conclusions/recommendations

Water resource development has modified the hydrological regimes of many EDBL, and this is widely recognised as the key threat to wetland function (*e.g.* Bunn *et al.* 1997, Puckridge 1999, Kingsford 2000a,b). Hydrology can have a significant effect on a wide range of ecosystem characteristics including water quality, nutrient cycling, primary production and biotic community structure and trophic interactions. Manipulating elements of the water regime and habitat connectivity thus represent the most significant tools available to managers for affecting ecological change and achieving desired ecological outcomes.

As a consequence of regulation many EDBL, including each of the Menindee Lakes, are now wetter for longer and dry periods are shorter or entirely absent. Recognition that the loss of a dry phase is as a major degrading force (*e.g.* Briggs 1988) has led to recommendations that these be reintroduced to a number of naturally ephemeral wetlands within the Murray-Darling Basin (*e.g.* Hydrotechnology 1995, Briggs 1998). However, rehabilitation may not in fact require complete drying. Partial drying or the reinstatement of greater variability in water levels may be sufficient to stimulate the development of vegetation and affect beneficial changes in nutrient processing, productivity and trophic structure.

Vegetation management should be the highest priority when managing a specific wetland. Vegetation is often considered a key indicator of a systems ability to support key processes and diverse biota and is often the primary focus of management actions (*e.g.* Reid and Brooks 1998, Tucker *et al.* 2002), however the focus of these actions will vary according to wetland type. In wetlands such as billabongs the focus is often on macrophyte communities. However, EDBL generally lack macrophytes and so much of the aquatic habitat values in EDBL are provided by inundated terrestrial lakebed vegetation. The loss of complete or partial lake drying events reduces the opportunity for lakebed vegetation to develop, thereby compromising post-inundation habitat values and productivity. The importance of vegetation as a driver of aquatic productivity and habitat need to be considered when developing management strategies for dry lakes that may include grazing and cropping activities.

At a landscape scale a diversity of hydrological regimes will produce a variety of wetlands that support different biotic communities. As a consequence, management of any specific wetland should be undertaken within a landscape context. Ensuring that there are a variety of flooding and drying regimes and a variety of depths amongst within wetland complexes will ensure the persistence of species and thus sustain system biodiversity.

It is widely acknowledged that Australia has a highly variable and unpredictable climate and under natural conditions the flooding and drying regime in any particular wetland will vary through time. This reinforces the need to consider the landscape in the management of wetlands. If the suitability of a wetland as habitat for any given species varies through time, then the need to disperse becomes very important and therefore connections among wetlands in the landscape should be managed explicitly. This is particularly important during drying phases or drought when animals need to find refuges if they are to survive. The work presented here reveals that the connection between a wetland will influence the movement of both materials and organisms into and out of the wetland.

The imposition of a dry phase on a wetland requires consideration of refuges for aquatic organisms. This does not necessarily mean ensuring that every organism survives the dry phase, but rather that species can persist in the landscape and are available to recolonize the wetland upon re-inundation. For fish, this means ensuring there is some permanent water in the landscape and for zooplankton and plants that the lakebed is managed with due regard for its role as a propagule bank.

While we have progressed some way toward understanding how ephemeral wetlands function, we have much more to do in understanding the impacts of change at larger spatial and temporal scales. Our model should, therefore, be viewed as a means for improving our ability to predict the outcomes of water resource development on individual wetlands and possibly providing guidance for attempts at restoration or rehabilitation of those wetlands.

PROJECT OVERVIEW

Background

Wetlands, including Ephemeral Deflation Basin Lakes (EDBL), are a critical component of lowland river floodplain ecosystems, providing habitat for large numbers of animals and plants, and environmental services such as water purification and flood mitigation. EDBL also represent a valuable resource for human activities with many being used as water storages to supply domestic and agricultural needs.

Water resource development, through the installation of weirs and levies, has led to numerous changes in EDBL. One of the major impacts of such development has been the alteration of the hydrological cycles, particularly the complete or partial loss of drying events and concomitant increases in the duration of inundation. These changes have been associated with declines in wetland water quality, diversity and productivity. The cycle of wetting and drying is believed to be key to the rehabilitation of these systems within the current supply regimes.

At present, our conceptual understanding of how changes in hydrology impact on EDBL ecosystem integrity is fragmented, and much of the available information is derived from temperate and tropical systems. In response to loss of ecosystem integrity, managers are seeking a more appropriate balance between exploitation and conservation. Examples of these initiatives include;

- Menindee Lakes Ecologically Sustainable Development Plan,
- Darling Anabranch Management Plan,
- Lake Victoria Management Plan, and
- Hattah Lakes Environment Action Plan.

Alteration of wetland hydrologic regime has been identified as the most important threat to wetland function (Bunn *et al.* 1997). Perhaps not surprisingly, the complete or partial loss of drying events appears to affect nearly every aspect of wetland ecology, including water quality, diversity and productivity.

Lake drying plays a potentially significant role in driving subsequent post-inundation aquatic processes, largely through its effects on the sediments. Sediments represent both the largest source and the largest sink for nutrients in freshwater ecosystems (Baldwin and Mitchell 2000). The drying of sediments affects the rate and mechanism of organic matter breakdown by re-aerating sediments, thereby allowing faster aerobic decomposition processes to flourish (Metzler and Smock 1990, Pattee and Chergui 1994, Nias 1999). Dried lakebed sediments have been shown to release a pulse of nitrogen (mainly as nitrate and ammonia) upon flooding (Qiu and McComb 1996, McComb and Qiu 1998, Baldwin and Mitchell 2000), and drying may also affect the release and uptake of phosphorus from sediments (Baldwin 1996, Mitchell and Baldwin 1998). Lake drying thus stimulates rates of carbon and nutrient cycling, which in turn may drive observed increases in productivity and diversity, but these linkages have yet to be demonstrated.

The loss of a dry phase is thought to significantly reduce wetland productivity, although evidence is limited. Invertebrate production (measured as abundance) has been found to increase after inundation (Maher and Carpenter 1984, Boutlon and Lloyd 1992, Jenkins and Boulton 1998). Macrophyte production has also been found to be greatest in the twelve months following a drying event (Briggs and Maher 1985). The loss of a dry phase seems to make wetlands less attractive to waterbirds (Thornton and Briggs 1994), while increases in water levels (*i.e.* flooding) are associated with increases in bird numbers (Frith 1982, Maher

and Carpenter 1984). The effect of dry phases on other groups, such as algae and fish, has received much less attention.

Ephemeral wetlands may have higher diversity than permanent wetlands (Belk 1998, Butcher 1999). Although in some cases the increase in diversity is partly due to the successional sequence initiated by flooding (Lake *et al.* 1989), ephemeral wetlands do tend to support a suite of early colonists that are usually absent from permanent wetlands (Williams 1998). A dry phase does not always increase diversity (Maltby 1991, Quinn *et al.* 2000), however, and we cannot confidently predict the effect of a dry phase on diversity in any given system. In particular, we do not understand how modification of hydrological regime affects a lake's response to drying.

Far less work has been done on the impact of prolonging the dry phase of an ephemeral wetland. The two groups of organisms that have been examined are macrophytes and zooplankton. Both groups rely on a combination of drought resistant stages and dispersal to survive prolonged dry periods. For both groups, prolonging the drying phase reduces the survival of seeds and eggs and potentially also lowers the diversity of germinating/emerging individuals when inundation occurs (*e.g.* Boulton and Lloyd 1992). It should be mentioned, however, that much of this work has been performed in laboratory experiments. The work of Jenkins in the Teryawynia and Menindee systems indicates that at least for zooplankton, colonisation from the incoming floodwaters has a significant role to play in determining the diversity of a flooding lake (Jenkins and Boulton 2003). This does, however, create issues for managers as floodwaters have higher abundances of zooplankton than base flows, and so the response of a lake to managed flooding may differ from that of a natural flood.

While increasing the duration of wet and dry phases is obviously important, they are not the only hydrological changes that have affected EDBL. As a consequence, managers require information on the role of other elements of wetland water regime that may be manipulated to improve wetland condition. These elements include variation in the depth of the lake, and the degree of lake inundation or drying.

Surveys of the distribution of littoral plants along the lower Murray River have found that 41 of 48 species occurred where fluctuations in water level were greatest (Walker *et al.* 1994, Blanch *et al.* 1999, 2000). Only a few species are dependent on permanently or very frequently flooded sites. As a consequence, increasing the variability of water levels can lead to the development of a more diverse plant community. We suspect that there may be important links between the formation of an abundant and diverse plant community on lakebeds and the hydrologic regime, and thus also on the ecology of the flooded lake, given that vegetation provides potentially important aquatic habitat, especially in EDBL where habitat structure and diversity is characteristically very low.

While flow regime has a significant impact on wetland ecology, it is important to consider the scale at which management and diversity conservation takes place. While ephemeral lakes may be more diverse, there may be some species that are reliant on permanent wetlands. As a result, management needs to manage wetland complexes rather than individual wetlands, as no single management strategy will benefit all species (*e.g.* Michener and Haeuber 1998, Schmidt *et al.* 1998), and some species may be put at risk by an overzealous desire to maximise diversity in individual wetlands. In EDBL and other wetlands in the Basin we need to determine if there are species that are found only in permanent wetlands, and develop strategies that are sensitive to their needs. This can only be achieved if the systems being managed are understood.

Objectives

The focus area for this study was the Menindee Lakes System, in western New South Wales, Australia. The Menindee Lakes is an integral part of the Murray-Darling Basin's water supply infrastructure, and in addition to its role in flood mitigation, this complex of arid-zone ephemeral deflation basin lakes (EDBL) is an important natural resource, providing significant breeding and nursery grounds for native fish within the Barwon-Darling River system (Harris 1995) and important wetland habitat for waterbirds (ANCA 1992; Jaensch *et al.* 2002). Due to their importance, the community, in partnership with government agencies, is in the process of reviewing the management of the Menindee Lakes. This study sought to provide information linking flow regime and ecological processes within the Lakes, which can be used to support the development of a management plan that is sensitive to environmental processes.

The widespread move to improve management of EDBL offers the community a chance to 1) enhance the environmental value of EDBL, 2) minimise the impact of regulation, and in some instances 3) produce significant water savings. To assist the community to achieve these goals this study sought to generate ecological information about EDBL to underpin their management. The specific objectives of the project were:

- 1 to develop an understanding of the ecological responses of EDBL water quality and biota to wetting and drying, and
- 2 to produce management guidelines for water regime management of these systems.

This report addresses the first of these aims and involved a mixture of field surveys, small-scale experiments and modelling as described below. Guidelines for the management of EDBL are presented as a separate document (refer to Scholz and Gawne 2004).

In Section 1 we review the hydrology of the Darling River, the principal source of water stored within the Menindee Lakes, review the impact that regulation has had on the hydrology of the Menindee Lakes since the 1960s, and describe the changes in water levels within the Lakes that occurred during the current study period (1996-2003). This hydraulic information provides a benchmark against which ecosystem responses to lake drying and flooding can be examined.

In Section 2 we review ecosystem responses, including water quality (Section 2.1), phytoplankton (Section 2.2), zooplankton (Section 2.3) and fish communities (Section 2.4), to wetting and drying for lakes within the Menindee System.

In Section 3 we test specific hypotheses relating to the interaction of hydrology and ecosystem function. Specifically, we examined the distribution and composition of plant seed banks present within lakes of differing hydrology, and used mesocosm-scale experimental ponds to examine post-inundation responses to changes in drying duration, lakebed grazing, habitat structure and predation pressure. Mesocosms have been used elsewhere to examine interactions between water regime and nutrients (Briggs *et al.* 1985), invertebrates (Nielsen *et al.* 1999) and macrophytes (Nielsen and Chick 1997, Brock 1998). Whilst the use of mesocosms overcomes difficulties inherent in imposing hydrological and experimental manipulations at the whole-lake scale, and provides for within-treatment replication that would otherwise not be possible, mesocosms have the potential to introduce certain scale-related artefacts. This prevents the scaling-up of quantitative results, but not of key processes.

Whilst the pressure placed on managers to achieve both environmental and water resource objectives has increased, the knowledge required to achieve these objectives is not readily

available. This is despite the increasing body of knowledge concerning various aspects of the ecology of ephemeral systems. Such knowledge is fragmented and is not integrated within a conceptual framework appropriate to EDBL that encompasses aspects of both wet and dry lake phases. In Section 4 we examine existing conceptual models that describe aspects of ephemeral lake ecology, review our knowledge of the ecological impacts of drying and inundation, and from these develop an heuristic conceptual model of EDBL function.

Finally, in Section 5 we test the validity of components of the conceptual model derived in Section 4 by examining field data obtained from other ephemeral systems.

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1: Hydrology of the Menindee Lakes System

O. Scholz

Introduction

The Menindee Lakes, situated on the Lower Darling River in NSW, have been subject to hydraulic regulation since the 1960s. Water resource development has the capacity to significantly modify aspects of the natural hydrological regime, including the frequency, duration, timing, magnitude and variability/predictability of flooding and drying events. Such alterations to wetland water regimes have been identified as the single most significant factor in disturbing wetland ecological processes and are thought responsible for declines in wetland values, such as water quality, productivity, habitat structure and biodiversity (Boulton and Lloyd 1992, Bunn *et al.* 1997, Boulton and Jenkins 1998).

In this section we review the hydrology of the Darling River, the source of most of the water stored within the Menindee Lakes, review the impact that regulation has had on the hydrology of the Menindee Lakes since the 1960s, and lastly, describe the changes in water levels within the Lakes that occurred during the current study period (1996-2003). This hydraulic information is needed to provide a benchmark against which ecosystem responses to lake drying and flooding can be examined.

Darling River

Australian dryland rivers, such as the Darling River, are naturally amongst the most hydrologically variable in the world (Puckridge *et al.* 1998). This is largely due to highly variable rainfall, low rainfall-runoff and high rates of evaporation. However, water resource development, through the construction of headwater dams, floodplain levies, main-channel weirs and the licensing of water extractors, has substantially altered the pattern of Darling River flows reaching the Menindee Lakes.

Darling River flows are dominated by subtropical summer monsoon precipitation and to a lesser extent by temperate winter storms. Both of these are strongly influenced by El Niño-Southern Oscillation (ENSO) cycles that are driven by changes in sea surface temperatures (Simpson *et al.* 1993, Chiew *et al.* 1998). For example, years with higher than mean sea surface temperature in the eastern equatorial Pacific Ocean often have lower than average rainfall and river discharges in SE Australia. ENSO events occur at frequencies ranging from every 2-8 years and impact more on summer than winter precipitation within the Darling River catchment. Although forecasting of ENSO-related sea surface temperatures from geophysical model calculations provides a potential mechanism for estimating probabilities of annual river discharge, such calculations are still in their infancy.

Upstream extractions of water from the Darling River have increased markedly since 1960. Between 1960 and 1994, the number of licenced extractors between Mungindi and Menindee increased from 20 to 267. Between 1936-96 mean and median flows in the Darling River at Wilcannia declined by 29% and 73%, respectively, indicating that small flood events (average recurrence interval <2 years) have been more significantly impacted than larger less frequent flow events (Thoms and Sheldon 2000).

Under 'natural' conditions (*i.e.* no regulation or diversions) maximum flows at Wilcannia occurred in March-April and September-October. Most water extraction occurs during summer, thereby altering the seasonal distribution of downstream flows. Water resource

development has thus increased both the predictability and consistency of annual and monthly Darling River flows entering the Menindee Lakes (Thoms and Sheldon 2000).

Since 1950, annual Darling River inflows to the Menindee Lakes ranged from 106-13,617 GL.yr⁻¹ (median 1973 GL.yr⁻¹) (Figure 1.1). By comparison precipitation contributes about 110 GL.yr⁻¹ (243.5 mm.yr⁻¹) to the Lakes. Monthly rainfall averages range from 7.5-10.7 GL (16.4-23.6 mm.month⁻¹). Surface runoff into the Lakes is negligible. Evaporation accounts for losses of approximately 753.8 GL.yr⁻¹ (2500 mm.yr⁻¹) (long-term average). Monthly rates of evaporation vary considerably, ranging from 18.8 GL in June to 110.7 GL in January. Evaporation accounts for as much as 49 % of annual water losses from the system (DWR 1994; DLWC 1997).

Darling River flows recorded at Wilcannia during the current study period (1996-2003) are shown in Figure 1.2. Most notable over this period were two periods of low flow between August 1997-August 1998 and from November 2001 until the end of the current study that coincided with ENSO events and contributed to the drying of the Menindee Lakes.

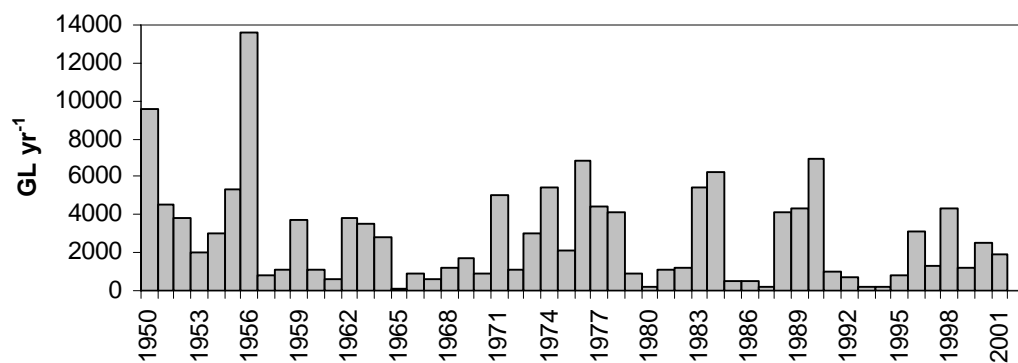


Figure 1.1: Annual Darling River inflows (GL year⁻¹) to the Menindee Lakes since 1950.

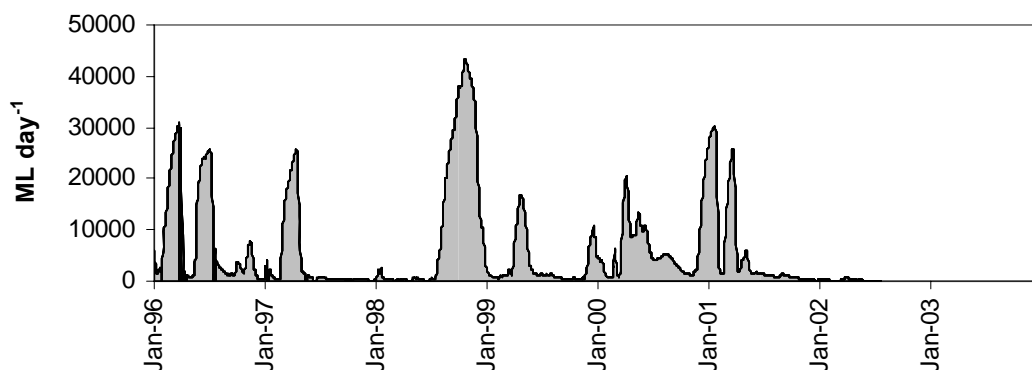


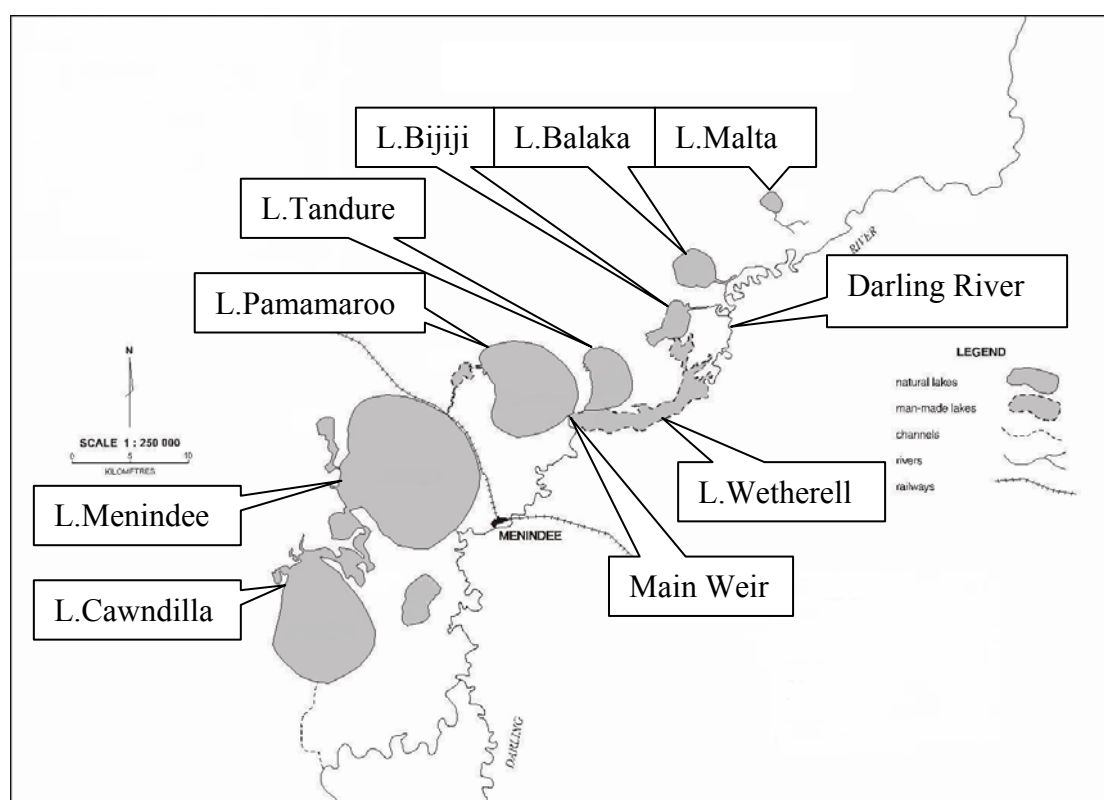
Figure 1.2: Darling River flows (ML day⁻¹) recorded at Wilcannia from January 1996 to December 2003.

Menindee Lakes

The Menindee Lakes are a series of shallow floodplain depressions or ephemeral deflation basin lakes (EDBL) situated on the Lower Darling River in far-west NSW. These lakes were formed by the erosive action of wind, a process known as deflation. On the eastern (lee) shorelines of the lakes are distinctive dunes called lunettes, formed by the deposition of lakebed material. The size of the lunettes generally reflects the size of the lake (Bowler 1973). Whilst Seddon and Briggs (1998) identified 567 deflation basin lakes larger than 100 ha in western NSW, the Menindee Lakes are unique because of their association with a major stream unlike other dune systems in the Murray Darling Basin (*e.g.* Teryaweynya Lakes). This association, in conjunction with the demand for increased supply and security of water, led to their development as a water storage facility during the 1960s.

The Menindee Lakes have been listed in the Directory of Important Wetlands (Environment Australia 2001) in Australia, as they are a good example of wetland type (*i.e.* EDBL) within the bioregion, provide important habitat for animals at critical stages in their life cycles, provide important refugia in drought or adverse conditions, are a significant habitat for water birds, support 1% or more of national populations of native plant or animal taxa, and support plant or animal populations that are considered endangered or vulnerable at the national level.

The Menindee Lakes Scheme comprises four major lakes: Pamamaroo, Menindee, Cawndilla and Wetherell. Lake Wetherell incorporates lakes Tandure, Bijiji, Balaka and Malta (Figures 1.3-1.6). These have a combined surface area of 457.3 km² and a storage capacity of 1613 GL at full supply level and a maximum storage capacity of 2527 GL when surcharged. The surcharge capacity is primarily reserved for flood mitigation.



■ **Figure 1.3: The Menindee Lakes System.**



■ Figure 1.4: Lakes Tandure, Pamamaroo and Menindee



■ Figure 1.5: Lake Bijiji.



■ **Figure 1.6: Lake Malta.**

The main control structure, the Main Weir, impounds the Darling River to form Lake Wetherell, to which lakes Malta, Balaka, Bijiji and Tandure are connected. Each lake within the system, with the exception of Lake Cawndilla, is individually connected to the Darling River. Lake Cawndilla is connected to Lake Menindee by Morton Bulka Channel. Water may be released from the Main Weir to the Darling River and/or to Lake Pamamaroo, which is joined in series to lakes Menindee and Cawndilla. Inlet and outlet structures allow for control of water levels in each of the storages. Water may be released to the Darling River through outlet regulators from lakes Wetherell, Pamamaroo and Menindee. Releases from Lake Cawndilla may be directed to the Great Darling Anabranh via Cawndilla Creek. No regulating structure currently exists between lakes Menindee and Cawndilla. The connecting channel between lakes Menindee and Cawndilla has a sill height of 55.50 mAHD.

Table 1.1 shows the physical and storage characteristics of each of the Menindee lakes. The emphasis of current storage operation is to reduce evaporative losses where possible by minimizing the surface area of the lakes. To achieve this, priority is given to filling Lake Wetherell to 59.80 mAHD, followed by filling lake Pamamaroo to full supply level (60.45 mAHD), then filling lakes Wetherell and Pamamaroo simultaneously to 61.67 mAHD. Once this has been achieved, Lakes Menindee and Cawndilla are filled to their respective full supply levels (59.84 mAHD). Any additional flows are used to fill, in order, lakes Wetherell and Pamamaroo then lakes Menindee and Cawndilla to their respective surcharge levels. The procedures for releasing water from the Menindee Lakes are based on the same considerations as the filling procedures, maintaining water levels in lakes Wetherell and Pamamaroo in preference to lakes Menindee and Cawndilla.

Lake	Bed level (mAHD)	Sill level (mAHD)	Full supply				Maximum surcharge	
			Level (mAHD)	Depth (m)	Area (ha)	Volume (GL)	Level (mAHD)	Volume (GL)
Malta	60.14	61.85	61.67	1.5	380	7	62.30	-
Balaka	59.23	59.78	61.67	2.4	1300	30.9	62.30	-
Bijiji	58.62	59.93	61.67	3.1	1050	25.9	62.30	-
Tandure	55.88	60.11	61.67	5.8	2190	101	62.30	-
Wetherell	-	-	61.67	-	5000	193	62.30	262
Pamamaroo	55.27	59.2	60.45	5.2	7100	270	62.00	380
Menindee	54.35	54.35	59.84	5.5	16000	600	61.50	880
Cawndilla	52.68	54.14	59.84	7.2	10000	550	61.50	720

■ **Table 1.1: Key physical characteristics of the Menindee Lakes (sources: DIPNR unpublished operation data, Bewsher Consulting 2000).**

Physical data describing the hydrological characteristics of each of the Menindee Lakes prior to regulation are scarce and that which exists is derived indirectly from Darling River flows. Estimations based on Darling River flood records from 1818-1886 (Russel 1886, cited Green 1997) suggest that ‘bank-full flows’ sufficient to inundate the Menindee Lakes, equivalent to about 22 GL.day⁻¹, occurred on average every 3.7 years. Modelling of inflows to each of the Menindee lakes prior to regulation has suggested that inflow events into each lake would have been relatively frequent. However, not all inflow events would have been sufficient to completely fill the lakes (Bewsher Consulting 1994).

Prior to regulation, lakes Cawndilla, Menindee, Pamamaroo and Tandure had similar characteristics in terms of flood frequency (Table 1.2). Inflows to these lakes would have occurred in about 30% of months, with the average frequency being one inflow per year. Larger inflows lasting more than one month would have been less frequent in lakes Menindee and Cawndilla (once every 2 years) than in lakes Pamamaroo and Tandure (once every year). The longest period of no inflows would have been about 3 years, or 4-5 years if smaller inflow events were excluded. Lake Cawndilla, being deeper and less prone to evaporative water losses would have generally been the last water body to dry during extended periods of no inflow. More frequent major inflow events and shorter periods of no inflow into lakes Tandure and Pamamaroo meant that these lakes were less likely to have experienced complete drying than lakes Menindee and Cawndilla.

In contrast to the larger lakes, lakes Malta, Balaka and Bijiji each received inflows in 15-17% of months, with the average frequency being every 2 years (Table 1.2). Excluding minor inflows, flooding would have occurred every 3 years. The longest period of no inflows would have been about 7 years, or 9-11 years if smaller inflow events are excluded. After flooding, most of the water in these smaller lakes would have drained back into the river, leaving residual pools to dry. Lake Malta would have been the first of these lakes to dry (Odeh 1994).

Lake	% of months inflow occurred (a)	Expected frequency of inflows (years) (a)	Max duration of inflows (months) (a)	Time required to dry (months) (b)	Max duration of no inflow (years) (a)
Malta	16 (14)	2 (3)	13	10	7 (11)
Balaka	17 (15)	2 (3)	14	14	7 (11)
Bijiji	15 (14)	2 (3)	12	16	7 (9)
Tandure	32 (29)	1 (1)	27	nd	3 (4)
Pamamaroo	33 (31)	1 (1)	27	nd	3 (4)
Menindee	29 (26)	1 (2)	26	24-36	3 (5)
Cawndilla	29 (26)	1 (2)	26	>36	3 (5)

■ **Table 1.2: Frequency of inflows to Menindee Lakes prior to regulation. Numbers in parentheses refer to estimates excluding small inflows of less than one month in duration. (Source: ^(a) Bewsher Consulting 1994, ^(b) Odeh 1994). nd – not determined.**

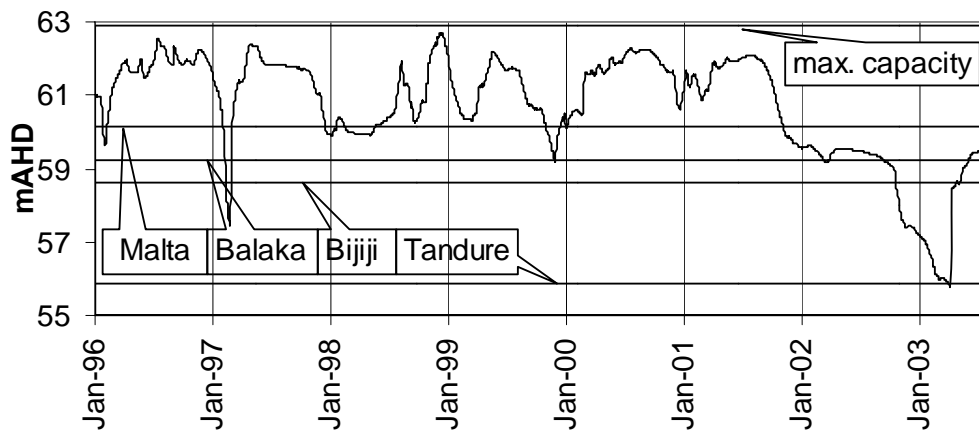
The impact of regulation on the frequency and duration of complete lake drying events was analysed here by comparing modelled ‘natural’ and ‘regulated’ hydrographs of each of the Menindee lakes between 1900-1991 using Menindee Plot software (DIPNR NSW, refer to Bewsher Consulting 2000 for model assumptions). Limitations of the Menindee Plot software, such as its lack of post-1991 data and its inability to generate ‘regulated’ simulations for lakes upstream of the Main Weir, were overcome by comparing known lake drying events since the commencement of regulation with the ‘natural’ hydrographs generated by Menindee Plot. Analysis of pre- and post-regulation wet and dry period durations and frequencies using Menindee Plot and historical data indicated that as a consequence of regulation, the main storages are now wetter for longer, and that when complete lake drying events occur they are generally shorter lived (Table 1.3).

Since the commencement of flow regulation within the Menindee lakes during the early 1960s, Lake Malta has dried completely on five occasions (in the early 1980s, 1986, 1994-5, 1998 and 2002-3), Lake Balaka four times (1986 and 1994-5, 1998 and 2002-3), Lake Bijiji three times (1983 and 1994-5, 2002-3), Lake Tandure once (2003), Lake Menindee on five occasions (1966-7, 1967-8, the early 1980s, 1994-5 and 2003), and Lake Cawndilla four times (1966-7, 1994-5, 1995-6 and 2003) (Withers 1994, Jenkins and Briggs 1997). It is worth noting that these records do not consider partial drying events, which are likely to have been important determinants of ecosystem function.

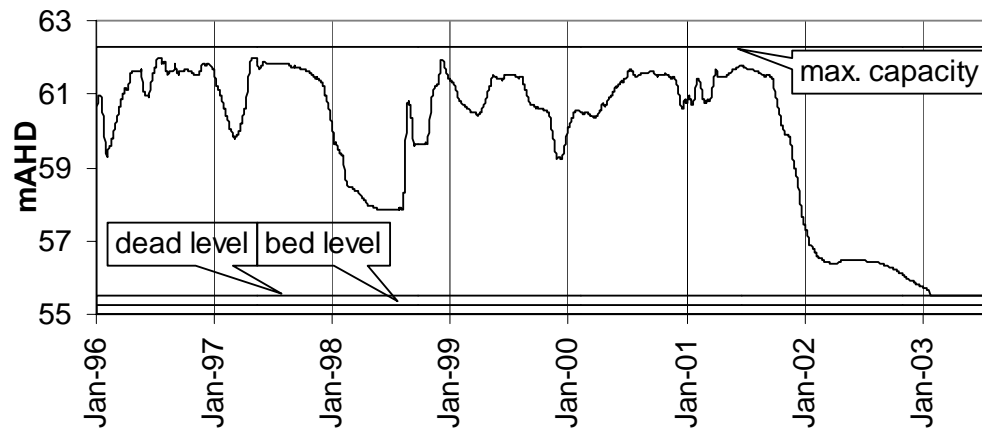
Storage volumes varied considerably during the 1996-2003 study period, ranging from full capacity to less than 1% capacity. The frequency, duration and timing of connections between lakes Malta, Balaka, Bijiji and Tandure to Lake Wetherell during this period are shown in Figure 1.7. Lake Malta, with a sill height of 60.14 mAHD, experienced the most frequent and longest periods of isolation from Lake Wetherell. Lake Malta was generally cut off from Lake Wetherell at some stage during each year. Lakes Balaka and Bijiji, with lower sills (59.23 mAHD and 58.62 mAHD, respectively) experienced fewer and shorter periods of disconnection from Lake Wetherell and were less prone to episodes of complete evaporative drying. Lake Tandure, with its even lower sill height of 55.88 mAHD did not become disconnected from Lake Wetherell until 2003. Changes in water levels in lakes Pamamaroo, Menindee and Cawndilla are shown in Figures 1.8, 1.9 and 1.10, respectively. Lakes Menindee and Cawndilla remained connected to each other until water levels dropped below 55.50 mAHD during November 2002.

Lake	Period of inundation (years)		Period between dry events (years)		Period of dryness (years)	
	Natural	Regulated	Natural	Regulated	Natural	Regulated
Malta	3.6±0.6	na	4.5±0.6	-- (8.6)	1.0±0.2	--
Balaka	0.9±0.1	na	1.7±0.1	-- (10.7)	0.8±0.1	--
Bijiji	1.8±0.2	na	3.0±0.2	-- (14.3)	1.2±0.2	--
Tandure	5.2±1.7	Perm	21.9±5.9	-- (Perm)	15.8±6.4	-- (0)
Pamamaroo	4.4±1.2	Perm	6.5±1.3	-- (Perm)	1.9±0.4	0.3±0.3 (0)
Menindee	0.8±0.1	4.3±0.1	1.6±0.1	5.1±0.9 (8.6)	0.7±0.1	0.9±0.1
Cawndilla	4.0±1.0	11.4±2.8	5.4±1.1	10.6±2.8 (14.3)	1.2±0.2	0.5±0.1

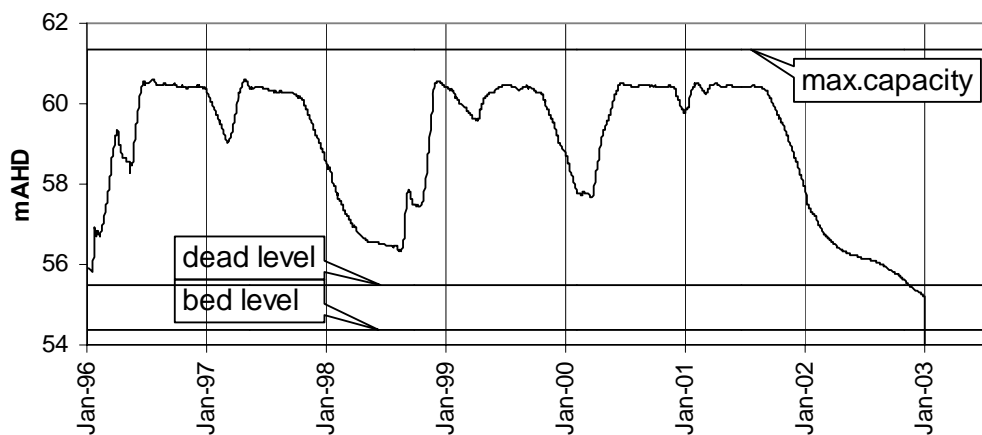
■ **Table 1.3: Frequency and duration of complete lake drying events experienced by each of the Menindee lakes under 'natural' and 'regulated' Darling River flow scenarios. Values shown as mean±se. Actual post-regulation values shown in parentheses. Perm = permanent.**



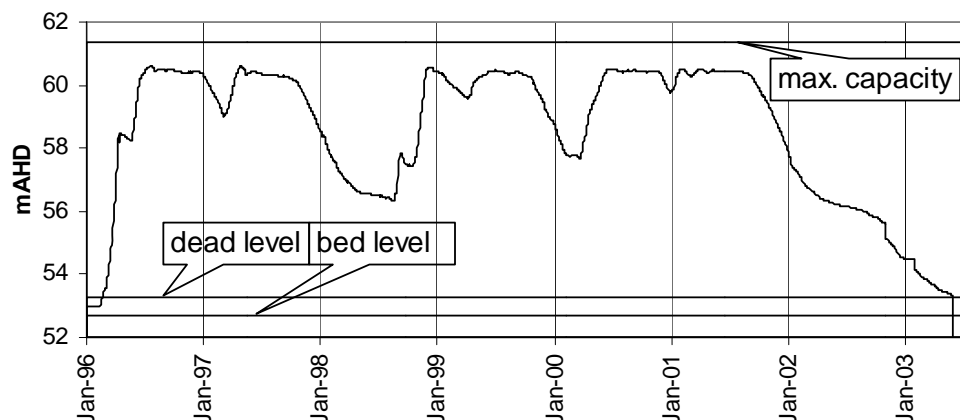
■ **Figure 1.7: Lake Wetherell water levels (mAHD) from January 1996 to July 2003. Sill heights of lakes Malta (60.14 mAHD), Balaka (59.23 mAHD), Bijiji (58.62 mAHD) and Tandure (55.88 mAHD) and maximum storage level (62.89 mAHD) are shown.**



■ Figure 1.8: Lake Pamamaroo water levels (mAHD) from January 1996 to July 2003. Lake bed (55.27 mAHD), dead storage (55.5 mAHD) and maximum storage (62.28 mAHD) levels are indicated.



■ Figure 1.9: Lake Menindee water levels (mAHD) from January 1996 to July 2003. Lake bed (54.35 mAHD), dead storage (55.3 mAHD) and maximum storage (61.36 mAHD) levels are indicated.



■ Figure 1.10: Lake Cawndilla water levels (mAHD) from January 1996 to July 2003. Lake bed (53.0 mAHD), dead storage (53.5 mAHD) and maximum storage (60.45 mAHD) levels are indicated.

Summary

Flow regulation since the late 1960s has altered the periodicity of flooding and complete drying events experienced by each of the Menindee lakes. The lakes are now wetter for longer and the dry periods much shorter. Since monitoring commenced in 1996, the Menindee Lakes have experienced two major drying episodes: August 1997 - August 1998 and November 2001 - >December 2003. Lake drying coincided with ENSO events, during which Darling River inflows to Lake Wetherell were reduced. Predictions of the ENSO index thus offer a mechanism for assessing upto one year in advance probabilities of annual river discharge and storage capacities.

Many ecosystem processes are directly influenced by components of the hydrological regime, such as the timing, duration and frequency of both wet and dry periods. Puckridge and Walker (1996) have suggested that ecosystem responses correlate with hydrological attributes measured over longer multi-cycle time frames, such as the frequency and variability of wetting and drying events, and not just to attributes of the most recent event (duration of wet/dry period). Environmental monitoring programs, therefore, require a longer time frame before more subtle impacts of altered hydrology on trophic function can be recognized.

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2: Monitoring (1996-2003)

2.1 Water Quality

O. Scholz

Introduction

Water quality monitoring in the Menindee Lakes commenced in 1962. Initially, emphasis was placed on monitoring salt movements through the system. Extensive algal blooms in the Darling River during 1991 prompted the expansion of the monitoring program to examine a broader range of water quality issues. This long-term monitoring of the larger and more permanent lakes Pamamaroo, Menindee and Cawndilla is undertaken by DIPNR for the MDBC. A separate water-quality monitoring program for the Menindee Lakes was initiated in August 1997 by MDFRC to collect information not currently provided by the DIPNR program. The MDFRC program included sampling of both the more permanent lakes (lakes Tandure, Menindee and Cawndilla) and the more ephemeral lakes (lakes Malta, Balaka, Bijiji) as identified in Table 1.3. In addition to electrical conductivity, turbidity and total suspended nitrogen and phosphorus concentrations, the dissolved inorganic fractions of nitrogen and phosphorus were sampled to permit the identification of changes in nutrient lability during episodes of lake drying and re-flooding. Data collected by both DIPNR and MDFRC over the period 1996-2002 are presented separately here.

2.1.1 DIPNR monitoring program

Methods

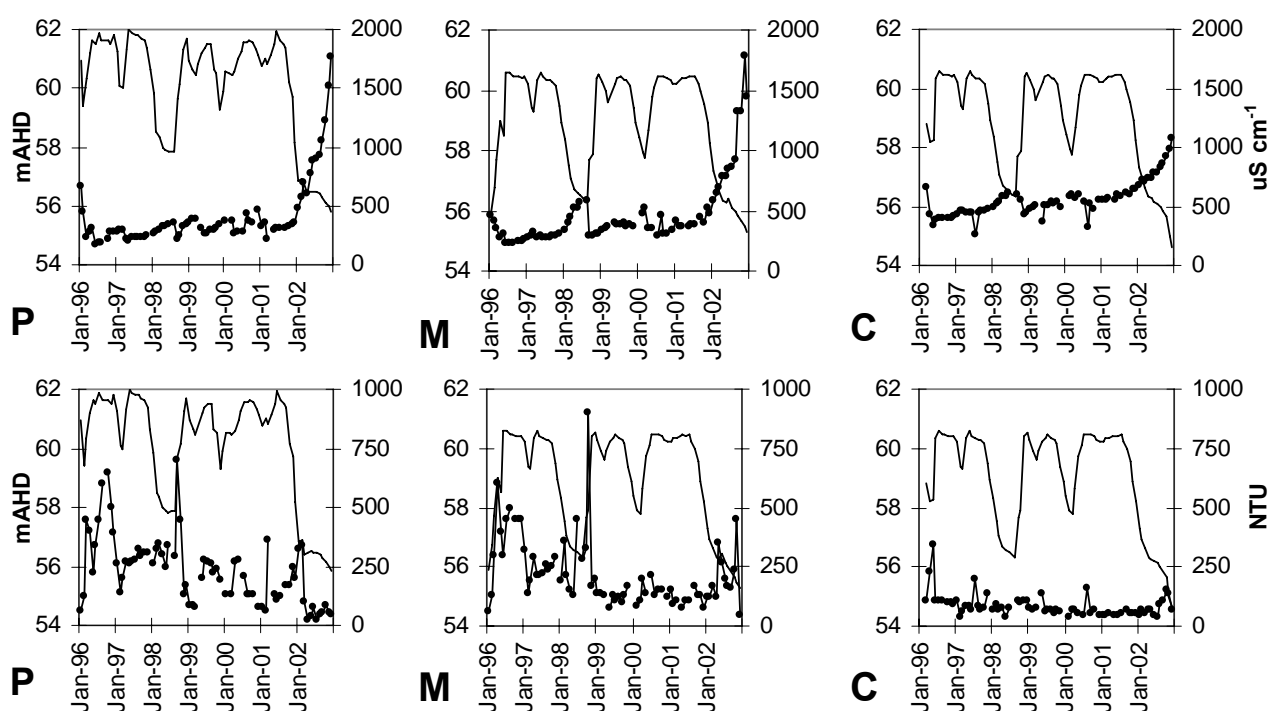
Water quality samples were collected from a single site in the centre of lakes Pamamaroo, Menindee and Cawndilla every month between January 1996 and December 2002. Additional samples were collected from a single mid-stream point along the Darling River adjacent to Lake Malta to provide a benchmark for the quality of source waters. Temperature ($^{\circ}\text{C}$), electrical conductivity standardized to 25°C (EC; $\mu\text{S cm}^{-1}$), and turbidity (NTU) were determined *in situ* at a depth of 0.25 m below the water surface using field turbidity and EC meters (WTW, Weilheim Germany). Unfiltered water samples for total suspended nitrogen (TN; mg N l^{-1}) and total suspended phosphorus (TP; mg P l^{-1}) were frozen until analysed. Total nitrogen present in collected samples was first converted to nitrate using $\text{NaOH-K}_2\text{S}_2\text{O}_8$, then reduced to nitrite using a cadmium column. Nitrogen as nitrite was then determined colorimetrically (APHA 1995). Total phosphorus present in collected samples was first converted to orthophosphate using $\text{NaOH-K}_2\text{S}_2\text{O}_8$. Phosphorus as orthophosphate was then determined colorimetrically using phosphomolybdate-blue (APHA 1995). Detection limits were $\text{TN} \pm 0.019 \text{ mg N l}^{-1}$ and $\text{TP} \pm 0.0025 \text{ mg P l}^{-1}$.

Raw time series-plots and descriptive statistics (percentiles) are presented for each variable for each site. Median values (50^{th} percentiles) were used in preference to means as they are not affected by extreme values and provide a more robust measure of central tendency of skewed data sets. Relationships between water level and water quality were examined using a 2-phase regression (least squares) model to calculate points of inflection ($\gamma \text{ mAHd} \pm \text{s.e.}$) and significance of linear trends either side of γ . These analyses were done using ODDJOB (V6.5; Dallal 1989), which is based on the procedures outlined by Hinkley (1971).

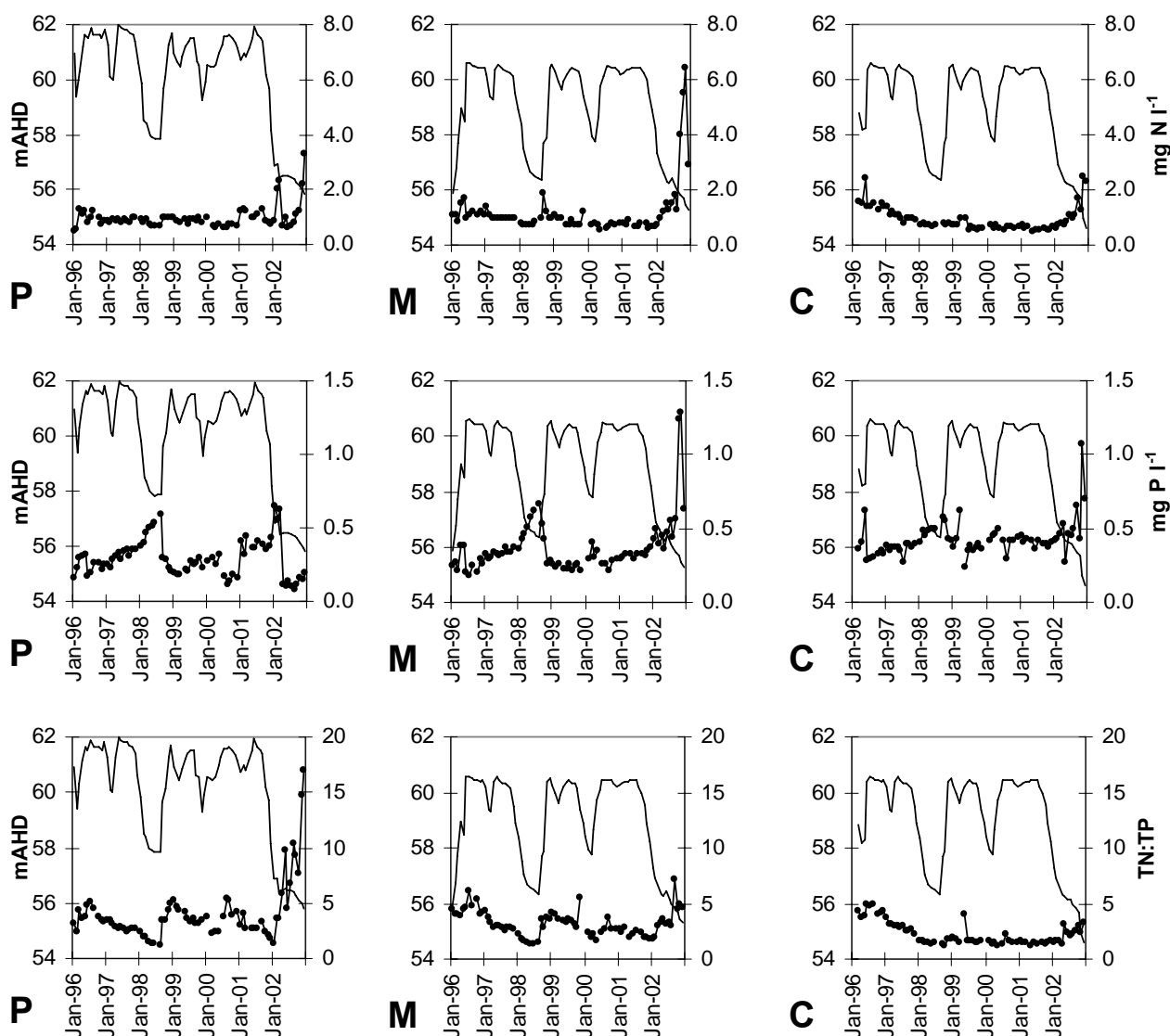
Results

Mean (\pm s.e.) monthly water temperatures (lake and year data pooled) ranged from 11.5 ± 0.2 °C in July to 26.4 ± 0.8 °C in February. Across all lakes, electrical conductivity (EC) and turbidity (NTU) ranged from 168-1780 $\mu\text{S cm}^{-1}$ and 25-900 NTU, respectively (Figure 2.1.1). Median salinity increased and median turbidity decreased through the lakes from Lake Pamamaroo to Lake Cawndilla (Table 2.1.1). Median EC and NTU values encountered in Lake Pamamaroo reflected closely those encountered in the Darling River.

Total nitrogen (TN) and total phosphorus (TP) concentrations ranged from 0.500-6.400 mg N l^{-1} and 0.077-1.290 mg P l^{-1} , respectively (Figure 2.1.2). Median TN concentrations were highest in Lake Menindee and median TP concentrations highest in Lake Cawndilla (Table 2.1.1). TN:TP ratios ranged between 1.19-16.92, with median values decreasing through the system from Lake Pamamaroo to Lake Cawndilla (Figure 2.1.2, Table 2.1.1). Median Darling River TN concentrations were greater and TP concentrations were lower than those recorded in the Darling River. This was also reflected by higher median TN:TP ratios.



■ **Figure 2.1.1: Electrical conductivity ($\mu\text{S cm}^{-1}$) and turbidity (NTU) plotted with water levels (mAHd) recorded in lakes Pamamaroo (P), Menindee (M) and Cawndilla (C) over the 1996-2002 study period.**



■ **Figure 2.1.2: Total nitrogen (mg N l^{-1}), total phosphorus (mg P l^{-1}) and total nitrogen:total phosphorus ratios (TN:TP) plotted with water levels (mAHD) recorded in lakes Pamamaroo (P), Menindee (M) and Cawndilla (C) over the 1996-2002 study period.**

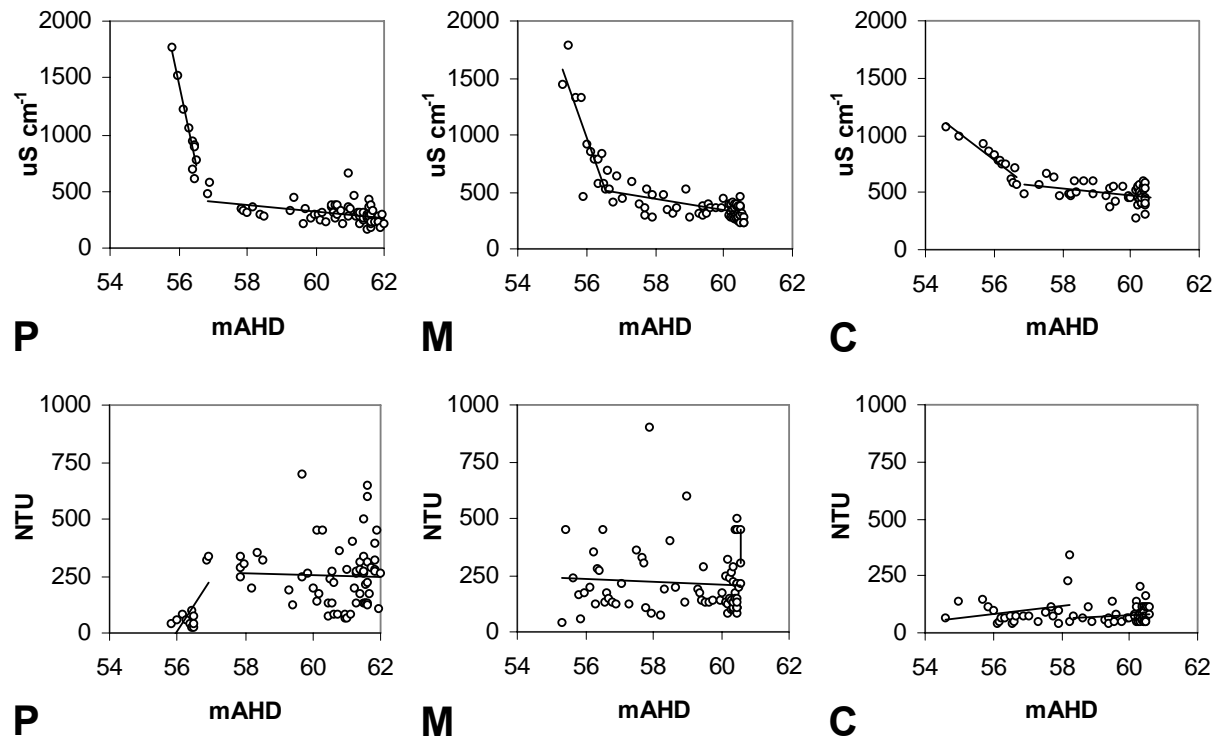
Maximum surcharge depths of lakes Pamamaroo, Menindee and Cawndilla are 6.73 m (55.27-62.00 mAHD), 7.15 m (54.35-61.50 mAHD) and 8.82 m (52.68-61.50 mAHD), respectively. Water levels during the study period fluctuated by 6.18 m (55.82-62.00 mAHD) in Lake Pamamaroo, 5.35 m (55.29-60.59 mAHD) in Lake Menindee, and 5.99 m (54.60-60.59 mAHD) in Lake Cawndilla. Whilst the lakes are managed so as to maintain full supply or maximum surcharge capacity when possible, two protracted periods during which there were no significant inflows occurred between August 1997-August 1998 and from November 2001 until the end of observations in December 2002. Water depths in lakes Pamamaroo, Menindee and Cawndilla prior to flooding during August 1998 were 2.59 m (57.86 mAHD), 1.99 m (56.34 mAHD) and 3.66 m (56.34 mAHD), respectively. Lake drying during 2001-02 was more severe, with water levels in lakes Pamamaroo, Menindee and Cawndilla falling as low as 0.55 m (55.82 mAHD), 0.94 m (55.29 mAHD) and 1.98 m (54.60 mAHD). Reductions in water level during these periods were driven by both releases and evaporation.

Parameter	Lake	Percentiles				
		0	10	50	90	100
EC ($\mu\text{S cm}^{-1}$)	Pamamaroo	168	222	307	749	1770
	Menindee	226	271	370	784	1780
	Cawndilla	269	401	540	746	1080
Turbidity (NTU)	Pamamaroo	25	65	220	397	700
	Menindee	45	103	170	450	900
	Cawndilla	40	45	70	140	340
TN (mg N l^{-1})	Pamamaroo	0.500	0.663	0.885	1.20	3.30
	Menindee	0.550	0.693	0.950	1.50	6.40
	Cawndilla	0.510	0.570	0.750	1.50	2.50
TP (mg P l^{-1})	Pamamaroo	0.077	0.144	0.275	0.462	0.651
	Menindee	0.180	0.223	0.325	0.542	1.29
	Cawndilla	0.240	0.325	0.410	0.526	1.07
TN:TP	Pamamaroo	1.19	2.05	3.45	5.75	16.9
	Menindee	1.32	1.77	2.99	4.58	7.10
	Cawndilla	1.22	1.38	1.71	3.96	5.00

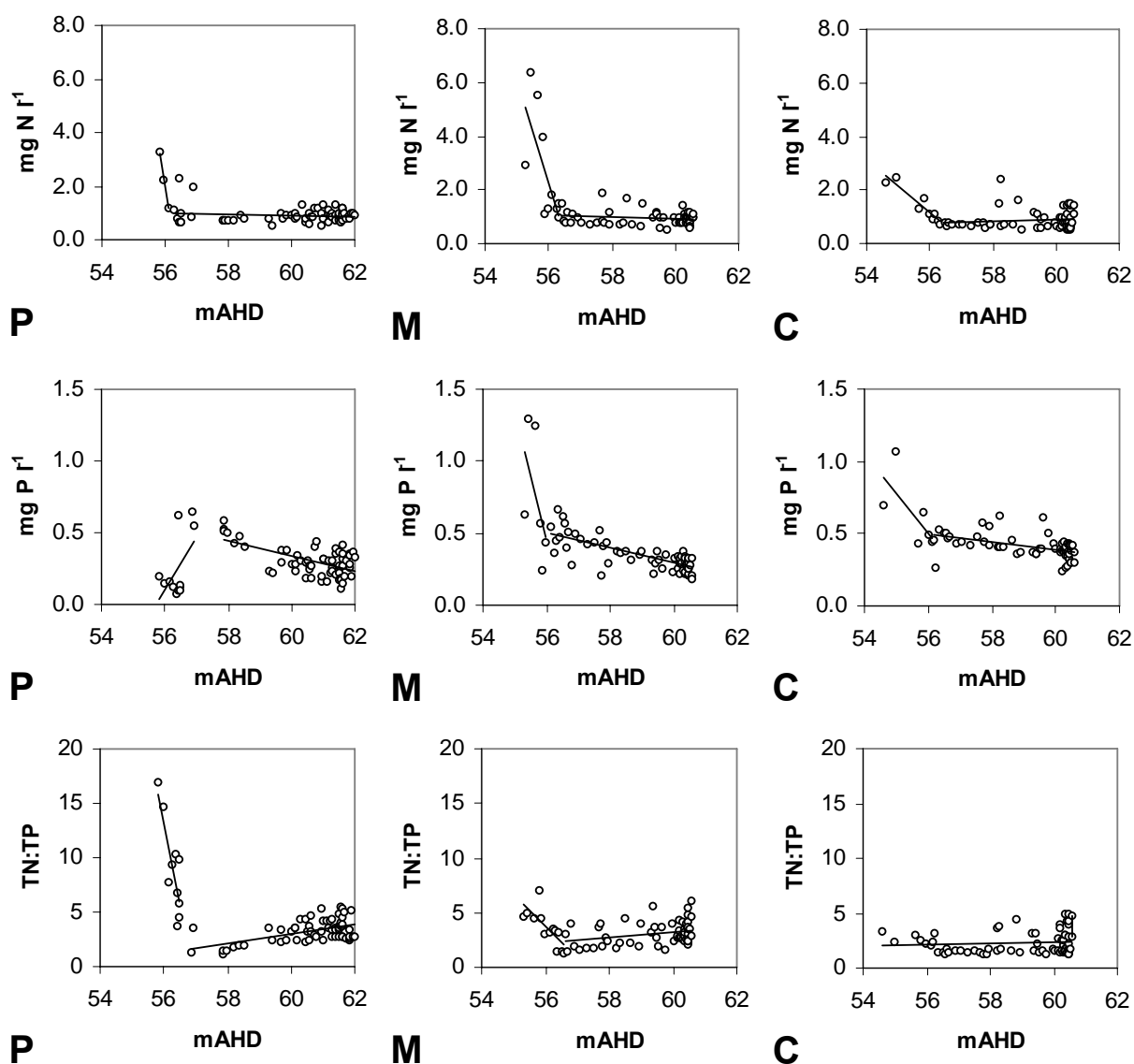
■ **Table 2.1.1: Summary statistics for monthly electrical conductivity (EC; $\mu\text{S cm}^{-1}$), turbidity (NTU), total nitrogen (TN; mg N l^{-1}), total phosphorus (TP; mg P l^{-1}) and TN:TP ratios recorded in the Darling River (n=48) and lakes Pamamaroo (n=74), Menindee (n=74) and Cawndilla (n=71) over the 1996-2002 study period.**

Water quality-water level relationships for most variables were non-linear (Figure 2.1.3 and 2.1.4). In most instances, differences between regression slopes fitted either side of a point of inflection, γ (β_0 for $\text{mAHD} < \gamma$, and β_1 for $\text{mAHD} > \gamma$) were significant at $p \leq 0.001$ (Table 2.1.2). β_1 values were either not significant or smaller in absolute terms than β_0 , indicating that water quality responses to changes in water level were weaker, though not necessarily insignificant, at water levels greater than γ . Whilst NTU in all lakes was not influenced by changes in water level either side of γ , responses of EC, TN and TP concentrations, and TN:TP ratios to lake drying were generally consistent between lakes, with all increasing more rapidly once water levels fell below γ . Exceptions to this included TP concentration responses in Lake Pamamaroo, which were influenced by the low TP concentrations recorded after April 2002, and TN:TP ratio responses in Lake Cawndilla, where the regression slopes β_0 and β_1 did not differ significantly from 0. Whereas EC increased steadily throughout lake drying episodes, increases in TN and TP concentrations did not persist, peaking at different intervals (e.g. 2001-2002).

Points of inflection ($\gamma \text{ mAHD} \pm \text{se}$) in water quality-water level relationships identified using 2-phase regression were generally consistent between water quality variables within lakes, but differed between lakes (Table 2.1.2). Mean γ values ranged from 56.16-57.10 mAHD (0.89-1.83 m depth) for Lake Pamamaroo, 55.99-56.57 mAHD (1.64-2.22 m depth) for Lake Menindee (excluding NTU estimate), and 56.12-56.75 mAHD (3.44-4.07 m depth) for Lake Cawndilla (excluding NTU and TN:TP estimates). Water levels fell below these thresholds after December 2001 in Lake Pamamaroo, between May and August 1998 and after February 2002 in Lake Menindee, and between April and August 1998 and after February 2002 in Lake Cawndilla.



■ Figure 2.1.3: 2-phase regression curves fitted to electrical conductivity ($\mu\text{S cm}^{-1}$) and turbidity (NTU) data plotted against water levels (mAHD) recorded in lakes Pamamaroo (P), Menindee (M) and Cawndilla (C) over the 1996-2002 study period.



■ Figure 2.1.4: 2-phase regression curves fitted to total nitrogen (mg N l⁻¹), total phosphorus (mg P l⁻¹) and total nitrogen:total phosphorus ratios (TN:TP) plotted against water levels (mAHD) recorded in lakes Pamamaroo (P), Menindee (M) and Cawndilla (C) over the 1996-2002 study period.

Lake	Water quality parameter	γ (mAHD \pm se)		β_0 ($<\gamma$)		β_1 ($>\gamma$)		$H_0: \beta_0 \neq \beta_1$
Pamamaroo	EC	56.72	0.04	-1470	*	-27.5	*	*
	NTU	57.10	0.46	+238	ns	-4.29	ns	*
	TN	56.16	0.04	-6.74	*	-0.017	ns	*
	TP	57.03	0.20	+0.377	*	-0.052	*	*
	TN:TP	56.81	0.07	-14.4	*	+0.437	*	*
Menindee	EC	56.57	0.09	-828.9	*	-49.7	*	*
	NTU	60.57	0.02	-5.52	ns	+15000	ns	ns
	TN	56.34	0.08	-3.87	*	-0.029	ns	*
	TP	55.99	0.11	-0.805	*	-0.051	*	*
	TN:TP	56.56	0.20	-2.741	*	+0.296	ns	*
Cawndilla	EC	56.75	0.24	-228.0	*	-39.91	*	*
	NTU	58.27	1.59	+8.508	ns	-9.780	ns	ns
	TN	56.36	0.20	-0.996	*	+0.020	ns	*
	TP	56.12	0.23	-0.261	*	-0.025	*	*
	TN:TP	60.56	0.02	+0.052	ns	+90.62	ns	ns

■ **Table 2.1.2: Summary of 2-phase regression analyses on lake height (mAHD)-water quality relationships. Data shown are; estimated points of inflection γ (mAHD \pm se), the direction and significance of each regression gradient (β_0 and β_1), and the significance of differences between fitted regression gradients (β_0 and β_1). ns – $p > 0.001$, and * – $p \leq 0.001$.**

Water quality of Lake Pamamaroo as it flooded between August-December 1998 closely reflected the quality of its source waters. During this period, the EC of inflows increased from 120-353 $\mu\text{S cm}^{-1}$ (Lake Pamamaroo 214-364 $\mu\text{S cm}^{-1}$), turbidity declined from 1600-16 NTU (Lake Pamamaroo 700-170 NTU), and TN and TP concentrations and TN:TP ratios in both approached median Darling River values. Although no overall relationship between turbidity and water level were observed, large increases in turbidity occurred in response to flooding (*e.g.* lakes Pamamaroo and Menindee during 1998). These turbid pulses declined rapidly over several weeks. The re-flooding of lakes during 1998 diluted the lake salt and TP concentrations initially present in lakes Menindee and Cawndilla. In contrast, flows carrying TN concentrations of 1.0 mg N l^{-1} from Lake Pamamaroo stimulated an initial increase in TN concentrations, and thus also TN:TP ratios, in Lake Menindee from 1.0 mg N l^{-1} to 1.9 mg N l^{-1} during the first month. This nitrogen pulse was short-lived, declining to 1.0 mg N l^{-1} by December 1998. No similar nitrogen pulse was recorded for Lake Cawndilla.

Discussion

Ephemeral deflation basin lakes (EDBL), such as the Menindee Lakes, naturally fluctuate between periods of flooding, involving two-way exchanges with the mainstream (*cf.* Flood Pulse Concept; Junk *et al.* 1989), followed by periods of hydraulic isolation during which they slowly dry. The regulation of water regimes within the main storages of the Menindee Lakes has altered the nature of exchanges between components of the floodplain, and decreased the frequency and duration of drying events. Reductions in the frequency and severity of episodes of lake drying have, firstly, reduced the frequency and amplitude of changes in salinity, turbidity and nutrients that would normally occur in ephemeral systems in response to flooding and drying, and secondly, reduced the extent and duration of lakebed exposure.

Observed reductions in median turbidity through the lakes were likely functions of both the serial connection of these lakes and of increases in the residence times of impounded water. These processes facilitate the sedimentation of suspended particulate matter, increasing photic depths and thus also the potential for primary production. Whilst there was no trend in median TN concentrations through the lakes, there was for TP concentrations, resulting in the sequential elevation of TN:TP ratios. As for TP concentrations, median EC values increased through the system. This suggests that the serial connection of these lakes has resulted in the net loading of sediments, especially in Lake Pamamaroo, and of phosphorus and salt in the terminal lake, Lake Cawndilla. Reinstating direct (pre-regulation) connections with the mainstream will likely reverse the tendency for the lakes to function as sediment, salt and nutrient sinks.

Electrical conductivity (EC), turbidity (NTU), total nitrogen (TN) and total phosphorus (TP) concentrations and TN:TP ratios varied greatly during the 1996-2002 study period. During normal operations, water levels in each of the lakes are maintained as close to full supply capacity as possible, whilst reserving storage capacity to receive riverine flood pulses so as to mitigate downstream flooding. For the most part, water quality is driven by the mass balance of exchanges into and out of the lakes. Although the extent of groundwater interactions on lake water budgets and water quality within the Menindee Lakes is currently poorly understood (DLWC 1998a,b), evaporation accounts for as much as 49 % of annual water losses from the system (DWR 1994, DLWC 1997) and is likely to be the key driver of changes in water quality, especially during periods of hydraulic isolation.

Turbidity (NTU) was not influenced by changes in water level. However, EC, TN and TP concentrations and TN:TP ratios were. Relationships between these and water level were not linear. At higher water levels, responses to changes in water level were either not significant or weaker than were responses at lower water levels. This was likely due to the interactions of inflows, outflows and evaporation at higher operating levels. The points of transition between these two responses were similar for EC and nutrients within lakes, but differed between lakes. Transition points were identified as occurring at between 56.16-57.03 mAHD (0.89-1.76 m depth) in Lake Pamamaroo, 55.99-56.57 mAHD (1.64-2.22 m depth) in Lake Menindee and 56.12-56.75 mAHD (3.44-4.07 m depth) in Lake Cawndilla. EC, TN and TP concentrations and TN:TP ratios increased significantly once water heights fell below these thresholds. Although inflows to each lake had ceased before these thresholds were reached, outflows had not. Thus, whilst evaporative concentration is likely to have been a key driver of water quality responses, the points of transition are likely to vary between drying episodes depending on the extent of drawdown.

As with lake drying, the re-flooding of all lakes following the lake-drying episode of 1997-8 initiated changes in water quality. These changes were generally short-term responses, lasting only one to two months, and generally reflected the quality of the inflowing waters. The increase in turbidity observed initially on the re-flooding of Lake Pamamaroo was attributable to the highly turbid Darling River flood pulse front. This turbid pulse flowed in to Lake Menindee, but not in to Lake Cawndilla. Higher post-flood turbidities were recorded in Lake Menindee than were in Lake Pamamaroo. Similarly, flooding stimulated increases in TN in Menindee above that present in the inflowing waters. As with turbidity, this post-flood pulse was short lived. Scholz *et al.* (2002) reported that much of this post-flood nitrogen pulse was attributable to releases of inorganic nitrogen from the sediments. Such releases are a commonly observed response to the inundation of previously exposed lakebeds (*e.g.* McComb and Qiu 1998, Baldwin and Mitchell 2000). Whilst concentrations of inorganic nitrogen in Lake Cawndilla also increased in response to flooding, their contribution to the post flood TN pool was smaller (*e.g.* Scholz *et al.* 2002). No post-flood increases in TN were recorded in lakes Pamamaroo or Cawndilla.

Whilst reinstating extremes in water quality are to be generally recommended on the basis that they more accurately reflect natural variability, evidence supporting the requirement of wetland biota for physico-chemical extremes *per se* to cue behavioural responses, such as the production of desiccation resistant eggs and cysts in micro-invertebrates, remains scarce. Substantially more evidence is available to suggest that the primary impacts of lake drying arise through changes in trophic structure as lakes dry (e.g. Hairston *et al.* 1990, and the following chapters of this report) and the exposure of lakebeds. Lakebed exposure facilitates the consolidation of sediments (van der Wielen *in press*), the mineralisation of nutrients within the sediments (Baldwin and Mitchell 2000), and the establishment of lakebed vegetation. On subsequent inundation, these processes have the potential to substantially increase aquatic productivity by reducing turbidity and thus increasing photic depths, by increasing nutrient availability derived from both the sediments and from inundated vegetation as it decomposes (Furch and Junk 1997), and by increasing the availability of substrates for algae, micro- and macro-invertebrates, and potentially important spawning habitat for fish (Geddes and Puckridge 1989, Lloyd *et al.* 1989, Gehrke 1990).

Hydraulic regulation of the main storages of the Menindee Lakes has increased the potential for sediment, salt and nutrient loading, and has reduced much of the variability in water quality normally associated with drying and flooding, and has reduced the potential for processes dependent on lakebed exposure. These changes are likely to have impacted on overall ecosystem function. Reinstating direct connections with the mainstream and reimposing greater variability in water levels thus represents a key step toward promoting wetland values.

2.1.2 MDFRC monitoring program

Methods

Water quality was monitored in lakes Malta, Balaka, Bijiji, Tandure, Menindee and Cawndilla over two periods; for 21 months as lakes dried and re-flooded between August 1997 and April 1999, and for 26 months between December 2000 and January 2003 as the lakes dried. Monitoring ceased once lakes were either dry or the last of the remaining water became inaccessible.

Water quality measurements were made and samples collected from three littoral sites in each lake. For each sampling event, electrical conductivity standardized to 25 °C (EC; $\mu\text{S cm}^{-1}$) and turbidity (NTU) was determined *in situ* at a depth of 0.25 m below the water surface using a U-10 multi-probe (HORIBA Ltd., Australia). Turbidity had a maximum level of detection of 1000 NTU. Unfiltered 200 ml samples for total nitrogen (TN; mg N l^{-1}), total phosphorus (TP; mg P l^{-1}) and 10 ml 0.45 μm filtered samples for dissolved oxides of nitrogen (NO_x ; mg N l^{-1}) and filterable reactive phosphorus (FRP; mg P l^{-1}) were frozen until analysed. NO_x was determined colorimetrically after its reduction to nitrite using a cadmium column (APHA 1995). Total nitrogen and ammonia were determined as for NO_x after pre-digestion in $\text{NaOH-K}_2\text{S}_2\text{O}_8$ and oxidation to nitrate. FRP was determined colorimetrically using the phosphomolybdate-blue method (APHA 1995). TP samples were determined as for FRP after pre-digestion in $\text{NaOH-K}_2\text{S}_2\text{O}_8$ and oxidation to orthophosphate. Detection limits varied between nutrient fractions; $\text{TN} \pm 0.019 \text{ mg N l}^{-1}$, $\text{TP} \pm 0.0025 \text{ mg P l}^{-1}$, $\text{NO}_x \pm 0.003 \text{ mg N l}^{-1}$ and $\text{FRP} \pm 0.001 \text{ mg P l}^{-1}$.

Raw time series plots (means \pm s.e.) and descriptive statistics (percentiles) are presented for each variable for each lake. Median values were used in preference to means as they are not affected by extreme values and provide a more robust measure of central tendency of skewed data sets. Differences in nutrient characteristics between sites were examined using fixed factor one-way ANOVAs. Analyses were done on square-root transformed data where variances were not homogeneous using SYSTAT[®] 10.2 (SPSS Inc. Chicago, USA). Data are presented as means \pm standard errors (n=3) or as individual replicate values where ranges are quoted.

Results

Two protracted drying events (1997-8 and 2001-3) and one re-flooding event (1998) were monitored between August 1997 and January 2003. The extent of drying during 1997-8 varied between lakes, ranging from 100 % exposure of lakebed sediments in lakes Malta and Balaka to only 5 % in Lake Tandure (Table 2.1.3). The greater duration of the 2001-3 drying event resulted in all lakes drying completely.

All lakes above the Main Weir, except Lake Tandure, were hydraulically isolated from Lake Wetherell prior to flooding in 1998. Flooding inflows into lakes Malta, Balaka, Bijiji and Tandure from Lake Wetherell, upstream of the Main Weir, commenced within a week prior to sampling in August 1998. Inflows into lakes Malta, Balaka and Bijiji lasted approximately one month, after which these lakes became hydraulically isolated. Lake Menindee received two controlled releases from Lake Pamamaroo, the first lasting 3 weeks between August and September 1998 sampling events and the second commencing 2 weeks prior to sampling in October and continued until early December 1998. Lake Cawndilla received all of its inflows from Lake Menindee.

Lake	Maximum depth (m) ^a	Area (ha) ^a	Lakebed area exposed (%)	
			1997-8	2001-3
Malta	1.5	380	100	100
Balaka	2.4	1300	100	100
Bijiji	3.1	1050	67	100
Tandure	5.8	2190	<5	>95
Menindee	5.5	16000	41	>95
Cawndilla	7.2	10000	10	>95

■ **Table 2.1.3: Physical characteristics of the Menindee Lakes and the extent of lakebed exposure during the 1997-8 and 2001-3 drying events. ^a Bewsher Consulting Pty. Ltd (2000).**

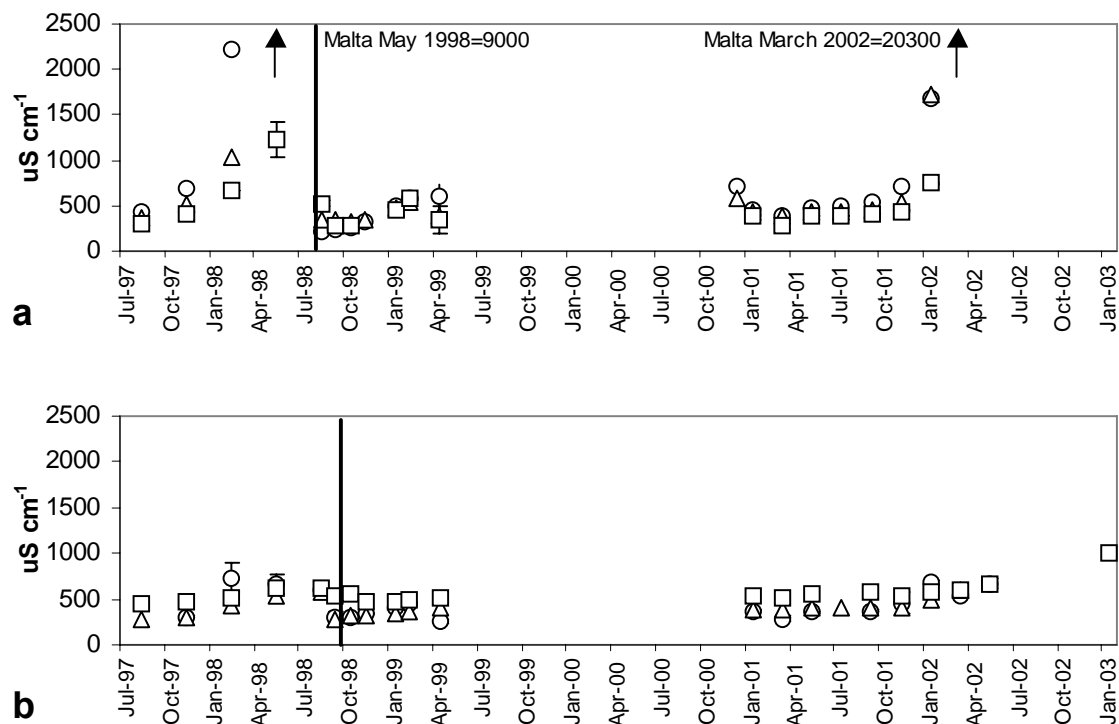
Summary statistics for each water quality parameter investigated are shown in Tables 2.1.4 and 2.1.5. Although robustness of these statistics is reduced by the small sample size ($n \leq 20$), these data are the first records for lakes Malta, Bijiji, Balaka and Tandure. Refer to Table 2.1.1 for percentile values based on a larger sample sizes ($n > 70$) for lakes Pamamaroo, Menindee and Cawndilla.

Electrical conductivity (EC) ranged from 207-20,300 $\mu\text{S cm}^{-1}$ (Table 2.1.4). Median lake salinities increased with distance upstream from the Main Weir; Lake Tandure (388 $\mu\text{S cm}^{-1}$), Lake Bijiji (405 $\mu\text{S cm}^{-1}$), Lake Balaka (435 $\mu\text{S cm}^{-1}$) and Lake Malta (522 $\mu\text{S cm}^{-1}$). Below the Main Wier, median lake salinity was higher in Lake Cawndilla (536 $\mu\text{S cm}^{-1}$) than in Lake Menindee (401 $\mu\text{S cm}^{-1}$) (*cf.* Table 2.1.1). EC increased in all lakes as they dried in 1998 and 2002, although observed increases in EC were greater and more rapid in the smaller lakes (lakes Malta, Balaka and Bijiji), than in the larger lakes (lakes Tandure, Menindee and Cawndilla) (Figure 2.1.5). Sampling frequency and inaccessibility to the water's edge as most lakes dried prevented measurements of remnant surface water pools. Sampling of such pools (surface area $< 100 \text{ m}^2$) in Lake Malta during May 1998 and March 2002 indicated EC maxima of 9000 $\mu\text{S cm}^{-1}$ and 20300 $\mu\text{S cm}^{-1}$, respectively. Re-filling during and after August 1998 reset all lake ECs and reduced differences between lakes. EC values of the flood pulse in Lake Wetherell ranged between 120-278 $\mu\text{S cm}^{-1}$ (DIPNR data). Post-flood lake minima were 207 $\mu\text{S cm}^{-1}$ (L. Malta), 328 $\mu\text{S cm}^{-1}$ (L. Balaka), 273 $\mu\text{S cm}^{-1}$ (L. Bijiji), 254 $\mu\text{S cm}^{-1}$ (L. Tandure), 276 $\mu\text{S cm}^{-1}$ (L. Menindee) and 448 $\mu\text{S cm}^{-1}$ (L. Cawndilla).

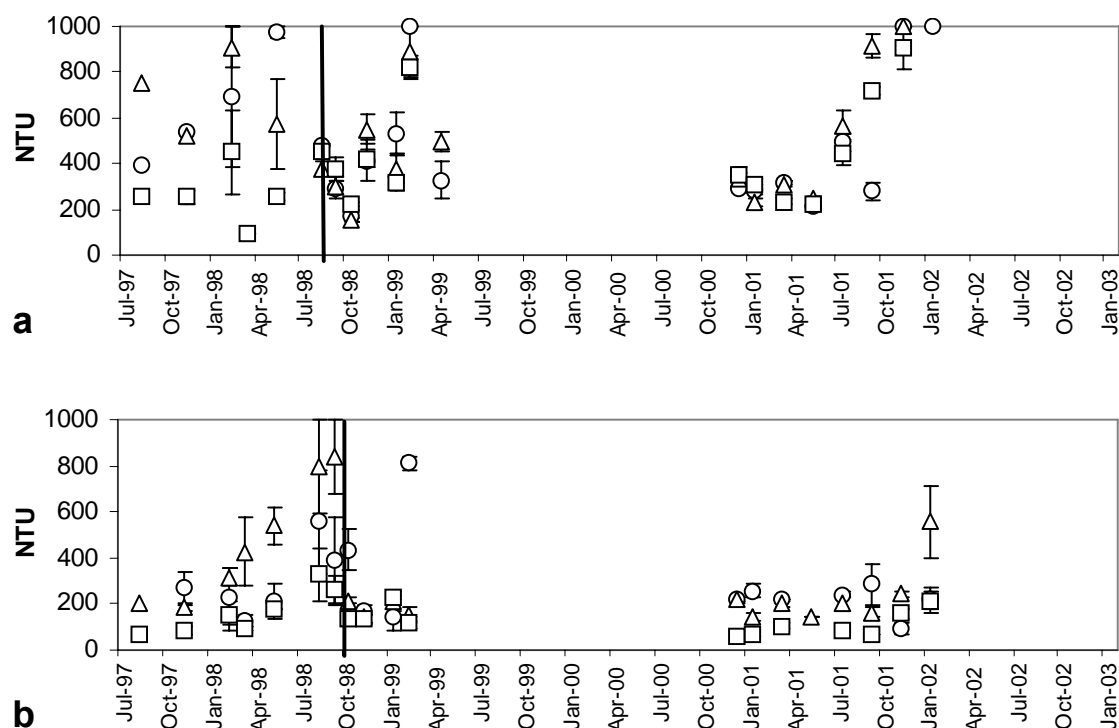
Turbidity (NTU) ranged from 92-999 (maximum level of detection) (Table 2.1.4). Median turbidities were higher in the shallower lakes (lakes Malta, Balaka and Bijiji) than in the deeper lakes (lakes Tandure, Menindee and Cawndilla). Turbidity generally increased in response to lake drying. Floodwater turbidities as high as 1600 NTU were recorded in Lake Wetherell during August 1998 (DIPNR data). Post-flood turbidity of lakes above the Main Weir declined rapidly (1-2 months) after re-filling as suspended material settled (Figure 2.1.6). Flows into Lakes Menindee and Cawndilla were less turbid (450-700 NTU and 330-900 NTU, respectively; DIPNR data) and post-flood changes in turbidity were not as great as that identified in the other lakes.

Parameter	Lake	Percentiles				
		0	10	50	90	100
EC ($\mu\text{S cm}^{-1}$)	Malta	207	265	522	2892	20300
	Balaka	328	338	435	721	1720
	Bijiji	273	283	405	699	1227
	Tandure	254	297	388	674	733
	Menindee	276	303	401	545	602
	Cawndilla	448	472	536	634	1007
Turbidity (NTU)	Malta	174	267	414	999	999
	Balaka	152	245	509	911	999
	Bijiji	92	224	332	748	906
	Tandure	93	136	231	484	811
	Menindee	141	144	212	605	839
	Cawndilla	57	68	127	238	327

■ Table 2.1.4: Summary statistics for electrical conductivity ($\mu\text{S cm}^{-1}$) and turbidity (NTU) recorded in each of the lakes between 1997-2003.



■ Figure 2.1.5: Electrical conductivity ($\mu\text{S cm}^{-1}$) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (\square), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (\square). The vertical bar indicates the 1998 flood event.



■ **Figure 2.1.6: Turbidity (NTU) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (□), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (□). The vertical bar indicates the 1998 flood event.**

Total nitrogen (TN) concentrations recorded within the lakes ranged from 0.305-280 mg N l⁻¹. (Table 2.1.5). Median TN concentrations were higher in the smaller lakes (lakes Malta, Balaka and Bijiji) than in the larger and deeper lakes (lakes Tandure, Menindee and Cawndilla). TN concentrations increased during 1997-8 as drying progressed in lakes Malta, Balaka, Bijiji and Tandure (One-way ANOVA: $p < 0.001$), but not in lakes Menindee (One-way ANOVA: $F = 0.994$, $p = 0.440$) or Cawndilla (One-way ANOVA: $F = 0.625$, $p = 0.576$). However, TN concentrations increased in all lakes as they dried during 2001-3 (One-way ANOVA: $p < 0.001$) (Figure 2.1.7). A maximum TN concentration of 280 mg N l⁻¹ was recorded in the last remaining pool of surface water in Lake Malta during March 2002.

TN concentrations in lakes Malta, Balaka, Bijiji and Tandure increased as they filled. Peak post-flood TN concentrations were recorded during September and October in lakes Malta (1.85 ± 0.25 mg N l⁻¹), Balaka (1.80 ± 0.36 mg N l⁻¹), Bijiji (2.79 ± 0.35 mg N l⁻¹) and Tandure (1.48 ± 0.25 mg N l⁻¹). These concentrations did not differ significantly from each other or from that present in Lake Wetherell floodwaters (1.79 ± 1.01 mg N l⁻¹) (One-way ANOVA: $F = 2.436$, $p = 0.178$). In contrast, flows carrying TN concentrations of 1.000 mg N l⁻¹ into Lake Menindee from Lake Pamamaroo (DIPNR data) stimulated an increase in TN concentrations from 1.13 ± 0.12 mg N l⁻¹ to 1.76 ± 0.11 mg N l⁻¹ within two months. This nutrient pulse was short lived, declining to 1.30 ± 0.05 mg N l⁻¹ by November, and did not appear to flow through to Lake Cawndilla, where TN concentrations remained below 1.0 mg N l⁻¹.

Total phosphorus (TP) concentrations recorded within the lakes ranged from 0.120-15.5 mg P l⁻¹. (Table 2.1.5). Median TP concentrations were higher in the smaller lakes (lakes Malta, Balaka and Bijiji) than in the larger and deeper lakes (lakes Tandure, Menindee and Cawndilla). TP concentrations increased in all lakes as they dried during both 1997-8 and 2001-3 (One-way ANOVAs: $p \leq 0.001$), except for Lake Tandure in 1997-8 (One-way

ANOVA: $F=1.857$, $p=0.236$) (Figure 2.1.8). A maximum TP concentration of 15.5 mg P l^{-1} was recorded in the last remaining pool of surface water in Lake Malta during March 2002. TP concentrations in lakes Malta, Balaka, Bijiji and Tandure increased as they filled. Peak post-flood TP concentrations were recorded during September and October in lakes: Malta ($0.45 \pm 0.07 \text{ mg P l}^{-1}$), Balaka ($0.43 \pm 0.05 \text{ mg P l}^{-1}$), Bijiji ($0.52 \pm 0.00 \text{ mg P l}^{-1}$) and Tandure ($0.39 \pm 0.05 \text{ mg P l}^{-1}$). These concentrations did not differ significantly from each other or from that present in Lake Wetherell floodwaters ($0.35 \pm 0.06 \text{ mg P l}^{-1}$) (One-way ANOVA: $F=1.011$, $p=0.481$). Regulated flows with TP concentrations of $0.29 \pm 0.05 \text{ mg P l}^{-1}$ into Lake Menindee from Lake Pamamaroo diluted lake TP concentrations from $0.63 \pm 0.04 \text{ mg P l}^{-1}$ to $0.44 \pm 0.03 \text{ mg P l}^{-1}$ within the first month. No pulse of TP occurred initially on flooding as was observed for TN. Differences in TP concentrations between Lake Cawndilla and the inflows from Lake Menindee were small and did not impact upon lake TP concentrations.

Dissolved oxides of nitrogen (NO_x) concentrations recorded within the lakes ranged from 0.000 - $0.610 \text{ mg N l}^{-1}$, but generally remained below 0.05 mg N l^{-1} and constituted less than 5 % of the TN pool (Table 2.1.5). During non-flood periods, NO_x concentrations were significantly higher (One-way ANOVA: $F=4.338$, $p=0.038$) and constituted a greater percentage of the TN pool (One-way ANOVA: $F=10.999$, $p=0.001$) in the larger and deeper lakes (lakes Tandure and Menindee) than in the smaller lakes (lakes Malta, Balaka and Bijiji). Whilst NO_x responses to drying were small, large increases in NO_x concentrations and NO_x :TN percentages were recorded shortly after the re-filling of each lake (Figures 2.1.9 and 2.1.10). Post-inundation NO_x concentration peaks in lakes: Malta ($0.61 \pm 0.08 \text{ mg N l}^{-1}$), Balaka ($0.58 \pm 0.12 \text{ mg N l}^{-1}$), Bijiji ($0.52 \pm 0.06 \text{ mg N l}^{-1}$) and Tandure ($0.29 \pm 0.13 \text{ mg N l}^{-1}$) did not differ significantly from each other or from that present in Lake Wetherell floodwaters ($0.68 \pm 0.26 \text{ mg N l}^{-1}$) (One-way ANOVA: $F=1.289$, $p=0.371$). NO_x concentrations peaked within a month of the first flooding inflows into Lake Menindee, increasing from $0.026 \pm 0.003 \text{ mg N l}^{-1}$ to $0.44 \pm 0.07 \text{ mg N l}^{-1}$. Although flooding had little impact on TN concentrations in Lake Cawndilla, NO_x concentrations rose from $0.067 \pm 0.048 \text{ mg N l}^{-1}$ prior to flooding to a peak of $0.25 \pm 0.03 \text{ mg N l}^{-1}$ in October. NO_x concentrations were not recorded for the in-flowing waters of either of these lakes. The post-flood NO_x pulse was rapidly assimilated in all lakes. Within 3 months of flooding both NO_x concentrations and NO_x :TN percentages were close to or at pre-flood concentrations.

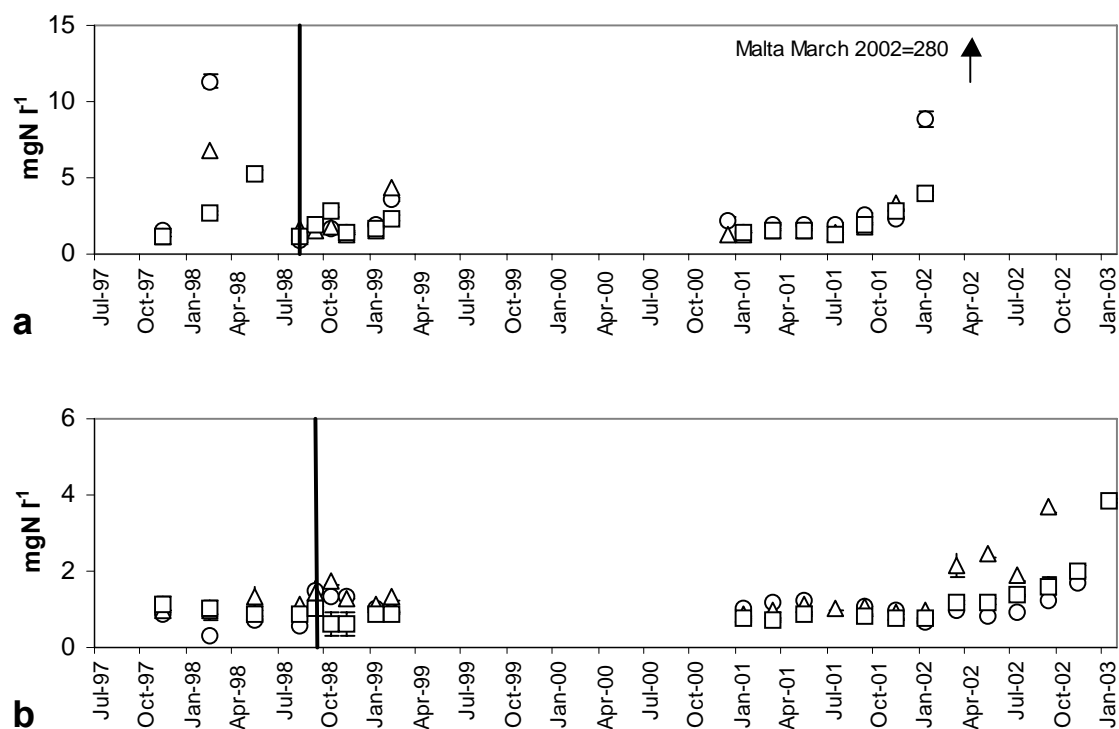
Filterable reactive phosphorus (FRP) concentrations recorded within the lakes ranged from 0.000 - $0.545 \text{ mg P l}^{-1}$. Median FRP concentrations and FRP:TP percentages did not differ greatly between lakes, ranging from 0.172 - $0.253 \text{ mg P l}^{-1}$ and 41.8-50.7 %, respectively (Table 2.1.5). FRP concentrations declined significantly as lakes dried between December 2001-January 2003 (One-way ANOVA: $F=4.323$, $p<0.001$) (Figure 2.1.11), and constituted an increasingly smaller proportion of the TP pool (One-way ANOVA: $F=3.341$, $p=0.002$) (Figure 2.1.12). Post-flood FRP concentrations in lakes Malta ($0.22 \pm 0.02 \text{ mg P l}^{-1}$), Balaka ($0.22 \pm 0.01 \text{ mg P l}^{-1}$), Bijiji ($0.21 \pm 0.04 \text{ mg P l}^{-1}$) and Tandure ($0.19 \pm 0.03 \text{ mg P l}^{-1}$) did not differ significantly from each other or from that present in Lake Wetherell floodwaters ($0.22 \pm 0.10 \text{ mg P l}^{-1}$) (One-way ANOVA: $F=0.299$, $p=0.876$). FRP concentrations in Lake Menindee declined from $0.43 \pm 0.03 \text{ mg P l}^{-1}$ to $0.22 \pm 0.02 \text{ mg P l}^{-1}$ within a month of releases from Lake Pamamaroo commencing. FRP concentrations in Lake Cawndilla were also diluted from $0.38 \pm 0.03 \text{ mg P l}^{-1}$ to $0.075 \pm 0.055 \text{ mg P l}^{-1}$ within two months of receiving inflows. FRP concentrations were not recorded for the in-flowing waters of either of these lakes, preventing comment on the relative significance of allochthonous FRP inputs and releases from the sediments. Whilst flooding did not greatly influence FRP concentrations, it did increase the lability of phosphorus (FRP:TP %) in all lakes (Figure 2.1.12). Post-flood FRP:TP percentages declined more rapidly in the smaller lakes than in the larger lakes. Within 3 months of flooding FRP:TP percentages were close to or at pre-flood concentrations.

Flooding not only stimulated increases in both NO_x :TN and FRP:TP percentages, but stimulated greater increases in NO_x than it did in FRP concentrations. Thus, median pre-flood

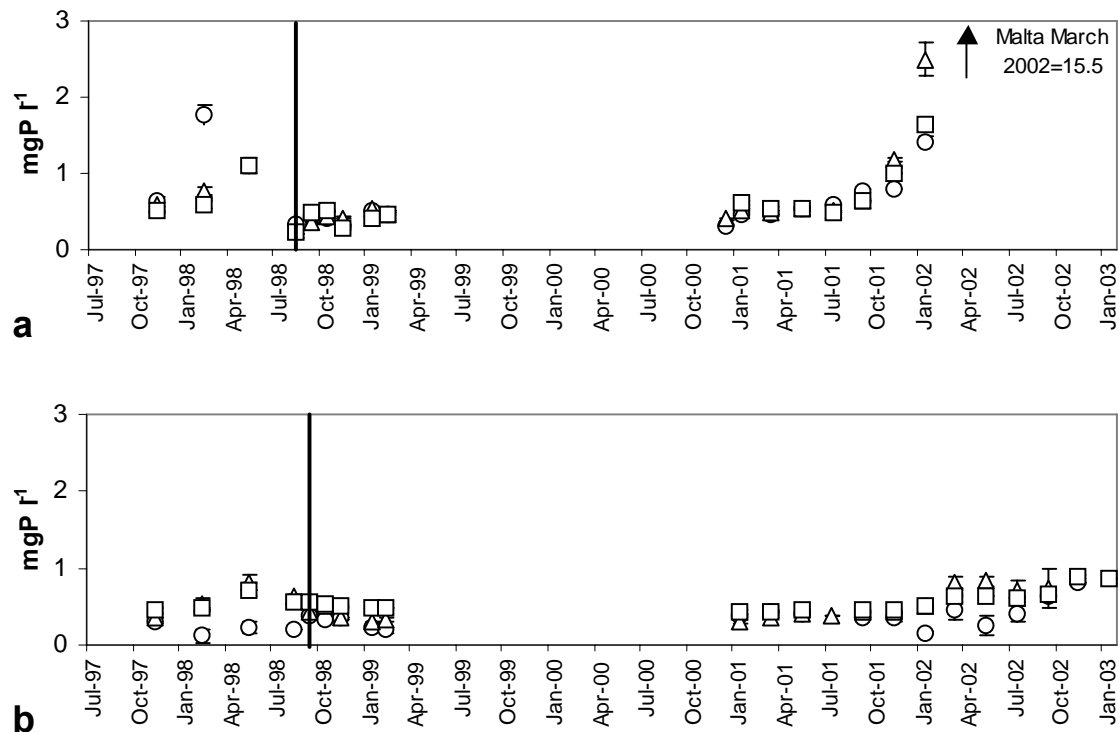
NO_x:FRP ratios ranged from 3.6-26.7 across the lakes, and increased to 152-386 after flooding (Table 2.1.5, Figure 2.1.13).

Parameter	Lake	Percentiles				
		0	10	50	90	100
TN (mg N l ⁻¹)	Malta	0.948	1.410	1.973	9.853	280.0
	Balaka	1.130	1.249	1.537	5.607	24.33
	Bijiji	1.133	1.247	1.788	3.425	5.193
	Tandure	0.305	0.633	0.988	1.368	1.675
	Menindee	0.852	0.977	1.123	2.197	3.670
	Cawndilla	0.598	0.705	0.890	1.612	3.848
NO _x (mg N l ⁻¹)	Malta	0.003	0.007	0.016	0.311	0.610
	Balaka	0.000	0.006	0.014	0.359	0.583
	Bijiji	0.000	0.010	0.012	0.128	0.515
	Tandure	0.005	0.006	0.021	0.170	0.287
	Menindee	0.005	0.006	0.023	0.287	0.435
	Cawndilla	0.000	0.006	0.009	0.152	0.247
NO _x :TN (%)	Malta	0.0	0.2	0.5	21.7	44.3
	Balaka	0.0	0.2	0.7	24.4	39.1
	Bijiji	0.0	0.3	0.8	6.3	27.6
	Tandure	0.4	0.6	3.0	14.1	19.3
	Menindee	0.1	0.3	2.5	22.8	31.3
	Cawndilla	0.0	0.3	1.1	21.6	40.5
TP (mg P l ⁻¹)	Malta	0.295	0.323	0.502	1.557	15.50
	Balaka	0.257	0.380	0.518	0.972	2.500
	Bijiji	0.223	0.335	0.525	1.058	1.633
	Tandure	0.120	0.193	0.346	0.468	0.815
	Menindee	0.293	0.329	0.434	0.811	0.835
	Cawndilla	0.430	0.445	0.507	0.723	0.882
FRP (mg P l ⁻¹)	Malta	0.017	0.048	0.210	0.306	0.353
	Balaka	0.013	0.016	0.241	0.369	0.545
	Bijiji	0.036	0.069	0.253	0.383	0.525
	Tandure	0.054	0.068	0.172	0.268	0.323
	Menindee	0.106	0.144	0.221	0.418	0.457
	Cawndilla	0.000	0.150	0.263	0.340	0.378
FRP:TP (%)	Malta	0.9	3.6	41.8	54.6	63.5
	Balaka	0.7	2.3	47.7	65.1	70.4
	Bijiji	7.9	16.7	44.5	65.5	76.5
	Tandure	26.7	34.3	47.5	83.4	89.3
	Menindee	0.0	21.6	50.7	69.5	84.0
	Cawndilla	0.0	24.9	50.5	76.4	77.9
NO _x :FRP	Malta	0.9	3.6	16.5	163.0	274.2
	Balaka	0.0	2.1	7.7	218.6	386.3
	Bijiji	0.0	2.4	13.9	100.2	245.2
	Tandure	2.4	3.1	26.7	97.3	152.2
	Menindee	1.1	2.5	5.9	158.0	202.3
	Cawndilla	1.9	2.4	3.6	56.0	328.9

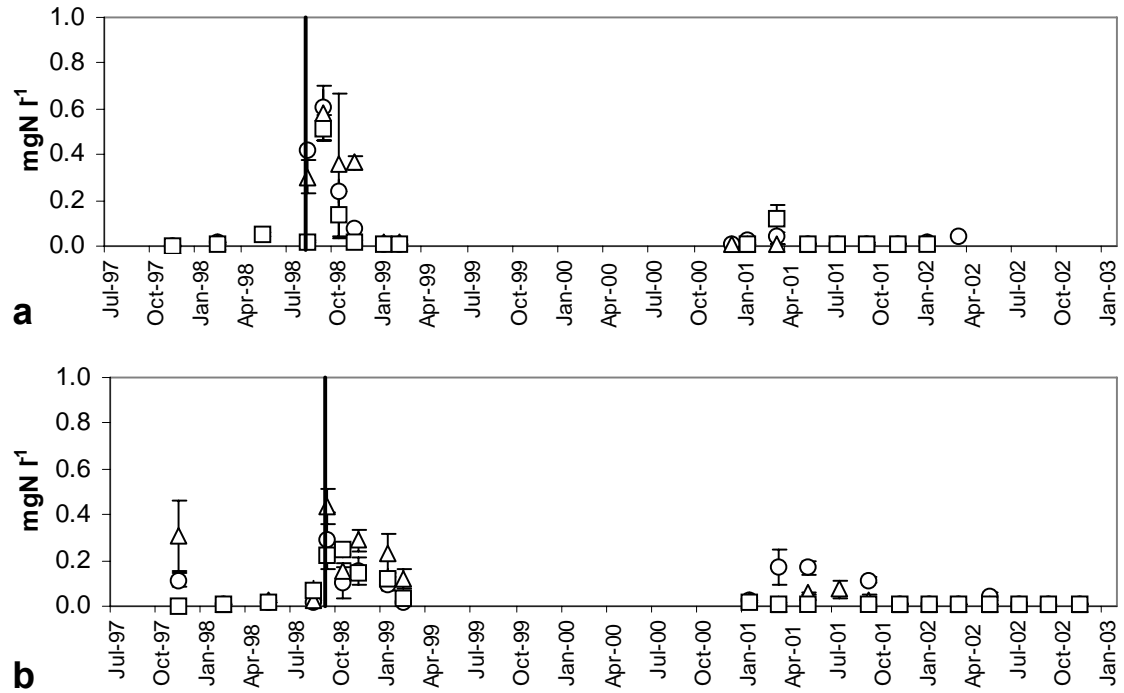
■ Table 2.1.5: Summary statistics for total nitrogen (mg N l⁻¹), dissolved oxides of nitrogen (mg N l⁻¹), NO_x:TN percentages, total phosphorus (mg P l⁻¹), filterable reactive phosphorus (mg P l⁻¹), FRP:TP percentages and NO_x:FRP ratios recorded in each of the lakes between 1997-2003.



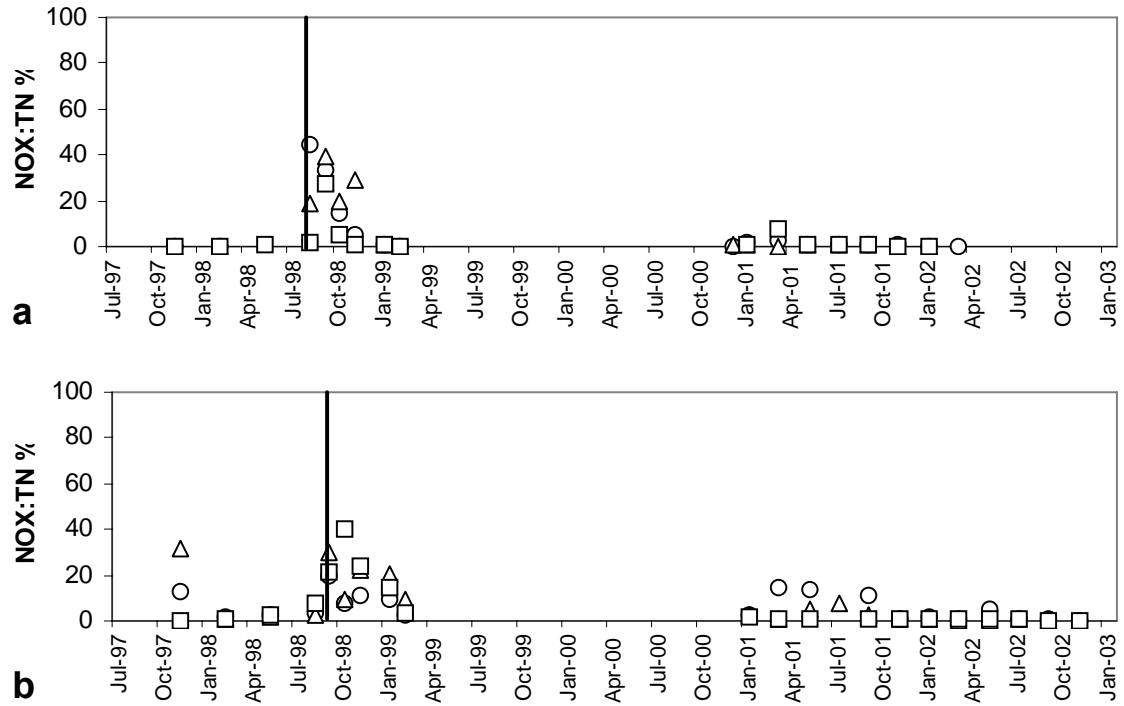
■ **Figure 2.1.7: Total nitrogen concentrations (mg N l⁻¹) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (□), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (□). The vertical bar indicates the 1998 flood event.**



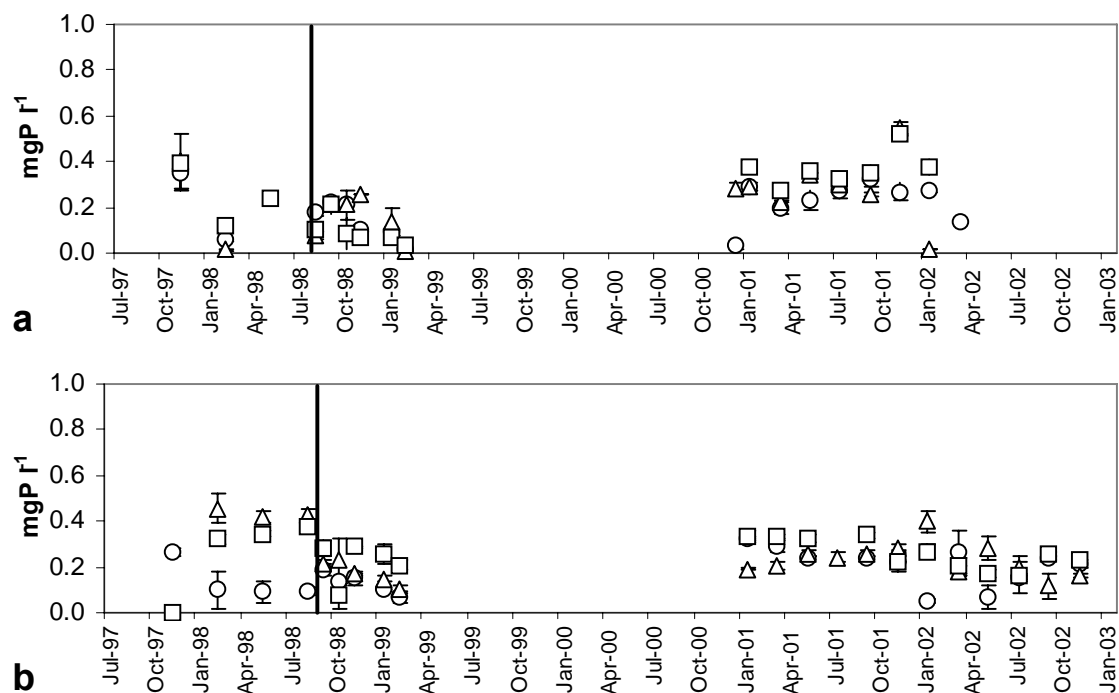
■ **Figure 2.1.8: Total phosphorus concentrations (mg P l⁻¹) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (□), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (□). The vertical bar indicates the 1998 flood event.**



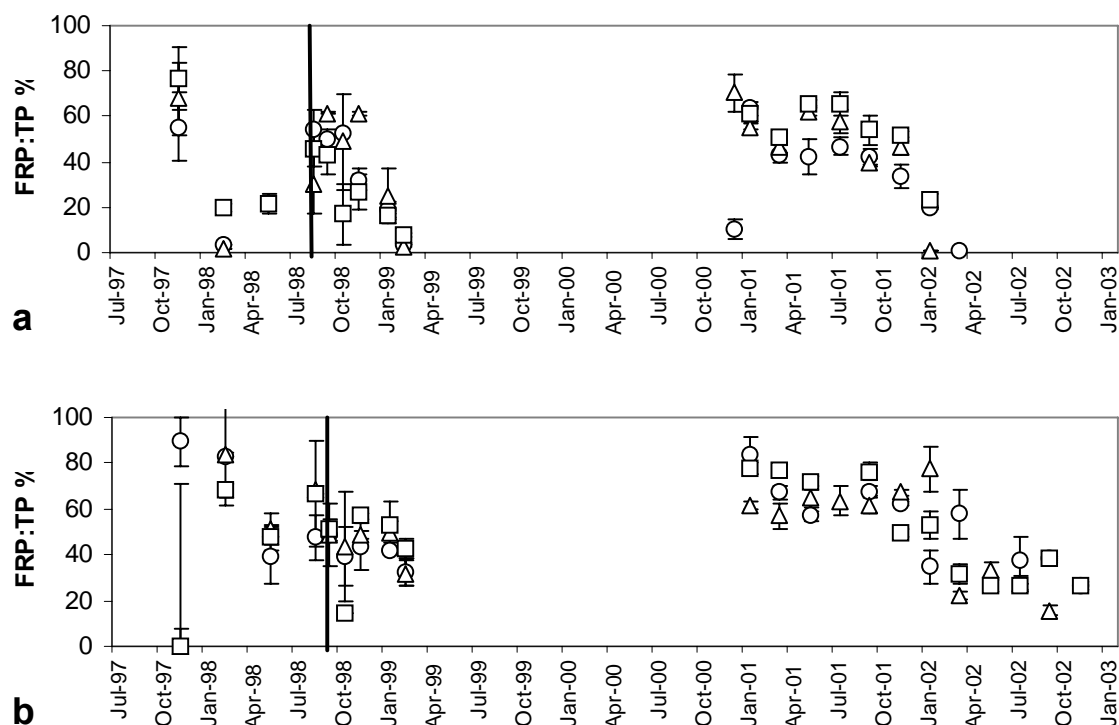
■ Figure 2.1.9: Oxides of nitrogen (NO_x) concentrations (mg N l^{-1}) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (\square), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (\square). The vertical bar indicates the 1998 flood event.



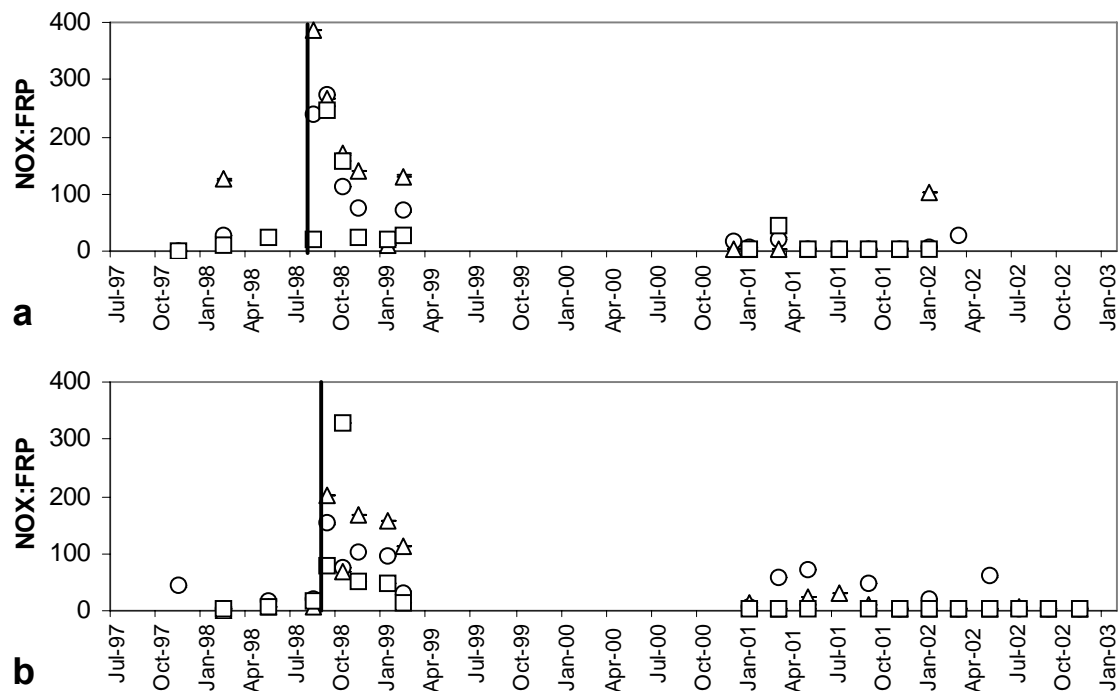
■ **Figure 2.1.10: Oxides of nitrogen:total nitrogen ($\text{NO}_x\text{:TN}$) percentages (%) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (\square), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (\square). The vertical bar indicates the 1998 flood event.**



■ **Figure 2.1.11: Filterable reactive phosphorus (FRP) concentrations (mg P l^{-1}) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (\square), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (\square). The vertical bar indicates the 1998 flood event.**



■ **Figure 2.1.12: Filterable reactive phosphorus:total phosphorus (FRP:TP) percentages (%) recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (\square), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (\square). The vertical bar indicates the 1998 flood event.**



■ **Figure 2.1.13: Dissolved oxides of nitrogen:filterable reactive phosphorus ($\text{NO}_x\text{:FRP}$) ratios recorded between 1997-2003 in a) lakes Malta (o), Balaka (Δ) and Bijiji (\square), and b) lakes Pamamaroo (o), Menindee (Δ) and Cawndilla (\square). The vertical bar indicates the 1998 flood event.**

Discussion

Water quality in six of the Menindee lakes was examined between 1997-2003. Of these, three were shallow (lakes Malta, Balaka and Bijiji) and three deeper (lakes Tandure, Menindee and Cawndilla). As a consequence of differences in lake profile and regulatory control, lakes Malta, Balaka and Bijiji are more prone to complete drying than are lakes Tandure, Menindee and Cawndilla. During the study period, the shallower lakes dried completely twice and the deeper lakes once. All lakes were flooded once between August and December 1998. Lake drying and re-flooding influenced water quality in each of the six lakes examined.

Median lake EC increased with distance upstream of the Main Wier, reflecting increases in the duration of hydraulic isolation from Lake Wetherell. As was identified by the DIPNR monitoring program, median EC was greater in Lake Cawndilla than in Lake Menindee and reflected the greater propensity for salt accumulation in Lake Cawndilla as a consequence of current flow regulation. Drying in all lakes was driven primarily by evaporation once they became disconnected from the mainstream. The shallower lakes (lakes Malta, Balaka and Bijiji) dried faster than did the deeper lakes (lakes Tandure, Menindee and Cawndilla). Maximum EC values in excess of $20,000 \mu\text{S cm}^{-1}$ were recorded in the remnant surface water pools. Re-filling reset all lake ECs to that of the floodwaters and reduced differences between lakes.

The smaller lakes were generally more turbid than the larger lakes, possibly reflecting differences in lake depth and susceptibility of the sediments to re-suspension by wind. Turbidity generally increased as lakes dried, possibly as a consequence of increasing sediment susceptibility to resuspension. The high turbidity of floodwaters that filled the lakes above the

Main Weir declined rapidly as suspended material settled. The lower turbidity of inflows to lakes Menindee and Cawndilla reduced the magnitude of post-flood responses in turbidity relative to those identified in the other lakes. Changes in the nature of lake connection (in series as opposed to direct connection) as a result of regulation plays a large role in this.

Median total nitrogen (TN) and total phosphorus (TP) concentrations were greater in the shallower lakes than in the deeper lakes. Both TN and TP concentrations increased as lakes dried during 1997-8 and 2001-3. Lakes Menindee and Cawndilla, where no significant response was identified during 1997-8, were exceptions to this. Similar findings were indicated in the previous section (Section 2.1.1). Post-flood TN and TP concentrations in lakes above the Main Weir reflected concentrations in the inflowing waters. In contrast to the lakes above the Main Weir, the nutrient content of inflows into Lake Menindee tended to be lower than that of the main flood pulse due to the sedimentation of entrained particles, abiotic associations and biotic assimilation during its passage via Lake Wetherell and Lake Pamamaroo. Post-flood TN concentrations in Lake Menindee were, however, initially much greater than could be accounted for by the floodwaters alone, suggesting that nutrient releases from the sediments may be important. No similar pulse of TP was identified. Changes in TN and TP concentrations following flooding of Lake Cawndilla were negligible.

During non-flood periods, dissolved oxides of nitrogen (NO_x) concentrations remained low ($<0.05 \text{ mg N l}^{-1}$) and constituted less than 5 % of the TN pool in all lakes. In contrast, filterable reactive phosphorus (FRP) concentrations were greater ($0.2\text{-}0.4 \text{ mg P l}^{-1}$) and constituted a much larger fraction of the TP pool (median 41.8-50.7 %), although FRP contributions to the total suspended phosphorus pool did tend to decline as drying progressed. Flooding in all lakes resulted in large increases in both NO_x concentrations, and NO_x :TN and FRP:TP percentages, though not FRP concentrations. Furthermore, flooding led to much greater increases in NO_x than FRP, which is consistent with the observations of Qiu and McComb (1996). As information regarding the NO_x and FRP content of floodwaters that entered lakes Menindee and Cawndilla was not available, comment as to the relative significance of floodwater contributions and sediment nutrient releases is not possible. Post-flood NO_x , NO_x :TN and FRP:TP pulses were rapidly assimilated in all lakes. Within 3 months of flooding these were close to or at pre-flood concentrations in all lakes. This is indicative of increasingly tighter coupling of biotic and abiotic release and uptake mechanisms.

Summary

Ephemeral deflation basin lakes (EDBL), such as the Menindee lakes, are naturally subject to periods of drying and re-flooding. Despite their geomorphic similarities, EDBL form a heterogeneous grouping of ephemeral environments that differ widely with respect to key determinants of ecosystem function, such as the nature of connection to other elements of the floodplain and their regimes of flooding and drying.

The regulation of water regimes within the Menindee Lakes system has decreased the frequency and duration of drying events in each lake (refer to Section 1). A reduction or even complete loss of a dry phase as a consequence of regulation is considered, firstly, to ameliorate the extremes in water quality, such as salinity, that are a natural component of ephemeral systems and upon which biota are thought to depend to cue life history changes (*e.g.* Boulton and Jenkins 1998), and secondly, to adversely impact upon wetland productivity through a reduction in nutrient bioavailability (*e.g.* Boulton and Lloyd 1992).

The water quality data presented in this review of DIPNR and MDFRC monitoring programs provides a clear indication of how salinity, turbidity and nutrients (nitrogen and phosphorus) within each of the Menindee lakes respond to episodes of drying and re-flooding. Changes in water quality observed during lake drying appeared to be driven by evaporation, however, little information currently exists regarding the role of groundwater interactions.

As lakes dried, salinity, total nitrogen and phosphorus concentrations and TN:TP ratios increased. There was no overall response of turbidity to changes in water level. Rates of change in water quality increased as water levels fell. In the larger storages this effect was most marked once water levels fell below 56.16-57.03 mAHD (0.89-1.76 m depth) in Lake Pamamaroo, 55.99-56.57 mAHD (1.64-2.22 m depth) in Lake Menindee, and 56.12-56.75 mAHD (3.44-4.07 m depth) in Lake Cawndilla. Because of differences in lake shape, threshold water levels/depths cannot be extrapolated to other lakes.

Changes in water quality in response to re-flooding generally reflected the quality of the inflowing waters. Post-inundation increases in turbidity were short lived. Flooding also stimulated a pulse of inorganic nitrogen and phosphorus that declined to low concentrations within 3 months after flooding. Relatively more inorganic nitrogen than phosphorus was made available following flooding to support biotic production.

Both the flood-pulse (*e.g.* Junk *et al.* 1989) and sediment-release (McComb and Qiu 1998, Baldwin and Mitchell 2000) mechanisms adequately account for observed increases in post-flood nitrogen and phosphorus concentrations, and account for the potential declines in wetland productivity that are believed to accompany changes in wetland hydrology. Firstly, regulation of inflows may reduce the net influx of nutrients by limiting the volume of flows or by limiting inflows to non-flood periods, when mainstream nutrient concentrations are likely to be lowest. Secondly, any reduction in the frequency or severity of lake drying will reduce lakebed exposure and thus inhibit the potential for nutrient releases from the sediments on flooding.

Flooding inflows appeared to be a more important driver of post-flood nutrient status, and hence of productive potential, than autochthonous releases from the sediments. However, significant nutrient (nitrogen) releases from the sediments were observed in Lake Menindee after flooding in 1998. Irrespective of nutrient source, flooding in all lakes examined led to increases in the lability of nitrogen, and to a lesser extent of phosphorus. This is in agreement with the observations of Qiu and McComb (1996). Other studies have indicated post-flood NO_x releases from the sediments to be rapid, peaking within a few days (Briggs *et al.* 1985,

Qiu and McComb 1996), whereas FRP releases tend to be slower (Qiu and McComb 1994, Mitchell and Baldwin 1998). It is possible that monthly observation may have missed much of the initial NO_x pulse and that sediment releases were more important in lakes Malta, Balaka and Bijiji than was indicated. Indeed, small-scale inundations of dried lakebed sediments collected from lakes Menindee and Balaka confirmed that both NO_x and FRP were being released from the sediments and that the release of NO_x was more rapid, peaking after 3-5 days, than was FRP, which peaked after 1-2 weeks (refer to Section 5).

Nutrient releases from newly inundated sediments are, however, by no means universal (*e.g.* Jacoby *et al.*, 1982; Baldwin, 1996; Mitchell and Baldwin, 1999). Nutrient transformations within the sediments are the net result of numerous inter-dependent interactions between physical, chemical and biological processes causing the sediment to act as nutrient sinks and/or sources. Identifying the links between wetting/drying and nutrient cycles in EDBL is an important first step towards developing management protocols aimed at preserving ecosystem integrity. As suggested above, increases in the frequency and duration of river flood pulses increases the potential for allochthonous inputs to floodplain wetlands. It also reduces the severity of drying events and thus also the potential for sediment nutrient transformations. Under these circumstances, organic matter may be expected to accumulate in EDBL causing them to function as net nutrient sinks. Indeed, this appears to be the case in lakes Malta, Balaka and Bijiji, where the organic content of the sediments is higher than that of the larger storages below the Main Weir (Scholz *et al.* 1999).

Hydraulic regulation has also modified the nature of connections between each of the lakes below the Main Weir and their primary source of water, the Darling River. Instead of being directly connected to the Darling River, the lakes are now connected in series, with riverine inflows directed through only one lake, Lake Pamamaroo. This has led to sequential decreases in median turbidity, due to increased residence times facilitating the settling of suspended particles, and to sequential increases in salt and phosphorus in the absence of flushing flows. The current hydraulic regime has thus increased the potential for sediment, salt and nutrient loading in these lakes. There is thus a real need to address the connectivity of these lakes and the potential for hydraulic management to address the issue of loading.

Although direct evidence supporting the ecological benefits to be gained by re-imposing episodes of lake drying is still limited, the re-imposition of drying phases has been recommended for a number of regulated wetlands within the Murray-Darling Basin (*e.g.* Briggs, 1988; Hydrotechnology, 1995). Other options include manipulating biotic processes, such as predation of fish by birds and/or grazing of exposed lakebeds. However, the efficacy of such tools cannot be established until appropriate numerical models that encapsulate the interrelations among the various pools and processes in EDBL have been developed. To this end, monitoring of the lakes was extended to include phytoplankton, zooplankton and fish communities. These data are presented in the following sections.

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2.2 Phytoplankton

O. Scholz

Introduction

The Menindee Lakes are representative of many of the shallow ephemeral floodplain depressions (ephemeral deflation basin lakes) that occur throughout the arid and semi-arid regions of the Murray-Darling Basin. Transitions between flooded and dry states are thought to drive both aquatic and terrestrial successional processes and facilitate biotic and abiotic exchanges between elements of the floodplain (*cf.* Flood Pulse Concept; Junk *et al.* 1989). The flooding of dry lakes is also thought to stimulate the release of potentially significant amounts of nutrients from the sediments (McComb and Qiu 1998, Baldwin and Mitchell 2000, Scholz *et al.* 2002) and inundated vegetation (Furch and Junk 1997), and drying of these characteristically turbid lakes has also been shown to lead to increases in both suspended nutrient concentrations (Section 2.1). Because of these responses, episodes of flooding and drying are thus likely to be periods of maximum aquatic primary production.

Hydraulic regulation since the 1960s of the Menindee Lakes has increased the permanency of water stored within each lake and reduced both the frequency and duration of complete lake drying episodes (Table 1.3). Whilst regulation is thought responsible for declines in wetland values, such as productivity and bio-diversity (Boulton and Lloyd 1992, Bunn *et al.* 1997, Boulton and Jenkins 1998), little site-specific ecological information is currently available to support these suppositions or to guide management actions such as the re-imposition of drying phases.

Awareness of the potential for flow regulation to stimulate phytoplankton bloom formation within the Menindee Lakes increased following the development of extensive cyanobacterial blooms (*Anabaena circinalis*) during 1991 both within the Menindee Lakes and its source waters, the Darling River (Hötzl and Croome 1994, Harriss *et al.* 1996). This led to the establishment of a phytoplankton and water-quality monitoring program within the main storages by the NSW Department of Infrastructure Planning and Natural Resources (DIPNR). In this first review of phytoplankton data collected from the Menindee Lakes between 1996-2002 we describe the communities present within each of the main storages (lakes Pamamaroo, Menindee and Cawndilla) and discuss temporal variations in community structure in relation to episodes of lake flooding and drying. This information will be useful for identifying both periods of greatest risk for the establishment of potentially nuisance algal blooms and for identifying the mechanisms responsible for such changes in phytoplankton communities.

Methods

Phytoplankton samples were collected from a single site in the centre of lakes Pamamaroo, Menindee and Cawndilla every month between January 1996 and December 2002. Phytoplankton were counted from an unfiltered 250 ml sample of water collected at a depth of 0.25 m and were preserved with Lugol's Iodine solution. Samples were concentrated by settling and a minimum of 200 cells or 10 % of the sample counted at 200x magnification using a Lund cell (APHA, 1995). Phytoplankton identifications to genera followed Prescott (1983), and Baker & Fabbro (1999). Whole-lake phytoplankton loads (cells lake⁻¹) were determined using 3rd order polynomial curve equations describing lake water level-volume relationships (NSW DIPNR 1988 unpublished data). Turbidity (NTU) and water temperature (°C) were determined *in situ* at the same sites and times as for phytoplankton at a depth of

0.25 m below the water surface using field turbidity and temperature meters (WTW, Weilheim Germany).

Multivariate analyses of phytoplankton community structure were performed using PRIMER (V5; Primer-E Ltd., 2000). Phytoplankton matrices were 4th-root transformed to down weigh the influence of individual taxa and to increase analytical robustness to zero values before calculating Bray-Curtis similarity co-efficients. Non-metric multidimensional scaling (NMDS) was used to examine multidimensional proximity of monthly samples for each lake. ANOSIM was used to test *a priori* hypotheses regarding differences between drying, non-drying and post-flood phase assemblages. Drying and non-drying phases for each lake were defined as water levels below 57 mAHD and above 57 mAHD, respectively. This boundary was based on the point of inflection in water quality responses to changes in water level described in Section 2.1.1. Post-flood assemblages were defined as those occurring within 4 months after the flooding of lakes in August 1998 and March 2000. ANOSIM R values reflect the degree of separation ($R \rightarrow 1$ maximum separation). SIMPER was used to identify species contributing most to group differences in cases where significant group differences were identified. BIOENV was used to explore the amount of variability in community structure accounted for by water level, turbidity and temperature. Environmental data (mAHD, NTU, °C) were not transformed before calculating normalised Euclidean similarity co-efficients. Normalising data adjusted for measurement unit differences between variables. Relationships between phytoplankton and environmental similarity matrices were expressed as Spearman rank correlation co-efficients (ρ). Values of ρ approaching 1 indicate increasing agreement between two sets of ranks. Because ranks were based on a large number of strongly inter-dependent similarity calculations, neither statistical significance or causality can be inferred from the regression co-efficients (ρ) (Clarke & Warwick, 1994).

Results

Sixty-five phytoplankton genera from 8 phyla were identified in 219 samples taken from lakes Pamamaroo, Menindee and Cawndilla between January 1996-December 2002. Of these, 11 taxa occurred in more than 30 % of all samples and 20 taxa were recorded in less than 1 % of samples (*i.e.* were rare) (Table 2.2.1). Twenty-eight taxa were common to all lakes. Chlorophyceae, Cyanobacteria and Bacillariophyceae were the most diverse phyla with 35, 10 and 10 taxa, respectively.

Distinct shifts in community composition at the phylum level were evident through the lakes from Lake Pamamaroo to Lake Cawndilla. These changes were characterised by an increase in the relative density of Chlorophyceae and by decreases in the relative densities of Cryptophyceae and Bacillariophyceae (Table 2.2.1). Total phytoplankton densities ranged from 63-378141 cells ml⁻¹. Median phytoplankton densities increased through the lakes from Lake Pamamaroo to Lake Cawndilla (Table 2.2.2).

Water levels during the 1996-2002 study period fluctuated by 6.18 m (55.82-62.00 mAHD) in Lake Pamamaroo, 5.35 m (55.29-60.59 mAHD) in Lake Menindee, and 5.99 m (54.60-60.59 mAHD) in Lake Cawndilla. Maximum surcharge depths of lakes Pamamaroo, Menindee and Cawndilla are 6.73 m (62.00 mAHD), 7.15 m (61.50 mAHD) and 8.82 m (61.50 mAHD), respectively. Whilst the lakes are managed so as to maintain full supply or maximum surcharge capacity when possible, two protracted periods of lake drying, during which there were no significant inflows, occurred between August 1997-August 1998 and from November 2001 until the end of observations in December 2002. Reductions in water level during these periods were driven by both releases and evaporation. Lakes Menindee and Cawndilla remained connected throughout the study period until November 2002 when water levels fell below 55.0 mAHD. Significant filling events during the study period raised water levels by

3.08 m (August 1998-January 1999), 1.27 m (November 1999-January 2000) and 0.85 m (December 2000-February 2001) in Lake Pamamaroo, and by 4.19 m and 5.00 m (August-December 1998) in lakes Menindee and Cawndilla, respectively, and by 0.58 m (March-May 1999) and 1.82 m (April-July 2000) in both lakes Menindee and Cawndilla. Relative changes in water level for each lake are shown in Figure 2.2.1a.

Phytoplankton taxa	Frequency of occurrence (%)	Relative abundance (%)		
		Pamamaroo	Menindee	Cawndilla
Chlorophyceae		53.4	78.6	81.8
Oocystis	88.6	28.0	9.2	17.9
Ankistrodesmus	75.8	6.3	2.2	2.1
Chlamydomonas	53.9	3.4	0.6	0.7
Scenedesmus	48.4	5.8	2.4	2.1
Planktonema	39.7	0.7	56.1	40.7
Crucigenia	36.1	3.6	4.3	12.3
Schroederia	35.2	0.6	0.3	0.3
Tetraedron	30.1	0.5	0.3	0.3
Closterium	17.4	0.1	<0.1	0.1
Dictyosphaerium	16.4	1.9	0.5	1.2
Chodatella	13.7	0.1	0.1	0.5
Sphaerocystis	13.7	0.8	0.5	0.5
Elakatothrix	11.0	0.3	0.1	0.3
Ankyra	7.3	<0.1	<0.1	<0.1
Coelastrum	7.3	0.2	0.7	0.3
Golenkinia	6.4	-	<0.1	0.2
Actinastrum	5.0	0.3	0.6	0.2
Pediastrum	3.2	0.1	0.3	0.2
Pteromonas	2.7	0.1	<0.1	-
Dimorphococcus	2.3	0.1	<0.1	-
Kirchneriella	1.8	<0.1	-	0.2
Tetrastrum	1.8	0.3	0.1	<0.1
Carteria	1.4	-	-	<0.1
Chlorella	1.4	-	-	0.4
Gloeactinium	0.9	0.1	0.1	-
Monoraphidium	0.9	0.1	0.1	-
Wislouchiella	0.9	<0.1	<0.1	-
Unidentified	0.5	-	-	0.8
Micractinium	0.5	<0.1	-	0.3
Chlorogonium	0.5	0.1	-	-
Botryococcus	0.5	<0.1	-	-
Coccomonas	0.5	-	<0.1	-
Cosmarium	0.5	-	-	<0.1
Eudorina	0.5	-	-	<0.1
Pandorina	0.5	-	-	<0.1

Phytoplankton taxa	Frequency of occurrence (%)	Relative abundance (%)		
		Pamamaroo	Menindee	Cawndilla
Cyanophyceae		12.1	11.4	9.0
Anabaena	16.0	3.2	6.5	2.3
Merismopedia	8.2	0.5	0.7	4.1
Anabaenopsis	5.0	<0.1	0.2	0.1
Aphanizomenon	3.7	4.1	1.8	0.2
Microcystis	1.8	0.6	<0.1	2.2
Oscillatoria	1.8	0.4	2.1	0.1
Pseudanabaena	1.8	3.3	<0.1	-
Lyngbya	0.5	-	<0.1	-
Planktolyngbya	0.5	-	0.1	-
Raphidiopsis	0.5	<0.1	-	-
Bacillariophyceae		7.8	4.7	1.6
Cyclotella	47.5	3.6	0.3	0.6
Nitzschia	20.5	0.9	3.8	0.3
Melosira/Aulacoseira	20.1	2.3	0.1	0.2
Navicula	8.2	0.1	0.2	0.1
Synedra	6.4	0.8	0.2	0.3
Fragilaria	1.8	-	<0.1	<0.1
Attheya/Acanthoceras	0.9	<0.1	<0.1	-
Hantzschia	0.5	-	<0.1	-
Pinnularia	0.5	-	<0.1	-
Surirella	0.5	<0.1	-	-
Cryptophyceae		25.0	4.6	7.2
Rhodomonas	91.3	20.7	3.9	6.0
Cryptomonas	68.9	4.3	0.7	1.2
Euglenophyceae		1.4	0.7	0.4
Euglena	29.2	0.8	0.3	0.3
Trachelomonas	20.1	0.5	0.2	0.1
Lepocinclis	1.4	<0.1	<0.1	<0.1
Strombomonas	0.9	<0.1	<0.1	-
Dinophyceae		0.3	<0.1	0.1
Peridinium	14.6	0.3	<0.1	0.1
Ceratium	0.5	-	<0.1	-
Chrysophyceae		0.0	0.0	<0.1
Mallomonas	1.4	-	-	<0.1
Chloromonadophyta		<0.1	0.0	<0.1
Merotrichia	1.4	<0.1	-	<0.1

■ Table 2.2.1: Phytoplankton taxa identified from lakes Pamamaroo (n=74), Menindee (n=74) and Cawndilla (n=71) over the 1996-2002 study period showing the frequency of occurrence of taxa in all collected samples (%) and their relative abundance (%) in samples from each lake.

Parameter	Lake	Percentiles				
		0	10	50	90	100
Phytoplankton abundance (cells ml ⁻¹)	Pamamaroo	63	429	2612	8103	60977
	Menindee	64	488	3586	64379	378141
	Cawndilla	225	1170	11318	24664	122801

■ **Table 2.2.2: Summary statistics for monthly phytoplankton abundance (cells ml⁻¹) recorded in lakes Pamamaroo (n=74), Menindee (n=74) and Cawndilla (n=71) over the 1996-2002 study period.**

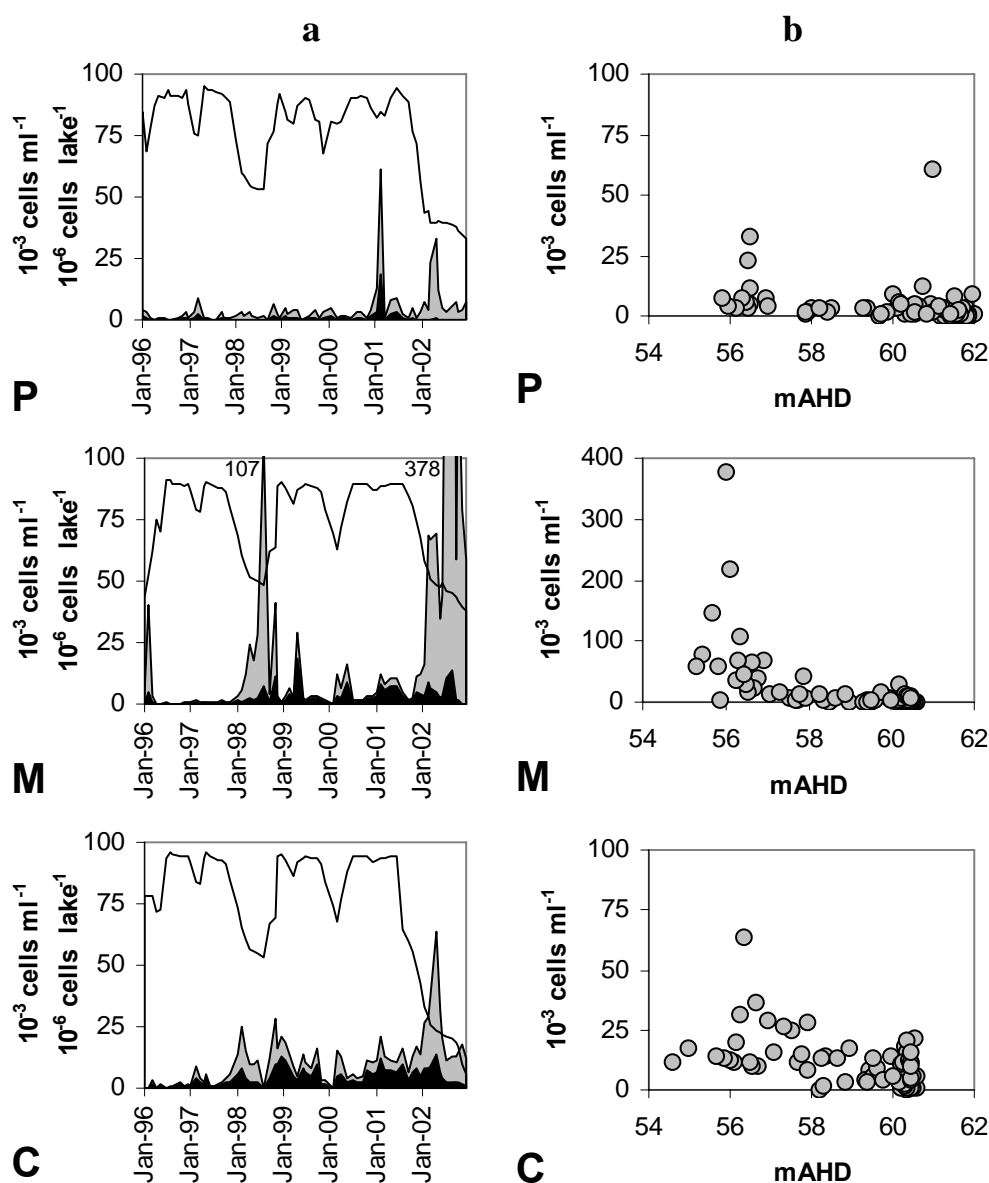
Following an initial dilution by the inflowing flood waters; lake flooding stimulated increases in both phytoplankton density and whole-lake phytoplankton populations (Figure 2.2.1a). Increases in post-flood phytoplankton cell densities in lakes Pamamaroo and Cawndilla were similar to those present in their source waters, lakes Wetherell and Menindee, respectively; suggesting that external loading primarily drove these increases. For example, maximum post-flood phytoplankton densities in Lake Pamamaroo of 6115 cells ml⁻¹ (August 1988-January 1999), 5214 cells ml⁻¹ (November 1999-January 2000) and 60988 cells ml⁻¹ (December 2000-February 2001) reflected those present in Lake Wetherell (10001 cells.ml⁻¹, 6555 cells ml⁻¹ and 47708 cells ml⁻¹, respectively: NSW DIPNR unpublished data). In contrast, increases in cell density observed in Lake Menindee after its re-flooding during August-December 1998 (max. 41081 cells ml⁻¹), March-May 1999 (max. 28743 cells ml⁻¹) and April-July 2000 (max. 15782 cells ml⁻¹) were much greater than could be attributed to loading from Lake Pamamaroo (6115 cells ml⁻¹, 3653 cells ml⁻¹, 1689 cells ml⁻¹, respectively). These data suggest that for Lake Menindee at least, flooding stimulated significant within lake population growth.

Highest phytoplankton cell densities were recorded during the episodes of lake drying that occurred during 1997-8 and 2001-2. Comparing plots of phytoplankton cell densities with whole-lake phytoplankton loads indicated that increases in cell density during these periods were due to both evaporative concentration and population growth (*e.g.* Lake Pamamaroo early-2001, Lake Menindee early and mid-2002, Lake Cawndilla late-2002) or primarily to evaporative concentration (*e.g.* Lake Pamamaroo early 2002, Lake Menindee mid-1998 and late-2002, Lake Cawndilla late 2002) (Figure 2.2.1a). Increases in phytoplankton cell density were most marked once water levels fell below about 57 mAHD (Figure 2.2.1b).

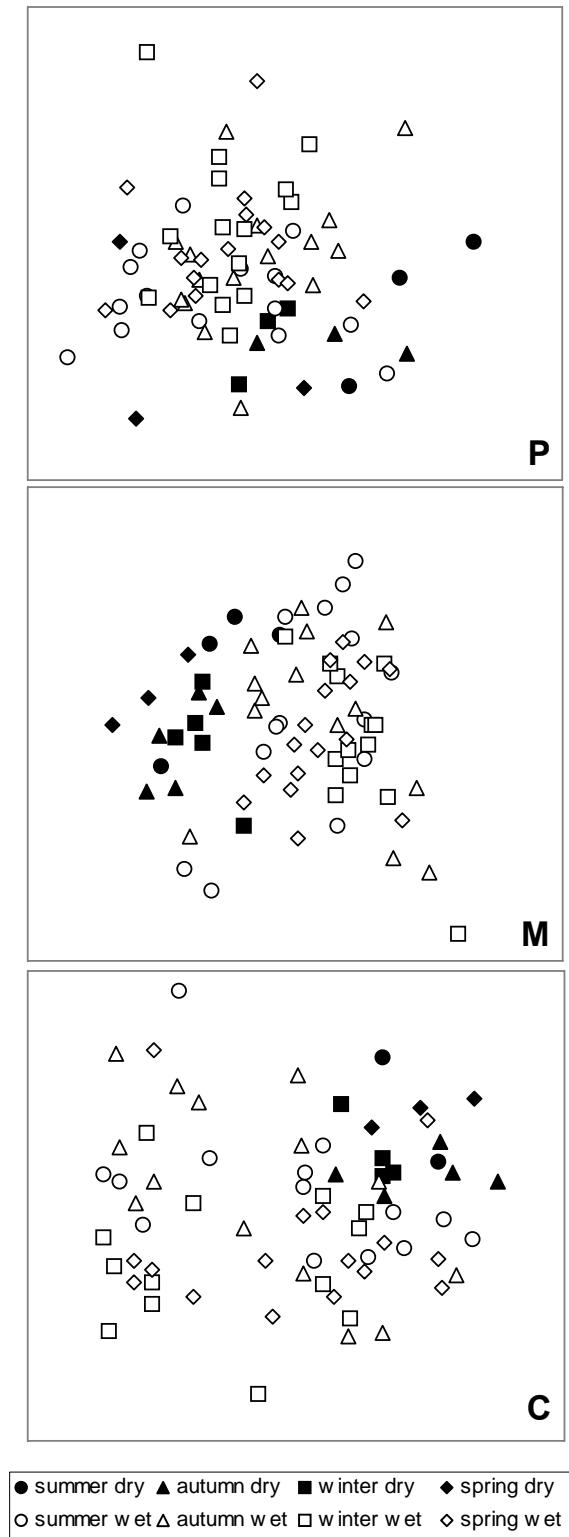
Two-dimensional NMDS plots of phytoplankton community structure (composition and density) are shown in Figure 2.2.2. For each lake, differences in community structure between drying (<57.0 mAHD) and non-drying (>57.0 mAHD) periods were significant (ANOSIM: Lake Pamamaroo $R=0.364$, $p<0.001$, Lake Menindee $R=0.574$, $p<0.001$, Lake Cawndilla $R=0.134$, $p=0.033$). Although drying episodes were not replicated in Lake Pamamaroo, they were in lakes Menindee and Cawndilla, indicating that community responses between successive drying events were uniform or predictable. SIMPER analyses of group differences indicated that changes in community structure associated with drying in each lake were characterised by increases in the chlorophytes *Planktonema* sp. (except in Lake Pamamaroo), *Oocystis* sp., *Ankistrodesmus* sp., *Scenedesmus* sp. and *Crucigenia* sp., cyanobacteria (especially *Anabaena* sp. and *Merismopedia* sp.), and euglenids (*Euglena* sp. and *Trachelomonas* sp.). Post-flood phytoplankton community structure varied between flooding events and did not differ significantly from that of communities present in either lake during non-drying periods (*i.e.* water levels >57 mAHD) (ANOSIM: $p>0.05$).

In addition to changes in lake water levels associated with episodes of lake flooding and drying, other factors such as temperature and turbidity, through their influence on algal productive potential, may also play important roles in determining both phytoplankton

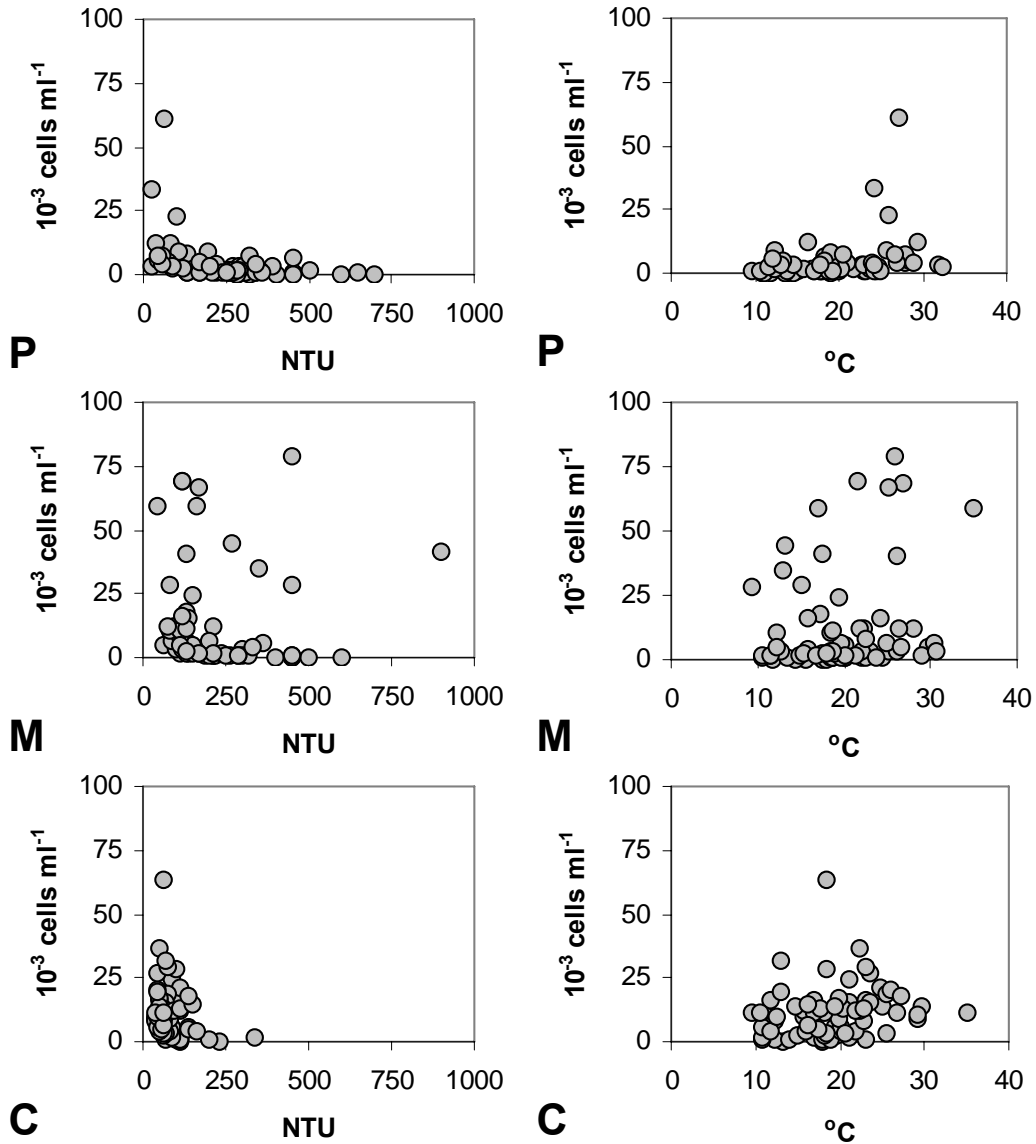
abundance and species composition. Mean (\pm s.e.) monthly water temperatures ranged from 11.5 ± 0.2 °C in July to 26.4 ± 0.8 °C in February. Turbidity ranged between 25-900 NTU, with median values declining through the lakes (Lake Pamamaroo 220 NTU, Lake Menindee 170 NTU, Lake Cawndilla 70 NTU) (Refer to Section 2.1.1 for a more detailed account of water quality throughout the study period). Figure 2.2.3 shows that phytoplankton densities tended to be higher when turbidity was low, and that responses to temperature were less pronounced. BIOENV analyses indicated that water level and turbidity combined explained more of the variability observed in the phytoplankton community structure in lakes Pamamaroo and Cawndilla than did temperature or turbidity either individually or in combination. Water level alone accounted for much of the variability in community structure encountered in Lake Menindee (Table 2.2.3).



■ Figure 2.2.1: a) Phytoplankton density ($10^3 \text{ cells ml}^{-1}$) (grey), phytoplankton load ($10^6 \text{ cells lake}^{-1}$) (black) and relative changes in water level, and b) relationships between phytoplankton density ($10^3 \text{ cells ml}^{-1}$) and water level (mAHd) level recorded between 1996-2002 in lakes Pamamaroo (P), Menindee (M) and Cawndilla (C).



■ **Figure 2.2.2: Non-metric multidimensional scaling plots of phytoplankton assemblages collected from lakes Pamamaroo (P), Menindee (M) and Cawndilla (C) between 1996-2002, showing relative seasonal positions and community responses to lake drying. Stress levels: 0.23 (P), 0.19 (M) and 0.19 (C).**



■ Figure 2.2.3: Relationships between phytoplankton density (10^3 cells ml^{-1}) and turbidity (NTU) and water temperature ($^{\circ}\text{C}$) recorded over the period 1996-2002 for lakes Pamamaroo (P), Menindee (M) and Cawndilla (C).

Lake	Spearman rank correlation co-efficient (ρ)						
	mAHD	$^{\circ}\text{C}$	NTU	mAHD and $^{\circ}\text{C}$	mAHD and NTU	$^{\circ}\text{C}$ and NTU	All
Pamamaroo	0.188	0.114	0.265	0.201	0.302	0.250	0.289
Menindee	0.545	0.050	0.149	0.424	0.531	0.149	0.448
Cawndilla	0.177	-0.010	0.237	0.130	0.302	0.148	0.242

■ Table 2.2.3: Spearman rank correlation co-efficients (ρ) calculated using BIOENV between phytoplankton communities and water level (mAHD), turbidity (NTU), and temperature ($^{\circ}\text{C}$). Highest ρ values for each lake are highlighted.

Discussion

Recent studies have shown that water quality throughout the Menindee Lakes fluctuates in response to disturbances such as lake drying and re-flooding (Scholz *et al.* 2002; Section 2.1). The large increases in nutrient concentrations that occur as lakes become dry and after they are flooded suggest that these events were also periods of potentially maximum aquatic production (Section 3). Regulation, through its reduction of the frequency and severity of lake drying events may thus reduce aquatic primary productivity by reducing nutrient availability (*e.g.* Baldwin and Mitchell 2000). This examination of phytoplankton data collected over the period 1996-2002 sought firstly to describe the communities present in each of the three main storages (lakes Pamamaroo, Menindee and Cawndilla) and secondly, to examine community responses throughout the hydrological cycle. Whilst changes in phytoplankton composition and abundance provide important information necessary for understanding links between hydrology and trophic processes, a better understanding of the conditions that lead to the establishment of potentially noxious algal blooms (*i.e.* blue-green algae) is of particular interest to water supply managers.

Lakes Pamamaroo, Menindee and Cawndilla are connected in series, with inflows from the Darling River (Lake Wetherell) passing initially through Lake Pamamaroo. The phytoplankton communities of Lake Pamamaroo were similar to those reported by Hötzel and Croome (1994) for the Darling River. Changes in phytoplankton community structure through the serially connected lakes were characterised by progressive increases in median total phytoplankton densities and the displacement of cryptophytes and diatoms by chlorophytes. These community changes corresponded with progressive decreases in turbidity and to sequential increases in salinity and phosphorus (Section 2.1.1). While median salinity increased through the system, much larger fluctuations in salinity occurred in response to evaporative concentration and dilution throughout the wetting and drying cycle (Section 2.1.1). Little salt sensitivity data is available to suggest what impacts cyclical changes in salinity associated with lake drying and re-flooding are likely to have on the planktonic flora (Hart *et al.* 1991, Bailey and James 2000). It is unlikely that salinity was a major determinant of phytoplankton community structure, as most phytoplankton taxa were recorded over the entire salinity range encountered during the study period (168-1780 $\mu\text{S cm}^{-1}$; Section 2.1).

Lake phytoplankton densities initially declined in response to the commencement of inflows. As flooding progressed both phytoplankton densities and whole lake phytoplankton loads increased. These increases could be attributed primarily to external loading. However, much higher post-flood phytoplankton densities were recorded in Lake Menindee during 1998 than were present in the floodwaters, suggesting that flooding had also stimulated in-lake population growth. Whilst flooding is likely to have stimulated phytoplankton growth in all lakes by increasing the availability of nutrients (Scholz *et al.*, 2002), much of this growth would have been masked by dilution as the lakes filled.

Phytoplankton densities generally increased as lakes dried. Phytoplankton responses to lake drying tended to become more pronounced as water levels fell below about 57 mAHd, or 1.2 m, 1.0 m and 2.4 m in lakes Pamamaroo, Menindee and Cawndilla respectively. These depths also marked transition points in water quality responses to drying, below which rates of increase in total nitrogen, total phosphorus and electrical conductivity increased significantly (Section 2.1). Increases observed in phytoplankton densities were driven by both population growth, possibly in response to increases in nutrient availability, and by evaporative concentration. Highest phytoplankton cell densities recorded during the 1996-2002 study period occurred during these drying episodes. Lake drying also stimulated significant changes in phytoplankton community composition that were consistent both between lakes and between drying events. These changes were characterised primarily by the numerical dominance of the chlorophytes *Planktonema* sp. (except in Lake Pamamaroo), *Oocystis* sp.,

Ankistrodesmus sp., *Scenedesmus* sp. and *Crucigenia* sp., euglenids (*Euglena* sp. and *Trachelomonas* sp.) and cyanobacteria (especially *Anabaena* sp. and *Merismopedia* sp.). From a management perspective, the risk of nuisance algal bloom development is thus increased during episodes of lake drying when the demand for potable water is also at its greatest.

Seasonality has been demonstrated to be a key driver of phytoplankton community structure (composition and density) across a wide range of lentic environments (e.g. Sommer *et al.* 1986, Anneville *et al.* 2002). However, seasonal temperature cycles appeared to be less important than water level and turbidity in accounting for temporal variations in phytoplankton populations. These findings concur with those reported for the phytoplankton present within the adjacent Darling River by Hötzel and Croome (1994). Whilst there was no overall relationship between water level and turbidity (Section 2.1), reductions in both are likely to have increased the photic zone/maximum lake depth ratio. This suggests that primary production in these characteristically turbid lakes was light limited, although this has yet to be empirically validated.

Our data indicates that changes in phytoplankton community structure may be mediated during cycles of lake flooding and drying by processes such as external loading and evaporative concentration, respectively, and growth, mediated by changes in nutrient availability and turbidity, respectively. Whilst ‘top-down’ trophic cascading effects on phytoplankton productivity by grazers have been well documented for temperate and tropical systems (e.g. Thornton *et al.* 1990, Mazumder 1994, Havens *et al.* 1996, Kjeldsen 1996, Kurmayer and Wanzenböck 1996, Reynolds 1999), we have no quantitative data to indicate the significance of such interactions within the Menindee Lakes. However, concurrent investigations of zooplankton, fish and bird communities present within the Menindee Lakes provide some evidence for trophic cascading initiated by lake drying (Sections 2.3 and 2.4, Jaensch *et al.* 2002). For example, the larger and more permanent lakes in arid regions, such as those examined here, tend to function as important water-bird refuges during drying events when many smaller water bodies disappear altogether (Kingsford and Porter 1999, Timms 2001, Kingsford *et al.* 2002). Thus, as these ‘refuge’ lakes dry and water-bird numbers increase, predation pressure by water-bird populations also increases. This may lead to the replacement of aquatic vertebrate predators (fish) by invertebrate predators, which may in turn increase predation pressures on invertebrate grazers. The increases in phytoplankton populations observed as lakes dry may thus also be attributable to reductions in ‘top-down’ control of phytoplankton populations.

Summary

We examined phytoplankton community structure in lakes Pamamaroo, Menindee and Cawndilla over a period of seven years (1996-2002) to identify responses to lake flooding and drying. Changes in community structure evident through these serially connected lakes were characterised by increases in median cell density, increases in Chlorophyceae, and decreases in Cryptophyceae and Bacillariophyceae. These changes corresponded with progressive reductions in median turbidity and increases in median total phosphorus concentrations.

Phytoplankton densities and whole lake phytoplankton loads increased in response to flooding. These increases were attributed to external loading and in-lake population growth. Post-flood population growth was likely stimulated by concomitant increases in nutrient availability. Phytoplankton densities and whole lake phytoplankton loads increased as lakes dried. These increases were attributed to evaporative concentration and population growth. Highest phytoplankton cell densities were recorded during episodes of lake drying. Phytoplankton communities at these times became numerically dominated by chlorophytes

(*Planktonema* sp., *Oocystis* sp., *Ankistrodesmus* sp., *Scenedesmus* sp., *Crucigenia* sp.), euglenids (*Euglena* sp. and *Trachelomonas* sp.) and cyanobacteria (*Anabaena* sp., *Merismopedia* sp.).

Seasonal temperature cycles were less important than were water level and turbidity in explaining temporal variations in phytoplankton populations. Reductions in both water level and turbidity increased the proportion of the water column occupied by the photic zone. This suggested that primary production in these characteristically turbid lakes was light limited.

Whilst temporal changes in phytoplankton community structure through cycles of lake flooding and drying could be attributed to processes such as external loading and evaporative concentration, respectively, and to growth, mediated by changes in nutrient availability and turbidity, we suggest that 'top-down' trophic cascading may play an equally important role in regulating the development of potentially nuisance algal blooms, especially as lakes dried.

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2.3 Zooplankton

O. Scholz

Introduction

Zooplankton provide major links in aquatic food chains by facilitating the transfer of nutrients, carbon and energy between bacteria, algae and higher consumers, such as fish and water fowl (*e.g.* Boon and Shiel 1990, Boulton and Jenkins 1998, Humphries *et al.* 1999). Because of this, zooplankton plays a key role in structuring ecosystem function (Shapiro *et al.* 1975, Lazzaro 1997). Zooplankton community structure is influenced by many factors, including life history characteristics, food availability, predation pressure, water quality, habitat diversity and complexity, and exchanges between lake and riverine environments (Wiggins *et al.* 1980, Shiel and Walker 1984, Williams 1985, Shiel 1985, 1986, 1995). Many of these factors are influenced by season and in ephemeral systems by drying and flooding. Despite potentially complex interactions between these factors, generalised responses of zooplankton to flooding and drying are to be expected, especially during the initial post-flood and late drying phases when changes in biotic and abiotic factors are likely to be greatest.

Few studies have examined the zooplankton of Australian dryland systems or tested hypotheses regarding the responses of zooplankton communities to aspects of water regime such as drying and flooding. Wetland inundation has been shown to initiate a successional sequence in zooplankton communities, with initial immigrants being replaced by emergents from the sediments during the first month after flooding (Jenkins and Boulton 2003), and to stimulate zooplankton productivity (*e.g.* Boulton and Lloyd 1992, Maher and Carpenter 1984). The few field and mesocosm studies that are available suggest that microinvertebrate productivity is linked to the frequency of inundation and to the duration of dry periods. For example, wetlands that experience frequent episodes of drying tend to be more productive than those that dry only infrequently (Boulton and Lloyd 1992, Jenkins and Boulton 1998), and longer dry phases tend to reduce the viability of aestivating individuals and of eggs and cysts deposited in the sediments (Moritz 1987, Hairston *et al.* 1995, Briggs *et al.* 1997, Jenkins and Briggs 1997). Further, as the period of inundation increases, biotic processes become relatively more important than abiotic processes in determining the distribution and abundance of invertebrate species (Wiggins *et al.* 1980, Boulton and Jenkins 1998). Prolonged inundation has also been shown to mediate a shift in community composition away from taxa with flexible life history strategies (Baird *et al.* 1987) and to reduce invertebrate abundance and productivity (Maher and Carpenter 1984). In comparison to post-inundation responses, relatively little is known of the responses of zooplankton communities to lake drying.

We have shown that wetland drying within ephemeral wetlands such as the Menindee Lakes is associated with increases in salt and suspended nutrient concentrations, and phytoplankton densities, and with reductions in fish abundances (*cf.* Scholz *et al.* 2002, and Sections 2.1, 2.2, 2.4.1 and 5). We hypothesised that wetland drying, through increases in potential food resource availability, reductions in predation pressure, and evaporative concentration, would lead to increases in zooplankton abundance. The aims of this Section were to examine changes in the composition and abundance of zooplankton assemblages as each of the Menindee lakes dried during 2001-2, and to identify the relative importance of potential structuring mechanisms, such as season, lake drying and phytoplankton biomass.

Methods

Zooplankton samples were collected from three littoral sites in lakes Malta, Balaka, Bijiji, Tandure, Menindee and Cawndilla every two months from January 2001 as the lakes dried. Low water levels prevented sampling without benthic contamination in lakes Malta, Balaka and Bijiji after November 2001, in Lake Menindee after July 2002, and in lakes Tandure and Cawndilla after November 2002.

Zooplankton were sampled by passing 75 l of lake water through a 50 μm mesh, and preserving with Lugol's Iodine solution. A minimum of 200 individuals or 10 % of each sample was counted using a Sedgewick-Rafter Cell (APHA 1995). Identifications to at least genus followed Shiel (1995) and Ingram *et al.* (1997). Species diversity was calculated as Shannon-Wiener H' (bits individual⁻¹), which accounts for differences in abundance between samples.

Water level data (mAHD) for lakes Menindee and Cawndilla were provided by DIPNR (refer to Section 2.1.1). Water temperature ($^{\circ}\text{C}$) and electrical conductivity (EC $\mu\text{S cm}^{-1}$) were measured using a U-10 multi probe (HORIBA Ltd., Australia) and samples taken for chlorophyll *a* (mg CHL l⁻¹) determinations at the same sites and times as zooplankton. Chlorophyll *a* determinations involved filtering (Whatman Pty. Ltd. GF/C) 500 ml of water collected at a depth of 0.25 m below the water surface, extracting CHL from the filtrates in hot ethanol (80 $^{\circ}\text{C}$ 5 minutes), and measuring the extracted CHL at 665 nm and 750 nm without acidification (APHA 1995).

Pearson correlations with Bonferroni adjusted *p*-values, one-way ANOVAs and *post hoc* Tukey multiple comparisons were calculated using SYSTAT[®] V10.2 (SYSTAT Inc., USA). Multivariate analyses of relationships between zooplankton community structure and lake drying and season were examined using PRIMER (V5; Primer-E 2000). Zooplankton data were 4th-root transformed to downweigh the influence of individual taxa and to increase analytical robustness to zero values before calculating Bray-Curtis similarity co-efficients. Nonmetric multidimensional scaling (NMDS) was used to graphically display temporal trajectories of zooplankton communities. ANOSIM was used to test for differences between groups. SIMPER was used to identify species contributing most to within group similarity.

BIOENV was used to determine relationships between zooplankton community structure and environmental variables indicative of season, lake drying and food availability. Water temperature ($^{\circ}\text{C}$) was used as an analog for season, and water level (mAHD) for drying. mAHD was significantly correlated with electrical conductivity (EC) in lakes Menindee (Pearson $r=-0.892$, $p=0.001$, $n=10$) and Cawndilla (Pearson $r=-0.811$, $p=0.002$, $n=11$), and this relationship was consistent across lakes (refer to Section 2.1.2). EC was therefore used as an analog of water level for lakes where no water level data was available. CHL provided an indirect estimate of phytoplankton biomass and was used as a measure of potential food resource availability. Environmental data ($^{\circ}\text{C}$, mAHD, EC and CHL) were not transformed before calculating normalised Euclidean similarity co-efficients. Relationships between zooplankton and environmental similarity matrices were expressed as Spearman rank correlation co-efficients (ρ). Values of ρ approaching 1 indicate increasing agreement between two sets of ranks. Whilst useful for exploring the amount of variability in community structure accounted for by season, drying and food availability, high values of ρ do not indicate causality. Because ranks were based on a large number of strongly inter-dependent similarity calculations, statistical significance cannot be inferred from the regression co-efficients (ρ) (Clarke and Warwick 1994).

Results

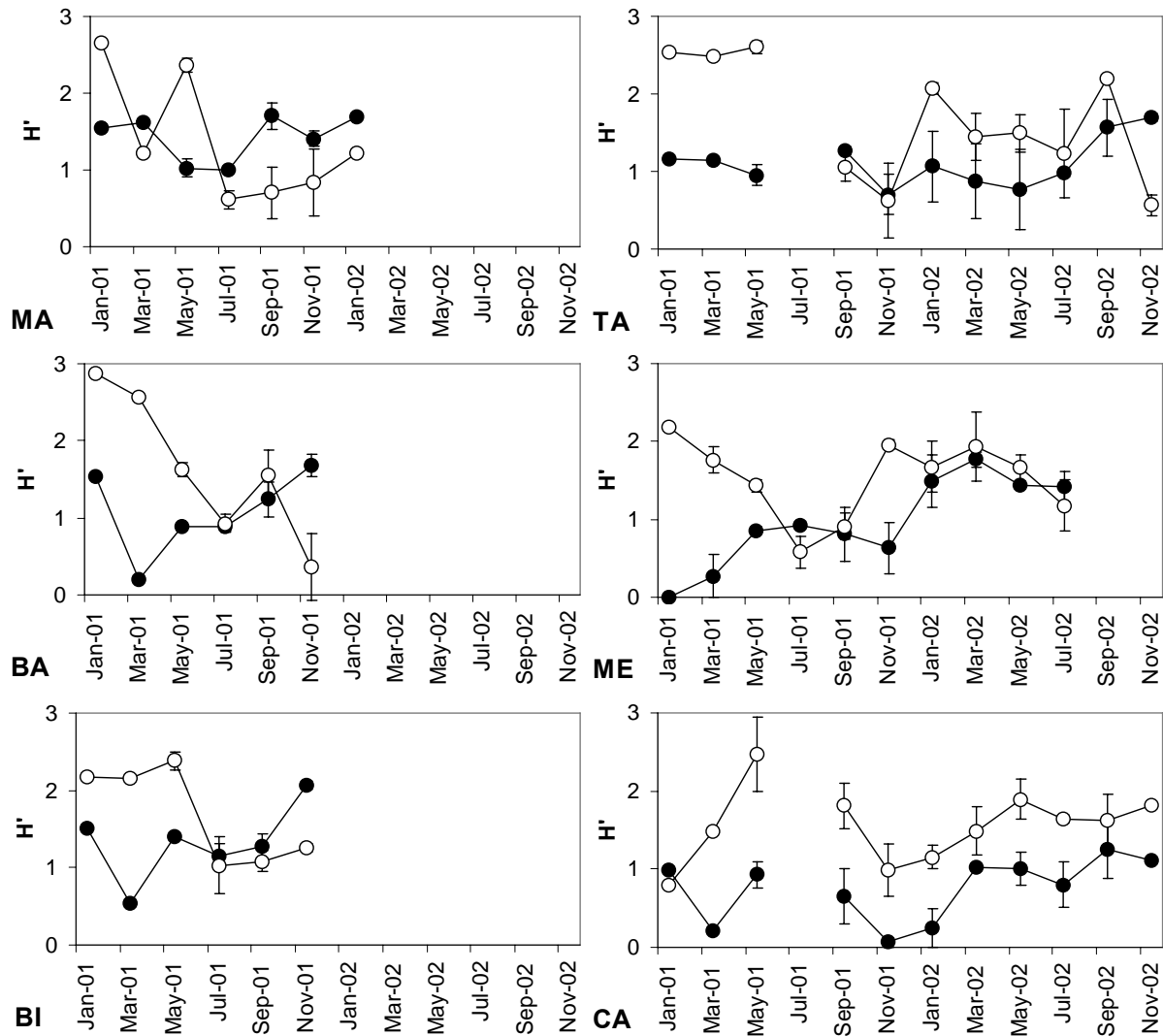
Thirty-nine zooplankton taxa were identified from 132 samples recovered from the Menindee lakes as they dried during 2001-2. These included 30 rotifers from 17 genera and 9 microcrustaceans (6 cladocerans, 2 copepods and 1 ostracod) (Table 2.3.1). The total number of taxa identified for each lake ranged from 28-33. Of these 18 taxa were common to all lakes. Eleven taxa were common, occurring in 50 % or more of samples and 5 taxa were rare, occurring in less than 5 % of samples. Eighteen rotifer taxa and 6 microcrustacean taxa (excluding nauplii) constituted at least 20 % of total abundance at some stage during the study period (Table 2.3.1). Of these, *Filinia* spp. and calanoid copepods (and their nauplii) were the most common dominants in all lakes. Whilst the composition of momentarily dominant taxa varied between lakes and times, dominant populations of *Brachionus calyciflorus gigantea*, *B. diversicornis* and *Moina* sp. developed only in the smaller lakes (Malta, Balaka and Bijiji), and *Polyarthra* spp. and *B. angularis* only in the larger lakes (Tandure, Menindee and Cawndilla).

Shannon-Wiener diversity (H') ranged from 0-2.95 for rotifer assemblages and from 0-2.16 for microcrustacean assemblages (Figure 2.3.1). Significant temporal changes in rotifer and microcrustacean H' were observed in all lakes, except Lake Cawndilla and Tandure (microcrustaceans) (Table 2.3.2). In the smaller lakes, which dried completely during the first year, lowest rotifer and highest microcrustacean diversities occurred during the second half of the year.

Momentary total zooplankton densities ranged from 63.0 ± 45.3 to 988.3 ± 8.3 individuals l^{-1} . Rotifer densities ranged from 5.0 ± 0.0 to 900.8 ± 24.2 individuals l^{-1} , and microcrustacean densities from 0.0 ± 0.0 to 353.3 ± 20.0 individuals l^{-1} (Figure 2.3.2). Significant temporal changes in rotifer densities were observed only in lakes Balaka and Menindee (Table 2.3.3). Rotifer densities declined steadily in Lake Balaka as it dried. Rotifer densities in Lake Menindee did not vary significantly throughout the study period except for a peak during May 2002, after which densities declined again shortly before the lake dried. Significant temporal changes in microcrustacean densities were observed in all lakes except Lake Tandure (Table 2.3.3). Microcrustacean densities tended to increase during November 2001 in lakes Malta, Balaka and Bijiji and during November 2002 in Lake Cawndilla, shortly before they dried. Significantly greater microcrustacean densities recorded in Lake Menindee during July 2001 were suggestive of a seasonal effect.

Zooplankton taxa	Combined frequency of occurrence (%)	Frequency of occurrence (%)					
		Malta	Balaka	Bijji	Tandure	Menindee	Cawndilla
Rotifers							
<i>Filinia</i> spp.	96.0	83.3	100.0	100.0	100.0	100.0	90.9
<i>Lecane</i> spp.	66.0	66.7	66.7	66.7	54.5	70.0	72.7
<i>Hexarthra mira</i>	64.0	33.3	33.3	50.0	81.8	60.0	90.9
<i>Brachionus urceolaris</i>	64.0	66.7	83.3	50.0	72.7	70.0	45.5
<i>Keratella australis</i>	58.0	33.3	33.3	50.0	45.5	80.0	81.8
<i>Brachionus calyciflorus gigantea</i>	56.0	83.3	100.0	50.0	54.5	30.0	45.5
<i>Polyarthra</i> spp.	50.0	0.0	50.0	50.0	54.5	80.0	45.5
<i>Conochilus</i> spp.	48.0	33.3	66.7	100.0	54.5	40.0	18.2
<i>Trichocerca</i> spp.	48.0	33.3	50.0	50.0	36.4	50.0	63.6
<i>Brachionus angularis</i>	44.0	33.3	33.3	33.3	36.4	70.0	45.5
<i>Brachionus rubens</i>	34.0	50.0	0.0	50.0	54.5	50.0	0.0
<i>Brachionus diversicornis</i>	28.0	33.3	16.7	16.7	36.4	30.0	27.3
<i>Bdelloida</i> spp.	26.0	16.7	33.3	16.7	18.2	50.0	18.2
<i>Brachionus novaezelandia</i>	24.0	50.0	33.3	16.7	9.1	20.0	27.3
<i>Asplanchna</i> spp.	18.0	16.7	16.7	0.0	18.2	40.0	9.1
<i>Brachionus calyciflorus</i>	18.0	33.3	16.7	0.0	18.2	30.0	9.1
<i>Brachionus quadridentatus</i>	18.0	33.3	33.3	33.3	18.2	0.0	9.1
<i>Synchaeta</i> spp.	16.0	0.0	0.0	0.0	18.2	30.0	27.3
<i>Dicranophorus</i> sp.	14.0	33.3	16.7	16.7	18.2	0.0	9.1
<i>Keratella tropica</i>	12.0	0.0	0.0	16.7	27.3	20.0	0.0
<i>Lepadella</i> spp.	12.0	16.7	16.7	0.0	27.3	0.0	9.1
<i>Proales</i> spp.	12.0	16.7	0.0	16.7	9.1	20.0	9.1
<i>Rotaria neptuna</i>	10.0	16.7	16.7	16.7	9.1	10.0	0.0
<i>Brachionus bidentatus</i>	10.0	16.7	16.7	0.0	9.1	0.0	18.2
<i>Brachionus keikoa</i>	10.0	0.0	0.0	16.7	18.2	10.0	9.1
<i>Brachionus budapestinensis</i>	8.0	0.0	16.7	16.7	18.2	0.0	0.0
<i>Brachionus falcatus</i>	4.0	0.0	0.0	16.7	9.1	0.0	0.0
<i>Cephalodella</i> spp.	4.0	16.7	0.0	16.7	0.0	0.0	0.0
<i>Brachionus leydigi</i>	2.0	0.0	0.0	16.7	0.0	0.0	0.0
<i>Tricotria tetracus</i>	2.0	0.0	0.0	0.0	0.0	10.0	0.0
Microcrustaceans							
Calanoid nauplii	98.0	100.0	100.0	100.0	100.0	90.0	100.0
<i>Calanoida</i> sp.	92.0	100.0	100.0	100.0	100.0	90.0	72.7
<i>Moina</i> sp.	62.0	83.3	33.3	66.7	81.8	60.0	45.5
<i>Chydorid</i> sp.	52.0	50.0	33.3	50.0	54.5	70.0	45.5
<i>Ostracoda</i> sp.	52.0	50.0	33.3	50.0	63.6	60.0	45.5
<i>Cyclopoida</i> sp.	38.0	33.3	33.3	33.3	45.5	20.0	54.5
<i>Daphnia lumholtzi</i>	32.0	50.0	16.7	33.3	18.2	50.0	27.3
<i>Daphnia carinata</i>	14.0	50.0	33.3	16.7	0.0	0.0	9.1
<i>Macrothrix</i> sp.	8.0	16.7	0.0	0.0	0.0	30.0	0.0
<i>Bosmina</i> sp.	4.0	16.7	0.0	0.0	0.0	0.0	9.1

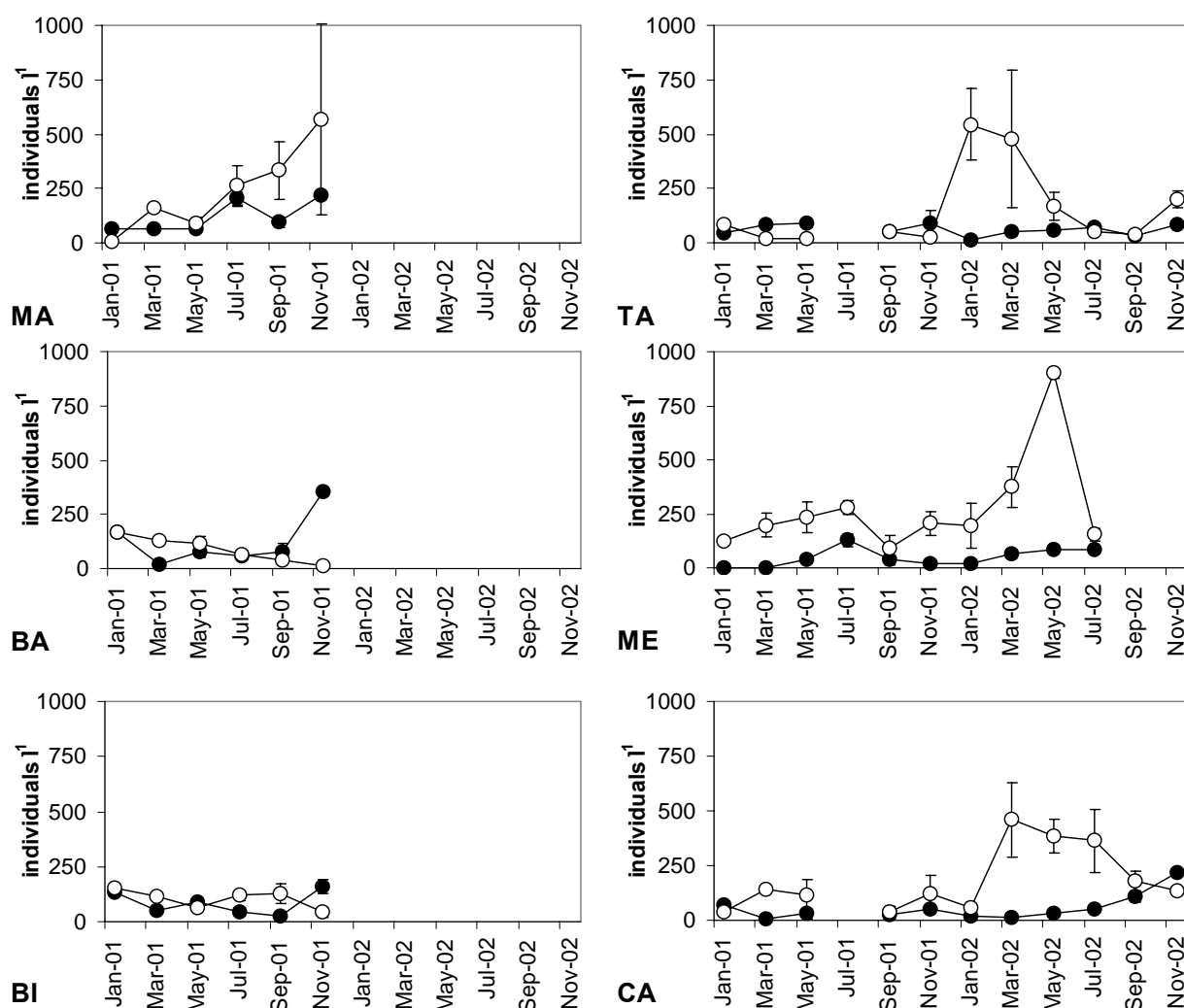
■ Table 2.3.1: Zooplankton taxa and their frequency (%) of occurrence in samples collected from lakes Malta (n=6), Balaka (n=6), Bijiji (n=6), Tandure (n=11), Menindee (n=10) and Cawndilla (n=11) over the 2001-2 study period. Instances where taxa were numerically dominant (>20 %) are indicated as bold.



■ **Figure 2.3.1: Shannon-Wiener diversity (H' mean \pm se) of rotifers (○) and microcrustaceans (●) collected from lakes Malta (MA), Balaka (BA), Bijiji (BI), Tandure (TA), Menindee (ME) and Cawndilla (CA) over the 2001-2 study period.**

Community	Lake	<i>p</i>	Tukey <i>post hoc</i> comparisons
Rotifers	Malta	0.015	May \neq Jul, May \neq Sept
	Balaka	0.006	Jan \neq Jul, Jan \neq Nov, Mar \neq Jul, Mar \neq Nov
	Bijiji	0.008	May \neq Jul, May \neq Sep, May \neq Nov
	Tandure	0.005	May'01 \neq Nov'02
	Menindee	0.009	Jul'01 \neq Nov'01, Jul'01 \neq Mar'02
	Cawndilla	0.111	ns
Micro-crustaceans	Malta	0.014	May \neq Sep, Jul \neq Sep
	Balaka	0.010	Jan \neq Mar, Mar \neq Sep, Mar \neq Nov
	Bijiji	0.003	Mar \neq Nov, May \neq Nov, Jul \neq Nov, Sep \neq Nov
	Tandure	0.705	ns
	Menindee	0.012	Mar'01 \neq Mar'02
	Cawndilla	0.130	ns

■ **Table 2.3.2: Summary ANOVA statistics for temporal trends in rotifer and microcrustacean diversity (H').**

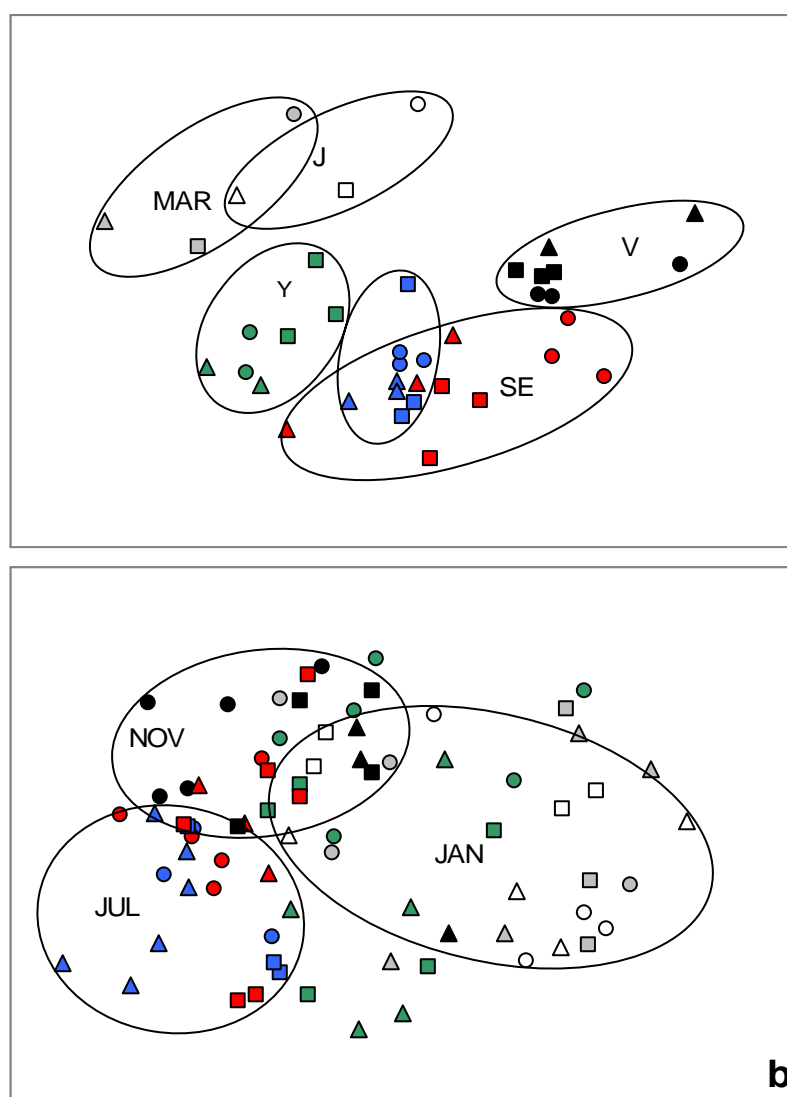


■ **Figure 2.3.2:** Densities (individuals l^{-1} mean \pm se) of rotifers (○) and microcrustaceans (●) collected from lakes Malta (MA), Balaka (BA), Bijiji (BI), Tandure (TA), Menindee (ME) and Cawndilla (CA) over the 2001-2 study period.

Community	Lake	<i>p</i>	Tukey <i>post hoc</i> comparisons
Rotifers	Malta	0.736	ns
	Balaka	0.013	Jan \neq Sep, Jan \neq Nov, May \neq Nov
	Bijiji	0.268	ns
	Tandure	0.103	ns
	Menindee	<0.001	May'02 \neq all others
	Cawndilla	0.056	ns
Micro-crustaceans	Malta	0.002	Jan \neq Nov, Mar \neq Nov, May \neq Nov, May \neq Jul, Jul \neq Sep, Sep \neq Nov
	Balaka	0.003	Mar \neq Nov, May \neq Nov, Jul \neq Nov, Sep \neq Nov
	Bijiji	0.006	Jul \neq Nov, Sep \neq Nov
	Tandure	0.486	ns
	Menindee	0.004	Jul'01 \neq all except Mar'01
	Cawndilla	0.002	Nov'02 \neq all others

■ **Table 2.3.3:** Summary ANOVA statistics for temporal trends in rotifer and microcrustacean density (individuals l^{-1}).

For each sampling event there were significant differences in community structure between the smaller lakes (Malta, Balaka and Bijiji) and the larger lakes (Tandure, Menindee and Cawndilla) (ANOSIM $p \leq 0.01$). The zooplankton communities of the smaller lakes monitored over one year prior to their drying followed a more clearly identifiable temporal trajectory than was apparent in the larger lakes, which were monitored over two years (Figure 2.3.3). Differences between successive sampling periods within both smaller and larger lake groups were significant (ANOSIM $p \leq 0.01$) for all except January-March 2001, where the number of replicates ($n=3$) was too low to achieve significance below the 10 % level (Clarke and Warwick 1994). For the larger lakes, differences between years were not significant (ANOSIM $p > 0.05$). Temporal shifts in zooplankton community structure identified using SIMPER for both lake groups are summarised in Table 2.3.4.



■ **Figure 2.3.3:** Non-metric multidimensional scaling plots of zooplankton assemblages collected from a) lakes Malta (●), Balaka (▲) and Bijiji (■) during 2001, and b) lakes Tandure (●), Menindee (▲) and Cawndilla (■) during 2001. 2. January-white, March-grey, May-green, July-blue, September-red, November-black. Stress levels 0.13 and 0.17, respectively.

TAXA	January	March	May	July	September	November
Rotifers						
<i>Filinia</i> spp.	●○	●○	●○	●○	●○	●○
<i>Brachionus urceolaris</i>	●	○	●			
<i>Brachionus angularis</i>	○					
<i>Hexarthra mira</i>	●○	●○	○		○	○
<i>Brachionus diversicornis</i>		●○				
<i>Trichocerca</i> spp.		●○				
<i>Polyarthra</i> spp.		○	○			
<i>Lecane</i> spp.			●			
<i>Brachionus calyciflorus gigantea</i>			●			
<i>Keratella australis</i>			○	○	○	○
<i>Conochilus</i> spp.					●	
Microcrustaceans						
Calanoid nauplii	●○	●○	●○	●○	●○	●○
<i>Calanoida</i> sp.	●○	●	●○	○	●○	●
<i>Moina</i> sp.	●					●
<i>Chydorid</i> sp.					○	●

■ **Table 2.3.4: Taxa contributing >5 % to within group similarity (as determined using SIMPER) of zooplankton communities sampled from lakes Malta, Balaka and Bijiji (●) and lakes Tandure, Menindee and Cawndilla (○) during 2001-2.**

Multivariate BIOENV analyses provided a more robust means for exploring relationships between zooplankton community structure and season and lake drying than was possible from examinations of diversity and abundance. Water temperature and water level were used as analogs for season and lake drying, respectively. As water level and electrical conductivity (EC) were co-linear, EC was used as an analog for water level where such data was not available. Because of this co-linearity, it was not possible to separate the effects of EC and water level. Little salt sensitivity data is available to suggest what impacts changes in salinity associated with lake drying are likely to have on the zooplankton (Hart *et al.* 1991, Bailey and James 2000). However, most zooplankton taxa were recorded over the entire range of EC encountered during this study (285-991 $\mu\text{S cm}^{-1}$; Section 2.1.2), and recorded EC values were relatively low in comparison to salinity tolerances reported for zooplankton (*e.g.* Hart *et al.* 1991).

Temperature and water level/EC combined explained more of the variability in rotifer communities of the smaller lakes (Malta, Balaka, Bijiji) than did either parameter individually (Table 2.3.5). Temperature explained more of the variability in the rotifer assemblages of lakes Tandure and Menindee, and drying was a greater influence in Lake Cawndilla. Water level/EC accounted for more of the variability observed in the microcrustacean communities of all lakes, except for Lake Menindee where the combined influences of temperature and water level/EC were more important. Taxa that exhibited strong temperature dependence (*i.e.* seasonality) included: *Hexarthra mira* (peak November-January), *Moina* sp. (peak November-January), *Chydorid* sp. (peak September-November), and *Brachionus calyciflorus gigantea* (peak May).

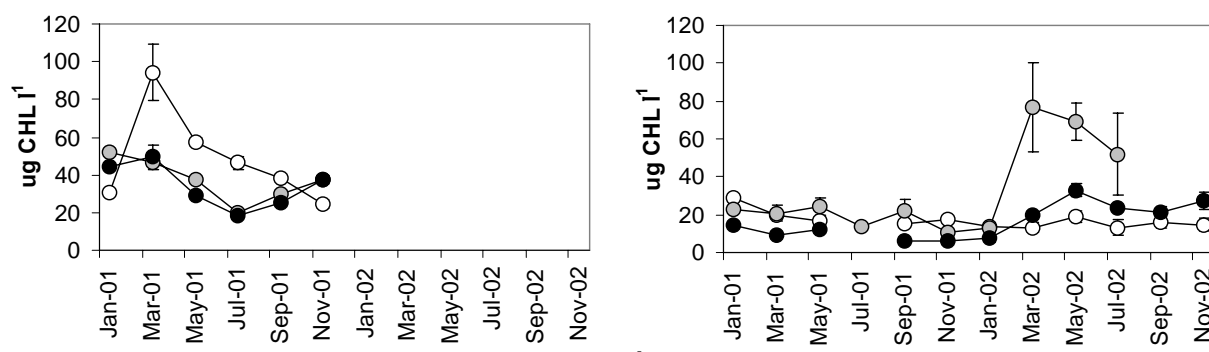
Chlorophyll *a* concentrations ranged from 4.63-122.4 $\mu\text{g CHL l}^{-1}$ (Figure 2.3.4). Significant temporal changes in CHL were observed in all lakes except Lake Tandure (Table 2.3.6). CHL concentrations were significantly correlated with temperature for lakes Balaka and Bijiji, with

maxima occurring during the warmer months (January and March) and minima during the cooler months (July) (Table 2.3.7). CHL concentrations declined steadily in Lake Malta from the March peak, and were not correlated with temperature. In contrast to the smaller lakes, CHL concentrations were significantly correlated with water level or EC in lakes Menindee and Cawndilla (Table 2.3.7). CHL concentrations in these lakes increased significantly after January 2002 (Table 2.3.6) and coincided with increases in rotifer densities (Figure 2.3.2).

CHL accounted for more of the variation within rotifer communities than it did for microcrustacean communities, although CHL ρ -values tended to be smaller than either temperature or water level or EC effects (Table 2.3.5). Comparatively lower rank correlations calculated for CHL and microcrustaceans than for CHL and rotifers may have been due a combination of factors including lag effects in community response times to food availability and different predation pressures.

Community	Lake	Spearman rank correlation co-efficient (ρ)					
		$^{\circ}\text{C}$	mAHD	EC	$^{\circ}\text{C}$ and mAHD	$^{\circ}\text{C}$ and EC	CHL
Rotifers	Malta	0.417	nd	0.524	nd	0.529	0.441
	Balaka	0.347	nd	0.365	nd	0.571	0.259
	Bijiji	0.436	nd	0.359	nd	0.650	0.384
	Tandure	0.759	nd	0.523	nd	0.691	0.257
	Menindee	0.633	0.358	0.441	0.622	0.598	0.151
	Cawndilla	0.199	0.378	0.343	0.341	0.337	0.345
Micro-crustaceans	Malta	0.244	nd	0.353	nd	0.308	0.363
	Balaka	-0.022	nd	0.562	nd	0.528	-0.058
	Bijiji	0.045	nd	0.413	nd	0.295	0.283
	Tandure	0.021	nd	0.459	nd	0.352	0.065
	Menindee	0.106	0.203	0.146	0.166	0.154	0.031
	Cawndilla	0.010	0.110	0.090	0.103	0.083	0.082

■ Table 2.3.5: Spearman rank correlation co-efficients (ρ) calculated using BIOENV between rotifer and microcrustacean communities and temperature ($^{\circ}\text{C}$), water level (mAHD), electrical conductivity (EC) and chlorophyll *a* (CHL) concentrations. Highest ρ values for each lake are highlighted. nd – no data.



■ **Figure 2.3.4: Chlorophyll a concentrations ($\mu\text{g CHL l}^{-1}$ mean \pm se) determined for a) lakes Malta (\circ), Balaka (\bullet) and Bijiji (\bullet), and b) lakes Tandure (\circ), Menindee (\bullet) and Cawndilla (\bullet) over the 2001-2 study period.**

Lake	<i>p</i>	Tukey <i>post hoc</i> comparisons
Malta	0.001	Mar \neq all others
Balaka	<0.001	Jan and Mar \neq all others, Jul \neq all others
Bijiji	<0.001	Mar \neq May-Sep, Jan \neq Jul, Jul \neq Sep
Tandure	0.156	ns
Menindee	0.006	Nov'01 and Jan'02 \neq Mar'02, Nov'01 \neq May'02
Cawndilla	<0.001	May'02 \neq all before, Sep'01-Jan'02 \neq all after

■ **Table 2.3.6: Summary ANOVA statistics for temporal trends in chlorophyll a concentrations ($\mu\text{g CHL l}^{-1}$).**

Lake	CHL vs $^{\circ}\text{C}$			CHL vs mAHD			CHL vs EC		
	<i>r</i>	<i>p</i>	<i>n</i>	<i>r</i>	<i>p</i>	<i>n</i>	<i>r</i>	<i>p</i>	<i>n</i>
Malta	0.098	0.853	6	nd	nd	nd	-0.719	0.107	6
Balaka	0.982	0.001	6	nd	nd	nd	-0.136	0.797	6
Bijiji	0.906	0.013	6	nd	nd	nd	-0.437	0.387	6
Tandure	0.305	0.361	11	nd	nd	nd	-0.383	0.349	8
Menindee	-0.017	0.963	10	-0.643	0.045	10	0.625	0.053	10
Cawndilla	-0.201	0.535	11	-0.762	0.006	11	0.689	0.019	11

■ **Table 2.3.7: Summary statistics of Pearson correlations for chlorophyll a concentrations ($\mu\text{g CHL l}^{-1}$) with season (as temperature $^{\circ}\text{C}$) and lake drying (as water level mAHD and salinity EC). Significant correlations ($p<0.05$) are highlighted. nd – no data.**

Discussion

Little is currently known of the zooplankton of the Menindee Lakes apart from a pilot study by the present authors (Scholz *et al.* 1999). Relatively more is known of the zooplankton of the adjacent Darling River (Shiel 1978, 1985, 1986, Shiel and Walker 1984, Shiel *et al.* 1982), and the emergence characteristics of zooplankton from the lakebeds of EDBL (Briggs *et al.* 1997, Jenkins and Briggs 1997, Jenkins and Boulton 2003, Scholz unpublished data). Despite large knowledge gaps concerning the zooplankton of this and other ephemeral systems, information available from other wetlands suggests that hydraulic regulation has the capacity to significantly modify not only zooplankton diversity and productivity, but also entire trophic structures (*e.g.* Boulton and Lloyd 1982, Bunn *et al.* 1997, Jenkins and Boulton 1998). The current study sought to examine the responses of zooplankton communities within six of the Menindee lakes as they dried during 2001-2, and to identify the relative importance of season, lake drying and phytoplankton biomass as determinants of community structure.

Thirty-nine zooplankton taxa (30 rotifers and 9 crustaceans) were identified from samples collected from the Menindee Lakes during 2001-2. Total community composition varied both temporally and between lakes, although *Filinia* spp. and calanoid copepods and their nauplii were present in most samples (96 % and 92-98 % of samples, respectively). Whilst the composition of momentarily dominant taxa varied between lakes and times, dominants generally reflected those reported earlier for Lake Menindee and the Darling River by Shiel (1978), Shiel *et al.* (1982), and Shiel and Walker (1984). Rotifers were generally more diverse and present in greater concentrations than were microcrustaceans.

Temporal changes in rotifer and microcrustacean diversity (Shannon-Wiener H') and density were significant in most lakes during the study period. Zooplankton community structure differed between the smaller lakes (lakes Malta, Balaka and Bijiji) and the larger lakes (lakes Tandure, Menindee and Cawndilla), but not within lake groups. Significant temporal shifts in community structure were recorded in all lakes. These differences were driven by only a few taxa including *Hexarthra mira*, *Moina* sp., *Chydorid* sp., and *Brachionus calyciflorus gigantea*. Seasonal shifts in zooplankton community structure were characterised by the dominance of rotifers during autumn/summer and micro-crustaceans in winter/spring. Similar seasonal shifts have been reported a Murray-Darling floodplain lake (Crome and Carpenter 1988) and temperate systems (*e.g.* Moore *et al.* 1996). Whilst season appeared to play an important role in structuring zooplankton assemblages in all lakes, the influence of drying was more difficult to resolve.

BIOENV analyses indicated that the relative importance of season and lake drying as community structuring agents varied both between rotifer and microcrustacean communities and between lakes. In the smaller lakes for which only one year of data was available, season and drying effects coincided to reduce rotifer diversity and concentrations during the second half of the year as these lakes dried. A much stronger seasonal response was identified for the rotifer communities in lakes Tandure and Menindee that were monitored over two years. However, rotifer responses to season and drying were weaker in Lake Cawndilla than was determined in the other lakes. This was likely due to the greater volume of water present within Lake Cawndilla than in the other lakes towards the end of the sampling period, which may have buffered responses. By comparison, microcrustacean responses to either season or lake drying were more consistent across lakes. Lake drying accounted for much more of the changes observed in the microcrustacean communities of all lakes than did season. Generally, microcrustacean communities became more diverse and more abundant as lakes dried. Evaporative concentration and reductions in predation pressure may have contributed to this response. Responses to both season and lake drying were examined at the community level. This may have masked stronger species level responses as indicated in Table 2.3.4. Overall,

zooplankton assemblages showed a response to drying and during non-drying periods were affected by season.

For each lake, phytoplankton biomass, measured as chlorophyll ($\mu\text{g CHL l}^{-1}$), accounted for consistently more of the variability of rotifer communities than it did for microcrustacean communities. These results suggest either that there was a tighter trophic coupling between phytoplankton and rotifers than there was between phytoplankton and microcrustaceans, or that rotifers were not subject to the same predator pressure that microcrustaceans were subject to. Despite variability in the chlorophyll content of phytoplankton (*e.g.* Riemann *et al.* 1989), a number of recent studies have demonstrated similar positive correlations between CHL and zooplankton densities (*e.g.* Beaver *et al.* 1999, Lund and Davis 2000, Branco *et al.* 2002). Whilst these data are suggestive of trophic links between plankton components, dietary preferences of zooplankton remain poorly understood (*e.g.* Merrick and Ganf 1988, Boon and Shiel 1990, Lougheed and Chow-Fraser 1998).

Summary

We examined zooplankton community structure in six of the Menindee Lakes between January 2001-July 2002 to identify responses to lake flooding and drying. Rotifer communities were generally more diverse and abundant than were crustaceans. Despite subtle differences in community composition between the smaller lakes (Malta, Balaka and Bijiji) and the larger lakes (Tandure, Menindee and Cawndilla), community composition and abundances varied temporally with *Filinia* spp. and calanoid copepods (incl. nauplii) the most persistent community dominants.

Rotifer assemblages varied more in response to season than did microcrustacea. Stronger positive rank-correlations of rotifers than microcrustaceans with phytoplankton biomass, though not demonstrating causality, suggest that this response was related to food preference and availability. Lake drying accounted for as much of the observed temporal variation of rotifers as did season, with lower temperatures and lake drying leading to reductions in both diversity and concentration. More of the variation encountered in microcrustacean assemblages was explained by lake drying than by season, and involved increases in both diversity and abundance. Changes in zooplankton community structure driven by both season and lake drying may thus modify food web interactions through changes in availability to fish and grazing pressure on lower trophic levels.

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2.4 Fish

2.4.1 Surveys 1997-2002

O. Scholz, B. Gawne and B. Ebner

Introduction

Native fish throughout the Murray-Darling Basin have been severely impacted by altered flow regimes, the loss of habitat, and barriers to passage (MDBMC 2002). Altered flow regimes, in particular, are thought to have impacted on the distribution of native fish species and to have favoured the expansion of alien species, such as carp (*Cyprinus carpio*) and mosquitofish (*Gambusia holbrooki*) (Harris and Gehrke 1997). Whilst fish distributions within the Darling River and its tributaries have been reported (Llewellyn 1983, Harris and Gehrke 1997), and responses of fish communities to flooding in Australian floodplain systems have received some attention (e.g. Gehrke 1991, 1994, Gehrke *et al.* 1997, McKinnon 1997, Humphries *et al.* 1999, King *et al.* 2003), community responses to lake drying have not been reported. Little data pertaining specifically to fish within the Menindee Lakes are available. That which is available reports on commercial fisheries catches and single surveys of lakes Pamamaroo and Wetherell within the wetland complex (Gehrke *et al.* 1997, Reid *et al.* 1997, SKM 2002).

We examined the fish communities present within the Menindee Lakes as they dried and re-flooded. We hypothesised that drying in these shallow lakes would lead to a reduction in both fish abundance and diversity due to increasing susceptibility to selective avian predation (e.g. Jaensch 2000), and that the significance of this response would differ between lakes depending on their depth. Further, we hypothesised that flooding would re-instate a diverse fish community and stimulate juvenile recruitment due as a consequence of immigration and the increased availability of suitable habitat and increases in post-flood aquatic productivity (e.g. Gehrke 1991, 1994, Gehrke *et al.* 1997, McKinnon 1997). Post-flood community structure within wetlands of the Menindee Lakes, we believed, would be dependent upon the extant lake and riverine fish communities and the duration of connection between these. Information concerning the responses of fish communities to episodes of lake drying and flooding is needed to support management actions, such as the imposition of drying phases and the timing of regulated inflows.

Methods

The fish populations of lakes Malta, Balaka, Bijiji, Tandure, Menindee and Cawndilla were surveyed on six occasions between 1997-2002, which included two drying events (1997-8 and 2001-3) and a single re-flooding event (1998). The severity of drying differed between drying events, with the smaller lakes (lakes Malta and Balaka) drying completely twice and lakes Bijiji, Tandure, Menindee and Cawndilla only once during 2002. The commencement of flooding inflows into lakes Malta, Balaka, Bijiji and Tandure from Lake Wetherell coincided with sampling in August 1998. The connection of lakes Malta, Balaka and Bijiji to Lake Wetherell lasted approximately one month as they re-flooded. Lake Malta was the first to become hydraulically isolated as the flood pulse receded, followed by Lake Balaka and then Lake Bijiji. Lake Tandure remained connected to Lake Wetherell throughout the survey period. Controlled releases into Lake Menindee commenced after the August 1998 survey and continued until early December 1998. Lake Cawndilla received all of its inflows from Lake Menindee via the inter-connecting channel (Morton Bulka Creek), and remained connected to Lake Menindee throughout the survey period.

Sampling was not possible in Lake Malta in February 1998, lakes Malta and Balaka in May 1998, and lakes Malta, Balaka and Bijiji in April 2002 when the lakes were either dry or too shallow (less than 15 cm deep) to effectively deploy the standard gear set used at other times. The extended dry period of 2002-3 precluded sampling of all lakes after April 2002. Three sites were sampled in each lake per sampling event. Sites were selected to encompass the range of available littoral habitat. This included bare sediments, inundated terrestrial grasses, lignum (*Muehlenbeckia cunninghamii*), sedge (*Cyperus gymnocaulos*), cumbungi (*Typha orientalis*), smartweed (*Persicaria*.sp.), and woody snags (refer to Taylor-Wood *et al.* 2002). Habitat diversity was greatest in Lake Tandure.

Each lake was sampled by deploying between 11 and 13 of each of two sizes of fyke net. Large fyke nets (LFN) had a central wing (8 m x 0.65 m) attached to the first supporting hoop ($\varnothing = 0.55$ m) with a mesh entry (0.32 m, stretched), and stretched mesh size of 28 mm. Small fyke nets (SFN) had dual wings (each 2.5 m x 1.2 m), with a first supporting hoop ($\varnothing = 0.4$ m) fitted with a square entry (0.15 m x 0.15 m) covered by a plastic grid with rigid square openings (0.05 m x 0.05 m). SFNs had a stretched mesh size of 2 mm. Fyke nets were set in the afternoon and collected the following morning. Fish identifications followed McDowall (1996). All carp gudgeons were identified to genus level only (*i.e.* *Hypseleotris* spp.) owing to the current taxonomic uncertainty at the species level (Bertozzi *et al.* 2000). Carp x goldfish hybrids may have been included in the counts for carp but not for goldfish. Fish from each species were counted and the smallest and largest total length (TL mm) recorded per net. All LFN and SFN data were standardised to a sampling effort of 200 net hours per lake (sites combined) to facilitate the examination of relative temporal and spatial variation in abundances between lakes.

Results

A total of 11 fish species were collected during the 1997-2002 surveys, of which eight species were native (Table 2.4.1). The four most abundant species (smelt, bony herring, carp gudgeon and carp) accounted for more than 93 % of the 34508 fish caught. Alien species (carp, goldfish and mosquitofish) accounted for 17.2 % of fish caught.

Six fish species were collected on all trips to the Menindee lakes, and five species were recorded in every lake at some stage (Table 2.4.2). Although no mosquitofish were recorded in fyke net catches from Lake Malta, they were present in seine net trawls in August 1997 and February 1998 (O. Scholz, unpublished data). All species recorded were encountered in open water areas and areas with submerged snags. Highest diversity of fish, and the only occurrences of crimson-spotted rainbowfish and silver perch, was recorded in Lake Tandure, which also had the greatest habitat diversity.

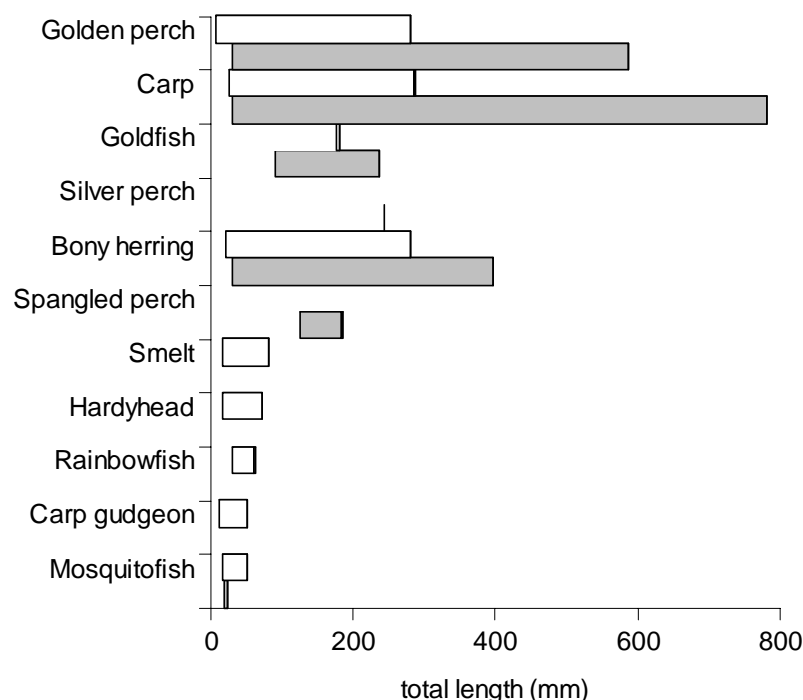
Two passive gear types, large fyke nets (LFN) and small fyke nets (SFN), were set in tandem to increase the probability of sampling a wider range of species and size classes. Two fish species (spangled perch, silver perch) caught in LFNs were not present in SFN catches, and four species (smelt, carp gudgeon, line-eyed hardyhead and crimson-spotted rainbowfish) caught in SFN catches were not present in LFN catches (Table 2.4.1). Fish caught using LFNs ranged in size from 18-780 mm and fish caught using SFNs ranged in size from 7-285 mm. (Figure 2.4.1).

Common name	Scientific name	Small fyke nets	Large fyke nets	Total
Australian smelt	<i>Retropinna semoni</i> (Weber)	13034	0	13034
Bony herring	<i>Nematalosa erebi</i> (Gunther)	4366	3820	8186
Carp gudgeon	<i>Hypseleotris</i> spp.	5864	0	5864
Carp*	<i>Cyprinus carpio</i> (Linnaeus)	1715	3509	5224
Golden perch	<i>Macquaria ambigua</i> (Richardson)	142	1281	1424
Mosquitofish*	<i>Gambusia holbrooki</i> (Girard)	706	2	706
Line-eyed hardyhead	<i>Craterocephalus stercusmuscarum fulvus</i> (Ivanstoff, Crowley and Allen)	31	0	31
Crimson-spotted rainbowfish	<i>Melanotaenia fluviatilis</i> (Castelnau)	19	0	19
Goldfish*	<i>Carassius auratus</i> (Linnaeus)	1	9	10
Spangled perch	<i>Leioptherapon unicolor</i> (Gunther)	0	8	8
Silver perch	<i>Bidyanus bidyanus</i> (Richardson)	0	1	1
TOTAL		25878	8630	34508

■ **Table 2.4.1: Total numbers of each fish species collected during the 1997-2002 surveys. *-alien species.**

Species	Nov 1997	Feb 1998	May 1998	Aug 1998	Nov 1998	Apr 2002	Malta	Balaka	Bijji	Tandure	Menindee	Cawndilla
Australian smelt	●	●	●	●	●	●	●	●	●	●	●	●
Bony herring	●	●	●	●	●	●	●	●	●	●	●	●
Carp gudgeons	●	●	●	●	●	●	●	●	●	●	●	●
Carp*	●	●	●	●	●	●	●	●	●	●	●	●
Golden perch	●	●	●	●	●	●	●	●	●	●	●	●
Mosquitofish*	●	●	●	●	●	●	●	●	●	●	○	●
Goldfish*	●	○	○	●	●	○	●	●	●	●	●	○
Line-eyed hardyhead	●	●	●	●	●	○	○	○	○	●	●	●
Crimson-spotted rainbowfish	●	●	○	●	○	○	○	○	○	●	○	○
Spangled perch	○	○	○	●	●	○	○	●	●	○	●	○
Silver perch	○	○	○	○	●	○	○	○	○	●	○	○

■ **Table 2.4.2: Presence (●) / absence (○) of species collected during each survey and species collected in each lake. *- alien species. ● – collected using seine net.**

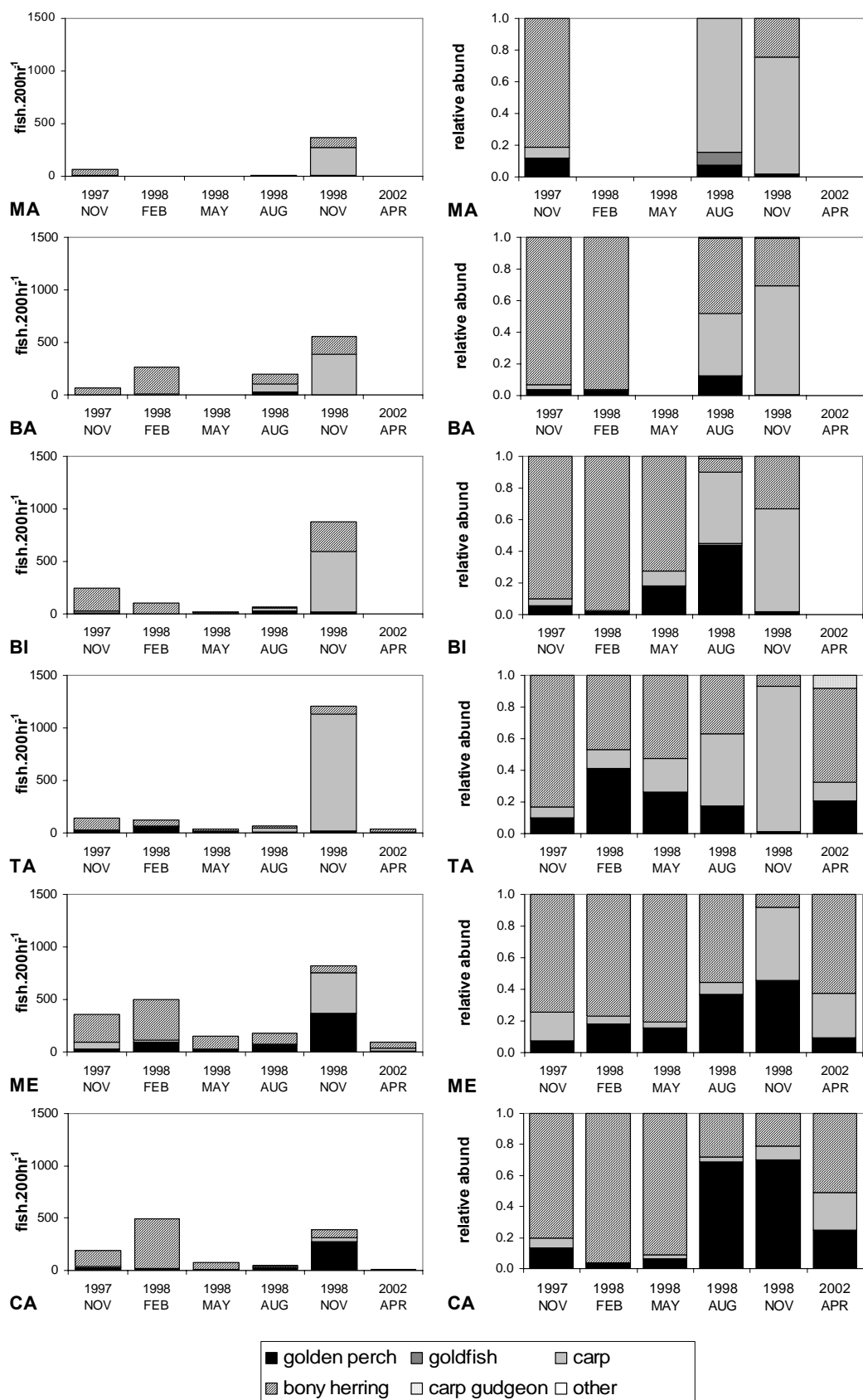


■ **Figure 2.4.1: Size ranges (total lengths mm) of fish species caught using large fyke nets (grey shading) and small fyke nets (no shading).**

Bony herring dominated LFN fish catches in all lakes as they dried during 1997-8. Golden perch and carp were sub-dominant, each generally constituting less than 20 % of the catch. Standardised LFN catches (fish 200 hr⁻¹) declined during 1997-8 as each lake dried (Figure 2.4.2). Large carp were the only species left stranded on the lakebeds of the smaller lakes (Malta and Balaka) as they dried completely (Figure 2.4.3). Fish abundances declined from 243 to 19.3 fish 200 hr⁻¹ in Lake Bijiji and from 146 to 37.3 fish 200 hr⁻¹ in Lake Tandure as they dried between November 1997 and May 1998. Fish abundances declined from 498.2 to 176.1 fish 200 hr⁻¹ in Lake Menindee and from 498 to 46.2 fish 200 hr⁻¹ in Lake Cawndilla as they dried between February 1998 and August 1998.

Re-flooding of the lakes above the Main Weir during August saw increases in both carp and golden perch numbers. By November, catches of carp had increased further, but catches of golden perch numbers had declined, suggesting that these had moved in during the initial filling of lakes had moved out again. Post-flood increases in LFN catches in each lake reflected the duration of connection to Lake Wetherell; Lake Tandure (1210 fish 200 hr⁻¹), Lake Bijiji (880 fish 200 hr⁻¹), Lake Balaka (560 fish 200 hr⁻¹), and Lake Malta (370 fish 200 hr⁻¹). Re-flooding of lakes below the Main Weir also led to increases LFN catches. November 1998 LFN catches were greater in Lake Menindee (820 fish 200 hr⁻¹) than in Lake Cawndilla (390 fish 200 hr⁻¹). Both carp and golden perch catches increased as Lake Menindee filled. Increases in the catches from Lake Cawndilla at the same time were due primarily to the recruitment of golden perch from Lake Menindee.

Sampling of fish populations using LFNs during April 2002 when lakes were again drying was only possible in lakes Tandure, Menindee and Cawndilla. LFN abundances were similar to those recorded prior to lake filling in 1998, and were again dominated by bony herring. Golden perch and carp contributions to total observed fish community structure were much lower than that recorded initially after flooding during November 1998.



■ **Figure 2.4.2: Abundance (fish 200hr⁻¹) and relative abundance of fish caught using large fyke nets set in lakes Malta (MA), Balaka (BA), Bijiji (BI), Tandure (TA), Menindee (ME) and Cawndilla (CA) between 1997-2002.**



■ **Figure 2.4.3: Large carp left stranded on Lake Malta as it dried (photo: O. Scholz April 2002).**

Fish community responses to lake drying as determined using SFNs differed between the smaller and larger lakes. As lakes Balaka and Bijiji dried, the community structure of SFN catches became less complex with mosquitofish becoming numerically dominant at the expense of bony herring, smelt, and golden perch (Figure 2.4.4). Lake Malta was only sampled once (November 1997) using SFNs, after which water levels were too low to effectively deploy fyke nets. Whilst SFN catches in Lake Malta during November were numerically dominated by bony herring and golden perch, seine netting during February 1998 indicated that only mosquitofish were present (O. Scholz unpublished data). The partial drying of lakes Tandure, Menindee and Cawndilla during 1997-8 also led to a loss of complexity in SFN catches. Drying in these lakes stimulated a shift in numerical dominance towards by smelt at the expense of carp gudgeons, bony bream and golden perch. Standardised SFN catches (fish 200 hr⁻¹) prior to flooding in 1998 were generally greater in the larger deeper lakes (lakes Tandure, Menindee and Cawndilla) than they were in the smaller shallower lakes (lakes Malta, Balaka and Bijiji).

Lake Tandure was the first of the lakes above the Main Weir to receive flooding inflows during August 1998. The initial flood pulse coincided with large increases in smelt numbers in SFN catches in Lake Tandure. Smaller increases in smelt abundances were also observed with the first inflows to lakes Malta and Bijiji during August. In contrast, bony herring and golden perch appeared to be the first to re-invade Lake Balaka during August. Differences in the composition of initial invaders between these lakes may be attributable to temporal differences in mainstream populations and/or to physical differences of the channels connecting the lakes with Lake Wetherell.

By November 1998, the smelt populations present in most lakes during August 1998 had declined. SFN fish catches were similar for all lakes above the Main Weir and were numerically dominated by carp, carp gudgeons and bony herring. SFN catches decreased as lakes Menindee and Cawndilla re-flooded. November 1998 SFN fish catch composition in Lake Menindee resembled that observed in lakes above the Main Weir with the addition of golden perch, which represented 9 % of the catch. Flooding of Lake Cawndilla via Lake

Menindee led to increases in the abundance of carp gudgeons and bony herring, and as was observed in LFN catches at this stage, relatively more golden perch than carp, although combined these constituted less than 2 % of the SFN catch.

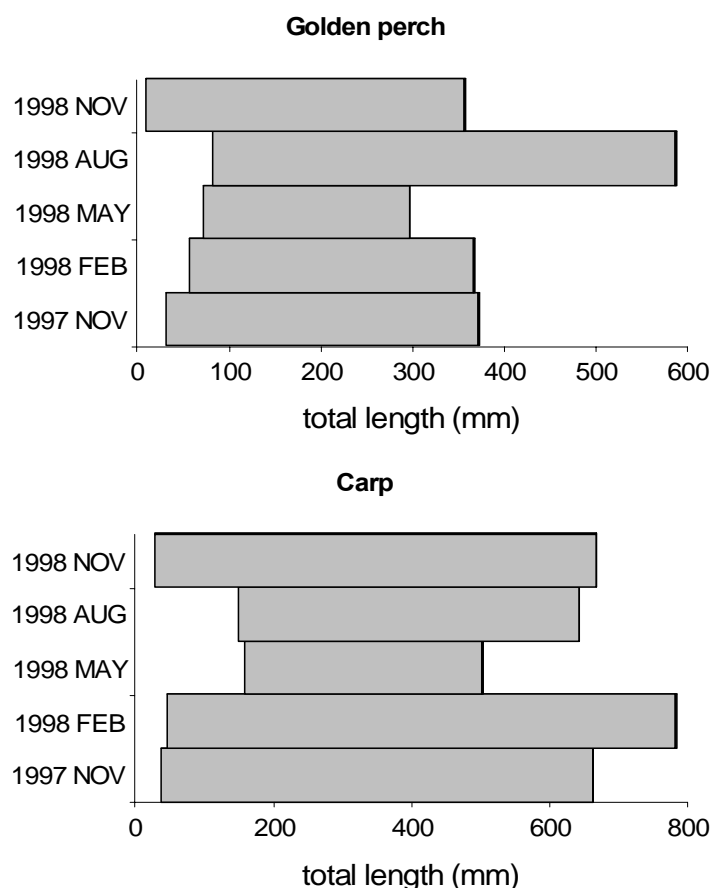
SFN fish compositions recorded during April 2002 as lakes Tandure, Menindee and Cawndilla were again drying were similar to those observed prior to lake filling in 1998. Bony herring, smelt and carp gudgeons numerically dominated catches at this time. As observed from LFN catches, golden perch and carp contributions to SFN catches were much lower than that recorded initially after flooding during November 1998.

The primary response to flooding in all lakes, as identified from both LFN and SFN catches was the increase in catches of both large and small sized golden perch and carp. The minimum size of fish caught provides a good indication of cohort progression throughout the year. November 1998 catch length data (lakes pooled within times) suggests that larval recruitment in both species had occurred (Figure 2.4.5). Figure 2.4.5 indicates that recruitment in both species had also occurred at about the same time during the previous year. Whether recruitment was due to local spawning or immigration was not established.

The minimum size of golden perch juveniles caught during November 1998 differed between lakes; 30-35 mm in lakes Malta, Balaka, Bijiji and Tandure, and 7-10 mm in lakes Menindee and Cawndilla. These sizes suggest ages of 75-85 days and less than 2 weeks, respectively (refer to Section 2.4.2), and correspond closely with the commencement of inflows into each of the lakes. Minimum lengths of carp juveniles caught during November 1998 also varied between lakes; 30 mm (Lake Malta), 25 mm (lakes Balaka and Bijiji), 50 mm (Lake Tandure), and 40 mm (lakes Menindee and Cawndilla), although the distribution of minimum carp sizes between lakes did not correspond as closely with the commencement of inflows as did golden perch.

Discussion

The eleven fish species encountered during the six surveys conducted between 1997-2002 have either been recorded previously or were expected based on their biogeographic distributions (Llewellyn 1983, McDowall 1996, Harris and Gehrke 1997). Four native fishes, line-eyed hardyhead (*Craterocephalus stercusmuscarum fulvus*), crimson-spotted rainbowfish (*Melanotaenia fluviatilis*), spangled perch (*Leioptherapon unicolor*) and silver perch (*Bidyanus bidyanus*) were rarely encountered in this study. In the case of hardyheads and rainbowfish, this may be related to the lack of macrophyte habitat in most lakes (Taylor-Wood *et al.* 2002). Spangled perch, however, are at the southern edge of their distribution at Menindee (Merrick 1996) and, as specimens were caught following lake re-flooding, may have arrived with floodwaters. Species that were not collected but expected included, catfish (*Tandanus tandanus*), and Murray cod (*Maccullochella peelii*). The absence of catfish in this study supports the reported large-scale reductions over recent decades of these species throughout much of the Murray-Darling Basin (Reid *et al.* 1997). Whilst anecdotal information (*i.e.* anglers and the 2004 fish-kill in the Lower Darling River) suggests that viable Murray cod populations remain in the Darling River System, the absence of cod in this lake survey probably reflects the affinity of the species for the channel environment and selectivity of the gear types used. To a certain extent channel affinity may also account for the absence of silver perch within the lakes. The single specimen recorded in this study was caught near the entrance of Lake Tandure. Other species, which were expected for the region but not collected, include the purple spotted gudgeon (*Mogurnda adspersa*) and olive perchlet (*Ambassis agassizii*). Larson and Hoese (1996) and Harris and Gehrke (1997) report that these species have become rare in the southern Murray-Darling Basin. There are no records of flatheaded gudgeon (*Philypnodon grandiceps*) in the Menindee section of the Darling River



■ **Figure 2.4.5: Size distribution (total lengths mm) of golden perch and carp caught during the 1997-8 surveys using large and small fyke nets. Lake data has been pooled.**

catchment and none were encountered during this investigation. Interestingly, this species has been recorded from upper tributaries of the Darling River and from the Murray River to the south.

As lakes dried during 1997-8, fish catches declined and community structure became increasingly numerically dominated by bony herring and smelt, and in the smaller lakes by mosquitofish, while abundances of golden perch and carp declined. Anecdotal information suggests that as lakes dry the larger native fish species (*e.g.* golden perch, bony herring) migrate from the lake into the main channel, leaving other species, such as carp, behind. However, the presence of these species in lakes Malta, Balaka and Bijijiji after their disconnection from the Darling River refutes such information. Whilst not recorded in LFN and SFN catches, only large carp were left stranded as these lakes dried. Declines in fish abundance during the drying phase suggests that individuals were being removed from the community, most probably by the opportunistic feeding of water birds, or dying as water levels fell and the quality of water declined (refer to Section 2.1). Increases in piscivorous water bird abundance were observed as the smaller lakes dried, more so than in the larger and deeper lakes during the study period (O. Scholz unpublished data). Similar responses of fish communities were observed as the system again dried during 2002.

Re-flooding of the lakes above the Main Weir re-set fish assemblages, with post-flood communities numerically dominated by golden perch carp, smelt, carp gudgeons and bony herring. The duration of connection of these lakes to Lake Wetherell during the flood pulse

influenced the period available for immigration and thus total recorded abundances. For example, Lake Tandure, which remained connected throughout the survey period, had the highest catch abundances, and Lake Malta, which had the shortest period of connection, had the lowest catch abundances. Golden perch were amongst the first to re-invade lakes above the Main Weir as they filled, but appeared to move out of the lakes after the initial flood pulse had passed. As Lake Menindee filled, a fish community similar to that observed in lakes above the Main Weir was established, albeit with a significantly greater golden perch population. Golden perch drove the smaller increase in total catch abundance observed in Lake Cawndilla as it filled during November 1998. These data suggest that golden perch were more mobile than were carp, and moved rapidly through the Menindee system below the Main Weir as each of the lakes filled in sequence.

Increases in golden perch and carp abundances following re-flooding of the lakes in 1998 were in part driven by the recruitment of juveniles. Whilst it was not possible to identify the relative significance of either local spawning or immigration, juvenile recruitment in both species was also evident in catches 12 months earlier during November 1997. Temperature and changes in flow or water level are generally considered important cues stimulating spawning in golden perch (Koehn and O'Connor 1990, Humphries *et al.* 1999) and carp (McDowall 1996, Smith and Walker 2004). Whilst spawning of golden perch in each of the Menindee Lakes coincided with lake flooding between August and November 1998, spawning also occurred between May and October 1997 in the absence of significant changes in water level (refer to Section 2.4.2). Relationships between water level and spawning activity in carp during both 1997 and 1998 were weak. These data suggest that spawning in golden perch and carp may be a response to prey availability and/or temperature through its effect on both prey production and fish physiology (*e.g.* Hanson *et al.* 1997, Wootton 1998, James *et al.* 2003).

The surveys reported here examined only the fish assemblages present within the Menindee Lakes where habitat diversity was very low, consisting of open water and submerged snags, and no macrophytes (Taylor-Wood *et al.* 2002). Highest fish diversity was recorded in Lake Tandure, where habitat diversity was greater than in the other lakes and connection to Lake Wetherell was permanent. The more extensive and diverse aquatic habitat present in Lake Wetherell suggests that total fish diversity within the entire Menindee Lakes system might be higher than that reported here. However, surveys of Lake Wetherell during 2000 and 2001 that targeted different habitat types did not encounter any fish species that were not recorded during our surveys of the lakes (SKM 2002).

2.4.2 Golden perch spawning 1997

O. Scholz, B. Gawne and B. Ebner

Introduction

Considerable effort has been expended documenting the changes in fish assemblages in the Murray-Darling Basin (MDB) (*e.g.* Llewellyn 1983, Harris and Gehrke 1997). However, causal links between environmental variables and the health of native fish populations remain poorly understood. Native fish in the MDB have evolved in an unpredictable, fluctuating environment in which large variations in population size are to be expected. Flow regulation has been implicated in the decline of native fish populations in the MDB through its influence on the flow regime and the movement of fish both up- and downstream and laterally into potentially critical floodplain habitat (*e.g.* Cadwallader 1978, Reynolds 1983, Mallen-Cooper *et al.* 1995). As these factors can be potentially managed to improve fish spawning and recruitment success, empirical links with life history stage requirements must be better understood.

Temperature and changes in flow or water level are generally considered important cues stimulating spawning of golden perch (*Macquaria ambigua* Percichthidae; Richardson) (Koehn and O'Connor 1990, Humphries *et al.* 1999). Spawning of golden perch has been reported to occur between October and April (Lake 1959, 1967d, Cadwallader 1977, Koehn and O'Connor 1990), when water temperatures exceed about 23 °C (Lake 1967a,b,c,d, Llewellyn and MacDonald 1980, Richardson 1984), or when warm temperatures coincide with a rise in water level (Lake 1967a, Mackay 1973, Richardson 1984, Gehrke 1991, Harris and Gehrke 1994). However, as early as the 1950s it was recognised that golden perch could spawn in response to both a rise and a fall in river height (Cadwallader 1977), and only more recently have studies confirmed the occurrence of spawning during non-flood periods (King *et al.* 2003, Mallen-Cooper and Stuart 2003).

Fish recruitment models, such as the 'flood-recruitment model' (Gehrke 1991, Harris and Gehrke 1994) and the 'low-flow recruitment hypothesis' (Humphries *et al.* 1999), have attempted to link spawning and subsequent recruitment success under different flow/water level conditions to food resource availability, as suggested by the 'prey match-mismatch hypothesis' (Cushing 1975, 1990). Whilst it appears that the spawning strategy of golden perch may be more flexible and not directly linked with flooding as originally thought (King *et al.* 2003, Mallen-Cooper and Stuart 2003), information describing links between water level, temperature and spawning in golden perch within the Basin remains limited, and little information is available for Darling River populations such as those associated with the Menindee Lakes (*e.g.* Gehrke *et al.* 1997). This study examined the links between water level, temperature and spawning of golden perch within the Menindee Lakes during 1997 with the intent of identifying potential mechanisms for managing this important native species.

Methods

The timing of golden perch spawning involved a back-calculation of fish age from the time of collection based on the examination of otolith microstructure. Seventy-two golden perch juveniles were collected from lakes Malta, Balaka, Bijiji, Tandure, Menindee and Cawndilla during August and November 1997 (Table 2.4.3). Fish were sampled using seine net trawls, and preserved in the field in 70 % ethanol. Both standard and total length measurements, rounded to the nearest millimetre, were recorded prior to preservation and otolith extraction. Extracted otoliths were stored in water for one week to displace any alcohol that may have caused them to crack on drying, thereby reducing readability. Air-dried otoliths were then weighed and growth increments counted at 1000x magnification. Age was estimated by counting increments along a radial transect originating at the primordium. Each prepared

specimen was counted twice to provide an indication of the error between age estimates. Error between age estimates was calculated as an index of average percent error (APE) developed by Beamish and Fournier (1987). APE was relatively high (3.49 %), but compared favourably with that of Anderson *et al.* (1992) (APE = 3.9 %).

Of the 72 fish otoliths examined, 35 possessed a major opaque increment near the outer edge. This usually corresponds to a period of slow somatic growth, and as increments were too fine and diffuse to count at 1000x magnification this prevented accurate daily age determinations. These fish, which included all those from Lake Cawndilla, were allocated to the 0+ age class and were excluded from further analysis. Of the remaining 37 fish, daily age estimates were reliably determined for 33. Estimates could not be determined for 4 preparations as increments were too irregular and diffuse to count accurately.

Water temperature and water level data for lakes Wetherell and Menindee were sourced from NSW DIPNR. Fluctuations in the water levels of lakes Malta, Balaka, Bijiji and Tandure were similar to those recorded for Lake Wetherell to which they were connected. Similarly, lakes Menindee and Cawndilla remained connected to each other throughout the study period. Pearson correlations and regression equations were calculated using SYSTAT®10.2 (SPSS Inc. Chicago, USA).

Lake	Date of capture	Number of individuals
Malta	7/8/1997	11
Malta	20-21/11/1997	10
Balaka	20/11/1997	9
Bijiji	25/11/1997	10
Tandure	26/11/1997	11
Menindee	24/11/1997	12
Cawndilla	27/11/1997	9

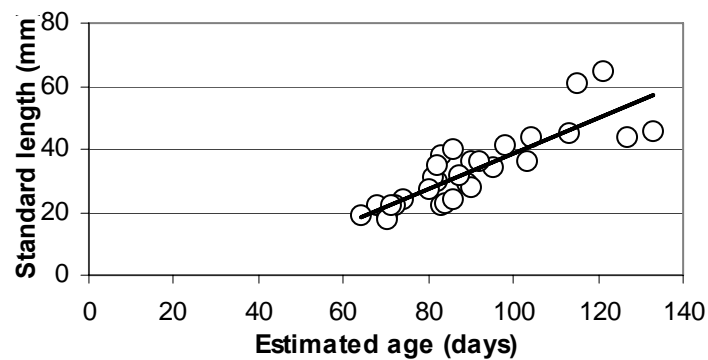
■ **Table 2.4.3: Location, date of capture, and number of golden perch juveniles used in this study.**

Results

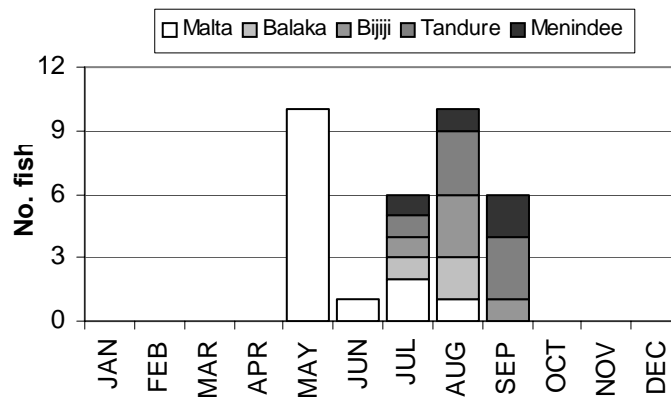
Standard length (SL) and total length (TL) data was available for 68 of the 72 fish caught. SL and TL were significantly positively correlated over the range examined (Pearson correlation: $r=1.00$, $p<0.001$, $n=68$; regression equation $SL=0.821TL+0.0021$, $R^2=0.999$), as were estimated daily age (EDA) and otolith weight (OW) (Pearson correlation: $r=0.745$, $p<0.001$, $n=33$; regression equation $EDA=0.0803OW-5.3857$, $R^2=0.555$), suggesting that both TL and OW may be used to estimate age.

Standard lengths of all fish examined ranged between 18-65 mm. Age estimates ranged between 64-133 days. Both EDA and SL data pairs were available for only 30 fish. Although EDA and standard length were significantly positively correlated (Pearson correlation: $r=0.85$, $p<0.01$, $n=30$; regression equation $SL=0.5605EDA-17.213$, $R^2=0.723$), the relationship appeared to weaken as fish grew (Figure 2.4.6). Growth rate of golden perch recovered from the Menindee Lakes appears to be slower than that reported by Rowland (1996) (30-40 mm at 40 days) and Arumugam and Geddes (1987) (30 mm at 40 days) for pond reared golden perch.

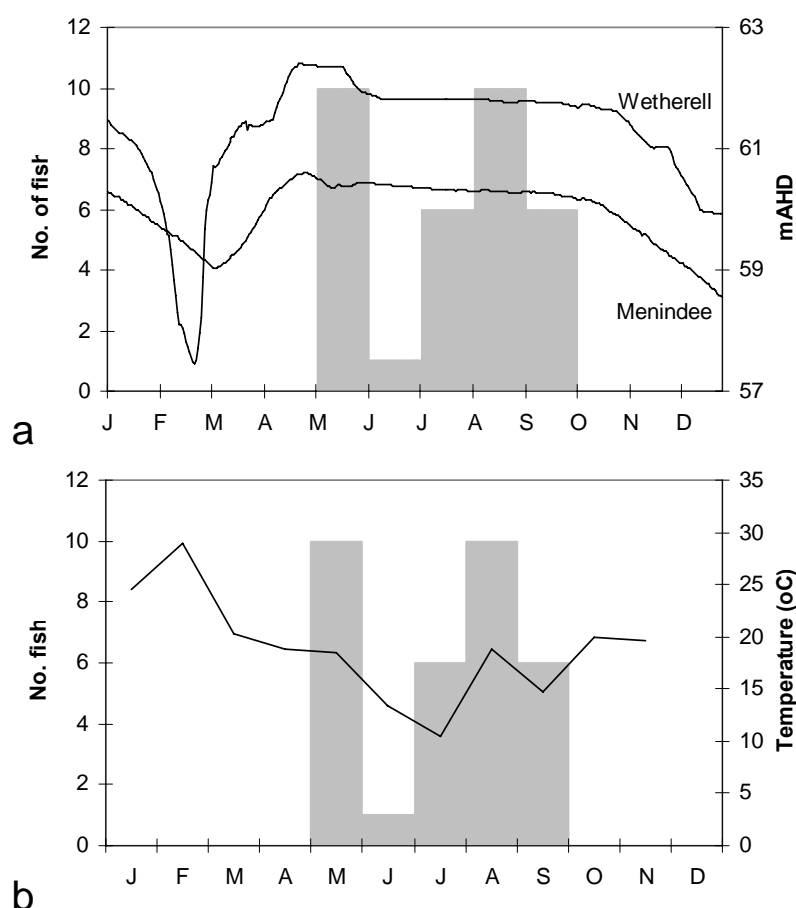
Spawning times based on the back calculation of age estimates from the date of capture are shown in Figure 2.4.7. All fish captured during August from Lake Malta were spawned between May and June (late autumn-early winter), several months after the commencement of inflows from Lake Wetherell (1st March). All fish captured during November were spawned between July and September (winter-early spring). Water levels during this second spawning period did not vary greatly (Figure 2.4.8a). Spawning by golden perch occurred over a water temperature range of 10.5-18.8 °C, with maximum spawning activity occurring during May and August when water temperatures were 18.5 °C and 18.8 °C, respectively (Figure 2.4.8b). Whereas autumn spawning was not preceded by large changes in temperature, the late winter spawning activity peak was associated with rising water temperatures.



■ Figure 2.4.6: The relationship between standard length (mm) and estimated age of fish (days).



■ Figure 2.4.7: Hatch date and lake distribution of the 33 fish for which age estimates were possible.



■ **Figure 2.4.8: Hatch date distribution of the 33 fish for which age estimates were possible plotted with a) water levels (mAHd) for lakes Wetherell and Menindee, and b) water temperature (°C).**

Discussion

Much of the literature relating to spawning cues in golden perch has focused on flood events (*cf.* ‘flood-recruitment model’ (FRM); Gehrke 1991, 1994), or more recently on periods of low flow (*cf.* ‘low-flow recruitment hypothesis’ (LFRH); Humphries *et al.* 1999). Whereas the FRM suggests that spawning and subsequent recruitment success is largely dependent on the floodplain inundation and the concomitant increases in suitable spawning habitat, nursery habitat, and food, the LFRH suggests that during periods of low flow, increased residence times promote increases in food resource availability, which in turn stimulate spawning and recruitment success (*cf.* ‘prey match-mismatch hypothesis; Cushing 1975, 1990). Warmer temperatures (>23°C) have also been implicated as important spawning cues in Murray River golden perch populations (*e.g.* Lake 1967a,b,c,d, Llewellyn and MacDonald 1980, Richardson 1984). This response may be due to the effect of temperature on both food resource availability and fish physiology (*e.g.* Hanson *et al.* 1997, Wootton 1998, James *et al.* 2003). As recent work (*i.e.* LFRH) has indicated that the coincidence of flood events and warm temperatures may not be as critical to spawning and recruitment success in golden perch as suggested by the FRM, a more flexible or opportunistic spawning and recruitment strategy appears to be operating (King *et al.* 2003, Mallen-Cooper and Stuart 2003). Differences in spawning windows for golden perch are thus to be expected between rivers, such as the Murray and Darling rivers, with widely differing flow regimes. However, direct

evidence either for or against flood/low-flow cued spawning remains scarce due in part to the difficulty of locating wild larvae (S. Meredith pers. comm.).

Spawning dates determined for 33 of the 72 juvenile golden perch caught from the Menindee Lakes indicated that spawning occurred between May and September 1997. However, as all lakes were connected with the Darling River during the identified period of spawning, it was not possible to determine whether fish had been spawned within the lakes or had moved in from the Darling River. Spawning of fish caught in Lake Malta during May occurred two months after the commencement of inflows from Lake Wetherell and coincided with highest water levels. No fish from the same spawning cohort were sampled from the other lakes. A second winter-early spring spawning period identified for fish recovered from five of the six lakes sampled did not coincide with marked changes in water level, suggesting that spawning was not obligately flood related. Spawning observed in the Menindee Lakes occurred over an extended period, much earlier and at lower temperatures (10.5-18.8 °C) than that reported previously.

Data presented here together with that published elsewhere (*e.g.* Koehn and O'Connor 1990) indicates that spawning in golden perch can occur throughout the year. Whilst our data also suggests that golden perch populations within the Menindee Lakes may not be obligate flood spawners as has been previously reported (*e.g.* Gehrke 1991), it does not discount the flood-dependence of larval recruitment success which we did not examine. For example, other large native fish species that do not require floods as a spawning cue tend to recruit best following floods when the availability of critical habitat and food resources is likely to be greatest (*e.g.* Mallen-Cooper and Stuart 2003).

Golden perch are highly fecund migratory fish that tend to spawn in particular localities rather than broadly throughout the adult habitat (Harris and Gehrke 1994). Ensuring spawning and subsequent larval recruitment success in key locations, such as the Menindee Lakes, depends upon a clear understanding of the links with key environmental variables. The responses to water level and temperature reported here and from throughout the Murray-Darling Basin clearly indicate that spawning activity in golden perch is not exclusively dependent on either flooding or season. Further work is necessary to clarify links with other potentially important cues, such as food resource availability and fish physiology.

Summary

Much of the information regarding the biology and life history of key native fish species has been summarised by Koehn and O'Connor (1990) and Tucker *et al.* (2002). However, key knowledge gaps still exist in our understanding of the dynamics of fish populations, specifically recruitment ecology.

In previous sections (Sections 2.1, 2.2 and 2.3) we demonstrated that periods of lake drying and subsequent re-flooding initiated predictable responses in water quality, phytoplankton and zooplankton. In this section we examined the fish communities present within the Menindee Lakes and their responses to lake drying and re-flooding, and also examined potential links between flow regime and spawning in Golden perch (*Macquaria ambigua*), the principal piscivore within the Lakes. Such information is needed to support proposed management actions, such as the re-imposition of drying phases and the timing of regulated inflows.

Eleven species of fish were recorded in six fyke net surveys conducted between 1997-2002 in the Menindee Lakes as they dried and re-flooded. Drying and re-flooding stimulated changes in the population structure of fish communities present within each of the Menindee Lakes. As lakes dried, the fish community became simplified and fish abundances declined. Drying led to the loss of the dominant piscivore (golden perch) and to the numerical dominance of bony herring, mosquitofish and smelt. Flooding re-seeded lakes with a fish fauna numerically dominated by golden perch, carp and bony herring. Golden perch were amongst the first to re-invade filling lakes and appeared to move sequentially through the Menindee system as each of the lakes filled. Whilst the extent of lake drying influenced the within-lake persistence of fish species and their contribution to post-flood assemblages, the composition of post-flood fish assemblages depended largely on the duration of lake connection with the main stream and on the momentary structure of the riverine fish community.

Flooding during 1998 also led to significant recruitment of golden perch and carp populations throughout the system. Temperature and changes in flow or water level are generally considered important cues stimulating spawning in golden perch (*Macquaria ambigua* Percichthidae; Richardson). Recent studies within the Murray-Darling Basin have decoupled these cueing mechanisms and suggested that spawning activity in golden perch may be more flexible. However, little empirical evidence is available to define more clearly the links between environmental factors and spawning activity, and how these might vary throughout the Basin. Ageing of golden perch larvae caught within the Menindee Lakes of far-west New South Wales, Australia, late in 1997 indicated that spawning occurred over an extended period between May and September, much earlier and for longer and at lower temperatures than previously reported. Whilst spawning commenced two months after the commencement of inflows and coincided with maximum lake water levels, spawning continued in the absence of further large changes in water level, suggesting that spawning was not obligately flood related. The responses to flow/water level and temperature reported here and from throughout the Murray-Darling Basin clearly indicate that spawning activity in golden perch is quite variable and not exclusively dependent on either flooding or season.

The changes in fish community structure observed through periods of drying and re-flooding might be expected to have a significant impact on trophic equilibria, leading to trophic cascading (e.g. Carpenter and Kitchell 1988, Lazzaro 1997). Whilst many population parameters, such as rate of population growth, age class structures, and the age/size dependent trophic interactions of individual fish species remain unknown, assertions of trophic cascading must remain tentative. However, we suggest (Section 5) that top-down trophic cascading initiated by lake drying through the loss of key species, such as golden perch, may

be as significant a factor in driving concomitant changes in phytoplankton and zooplankton community structure (Sections 2.2 and 2.3) as bottom-up forcing identified in Section 2.1.

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3: Targeted investigations

3.1 The influence of hydrology on plant seed banks

J. Nicol and O. Scholz

Abstract

Hydrology is considered to be an important structuring agent of wetland seed banks and plant communities. We examined the distribution, size and composition of seed banks present within the Menindee Lakes and their relation to hydrology. Fifty-eight plant species were recorded from the seedbanks of the Menindee Lakes. The seed bank of Lake Malta was much larger (70,000-80,000 seeds m⁻²), more diverse (32 species), contained more species with persistent seed banks, and was more evenly distributed throughout the elevation range than that recorded in the relatively much larger lakes Tandure, Menindee and Cawndilla. Seed banks within the larger lakes had a combined species richness of 27 species, and 90 % of the seeds were concentrated within a distinct and narrow strandline that generally contained less than 10,000 seeds m⁻². These differences were consistent with hypothesised hydraulic structuring processes. In the larger lakes, greater wave energy and steeper littoral gradients are likely to have influenced the distribution of seeds, and to have negatively impacted on the establishment of lakeshore plants, reducing the potential for plant regeneration to a narrow littoral zone, and thus also local replenishment of the seedbank. Further, regulation has decreased the connectivity of these lakes with other elements of the fluvial system thereby reducing the potential for external seed contributions, especially during flood pulses when seed loads are likely to be highest.

Introduction

A recent vegetation survey of the Menindee Lakes (January 2000) provided a snapshot of the distribution of different vegetation communities present within the lakes (Taylor Wood *et al.* 2001). Taylor-Wood *et al.* (2001) identified five broad categories for vegetation types within the areas subject to inundation of Menindee Lakes.

1: Floodplain woodland: floodplain woodland dominated by either river red gum (*Eucalyptus camaldulensis*) or black box (*E. largiflorens*), rarely flooded woodland, woodland with lignum (*Muehlenbeckia florulenta*), and introduced species.

2: Shrubland: chenopod shrubland.

3:Herbfield/Sedges/Grasslands: sandy lake fringe, dry lakebed herbfield/sedgeland/grassland.

4:Freshwater Wetlands: shallow freshwater marsh, shallow freshwater marsh (dead trees), lignum swamp, dead trees with *Persicaria* and/or lignum.

5: Areas with little or no vegetation: open water, open water with dead trees, recently exposed lakebed, open water channel and inflow-outflow channel.

For the most part, the lakes have areas of open water fringed by floodplain woodland consisting of either river red gum (*Eucalyptus camaldulensis*) or black box (*E. largiflorens*) over story. Lakebed sediments vary from fine clay/silts to coarse red and white sands. Areas of exposed lakebed sediment become herbfields/grasslands/sedgelands when water levels are

drawn down. Increased permanency of water within these lakes has also led to the death of lower lying eucalypts. Vegetation within Lake Wetherell and the connecting channels tend to be more complex, support a greater number of vegetation types, and are not dominated by large areas of open water. Whilst all vegetation types found within the lakes are represented, freshwater wetlands dominated by *Persicaria* predominate in the lower reaches of Lake Wetherell (towards the Main Weir).

In January 2000 the lakes were at approximately 50% capacity. At this time, open water areas accounted for 51 % of the vegetation/habitat surveyed, rarely flooded woodland (11 %), open water lake (dead trees) (11 %), floodplain woodland (*E. camaldulensis*) (9 %), floodplain woodland (*E. largiflorens*) (4 %) and shallow freshwater marsh (3 %) (Taylor-Wood *et al.* 2001).

The vegetation of the Menindee Lakes responds dynamically to changes in season and water level. Inundation and desiccation are key drivers of vegetation community structure in ephemeral systems, leading to differences between lakes of differing hydrologies, and within lakes to the zonation of lakeshore plants with respect to exposure and submergence. Moore and Keddy (1988) have suggested that observed patterns of zonation parallel to the water's edge is caused by the differential germination of seeds at different elevations rather than to differences in the composition of the seed bank as reported by Stone (2001).

The seed bank is defined as the reserves of viable seed present in and on the soil surface (Roberts 1981). Seed banks ensure the survival of plant species through periods of unfavourable conditions for germination, growth and survival (*e.g.* van der Valk 1976, Thompson and Grime 1979, Keddy and Reznicek 1982, Leck 1989, Brock and Britton 1995, Leck and Brock 2000). The size of the seed bank, the contribution made to it by the different species, and patterns of seed distribution reflect the seed production by the resident plant community and of surrounding plant communities not only in the preceeding year, but perhaps in many previous years (Roberts 1981). Thompson (1992) has suggested that differences in the size of seed banks may be related to the extent of water level, with more variable environments commonly having larger seed banks.

Spatial heterogeneity of seed banks has been well documented (*e.g.* Roberts 1981, Bigwood and Inouye 1988, Benoit *et al.* 1989, Reinhardt *et al.* 2000, Grandin 2001). Spatial patterns of seed bank composition may arise through the accumulation and deposition of floating seeds in strandlines on the lee shores. Strandlines are areas around the shorelines of lakes where the deposition of organic debris has occurred. They are formed by the sorting action of waves (especially in large lakes), or by the stranding of floating material around the edge of the lake. The accumulation of seeds within strandlines, and their subsequent germination is also influenced by seed properties, such as the number of seeds released, seed buoyancy, and the ability to tolerate strandline conditions (van der Valk 1986, Smith 1990, Facelli 1991, Nilsson *et al.* 2002). In the Menindee Lakes, strandlines form multiple discontinuous rings around the edges of lakes (Figure 3.1.1). There is evidence to suggest that strandlines are areas where seeds of floodplain species and organic matter have become concentrated (J. Nicol unpublished data) and in turn, plant germination and recruitment are concentrated.

Given the differences in water regime experienced by each of the Menindee lakes and differences in their connectivity with other components of the floodplain, one might also expect differences in the seed banks and thus the regenerative potential of lakebed vegetation assemblages in response to disturbances such as flooding and drying.

In this section, we examined the distribution, size and composition of seed banks present within the Menindee Lakes, and their relation to hydraulic influences. This work was carried out by one of the authors (J. Nicol) as part of a Ph.D. funded within the current project. For brevity, we present only a summary of the most pertinent results, and we refer you Nicol

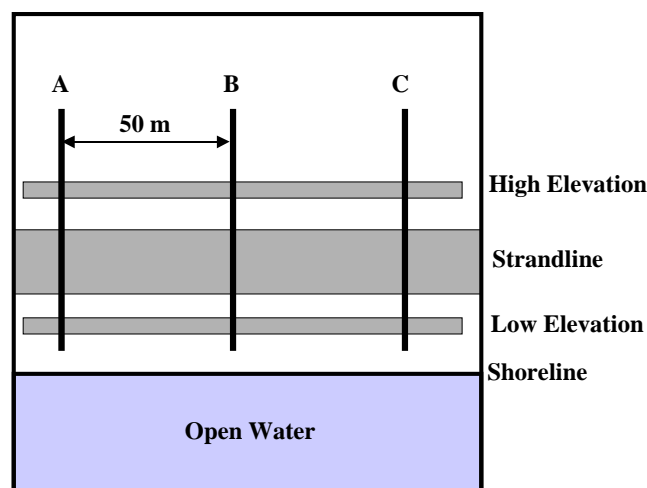
(2004) for a full account of the statistical analyses and other investigations of the vegetation of the Menindee Lakes.



■ **Figure 3.1.1: A well developed strandline on the northern shore of Lake Cawndilla.**

Methods

Seed banks were examined from sediment samples collected from lakes Malta, Tandure, Menindee and Cawndilla in June 2001. Three replicate transects 50 m apart were established on the northeastern shores of lakes Malta, Tandure, Menindee and Cawndilla. Five composite sediment cores (5 cm diameter, 5 cm deep) were taken from 4 sites on each transect: above the strandline ('high' elevation), the strandline (on top of the sediments), the sediments underneath the strandline, and below the strandline ('low' elevation) (Figure 3.1.2).



■ **Figure 3.1.2: Strandline sampling strategy.**

Sediment samples were dried at 40 °C until constant weight was achieved. Two hundred grams of each replicate sediment sample was then spread evenly over 4 cm of 60-40 sandy loam contained in 170 x 115 mm plastic containers. Two holes were drilled in the side each container 10 mm from the bottom which allowed water to drain. The samples were placed in random positions in a glasshouse and watered daily. In addition to the seed bank samples, fifteen blanks consisting of only sandy loam were randomly placed amongst the samples to determine if there was any contamination in the sandy loam or from the glasshouse. Every two weeks seedlings were counted, identified and removed and the position of the samples in the glasshouse re-randomised. Seedlings that could not be identified were transplanted and grown to a stage at which they could be identified. Plants were identified using keys in Jessop and Tolken (1986), Sainty and Jacobs (1981, 1994) and Cunningham *et al.* (1981). Nomenclature follows Jessop and Tolken (1986).

Plants were watered daily for 12 weeks then dried and not watered for six weeks. Twelve weeks was considered long enough for one wetting cycle because germination had slowed dramatically and in most cases ceased after six weeks. This wetting and drying cycle was repeated four more times for a total of five wetting and drying cycles.

The number of germinants was converted to seeds.m⁻² by calculating the bulk density of the sediment, then calculating the total mass of sediment for 1 m² to a depth of 5 cm. The high elevation, low elevation and below strandline samples from all lakes had bulk density of 1.4 g cm⁻³, the strandline samples had a bulk density of 0.9 g cm⁻³. This equated 70 kg of sediment m⁻² for the high elevation, low elevation and below strandline samples and 45 kg of sediment m⁻² for the strandline samples. The formula for converting the number of germinants to seeds m⁻²:

$$\text{No. Seeds m}^{-2} = \text{No. Germinants} \times \frac{\text{Mass of Sediment m}^{-2}}{\text{Sample Mass}}$$

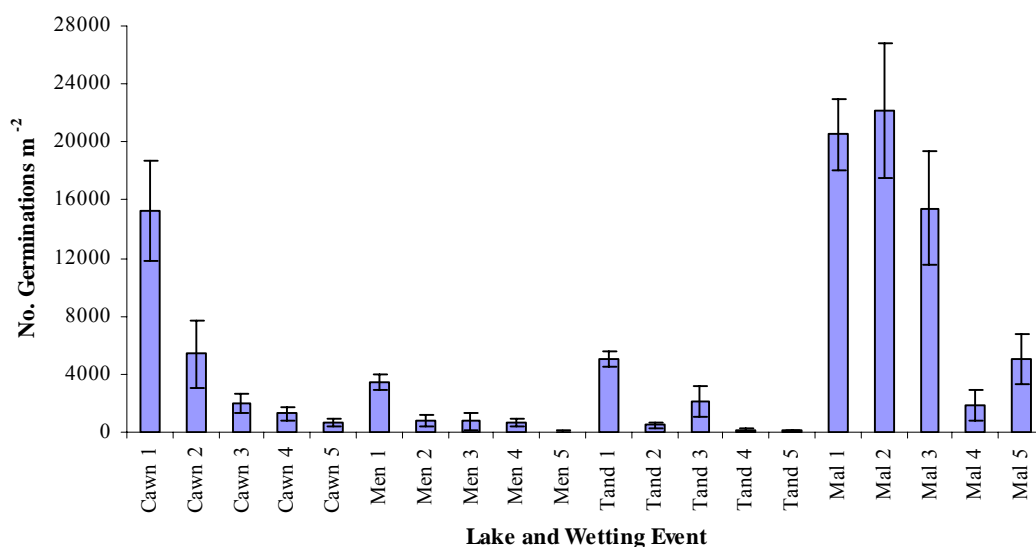
Differences in species composition between lakes and locations along transects within each lake were analysed with NMS ordination based on Bray-Curtis similarities using the package PCOrd (McCune and Mefford 1999). Single-factor NPMANOVA was used to identify differences in seed bank densities and richness between sites (Anderson 2001). Multiple comparisons were performed using a Tukey test for ranked data (Zar 1984).

Results

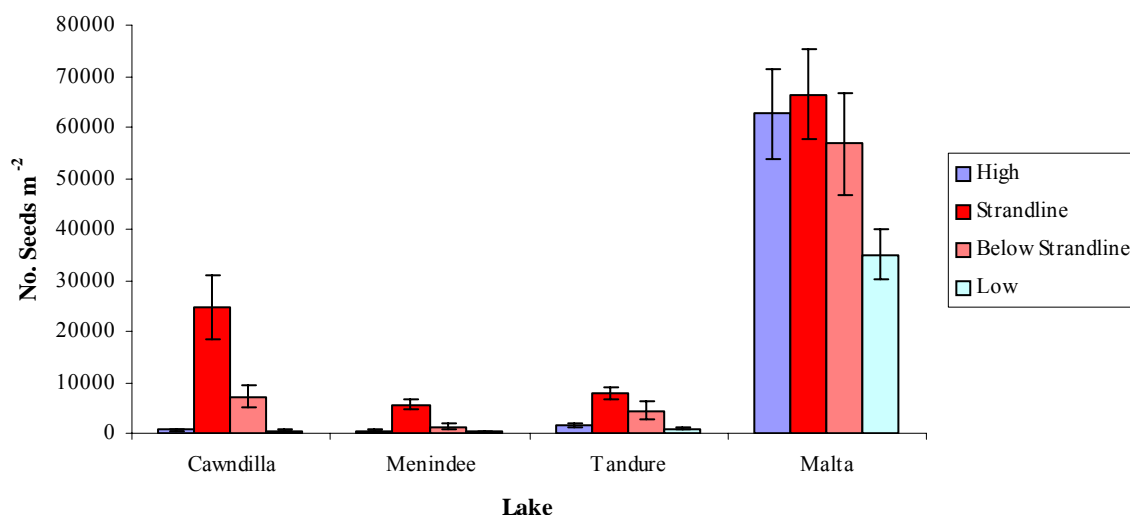
Numbers of germinants decreased with each successive wetting of strandline samples collected from lakes Malta, Tandure, Menindee and Cawndilla. Numbers decreased rapidly after the first wetting in samples from the larger lakes. In contrast, germinant numbers in samples from Lake Malta did not begin to decline until after the third wetting (Figure 3.1.3).

More seeds were recorded in the sediments and strandline of Lake Malta than were recorded in lakes Tandure, Menindee and Cawndilla. Seed density did not differ with elevation in Lake Malta, but did in lakes Cawndilla, Menindee and Tandure, where most seeds were associated with the strandline and to a lesser extent with the sediments underneath the strandline (Figure 3.1.4).

A total of 58 species were recorded from the seed banks of Lakes Malta, Tandure, Menindee and Cawndilla (Table 3.1.1). For all lakes, the number of species encountered decreased after the first wetting cycle. No new species were detected after the first wetting cycle. Subsequent wettings led to further losses of species richness, especially after the third wetting cycle (Figure 3.1.5). These data suggest that the species represented within the seed banks utilised different strategies. Whilst some species had transient seed banks, *i.e.* the entire viable seed reserve of the species germinated in response to a single wetting, others had persistent seed banks, *i.e.* only a portion of the viable seed bank germinated in response to each wetting until its seed bank was depleted. This response allows species to hedge their bets with respect to wetting events. This is perhaps a favourable adaptation to ephemeral environments, in which the timing and/or magnitude of inundation prove unsuitable for subsequent recruitment and seed set. Of the species recorded, 21 species were only detected in the first wetting cycle indicating they had transient seed banks (Table 3.1.1).



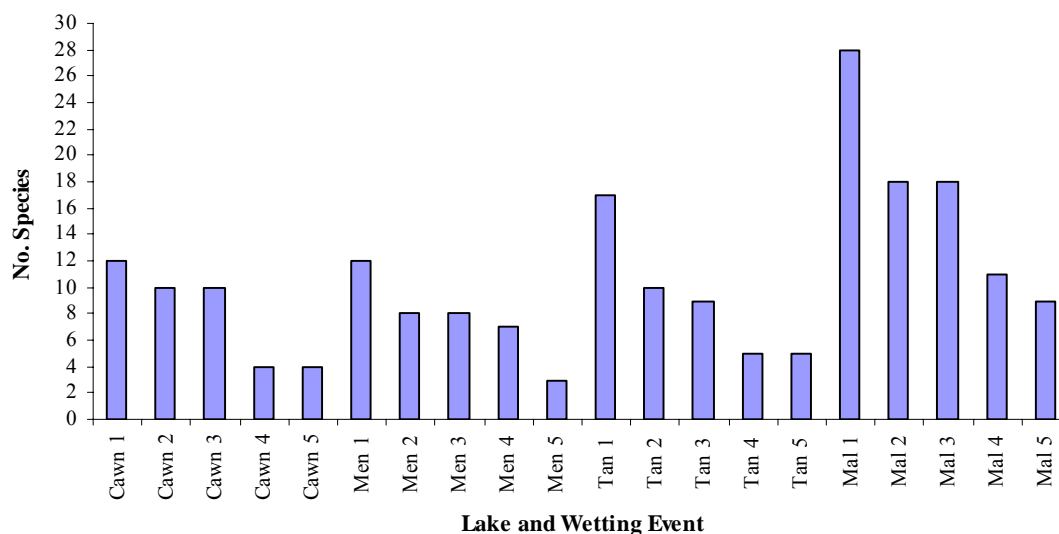
■ **Figure 3.1.3: Number of germinations.m⁻² for the strandlines of Lakes Cawndilla, Menindee, Tandure and Malta for each wetting event (error bars are ± 1 SE) (only strandlines were plotted because the number of germinants from other samples in Lakes Cawndilla, Menindee and Tandure were extremely low) (Cawn = Cawndilla, Men = Menindee, Tand = Tandure and Mal = Malta) (1–5 = wetting event).**



■ **Figure 3.1.4: Total number of germinations.m⁻² (after five wetting events) for strandlines and adjacent sediment collected from lakes Cawndilla, Menindee, Tandure and Malta (error bars are ± 1 SE, n = 15).**

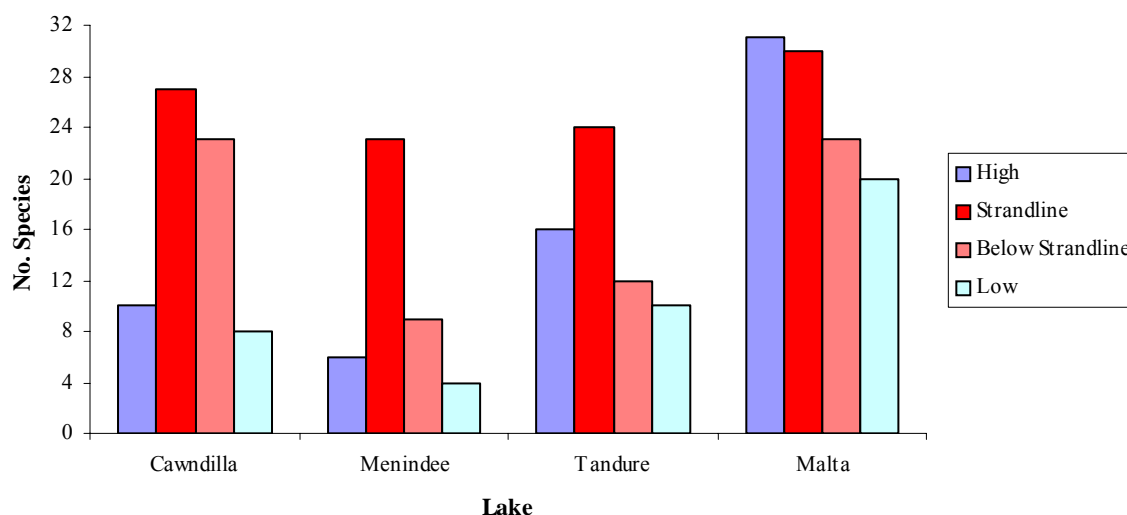
Species with persistent seed banks		Species with transient seed banks
<i>Alisma</i> sp.	<i>Medicago</i> sp.*	<i>Daucus glochidiatus</i>
<i>Alternanthera denticulata</i>	<i>Mollogo cerviana</i>	<i>Eucalyptus largiflorens</i>
<i>Ammania multiflora</i>	<i>Morgania floribunda</i>	<i>Euphorbia drummondii</i>
<i>Argemone ochroleuca</i> *	<i>Myriocephalus stuartii</i>	<i>Heliotropium amplexicaule</i> *
<i>Azolla</i> sp.	<i>Myriophyllum verrucosum</i>	<i>Heliotropium europaeum</i> *
<i>Centipeda minima</i>	<i>Nicotiana glauca</i>	<i>Iseotopsis graminifolia</i>
<i>Chenopodium pumilio</i>	<i>Pachychnia tenuis</i>	<i>Isolepis australiensis</i>
<i>Chloris truncata</i>	<i>Persicaria lapathifolium</i>	<i>Juncus aridicola</i>
<i>Convolvulus arvensis</i>	<i>Polygonum plebium</i>	<i>Lemna</i> sp.
<i>Crassula sieberana</i>	<i>Rumex bidens</i>	<i>Ludwigia peploides</i>
<i>Cyperus gymnocaulos</i>	<i>Schlerolaena</i> sp.	<i>Myosurus minima</i>
<i>Epaltes australis</i>	<i>Scleroblitum atriplicinum</i>	<i>Nicotiana velutino</i>
<i>Eragrostis dielsii</i>	<i>Solanum oligacanthum</i>	<i>Polygonum aviculare</i> *
<i>Eragrostis parvifolia</i>	<i>Sporobolus mitchelli</i>	<i>Ptilotus obovatus</i>
<i>Galenia secunda</i> *	<i>Tetragonia tetragonoides</i>	<i>Ricinis communis</i> *
<i>Glinus lotoides</i>	<i>Wahlenbergia communis</i>	<i>Rumex crispus</i> *
<i>Gnaphalium luteo-album</i>		<i>Senecio</i> sp.
<i>Haloragis aspera</i>		<i>Sinapis alba</i> *
<i>Heliotropium curassivicum</i>		<i>Solanum karsensis</i>
<i>Hypochoeris radicata</i> *		Unidentified dicotyledon
<i>Limosella australis</i>		<i>Xanthium occidentale</i> *

■ **Table 3.1.1: Plant species and seed bank strategy of taxa detected from the seed banks of lakes Malta, Tandure, Menindee and Cawndilla (* denotes exotic species).**



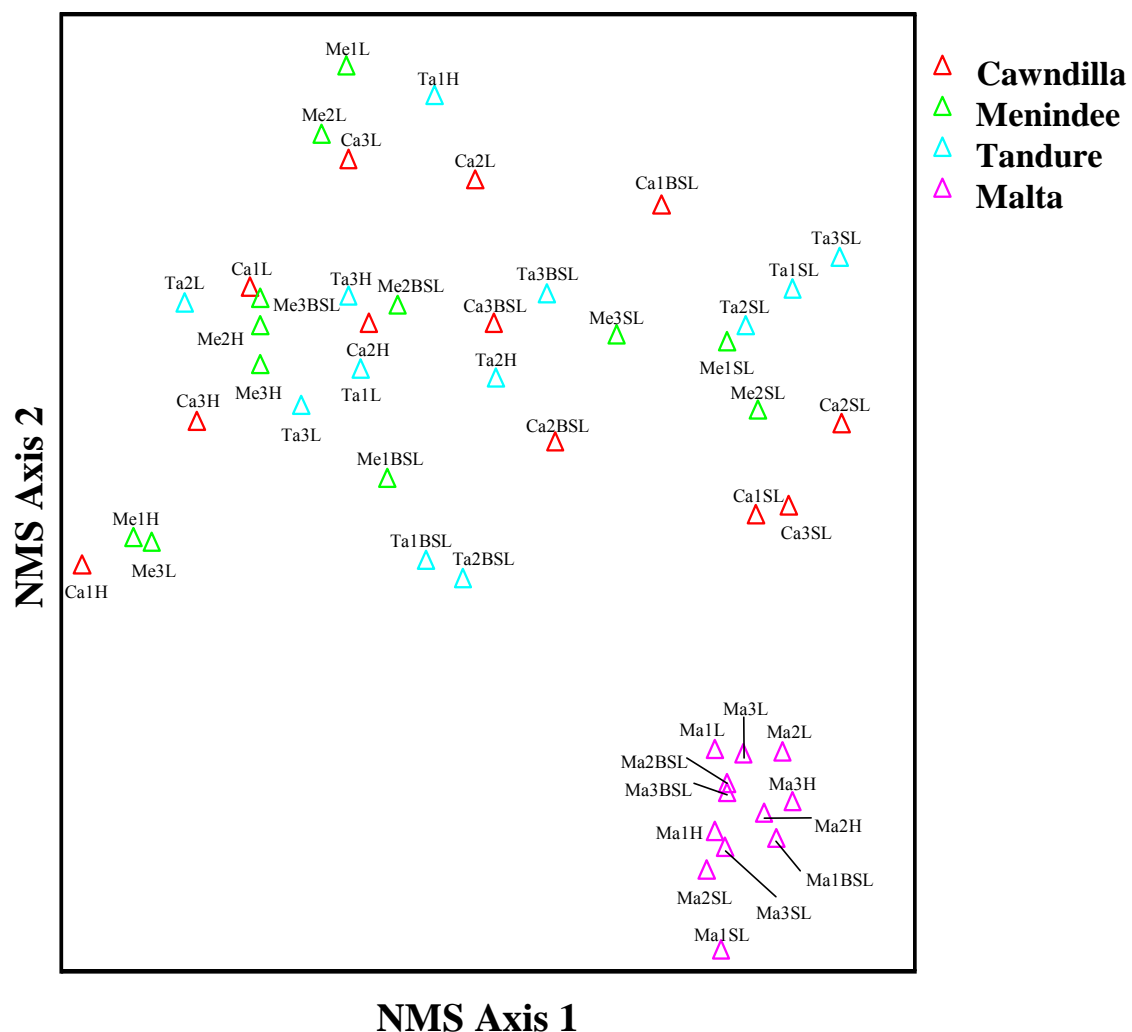
■ **Figure 3.1.5: Number of species detected in the seed banks (strandline and adjacent sediment) of lakes Malta, Tandure, Menindee and Cawndilla for each wetting event. (Cawn = Cawndilla, Men = Menindee, Tand = Tandure and Mal = Malta) (1–5 = wetting event).**

More species were recorded in the seedbank of Lake Malta than were recorded in lakes Tandure, Menindee and Cawndilla. Seedbank species richness decreased with elevation in Lake Malta. Seedbank species richness was concentrated within the strandline in lakes Tandure, Menindee and Cawndilla. The species rich sediment seed bank present around the edge of Lake Malta was absent from the larger lakes (Figure 3.1.6).



■ **Figure 3.1.6: Total number of species detected for the strandlines and adjacent sediment in lakes Cawndilla, Menindee, Tandure and Malta after five wetting events.**

NMDS-ordination indicated that the species composition of the Lake Malta seed bank differed markedly from that of lakes Tandure, Menindee and Cawndilla (Figure 3.1.7). Although strandline composition was more similar between the larger lakes than were similarities with other samples taken from along the elevation gradient within lakes, strandline compositions differed significantly between lakes (NPMANOVA: $F_{3, 56}=14.61$, $P=0.0004$; differences confirmed by Tukey HSD: Cawndilla \neq Menindee \neq Tandure \neq Malta). Whilst the distribution of samples from Lake Malta formed a much tighter grouping in multi-dimensional space that did sample from the other lakes, differences between sites along transects were significant (NPMANOVA: $F_{3, 56}=5.18$, $P=0.0006$. Tukey HSD: high elevation \neq strandline \neq below strandline \neq low elevation).



■ **Figure 3.1.7: NMS ordination of the species composition of the seedbanks of lakes Malta, Tandure, Menindee and Cawndilla (stress = 17.8%) (Ma = Malta, Ta = Tandure, Me = Menindee, Ca = Cawndilla, 1, 2 or 3 = transect, H = high elevation, SL = strandline, BSL = below strandline, L = low elevation).**

Discussion

Seed bank distribution

The strandline and the underlying sediments accounted for over 90% of the seeds detected in lakes Tandure, Menindee and Cawndilla, suggesting that this narrow zone of organic matter and seed deposition is extremely important in the vegetation dynamics of the edges these lakes. If flooding, drought or grazing kills the extant vegetation around the edges of the large lakes the strandline provides almost all of the seed reserves for regeneration. In contrast, seed bank densities in Lake Malta were an order of magnitude higher than that encountered in the larger lakes, and was more evenly distributed throughout the range of elevations examined.

Lake morphology and hydrology may account for the differences in seed bank distribution observed between Lake Malta and the larger lakes. Lake Malta is much smaller (max. diameter 3 km) and shallower (max. depth 1.5 m) than lakes Tandure, Menindee and Cawndilla (maximum diameters 8 km, 20 km and 12 km, respectively, and max. depth 5.8 m, 5.5 m and 9.6 m, respectively). Lake Malta also dries more frequently than the larger lakes (refer to Section 1 Tables 1.2 and 1.3). In lakes Cawndilla, Tandure and Menindee, the combination of these factors increases the potential for wave action to mobilise organic matter and seeds to the littoral fringes where they are deposited as narrow strandlines. The smaller size, flatter profile, and more ephemeral nature of the water regime in Lake Malta reduces wave energy and the increases the zone of seed deposition.

Wave action has been shown to have a negative impact on the establishment and growth of lakeshore plants (Wilson and Keddy 1985, Foote and Kadlec 1988, Coops and van der Velde 1996, Doyle 2001, Riis and Hawes 2003). If plants are unable to establish in areas subject to wave action the seed bank could become, through time, depauperate if there is no external seed input. The Menindee Lakes scheme was completed in the 1960s, which is probably sufficient time for this to occur.

Seed bank size

The seedling emergence technique used in this study tends to underestimate the total seed bank density relative to methods where seeds are physically separated from the sediments (Roberts 1981, Gross 1990, Brown 1992). However, the seedling emergence technique does have its advantages in that it is less labour intensive, species are easier to identify, there is no bias against small seeded species, and only the viable, and therefore ecologically relevant, seed store is quantified (Roberts 1981, Gross 1990, Brown 1992). Note that tetrazolium staining is required to conclusively determine viability when using seed separation techniques. The seedling emergence technique was chosen for this study because many of the species present in the extant vegetation have small (<1 mm diameter) seeds (*e.g.* *Epaltes australis*, *Gnaphalium luteo-album*, *Sporobolus mitchelli*, *Centipeda minima*, *Glinus lotoides*, *Chenopodium pumilio* and *Morgania floribunda*), which could be easily missed by seed separation techniques.

The seed banks of terrestrial systems are extremely variable depending on the type of system (Roberts 1981). In cultivated systems, seed densities as high as 500,000 seeds m⁻² have been reported (Roberts 1981). In low disturbance systems, dominated by long-lived species, such as forests and woodlands, seed densities are generally lower (<5000 seeds m⁻²) (Roberts 1981, Brown 1992).

Seed density was much higher in Lake Malta (70,000-80,000 seeds m⁻²) than in the larger lakes (generally <10,000 seeds m⁻², although 25000 seeds m⁻² were recorded in the strandline of Lake Cawndilla), despite the concentration of seeds within a narrower standline zone in the

larger lakes. Seed bank densities were generally greater, especially in Lake Malta, than that reported for overseas wetland systems (*e.g.* 1300 seeds m⁻² (Brock and Rogers 1998), 0-2,335 seeds m⁻² (Haag 1983), 707-4,607 seeds m⁻² (Leck and Simpson 1995), 2,300 seeds m⁻² (Le Page and Keddy 1998), and 21,445-42,615 seeds m⁻² (van der Valk and Davis 1978), but were comparable to those reported for other Australian wetland systems. For example, Nicol *et al.* (2003) detected between 20,000-90,000 seeds m⁻² in the seed bank of a South Australian temporary wetland, Finlayson *et al.* (1990) detected 3,800-15,400 seeds m⁻² in the seed banks of a Northern Territory floodplain, and McIntyre (1985) showed the seed banks of rice fields on the Murrumbidgee floodplain were extremely large containing 100,000-300,000 seeds m⁻².

Differences in seed bank density between Lake Malta and the larger lakes may be attributable to a combination of factors including differences in wave energy and connectivity with other elements of the fluvial system. For example, greater wave energy in the larger lakes may reduce germination success and thus the potential for autochthonous seed set (*e.g.* Wilson and Keddy 1985, Foote and Kadlec 1988, Coops and van der Velde 1996, Doyle 2001, Riis and Hawes 2003). In addition, allochthonous seed inputs are likely to be much higher in Lake Malta, which is connected directly to the Darling River during flood events when seed loads are likely to be greatest. In contrast, flows into lakes Menindee and Cawndilla are regulated and pass first through Lake Pamamaroo, in which much of the allochthonous seed loads entering from Lake Wetherell may be deposited. The seed banks of Lake Pamamaroo were not examined in this study, but we would anticipate that seed densities and species richness are likely to be greater than that encountered in lakes Menindee and Cawndilla. Whilst Lake Tandure has a direct connection with Lake Wetherell, the mixing of waters is to a large extent limited to the mouth of Lake Tandure.

Seed Bank Composition

Fifty-eight plant species were recorded from the seed banks of Lakes Malta, Tandure, Menindee and Cawndilla. Seed bank species richness was greater in Lake Malta (32 species) than in that identified in the larger lakes (upto 27 species in Lake Cawndilla). This compares with seed bank diversities reported for other Australian wetland systems of 28 species (Nicol *et al.* 2003), 33 species (Finlayson *et al.* 1990), 68 species (Britton and Brock 1994), and 73 species (Brock *et al.* 2003). Seed species richness encountered within the Menindee Lakes tended to be greater than that reported for overseas wetlands. For example 14 species (LaDeau and Ellison 1999), 18 species (Brock and Rogers 1998), 22 species (ter Heerdt and Drost 1994), 22 species (Leck and Graveline 1979), 23 species (van der Valk and Davis 1976), and 37 species (Le Page and Keddy 1998).

The distribution of seed bank species richness within lakes reflected that of seed bank density. Seed bank species richness in Lake Malta was greatest within, or at elevations above, the strandline. For the larger lakes, seed bank species richness was concentrated within the relatively narrower strandline zone. In all lakes, especially in the larger lakes, the composition of the strandline differed markedly from that present within the sediments. Many of the species present within the strandline of the large lakes had large seeds (*e.g.* *Ludwigia peploides*, *Rumex bidens*, *Xanthium occidentale*, *Persicaria lapathifolium*). *Alternanthera denticulata*, was also present in significant numbers within the strandline of all lakes. Although small-seeded, its seed have small papery wings that are probably an adaptation for wind dispersal, but which also assist its buoyancy and capacity for hydraulic dispersion. Many of the species unique to Lake Malta were small seeded. These taxa may be more prone to exclusion from the larger lakes due to their susceptibility to greater wave action upon germination. The non-seed component of the strandline has also been reported to inhibit the germination of small seeded species by burial (van der Valk 1986, Facelli and Pickett 1991, Middleton *et al.* 1991), effectively removing them from the viable seed bank.

Eleven exotic species were detected from the seed banks of all lakes (Table 3.1.1). Seven out of 21 species that had transient seed banks were exotic (Table 3.1.1) and most were present only in the large lakes. Only one exotic taxon (*Medicago* spp.) was detected only in the seed bank of Lake Malta at densities of 0-700 seeds m⁻². Lake Mata is grazed by domestic stock when dry and annual medics have been sown by the landholders to provide high nutrition pasture (D. Barnes pers. com.). The majority of studies from freshwater and terrestrial systems have neglected to indicate which species are exotic in their species lists. Exceptions to this include Nicol *et al.* (2003), who detected 7 exotic species (28 species total) in the seed bank of a seasonal southern Australian wetland, Brock and Casanova (1997), who detected 11 exotics (60 species total), and Casanova and Brock (2000), who detected 12 exotics (72 total) from the seed banks of northern New South Wales temporary wetlands.

For all lakes, the number of species encountered decreased after the first wetting cycle, indicating that the seed reserves of some species were either very low and/or that all seeds present germinated in response to a single wetting. Of the 58 species recorded, 21 species utilised this 'transient' strategy, which is possibly an adaptation to more permanent environments where subsequent recruitment conditions are likely to remain favourable. All other species were 'persistent', in that only a portion of their viable seed reserves germinated after each cycle of wetting. This process continued until seed reserves became depleted after the third wetting cycle, although 12 taxa were still present after the 5 wetting cycles used in this study. In a similar study, Leck and Brock (2000) found that the seed bank had become depleted but not exhausted after eight wetting cycles. 'Persistence' is a likely beneficial adaptation to ephemeral systems, in which favourable post-germination conditions are not ensured. This strategy enables species to 'hedge their bets' and increase their ability to persist. Leck and Brock (2000) demonstrated that all the species from temporary and semi-permanent wetlands on the New South Wales northern tablelands bet hedged (no reduction in the number of species was recorded between the first and second wetting events). They also reported that the seeds of many species remained viable for at least nine years in dry storage.

Long-lived species tend not to form a persistent seed bank because they produce seeds more than once throughout their life cycle that will ensure survival of the species if the system is prone to false starts (Roberts 1981, Leck and Brock 2000). Indeed, this was the case for black box (*E. largiflorens*). No red gum (*E. camaldulensis*) seeds were recorded in the seed banks of any of the lakes examined.

A further adaptive response to the unpredictability of ephemeral environments is the ability to germinate and set seed rapidly. For most species, on average, over 50% of the germination occurred in the first two weeks after the initial watering with more than 90% of the germination occurring in the first six weeks (J. Nicol unpublished data). *Iseotopsis graminifolia* has been observed in the field to flower and set seed in less than four weeks (J. Nicol pers. obs.) and if the seed can survive in dry sediment for extended periods there is no need to bet hedge.

Yet another means of persistence is the ability to reproduce asexually. For example, *Lemna* sp. produces new plants by budding (Johansson and Nilsson 1993), *Juncus aridicola* by rhizomes and *Ludwigia peploides* produces roots at nodes that can produce new plants by fragmentation (Cunningham 1981). Species that form rhizomes or other belowground perennating structures are able to survive periods of desiccation by allocating more resources to the below ground organs (Rea 1994). Plants that produce asexual reproductive structures such as rhizomes have an advantage over those species that are totally reliant on seeds, because asexual offspring are generally more developed, larger and able to utilize resources more efficiently than sexual offspring (Grace 1993). Asexual reproduction is not limited to 'transient' species. *Azolla* sp., *Cyperus gymnocaulos*, *Heliotropium curassivicum*, *Limosella australis*, *Myriophyllum verrucosum* and *Sporobolus mitchelli* all have asexual modes of reproduction (Cunningham 1981).

Summary

Wetland sediment seed banks play a key role in the persistence of plant species through unfavourable periods, such as inundation for terrestrial species and lake drying for aquatic species. Hydrology has been implicated as an important structuring agent of seed banks and plant communities within wetland systems through its ability to influence the exchange of seeds between wetland components, its ability to influence the distribution of seeds within a wetland, and its ability to influence the recruitment success of germinants. We examined the distribution, size and composition of seed banks present within the Menindee Lakes and their relation to hydrology.

A total of 58 plant species were identified from the seedbanks of the Menindee Lakes. The seed bank of Lake Malta was much larger (70,000-80,000 seeds m⁻²), more diverse (32 species), and more evenly distributed throughout the elevation range than that recorded in the relatively much larger lakes Tandure, Menindee and Cawndilla. Seedbanks within the larger lakes had a combined species richness of 27 species, and 90 % of the seeds were concentrated within a distinct and narrow strandline that generally contained less than 10,000 seeds m⁻². Seed banks contained species that were either 'transient' (*i.e.* all viable seeds germinated after a single wetting) or 'persistent' (*i.e.* only a portion of the viable seeds germinated after a single wetting). Persistence is thought to be a favourable adaptation to ephemeral systems in which favourable post-germination conditions are not ensured. More 'persistent' species were present in Lake Malta, which experiences a more variable hydraulic regime, than were present in the relatively more permanent larger lakes.

The differences in seedbank density and species richness observed between lakes were consistent with previously described hydraulic structuring processes, and suggest that lake shape and connectivity play an important role in structuring wetland vegetation. Whilst these latter aspects have been shown to influence zooplankton (Dodson 1992, Dodson *et al.* 2000), mollusc (Browne 1981), and fish assemblages (Barbour and Browne 1974, Browne 1981, Hershey *et al.* 1999) (*sensu* the Geomorphic Trophic Model, refer to Section 4), similar responses to the vegetation have not previously been reported.

In the larger lakes, greater wave energy and steeper littoral gradients are likely to have influenced the distribution of seeds within distinct strandlines, and to have negatively impacted on the establishment and growth of lakeshore plants, reducing the potential for plant regeneration to a narrow littoral zone, and local recruitment to the seedbank. Further, regulation has decreased the connectivity of these lakes with other elements of the fluvial system thereby reducing the potential for external seed contributions, especially during flood pulses when seed loads are likely to be highest.

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3.2 Effects of drying duration on post inundation responses

O. Scholz and B. Gawne

Abstract

Flow regulation can modify key aspects of the natural hydrological regime in ephemeral deflation basin lakes (EDBL), including the duration of the dry phase. We examined water quality and biotic responses for one month after re-flooding in constructed ponds (25000 l capacity) that had been allowed to dry for either 3½ or 6½ months. More terrestrial vegetation was present prior to inundation on pondbeds that had been dry for longer. Although no significant post-inundation nutrient pulse or treatment effects on nutrients were observed, more algae developed in ponds that had been drier for longer. Large sample variances reduced our ability to discern treatment or time effects for zooplankton abundances. However, ponds that had been drier longer supported a greater diversity of zooplankton. This difference was due primarily to increases in the number of rotifer taxa. These data suggest that reductions in the duration of lake drying events of EDBL may compromise aquatic primary production, and biotic diversity through its impact on habitat structure. These data also highlight the important link between terrestrial and aquatic phases in EDBL and the need to better understand the potential for dry lakebed management.

Introduction

Ephemeral deflation basin lakes (EDBL) are widespread throughout the arid and semi-arid regions of the Murray-Darling Basin in Australia (Seddon *et al.* 1997, Seddon and Briggs 1998). These lowland river floodplain environments naturally fluctuate between terrestrial and aquatic states. Transitions between these states are thought to drive both aquatic and terrestrial successional processes and facilitate biotic and abiotic exchanges between elements of the floodplain and the riverine environment (*cf.* Flood Pulse Concept; Junk *et al.* 1989).

The flooding of dry lakes is also thought to stimulate the release of potentially significant amounts of nutrients and organic matter from the sediments (McComb and Qiu 1998, Baldwin and Mitchell 2000, Scholz *et al.* 2002) and the emergence of micro-invertebrates from eggs and cysts deposited in the sediments during previous periods of inundation (*e.g.* Boulton and Lloyd 1992, Boulton and Jenkins 1998, Nielsen *et al.* 2000). As lakes dry, terrestrial plants often rapidly colonize their beds. Whilst such vegetation provides important habitat for terrestrial fauna when lakes are dry (*e.g.* Briggs 1996, Briggs *et al.* 2000), it also provides habitat structure for a range of algae, micro- and macroinvertebrates and suitable spawning habitat for native fish (Geddes and Puckridge 1989, Lloyd *et al.* 1989, Gehrke 1990) and provides an additional source of organic matter and nutrients as it decomposes (Furch and Junk 1997) following inundation. Because of these responses to drying and re-flooding, post-flood EDBL are potentially sites of high productivity and diversity within arid floodplain ecosystems.

The duration of lake drying events has the potential to modify post flood aquatic ecosystem responses by influencing the abundance and composition lakebed vegetation, the mineralization and subsequent exchanges of nutrients between the sediments and water column (Baldwin and Mitchell 2000), and the viability of sediment egg and cyst reserves (Moritz 1987, Boulton and Lloyd 1992, Hairston *et al.* 1995, Jenkins and Briggs 1997).

For many EDBL, flow regulation has increased the permanency of stored water and reduced the frequency and duration of complete lake drying episodes (*e.g.* Menindee Lakes System;

Section 1 Table 1.3). Whilst guidelines exist for reinstating drying events (*e.g.* Briggs 1998), no empirical data is available to suggest how differences in the duration of lake dryness might impact on the ecological function of EDBL. In this study we examined how the duration of lake drying through its control of the extent of terrestrial plant growth may affect post-flood water quality, nutrient availability, plankton abundance and biodiversity in arid-zone EDBL. We hypothesised that submerged terrestrial vegetation constitutes both an important source of organic matter as it decomposes and modifier of aquatic habitat structure, and that these would stimulate aquatic productivity and diversity. This has implications not only for hydraulic management but also for the management of lakebed vegetation, which may be compromised by activities such as grazing.

Methods

Six ponds measuring approximately 6.5 m x 6.0 m and 1 m deep (volume 25,000 l) were constructed on the lakebed of Lake Tandou, an arid-zone ephemeral deflation basin lake associated with the Darling River in southwest New South Wales. Ponds were filled to capacity during February 2001 with unfiltered river water. After 2 months when water levels had declined to half capacity, 3 ponds were randomly selected and drained. The remaining three ponds were left a further 3 months to dry completely.

Each of the experimental ponds was re-filled in November 2001, 3½ and 6½ months after having dried, with unfiltered river water. Ponds were monitored for one month (days 0, 1, 3, 5, 7, 14 and 28) after filling. On each sampling event, water column electrical conductivity standardised to 25°C (EC; $\mu\text{S cm}^{-1}$), pH and dissolved oxygen (DO, mg O l^{-1}) were recorded using a U-10 multi-probe (HORIBA Ltd., Australia). All sampling occurred between 11 am and 1 pm to minimise potential diel effects.

Concentrations of suspended particulate matter were determined by passing 500 ml of pond water through ashed (at 550 °C) and weighed filters (Whatman Pty. Ltd. GF/C). Reweighing these after drying at 105 °C and re-ashing enabled the calculation of total suspended particulate dry weight (mg DW l^{-1}) and of the organic matter component (mg POM l^{-1}). From each pond on each sampling event 200 ml of unfiltered water was stored frozen for total nitrogen (TN, mg N l^{-1}) and total phosphorus (TP, mg P l^{-1}) determinations. Three replicate 10ml aliquots of 0.45 μm filtered water were stored frozen for determinations of labile nitrogen (oxides of nitrogen: NO_x , mg N l^{-1}) and labile phosphorus (filterable reactive phosphorus: FRP, mg P l^{-1}). NO_x was determined colorimetrically after its reduction to nitrite using a cadmium column (APHA 1995). TN was determined as for NO_x after its pre-digestion in NaOH- $\text{K}_2\text{S}_2\text{O}_8$ and oxidation to nitrate. FRP was determined colorimetrically using the phosphomolybdate-blue method (APHA 1995). TP samples were determined as for FRP after pre-digestion in NaOH- $\text{K}_2\text{S}_2\text{O}_8$ and oxidation to orthophosphate. Detection limits were $\text{TN} \pm 0.019 \text{ mg N l}^{-1}$ and $\text{TP} \pm 0.0025 \text{ mg P l}^{-1}$.

Phytoplankton biomass was measured as chlorophyll *a* ($\mu\text{g CHL l}^{-1}$). Chlorophyll *a* determinations involved filtering (Whatman Pty. Ltd. GF/C) 500 ml of water, extracting CHL*a* from the filtrates in hot ethanol (80 °C 5 minutes), and measuring the extracted CHL*a* at 665 nm and 750 nm without acidification (APHA 1995). Zooplankton was sampled by straining 75 l of pond water through 50 μm mesh size plankton nets. Filtered samples were preserved with Lugol's iodine solution. At least 250 individuals were counted from at least 3 Sedgewick-Rafter Cell preparations per sample. Identifications followed Shiel (1995) and Ingram *et al.* (1997). Though counted separately, calanoid adults and nauplii were pooled prior to statistical analysis.

Data are presented as means \pm standard errors unless stated otherwise. Repeated measures ANOVA (RMA), one-way ANOVA and Pearson correlations with Bonferroni *post hoc* adjustment were calculated using SYSTAT® V10.2 (SPSS Inc., Chicago USA). RMA probabilities are presented as *p* and G-G adjusted *p* values. Similarities in zooplankton community structure (composition and abundance) between treatments and times were examined using the SIMPER module in PRIMER (V5; Primer-E Ltd., 2000). Data for these analyses were 4th-root transformed to downweigh the influence of individual taxa and to increase analytical robustness to zero values before calculating the Bray-Curtis similarity matrices. Statistical significance of time/treatment groups was not determined, as the number of replicates (n=3) was too low to achieve significance below the 10 % level (Clarke and Warwick 1994).

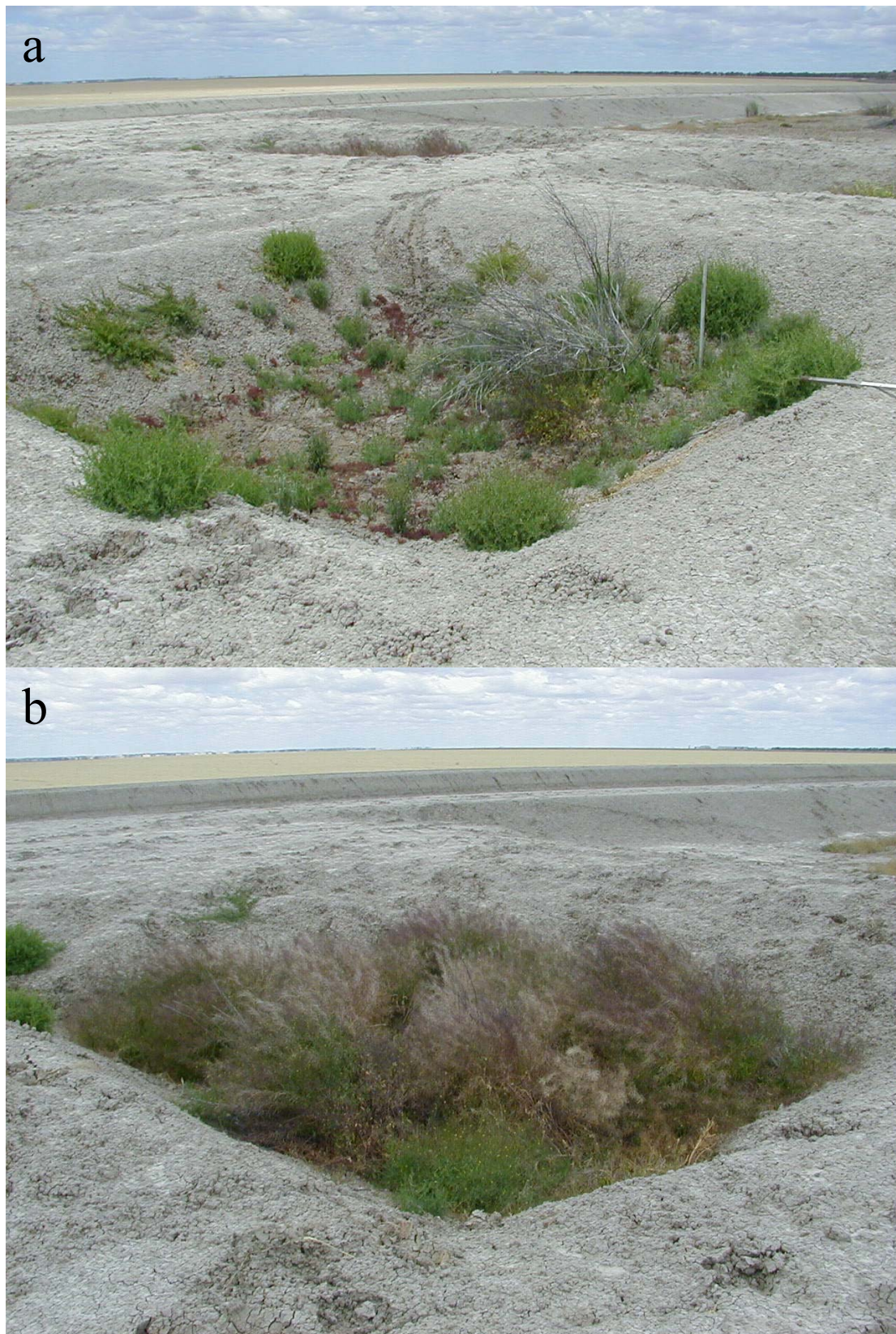
Results

Prior to experimental re-flooding terrestrial vegetation had become established in each of the dry ponds. More vegetation was present and maximum canopy height was greater in ponds that had been dry for 6½ months (62 \pm 7 % area coverage, max. canopy height 1.5 m) than in the ponds that had been dry for 3½ months (20 \pm 3% area coverage, max. canopy height 0.4 m) (Figure 3.2.1). Dominant plant species included prickly saltwort (*Salsola kali*), common sneezeweed (*Centipeda cunninghamii*) and spreading nut-heads (*Epalties australis*).

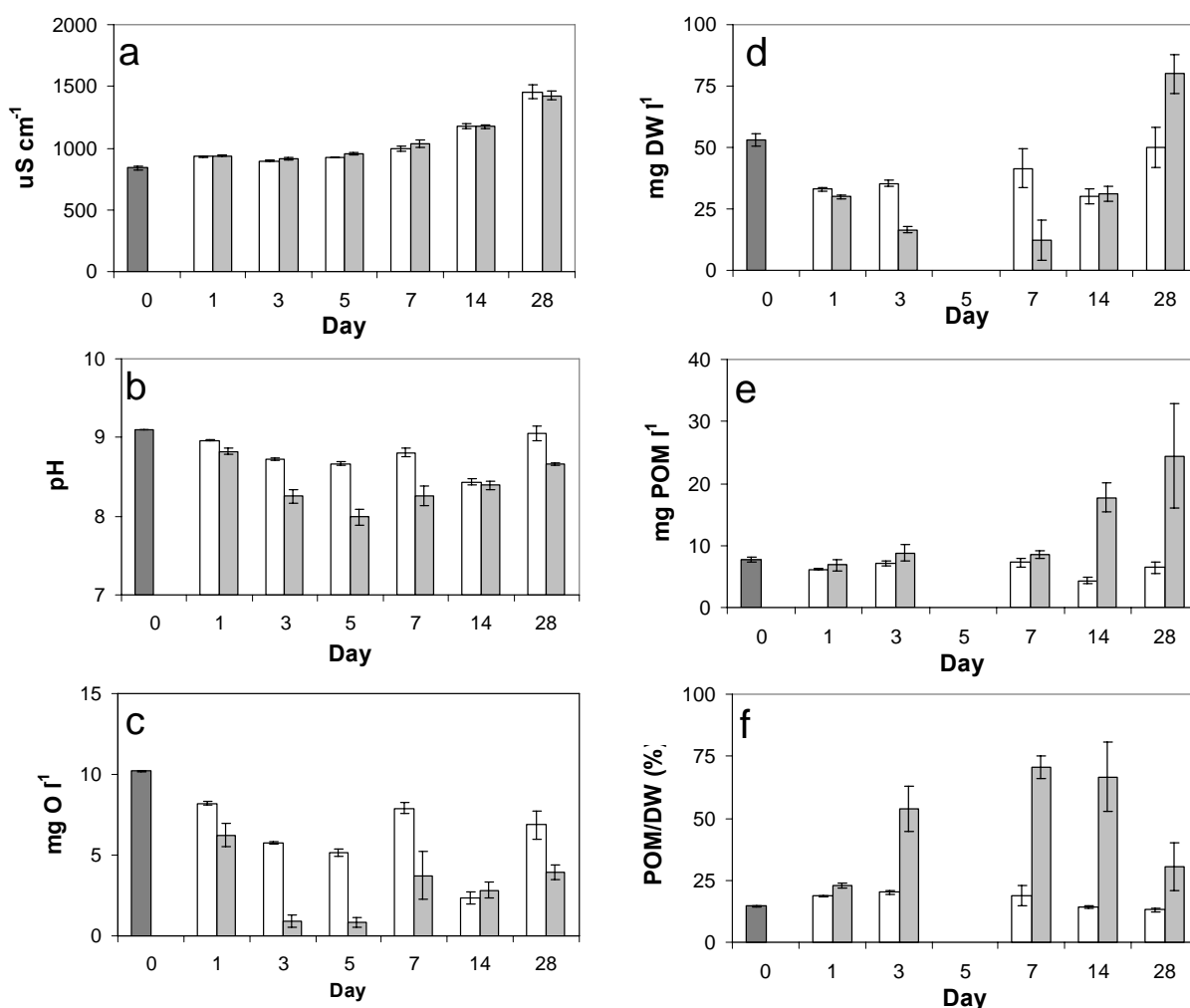
After experimental re-flooding, water-colour within ponds that had been dry for longer turned dark brown, possibly due to the leaching of tannins, phenolics and dissolved organic carbon from the inundated vegetation. No similar response was observed in ponds that had been dry for a shorter period. These treatment differences gradually disappeared over the study period (O. Scholz pers. obs.).

Pond volumes declined by 59-73 % over the 28-day study period due to both evaporation and seepage. Over the same period, electrical conductivity (EC) increased by 58 % from 839 \pm 12 μ S cm⁻¹ to 1439 \pm 31 μ S cm⁻¹ (Figure 3.2.2a). These increases over time were significant (RMA: G-G<0.001, n=42) and did not differ between treatments (RMA: *p*=0.670, n=42). Measured pH and dissolved oxygen (DO) ranged from 7.8-9.2 and 0.15-10.25 mg O l⁻¹, respectively (Figures 3.2.2b,c). Treatments responded differently over time for both pH and DO (RMA: G-G_{pH}<0.01, n=42 and G-G_{DO}<0.05, n=42). Daily comparisons indicated that pH and DO were significantly lower during the first week in ponds that had been drier longer (ANOVA: *p*_{pH}<0.015, n=6 for days 1-7, and *p*_{DO}<0.001, n=6 for days 3-7).

The dry weight (DW) of suspended particulate matter within the ponds ranged from 9.8-123.3 mg DW l⁻¹ over the study period (Figure 3.2.2d). DW changed significantly over time (RMA: G-G<0.05, n=36). Although there was no treatment effect over the entire study period (RMA: *p*=0.459, n=36), significantly less suspended particulate matter was present on days 3 and 7 in ponds that had been dry longest (ANOVA: *p*<0.05 and n=6 for each day). Suspended particulate organic matter (POM) loads ranged from 3.8-35.8 mg POM l⁻¹ (Figure 3.2.2e). POM concentrations did not vary significantly over time (RMA: G-G<0.155, n=36). However, treatment effects were significant (RMA: *p*<0.01, n=36), with more POM present after day 14 in ponds that had been drier for longer (ANOVA: *p*<0.01, n=6 for each day). POM constituted between 12.4-89.7 % of total suspended particulate loads (Figure 3.2.2f). Temporal trends in the POM:DW ratio differed between treatments (RMA: G-G<0.01, n=36). POM:DW ratios were greater in ponds that had been dry longer.

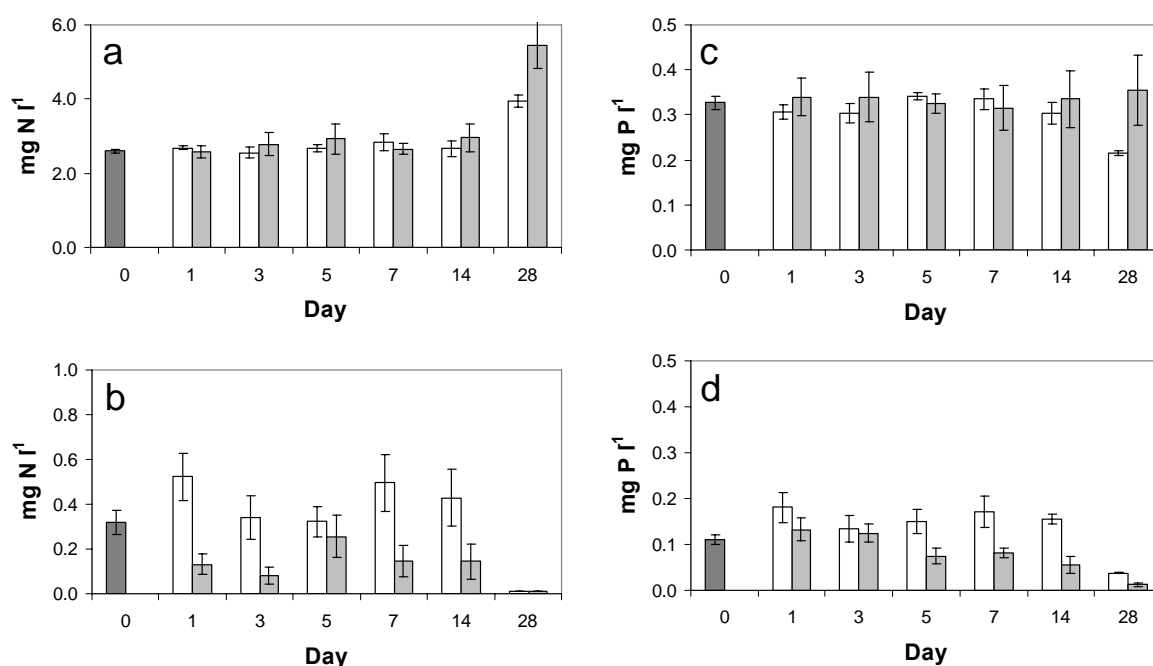


■ Figure 3.2.1: Experimental ponds showing differences in terrestrial vegetation present in ponds that had been dry for 3½ months (a) and 6½ months (b). Photographed shortly before flooding. Photos by O. Scholz.



■ **Figure 3.2.2: a) Electrical conductivity ($\mu\text{S cm}^{-1}$), b) pH, c) dissolved oxygen (mg O l^{-1}), d) suspended dry weight (mg DW l^{-1}), e) suspended particulate organic matter (mg POM l^{-1}), and f) percentage contribution of organic matter to total suspended loads plotted over time after re-flooding of ponds that had been dry for 3½ months (\circ) and 6½ months (\bullet)(mean \pm se, $n=3$). Day 0 common to both treatments.**

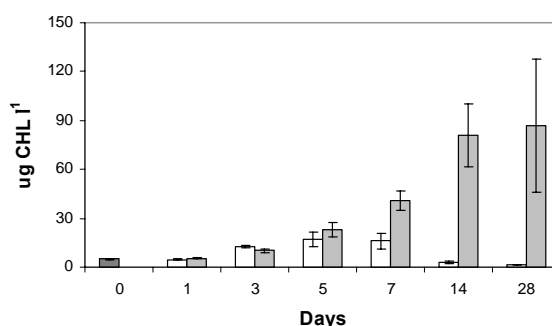
Total nitrogen (TN) concentrations ranged from 2.26-6.54 mg N l^{-1} (Figure 3.2.3a). Total phosphorus (TP) concentrations ranged from 0.20-0.46 mg P l^{-1} (Figure 3.2.3c). Treatment effects were not significant for either TN (RMA: $p=0.130$, $n=42$) or TP (RMA: $p=0.458$, $n=42$). In contrast to TP concentrations, which did not vary through time (RMA: $G-G=0.621$, $n=42$), TN concentrations increased significantly (RMA: $G-G<0.01$, $n=42$). This elevated TN:TP ratios, which ranged from 7.9-9.0 (days 0-14) to 15.4-18.4 (day 28). NO_x concentrations ranged from 0.006-1.035 mg N l^{-1} (Figure 3.2.3b). FRP concentrations ranged from 0.004-0.335 mg P l^{-1} (Figure 3.2.3d). Treatment effects were not significant for either NO_x (RMA: $p=0.239$, $n=42$) or FRP (RMA: $p=0.244$, $n=42$), and NO_x or FRP concentrations did not change significantly over time (RMA: $G-G_{\text{NO}_x}=0.163$, $n=21$ and $G-G_{\text{FRP}}=0.056$, $n=21$). With time after re-flooding, NO_x and FRP constituted a decreasing fraction of the TN and TP pools. NO_x :TN ratios fell from 12.3 % at day 0 to <0.3 % at day 28 and FRP:TP ratios fell from 33.8 % to <17.3 % by day 28. NO_x :FRP ratios also declined during the study, falling from 2.9 to <0.8 by day 28.



■ **Figure 3.2.3: a) Total suspended nitrogen (mg N l⁻¹), b) labile nitrogen (NO_x) (mg N l⁻¹), c) total suspended phosphorus (mg P l⁻¹), and d) labile phosphorus (FRP) (mg P l⁻¹) concentrations plotted over time after re-flooding of ponds that had been dry for 3½ months (○) and 6½ months (●) (mean ± se, n=3). Day 0 common to both treatments.**

Chlorophyll *a* concentrations ranged from 1.51-146 µg CHL l⁻¹. Ponds were filled with water containing 4.9±0.2 µg CHL l⁻¹. Treatment effects were not significant prior to day 7 (RMA: $p=0.552$, $n=24$). Whereas CHL_a peaked at only 17.1±4.3 µg CHL l⁻¹ after 5 days in ponds that had been dry for 3½ months, CHL_a continued to increase throughout the study period in ponds that had been dry for 6½ months, peaking at 86.9±41.1µg CHL l⁻¹ on Day 28 (Figure 3.2.4).

CHL_a was significantly positively correlated with POM in both short (Pearson $r=0.595$, $p<0.05$, $n=15$) and long (Pearson $r=0.545$, $p<0.05$, $n=15$) dry treatments, suggesting that phytoplankton constituted much of the suspended POM. Though not quantified, thick epiphytic algal loads developed on the submerged vegetation. Epiphytic algae appeared more abundant in ponds with more submerged vegetation.

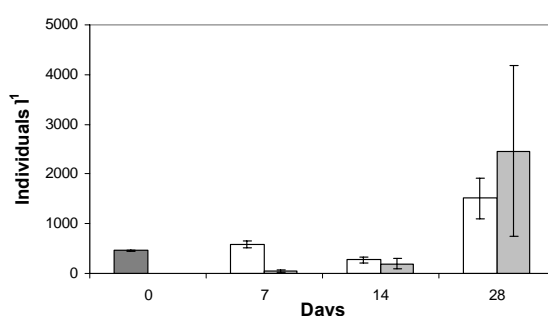


■ **Figure 3.2.4: Phytoplankton biomass measured as chlorophyll *a* (µg CHL l⁻¹) plotted over time after re-flooding of ponds that had been dry for 3½ months (○) and 6½ months (●) (mean ± se, n=3). Day 0 common to both treatments.**

Sixteen micro-invertebrate species were identified in samples collected from the experimental ponds during the 28-day post-flood period. These included 11 rotifer and 5 crustacean taxa (Table 3.2.1). Four crustacean taxa (excluding copepod nauplii) and no rotifer taxa were present at day 0. After 28 days a total of 9 taxa had been recorded from ponds that had been dry for 3½ and 15 taxa from those that had been dry for 6½ months. Rotifers accounted for almost all increases in diversity in both treatments.

Zooplankton densities ranged from 5–5890 individuals l⁻¹ during the study period (Figure 3.2.5). Due to large replicate variances, overall treatment and time effects were not significant (RMA: $p=0.862$, $n=24$ and G-G=0.136, $n=24$, respectively). However, total zooplankton densities did decrease significantly between days 0 and 7 in the 6½ month dry treatment (ANOVA: $p=0.000$, $n=6$), but not in the 3½-month dry treatment (ANOVA: $p=0.133$, $n=6$). This strong treatment effect followed a period of greatly reduced DO concentrations in the 6½-month dry treatment.

Calanoid copepods and their nauplii generally dominated zooplankton communities (Table 3.2.1). Similarities in zooplankton community structure between treatments declined progressively over time (SIMPER: day 7=72.2 %, day 14=59.4 %, day 28=47.6 %), reflecting the increased appearance of rotifer taxa in the 6½-month dry treatment relative to the 3½-month dry treatment. Zooplankton community structure varied less between replicates within times for the 3½-month treatment (SIMPER: day 7=84.1 %, day 14=85.4 % and day 28=79.0 %) than it did for the 6½-month treatment (SIMPER: day 7=39.8 %, day 14=22.9 % and day 28=47.0 %), and likely reflects the greater variation in habitat structure present within the ponds that had been dry for longer (O. Scholz pers. obs.).



■ Figure 3.2.5: Total zooplankton abundances (individuals l⁻¹) plotted over time after re-flooding of ponds that had been dry for 3½ months (○) and 6½ months (●) (mean ± se, $n=3$). Day 0 common to both treatments.

TAXA	Day 0	Day 7		Day 14		Day 28	
	3 ½ and 6 ½	3 ½	6 ½	3 ½	6 ½	3 ½	6 ½
Rotifers							
<i>Asplanchna</i> sp.	-	-	-	-	-	-	<0.1
<i>Brachionus calyciflorus</i>	-	-	-	-	26.0	-	-
<i>B. calyciflorus gigantea</i>	-	0.4	0.9	-	-	<0.1	1.4
<i>B. leydigi</i>	-	-	-	-	-	-	0.1
<i>B. novaezelandia</i>	-	1.2	7.9	2.4	1.6	-	2.8
<i>B. quadridentatus</i>	-	-	-	-	0.7	-	0.1
<i>B. urceolaris</i>	-	-	-	-	5.6	-	-
<i>Lecane</i> sp.	-	-	0.4	-	-	-	<0.1
<i>Proales</i> sp.	-	-	-	0.2	-	-	-
<i>Polyarthra</i> sp.	-	-	-	-	-	0.9	26.8
<i>Trichocerca</i> sp.	-	-	20.2	-	-	-	-
Crustaceans							
<i>Calanoida</i> sp. nauplii	47.2	66.3	47.6	2.5	59.4	96.5	53.9
<i>Calanoida</i> sp.	49.4	22.2	13.4	58.1	5.3	2.0	1.4
<i>Cyclopoida</i> sp.	-	0.2	7.0	-	-	0.1	1.1
<i>Daphnia carinata</i>	0.7	1.2	0.3	22.1	0.4	0.6	11.6
<i>Moina</i> sp.	2.0	8.5	2.5	14.7	1.0	-	0.6
<i>Ostracoda</i> sp.	0.7	-	-	-	-	-	-
Total abundance (individuals l⁻¹)	456 ± 10.4	588 ± 69.0	45.8 ± 25.7	275 ± 55.2	192 ± 109	1508 ± 414	2457 ± 1717

■ **Table 3.2.1: Total abundances (individuals l⁻¹) and relative abundances (%) of rotifer and crustacean taxa recorded 0, 7, 14, and 28 days after re-flooding in ponds that had been dry for 3½ and 6½ months (mean ± se, n=3).**

Discussion

A growing body of evidence suggests that water resource development on arid-zone ephemeral deflation basin lakes (EDBL) has had detrimental impacts on system productivity and diversity (Boulton and Lloyd 1992, Bunn *et al.* 1997, Boulton and Jenkins 1998, Kingsford 2000). For many EDBL, such as the Menindee Lakes, where flow regulation has increased the permanency of stored water and reduced the frequency and duration of complete lake drying episodes, there is little information to suggest how differences in the duration of lake dryness might impact on the post-flood ecological function of EDBL.

After re-flooding, the colour of the water within experimental ponds differed noticeably between treatments. Water in ponds that had been dry for longer turned dark brown. This was likely due to the leaching of tannins, phenolics and dissolved organic carbon from the submerged vegetation (*e.g.* Putz 1997, Entry 2000). No similar response was observed in ponds that had been dry for a shorter period. The significant reductions in pH and DO observed during the first week after re-flooding in the 6½ month dry treatment relative to the 3½ month dry treatment are consistent with elevated aerobic microbial activity associated with the decomposition of the greater organic loads (*i.e.* submerged vegetation) present. The

presence of submerged vegetation also facilitated the sedimentation of particles (DW), mostly the inorganic fraction, by reducing water column turbulence.

Increases in aquatic productivity are commonly witnessed upon the flooding of dry wetlands (Crome and Carpenter 1988, Briggs and Maher 1985, Boulton and Lloyd 1992, Jenkins and Boulton 1998). Sediment drying promotes the release of potentially significant amounts of bio-available N and P on re-wetting. The magnitude of such responses is influenced in part by duration of sediment exposure (reviewed by McComb and Qiu 1998, Baldwin and Mitchell 2000). Lake drying also permits the establishment of terrestrial vegetation. Such vegetation has the capacity to mobilise nutrients from deeper sediment layers that would otherwise remain inaccessible and make them available through decomposition when inundated. Longer periods of lake drying may thus increase the potential for sediment nutrient transformations and terrestrial vegetation establishment, thereby increasing production potential and habitat structure during both dry and wet phases. The establishment of terrestrial lakebed vegetation is likely to be especially important in turbid EDBL where macrophyte development is generally absent and habitat structure/diversity is limited to a narrow riparian margin (*e.g.* Taylor-Wood *et al.* 2002).

Contrary to expectations, post-flood nutrient concentrations did not differ between experimental treatments and there was no significant initial nutrient pulse. TN:TP ratios increased and NO_x:TN, FRP:TP and NO_x:FRP ratios decreased progressively after flooding, irrespective of treatment. Similar post-inundation responses of nutrient ratios have been observed at the lake scale (Scholz *et al.* 2001, Scholz *et al.* 2002). These decreases are indicative of increasingly tighter couplings between nutrient synthesis and biotic and abiotic uptake processes and of a higher biotic demand for nitrogen than phosphorus (*e.g.* Rhee and Gotham 1980). Although nutrient responses did not differ between treatments, phytoplankton biomass increased in ponds that had been dry for longer, and extensive epiphyte loads developed on submerged vegetation. Whilst we did not estimate benthic algal loads or total aquatic primary production, this finding lends support to the hypothesis that increases in drying duration stimulates aquatic production.

Zooplankton assemblages present initially within the floodwaters contained only crustacea, predominantly *Calanoida* sp. and their nauplii. Increases in assemblage diversity over time were recorded in both treatments. These increases were driven primarily by the emergence of rotifers from the sediments (*e.g.* Boulton and Lloyd 1992, Boulton and Jenkins 1998, Nielsen *et al.* 2000), rather than by slower aerial invasion (*e.g.* Boulton and Suter 1986). More than twice as many rotifer taxa were encountered in ponds that had been dry for longer. As treatments were randomly assigned to the newly constructed ponds on the dry bed of Lake Tandou, differences in sediment egg banks between treatments were likely to have been negligible. This treatment effect we attributed to the presence of greater habitat structure provided by the submerged plants. Similar diversity-habitat relationships have been described for a variety of organisms across a range of aquatic environments (*e.g.* Menge and Sutherland 1976, Richlefs 1987, Arscott *et al.* 2000, Burks *et al.* 2001).

Large replicate variances reduced our ability to detect statistically significant treatment or time effects for zooplankton abundance. However, multivariate analyses did show that zooplankton community structure varied less between replicates within times for the 3½ month treatment than it did for the 6½ month treatment. This is a likely reflection of the differences in habitat heterogeneity between treatments, and supports the significance attributed to habitat structure on structuring zooplankton assemblages.

This study suggests that reductions in the duration of lake drying events, as has occurred in the Menindee Lakes, may compromise aquatic autotrophic productivity and, through its impact on habitat structure, zooplankton diversity. Whilst reimposing drying episodes is generally to be recommended, longer drying periods increase the opportunity dry lakebed

cropping and grazing. These activities occur in many EDBL within the Murray-Darling Basin, including the lakes Malta, Balaka and Bijiji (Briggs and Jenkins 1997, Seddon and Briggs 1998). Our data highlights the important link between terrestrial and aquatic phases in EDBL. At present, information regarding the potential impacts of lakebed cropping and grazing on EDBL ecosystem processes remains scarce (*e.g.* Briggs and Jenkins 1997, Robertson 1998).

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3.3 Effects of lakebed vegetation and grazing on post-inundation responses

O. Scholz and B. Gawne

Abstract

The presence of terrestrial lakebed vegetation was thought to stimulate post-inundation aquatic productivity and diversity by providing organic material and important habitat structure. The presence and structure of lakebed vegetation may be influenced by both the duration of the dry phase and by grazing. We examined post-inundation responses of nutrients, algae and zooplankton in mesocosms assigned to one of three treatments: no-vegetation, grazed and un-grazed. Post-inundation responses did not differ between treatments for nitrogen, phosphorus and dissolved organic carbon concentrations, or for algal biomass. Emergence of zooplankton from the sediments contributed greatly to initial mesocosm diversity and did not differ between treatments. Most rotifers appeared with one week and crustacea within two weeks. Increases in predator numbers were similar between treatments, and reduced prey abundances uniformly across treatments. However, the presence of habitat structure reduced the rate of species lost to predation. Whilst these data suggest that the presence of lakebed vegetation or grazing has little impact on aquatic production, inundated vegetation provides habitat structure necessary for the maintenance of micro-invertebrate diversity.

Introduction

Ephemeral deflation basin lakes (EDBL) are widespread throughout the arid and semi-arid regions of the Murray-Darling Basin in Australia (Seddon *et al.* 1997, Seddon and Briggs 1998). These lowland river floodplain environments naturally fluctuate between terrestrial and aquatic states. Transitions between these states are thought to drive both aquatic and terrestrial successional processes and to facilitate biotic and abiotic exchanges between elements of the floodplain and the riverine environment (*cf.* Flood Pulse Concept; Junk *et al.* 1989). Modification of the wet/dry regime through hydraulic regulation thus has the potential to disrupt many of these processes and exchanges, and has been identified as a key threat to ecosystem productivity and diversity (Boulton and Lloyd 1992, Bunn *et al.* 1997, Boulton and Jenkins 1998, Kingsford 2000).

In naturally ephemeral wetlands, such as the Menindee Lakes, flow-regulation has increased the permanency of inundation and reduced the duration and frequency of drying events (Section 1 Table 1.3). The loss of complete or partial drying may lead to a reduction in rates of nutrient cycling and thus of productivity (Baldwin and Mitchell 2000), and modify both aquatic and terrestrial plant community structure (Roberts and Marston 2000). Taylor-Wood *et al.* (2002) has shown for the Menindee Lakes that regulation has adversely impacted on fringing terrestrial vegetation able to tolerate only shorter periods of inundation than is currently the case. Regulation has also reduced the time available for the establishment of dry lakebed vegetation. When inundated, terrestrial lakebed vegetation represents a potentially significant source of organic-matter and nutrients as it decomposes (Furch and Junk 1997), provides habitat structure for a range of algae, micro- and macro-invertebrates, and spawning habitat for native fish (Geddes and Puckridge 1989, Lloyd *et al.* 1989, Gehrke 1990), and is thus likely to influence biodiversity (Beck 2000, Taniguchi *et al.* 2003). Such habitat is likely to be crucial in EDBL where aquatic habitat diversity is characteristically very low (Taylor-Wood *et al.* 2002).

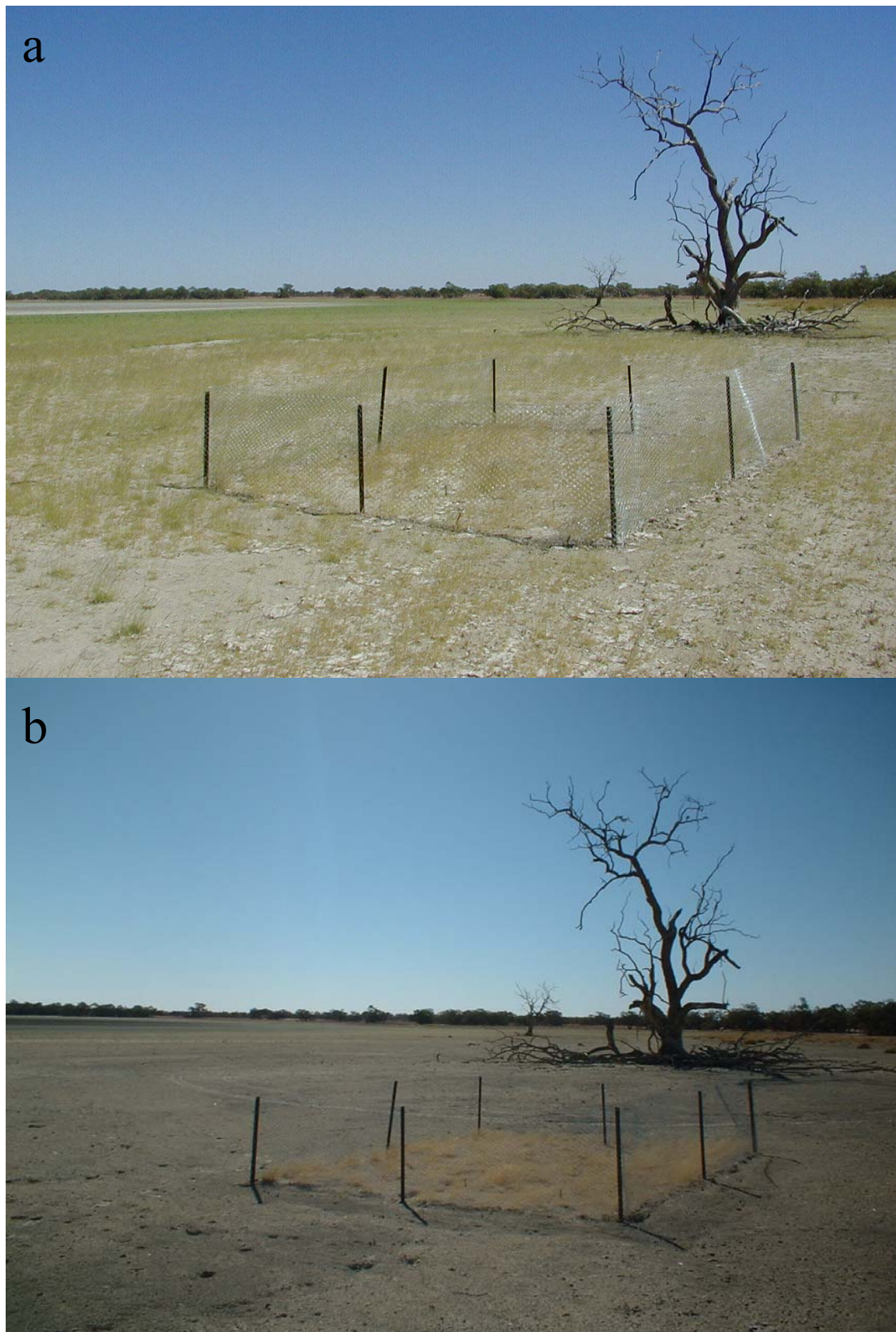
Grazing of lakebed vegetation has the potential to modify plant community structure either directly by selective grazing and trampling (Wahren *et al.* 1999, Jansen and Robertson 2001, Jutila 2001), or indirectly by altering the composition of the soil seed bank (Jutila 1998, Bertiller 1992, O'Connor and Pickett 1992). Whilst grazing has been identified as another potentially significant threat to wetland processes (Bunn *et al.* 1997, Robertson 1998), its impacts on wetland function are likely to differ between wetland types. For example, in non-ephemeral wetlands where there is direct access by stock to open water and where aquatic littoral vegetation provides a food resource, selective grazing, damage to banks and contamination of wetland waters (*e.g.* increased turbidity, faecal deposition) have all been linked to altered wetland function (Robertson 1998). However, for EDBL direct access to open water is often physically restricted by expanses of mud, and macrophytes are largely absent. In these systems grazing impacts are focused on the dry lakebed. These impacts include the reduction of vegetation standing crop, which can be significant (*e.g.* Figure 3.3.1), and the modification of nutrient cycles through the conversion of plant biomass to locally deposited manure and exported animal biomass. At present no study has specifically examined the role of dry lakebed grazing in directing post-flood aquatic processes in EDBL. Given that land use within the semi/arid region of the Murray-Darling Basin is primarily pastoral and many EDBL are subject to grazing, including the Menindee Lakes, this issue warrants attention.

This study examines two hypotheses. Firstly, that the presence of vegetation increases post-flood aquatic productivity, and that grazing reduces potential post-flood production through the removal of nutrients that would otherwise be released as plants decompose. And secondly, that grazing eliminates much of the potential post-inundation habitat structure and niche diversity, resulting in a more simplified trophic structure.

Methods

Twelve 500 l mesocosms (1.0 m diameter x 0.5 m deep) were each filled with 0.1 m (*ca.* 100 l) of surface sediment (top 5 cm) collected from the dry bed of Lake Malta. Mesocosms were randomly assigned to one of three experimental treatments: no-vegetation, grazed and un-grazed. Grazed and un-grazed treatments were sown with 100 g of rye grass seeds (*Lolium perenne*). No-vegetation treatments were not sown. All mesocosms received 2 l of RO (reverse osmosis) filtered water every 2 days. This was sufficient to facilitate grass growth but not enough to waterlog the sediments. Grass was grown to a length of approximately 15 cm over 2 months. To simulate grazing, all grass present in grazed mesocosms was harvested, leaving a short stubble (<0.5 mm), and replaced with dry sheep/kangaroo manure collected from Lake Malta. Harvested grass biomass ranged from 46.3-100.8 g (mean 70.4±11.3 g) dry weight per mesocosm. This equated to 40 g of dry intact faeces, assuming a dry matter digestibility of 60 % (pers. com. R. Inglis, NSW Agriculture).

Mesocosms were filled during February 2002 with freshly collected unfiltered Darling River water, and were monitored for one month (days 0, 1, 3, 5, 7, 14 and 28) after filling. On each sampling event, water column turbidity (NTU) was recorded using a U-10 multi-probe (HORIBA Ltd., Australia). Dissolved organic carbon (DOC) was determined from 20 ml of 0.2 µm filtered water that was fixed with phosphoric acid, and stored frozen until analysis by wet oxidation in sodium persulphate at 100 °C. From each pond on each sampling event 200 ml of unfiltered water was stored frozen for total nitrogen (TN; mg N l⁻¹) and total phosphorus (TP; mg P l⁻¹) determinations, and 10 ml aliquots of 0.45 µm filtered water were frozen for determinations of labile nitrogen (oxides of nitrogen, NO_x; mg N l⁻¹) and labile phosphorus (filterable reactive phosphorus, FRP; mg P l⁻¹). NO_x was determined colorimetrically after its reduction to nitrite using a cadmium column (APHA 1995). TN was determined as for NO_x after its pre-digestion in NaOH-K₂S₂O₈ and oxidation to nitrate. FRP was determined



■ Figure 3.3.1: Grazing enclosure (4 m x 5 m) on Lake Malta showing a) the extent of lakebed vegetation in March 2002, 4 months after lakebed exposure, and b) the impact of grazing 8 months later (November 2002). Photos by O. Scholz.

colorimetrically using the phosphomolybdate-blue method (APHA 1995). TP samples were determined as for FRP after pre-digestion in NaOH-K₂S₂O₈ and oxidation to orthophosphate. Detection limits were TN±0.019 mg N l⁻¹ and TP±0.0025 mg P l⁻¹.

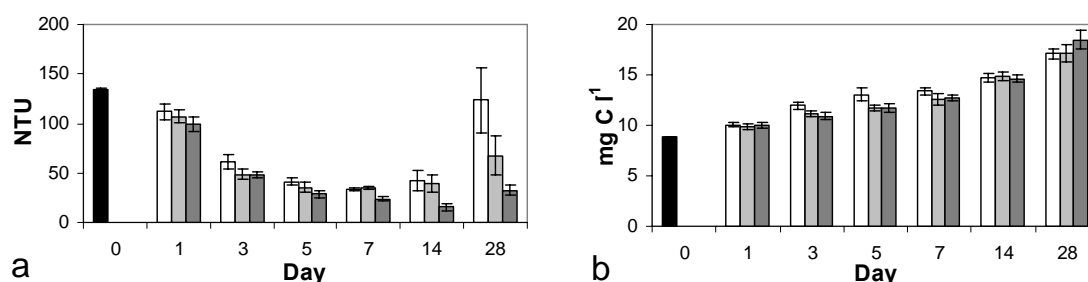
Panktonic, benthic and epiphytic (mesocosm wall) algal fractions were collected; 500 ml sub-surface water for plankton and 25 cm² cores for benthos and epiphyton. Grass shoots were removed from samples where they occurred prior to analysis. Algal biomass was measured as chlorophyll *a* (CHL*a*) using hot ethanol extraction and spectrophotometric measurement at 665 nm and 750 nm without acidification (APHA 1995). Expressing CHL *a* concentrations as loads per mesocosm allowed for comparisons between the different fractions. Zooplankton was sampled by straining 10 l of mesocosm water through 50 µm mesh size plankton nets. Filtrates were preserved with Lugol's Iodine solution. Filtered water was returned to mesocosms. At least 250 individuals were counted per sample using a Sedgewick Rafter cell. Identifications followed Shiel (1995) and Ingram *et al.* (1997).

Data are presented as means±standard errors unless stated otherwise. One-way ANOVA and repeated measures ANOVA (RMA) were calculated using SYSTAT® V10.2 (SYSTAT Software Inc., USA). RMA probabilities are presented as *p* and G-G adjusted *p* values.

Results

Turbidity ranged from 11-195 NTU (Figure 3.3.2a). Although treatments responded differently over time (RMA_{treatment×time}: G-G=0.003, n=81), turbidity declined in all mesocosms over the first two weeks. Lower water levels and strong winds prior to sampling on day 28 resulted in the re-suspension of particulate matter. Within times, turbidity tended to be lowest in un-grazed and highest in no-vegetation treatments, suggesting that the presence of vegetation facilitated the settling of suspended matter and reduced re-suspension.

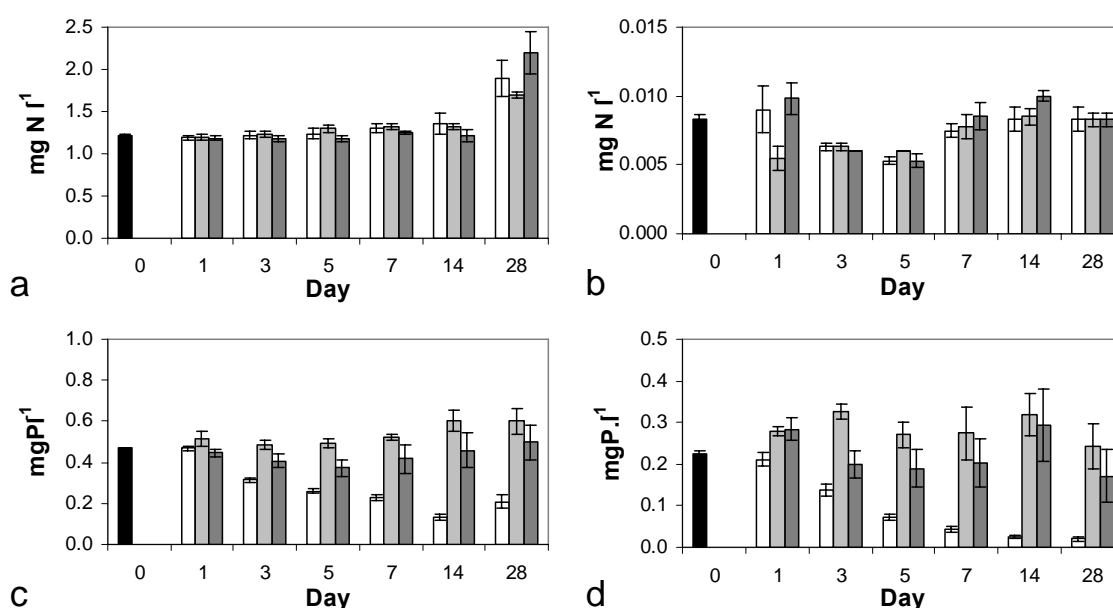
Dissolved organic carbon (DOC) concentrations ranged from 8.85-20.8 mg C l⁻¹ (Figure 3.3.2b). Treatment effects were not significant (RMA: *p*=0.547, n=81), but time effects were (RMA: G-G<0.001, n=81). There was no significant interaction between factors (RMA: G-G=0.184, n=81). During the study, DOC increased by 97.5 %. As water volumes declined by only 30 % over the same period, observed increases were attributed to both evaporative concentration and leeching of carbon from the sediments.



■ Figure 3.3.2: (a) Turbidity (NTU) and (b) dissolved organic carbon concentration (mg C l⁻¹) determined after re-flooding of no-vegetation (○), grazed (●) and un-grazed (◐) mesocosms (mean ± se, n=4). Day 0 common to all treatments.

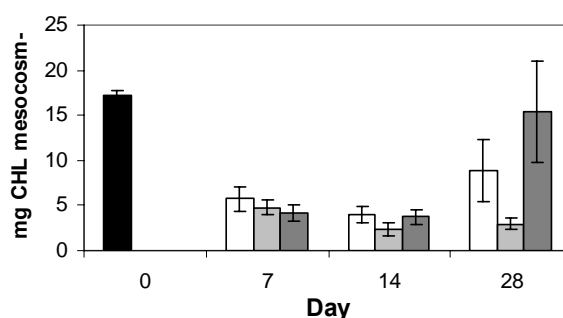
Total nitrogen (TN) concentrations ranged from 1.10-2.66 mg N l⁻¹ (Figure 3.3.3a). Treatment effects were not significant (RMA: $p=0.718$, $n=81$), but time effects were (RMA: $G-G<0.001$, $n=81$), with highest TN concentrations measured on day 28. There was no significant interaction between treatments and time (RMA: $G-G=0.081$, $n=81$). NO_x concentrations ranged from 0.004-0.012 mg N l⁻¹ (Figure 3.3.3b). Treatment effects were not significant (RMA: $p=0.264$, $n=81$), but time effects were (RMA: $G-G=0.004$, $n=81$), decreasing for the first 5 days after inundation. There was no significant interaction between treatments and time (RMA: $G-G=0.066$, $n=81$).

TP concentrations ranged from 0.105-0.750 mg P l⁻¹ (Figure 3.3.3c). The interaction between treatments and time was significant (RMA: $G-G=0.015$, $n=81$). Whilst TP concentrations decreased in the no-vegetation treatment, differences between grazed and un-grazed treatments were not significant (RMA: $p=0.069$, $n=56$) and did not vary through time (RMA: $G-G=0.241$, $n=56$). FRP concentrations ranged from 0.009-0.046 mg P l⁻¹ (Figure 3.3.3d). Both treatment and time effects were significant (RMA_{treatment}: $p=0.014$, $n=81$; RMA_{time}: $G-G=0.024$, $n=81$) and there was no interaction between factors (RMA: $p=0.055$, $n=56$). Differences between grazed and un-grazed treatments were not significant (RMA: $p=0.141$, $n=56$), and they did not vary through time (RMA: $G-G=0.200$, $n=56$).



■ **Figure 3.3.3: (a) Total suspended nitrogen (mg N l⁻¹), (b) labile nitrogen (NO_x) (mg N l⁻¹), (c) total suspended phosphorus (mg P l⁻¹), and (d) labile phosphorus (FRP) (mg P l⁻¹) concentrations determined after re-flooding of no-vegetation (○), grazed (◐) and un-grazed (●) mesocosms (mean ± se, $n=4$). Day 0 common to all treatments.**

Total mesocosm chlorophyll *a* loads (planktonic+benthic+epiphytic fractions) ranged from 1.17-23.34 mg CHL mesocosm⁻¹ (Figure 3.3.4). Treatment effects were not significant between days 0-14 (RMA: $P=0.323$, $n=33$). Plankton contributions to total CHL_a loads decreased from 100 % to 41-49 % over the first 14 days. Over the same period, benthic loads increased from 0 % to 51-59 %. At no stage did epiphytes growing on mesocosm walls contribute more than 0.6 % to total CHL_a loads. Increases in total CHL_a loads on day 28 in no-vegetation and un-grazed treatments were primarily due to increases in plankton. It was not possible to establish whether this arose through the re-suspension of benthic algae.



■ **Figure 3.3.4: Total chlorophyll a (mg CHL mesocosm⁻¹) determined after re-flooding of no-vegetation (○), grazed (◐) and un-grazed (◑) mesocosms (mean ± se, n=4). Day 0 common to all treatments.**

Twenty-seven micro-invertebrate taxa were identified in samples collected from the experimental mesocosms during the 28-day post-flood period. These included 18 rotifer, 8 crustacean (5 branchiopods, 2 copepods excluding nauplii and 1 ostracod) and 1 euglenid taxa. Of these, 12 rotifer, 5 crustacean and the single euglenid taxa were common to all treatments (Table 3.3.1).

Total zooplankton taxa richness within treatments and times ranged from 9-19 taxa. *Euglena* sp. was encountered in all but day 28 samples. Crustacean richness ranged from 1 taxon initially (calanoid copepods and their nauplii) to 7 taxa (day 28). Treatment effects were not significant (RMA: $p=0.505$, $n=36$), but time effects were (RMA: $G-G<0.001$, $n=36$). Crustacean richness in all treatments increased significantly between days 7 and 14 (one-way ANOVAs: $p_{\text{no-vegetation}}=0.032$, $p_{\text{grazed}}=0.002$, $p_{\text{un-grazed}}=0.024$, $n=8$) (Figure 3.3.5a).

Rotifer richness increased from 7 taxa at day 0 to as many as 12 after 1 week (Figure 3.3.5b). Treatment differences at that stage were not significant (one-way ANOVA: $p=0.702$, $n=12$). Between days 7 and 14, rotifer richness declined significantly in the no-vegetation treatment (one-way ANOVA: $p=0.001$, $n=8$), where only *Filinia australis* and *Keratella tropica* remained. Rotifer richness declined less sharply over the same interval in the grazed treatment (one-way ANOVA: $p=0.006$, $n=8$), with only four taxa remaining (*F. australis*, *K. tropica*, *Hexarthra* sp. and *Polyarthra* sp.). No significant change in richness was observed in the un-grazed treatment between days 7 and 14 (one-way ANOVA: $p=0.903$, $n=8$). By day 28, richness in each treatment had declined to two or three taxa.

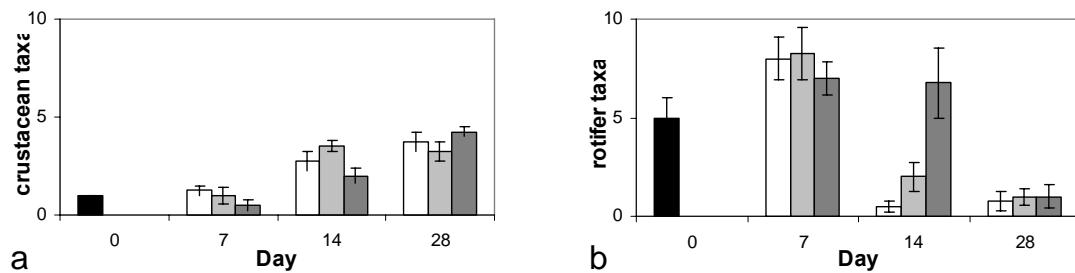
Changes in zooplankton abundance reflected those described above for diversity. Total zooplankton densities ranged from 160-11620 individuals l⁻¹ during the study period. Total densities at day 0 were 4490±1030 individuals l⁻¹ and were dominated by *Polyarthra* sp. and *Euglena* sp. (Table 3.3.1). Crustacean densities ranged from 0-580 individuals l⁻¹ and were dominated by calanoid copepods and their nauplii in all treatments and times (Figure 3.3.6a). Treatment effects were not significant (RMA: $p=0.813$, $n=36$), but time effects were (RMA: $G-G=0.002$, $n=45$). Crustacean densities increased significantly between days 7 and 14 in the no-vegetation treatment (one-way ANOVA: $p=0.034$, $n=8$) and in the un-grazed treatment (one-way ANOVA: $p=0.002$, $n=8$), but not in the grazed treatment (one way ANOVA: $p=0.093$, $n=8$).

Rotifer densities ranged from 0-9800 individuals l⁻¹ (Figure 3.3.6b). Rotifer abundances in all treatments did not change significantly between days 0 and 7 (one way ANOVAs: $p_{\text{no-vegetation}}=0.741$, $p_{\text{grazed}}=0.790$, $p_{\text{un-grazed}}=0.171$, $n=8$). Rotifer densities decreased significantly between days 7 and 14 in the grazed treatment (one way ANOVA: $p=0.011$, $n=8$) and the ungrazed treatment (one way ANOVA: $p=0.022$, $n=8$), but not in the no-vegetation treatment

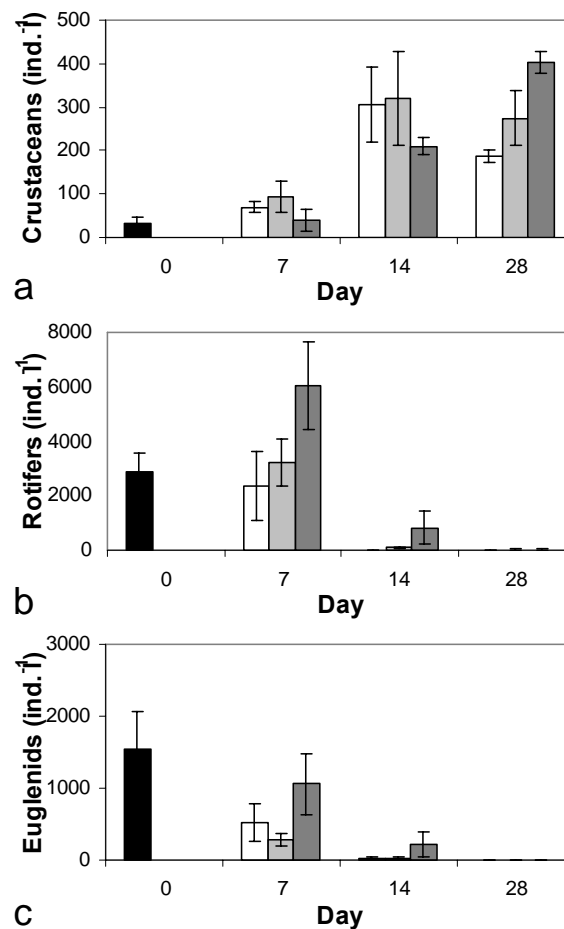
(one way ANOVA: $p=0.117$, $n=8$). Euglenid densities ranged from 0-2580 individuals l^{-1} and responses were similar to those of rotifers (Figure 3.3.6c). Treatment effects were not significant (RMA: $p=0.841$, $n=33$), but time effects were (RMA: G-G=0.001, $n=33$). Large sample variances limited the ability to detect significant differences between times.

TAXA	Day 0	Day 7			Day 14			Day 28		
	Flood water	No vegetation	Grazed	Un-grazed	No vegetation	Grazed	Un-grazed	No vegetation	Grazed	Un-grazed
Rotifera										
<i>Asplanchna</i> sp.	-	1.2	1.8	0.2	-	-	1.8	-	-	-
<i>Brachionus angularis</i>	-	0.1	-	-	-	-	-	-	-	-
<i>B. budapestinensis</i>	-	0.1	0.1	-	-	-	-	-	-	-
<i>B. calyciflorus</i>	-	-	-	-	-	-	0.7	-	-	-
<i>B. novazealandea</i>	-	-	-	-	-	-	-	2.4	2.5	-
<i>B. urceolaris</i>	-	1.9	0.1	-	-	-	1.5	-	-	-
<i>Filinia australis</i>	-	5.3	6.1	1.8	1.8	14.4	7.7	-	-	1.2
<i>F. terminalis</i>	0.8	2.6	2.8	2.0	-	-	0.1	-	-	-
<i>Hexarthra</i>	5.2	3.6	12.1	5.1	-	0.8	3.8	-	-	-
<i>Keratella australis</i>	-	-	-	-	-	-	0.6	2.4	7.8	1.0
<i>K. cochlearis</i>	0.1	0.4	-	0.4	-	-	0.1	-	-	-
<i>K. tropica</i>	0.2	4.2	0.7	<0.1	0.8	5.0	4.5	-	-	-
<i>Lecane</i> sp.	0.1	-	0.1	-	-	-	-	2.5	-	2.2
<i>Polyarthra</i> sp.	57.0	31.6	56.5	63.5	-	3.0	28.2	-	-	-
<i>Synchaeta</i> sp.	-	0.1	0.2	0.2	-	-	0.1	-	-	-
<i>Trichocerca</i> sp.	1.4	0.2	0.5	0.4	-	-	0.4	-	-	-
<i>Trichotria</i> sp.	-	-	-	-	-	-	0.1	-	-	-
Unident rotifer sp.	-	21.1	7.7	12.7	-	-	1.2	-	-	-
Crustaceans										
<i>Calanoida</i> sp. nauplii	0.3	4.4	2.5	0.2	49.5	33.1	21.6	21.0	34.9	55.8
<i>Calanoida</i> sp.	0.5	3.6	0.8	1.2	24.2	11.9	7.2	23.9	20.5	10.9
<i>Cyclopoida</i> sp.	-	-	-	-	3.9	7.6	-	3.1	4.9	11.1
<i>Bosmina</i> sp.	-	-	-	-	-	-	-	5.6	1.6	-
<i>Daphnia carinata</i>	-	-	-	-	-	1.4	-	3.5	2.5	-
<i>Macrothrix</i> sp.	-	-	-	-	1.8	0.8	-	2.4	1.1	5.2
<i>Moina</i> sp.	-	0.2	0.4	-	5.4	16.5	7.1	13.0	24.1	7.8
<i>Sididae</i> sp.	-	-	-	-	-	-	-	-	-	4.8
<i>Ostracod</i> sp.	-	-	-	-	5.1	-	1.5	20.3	-	-
Euglenids										
<i>Euglena</i> sp.	34.4	19.4	7.6	12.3	7.6	5.5	11.4	-	-	-
Total abundance (individuals l^{-1})	4490±1030	2930±1390	3610±896	7150±1970	342±97	446±114	1260±779	202±15	299±56	422±33

■ Table 3.3.1: Total abundances (individuals l^{-1}) and relative abundances (%) of zooplankton taxa recorded in no-vegetation, grazed and un-grazed treatments after re-flooding (mean ± se, $n=4$).



■ Figure 3.3.5: (a) Numbers of crustacean and (b) rotifer taxa recorded after re-flooding of no-vegetation (○), grazed (◐) and un-grazed (◑) mesocosms (mean \pm se, n=4). Day 0 common to all treatments.



■ Figure 3.3.6: (a) Crustacean, (b) rotifer and (c) euglenid abundances (individuals l⁻¹) in no-vegetation (○), grazed (◐) and un-grazed (◑) treatments over 28 days post-inundation (mean \pm se, n=4). Note scale differences. Day 0 common to all treatments.

Discussion

Inundated terrestrial vegetation represents a potentially significant source of organic-matter as it decomposes (Furch and Junk 1997), and potentially significant habitat structure for a range of aquatic organisms (Geddes and Puckridge 1989, Lloyd *et al.* 1989, Gehrke 1990, Arscott *et al.* 2000). Water resource development has increased the permanency of inundation and reduced the duration and frequency of drying events in EDBL, such as the Menindee Lakes. This effectively reduces the time available for dry lakebed vegetation to establish, and thus also the ecological benefits that these communities provide under natural (*i.e.* more ephemeral) hydrological regimes.

Just as the timing and duration of drying episodes are potentially important determinants of lakebed plant community structure, so too may be grazing by both native animals and stock (Wahren *et al.* 1999, Jansen and Robertson 2001). Many arid-zone EDBL, including lakes of the Menindee system, are subject to significant grazing pressure (*e.g.* Figure 3.3.1). It was hypothesized that lakebed vegetation increases post-flood aquatic productivity, that grazing reduced this potential through the net removal of nutrients, and that grazing reduces habitat structure and thus also post-flood biotic diversity (Beck 2000, Taniguchi *et al.* 2003). These were tested using 500 l mesocosms assigned to one of three treatments: no-vegetation (bare sediment), grazed (rye-grass removed and manure added) and un-grazed (rye-grass).

After inundation, suspended matter in each of the mesocosms took several days to settle. The presence of vegetation aided the settling of suspended matter and reduced susceptibility to sediment re-suspension. Concentrations of dissolved organic carbon (DOC) did not differ between treatments, suggesting that neither the presence of vegetation nor its transformation into manure were significant sources of carbon. However, DOC concentrations did increase steadily during the 28-day post-flood period. These increases were greater than could be attributed to evaporative concentration alone, suggesting that carbon was being released from the sediments.

No treatment effects were observed for TN and NO_x, which remained constant or rose slightly. In contrast, TP and FRP concentrations declined markedly in the no-vegetation treatment relative to grazed and un-grazed treatments. This response is difficult to explain. Lake flooding is generally associated with a nutrient pulse that fuels productivity (*e.g.* Briggs *et al.* 1985, Junk *et al.* 1989, Baldwin and Mitchell 2000, Scholz *et al.* 2002). However, no post-flood nutrient pulse was observed. This was a likely consequence of mesocosm preparation, during which soils in all treatments were kept moist as grass was grown, and would have stimulated microbial assimilation of bio-available nutrients.

Few studies have examined the relative contributions of phytoplankton and epiphyton/phytobenthos to total algal biomass and primary production. Gawne *et al.* (2000) indicated that phytoplankton contributed more biomass and more to system productivity than did benthic algae in the Murray River, and that this was due largely to the narrowness of the littoral zone. In contrast, Wetzel (1964) indicated that littoral productivity could easily exceed that of the phytoplankton in large shallow lakes, such as EDBL. Wetzel *et al.* (1972), Stanley (1976), and Loeb *et al.* (1983) have reported similar results. As might be expected from the post-flood responses of DOC and nutrients, there was no treatment effect on total algal biomass. After flooding, phytoplankton biomass decreased and benthic contributions to total algal biomass increased. This suggests that primary production was either benthic driven and/or that benthic grazing pressure was lower than was plankton grazing pressure. As benthic grazer populations were not examined, no definitive assessment of the relative contributions to system production of benthic and planktonic algae was possible.

Greater micro-invertebrate diversity was encountered in all experimental mesocosms after flooding than was present initially in the floodwaters. These increases were driven primarily by emergence from the sediments. Many wetland invertebrate species, particularly rotifers and micro-crustaceans, produce resting stages (eggs, cysts) that allow them to bridge periods of adverse environmental conditions, such as lake drying. In turn, lake flooding triggers the emergence of a succession of invertebrate communities (*e.g.* Boulton and Lloyd 1992, Nielsen *et al.* 2000). Rotifers took approximately 1 week and micro-crustaceans 2-4 weeks to emerge. These times were similar to those reported by Boulton and Lloyd (1992). The declines in rotifer and euglenid abundance and diversity after day 7 coincided with the appearance of predatory mosquito larvae (Diptera fam. Culcidae). Though not sampled, mosquito larval densities in all mesocosms peaked around day 14 at densities of *ca.* 50-100 mesocosm⁻¹. Selective predation of soft bodied and less motile taxa was thus most likely to have contributed to the crash in rotifer and euglenid populations. Such severe responses to predation were a likely consequence of artificially high predator/prey ratios within the mesocosms. At the lake scale, these ratios are kept low by the presence of larger predators (macro-invertebrates and fish), which were absent from mesocosms. Whilst there were no treatment effects regarding the loss of rotifer abundances after day 7, the presence of vegetation did reduce the rate of rotifer species loss. Habitat structure may have thus provided important refuge from predation.

We hypothesized that lakebed vegetation and grazing would modify post-flood aquatic production and micro-invertebrate diversity in comparison to un-vegetated lakebeds that are characteristic of short drying episodes. The absence of treatment effects for nutrients, DOC and algal biomass suggest that lakebed management had no impact on aquatic production, although invertebrate grazing pressure or primary production were not measured. However, the presence of habitat structure did improve the resilience of zooplankton species to predation by invertebrates.

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3.4 Effects of organic matter and habitat structure on post-inundation responses

O. Scholz and B. Gawne

Abstract

The presence of terrestrial lakebed vegetation was thought to stimulate post-inundation aquatic productivity and diversity by providing organic matter and important habitat structure. We examined nutrient concentrations, phytoplankton biomass, primary productivity and zooplankton community structure for four weeks after flooding in mesocosms assigned to one of four treatments designed to isolate the effects of habitat structure (H) and organic matter supply (OM) provided by inundated vegetation: no-vegetation (-H, -OM), artificial vegetation (+H, -OM), cut grass (-H, +OM), and grass (+H, +OM). Nutrients leached from inundated vegetation increased the potential for primary production, although this decreased once bio-available nitrogen and phosphorus pools became depleted. Zooplankton communities showed no consistent response to either the presence/absence of habitat structure or to nutrient inputs from inundated vegetation. These data suggest that management actions that impair the establishment of lakebed vegetation, such as reductions in the duration of lake drying events and grazing, may reduce post-inundation aquatic productivity, but have little impact on zooplankton communities, an important food resource for fish.

Introduction

Ephemeral deflation basin lakes (EDBL) are widespread throughout the arid and semi-arid regions of the Murray-Darling Basin in Australia (Seddon *et al.* 1997, Seddon and Briggs 1998). These lowland river floodplain environments naturally fluctuate between terrestrial and aquatic states. Transitions between these states are thought to drive both aquatic and terrestrial successional processes and facilitate biotic and abiotic exchanges between elements of the floodplain and the riverine environment (*cf.* Flood Pulse Concept; Junk *et al.* 1989). Modification of the wet/dry regime through hydraulic regulation thus has the potential to disrupt many of these processes and exchanges, and has been identified as a key threat to ecosystem productivity and diversity (Boulton and Lloyd 1992, Bunn *et al.* 1997, Boulton and Jenkins 1998, Kingsford 2000).

The flooding of dry lakes is also thought to stimulate the release of potentially significant amounts of nutrients and organic matter from the sediments (McComb and Qiu 1998, Baldwin and Mitchell 2000, Scholz *et al.* 2002) and vegetation (Furch and Junk 1997). These releases have the potential to fuel a post-flood pulse of autotrophic and heterotrophic productivity, but this has not yet been demonstrated.

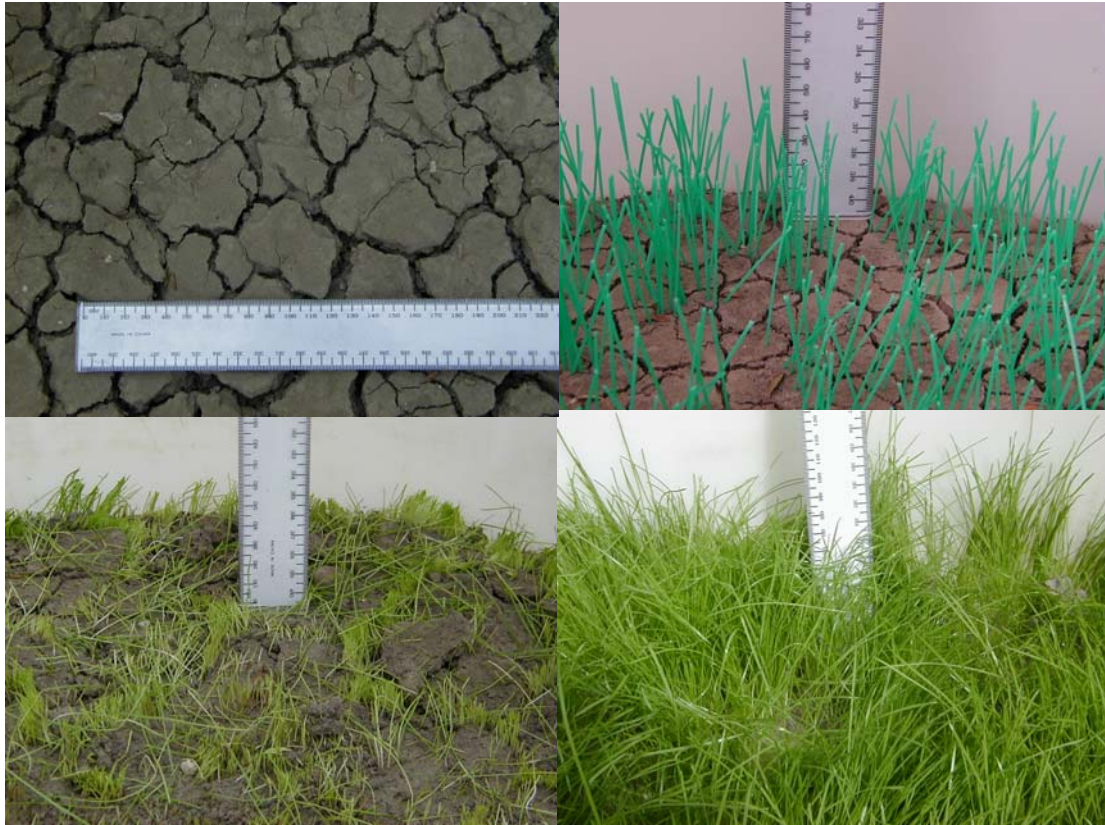
Flooding has also been shown to stimulate the emergence of micro-invertebrates from eggs and cysts deposited in the sediments during previous periods of inundation (*e.g.* Boulton and Lloyd 1992, Boulton and Jenkins 1998, Nielsen *et al.* 2000). The deposition of eggs and cysts into the sediments provides a mechanism for organisms to persist locally during dry periods, and their emergence shortly after re-flooding is thought to enable them to utilise the post-flood increases in food resources. Whilst post-inundation emergence rates and diversity have been documented across a range of ephemeral environments, no studies have concurrently examined potential interactions between micro-invertebrate assemblages emerging from the sediments after flooding and the supposed post-flood pulse of autotrophic and heterotrophic productivity.

As lakes dry, terrestrial plants often rapidly colonize their beds. On re-flooding, the presence of such vegetation has been shown not only to provide nutrients as they decompose (Furch and Junk 1997), but also habitat structure for a range of algae, micro- and macroinvertebrates and suitable spawning habitat for native fish (Geddes and Puckridge 1989, Lloyd *et al.* 1989, Gehrke 1990). The habitat structure provided by inundated vegetation is thus likely to support greater aquatic biodiversity (Beck 2000, Taniguchi *et al.* 2003), especially in EDBL where habitat diversity is characteristically very low (Taylor-Wood *et al.* 2002). For many EDBL, flow regulation has increased the permanency of stored water and reduced the frequency and duration of complete lake drying episodes (*e.g.* Menindee Lakes System; Section 1 Table 1.3). Such changes in flow regime have the potential to reduce the time available for lakebed vegetation to establish, and thus also the potential to alter post-inundation aquatic processes.

In this study we examined whether the presence of lakebed vegetation (*i.e.* grass) affects post-flood nutrient availability, primary productivity, and zooplankton abundance and diversity in arid-zone EDBL. We hypothesised that submerged terrestrial vegetation constitutes both an important source of nutrients as it decomposes and modifier of aquatic habitat structure, and that these would stimulate aquatic productivity and diversity. This has implications not only for hydraulic management, but also for the management of lakebed vegetation, which may be compromised by activities such as grazing.

Methods

Twelve 85 l mesocosms (0.6 m diameter x 0.4 m deep) were each filled with 0.1 m (*ca.* 20 l) of surface sediment (top 5 cm) collected from the dry bed of Lake Malta. Mesocosms were randomly assigned to one of four experimental treatments designed to isolate the effects of habitat structure (H) and organic matter supply (OM) from inundated vegetation on post inundation aquatic responses: no-vegetation (-H, -OM), artificial vegetation (+H, -OM), cut grass (-H, +OM), and grass (+H, +OM) (Figure 3.4.1). Artificial vegetation was constructed using round green plastic flex (1 mm diameter) fixed into a polystyrene base at *ca.* 1 cm spacings, which was then covered with soil, leaving 5-7 cm of flex protruding above the sediment surface. Grass and cut grass treatments were sown with 100 g of rye grass seeds (*Lolium perenne*). All mesocosms received 1 l of RO (reverse osmosis) filtered water every 2 days. This was sufficient to facilitate grass growth but not enough to waterlog the sediments. Grass was grown to a length of approximately 15 cm over 2 months. All grass present in cut grass mesocosms was then harvested, leaving a short stubble (*ca.* 1 cm). Harvested grass biomass ranged from 91.3-179.1 g wet weight (mean 136.2 ± 25.4 g) per mesocosm. 125 g of harvested grass was returned to these mesocosms suspended in 50 μ m mesh bags to exclude micro-invertebrates, but permit the diffusion of organic matter.



■ **Figure 3.4.1: Experimental treatments (a) bare sediment, (b) artificial grass, (c) grazed grass, and (d) grass.**

Mesocosms were filled during April 2003 to a depth of 0.3 m with freshly collected unfiltered Darling River water, and were monitored for one month (days 0, 1, 3, 5, 7, 14 and 28) after filling. Mesocosms were filled so as to minimise disturbance of the sediments. On each sampling event, water column turbidity (NTU) was recorded using a U-10 multi-probe (HORIBA Ltd., Australia). Dissolved organic carbon (DOC) was determined from 20 ml of 0.2 μm filtered water that was fixed with phosphoric acid, and stored frozen until analysis by wet oxidation in sodium persulphate at 100 °C. From each pond on each sampling event 200 ml of unfiltered water was stored frozen for total nitrogen (TN; mg N l^{-1}) and total phosphorus (TP; mg P l^{-1}) determinations, and 10 ml aliquots of 0.2 μm filtered water were frozen for determinations of labile nitrogen (oxides of nitrogen, NO_x ; mg N l^{-1}) and labile phosphorus (filterable reactive phosphorus, FRP; mg P l^{-1}). NO_x was determined colorimetrically after its reduction to nitrite using a cadmium column (APHA 1995). TN was determined as for NO_x after its pre-digestion in $\text{NaOH-K}_2\text{S}_2\text{O}_8$ and oxidation to nitrate. FRP was determined colorimetrically using the phosphomolybdate-blue method (APHA 1995). TP samples were determined as for FRP after pre-digestion in $\text{NaOH-K}_2\text{S}_2\text{O}_8$ and oxidation to orthophosphate. Detection limits were $\text{TN} \pm 0.019 \text{ mg N l}^{-1}$ and $\text{TP} \pm 0.0025 \text{ mg P l}^{-1}$.

Phytoplankton biomass was measured as chlorophyll *a* concentration (mg CHL l^{-1}). Chlorophyll *a* determinations involved filtering (Whatman Pty. Ltd. GF/C) 500 ml of water, extracting CHL from the filtrates in hot ethanol (80 °C for 5 minutes), and measuring the extracted CHL at 665 nm and 750 nm without acidification (APHA 1995).

Community metabolism was determined by measuring diurnal changes in temperature and dissolved oxygen concentrations (YSI 5775 oxygen probe YSI Inc., Ohio, WP-82 data logger

TPS Pty Ltd., Brisbane QLD) and light intensities (ODYSSEY light logger, Dataflow Systems PTY. Ltd., Cooroy QLD) at 10-minute intervals over 24 hours in open systems. A 12 V in line pump (11 l min⁻¹ Whale 991 in-line pump, Munster Sims, Bangor Nth. Ireland) maintained flow over the dissolved oxygen probe, preventing the development of oxygen gradients around the membrane. Net primary production (NPP), or net daily metabolism, was calculated as the difference between gross primary production (GPP g C m⁻³ d⁻¹) and community respiration (CR₂₄). GPP represents the change in oxygen during daylight hours; CR₂₄ represents the loss of oxygen as a result of community respiration over 24 hours. Oxygen data were converted to units of carbon using a photosynthetic quotient of 1 and a ratio of 1 mg O₂ = 0.375 mg C.

Zooplankton was sampled by straining 8 l of mesocosm water through 50 µm mesh size plankton nets. Filtrates were preserved with Lugol's iodine solution. Filtered water was returned to mesocosms. Rotifers were counted from sub-samples using Sedgewick Rafter cell preparations. Whole sample counts were made of micro-crustaceans and larger bodied invertebrates. Identifications followed Shiel (1995) and Ingram *et al.* (1997). Treatment zooplankton abundances (individuals l⁻¹) were calculated by averaging replicates. Species diversity was calculated as Shannon-Wiener H' (bits individual⁻¹), which adjusts for differences in abundance between samples.

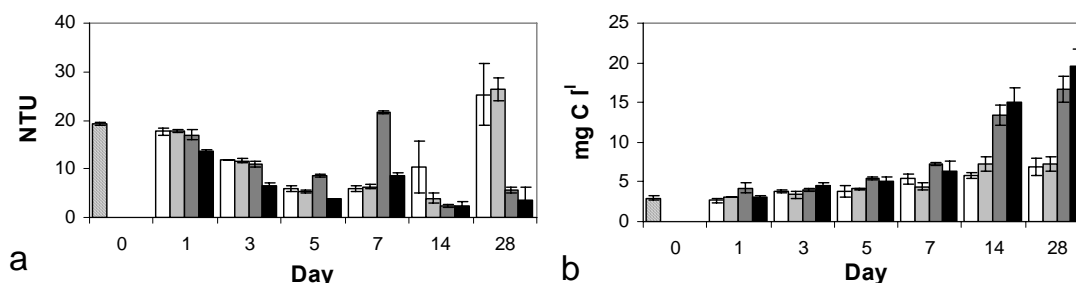
Data are presented as means±standard errors unless stated otherwise. Two-way repeated measures ANOVA (RMA) and one-way ANOVA with Tukey's *post hoc* testing were calculated using SYSTAT® V10.2 (SPSS Inc., Chicago USA). RMA probabilities are presented as *p* and G-G adjusted *p* values. Data did not require transformation to satisfy assumptions of homoscedasticity. Multivariate analyses of treatment responses of zooplankton assemblages were calculated using PRIMER (V5; Primer-E Ltd., 2000). Non-metric multidimensional scaling (NMDS) was used to display relative similarities between experimental treatments and days since trough inundation. ANOSIM was used to test for differences between groups, where R-values reflect the degree of separation (R→1 maximum separation) and *p* the level of significance. Zooplankton data were 4th-root transformed to downweigh the influence of individual taxa and to increase analytical robustness to zero values before calculating Bray-Curtis similarity co-efficients.

Results

Turbidity ranged from 1-38 NTU (Figure 3.4.2a). Although habitat structure and organic matter addition effects interacted (2-way RMA_{HxN}: F=10.931, *p*=0.011), and this interaction varied over time (2-way RMA_{HxNxT}: F=31.529, *p*<0.001), turbidity generally declined in all mesocosms during the study period. Over the first 5 days, turbidity was lowest in the grass treatment (one-way ANOVAs within times: *p*<0.01), suggesting that the presence of vegetation facilitated the settling of suspended matter. Increases in turbidity on day 7 in the cut grass and to a lesser extent in the grass treatment were attributable to elevated phytoplankton concentrations (refer to Figure 3.4.4). Strong winds prior to sampling on day 28 resulted in the re-suspension of particulate matter in bare sediment and artificial habitat treatments, in which consolidating benthic microbial-algal mats were less developed than in the other treatments (O. Scholz pers. obs.).

Dissolved organic carbon (DOC) concentrations ranged from 2.10-23.85 mg C l⁻¹ (Figure 3.4.2b). Although habitat structure and organic matter addition effects interacted (2-way RMA_{HxN}: F=43.062, *p*<0.001), and this interaction varied over time (2-way RMA_{HxNxT}: F=34.588, *p*<0.001), there was a tendency for DOC concentrations to increase in all mesocosms during the study period. These increases were greater in the cutgrass and grass treatments, especially after day 7, indicating that vegetation contributed significant amounts

of DOC to the water column as it decomposed. After 3 days, DOC concentrations in the cut grass and grass treatments were significantly higher than in the bare sediment and artificial grass treatments (one-way ANOVAs within times: $p < 0.05$).



■ **Figure 3.4.2: (a) Turbidity (NTU) and (b) dissolved organic carbon concentration (mg C l⁻¹) determined after flooding of no-vegetation (○), artificial grass (◐), grazed grass (◑), and grass (●) mesocosms (mean ± se, n=3). Day 0 common to all treatments.**

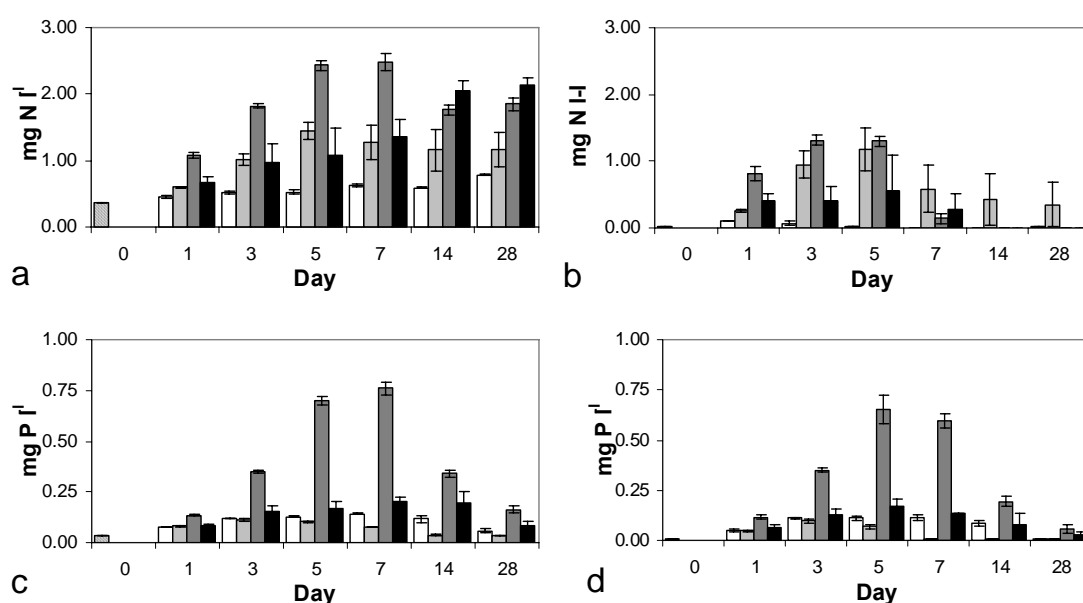
Total nitrogen (TN) concentrations ranged from 0.365-2.650 mg N l⁻¹ (Figure 3.4.3a). Habitat structure and organic matter addition effects interacted (2-way RMA_{HxN}: $F=33.419$, $p < 0.001$), and this interaction varied over time (2-way RMA_{HxNxT}: $F=14.336$, $p < 0.001$). TN concentrations increased significantly in the bare sediment treatment from 0.372±0.004 mg N l⁻¹ on day 0 to 0.782±0.011 mg N l⁻¹ on day 28 (one-way ANOVA: $F=1080.643$, $p < 0.001$). TN concentrations peaked on days 5 and 7 in the cut grass treatment and peaked on days 14 and 28 in the grass treatment, suggesting that the vegetation contributed significant amounts of nitrogen to the water column as it decomposed, and that the rate of release of nitrogen was faster from cut grass. Contrary to expectations, TN concentrations in the artificial grass treatment was significantly higher during the first week after inundation than in the bare sediment treatment (one-way ANOVAs within times: $p < 0.001$).

NO_x concentrations ranged from 0.005-1.710 mg N l⁻¹ (Figure 3.4.3b). NO_x concentrations on day 0 were 0.011±0.002 mg N l⁻¹, which constituted 3.1±0.7 % of the TN present. Flooding stimulated an increase in NO_x concentrations in all treatments. These increases were smallest in the bare sediment treatment, which peaked on day 1 with 0.109±0.008 mg N l⁻¹ with a NO_x:TN ratio of 24.2±2.0 %. Although it took up to 5 days for NO_x concentrations to peak in the other treatments, highest NO_x:TN ratios occurred on day 1 for cut grass (75.2±8.8 %) and grass (57.0±10.5 %) treatments. These responses suggest that flooding stimulated an initial release of NO_x from the sediments and a more protracted and larger release from the vegetation where present. By day 14, NO_x concentrations and NO_x:TN ratios in the bare sediment, cut grass and grass treatments had declined to below that determined on day 0. These declines in NO_x concentrations suggest that rates of NO_x generation decreased relative to rates of biotic and abiotic uptake.

As for TN, much greater NO_x concentrations (1.180±0.318 mg N l⁻¹) and NO_x:TN ratios (max 91.8±11.9 % on day 3) were recorded in the artificial grass treatment than in the bare sediment treatment, suggesting that significant amounts of NO_x was being contributed by the artificial grass. This resulted in there being a significant habitat effect on nutrient additions (2-way RMA_H: $F=8.040$, $p=0.022$) rather than a significant effect of nutrient additions from cut grass and grass treatments as was expected (2-way RMA_N: $F=0.648$, $p=0.432$).

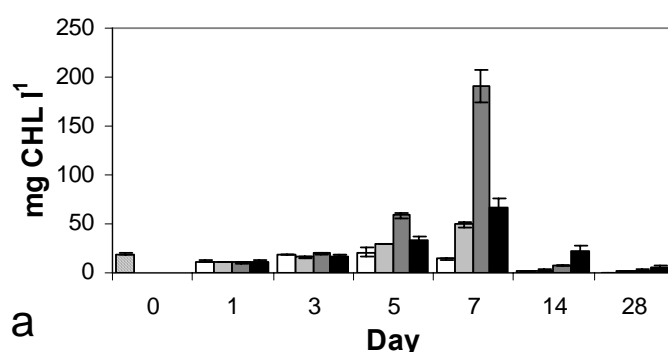
TP concentrations ranged from 0.035-0.800 mg P l⁻¹ (Figure 3.4.3c). Habitat structure and organic matter addition effects interacted (2-way RMA_{HxN}: F=1018.528, *p*<0.001), and this interaction varied over time (2-way RMA_{HxNxt}: F=62.972, *p*<0.001). Bare sediment and artificial grass treatments did not differ significantly from each other over the first 3 days (one-way ANOVAs within times: *p*>0.05), during which TP concentrations increased from 0.038±0.000 mg P l⁻¹ to 0.114±0.003 mg P l⁻¹. After day 3, TP concentrations declined more rapidly in the artificial grass treatment. After day 1, TP concentrations were significantly higher in both cut grass and grass treatments than in the bare sediment and artificial grass treatments. Much more TP was released from the cut grass than the intact grass over the study period. Decreases in TP concentrations were observed after the first week in bare sediment, cut grass and grass treatments, and by day 28 had approached those observed on day 0.

FRP concentrations ranged from 0.004-0.735 mg P l⁻¹ (Figure 3.4.3d). Habitat structure and organic matter addition effects interacted (2-way RMA_{HxN}: F=319.880, *p*<0.001), and this interaction varied over time (2-way RMA_{HxNxt}: F=33.892, *p*<0.001). As with NO_x concentrations, flooding initiated a pulse of FRP in all treatments. Bare sediment and artificial grass treatments did not differ significantly from each other over the first 3 days (one-way ANOVAs within times: *p*>0.05), during which FRP concentrations increased from 0.006±0.000 mg P l⁻¹ to 0.103±0.006 mg P l⁻¹ and FRP/TP ratios increased from 16.8±1.8 % to 93.1±3.7 %. As with TP, subsequent declines in FRP concentrations were more rapid in the artificial grass treatment, returning to the concentrations encountered on day 0 by day 7. This suggests that FRP was being actively taken up either by the plastic flex or by biofilms associated with the flex. Increases in FRP concentration were larger in cut grass and grass treatments than in bare sediment and artificial grass treatments and accounted for all of the TP encountered on days 3 and 5, respectively. Decreases in FRP concentration observed after day 5 in all treatments to levels approaching that of day 0 suggests that rates of FRP generation decreased relative to rates of biotic and abiotic uptake.



■ Figure 3.4.3: (a) Total suspended nitrogen (mg N l⁻¹), (b) available nitrogen (NO_x) (mg N l⁻¹), (c) total suspended phosphorus (mg P l⁻¹), and (d) available phosphorus (FRP) (mg P l⁻¹) concentrations, determined after flooding of no-vegetation (○), artificial grass (●), grazed grass (●), and grass (●) mesocosms (mean ± se, n=3). Day 0 common to all treatments.

Phytoplankton chlorophyll *a* concentrations ranged from 0.73-214.63 mg CHL l⁻¹ (Figure 3.4.4). Habitat structure and organic matter addition effects interacted (2-way RMA_{HxN}: F=88.414, *p*<0.001), and this interaction varied over time (2-way RMA_{HxNxt}: F=84.056, *p*<0.001). Treatment effects were not significant for the first 3 days after flooding (one-way ANOVA within times: *p*>0.05). However, by day 7 CHL*a* concentrations had increased significantly in the artificial grass, cut grass and grass treatments (one-way ANOVAs within treatments: *p*<0.01). CHL*a* concentrations declined significantly in each treatment after day 7 (one-way ANOVAs within treatments: *p*<0.001, *n*=6). These decreases coincided with declines in NO_x concentrations in the bare sediment, cut grass and grass treatments, and with decreases in FRP concentrations in the artificial grass treatment.

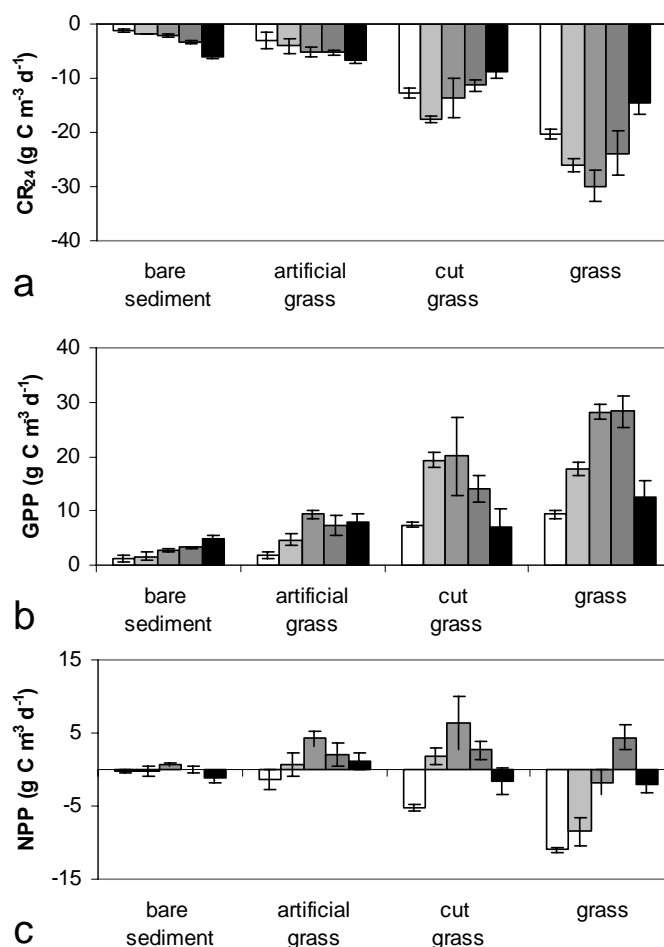


■ **Figure 3.4.4: Phytoplankton chlorophyll *a* (mg CHL l⁻¹) determined for bare sediment (○), artificial grass (◐), cut grass (◑), and grass (●) treatments after flooding (mean ± se, *n*=3). Day 0 common to all treatments.**

Community respiration (CR₂₄) ranged from 0.77 to 33.45 g C m³ d⁻¹ (Figure 3.4.5a). The influence of organic matter supply on CR₂₄ differed significantly between habitat structure treatments (2-way RMA_{HxN}: F=10.665, *p*=0.014). CR₂₄ varied significantly over time (RMA_t: F=8.683, *p*=0.004), and responses were dependent on organic matter supply (RMA_{txN}: F=19.956, *p*<0.001), but not on habitat structure (RMA_{txH}: F=2.117, *p*=0.158). CR₂₄ increased steadily in the bare sediment and artificial grass treatments throughout the 28-day study period to 5.91±0.37 g C m³ d⁻¹ and 6.77±0.056 g C m³ d⁻¹, respectively, at which stage they did not differ significantly (one-way ANOVA: F=1.618, *p*=0.272). In contrast, CR₂₄ increased during the first week in both cut grass and grass treatments, with CR₂₄ in the grass treatment peaking at a higher concentration (29.88±2.97 g C m³ d⁻¹) and later (day 7) than in the cut grass treatment (17.52±0.53 g C m³ d⁻¹ on day 5). Subsequent declines in CR₂₄ in these treatments corresponded with declines in readily available nutrient concentrations (NO_x and FRP) and phytoplankton biomass.

Gross primary production (GPP) ranged from -0.05-33.33 g C m³ d⁻¹ (Figure 3.4.5b). GPP was significantly influenced by habitat structure (RMA_H: F=17.444, *p*=0.004) and organic matter supply (RMA_N: F=172.596, *p*<0.001). There was no interaction between these effects (RMA_{HxN}: F=0.256, *p*=0.629). GPP increased steadily in the bare sediment treatment, rising to 4.83±0.53 g C m³ d⁻¹ by day 28. GPP increased over the first week in the other treatments, peaking at 9.32±0.87 g C m³ d⁻¹ in the artificial grass, 20.12±7.19 g C m³ d⁻¹ in the cut grass, and 28.15±1.37 g C m³ d⁻¹ (28.29±2.93 g C m³ d⁻¹ on day 14) in the grass treatments. As with CR₂₄, subsequent declines in GPP corresponded with declines in readily available nutrient concentrations (NO_x and FRP) and phytoplankton biomass.

Net primary production (NPP) ranged from -11.53 to $+11.91$ $\text{g C m}^{-3} \text{d}^{-1}$ (Figure 3.4.5c). The influence of organic matter supply on NPP differed significantly between habitat structure treatments (2-way RMA_{HxN} : $F=14.740$, $p=0.006$), and this interaction varied through time (2-way $\text{RMA}_{\text{HxNxt}}$: $F=7.089$, $p>0.001$). Thus, although all treatments displayed similar temporal responses, treatment differences arose principally from differences in the magnitude of NPP and the timing of transitions between net heterotrophy and autotrophy. NPP ranges in the bare sediment (-1.08 ± 0.85 to $+0.66 \pm 0.22$ $\text{g C m}^{-3} \text{d}^{-1}$) and artificial grass (-1.37 ± 1.47 to $+4.27 \pm 0.99$ $\text{g C m}^{-3} \text{d}^{-1}$) treatments was lower than those of cut grass (-12.66 ± 0.87 to $+6.38 \pm 3.55$ $\text{g C m}^{-3} \text{d}^{-1}$) and grass treatments (range -11.01 ± 0.30 to $+4.39 \pm 1.78$ $\text{g C m}^{-3} \text{d}^{-1}$).



■ **Figure 3.4.5: (a) Community respiration (CR_{24}) ($\text{g C m}^{-3} \text{d}^{-1}$), (b) gross primary production (GPP) ($\text{g C m}^{-3} \text{d}^{-1}$), and (c) net primary production (NPP) ($\text{g C m}^{-3} \text{d}^{-1}$) determined for each treatment on days 3 (○), 5 (◐), 7 (◑), 14 (●), and 28 (●) after flooding. (mean \pm se, $n=3$).**

Forty-six micro-invertebrate taxa were identified in samples collected from the experimental mesocosms during the 28-day post-flood period (Tables 3.4.1 and 3.4.2). These included 28 rotifers, 10 cladocerans, 5 copepods, 2 ostracods, and one dipteran (mosquito). Of these, 20 taxa (11 rotifers, 4 cladocerans, 2 copepods, 2 ostracods and mosquito larvae/pupae) were common to all treatments. Sixteen taxa were introduced with the floodwater to each mesocosm on day 0. By the end of the study period, at least 27 new taxa (15 rotifers, 9

cladocerans, 2 ostracods and mosquito larvae/pupae) had been recorded. These additions are most likely to have emerged from eggs or resting stages deposited in the sediments, except for the aerial invasion by mosquitos. Copepodites constituted a significant component of the micro-invertebrates introduced at day 0. No copepodites were recorded after day 7. As copepods take from 2-4 weeks to emerge from the sediments (Boulton and Lloyd 1992), most of the adult copepods encountered are likely to have been introduced with the floodwater.

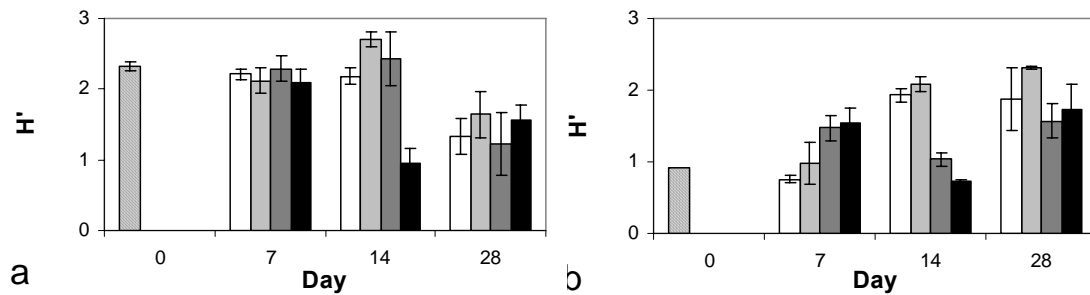
Relative abundance (%)													
DAY	0	7				14				28			
TAXA		Bare sediment	Artificial grass	Cut grass	Grass	Bare sediment	Artificial grass	Cut grass	Grass	Bare sediment	Artificial grass	Cut grass	Grass
<i>Brachionus angularis</i>	-	-	0.6	2.1	1.6	-	0.8	-	-	-	-	-	-
<i>B. bidentatus</i>	1.2	-	-	0.7	-	5.7	2.0	0.5	-	-	-	-	-
<i>B. budapestinensis</i>	2.8	1.3	-	-	1.8	-	2.0	-	-	-	-	-	-
<i>B. calyciflorous</i>	-	-	-	-	-	9.3	1.2	0.9	-	-	-	-	-
<i>B. calyciflorous gigantia</i>	-	-	-	-	-	18.0	3.5	-	-	-	0.6	0.5	-
<i>B. diversicornus</i>	13.1	-	4.3	3.2	-	-	-	-	-	-	-	-	-
<i>B. falcatus</i>	1.2	-	-	-	-	1.1	-	-	-	-	-	-	-
<i>B. leydigia</i>	-	-	-	-	-	2.2	-	-	-	4.3	1.1	1.1	12.9
<i>B. novaezealandia</i>	-	-	-	0.7	-	-	0.7	7.8	-	-	-	-	-
<i>B. quadridentatus</i>	-	0.6	-	-	-	-	6.3	3.7	-	24.8	15.3	57.1	12.9
<i>B. urceolaris</i>	-	1.9	4.8	6.3	0.6	2.7	16.2	5.8	16.7	-	-	-	-
<i>Keratella australis</i>	1.6	5.6	-	0.5	1.0	-	-	-	-	-	-	2.2	-
<i>K. cochlearis</i>	1.2	1.9	1.1	0.5	3.1	3.0	-	-	8.5	-	-	-	2.7
<i>K. procurva</i>	21.3	29.0	15.9	14.2	22.5	32.9	19.4	32.1	49.5	5.0	8.6	7.2	6.7
<i>K. valga</i>	-	1.9	2.3	5.8	-	-	-	0.5	-	-	-	-	-
<i>Filinia</i> spp.	10.1	1.3	-	1.6	3.8	2.2	-	-	-	-	-	-	1.7
<i>Polyarthra</i> sp	18.1	41.0	44.5	51.8	46.8	-	4.8	-	-	-	-	-	-
<i>Synchaeta</i> sp	1.7	0.6	-	-	-	-	-	1.8	-	-	-	-	-
<i>Lecane</i> spp.	1.6	4.6	0.6	-	-	7.9	5.9	10.3	-	61.1	60.0	28.1	57.2
<i>Lepadella</i> sp.	-	-	-	-	-	1.9	8.0	8.2	8.7	-	2.4	-	-
<i>Hexarthra mira</i> .	16.7	1.6	-	4.4	-	-	-	-	-	-	-	-	-
<i>Trichocerca</i> sp.	9.6	4.8	7.1	3.2	6.0	-	1.5	8.9	16.7	4.9	9.0	-	2.7
<i>Trichotria tetractis</i>	-	-	-	-	-	-	6.1	2.3	-	-	1.7	2.4	-
<i>Dicranophorus</i> sp.	-	0.6	18.8	4.2	12.7	0.6	-	-	-	-	0.2	0.3	-
<i>Cephalodella</i> spp.	-	0.9	-	0.7	-	-	-	2.9	-	-	1.1	-	3.3
<i>Mytilinia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	1.2	-
<i>Proales</i> sp.	-	2.5	-	-	-	11.1	21.5	14.3	-	-	-	-	-
<i>Euchlanis</i> sp.	-	-	-	-	-	1.4	-	-	-	-	-	-	-
Total abundance (individuals l ⁻¹)	3075±379	6333±1264	5033±1351	7345±1718	6926±1468	577±274	4122±2698	2428±1149	3941±963	853±157	3814±1512	4736±517	10032±4764

■ Table 3.4.1: Total abundances (individuals l⁻¹) and relative abundances (%) of rotifers identified from no-vegetation, artificial grass, grazed grass, and grass mesocosms on days 0, 7, 14, and 28 after flooding.

Relative abundance (%)													
DAY	0	7				14				28			
TAXA		Bare sediment	Artificial grass	Cut grass	Grass	Bare sediment	Artificial grass	Cut grass	Grass	Bare sediment	Artificial grass	Cut grass	Grass
Copepods: Calanoida													
<i>Boeckella triarticulata</i>	-	-	-	-	-	33.5	27.1	2.1	0.7	23.3	28.7	5.4	1.3
<i>Calamoecia canberra</i>	-	-	-	-	-	2.6	13.4	-	0.2	3.7	4.0	-	-
copepodite	50.0	85.1	80.7	28.6	25.4	-	-	-	-	-	-	-	-
Copepods: Cyclopoida													
<i>Acanthocyclops vernalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	2.6
<i>Mesocyclops</i> sp.	-	0.6	0.5	-	-	9.3	8.9	1.1	2.8	3.9	3.7	1.7	13.9
<i>Microcyclops</i> sp.	-	-	-	-	-	-	-	-	-	0.1	-	-	-
copepodite	33.3	10.0	8.5	7.3	19.1	-	-	-	-	-	-	-	-
Cladocera:													
<i>Macrothrix</i> sp.	-	-	-	-	-	1.2	1.0	-	-	12.1	6.5	1.0	-
<i>Moina</i> sp.	-	3.2	3.6	2.0	3.1	15.0	17.4	0.7	0.5	43.5	27.5	36.3	0.3
<i>Bosmina meridionalis</i>	16.7	-	0.7	-	-	-	-	-	-	-	-	-	-
<i>Ceriodaphnia</i> sp.	-	1.1	-	-	-	1.1	-	-	-	-	1.4	0.7	1.5
<i>Daphnia carinata</i>	-	-	-	0.2	-	0.1	1.3	0.1	-	0.4	0.2	0.5	-
<i>Daphnia lumholtzi</i>	-	-	1.0	1.0	-	-	1.1	-	-	-	5.3	-	0.5
<i>Pleuroxus</i> sp.	-	-	-	-	-	-	0.3	-	-	-	0.1	-	3.4
<i>Alona</i> sp.	-	-	-	-	-	0.1	-	-	-	5.7	4.0	1.1	2.0
<i>Chydrous</i> sp.	-	-	-	0.2	-	-	0.5	0.1	1.0	0.9	0.2	2.5	7.8
<i>Archipleuroxus bayli</i>	-	-	-	-	-	-	-	-	-	-	0.2	-	-
Ostracoda:													
<i>Cypricercus</i> sp.	-	-	-	-	-	-	1.6	30.9	7.7	0.2	1.2	2.5	3.0
<i>Ilyocyprus australiensis</i>	-	-	-	-	-	-	-	-	-	1.2	0.4	0.3	1.1
juvenile	-	-	-	3.2	-	-	-	-	-	-	-	-	-
Insecta: Diptera													
Culicidae: larvae/pupae	-	-	5.1	57.4	52.4	37.0	27.4	65.1	87.1	5.0	16.9	48.3	62.4
Total abundance (individuals l ⁻¹)	0.3±0.1	9.2±1.4	15.0±6.8	15.3±4.2	3.9±2.9	22.2±5.3	30.0±2.4	38.6±12.3	13.7±2.6	117.0±70.8	105±50.2	195.5±50.7	59.6±35.5

■ **Table 3.4.2: Total abundances (individuals l⁻¹) and relative abundances (%) of micro-invertebrates identified from no-vegetation, artificial grass, grazed grass, and grass mesocosms on days 0, 7, 14, and 28 after flooding.**

Momentary rotifer taxon richness ranged from 2-12 for rotifers and from 0-10 for other micro-invertebrates. Temporal trends in species diversity (Shannon-Wiener H') for each treatment are shown in Figure 3.4.6. Habitat structure and nutrient addition effects on diversity were not significant for rotifers (2-way RMA_H: F=0.329, *p*=0.582, 2-way RMA_C: F=2.350, *p*=0.164) or for other micro-invertebrates (2-way RMA_H: F=0.028, *p*=0.870, 2-way RMA_C: F=3.743, *p*=0.089). However, there was a significant interaction between organic matter treatments and time for micro-invertebrates (2-way RMA_{Nxt}: F=26.172, *p*<0.001). This was driven primarily by the loss of diversity in the grass and cut grass treatments on day 14 (one-way ANOVA: F=59.392, *p*<0.001).



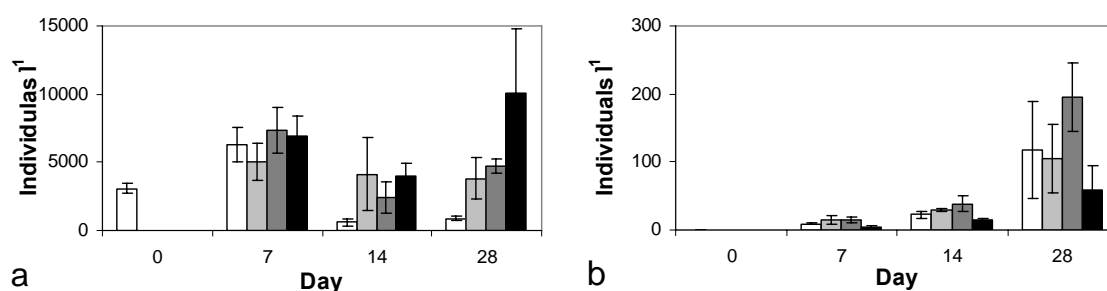
■ **Figure 3.4.6: Sannon-Wiener diversity (H' mean \pm se) of (a) rotifers and (b) other micro-invertebrates identified from no-vegetation (○), artificial grass (●), grazed grass (◐), and grass (●) mesocosms (mean \pm se, $n=3$). Day 0 common to all treatments.**

Rotifer densities ranged from 188-19011 individuals l^{-1} (Table 3.4.1, Figure 3.4.7a). Total densities at day 0 were 3075 ± 379 individuals l^{-1} and were dominated by *Keratella procurva*, *Polyarthra* sp., and *Hexarthra mira*. Habitat structure and organic matter effects on rotifer density were not significant (2-way RMA_H : $F=0.028$, $p=0.871$, 2-way RMA_C : $F=2.703$, $p=0.139$), but time was (2-way RMA_t : $F=4.366$, $p=0.014$). Rotifer densities increased significantly between days 0-7 (one way ANOVA treatments pooled: $F=23.011$, $p<0.001$), decreased between days 7-14 (one-way ANOVA treatments pooled: $F=12.306$, $p=0.002$), and did not change between days 14-28 (one-way ANOVA treatments pooled: $F=1.581$, $p=0.222$).

Micro-invertebrate densities (excl. rotifers) ranged from 0-295.9 individuals l^{-1} (Table 3.4.2, Figure 3.4.7b). Total densities at day 0 were 0.3 ± 0.1 individuals l^{-1} and consisted entirely of copepodites and *Bosmina meridionales*. Habitat structure and organic matter effects on micro-invertebrate density were not significant (2-way RMA_H : $F=2.254$, $p=0.172$, 2-way RMA_C : $F=0.059$, $p=0.814$), but time was (2-way RMA_t : $F=16.939$, $p=0.003$). One-way ANOVAs (treatments pooled) showed that micro-invertebrate density increased significantly between each time interval ($p<0.01$).

Multivariate analyses of rotifer communities indicated that community structure (density and composition) changed significantly between successive sampling events (ANOSIM: $R_{day0-7}=0.572$, $p=0.007$, $R_{day7-14}=0.682$, $p=0.001$, $R_{day14-28}=0.468$, $p=0.001$) (Figure 3.4.8a). Habitat effects (artificial grass and grass treatments pooled, bare sediment and cut grass treatments pooled) were not significant on day 7 (ANOSIM: $R=0.083$, $p=0.740$) or day 28 (ANOSIM: $R=0.004$, $p=0.400$), but were on day 14 (ANOSIM: $R=0.239$, $p=0.048$). Organic matter effects (artificial grass and bare sediment treatments pooled, grass and cut grass treatments pooled) were not significant throughout the study period (ANOSIM: $R_{day7}=0.187$, $p=0.067$, $R_{day14}=0.200$, $p=0.067$, $R_{day28}=0.130$, $p=0.117$).

Multivariate analyses of micro-invertebrate communities indicated that community structure (density and composition) changed significantly between successive sampling events (ANOSIM: $R_{day0-7}=0.964$, $p=0.013$, $R_{day7-14}=0.986$, $p=0.001$, $R_{day14-28}=0.345$, $p=0.001$) (Figure 3.4.8b). Habitat effects (artificial grass and grass treatments pooled, bare sediment and cut grass treatments pooled) were significant within each sampling time (ANOSIM: $R_{day7}=0.624$, $p=0.006$, $R_{day14}=0.878$, $p=0.002$, $R_{day28}=0.435$, $p=0.002$), but organic matter effects (artificial grass and bare sediment treatments pooled, grass and cut grass treatments pooled) were not (ANOSIM: $R_{day7}=0.128$, $p=0.162$, $R_{day14}=0.056$, $p=0.578$, $R_{day28}=0.031$, $p=0.554$).



■ **Figure 3.4.7: (a) Rotifer and (b) micro-invertebrate abundances (individuals l⁻¹) determined for bare sediment (○), artificial grass (◐), cut grass (◑), and grass (●) treatments after flooding (mean ± se, n=3). Day 0 common to all treatments. Note scale differences.**

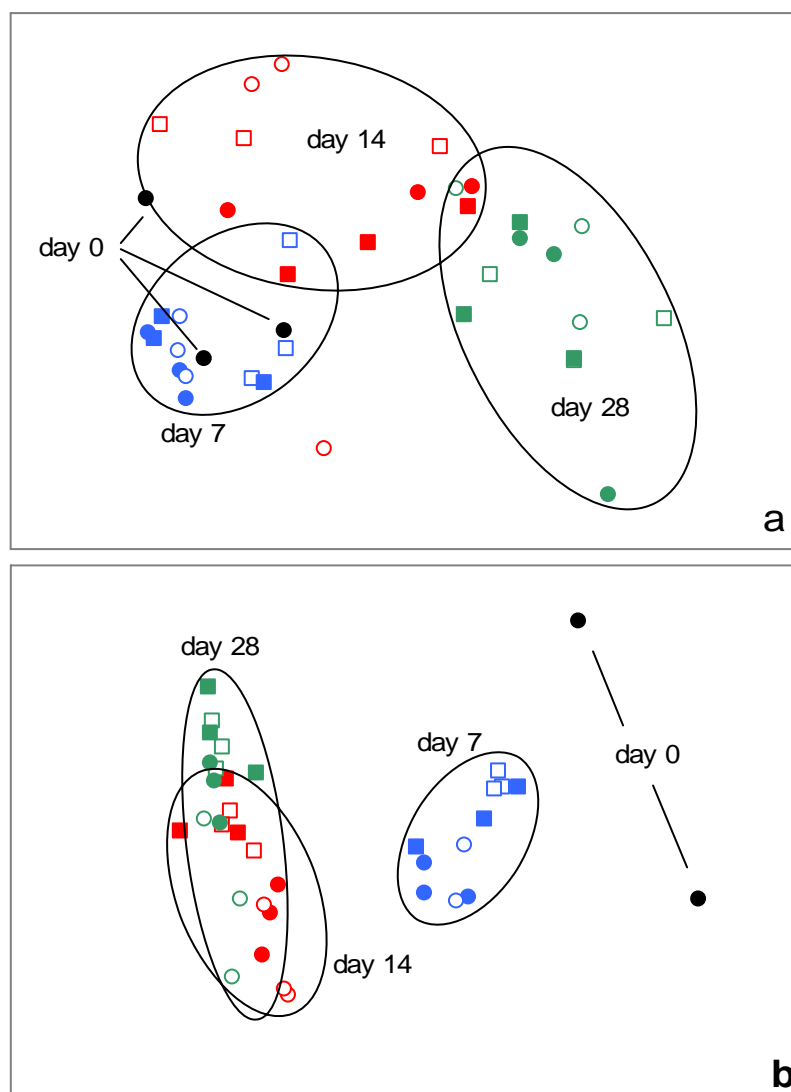
Discussion

Water resource development has increased the permanency of inundation and reduced the duration and frequency of drying events in some EDBL, such as the Menindee Lakes. This effectively reduces the time available for dry lakebed vegetation to establish, and thus also the ecological benefits that these communities provide when inundated such as the leeching of nutrients and organic-matter as they decompose (e.g. Furch and Junk 1997) and critical habitat structure for a range of aquatic organisms (Geddes and Puckridge 1989, Lloyd *et al.* 1989, Gehrke 1990, Arscott *et al.* 2000). We tested whether post-inundation responses of dissolved organic carbon, nutrients, primary production and zooplankton communities were influenced by the presence of submerged vegetation, and whether these responses related either to the leeching of organic matter from the vegetation as it decomposed or to the presence of habitat structure.

Lake flooding is generally associated with increased turbidity derived from particulate matter flushed from catchment floodplains, instream erosion, and lakebed re-suspension. This suspended particulate matter quickly settles, reducing turbidity and increasing light availability for autotrophic production (*cf.* Baranyi *et al.* 2002). After inundation, turbidity declined in all treatments. The presence of intact vegetation initially aided the settling of suspended matter. Treatments with nutrient inputs from vegetation developed more extensive benthic biofilms that consolidated the sediments and reduced their susceptibility to re-suspension.

Dissolved organic carbon (DOC) concentrations increased in all treatments during the study period, but more so in those with (natural) vegetation. These data indicate that both the sediments and vegetation are potentially important sources of carbon for both autotrophic and heterotrophic production. The sediments and submerged vegetation were also important sources of nitrogen and phosphorus, principally as NO_x and FRP, with more NO_x than FRP being released. Flooding initiated an initial pulse of nutrients from the sediments (peak within 1 day), followed by a slower, but larger, pulse from the vegetation (peak within 1 week). Irrespective of habitat structure or nutrient additions, NO_x and FRP concentrations declined steadily towards the end of the 4-week study period, approaching concentrations similar to those initially present within the floodwaters. These declines observed after 5 days in all treatments suggests that rates of NO_x and FRP generation decreased relative to rates of biotic and abiotic uptake. These results support existing models in which the flooding of previously dried lakebed sediments stimulates the release of inorganic nutrients, nitrogen more so than

phosphorus (Qiu and McComb 1996, McComb and Qiu 1998, Mitchell and Baldwin 1998, Baldwin and Mitchell 2000).



■ **Figure 3.4.8: Non-metric multidimensional scaling plots of (a) rotifer and (b) micro-invertebrate assemblages determined on days 0, 7, 14 and 28 after flooding. Square icons–habitat structure present, round icons–habitat structure absent, shaded icons–with nutrient inputs, unshaded icons–without nutrient inputs. Stress levels 0.12 and 0.07, respectively.**

An unanticipated outcome was the generation of significant amounts of NO_x and the more rapid decline in FRP concentrations within the artificial habitat treatment relative to the bare sediment treatment. It is possible that these release and uptake processes, respectively, were related to either the plastic flex used in constructing the artificial grass or to microbial biofilms attached to the flex, especially considering the large increase in surface area presented by the artificial habitat (*ca.* $0.74 \text{ m}^2 \cdot \text{mesocosm}^{-1}$) relative to benthic ($0.28 \text{ m}^2 \cdot \text{mesocosm}^{-1}$) and mesocosm wall ($0.56 \text{ m}^2 \cdot \text{mesocosm}^{-1}$) surface areas.

Phytoplankton biomass, estimated as chlorophyll *a*, increased in all treatments during the first week. Highest concentrations developed in those treatments with vegetation derived organic matter inputs. Subsequent decreases coincided with declines in labile nitrogen (NO_x) in all but the artificial habitat treatment, where FRP concentrations rather than NO_x concentrations declined.

Net primary production (NPP) ranged from -11.53 to $11.91 \text{ g C m}^{-3} \text{ d}^{-1}$. All treatments displayed similar temporal responses, with treatment effects altering the magnitude of NPP and the timing of transitions between net heterotrophy and autotrophy. Treatments that had greater organic matter inputs (*i.e.* those with vegetation) varied most, being both most productive and most consumptive. For all treatments, net primary production (NPP) shifted from net heterotrophy to net autotrophy during the first week, then (except for the artificial grass treatment) reverted to net heterotrophy by day 28. This shift is consistent, firstly, with heterotrophs (*i.e.* microbes) responding more rapidly than autotrophs (*i.e.* algae) to flooding and the concomitant increases in available organic matter and light (*i.e.* reduced turbidity), and secondly, with algal senescence fueling heterotrophic activity.

Of the 46 micro-invertebrate taxa encountered during the study, at least 27 were not present initially in the floodwaters. Numerous studies have shown that rotifers and other micro-invertebrates produce resting stages (eggs, cysts) that allow them to bridge periods of adverse environmental conditions, such as lake drying, and that lake flooding triggers the emergence of a succession of invertebrate communities (*e.g.* Hairston *et al.* 1995, Boulton and Lloyd 1992, Jenkins and Briggs 1997, Jenkins and Boulton 1998, Nielsen *et al.* 2000). Rotifer abundances increased significantly during the first week post-inundation, and new rotifer taxa were recorded on each sampling occasion. As generation times for these taxa lie in the order of 3-4 days (Allan 1976), it is most likely that these new taxa emerged from the sediments at different rates. A similar process was apparent for other micro-invertebrate taxa, although abundances were orders of magnitude lower and rates of emergence slower than for rotifers. These timings of emergence were similar to those reported by Boulton and Lloyd (1992), and reflect changes in rotifer and crustacean biomass reported by Baranyi *et al.* (2002). For example, Baranyi *et al.* (2002) reported that crustacean biomass exceeded rotifer biomass after approximately 14 days, after which rotifer biomass declined. Rotifers are suppressed and often excluded by large cladocerans (Brooks and Dodson 1965, Gilbert 1988) through exploitative competition for the same phytoplankton food resources (Kirk 1991) and mechanical interference (Gilbert and Stemberger 1985, Burns and Gilbert 1986). As we did not record zooplankton size structure, such interactions could not be identified. Copepodites constituted a significant component of the micro-invertebrates introduced at day 0. These take about 14 days to reach reproductive maturity (Allan 1976, Ingram *et al.* 1997). As no copepodites were recorded after day 7, it is unlikely that recruitment of these taxa from the sediments occurred. The appearance of mosquito larvae/pupae after day 0 was most likely the result of aerial invasion. Mosquitos, the principal predator recorded during the study, showed a preference for nutrient treatments (grass and cut grass). However, their impact on zooplankton community structure, in terms predation, could not be determined.

Significant temporal shifts in community structure after flooding were observed for both rotifers and micro-crustaceans. Whilst no significant habitat or organic matter effects were detected for either rotifer or micro-crustacean abundances or diversity, a significant habitat effect was identified for micro-crustacean community structure (incorporating both abundance and diversity information).

We hypothesised that submerged terrestrial vegetation constitutes both an important source of organic matter as it decomposes and modifier of aquatic habitat structure, and that these would stimulate aquatic productivity and diversity. Whilst inundated sediments were a source of carbon, nitrogen and phosphorus, these were also released from the inundated vegetation. The presence of vegetation thus increased the potential for primary production, measured both

as CHL_a and NPP. However, both algal biomass and NPP decreased once labile nitrogen and phosphorus pools became depleted after the first week. These results highlight the link between nutrient availability and aquatic productivity. This has implications not only for management actions that reduce the frequency and duration of lake drying episodes, and thus the time available for lakebed vegetation to develop, but also for the management of lakebed vegetation, which may be compromised by activities such as grazing or cropping (e.g. Robertson 1998, Seddon and Briggs 1998).

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3.5 Effects of lake drying and predation on post-inundation responses

B. Gawne and O. Scholz

Abstract

The drying of ephemeral lakes has been found to lead to an increase in productivity upon re-inundation. The mechanisms underlying this disturbance mediated increase in productivity are poorly understood. Observations of ephemeral systems indicate that drying leads to both changes in lake trophic structure and nutrient availability. Both these changes have been found to affect the productivity of wetland systems and so an experiment was conducted to determine the role of bottom-up and top-down effects in determining post-flood productivity in ephemeral lakes. The mesocosm experiment manipulated hydrological regime and predator presence in a two-way factorial design and observed the impact on water quality, algal biomass and productivity and zooplankton community structure. The results indicate that both predator presence and nutrient releases from dried sediments have an impact on lake response to flooding after a drying event. The results also indicate that other factors have the potential to interact in complex ways to influence the response of biota to wetland drying and flooding cycles. Developing a better understanding of the factors that influence an ephemeral wetland's response to flooding will help explain variable responses to flooding observed in natural systems.

Introduction

Water Resource Development has lead to numerous changes in EDBL function with the installation of weirs and levies. Prior to such developments EDBL would be filled by floodwaters from the main channel, or directly by local rainfall and then dry. Regulatory operations have significantly modified the natural hydrological regime of many of these lakes with impacts on the frequency, duration, timing, magnitude and variability/predictability of flooding and drying events. One common impact has been the loss of a dry phase. This loss is associated with declines in water quality, biodiversity and productivity (*e.g.* Boulton and Lloyd 1992, Robertson *et al.* 1999, Kingsford 2000).

Drying affects every aspect of the ecology of ephemeral lakes, but two phenomena that appear common to ephemeral lakes are changes in the availability of nutrients as dried lakes fill (Podrabsky *et al.* 1998, Baldwin and Mitchell 2000) and changes in the trophic structure of lakes as they flood and dry (Batzler and Wissinger 1996, Corti *et al.* 1997, Lake *et al.* 1989, Timms and Boulton 2001). The Flood Pulse Concept (Junk *et al.* 1989) suggests that the flooding of dried floodplain habitats initiates a 'bottom-up' cascade of energy transfer commencing with the autotrophic (bacterial and photosynthetic) utilisation of freely available nutrients. This in turn benefits the secondary and tertiary consumers. Production at each successive trophic level increases until the driving resource, be it nutrients or food, becomes limiting. This hypothesis is based on the observation that flooding provides a pulse of nutrients through the import of nutrients to the system and the Birch effect releasing a pulse of available nutrients from dried sediments (McComb and Qiu 1998, Baldwin and Mitchell 2000). While drying mediated increases in productivity have been observed in algae (Wetzel 1983, Crome and Carpenter 1988), macrophytes (Briggs and Maher 1985) and invertebrates (Maher 1984, Boulton and Lloyd 1992, Jenkins and Boulton 1998), flood mediated increases in nutrients are by no means ubiquitous (McComb and Qiu 1998) and so their role in fuelling an increase in productivity is uncertain. To date there have been very few detailed investigations of the effects of drying on productivity or of the underlying mechanisms driving the observed changes.

In contrast to the Flood-Pulse Concept, which is a 'bottom-up' or resource controlled model of trophic structure, 'top-down' models emphasise the effects of higher trophic levels on the biomass and productivity of lower trophic levels (Hairston *et al.* 1960, Carpenter *et al.* 1985, Carpenter and Kitchell 1987, 1992). After re-filling, lake herbivore and predator populations tend to be at their lowest due to the extirpation of animals during the dry phase and subsequent dilution of survivors (Crome and Carpenter 1988, Lake *et al.* 1989, Neckles *et al.* 1990, Corti *et al.* 1997). Top-down models would tend to suggest that the increase in productivity might, therefore, be due to lower consumer pressure upon reflooding and the greater resilience of algae and zooplankton communities.

The objective of this study was to examine the role of bottom-up and top-down forces in determining post-flood primary productivity in lakes that have dried.

Methods

Twelve identical 500 l stock troughs (diameter = 1.13 m, depth = 0.5 m) were placed in two rows in the open such that neither received more or less exposure to shade or sunlight. In early 1998 wet sediment was collected from Lake Tandure, an arid-zone ephemeral deflation basin lake associated with the Darling River in SW NSW. This sediment was placed in each trough to a depth of 0.1 m and covered with 0.25 m unfiltered water from the Darling River. Half the troughs were randomly allocated to a 'Dry' treatment in which water was allowed to evaporate for several months, reflecting natural drying rates. The sediments were then kept dry for three months. The sediment in the other six troughs were allocated to a 'Wet' treatment that was kept under at least 0.10 m of water by periodic addition of Darling River water.

On April 27 1999, water from the Darling River was added to each trough to a maximum depth of 0.4 m (*ca.* 480 l). The water was passed through a 50 μm mesh filter. Throughout the course of the experiment the troughs were periodically topped up with aged tap water in order to maintain a depth of at least 0.3 m. Once filled, twenty notonectids were added to each of three randomly selected Wet and three Dry troughs ('Predator' treatment). Notoonectids were selected as the predator because they are ubiquitous in EDBL, and ethically the use of vertebrates should be avoided. The effects of notonectid and fish predation have been found to be similar in other studies (Arner *et al.* 1998, Riessen 1999) and so notonectids provided a realistic substitute for fish. All troughs were covered with mosquito netting to reduce predator emigration. Where necessary, additional notonectids were added to maintain predator densities.

Nutrients and water quality were sampled 1 and 6 hours after water was added and then on days 3, 7, 14, 28, 56 and 90. On each sampling date, water column pH, turbidity and temperature were recorded at 7 am and 1 pm, using a U-10 multi-probe (HORIBA Ltd., Australia). From each trough on each sampling event 200 ml of unfiltered water was frozen for total nitrogen (TN) and total phosphorus (TP) determinations. Two replicate 10 ml aliquots of 0.45 μm filtered trough water were frozen for determinations of oxides of nitrogen (NO_x) and filterable reactive phosphorus (FRP). Total nitrogen was first converted to nitrate using $\text{NaOH-K}_2\text{S}_2\text{O}_8$, then reduced to nitrite using a cadmium column. Nitrogen as nitrite was then determined colorimetrically (APHA 1995). Total phosphorus was first converted to orthophosphate using $\text{NaOH-K}_2\text{S}_2\text{O}_8$. Phosphorus as orthophosphate was then determined colorimetrically using the phosphomolybdate-blue method (APHA 1995). Detection limits were $\text{TN} \pm 0.019 \text{ mg N l}^{-1}$ and $\text{TP} \pm 0.0025 \text{ mg P l}^{-1}$.

Suspended chlorophyll *a* concentrations (phytoplankton fraction) were determined on days 0, 2, 7, 28, 56 and 90. 500 ml of water was filtered through Whatman GF/C filters and the

chlorophyll extracted using hot ethanol with acid-correction for phaeophytin to distinguish viable from non-viable algal biomass (APHA 1995). Additional 25 cm² samples were collected on days 28, 56 and 90 from the trough sides (biofilm fraction), and the sediment surface (benthic fraction). For the biofilm fraction, a 4 cm² template was used to define an area of wall from which algae was removed by scraping with a cloth which was then placed in ethanol treated as described above. Three 1 cm sediment cores were collected and pooled to determine benthic chlorophyll. These samples were then placed in ethanol and analysed using the same technique described above.

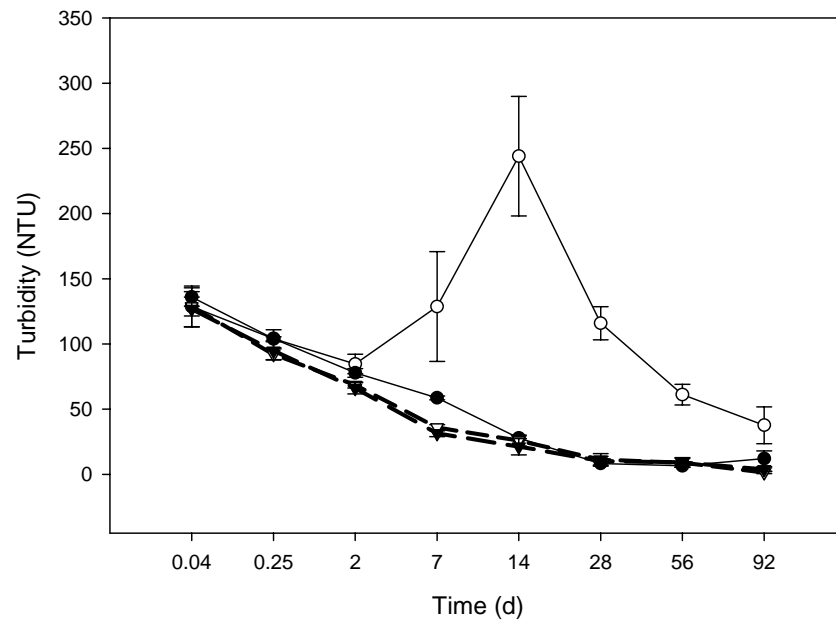
Community metabolism in each trough was estimated by measuring diurnal changes in dissolved oxygen concentration in enclosed 1.5 l clear perspex chambers (9.5 cm radius x 25 cm height). A single chamber was pushed into the sediments of each trough on days 3, 7, 14, 28, 56, and 90. A recirculating 12 V in line pump (11 l min⁻¹ Whale 991 in-line pump, Munster Sims, Bangor Nth. Ireland) was used to circulate water within each chamber. Oxygen concentration was measured electronically and recorded every ten minutes (YSI 5775 dissolved oxygen probe, YSI Inc. Ohio, connected to a WP-82 dissolved oxygen and temperature meter, TPS Pty Ltd., Brisbane). Changes in oxygen concentration were monitored for at least 24 h. at 15 minute intervals Oxygen data were converted to units of carbon using a photosynthetic quotient of 1 and a ratio of 1 mg.O₂ = 0.375 mg.C. Data are reported as mg C h⁻¹ as we could not determine the proportion of benthic production relative to the water column.

Zooplankton was sampled on days 2, 7, 14, 28, 56, and 91 by passing 10 l of water through 50 µm mesh size plankton nets. Filtered samples were preserved with Lugol's Iodine solution (APHA 1995). Depending on densities, between 4 and 12 transects were examined from each of four Sedgewick-Rafter cell preparations until at least 250 organisms had been counted. Identifications for rotifers, cladocerans and copepods followed Shiel (1995) and for arthropods Williams (1980).

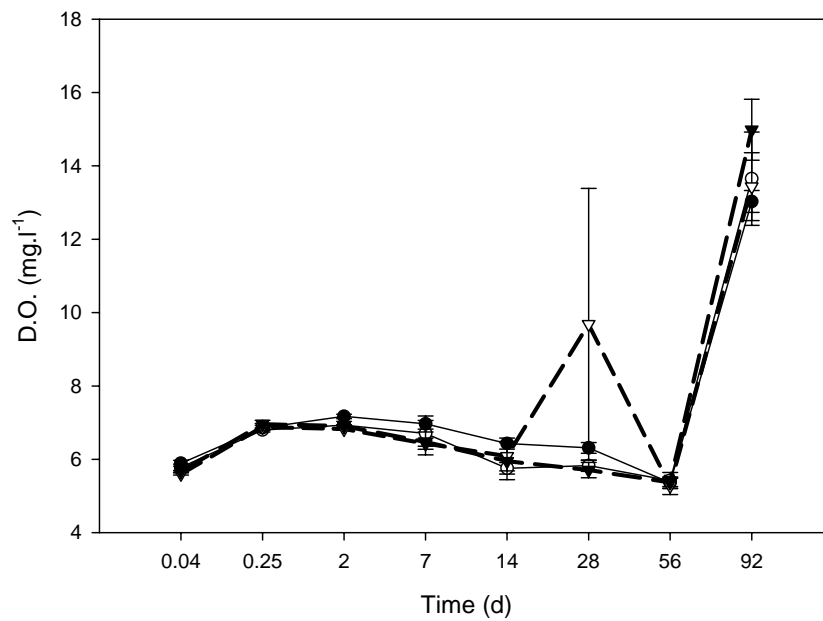
All water quality, nutrient, chlorophyll, production, phytoplankton and zooplankton abundance data were analysed as two-way repeated measures ANOVA (RMA) with water regime and predator presence as fixed factors. Data for each sampling date were also analysed by two-way ANOVA. ANOVAs were calculated using SYSTAT[®] V10.2 (SPSS Inc., Chicago USA). RMA probabilities are presented as *p* and G-G adjusted *p* values. Similarities in zooplankton community structure (composition and abundance) between treatments and times were examined using MDS and ANOSIM using PRIMER (V5; Primer-E Ltd., 2000). Data for these analyses were square-root transformed to down-weight the influence of individual taxa and to increase analytical robustness to zero values before calculating the Bray-Curtis dissimilarity matrices.

Results

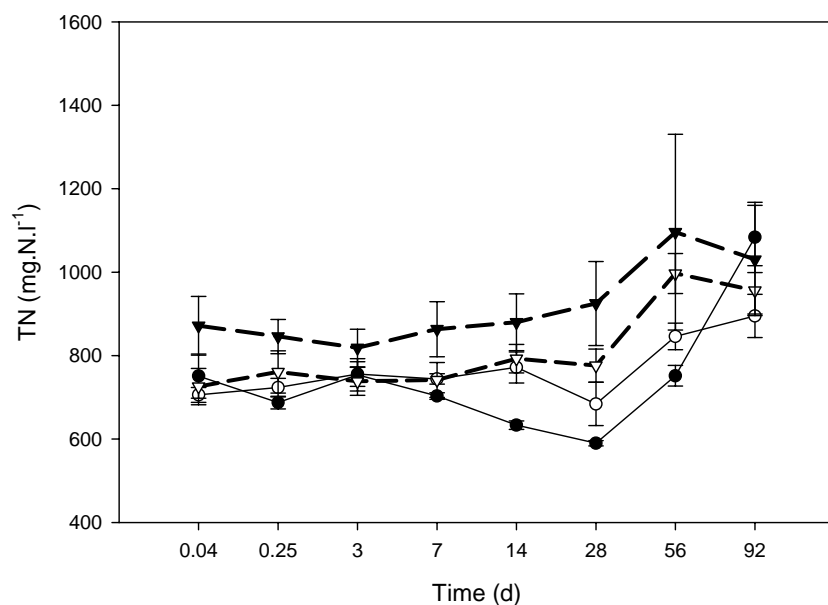
All measured water quality parameters changed significantly through time (RMA: G-G < 0.00001). Turbidity (Figure 3.5.1) declined through time while conductivity increased. The lowest dissolved oxygen concentrations (Figure 3.5.2) and maximum pH were recorded on day 56. Total nitrogen concentrations increased through time, while NO_x, TP and FRP all declined over the course of the experiment (Figures 3.5.3-3.5.6).



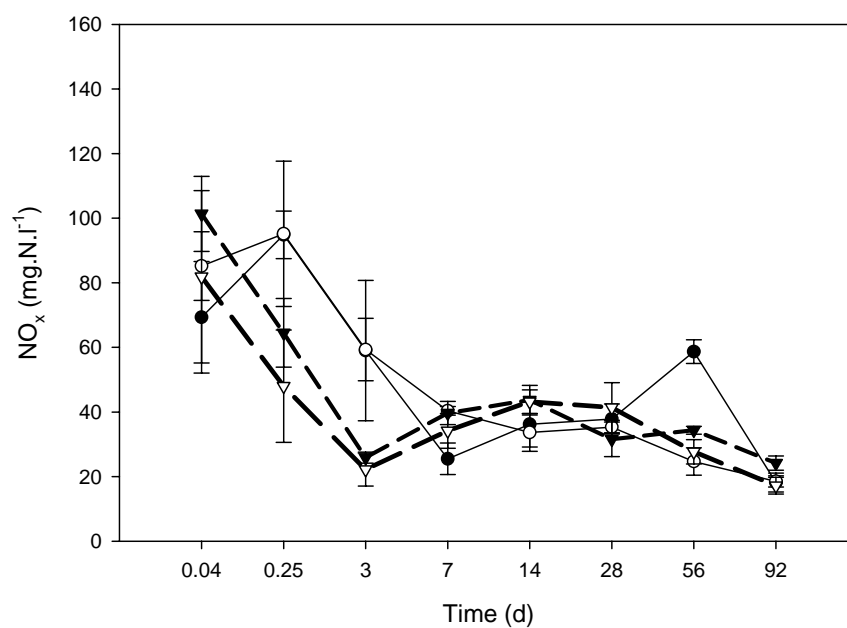
■ Figure 3.5.1: Turbidity (NTU) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean ± se).



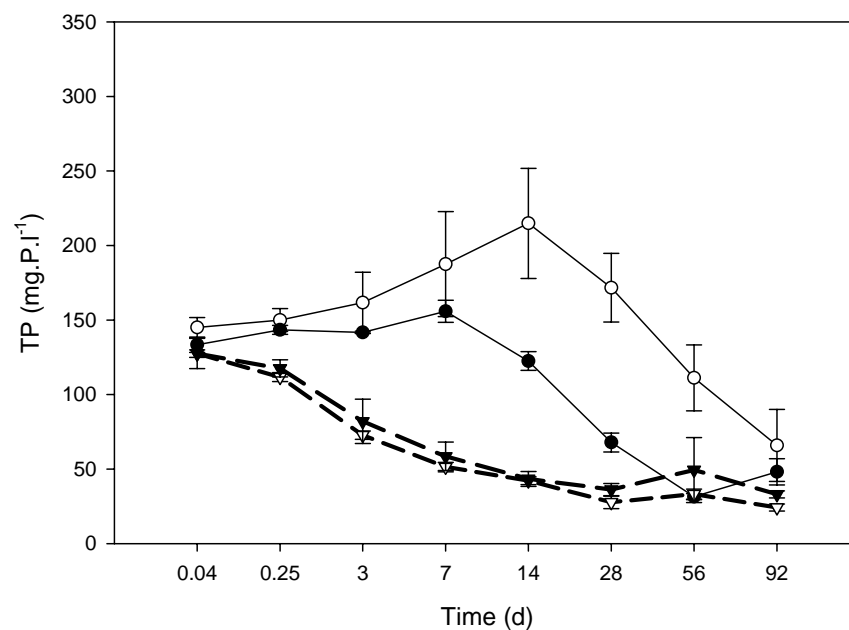
■ Figure 3.5.2: Dissolved oxygen (mg l⁻¹) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean ± se).



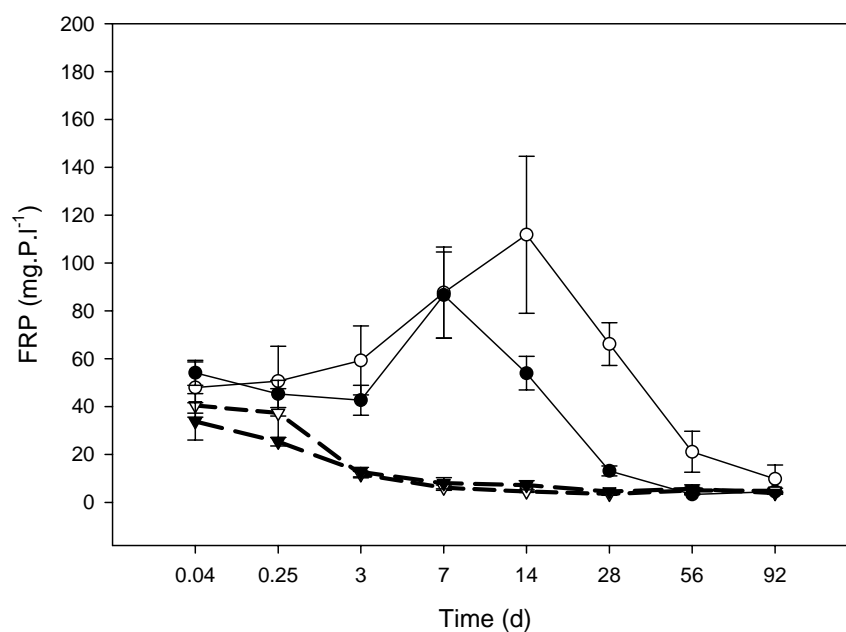
■ Figure 3.5.3: Total nitrogen (TN; mg N l⁻¹) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean ± se).



■ Figure 3.5.4: Oxides of nitrogen (NO_x; mg N l⁻¹) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean ± se).



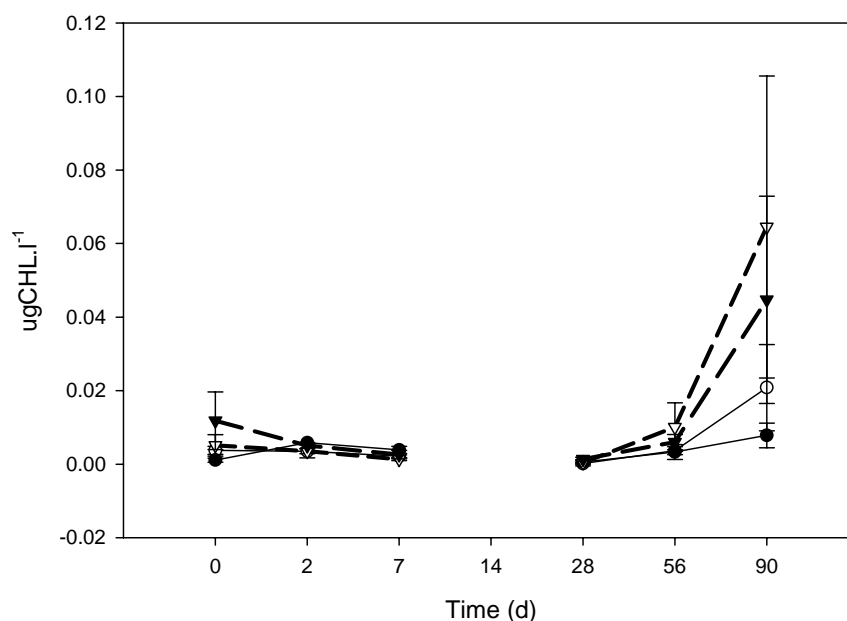
■ Figure 3.5.5: Total phosphorus (TP; mg P l^{-1}) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (Δ), and wet/predator (▲) treatments (mean \pm se).



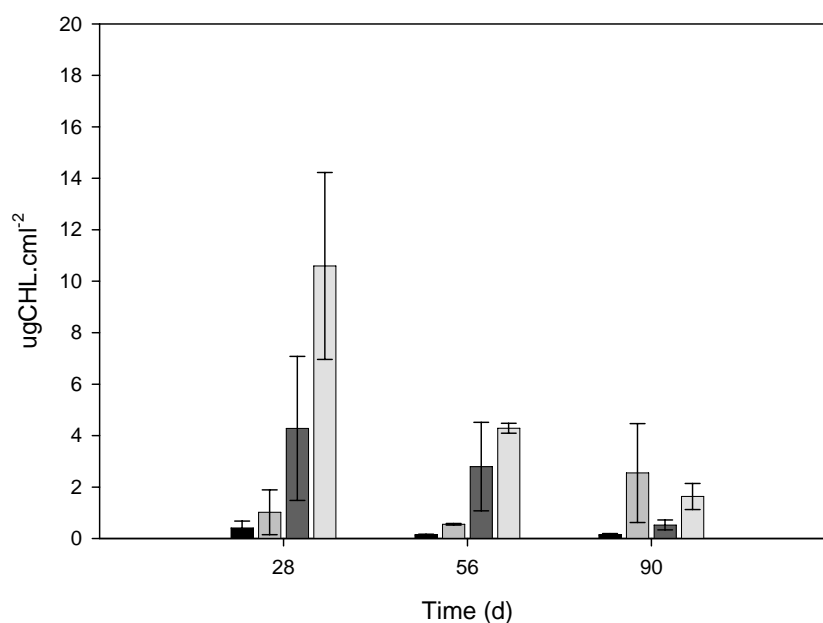
■ Figure 3.5.6: Filterable reactive phosphorus (FRP; mg P l^{-1}) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (Δ), and wet/predator (▲) treatments (mean \pm se).

The presence of predators or the imposition of a dry phase affected a number of water quality parameters. Troughs that remained wet had significantly higher conductivity, TP and TN concentrations (RMA: $p < 0.042$). These differences are probably due to the additional water, with associated salts and nutrients that was added to these troughs in order to keep them wet. There were significant changes in the concentration of TN and TP through time with the changes being influenced by drying in the case of TN (RMA: $p = 0.0011$) and by both drying and the presence of predators in the case of TP (RMA: $p = 0.0014$). NO_x concentrations varied significantly through time (RMA: $G\text{-}G = 0.00001$), and these changes differed between drying treatments (RMA: $G\text{-}G = 0.0064$). FRP was influenced by an interaction among predator presence and drying (RMA: $p = 0.047$) with the presence of predators leading to lower FRP when the trough dried and similar FRP concentrations in the absence of a dry phase.

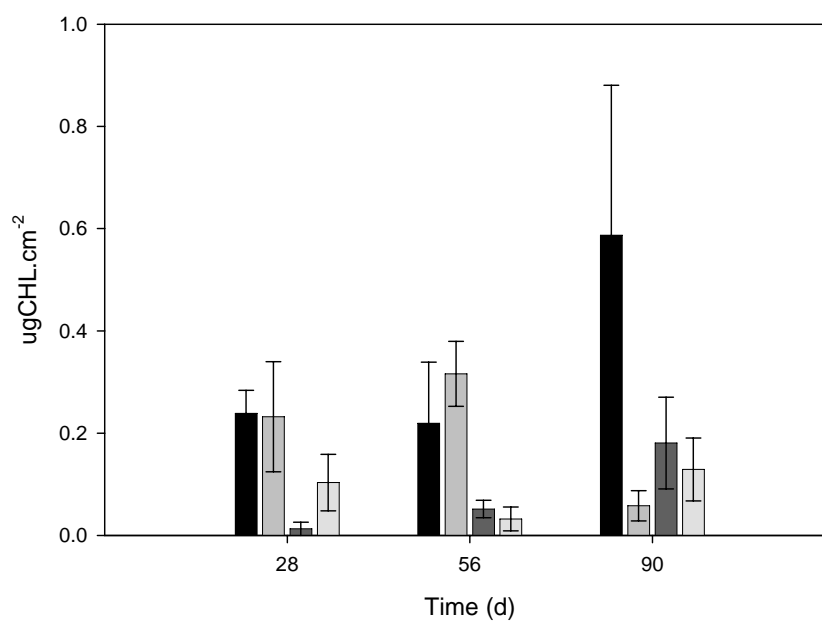
Phytoplankton biomass (Figure 3.5.7), measured as chlorophyll *a*, initially declined and then increased significantly in all treatments (RMA: $G\text{-}G = 0.039$). Treatments had no effect on phytoplankton biomass (RMA: $p > 0.095$). The most obvious difference among Wet and Dry treatments was the accumulation of thick benthic mats of algae that provided a complex three-dimensional structure to Wet treatments. Benthic algae were not one of the initial suite of parameters assessed, and so data for the early sampling dates are not available. Wet treatments had significantly greater sediment chlorophyll *a* (ANOVA: $p = 0.0056$, Figure 3.5.8) and significantly less chlorophyll *a* on trough walls (ANOVA: $p = 0.026$, Figure 3.5.9) on day 28 but not on subsequent dates (ANOVA: $p > 0.105$). On day 90, sediment chlorophyll analysis revealed a significant interaction between predator presence and a dry phase (ANOVA: $p = 0.037$).



■ **Figure 3.5.7: Phytoplankton biomass ($\mu\text{g CHL l}^{-1}$) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean \pm se).**

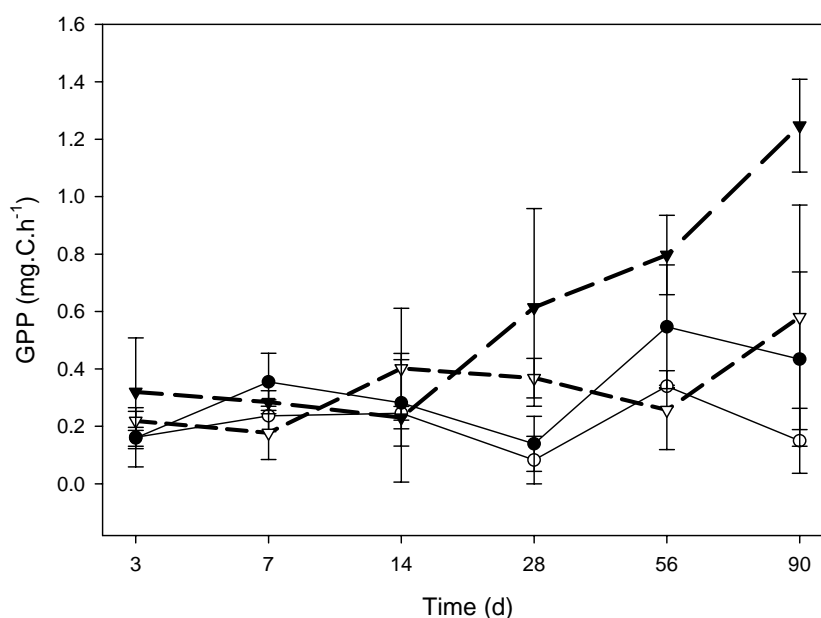


■ Figure 3.5.8: Benthic algal biomass ($\mu\text{g CHL cm}^{-2}$) determined after re-flooding of dry/no predator (■), dry/predator (■), wet/no predator (■), and wet/predator (■) treatments (mean \pm se).

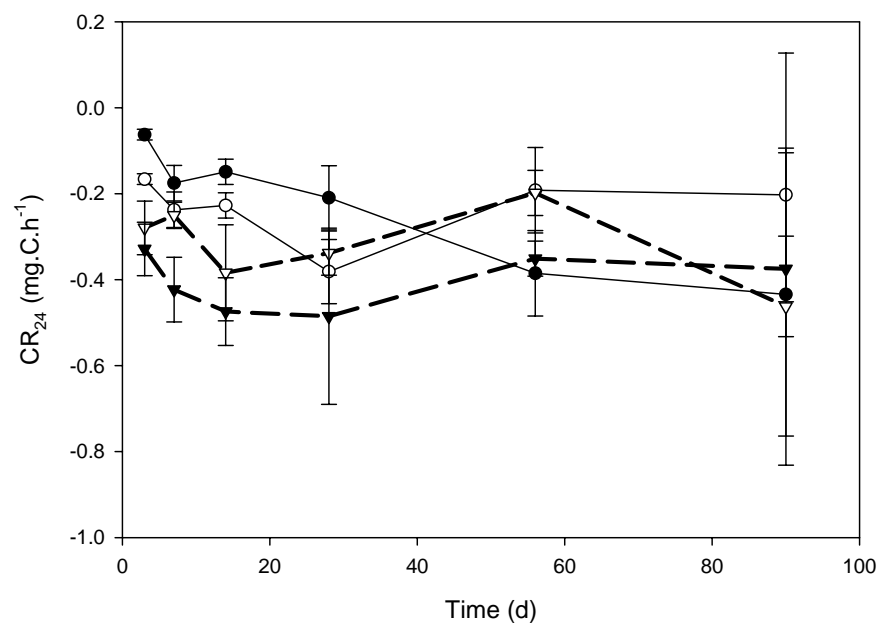


■ Figure 3.5.9: Trough wall biofilm algal biomass ($\mu\text{g CHL cm}^{-2}$) determined after re-flooding of dry/no predator (■), dry/predator (■), wet/no predator (■), and wet/predator (■) treatments (mean \pm se).

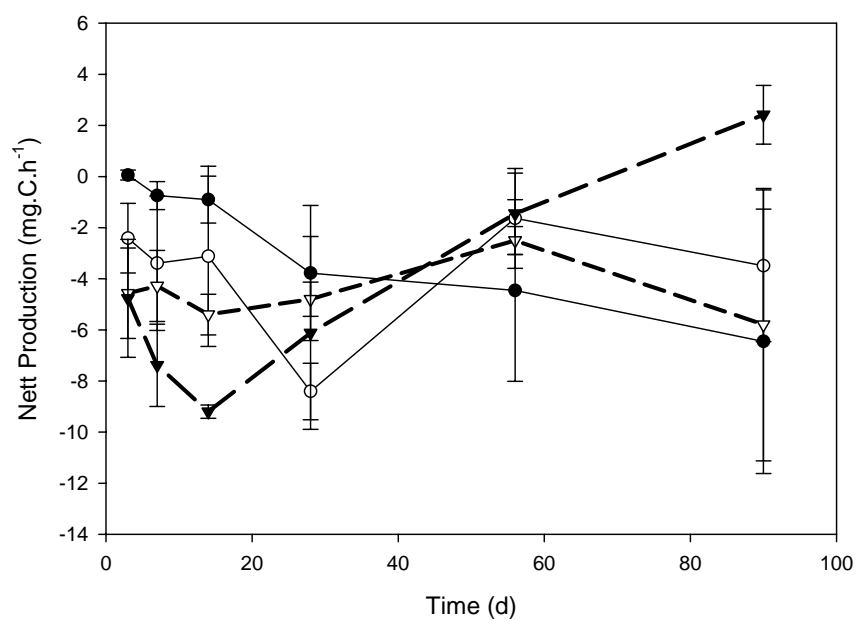
There were no significant trends in GPP or CR₂₄ through time (RMA: $G-G>0.064$), although the Wet treatments with predators started with the lowest NPP and had the highest NPP after three months, while dried troughs with predators started with the highest NPP and had the lowest after three months (Figure 3.5.10). Rates of GPP were similar in all treatments for the first month, after which the Wet treatments increased rates of GPP, which lead to a significant effect of drying on rates of GPP (RMA: $p=0.037$) (Figure 3.5.10a). A comparison of treatments with and without predators revealed a similar trend of increasing GPP through time that meant that over the course of the experiment troughs with predators had higher rates of GPP (RMA: $p=0.049$). There was no significant interaction between Predation and Dry treatments (RMA: $p=0.484$). Wet troughs had significantly higher rates of CR₂₄ (RMA: $p=0.039$), although these differences diminished through the course of the experiment (Figure 3.5.10b). The presence of predators only affected CR₂₄ on day 56 (ANOVA: $p=0.043$), when troughs with predators had higher rates of CR₂₄. The higher rates of CR₂₄ in Wet treatments for the first two weeks of the experiment meant that NPP in Wet treatments was significantly lower on days 3, 7 and 14 (ANOVA: $p<0.037$, Figure 3.5.10c), but the repeated measures ANOVA did not reveal a significant effect of drying on NPP (RMA: $p=0.19$).



■ Figure 3.5.10a: Gross primary production (GPP; mg C h⁻¹) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean ± se).

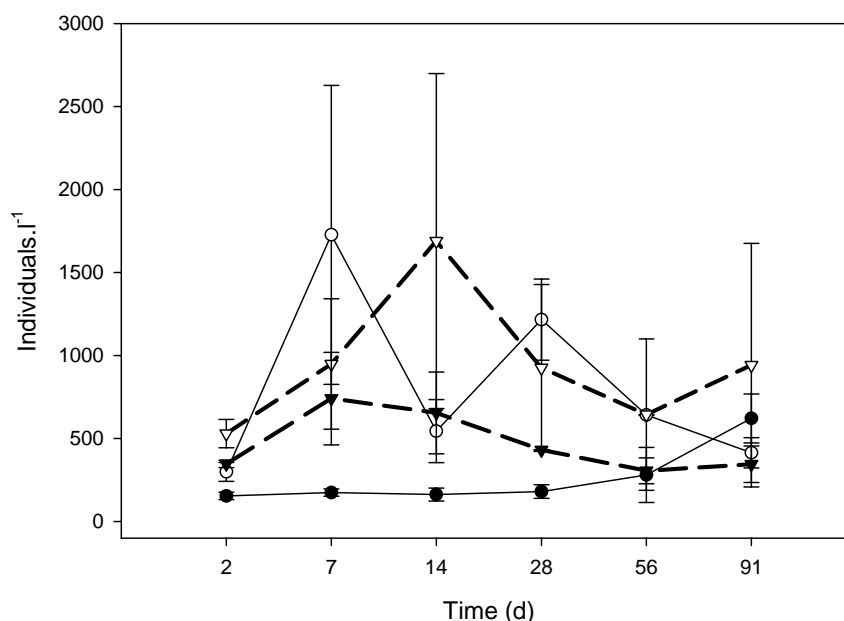


■ Figure 3.5.10b: Community respiration (CR_{24} ; $mg\ C\ h^{-1}$) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean \pm se).



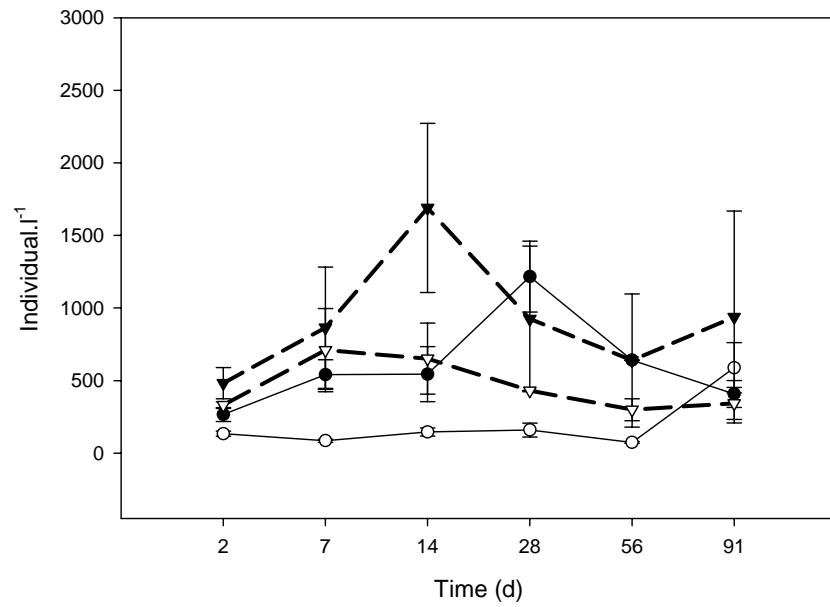
■ Figure 3.5.10c: Net primary production (NPP; $mg\ C\ h^{-1}$) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean \pm se).

There were no significant changes in zooplankton abundance (Figure 3.5.11) or number of taxa through time (RMA: $G\text{-}G>0.096$). Over the course of the experiment, troughs with predators had lower abundances of zooplankton (RMA: $p=0.048$), but there were no consistent differences due to drying. Drying did have a significant effect (ANOVA: $p<0.033$) on zooplankton abundance on days 3 and 14 when Dry troughs had lower zooplankton abundance.

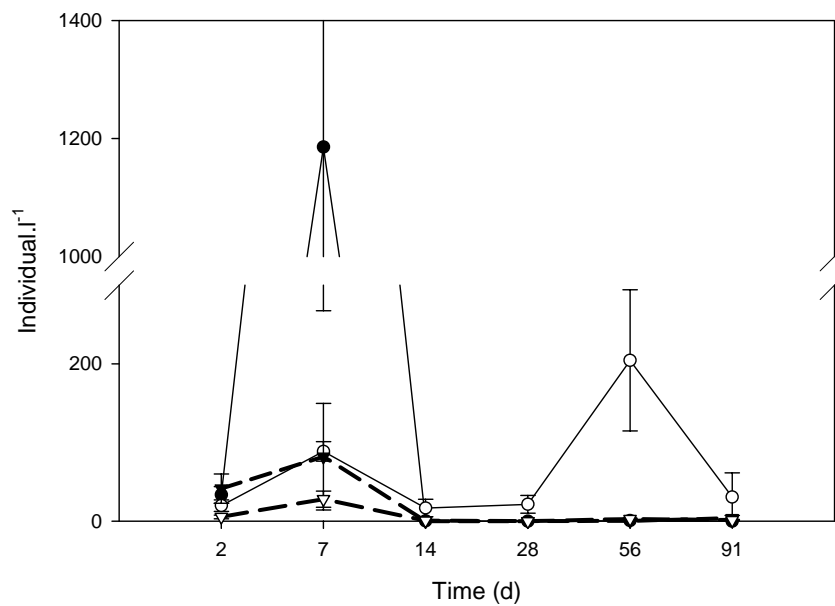


■ **Figure 3.5.11: Zooplankton abundance (individuals l^{-1}) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean \pm se).**

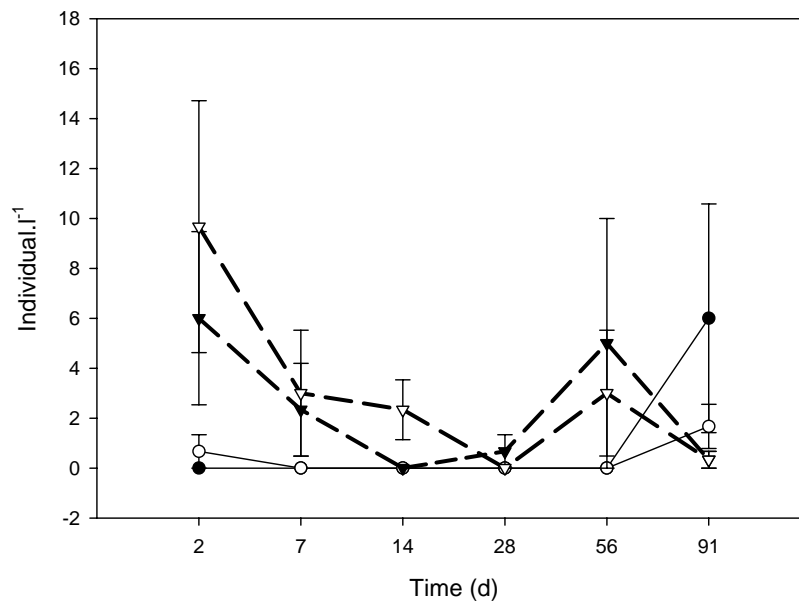
A separate analysis of crustacean (Figure 3.5.12) and rotifer abundance (Figure 3.5.13) did reveal significant changes through time (RMA: $G\text{-}G<0.039$) and significant treatment effects (RMA: $p<0.018$). Crustacean abundance was lower in Dry treatments and lower in Predator treatments (RMA: $p=0.018$). Rotifer abundance reached a peak in the first week after inundation and then declined in all treatments except Dry with Predators (Figure 3.5.13). Over the course of the experiment rotifers were more abundant in Dry treatments (RMA: $p=0.0077$). Insect abundance was greatest in Wet treatments (RMA: $p=0.035$) and only started accumulating in Dry treatments toward the end of the experiment (Figure 3.5.14). The presence of predators had no significant effect on insect numbers (RMA: $p=0.728$).



■ Figure 3.5.12: Crustacean abundance (individuals l⁻¹) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean ± se).



■ Figure 3.5.13: Rotifer abundance (individuals l⁻¹) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean ± se).

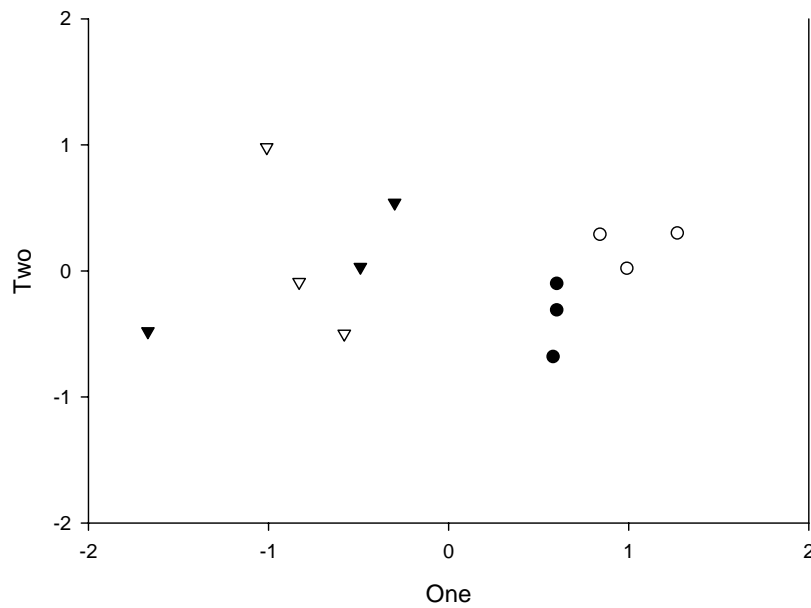


■ **Figure 3.5.14:** Insect abundance (individuals l^{-1}) determined after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (mean \pm se).

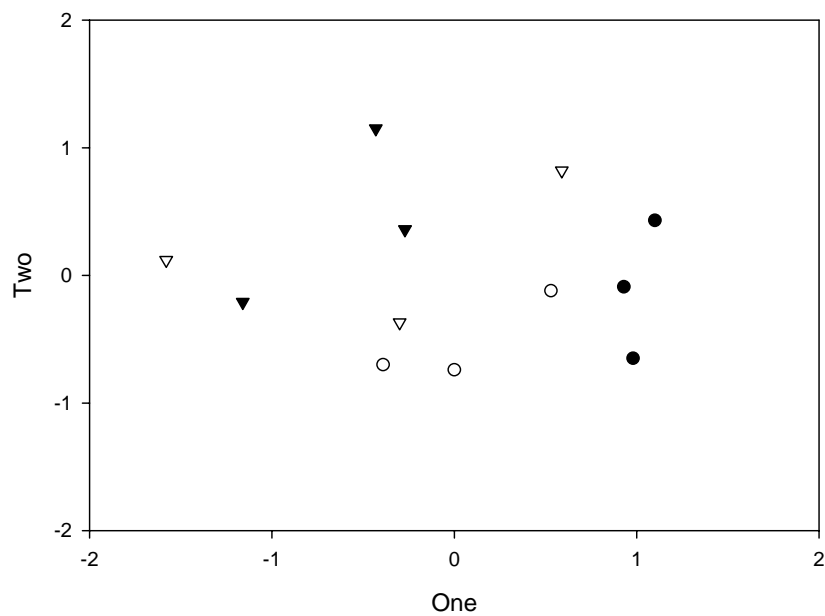
Multivariate analyses of the zooplankton communities indicated that the significance of drying and predator treatment effects varied through time (Table 3.5.1). For example, on day 3 both drying and predator treatment effects were significant (Figure 3.5.15). By day 14 there was only a significant drying treatment effect (Figure 3.5.16), and after 28 days there was only predator treatment effect (Figure 3.5.17).

Days after inundation	Drying effect	Predator effect
	<i>p</i>	<i>p</i>
3	0.03	0.01
7	0.01	0.10
14	0.03	0.25
28	0.10	0.01
56	0.45	0.85
90	0.03	0.12

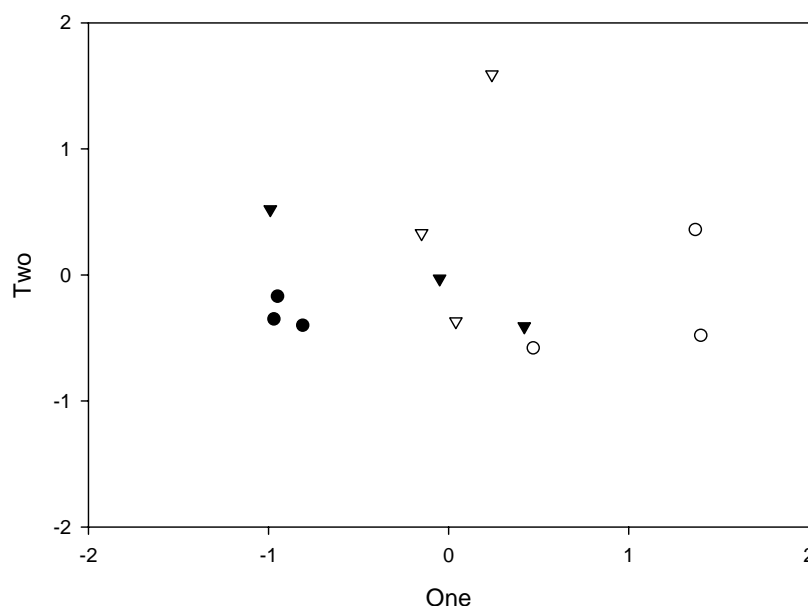
■ **Table 3.5.1:** ANOSIM results showing level of significance (*p*) of drying and predator treatment effects on zooplankton assemblage structure over time after inundation.



■ Figure 3.5.15: Non-metric multidimensional scaling plot of zooplankton assemblages determined on day 3 after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (stress 0.08).



■ Figure 3.5.16: Non-metric multidimensional scaling plot of zooplankton assemblages determined on day 14 after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (stress 0.09).



■ **Figure 3.5.17: Non-metric multidimensional scaling plot of zooplankton assemblages determined on day 28 after re-flooding of dry/no predator (○), dry/predator (●), wet/no predator (△), and wet/predator (▲) treatments (stress 0.05).**

Discussion

The results indicate that both bottom-up and top-down forces influence an ephemeral wetland's response to flooding. The effects of experimental manipulations of sediment desiccation and the food web interacted in complex ways to determine the overall response.

One of the disadvantages of conducting experiments in mesocosms is that they produce artefacts. The experimental set up used in this study is no different. The major difference observed between the experimental troughs and natural lakes was the accumulation of mats of benthic algae. In natural lakes, consumption and disturbance would limit the accumulation of benthic algae. Subsequent interpretation of the results is therefore couched in terms of this difference between lakes and mesocosms.

A second limitation of this study is that in order to impose the treatments, water was added to Wet treatment troughs. This had a significant effect on the concentrations of nitrogen, phosphorus and salt, which makes interpretation of trends in water quality difficult to interpret strictly in terms of a response to drying. We believe that the addition of water to the troughs provided an appropriate representation of what happens to regulated wetlands where water is added to offset evaporative and consumptive losses and, therefore, the comparison between Dry and Wet troughs is similar to the comparison between natural ephemeral wetlands and those in which the dry phase has been lost due to regulation.

One of the predictions was that drying the sediments would lead to the release of nutrients upon inundation (Birch Effect; McComb and Qiu 1998, Baldwin and Mitchell 2000) and that this would lead to an increase in productivity. Although there were no significant differences in the initial concentrations of available nitrogen between treatments, greater total nitrogen and total phosphorus concentrations developed in the troughs in which the sediments had been dried. It is not clear whether this change was due to the release of available nitrogen from dried sediments or whether the biological demand for nitrogen was lower in dried

treatments. The lack of significant differences in photosynthesis rates suggest that the demand by primary producers for nitrogen may have been similar, but higher rates of respiration suggest that heterotrophic demand for nitrogen may have been higher in troughs that remained wet. Drying also affected the concentration of available phosphorus with significantly higher concentrations in dried troughs on days 7, 14 and 28. In this instance, it would appear that releases from the sediments contributed to the observed increases in total phosphorus concentrations.

If the Birch Effect were to produce a trophic cascade, then we would expect that the dried troughs, with higher concentrations of available phosphorus and slower declines in the availability of NO_x , would support higher rates of primary and heterotrophic production and that this might fuel increases in zooplankton abundance. It would appear that sediment nutrient releases had only limited effects up the food web. Dried troughs had similar rates of photosynthesis and lower rates of respiration. Only rotifer numbers were significantly higher in dried treatments with total zooplankton abundances being similar among dried and continually wet treatments. This pattern does not support the classic trophic cascade model, but does suggest that increased nutrients may have limited effects up the food web.

Regardless of the Birch effect, the results presented here reveal that respiration rates and changes in chlorophyll *a* were affected by sediment drying. The results indicate that drying is a disturbance that eliminates algae so that benthic algal abundance is greater in troughs that remained wet. Rates of respiration were also higher in troughs that remained wet indicating that a greater proportion of the carbon fixed was respired compared to troughs that were dried and had similar rates of photosynthesis. This suggests that a greater proportion of the carbon fixed in dry troughs was used to support algal growth or was consumed.

Wetland drying is a major disturbance for aquatic organisms that results in the mortality of many species. We hypothesized that changes in the number of predators in a system due to drying might have a significant impact on prey organisms and that these effects may cause a trophic cascade that would affect algal productivity and/or abundance. Our results indicate that the presence of predators has a significant negative impact on some prey species (crustacean zooplankton) but a positive effect on others (rotifers). This type of predator effect is similar to studies performed in rock pools (Arner *et al.* 1998) and farm dams (Geddes 1986) in which notonectids significantly decrease the abundance of crustacean zooplankton.

In only two instances did the presence of predators cascade down to affect either algal abundance or production. The first was on day 56 when predation did produce the expected increase in photosynthesis and respiration. The reason for the lack of predator effects on the other dates sampled is not clear. Day 56 did not represent a peak in zooplankton abundance and predator numbers were kept relatively constant throughout the experiment, so a change in consumer pressure seems unlikely. The second instance was that predators affected the change in chlorophyll *a* through time on the trough walls even though there were no significant differences in chlorophyll *a* among the three times sampled.

The presence of predators in the system significantly decreased FRP concentrations on days 28 and 56. This decrease suggests that predator effects did cascade down the food web and affect nutrient concentrations. This type of effect has been found in other lakes (Hansson and Tranvik 1997, Schaus and Vanni 2000), but external nutrient loading from the catchment (Vanni *et al.* 1992) and nutrient re-cycling by predators (Vanni and Layne 1997, Persson 1997, Reissig *et al.* 2003) have the capacity to overwhelm the direct depletion of nutrients by algae. The reasons that predator effects on FRP concentrations were not more consistent through time in the current experiment are not clear.

The current experiment provides limited evidence for both a bottom up and top down trophic cascade in response to drying and changes in trophic structure, but the cascading effects are weak and variable. Two broad situations have been identified that may dampen or eliminate

cascading effects in lentic systems. The first is where other stresses are acting on the system (Phillips *et al.* 1999). It is possible that the mesocosm placed some additional stress on the systems or that the simultaneous manipulation of bottom up and top down manipulations produced greater variability in response than would be expected from a manipulation of either predator pressure or drying alone.

Trophic cascades have also been found to be weaker in complex systems (Shapiro 1990, Lazzaro 1997). We did not anticipate the extensive growth of filamentous algae in the permanently inundated troughs, but these mats of algae provided a far more structurally complex habitat than that present in the dried troughs. This complexity may have reduced the ability of predators to forage (Schriver *et al.* 1995, Stephen *et al.* 1998) or may have reduced the ability of zooplankton to have a significant effect on productivity in permanently inundated troughs.

Top down cascades have also been dampened when the zooplankton community is dominated by small taxa such as rotifers (Pace 1984, Angeler *et al.* 2000). In the current experiment, notonectid predation increased rotifer abundance. This change may have decreased the zooplankton community's capacity to affect the phytoplankton community due to their lower clearance rates (Vanni *et al.* 1992) and because rotifers tend to feed on small algae and bacteria (Boon and Shiel 1990). Perhaps there was a dampening of cascade due to the increase in rotifers abundance, which may have maintained grazing pressure on algae.

The Flood Pulse Concept (Junk *et al.* 1989) and studies of birds (Kingsford 2000), zooplankton (Jenkins and Boulton 1998), and macroinvertebrates (Maher and Carpenter 1984, Boulton and Lloyd 1992) suggest that flooding leads to an increase in productivity. It was, therefore, surprising that there was neither a significant pulse in primary production after inundation or greater differences in the primary productivity of the dried and permanently inundated treatments. The lack of significant differences is also surprising given the different nutrient environments and the different amounts of algae on the walls and sediments of dried compared to permanently inundated treatments. These data suggest that there was some additional factor limiting photosynthesis in the mesocosms. The effects of flooding have been found to vary in response to nutrients (Bukavekas and Crane 2002), depth (Briggs *et al.* 1993, Poizat and Crivelli 1997), flood timing (Nielsen and Chick 1997, Poizat and Crivelli 1997), lake shape (Hamilton and Lewis 1990), and connectivity (Tockner *et al.* 1999). As all these parameters were either consistent among treatments or were part of the manipulation, we have no data to indicate what may have been limiting primary productivity in the mesocosms.

The lack of significant differences in productivity between experimental treatments suggests that the rates of primary production in dried systems could be similar to those in permanently inundated systems. The data also suggest a mechanism whereby drying and flooding may still lead to an increase in secondary production despite similar rates of primary productivity. While the amount of carbon being fixed by algae in permanently inundated systems was similar to that in dried systems, the rates of respiration were higher. This suggests that the microbial loop was consuming a greater proportion of primary production and, therefore, that less carbon was available for consumption by higher trophic levels. The microbial loop is acknowledged as being an important metabolic pathway in lentic systems (Serruya 1990, Hart *et al.* 2000, Bunn *et al.* 2003). The data presented here suggests that the proportion of organic matter passing through the microbial loop may be affected by drying events.

The current data suggest that higher trophic levels did not respond to the greater rate of accumulation of organic matter in dried treatments. The reasons for this may be related to a variety of factors including the standing stock of algae, which was greater in permanently inundated troughs or the habitat in which the primary production was occurring. In this experiment, algae that accumulated on the walls of the dried troughs may not have been accessible to the zooplankton sampled. It would also appear that the ability of consumers to

benefit from higher productivity might depend on the presence of predators that are capable of affecting prey numbers.

The preceding paragraphs should not be considered to be an argument for drying and flooding producing any specific effect; rather this experiment provides some insight into the complex interactions among factors that change during a dry-flood cycle. We manipulated two of the factors known to vary during a drying-flooding cycle; sediment mediated nutrient cycles and predator abundance, and found that both bottom-up and top-down influences have some impact although these effects may vary through time.

In this experiment, the effects of flooding also appear to be related to the persistence, in permanently inundated troughs, of large mats of filamentous algae which were able to rapidly utilize the nutrients added when all the troughs were filled. The filamentous algae also provided a complex habitat for zooplankton, which may have affected foraging by notonectids (Gotceitas and Colgan 1989). These effects suggest that the response to flooding will depend on the suite of organisms present in the system and their capacity to respond to inundation.

The effects of drying and flooding may also affect the fate of organic matter in floodplain systems. Examinations of the effects of drying on sediment microbial communities have revealed that drying is a major disturbance that has the potential to affect nutrient cycling within wetlands (Baldwin and Mitchell 2000). The current work reveals that drying of the microbial and algal community also has the potential to affect the amount of organic matter that is available to higher trophic levels. The consequences of this type of change needs further investigation, but could provide further insight into the role of drying in determining post-flood secondary productivity.

The Flood Pulse Concept and work on sediment-nutrient cycles has suggested that floods are important primarily because of their influence on post-flood productivity. The work presented here suggests that other interactions that occur during dry-flood cycles may also be important in determining post-flood aquatic ecosystem response. In an era where managers are attempting to restore flooding ecosystems, understanding the role of some of these other factors (food web alterations, persistence and the microbial loop) and their interactions may help us to better predict the outcomes from particular water management strategies.

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4: Conceptual model of EDBL function

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Abstract

Ephemeral deflation basin lakes (EDBLs) occur throughout the arid and semi-arid regions of the Murray-Darling Basin in Australia. They are diverse and productive habitats whose management has generally lead to significant declines in wetland condition. Managers are currently trying to protect or restore these systems without an adequate theoretical framework on which to base management decisions. Existing conceptual models provide little insight into the effects of any component of the flow regime except flooding and are therefore inadequate. We review the effects of flooding and drying on lakes and use the information to propose a conceptual model that identifies 5 stages in the cycle of flooding and drying. The conceptual model incorporates elements of the Flood Pulse Concept, Trophic Cascade and Geomorphic Trophic models as they apply to these highly variable systems.

Introduction

Ephemeral deflation basin lakes (EDBLs) are widespread throughout the arid and semi-arid regions of the Murray-Darling Basin in Australia where evaporation exceeds rainfall. They are important both as wetlands and as components of the larger floodplain ecosystem (Ward 1989, Ward and Stanford 1995). They support diverse and productive plant and animal communities and provide, for example, critical nursery habitat for native fish (Puckridge 1999) and breeding and feeding habitat for birds (Kingsford 2000a). In addition to these values, EDBL represent a valuable resource for human activities, with many now used to grow crops, as water storages and recreational areas. A growing body of evidence suggests that the impacts of water resource and agricultural development on arid-zone EDBL have generally been detrimental in terms of net ecosystem productivity and diversity (Kingsford 2000a,b).

EDBL are lowland river floodplain environments that fluctuate between terrestrial and aquatic states. Water resource management has significantly altered the hydrological regime of many EDBL within the Murray Darling Basin. This has given rise to three broad categories of EDBL. Those that have not been affected by water resource development, those that are dry more frequently than natural, and those that are wet for longer or more frequently than natural (35% of Murray R. wetlands; Pressey 1990) (Seddon and Briggs 1998). These hydrological changes strongly influence biotic and abiotic processes.

It is generally agreed that both wet and dry periods are important in maintaining ecosystem integrity in ephemeral wetlands (Boulton and Lloyd 1992, Bunn *et al.* 1997, Boulton and Jenkins 1998). Disturbances, such as flooding and drying, drive aquatic and terrestrial successional processes and facilitate biotic and abiotic exchanges between elements of the floodplain and the riverine environment (*cf.* Flood Pulse Concept; Junk *et al.* 1989). Because of this EDBL are potentially sites of high productivity and diversity within arid zone floodplain ecosystems. As a consequence, the management of these systems has implications for the productivity and diversity at a landscape scale.

Whilst the pressure placed on managers to achieve both environmental and water resource objectives has increased, the knowledge required to achieve these objectives is not readily available. This is despite the increasing body of knowledge concerning various aspects of the ecology of these systems. Such knowledge is fragmented and is not integrated within a

conceptual framework appropriate to EDBL that encompasses aspects of both wet and dry lake phases. For example, although the Flood Pulse Concept (Junk *et al.* 1989) predicts that the loss of flooding would be expected to have a detrimental effect on wetland condition, there are no similar conceptual models to predict the effect of the loss of drying episodes.

This review examines existing conceptual models of ephemeral lake ecology and reviews our knowledge of the ecological impacts of drying and inundation in an attempt to construct an heuristic conceptual model of EDBL.

EDBL distribution

The majority of EDBL of the Murray Darling Basin occur within western New South Wales. In their survey of lakes in this region, Seddon and Briggs (1998) identified 567 deflation basin lakes larger than 100 ha. Although numerous smaller deflation basins have been identified and mapped, little if any information exists for the majority of lakes. Seddon *et al.* (1997) have compiled a database of lake attributes and published literature for EDBL (>100 ha) within western New South Wales. Though not restricted to EDBL alone, similar information covering smaller wetlands and those considered important from a conservation stand point throughout the Basin has been compiled by ANCA (1996).

Geomorphically, EDBL are floodplain depressions formed by wind and wave action moving material from their beds eastwards with the prevailing winds. Sand dunes or lunettes formed by the deposition of these eroded materials commonly occur on the eastern margin of lake basins. Lakebeds generally consist of fertile clay soils deposited by successive flooding events, and differ markedly from the soils on surrounding higher ground (Bowler 1990, Pressey 1990). These lakes receive water only intermittently through connection to their riverine supply during periods of high flow or from local rainfall. They are thus subject to episodes of rapid flooding followed by more protracted periods of evaporative drying. The periodicity of these wet/dry phases varies considerably between lakes. Whereas some lakes receive water from annual high river levels and fill frequently, others may remain dry for many years or even never fill where the supply channels have been cut. Variations in groundwater interactions between lakes may also impact upon hydrologic regimes. At present, however, little information concerning these processes is available. Despite their geomorphological similarity, EDBL are heterogeneous. Flood frequency, flood duration, salinity and source of water vary greatly between lakes (Seddon and Briggs 1998).

The periodicity of flooding and drying is not well documented for most EDBL. Records are available for some of the more actively managed storages, such as Lake Victoria (SA Water) and the Menindee Lakes (NSW DIPNR), and for those on the Darling Anabranch (Withers 1994) and Talyawalka Creek (Withers 1996). Similar records are, however, not usually kept for rainfall filled lakes, which are often excluded from management strategies because they do not occur on the floodplains of gauged rivers. It has become clear over the last two decades that all EDBL are very vulnerable to water resource development (Kingsford 2000b, Roshier *et al.* 2001)

Existing conceptual models

In order to manage EDBL in a sustainable manner and protect their environmental values, managers require conceptual models on which to base management strategies and design monitoring programs to evaluate environmental outcomes. There are several conceptual models available to scientists and managers concerning lake ecology that could be used to

guide management of EDBLs, but they are all derived from Northern Hemisphere lakes or tropical rivers and, therefore, are not always appropriate in an Australian context.

Alternate Stable States

The first of these conceptual models regards lakes as oscillating between stable states of macrophyte domination or phytoplankton domination (Scheffer *et al.* 1993, Casanova *et al.* 1997, Bachmann *et al.* 1999). These states are influenced by the distribution and concentration of nutrients. The loss of macrophytes has the effect of eliminating habitat for a range of invertebrates (Diehl and Kornijow 1992, Schriver *et al.* 1995, Burks *et al.* 2001), thereby altering trophic structure. While this idea may have some utility in EDBL, it hasn't currently been linked to hydrological regime. It is, however, widely recognised that changes to the hydrological regime have a significant impact on the macrophyte community (Poiani and Johnson 1993, Casanova 1994, Blanch *et al.* 1999). The idea of alternative stable states, therefore, only provides managers with guidance on nutrient management and erosion, not hydrological management.

Trophic Cascade

Trophic cascade or food web models may also have some relevance to the management of EDBL. These models suggest that lake productivity and community composition are determined by a combination of top-down and bottom-up forces, such that changes in the fish community can influence algal abundance and water quality. While food web manipulations have been successful in achieving improvements in water quality and reducing algal blooms (Carpenter and Kitchell 1988, Carpenter *et al.* 2001), there are some situations in which they are inappropriate. Trophic cascades appear to be weakened as the food web or habitat becomes more complex (Shapiro 1990, Lazzaro 1997), or where other stresses such as sedimentation plays a role (Phillips *et al.* 1999). The trophic cascade models do not consider water regime and are, therefore, of only limited utility to those concerned with the effects of water resource development.

Flood Pulse Concept

The third conceptual model is the Flood Pulse Concept (FPC) (Junk *et al.* 1989, Lewis *et al.* 2000), which states that the flood pulse stimulates aquatic productivity. While formulated to describe the ecology of river-floodplain ecosystems rather than individual wetlands, floods have been found to be important in determining the productivity and diversity of lake communities. Whilst several recent Australian studies have indicated that alterations of flooding regimes has had a detrimental impact on Australian wetlands (Briggs *et al.* 1998, Kingsford 2000a), the FPC makes no reference to either long term flow regimes or other important hydrological events such as drying (Walker *et al.* 1995, Puckridge *et al.* 2000). As a consequence, the FPC provides advice for only one component of the water regime within ephemeral lakes.

Geomorphic Trophic Model

The fourth conceptual model is the Geomorphic Trophic Model (GTM). This model suggests that variation in bio-geochemical and biotic processes between floodplain lakes can be largely understood and predicted on the basis of morphometric and hydrologic factors. The GTM has been invoked in Orinoco floodplain lakes, where lake shape affects turbidity which in turn

affects the biotic community (Lewis *et al.* 2000), and in Arctic lakes, where lake shape affects the persistence of fish through the winter freeze (Hershey *et al.* 1999). Lake shape also affects diversity with positive correlations having been reported between lake surface area and the diversity of zooplankton (Dodson 1992, Dodson *et al.* 2000), fish (Barbour and Brown 1974, Browne 1981) and mollusc (Browne 1981) species. The increase in diversity with lake surface area appears to be an example of the species-area relationship, although the mechanism producing these patterns has received little attention (Douglas and Lake 1994).

Lake morphology also affects lake productivity with shallower lakes being more productive (Hamilton and Lewis 1990, Serruya 1990, Perin *et al.* 1996). The mechanisms underlying this pattern include mixing/stratification, oxygenation, the relative contribution of the littoral zone and the input of nutrients (Hamilton and Lewis 1990, Serruya 1990, Perin *et al.* 1996). Because there is a relationship between lake depth and lake hydroperiod, it is possible that observed patterns of productivity in ephemeral lakes are due to the fact that ephemeral lakes tend to be shallower than permanent lakes of similar volume. However, this hypothesis does not explain why water resource development has such detrimental effects on EDBL.

What emerges from this summary is that none of the existing conceptual models adequately describe the relationship between water regime and lake ecology. The lack of a conceptual model is partly due to the lack of data about the changes that occur in lakes as they undergo cycles of flooding and drying. There is, however, a growing body of information about the ecology of floodplain and ephemeral wetlands and the rest of this review will attempt to synthesise the available information with an examination of changes associated first with drying and then with flooding.

Ecological consequences of lake drying and flooding

Lake drying

Drying occurs through the combined effects of draining, evaporation and groundwater infiltration with the relative importance of each process varying among lakes and drying stage. Most of the available literature appears to concern lakes and wetlands in which evaporation is the dominant process. As lakes and wetlands evaporate, a number of predictable changes appear to occur. There is a concentration of nutrients, salt and organisms and an increase in turbidity (Talling 1992, Thormann *et al.* 1998). Increases in algal abundance and changes in algal species composition have also been reported (Talling 1992, Ibanez 1998).

A further common feature of drying lakes is that biotic interactions such as predation and competition increase (Schneider and Frost 1996, Golladay *et al.* 1997, Tockner *et al.* 1999). These changes are linked to declining habitat availability (Golladay *et al.* 1997) and to increases in the proportion of predatory taxa (Batzler and Wissinger 1996, Corti *et al.* 1997, Moorehead *et al.* 1998, Lake *et al.* 1989), although this trend is not universal (Timms and Boulton 2001). Increases in predator abundance have been explained primarily in terms of the progressive colonisation of ephemeral lakes and wetlands by predators (Wiggins *et al.* 1980, Lake *et al.* 1989, Jeffries 1994).

While the number of predatory taxa increases with drying, the situation is complicated by changes in habitat availability that occurs as a result of drying. Top-down control has been found to be more important in shallow lakes (Jeppesen *et al.* 1997), so as lakes dry and become shallower predation may become more intense without additional colonisation by predatory taxa. As an example of the way in which predator pressure may change, deep lakes

offer fish refuge from avian predation, but eventually this refuge is lost and while some fish may attempt to find their way back to deeper refuges, many remain isolated (Kahl 1964, Kushlan 1976). Without a refuge the fish community may undergo a dramatic reduction as avian predation becomes more effective (Kushlan 1976, Scholz *et al.* 1999). The reduction in fish numbers may offer invertebrate predators (*e.g.* notonectids, dytiscid beetles) an opportunity to proliferate (Boulton and Lloyd 1991, Jeffries 1994).

In the final stages of drying the concentration of nutrients and salts can be extreme and fluctuations in water quality also increase as the buffering capacity of the volume of water is diminished and the lake becomes more exposed to the weather (Talling 1992, Balla and Davis 1995, Podrabsky *et al.* 1998). When the lake finally dries there is typically a well established vertical zonation of terrestrial, flood dependent vegetation surrounding an area of dry cracked mud where salt levels were too high, or drying conditions too extreme to allow the development of vegetation. Within the sediments there remain the drought resistant propagules of micro-invertebrates (Boulton and Jenkins 1998, Jenkins and Boulton 1998), algae (Robson 2000, Stanley *et al.* 2004) and plants (Brock 1998) awaiting cues for germination. Other animals may find refuge in burrows (yabbies, frogs) or in moist habitats under litter (Wiggins *et al.* 1980, Boulton 1989).

Drying also consolidates sediments on the lake bed (van der Wielen *in press*). This process is affected by the duration of the dry phase, but can, upon re-inundation decrease rates of sediment resuspension and increase rates of particle settlement. This has the ultimate effect of increasing light penetration into the water and thus also primary production.

The loss of lake drying

Even though many taxa have found ways of surviving periods of drying, there can be little doubt that drying is a major disturbance. The loss of a dry phase has been found to lead to significant changes that are often perceived as being deleterious. For example, invertebrate productivity (Brinson *et al.* 1981, Maher and Carpenter 1984, Briggs and Maher 1985) and diversity (Leslie *et al.* 1997, Boulton and Jenkins 1998) have been shown to suffer in response to the loss of wetland drying. The loss of a dry phase has also been associated with an increase in introduced species such as carp (*Cyprinus carpio*) (Gehrke *et al.* 1995, Boulton and Jenkins 1998, Gehrke *et al.* 1999). Significant changes have also been observed in the vegetation community with loss of lignum (*Muehlenbeckia cunninghamii*) and red gums (*Eucalyptus camaldulensis*) (Walker and Thoms 1993, Thornton and Briggs 1994) and changes in the macrophyte community (Brock and Casanova 1991, Poiani and Johnson 1993, Walker *et al.* 1994). While far less is known about changes in ecological processes it would appear that the loss of a dry phase leads to an increase in the importance of anaerobic decomposition of organic matter (Brinson *et al.* 1981, Boon *et al.* 1996).

In regulated systems, a greater proportion of the water is drained for consumptive use. This may have implications for the ecology of regulated lakes by facilitating the export of nutrients, salt and organisms such as algae and micro-invertebrates. We are not currently aware of any data that would allow determination of the effects of these changes on lake ecology, but it is possible that it may have some effect on the post-flood nutrient pulse. There are concerns that accelerated draw-down may alter the rate of concentration of solutes in a lake and that this may deprive some micro-invertebrates of the cues or time required to stimulate the production of resting stages (Kalk and Schulten-Senden 1977, Ricci 2001). To date, there is little Australian evidence to support this hypothesis (SKM 2002).

Lake flooding

Floods are highly variable phenomena, particularly in Australia where flood frequency, magnitude, timing and duration are all highly unpredictable (Puckridge *et al.* 1998). Flood effects vary with timing (Boulton and Jenkins 1998, Nielsen *et al.* 1999), depth (Briggs *et al.* 1993b, Leeper and Taylor 1998), mode of flooding (Quinn *et al.* 2000) and flood water quality (Leeper and Taylor 1998, Rabalais *et al.* 1998, Lewis *et al.* 2000). Despite this variation some effects are common to all floods.

Floods are associated with a pulse of nutrients and organic matter. Nutrients and organic matter are released from dried sediments (Qui and McComb 1996, Baldwin and Mitchell 2000) and vegetation (Furch and Junk 1997), and/or imported with the flood water (Hillbricht-Ilkowska 1999, Tockner *et al.* 1999, Lewis *et al.* 2000). Floods are also associated with increases in the abundance or productivity of invertebrates (Hart 1985, Junk 1997, Lewis *et al.* 2000), macrophytes (Brinson *et al.* 1981, Poiani and Johnson 1993, Nielsen and Chick 1997), fish (Holcik 1996, Poizat and Crivelli 1997, Gutreuter *et al.* 1999, Puckridge *et al.* 2000) and birds (Briggs and Thornton 1999, Kingsford *et al.* 1999). The Flood Pulse Concept argues that it is the pulse of nutrients that drives the observed increases in the productivity of plants and animals. However, if this were the only effect of floods, similar effects might be expected in response to eutrophication. While, moderate eutrophication has been associated with increases in productivity (Gowns *et al.* 1992, Carpenter *et al.* 1998), we are not aware of any studies that suggest that eutrophication and flooding have the same ecological outcomes.

We suggest that a nutrient pulse is just one of at least three changes that occur during flooding of ephemeral wetlands. The second change is the expansion of aquatic habitat and habitat complexity. At small spatial scales complex habitat patches are created through either inundation of terrestrial vegetation or by stimulating the growth of macrophytes. Numerous studies have found that this type of spatially complex habitat provides refuge for prey organisms allowing the development of more diverse and abundant invertebrate communities (Boulton and Lloyd 1991, Balla and Davis 1995, Leslie *et al.* 1997, Battle and Golladay 2001). The drowned vegetation may provide both a refuge habitat and a source of organic carbon to fuel a highly productive community (Lewis *et al.* 2000, Battle and Golladay 2001). Whilst amphibious plant species, such as lignum (*Muehlenbeckia cunninghamii*), black box (*Eucalyptus largiflorens*) and red gums (*E. camaldulensis*) that are commonly present within EDBL, continue to provide spatial complexity for as long as they are inundated, many of the terrestrial grasses and herbs decompose and so offer only ephemeral habitat for aquatic invertebrates (Battle and Golladay 2001). In some lakes, the bed of the lake may support the growth of submerged or emergent macrophytes, but this is highly variable and depends on a variety of other environmental factors.

At a larger spatial scale floods create a mosaic of habitat types including deep pools, large areas of shallow water and vegetated islands. These habitats are important for different groups of organisms with, for example, vegetated islands providing important breeding habitat for birds (Briggs *et al.* 1993a) and shallow water providing important feeding habitat for wading birds (Kingsford *et al.* 1999).

The third important change that occurs during flooding of ephemeral wetlands is the reduction of predator densities (Lake *et al.* 1989, Batzer and Wissinger 1996, Battle and Golladay 2001). The use of lakebed sediments as a drought refuge means that micro-invertebrates have the capacity to rapidly colonise after a flood event, while their predators (invertebrates and fish) take longer to colonise and reproduce. This contention is supported by studies that record the slow accumulation of predators in ephemeral lakes and the presence of predator intolerant species during the early stages of flooding (Jeffries 1994, Collinson *et al.* 1995,

Batzer and Wissinger 1996, Timms 1997). The initial scarcity of predators after flooding allows the micro-invertebrate community to take maximum advantage of the increased autotrophic and heterotrophic productivity associated with a flood as predicted by the trophic cascade model (*e.g.* Carpenter and Kitchell 1988).

The loss of lake flooding

Given the effects of floods on nutrient dynamics, aquatic habitat and community composition, it is not surprising that the dramatic changes associated with the loss of flooding have been reported. These include changes in the species composition of floodplain vegetation (Bren 1992, Brereton 1994, Nielsen and Chick 1997) and declines in invertebrate diversity (Boulton and Lloyd 1991, Jenkins and Boulton 1998), fish (Kingsford 2000a, Gehrke and Harris 2001) and birds (Kingsford and Thomas 1995, Leslie 2001). As a consequence, the effects of water resource development on flooding characteristics is one of the major threats facing managers of EDBL (Walker *et al.* 1997, Kingsford 2000a).

Conceptual model of EDBL function

EDBL undergo cycles of flooding and drying in which we believe there are five phases beginning and ending with a dry lakebed (Figure 4.1).

The first phase occurs after the flooding of a dry or partially dried lake (Figures 4.1a,b). This initial flooding phase is characterised by high habitat abundance and diversity provided primarily by inundated terrestrial vegetation, such as grasses, and by high productivity fuelled by the inflow of nutrients and organic matter with the floodwaters and by releases from the sediments and the decomposition of inundated terrestrial vegetation. Changes in primary and secondary production following wetland inundation tend to follow a predictable successional sequence. Inorganic nutrient pools (especially nitrogen) tend to decline rapidly after flooding (within the 1st week) through tighter coupling of biotic and abiotic nutrient release and uptake mechanisms. Primary production generally peaks within the first three weeks after flooding. Secondary production generally peaks after the 3rd or 4th week after inundation.

During the late flood phase (Figure 4.1c), fish populations increase due to both immigration and local recruitment, and provide increasing top-down pressure on secondary production. As water levels continue to increase, the inundation of littoral fringe vegetation, such as lignum, black box and red gum provides additional aquatic habitat, although at this time also much of the habitat structure and complexity across the lakebed provided by inundated grasses and herbs begins to decline as they decompose.

During the late wet phase (Figure 4.1d), fish populations are established, the productive pulse fuelled by nutrient releases from the sediments and decomposing vegetation subsides, and habitat structure/complexity is restricted to the littoral fringe.

The drying phase commences with disconnection from the mainstream (Figure 4.1e). As this phase progresses the lake contracts, littoral habitat is exposed, water quality changes (elevated salt, nitrogen and phosphorus concentrations) and becomes less buffered to diel fluctuations in temperature. During this period aquatic organisms become concentrated and once the lake becomes too shallow to offer fish refuge, avian predation of fish increases. These processes impact on trophic interactions. This process continues until physical conditions become too harsh and the lake ultimately dries.

Finally, once the lakebed has been exposed it becomes an important terrestrial habitat for a range of plants and animals (Figure 4.1f).

This conceptual model incorporates aspects of the Flood Pulse Concept, Trophic Cascade/Food Web and Geomorphic Trophic models. As discussed above, whilst floods have the potential to stimulate productivity through bottom-up forcing, as suggested by the FPC, and to create aquatic habitat, these ecological benefits are to a large extent reliant on the occurrence of dry phases that allow lakebed vegetation to develop, organic matter to accumulate and sediment nutrients to be mineralised. Our model also indicates that lake wetting and drying influences the significance of top-down forcing on food webs by key predators as suggested by the trophic cascade model. The Geomorphic-Trophic model also plays a role in our model in so far as some of the observed changes appear to be driven by the changes in lake shape and size that occur as the lake dries.

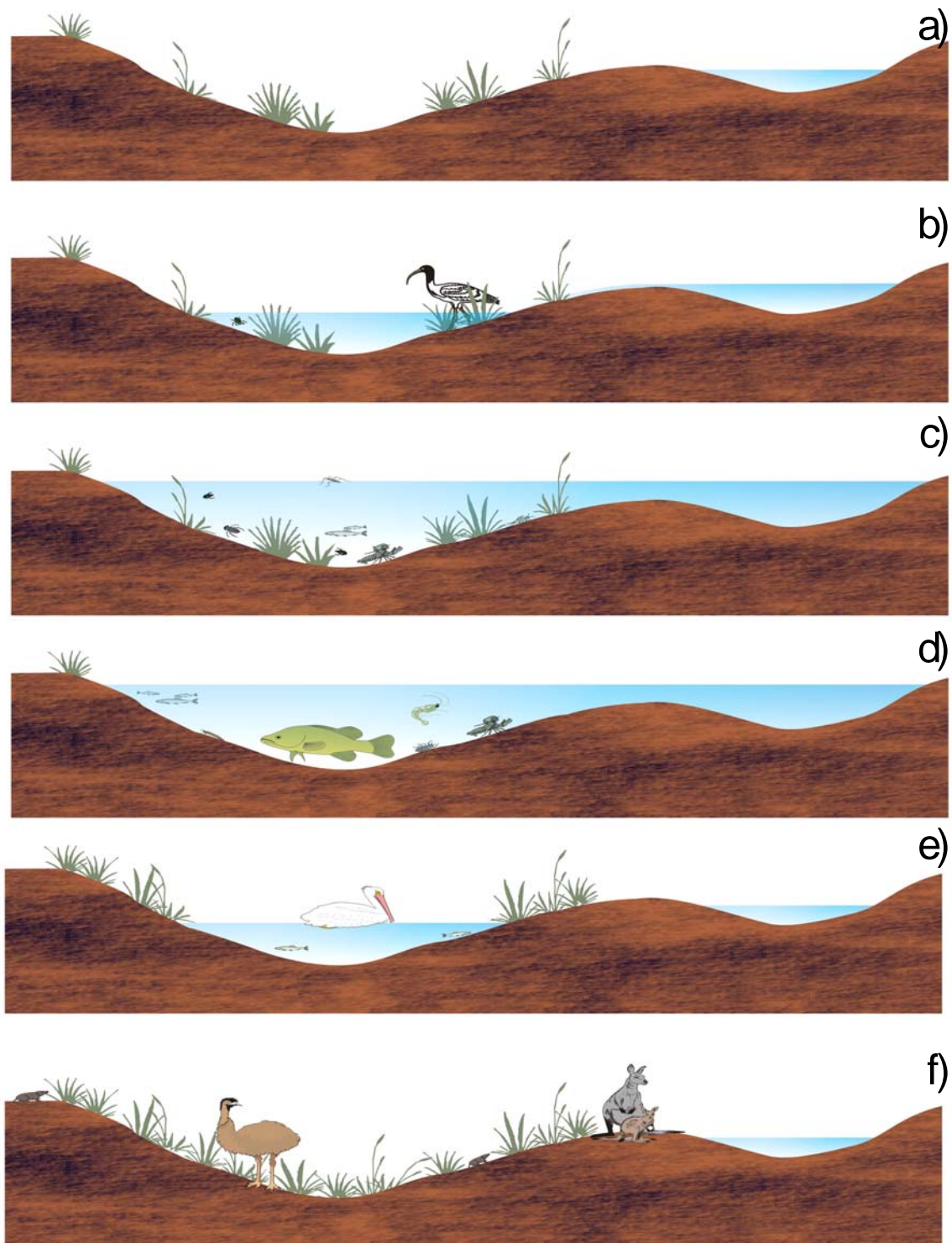
We recognise that the knowledge base on which our model is founded is far from complete and that there may be areas where the model is inappropriate. We believe, however, that synthesis of the available information, including that detailed in previous chapters will provide a reference point for researchers and a tool for managers who currently do not have an adequate knowledge base on which to base the management of these productive and diverse systems.

Management Implications

EDBL management should consider the roles and nature of flooding, drying and connectivity. Any change to the depth or duration of flooding will have a significant impact on ephemeral lakes by changing the ability of organisms to colonise the lake and changing trophic relationships. These changes in hydrology have already been widely recognised as significant degrading forces in Australian wetlands (Puckridge 1999, Kingsford 2000a,b).

The loss of a dry phase has also been recognised as a major degrading force (Briggs 1988). The conceptual model presented here, suggests that this is because permanent inundation allows the accumulation of predatory species that have the potential to exclude predator intolerant species and force the lake into a trophic configuration in which productivity and diversity are reduced. The loss of a dry phase may also lead to the loss of habitat heterogeneity with similar effects on production and diversity. The conceptual model suggests that rehabilitation may not require complete drying, but that restoration of a hydrological cycle that produces changes in trophic structure and the development of vegetation on the lake bed will be important in the management of these systems.

Our conceptual model attempts to describe the ecology of individual wetlands and implies that any change to the hydrological cycle in is likely to lead to changes in wetland condition. The consequences of these changes need to be viewed from both the perspective of the individual wetland and from a landscape perspective that would have contained wetlands with a diversity of hydrological regimes. While this review reveals that we have progressed some way toward understanding how ephemeral wetlands function, we have much more to do in understanding the impacts of change at larger spatial and temporal scales. This model should, therefore, be viewed as a means for improving our ability to predict the outcomes of water resource development on individual wetlands and possibly providing guidance for attempts at restoration or rehabilitation of those wetlands.



■ Figure 4.1: Illustration of the five stages of lake filling and drying. a) dry lake bed with forbs and grasses, b) shallow flooding creates a heterogeneous, nutrient rich aquatic habitat, c) late flood phase with established invertebrate and fish communities, d) late flooding cycle with low habitat heterogeneity and well established predatory fish community, e) drying lake during which aquatic populations are concentrated and avian predation becomes dominant, and f) dry lake providing productive habitat for terrestrial plants and animals.