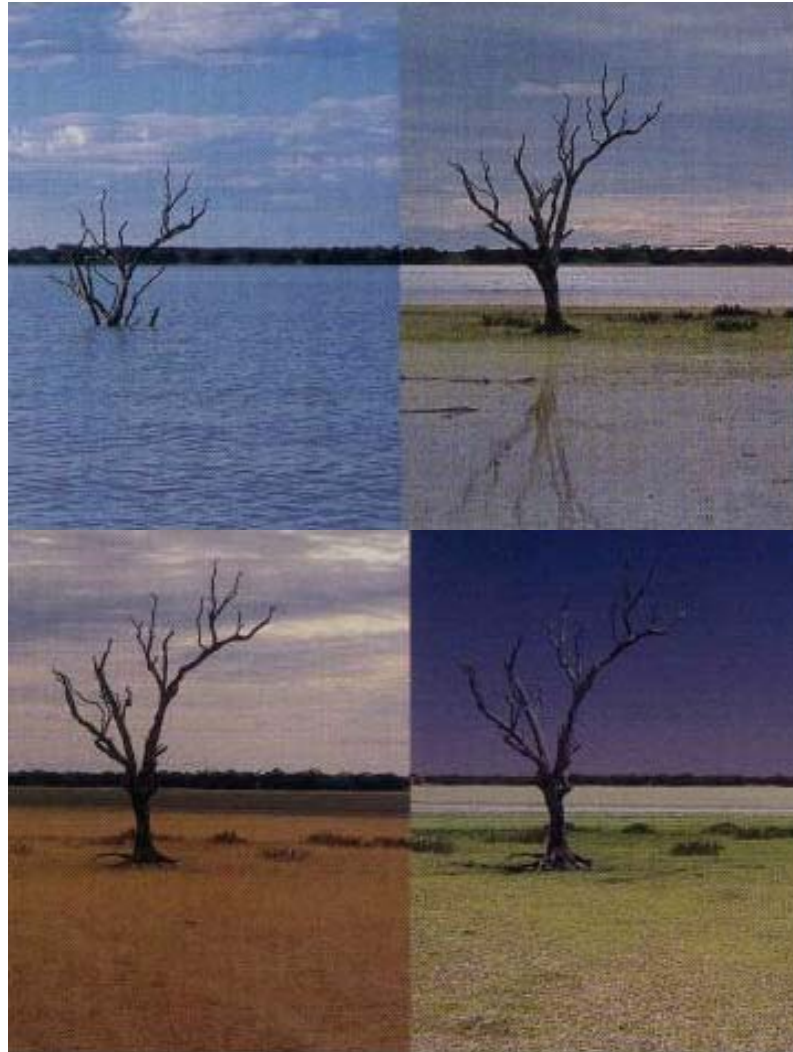


Aquatic ecosystem responses to flooding of the Menindee Lakes in 2004

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December 2004



Acknowledgements

This report was produced for the Murray-Darling Basin Commission as part of the Strategic Investigation Program – Rivers - Project R4013. We gratefully acknowledge their support and thank Mike Arandt and Barry Philp (NSW DIPNR) for their assistance, Robert Walsh and Lara Sutor (MDFRC Mildura) for invertebrate sample analyses, John Pengelly (MDFRC Albury) for nutrient analyses, and those from the MDFRC Mildura who assisted in the field: Clayton Sharpe, Iain Ellis, Nick Whiterod, Nicole McCasker and Sally Muston. Finally, we take this opportunity to thank the owners/managers of ‘Black Gate’, ‘Balaka’ and ‘Rochdale’ stations for their assistance and for allowing free access to their properties.

Report Citation

Scholz O. and Gawne B. (2004). Aquatic ecosystem responses to flooding of the Menindee Lakes in 2004. Report to the Murray-Darling Basin Commission, Canberra. Project R4013. Murray-Darling Freshwater Research Centre, Mildura.

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The contents of this publication do not purport to represent the position of the Murray-Darling Basin Commission. They are presented to inform discussion for improvement of the Basin’s natural resources.

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

Summary

This MDBC funded project (Project R4013), an adjunct to MDBC Project R1011 (*'The ecology of Ephemeral Deflation Basin Lakes (EDBL)'*) examined aquatic responses to flooding of the Menindee Lakes during 2004. This enabled us to refine our conceptual model of EDBL function through wetting and drying cycles developed as part of Project R1011, thereby providing a more informed ecological basis for the development of water management strategies for this and other ephemeral ecosystems. The objectives of this investigation were firstly to examine post-flood responses of four deflation basin lakes within the Menindee Lakes complex, each differing in their hydraulic history, and secondly, to test key responses predicted by our conceptual model.

The conceptual model predicted that flooding would;

- lead to an increase in productivity stimulated by sediment and vegetation nutrient release,
- increase invertebrate abundance through the provision of submerged vegetation that would provide important habitat, and
- initiate an increase in the productivity of the fish community.

The fact that the 4 lakes studied had different hydraulic histories provided an opportunity to examine the impact of drying history on lake's response to inundation. It was predicted that historical reductions in both the frequency and severity of episodes of lake drying would;

- reduce the potential for nutrient mobilization from the sediments following inundation, thereby reducing the potential for primary production. and
- affect the amount and type of organic matter on the lake bed which would have impacts on the type of habitat being provided for invertebrates.

We also hypothesized that submerged terrestrial vegetation would constitute an important source of nutrients, and that this would stimulate aquatic primary production. The leeching of nutrients from inundated vegetation in Lake Malta was inferred by the development of thick epiphytic biofilms over the supporting vegetation. However, only net increases in water column phosphorus concentrations were observed, suggesting firstly that the epiphytes had a higher demand for nitrogen than for phosphorus, and secondly that less nitrogen was available to support phytoplankton growth. Whereas phytoplankton biomass in the absence of inundated vegetation decreased once sediment derived labile nitrogen and phosphorus pools became depleted, substantially more epiphyte biomass developed and persisted in response to the slower and more protracted release of nutrients from the inundated vegetation.

In addition to its role as nutrient source, the presence of inundated vegetation was thought to provide potentially important aquatic habitat structure for a range of organisms, increasing the system's capacity to support greater organism biomass. Whilst no habitat effect was identified for zooplankton, some evidence was available to indicate that it did support greater macro-invertebrate abundances.

As predicted, the magnitudes of the initial post-flood pulse in zooplankton abundance differed between lakes, with the lowest occurring in the most permanent lake, Lake Tandure. However, it was not possible to determine whether these reflected 'real' differences in zooplankton productivity driven by hydraulically mediated differences in both food resource availability and re-colonization potential from the sediments, or 'apparent' differences in zooplankton productivity driven by differences in predation pressure.

Littoral benthic substrate composition changed along a gradient of decreasing lake permanence, with that of Lake Tandure consisting almost entirely of woody debris derived

from fringing black box trees and that of the smaller more ephemeral lakes primarily of fibrous plant debris derived from inundated lakebed grasses and herbs. These differences in substrate composition accounted for much of the differences in benthic macro-invertebrate community structure encountered between the lakes, suggesting that hydrology had the capacity to indirectly modify lake trophic structure through its effect on particulate organic matter inputs.

We predicted that the inundation of lakes would stimulate increases in lake fish populations, both as a consequence of immigration and recruitment following flood induced spawning, and that these increases would be linked with concomitant increases in the availability of potential food resources and floodplain spawning/nursery habitat. Fish catches in each of the four lakes investigated increased during the first month of inundation before declining towards the end of the study period. These increases coincided with observed increases in zooplankton abundances. Emigration of fish following subsidence of the post-inundation zooplankton pulse and avian predation likely accounted for the subsequent declines in fish catches.

The ability of carp to adapt their spawning seasonality to local flow conditions is a key characteristic underpinning the success of this invasive species. Flooding during February stimulated a significant spawning event in carp and was followed by successively smaller spawning events at intervals of 5-6 weeks. Whilst the initial spawning event occurred with the rising limb of the flood pulse within the main channel, subsequent spawning also occurred within the lakes (Lake Malta). Lowest larval and juvenile abundances were recorded in Lake Tandure. This was a likely consequence of greater initial predation pressure by macro-invertebrates rather than a response to differences in lake drying history and food resource productivity. Although differences in growth rates between lakes were not examined, comparisons with data available for both mainstream and floodplain environments support our expectations of floodplains being more productive environments for fish.

Differences in hydraulic regime and/or the severity of the most recent lake drying episode between lakes had demonstrable effects on aquatic primary and secondary productivity and on invertebrate community structure. Most of the post-inundation responses and differences between lakes were observed during the first month of inundation. However, within six months many of these differences among lakes had disappeared as seasonality began to play an increasingly important role.

Our results provide evidence for the existence of links between the frequency and severity of lake drying episodes, nutrient releases from both sediments and inundated vegetation and post-inundation aquatic primary and secondary production. These links have important implications not only for management actions that reduce the frequency and duration of lake drying episodes, and thus also the time available for lakebed vegetation to develop, but also for the management of lakebed vegetation itself, which may be compromised by activities such as grazing or cropping.

EDBL occur throughout the drier regions of the Murray-Darling Basin. Despite certain geomorphological similarities, key determinants of ecosystem function such as the prevailing hydrologic regime naturally vary greatly between lakes and have been modified through water resource development initiatives. Whilst reductions in the frequency and severity of lake drying events is widely considered to be a major degrading force (*e.g.* Bunn *et al.* 1997, Briggs 1998, Kingsford 2000a,b) and 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), consideration needs to be given to maintaining, or indeed increasing, the diversity of hydrologic regimes at the landscape scale. Such an approach is most likely to facilitate the persistence of species at that scale, by providing both temporal and spatial heterogeneity in the timing of developmental cues and refuges during dry periods.

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Introduction

The MDBC funded a project from 2000 to 2003 (Project R1011 *The ecology of ephemeral deflation Basin Lakes*) which aimed to better understand the ecology of deflation basin lakes in the Murray-Darling Basin and to produce guidelines to assist in their management. The objectives of Project R1011 were to develop a conceptual model of the ecological responses to wetting and drying, and to produce management guidelines for water regime management of these systems (refer to Scholz and Gawne 2004a,b). Project R1011 examined changes in the Menindee Lakes during two drying phases and a single flooding event. However, due to the timing of funding cycles and the protracted drought of 2001-4, project R1011 missed a second flood event that reduced its ability to validate ecosystem responses to flooding. The current project (R4013) addresses this knowledge gap by examining ecosystem responses to the re-flooding of the Menindee Lakes that occurred during 2004.

The re-flooding of the Menindee Lakes during 2004 was a relatively unusual event that represented the end of a severe drought during which most of the lakes dried completely. This afforded the unique opportunity to compare post-flood responses between lakes that varied in both historical drying frequency, ranging from 1 in 8.6 years to virtually permanent, and in drying duration, ranging from 15 to 23 months.

The conceptual model of deflation basin lake function through cycles of wetting and drying developed by Project R1011 integrated field data, targeted investigations and published information to derive 5 ecologically distinct stages:

- 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 previously exposed 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 producers. 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. This process continues until physical conditions become too harsh for aquatic organisms 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.

These stages formed the basis for generating testable hypotheses. For example, shorter periods of lakebed exposure are likely to reduce the potential for nutrient mineralisation within the sediments and thus their release on becoming inundated, thereby reducing the potential for primary production. Further, differences in lakebed characteristics, such as the presence of lakebed vegetation, are likely to play a key role in determining the pool of

nutrients available to support primary production. We suspect also that the presence of inundated vegetation and benthic particulate matter may play a role in facilitating the establishment of more diverse aquatic communities by increasing niche diversity.

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). Whilst flow regulation has been implicated in the decline of native fish populations in the MDB through its influence on 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), flood events have been shown to stimulate recruitment in both native and introduced species (e.g. Cushing 1975, 1990, Gehrke 1991, Harris and Gehrke 1994, Gehrke *et al.* 1995, Driver *et al.* 1997). As fish depend on zooplankton for food from shortly after hatching until they are large enough to switch to other prey (Culver and Geddes 1993, Arumugam and Geddes 1996, Rowland 1996), it is likely that such post flood responses in fish populations to pulses in zooplankton productivity (Cushing 1975, 1990). Our model suggests that post-flood increases in lake fish populations would occur both as a consequence of immigration from the riverine environment and recruitment following flood induced spawning.

Earlier work has shown that introduced carp (*Cyprinus carpio* L.) constitute a significant component of the fish community of the Menindee Lakes (Scholz and Gawne 2004a). Although carp in the Murray-Darling Basin have demonstrated strong population growth in response to flow regulation and episodic flood events (e.g. Gehrke *et al.* 1995, Driver *et al.* 1997, Stuart and Jones 2002), empirical relationships linking the timing of spawning with flow characteristics remain scarce. We used this opportunity to examine this relationship so as to improve predictive capacity regarding responses of carp to flood events.

The objectives of this project were to examine the post-flood responses in four ephemeral lakes within the Menindee Lakes complex, each differing in their hydraulic history and lakebed characteristics. Examining the responses of water quality and of aquatic communities (phytoplankton, zooplankton, macro-invertebrates and fish) to flooding during 2004 at greater temporal resolution than was possible during the 1998 flood reported on previously (Scholz and Gawne 2004a) allowed us to test and refine our conceptual model, thereby benefiting our understanding of how the Menindee Lakes system functions and providing a more informed basis upon which to formulate water management strategies for this and other ephemeral ecosystems.

Methods

Benthic coarse particulate organic matter (CPOM), water quality, phytoplankton, zooplankton, macro-invertebrate and fish were sampled from three littoral sites in lakes Malta, Balaka, Bijiji and Tandure on ten occasions between February and September 2004. A staggered sampling regime was necessary as lakes commenced to flood on different dates (Table 1). Sites were selected to encompass the range of available littoral habitat consisting primarily of bare sediments, inundated terrestrial grasses and woody snags. Sampling of these lakes commenced with their re-flooding during February once water levels in Lake Wetherell exceeded their respective sill heights. Hydrological and water quality data (electrical conductivity, turbidity, total nitrogen and total phosphorus) for sites in Lake Wetherell adjacent to the inflows to each of the lakes were sourced from NSW DIPNR.

Benthic CPOM was sampled by sweep netting (250 μm mesh size) a single 10 m reach of littoral habitat per site. Each sample was first passed through a 1.1 mm mesh to remove smaller debris, and then any remaining organisms and inorganic particles (*i.e.* stones) were removed. Samples were then oven dried at 80 °C for 48 hr and weighed to obtain dry mass (g CPOM m^{-2}). CPOM was separated into four components (woody debris including leaves, seed

Pods, bark and twigs, fibrous plant debris, consisting principally of grasses and herbaceous vegetation, faeces originating primarily from sheep, and larger (>0.5 mm) unidentified seeds. The contribution by volume of each component was expressed as a percentage of the total.

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 labile nitrogen (dissolved oxides of nitrogen: NO_x; mg N l^{-1}) and labile phosphorus (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 was determined as for NO_x after pre-digestion in NaOH-K₂S₂O₈ 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-K₂S₂O₈ and oxidation to orthophosphate. Detection limits varied between nutrient fractions; TN \pm 0.019 mg N l^{-1} , TP \pm 0.0025 mg P l^{-1} , NO_x \pm 0.003 mg N l^{-1} and FRP \pm 0.001 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).

Sampling event	Date	Lake Tandure	Lake Bijiji	Lake Balaka	Lake Malta
1	17-Feb-04	6	-	-	-
2	25-Feb-04	14	6	0	-
3	2-Mar-04	20	13	6	-
4	9-Mar-04	27	20	12	9
5	17-Mar-04	35	28	20	17
6	24-Mar-04	41	34	27	24
7	30-Mar-04	47	40	33	30
8	6-May-04	84	77	71	68
9	22-Jun-04	131	124	118	115
10	7-Sep-04	208	201	195	192

■ **Table 1: Dates of sampling events and the corresponding number of days after the commencement of inflows into each lake samples.**

Zooplankton were sampled by passing 75 l of lake water through a 50 μm mesh and were preserved in 70 % ethanol. A minimum of 200 individuals or 10 % of each sample were 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. Juvenile copepods (nauplii and copepodites) were counted and treated as separate taxa.

Macro-invertebrates were sampled using the rapid bio-assessment protocol of Tiller and Metzeling (1998) (see also Coysh *et al.* 2001). Macro-invertebrates were sampled by sweep netting (250 μm mesh size) a single 10 m reach of littoral habitat at three sites within each lake. Compared with other commonly used active and passive sampling methods, sweep netting provides similar diversity though lower abundances (Humphries *et al.* 1998).

Collected samples were preserved in 70 % ethanol. Identifications to family followed Williams (1980) and Hawking and Smith (1997).

The fish communities of each lake were sampled by deploying 3 of each of two sizes of fyke net. These passive gear types were set in tandem to increase the probability of sampling a wider range of species and size classes. 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. All fish were counted and total lengths (TL mm) recorded in the field for the first 30 individuals of each species per net. All LFN and SFN data were standardised to a sampling effort of 200 net hours per lake (sites combined) to facilitate both the examination of relative temporal and spatial variation in abundances between lakes and comparisons with earlier fish surveys.

The timing of carp spawning was determined by back-calculating fish age from the time of collection. This was done by determining the age-length relationship of a subset of fish caught from each lake, then applying this to all carp caught. Both standard length (SL) and total length (TL) of individuals retained for the determination of the age-length relationship were recorded prior to their preservation in 95 % ethanol. Age determinations based on the examination of otolith daily growth increments were only possible for carp <50 mm SL, above which daily increments became obscured by the deposition of annular growth rings (*cf.* Vilizzi 1998, Smith and Walker 2003).

Following extraction, sagittal otoliths were mounted on microscope slides using Crystalbond (Aremco, Valley Cottage, NY, USA) thermoplastic cement. Thicker otoliths required grinding and polishing using 2000 grit size sand paper and 1.0 μ m diamond polishing compound (Leco Corporation MI, USA), respectively, to more clearly expose growth increments. Each prepared specimen was counted three times 'blind' (*i.e.* without reference to previous counts) at 400x magnification. Co-efficients of variation between counts did not exceed 15 %. Otolith increment counts were reduced by three days to adjust for the estimated four day period between spawning and hatching and the deposition of the first increment prior to hatching (Smith and Walker 2003, Wilson unpublished).

Differences between sample means were tested using Students *t*-test. Pearson correlations with Bonferroni adjusted *p*-values and regression analyses were done using SYSTAT[®] V10.2 (SPSS Inc. Chicago, USA), as were analyses of temporal trends using fixed factor one-way ANOVAs with Tukey's *post hoc* testing at $\alpha=0.05$. Data did not require transformation to satisfy assumptions of normality.

Temporal shifts in invertebrate community structure were examined using PRIMER (V5; Primer-E 2000). Invertebrate data 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 graphically display relative temporal trajectories of zooplankton communities. ANOSIM was used to test for differences between groups where *R* reflects the degree of separation ($R \rightarrow 1$ maximum separation) and *p* the level of significance. SIMPER was used to identify species contributing most to within group similarities and to between group differences.

Results

Hydrology and lake characteristics

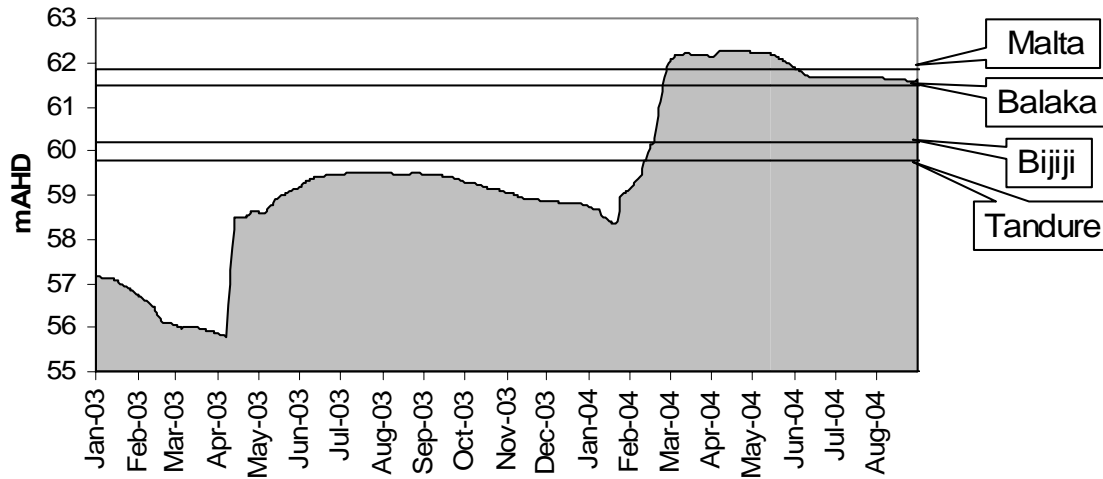
February 2004 marked the end of an extended drought during which Darling River flows upstream of the Menindee Lakes at Wilcannia ceased altogether between 25th January 2003 and 4th April 2003 and between 24th October 2003 and 14th January 2004. This extended dry period, the most severe recorded since the commencement of flow regulation in the 1960s, resulted in the complete drying of lakes Bijiji, Balaka and Malta and in the almost complete drying of Lake Tandure (> 95 % dry).

The physical and hydrological characteristics of lakes Tandure, Bijiji, Balaka and Malta are summarised in Table 2. Whereas each of the smaller lakes dry periodically, Lake Tandure, the largest and deepest of the four lakes above the Main Weir, between 2002-4 was the first such event since the commencement of regulated flows in the 1960s. Differences in rates of drying between lakes resulted in a gradient of periods for which each of the lakes had been dry prior to February 2004: Lake Tandure (15 months), Lake Bijiji (19 months), Lake Balaka (21 months) and Lake Malta (23 months).

Inflows from the Darling River to Lake Wetherell during January and February 2004 resulted in the sequential flooding of each lake once their sill heights had been breached. Inflows into the four lakes commenced on 11th February (L. Tandure), 18th February (L. Bijiji), 25th February (L. Balaka), and 28th February (L. Malta) (Figure 1). Lakes Tandure, Bijiji and Balaka remained connected to Lake Wetherell throughout the study period. Lake Malta became disconnected from Lake Wetherell on 3rd June.

Lake	Bed level (mAHD)	Sill level (mAHD)	Full supply level (mAHD)	Full supply depth (m)	Full supply area (ha)	Full supply volume (GL)	Period between dry events (years)	Time required to dry (months)
Tandure	55.88	59.80	61.67	5.8	2190	101	Perm	Perm
Bijiji	58.62	60.19	61.67	3.1	1050	25.9	14.3	16
Balaka	59.23	61.50	61.67	2.4	1300	30.9	10.7	14
Malta	60.14	61.85	61.67	1.5	380	7	8.6	10
Wetherell	-	-	61.67	-	5000	193	Perm	Perm

- Table 2: Key physical and hydrological characteristics of the Menindee Lakes (sources: DIPNR unpublished operation data, Bewsher Consulting 2000). Sill heights shown are based on Lake Wetherell gauge height on the day inflows commenced. These differ from those reported by Bewsher Consulting (2000): 60.11 m AHD, 59.93 mAHD and 59.78 mAHD for lakes Tandure, Bijiji and Balaka, respectively. Period between dry events and time required for each lake to dry following disconnection from Lake Wetherell were calculated for the period between the commencement of regulation in the 1960s and the most recent drying episode (2001-4). Permanent.**



■ **Figure 1: Lake Wetherell water levels (mAHD) from January 2003 to September 2004. Sill heights of lakes Malta (61.85 mAHD), Balaka (61.50 mAHD), Bijiji (60.19 mAHD) and Tandure (59.80 mAHD) are shown.**

Differences in the nature of connection of each lake with Lake Wetherell may be expected to play an important role in modifying the quality of water and the composition and rates of organisms entering the lakes. In contrast to Lake Tandure, which has a direct connection with the mainstream, Lake Balaka is connected on two sides by large floodplain depressions that remain inundated for extended periods and provide significant shallow habitat for aquatic organisms. Further upstream in Lake Wetherell, channel connections with lakes Balaka and Malta are more constrained. Whereas Lake Balaka is fed from a relatively simple channel of only 6 km length, flows into Lake Malta must pass through a 14 km convoluted creek system.

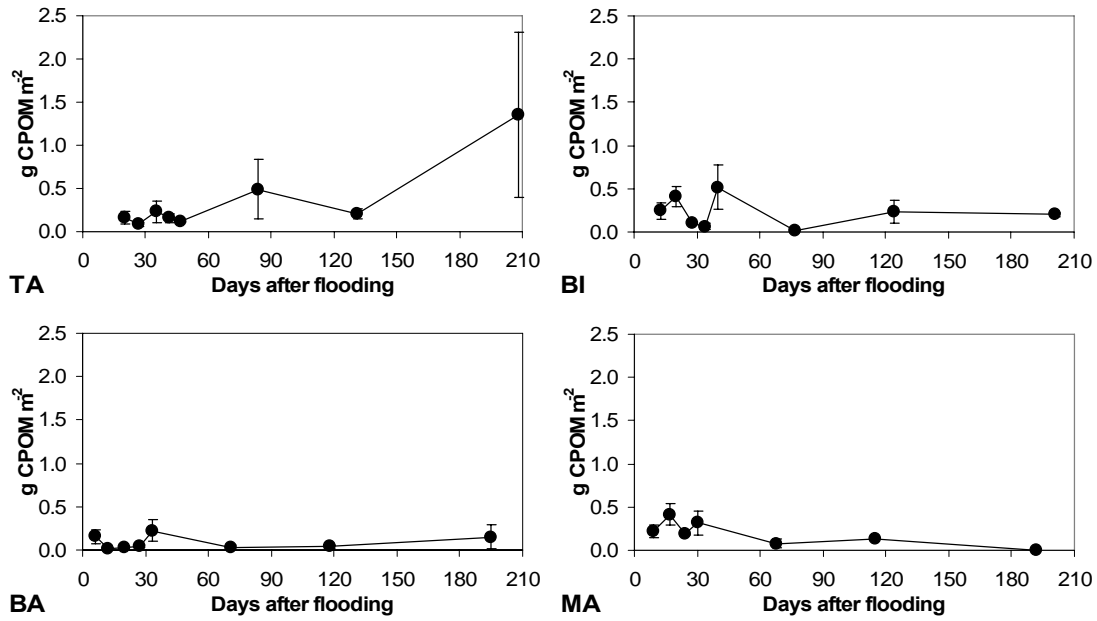
Differences in lake characteristics described above have contributed to influencing the structure and distribution of littoral vegetation in each lake. The littoral margins of each lake were rapidly colonized by a similar suite of herbs, sedges and grasses as they dried. Refer to Taylor-Wood *et al.* (2001) and Nicol (2004) for a full description of these assemblages. The most noticeable differences between lakes with respect to these communities were that Lake Tandure did not support large groundcover species around the margins, and that in Lakes Bijiji and Balaka the dominant lake bed plant was *Cyperus gymnocaulos* while, at higher elevations, patches of *Lignum* sp. were present. Lakebed vegetation in Lakes Tandure, Bijiji and Balaka was restricted to the lake margins and the central lakebed consisting of bare fine-grained sediments, terrestrial vegetation. In contrast, Lake Malta, the shallowest and most frequently dry lake, lake bed vegetation extended across the entire lakebed, (Figure 2). The lakebed vegetation of all lakes was subject to grazing by both stock (sheep and cattle) and native animals (*e.g.* kangaroos). The impact of this was most severe on the fringing herb and grass communities in lakes Tandure (shown in Figure 2) and Malta; however, this did not extend into the more erect vegetation covering the inner lakebed of Lake Malta.

Longer-term increases in mean water levels as a consequence of regulation has increased the duration of inundation of black box (*Eucalyptus largiflorens*) resulting in their death and the accumulation of large woody debris in lakes Tandure and Bijiji. In contrast to the smaller lakes, steeper littoral gradients in Lake Tandure have resulted in the fringing black box extending to the waters edge, where they provide both shade and contribute coarse particulate organic material (CPOM).

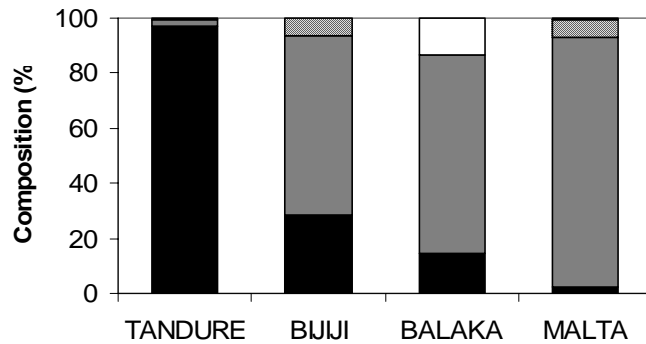


■ **Figure 2: Lakebed vegetation of lakes Tandure, Bijiji, Balaka and Malta (photos: O. Scholz).**

CPOM standing stocks ranged from <0.001 - 3.229 g m^{-2} (Figure 3). Temporal variations in CPOM standing stocks within each lake were not significant (One-way ANOVA: Tandure $p=0.336$, Bijiji $p=0.163$, Balaka $p=0.401$, Malta $p=0.239$), nor were differences between lakes (times pooled) significant (One-way ANOVA: $p=0.127$). However, there were significant compositional differences between lakes (Figure 4). Woody debris and fibrous plant debris accounted for 86.7-99.6 % of total CPOM standing stocks within the lakes. Lake Tandure had significantly more woody debris than did the other lakes (One-way ANOVA: $p<0.001$. Tukey *post hoc* test: Tandure> all lakes, Bijiji>Malta) and conversely also the least fibrous plant debris (One-way ANOVA: $p<0.001$. Tukey *post hoc* test: Tandure>all lakes, Bijiji>Malta). Fecal matter constituted $6.5\pm 3.1 \%$ and $6.6\pm 3.8 \%$ of total CPOM standing stocks in lakes Bijij and Malta, respectively, and large seeds constituted $13.1\pm 6.0 \%$ of total CPOM standing stocks in Lake Balaka.



■ Figure 3: Coarse particulate organic matter standing stocks (g CPOM m⁻², mean±se) recorded for lakes Tandure (TA), Bijji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period.



■ Figure 4: Relative compositions of CPOM collected from each lake during the 2004 post-flood study period. Woody debris (black), fibrous plant debris (grey), faeces (diagonal) and large seeds (white).

Water quality

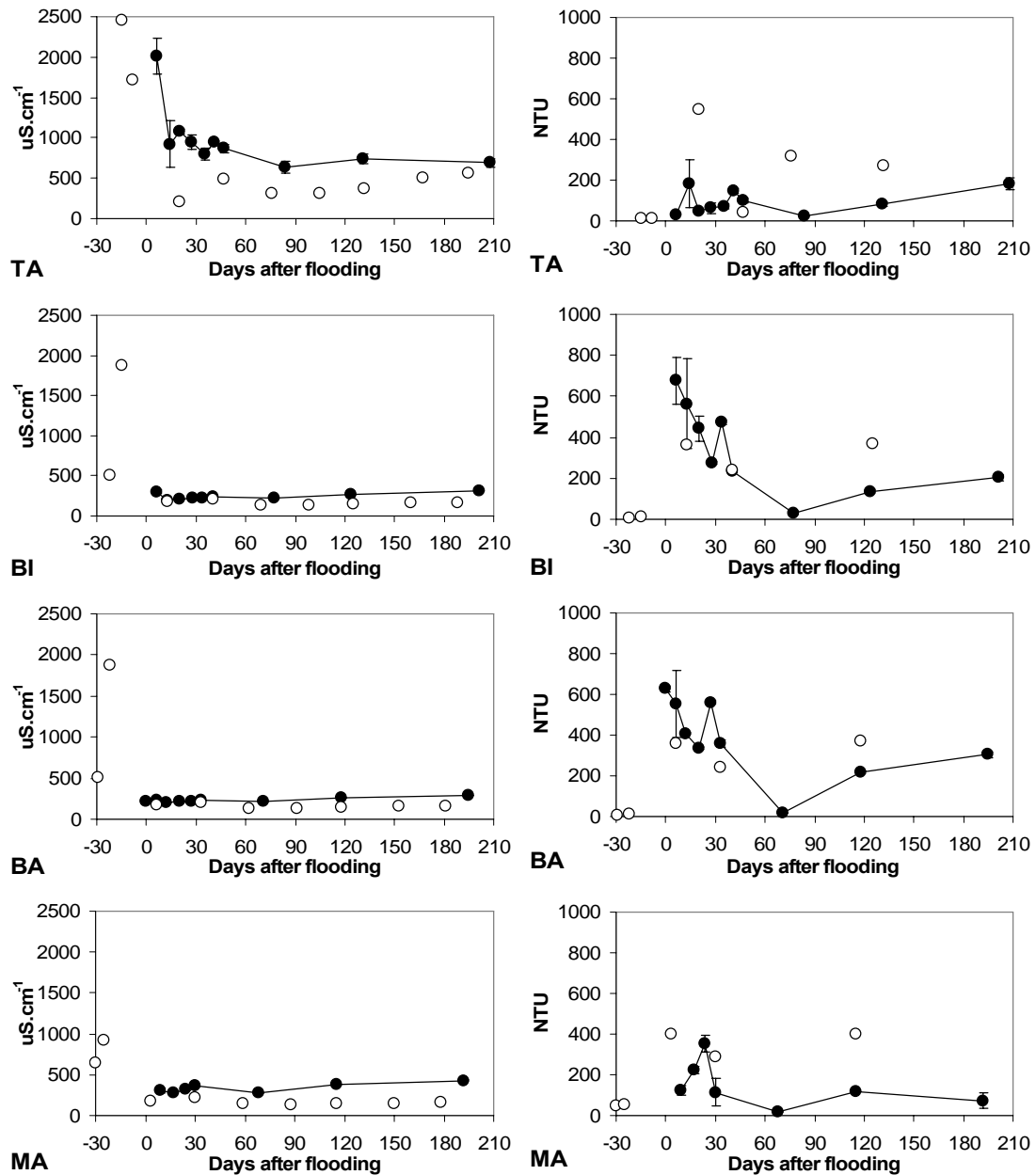
Electrical conductivity (EC) recorded in each lake after flooding ranged from 496-2340 $\mu\text{S cm}^{-1}$ in Lake Tandure, 190-343 $\mu\text{S cm}^{-1}$ in Lake Bijiji, 190-297 $\mu\text{S cm}^{-1}$ in Lake Balaka, and 247-448 $\mu\text{S cm}^{-1}$ in Lake Malta (Figure 5).

EC recorded in Lake Wetherell on 27th January as the Darling River flood pulse arrived ranged from 646 $\mu\text{S cm}^{-1}$ upstream of Lake Malta to 2460 $\mu\text{S cm}^{-1}$ close to the Main Weir. Despite diluting inflows from the Darling River, the EC gradient in Lake Wetherell persisted throughout the study period, ranging from 130-216 $\mu\text{S cm}^{-1}$ in its upper reaches and from 214-560 $\mu\text{S cm}^{-1}$ downstream towards the Main Weir. This reduced the potential for inflows to dilute salt loads in Lake Tandure, thereby maintaining higher salt concentrations in Lake Tandure relative to the other lakes. Post-flood EC was initially greatest in Lake Tandure (2013 \pm 222 $\mu\text{S cm}^{-1}$ day 6) compared with lakes Bijiji (300 \pm 22 $\mu\text{S cm}^{-1}$ day 6), Balaka (226 \pm 11 $\mu\text{S cm}^{-1}$ day 6) and Malta (302 \pm 28 $\mu\text{S cm}^{-1}$ day 9). In contrast to the smaller lakes, relatively large EC gradients were observed in Lake Tandure initially as it filled. EC in Lake Tandure during this period was characteristically greatest at points furthest from its mouth.

Turbidity (NTU) recorded in each lake after flooding ranged from 13-406 NTU in Lake Tandure, 21->999 NTU in Lake Bijiji, 14-888 NTU in Lake Balaka, and 17-423 NTU in Lake Malta (Figure 5).

Turbidity in Lake Wetherell prior to flooding decreased with distance downstream, ranging from 9.7-11 NTU immediately upstream of the Main Weir to 50-55 NTU upstream of Malta Creek. The flooding of Lake Wetherell led to initial increases in turbidity to 360-550 NTU (recorded 2nd March). Within a month of the flood peak, turbidity in Lake Wetherell had decreased to 40-290 NTU. Turbidity declined more rapidly and to lower levels with distance downstream through Lake Wetherell due to sedimentation.

As flows into Lake Tandure commenced with the arrival of the flood pulse front, the turbidity of its inflows gradually increased resulting in a distinct turbidity gradient within the lake. Turbidity in Lake Tandure was characteristically lowest at points furthest from its mouth. This was likely due to longer residence times facilitating sedimentation. For example, 2 weeks after inflows had commenced (25th February), a turbidity gradient of 18-120-406 NTU between the three sampling sites had been established. The onset of filling of the smaller lakes coincided with the peak in Lake Wetherell turbidity, resulting in initially higher turbidities in Lake Bijiji (667 \pm 113 NTU day 6) and Lake Balaka (627 \pm 12 NTU day 0). The re-suspension of lakebed sediments on lake filling may have also contributed to the increases in observed turbidity. The first sampling of Lake Malta did not occur until 9 days after flooding, at which time turbidity was 122 \pm 24 NTU. Turbidity decreased steadily in each lake during at least the first month after flooding as entrained particles settled. Thereafter, changes in turbidity appeared to be driven principally by wind driven re-suspension. This had the capacity to influence turbidity at both the system level (*e.g.* low wind velocities in the days prior to sampling between days 70-80 account for reductions in the turbidity of each lake) and the lake scale (*e.g.* larger within lake differences encountered during the last sampling event in Lake Malta) (Figure 5).



■ Figure 5: Electrical conductivity ($\mu\text{S cm}^{-1}$ mean \pm se) and turbidity (NTU mean \pm se) recorded for lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) (●) and Lake Wetherell adjacent to the inflows of each lake (○) during the 2004 post-flood study period.

Total nitrogen (TN), dissolved oxides of nitrogen (NO_x), total phosphorus (TP) and filterable reactive phosphorus (FRP) concentrations recorded for each lake during the post-flood study period are shown in Figure 6.

TN concentrations during the first week of flooding did not differ significantly between lakes Bijiji (2.163 ± 0.057 mg N l⁻¹), Balaka (1.960 ± 0.261 mg N l⁻¹) and Malta (1.840 ± 0.165 mg N l⁻¹) and were greater than those recorded in both lakes Tandure (1.035 ± 0.152 mg N l⁻¹) and Wetherell (1.120 ± 0.078 mg N l⁻¹) (One-way ANOVA: $p=0.001$. Tukey *post hoc* test: Wetherell=Tandure<Bijiji=Balaka=Malta). Such differences between source and lake waters suggest that nitrogen was contributed from within each of the smaller lakes as they flooded.

Significant temporal changes in TN concentrations were recorded only in the smaller lakes (Table 3). In these lakes, TN concentrations declined significantly during the first month as a likely consequence of continued diluting inflows and the settling of entrained organic matter (*cf.* turbidity decreases). The TN peak recorded in Lake Tandure on day 47 was due to a single sample (2.250 mg N l⁻¹) collected from the site furthest from the mouth of the lake. By the end of the study period there were no significant differences in TN concentrations between lakes Tandure (1.507 ± 0.354 mg N l⁻¹), Bijiji (1.247 ± 0.097 mg N l⁻¹), Balaka (1.203 ± 0.058 mg N l⁻¹) or Malta (1.173 ± 0.079 mg N l⁻¹) (One-way ANOVA: $p=0.607$).

Significant temporal variations in NO_x concentrations were identified for each lake (Table 3). The largest post-inundation NO_x concentrations were recorded in lakes Bijiji (0.318 ± 0.028 mg N l⁻¹) and Balaka (0.455 ± 0.006 mg N l⁻¹) on days 77 and 33, respectively. NO_x concentrations did not exceed 0.210 ± 0.009 mg N l⁻¹ in Lake Tandure (day 131) and 0.138 ± 0.030 mg N l⁻¹ in Lake Malta (day 68). As NO_x concentrations increased so too did their relative contribution to the TN pool (Figure 7). Despite comparable TN concentrations between the smaller lakes, NO_x concentrations and their contribution to the suspended TN pool remained much lower in Lake Malta. By the end of the study period NO_x concentrations were significantly greater in Lake Tandure (0.157 ± 0.025 mg N l⁻¹) than they were in lakes Bijiji (0.016 ± 0.006 mg N l⁻¹), Balaka (0.083 ± 0.009 mg N l⁻¹) and Malta (0.020 ± 0.007 mg N l⁻¹) (One-way ANOVA: $p<0.001$. Tukey *post hoc* test: Tandure>Bijiji, Balaka, Malta, and Bijiji<Balaka).

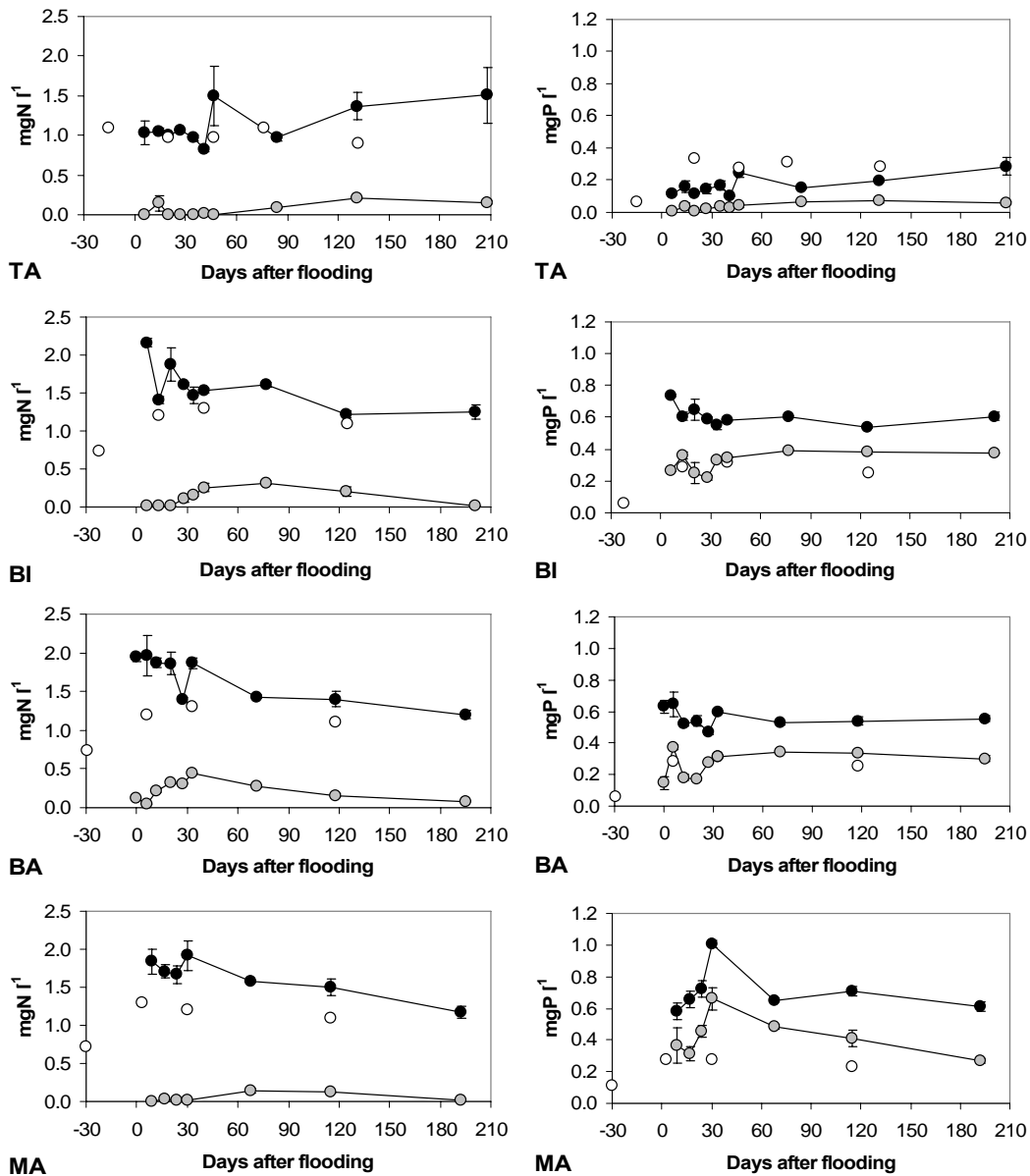
TP concentrations during the first week of flooding did not differ significantly between lakes Bijiji (0.738 ± 0.007 mg P l⁻¹), Balaka (0.645 ± 0.075 mg P l⁻¹) and Malta (0.580 ± 0.051 mg P l⁻¹) and were greater than those recorded in both lakes Tandure (0.113 ± 0.006 mg P l⁻¹) and Wetherell (0.291 ± 0.014 mg P l⁻¹) (One-way ANOVA: $p<0.001$. Tukey *post hoc* test: Tandure<Wetherell< Bijiji=Balaka=Malta). Such differences between source and lake waters suggest that phosphorus was contributed from within each of the smaller lakes as they flooded.

Significant temporal changes in TP concentrations were recorded in each lake (Table 3). For lakes Bijiji and Balaka, TP concentrations decreased significantly during the first 34 and 27 days of inundation. This was likely due to continued diluting inflows and the settling of particle associated phosphorus (*cf.* turbidity decreases). Increases in TP during the first 30 days in Lake Malta were attributed to increases in FRP concentrations recorded during that period. Although a significant peak in TP concentration was recorded 47 days after first filling in Lake Tandure (0.248 ± 0.028 mg P l⁻¹) this was still lower than that present within Lake Wetherell during that period (0.300 ± 0.015 mg P l⁻¹) (Student *t*-test: $t=-1.275$, $p=0.271$). By the end of the study period differences in TP concentrations between lakes Tandure (0.287 ± 0.052 mg P l⁻¹), Bijiji (0.607 ± 0.027 mg P l⁻¹), Balaka (0.553 ± 0.020 mg P l⁻¹) and Malta (0.610 ± 0.030 mg P l⁻¹) remained significant (One-way ANOVA: $p<0.001$. Tukey *post hoc* test: Tandure<Bijiji=Balaka=Malta).

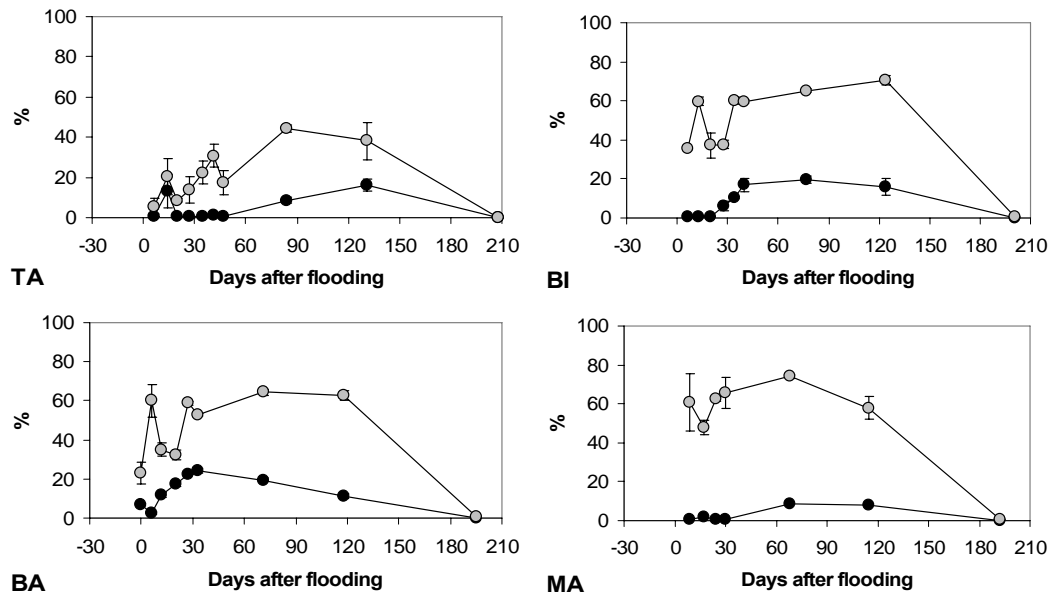
Significant temporal variations in FRP concentrations were identified for each lake after re-flooding (Table 3). FRP concentrations during the first two weeks of inundation were significantly greater in lakes Bijiji ($0.362 \pm 0.022 \text{ mg P l}^{-1}$), Balaka ($0.375 \pm 0.015 \text{ mg P l}^{-1}$) and Malta ($0.363 \pm 0.112 \text{ mg P l}^{-1}$) than in Lake Tandure ($0.038 \pm 0.018 \text{ mg P l}^{-1}$) (One-way ANOVA: $p=0.004$. Tukey *post hoc* test: Tandure<Bijiji=Balaka=Malta). These differences between lakes were attributed to releases from the sediments. Subsequent declines over the following two weeks in lakes Bijiji and Balaka were a likely consequence of continued diluting inflows. Increases in FRP concentrations after this in lakes Bijiji (maximum $0.393 \pm 0.003 \text{ mg P l}^{-1}$ on day 77) and Balaka (maximum $0.340 \pm 0.001 \text{ mg P l}^{-1}$ on day 71) suggest that releases from the sediment continued after inflows had ceased. Whilst a similar pattern was apparent in Lake Malta, increases in FRP following the lake filling period were much greater (maximum $0.660 \pm 0.070 \text{ mg P l}^{-1}$ on day 30), suggesting the presence of an additional source, most probably releases from the inundated decomposing vegetation. By the end of the study period much less FRP was present in Lake Tandure than was present in the other lakes; Lake Tandure ($0.059 \pm 0.005 \text{ mg P l}^{-1}$), Lake Bijiji ($0.377 \pm 0.002 \text{ mg P l}^{-1}$), Lake Balaka ($0.302 \pm 0.020 \text{ mg P l}^{-1}$) and Lake Malta ($0.267 \pm 0.016 \text{ mg P l}^{-1}$) (One-way ANOVA: $p<0.001$. Tukey *post hoc* test: Tandure<Bijiji>Balaka=Malta).

Nutrient fraction	Lake	<i>p</i>	Tukey <i>post hoc</i> comparisons
TN	Tandure	0.142	ns
	Bijiji	<0.001	day 6 > all subsequent days except day 20 day 13 < day 20 > days 124, 201
	Balaka	<0.001	days 0, 6, 12, 20, 33 > day 195
	Malta	0.014	day 9 > days 30, 192
NO _x	Tandure	0.001	day 131 > all days except days 14 and 131
	Bijiji	<0.001	days 6, 13, 20 < days 40, 77, 124> day 201 days 28, 34 < day 77
	Balaka	<0.001	day 0 > day 6 < days 12, 20, 27, 33, 71, 118 > day 195
	Malta	<0.001	days 9, 17, 24, 30 < days 68, 115 > day 192
TP	Tandure	0.001	days 6, 20, 27, 41, 84 < day 208 days 6, 41 < day 47
	Bijiji	0.003	day 6 > days 28, 34, 40, 124
	Balaka	0.032	day 0 = day 6 > day 27
	Malta	<0.001	days 9, 17, 24 < day 30 > days 68, 115, 192
FRP	Tandure	0.002	days 6, 20 < days 84, 131 day 27 < day 131
	Bijiji	<0.001	day 13 > day 28 < all subsequent days
	Balaka	<0.001	day 0 < day 6 > days 12, 20, 27 day 12 = day 20 < all subsequent days
	Malta	0.007	days 9, 17 < day 30 > day 192

■ **Table 3: Summary ANOVA statistics for temporal trends in TN, NO_x, TP, and FRP concentrations in lakes Tandure, Bijiji, Balaka and Malta during the 2004 post-flood study period.**



■ Figure 6: Total nitrogen (TN mg N l⁻¹) (●), dissolved oxides of nitrogen (NO_x mg N l⁻¹) (●), total phosphorus (TP mg P l⁻¹) (●) and filterable reactive phosphorus (FRP mg P l⁻¹) (●) concentrations recorded in lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period. All values are mean ± se. Total nitrogen (TN mg N l⁻¹) and total phosphorus (TP mg P l⁻¹) concentrations recorded in Lake Wetherell adjacent to the inflows of each lake are indicated as ○.



■ **Figure 7: Percentage contributions of NO_x to TN concentrations (%) (●) and FRP to TP concentrations (%) (○) determined for lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period. All values are mean±se.**

Phytoplankton

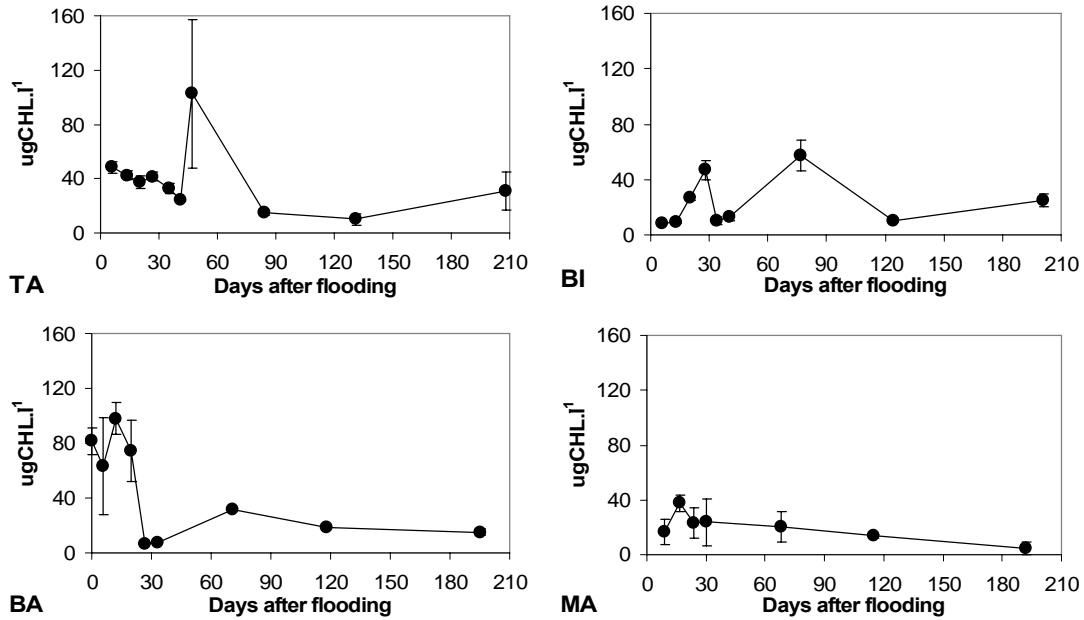
Phytoplankton biomass, estimated indirectly as chlorophyll *a* pigment concentration, across all lakes ranged from 0.010-212.20 µg CHL l⁻¹ (Figure 8). Chlorophyll *a* concentrations during the first week of flooding differed significantly between lakes Tandure (42.39±3.41 µg CHL l⁻¹), Bijiji (8.60±0.34 µg CHL l⁻¹), Balaka (81.7±10.0 µg CHL l⁻¹) and Malta (16.86±9.38 µg CHL l⁻¹) (One-way ANOVA: $p < 0.001$. Tukey *post hoc* test: Balaka > Tandure = Malta > Bijiji). No data was available regarding the chlorophyll content of inflows.

No significant temporal variations in chlorophyll *a* concentrations were identified for lakes Tandure (One-way ANOVA: $p = 0.096$) or Malta (One-way ANOVA: $p = 0.455$) (Table 4). Mean chlorophyll *a* concentrations in lakes Tandure and Malta were 38.54±8.11 µg CHL l⁻¹ and 19.94±3.79 µg CHL l⁻¹, respectively. Although lowest plankton chlorophyll *a* concentrations were recorded in Lake Malta, extensive algal biofilms (dominated by the filamentous chlorophyte *Oedogonium* sp.) were associated with the inundated vegetation. Similar biofilm loads did not develop on the littoral vegetation in the other lakes. Large algal mats became dislodged and accumulated around the margins of the lake as the supporting lakebed vegetation in Lake Malta decomposed. These were subsequently stranded as water levels receded, forming a crust on the exposed sediments (Figure 9).

The chlorophyll *a* peak recorded in Lake Tandure on day 47 was due to a single sample (212.20 µg CHL l⁻¹) collected from the site furthest from the mouth of the lake where mixing currents were likely to have been lowest. This maximum in chlorophyll *a* concentration corresponded with the relatively high TN concentrations recorded at the same time.

Significant temporal changes in chlorophyll *a* concentration were observed in lakes Bijiji (One-way ANOVA: $p < 0.001$) and Balaka (One-way ANOVA: $p = 0.001$) (Table 4). Chlorophyll *a* concentrations increased significantly during the first 28 days in Lake Bijiji (maximum 46.84±6.92 µg CHL l⁻¹) and 20 days in Lake Balaka (maximum 97.97±11.42 µg

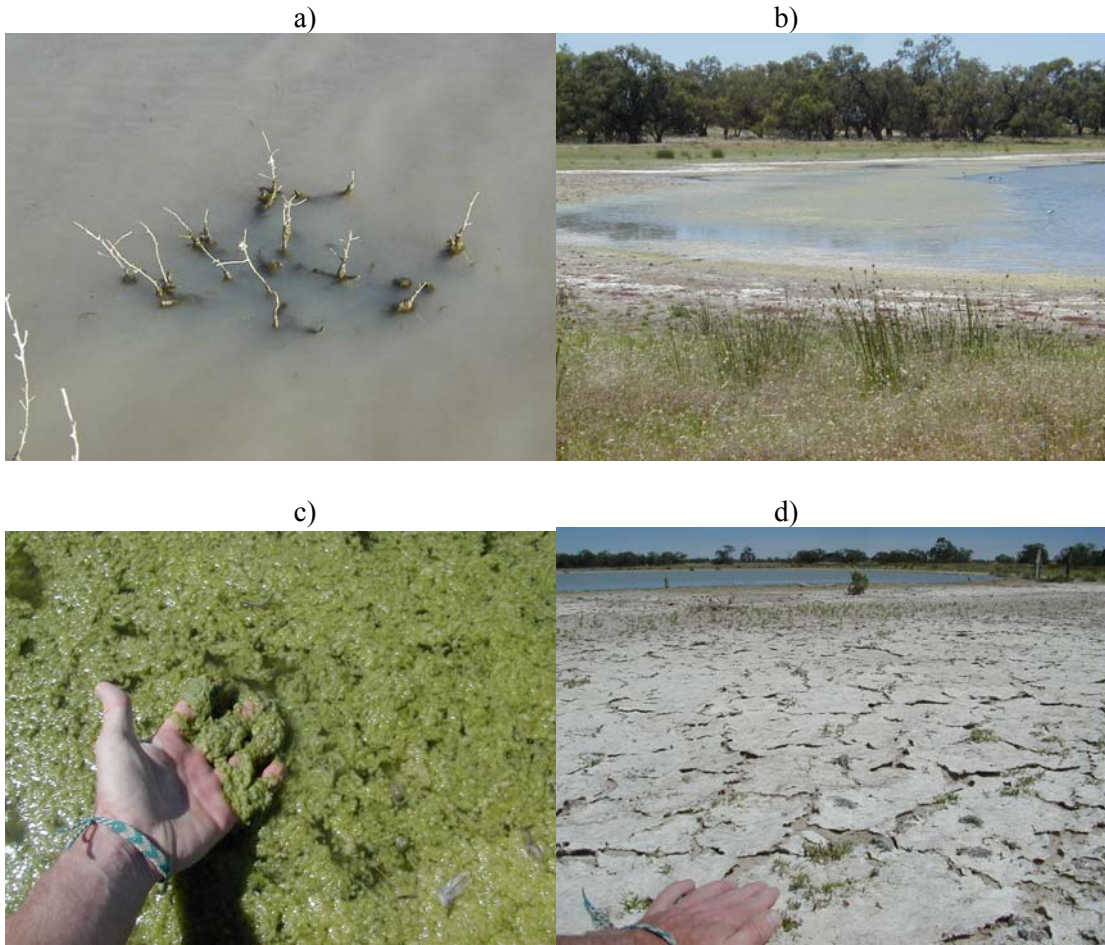
CHL l⁻¹) before declining. Chlorophyll *a* concentrations determined for the last sampling event did not differ significantly between lakes; Lake Tandure (30.78±14.35 µg CHL l⁻¹), Lake Bijiji (25.04±4.34 µg CHL l⁻¹), Lake Balaka (15.18±2.57 µg CHL l⁻¹) and Lake Malta (4.97±4.69 µg CHL l⁻¹) (One-way ANOVA: *p*=0.187).



■ Figure 8: Chlorophyll *a* (µg CHL l⁻¹ mean±se) (●) concentrations recorded for lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period. All values are mean±se.

	Lake	<i>p</i>	Tukey <i>post hoc</i> comparisons
CHL	Tandure	0.096	ns
	Bijiji	<0.001	days 6, 13 > day 28 > days 35, 40 < day 77 > days 124, 210
	Balaka	0.001	day 12 > days 27, 33, 118, 195
	Malta	0.455	ns

■ Table 4: Summary ANOVA statistics for temporal trends in chlorophyll *a* concentrations in lakes Tandure, Bijiji, Balaka and Malta during the 2004 post-flood study period.



■ **Figure 9: Algal biofilm development in Lake Malta: a) biofilm attached to inundated vegetation, b) and c) the accumulation of algal mats around the lake margins, and d) algal crusts deposited as water levels recede (photos O. Scholz).**

Zooplankton

Sixty-seven zooplankton taxa were identified from 119 samples recovered from the Menindee lakes as they flooded during 2004. These included 49 rotifers from 27 genera and 18 micro-crustaceans (7 cladocerans, 3 copepods and 1 ostracod) (Tables 5 and 6). The total number of taxa identified for each lake ranged from 44-56. Of these 34 taxa were common to all lakes. Four taxa were common, occurring in 50 % or more of samples and 25 taxa were rare, occurring in 5 % or less samples. Twenty-nine rotifer taxa and 9 micro-crustacean taxa constituted at least 20 % of total abundance at some stage during the study period.

Shannon-Wiener diversity (H') ranged from 0-3.86 bits individual⁻¹ for rotifer assemblages and from 0-2.84 bits individual⁻¹ for micro-crustacean assemblages (Figure 10). Significant temporal changes in rotifer H' were observed in each lake (Table 7). Rotifer diversity declined significantly in each lake after 12-20 days. Maximum rotifer diversities recorded prior to these declines did not differ significantly between lakes (One-way ANOVA: $R^2=0.509$, $p=0.111$), nor did they differ between lakes at the final sampling event (192-208 days) (One-way ANOVA: $R^2=0.309$, $p=0.372$). Initial micro-crustacean diversities did not differ significantly between lakes (One-way ANOVA: $R^2=0.634$, $p=0.058$). Significant temporal fluctuations in micro-crustacean H' were observed only in lakes Bijiji, Balaka and Malta (Table 7). Although temporal fluctuations in these lakes varied, significant declines were recorded in lakes Bijiji and Balaka during the first month after flooding. By the end of the study period micro-crustacean diversity was significantly higher in lakes Bijiji and Malta than in lakes Tandure and Balaka (One-way ANOVA: $R^2=0.795$, $p=0.004$. Tukey *post hoc* test: Tandure = Balaka < Bijiji = Malta).

Momentary total zooplankton densities ranged from 107-3840 individuals l⁻¹. Rotifer densities ranged from 3.30-3600 individuals l⁻¹, and micro-crustacean densities from 0-2830 individuals l⁻¹ (Figure 11). Significant temporal changes in rotifer density were observed in each lake after flooding (Table 8). Initial density maxima were significantly greater in Lake Malta (3751±42 individuals l⁻¹, day 9) than those recorded in lakes Tandure (943±331 individuals l⁻¹, day 20), Bijiji (318±35 individuals l⁻¹, day 20) or Balaka (635±168 individuals l⁻¹, day 12) (One-way ANOVA: $R^2=0.948$, $p<0.001$. Tukey *post hoc* test: Malta > Tandure = Balaka = Bijiji).

Rotifer densities in lakes Malta and Balaka declined significantly by days 17 and 20, respectively, but took much longer (47-84 days) in Lake Tandure and did not change significantly over the first 40 days in Lake Bijiji. Rotifer densities varied little after these initial decreases in lakes Tandure and Malta. In contrast, rotifer densities in both lakes Bijiji and Balaka increased significantly after 34 and 27 days, respectively. By the end of the study period rotifer densities did not differ significantly between lakes (One-way ANOVA: $R^2=0.497$, $p=0.122$).

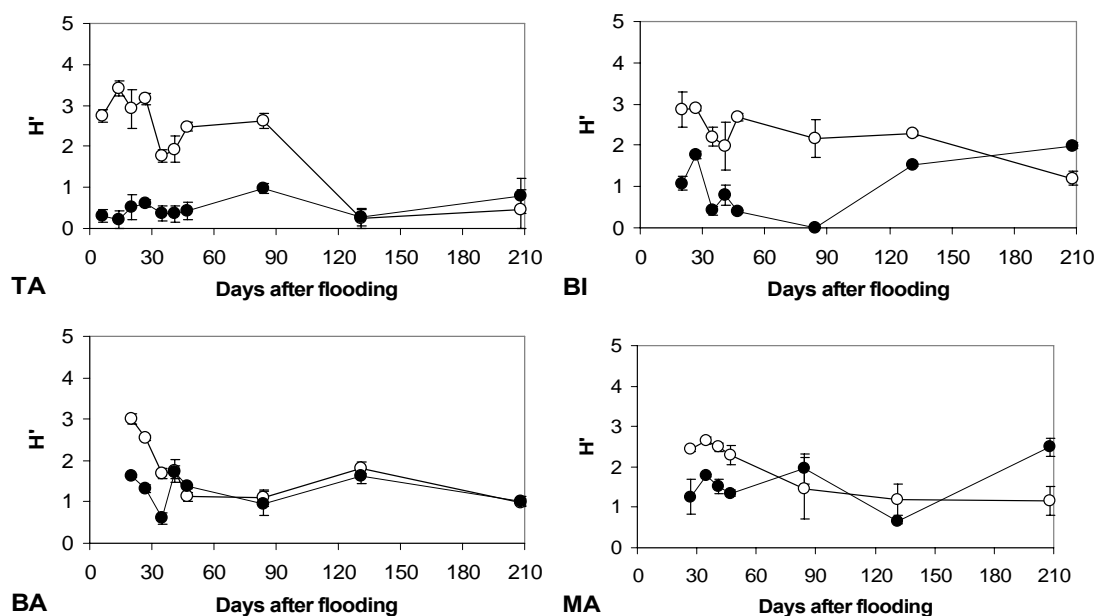
Initial micro-crustacean densities did not differ significantly between lakes (One-way ANOVA: $R^2=0.628$, $p=0.062$). Significant temporal fluctuations in micro-crustacean density were observed only in lakes Bijiji, Balaka and Malta (Table 8). In these lakes, micro-crustacean densities increased significantly until 17th March, days 28, 20 and 17, respectively, after which densities declined significantly in lakes Bijiji and Balaka. Changes in micro-crustacean density in Lake Malta after day 17 were not significant. By the end of the study period micro-crustacean densities did not differ significantly between lakes (One-way ANOVA: $R^2=0.489$, $p=0.129$).

Rotifer taxa	Combined frequency of occurrence (%)	Frequency of occurrence (%)			
		Tandure	Bijiji	Balaka	Malta
<i>Lecane</i> sp.	58.0	70.0	63.3	51.7	46.7
<i>Polyarthra</i> sp.	40.3	73.3	33.3	34.5	20.0
<i>Brachionus leydigi</i>	33.6	53.3	30.0	20.7	30.0
<i>Brachionus quadridentatus</i>	31.9	53.3	23.3	10.3	40.0
<i>Trichocerca</i> spp.	31.9	70.0	36.7	10.3	10.0
<i>Conochilus</i> sp.	31.1	33.3	46.7	27.6	16.7
<i>Keratella australis</i>	30.3	3.3	46.7	48.3	23.3
<i>Lepadella</i> sp.	29.4	53.3	30.0	20.7	13.3
<i>Asplanchna</i> sp.	28.6	33.3	30.0	31.0	20.0
<i>Brachionus angularis</i>	27.7	63.3	10.0	20.7	16.7
<i>Brachionus bidentatus</i>	27.7	23.3	40.0	13.8	33.3
<i>Filinia passa</i>	26.1	46.7	16.7	24.1	16.7
<i>Filinia australiensis</i>	24.4	20.0	20.0	37.9	20.0
<i>Epiphanes brachionus</i>	23.5	26.7	16.7	27.6	23.3
<i>Keratella procurva</i>	22.7	46.7	26.7	13.8	3.3
<i>Bdelloidae</i>	21.0	43.3	20.0	17.2	3.3
<i>Proales</i> sp.	19.3	30.0	20.0	6.9	20.0
<i>Anuroopsis fissa</i>	16.0	40.0	13.3	6.9	3.3
<i>Cephalodella</i> sp.	14.3	30.0	16.7	0.0	10.0
<i>Hexarthra mira</i>	13.4	50.0	3.3	0.0	0.0
<i>Synchaeta</i> sp.	12.6	23.3	13.3	10.3	3.3
<i>Brachionus urceolaris</i>	11.8	13.3	3.3	10.3	20.0
<i>Brachionus budapestinensis</i>	10.9	26.7	3.3	3.4	10.0
<i>Dicranophoridae</i>	10.9	13.3	20.0	3.4	6.7
<i>Cephalodella gibba</i>	10.1	6.7	23.3	0.0	10.0
<i>Brachionus diversicornis</i>	8.4	33.3	0.0	0.0	0.0
<i>Gastropus hyptopus</i>	8.4	3.3	13.3	6.9	10.0
<i>Brachionus calyciflorus</i>	7.6	26.7	3.3	0.0	0.0
<i>Keratella tropica</i>	7.6	16.7	10.0	0.0	3.3
<i>Pompholyx</i> sp.	5.9	10.0	3.3	6.9	3.3
<i>Testudinella</i> sp.	5.9	3.3	10.0	10.3	0.0
<i>Keratella shieli</i>	4.2	13.3	3.3	0.0	0.0
<i>Keratella slacki</i>	4.2	0.0	13.3	3.4	0.0
<i>Platyias quadricornis</i>	4.2	3.3	10.0	3.4	0.0
<i>Brachionus falcatus</i>	3.4	13.3	0.0	0.0	0.0
<i>Brachionus rubens</i>	3.4	13.3	0.0	0.0	0.0
<i>Brachionus kiekoa</i>	2.5	0.0	0.0	0.0	10.0
<i>Filinia pejlerei</i>	2.5	0.0	0.0	10.3	0.0
<i>Fosculariidae</i>	2.5	3.3	0.0	3.4	3.3
<i>Brachionus novazealandi</i>	1.7	0.0	0.0	0.0	6.7
<i>Conochilus unicornis</i>	1.7	6.7	0.0	0.0	0.0
<i>Euchlanis</i> sp.	1.7	0.0	3.3	0.0	3.3
<i>Filinia terminalis</i>	1.7	3.3	0.0	3.4	0.0
<i>Keratella quadrata</i>	1.7	6.7	0.0	0.0	0.0
<i>cf Notomatidae</i>	1.7	0.0	6.7	0.0	0.0
<i>Rotatoria</i> sp.	1.7	3.3	3.3	0.0	0.0
<i>Ascomorpha</i> sp.	0.8	0.0	0.0	3.4	0.0
<i>Brachionus lyratus</i>	0.8	3.3	0.0	0.0	0.0
<i>Forficula</i> sp.	0.8	0.0	3.3	0.0	0.0

■ Table 5: Rotifer taxa and their frequency (%) of occurrence in samples collected from lakes Tandure (n=30), Bijiji (n=30), Balaka (n=29) and Malta (n=30) during the 2004 post-flood study period. Taxa that were numerically dominant (>20 %) at some stage are indicated as bold.

Micro-crustacean taxa	Combined frequency of occurrence (%)	Frequency of occurrence (%)			
		Tandure	Bijiji	Balaka	Malta
Calanoid nauplii	77.3	83.3	76.7	79.3	70.0
Calanoid copepodite	67.2	63.3	66.7	72.4	66.7
<i>Boeckella triarticulata</i>	50.4	26.7	50.0	65.5	60.0
<i>Cyclopoida</i> sp:	34.5	10.0	33.3	48.3	46.7
<i>Moina</i> sp.	27.7	6.7	33.3	34.5	36.7
<i>Daphnia lumholtzi</i>	21.0	3.3	13.3	13.8	53.3
<i>Ostrococha</i>	18.5	20.0	13.3	13.8	26.7
<i>Ceriodaphnia</i> sp.	15.1	3.3	16.7	24.1	16.7
<i>Alona</i> sp.	13.4	13.3	10.0	17.2	13.3
<i>Diaphanosoma</i> sp.	10.9	10.0	6.7	10.3	16.7
<i>Bosmina meridionalis</i>	5.0	0.0	0.0	10.3	10.0
<i>Chydorus</i> sp.	4.2	3.3	0.0	6.9	6.7
<i>Macrothrix</i> sp.	4.2	13.3	0.0	3.4	0.0
<i>Calamoecia canberri</i>	2.5	0.0	6.7	0.0	3.3
<i>Simocephalus</i> sp.	2.5	0.0	3.3	0.0	6.7
<i>Ilyocryptus</i> sp.	2.5	10.0	0.0	0.0	0.0
<i>Harpacticoida</i>	1.7	3.3	3.3	0.0	0.0
<i>Leydigia</i> sp.	0.8	3.3	0.0	0.0	0.0

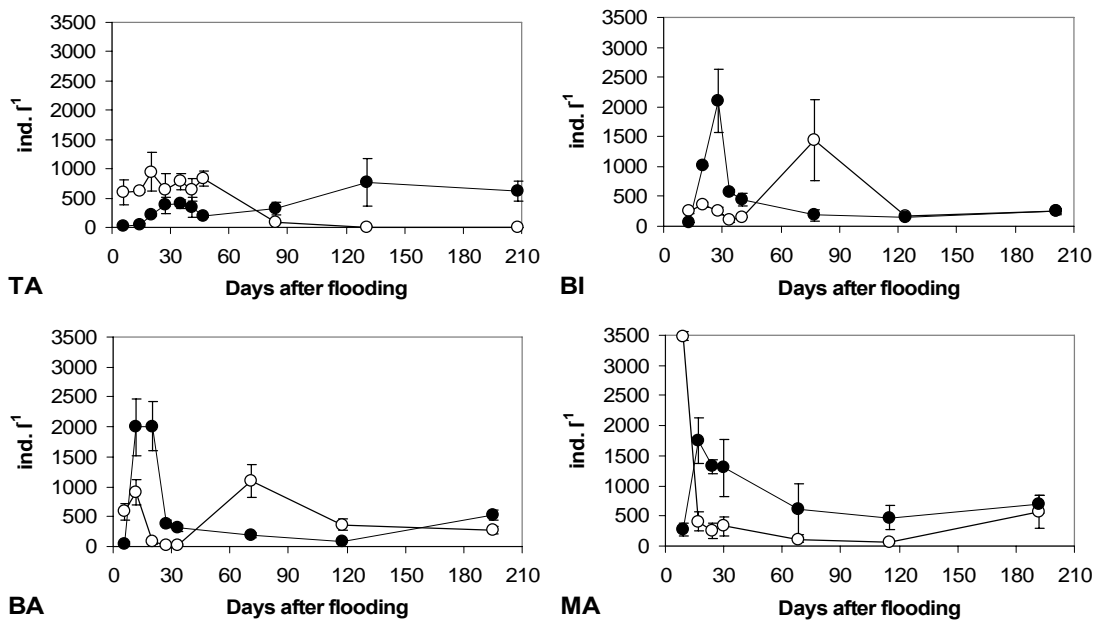
■ Table 6: Micro-crustacean taxa and their frequency (%) of occurrence in samples collected from lakes Tandure (n=30), Bijiji (n=30), Balaka (n=29) and Malta (n=30) during the 2004 post-flood study period. Taxa that were numerically dominant (>20 %) at some stage are indicated as bold.



■ Figure 10: Shannon-Wiener diversity (H' mean \pm se) of rotifers (\circ) and micro-crustaceans (\bullet) collected from lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period.

Community	Lake	<i>p</i>	Tukey <i>post hoc</i> comparisons
Rotifers	Tandure	<0.001	days 6, 14, 27, 41, 47, 84 > days 131, 208 day 14 > days 35, 41, 84, 131 day 35 > day 131
	Bijiji	0.030	days 13, 20 > day 201
	Balaka	<0.001	day 6 = day 12 > all subsequent days day 118 > day 192
	Malta	0.031	day 17 > day 192
Micro-crustaceans	Tandure	0.379	ns
	Bijiji	<0.001	day 13 < day 20 > days 28, 34, 40, 77 day 77 < days 124, 201
	Balaka	0.002	day 6 > day 20 < days 27, 118
	Malta	0.003	day 9 < day 192 day 68 > day 115 < day 192

■ Table 7: Summary ANOVA statistics for temporal trends in rotifer and micro-crustacean diversity H' (bits individual⁻¹).



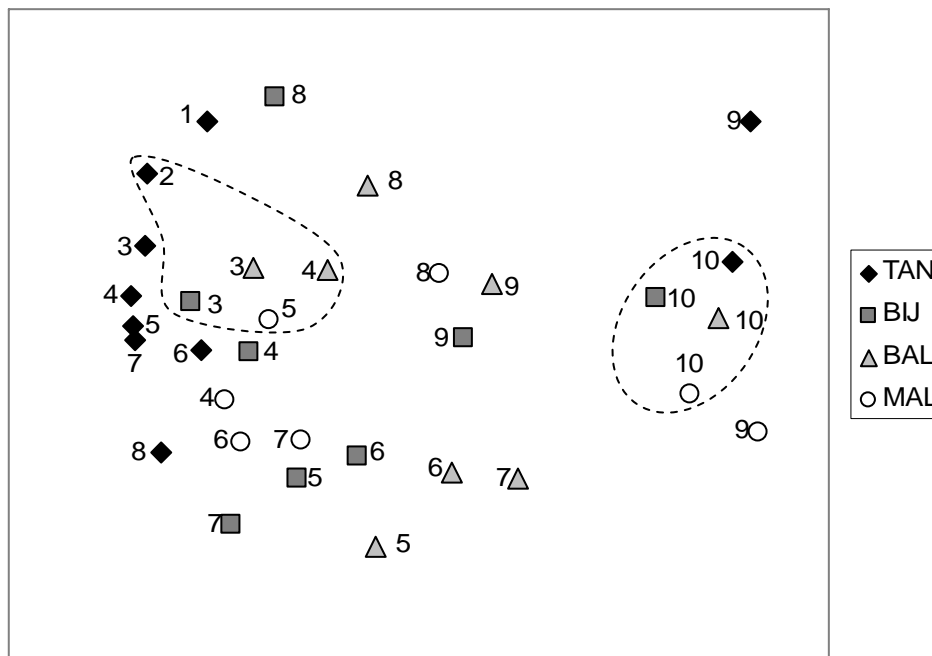
■ Figure 11: Densities (individuals l^{-1} mean \pm se) of rotifers (\circ) and micro-crustaceans (\bullet) collected from lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period.

Community	Lake	<i>p</i>	Tukey <i>post hoc</i> comparisons
Rotifers	Tandure	0.004	day 20 > days 84, 131, 208
	Bijiji	0.025	days 13, 28, 34, 40 < day 77 > days 124, 201
	Balaka	<0.001	day 12 > days 20, 27, 33 < day 71 > days 118, 195
	Malta	<0.001	day 9 > all subsequent days
Micro-crustaceans	Tandure	0.083	ns
	Bijiji	<0.001	day 13 < day 20 < day 28 > all subsequent days
	Balaka	<0.001	day 6 < day 12 = day 20 > all subsequent days
	Malta	0.031	day 9 > day 17

■ Table 8: Summary ANOVA statistics for temporal trends in rotifer and micro-crustacean density (individuals l^{-1}).

Two-dimensional NMDS was used to display multidimensional relationships between sampled zooplankton communities (rotifers and micro-crustaceans combined) (Figure 12). We first tested the *a priori* hypothesis that zooplankton communities differed between lakes. For this we pooled all sampling times within lakes. The zooplankton communities of Lake Tandure differed significantly from those in Lake Balaka (ANOSIM: $R=0.248$, $p=0.014$) and Malta (ANOSIM: $R=0.229$, $p=0.030$), but not from those in lakes Bijiji (ANOSIM: $R=0.071$, $p=0.150$). Zooplankton communities did not differ significantly between the three smaller lakes (ANOSIM: $R_{\text{Bijiji-Balaka}}=-0.012$, $p=0.467$; $R_{\text{Bijiji-Malta}}=0.012$, $p=0.336$; $R_{\text{Balaka-Malta}}=-0.074$, $p=0.762$). SIMPER analyses indicated that calanoid nauplii, copepodites and *Lecane sp.* were important structural components of communities in each lake. Key distinguishing taxa for each lake (*i.e.* those that contributed more than 5 % to total group similarity) are shown in Table 9.

We then tested the *a priori* hypothesis that zooplankton community structure changed over time in all lakes. Analyses of differences either within times between lakes or between times within lakes was compromised by the number of replicates per lake/time ($n=3$) being too low to achieve significance below the 10 % level (Clarke and Warwick 1994). We therefore pooled lakes within two selected sampling times; 2 weeks after inundation (*i.e.* sampling events 2, 3, 4 and 5 in lakes Tandure, Bijiji, Balaka and Malta, respectively) and 6-7 months after inundation (*i.e.* the last sampling event). We selected 2 weeks after inundation as our starting point as it was the first time for which data was available for each lake (*i.e.* where $n>3$). Early and late inundation community groups differed significantly (ANOSIM: Global $R=1.0$, $p=0.029$). SIMPER analyses indicated an average dissimilarity of 74.04 % between the two groups, with the early flood community distinguished by more rotifer taxa and late flood communities distinguished by more micro-crustaceans (Table 10).



■ **Figure 12: Non-metric multidimensional scaling plot of zooplankton community structure for samples collected from lakes Tandure, Bijiji, Balaka and Malta during the 2004 post-flood study period. Bound areas encompass 2 week and 6-7 month post-inundation groups. Icon labels refer to sampling events (refer to Table 1). Stress level = 0.16.**

Taxa	Percentage contributions to within lake similarity			
	Tandure	Bijji	Balaka	Malta
Calanoid nauplii	18.28	21.57	23.07	16.19
Calanoid copepodite	8.87	8.51	13.58	11.04
<i>Lecane</i> sp.	5.78	9.63	7.35	7.61
<i>Polyarthra</i> sp.	8.48			
<i>Brachionus angularis</i>	5.35			
<i>Conochilus</i> sp.		6.28		
<i>Boeckella triarticulata</i>		5.15	12.42	11.44
<i>Keratella australis</i>			8.34	
<i>Cyclopoida</i> sp:			6.71	5.65
<i>Daphnia lumholtzi</i>				7.45
<i>Brachionus quadridentatus</i>				5.33
<i>Brachionus bidentatus</i>				5.24

■ **Table 9: Zooplankton taxa most representative of community structures in each lake (i.e. those contributing > 5 % to group similarity).**

Early post-flood (2 weeks)	Contribution to group dissimilarities (%)	Late post-flood (6-7 months)	Contribution to group dissimilarities (%)
Rotifers			
<i>Brachionus quadridentatus</i>	4.59	<i>Keratella australis</i>	5.12
<i>Brachionus leydigi</i>	3.87	<i>Filinia australiensis</i>	3.99
<i>Filinia passa</i>	3.66	<i>Conochilus</i> sp.	3.09
<i>Polyarthra</i> sp.	3.53	<i>Brachionus novazealandi</i>	1.19
<i>Trichocerca</i> spp.	3.43		
<i>Brachionus angularis</i>	3.32		
<i>Lecane</i> sp.	3.03		
<i>Epiphanes brachionus</i>	2.55		
<i>Gastropus hyptopus</i>	2.33		
<i>Asplanchna</i> sp.	2.32		
<i>Brachionus bidentatus</i>	2.27		
<i>Proales</i> sp.	2.09		
<i>Brachionus budapestinensis</i>	2.06		
<i>Anuroopsis fissa</i>	2.05		
<i>Brachionus calyciflorus</i>	1.72		
<i>Brachionus urceolaris</i>	1.72		
<i>Keratella procurva</i>	1.37		
<i>Lepadella</i> sp.	1.31		
<i>Dicranophoridae</i>	1.02		
Micro-crustaceans			
<i>Moina</i> sp.	3.10	<i>Boeckella triarticulata</i>	3.75
<i>Cyclopoida</i>	2.69	<i>Ceriodaphnia</i> sp.	2.85
Nauplii	2.40	<i>Alona</i> sp.	2.01
Copepodite	1.82	<i>Ostracoda</i>	1.97
		<i>Calamoecia canberri</i>	1.63
		<i>Daphnia lumholtzi</i>	1.62
		<i>Harpacticoida</i>	1.37

Table 10: Zooplankton taxa most representative of differences between communities sampled two weeks and 6-7 months after lake inundation (i.e. those contributing > 1 % to dissimilarity between times).

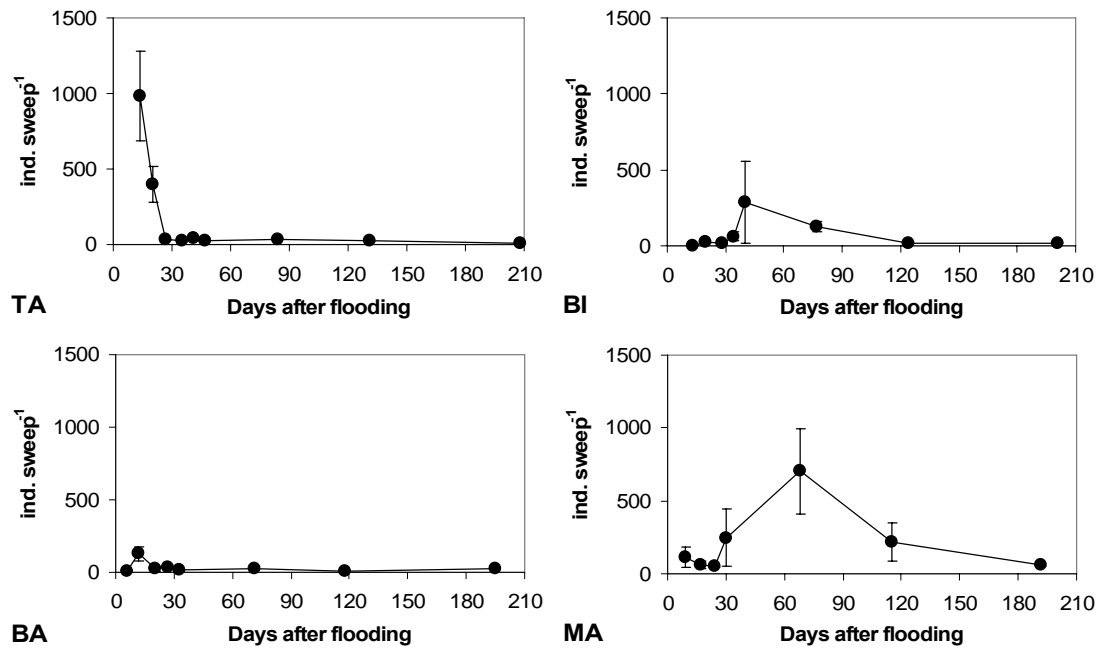
Macro-invertebrates

Twenty-four macro-invertebrate taxa were identified from 95 samples recovered from the Menindee lakes as they flooded during 2004. These included 18 insects (6 orders), 4 crustaceans (3 orders), 1 gastropod and 1 arachnid (Table 11). The total number of taxa identified in each lake ranged from 9-16. Of these, 6 taxa were common to all lakes. Three taxa were common, occurring in 50 % or more of samples and 16 taxa were rare, occurring in 5 % or less samples. Eleven taxa constituted at least 20 % of total abundance at some stage during the study period.

Macro-invertebrate densities ranged from 1-1348 sweep⁻¹ (Figure 13). No significant temporal change in macro-invertebrate density was detected in lakes Bijiji (One-way ANOVA: $p=0.462$) and Malta (One-way ANOVA: $p=0.074$). Significant temporal changes in macro-invertebrate density identified in lakes Tandure (One-way ANOVA: $p<0.001$. Tukey *post hoc* test: day 14 > all subsequent days) and Balaka (One-way ANOVA: $p=0.007$. Tukey *post hoc* test: day 6 < day 13 > all subsequent days) were principally due to declines in notonectids and corixids in Lake Tandure and to changes in corixid numbers in Lake Balaka.

Class	Order (sub-order)	Family (sub-family)	Frequency of occurrence (%)				
			Combined	Tandure	Bijiji	Balaka	Malta
Insecta	Hemiptera	Corixidae	87.4	92.6	79.2	87.5	90.0
Insecta	Hemiptera	Notonectidae	71.6	48.1	66.7	83.3	95.0
Insecta	Diptera	Chironomidae (Chironominae)	61.1	77.8	58.3	33.3	75.0
Insecta	Coleoptera	Dytiscidae	30.5	22.2	33.3	20.8	50.0
Insecta	Trichoptera	Leptoceridae	18.9	14.8	29.2	16.7	15.0
Crustacea	Decapoda	Palaemonidae	13.7	33.3	4.2	0.0	15.0
Insecta	Coleoptera	Haliplidae	12.6	7.4	8.3	20.8	15.0
Crustacea	Decapoda	Atyidae	10.5	33.3	4.2	0.0	0.0
Insecta	Diptera	Chironomidae (Tanypodinae)	4.2	7.4	8.3	0.0	0.0
Insecta	Coleoptera	Hydrophilidae	3.2	7.4	4.2	0.0	0.0
Insecta	Diptera	Blephariceridae	3.2	0.0	4.2	8.3	0.0
Insecta	Diptera	Ceratopogonidae	3.2	7.4	0.0	4.2	0.0
Insecta	Diptera	Athericidae	3.2	0.0	4.2	8.3	0.0
Insecta	Trichoptera	Ecnomidae	3.2	0.0	8.3	0.0	5.0
Gastropoda		Physidae	2.1	7.4	0.0	0.0	0.0
Crustacea	Anostraca	Thamnocephalidae	2.1	0.0	0.0	0.0	10.0
Crustacea	Isopoda	Cirolanidae	2.1	7.4	0.0	0.0	0.0
Insecta	Odonata (Zygoptera)	Lestidae	2.1	3.7	0.0	0.0	5.0
Insecta	Coleoptera	Hygrobiidae	2.1	0.0	4.2	0.0	5.0
Arachnida	Acarina	Hydrachnidae	1.1	0.0	0.0	0.0	5.0
Insecta	Ephemeroptera	Baetidae	1.1	3.7	0.0	0.0	0.0
Insecta	Odonata	Coenagrionidae	1.1	0.0	0.0	0.0	5.0
Insecta	Trichoptera	Odontoceridae	1.1	3.7	0.0	0.0	0.0
Insecta	Trichoptera	Calocidae/Helicophidae	1.1	0.0	4.2	0.0	0.0

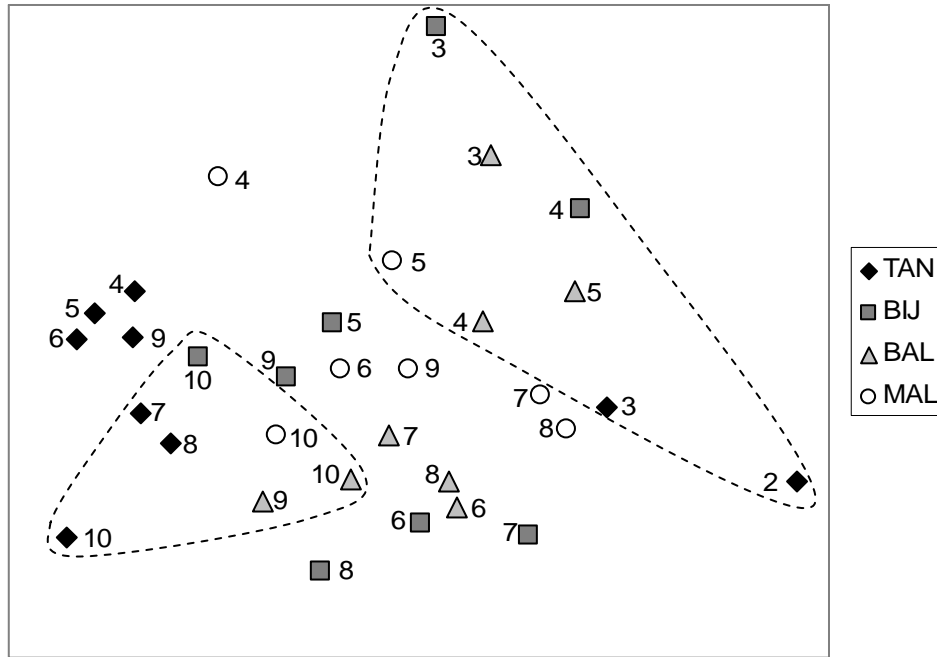
■ **Table 11: Macro-invertebrate taxa and their frequency (%) of occurrence in samples collected from lakes Tandure (n=27), Bijiji (n=24), Balaka (n=24) and Malta (n=20) during the 2004 post-flood study period. Taxa that were numerically dominant (>20 %) at some stage are indicated as bold.**



■ **Figure 13: Densities (individuals sweep⁻¹ mean±se) of macro-invertebrates collected from lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period.**

Two-dimensional NMDS was used to display multidimensional relationships between sampled macro-invertebrate communities (Figure 14). We first tested the *a priori* hypothesis that macro-invertebrate communities differed between lakes. For this we pooled all sampling times within lakes. The macro-invertebrate communities of Lake Tandure differed significantly from those in lake Balaka (ANOSIM: $R=0.401$, $p=0.003$), but not in lakes Bijiji (ANOSIM: $R=0.132$, $p=0.054$) or Malta (ANOSIM: $R=0.186$, $p=0.058$). Whilst the macro-invertebrate communities of Lake Bijiji did not differ significantly from those of lakes Balaka (ANOSIM: $R=0.066$, $p=0.185$) and Malta (ANOSIM: $R=0.064$, $p=0.191$), those of lakes Balaka and Malta did differ significantly (ANOSIM: $R=0.364$, $p=0.001$). SIMPER analyses indicated that corixids, notonectids and chironomids were important structural components of communities in each lake. Key distinguishing taxa for each lake (*i.e.* those that contributed more than 5 % to total group similarity) included dytiscids in lakes Bijiji and Malta, and atyids (freshwater shrimps) and palaemonids (freshwater prawns) in Lake Tandure (Table 12).

We then tested the *a priori* hypothesis that macro-invertebrate community structure changed over time in all lakes, and that differences in structure between lakes decreased over time. Analyses of differences either within times between lakes or between times within lakes was compromised by the number of replicates per lake/time ($n=3$) being too low to achieve significance below the 10 % level (Clarke and Warwick 1994). We therefore pooled lakes within two selected sampling times; 2 weeks after inundation (*i.e.* sampling events 2, 3, 4 and 5 in lakes Tandure, Bijiji, Balaka and Malta, respectively) and 6-7 months after inundation (*i.e.* the last sampling event). We selected 2 weeks after inundation as our starting point as it was the first time for which data was available for each lake (*i.e.* where $n>3$). Early and late inundation community groups differed significantly (ANOSIM: Global $R=0.5$, $p=0.029$). SIMPER analyses indicated an average dissimilarity of 57.39 % between the two groups, with the early flood community distinguished by more taxa (Table 13). SIMPER also indicated that community similarities between lakes increased from 44.86 % shortly after flooding to 68.98 % by the end of the study period.



■ **Figure 14: Non-metric multidimensional scaling plot of macro-invertebrate community structure for samples collected from lakes Tandure, Bijiji, Balaka and Malta during the 2004 post-flood study period. Bound areas encompass 2 week and 6-7 month post-inundation groups. Icon labels refer to sampling events (refer to Table 1). Stress level = 0.19.**

Taxa	Percentage contributions to within lake similarity			
	Tandure	Bijiji	Balaka	Malta
Corixidae	31.08	34.88	43.36	33.78
Notonectidae	14.74	26.98	34.95	24.66
Chironomidae (Chironominae)	24.37	24.81	13.92	27.04
Dytiscidae		8.88		10.75
Atyidae	6.96			
Palaemonidae	13.49			

■ **Table 12: Taxa most representative of community structures in each lake (i.e. those contributing > 5 % to group similarity).**

Time 4 (9 th March)	Contribution to group dissimilarities (%)	Time 10 (7 th September)	Contribution to group dissimilarities (%)
Corixidae	17.15	Leptoceridae	12.45
Notonectidae	16.30	Palaemonidae	8.04
Chironomidae (Chironominae)	12.95		
Dytiscidae	10.61		
Hydrophilidae	5.85		
Hygrobiidae	5.78		
Haliplidae	3.13		
Hydrachnidae	2.57		
Thamnocephalidae	1.95		

■ **Table 13: Macro-invertebrate taxa most representative of differences between communities sampled initially on lake inundation and six months later.**

Fish

A total of 10 fish species (7 native, 3 alien) were recorded during the ten 2004 post-flood surveys (Table 14). Alien species (carp, goldfish and mosquitofish) accounted for 22.6 % of fish caught. The four most abundant species (carp gudgeon, carp, bony herring and smelt) accounted for more than 97.6 % of the 21257 fish caught.

Seven fish species were common to all lakes: carp gudgeons, carp, bony herring, smelt, golden perch, goldfish and spangled perch. Mosquitofish were not recorded in Lake Bijiji. Crimson-spotted rainbowfish were only recorded in lakes Bijiji and Tandure, and silver perch only in lakes Balaka and Bijiji.

Species	Scientific name	Large fyke nets	Small fyke nets	Total
Carp gudgeon	<i>Hypseleotris</i> spp.	0	13423	13423
Carp*	<i>Cyprinus carpio</i> (Linnaeus)	309	4326	4635
Bony herring	<i>Nematalosa erebi</i> (Gunther)	897	1117	2014
Australian smelt	<i>Retropinna semoni</i> (Weber)	0	667	667
Golden perch	<i>Macquaria ambigua</i> (Richardson)	71	228	299
Mosquitofish*	<i>Gambusia holbrooki</i> (Girard)	0	127	127
Goldfish*	<i>Carassius auratus</i> (Linnaeus)	37	6	43
Spangled perch	<i>Leioptherapon unicolor</i> (Gunther)	3	39	42
Crimson-spotted rainbowfish	<i>Melanotaenia fluviatilis</i> (Castelnaud)	0	5	5
Silver perch	<i>Bidyanus bidyanus</i> sp.(Richardson)	0	2	2
TOTAL		1317	19940	21257

■ **Table 14: Total numbers of each fish species collected during the 2004 post-flood surveys using both large and small fyke nets. *-alien species.**

Large fyke net (LFN) CPUE for each lake are shown in Figure 15. Bony herring were numerically dominant in catches from lakes Tandure, Bijiji and Balaka on all but the last survey.

In Lake Tandure total CPUE declined steadily from a peak 191.7 fish 200 hr⁻¹ on day 27 to 26.9 fish 200 hr⁻¹ on day 208. Catches of bony herring were greatest during the first 4-5 weeks after inundation. Catches of bony herring declined from a maximum of 88.3 fish 200 hr⁻¹ on day 27 to only 10.1 fish 200 hr⁻¹ by day 208. Catches of golden perch were highest on day 14 (24.8 fish 200 hr⁻¹, TL=73-90 mm). Much larger golden perch, albeit in smaller numbers, were caught only towards the end of the survey period (day 84 TL=312 mm, day 208 TL=212-236 mm). Carp caught during the first 35 days ranged in size from 107-676 mm TL. Goldfish caught on days 14, 35 and 208 ranged in size from 135-233 mm TL. Spangled perch were only caught on day 14 (3.3 fish 200 hr⁻¹).

In Lake Bijiji total CPUE declined steadily from a peak of 272.2 fish 200 hr⁻¹ on day 20 to 64.7 fish 200 hr⁻¹ on day 201. Catches of bony herring were greatest during the first 4-5 weeks after inundation. Catches of bony herring declined from a maximum of 204.4 fish 200 hr⁻¹ on day 20 to only 17 fish 200 hr⁻¹ by day 201. Golden perch were only caught on days 124 (2.7 fish 200 hr⁻¹, TL 195 mm) and 201 (6.8 fish 200 hr⁻¹, TL 133-156 mm). Catches of carp were

greatest on day 34 after inundation (152.2 fish 200 hr⁻¹). Carp caught throughout the survey period ranged in size from 50-562 mm TL. Goldfish caught on day 24 ranged in size from 163-265 mm TL (58.9 fish hr⁻¹). The single goldfish caught on day 40 belonged to a smaller cohort (77 mm TL).

In Lake Balaka total CPUE declined from a peak of 208.3 fish 200 hr⁻¹ on day 12 to 17.1 fish 200 hr⁻¹ on day 33 before increasing again to 195.2 fish 200 hr⁻¹ on day 118. Most of this variability was due to fluctuations in the catches of bony herring (193.0 fish 200 hr⁻¹ on day 20, 11.4 fish 200 hr⁻¹ on day 33 and 190.5 fish 200 hr⁻¹ on day 118). Only 3.4 fish 200 hr⁻¹ were caught on day 195. Golden perch catches between days 12 and 118 ranged from 0-6.5 fish 200 hr⁻¹. This increased on day 195 to 148.9 fish 200 hr⁻¹. All golden perch catches included both small and large sized fish (range 31-340 mm TL). Catches of carp between days 12 and 33 ranged from 0- 5.7 fish 200 hr⁻¹ and were all mature (180-560 mm TL). All carp caught on days 71 (3.3 fish 200 hr⁻¹) and 195 (16.9 fish 200 hr⁻¹) were smaller (71-111 mm TL). Goldfish were only caught on day 12 (25.0 fish 200 hr⁻¹, TL=165-208 mm). Spangled perch were only caught on day 12 and 195 (2.8 fish 200 hr⁻¹ and 3.4 fish 200 hr⁻¹, respectively).

In Lake Malta total CPUE fluctuated greatly, peaking on days 30 (274.7 fish 200 hr⁻¹) and 115 (327.8 fish 200 hr⁻¹). These peaks were due principally to increases in carp numbers (261.9 fish 200 hr⁻¹ and 294.5 fish 200 hr⁻¹, respectively). Carp size class distribution ranged from 61-476 mm TL. Goldfish were only caught on days 9 and 17 (5.8 fish 200 hr⁻¹ and 6.3 fish 200 hr⁻¹, respectively, size range 95-190 mm TL). Golden perch were only caught on days 24 and 30 (3.1 fish 200 hr⁻¹ and 9.6 fish 200 hr⁻¹, respectively, size range 58-99 mm TL). Bony herring catches were much lower than those recorded in the other lakes, peaking on day 33 at 33.3 fish 200 hr⁻¹.

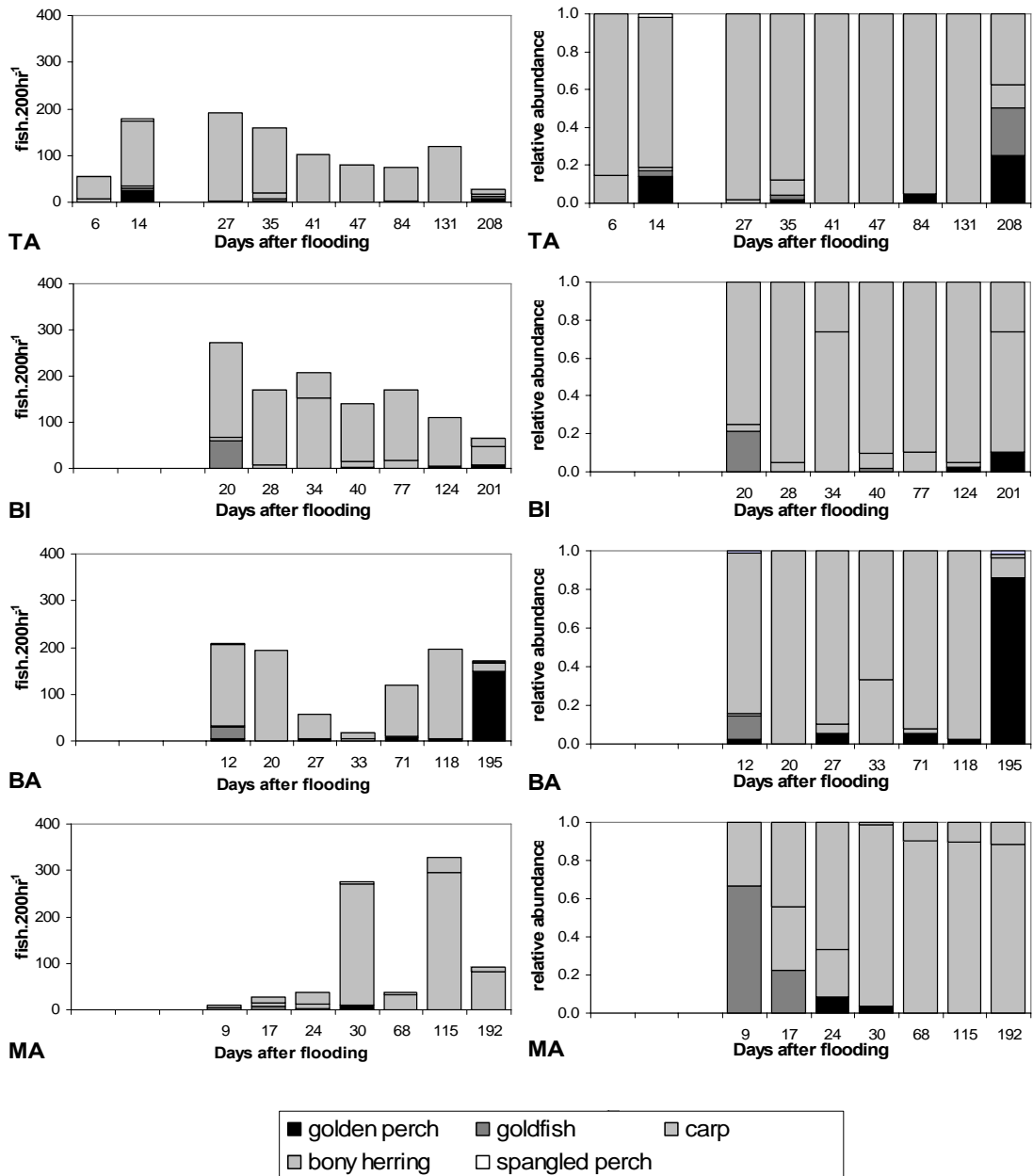
Small fyke net (SFN) CPUE were higher in Lake Tandure (range 2538-7407 fish 200 hr⁻¹) than those in lakes Bijiji (range 71.4-3466 fish 200 hr⁻¹), Balaka (range 71.1-1463 fish 200 hr⁻¹) or Malta (range 59.7-605.8 fish 200 hr⁻¹) (Figure 16). In all lakes total SFN catches increased as lakes filled, peaking on days 35, 40, 33 and 17, respectively, before declining towards the end of the survey period.

SFN CPUE from Lake Tandure were numerically dominated by carp gudgeon throughout the survey period (range 1200-7049 fish 200 hr⁻¹). Bony herring numbers were highest on day 27 (1141 fish 200 hr⁻¹), carp on day 35 (63.1 fish 200 hr⁻¹), mosquitofish on day 47 (310.6 fish 200 hr⁻¹) and Australian smelt on day 131 (1259 fish 200 hr⁻¹). Relatively few golden perch were caught (\leq 3.3 fish 200 hr⁻¹ on days 14 and 27).

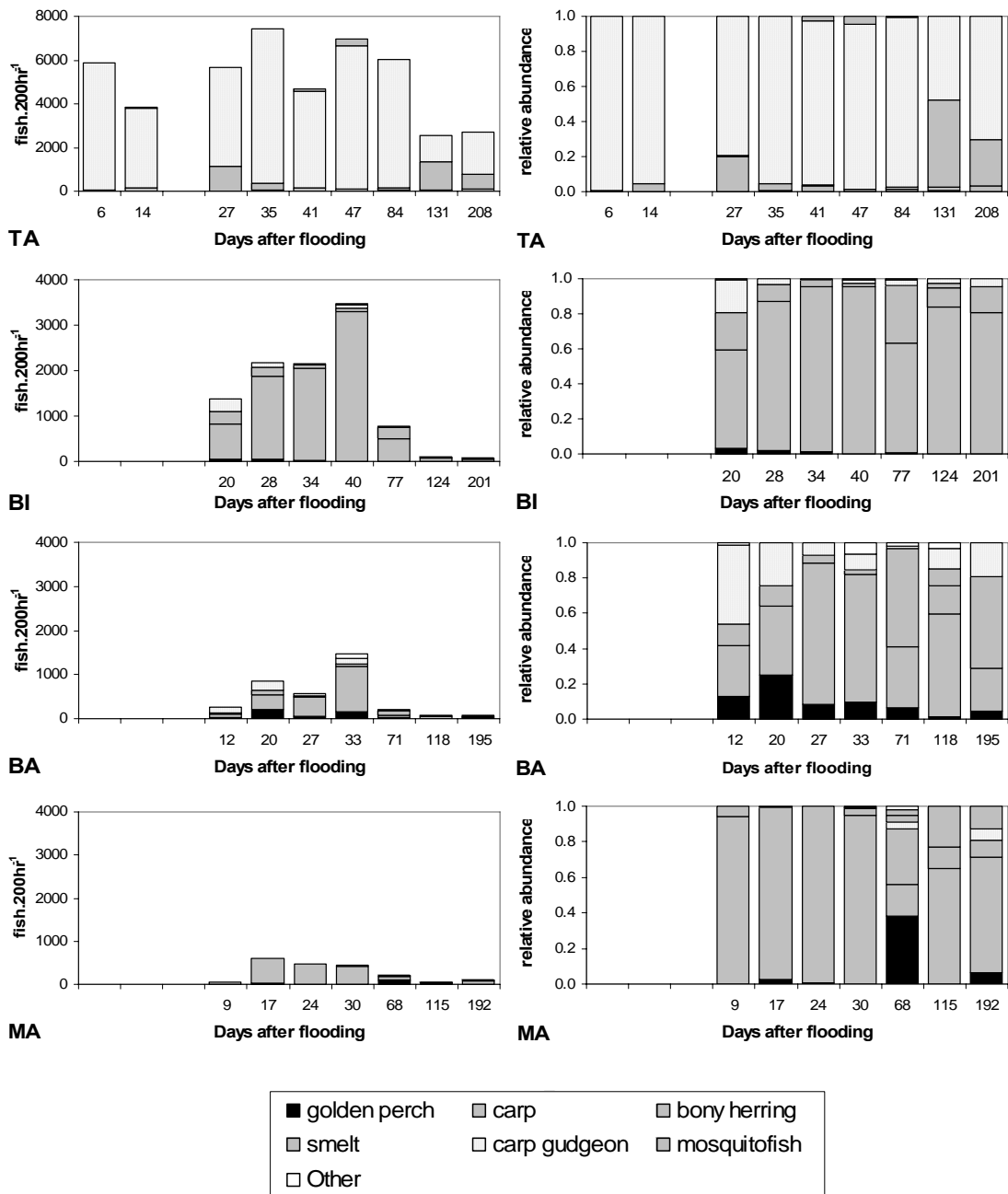
SFN CPUE from Lake Bijiji were numerically dominated by carp, whose numbers increased to 3293 fish 200 hr⁻¹ by day 40. Greatest numbers of bony herring (285.6 fish 200 hr⁻¹), carp gudgeons (261.7 fish 200 hr⁻¹) and golden perch (46.1 fish 200 hr⁻¹) were recorded during the first survey (day 20). Only a few Australian smelt (2.7 fish 200 hr⁻¹) were caught on day 124.

Temporal changes in the species composition of SFN fish catches from Lake Balaka were similar to those from Lake Bijiji. Carp numbers increased to 1056 fish 200 hr⁻¹ by day 33. Greatest numbers of bony herring (95.1 fish 200 hr⁻¹), carp gudgeons (208.5 fish 200 hr⁻¹) and golden perch (214.6 fish 200 hr⁻¹) were recorded on 20 day. Australian smelt only appeared in catches after one month, peaking at 137.2 fish 200 hr⁻¹ on day 195.

SFN catches from Lake Malta were numerically dominated by carp, whose numbers declined from a peak of 587.2 fish 200 hr⁻¹ on day 17 to 35.8 fish 200 hr⁻¹ by day 68, at which time maximum numbers of carp gudgeon (7.5 fish 200 hr⁻¹), bony herring (63.9 fish 200 hr⁻¹) and golden perch (77.8 fish 200 hr⁻¹) were recorded. Australian smelt only appeared in catches after 68 days, increasing to 14.1 fish 200 hr⁻¹ by day 192.



■ Figure 15: CPUE (fish 200hr⁻¹) and relative abundance of fish caught using large fyke nets set in lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period. Missing columns – not sampled.



■ Figure 16: CPUE (fish 200hr⁻¹) and relative abundance of fish caught using small fyke nets set in lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period. Note scale difference for Lake Tandure. Missing columns – not sampled.

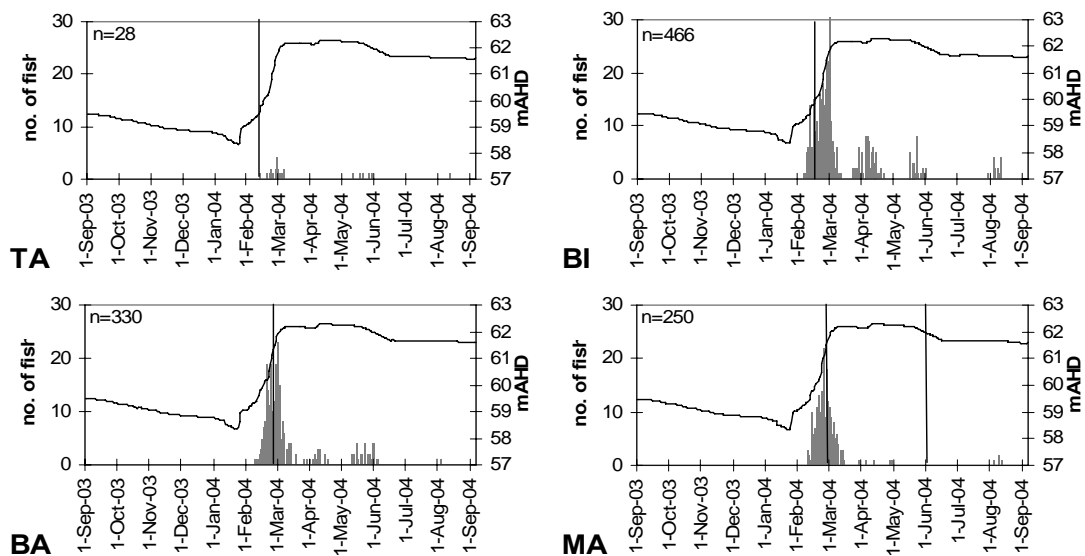
Spawning dates were determined for 1074 carp <50 mm SL by subtracting estimated fish ages from the date of capture using the following SL-TL and age-length relationships:

$$SL \text{ (mm)} = 0.7783 \times TL \text{ (mm)} + 0.5955 \quad (r^2=0.9971, n=141)$$

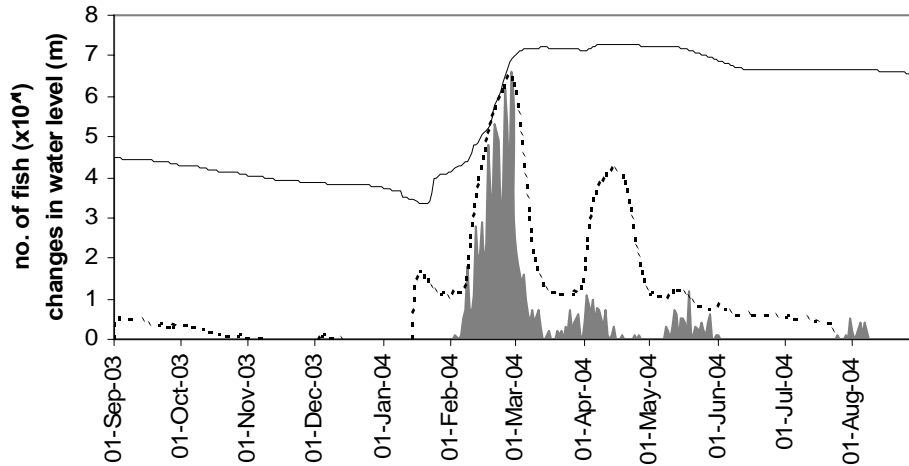
$$\text{Age (in days)} = 0.7659 \times SL^{1.0569} \quad (r^2=0.9225, n=16)$$

Multiple spawning events were identified for carp caught in each lake (Figure 17). Peak spawning activity in each lake occurred during late February-early March and coincided with the arrival of the Darling River flood pulse, which raised water levels in Lake Wetherell (Figure 18). Spawning commenced prior to the flooding of the smaller lakes, indicating that fish from the initial spawning event were part of the first spawning cohort. Subsequent smaller spawning events occurred at intervals of 5-6 weeks, in mid-April, late-May and early-mid August. The duration of successive spawning events decreased from approximately 41 days for the initial flood-pulse event to 33 days, 24 days and as short as 14 days for the last event.

As lakes Tandure, Bijiji and Balaka remained connected to Lake Wetherell throughout the survey period, it was not possible to determine where spawning during these periods had taken place. However, the last identified spawning event in Lake Malta occurred approximately two months after its disconnection from Lake Wetherell, indicating that spawning had taken place within the lake.

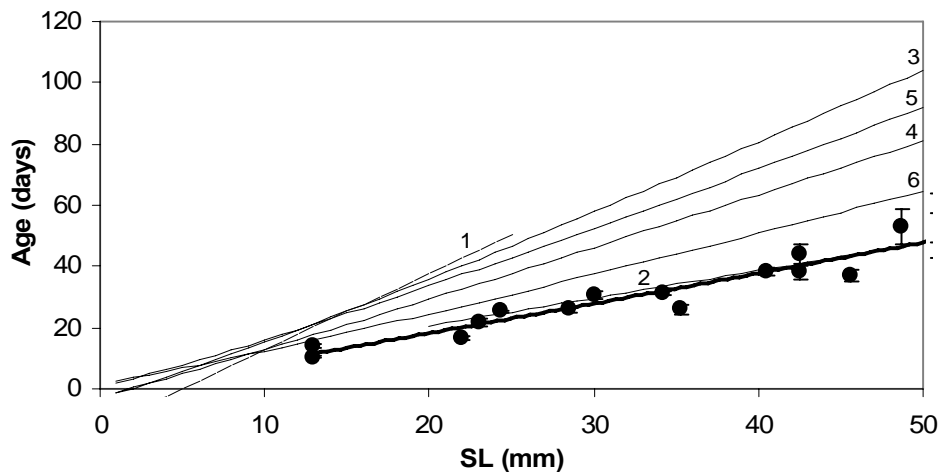


■ **Figure 17: Spawning date distribution of carp caught from lakes Tandure (TA), Bijiji (BI), Balaka (BA) and Malta (MA) during the 2004 post-flood study period. Solid line indicates water levels (mAHHD) recorded in Lake Wetherell. Vertical lines indicate the onset of lake flooding, and for Lake Malta also the timing of disconnection from Lake Wetherell.**



■ **Figure 18: Spawning date distribution of carp collected from all lakes during the 2004 post-flood study period plotted against changes in water levels (m) of Darling River at Wilcannia (dashed line) and Lake Wetherell (solid line).**

The growth rate determined for larval and juvenile carp (cohorts and lakes pooled) (slope of the age-length equation shown above) was similar to that determined for juvenile carp collected from backwaters of the Murray River near Berri (Gurra Lakes) and Swan Reach (Vilizzi 1998), but greater than those determined for mid-stream River Murray populations collected from Punyelroo and Walker Flat over two years (Smith 2004) (Figure 19). These differences between populations indicate that growth rates of carp vary both spatially and temporally and that lake populations tend to grow faster than do river populations.



■ **Figure 19: Age-length relationships determined for carp in the present study (solid line, mean±se), by Vilizzi (1998) for larvae (1) and juveniles (2) collected from Murray River backwaters, and by Smith (2004) for carp collected mid-stream from two sites in the Murray River over two years: (3) Walker Flat 2001-2 (4) Walker Flat 2002-3, (5) Punyelroo 2001-2 and (6) Punyelroo 2002-3.**

Discussion

Ephemeral deflation basin lakes (EDBL) are lowland river floodplain environments that fluctuate between terrestrial and aquatic states. 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 productivity and diversity at a landscape scale.

Water resource management has significantly altered the hydrological regime of many EDBL within the Murray Darling Basin. Within the Menindee Lakes system, for example, flow regulation has increased the permanency of inundation and reduced the frequency and severity of lake drying events. Whilst a growing body of evidence suggests that the impacts of water resource development on arid-zone EDBL have generally been detrimental in terms of net ecosystem productivity and diversity (*e.g.* Kingsford 2000a,b), empirical evidence to support this remains scarce.

This project was initiated to examine aquatic ecosystem responses of four of the Menindee Lakes as they flooded during 2004, and to test hypotheses generated by the conceptual model of EDBL function throughout the wet/dry cycle developed as part of MDBC Project R1011 (Scholz and Gawne 2004a,b).

Each of the floodplain lakes chosen for this investigation was situated adjacent to Lake Wetherell, an impoundment of the Darling River behind the Menindee Lakes Main Weir. Prior to their re-flooding during February 2004, each of the smaller floodplain lakes were completely dry and only a remnant pool covering less than 5 % of the surface area of Lake Tandure remained. The severity of this drying event was unique insofar as Lake Tandure had not dried as extensively since the commencement of flow regulation during the 1960s. The 2004 flood event thus provided an opportunity to examine post-inundation responses in lakes covering a gradient of historical lake drying frequencies: L. Tandure (permanent prior to 2003), L. Bijiji (1 in 14.3 years), L. Balaka (1 in 10.7 years) and L. Malta (1 in 8.6 years). Also, differences in rates of drying between lakes resulted in a gradient of periods for which each of the lakes had been dry prior to re-flooding: Tandure (15 months), L. Bijiji (19 months), L. Balaka (21 months) and L. Malta (23 months). Much of the difference in historical drying frequencies and drying durations between lakes since the regulation of Lake Wetherell during the 1960s is attributable to progressively higher sill heights (and therefore less frequent inflow events) and surface area:volume ratios (*i.e.* greater exposure to evaporation) with distance upstream from the Main Weir.

Based on the conceptual model developed earlier (Scholz and Gawne 2004a), we predicted that these differences in lake characteristics would modify post-inundation responses in each lake with respect to water quality and the structure of invertebrate and fish assemblages. Specifically, more frequent and protracted drying periods were likely to increase the capacity for nutrient mobilization from the lakebed sediments following lake inundation (*sensu* Baldwin and Mitchell 2000), increasing the potential for primary and secondary production. Whilst we predicted that differences in the composition of benthic litter (CPOM) between lakes were likely to modify nutrient fluxes as it decomposed (*e.g.* Brinson 1977), the presence of inundated lakebed vegetation in Lake Malta was predicted to provide an additional nutrient source and to provide habitat structure capable of supporting a greater abundance and diversity of biota than was possible in the other lakes (Briggs and Maher 1985, Furch and Junk 1997).

Water quality

Prior to flooding, EC in Lake Wetherell had increased to $2460 \mu\text{S cm}^{-1}$ near the Main Weir. Much of this saline water was pushed into Lake Tandure, the first lake to flood. Subsequent less saline Darling River inflows diluted salt concentrations in Lake Wetherell prior to the commencement of inflows into the other lakes, resulting in lower post-flood ECs in the smaller lakes. Initial post-flood ECs recorded in each lake were thus influenced by the timing of re-connection with Lake Wetherell.

Turbidity in Lake Wetherell prior to flooding decreased with distance downstream, ranging from 9.7-11 NTU close to the Main Weir to 50-55 NTU upstream of Malta Creek. This was likely to have been a function of the slower flow environment (*i.e.* increased channel width, depth and density of submerged vegetation) facilitating the sedimentation of entrained particles. Subsequent flood water inflows to Lake Wetherell from the Darling River led to a rapid initial increase in turbidity (range 360-550 NTU). Differences in both the timing of inflows and position of each of the floodplain lakes resulted in Lake Tandure (the first to flood) receiving inflows that were less turbid than the other lakes. Post-inundation turbidities in the smaller lakes declined steadily during the first two months in lakes Bijiji and Balaka as suspended matter settled. However, the post-inundation decrease in turbidity in Lake Malta was more rapid (within one month) and likely facilitated by the presence of lakebed vegetation acting to reduce turbulence.

Lake inundation was associated with an increase in nutrient concentrations through both the importation of nutrients with flood waters and sediment release. Both flood-pulse (*e.g.* Junk *et al.* 1989) and sediment-release (McComb and Qiu 1998, Baldwin and Mitchell 2000) mechanisms have been proposed to account for increases in post-flood nitrogen and phosphorus concentrations commonly observed in response to the inundation of previously exposed lakebeds. These models suggest that the loss of flood pulses and drying mediated nutrient release may account for the potential declines in wetland productivity that are believed to accompany changes in wetland hydrology. However, field data supporting either remains scarce (*e.g.* Scholz *et al.* 2002).

Post-inundation nutrient responses varied between lakes and tended to support the relative importance of sediment releases over flood pulse inflows in these lakes. For example, flooding stimulated initial increases in total suspended nitrogen (TN) and phosphorus (TP) concentrations in the smaller lakes (lakes Bijiji, Balaka and Malta) above that present in their source waters. In contrast to these lakes, which had each experienced more frequent and longer drying than Lake Tandure, no similar post flood nutrient pulse was observed in Lake Tandure.

Despite comparable TN concentrations between the smaller lakes, NO_x concentrations and their contribution to the suspended TN pool remained much lower in Lake Malta. This difference between the smaller lakes was likely due to the presence of biofilms associated with the submerged vegetation, and their capacity for denitrification and/or greater demand for labile N. In contrast to NO_x, much higher FRP concentrations were recorded in Lake Malta relative to the other lakes, and were likely being leached from the senescing vegetation (*e.g.* Furch and Junk 1997).

These data suggest that increases in lake drying frequency and/or drying duration stimulated the release of nitrogen and phosphorus from the sediments, increasing the potential for primary production. The presence of senescing vegetation in Lake Malta contributed further

to the pool of available nutrients, with the lower biotic demand for phosphorus than for nitrogen resulting in the accumulation of phosphorus within the water column.

Phytoplankton

Our conceptual model predicted that primary production (measured as phytoplankton biomass) would increase in response to nutrient availability, and hence would increase more in lakes that had dried more frequently and/or for longer. Significant increases in phytoplankton biomass were observed only in lakes Bijiji and Balaka. These increases coincided with increases in nutrient concentrations, providing a circumstantial link between nutrient release and capacity for primary production. This link was also supported by the lack of changes in phytoplankton biomass observed in Lake Tandure where no post-flood nutrient pulse was recorded. However, in Lake Malta where nutrient releases were likely to have been greatest no change in phytoplankton biomass was observed. Indeed, of the four lakes examined, phytoplankton biomass was lowest in Lake Malta. Further, turbidity was generally lower in Lake Malta than it was in lakes Bijiji and Balaka, suggesting that light availability and hence capacity for primary production would have been greater.

Although phytoplankton biomass was much lower in Lake Malta, substantial epiphytic loads developed on the inundated terrestrial vegetation. These biofilms became dislodged and accumulated around the margins of the lake as they exceeded the capacity of the inundated vegetation to support them and as the inundated vegetation in Lake Malta decomposed. Epiphytes were much less apparent in the other lakes where suitable substrata (*i.e.* vegetation, woody debris) were restricted to a relatively narrow littoral margin. The presence of inundated vegetation in Lake Malta thus appeared to stimulate a shift in the partitioning of algal production from the plankton to the epiphyton. Whilst a similar shift in algal partitioning in response to the presence of inundated vegetation was reported in an earlier mesocosm-scale study (Section 3.3 Scholz and Gawne 2004a), this is the first demonstration of this effect at the lake-scale. Though several studies have shown that biofilm productivity can exceed that of the phytoplankton in large shallow lakes, such as deflation basin lakes (Wetzel 1964, Wetzel *et al.* 1972, Stanley 1976, Loeb *et al.* 1983), these made no link with lake hydrology.

Whereas phytoplankton biomass in the absence of inundated vegetation decreased once sediment derived labile nitrogen and phosphorus pools became depleted, epiphyte biomass appeared to increase and persist in response to the slower and more protracted release of nutrients from the inundated vegetation. This suggested that net primary productivity may have been greater in the presence of inundated vegetation. These findings are similar to those we reported earlier for mesocosm scale experiments (Scholz and Gawne 2004b).

The partitioning of primary production as described for Lake Malta is likely to have influenced the accessibility of food resources available to aquatic grazer populations, and thus possibly also influenced other trophic interactions. This has potentially important implications for the management of lake drying regimes (*i.e.* longer drying increases the potential for sediment nutrient mineralization and for lakebed vegetation to develop) and dry lakebed vegetation (*e.g.* grazing and cropping) (*e.g.* Robertson 1998, Seddon and Briggs 1998).

Zooplankton

Flooding has 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, Hairston *et al.* 1995, Boulton and Jenkins 1998, Nielsen *et al.* 2000). The presence of such propagules within 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. Flooding thus initiates a successional sequence in zooplankton communities, with flood borne immigrants being replaced initially by emergents followed by a more depauperate suite of taxa as pioneer species disappear. Zooplankton community diversity and abundance are thus likely to be greatest during the initial post-flood period when food resources are abundant (*e.g.* Maher and Carpenter 1984, Boulton and Lloyd 1992, Jenkins and Boulton 2003).

The few field and mesocosm studies that are available suggest that zooplankton 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). Accordingly, we predicted that post-inundation productivity would be lower in Lake Tandure than in the other lakes that had a history of more frequent drying.

The zooplankton communities of all lakes characteristically included calanoid copepods and copepodites and the rotifer *Lecane* sp. Whilst differences in key distinguishing taxa for each lake were identified, differences between lakes Bijiji, Balaka and Malta were not significant, whilst those of Lake Tandure differed significantly from those in lakes Balaka and Malta (refer to Table 9).

Increases in rotifer and micro-crustacean abundances during the first month of inundation were greatest in the smaller lakes, conforming to our predictions. Rotifer abundances in each lake peaked earlier than did that of micro-crustaceans. This reflected the changes in rotifer and micro-crustacean abundances reported elsewhere (Allan 1976, Boulton and Lloyd 1992, Ingram *et al.* 1997 Baranyi *et al.* (2002) and was a likely consequence of the shorter embryonic development times of rotifers (Herzig 1983, Townsend *et al.* 1997).

Baranyi *et al.* (2002) reported that micro-crustacean biomass exceeded rotifer biomass after approximately 14 days, after which rotifer biomass declined. A similar response was observed in each of the lakes we examined. This negative response by rotifers has been attributed in other studies to their suppression and exclusion by large cladocerans (Brooks and Dodson 1965, Gilbert 1988), to exploitative competition for the same phytoplankton food resources (Kirk 1991) to mechanical interference (Gilbert and Stemberger 1985, Burns and Gilbert 1986) and to predation (Lapesa *et al.* 2002).

Fluctuations in community abundances following the initial post-inundation emergence-driven peaks were more difficult to account for. Wiggins *et al.* (1980) and Baranyi *et al.* (2002) indicated that as the period of inundation increases, biotic processes become relatively more important than abiotic processes in determining the distribution and abundance of invertebrate species. Prolonged inundation, beyond the initial post-flood pulse of production, has also been shown to lead to reductions in both invertebrate abundance and productivity (Maher and Carpenter 1984). Comparisons between initial and final (six months) post-inundation communities indicated firstly, that significant changes in community structure had occurred, and secondly, that similar changes had occurred within each of the lakes. These changes were attributable to the replacement of the initial post-flood community by a more depauperate suite of rotifers and a more diverse suite of micro-crustaceans. Comparable shifts in community structure have been attributed to season (Crome and Carpenter 1988, Moore *et al.* 1996, Scholz and Gawne 2004a) and to differences in species environmental preference. For example, as lakes fill the rotifer-dominated communities more closely reflect those typical of river environments and the subsequent transition to micro-crustacean-dominated communities more closely reflect those typical of lake environments (*e.g.* Shiel *et al.* 1982, Shiel and Walker 1984, Shiel 1986, Baranyi *et al.* 2002).

As mentioned earlier, there was a significant difference in the magnitude of initial post-inundation zooplankton abundance peaks between Lake Tandure and the smaller lakes. Three mechanisms to account for this difference are suggested. Firstly, the relative infrequency of drying episodes in Lake Tandure (once in the last 40 years) reduced the availability of food resources. Secondly, the relative infrequency of drying episodes in Lake Tandure may have reduced the potential for zooplankton regeneration from the sediments following inundation. This explanation is based on a number of supportable assumptions, such as the deposition of propagules being cued by lake drying, and propagule viability decreasing with time (*e.g.* Kalk and Schulten-Senden 1977, Moritz 1987, Hairston *et al.* 1995, Briggs *et al.* 1997, Jenkins and Briggs 1997, Boulton and Jenkins 1998, Brock *et al.* 2003). And thirdly, there was no difference in post-inundation zooplankton productivity, but rather that the standing crop was reduced by predation (*e.g.* Reynolds and Geddes 1984, Geddes 1986, Hillman and Shiel 1997).

Positive associations between zooplankton abundance and diversity and habitat structure are well documented (Beck 2000, Taniguchi *et al.* 2003). These associations are based on the increases in food availability, shelter and niche diversity afforded by complex habitat. The second prediction of our model, namely that the presence of habitat structure, such as inundated vegetation in Lake Malta, would support both higher zooplankton abundances and diversity was not supported.

Macro-invertebrates

Upon inundation macro-invertebrate communities in all lakes underwent significant temporal changes with rapid colonization by a diverse macro-invertebrate community dominated by notonectids and corixids. Over time the community changed with declines in the numbers of corixids and notonectids and increases in the numbers of crustaceans. Numerous studies have shown water-level variability to be a major determinant of macro-invertebrate community structure and productivity (Wiggins *et al.* 1980, Bataille and Baldassarre 1993, Jeffries 1994). Although differences in the structure of macro-invertebrate communities of ephemeral and more permanent wetlands have been documented (*e.g.* Schalles and Shure 1989, Batzer and Resh 1992, Jeffries 1994), little consensus exists as to whether ephemeral systems are intrinsically more productive habitats for macro-invertebrates than more permanent systems (Batzer and Wissinger 1996).

The re-colonization of newly inundated wetlands by macro-invertebrates occurs via pathways such as emergence from the sediments of desiccation resistant immature stages (eggs and larvae) or desiccation resistant adults, passive movement with the incoming waters, active migration during the period of connection, chance introduction by other animals and aerial dispersal (Talling 1951, Wiggins *et al.* 1980, Batzer and Wissinger 1996, Hillman and Quinn 2002). Aerial invaders such as corixids and notonectids were the first macro-invertebrate taxa to re-colonize Lake Tandure as it filled. Densities of these taxa during the first two weeks before inflows into the other lakes had commenced were significantly greater than were recorded at any other stage during the study in any of the other lakes. This likely reflected the absence of alternative habitat suitable for colonization during that initial period. The presence of these omnivorous and carnivorous taxa, respectively, at densities as high as 892 corixids 10 m sweep⁻¹ and 1120 notonectids 10 m sweep⁻¹ during the first few weeks of inundation may have represented a significant top-down pressure in zooplankton communities, and accounted for the lower zooplankton abundances recorded in Lake Tandure relative to the other lakes during that period (*e.g.* Reynolds and Geddes 1984, Geddes 1986, Jeffries 1996, Arner *et al.* 1998).

Apart from reductions in corixid and notonectid abundances in Lake Tandure and corixid abundances in Lake Balaka during the first three weeks of inundation, macro-invertebrate abundances did not vary significantly throughout the study period. Although large sample variances reduced the power to detect changes, highest abundances in Lake Malta were recorded 68 days after inundation (range 222-1234 individuals 10 m sweep⁻¹). Subsequent declines in abundance coincided with noticeable reductions in habitat structure provided by the inundated vegetation (O. Scholz pers. obs).

Temporal changes in macro-invertebrate community structure following lake inundation are driven initially by species succession initiated via the re-colonization pathways already stated. Over time, however, seasonal changes in the food base, habitat quality and aerial invasion are likely to become increasingly important. This suggests firstly, that temporal changes in the community structure of permanent water bodies will be driven primarily by seasonal influences, and secondly, that the community structure of ephemeral water bodies will converge both with each other and with that of permanent systems irrespective of initial differences in the composition of early colonizers (*sensu* Hillman and Quinn 2002). It is important to note here that convergence is only possible for water bodies between which species exchanges occur. Our data supported this hypothesis, with community similarities between lakes increasing from 44.86 % shortly after flooding to 68.98 % by the end of the study period.

Macro-invertebrate community structures differed significantly between Lake Tandure and the smaller lakes, but not between the smaller lakes. Corixids, notonectids and chironomids (omnivores) were important structural components of the macro-invertebrate communities in each lake (and also of the Darling River, *e.g.* Sheldon 1996, Sheldon and Walker 1998), reflecting the mobility of these taxa. Key distinguishing taxa between lakes included dytiscids (carnivores) in lakes Bijiji and Malta, and atyids (*Paratya australiensis* freshwater shrimp) and palaemonids (*Macrobrachium australiense* freshwater prawns) in Lake Tandure. Lake Tandure was also the only lake in which parastacidae (*Cherax destructor* freshwater crayfish) were encountered (O. Scholz unpublished data). The preference of these decapods for more permanent water bodies has been commented on by Hillman and Quinn (2002). Although Lake Tandure was the only lake in which a residual pool providing refuge persisted, we suggest that the presence of these shredders in Lake Tandure was also likely influenced by differences in the composition of benthic CPOM. Although decapods are widely distributed throughout the Darling River (Sheldon 1996), Gladden and Smock (1990) reported that far more shredder production occurred in the floodplain than in the channel of lowland systems they investigated. The processing of CPOM to fine particulate organic matter (FPOM) by these shredder communities and the subsequent movement of FPOM to the channel as indicated by Edwards and Meyer (1987) and Cuffney (1988), suggests that shredders likely play an important role in the detrital dynamics of the entire system.

We have shown previously that lake hydrology has the capacity to modify the sediments by facilitating greater deposition of particulate matter within the smaller lakes than in Lake Tandure (*e.g.* Scholz *et al.* 2002). In this study, the significant differences in substratum quality (benthic CPOM) identified between the lakes was attributed to differences in littoral vegetation and terrestrial inputs. Whereas CPOM in the smaller lakes consisted primarily of fibrous plant matter derived from inundated lakebed grasses and herbs, the CPOM in Lake Tandure consisted almost entirely of woody debris contributed by fringing black box (*Eucalyptus largiflorens*). As littoral substrate quality is widely considered a key determinant of macro-invertebrate communities in both flowing and non-flowing environments (*e.g.* McLachlan 1977, Pringle *et al.* 1988, Van den Brink *et al.* 1994, Sheldon and Puckridge 1998), we predicted that these differences between lakes would impact on the littoral macro-invertebrate communities examined.

The data presented here indicate that macro-invertebrate colonization of inundated lakes is rapid and that once established the community undergoes a series of changes. Early in the successional sequence macro-invertebrate community structure appears to be influenced by habitat structure, particularly the amount and type of vegetation on the lake bed. These findings highlight once again the importance of dry lake bed management in determining the ecological response to inundation.

Fish

We predicted that post-flood lake fish populations would increase as a consequence of both immigration and recruitment following flood induced spawning, and that these increases would be linked with concomitant increases in the availability of potential food resources and floodplain spawning/nursery habitat. Whilst several recruitment models have been postulated (Cushing 1975, 1990, Gehrke 1991, Harris and Gehrke 1994, Humphries *et al.* 1999.) little empirical data is currently available to indicate whether spawning in key species, such as carp, occurs in-stream in response to rises in water level or in-lake in response to the increased availability of food and floodplain spawning/nursery habitat. We examined this by aging juvenile fish to determine the location of spawning.

Each of the ten fish species (7 native and 3 alien) encountered during the current six month post-inundation study period were also recorded during earlier surveys (Scholz and Gawne 2004a). The only previously recorded species not encountered in the current study was the line-eyed hardyhead (*Craterocephalus stercusmuscarum fulvus*). This species was only encountered in small numbers previously, and its absence or rarity in both surveys likely reflects the lack of suitable (*i.e.* macrophyte) habitat (Pusey *et al.* 2004).

Large fyke net (LFN) and small fyke net (SFN) catches in each of the four lakes investigated increased during the first month of inundation before declining towards the end of the study period. These increases coincided with observed increases in zooplankton abundances and newly available habitat. The decline in fish numbers after 30 to 40 days may be related to emigration of fish following subsidence of post-inundation zooplankton pulse and avian predation.

LFN catches were numerically dominated by bony herring and carp. Lowest total catches were generally recorded in Lake Malta, which provided the smallest catch of bony herring and the largest catch of carp. Differences among lakes likely reflected the timing of connection of each lake with Lake Wetherell and differences in the nature of connection with Lake Wetherell.

Small fyke net catches were much greater in Lake Tandure than in the other lakes. Lowest catches were recorded in Lake Malta. In contrast to the smaller lakes in which carp were most abundant, SFN catches in Lake Tandure were numerically dominated by carp gudgeon. This difference likely reflects the susceptibility of carp gudgeons to passive dispersal with the initial flood pulse. As carp gudgeon spawn during the warmer summer months (Meredith *et al.* 2002), the timing of flooding likely accounts for the large numbers recorded. By comparison, far fewer carp gudgeon were encountered after the previous flood event during August 1998. At that time SFN catches consisted primarily of smelt (spring spawners; McDowell 1996, Allen *et al.* 2002) and carp (Scholz and Gawne 2004a).

Most of the large carp (both ♀ and ♂) caught in Lake Tandure during the first post-flood survey were ripe and all nets set at that time were covered by large numbers of deposited carp eggs (O. Scholz pers. obs.). This in conjunction with the absence of adult carp from subsequent surveys, suggest that carp had moved in to Lake Tandure to spawn before returning to Lake Wetherell. However, far fewer carp larvae and juveniles were caught in

Lake Tandure than were caught in the other lakes. Two mechanisms to account for this are suggested. Firstly, abundances of carp larvae and juveniles may have been reduced by the greater abundances of potential invertebrate predators present initially after flooding in Lake Tandure (discussed above), and secondly, peak spawning activity of carp coincided with the commencement of inflows to Lake Bijiji, where most larvae were encountered.

Age determinations of larval and juvenile carp caught during the survey period from each lake indicated the presence of flood pulse spawned and multiple post-flood pulse spawned cohorts. Methodological constraints (*i.e.* otolith increment visibility) prevented the examination of cohorts that had been spawned more than 46 days prior to the first survey (*i.e.* pre-2004). The timing of the initial spawning event to which most fish caught belonged coincided with rising limb of the flood pulse and preceded the commencement of inflows into each of the smaller lakes. Although spawning and egg deposition was observed in Lake Tandure, this was not observed in the other lakes. These data, whilst not excluding the possibility of in-lake spawning, suggest that the initial flood pulse stimulated spawning within Lake Wetherell as water levels increased, and that the larvae and juveniles caught within each lake likely belonged to the same riverine cohort.

The spawning of three subsequent cohorts at intervals of 5-6 weeks was synchronous between lakes, irrespective of lake connection with Lake Wetherell or changes in river discharge. For example, the last recorded spawning event occurred in Lake Malta after it had become hydraulically isolated. These data suggest that flooding not only stimulated the initial spawning response, but also subsequent spawning events.

Intermittent or batch-wise spawning by carp at intervals of 1-5 weeks, with the number of eggs released decreasing in successive batches is a recognized phenomenon (*e.g.* Swee and McCrimmon 1966, Ivanov 1971, Vilizzi 1998). This likely accounts for the decreases in catches of successive cohorts in each lake during this study. The spawning period for each cohort also decreased over successive batches, ranging from 41 days for the initial batch to only 14 days for the last recorded batch. Similar responses reported elsewhere were attributed to sequential releases over a period of days of portions of each batch of eggs (Mills 1991). The ability to respond quickly to changes in water level and thus to increases in potential resource availability (food and habitat) in conjunction with the capacity to rapidly regenerate depleted egg reserves confers upon carp a considerable competitive advantage over native fish species.

Lowest larval and juvenile abundances were recorded in Lake Tandure. This was a likely consequence of greater initial predation pressure by notonectids relative to the other lakes rather than a response to differences in lake drying history and food resource productivity. Few studies have compared growth rates of carp from different environments (*e.g.* Smith 2004), and none have examined changes in growth in response to flooding. Given the overall increases in post-inundation ecosystem productivity suggested by our data we might expect that this would also produce increased growth. Although we did not examine differences in growth rates between lakes, our estimate of the growth rate of flood-pulse spawned carp was similar to that reported for backwaters associated with the Murray River by Vilizzi (1998) and greater than that of mid-stream Murray River populations reported by Smith (2004). Whilst this may be indicative of differences between the two types of environment, we recognize that temporal variability both within and between cohorts and populations are likely to be considerable.

Our results strongly suggest that response to inundation depends on the timing of flooding and connection between lake and river. Carp appear to have flexible reproductive strategy that enables them to reproduce regardless of flood timing whereas some native species appear to be very sensitive to the timing of floods *e.g.* Australian smelt and gudgeon. Overall results

confirm predictions of conceptual model but further information is required on factors affecting successful recruitment of both native and introduced species.

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