THE INFLUENCE OF SEASONALITY AND DURATION OF FLOODING ON ZOOPLANKTON IN EXPERIMENTAL BILLABONGS

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ABSTRACT

The regulation of Australian lowland rivers such as the River Murray has resulted in changes to the flooding characteristics of many associated wetlands. It has been suggested that these changes in flooding have changed the pattern of response of many wetland biota. The substantial variability in the size and shape of these wetlands makes limited field observations difficult to interpret. To overcome this variability 16 experimental billabongs were constructed in which factors that may cause changes to populations within billabongs could be manipulated. In this paper we report on experiments that test the hypothesis that changing the pattern of flooding alters the density and diversity of rotifers and microcrustaceans in billabongs. The experimental billabongs were sampled fortnightly for two years. During this time four flood events were imposed. Flooding of the experimental billabongs resulted in increased microcrustacean abundance. Rotifer abundance rarely increased following flooding. Changing the time of flooding did not modify this response. Observed changes in community structure following flooding result from changes in the relative densities of taxa already present rather than changes in the community composition. Copyright © 2002 John Wiley & Sons, Ltd.

KEY WORDS: rotifers; microcrustaceans; zooplankton; cut-off meanders; billabongs; floodplain; flooding; mesocosms

INTRODUCTION

Australia has a diverse range of wetlands that cover approximately 3% of the land, but the majority of these are ephemeral (Mitchell, 1994). Non-riverine wetlands have their own local catchment or are filled from groundwater, such as mound springs in central Australia (Robins, 1999). Riverine wetlands are associated with rivers during flooding. Often these are formed by the meanderings of lowland rivers and are commonly termed billabongs, cut-off meanders, oxbows or lagoons.

Communities within billabongs vary geographically and seasonally. The variability in hydrology of floodplain billabongs has promoted specialized adaptations, particularly in animals that are capable only of passive dispersal (Hillman, 1986). They survive in a constantly changing chemical and physical environment that creates a range of stresses from extremes of temperature, fluctuating salinity and low oxygen levels to complete drying (Williams, 1985).

Much of the high diversity in floodplain environments is assumed to be driven by variations in the flooding regime (Hillman, 1986; Bonecker and Lansac-Tôha, 1996; García *et al*., 1997). Incoming flood waters supply allochthonous nutrients (Welcomme, 1979; García *et al*., 1997) and make available nutrients from decaying material (Bonecker and Lansac-Tôha, 1996). The release of nutrients fuels a pulse of primary productivity, which in turn stimulates zooplankton growth and abundance (Hall *et al*., 1970; Junk *et al*., 1989). The increased biomass of zooplankton may form a resource for juvenile fish either in the billabong (Geddes and Puckridge, 1989) or in the river channel as flood waters recede (Humphries *et al*., 1999).

Abiotic processes have an important role in determining community structure (Bonner *et al*., 1997). Following flooding, zooplankton abundance rapidly increases due to the activation of resting stages such as eggs and diapausing juveniles (Morton and Bayly, 1977; Boulton and Lloyd, 1992). The species that survive

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to take advantage of the new environment are those best adapted to the physical and chemical environment (King *et al.*, 1996), with individual species having their own specialized requirements (Bérzins and Pejler, 1989). The critical chemical parameters (dissolved oxygen, pH, conductivity) affecting floodplain microinvertebrates appear to be similar globally (Shiel, 1979), and these parameters are known to be influenced by the hydrology of the system (Van den Brink and Van der Velde, 1994; Van den Brink *et al.*, 1994). Billabong hydrology is influenced by spatial and temporal patterns of high flow and, as a result, quite proximal billabongs can have very different hydrological patterns based on their position on the floodplain (Walker and Thoms, 1993).

The high natural variability of billabongs makes adequate replication for field experimentation difficult. The use of experimental billabongs has the potential to shed light on many of the processes that occur in natural billabongs, by standardizing the size and structure controlling many of the processes that occur. Mesocosms have been widely used in ecotoxicological experiments as an experimental link between the laboratory and natural environment (Crossland and La Point, 1992). While scaling up from mesocosm experiments to natural systems is not always possible, the same biological processes and successional patterns occur (Odum, 1969).

This paper examines the hypothesis that changes in the duration of flooding and in the seasonality of flooding influence the density and diversity of rotifer and microcrustacean populations.

METHODS

Experimental design

Sixteen mesocosms were constructed on the floodplain of the River Murray, 4 km south of Albury, New South Wales, Australia. Each mesocosm was constructed from circular corrugated galvanized iron with a diameter of 4.5 m and height of 1.2 m and was sunk into the ground to a depth of approximately 0.8 m. Overflow pipes were installed into each mesocosm to regulate the maximum depth to approximately 0.9 m.

Each mesocosm was profiled to provide a shallow, ephemeral area and a deeper area (Figure 1). The profile was overlaid with a plastic liner. All were then alternately filled with river water and drained over a fortnightly cycle for three months to remove any plastic residues leaching from the liners.

Soil (32 m^3) was collected from the nearby floodplain, homogenized and distributed evenly between the billabongs, giving a sediment depth of approximately 15 cm. Ten litres of dry sediment from the margin of an adjacent ephemeral billabong—typically flooded in winter or early spring from rainfall events —were added to each half of each billabong to provide an inoculum of 'local' biota.

The shallow area in each half of each billabong was planted with *Myriophyllum papillosum* Orch., and *Vallisneria americana* Graebner. During the course of the experiment a further 12 plant taxa colonized the experimental billabongs (Nielsen and Chick, 1997).

Flood patterns

One of four hydrological flood-patterns (Fp) was assigned randomly to each of the 16 experimental billabongs giving four replicates of each. The four flood-patterns are described in Table I.
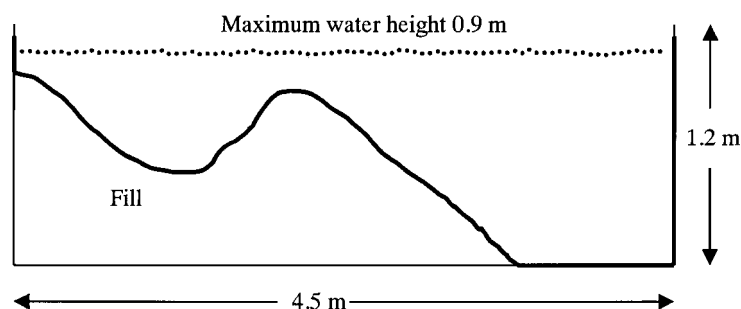

Figure 1. Profile of an experimental billabong

Table I. Flood pattern imposed on the 16 artificial billabongs

Flood pattern	Description
Unflooded/Control	Mimicking natural billabongs that are infrequently inundated. Water levels allowed to fluctuate with rainfall and evaporation.
Permanent	Mimicking flooding that has been caused by the construction of dams and weirs downstream. Water levels maintained at maximum depth.
Spring	Mimicking releases used for environmental flows. Water levels allowed to fluctuate with rainfall and evaporation. Billabongs artificially flooded to maximum depth September 1995 and 1996.
Summer	Mimicking flooding caused by releases from upstream water storages for irrigation. Water levels allowed to fluctuate with rainfall and evaporation. Billabongs artificially flooded to maximum depth January 1995 and 1996.

When flood events were imposed on the summer and spring flood-patterns, water was pumped from Ryans Creek, a nearby anabranch of the River Murray, through a 50 μm filter to remove any rotifers and microcrustaceans. In all four imposed flood events the volume of water approximately doubled.

Sampling

A single quantitative sample was collected from each experimental billabong using a Jabsco self-priming pump (model number 22050-200), pumping at 14 litres per minute at each sampling time. Pump flows were measured using a Fisher and Porter variable area flow meter. The inlet pipe was moved in a zig-zag pattern up and down through the water column while moving the inlet pipe backwards and forwards across the billabong so that both deep and shallow areas were sampled over a two minute period. The sampled volume was filtered through a 35 μm mesh net and the filtrate was returned to the billabong. The collected sample volume was recorded and a 10 ml subsample extracted and preserved in 70% ethanol. The remaining organisms were returned live to their respective billabongs. In the laboratory successive 1 ml aliquots were taken from the 10 ml subsample and counted in a Sedgwick-Rafter counting chamber and identified using a darkfield microscope, until a minimum of 200 individuals had been counted. These were identified to the level of genus following Shiel (1995). All counts were converted to animals per litre (density) and animals per billabong (abundance) prior to analysis.

During the period from January 1995 to November 1996 samples were collected every two weeks. However, after July 1995 only every second sampling event was sorted and identified. When flood events were imposed on either the summer or spring flood patterns, sampling of the relevant flood-pattern and the unflooded flood-pattern was intensified to every second day for the week preceding the flood and on an expanding (0, 0.5, 1, 3, 6, 9, 14, 21 days) post-flood. Sampling of these treatments then reverted back to the normal two-weekly sampling event. Any increases in the number of animals within the billabong as a result of flooding were expected to occur within a three-week period (Tan and Shiel, 1993). For the flood events the unflooded flood-pattern was used as a reference against which the flooded billabongs were compared.

Statistical analysis

Systat® (Ver. 6.0.1) was used for univariate analysis of variance (ANOVA). Data (zooplankton density and abundance) were subjected to fourth root transformation to remove heterogeneity of variances and the dependency of variance and mean. The analysis of variance was based on a split-plot design: treatments applied to the billabongs (plots) and fish/no fish to separate halves within the billabongs. The model was used to analyse both the long-term data set and the four sets of flood data. When significant differences between treatments were indicated, Bonferroni Pairwise comparisons were applied.

Definitions

Density is defined as the number of animals in one litre of water, and abundance refers to the number of animals occurring in each billabong (i.e. the number of animals per litre multiplied by the volume of water in each billabong at the time). Assuming negligible input of zooplankton with incoming water, the immediate result of flooding is a dilution of animals (i.e. lower density) with abundance largely unaltered. A significant ANOVA will indicate if imposed flooding results in an increase in the abundance of zooplankton. Importantly, the null hypothesis proposes a change in densities, relative to dilution, and proposes no change in abundance. This distinction is critical in interpreting the ANOVA results in this study.

RESULTS

Hydrology

The fluctuation in the volume of the experimental billabongs was an important component of the experiment. The four flooding events (two spring and two summer) all resulted in an approximately two-fold increase in the volume of the experimental billabongs. The timing of these floods was important in the development of the various communities.

The four flood-patterns imposed on the billabongs could be rated in terms of the amount of fluctuation that occurred in their water levels (Figure 2). The permanent treatment had no variability in water levels. Water lost via evaporation was continually replaced with rainwater previously collected in tanks. The summer flood treatment had reduced depth variability because the two summer flood events occurred at the time when evaporation was greatest, thus refilling them at a time when evaporation would have otherwise reduced depth substantially. This reduced the amount of time that terrestrial areas were exposed each year to one to two months. The unflooded and spring flooded treatments both had more variability in their depth. The two spring flood events corresponded with natural spring rainfall that filled the unflooded treatment at about the same time. Both the unflooded and spring flooded treatments lost substantial amounts of water through evaporation particularly over the summer months, exposing large amounts of sediments for up to six months each year.

Duration of inundation

There were significant differences in the abundance of rotifers between treatments over the 20 month period with a greater abundance of rotifers in the permanently flooded treatment (Fp $\times$ T: $P = 0.010$) (Figure 3). The greater abundance of rotifers in the permanently flooded treatment resulted from this treatment supporting a higher density of animals (Fp $\times$ T: $P = 0.011$) (Figure 3). The population density of *Conochilus* sp. (Fp $\times$ T: $P = 0.006$) was higher in the permanent treatment over the 20 months than in any other treatment (Figure 4).

Over the 20 month period there was a significant difference between treatments in the abundance of micro-crustaceans. There was a greater abundance in the more permanently flooded treatments (Fp $\times$ T: $P < 0.001$) (Figure 3). There was also a higher density of microcrustaceans in the permanent treatment over the summer period (Fp $\times$ T: $P = 0.022$) (Figure 3). Two groups of microcrustaceans displayed differences in population densities between treatments over this period. The chydorids had a higher density in the permanently filled treatment (Fp $\times$ T: $P = 0.001$) (Figure 4). The ostracod *Newnhamia* sp. had higher densities in the unflooded and spring flooded treatments (Fp $\times$ T: $P < 0.001$) (Figure 4).

Timing of inundation

Summer flooding. Analysis of the data from the two summer floods revealed that there was no change in either the density or abundance of rotifers. After the flood in the summer of 1996 two rotifer taxa showed significant variations in their densities between times. The densities of *Anuraeopsis* sp. (Fp $\times$ T: $P = 0.016$) and *Trichocerca* sp. (Fp $\times$ T: $P < 0.001$) (Figure 5) populations were diluted and did not return to pre-flood densities during the sampling period.
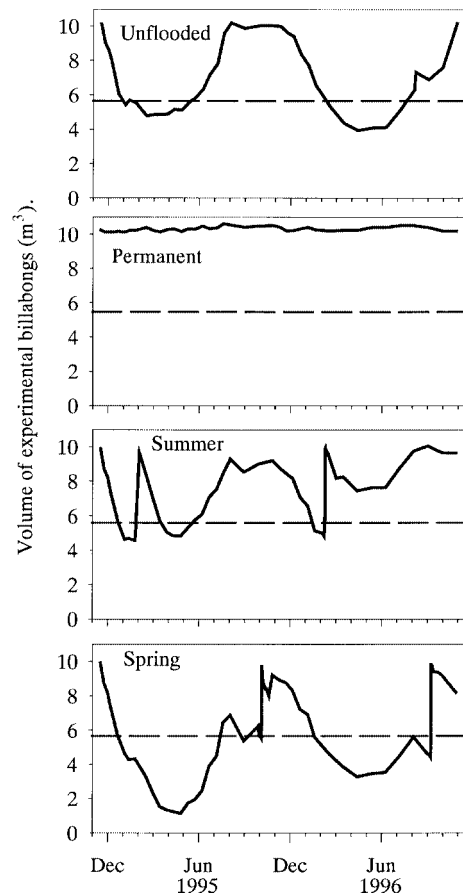
Figure 2. Variation in the volume of the experimental billabongs over the two year period. Dashed line indicates volume of water needed to completely inundate the sediment

There was no increase in the density of microcrustaceans after either the 1995 or 1996 floods. Nor was there an increase in their abundance after the 1995 flood. There was a significant difference in the abundance of microcrustaceans between times after the 1996 flood (Fp × T: $P < 0.001$) (Figure 5), with numbers rising slowly after the flood event.

Spring flooding. Analysis of the data from the spring floods reveals that there was no change in either the density or abundance of rotifers and microcrustaceans after either the 1995 or 1996 floods.

Following the spring flood in 1995 population densities of two taxa had significant variations between times. The population of *Filinia* sp. recovered from the initial dilution and rapidly increased in density after flooding in 1995 (Fp × T: $P < 0.001$) (Figure 6). The densities of *Keratella* sp. population remained diluted after the 1995 spring flood (Fp × T: $P < 0.001$) (Figure 6).

DISCUSSION

The densities of both rotifers and microcrustaceans in the experimental billabongs varied seasonally as found in other freshwater systems (e.g. Orcutt and Pace, 1984). Rotifers constituted most of the zooplankton identified in the experimental billabongs.

Duration of Inundation

The permanent and summer treatments had higher abundance of both rotifers and microcrustaceans, especially over the drier summer months when water levels in the unflooded and spring flooded billabongs became
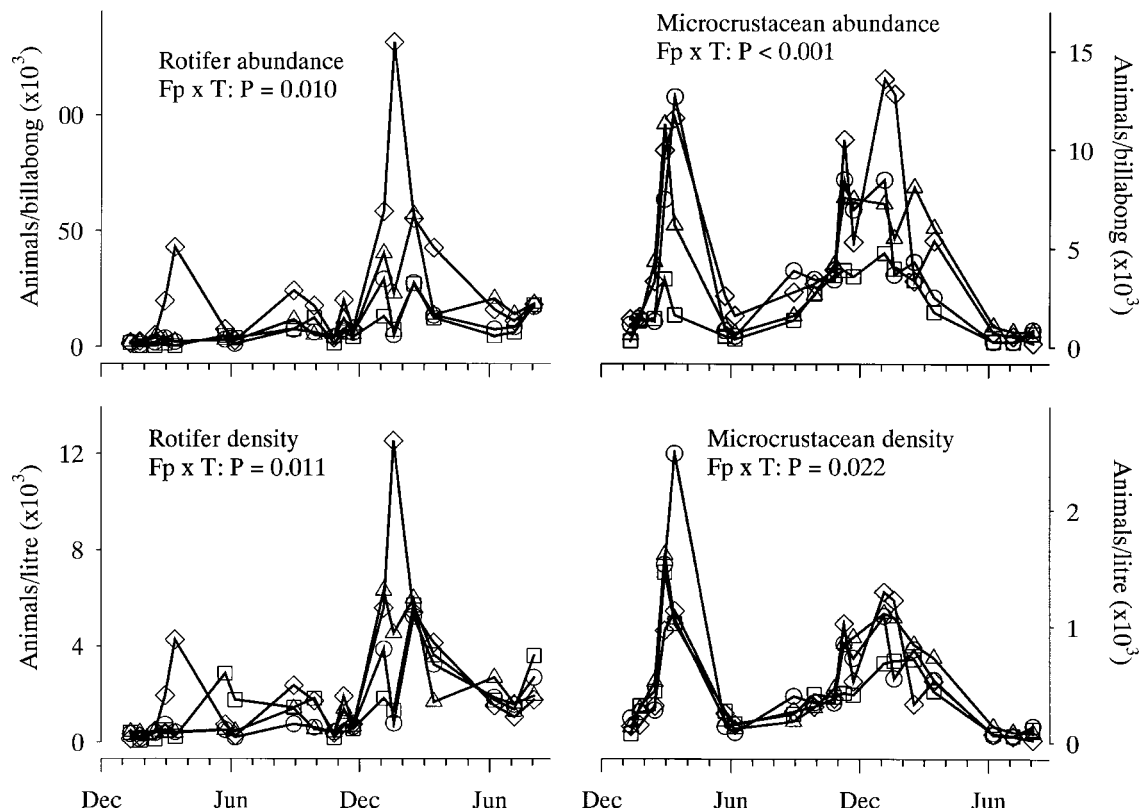
Figure 3. The abundance and density of rotifers and microcrustaceans in the four treatments for 1995–1996. Mean values only.
$\bigcirc$ = unflooded; $\Diamond$ = permanent; $\triangle$ = summer, $\square$ = spring. Fp × T: *P* is the probability of a significant difference between treatments
(Fp) over time (T)

low. The densities of both rotifer and microcrustacean populations in the four treatments appeared to change in cyclic patterns that were unrelated to the hydrology of the billabongs. In the experimental billabongs, permanent flooding had only a minor effect on the structure of the zooplankton community. The rotifer *Conochilus* sp. and the cladoceran family Chydoridae were the only taxa that were more numerous in the permanently inundated treatment than in the others. Large waterbodies have been found to have more diverse chydorid communities than small waterbodies, owing to the greater diversity of habitat (Fryer, 1968, 1985). The increase in macrophyte cover that was observed in the permanently inundated treatment (Nielsen and Chick, 1997) may have provided increased habitat in this study (Bonecker and Lansac-Tôha, 1996). The increased macrophytes may also have allowed the planktonic rotifer *Conochilus* sp. to coexist with competitors and obtain refuge from predators.

The density of the ostracod *Newnhamia* sp. was reduced by permanent inundation. In the unflooded and spring flood-patterns there were strong seasonal peaks in densities in early summer that were absent from the permanently flooded treatments and weak in the summer flooded treatments. Many ostracod taxa are early colonizers of temporary waterbodies and *Newnhamia fenestrata* has been recorded soon after inundation (Lake *et al.*, 1989). Loss of variability in hydrology may potentially remove those environmental cues necessary to trigger emergence from resting eggs deposited by previous generations (Wiggins *et al.*, 1982; Neckles *et al.*, 1990). Hence, loss of flooding variability may represent a disturbance to this crustacean (Golladay *et al.*, 1997).

Seasonality of flooding

In many systems flood events are predictable and seasonal, and result in substantial increases in the biomass of the microfauna that is then utilized by animals at higher trophic levels (Junk *et al.*, 1989). It is expected
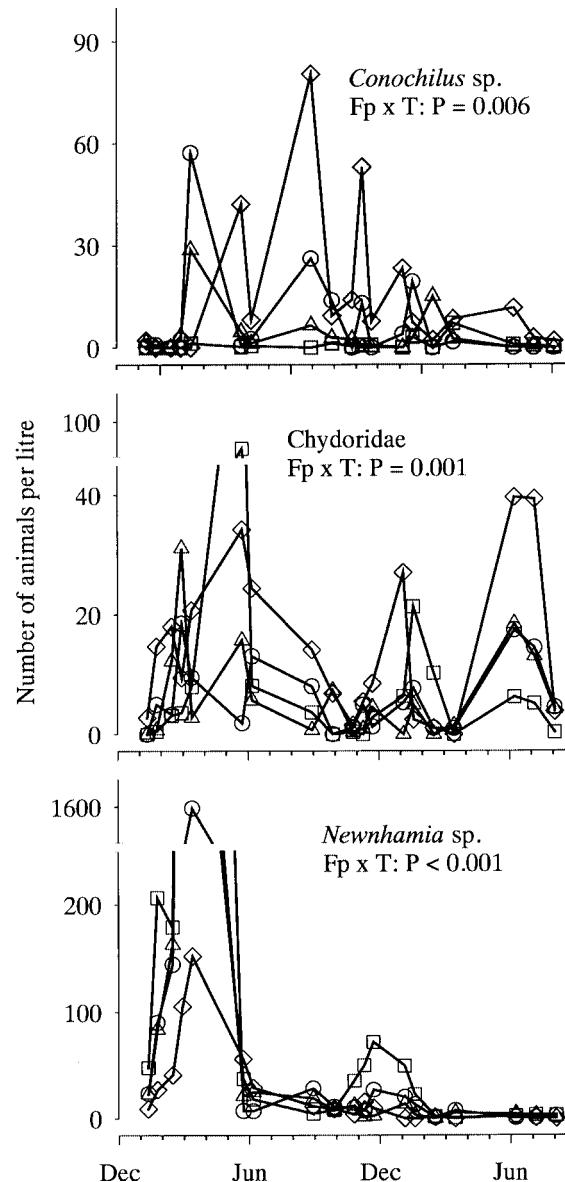
Figure 4. Rotifer and microcrustacean taxa with significant variations in their densities (animals/litre) under the different flooding patterns during 1995–1996. Mean values only. O = unflooded; ◊ = permanent; △ = summer, □ = spring. Fp × T: P is the probability of a significant difference between treatments (Fp) over time (T)

that flood events on temperate floodplains in Australia should have a similar effect (Lloyd *et al.*, 1994). In this study, the response of both rotifers and microcrustaceans after the four floods was not predictable and varied between years. Rotifers did not increase in density or abundance after either summer flood or spring floods. Only after one summer flood did microcrustacean abundance increase. Under natural circumstances, the emergence of animals from the egg-bank will vary depending on the relative proportion of wet or dry sediment covered by inundation. In this instance, the experimental billabongs, with mostly vertical sides, are an extreme case with only limited sediment available for rewetting.

These results suggest that the seasonality of flooding may not be important to rotifers and microcrustaceans in these systems. Wiggins *et al.* (1982) suggest that emergence of animals from resting eggs is dependent not only on the availability of water but also on receiving the right cues in the right sequence. There was a
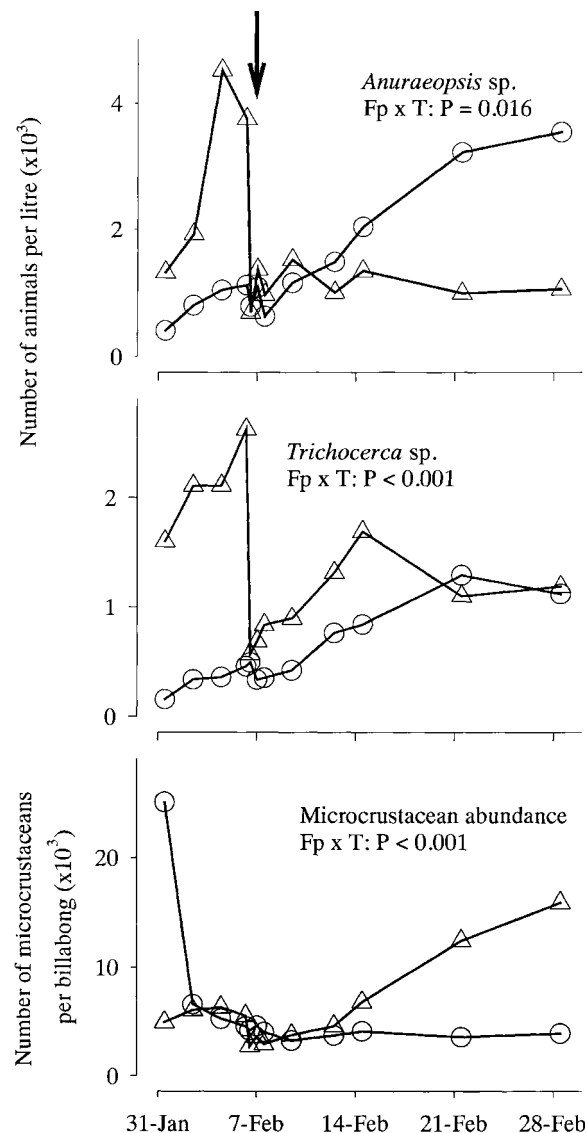
Figure 5. The density of *Anuraeopsis* sp. and *Trichocerca* sp. and the abundance of microcrustaceans with significant changes in density after the summer flood in 1996. Mean values only. ○ = unflooded; △ = flooded. Fp × T: *P* is the probability of a significant difference between treatments (Fp) over time (T). Arrow indicates time of flood event

substantial reservoir of resting zooplankton eggs in the sediments of all the experimental billabongs (Nielsen *et al.*, 2000), which implies that even though water was supplied, the correct environmental cues were not. The lack of response following flooding may have been through delayed emergence of these resting eggs.

Individual microinvertebrate genera varied in their response to flooding, broadly following patterns reported by Tan and Shiel (1993). Populations can be classified as having three types of response to flooding. Type A response resulted in a dilution of the population densities. Populations did not undergo rapid recruitment after flooding and remained diluted for an indefinite period of time. Type B response resulted in a dilution of population densities. Populations rapidly undergo a period of recruitment resulting in population densities exceeding pre-flood densities. Type C response resulted in a dilution of population densities. Populations rapidly undergo a period of recruitment until pre-flood densities are regained. The response of animals to flooding in this experiment was not consistent across seasons or time.
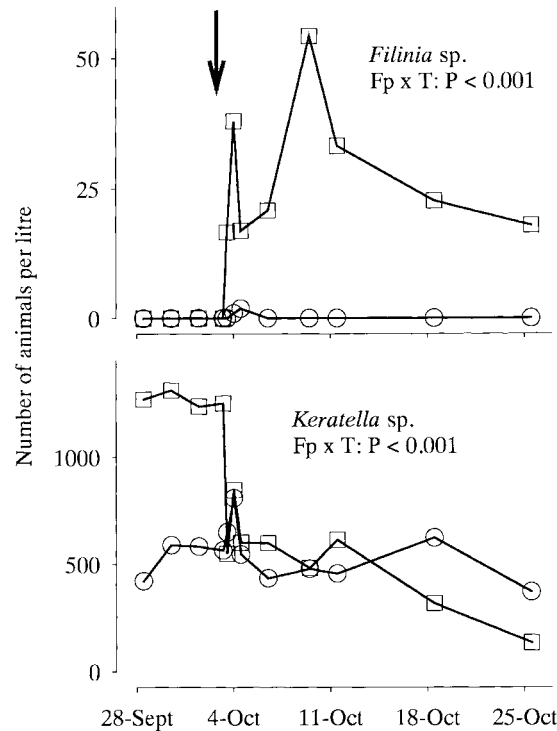
Figure 6. The density of *Filinia* sp. and *Keratella* sp. after the spring flood in 1995. Mean values only. ○ = unflooded; □ = flooded. Fp × T: *P* is the probability of a significant difference between treatments (Fp) over time (T). Arrow indicates time of flood event

There were only minor changes in the taxonomic composition of the two assemblages. Over the two year period of the study different hydrological patterns appeared to result (often indirectly) in changed population densities for some genera but to a large extent the zooplankton communities appeared to be independent of hydrological pattern over time. This is analogous to the response of macrophytes that live in these environments. A response (germination or hatching) appears to be related to environmental factors other than hydrology (Brock and Casanova, 1997).

Changes in the community were related to changes in population densities, rather than changes in the community composition. This may be due to the taxonomic resolution used, but previous studies have also shown only a limited effect of flooding on the recruitment of new taxa (Tan and Shiel, 1993; Pechar *et al.*, 1996). Despite this, studies of emergence after wetting sediment (e.g. Boulton and Lloyd, 1992) and estimates of numbers of dormant eggs (De Stasio, 1989; Hairston, 1996) indicate a significant potential for recruitment from the sediment. The method and frequency of sampling used in this study should have permitted the detection of taxa present in all but very low numbers. This suggests that either all the taxa emerging from sediments after flooding were already represented in the water column or that new emergent taxa failed to become established either because current environmental factors were unsuitable or through their inability to compete with taxa already present. Flood-induced recruitment in billabongs that have not dried out may be much less significant than the phenomenon in dry, episodic systems. The egg-bank in the latter is the foundation for successional processes. This suggests the egg-bank may not be as important in influencing the productivity of permanent billabongs as it is in ephemeral billabongs. As with the macrophyte communities (Brock and Casanova, 1997), increasing either the permanency of flooding or the duration of the dry period may result in a loss of diversity from the microfauna.

The regulation of lowland rivers and storage of water for irrigation releases in temperate regions has had two substantial effects. Within the River Murray system much of the hydrologic variability has been removed resulting in some wetlands becoming more permanently inundated with little fluctuation in water

levels (Walker and Thoms, 1993). Secondly, water releases from impoundments for irrigation have resulted in a shift from a predominantly winter flood pattern to a summer flood pattern (Hillman, 1986). Historically, the biota of these wetlands has been considered to be sensitive to changing environmental conditions (Walker and Thoms, 1993). This study suggests that at the scale of microfauna the biota are robust, with populations within the communities exhibiting varying degrees of resilience to environmental change. However, invertebrates that are adapted to a cycle of wetting and drying may be lost from the system, possibly due to the loss of environmental cues. This suggests that, to maintain a high level of diversity on the floodplain, management practices need to be aimed at maintaining a diversity of hydrological regimes, ranging from permanently flooded billabongs to ephemeral billabongs.

REFERENCES

Bérzins B, Pejler B. 1989. Rotifer occurrence in relation to oxygen content. *Hydrobiologia* **183**: 165–172.

Bonecker CC, Lansac-Tôha FA. 1996. Community structure of rotifers in two environments of the upper River Parana floodplain (MS)-Brazil. *Hydrobiologia* **325**: 137–150.

Bonner LA, Diehl WJ, Altig R. 1997. Physical, chemical and biological dynamics of five temporary dystrophic forest pools in central Mississippi. *Hydrobiologia* **353**: 77–89.

Boulton AJ, Lloyd LN. 1992. Flooding frequency and invertebrate emergence from dry floodplain sediments of the River Murray, Australia. *Regulated Rivers: Research and Management* **7**: 137–151.

Brock MA, Casanova MT. 1997. Plant life at the edge of wetlands: ecological responses to wetting and drying patterns. In *Frontiers in Ecology*, Klomp N, Lunt I (eds). Elsevier Science: Oxford; 181–192.

Crossland NO, La Point TW. 1992. Editorial: the design of mesocosm experiments. *Environmental Toxicology and Chemistry* **11**: 1–4.

De Stasio BT Jr. 1989. The seedbank of a freshwater crustacean: copepodology for the plant ecologist. *Ecology* **70**: 1377–1389.

Fryer G. 1968. Evolution and adaptive radiation in the Chydoridae (Crustacea: Cladocera): A study in comparative functional morphology and ecology. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* **254**: 221–385.

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

García CM, García-Ruiz R, Rendón M, Niell FX, Lucena J. 1997. Hydrological cycle and interannual variability of the aquatic community in a temporary saline lake (Fuente de Piedra, Southern Spain). *Hydrobiologia* **345**: 131–141.

Geddes MC, Puckridge JT. 1989. Survival and growth of larval and juvenile native fish: the importance of the floodplain. In *Proceedings of the Workshop on Native Fish Management*, Lawrence B (ed.). Murray-Darling Basin Commission: Canberra; 101–115.

Golladay SW, Taylor BW, Palik BJ. 1997. Invertebrate communities of forested limesink wetlands in southwest Georgia, USA: habitat use and influence of extended inundation. *Wetlands* **17**: 383–393.

Hairston NG Jr. 1996. Zooplankton egg banks as biotic reservoirs in changing environments. *Limnology and Oceanography* **41**: 1087–1092.

Hall DJ, Cooper WE, Werner EE. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* **15**: 839–928.

Hillman TJ. 1986. Billabongs. In *Limnology in Australia*, De Deckker P, Williams WD (eds). Junk: Dordrecht; 457–470.

Humphries P, King AJ, Koehn JD. 1999. Fish, flows and floodplains: links between freshwater fishes and their environments in the Murray–Darling River system, Australia. *Environmental Biology* **56**: 129–151.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river–floodplain systems. In *Proceedings of the International Large River Symposium*, Dodge PD (ed.). Canadian Special Publication of Fisheries and Aquatic Sciences **106**: 110–127.

King JL, Simovich MA, Brusca RC. 1996. Species richness, endemism and ecology of crustacean assemblages in northern California vernal pools. *Hydrobiologia* **328**: 85–116.

Lake PS, Bayly IAE, Morton DW. 1989. The phenology of a temporary pond in western Victoria, Australia, with special reference to invertebrate succession. *Archiv für Hydrobiologie* **115**: 171–202.

Lloyd L, Atkins B, Boon P, Jacobs T, Roberts J. 1994. Natural processes within Murray–Darling floodplain wetlands. In *Proceedings of the Floodplain Wetlands Management Workshop*, Sharley T, Huggan C (eds). Murray–Darling Basin Commission: Canberra; 6–23.

Mitchell D. 1994. Floodplain wetlands of the Murray-Darling Basin: Management issues and challenges. In *Proceedings of the Floodplain Wetlands Management Workshop*, Sharley T, Huggan C (eds). Murray–Darling Basin Commission: Canberra; 1–5.

Morton DW, Bayly IAE. 1977. Studies on the ecology of some temporary freshwater pools in Victoria with special reference to microcrustaceans. *Australian Journal of Marine and Freshwater Research* **28**: 439–454.

Neckles HA, Murkin HR, Cooper JA. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. *Freshwater Biology* **23**: 311–322.

Nielsen DL, Chick AJ. 1997. Flood-mediated changes in aquatic macrophyte community structure. *Marine and Freshwater Research* **48**: 153–157.

Nielsen DL, Smith FJ, Hillman TJ, Shiel RJ. 2000. Impact of water regime and fish predation on zooplankton resting egg production and emergence. *Journal of Plankton Research* **22**: 433–446.

Odum EP. 1969. The strategy of ecosystem development. *Science* **164**: 262–270.

Orcutt JD, Pace ML. 1984. Seasonal dynamics of rotifer and crustacean zooplankton populations in a eutrophic, monomictic lake with a note on rotifer sampling techniques. *Hydrobiologia* **119**: 73–80.

Pechar L, Hrbácek J, Pithart D, Dvorák J. 1996. Ecology of pools in the floodplain. In *Floodplain Ecology and Management*, Prach K, Jeník J, Large ARG (eds). SPB Academic Publishing: The Netherlands; 209–226.

Robins R. 1999. Clocks for rocks: An archaeological perspective on the Currawinya Lakes. In *A Free-flowing River: The Ecology of the Paroo River*, Kingsford RT (ed). New South Wales National Parks & Wildlife Service: Hurstville; 150–178.

Shiel RJ. 1979. Synecology of the rotifer of the River Murray, South Australia. *Australian Journal of Marine and Freshwater Research* **30**: 255–263.

Shiel RJ. 1995. *A Guide to Identification of Rotifers, Cladocerans and Copepods from Australian Inland Waters*. Co-operative Research Center for Freshwater Ecology: Canberra.

Tan L, Shiel RJ. 1993. Responses of billabong rotifer communities to inundation. *Hydrobiologia* **255/256**: 361–369.

Van den Brink FWB, Van der Velde G. 1994. Impact of hydrology and water chemistry on floodplain lake communities along the Lower Rhine and Meuse. *Water Science and Technology* **29**: 57–60.

Van den Brink FWB, Van Katwijk MM, Van der Velde G. 1994. Impact of hydrology on phyto- and zooplankton community composition in floodplain lakes along the lower Rhine and Meuse. *Journal of Plankton Research* **16**: 351–373.

Walker KF, Thoms MC. 1993. Environmental effects of flow regulation on the lower Murray River, Australia. *Regulated Rivers: Research and Management* **8**: 103–119.

Welcomme RL. 1979. *Fisheries Ecology of Floodplain Rivers*. Longman: New York.

Wiggins GB, Mackay RJ, Smith IM. 1982. Evolutionary and ecological strategies of animals in annual temporary pools. *Archiv für Hydrobiologie Supplementband* **58**: 97–206.

Williams WD. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* **125**: 85–110.