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Responses of billabong rotifer communities to inundation

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Abstract

Daily plankton collections were taken from a billabong of the River Murray for two weeks prior to inundation in March 1990, and continued for ten days after flooding. Quantitative responses of the plankton community and the component species were analysed against measured environmental variables and between species. Rotifers and copepod nauplii were the predominant net plankton (> 53 μm). Significant negative or positive responses to inundation were detected for most common taxa of 63 rotifer species recorded. A four-fold dilution from intrusion of river water masked rapid population increases. Opportunistic responses to inundation appear to be a survival strategy in the highly unpredictable billabong environment.

Introduction

Billabongs are remnants of past river meanders along Australia's low gradient floodplains. They are similar in morphology and formation to oxbows elsewhere, but their ecology reflects a unique evolutionary time-scale. The Murray-Darling river system, for example, occupied its present drainage basin 60 million years ago in Gondwana. For millions of years, as Australia moved north, the low-gradient rivers meandered back and forth across their floodplains – billabongs formed and re-formed. In this ancient and highly stable river system, extant billabongs may have occupied the same position for thousands of years. They have been subjected to variations of climate, from tropical to arid, but have not been scoured by glaciation. During periods of aridity billabongs may have provided refugia and foci of speciation, and a source of colonizing biota when the climate became wetter. The present biota of billabongs has a range of strategies to cope with a flood-drought environment. For a detailed review of the history and ecology of the Basin, see Mackay & Eastburn (1990), and for billabong ecology Hillman (1986) and Boon *et al.* (1990).

Preliminary evidence of the richness of the rotifer communities of billabongs of tropical Australia was provided by Koste (1981). Later studies were reviewed by Shiel & Williams (1990). Comparable rotifer species diversity was recorded in temperate River Murray billabongs during a 1988–89 study, when >200 species were identified from weekly plankton samples from one billabong. Daily sampling at the break of season during this study demonstrated rapid replacement of rotifer species dominants, *ca.* 3–4 days during summer (Hillman & Shiel, 1991).

Given the habitat heterogeneity of billabongs – an 'environmental mosaic' (Hillman, 1986), such rapid replacement times suggested a selective advantage where the fastest (in terms of reproduction or production of resistant stages) survive. Could a long evolutionary association under intense selective forces explain the species diversity of these habitats, and the degree of endemicity of the rotifer fauna? Rotifers are known from floodplain environments in the Eocene of south-eastern Australia (Southcott & Lange, 1971). More than half of 60 apparently indigenous monogonont rotifer taxa are known only from billabongs, with a further 25% described from riverine collections, possibly of floodplain origin.

As part of a long-term study of microfaunal ecology in billabongs, we report here on the species composition and population dynamics of the resident rotifer community in a River Murray billabong pre- and post-flooding in summer 1990. The significance of microfaunal community responses is then considered in relation to the billabong ecosystem, particularly in the context of floodplain food webs.

Study area

Ryan's 1 is a broad crescentic meander loop (650 x 50–75 m) located on the River Murray floodplain near Wodonga in northeastern Victoria (36° 09′ S 146° 56′ E) (Fig. 1), *ca* 650 m from the present river channel. The billabong is 0.5–2.5 m in depth, fringed with *Juncus* and *Eleocharis*, with a diverse submerged and floating macrophyte flora (Boon *et al.*, 1990). During late summer 1990, the volume of Ryan's 1 (Fig. 2) had been decreasing since the previous winter; the depth was 0.45 m during sampling prior to flooding. Decomposition of stranded vegetation, a bloom of the cyanobacterium, *Microcystis*, and concentration effects contributed to a decline in water quality.

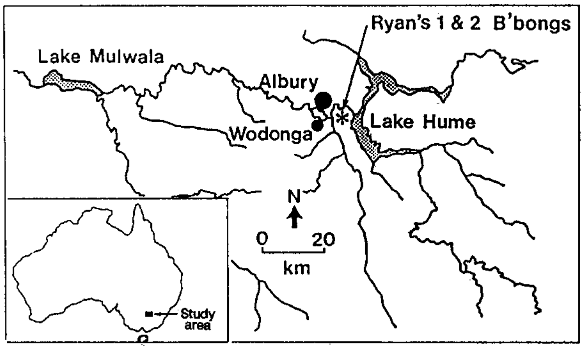

Fig. 1. Location of the study site on the River Murray floodplain in northern Victoria, Australia.

Daily sampling had been conducted from the 1st to the 14th of March. Irrigation releases from an upstream reservoir, Lake Hume, flooded the study site on March 17 to a depth of 2.0 m. This flood event, albeit 'anthropogenic', provided an opportunity to quantify the responses of the microfaunal community to rapid changes in water quality resulting from inundation. When the water level stabilized after flooding, sampling was continued from the 19–28th of March.

Methods

Measurements taken in the field were: depth (from a 2 m depth gauge placed permanently in each billabong); temperature at *ca* 30 cm depth (hand-held mercury thermometer) and pH (Analite pH/mV meter). Replicate water samples for dissolved oxygen were fixed in the field (Winkler method), followed by laboratory acidification, and titration using a Metrohm 672 titroprocessor and 655 Dosimat. Conductivity was measured with a Radiometer CDM 2e meter from 500 ml or 1 l volumes collected in polyethylene bottles and returned to the laboratory, generally 20–30 min after collection. Turbidity was determined from the same samples using a Hach 2100A turbidimeter against Hach Gelex standards.

Qualitative plankton tows for community composition were taken with a Birge cone net (30 cm diam., 53 μm-mesh); quantitative plankton samples were collected in a cylindrical Haney-type perspex trap (13.8 l) with removable net (53 μm stainless steel mesh), which was backwashed into 60 ml Wheaton bottles. Zooplankton counts (Zeiss stereo microscope, dark-field stage with a milled perspex counting tray, max. magnification 64 x) were made on multiple 0.5–1 ml aliquots drawn from an agitated sample. Some counts were made on 100–500 μl aliquots, counted in a haemocytometer or Sedgwick-Rafter cell on an

Fig. 2. Ryan's 1 billabong, view west over *Eleocharis* bed, sampling site in open water, centre of view.

Olympus BH-2 microscope with Nomarski Interference Contrast optics (max. magnification 1600 x). Taxonomic references used were Kutikova (1970), Koste (1978), Koste & Shiel (e.g. 1990). The Shannon-Wiener Diversity Index (H′) and the Spearman's Rank Correlation Coefficient were calculated, and cluster analyses (Czeckanowski's and Raabe's Similarity Indices and Sokal's Niche Distance (Hellawell 1978)) were performed.

Results and discussion

Water physicochemistry

There were significant changes in all measured parameters following inflows of river water. We have estimated from conductivity decrease and depth gauge, that a four-fold volume increase occurred during the flood. The incoming water was slightly cooler (Fig. 3a) and of lower conductivity (Fig. 3d) than the billabong water. The steady increase in turbidity seen in Fig. 3e was biogenic, reflecting the bloom of *Microcystis*, with associated pH levels ≥ 10. The disappearance of *Microcystis* from the water column following inundation was accompanied by abrupt decreases in pH (Fig. 3c) and turbidity (Fig. 3e). Changes in dissolved oxygen (Fig. 3b) to supersaturation levels after inundation reflect both the well-oxygenated incoming water (turbulent release from the reservoir 10 km upstream) and the rapid growth of phytoflagellates which followed the *Microcystis* collapse.

Zooplankton community

'Zooplankton' is used here for convenience to describe the microfaunal assemblage of open water in the billabong. Commonly, true plankters, facultative plankters, and dislodged epiphytic and epibenthic taxa from submerged and floating macrophytes are collected, especially at low water levels. Total zooplankton density over the study (Fig. 3f) declined from 2034–13,264 ind. l^{-1} preflooding ($\bar{x} = 6525$) to 1076–5539 ind. l^{-1} post-

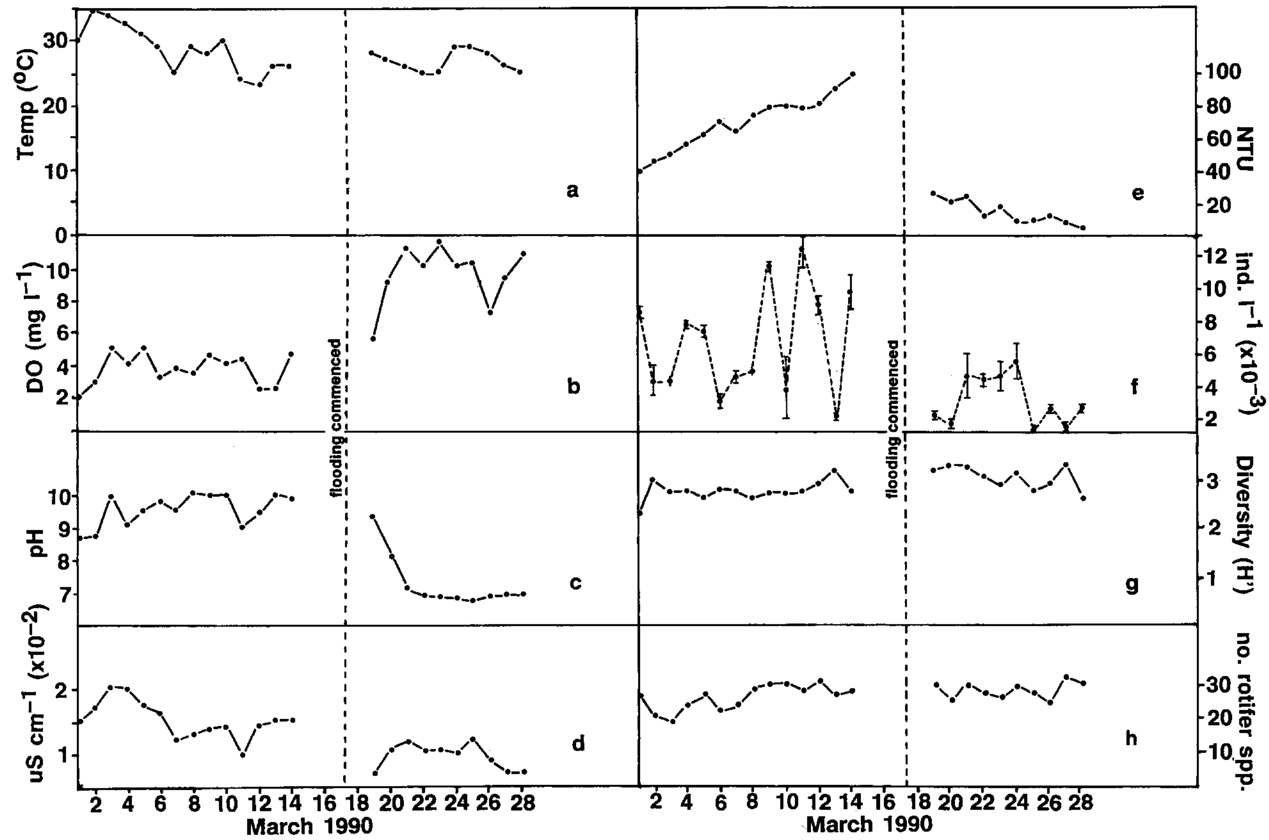

Fig. 3. Changes in measured water quality variables and plankton population parameters during March 1990, Ryans's 1 Billabong: a. temperature, b. dissolved oxygen, c. pH, d. conductivity, e. turbidity, f. total zooplankton density, g. species diversity (Shannon-Wiener H'), h. no. of rotifer species coll.$^{-1}$.

flooding ($\bar{x} = 3443$). Community diversity, (H') (Fig. 3g) remained high throughout. A total of 69 taxa was identified from the 24 dates, with rotifers (63 spp., Table 1) numerically abundant on all occasions. Only cyclopoid copepodites and nauplii (*Eucyclops*/*Microcyclops* spp.) occurred in appreciable numbers, but they rarely constituted more than 10% of the community. Other taxa present were calanoid copepods (*Boeckella fluvialis*), chydorid and macrothricid cladocerans, generally in low numbers, and not treated further here.

To what extent are these community events intrinsic to the billabong 'plankton' rather than a reflection of the river intrusion? Of the 63 taxa listed in Table 1, *ca* 30% also have been recorded in the plankton of the upstream reservoir, generally in small numbers. Lake Hume has a microcrustacean limnoplankton typical of short retention-time storages in the Basin (Shiel 1990), but undoubtedly past floods and reservoir spills have passed viable plankton assemblages into downstream billabongs, where some taxa survive. *Calamoecia lucasi* is the predominant plankter in the reservoir during March, so if Lake Hume limnoplankton intruded into Ryan's 1 on March 17, we would expect increases in calanoid copepodites and nauplii. The pre-flood density of copepod nauplii in Ryan's 1 was 710 ind. l^{-1}, post flood 201 ind. l^{-1} ($t = 4.04$, $P < 0.001$), i.e. a dilution. Additionally, only three planktonic taxa listed in Table 1 were recorded post-flooding and not pre-flooding (*C. dossuarius*, *F. longiseta*, *L. flosculosa*), all of which occurred in the billa-

Table 1. Rotifer species recorded in Ryan's 1 Billabong pre- and post-flooding March 1990. Representation of most abundant taxa is shown: (%pre/%post). Endemic or Australian species are asterisked.

1. _Anuraeopsis navicula_
2. _Ascomorpha saltans_
3. _Asplanchna asymmetrica_*
4. _Brachionus angularis_ (6.4/12.9)
5. _B. budapestinensis_ (38.6/23.1)
6. _B. calyciflorus_
7. _B. dichotomus reductus_* (18.4/6.4)
8. _B. falcatus_ (0.4/5.5)
9. _B. lyratus_* (4.4/0/2)
10. _B. patulus_*
11. _B. quadridentatus_
12. _Cephalodella gibba_
13. _Collotheca_ sp.
14. _Colurella uncinata_
15. _Conochilus dossuarius_
16. _Euchlanis incisa_
17. _Filinia longiseta_
18. _F. opoliensis_ (0.5/4.7)
19. _F. 'passa'_
20. _F. pejleri_ (3.7/2.2)
21. _Heterolepadella ehrenbergi_
22. _Hexarthra intermedia_
23. _Keratella cochlearis_
24. _K. procurva_
25. _K. slacki_*
26. _K. tropica_ (12.8/28.7)
27. _Lacinularia flosculosa_
28. _Lecane ludwigi_
29. _L. luna_
30. _L. ohioensis_
31. _L. mira_
32. _L. tenuiseta_
33. _L. ungulata australiensis_*
34. _Lepadella patella_
35. _L. rhomboides_
36. _L. triptera_
37. _Macrochaetus collinsi_
38. _Monostyla bulla_
39. _M. hamata_
40. _M. lunaris_
41. _M. papuana_
42. _Mytilina ventralis_
43. _Notommata glyphura_
44. notammatid, indet.
45. notammatid, indet.
46. _Polyarthra vulgaris_ (1.0/3.0)
47. _Pompholyx complanata_
48. _Proalides tentaculatus_
49. _Rotaria neptunia_
50. _Synchaeta pectinata_
51. _Testudinella patina_
52. _Trichocerca chattoni_
53. _T. intermedia_
54. _T. pusilla_
55. _T. rattus carinata_
56. _T. similis_
57. _T. similis grandis_
58. _T. tenuoir_
59. _Trichotria tetractis_
60. _Tripleuchlanis plicata_
61. _Tripleuchlanis_ sp.
63. other, indet.

bong plankton during the previous two-year study. March releases for irrigation are drawn off from the hypolimnion (> 30 m deep) through a pressure tunnel, hence we consider it unlikely that limnoplankton survives into the downstream river during irrigation releases. Research on such survival is lacking in Australian reservoir/river systems.

Rotifer community

About half of the recorded rotifer taxa (Table 1) are resident in floating _Azolla/Ricciocarpus_ mats at the study site (De Manuel & Shiel in press), e.g. _Lecane_, _Lepadella_, _Monostyla_ spp. They were recorded as single individuals or in low numbers. Of 24–33 taxa present on each date (Fig. 3h), true plankters comprised more than 80% of the community. Only four species reached proportions over 10% of the rotifer population: _Brachionus angularis_, _B. budapestinensis_, _B. dichotomus reductus_, and _Keratella tropica_. These were dominant before and after flooding, although relative proportions changed (Table 1). Only three further taxa reached 3–5% of the pre-flooding population: _Brachionus lyratus_, _Filinia pejleri_ and _Monostyla bulla_. Post-flooding, _B. falcatus_, _F. opoliensis_, _Polyarthra vulgaris_ and _Proalides tentaculatus_ replaced them as community subdominants. Population dynamics of these species are shown in Fig. 4. Some minor species also had significant changes in population density following inundation, e.g. maximum densities of 180 ind. l^{-1} were recorded for *A. navicula*, 50 ind. l^{-1} for *B. quadridentatus*, 150 ind. l^{-1} for *H. ehrenbergi* and 62 ind. l^{-1} for *T. patina*. Post-flooding, the first two taxa declined to 1–2 ind. l^{-1} within a week of the flood event, the last two disappeared entirely, i.e. there were more extreme responses than expected for a dilution effect, or for intra-habitat population movements.

Raabe's Similarity Index showed that clear pre- and post-flood assemblages could be discriminated (Fig. 5). The only exception was March 13, which clustered with post-flood dates as an outlier. This reflects the low density of plankters collected on that date, a result of intra-habitat patchiness (Fig. 3f). Consecutive days tended to have more similar rotifer assemblages than did more widely-separated dates.

Significance of differences in pre- and post-flood mean densities for each major taxon were then tested by *t*-statistic (2 means). Measured environmental variables were related to population events for the 18 most common taxa using Spear-

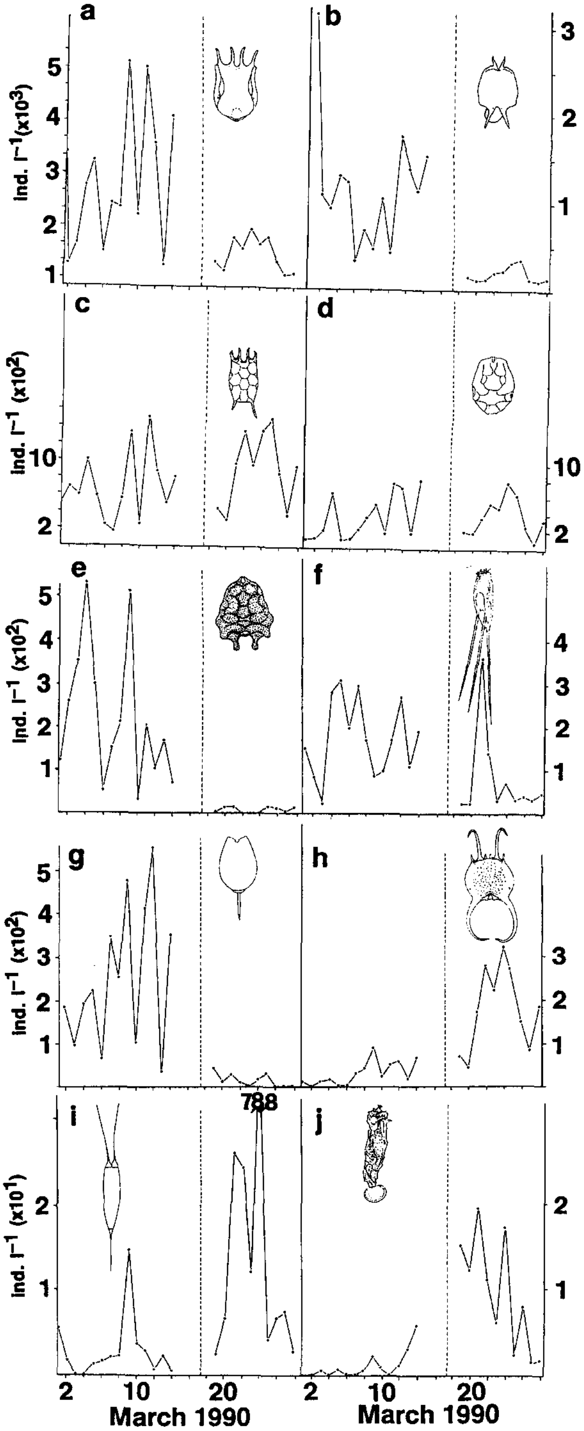

Fig. 4. Population events for community dominants in Ryan's 1 rotifer assemblage pre- and post-flooding, March 1990. a. *Brachionus budapestinensis*, b. *B. dichotomus reductus*, c. *Keratella tropica*, d. *B. angularis*, e. *B. lyratus*, f. *Filinia pejleri*, g. *Monostyla bulla*, h. *B. falcatus*, i. *F. opoliensis*, j. *Proalides tentaculatus*.

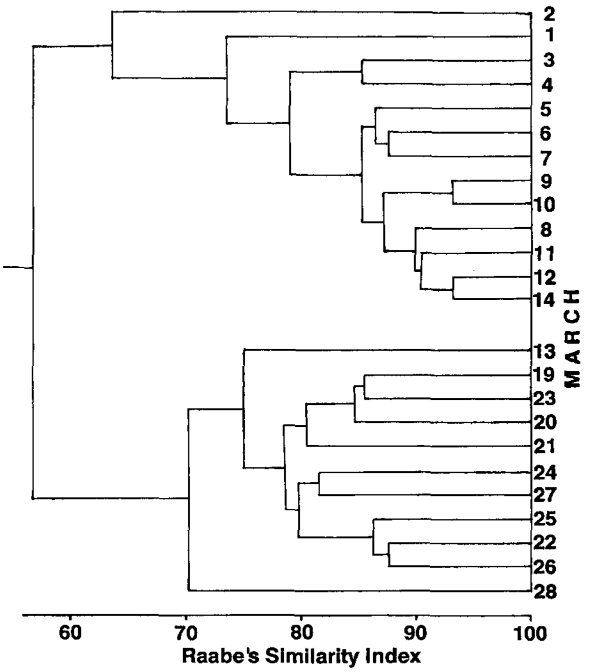

Fig. 5. Similarity of pre- and post-flooding rotifer communities on each sampling date clustered using Raabe's Similarity Index.

man's Rank Correlation Coefficient, and pre- and post-flood egg ratios for each species also were analysed to detect flood effects. Three population responses were evident:

Marked collapse indicative of dilution or deleterious effect of inundation (cf. Figs 4a, b, e, g): *A. navicula* ($t = 5.17$, $P < 0.001$), *B. budapestinensis* ($t = 3.43$, $P < 0.01$), *B. dichotomus reductus* ($t = 3.63$, $P < 0.01$), *B. lyratus* ($t = 4.26$, $P < 0.001$), *B. quadridentatus* ($t = 5.58$, $P < 0.001$), *H. ehrenbergi* ($t = 2.87$, $P < 0.01$), *K. slacki* ($t = 2.07$, $P < 0.05$), *M. bulla* ($t = 4.53$, $P < 0.001$), and *T. patina* ($t = 4.43$, $P < 0.001$) (all DF = 22). Dilution effects were evident in *B. budapestinensis* and *B. dichotomus reductus* (Fig. 4a, b), which responded to the flood event by significant increases in egg production. *B. lyratus* and *M. bulla* (Fig. 4e, g), however, did not recover after flooding, did not increase egg production and virtually disappeared from the site.

Maintenance of pre-flooding levels in populations of *A. asymmetrica*, *B. angularis*, *B. calyciflorus*, *K. tropica*, *P. vulgaris*, and *T. similis*. There was no significant difference in population means, despite the four-fold dilution. *K. tropica* and *B. angularis*, for example (Fig. 4c, d), both declined post-flood, however the decline was within the sampling variability. There was no significant change in egg production, and no evidence of resting egg hatching. In these taxa, population responses are not readily explained, but may reflect intra-habitat patchiness, with movement of these taxa into the sampled patch.

Population pulses exceeding pre-flood densities (e.g. Fig. 4f, h, l) for *B. falcatus* ($t = 5.54$, $P < 0.001$), *F. opoliensis* ($t = 2.39$, $P < 0.05$), *F. pejleri* ($t = 2.4$, $P < 0.05$) (pulse and decline), *P. tentaculatus* ($t = 4.68$, $P < 0.001$), and *T. pusilla* ($t = 2.9$, $P < 0.01$). These rotifers appeared to be cued by the flood event. *B. falcatus*, and both species of *Filinia*, increased egg production, although in the case of *F. opoliensis*, production was inadequate to account for the increase in population density post-flooding. *F. opoliensis* showed strong negative responses to the *Microcystis* bloom, and had almost disappeared from the site pre-flooding. The fourfold population peaks beginning one day post-flooding suggest cueing of resting-egg hatching, with resultant pulses in the population. *P. tentaculatus* and *T. pusilla* are problematic – both had marked population increases but no change in egg production; if resting eggs contributed to the populations, their hatching seems to have been serial (cf. Fig. 4j) rather than in a pulse as for *Filinia opoliensis*. Other taxa were insufficient in numbers or occurrence for analysis.. For the 18 most common species in the pre-flood community, responses to measured environmental variables significant at $P < 0.01$ were indicated for six taxa, and at $P < 0.05$ for a further seven (Table 2). *B. falcatus*, for example, had significant negative correlations with temperature and pH, and a positive correlation with turbidity. Similarly, *B. dichotomus reductus* was negatively affected by the high pH levels during the *Microcystis* bloom. *M. bulla* had significant positive correlations with turbidity and pH (i.e. the *Microcystis* bloom), but a negative correlation with dissolved oxygen levels. The strong positive correlation of *M. bulla* with turbidity pre-flooding may be a grazing association related to high bacterial levels accompanying such blooms (cf. Boon & Shiel, 1990). Other taxa with a similar strong positive pre-flooding association with the cyanobacterial bloom (Table 2) and significant post-flood decline (*A. navicula*, *B. quadridentatus*, *H. ehrenbergi* and *T. patina*) are all small species, and known or likely bacteriovore/detritivores, all probably grazing in the clumps of *Microcystis*.

Eleven taxa had sufficient eggs for analysis, and all but one had a higher proportion of egg-carrying females post-flooding. However, *t*-tests indicated that these differences were significant in only four taxa: *B. budapestinensis* ($t = 2.62$, $P < 0.05$), *B. dichotomus reductus* ($t = 2.93$, $P < 0.01$), *B. falcatus* ($t = 3.32$, $P < 0.01$) and *F. opoliensis* ($t = 2.07$, $P < 0.05$). Spearman's rank correlation analysis of egg ratios gave significant associations for *B. dichotomus reductus* (RS = – 0.80 with turbidity, -0.69 with pH, 0.67

Table 2. Significant Spearman Rank RS values for Ryan's 1 plankton vs. phys-chem. parameters. Pre-flooding and total data set ($n = 24$). (* $P < 0.05$; ** $P < 0.01$).

Species	Temp.		DO		pH		Cond.		Turb.	
	Pre-	Total	Pre-	Total	Pre-	Total	Pre-	Total	Pre-	Total
1. *Anuraeopsis navicula*			- 0.72**		0.78**			0.52*		0.85**
3. *Asplanchna asymmetrica*							0.67*			
4. *Brachionus angularis*	- 0.57*	- 0.46*					- 0.55*			
5. *B. budapestinensis*						0.41*				0.60**
6. *B. calyciflorus*					- 0.65*					
7. *B. dichotomus reductus*				- 0.53*	- 0.71			0.55**		0.51*
8. *B. falcatus*	- 0.74**	- 0.57**		0.75**	- 0.72*	- 0.62**		- 0.72**	0.65*	- 0.56**
9. *B. lyratus*		0.44**		- 0.64**		0.67**		0.73**		0.65**
11. *B. quadridentatus*	- 0.60*			- 0.69**		0.73**		0.47*		0.81**
18. *Filinia opoliensis*				0.59**	- 0.66*	- 0.68**		- 0.71**		- 0.64**
20. *F. pejleri*										0.54**
21. *Heterolepadella ehrenbergi*				- 0.67**		0.63**		0.62**		0.75**
26. *Keratella tropica*			0.42*							
38. *Monostyla bulla*			- 0.68**		0.69**		0.53*		0.81**	
46. *Polyarthra vulgaris*					- 0.59**				- 0.46*	
48. *Proalides tentaculatus*			0.63**					- 0.43*		
51. *Testudinella patina*			- 0.64**		0.58**		0.49*		0.67**	
56. *Trichocerca similis*	- 0.71**									

with DO, all $P < 0.01$), *B. falcatus* (RS = 0.70 with conductivity, $P < 0.05$) and *F. opoliensis* (RS = − 0.92 with turbidity, $P < 0.01$).

In such a heterogeneous and rapidly changing environment, how 'real' an interpretation of our observations can we provide? We were sampling a patch of a very patchy habitat – a 'harlequin environment' (cf. Horn & Macarthur, 1972) – in which most mobile or wind-influenced planktonic taxa are distributed unevenly, both horizontally and vertically. Assuming minimal intrusion of reservoir plankton, how accurately can we distinguish 'normal' population events from those induced by flooding? Clearly, although dilution is one effect of river water intrusion on billabong plankton, accompanying changes in water quality, phytoplankton, etc, modify population cycles. Correlation coefficients, as in Table 2, provide some measure of these modifications, however their interpretation is constrained when the variables are not independent and the populations are not distributed normally.

Clearly, although this flood event could not be considered catastrophic, in the sense that the billabong had not dried out completely, and represented simply a dilution of the environment, components of the rotifer plankton responded differently to the intrusion of river water. No single variable is identifiable as a stimulus for species' responses, indeed it is unlikely that a single stimulating variable is to be expected. The changes which induced the break-up of the *Microcystis* bloom rapidly affected taxa associated with it; the subsequent increase in phytoflagellates post-flooding provided a resource for a different rotifer assemblage. Water quality changes appear to have been sufficient to cue resting egg hatching in some taxa, but not others, even though resting stages of all species which occur over the seasonal cycle must be present in the billabong (cf. May, 1986). Further investigation is required, particularly for more extreme environmental perturbations such as complete drying out of the billabong.

Our observations suggest that each taxon has a suite of optima which are met for only a relatively short time in the continuously changing billabong environment, inducing similarly rapid population events in resident rotifer communities. The heterogeneity of billabong environments, each with different catchment and substratum characteristics, water quality, macrophyte and phytoplankton associations, provides a diversity of niches unavailable in river or lacustrine ecosystems. Such niche diversity, together with great geological age of the habitat, may account for the species richness of billabong planktonic and littoral rotifer communities, and the disparity between the communities of different billabongs. There is, as yet, no comparable information on the rotifer fauna of floodplain habitats elsewhere, but such diversity may, indeed, be a feature of all such environments.

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