

# **CRC Freshwater Ecology Project A240**

**Quantifying flow habitat biota relationships in riverine ecosystems.**

## **Successional processes in lowland river slackwaters**

**FINAL REPORT  
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Second Year Report

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Rainbow Bee-eater  
Photo: Ben Gawne

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## Introduction

Flow is regarded as the major variable in riverine ecology. Within a patch, hydraulic conditions affect the distribution and community composition of a wide variety of organisms including macroinvertebrates (Gore and Hamilton 1996; Doisy and Rabeni 2001; Gore et al. 2001), microinvertebrates (Pourriot et al. 1997; Reckendorfer et al. 1999; Viroux 1999), algae (Ameziane et al. 2003; Hein et al. 2004; Sommer et al. 2004) and fish (Gore and Hamilton 1996; Koehn 1996; Barko et al. 2004). At the reach scale flow maintains habitat heterogeneity either directly (Hart and Finelli 1999; Tockner et al. 2000) or by acting as a disturbance (Peterson and Stevenson 1992; Reice 1994; Downes et al. 1998; Dent et al. 1999). Temporal variation in flow is also important because changes in flow are complex events in lowland rivers that have a major role in maintaining habitat heterogeneity (Tockner et al. 2000).

Due to the interaction between temporal flow variability and spatial heterogeneity, changes in the flow regime may have an impact on both spatial heterogeneity within the river channel and hydraulic variability within a patch. Discharge in Australian rivers systems is inherently variable (Puckridge et al. 1998, Thoms and Sheldon 2000), therefore patch variability within many Australian river systems is also highly dynamic. However, as with many of the world's rivers, the natural flow variability of these river systems has been altered by river regulation (Ward and Stanford 1979; Petts 1984) and this has altered the spatial and temporal dynamics of habitat patches (Bowen et al. 2003). Regulation has reduced this variability at a variety of temporal scales including short-term variation potentially affecting the ecological condition of these systems (Stewardson and Gippel 2003).

Changes in flow may alter the hydraulic characteristics of instream patches, thereby changing their habitat value. Flow changes vary in magnitude from extreme events such as floods or droughts that clearly act as disturbances with significant effects on the abundance and species composition of the biotic community (Dodds et al. 2004). Flow changes may also be relatively subtle such as daily changes in discharge. These types of changes may still have significant effects on patch hydraulic conditions but these flow changes have received far less attention. In lowland rivers small scale flow variations have been found to have an influence on biofilm species composition (Sheldon and Walker 1997; Burns and Walker 2000) and littoral vegetation (Blanch et al. 2000; Capon 2003). The response of the in channel biotic community to changes in the hydraulic character of patches remains largely unknown.

In floodplain environments, variations in flow may establish a patch mosaic at a variety of successional stages (Ward et al. 1999). There is less evidence for changes in flow leading to in-channel successional changes, but if flow changes act as disturbance, they may create habitat for fugitive species (*sensu* Downes and Lake 1991), or facilitate the persistence of competitively inferior species (McAuliffe 1983; Hemphill 1991). Examination of small scale flow changes in low-order streams indicates reasonably rapid response among some biotic components that this resilience is a characteristic of systems with a long history of frequent disturbance. Examinations of this sort are rare in lowland rivers and so we do not know whether lowland rivers demonstrate similar resilience or what the consequences of removing these short term variations in flow might be for the system.

Slackwaters are increasingly being recognised as important patches in lowland river systems. Slackwaters have been found to support higher rates of respiration (Nelson and Scott 1962; Mulholland et al. 2001) and denitrification (Melody and Dodds 2002; Strauss et al. 2004) both of which may be related to litter accumulation (Nelson and Scott 1962; Mulholland et al. 1997, 2001; Melody and Dodds 2002). Slackwaters may support greater abundances of algae (Sommer et al. 2004) and phytoplankton (Ameziane et al. 2003; Hein et al. 2004) and a discrete flora (Chernoff et al. 2004). Slackwaters appear to be patches of high zooplankton abundance (Tans et al. 1998; Reckendorfer et al. 1999; Speas 2000; Keckeis et al. 2003; King 2004; Nielsen et al. 2005) and provide critical fish habitat for either reproduction (Niehaus et al. 1997; Gurtin et al. 2003; Barko et al. 2004; King 2004) or adults (Hirzinger et al. 2004; Hohausova 2000, Hohausova et al. 2003). The macroinvertebrate community within slackwaters also appears to be different from that found in other patch types within the main channel (Buffagni et al. 2000; Doisy and Rabeni 2001). The discrete community and important metabolic functions that occur within slackwaters mean that they play a key role in the ecology of lowland rivers and understanding slackwater ecology will facilitate understanding lowland river ecology more generally.

Slackwaters are created during both increases and decreases in flow. Increasing discharge creates slackwaters through inundation of protected areas of, or embayments in the river bank while decreasing flow converts flowing patches to slackwaters (Schiemer et al. 2001) Succession may be considered to be the orderly development of biotic communities that is both directional and predictable (Odum 1969).

The objective of this study was to mimic the alteration of flowing water patches to slackwaters by creating slackwater patches in a flowing patch of the main river channel, and to track the metabolic and biotic changes that took place once the flowing area had become a slackwater, over a 14 day period. We hypothesize that the biotic and abiotic nature of the created slackwater patches will rapidly come to resemble that of natural (reference) slackwaters.

## **Methods**

### ***Site Description***

The Broken River, a mid-slope tributary of the Goulburn River (**Figure 1**), has a mean annual discharge of 200,000 ML and approximately 10% is diverted for off-stream use. The impoundments, Lakes Nillahcootie (built 1967) and Mokoan (built 1971), are the primary regulating bodies and irrigation flows are released during summer and autumn. The lower reaches of the Broken River where this study was conducted consist mostly of long, meandering runs, comprising alternating shallow (<1 m) and deep (1-3 m) areas with still to moderate velocities (0-0.5 m s<sup>-1</sup>). Instream structure comprises snags derived from riparian river redgums (*Eucalyptus camaldulensis*) and aquatic macrophytes dominated by common reed (*Phragmites australis*).

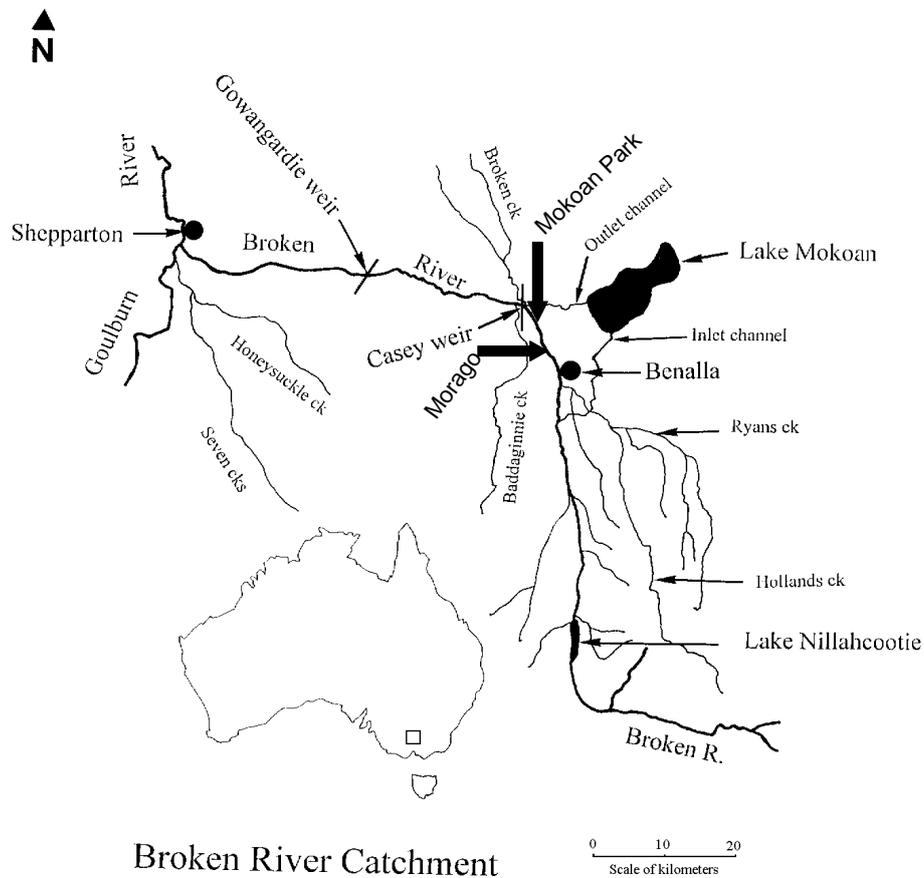
### ***Experimental Design***

The slackwater manipulation experiment was conducted in the Broken River between Scholes Rd, just north of Benalla (36° 31' S, 145° 57' E) and Casey Weir (36° 28' S, 145° 56' E) from 19 October to 15 December 2004. This section of the Broken River was chosen to maximise the pool of potential fish species that could be affected by the alterations to the slackwater habitats.

Approximately 10 species of fish have previously been identified from this river (Humphries and Lake 2000) and to minimise changes in river height during the experiment due to irrigation releases. Access to these sites was through two private properties “Morago” and “Mokoan Park”.

Prior to commencement of the study six flowing sites were identified for modification to a slackwater habitat. Six reference (natural) slackwaters were also identified for sampling at the same time as the created slackwater experimental units.

Six 2000 litre tanks (diameter 2 m, height 1 m, Polymaster aquaculture tanks) were used to create slackwater habitats in naturally flowing areas (velocity approx  $0.2 \text{ ms}^{-1}$ ) adjacent to the River’s edge. The tanks had their base removed and a 1.5 m x 0.6 m slot cut into the downstream end of the tank. These modifications enabled the tank to be immersed into the benthos to a depth of approximately 10 cm and allowed exchange of water and biota.



**Figure 1.** Broken River Catchment indicating sampling sites, Mokoan Park and Morago.

Tanks were secured in place using 2 m star pickets with fencing wire secured to the tanks through holes in the upper edge (Figure 2). Sand bags were used to reinforce the upstream edge of the tanks and to prevent geomorphic undermining. The six created and six reference slackwater sites (12 sampling units) were sampled on days 1, 3, 9 and 14 after the tanks were installed.



**Figure 2.** Tank installed to create a slackwater.

### ***Snag Construction and Deployment***

Three hundred and sixty natural snags (diameter 30-50 mm; length 30 cm) were cut from submerged woody debris from the experimental reach of the Broken River.

Each snag was numbered and its surface area measured. Eight snags were attached to a Dexion “L” cross member (length 60 cm) using electrical cable ties. This cross member was bolted to one end of a 10 cm x 10 cm x 50 cm masonry block (Figure 3) to ensure the snags remained submerged just above the benthos. Three of these racks of snags were deployed in each of the 12 identified sampling units in September 2004 (four weeks prior to the commencement of the experiment) to allow colonisation.



**Figure 3.** Experimental snags ready for deployment.

### ***Physico-chemical Analyses***

Physico-chemical and habitat data were collected from all 12 sampling units on each sampling occasion. Temperature, dissolved oxygen, turbidity, conductivity and pH were measured *in situ* using a Horiba U-10 Water Quality Checker. Current velocity was measured *in situ* using a Flow Mate 2000 (Marsh M<sup>c</sup>Birney). A 300 ml water sample was filtered onto a pre-weighed 45 mm Whatman GFF filter paper for total suspended solids (TSS) analysis. In the laboratory, the sample was dried at 105 °C for 24 hrs, allowed to cool within a desiccator and weighed again to determine TSS.

Particulate organic matter (POM) was determined by combusting the dried TSS sample at 550 °C for one hour and recording the difference in mass (Ash Free Dry Mass (AFDM)).

### ***Open Water Chlorophyll a***

Open water chlorophyll *a* concentration was determined for each of the 12 sampling units on each sampling occasion identified above. A known volume of water was filtered through a Whatman GF/C Filter, which was immediately transferred to a 10 ml polypropylene centrifuge tube (Sarstedt) and frozen for later analysis in the laboratory. Total chlorophyll *a* concentration was determined following extraction in boiling, 90% ethanol (ISO 1992). Chlorophyll *a* concentrations were determined by optical adsorption at 665 and 750 nm using standard spectrophotometric methods.

### ***Benthic Organic Matter and Chlorophyll a***

Benthic samples were collected from each of the 12 sampling units on each sampling occasion identified above by taking a sediment core using a 60 ml syringe with the needle end removed. The plunger of the syringe and a small flexible metal paint scraper were used to remove excess sample from the core so that the core contained only the upper most 5 ml of benthos. Three cores were randomly collected from within the patch and placed into a sterilised, 70 ml polypropylene sample jar (Sarstedt) and immediately frozen for laboratory analysis of organic matter content (AFDM). A further three samples were collected, which had 47.5 ml of 100% ethanol added (to reach a final concentration of 90%) and these samples were stored on ice in the dark until they were taken to the laboratory for chlorophyll *a* analysis. Total chlorophyll *a* concentration was determined following extraction in boiling, 90% ethanol (ISO 1992) as described above. AFDM was determined as the difference in mass of the sediment before and after one hour of combustion at 550 °C in a ceramic crucible following drying for 24 hours at 105 °C. Sampling locations within each patch were documented on each occasion to avoid re-sampling.

### ***Open Water Metabolism***

Dissolved oxygen loggers (TPS-WP82Y) were deployed for 24 hours on metal frames that were pushed into the sediment in each of the sampling units and on each of the sampling occasions identified above. A small submersible water pump was also attached to each metal frame beneath the probe to ensure water circulation over the probe. Light loggers (Odyssey) were deployed as close as possible to the probes to measure concurrent incident photosynthetically active radiation (PAR). Both dissolved oxygen and PAR were logged at 10 minute intervals.

### ***Snag Biofilm Metabolism***

Snag production chambers were constructed from 50 cm lengths of 40 mm diameter Perspex tube. Each chamber was capped with rubber pan cones. Flexible tubing connected each end to a small submersible pump to reticulate water through each chamber. A rubber bung sealed one end of the chamber and an “YSI” dissolved oxygen probe fitted with a bung sealed the other end. Each chamber was attached to the same frame as that used for open water production in the slackwater to ensure similar light conditions.

One seasoned snag segment was collected from each of the 12 sampling units on each sampling occasion and carefully placed in a chamber that had been purged of air.

Dissolved oxygen was logged every 10 minutes for 24 hours. Snags were then removed from the chambers and biofilm sub-samples of known area were collected, filtered on to GFC and transferred to a 15 mL centrifuge tube before being frozen and returned to the laboratory for chlorophyll-*a* analysis. Total chlorophyll *a* concentration was determined following extraction in 10 ml of boiling, 90% ethanol (ISO 1992) as described above.

The snags were then returned to the slackwaters where they were reattached to the rack using a different coloured cable tie so that the used snags could easily be identified and not re-sampled.

For both open water and snag biofilm metabolism, respiration was determined by the rate of oxygen uptake in the absence of sunlight. Gross primary production (GPP) was determined as the rate of increase in oxygen concentration during daylight hours. Nett primary production (NPP) was determined by adding the daily estimate of respiration to GPP.

### ***Microinvertebrates***

Microinvertebrates samples were collected from each of the 12 sampling units on each of the sampling occasions identified above by pumping (12-volt submersible “Conga”) 10 L water through a 50 µm mesh net at 25 litres per minute. Samples were collected from the slackwaters by maintaining the pump inlet within 2 cm of the sediment and moving the pump horizontally across the benthic surface. Samples were preserved in 70% ethanol and returned to the laboratory for identification and counting. Samples were counted in a Sedgewick-Rafter counting chamber and identified using a darkfield microscope (Zeiss). Microinvertebrates were identified to the level of Family or Genus following keys in Shiel (1995), with the exception of ostracods that were identified to Class.

### ***Macroinvertebrates***

Macroinvertebrates were sampled from each of the 12 sampling units on each of the sampling occasions identified above from the racks of snags mentioned above (see Snag Construction and Deployment, above).

On each sampling occasion, one snag was randomly selected from each of the three racks within the sampling unit (three snags per sampling unit). To ensure maximum capture of macroinvertebrates the snags were collected using 90 mm PVC storm water pipe with a 500  $\mu$ m mesh screen fitted to one end and held in place with a joining sleeve. The pipe was gently placed over the snag and the cable tie cut to free the snag from the rack. The snag and any dislodged material was then washed into a plastic bucket and scrubbed down using a stiff nail brush, to remove all the animals from the surface. The scrubbed snags were returned to the slackwater where they were reattached to the rack using a different coloured cable tie so that the used snags could easily be identified and not re-sampled. The samples were preserved in 70 % ethanol and returned to the laboratory for counting and identification to lowest taxa level following the keys listed in Hawking (2000).

### ***Fish and Macrocrustaceans***

Fish and shrimp samples were collected on each of the sampling occasions identified above using modified quatrefoil light traps (Humphries et al. 2002), which were placed in each of the 12 sampling units near sunset. The samples were collected the following morning, washed into 300 ml polypropylene jars (Sarstedt), preserved in 70% ethanol and returned to the laboratory for counting and identification using the key of Serafini and Humphries (2003). Adult and juvenile shrimp were identified using keys modified from Williams (1980). Larval shrimp were counted, but not identified.

## **Data analysis**

### **Physico-chemical and Metabolism Data.**

Analysis of variance (ANOVA) was performed using the statistical package Systat (Version 10, SPSS inc., Chicago, IL, USA). ANOVA of untransformed physico-chemical data was performed using the model:  $DV = constant + time + treatment + time \times treatment$  to assess the differences between treatments and between treatments over time.

### **Biotic Data**

Repeated measures ANOVA was used to assess differences among treatments using the model:  $DV \text{ t1 t3 t9 t14/ repeat} = 4 (1, 3, 9, 14)$ .

For macroinvertebrates (excluding macrocrustaceans) the mean number of animals collected from the three snags sampled in each replicate was calculated. Numbers were then expressed as numbers of animals per  $m^2$ . Microinvertebrate counts were converted to number of animals  $L^{-1}$ . Fish and macrocrustacean numbers were expressed as numbers per unit.

All microinvertebrates and macroinvertebrate data were subjected to a logarithmic transformation ( $\log\{x+1\}$ ) prior to analysis, which removed heterogeneity of variances, as a pre-requisite for parametric analysis (Underwood 1997).

Multivariate analysis including non-metric multidimensional scaling (nMDS) and SIMPER using Primer v5 (Clarke and Warwick 2001). PERMANOVA (Anderson 2005) was used to determine if differences occurred between groups. Data was analysed as transformed abundance data (4<sup>th</sup> root) and presence-absence data.

Multivariate analysis was performed on macroinvertebrate and microinvertebrate groups. Due to the low diversity of fish and macrocrustaceans these were not analysed.

SIMPER was used to analyse the total biotic data set (microinvertebrates, macroinvertebrates, shrimp and fish) for underlying patterns following presence absence transformation. BIOENV was used to relate patterns in the biotic data set with a range of environmental variables (listed above).

## **Results**

### ***Physico-chemical***

With the exception of turbidity there were no significant differences between any of the measured parameters. Turbidity varied between treatments and over time, primarily driven by higher turbidity in the tanks in the first days after setting up. For the majority of time turbidity was higher in the reference slackwaters (Table 1).

### ***Metabolism Carbon and Chlorophyll a***

There was no difference between the two treatments for either gross primary production (GPP), respiration and net respiration in either the open water or on the snags nor was there any differences between treatments in the open water chlorophyll-*a* and total suspended solids (TSS) and sediment carbon.

Within the created slackwaters there was significantly less particulate organic matter (POM) and chlorophyll *a* in the water column but on the sediment and snags there was more chlorophyll *a* in the created slackwaters compared to the reference slackwaters, except for sediment chlorophyll *a* on day 1 where there was no difference between treatments. Overall, the sediments contained three times more Chlorophyll *a* than the snags (Table 1; **Figure 4** and Figure 5).

**Table 1.** Summary table of P-values derived from ANOVA of physico-chemical and metabolism data.

Parameter	Treatment	Time	Treatment x Time
pH	0.878	<0.001	0.523
Conductivity	0.842	0.296	0.930
Turbidity	<0.050	<0.050	<0.001
Dissolved Oxygen	0.166	<0.001	0.281
Temperature	0.097	<0.001	0.501
Open water - GPP	0.327	<0.050	0.088
Open water - respiration	0.792	<0.050	0.113
Open water – net production	0.828	<0.050	0.134
Open water – chlorophyll <i>a</i>	0.080	0.322	0.999
Open water - POC	<0.050	<0.050	0.420
Open water - TSS	0.101	0.372	0.523
Snag – GPP	0.174	<0.001	0.399
Snag - respiration	0.878	<0.050	0.794
Snag – net production	0.409	0.537	0.499
Snag – chlorophyll <i>a</i>	<0.050	0.067	0.568
Sediment – chlorophyll <i>a</i>	<0.050	0.788	0.302
Sediment Carbon	0.478	0.136	0.631

### ***Microinvertebrates***

A total of 39 microinvertebrates taxa were collected during this study, 30 from the reference slackwaters and 31 from the tanks. There was no significant difference in the number of taxa collected among treatments. There was however a significant difference in the number of animals collected with more collected from the reference slackwaters. Numbers of animals followed a similar patten across time (Table 2, Figure 7A, B).

**Table 2.** Summary table of P-values derived from repeated measures ANOVA invertebrates, fish and macrocrustacean numbers and richness.

Group	Parameter	Treatment	Time	Treatment x Time
Microinvertebrates	density	<0.050	0.249	0.209
	diversity	0.298	<0.050	0.408
Macroinvertebrates	density	<0.001	<0.001	<0.001
	diversity	0.650	<0.050	0.172
Fish	density	0.580	<0.050	0.329
	diversity	0.516	0.195	0.918
Macrocrustaceans	density	0.887	0.211	0.678
	diversity	0.901	0.912	0.999

Multivariate analysis of the microinvertebrate community data indicates that there were significant differences occurring between treatments and between treatments over time using both abundance data and presence-absence data. There were also significant differences occurring between treatments on individual sampling occasions (Table 3; Figure 8A, B). There were significant differences in abundance data between treatments on days 1, 3 and 14 and significant differences in presence absence data on days 1 and 9.

**Table 3.** Results of 2 factor PERMANOVA analysis comparing the treatment and days and examining differences between treatments on individual days.

Parameter	Microinvertebrates		Macroinvertebrates	
	Abundance	Diversity	Density	Diversity
Treatment	<0.050	<0.050	<0.050	<0.050
Day	<0.050	0.179	<0.050	<0.050
Treatment x Day	<0.050	<0.050	<0.050	<0.050
Day 1	0.062	<0.050	<0.050	<0.050
Day 3	<0.050	<0.050	<0.050	<0.050
Day 9	0.309	0.520	<0.050	<0.050
Day 14	<0.050	<0.050	<0.050	<0.050

## ***Macroinvertebrates***

A total of 51 taxa were collected as part of the study, 46 in the reference slackwater and 41 in the experimental tanks. There was no significant difference in the number of taxa collected among treatments. There was however a significant difference in the numbers of macroinvertebrates collected with more animals collected from the tanks compared to the reference slackwaters. Numbers of animals remained constant across time in the reference slackwaters but decreased over time in the tanks (Table 2; Figure 7C, D).

Multivariate analysis macroinvertebrate community data indicates that there were significant differences occurring between treatments and between treatments over time using both abundance data and presence-absence data. There were also significant differences occurring between treatments on individual sampling occasions (Table 3, Figure 8D). The difference in communities was still apparent after day 14.

## ***Fish***

A total of 1195 adult and larval fish were collected during this study. The fish assemblage was dominated by common carp larvae (94%) with carp gudgeon contributing 4.6%, smelt and mosquito fish both contributing less than 1% to the fish abundance. Neither the abundance nor the species richness of fish were significantly different between treatments (Table 2; Figure 7E).

## ***Macrocrustaceans***

A total of 526 adult and larval microcrustaceans were collected. The population was dominated by unidentified shrimp larva (72%), but also included *Parataya* (18%), *Caridina* (8%) and *Macrobrachium* (1%). Neither the abundance nor the species richness of macrocrustaceans was significantly different among treatments (Table 2; Figure 7F).

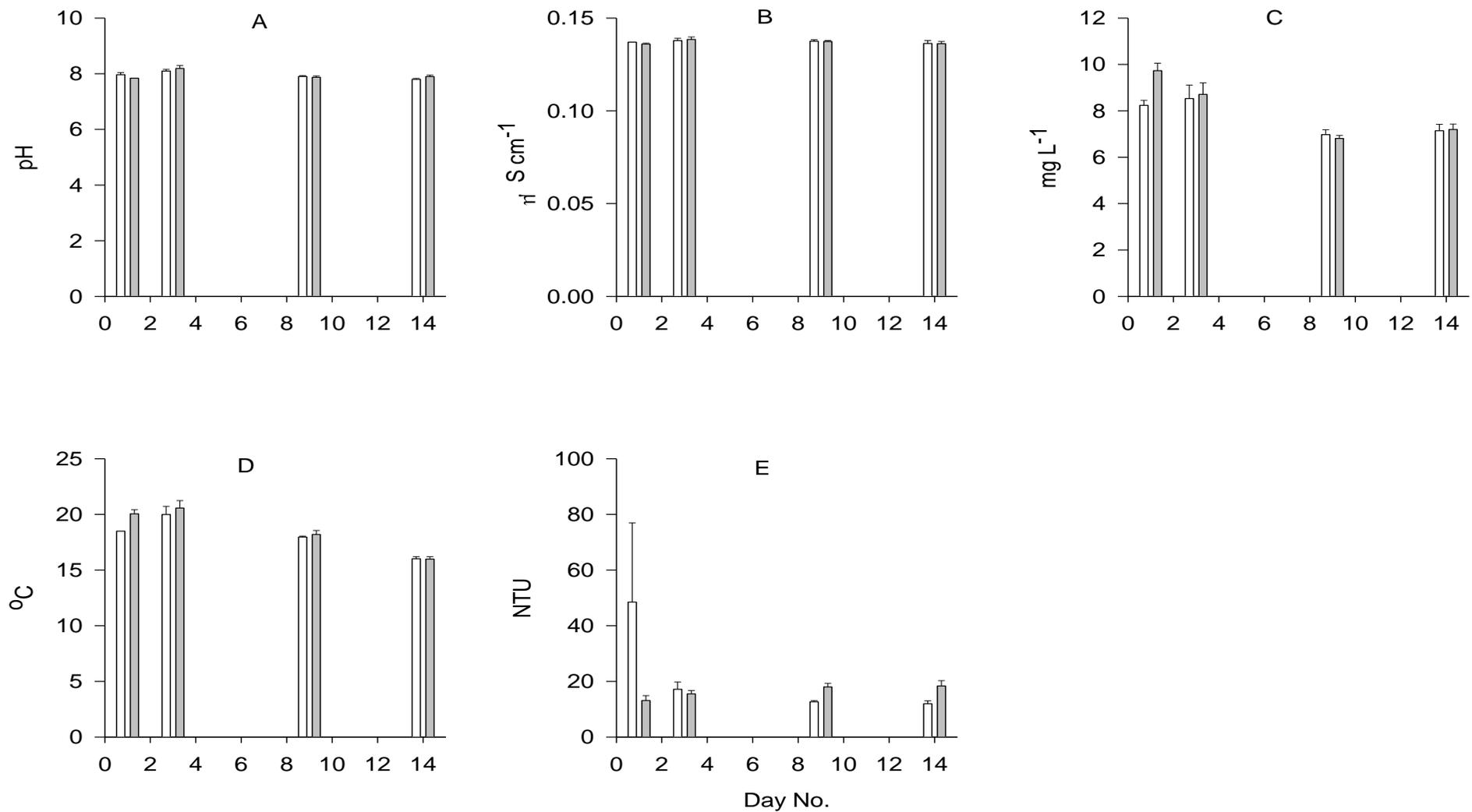
SIMPER analysis was performed on all on biotic groups and indicated that no individual taxa contributed a large percentage to the dissimilarities between either treatment on either day 1 and day 14. All taxa that contributed to 50% of the dissimilarity contributed less than 5% (Table 4). Taxa that are commonly found in flowing environments were abundant in the created slackwaters on day 1 but were substantially reduced in numbers or absent by day 14. The most abundant taxa on day 14 were primarily predators or omnivores.

## ***Correlation of multivariate biotic patterns with environmental variables***

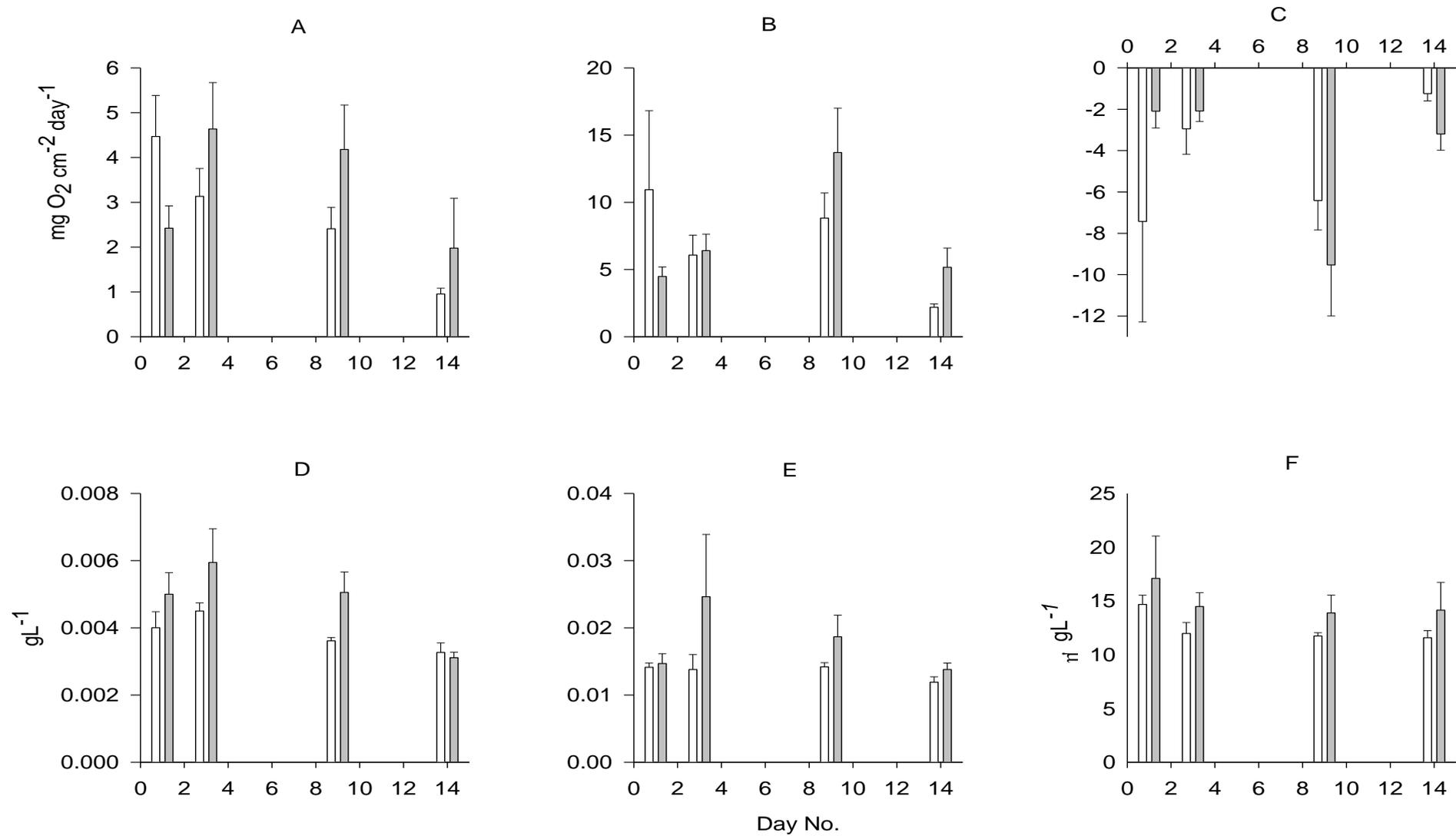
Bioenv analysis was used to correlate multivariate patterns in biotic community with environmental variables. The variable which correlated most strongly with the biotic patterns was particulate organic carbon ( $R = 0.137$ ). The best combination of maximum three variables was; particulate organic carbon and snag gross primary production ( $R = 0.163$ ). The best combination of maximum five variables was; total suspended solids, particulate organic carbon, snag gross primary production and open water gross primary production ( $R = 0.168$ ).

**Table 4.** The average abundance of taxa contributing to 50% of the dissimilarity between experimental units on day 1 and day 14 (empty cells indicates minimal contribution to dissimilarity). MC = macrocrustacean, MI = macroinvertebrate, MF = microinvertebrates. B = bacteriovore, C = carnivore, Co = collector, D = detritivore, E = engulfer, F = filterer, G = gatherer, H = herbivore O = omnivore, P = piercer, Pa = parasite, S = shredder, Sc = scraper, Su = sucker (Bauchsbaum et al. 1987; Shiel 1995; Hawking and Smith 1997).

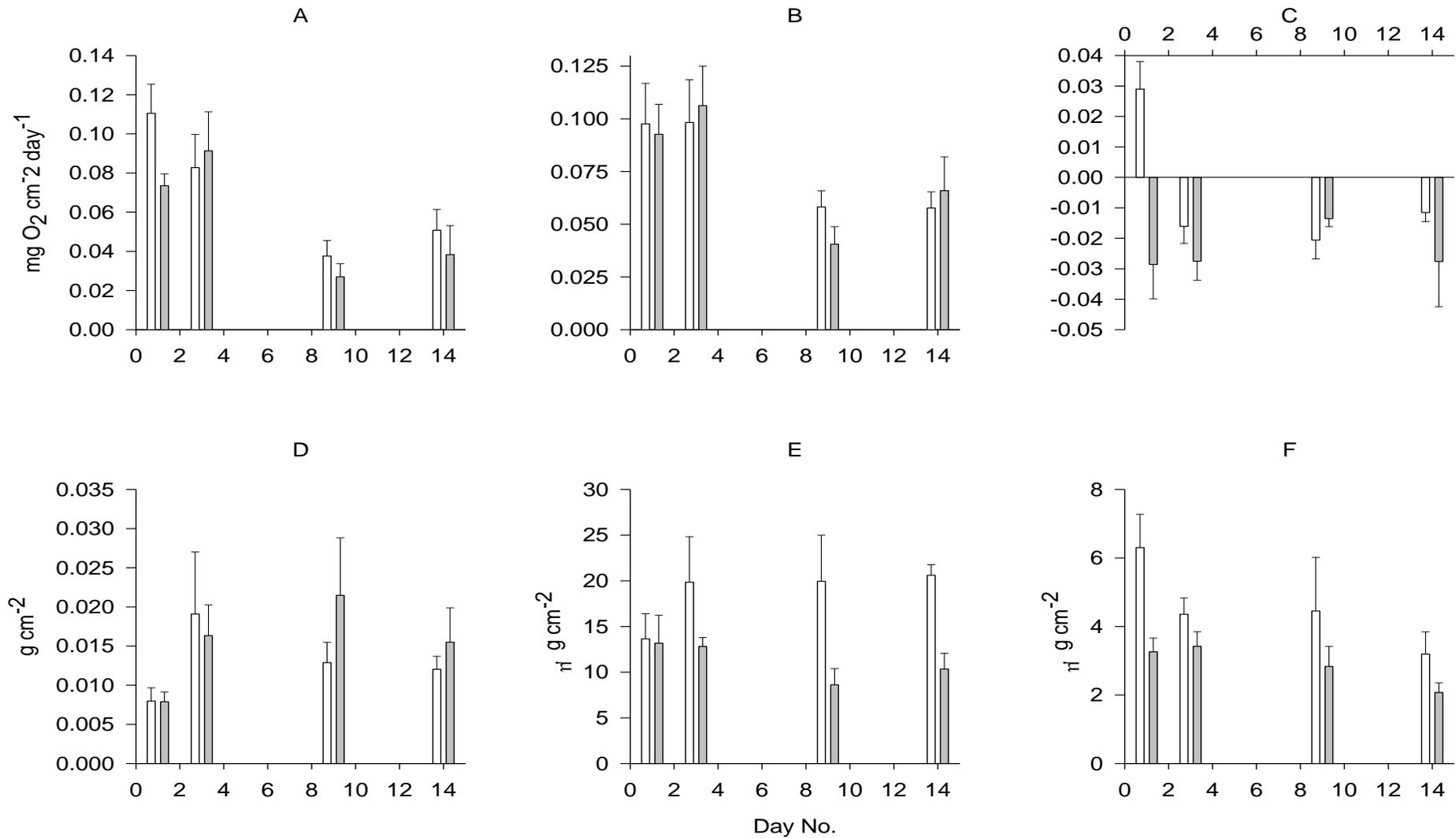
Taxa	Group	FFG	Day 1			Day 14		
			reference	tank	%	reference	tank	%
Caridina	MC	O, G	1.00	0.50	2.23	1.50	0.33	2.54
Larval shrimp	MC	O, G				1.33	4.17	2.30
Parataya	MC	O, G	0.67	1.83	2.25	0.83	1.00	2.57
Baetidae	MI	H, D	1.66	186.34	3.77	6.62	23.92	2.29
Bryozoa	MI	O, F				12.9	24.33	2.3
Calamoceratidae	MI	H, D	12.05	0.00	3.02	16.16	1.66	2.31
Ceratopogonidae	MI	C, E, Co, G				12.04	10.01	2.30
Corixidae	MI	O, P				10.17	289.20	2.80
Dugesiididae	MI	C				101.39	7.92	2.31
Elmidae	MI	H, Sc,	4.33	15.14	2.33	12.18	53.36	2.32
Empididae	MI	C, E	1.20	14.45	2.71	4.50	124.87	3.94
Hydra	MI	C	31.56	3.16	2.82	19.00	46.40	2.34
Hydracarina	MI	C, P, Su, Pa				38.87	12.43	2.74
Hydropsychidae	MI	O, F	6.29	305.24	3.81			
Isostictidae	MI	C				60.91	30.33	2.29
Leptoceridae	MI	H, O, D, C	20.03	4.25	2.79	28.7	58.82	2.80
Leptophlebiidae	MI	D, S	32.27	15.07	2.83			
Oribatida	MI	C, P, Su,	0.00	91.11	4.54	25.98	25.67	2.59
Physidae	MI	H, Sc	22.06	7.11	2.80	45.12	94.42	2.33
Simuliidae	MI	O, Co, F	7.91	70.67	2.29			
Bdelloid	MF	unknown	2.19	2.55	2.25	1.57	2.45	2.88
Euchlanis	MF	D, H	1.15	4.87	2.28			
Keratella	MF	B, H				1.98	1.70	2.36
Monostyla	MF	B, H	0.50	1.25	2.24			
Trichocerca	MF	P, H	2.72	1.11	2.25			
Trichotria	MF	H, D	2.62	1.10	2.25			
Neothrix	MF	H, D				49.85	48.13	2.36



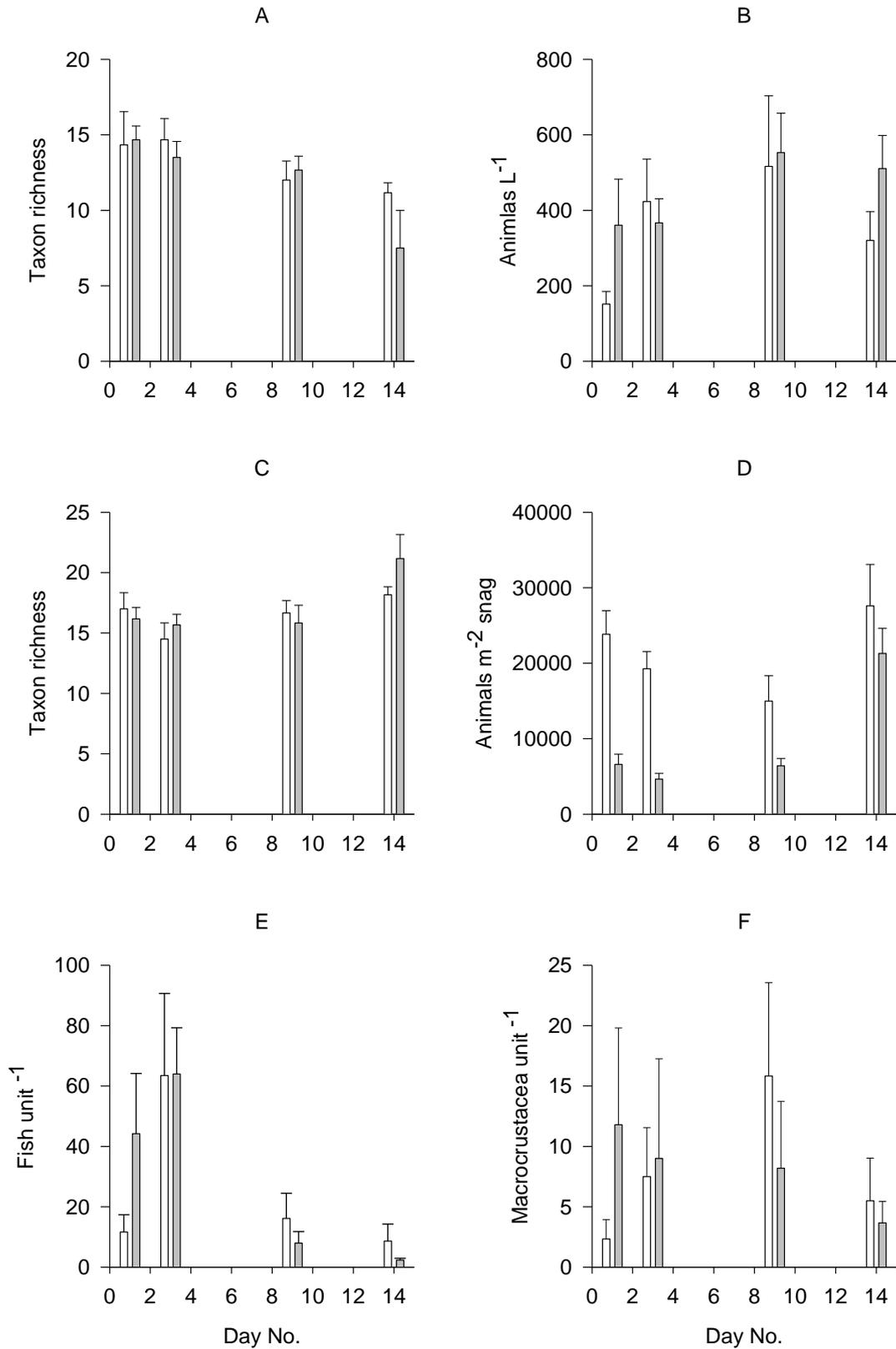
**Figure 4.** Physico-chemical data. A) pH; B) conductivity; C) dissolved oxygen; D) temperature and E) Turbidity. Open bars = created slackwaters; Grey bars reference slackwaters. (All data mean  $\pm$  s.e.)



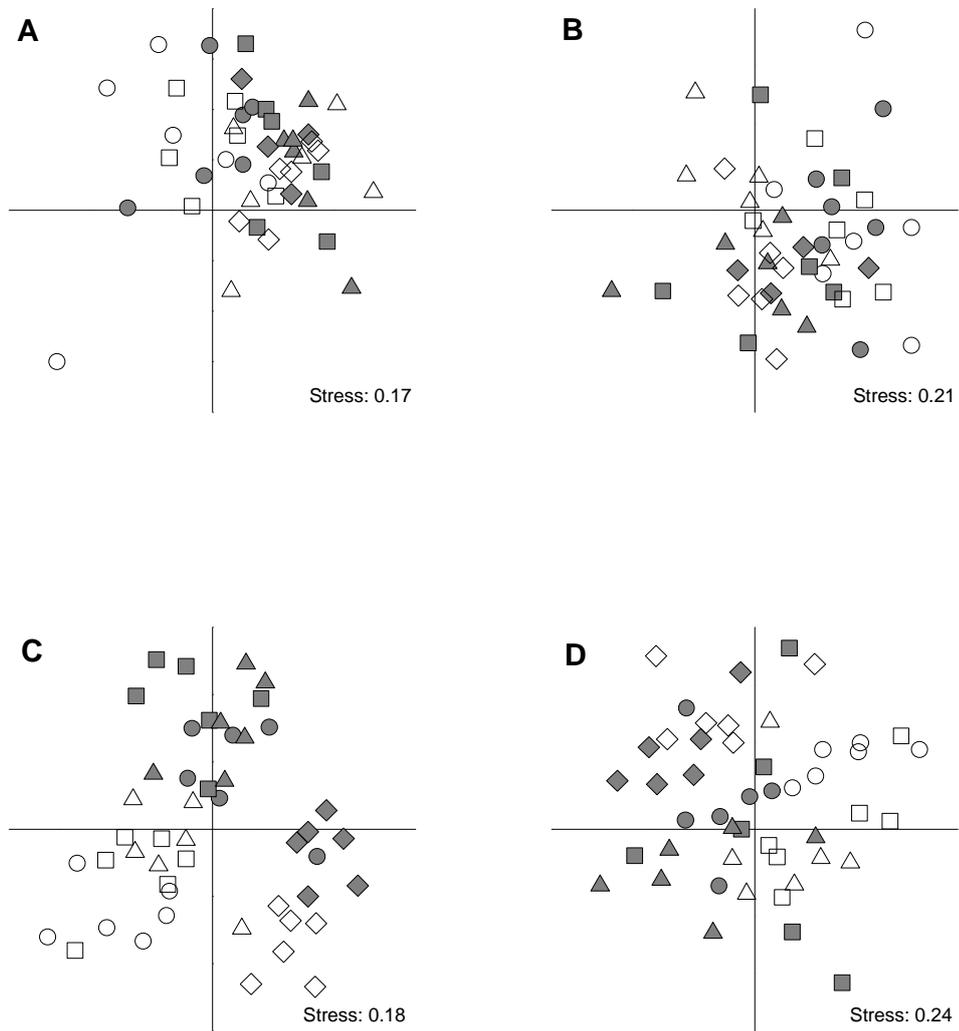
**Figure 5.** Open water metabolism, carbon and chlorophyll-*a*. A) Gross primary production; B) Respiration; C) Net production; D) Particulate organic carbon; E) Total suspended solids and F) Chlorophyll *a*. Open bars = created slackwaters; Grey bars reference slackwaters. (All data mean  $\pm$  s.e.)



**Figure 6.** Biofilm metabolism, carbon and chlorophyll-*a*. A) Snag biofilm gross primary production; B) Snag biofilm respiration; C) Snag biofilm net production; D) Sediment organic carbon; E) Sediment Chlorophyll-*a* and F) Snag biofilm chlorophyll *a*. Open bars = created slackwaters; Grey bars reference slackwaters. (All data mean  $\pm$  s.e.)



**Figure 7.** Measures of biota. The richness of and abundance of microinvertebrates (A, B); macroinvertebrates (C, D) and abundance of fish (E) and macrocrustaceans (F). Open bars = created slackwaters; Grey bars = reference slackwaters. (All data mean  $\pm$  s.e.)



**Figure 8.** nMDS of microinvertebrates communities (A = abundance data; B = presence absence data) and macroinvertebrate communities (C = abundance data; D = presence absence data)  
 Open symbols = created slackwaters; closed symbols = reference slackwaters.  
 ● = day 1; ■ = day3; ▲ =day 9; ◆ = day 14.

## **Discussion**

The structural heterogeneity of the wetted area of a river channel provides a myriad of habitat patches at a variety of scales. Within channel slackwater patches have been shown to be significant refuges from flow and sites for recruitment of larval fish (Humphries et al. 1999) and invertebrates (Scrimgeour and Winterbourne 1989; Negishi et al. 2002). These patches vary both in size and shape but also in their degree of permanence. As channel flow varies new slack water areas may be created or modified (Schiemer et al. 2001; Bowen et al. 2003). Earlier studies on the Broken River (Gawne et al. 2004; P. Humphries unpublished data) have shown distinct differences in the fauna between main channel flowing habitats and temporary slackwaters created in the main channel and, for at least microinvertebrates, it appeared that the slackwater communities were well established within the first month (Gawne et al. 2004). In this study the primary aim was to determine the rate of change in both biotic and abiotic variables and attempt to identify the driving processes.

### ***Physio-chemical parameters***

There was no significant difference between the physico-chemical parameters measured between the reference and created slackwater treatments. The lack of detectable differences in the physico-chemical parameters measured indicates that there is a continual exchange and mixing of water between the flowing environment and the more static environments. Previous studies on lowland rivers comparing slackwater habitats to flowing habitats have also indicated that there is continual exchange and mixing of water facilitated by connectivity (Schiemer et al. 2001).

## ***Metabolism Carbon and Chlorophyll-a***

The metabolism parameters also indicate rapid changes occur when flowing habitats are changed to non-flowing habitats. Studies of metabolism in alpine streams have reported rapid responses (<4 days) following flooding at temperatures of 6 °C (Uehlinger et al. 2003), therefore it is quite possible that at temperatures of around 18 °C as were occurring in the Broken River during the duration of this experiment metabolism could respond substantially quicker.

This data also indicates that slackwaters zones act as sinks for organic material. Particulate organic matter was higher in the reference slackwaters compared to the created slackwaters but by day 14 there was no difference. The higher organic parameters in the reference slackwaters presumably contribute to increased open water metabolism in these treatments.

There is conflicting evidence of the relationship between flow and chlorophyll *a* and it is usually perceived as a negative relationship (Sommer et. al. 2004) but previous studies on the Broken River have indicated a positive relationship (R. Oliver unpublished data). Snag biofilm (algae) appeared to respond rapidly to the change in flow regime. Chlorophyll *a* was much higher initially on the snags from the created slackwaters (preconditioned in the flow) and although it decreased over time in both treatments and the snags from the created slackwaters consistently contained more chlorophyll *a* than those from the reference slackwaters, they did become more similar.

A similar trend was not evident in chlorophyll *a* from the sediments. On day 1 sediments from both treatments contained the similar amounts of chlorophyll. Within days; however, the amount of chlorophyll in the sediment within the created slackwaters had significantly increased compared to the reference slackwaters. Modification of the flow regime allowed for rapid increases in algal biomass which was not reduced over the 14 day sampling period.

Generally there is less chlorophyll *a* present in habitats with low complexity (i.e. river channel) compared to more complex habitats (i.e. slackwaters) (Taniguchi and Tokeshi 2004). In part, these differences in chlorophyll *a* could be a consequence of the more complex habitats supporting a greater diversity of grazers. Previous studies have shown that slackwaters do support more diverse and abundant communities of grazers (King 2004; Nielsen et al. 2005) and there is a substantial amount of published research on phytoplankton – zooplankton interactions (Sommer et al. 1986).

In this study the grazer community of microinvertebrates also responded rapidly to the creation of the slackwaters but it would appear that there is a lag period before the grazers can substantially reduce the amount of algal production.

### ***Biota***

Microinvertebrates and macroinvertebrate communities responded rapidly to the creation of the slackwaters. For both the invertebrate communities shifts in community structure occurred from those communities adapted to flowing environments to those adapted to more static environments.

Although univariate analysis does not indicate any differences in the richness of microinvertebrates it does show significant differences in abundance between treatments on day one, however, by day three these differences were not apparent. Multivariate analysis using presence and absence data does however indicate that different communities were occurring between the two treatments. Initially the community structure is significantly different (days 1 and 3) but from then onwards the communities are similar. Therefore, despite similar numbers of taxa in both treatments at day 1, structurally they were distinct.

This response is most likely due to microinvertebrates drift into the newly created slackwaters (Speas 2000; Schiemer et al. 2001). Previous work has shown that flowing habitats are generally low in both diversity and abundance of microinvertebrates (King 2004; Nielsen et al. 2005). Within a period of one day there was no difference in the diversity of microinvertebrates between the reference and created slackwaters and within three days there was no difference in the abundance of animals. This suggests that recolonisation is primarily coming from animals drifting in to these newly created area (M. Carey unpublished data). The majority of animals that comprised the microinvertebrate communities have previously been recorded from flowing habitats and in the drift within the Broken River (M. Carey unpublished data; Nielsen et al. 2005). Animals that are capable of rapid reproduction and population growth and continually drifting in low numbers will have a competitive advantage when new habitats become available. There is evidence from the Danube and Rhine Rivers that the microinvertebrates that are always present in the drift are derived from slackwater habitats (Schiemer et al. 2001).

Univariate analysis of the macroinvertebrate data also indicates no difference in the number of taxa present between treatments but substantial difference in the abundance of animals. On all sampling occasions there were more animals in the created slackwaters compared to the reference slackwaters but by day 14 these differences were very much reduced. Not only were there more animals in the created slackwaters the communities were significantly different on all sampling occasions between treatments. This may in part be driven by the greater abundance benthic algal as indicated by higher chlorophyll *a* in the created slackwaters favouring grazers throughout the 14 day period but also by habitat preference. Initially as expected the macroinvertebrate communities in the created slackwaters were dominated by taxa adapted to flowing habitats (e.g. Baetidae, Hydropsychidae, Oribatidae, Simuliidae) and by day 14 these animals were not present or in much reduced numbers. At day 14 there were still differences in the communities but these differences were driven by the presence of predators (i.e. Empididae) and herbivores (i.e. Corixidae) in the created slackwaters.

Both fish and shrimp were collected in abundant numbers but neither group exhibited any differences between treatments. Both of these groups are much more mobile compared to either of the invertebrate groups. Presumably individuals of these groups would move longitudinally along the river utilising new habitats as stream flow changes.

Temporary water bodies associated with lowland rivers are influenced by the spatial and temporal patterns of flow (Walker and Thoms 1993) which in turn promotes a diverse array of biotic communities within the landscape. Slackwater habitats within the main river channel are also influenced by the spatial and temporal pattern of flows. These habitats will vary from temporary through to permanently inundated depending on their size and location within the river channel and their duration and availability will be shortened or extended with water level fluctuations (Schiemer et al. 2001). Such a diversity of slackwater habitats should promote a greater diversity of biota within the river channel similar to that what occurs within a heterogenous floodplain landscape (Shiel et. al. 1998). As slackwaters are inundated they will become sinks for nutrients with organic material being washed in and make available nutrients from decaying matter previously deposited (Bonecker and Lansac-Tôha 1996). The release of nutrients will fuel a pulse of productivity, which in turn stimulates invertebrate growth and abundance (Hall et al. 1970; Junk et al. 1989). The increased abundance may then form a resource for juvenile fish and other predators within the river channel (Humphries et al. 1999).

This study suggests that the biota associated with slackwaters with lowland rivers are robust, with populations within the communities exhibiting varying degrees of resilience to environmental change. In this study there was a rapid response to changed flow regime for all biological and physical parameters measured. For some parameters the response appears to occur within minutes to hours (i.e. physico-chemical parameters); hours to days (microinvertebrates); days to weeks (macroinvertebrates). The study indicates that modification of flow regimes that result

in the loss of slackwater habitats will impinge on the productivity and diversity of lowland rivers.

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