

CREATING A DISTURBANCE: MANIPULATING SLACKWATERS IN A LOWLAND RIVER

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ABSTRACT

The dynamic nature of habitat patches in rivers is driven primarily by flow regime. Altered hydrology, through river regulation, can limit the size and distribution of slackwater patches; important areas for the development of young fish and for shrimp in lowland rivers. Between late October 2002 and late January 2003, we investigated responses of fish, shrimp and their potential prey to the experimental creation of slackwaters and, conversely, to the experimental creation of flowing patches, by diverting water away from flowing patches and into slackwater patches, respectively. A pre-experimental survey indicated that slackwaters contained many more fish than flowing patches, and fish larvae were flushed out of slackwaters during the construction of flowing patches. Creation of slackwaters resulted in increased abundance of fish and shrimp, with the opposite occurring when slackwaters were changed into flowing patches. Converting slackwaters into flowing patches, and *vice versa*, altered the species composition of zooplankton and microbenthic assemblages but did not change their densities. Thus, standing crop of potential prey alone could not explain the differences in fish or shrimp abundance found between patch types. We hypothesize that slackwaters primarily act as refuges from current and provide energetic advantages to the young stages of fish and to shrimp. River regulation has the potential to affect the recruitment success of fish and shrimp by affecting the size, arrangement and availability of slackwater patches. Copyright © 2006 John Wiley & Sons, Ltd.

KEY WORDS: fish; shrimp; river regulation; experiment; larvae

INTRODUCTION

Habitat patches in rivers are formed by interactions among hydrology, geomorphology and structural elements, such as coarse woody debris, boulders or macrophytes (Thorp *et al.*, in press). The dynamic nature of these habitat patches is driven primarily by characteristics of the flow regime (Hill *et al.*, 1991). This dynamism is most obvious during flooding, when ephemeral off-channel habitat patches, such as billabongs (oxbow lakes) and other floodplain wetlands, become inundated and connected to the main channel. Prior to inundation, these habitat patches are terrestrial in nature; and it is only once flooded that they become available to aquatic organisms (Boulton and Lloyd, 1992; Nielsen *et al.*, 2002; Brock *et al.*, 2003). This shifting nature of habitat patches may also occur within the main channel of rivers; thus, a patch that may act as a pool (slow flowing or still) under particular flow conditions may act as a run (fast current, unbroken water) under other flow conditions.

The persistence of habitat patches is dependent on temporal characteristics of a flow regime: timing, duration and variation. A patch may begin to exhibit the characteristics of a pool as flow declines into the normally dry period (timing). This pool may persist for several months (duration), although local rainfall events may disrupt its pool-like nature temporarily (variation). Riverine biota must run the gauntlet of the variation in habitat patches due to changes in flow, although in the case of highly mobile organisms, such as adult fish, it should not normally cause undue stress. This is partly because of their typically more generalist requirements (e.g. food, shelter, depth) relative to younger stages, partly because they can move from one patch to another as flow changes, and partly

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because of the often predictable nature of broad, seasonal hydrological patterns within which biota have evolved (Lytle and Poff, 2004). However, for less mobile organisms or life stages—such as attached eggs and undeveloped larvae of fish—changes to flow, and the resulting effect on critical rearing habitat, may result in significant mortality (Harvey, 1987; Schlosser and Angermeier, 1990; Chapman and Kramer, 1991; De Angelis *et al.*, 1997) and may be a significant determinant of recruitment success in any one year.

Alterations to natural patterns of river flow are extremely common throughout the world, as part of the widespread regulation of rivers (Ward and Stanford, 1979; Petts, 1984). The natural hydrologies of reaches, sections and sometimes entire rivers have been disrupted by the capture of rainfall and the subsequent release of water from dams, often for hydro-electric or irrigation purposes. This flow alteration, by definition, has resulted in altered type, frequency and extent of particular habitat patches. In the case of the lower River Murray in South Australia for example, normally free-flowing sections of river have been turned into virtual lakes by a series of 11 locks (Walker, 1986, 1992). In other cases, capture of runoff in dams has reduced flooding frequency and floodplain connectivity (Ward and Stanford, 1979; Petts, 1984). Less obvious changes to habitat patches, however, may occur within the main channel of rivers, especially when flows are only moderately altered. For example, artificially enhanced flows in rivers during typically low-flow periods—summer in southern Australia—increases current speed and depth within slackwater patches (areas with little or no discernible current) (Thorp and Casper, 2003). This can result in the loss of a substantial proportion of this type of habitat (Bowen *et al.*, 2003), sometimes for short periods—such as during hydro-peaking—and sometimes for months at a time, during irrigation releases. Because slackwaters are important nursery habitats for some species of fishes (Humphries *et al.*, 1999, 2002; Humphries and Lake, 2000; Dieterman and Galat, 2004; King, 2004b) and for shrimp (Richardson *et al.*, 2004), there is the potential for significant harm to recruitment should their extent be diminished.

In this study, we investigated the effects on fish, shrimp and measures of potential food (microfauna, benthic chlorophyll-*a* and organic content) of changes to slackwater patches within a lowland river in southern Australia, through two hydraulic manipulations. In the first manipulation, we diverted flow through natural slackwaters, increasing the current speed considerably (and thus simulating enhanced flows due to releases from dams). In the second manipulation, we diverted flow away from naturally flowing patches, thus stopping the current and effectively 'creating' slackwaters. We hypothesized that increasing current speed through natural slackwaters would reduce the abundance of fish, shrimp and microinvertebrates, and reduce the benthic chlorophyll-*a* and organic content relative to controls. We hypothesized that stopping the current in naturally flowing habitats would have the opposite effects.

STUDY LOCATION

The study was conducted in the Broken River, Northeastern Victoria, Australia. This river arises at about 1000 m a.s.l., just north of the Great Dividing Range and has a total length of approximately 180 km. The mean annual discharge of the Broken River is about $230 \times 10^6 \text{ m}^3$, with highest flows between June and September, when water temperatures are coldest ($\sim 7^\circ\text{C}$) and lowest flows between December and April, when water temperatures can reach $> 30^\circ\text{C}$. The Broken River is moderately regulated, with some storage of winter/spring flows in two impoundments (Lakes Nillahcootie and Mokoan) and later release of this over summer. Two substantial weirs (Casey and Gowangardie weirs), downstream of the major impoundments, are impediments to movement of fish upstream, but have little effect on the hydrology of the river. Much of the catchment has been cleared for agriculture.

The experiments were carried out at Morago ($145^\circ 57' 20'' \text{ E}$, $36^\circ 31' 18'' \text{ S}$ – $145^\circ 57' 28'' \text{ E}$, $36^\circ 31' 31'' \text{ S}$), which typically does not experience enhanced flows over the spring/summer period (as releases from Lake Nillahcootie are routed through Lake Mokoan and re-enter the Broken River downstream of our study reach) and so discharge is relatively stable during the time the experiment was conducted. The study reach was approximately 1 km in length, its width ranged from 20 to 50 m, it consisted of alternating pools (slow current speed, between 1 and 2 m deep) and runs (moderate current speed, between 0.2 and 1 m deep), with frequent piles of large woody debris throughout and less frequent patches of aquatic macrophytes (predominantly *Phragmites australis* and *Vallisneria spiralis*).

Eight species of fish have been commonly caught in this region of the Broken River (Humphries *et al.*, 2002) and include Australian smelt (*Retropinna semoni*), carp gudgeons (*Hypseleotris* spp., see below), Murray cod (*Maccullochella peelii*), crimson-spotted rainbowfish (*Melanotaenia fluviatilis*), mountain galaxias (*Galaxias olidus*), European perch (*Perca fluviatilis*), common carp (*Cyprinus carpio*) and eastern gambusia (*Gambusia holbrooki*). The adults of all of these species can be found in both flowing and non-flowing habitats in the Broken River (Humphries unpublished data), although Murray cod and mountain galaxias only rarely in the latter. None of the species could be termed obligate rheophils or obligate limnophils as most exhibit ontogenetic changes in habitat use (see King, 2004b).

Three species of shrimp—the atyids *Paratya australiensis* and *Caridina mccullochi* and the palaemonid *Macrobrachium australiense*—are common in this region of the Broken River (Richardson *et al.*, 2004). Larvae of all three shrimp species can be found in slackwater areas, as do juvenile and adult *Paratya* and *Caridina*: adult *Macrobrachium* more commonly occur in flowing channel habitats (Richardson *et al.*, 2004).

METHODS

Experimental set-up

An initial survey of Morago was undertaken to determine candidate sites for manipulation. Manipulating current to 'create' slackwaters (hereafter, referred to as created slackwaters or CRSW) necessitated locating littoral sites experiencing moderate to fast currents, which could have sand bag walls built out from the banks (Figure 1). Manipulating current to 'destroy' slackwaters or create flowing habitats (hereafter, referred to as created flow or CRFL) necessitated locating existing slackwaters appropriately positioned such that sand bag walls could be built to divert current through them. This meant that large slackwaters (approximately $>5 \times 5$ m) could not be destroyed and that we were limited to diverting current through slackwaters which resulted from the presence of woody debris piles and from relatively small slackwaters (the area affected was typically 10–20 m²). Slackwaters which contained dense stands of macrophytes were avoided because of their potential to influence greatly the abundance of fish and because of the difficulties of sampling within them.

After trying several alternative methods of diverting water, sand bag walls were chosen. A temporary wall was first constructed to enable rapid deployment and to make small adjustments of orientation; this also avoided undue disturbance during construction of the main wall. This wall was made from 2 m metal stakes, medium-mesh fencing wire and plastic sheeting, in the position where the sand bag wall was to be built. Sand bags were then placed along the outside edge of the temporary wall. Each sand bag wall was built so that it was approximately 0.2 m above the water surface and all walls remained intact for the 3 months of the study (both manipulations were carried out concurrently).

Six replicate CRFL and six replicate CRSW treatments were set up, with the same number of controls (a total of 24 experimental units). Controls (COSW and COFL) were simply either slackwater or flowing habitat patches which were not manipulated, which were of similar dimensions to treatments and which were chosen randomly from a range of possible patches. Each treatment and control unit was marked individually and sampled on each visit. The experimental units were set up on 24–25 October 2002 and were distributed throughout the reach. Sampling of five replicates of each patch type was conducted every two weeks for 2 months (7–8 November, 20–21 November, 5–6 December, 19–20 December) and then 6 weeks later on 28–29 January 2003. The reason for the gap between the penultimate and last sampling occasion was simply to vary the amount of time that the patches were left between samplings. The sixth replicate of each type functioned as a back-up in case of loss due to some extraneous cause, but was not needed.

Sample collection

The larvae, juveniles and adults of fish and shrimp were collected from five randomly chosen slackwaters and five randomly chosen flowing patches—which were entirely separate patches, not involved as controls or experimental units, but located within the same study reach—on 23 October 2002 (the day before slackwaters were

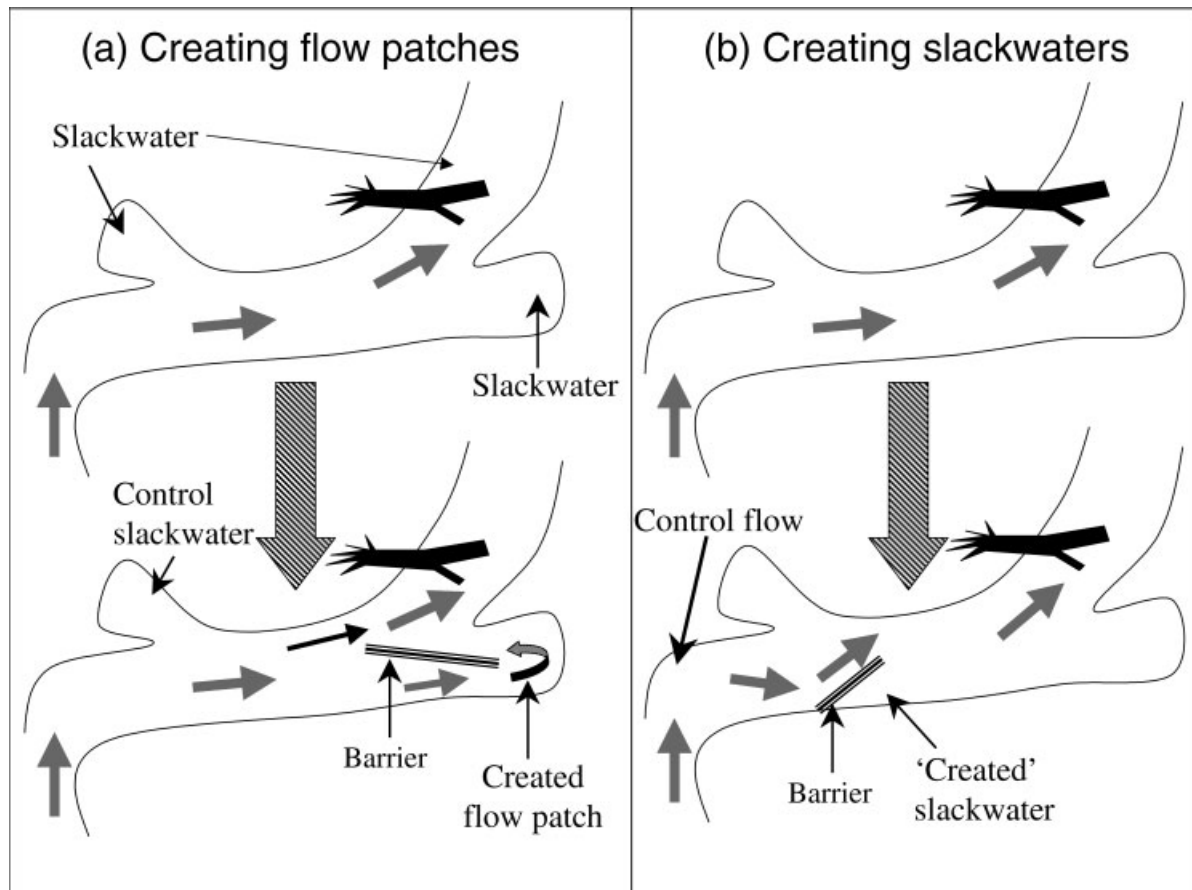


Figure 1. Schematic of section of river, showing how (a) slackwaters were altered to become created flow patches (CRFL) and (b) flow patches were altered to become created slackwaters (CRSW)

constructed) to establish the conditions at the commencement of the experiments. They were collected in the same manner as for the routine sampling, described below.

During construction of CRFL units, two drift nets ($1 \times 500 \mu\text{m}$ and $1 \times 250 \mu\text{m}$ mesh) were deployed for 1 hr at the downstream end of each CRFL unit in order to collect fish and shrimp displaced by the sudden increase in current speed. A further two nets of the same mesh size were deployed as controls in an area adjacent to each CRFL unit, where the current was fastest.

Fish and shrimp were collected using a sweep-net electrofisher (King and Crook, 2002; 25 cm width, 500 μm mesh) the day before the other biotic sampling was conducted, because we were concerned that electrofishing may have affected the other components of the patches if we had sampled them immediately afterwards. The sweep-net electrofisher was swept through 4 m of the habitat patch, ensuring the entire depth of the patch was sampled. The fish and shrimp from these samples were combined with those from samples taken the following day using a macroinvertebrate sweep-net (25 cm width, 250 μm mesh), swept just above the substratum through 1 m of habitat patch, after it was realized that both methods were effective in catching both taxa. The location of sampling within each habitat patch was chosen randomly and every attempt was made to avoid disturbance of other parts of the patch. Samples were preserved immediately in 95% ethanol. Zooplankton was collected by taking, from random depths and locations within the habitat patch, 10×1 L flasks of water and filtering the total volume through a 60 μm mesh net. Samples were immediately preserved in 70% ethanol. Benthic macroinvertebrates (microbenthos) were collected by taking, from random locations in the habitat patches, 3×4.5 cm diameter cores to a depth of 2 cm in a similar manner to King (2004a); this resulted in collecting about 3 cm of water above the substratum as well as sediment. Briefly, the corer was pushed 2 cm into the substratum, a cap placed on the top to create a seal,

the corer carefully raised until its base was flush with the substratum, a flat-bladed trowel slid under the base and the corer and trowel quickly placed in a bucket of filtered water. The three cores were combined and alternately stirred in the bucket and poured through a 53 μm mesh net until no benthic invertebrates remained (King [2002] showed that this method left virtually no animals or organic material within the sediment). The decanted material was concentrated and preserved in 70% ethanol.

Water column chl-*a* samples were collected from immediately below the water surface using a 600 ml opaque plastic jar. The sample was immediately placed on ice and kept dark. Benthic samples for chl-*a* and organic content were collected by using a core-like 29 mm diameter, 60 ml syringe with the end removed. The syringe plunger and a flat bladed trowel were used to remove excess sample from the core so that the sample contained only the upper 5 mm of the substratum. For both chl-*a* and organic matter, three replicates were collected randomly from each habitat patch, placed into a 60 ml centrifuge tube and immediately stored on ice.

Laboratory procedures

The larvae, juveniles and adults of fish were identified with the aid of a dissecting microscope and taxonomic keys (McDowall, 1996; Serafini and Humphries, 2004). Only carp gudgeons (*Hypseleotris* spp.) were not identified beyond genus, because of uncertainty with their taxonomy (Bertozzi *et al.*, 2000).

All shrimp were identified to species using a dissecting microscope. Adult and juvenile shrimp were identified using a key modified from Williams (1980), and larvae were identified to species using Benzie (1982) and Walsh (1993).

Benthic and planktonic microinvertebrates were subsampled prior to sorting. Individual samples were first filtered through a 60 μm sieve, then transferred to a 100 ml measuring cylinder and made up to a known volume. This sample was then thoroughly mixed, and a known volume, generally between 1 and 3 ml, was removed using a 10 ml Gilson pipette for sorting and identification. The subsample was placed in a 5-ml Sedgewick–Rafter cell and then sorted and identified using dark field microscopy. Microcrustacea were identified to Family, rotifers to Rotifera and testate amoebae to testate amoebae.

Water column and benthic chl-*a* samples were filtered through 0.45- μm Whatman GF/C filter paper and extracted overnight in 90% ethanol using standard methods (International Standards Organization, 1994). For the benthic chl-*a*, 47.5 ml 100% AR grade ethanol was added to each sample, which allows for 50% water in the sample.

Benthic dry weight and organic matter content was determined by placing the individual samples into pre-weighed 30 ml crucibles and dried at 105°C to a constant weight (generally between 24 and 30 hr), then cooled in a desiccator and weighed. Samples were then fired at 550°C for 1 hr, cooled in a desiccator and weighed to determine loss on ignition (organic content).

Physico-chemical parameters

Temperature, dissolved oxygen, turbidity, pH and conductivity were measured on each sampling occasion, using a Horiba Water Checker. In addition, Onset Optic Stowaway temperature loggers were placed on the substratum of three treatment and three control habitat patches for each experimental type (CRFL, CRSW) and set to log temperature hourly.

Data analysis

In most cases, data were of the form of counts of organisms per sample. In the case of fish and shrimp, data were presented as numbers per unit sampling effort. Microinvertebrates were standardized to numbers per litre. This involved simply dividing the total number of planktonic microinvertebrates by 10, but was not as straightforward for the microbenthos and involved some assumptions. The depth of material—both water and sediment—collected in the benthic corer, was 5 cm (3 cm of water and 2 cm of sediment). To determine the density of microbenthos per litre, we calculated the volume of material sampled with one core (79.52 cm³), multiplied this by three cores (238.56 cm³) and then standardized to 1 L. We assumed that microbenthos were evenly spaced within the material

collected in the core, whereas it is most likely that the majority of the organisms were associated with the surface and first centimetre of the substratum. Thus, our estimates of density will be underestimates of the true density. Water column and benthic chl-*a* concentration was calculated as $\mu\text{g/L}$. Benthic dry weight was calculated as g/ml by dividing sample dry weight by sample volume. The percentage organic content was determined by dividing loss on ignition by sample dry weight multiplied by 100.

In the majority of cases, data were $\log_{10}(x + 1)$ transformed to satisfy the assumptions of *t*-tests and analysis of variance (ANOVA). This was not the case, however, for the physico-chemical variables, which were all homoscedastic and approximated a normal distribution.

Paired *t*-tests were performed to compare the number of fish and shrimp flushed from CRFL habitat patches, relative to the main channel controls. A two-sample *t*-test was performed, comparing the number of fish (fish and fish larvae) in natural slackwaters with natural flowing habitat patches immediately prior to the commencement of the experiment.

One-way repeated-measures ANOVAs ('Trip' being repeated five times and 'Habitat' being the factor) were conducted for each of the two manipulations separately CRSW versus COFL and CRFL versus COSW on: temperature, dissolved oxygen, conductivity, turbidity, current speed, water depth, abundance of total fish, common carp (*Cyprinus carpio*), crimson-spotted rainbowfish (*Melanotaenia fluviatilis*), total shrimp, *Paratya australiensis*, *Caridina mcccullochi*, *Macrobrachium australiense*; density and taxon richness of zooplankton and microbenthos; dry weight and percentage of organic content of sediment; and the sediment and water column concentration of chl-*a*.

Multivariate analysis of planktonic microinvertebrates and microbenthos communities was performed using non-metric multidimensional scaling (NMDS) and Analysis of Similarity (ANOSIM) using Primer v5 statistical package (Clarke and Warwick, 2001). All four habitat patch types were included in a single analysis.

RESULTS

Physico-chemical variables

For all physico-chemical variables, except for pH and current speed, the effect of Habitat—for both the COSW versus CRFL and the COFL versus CRSW manipulations—was non-significant (repeated-measures ANOVAs, Table I, Figure 2). Indeed, Time contributed the most to variation in all variables, except for current speed and depth. Slackwaters had zero current speed in all experimental and control units, whereas flowing patches experienced mean current speeds of between 0.15 and almost 0.4 m/sec. Depth was not significantly different between slackwater patches and their flowing water counterparts, although there was a trend for greater depths in flowing water patches than the corresponding slackwater patches. In all slackwater habitats, created and control, pH values were consistently greater than in their flowing habitat counterparts.

Flushing from slackwaters

Although a total of 21 fish (20 larvae of common carp, *Cyprinus carpio* and 1 larva of Australian smelt, *Retropinna semoni*) were caught during the initial flush from CRFL patches (formerly slackwaters) compared with only 2 fish (common carp) caught in nets in the adjacent main channel, a *t*-test indicated that the mean number of fish collected was not significantly different between each habitat type ($df = 10$, $t = 1.566$, $p = 0.074$). There was also no significant difference in the mean number of shrimp flushed from the slackwaters (total of one) relative to the number in the main channel (total of five; $df = 10$, $t = -1.034$, $p > 0.10$).

Fishes

Prior to the commencement of the experiment, the mean (± 1 SE) number of fish collected in slackwaters (7.14 ± 1.66) was significantly greater than that in flowing habitats (where no fish were found) (*t*-test, $df = 8$, $t = 3.868$, $p < 0.01$).

Five species of fish were collected during the main experiments: common carp was the most abundant (total of 51 fish, of which, 37 were larvae and 14 juveniles), next most common was crimson-spotted rainbowfish

Table I. Mean squares and significance levels for repeated-measures ANOVAs investigating the effects of Habitat type and Time on physico-chemical variables, comparing created flow (CRFL) with control slackwaters (COSW) and created slackwaters (CRSW) with control flow (COFL).

Variable	Created Flow vs. Control Slackwater				Created Slackwater vs. Control Flow				
	Habitat	Error	Time	Time × Habitat	Habitat	Error	Time	Time × Habitat	Error
Temperature (°C)	0.871	1.140	144.798***	0.374	1.514	0.448	144.408***	0.172	0.144
Dissolved oxygen (mg/L)	0.303	0.412	4.956***	0.177	3.251**	0.431	5.791***	0.481	0.203
pH	0.764**	0.055	1.404***	0.106**	0.210**	0.025	1.913***	0.026	0.020
Conductivity (µS/cm)	5.618 × 10 ⁻⁵	1.129 × 10 ⁻⁵	0.002***	2.18 × 10 ⁻⁶	1.058 × 10 ⁻⁵	8.415 × 10 ⁻⁶	0.002***	1.630 × 10 ⁻⁶	1.817 × 10 ⁻⁶
Turbidity (NTU)	48.020	46.300	463.580**	27.620	180.500	95.413	634.220***	29.300	19.260
Current speed (m/sec)	0.461**	0.028	0.009**	0.009**	1.095**	0.002	0.012	0.012	0.005
Depth (cm)	290.746	288.068	79.581	21.439	234.090	28.158	49.898	45.076	45.005

Degrees of freedom for each analysis were: Habitat/Error—1, 8; Time/Time × Habitat/Error—4, 4, 32; ***p* < 0.01, ****p* < 0.001.

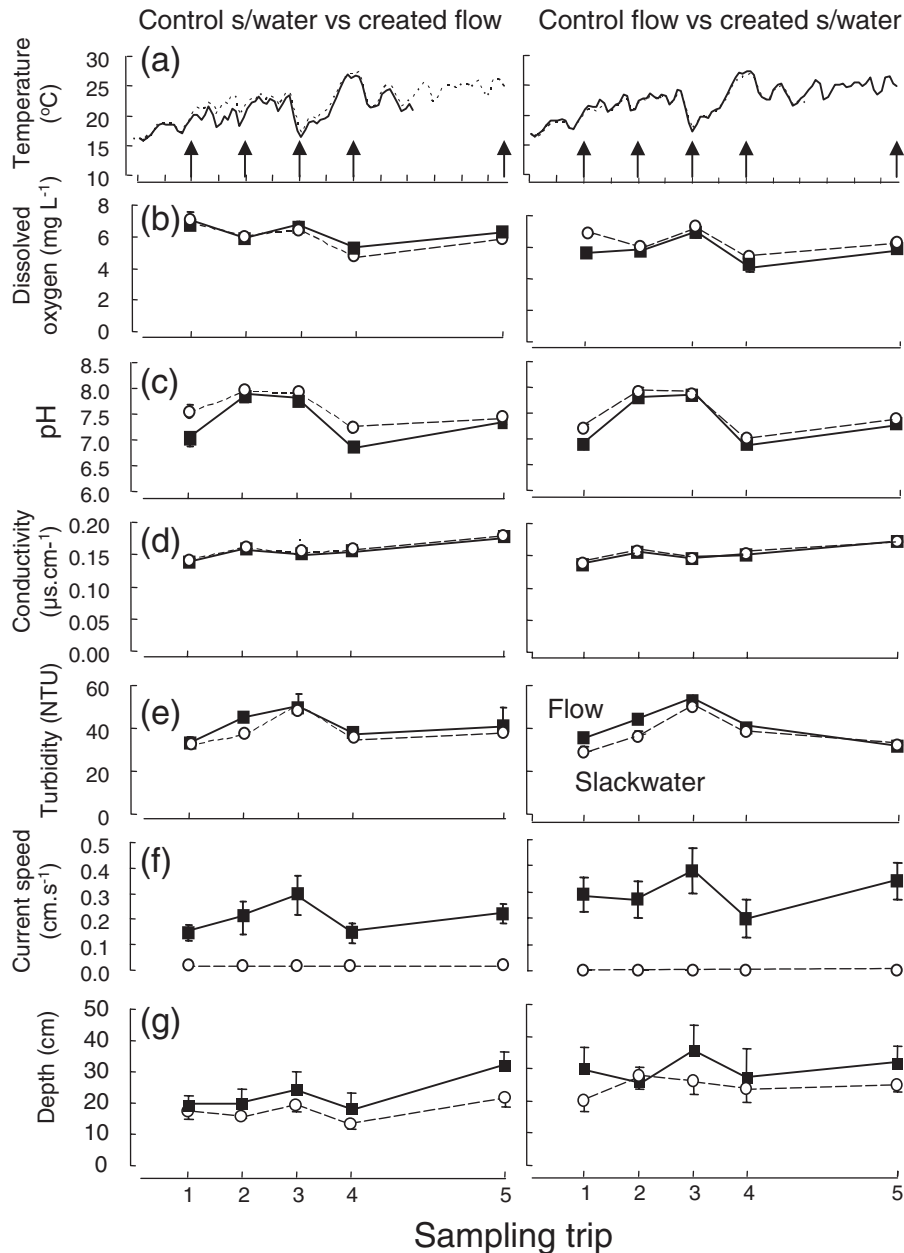


Figure 2. Mean (± 1 SE) (a) temperature, (b) dissolved oxygen, (c) pH, (d) conductivity, (e) turbidity (f) current speed and (g) depth for the five sampling trips, comparing control slackwaters (COSW) with created flow (CRFL) patches and control flow (COFL) patches with created slackwaters (CRSL). Slackwaters = dashed lines and open circles, flowing patches = solid lines and filled squares. Temperature was logged hourly and these data are presented here. Vertical arrows indicate the five biological sampling times

(total = 20: 17 larvae, 3 juvenile), carp gudgeons (*Hypseleotris* spp.: 10 juvenile/adults), gambusia (*Gambusia holbrooki*: 9 juvenile/adults) and Australian smelt (1 larva). A total of 84 fish were collected from slackwater patches (COSW = 44, CRSW = 40) but only 7 from flowing patches (COFL = 2, CRFL = 5).

Repeated-measures ANOVAs comparing COSW vs. CRFL patches indicated that there was a significantly greater mean abundance of total fish and common carp in the COSW patches than in the CRFL patches ($p < 0.05$; Table II, Figure 3). Repeated measures ANOVAs comparing COFL vs. CRSW patches showed that there was a significantly greater mean abundance of total fish and common carp in CRSW than in COFL patches

Table II. Mean squares and significance levels for repeated-measures ANOVAs investigating the effects of Habitat type and Time on biotic and abiotic variables, comparing created flow (CRFL) with control slackwaters (COSW) and created slackwaters (CRSW) with control flow (COFL).

Variable	Created Flow versus Control Slackwater				Created Slackwater vs Control Flow				
	Habitat	Error	Time	Time × Habitat	Habitat	Error	Time	Time × Habitat	Error
Total fish	0.907*	0.096	0.094	0.065	1.063**	0.079	0.043	0.045	0.039
Carp	0.556*	0.090	0.153**	0.113*	0.564***	0.016	0.117	0.117	0.480
Rainbowfish	0.096	0.061	0.004	0.026	0.086	0.033	0.014	0.016	0.023
Total shrimp	5.205*	0.481	2.568***	0.598**	3.274***	0.101	1.286***	0.499**	0.064
<i>P. australiensis</i>	1.970*	0.342	2.229***	0.277	1.908***	0.042	1.494***	0.630***	0.044
<i>C. maculochi</i>	5.853**	0.353	1.083***	0.792***	0.359*	0.053	0.085	0.052	0.042
<i>M. australiense</i>	0.249	0.124	0.124	0.251**	0.229*	0.028	0.050	0.110*	0.031
Zooplankton density	0.042	0.009	0.626***	0.095	0.012	0.023	0.842***	0.022	0.025
Zooplankton taxon rich	8.000*	1.190	2.230	3.250*	0.980	0.790	6.900***	0.180	0.965
Microb. density	0.062	0.256	0.026	0.143	0.013	0.113	0.083	0.156*	0.042
Microb. taxon rich	7.220*	1.160	0.950	1.770	62.720***	1.100	3.730**	0.870	0.775
Sed. dry weight	0.011	0.005	0.004***	0.000	0.045**	0.003	0.004***	0.001*	0.000
Sed. % organic	0.015*	0.002	0.001	0.001	0.016*	0.002	0.001	0.001	0.000
Sed. chl- <i>a</i>	0.043	0.019	0.107**	0.008	0.000	0.045	0.239**	0.074	0.039
Water chl- <i>a</i>	0.026*	0.005	0.202***	0.013	0.053	0.013	0.257***	0.001	0.003

Degrees of freedom for each analysis were: Habitat/Error—1, 8; Time/Time × Habitat/Error—4,4,32. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

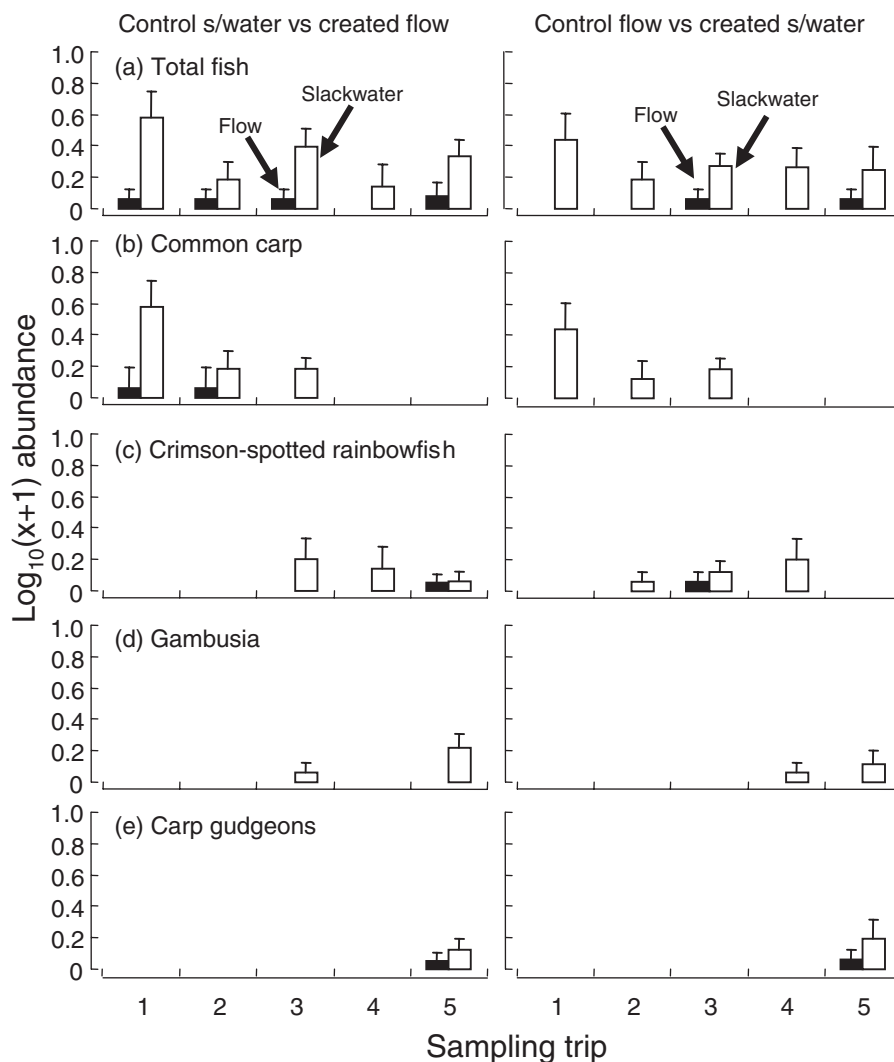


Figure 3. Mean abundance (+1 SE) of (a) total fish, (b) common carp, (c) crimson-spotted rainbowfish, (d) gambusia and (e) carp gudgeons for the five sampling trips, comparing COSW with CRFL patches and COFL patches with CRSL. Slackwaters = open columns, flowing patches = filled columns

($p < 0.01$ and $p < 0.001$, respectively). Carp abundance also differed significantly by Time and there was a significant Time \times Habitat interaction, but mean square values for these factors were between 1/4 and 1/5 that of Habitat. The mean abundance of crimson-spotted rainbowfish in slackwater habitats—both created and control—was close to, but not significantly different from, the associated flowing habitat patches (repeated-measures ANOVAs: CRFL vs. COSW, $p = 0.12$; CRSW vs. COFL $p = 0.059$; Table II). For each of the above groups, there were comparable abundances of fish in COSW as there were in CRSW patches, although this was not tested formally. Although analyses of the abundance of gambusia and carp gudgeons were not conducted because of the low numbers of fish collected, these two species were rarely collected from flowing habitat patches. The single Australian smelt (larva) was collected from a CRFL patch.

Shrimps

Three shrimp species were collected during this study: two atyids, *Caridina mccullochi* and *Paratya australiensis* and a palaemonid, *Macrobrachium australiense*. *Paratya australis* was the most common (817: 10 larvae, 807

juvenile/adults), then *C. mccullochi* (628: 74 larvae, 554 juvenile/adults) and lastly, *M. australiense* (86: 55 larvae, 31 juvenile/adults). A total of 1427 shrimp were collected from slackwater patches (COSW = 1085, CRSW = 342) and 104 shrimp were collected from flowing patches (COFL = 22, CRFL = 82).

Repeated-measures ANOVAs showed that there was a significantly greater mean abundance of total shrimp, *P. australiense* and *C. mccullochi* in slackwater habitats than flowing habitats in both types of manipulations (COSW vs. CRFL and CRSW vs. COFL) and significantly greater mean abundance of *M. australiense* in CRSW than in COFL (Table II, Figure 4). Results also indicated that there were significant increases in abundance of most of these variables with Time and that, typically, there were significant interactions between Time and Habitat. The abundance of *M. australiense* did not differ consistently between CRFL and COSW patches (Figure 4d). In only the case of *C. mccullochi* was there a clear example of greater abundance of shrimp in COSW patches than those which we created (CRSW).

Microfauna

The density of both zooplankton and microbenthos did not differ significantly with Habitat in either manipulation (Repeated-measures ANOVAs of COSW vs. CRFL and COFL vs. CRSW, Table II, Figure 5). In the case of zooplankton, density varied significantly with Time ($p < 0.001$). In the case of microbenthos comparing COFL with CRSW, density at the start of the experiment was greater in CRSW patches, but by the third sampling trip,

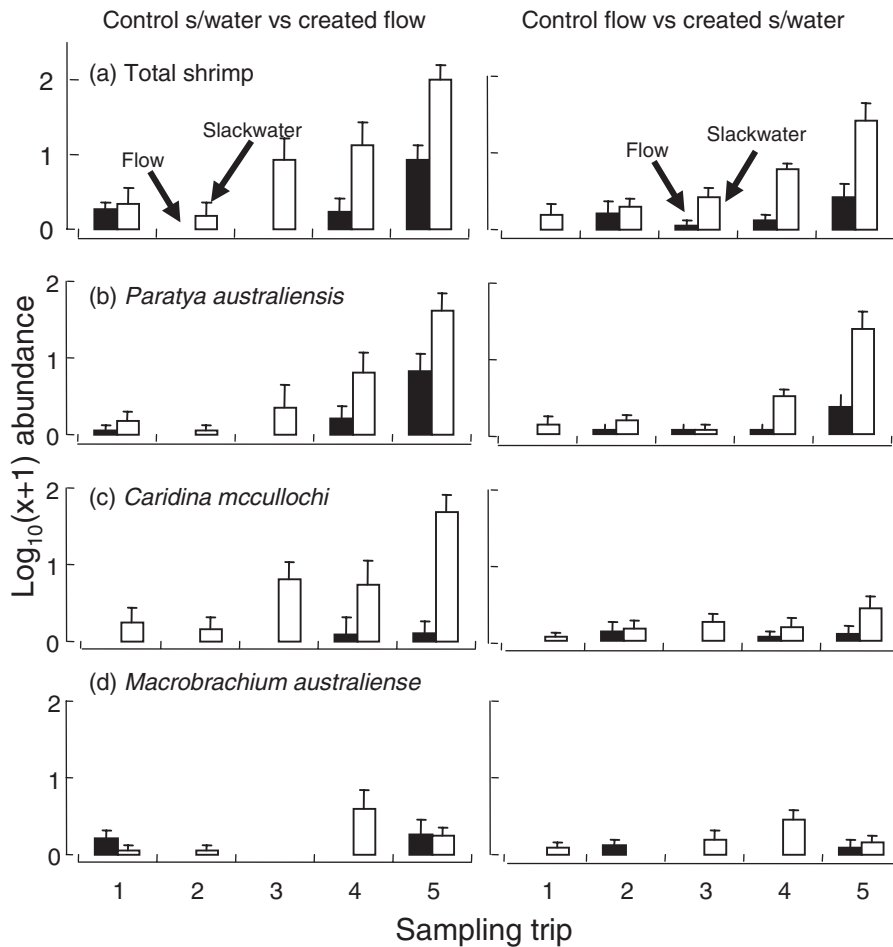


Figure 4. Mean abundance (+1 SE) of (a) total shrimp, (b) *Paratya australiense*, (c) *Caridina mccullochi* and (d) *Macrobrachium australiense* for the five sampling trips, comparing COSW with CRFL patches and COFL patches with CRSW. Slackwaters = open columns, flowing patches = filled columns

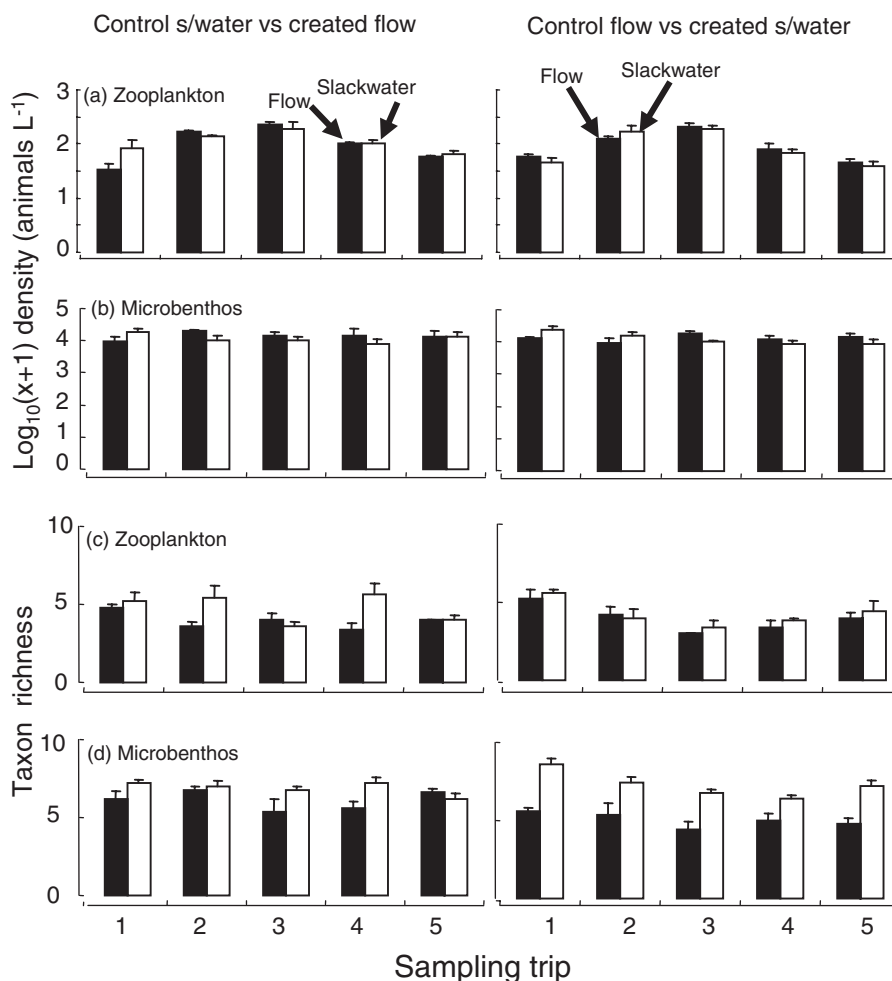


Figure 5. Mean (+1 SE) density of (a) zooplankton and (b) microbenthos and taxon richness of (c) zooplankton and (d) microbenthos for the five sampling trips, comparing COSW with CRFL patches and COFL patches with CRSL. Slackwaters = open columns, flowing patches = filled columns

density was greater in COFL patches (Time \times Habitat, $p < 0.05$). By contrast, zooplankton and microbenthos taxon richness differed significantly with Habitat for all comparisons, except for zooplankton CRSW with COFL; indeed, in each case, Habitat had by far the greatest mean square and there was a greater number of taxa overall in slackwater habitats than flowing habitats. This same trend was apparent also for zooplankton in the CRSW versus COFL experiment, but the difference was non-significant.

Analysis of community composition of zooplankton (Figure 6a) and microbenthos (Figure 6b) indicated that there was a separation of slackwater from flowing habitats, although this was more obvious and significant for the zooplankton (ANOSIM: CRSW vs. COFL, $R = 0.573$, $p < 0.01$; COSW vs. CRSW, $R = 0.099$, $p < 0.01$) than for the microbenthos (CRSW vs. COFL, $R = -0.021$, ns; COSW vs. CRSW, $R = 0.142$, $p < 0.01$). There was, however, no significant separation of created habitats from control habitats of the same flow type.

Water column chlorophyll-a, benthic chlorophyll-a, dry weight and percentage of organic matter

The only significant Habitat difference in chl-*a* concentrations was for water column chl-*a* between COSW and CRFL; the effect was only marginally and significantly in favour of COSW patches (Table II, Figure 7a,b; $p = 0.046$). Water column and sediment chl-*a* concentration did, however, change significantly with Time in both manipulations ($p < 0.01$ and $p < 0.001$).

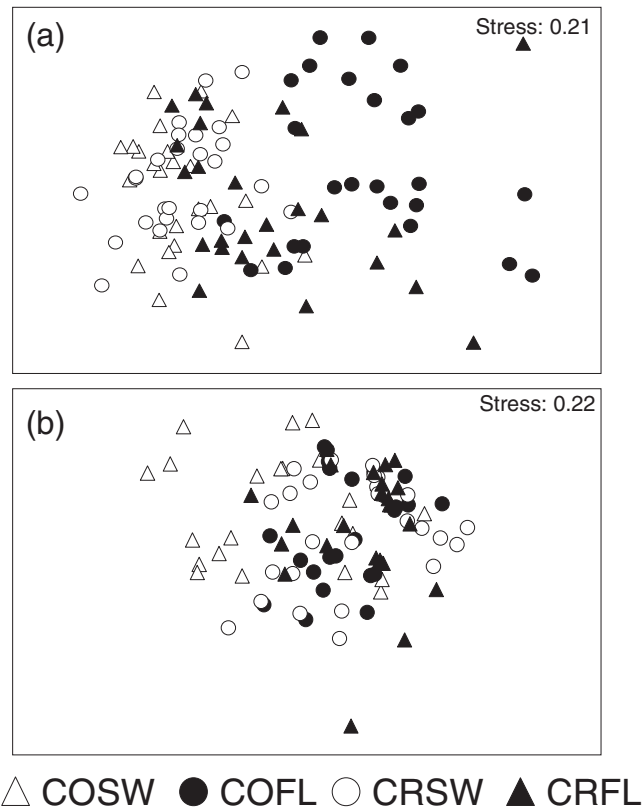


Figure 6. Multidimensional scaling plots of (a) zooplankton and (b) microbenthos for the five sampling trips, for COSW, COFL, CRSW and CRFL

Although the dry weight of sediment did not show consistent differences between slackwater and flowing habitats in either manipulation (COSW vs. CRFL and COFL vs. CRSW), this was not the case for percent organic matter (Table II, Figure 7c,d). Thus, there was a significantly greater percent organic content of the sediment in both COSW and CRSW patches than in their flowing counterparts.

DISCUSSION

Initial sampling indicated that fish larvae were present in natural slackwater patches, but not in natural flowing patches. We also collected significantly more fish larvae being flushed from slackwaters, as we diverted flow through them, than were in adjacent control habitats. There was no difference, however, for shrimp. These patterns in habitat use for fish larvae are consistent with the results obtained by King (2004b) in the Broken River, who found widespread use of natural slackwaters by the larvae and juveniles of most species of fish, irrespective of whether they were limnophilic or rheophilic as adults. The larvae of many riverine fish species elsewhere in the world similarly utilize slackwater and low-velocity patches (e.g. Poizat and Pont, 1996; Pusey *et al.*, 2002), although there are others—such as some salmonids and cyprinids—that are obligate rheophils throughout their life cycle and so do not use slackwater patches as commonly (see Matthews, 1998; Dieterman and Galat, 2004).

The results of our hydraulic manipulations indicated that an order of magnitude more fish and shrimp were collected from slackwaters—both created and natural—than from flowing patches. The only exception to this pattern of habitat use was a single Australian smelt, which was collected from a created flow patch. Of the six taxonomic groups analysed statistically, there were consistent and significantly greater abundances of four of them—total fish, common carp, *Paratya australiensis* and *Caridina mccullochi*—in natural and created slackwaters than in

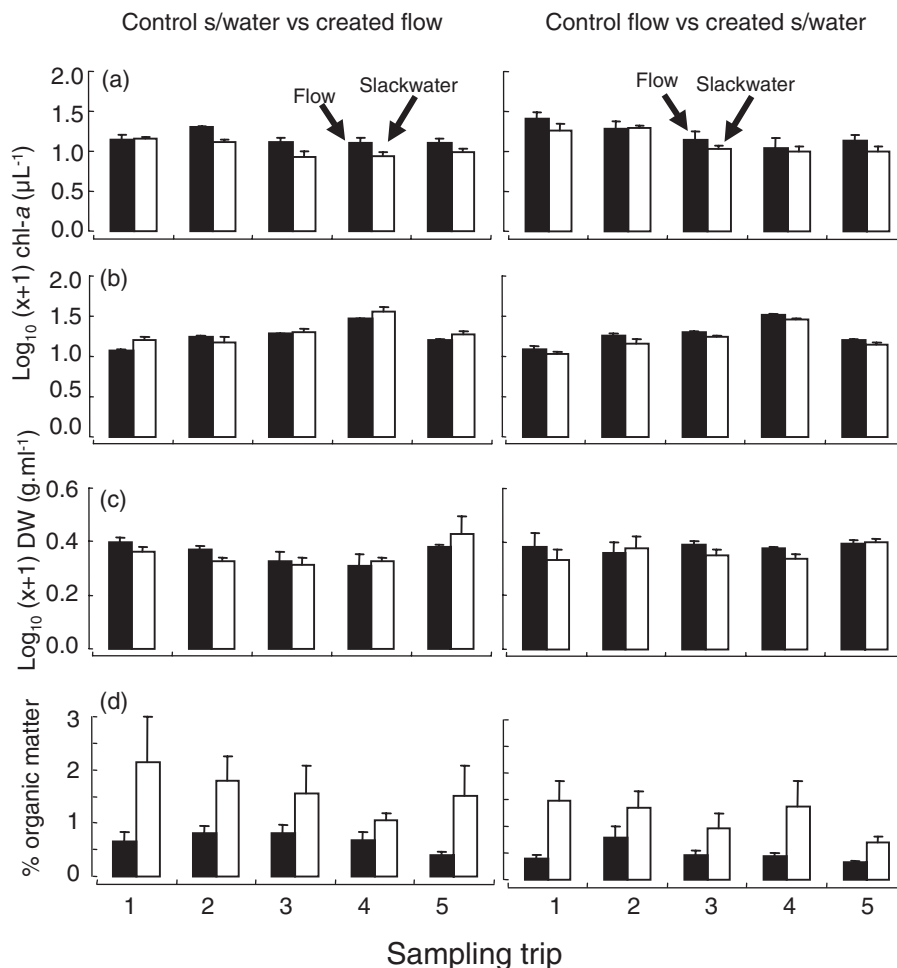


Figure 7. Mean (+1 SE) (a) sediment chlorophyll-*a*, (b) water column chlorophyll-*a*, (c) dry weight of sediment organic matter and (d) per cent sediment organic matter for the five sampling trips, comparing COSW with CRFL patches and COFL patches with CRSL. Slackwaters = open columns, flowing patches = filled columns

their flowing counterparts. The created slackwaters and those destroyed to create flowing patches, were, admittedly, relatively small: we were unable to manipulate slackwaters larger than about 20 m^2 in area. This does limit the generality of our results to some degree, since many slackwaters are considerably larger than 20 m^2 . However, ours and others' experience with sampling natural slackwaters has indicated that there are many slackwaters in this type of river of similar size or smaller to the ones we manipulated, and that the larvae and juveniles of several large species and all life stages of smaller species will often utilize slackwaters much smaller than this (Humphries *et al.*, 2002; King, 2004b; Price, unpublished data). Nevertheless, recent work has indicated that the abundance of fish larvae increases with slackwater area (Price, unpublished data) and there are undoubtedly effects, such as those relating to area versus perimeter of slackwater, which we were unable to come to grips with during our study. Manipulation of slackwaters of different sizes, orientations and shapes in future experiments could be very informative.

Our fish samples were dominated by the alien common carp and the native crimson-spotted rainbowfish, although in total we recorded five species. Larvae made up 76% of the two main species and juveniles the remainder. The species which were collected in the present study also predominated in the samples of King (2004b) and Humphries *et al.* (2002) in the same river. The main exceptions were Australian smelt and Murray cod. Of the former species, in the present study we caught only one, whereas it contributed approximately 50% and 20% to

the larval fish fauna collected by Humphries *et al.* (2002) and King (2004b) respectively. However, our collections were at a time of the year after the peak abundance of the larvae of this species would normally have passed, and its adults tend to occupy mid-channel habitats, which were not included in our study. As regards Murray cod, its larvae are considered obligate drifters, and all life stages are found rarely in slackwater habitats (Humphries *et al.*, 2002; King, 2004b; Humphries, 2005; Koehn and Harrington, 2005).

Of the two species of fish which made up the bulk of our samples, common carp is widely regarded as a habitat generalist (Koehn, 2004), although larvae and juveniles tend to occur most commonly in slackwater habitats—as we also found—whereas adults occupy main channel habitats (King, 2004b). Larvae and juveniles of crimson-spotted rainbowfish are commonly recorded from slackwater habitats (King, 2004b), whereas adults tend to be more generalist in their habitat associations (Lukies, 2004; Price, unpublished data). Like its congener Duboulay's rainbowfish (*Melanotaenia duboulayi*), crimson-spotted rainbowfish adults tend to form shoals and be associated with macrophyte beds in areas of relatively low water velocity (Pusey *et al.*, 2004). In the Broken River, adults are most commonly caught in the main river channel associated with stands of common rush, *Phragmites australis*, (Lukies, 2004), which baffle the current to a large extent.

All three species of shrimp commonly collected from the Broken River (Richardson *et al.*, 2004) were collected in our samples. In virtually all cases, there were significant increases in abundance of shrimp when slackwater patches were created from normally flowing patches and decreases in abundance when flowing patches were created from regions of slackwater. The exception to this pattern was for *Macrobrachium australiense*, which showed no difference between CRFL and COSW patches. A recent study in the Broken River and the nearby Campaspe River indicated that shrimps were abundant in slackwater patches, particularly during early stages of their life cycles (Richardson *et al.*, 2004). Follow-up investigations found that *C. mccullochi* was strongly associated with zero-velocity habitats at all stages of development, and whilst *M. australiense* larvae occurred in slackwaters only, adult *M. australiense* were associated with flowing channel habitats (Richardson, unpublished data). Although *Paratya australiensis* may be more abundant in slackwater areas, they appear to be less reliant than the other two species on this particular habitat type (Richardson *et al.*, 2004).

Slackwaters have been hypothesized as providing refuge for the young stages of fishes and shrimps from current and/or predation and as sites where food is abundant (Humphries *et al.*, 1999; Aoyagui and Bonecker, 2004; King, 2004a,b; Richardson *et al.*, 2004). Although these hypotheses are largely untested, King (2004a) has also shown in the Broken River that the density of benthic microfauna, seemingly an important food source for larval fish, was not different between flowing and still habitats. Similarly, the results from our manipulations indicated that the density of benthic microfauna and zooplankton did not differ consistently between flowing and slackwater patches. Therefore, the greater abundance of fish and shrimp in created slackwater patches and lower abundance in created flow patches cannot be explained by the density of potential prey. There was, however, a significant difference in the community composition of microfauna between slackwater and flowing patches, and slackwater patches had a greater amount of benthic organic matter, which is a potential food resource for shrimp (Burns and Walker, 2000).

Because we only measured standing crop of potential, and not production or ultimate, trophic sources, it is important to consider these factors for comparisons of slackwater and flowing patches. Several recent studies and reviews have either implicitly or explicitly proposed that slackwater (or high retention) patches are important sites for production in rivers. Thorp and DeLong (1994, 2002) emphasized the significance of the main channel of rivers as a site of production in their riverine productivity model, and Bunn *et al.* (2003) coined the term 'bathtub ring' to describe their observations of the conspicuous band of algae (which is the primary driver of food webs during low flows) along the edge of Australian dryland rivers. Humphries *et al.* (1999) proposed the 'low flow recruitment hypothesis' which suggested that low-flow conditions in main channel slackwater habitats and benthic microfauna could hold the key to within-channel fish recruitment. Additionally, regions of high flow retention have been identified as having important, perhaps primary, roles in food webs (see Schiemer *et al.*'s (2001); 'inshore retentivity concept'). We were able to detect only a slight—but significant—lower concentration of water column chl-*a* in CRFL patches relative to COSW. Whilst this result is perhaps indicative of the influence of prolonged water retention in slackwaters on phytoplankton, we have not in our study established a link between standing crop and primary production or the overall food web. Research in these areas is clearly needed.

Although trophic resources in our flowing versus slackwater patches remains somewhat problematic, the other component relating to our manipulations is the physical effects of altering the hydraulic conditions for fish and

shrimp. Slackwaters and low-velocity patches provide areas in rivers that may act as refuges from current, especially for the early life stages of fish and for shrimp (Humphries *et al.*, 1999; Keckeis and Schiemer, 2002; King, 2004a, b; Richardson *et al.*, 2004). This is more likely to explain the response of larvae—which are typically poor swimmers—than it is of juveniles and adults. Energetically, there is evidence for fish larvae that is advantageous to be associated with still or low-velocity patches (see Flore and Keckeis, 1998; Matthews, 1998; Flore *et al.*, 2001). Larval shrimp may be similarly advantaged by slackwater habitat patches (Richardson *et al.*, 2004). An ability to maintain position or move against slow water currents does not develop in *P. australiensis* or *M. australiense* until the juvenile stage (Lee and Fielder 1984; Hancock and Bunn 1999), and probably later, if at all, in *C. mccullochi* (Richardson, unpublished data).

Concluding remarks

Hydrology largely drives the dynamic nature and extent of habitat patches in river systems (Hill *et al.*, 1991). River regulation has altered the natural hydrology in many of the world's rivers and consequently has altered both the temporal and spatial nature of riverine habitat patches. Many aquatic species have life history strategies which are synchronized with the long-term flow patterns (Lytle and Poff, 2004); strategies that may have evolved to take advantage of the seasonal availability of habitat patches and which may involve ontogenetic shifts in habitat use (King, 2004b). Alterations to the natural flow regime may alter the size, depth, complexity and spatial arrangement, and spatial and temporal availability of slackwater patches (Bowen *et al.*, 2003). In this study we have shown that increasing velocity through slackwaters, which is one of the ways in which increasing flows for irrigation purposes may affect slackwater habitats, has a significant impact on the use of these patches by fish and shrimp.

Our results for fish were dominated by two species of fish only, and a large proportion comprised common carp: an alien species. It is unfortunate, but a reality, that most Australian lowland rivers are now dominated by alien species. All species of shrimp, by contrast, were native. Notwithstanding the origins of the species collected, our results clearly showed that by manipulating the hydraulic conditions, through either stopping flow or increasing it, the abundance of fish and shrimp were affected relative to controls. This study is unusual in that it attempted to manipulate hydraulic conditions *in situ*. We hope that, as a preliminary step, it inspires others to improve our design and conduct bigger and better manipulations in the future. There is no doubt that further research into the ecological role of slackwater patches in lowland rivers is badly needed. We consider that, despite our poor understanding of their ecological role in lowland rivers, low-velocity and slackwater patches must be taken into consideration during management.

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