

## Dams and flow in the Cotter River, Australia: effects on instream trophic structure and benthic metabolism

Heath Chester\* & Richard Norris

*Cooperative Research Centre for Freshwater Ecology, University of Canberra, Canberra, ACT 2601, Australia*

(\*Author for correspondence: E-mail: richard.norris@canberra.edu.au)

Received 13 May 2005; in revised form 27 March 2006; accepted 1 April 2006; published online 3 July 2006

*Key words:* metabolism, periphyton, macroinvertebrates, diet, environmental flows, stable isotopes

### Abstract

This study assessed benthic macroinvertebrates and periphyton and its responses to managed river-flows, in riffles downstream of three dams on the Cotter River, Australian Capital Territory. Benthic macroinvertebrates and periphyton were also assessed in adjacent tributaries of the river, as well as in a nearby unregulated river and its tributaries. Food sources of four macroinvertebrate taxa (Leptophlebiidae, Elmidae, Glossosomatidae and Orthocladiinae) were determined by stable isotope analysis of the invertebrates and their potential food, in conjunction with examination of the gut contents of individual invertebrates. Components of benthic periphyton were the main food source for the selected taxa. Orthocladiinae consumed primarily amorphous detritus, while Elmidae, Glossosomatidae and Leptophlebiidae consumed diatoms. Enclosed benthic chambers were used to measure the response of benthic metabolism to monthly flow spikes released from one of the dams. The balance of benthic metabolism as measured by the Production/Respiration ratio (P/R) showed a shift towards production after the release of flow spikes. At sites downstream of the dams, there was more periphyton chlorophyll-a in the form of filamentous green algae than at sites in the unregulated river and the tributaries, and macroinvertebrate taxa using periphyton as a food resource were missing or reduced in abundance relative to sites without dams. However, the site downstream of the dam with environmental flow releases had more macroinvertebrate taxa and less periphyton chlorophyll-a content than sites downstream of dams without managed environmental flows, suggesting that a more suitable food supply resulting from environmental flow releases shifted macroinvertebrate communities towards those of unregulated streams.

### Introduction

Most benthic communities downstream of dams are altered in ways that are considered detrimental when compared with similar unregulated streams (Ward & Stanford, 1979; Walker, 1985). In these communities, many macroinvertebrate taxa are either absent or only present in reduced abundance. Yet these taxa are often predicted with high probabilities to be present in the absence of river regulation (Marchant & Hehir, 2002). Dams alter the downstream benthic algal community also,

through altered thermal regimes (DeNicola, 1996), changed flow patterns (Reiter, 1986; Biggs, 1996) and changes to the disturbance regime (Mosisch & Bunn, 1997). This changed structure of the algal community is likely to have a flow-on effect to the communities of consumer organisms because, as is being increasingly recognised, benthic algae are an important food resource in upland forest streams (Mulholland et al., 2000; Rainer et al., 2001; Salas & Dudgeon, 2001; Woodward & Hildrew, 2002). For an overall perspective, it is probable that stream metabolism can provide an integrative

measure of stream ecosystem functioning (Bunn et al., 1999; Udy et al., 2001); it may also indicate the biological response of a stream to a specific flow-based event (Osborne, 1983). As such it may provide a method for observing a direct biological response to manipulations of flows from dams.

The alteration of many rivers by regulation undermines the ecological condition of the water resources upon which humans depend. As such there is increasing recognition of the need to preserve them, and environmental flows have been recommended as one way of achieving this (Walker, 1985; Reiser et al., 1989; Cullen & Lake, 1995). However, such is the demand for water that there is pressure on water managers to allocate only the minimum amount of water to environmental needs. While many aspects of the effects of river regulation and water abstraction on the ecology of flowing waters throughout the world have been investigated and documented (Petts, 1980; 1984; Walker, 1985; Maddock, 1999) the potential benefits of environmental flows are not fully known. It is essential to determine the causes of the declining state of dammed rivers, and subsequently to monitor the effects of any remedial flow releases, if management strategies are to be successful.

This study aimed to investigate the effects of the dams and their operation on the ecology of stream periphyton and benthic macroinvertebrates in the Cotter River compared with the nearby similar but unregulated Goodradigbee River and its tributaries (Fig. 1). It was intended to determine whether dams had a direct effect on macroinvertebrate composition and abundance and if indirect effects on stream metabolism and food resources were important. If the latter were found to be important, it may be that the environmental flows could be better managed to maximise their ecological benefits.

## Methods

### *Study area*

This study was conducted in the regulated Cotter River and the unregulated Goodradigbee River, both of which are located in the Brindabella mountain range along the western side of the

Australian Capital Territory (ACT; Fig. 1). These permeable catchments are mostly forested with stable soils and a long-term average rainfall of 934 mm, with the most consistent rainfall occurring in August to October. The Cotter River supplies water for Australia's national capital, Canberra. Its catchment is largely protected from human activities, is undisturbed, and most of its features and much of the river are in a near natural state, except for a small area of plantation forestry. However, there are three dams on the Cotter River and Canberra's water is piped from the middle dam, Bendora, with environmental flow releases also made from this dam. Even with considered management of the environmental flow releases, the macroinvertebrate benthic communities downstream of Bendora Dam have been altered (Marchant & Hehir, 2002).

The daily release of environmental water from Bendora Dam (Fig. 1) during the study period was 75% of the daily 80th flow percentile (calculated from the average for the month) with variations applied by operational issues such as maintenance of dam equipment. At the end of each month a "spike" release was made for 2 days so that the total released for the month was equivalent to each month's 80th percentile flow calculated from long-term pre-dam flow records. Bendora Dam is currently the only dam that makes variable releases; Corin Dam releases large amounts of water at a relatively constant rate to keep the Bendora storage at the optimum level for supplying water to Canberra, and the Cotter Dam is a small surface-release reservoir which is left as an emergency supply.

### *Sampling*

Macroinvertebrates, periphyton and detritus were sampled from a riffle downstream of each dam along the Cotter River and from the nearest downstream tributary. Corresponding sites were chosen in the Goodradigbee River and its tributaries (Fig. 1) based on obtaining the best match of physical habitat variables (Parsons & Norris, 1996) and on previous research showing that these sites were physically similar to the Cotter River (Sloane et al., 1998; 1999). Sampling was conducted during October to November 2001.

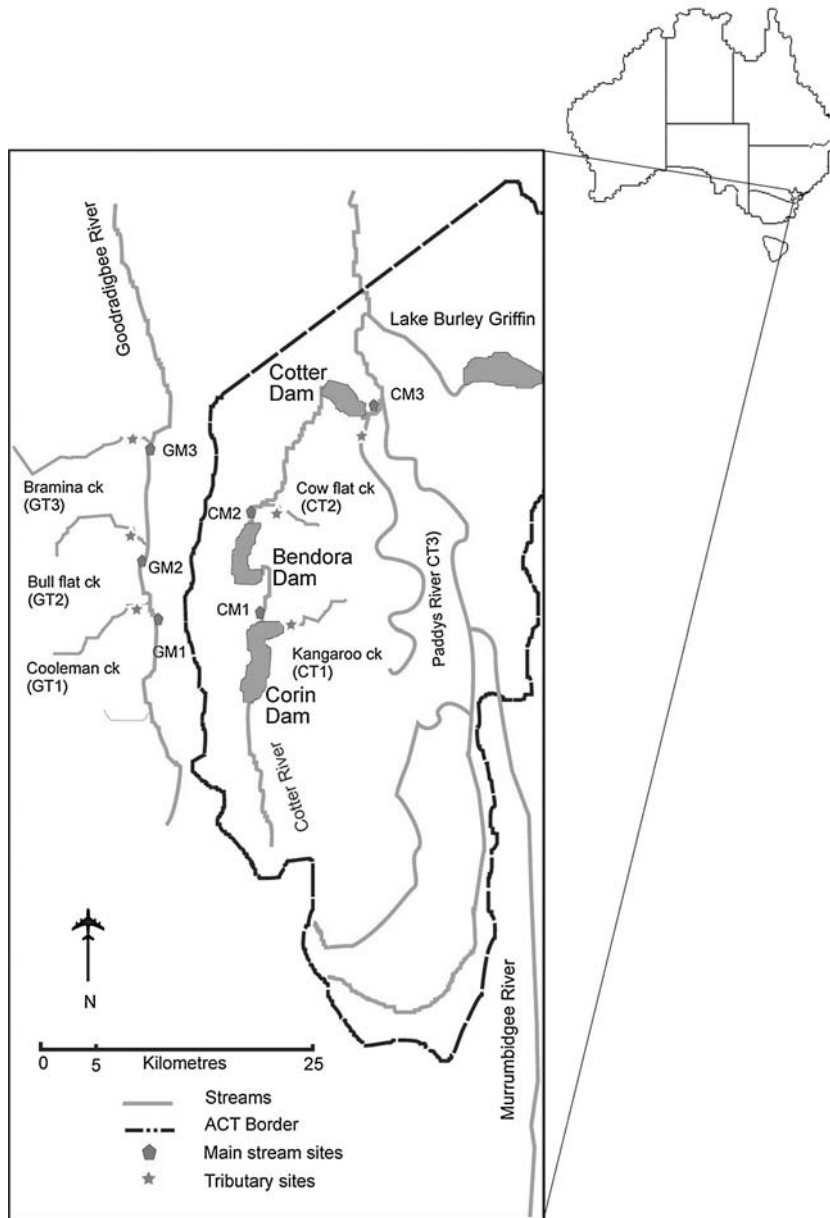


Figure 1. Study area and sampling sites in the Cotter and Goodradigbee Rivers, Australian Capital Territory.

Macroinvertebrates, water quality and physical habitat variables were sampled according to protocols used in the AUSRIVAS (Australian River Assessment System) sampling and processing manual for ACT (Coysh et al., 2000) from the riffle habitat. Benthic macroinvertebrates were sampled from 10 m of riffle with a framed net 350 mm across the bottom with a mesh size of 250  $\mu\text{m}$  and samples were preserved in ethanol. In

the laboratory, preserved samples were placed in a sub-sampling box comprising 100 cells (Marchant, 1989) and agitated until evenly distributed. Contents of each randomly selected cell were removed until approximately 200 animals from each sample were identified. Macroinvertebrates were identified to family except Chironomidae, which were identified to sub-family, and worms (Oligochaeta) and mites (Acarina), which were identified to class and

order, respectively. The use of the ACT AUSRIVAS protocol enabled estimation of abundances, unlike livepick versions of the AUSRIVAS sampling protocols used in other states of Australia that provide only presence/absence data.

From each site after initial identification and analyses at family taxonomic level, four taxa were selected, three of which were identified to species and a fourth, Orthoclaadiinae, to sub-family. This selection was based on previous research indicating that these taxa were affected by regulation in the Cotter River (Sloane et al., 1998; 1999; Marchant & Hehir, 2002) and constituted a significant component of the diet of native fish (Lintermans, 1998; Cadwallader & Eden, 1979). Five individuals of each of the selected taxa at each site were dried for approximately a minute; then the thorax was opened and the gut contents expelled into a drop of water on a glass slide, covered with a cover slip and scanned at magnifications ranging from 100× to 1000×. Food items were classified into categories: blue-green coccoid, diatom, green filament, and detritus. Each category was given a percent ranking assessed subjectively according to the area of slide covered for the digestive tract of each animal (Chessman, 1986; Ledger & Hildrew, 1998).

Animals that had their gut contents removed were grouped with individuals of the same taxon and catchment except for Orthoclaadiinae, which were all pooled. This ensured enough material for stable isotope analysis (SIA) and still gave signatures representative of the populations (Lancaster & Waldron, 2001). Samples were dried for 24 h at 40 °C, then ground to a fine powder and analysed for stable isotopes of carbon and nitrogen. Samples were oxidised at high temperature and the resultant CO<sub>2</sub> and N were analysed with a continuous-flow ratio mass spectrometer (Udy et al., 2001; McCutchan & Lewis, 2002). Ratios of <sup>13</sup>C/<sup>12</sup>C and <sup>14</sup>N/<sup>15</sup>N were expressed in δ notation as the relative per mil (‰) difference between the sample and conventional standard (sucrose for carbon and ammonium sulphate for nitrogen), i.e.

$$\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000,$$

where  $R = {}^{13}\text{C}/{}^{12}\text{C}$ .

Detritus, such as leaves and twigs, was collected from a riffle at each site, placed in plastic bags and kept on ice for return to the laboratory where the

bags were immediately frozen for later processing. In the laboratory, samples were thawed, gently scrubbed and rinsed in distilled and de-ionised water to remove any attached algal/bacterial material. They were then dried at 60 °C for 24 h and ground into a powder using a ring mill. SIA was performed on the samples as for the invertebrate samples above.

Periphyton was sampled from a 1-m-wide transect laid across a riffle at each site. The periphyton was removed from the upper surface of the streambed in situ using a syringe sampler similar to that described by Loeb (1981). The sampler scrubbed an area of 637 mm<sup>2</sup>, collecting adnate and loose forms of periphyton as well as organic/inorganic detritus in the periphyton matrix. Eighteen samples were collected from each transect and randomly divided into three groups of six, then 5-ml aliquots were taken from each replicate sample of one group and combined into a glass vial filled with ethanol for later identification. Biomass and chlorophyll-a samples were filtered onto individual glass fibre filters and frozen, and samples for SIA were frozen. Biomass samples were dried at 45 °C for 24 h, weighed and then placed into a 500 °C furnace for 1 h then weighed again. The difference of the two weights represents ash free dry mass (AFDM) and was scaled to gm<sup>-2</sup>. Chlorophyll pigments were extracted from the filters in 90% ethanol and measured in a spectrophotometer (Franson, 1985).

Periphyton stable isotope samples were defrosted and decanted into 50-ml centrifuge tubes, then centrifuged at 2500 rpm for 10 min. The top layer of water was removed and the remaining solutions were combined and spun for another 10 min. This was repeated until a 20 ml concentrated solution representing the six replicates from a site was obtained. This sample was dried at 60 °C for 24 h and subjected to SIA as above for the invertebrate samples.

Samples of periphyton preserved in vials were agitated vigorously and a 20 μl portion was drawn from each, placed on a glass slide, covered with a glass slip and sealed with acrylic varnish. A minimum of two replicates per site were analysed. Material in each sample was scanned at magnifications ranging from 100× to 1000× and classified into five categories: filamentous green, diatom, detritus, blue-green filament and coccoid. The

proportion of each category as a percentage was subjectively estimated (Ledger & Hildrew, 1998).

Benthic metabolism was measured using pairs of enclosed chambers (Bunn et al., 1999; Udy et al., 2001) placed at three sites along the reach between Bendora Dam and Cotter Dam (Fig. 1). Measurement of metabolism for 24 h was timed to finish within 1–3 h of the beginning of an environmental flow release from Bendora Dam and then measured again for 24 h within 24 h of the flow returning to pre-release levels. Measurements of Gross Primary Production (GPP), Respiration (R24) and the Production to Respiration ratio (P/R) were made during 2002 for the releases in February, March, and May.

#### Data analyses

Similarity in macroinvertebrate composition among sites, based on family-level relative abundance data fourth root transformed (applied to reduce the high range and skewed distributions of relative abundance; Clarke and Warwick, 2001), were determined using cluster analyses in the PC-ORD multivariate analysis package, version 4.20 (McCune & Mefford, 1999). The Bray–Curtis distance measure was used, because it is a robust measure of association for cluster analysis (Faith et al., 1987) with the agglomerative clustering technique, flexible Unweighted Pair-Group Arithmetic Averaging (UPGMA), to form site groupings. A beta value of  $-0.1$  was used, as recommended for flexible UPGMA classifications (Belbin & McDonald, 1993). Site groupings were displayed in two-dimensional plots following non-metric multidimensional scaling (NMDS) ordination (McCune & Mefford, 1999). Differences in periphyton chlorophyll-a content and AFDM between sites were determined using ANOVA, and where a significant effect was revealed the sites that were different were identified using Tukey–Kramer multiple comparison tests. Differences in benthic metabolism along the reach between Bendora and Cotter dams before and after the release of an environmental flow was compared using paired *t*-tests.

#### Results

All spot water quality measurements recorded as per AUSRIVAS ACT protocols were within the

Australian guidelines for maintaining ecosystem health (ANZECC & ARMCANZ, 2000). There were no significant variations among sites to indicate a water quality issue.

Fifty-one taxa of macroinvertebrates were identified and the taxonomic composition was typical of upland montane regions, with the insect taxa Ephemeroptera, Trichoptera, Plecoptera, Coleoptera and Diptera dominating abundance and richness. Elmidae were abundant at almost all sites except those downstream of dams, while Orthoclaadiinae were more abundant at sites downstream of dams [www.macrotable1.cjb.net]. Oligochaeta occurred at all sites but were notably more abundant downstream of the Cotter Dam (CM3). The only taxon absent from sites downstream of the dams but present at all other sites was the caddisfly Glossosomatidae. Elmidae, Baetidae and Coloburiscidae, occurred at most of the reference or tributary sites and were either absent downstream of dams or present only in small numbers. Crustaceans Calanoida and Cladocera were recorded from two of the sites downstream of the dams Bendora (CM2) and Corin (CM1). Two of the sites downstream of dams, CM1 and CM3 had the lowest taxonomic richness [www.macrotable1.cjb.net]. The sites downstream of dams in the Cotter River had a different macroinvertebrate composition from all other sites (Fig. 2). The site downstream of the largest dam (CM1) was also different from the other two smaller dam sites (CM2 and CM3). Site CM1 had a lower overall abundance than the other sites, and also contained two taxa (Gastropoda: Physidae and Trichoptera: Tasimiidae) that were collected only from this site. The Cotter River tributary sites (CT1, CT2 and CT3) were more similar to the Goodradigbee River sites than they were to the sites downstream of dams (Fig. 2).

Orthoclaadiinae species which were in greater relative abundance downstream of the dams had gut contents comprising ultrafine detritus (Fig. 3) while the other taxa, thought to be negatively affected by dams, that were examined Leptophlebiidae *Austrophlebioides pusillus*, Elmidae *Austrolimnius* sp. *L65E* and Glossosomatidae *Agapetus* sp. *AV1* consumed mainly diatoms and ultrafine detritus (Fig. 3).

Chlorophyll-a ranged from 1.3 to 28.7 mg m<sup>-2</sup> and was significantly higher at the sites

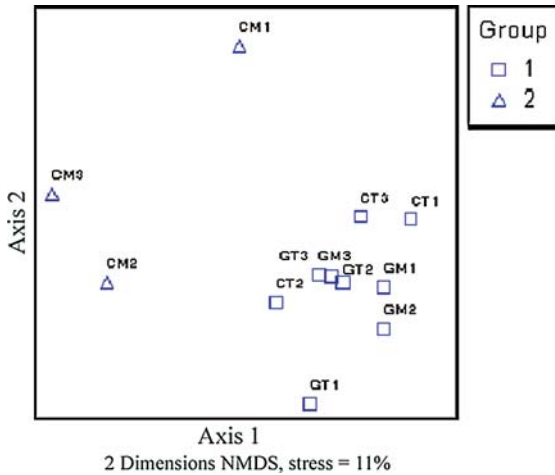


Figure 2. Grouping of sites in the Cotter River (CM1, CM2, CM3), tributaries of the Cotter River (CT1, CT2, CT3), the Goodradigbee River reference sites (GM1, GM2, GM3) and tributaries of the Goodradigbee River (GT1, GT2, GT3) based on invertebrate composition. Groups determined by UPGMA classification and plotted using the first two dimensions of an NMDS ordination.

downstream of dams compared to tributary and reference sites (Tukey–Kramer HSD,  $p < 0.005$ ,  $n = 18$ ) (Table 1). However, there were no significant differences among sites in the amount of AFDM (Table 1). Periphyton at sites downstream of the dams contained relatively higher

proportions of green filamentous material, typically Chlorophytes including *Stigeoclonium*, *Draparnaldia*, *Audouinella* and *Spirogyra* (Fig. 4). Structurally the matrix of periphyton downstream of dams was of large chlorophyte filaments covered with clusters of stalked diatoms interspersed with varying amounts of detritus. All the other sites comprised predominantly detritus and diatoms and occasional clumps of cyanobacteria (bluegreen filament) (Fig. 4). The structure of these clumps consisted of detritus densely surrounded and infiltrated by stalked and free-form diatoms.

Carbon and nitrogen stable isotope signatures for the four macroinvertebrate taxa were similar to each other regardless of their collection site. Values for detritus were consistent across both catchments while periphyton showed most variation among sites (Fig. 5). There was a clear separation between the isotope signatures of detritus and periphyton for both  $\delta^{13}\text{C}$  ( $F_{1,18} = 82$ ,  $P < 0.001$ ) and  $\delta^{15}\text{N}$  ( $F_{1,18} = 64$ ,  $P < 0.001$ ) (Fig. 5). The shift in SIA signatures from the diet to the consumer are around  $+0.5\text{‰}$  for  $\delta^{13}\text{C}$  and  $+2\text{--}4\text{‰}$  for  $\delta^{15}\text{N}$  (Vander Zander & Rasmussen, 1999; McCutchan & Lewis, 2002). The taxa had signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  that were too far away from the detritus to have assimilated material directly from detritus (Fig. 5). The more likely

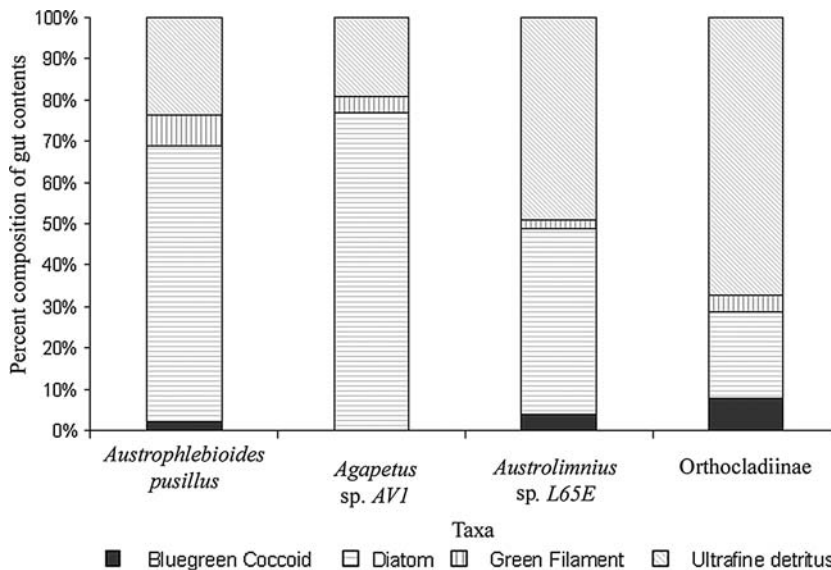


Figure 3. Composition of gut contents for Leptophlebiidae *Austrophlebioides pusillus*, Glossosomatidae *Agapetus sp. AV1*, Elmidae *Austrolimnius sp. L65E* and Chironomidae *Orthoclaadiinae*.

Table 1. Chlorophyll-a content and ash free dry mass of periphyton for sites downstream of the dams along the Cotter River (CM1, CM2, CM3), tributaries of the Cotter River (CT1, CT2, CT3), the Goodradigbee River reference sites (GM1, GM2, GM3) and tributaries of the Goodradigbee River (GT1, GT2, GT3)

	Site code											
	CM1	CM2	CM3	CT1	CT2	CT3	GM1	GM2	GM3	GT1	GT2	GT3
Chlorophyll-a, mg m <sup>-2</sup>	16.77	28.69	18.95	4.49	5.03	6.55	1.69	1.69	3.42	3.04	1.72	1.27
Standard error	6.97	9.23	6.50	1.64	3.02	2.58	0.46	0.41	1.00	1.33	0.40	0.43
AFDM, g m <sup>-2</sup>	18.08	16.64	10.55	10.01	7.79	4.57	6.92	18.16	14.68	10.61	1.38	9.43
Standard error	5.20	5.81	2.41	4.25	2.57	0.39	1.22	7.75	11.40	6.40	0.61	5.50

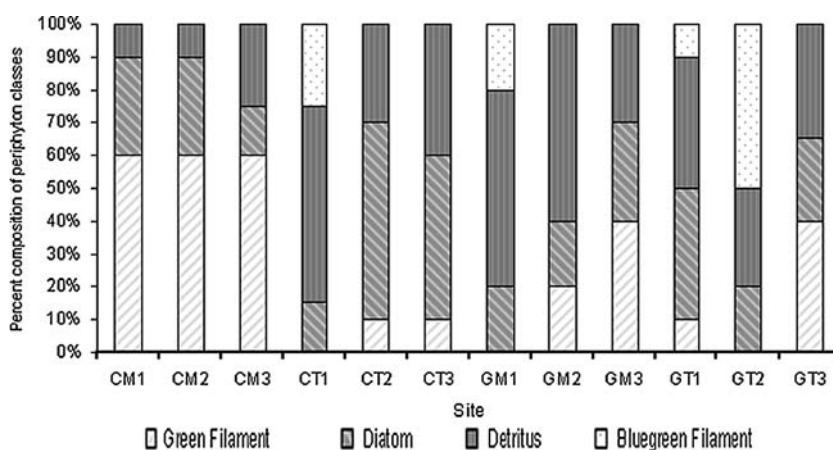


Figure 4. Percentage composition of periphyton for sites downstream of the dams along the Cotter River (CM1, CM2, CM3), tributaries of the Cotter River (CT1, CT2, CT3), the Goodradigbee River reference sites (GM1, GM2, GM3) and tributaries of the Goodradigbee River (GT1, GT2, GT3).

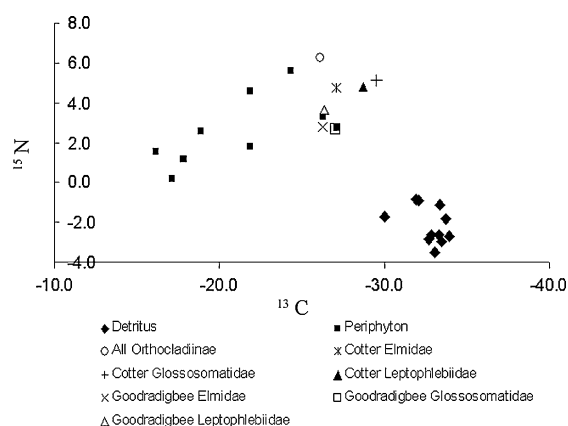


Figure 5.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for detritus, periphyton and macroinvertebrate samples for all sites sampled in the Cotter River and Goodradigbee River catchments October–November 2001.

source of carbon and nitrogen was periphyton, with some fraction of carbon coming from detrital material in the periphyton.

The range of net daily metabolism (GPP minus R24) amongst individual replicates was 227 to  $-106 \text{ mg C m}^{-2} \text{ day}^{-1}$ . After each flow release there were significant increases in the level of gross primary production (GPP) (one-tailed paired  $T = 2.75$ ,  $p < 0.008$ ,  $n = 6$ ) but no significant change in the amount of respiration (R24). There was variation in response of levels of GPP and R24 to each flow release (Fig. 6). However, the net effect for the reach was that the P/R ratio was elevated significantly (one-tailed paired  $T = 4.15$ ,  $p < 0.001$ ,  $n = 6$ ) after each flow release (Fig. 6). Metabolism in the reach shifted from being slightly heterotrophic to autotrophic.

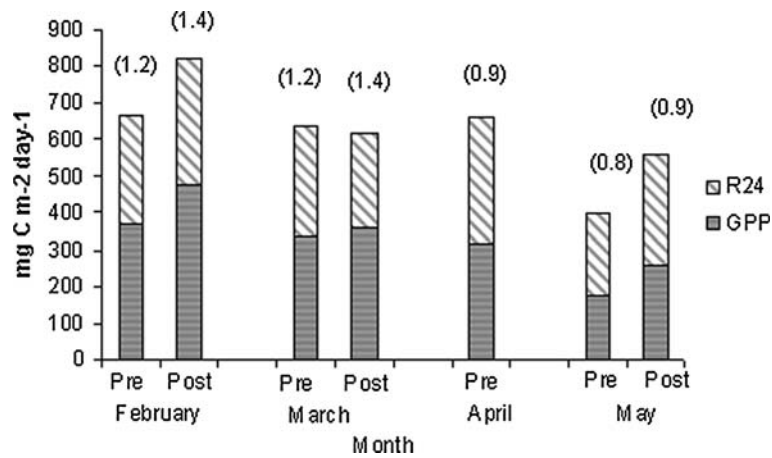


Figure 6. Gross primary production (GPP), respiration (R24) values and P/R ratios (shown in brackets) for each site before and after flow release along the reach of the Cotter River between Bendora Dam and the Cotter Dam 2002 (no release was made in April).

## Discussion

Previous investigations in the Cotter River catchment have shown no difference in major cations and anions (Talsma & Hallam, 1982; Talsma, 1983), nutrients, water quality and instream physical habitat (Sloane et al., 1998; 1999) between sites downstream of dams, sites along reaches of the Cotter River and surrounding tributaries. However, a remaining impact of the dams on the Cotter River is alteration of the flow regime. A hydrology study (CRCFE, 2003) characterised the post- and pre-regulation hydrology of the Cotter River and has shown that, aside from a reduction in gross discharge, there has been a marked reduction in the number and nature of small (<2 year return) flow events. This reduction in small flow events, together with the typical reduction in sediment transport that is commonly caused by the physical barrier of the dams, could be expected to alter instream processes and biotic communities in reaches downstream of the dams.

The periphyton at sites downstream of the dams in the Cotter River contained more chlorophyll a and had more green filamentous chlorophytes than the reference and tributary sites (Table 1, Fig. 4). Reference and tributary site periphyton had proportionally more diatoms and detritus (Fig. 4), with the detritus containing unicellular green algae, protists, bacteria and fungi that were difficult to identify because of the preservation method (Chessman, 1986; Entwisle et al., 1997). Given that the sites downstream of dams

are physically and chemically similar to the unregulated sites it might be expected that they would have a similar periphyton community (Cattaneo et al., 1997; Kutka & Richards, 1996). However, the differences in the periphyton community downstream of dam sites probably results from less frequent disturbance because of the reduction in small events caused by regulation, as the principal periphyton habitat template is stream nutrient status and time since last flow disturbance (Biggs, 1995). The lack of difference in AFDM among sites (Table 1) probably reflects the limit of material that can accumulate on rocks in riffles under the shear stress of even moderate flows (Biggs, 1996; Lau & Liu, 1993). Therefore, the reduction in disturbance, particularly from small events, in the Cotter River because of dam operation has changed the composition and structure of periphyton on rocks. This change might reasonably be expected to produce effects on trophic status and food for animals if it is a major food source.

The overall community composition of macroinvertebrates at sites downstream of dams was not similar to unregulated sites, and some taxa found at all the unregulated sites (e.g. Glossosomatidae) were missing downstream of the dams. Sites downstream of dams in the Cotter River were numerically dominated by Diptera and Oligochaeta. Ephemeroptera and Coleoptera, while present downstream of dams, were much more abundant at the reference and tributary sites. Reduced abundance and displaced taxa are commonly



reported changes downstream of dams (Petts & Greenwood, 1981; Weisberg et al., 1990; Gowns & Gowns, 2001). However, macroinvertebrate communities can be near their natural state without loss of characteristic taxa for that river if flow diversion is not large enough to affect the magnitude of flow variations (Russell & Belish, 1999) or the right combinations of conditions exist. For example, the release pattern and the heterogenous nature of the substratum downstream of Cow Green Reservoir in Britain increased numbers of certain taxa without displacing the pre-dam fauna (Armitage, 1978).

Some of the macroinvertebrate taxa affected at sites downstream of the dams on the Cotter River were Leptophlebiidae, Glossosomatidae, Elmidae and Orthocladiinae. All these taxa are classified as algal/detrital feeders (Hawking, 1997; Chessman, 1986) and like many Australian macroinvertebrate taxa are described as omnivores with plastic feeding habits (Boulton & Brock, 1999). However, it has been shown that invertebrates can be discriminating with the food they prefer (Becker, 1994) and may require food of a certain type to meet their metabolic requirements (Sheldon & Walker, 1997). Analysis of dietary composition of the animals shows that three taxa negatively affected by the dams (Leptophlebiidae, Glossosomatidae and Elmidae) ingest and assimilate periphyton containing mostly diatoms and detritus (a category that includes unicellular green algae, bacteria fungi and ultrafine organic particles) (Figs. 3 and 5). Orthocladiinae also derive carbon from this source (Fig. 5) although dietary analysis showed that they primarily consume the smaller detrital component from a matrix of large filamentous chlorophytes (Fig. 5) similar to other small invertebrates that feed within the periphyton matrix (Brennan et al., 1978). Although in this study the SIA signatures for periphyton carbon were higher than the invertebrates it is possible that periphyton may be undergoing seasonal changes in  $\delta^{13}\text{C}$  (McCutchan & Lewis, 2002). There is some indication of that possibility given the spread of periphyton carbon values and it may be expected then that the  $\delta^{13}\text{C}$  signatures for macroinvertebrates would lag behind changes to periphyton because growth and assimilation rates will be slower than the rate of change in food sources values. If this was occurring then

periphyton is the dominant carbon source for the investigated taxa (McCutchan & Lewis, 2002). The value of using both carbon and nitrogen to discern trophic pathways is demonstrated as contemporaneous sampling of consumer and diet using carbon alone would have indicated detritus as the probable invertebrate food source however, the difference in nitrogen values between macroinvertebrates and detritus rules this out. The feeding preferences for the investigated taxa match the composition of the periphyton in sites downstream of the dams, which was different from the reference and tributary sites. Sites downstream of dams in the Cotter River had a matrix of detritus bound up in large filamentous chlorophytes in which the Orthocladiinae midges may reside, feed and possibly avoid predation, while the reference and tributary sites had a more accessible prostrate mix of diatoms, cyanobacteria, metazoans, fungi and detritus in a matrix of polysaccharide and polymer exudates, which is reported as the preferred form for many grazers (Lamberti, 1996) such as Leptophlebiidae and Elmidae.

Measures of stream metabolism (Fig. 6) were in the middle of the ranges (GPP 25–3200  $\text{mg C m}^{-2} \text{ day}^{-1}$ , R24 80–2850  $\text{mg C m}^{-2} \text{ day}^{-1}$  and P/R 0.4–1.9) measured elsewhere in Australia (Davies, 1997; Bunn et al., 1999; Mathieu, 1996). Metabolism shifted towards production (Fig. 6) and levels of GPP increased in the reach of the Cotter River between Bendora and Cotter dams after the release of 2-day spike discharges from Bendora Dam. Increased nutrient diffusion (Lock & Peter, 1979), removal of inorganic particles and dead or senescent cells (Jan Stevenson, 1996) are likely mechanisms stimulating GPP that would have been influenced by the flow releases. The response of R24 is not as clear as GPP, with no significant effect of the spike flow measured (Fig. 6). The R24 measure represents processes from a more complex community (autotrophs and a suite of heterotrophs), and the various biotic components inhabiting the substrate may respond differently to the elevated flow. Microbial heterotrophs associated with dead cells, organic and inorganic particles may be removed with the elevated flow (Peterson, 1996). Invertebrates, which make up a component of the heterotrophic side of metabolism, may drift or seek refuge in response to changes in the flow (Gore, 1977; Poff & Ward,

1991). The removal/redistribution of these components of R24 may offset the increase in metabolic respiratory activity of the autotrophic organisms. However, overall the response of metabolic processes in the Cotter River shows that the balance of metabolism (P/R ratio) shifted towards autotrophy, and levels of production (GPP) increased after the release of flow spikes. Thus, even small changes in flow (7–8 times base flow) stimulated a significant increase in GPP; a fundamental ecological process that supports higher trophic levels.

The implications of the short 2-day releases from Bendora dam are important. That the spike flow releases elicit a metabolic response indicates that there are changes to the dynamics within the periphyton community caused by moderate flow manipulations. This would be expected to have flow-on effects to higher trophic levels such as invertebrates and fish, and instream processes such as nutrient uptake or release by the periphyton (Uehlinger, 1991). The increase in levels of GPP with no clear directional effect on levels of R24, shows that disturbance of a magnitude thought to reset the periphyton community from a climax state of filamentous algae to that thought to represent colonisation conditions where respiration becomes more dominant (Peterson, 1996) has not been reached. This indicates that the environmental flows from Bendora dam do not fully recreate conditions in the Cotter River that could suit a periphyton community of prostrate diatoms in a detrital matrix similar to that found in nearby unregulated streams in the region (Fig. 4).

Amongst the dams there were some differences in the macroinvertebrate community composition downstream of each of the dams (Fig. 2). Bendora had most animals and taxa, while Corin Dam was dominated by the high abundance of Orthocladinae. Cotter Dam had the poorest, macroinvertebrate community with the lowest taxa richness and was numerically dominated by Oligochaetes and Orthocladinae midges. The difference in flow releases between the dams in the Cotter River is reflected in differences in periphyton and the macroinvertebrate communities. If releases could effect responses similar to those reported for natural disturbances (Osborne, 1983; Power & Stewart, 1985; Uehlinger & Naegeli, 1998), then changes to the periphyton community and

subsequent trophic interactions with invertebrate grazers could result in instream communities more similar to unregulated streams of the area. However, given that flow releases can have significant effects, the timing frequency and magnitude of such releases may need to take into account natural occurrence of such events otherwise flow releases that are out of character with the natural history of river may have negative effects on aspects of the ecosystem.

In these two forested upland gravel bed streams autotrophy is an important pathway. Gut content examination shows that some of the taxa affected, whether positively or negatively, foraging in periphyton. SIA shows the trophic pathway for these taxa is also periphyton. Dams, through the release of clear water and stable flow, can enhance the importance of autotrophy in reaches immediately downstream and this may initially facilitate a greater food resource for macroinvertebrates and enable greater stream productivity. However, the shift from a periphyton matrix dominated by diatoms and other small microflora to one of filamentous algae reduces the availability of useable food for large grazers such as Leptophlebiidae mayflies and enables other taxa such as Orthocladinae to numerically dominate. Flow releases from dams have the potential to affect instream processes and facilitate a change in periphyton structure that will promote trophic interactions similar to that found in reference and tributary sites.

### Acknowledgements

The authors are grateful to the Cooperative Research Centre for Freshwater Ecology (University of Canberra), Environment ACT and ActewAGL for logistic and material support. Dr Richard Marchant for comment and assistance with the study concept and supervision. Matthew O'Brien, Tom Nelson, Amara Barlow, Catherine Lemann Sue Nichols, Simon Godschalx for laboratory and field assistance.

### References

- ANZECC & ARMCANZ, 2000. National Water Quality Management Strategy: Australian and New Zealand

- Guidelines for Fresh and Marine Water Quality. Australian and New Zealand Environment and Conservation Council and the Agriculture and Resource Management Council of Australia and New Zealand. <http://www.ea.gov.au/water/quality/nwqms/index.html>.
- Armitage, P. D., 1978. Downstream changes in the composition, numbers and biomass of bottom fauna in the Tees below Cow Green reservoir and in an unregulated tributary Maize Becke, in the first five years after impoundment. *Hydrobiologia* 58: 145–156.
- Becker, G., 1994. Food preference by five trichopteran scrapers. *Hydrobiologia* 273: 171–178.
- Belbin, L. & C. McDonald, 1993. Comparing three classification strategies for use in ecology. *Journal of Vegetation Science* 4: 341–348.
- Biggs, B. F., 1996. Hydraulic habitat of plants in streams. *Regulated Rivers: Research and Management* 12: 131–144.
- Biggs, B. J. F., 1995. The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. *Freshwater Biology* 33: 419–438.
- Boulton, A. J. & M. A. Brock, 1999. *Australian Freshwater Ecology: Processes and Management*. Gleneagles Publishing, Glen Osmond, Australia.
- Brennan, A., A. J. McLachlan & R. S. Wotton, 1978. Particulate material and midge larvae (Chironomidae: Diptera) in an upland river. *Hydrobiologia* 59: 67–73.
- Bunn, S. E., P. M. Davies & T. D. Mosisch, 1999. Ecosystem measures of river health and their response to riparian catchment degradation. *Freshwater Biology* 41: 333–345.
- Cadwallader, P. L. & K. A. Eden, 1979. Observations on the food of Maquarie Perch, *Maquaria australasica* (Pisces: Percichthyidae), in Victoria. *Australian Journal of Marine and Freshwater Research* 30: 401–409.
- Cattaneo, A., T. Keriman, M. Roberge & J. Marty, 1997. Periphyton distribution and abundance on substrata of different size along a gradient of stream trophy. *Hydrobiologia* 354: 101–110.
- Chessman, B. C., 1986. Dietary studies of aquatic insects from two Victorian rivers. *Australian Journal of Marine and Freshwater Research* 37: 129–146.
- Clarke, K. R. & R. M. Warwick, 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation* (2nd edn). PRIMER-E Ltd. Plymouth, United Kingdom.
- Coysh, J. L., S. J. Nichols, J. C. Simpson, R. H. Norris, L. A. Barmuta, B. C. Chessman & P. Blackman, 2000. *Australian RIVER Assessment System (AUSRIVAS) National River Health Program Predictive Model Manual*. Cooperative Research Centre for Freshwater Ecology.
- Cullen, P. & P. S. Lake, 1995. *Water Resources and Biodiversity: Past Present and Future Problems and Solutions*. Conserving Biodiversity threats and solutions, Beatrice and Sons: 115–135.
- Davies, P. M., 1997. Assessing river health by measuring community metabolism. Report to the Land and Water Research Development Corporation UWA14. Canberra.
- DeNicola, D. M., 1996. Periphyton response to temperature at different ecological levels. In Jan Stevenson, R., M. I. Bothwell & R. L. Lowe (eds), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press Inc, California.
- Entlewise, T. J., J. A. Sonneman & S. H. Lewis, 1997. *Freshwater Algae in Australia*. Sainty and Associates Pty Ltd, Potts Point, New South Wales.
- Faith, D. P., P. R. Minchin & L. Belbin, 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57–68.
- Franson, M., 1985. *Standard Methods for the Examination of Water and Wastewater*. American Public Health Association, American Water Works Association and Water Pollution Control Federation, Washington DC.
- Gore, J. A., 1977. Reservoir manipulations and benthic macroinvertebrates on a prairie river. *Hydrobiologia* 55: 113–123.
- Growns, I. O. & J. E. Gowns, 2001. Ecological effects of flow regulation on macroinvertebrate and periphytic diatom assemblages in the Hawkesbury-Nepean River, Australia. *Regulated Rivers: Research and Management* 17: 275–293.
- Hawking, J. H., 1997. *Colour guide to freshwater invertebrates of Australian inland waters*. Albury: Cooperative Research Centre for Freshwater Ecology.
- Jan Stevenson, R., 1996. The stimulation and drag of current. In Jan Stevenson, R., M. I. Bothwell & R. L. Lowe (eds), *Algal Ecology: Freshwater Benthic Ecosystems*. Academic Press Inc, California.
- Kutka, F. J. & C. Richards, 1996. Relating diatom assemblage structure to stream habitat quality. *Journal North American Benthological Society* 15: 469–480.
- Lamberti, G. A., 1996. The role of periphyton in benthic food webs. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), *Algal Ecology, Freshwater Benthic Ecosystems*. Academic Press, California, 753.
- Lancaster, J. & S. Waldron, 2001. Stable isotope values of lotic invertebrates: sources of variation, experimental design, and statistical interpretation. *Limnology and Oceanography* 46: 723–730.
- Lau, Y. L. & D. Liu, 1993. Effect of flow rate on biofilm accumulation in open channels. *Water Resources* 27: 355–360.
- Ledger, M. E. & A. G. Hildrew, 1998. Temporal and spatial variation in the epilithic biofilm of an acid stream. *Freshwater Biology* 40: 655–670.
- Lintermans, M., 1998. The Ecology of the Two-spined Blackfish *Gadopsis bispinosus* (Pisces: Gadopsidae). Division of Botany and Zoology. Australian National University, Canberra.
- Lock, M. A. & J. H. Peter, 1979. The effect of flow patterns on uptake of phosphorus by river periphyton. *Limnology and Oceanography* 24: 376–383.
- Loeb, S. L., 1981. An in situ method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. *Limnology and Oceanography* 26: 394–400.
- Maddock, I., 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* 41: 373–391.
- Marchant, R., 1989. A subsampler for samples of benthic invertebrates. *Bulletin of the Australian Society of Limnology* 12: 49–52.

- Marchant, R. & G. Hehir, 2002. The use of AUSRIVAS predictive models to assess the response of lotic macroinvertebrates to dams in south-east Australia. *Freshwater Biology* 47: 1033–1050.
- Mathieu, J., 1996. Epilithic metabolism resulting from altered nutrient and grazing conditions and from a point source of sewage effluent. Canberra, Ecology and Environmental Science, University of Canberra.
- McCune, B. & M. J. Mefford, 1999. *Multivariate Analysis of Ecological Data Version 4.20*. MjM Software, Gleneden Beach, Oregon, USA.
- McCutchan, J. H., W. M. Lewis & Jr., 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography* 47: 742–752.
- Mosich, T. D. & S. E. Bunn, 1997. Temporal patterns of rainforest stream epilithic algae in relation to flow-related disturbance. *Aquatic Botany* 58: 181–193.
- Mulholland, P. J., J. L. Tank, W. M. Sanzone, B. J. Peterson, J. R. Webster & J. L. Meyer, 2000. Food resources of stream macroinvertebrates determined by natural-abundance stable C and N isotopes and a  $^{15}\text{N}$  addition. *Journal North American Benthological Society* 19: 145–157.
- Osborne, L. L., 1983. Colonization and recovery of lotic epilithic communities: A metabolic approach. *Hydrobiologia* 99: 29–36.
- Parsons, M. & R. H. Norris, 1996. The effect of habitat-specific sampling on biological assessment of water quality using a predictive model. *Freshwater Biology* 36: 419–434.
- Peterson, C. G., 1996. *Response of Benthic Algal Communities to Natural Physical Disturbance*. Academic Press Inc, California.
- Petts, G. E., 1980. Long-term consequences of upstream impoundment. *Environmental Conservation* 7: 325–332.
- Petts, G. E., 1984. *Impounded Rivers*. John Wiley and Sons, New York.
- Petts, G. E. & M. Greenwood, 1981. *Habitat changes below Dartmoor Reservoirs. Reports and transactions*. Devonshire Association for the Advancement of Science, Literature and Art 113: 13–27.
- Poff, L. N. & J. V. Ward, 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fish and Aquatic Science* 48: 1926–1936.
- Power, P. E. & A. J. Stewart, 1985. Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *The American Midland Naturalist* 117: 333–345.
- Rainer, Z., P. Burgherr, S. M. Bernasconi & U. Uehlinger, 2001. Stable isotopes analysis of macroinvertebrates and their food sources in a glacier stream. *Freshwater Biology* 46: 871–882.
- Reiser, D. W., M. P. Ramey & T. A. Wesche, 1989. *Flushing Flows*. CRC Press, Boca Raton.
- Reiter, M. A., 1986. Interactions between the hydrodynamics of flowing water and the development of a benthic algal community. *Journal of Freshwater Ecology* 3: 511–517.
- Russell, R. B. & T. A. Belish, 1999. Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management* 15: 353–363.
- Salas, M. & D. Dudgeon, 2001. Stable-isotope determination of mayfly (Insecta: Ephemeroptera) food sources in three tropical Asian streams. *Archiv für Hydrobiologia* 151: 17–32.
- Sheldon, F. & K. F. Walker, 1997. Changes in the biofilms induced by flow regulation could explain extinctions of aquatic snails in the lower River Murray, Australia. *Hydrobiologia* 347: 97–108.
- Sloane, P., N. Davies & R. Norris, 1999. *ACT Component of the First National Assessment of River Health: Interim Report Spring (1999)*. Department of Urban Services, Canberra.
- Sloane, P., J. Simpson & R. Norris, 1998. *ACT Component of the Monitoring River Health Initiative: Final Report*. Department of Urban Services, Canberra 45 pp.
- Talsma, T., 1983. *Soils of the Cotter Catchment Area, A.C.T.: Distribution, chemical and physical properties*. Australian Journal of Soil Research 21: 241–255.
- Talsma, T. & P. M. Hallam, 1982. Stream water quality in forest catchments in the Cotter Valley, ACT. In O'Loughlin, E. M. & J. L. Bren (eds), *The First National Symposium on Forest Hydrology*. Institute of Engineers Australia, Canberra, 50–60.
- Udy, J. W., J. E. Clapcott, C. S. Fellows, B. D. Harch, S. E. Bunn & P. M. Davies, 2001. *Measures of Primary Production as Indicators of Ecosystem Health*. Center for Catchment and Instream Research, Griffith University and South east Regional Water Quality Management Strategy, Brisbane.
- Uehlinger, U., 1991. Spatial and temporal variability of periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie* 123: 219–237.
- Uehlinger, U. & M. W. Naegeli, 1998. Ecosystem, disturbance and stability in a prealpine gravel bed river. *Journal of the North American Benthological Society* 17: 165–178.
- Vander Zander, M. J. & J. B. Rasmussen, 1999. Primary consumer  $^{13}\text{C}$  and  $^{15}\text{N}$  and the trophic position of aquatic consumers. *Ecology* 80: 1395–1404.
- Walker, K. F., 1985. A review of the ecological effects of river regulation in Australia. *Hydrobiologia* 125: 111–129.
- Ward, J. V. & J. A. Stanford (eds.), 1979. *The Ecology of Regulated Streams*. In *Proceedings of the First International Symposium on Regulated Streams Held in Erie, April 18–20, 1979*. Plenum Press, New York.
- Weisberg, S. B., A. J. Janicki, J. Gerritsen & H. T. Wilson, 1990. Enhancement of benthic macroinvertebrates by minimum flow from a hydroelectric dam. *Regulated Rivers: Research and Management* 5: 265–277.
- Woodward, G. & A. G. Hildrew, 2002. Food web structure in riverine landscapes. *Freshwater Biology* 47: 777–798.