

Linking pattern and process: the effects of hydraulic conditions on cobble biofilm metabolism in an Australian upland stream

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Abstract Mesoscale variability in hydraulic conditions plays an important role in stream ecosystem structure and function. While the structural effects of variability have been widely tested, its influence on ecosystem processes is less well understood. This study examines the influence of spatial hydraulic variability on cobble biofilm metabolism in a regulated Australian upland stream. Primary production and respiration on stream cobbles forming the substrate in areas subject to three different flow conditions were measured using benthic chambers. Overall the cobble biofilms were found to be strongly autotrophic ($P/R \gg 1$). Rates of respiration and, to a lesser extent, production were greatest where flow velocities and turbulence were low. Concentrations of chlorophyll *a*, pheophytin *a* and organic material were also highest in areas of lowest flow velocities. Hydraulic conditions did not affect P/R ratios. The degree of autotrophy is likely to reflect the effects of a recent fire in reducing shading and increasing nutrient influx. The observed spatial patterns can be partly explained by the greater accumulation of biomass in low flow velocity areas, but qualitative differences in biofilms are also likely to be important.

Key words flow management; hydraulic variability; primary production; respiration; surface flow type

INTRODUCTION

Development of environmentally sound flow management techniques requires knowledge of the influence of flow on biological processes. Flow exerts a strong influence on the distribution and abundance of stream biota. This can be direct, for example, through its effect on the capacity of biota to move or maintain position within favoured habitat, or indirect, for example, through its effect on the spatial distribution of resources. Flow is therefore a fundamental component of the physical habitat template in streams, and variation in flow control contributes greatly to the overall diversity of the physical environment in streams. Variation in hydraulic conditions is likely to be greatest in upland, lower-order streams because of the generally higher heterogeneity in bed morphometry and because the relatively shallow depths mean that the effect of bed morphometry is expressed through most, if not all, of the water column (Emery *et al.*, 2003). The result is a spatial mosaic of patches delineated by distinct hydraulic conditions or flow types (Newson & Newson, 2000).

The biological effects of mesoscale spatial variation in hydraulic conditions have been demonstrated for a range of stream communities including periphyton (Biggs *et al.*, 1998), stream macrophytes (Riis & Biggs, 2001), macroinvertebrates (Brooks *et*

al., 2005) and fish (Maddock *et al.*, 2004). Several studies have also shown that variability plays an important role in ecosystem processes such as primary productivity, respiration and nutrient cycling (Uehlinger, 2000; Larned *et al.*, 2004). Although the effects of mesoscale flow variability on structural patterns in stream biota have been examined in several studies in Australia, its effect on ecosystem processes has not been widely tested.

This study examines the relationship between spatial variation in hydraulic conditions and the ecosystem process of benthic metabolism in an upland stream affected by flow regulation. It is part of a broader study that also incorporates an examination of the effects of temporal variation in flow as well as the interaction between the two. The answers to the questions raised in this study will be used to demonstrate ways that mesoscale flow variability can be managed to maximize ecological benefit.

METHODS

Study area

The Cotter River is an upland cobble and gravel-bed river that drains a catchment of approximately 483 km² located within the Brindabella Ranges in the Australian Capital Territory (Fig. 1). Three dams regulate flow for the purpose of supplying water for the city of Canberra (pop. ~322 000); however, environmental flow releases designed to minimize the impact of the dams and mimic the natural flow regime are made. Sites included in the study are all situated on the reach of the Cotter River between the Bendora and Cotter dams (Fig. 1) at altitudes ranging from ~700 to 500 m above sea level. The climate is temperate with hot summers and cold winters. Average precipitation ranges from 990 to 1080 mm, with the wettest months between July and October. Although the catchment is largely unmodified by human land use, severe and extensive fires during the summer of 2003 burnt most of the Cotter River catchment above the Cotter Dam.

Study design

Sampling was carried out during February and March 2005. Treatments were “surface flow types” (SFTs), which are spatially distinct flow patches that can be readily distinguished visually, but which also represent distinct hydraulic environments (Newson & Newson, 2000). Seven flow types were identified in the river, and three of these were included in this study: no perceptible flow (NPF), ripple flow (RF) and standing broken wave (SBW). These flow types cover a broad range of hydraulic conditions (Reid *et al.*, 2005) and together make up approximately 50% of the total stream surface area within the study reach (Dyer & Thoms, 2006). Each of the three SFTs was sampled at six locations within the study reach (Fig. 1). Sampling took place following eight weeks of low flow (<50 ML day⁻¹) on two occasions separated by 12 days that incorporated a two-day environmental flow release, which peaked at 185 ML day⁻¹.

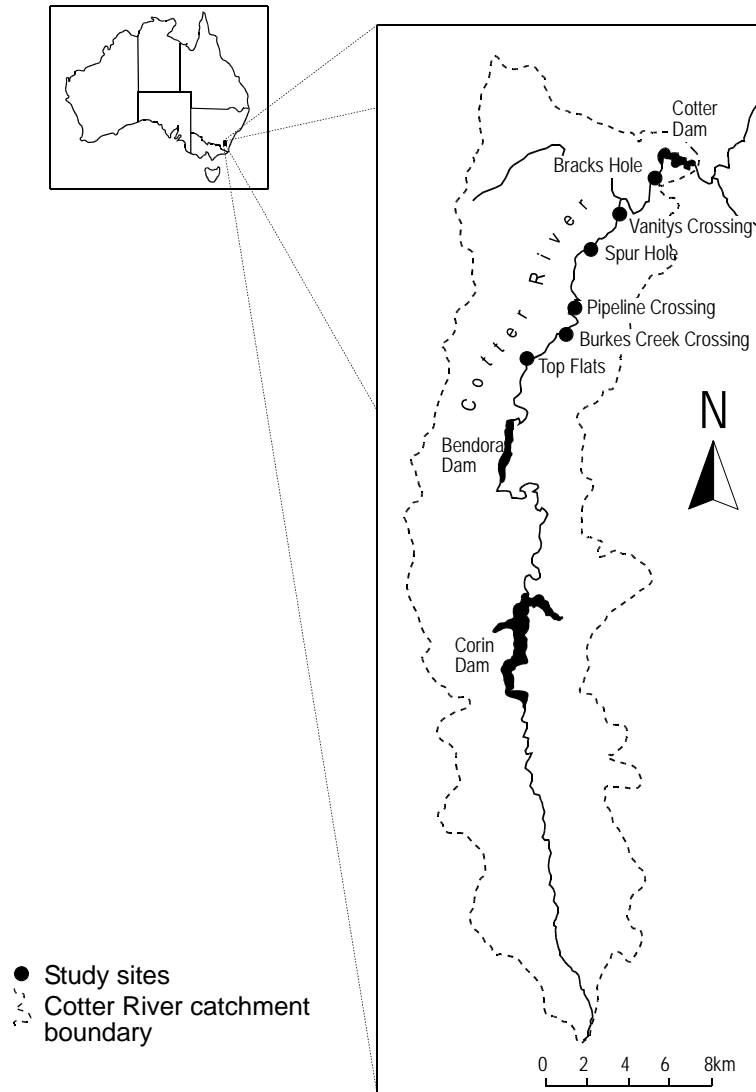


Fig. 1 Location of the Cotter River catchment and study sites.

Field and laboratory methods

Biofilm metabolism was measured by calculating fluxes of dissolved oxygen within enclosed chambers placed on the streambed. Benthic chambers were Perspex domes with total enclosed volumes of between 9700 and 10 000 cm³. Single cobbles were collected from each of the three different flow types at each site and placed within the benthic chambers. These were then placed in the stream away from areas of high flow to minimize disturbance at depths sufficient to completely cover the chamber.

Oxygen production and consumption rates within the domes were calculated through change in dissolved oxygen concentrations measured with a dissolved oxygen probe (YSI 5739) and recorded every 10 min by data loggers (TPS WP-82Y) over at least a full 24-h cycle. A battery powered pump circulated water within the dome to reduce boundary layer effects at the rock-water interface. A tight-fitting plastic base provided a basal seal for the chamber.

At the completion of each measurement period, rocks were retrieved and scrubbed to remove biofilms. The recovered material was then thoroughly mixed and divided into two equal sub-samples. The first sub-sample was dried at 80°C for at least 24 h and weighed to determine dry weight. Dried material was then ignited at 550°C for 1 h to calculate ash-free dry weight (*AFDW*). The second sub-sample was used to determine chlorophyll *a* and pheophytin *a* concentrations. To achieve this, known volumes of material were filtered onto glass fibre filters (Whatman GC-50), which were heated at 80°C in a 90% ethanol solution for 5 min to extract pigments. Chlorophyll *a* concentrations in extracts were calculated from spectrophotometer measurements of absorbance at 664 and 750 nm (APHA, 1992). Measurements were repeated on acidified samples to correct for pheophytin *a* (APHA, 1992).

Rock volumes were calculated by water displacement and rock surface area was calculated by weighing the amount of aluminium foil required to cover each rock, having first determined the weight:surface area ratio (McCreadie & Colbo, 1991). The metabolically active area of the rock was assumed to be half the total surface area (Fellows *et al.*, 2006).

Carbon production and consumption rates were calculated from changes in dissolved oxygen concentrations within the domes during the measurement period assuming a mol of carbon is exchanged for each mol of O₂ exchanged (i.e. 1 mg O₂ is required to produce 0.375 mg of C and *vice versa*: Bunn *et al.*, 1999). These data were used to calculate gross daily primary productivity (*GPP*), daily respiration (*R*₂₄) and net biofilm production ($NBP = GPP - R_{24}$) per unit area, as well as the ratio of production to respiration (*P/R*) and the rate of primary production per mg of chlorophyll *a* (*RPP*).

Data analysis

Results were analysed using analysis of variance (ANOVA) in the SPSS statistical computer program (version 11.5.0, SPSS, 2002). A randomized complete block design, with SFT (Surface Flow Types) ($df = 2$) and trip ($df = 1$) blocked across sites ($df = 5$), was employed to test the effects of SFT, trip and site on the dependent variables (*GPP*, *R*₂₄, *NBP*, *P/R*, *RPP*, chlorophyll *a*, pheophytin *a*, *AFDW* and dry weight). Data were transformed where appropriate to fulfil the requirements of equal variances between groups.

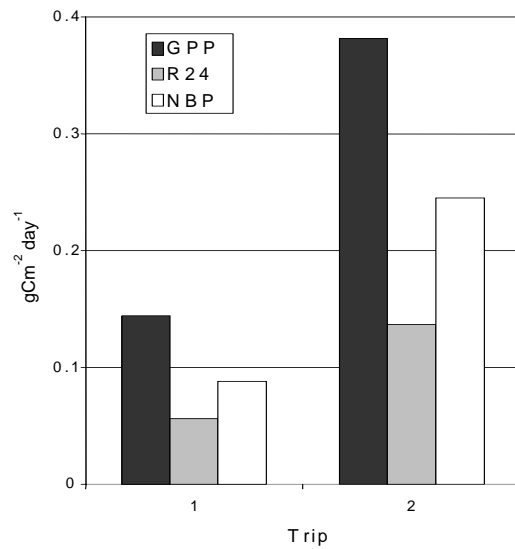
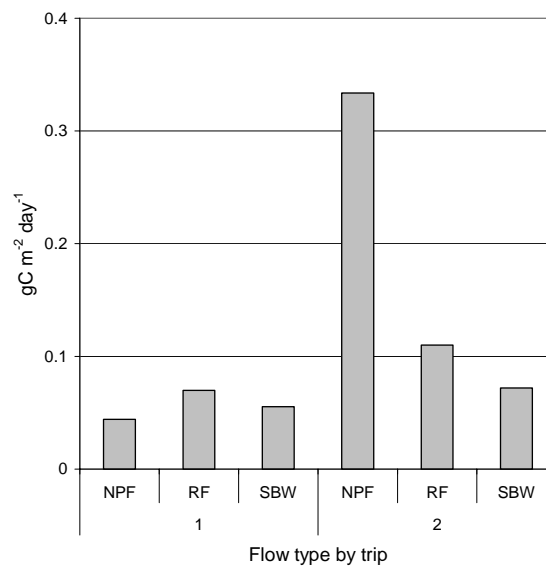
RESULTS

Pump failure, incomplete seals on chambers and faulty DO probes and loggers meant that metabolism data could not be used for several replicates for each sampling event. This reduced the total number of measurements for *GPP*, *R*₂₄, *NBP*, *P/R* and *RPP* from 36 to 26 (Table 1). Despite this, there were sufficient replicates to test each factor. The number of measurements for chlorophyll *a*, pheophytin *a*, *AFDW* and dry weight were not affected by malfunctions in the benthic chambers.

Summary statistics for the dependent variables (Table 1) show that the cobble biofilms of the Cotter River were net producers (autotrophic) during the sampling period.

Table 1 Summary statistics for dependent variables.

	<i>N</i>	Minimum	Maximum	Mean	SD
R_{24} (mg C m ⁻² day ⁻¹)	26	3.12	793.08	180.91	197.51
<i>GPP</i> (mg C m ⁻² day ⁻¹)	26	18.67	1526.19	488.39	428.21
<i>NBP</i> (mg C m ⁻² day ⁻¹)	26	-122.45	1202.86	307.48	362.92
<i>P/R</i>	26	0.82	20.73	4.86	5.26
<i>PP</i> rate (mg C (mg chl a) ⁻¹ day ⁻¹)	26	0.01	0.33	0.15	0.10
Dry weight (gm ⁻²)	36	3.11	124.15	24.06	29.63
<i>AFDW</i> (g m ⁻²)	36	1.03	15.02	4.34	3.69
<i>Chl a</i> (mg m ⁻²)	36	0.16	10.90	3.73	2.76
<i>Pheo a</i> (mg m ⁻²)	36	0.27	21.31	2.95	3.57

**Fig. 2** Estimated marginal means for *GPP*, R_{24} and *NBP* by trip.**Fig. 3** Estimated marginal means for R_{24} from no perceptible flow (NPF), ripple flow (RF) and standing broken wave (SBW) areas for each sampling trip.

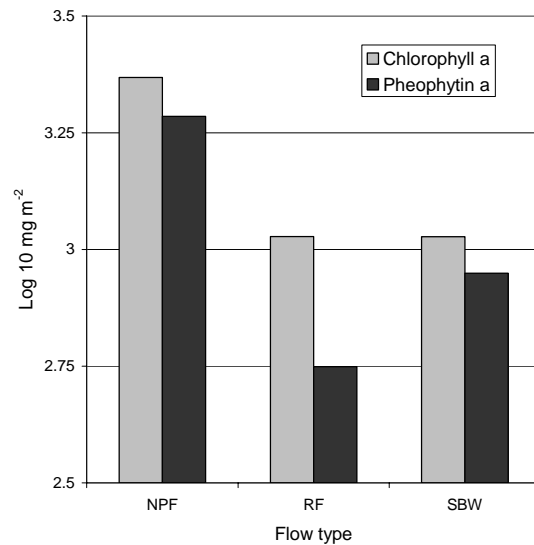


Fig. 4 Log₁₀ of chlorophyll *a* and pheophytin *a* concentrations from no perceptible flow (NPF), ripple flow (RF) and standing broken wave (SBW) areas.

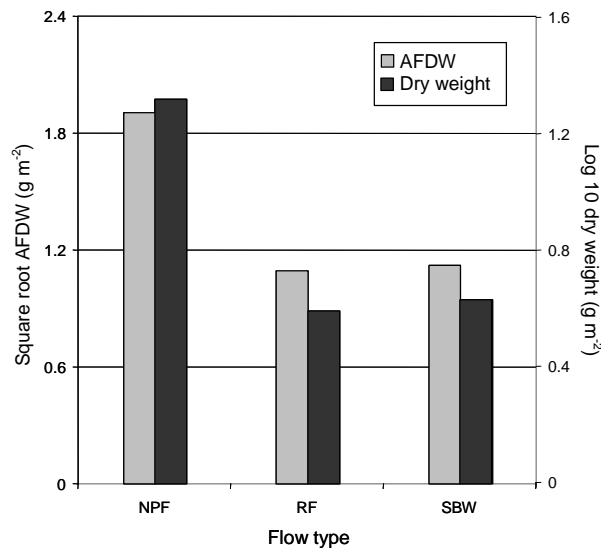


Fig. 5 Estimated marginal means for log₁₀ of dry weight and square root of *AFDW* from no perceptible flow (NPF), ripple flow (RF) and standing broken wave (SBW) areas for each sampling occasion.

Gross primary productivity (*GPP*), *NBP* and R_{24} were all significantly higher for the second sampling occasion (Table 2; Fig. 2). Both *GPP* and R_{24} were highest overall in NPF areas and lowest in SBW areas, but these differences were not significant at the 0.05 level (Table 2). In the case of R_{24} , there was a significant interaction of flow type with trip, whereby the increase in R_{24} from trip 1 to trip 2 was greatest in NPF areas (Fig. 3; Table 2). Chlorophyll *a* and pheophytin *a* concentrations (Fig. 4), as well as dry weight and *AFDW* (Fig. 5), were all influenced by flow type, and were greatest within NPF areas.

Table 2 Summary of the results of ANOVA (three-factor randomized complete block) carried out on metabolism data showing F-values (*F*) and probabilities (*p*) for “Trip”, “Flow-type”, “Site” and interaction effects.

Dependent variables	Transform	Trip:		Flow type:		Site:		Trip × Flow type:		Trip × Site:		Flow type × Site:	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
		16.45	0.020	3.12	0.098	0.46	0.792	0.84	0.543	1.64	0.413	1.53	0.456
<i>NBP</i>	none	9.40	0.044	1.04	0.393	0.17	0.960	0.07	0.939	1.75	0.396	2.24	0.347
<i>R</i> ₂₄	none	35.06	0.005	3.10	0.095	1.38	0.305	85.15	0.012	4.12	0.205	17.29	0.056
<i>P/R</i>	square root	0.39	0.570	1.48	0.283	1.57	0.369	3.95	0.202	1.85	0.380	1.99	0.380
Rate of <i>PP</i>	none	5.95	0.087	1.78	0.233	3.05	0.623	0.23	0.810	1.01	0.552	0.81	0.664
<i>Chl a</i>	log 10	4.40	0.090	5.44	0.025	1.33	0.486	1.77	0.220	1.08	0.428	0.80	0.634
<i>Pheo a</i>	log 10	1.48	0.279	37.26	0.000	5.72	0.331	0.57	0.586	1.37	0.314	0.29	0.967
<i>DW</i>	log 10	0.73	0.433	43.04	0.000	0.52	0.756	0.46	0.644	2.11	0.147	0.75	0.672
<i>AFDW</i>	square root	0.26	0.632	39.56	0.000	0.61	0.707	0.78	0.485	2.73	0.083	0.48	0.869

DISCUSSION

Overall rates of productivity and respiration

The results suggest that the cobble biofilms are strongly autotrophic (net producers of carbon) with the *P/R* ratio averaging almost 5 (Table 1). This level of autotrophy contrasts with that detected in a previous study carried out in the Cotter River, which found *P/R* ratios of around 1 (Chester, 2003). Importantly, the previous study was carried out prior to the recent severe fires. These fires have reduced riparian shading substantially and the resultant increase in light availability is likely to have increased benthic production (Bunn *et al.*, 1999). In addition, the removal of understorey and groundcover vegetation, as well as the liberation of mineral nutrients in burnt vegetation, are likely to have contributed to a net increase in nutrient inputs to the stream (Spencer *et al.*, 2003; Norris & Thoms, 2004). It would appear, therefore, that the combination of low disturbance frequency, which allows for high algal biomass to develop (Biggs *et al.*, 1998), along with high light and nutrient availability has contributed to a strongly autotrophic system.

Spatial variation in cobble biofilm metabolism

Metabolism and biofilm quantity and quality were measured on cobbles sampled across a broad range of hydraulic conditions, from NPF areas where there is no or negligible flow through to SBW areas, which previous studies have shown exhibit the highest near-bed flow and turbulence conditions in the study reach (Reid *et al.*, 2005). Despite this, although both *GPP* and *R*₂₄ were found to be higher in NPF areas, the difference was significant only for *R*₂₄ and this pattern itself varied over time (Fig. 3). Moreover, none of the remaining measures of the process of cobble biofilm metabolism (*NBP*, *P/R* or rate of *PP*) differed significantly across the three flow types. This result contrasts with those for the measures of biofilm quality and quantity, all of which were found to differ significantly across flow types, with values consistently

highest in NPF areas (Figs 4 and 5). The higher values for dry weight, *AFDW*, chlorophyll *a* and pheophytin *a* in NPF areas are unsurprising and clearly reflect the capacity for greater amounts of algae, bacteria and organic detritus to accumulate in low flow areas.

At face value it would seem that the higher R_{24} in NPF areas is a direct reflection of the greater accumulation of biofilms in these areas. However, the interaction between trip and flow type for R_{24} , when no interaction was found for the structural measures, suggests that the temporal effect is also driven by changes in the rates of respiration within the biofilms between trips. These changes may, in turn, reflect a qualitative change in the biofilm communities of NPF areas before and after a high flow event. For example, there may have been an increase in the ratio of bacteria to organic detritus following the high flow event. It is unclear why this temporal effect should be strongest in NPF areas.

Although several measured variables exhibited spatial variation at the mesoscale of SFT patches, it is noteworthy that no differences were detected between sites. This is likely to be because the three flow types sampled were distributed equally across sites. This does not preclude the possibility that overall biofilm composition and metabolic activity could vary along the study reach, but does suggest that any such variation would reflect between-site variation in the relative proportion of each flow type (Dyer & Thoms, 2006).

CONCLUSIONS

The results of this study highlight the variable spatial and temporal effects of flow on cobble biofilm metabolism. At a general level, the study indicates that rates of respiration and, to a lesser extent, productivity are highest in areas where flow velocity and turbulence are low. These differences can be partly attributed to the quantity of material accumulated within the biofilms under different flow conditions, although there is evidence that qualitative differences in the composition of biofilms beyond the coarse measures of dry weight, *AFDW*, chlorophyll *a* and pheophytin *a*, are important. Spatial variation also appears to be more related to mesoscale hydraulic variation rather than reach scale differences, highlighting the potential influence that variation in hydraulic conditions at these smaller spatial scales can have on benthic systems.

As noted previously, the range of hydraulic conditions present within streams such as the Cotter represent a dynamic spatial mosaic, with both the area and arrangement of hydraulic conditions varying in response to changing discharge. The variation in composition and metabolic activity of biofilm communities detected across different flow types demonstrates that an understanding of how the distribution of these patches of distinct hydraulic character change in response to changing flow will increase our understanding of the ecological consequences of flow management practices.

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