

## Benthic metabolism as an indicator of stream ecosystem health

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### Abstract

We tested direct and indirect measures of benthic metabolism as indicators of stream ecosystem health across a known agricultural land-use disturbance gradient in southeast Queensland, Australia. Gross primary production (GPP) and respiration ( $R_{24}$ ) in benthic chambers in cobble and sediment habitats, algal biomass (as chlorophyll *a*) from cobbles and sediment cores, algal biomass accrual on artificial substrates and stable carbon isotope ratios of aquatic plants and benthic sediments were measured at 53 stream sites, ranging from undisturbed subtropical rainforest to catchments where improved pasture and intensive cropping are major land-uses. Rates of benthic GPP and  $R_{24}$  varied by more than two orders of magnitude across the study gradient. Generalised linear regression modelling explained 80% or more of the variation in these two indicators when sediment and cobble substrate dominated sites were considered separately, and both catchment and reach scale descriptors of the disturbance gradient were important in explaining this variation. Model fits were poor for net daily benthic metabolism (NDM) and production to respiration ratio (P/R). Algal biomass accrual on artificial substrate and stable carbon isotope ratios of aquatic plants and benthic sediment were the best of the indirect indicators, with regression model  $R^2$  values of 50% or greater. Model fits were poor for algal biomass on natural substrates for cobble sites and all sites. None of these indirect measures of benthic metabolism was a good surrogate for measured GPP. Direct measures of benthic metabolism, GPP and  $R_{24}$ , and several indirect measures were good indicators of stream ecosystem health and are recommended in assessing process-related responses to riparian and catchment land use change and the success of ecosystem rehabilitation actions.

### Introduction

Stream and river health assessment has been traditionally dominated by the measurement of the distribution and abundance of plant and animal species (Marchant et al., 1984; Bunn, 1995; Harris, 1995; Reid et al., 1995; Whitton & Kelly, 1995; Wright, 1995). However, there is growing concern

that measures of ecosystem health should include not only aspects of their organization (e.g. biodiversity, species composition, food web structure), but also their vigour (e.g. rates of production, nutrient cycling) and resilience (e.g. ability to recover from disturbance) (Rapport et al., 1998). Furthermore, many goals of river management relate to the maintenance of natural ecological

processes and ecosystem function yet measurement of these processes is often neglected in assessment programs (Bunn & Davies, 2000).

Bunn et al. (1999) and Bunn and Davies (2000) have previously argued that direct measures of ecosystem processes, such as benthic community metabolism, are important considerations in aquatic ecosystem health monitoring. Benthic community metabolism is a particularly important indicator because the component processes of metabolism, respiration and primary production, both respond to environmental variables that are commonly influenced by catchment disturbance, such as light and temperature regimes and nutrient loads (Bunn et al., 1999). Gross primary production (GPP) in forested streams should be low and light-limited due to shading by riparian vegetation at minimally disturbed sites but should increase across a gradient of catchment disturbance due to increased light and nutrient availability. Respiration ( $R_{24}$ ) may also be expected to increase with increasing disturbance, not only due to higher in-stream GPP but also because of inputs of organic carbon and sediment from the catchment (Bunn et al., 1999).

Methods used to assess benthic metabolism vary in the level of information obtained as well as in the cost and technical expertise required. Three common methods are: (1) direct measures of benthic community metabolism using dissolved gas fluxes in enclosed chambers (Bott et al., 1985); (2) measures of static biomass of primary producers (Morin et al., 1999); and (3) growth rate of primary producers measured by biomass accrual on bare substrate (Kevern & Ball, 1965). Direct measurements of rates of benthic community metabolism have been used as an important tool in stream ecosystem ecology for nearly four decades (McIntire et al., 1964; Bott et al., 1978; Dodds et al., 1996; Craft et al., 2002), but have not been widely adopted in monitoring ecosystem health (but see Hill et al., 2000), perhaps due in part to the perception that the measurements are technically difficult and costly.

Many studies and monitoring programs measure static algal biomass on natural substrate as a surrogate of primary production (e.g. Morin et al., 1999), which is less expensive and less time consuming than making rate measurements. It is important to realize that algal biomass may not necessarily relate directly to the rate of metabolism

because it represents the result of interactions between net primary production, activity of grazing invertebrates, and the physical disturbance regime. Additionally, the relationship between primary production and biomass has been shown to be density dependent (Pfeifer & McDiffet, 1975; Morin et al., 1999). Nonetheless, production and biomass are often found to be positively correlated in many different types of systems (Enriquez et al., 1996; Morin et al., 1999). Measurement of algal biomass may be a useful indicator of stream health independent of its relationship with production because high algal biomass is often viewed as a symptom of unhealthy streams. Measuring algal biomass on artificial substrates placed in streams for a set duration can provide an estimate of algal growth and may help to standardize inter-site comparisons by controlling substrate type and biofilm age (e.g. Mosisch et al., 2001).

An additional and perhaps novel way of estimating benthic primary production in streams may be derived from the measurement of stable carbon isotope signatures of algae and other aquatic plants. Stable isotopes have been used extensively to determine the energy base of stream and river food webs (Peterson & Fry, 1987; Finlay, 2001). Difficulties in interpretation often arise because many factors other than the mode of photosynthesis influence the carbon isotope signatures of aquatic plants, including light intensity, water velocity, and carbon dioxide concentration (O'Leary et al., 1992; France, 1995; France & Holmquist, 1997; MacLeod & Barton, 1998; Finlay, 2001). In recent work on a range of biomes in Australia, Bunn et al. (1999; and unpublished data) have found that a significant proportion of the observed variation in  $\delta^{13}\text{C}$  values of algae is explained by variation in benthic GPP. Measures of the carbon isotope signatures of plant tissues are likely to reflect the rate of primary production, especially if other key factors such as water velocity do not vary greatly across sites. Depending on the source of organic carbon in sediments,  $\delta^{13}\text{C}$  values of sediment might also reflect benthic GPP. Although the measurement of  $\delta^{13}\text{C}$  requires the use of a technically precise analytical instrument (isotope ratio mass spectrometer), it is relatively easy to collect the samples and the analyses are routinely undertaken in many research laboratories at low cost.

The aim of this study was to compare the performance of these four measures of benthic metabolism across a diffuse land-use gradient, as part of a larger study investigating potential indicators of ecosystem health for streams and rivers in southeast Queensland, Australia (Abal et al., 2005). A particular focus was on the relative response of the four ecosystem process measures to reach scale versus catchment scale descriptors of disturbance.

## Methods

### *The southeast Queensland study*

This study forms part of the scientific work undertaken as part of the Southeast Queensland Regional Water Quality Strategy for what is now known as the Moreton Bay Waterways and Catchments Partnership (Abal et al., 2005). The study area covers six catchments and 15 major rivers of the Moreton region of Queensland in southeastern Australia (22,353 km<sup>2</sup>) and incorporates 19 local government regions. The region lies in a transitional zone between tropical and temperate climates, though much of the rainfall (55%) occurs during the summer wet season (December to March). Stream flow varies greatly with season and many streams, particularly in the headwaters, are ephemeral and flow only during the wet season. Upland endemic riparian vegetation includes notophyll vine rainforests, dry eucalypt-dominated forests, and fern thicket/hoop pine (*Araucaria cunninghamii*) scrub. Endemic riparian vegetation of lowland areas is dominated by semi-evergreen vine thickets/hoop pine scrub and dry notophyll vine forest, river sheoak (*Casuarina* spp.), red bottlebrush (*Calistemon* spp.) and lilly-pilly (*Syzygium* spp.). Riparian zones along southeast Queensland's streams have been heavily disturbed since European settlement and less than 60% of endemic vegetation remains in many subcatchments (Catterall & Kingston, 1993).

The project on Design and Implementation of a Baseline Monitoring program for streams and rivers in the region (DIBM) formed a key component of the science framework of the Partnership (1999–2001) (Abal et al., 2005). The aim was to develop a cost-effective, coordinated ecosystem health monitoring program for freshwaters of the region that

can be used to measure and report on current status and future changes in ecological health. To do this, the DIBM study adopted an approach similar to that previously used to detect anthropogenic impacts in marine systems (Bayne et al., 1988; Addison & Clarke, 1990; Stebbing & Dethlefsen, 1992). These studies by the Group of Experts on Environmental Pollution (GEEP) evaluated a broad range of indicators against a known disturbance gradient and identified those that best responded.

The major land uses in southeast Queensland are grazing and cropping, and these were chosen as the primary disturbance gradient against which indicators were evaluated. Data on the percentage of catchment cleared was derived from GIS, while other attributes or *descriptors* of the disturbance gradient were measured in the field. The disturbance gradient descriptors were assigned to one of six broad categories to simplify reporting and allow direct comparison of different indicators (Table 1).

A suite of potential indicators of stream health was measured at 53 sites on first to third order streams that varied in the degree of land use disturbance (from undisturbed rainforest to cleared catchments) in September and October 2000. These indicators fell into five groups: macroinvertebrates, fish, water chemistry, nutrients and nutrient cycling, and benthic metabolism (Abal et al., 2005). The response of these indicators to descriptors of reach and catchment scale disturbance was investigated using generalised linear regression modelling (see the section 'Data analysis'). This paper focuses on the results from measures of benthic metabolism and results from other aspects of the DIBM study can be found in this issue (Kennard et al., 2006; Udy et al., 2006) and in Smith & Storey (2001) and Abal et al. (2005).

### *Disturbance gradient descriptors*

Over 80 disturbance descriptors of the catchment land use disturbance gradient were derived from measurements made at the sites as well as catchment GIS data for the DIBM study. A subset of the descriptors was chosen for the analysis of each group of indicators based on conceptual models of factors influencing the indicators. For the benthic metabolism indicators, this subset included 13 descriptors from 4 categories (Table 1). *Land-use* descriptors % Cleared and % Crop cover were obtained using GIS

Table 1. Categories of disturbance gradient descriptors and the specific descriptors chosen for use in generalised linear regression modelling of benthic metabolism indicators

Descriptor category/Descriptor	Explanation
<i>1. Land-use (Catchment scale)</i>	
% Cleared	Percentage of total catchment area cleared
% Crop cover	Percentage of total catchment area cropped
<i>2. Channel Conditions (Reach scale)</i>	
Channel condition	Categorical variable, Scale 1–4, where 1 = Much aggradation/degradation, 4 = None
<i>3. Riparian Conditions (Reach scale)</i>	
HEMIPHOT cover	Measure of % riparian canopy cover at the specific site of benthic metabolism measurements using fish-eye lens (hemi) photography and image analysis
Riparian vegetation	Categorical variable, Scale 0–4, where 0 = No riparian vegetation, 4 = Excellent riparian vegetation
<i>4. Water/sediment chemistry (Reach and catchment scale)</i>	
All descriptors based on laboratory analyses of water samples taken at the time of metabolism measurements (with the exception of maximum temperature)	
Ions gradient (PCA 1)	PCA variable 1 explained 53% of the variation in site water chemistry and represented inorganic ions
NO <sub>2</sub> + NO <sub>3</sub>	Dissolved nitrite + nitrate-N concentration (mg l <sup>-1</sup> )
NH <sub>4</sub>	Dissolved ammonium-N concentration (mg l <sup>-1</sup> )
TN	Total N (mg l <sup>-1</sup> )
PO <sub>4</sub>	Filterable reactive phosphate (mg l <sup>-1</sup> )
TP	Total phosphate (mg l <sup>-1</sup> )
Maximum temperature	Maximum water temperature recorded by data logger over 24 h in open water
Turbidity	Turbidity (NTU)
<i>5. In-stream habitat – none included</i>	
<i>6. Flow related – none included</i>	

See text for a more detailed description of the methods used to quantify the descriptors.

analysis of subcatchment boundaries and State Land and Tree Survey (SLATS) data from 1999 (Queensland Natural Resources and Mines). Channel condition (*Channel Conditions* category) was assessed using a method modified from Rosgen (1994). Two measures of *Riparian Conditions* were employed: fish-eye lens photography and HEMIPHOT software (Ter Steege, 1994) were used to quantify riparian canopy cover at the location where benthic metabolism measurements were made while a categorical assessment of riparian vegetation was made over the 100 m study reach (modified from Anderson, 1993). Eight descriptors were chosen from the *Water and Sediment Chemis-*

*try* category. Maximum temperature was the maximum value recorded by a data logger left in the stream over a 24 h period (TPS 601). The remainder of the descriptors were derived from three water samples collected at each site: (1) unfiltered for total ionic composition and turbidity, (2) unfiltered for total concentrations of nutrients, and (3) filtered for concentrations of dissolved nutrients. Principal components analysis (PCA) was used to reduce the total number of water chemistry variables. PCA variable 1 explained 53% of the variation in site water chemistry and represented primarily inorganic ions (e.g. alkalinity, conductivity, chloride). Nutrients were considered individually

(nitrate + nitrite, ammonium, total nitrogen, filterable reactive phosphate, and total phosphate). No descriptors from the *In-stream Habitat* or *Flow Related* categories were chosen for analysis of the benthic metabolism indicators.

#### *Direct measurement of benthic metabolism*

In many streams and rivers, the benthic zone is the major region of organic matter processing, and negligible rates of metabolism occur in the water column (Keithan & Lowe, 1985; Davies, 1994). This is especially the case in small streams, which were the particular focus of work undertaken within the DIBM project.

Benthic metabolism was determined by measuring the net change in dissolved oxygen within a dome-shaped Perspex chamber (diameter = 29.5 cm, total height = 25 cm, total volume = 10 l) over a 24 h period at each site. A dissolved oxygen (DO) sensor (YSI 5739, USA) was located in the top of each chamber and a pump recirculated water to reduce boundary layer effects at the sediment-water interface and ensure flow saturation across the membrane of the oxygen probe. Each probe was attached to a data-logger (TPS 601), which recorded DO and water temperature at 10 min intervals. Where the streambed consisted predominantly of large cobbles, one or more cobbles were placed inside the chamber with a plastic base to provide a watertight seal. In streams with a substrate of sediment (sand or mud), the chambers were pushed into the sediment to a depth of approximately 10 cm, with an enclosed surface area of substrate of 0.068 m<sup>2</sup>. The volume of water in the chamber was measured by subtracting the volume of the cobble or sediments from the total volume. Cobble surface area was measured by wrapping the cobbles in aluminium foil, weighing the foil used to cover the rock, and using a weight-area relationship for the foil to calculate area (after McCreadie & Colbo, 1991). The metabolically "active" surface area of each cobble was assumed to be half the total cobble area (Naiman, 1983; Davies, 1994).

Different components of benthic metabolism were calculated by comparing the rate of change of DO concentration in the chambers at different times of the day. The mean rate of change at night was taken as the rate of respiration, and daily

respiration ( $R_{24}$ ) was calculated by assuming the rate was constant and multiplying by 24 h. Gross primary production (GPP) was calculated as the sum of the DO production during daylight hours plus the DO consumed by respiration during that period of time based on the night time respiration rate. Net daily metabolism (NDM) was calculated as the difference between GPP and  $R_{24}$  and P/R ratio was calculated as GPP divided by  $R_{24}$ . Changes in DO concentrations over time (mg O<sub>2</sub> l<sup>-1</sup> h<sup>-1</sup>) were multiplied by chamber volume and divided by substrate surface area to obtain values in units of mg O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>. These rates were converted to units of carbon assuming that one mole of C is equivalent of one mole of O<sub>2</sub> for both respiration and photosynthesis (i.e. 1 mg O<sub>2</sub> = 0.375 mg C, Lambert, 1984; Bender et al., 1987).

Benthic metabolism measurements were made using duplicate domes at 51 of the 53 sites. Of these 51 sites, the benthic substrate was dominated by cobbles at 26 sites and finer sediment at 25 sites. Poor equipment performance at two of the sediment substrate sites meant that usable data were collected from 49 of the sites.

#### *Algal biomass on natural substrates*

Different approaches to measuring algal biomass can be grouped into three broad categories: ash-free dry mass, pigment analysis, and biovolume of algal cells (Steinman & Lamberti, 1996). Pigment analysis using chlorophyll *a* content of benthic biofilms was used to measure benthic algal biomass in this study because it is a relatively simple technique and it removes the influence of other potential organic components of the biofilm (Steinman & Lamberti, 1996). Measurement of chlorophyll *a* on natural substrates on a particular day represents a static measure of algal biomass.

Samples were collected from the stream-bed for algal biomass determination using different techniques for the two types of bed substrate. For cobbles, algae were collected from the top surface using a Perspex cylinder that isolated 0.0015 m<sup>2</sup> with a gasket and contained a circular brush. The biofilm was scrubbed loose as ambient stream water was pumped through the cylinder and into a collection vessel. The slurry was filtered onto 0.7 μM glass fibre filters using a hand vacuum pump, and filters were frozen until analysis. A sample was

taken from each cobble used in benthic chamber measurements as well as one additional cobble, for a total of three samples from each of the 26 sites. A sample of the ambient stream water at each site was also filtered and analysed to correct the cobble values for any chlorophyll *a* in the stream water.

For sites without cobbles, small cores (surface area = 0.0006 m<sup>2</sup>) were taken using modified 60 ml plastic syringes to collect algae on sediment substrates. The top 2 cm of each core was retained and frozen until analysis. Two cores were taken at each site near the location where benthic chambers were deployed. Removal of the chambers disturbed the sediment too much to allow sediment samples to be taken from the sediment that had been enclosed in the chambers. Samples were obtained from 21 of the 22 sediment sites.

Chlorophyll *a* analysis was performed according to the methods of Parsons et al. (1984). Following extraction in 90% acetone, the solution was centrifuged and the supernatant analysed for chlorophyll *a* concentration by spectrophotometer, using an acidification step to account for phaeophytin content. Chlorophyll *a* concentration was expressed as mg m<sup>-2</sup> for all substrates.

#### *Algal growth on artificial substrates*

The control treatment of an algal bioassay experiment (see Udy et al., 2006) provided an artificial substrate for measuring growth of benthic algae. The biomass of algae at the end of deployment represents net algal accrual over the period and was considered a measure of net algal growth. Artificial substrates were made from plastic pots with lids containing a 6 cm diameter circle of 100- $\mu$ m nylon mesh. Control pots used here did not have added nutrients (treatment pots contained slow-release fertiliser; Udy et al., 2006). Two sets of pots were deployed at each site the day after benthic metabolism measurements were made, and were left for approximately four weeks prior to collection. The mesh and any attached algae was removed and frozen until analysis, resulting in two replicate samples per site. Chlorophyll *a* concentration was measured as described for natural substrates. Data from artificial substrates were not obtained for 19 of the 51 sites due to a variety of factors including exposure from falling stream levels, burial by sediment, and vandalism.

#### *Stable carbon isotopes*

Where present, aquatic plant samples (filamentous algae and submerged vascular macrophytes) were collected by hand for  $\delta^{13}\text{C}$  analysis (23 sites). Sediment samples were collected using modified 60 ml plastic syringes, with the top 5 cm of sediment retained. Sediments were collected from all the sites dominated by sediment substrate as well as cobble sites where pockets of sediment could be found, for a total of 43 sites. These samples presumably included microalgae growing on the sediment surface as well as any particulate organic matter present. All samples were frozen during transportation to the laboratory and subsequently kept frozen until prepared for stable isotope analysis. Plant samples were cleaned and rinsed in distilled water and oven-dried at 60°C for 36–48 h. Sediment samples were dried at 60°C until completely dry (up to 6 days). Dried plant and sediment samples were ground to a powder-like consistency using mortar and pestle. Ground samples were oxidised at high temperature using an elemental analyser and the resultant carbon dioxide was analysed with a continuous-flow ratio mass spectrometer (IsoPrime, Micromass, UK). Ratios of  $^{13}\text{C}/^{12}\text{C}$  were expressed in  $\delta$  notation as the relative per mil (‰) difference between the sample and conventional standard (PeeDee Belemnite carbonate):

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

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

#### *Data analysis*

In keeping with the GEEP-style approach (Bayne et al., 1988), a protocol for data analysis was devised to simplify the process of comparing the eight indices of benthic metabolism (GPP,  $R_{24}$ , P/R, NDM, chlorophyll *a* on natural substrate, chlorophyll *a* on artificial substrate,  $\delta^{13}\text{C}$  plants, and  $\delta^{13}\text{C}$  sediment). This subsequently allowed direct comparison of all the results across the various ecological indicators used in the DIBM study. Initially, distributional properties of the data were checked to identify outliers and any required transformations for subsequent statistical analyses. Preliminary investigation of relationships between

descriptors of the disturbance gradient and indices were explored using scatter plots and Spearman rank correlation coefficients to ascertain whether any simple bivariate relationships existed. A Generalised Linear Modelling (GLM) framework was used to determine whether particular metabolism indices could be used to detect the underlying disturbance gradient. While a number of multivariate approaches could have been taken, stepwise regression modelling (simultaneously searching both forwards and backwards) was employed because it not only accommodates for the different distributional forms of the indices (e.g. normal, poisson, binomial), but it also identifies which disturbance gradients account for the variability in each of the indices, and additionally quantifies the proportion of variation accounted for by each disturbance measure. The Akaike Information Criterion (AIC) was used for variable selection within the modelling procedure. Indicators were assessed in terms of the approximate amount of variation explained (approximate  $R^2$  value) by the model and the proportion of this variation explained by individual descriptors of the disturbance gradient. Data were analysed using the S-PLUS 2000 – Professional Release 3 (MathSoft Inc.) statistical software.

Only a limited number of the over 80 disturbance descriptors of the catchment land use disturbance gradient were included in the GLM to avoid over-parameterization of the regression models. In the case of the benthic metabolism indicators, 13 descriptors from 4 of the categories were chosen as the most appropriate based on conceptual models of factors influencing metabolism (Table 1), with these chosen to avoid multicollinearity. These 4 categories were described as containing measures made at the catchment scale (*Land-use*), the reach scale (*Channel Conditions* and *Riparian Conditions*), or influenced by both scales (*Water and Sediment Chemistry*).

Due to the potential for large differences between streams of different substrate types, cobble and sediment streams were analysed both separately and combined, so that it was possible to identify trends that occurred in only one of the substrate types as well as overall trends. Mean site values were used in analyses for measures where there were two or more replicates per site. Two sites were downstream of sewage treatment plants

and had total and dissolved nutrient concentrations that were two orders of magnitude greater than most other sites. These high values prevented the successful transformation of the nutrient data, so the two sites were removed from the dataset. No transformations of descriptors were required after these two sites were removed. The two sites at which benthic metabolism equipment failed were also dropped from the data set, and further analyses therefore involved 22 sediment and 25 cobble sites. Simple linear regression analysis was performed between GPP and riparian cover for comparison with previous studies as well as between GPP and several of the indirect measures to assess whether any were suitable surrogate measures.

## Results

### *Direct measures of benthic metabolism*

Rates of GPP and  $R_{24}$  varied by up to two orders of magnitude among the 47 sites included in analyses. GPP and  $R_{24}$  exhibited similar maximum, minimum, and mean values (Table 2). Mean GPP was  $610 \text{ mg C m}^{-2} \text{ d}^{-1}$  with a range from 0.01 to 2990, and mean  $R_{24}$  was  $600 \text{ mg C m}^{-2} \text{ d}^{-1}$ , with a range of 10 to 2340. Mean NDM was negative, and mean P/R was greater than 1. Slightly over half of the sites had values of P/R greater than 1. Sediment sites had greater mean values of GPP and  $R_{24}$  compared to cobble sites, but mean NDM and P/R were greater at cobble sites.

Regression modelling showed that much of the observed variability among sites in GPP and  $R_{24}$  could be explained by disturbance gradient descriptors in the *Water and sediment chemistry*, *Riparian condition*, and *Land-use* categories (Table 3). For cobble-bed streams, 89% of the variation in GPP could be explained by the overall model (Fig. 1a). Descriptors in the *Water and sediment chemistry* category contributed most to the high approximate  $R^2$  value, with Total N concentration alone contributing 59%. The Ions gradient explained an additional 11%, and the relationships of both variables with GPP had positive slopes. The ability of the disturbance

Table 2. Values of benthic metabolism indicators measured in 47 first to third order Southeast Queensland streams, September and October 2000

	All sites mean (min, max)	Cobble sites mean (min, max)	Sediment sites mean (min, max)
Gross primary production (GPP, mg C m <sup>-2</sup> d <sup>-1</sup> )	610 (0.01, 2990)	490 (0.01, 2990)	750 (31, 2100)
Respiration (R <sub>24</sub> , mg C m <sup>-2</sup> d <sup>-1</sup> )	600 (10, 2340)	330 (10, 1334)	900 (70, 2340)
Net daily metabolism (NDM, mg C m <sup>-2</sup> d <sup>-1</sup> )	-10 (-1140, 1840)	150 (-500, 1840)	-150 (-1140, 490)
P/R	1.3 (<0.01, 8.6)	1.7 (<0.01, 8.6)	0.8 (0.15, 1.3)
Algal biomass (natural substrate, mg chlorophyll <i>a</i> m <sup>-2</sup> )	52 (1, 614)	7 (1, 23)	105 (5, 614)
Algal growth (artificial substrate, mg chlorophyll <i>a</i> m <sup>-2</sup> )	11 (1, 64)		
δ <sup>13</sup> C plants (‰)	-26 (-39, -15)		
δ <sup>13</sup> C sediment (‰)	-25 (-29, -14)		

Values represent mean, minimum, and maximum for all sites ( $n = 47$ , except for algal and stable isotope values, see text for details), or cobble substrate sites ( $n = 25$ ) and sediment substrate sites ( $n = 22$ ) considered separately.

gradient descriptors to explain the variability in GPP for sites with sediment substrate was slightly weaker ( $R^2 = 79\%$ , Fig. 1b) and included factors related to *Riparian condition* and *Water and sediment chemistry*. Riparian vegetation explained 44% of the variation and the relationship had a negative slope, while relationships with Turbidity and the Ions gradient had positive slopes and  $R^2$  values of 11 and 10%, respectively. The model for all sites explained less of the variation in GPP than either substrate alone (Fig. 1c) and also included *Riparian condition* and *Water and sediment chemistry* as major descriptors. Similar to the model for sediment sites, the relationship with Riparian vegetation explained the largest portion of the variation (32%) and exhibited a negative slope, while  $\text{NH}_4^+$  concentration and the Ions gradient had  $R^2$  values of 14 and 13%, respectively, and both had positive slopes with GPP.

Canopy cover alone explained 41% of the variation in GPP across all sites when analysed using simple linear regression analysis ( $p < 0.001$ ; Fig. 2). GPP decreased with increasing canopy cover, and the relationships were very similar when sites were partitioned by substrate, with  $R^2$  values of 42% for cobbles and 37% for sediment. Note that in the case of the cobble stream sites, this relationship was not obvious in the GLM, as much of this variance is likely to have been removed in the stepwise model by Total N concentration in the *Water and sediment chemistry* category (Table 3).

As with GPP, a large proportion of the variation in  $R_{24}$  was explained by *Water and sediment chemistry* (Table 3). For cobble sites, *Land-use* was also an important descriptor category, contributing over half of the total approximate model  $R^2$  of 84% (Fig. 1d). The two *Land-use* descriptors, % Crop cover and % Cleared, made similar contributions to the total  $R^2$  at 24.4 and 21.4%, respectively. Both of these descriptors and Maximum temperature (partial  $R^2 = 38\%$ ) had relationships with  $R_{24}$  of positive slope. Descriptors in the *Riparian condition* category explained nearly half of the total 85% for sediment sites (Fig. 1e), with values of 22% for Hemiphot cover and 17% for Riparian vegetation. Similar to GPP, values of  $R_{24}$  decreased with increasing values for both *Riparian condition* descriptors. The Ions gradient in the *Water and sediment chemistry* category explained another 23% and exhibited a positive slope. Only *Water and sediment chemistry* descriptors contributed to the model for all sites (total  $R^2 = 58\%$ , Fig. 1f). The Ions gradient and Total N contributed 35 and 23%, respectively, and both relationships with  $R_{24}$  had positive slopes.

With the exception of NDM at cobble sites, descriptors of the disturbance gradient did not explain as much of the variability in net NDM and P/R as they did for GPP or  $R_{24}$  (Table 3). For both of these variables, model values of  $R^2$  were much lower for sediment sites than cobble sites, and the combined models had intermediate values. The model fit for P/R of sediment sites was very



Table 3. Regression modelling results for benthic metabolism indicators against catchment and reach scale descriptors of the disturbance gradient

Process indicators	Approximate R <sup>2</sup> overall model %	Disturbance gradient categories				Number of sites used in analysis
		Land-use %	Channel condition %	Riparian conditions %	Water & sediment chemistry %	
<i>Direct measures of benthic metabolism</i>						
Gross primary production (GPP)						
Cobble sites	89		9		80	25
Sediment sites	79		7	44	28	22
All sites	63	4		32	27	47
Respiration (R <sub>24</sub> )						
Cobble sites	84	46			38	25
Sediment sites	85		5	39	41	22
All sites	58				58	47
NDM						
Cobble sites	90	18	3		69	25
Sediment sites	49	14			35	22
All sites	38		1		36	47
P/R						
Cobble sites	25				25	25
Sediment sites	— <sup>a</sup>					22
All sites	10				10	47
<i>Algal biomass</i>						
Cobble sites	43	5	21		17	25
Sediment sites	81		6	37	38	21
All sites	29					46
<i>Algal growth</i>						
Artificial substrate	66	20		9	37	30
<i>Stable isotopes</i>						
δ <sup>13</sup> C (plants)	60	15			45	20
δ <sup>13</sup> C (sediment)	49	35	3		11	43

Total variation explained by each model is shown in the first column, and a break down of that variation into the categories in which the disturbance descriptors are grouped is shown in subsequent columns.

<sup>a</sup>very poor model fit; R<sup>2</sup> not reported.

poor and little of the observed variation was explained by any disturbance parameters.

#### *Algal biomass*

Chlorophyll *a* concentrations ranged from 1 to greater than 600 mg m<sup>-2</sup>, with a mean of 52 mg m<sup>-2</sup> (Table 2). The mean concentration on sediment substrates was over 10 times greater than that of cobble substrates. Very little of the variation in chlorophyll *a* concentrations at cobble sites or all

sites combined was explained by the disturbance gradient (Table 3, Fig. 3a and c). The model for sediment sites explained much of the variation in ambient chlorophyll *a* concentrations (Fig. 3b), with about half of this contributed by *Water and sediment chemistry* (35% from the Ions gradient) and half from *Riparian condition* category (37% from Riparian vegetation). The relationship between chlorophyll *a* and the Ions gradient had a positive slope, while the relationship with Riparian vegetation had a negative slope.

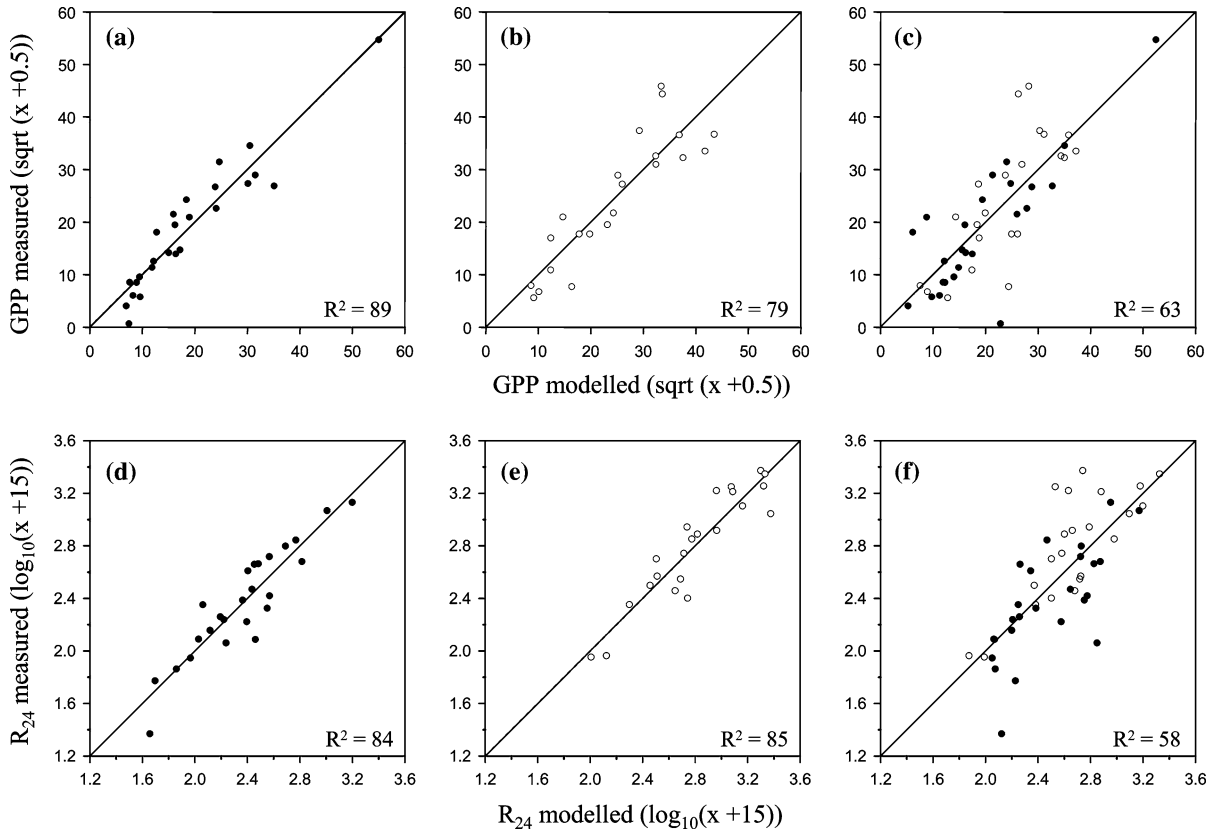


Figure 1. Regression modelling results for gross primary production (GPP) and respiration ( $R_{24}$ ) at sites with (a and d) cobble or (b and e) sediment substrate and all sites (c and f). Measured values are plotted against the modelled values using a model of disturbance gradient descriptors developed in a Generalised Linear Modelling (GLM) framework using stepwise (simultaneous forward and backward) regression modelling. The Akaike Information Criterion (AIC) was used for variable selection. Square root ( $\text{GPP} + 0.5$ ) and  $\log_{10}(\text{R}_{24} + 15)$  transformations were used for modelling. Untransformed units are  $\text{mg C m}^{-2} \text{d}^{-1}$ . Cobble sites are designated with filled circles and sediment sites are designated with open circles.

### Algal growth on artificial substrate

Chlorophyll *a* concentrations on artificial substrates ranged from 1 to 64  $\text{mg chlorophyll } a \text{ m}^{-2}$  (mean = 11,  $n = 30$ , Table 2). These equate to net biomass accrual rates of 0.03 to 2  $\text{mg chlorophyll } a \text{ m}^{-2} \text{d}^{-1}$ . Regression modelling showed that about two thirds of the variability in the chlorophyll *a* concentrations on the artificial substrates could be explained by disturbance gradient descriptors of *Water and sediment chemistry*, *Land-use*, and *Riparian conditions* (Table 3, Fig. 4). The main descriptors contributing to the model were Maximum temperature (22%),  $\text{PO}_4$  (15%), and % Cleared (14%). All three had positive relationships with chlorophyll *a*.

### Stable carbon isotopes

The  $\delta^{13}\text{C}$  values of filamentous algae and vascular macrophytes ranged from  $-39\text{‰}$  to  $-15\text{‰}$  for the 20 sites from which samples were available (Table 2). Regression modelling showed that 60% of the variability in  $\delta^{13}\text{C}$  values for aquatic vegetation could be explained by descriptors of *Water and sediment chemistry*, and *Land-use* (Table 3, Fig. 5a). Within *Water and sediment chemistry*, the Ions gradient contributed 26% and had a relationship of positive slope, while  $\text{NO}_2 + \text{NO}_3$  explained 14% but had a negative slope. An additional 15% was explained by % Cleared, with a positive slope. The range in the  $\delta^{13}\text{C}$  values of the sediment ( $-29\text{‰}$  to  $-14\text{‰}$ ,  $n = 43$  sites,

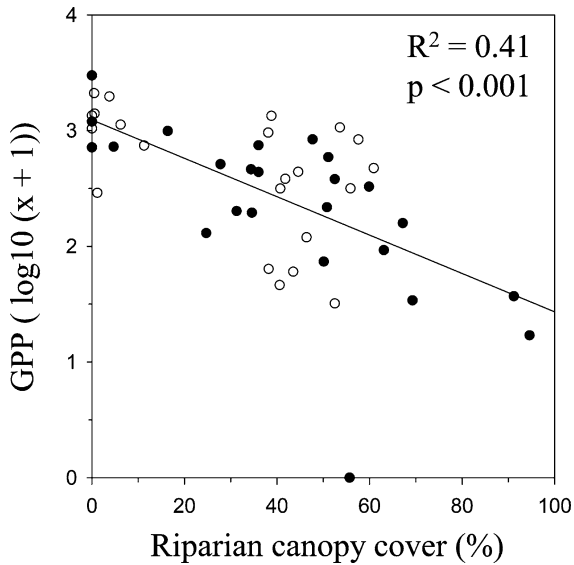


Figure 2. Relationship between gross primary production (GPP,  $\text{mg C m}^{-2} \text{d}^{-1}$ ) and riparian canopy cover as measured using fish eye lens photography and image analysis. Results of regression analysis are shown with a best fit line. Symbols as in Figure 1.

Table 2) was smaller than the range of values obtained for aquatic plants. Although the model fit for  $\delta^{13}\text{C}$  values was weaker (49%), it was also dominated by descriptors of *Land-use* (% Cleared, 35% with a positive slope) and *Water and sediment chemistry* (Ions gradient, 11%, with a positive slope)(Table 3, Fig. 5b).

### Relationships among measures of benthic metabolism

No strong relationships were found between direct measures of benthic metabolism and indirect measures. There was a reasonable positive relationship between GPP and chlorophyll *a* on natural substrates at cobble sites ( $R^2 = 44\%$ ,  $p < 0.001$ ) but the relationship for sediment sites was not significant ( $R^2 = 18\%$ ,  $p = 0.054$ ; Fig. 6). The trend was weak when all sites were considered ( $R^2 = 12\%$ ,  $p = 0.021$ ). There was no relationship between GPP and algal biomass accrual (as chlorophyll *a*) on artificial substrates ( $R^2 < 1\%$ ,  $p = 0.68$ ). Aquatic plants from sites with higher GPP generally had more enriched  $\delta^{13}\text{C}$  values ( $R^2 = 34\%$ ,  $p = 0.007$ ; Fig. 7a). A similar relationship was found between sediment  $\delta^{13}\text{C}$  values and GPP, but GPP explained only 19% of the variation (Fig. 7b). When sites of differing substrate were considered separately, the relationship was improved for sediment sites ( $R^2 = 31\%$ ,  $p = 0.009$ ) but was not significant for cobble sites ( $R^2 = 15\%$ ,  $p = 0.08$ ).

## Discussion

### Performance of ecosystem process indicators

An important feature of a good ecosystem health indicator is that it responds to the disturbance

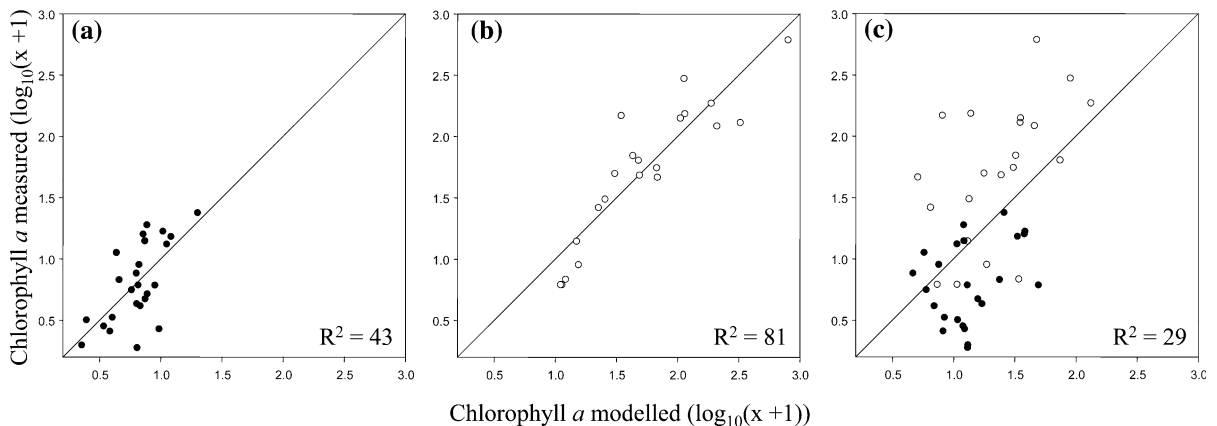


Figure 3. Regression modelling results (GLM) for chlorophyll *a* concentrations on natural substrates at sites with (a) cobble or (b) sediment substrate and all sites (c). The transformation  $\log_{10}(\text{chlorophyll } a + 1)$  was used in the model and untransformed units are  $\text{mg chlorophyll } a \text{ m}^{-2}$ . Other details are as in Figure 1.

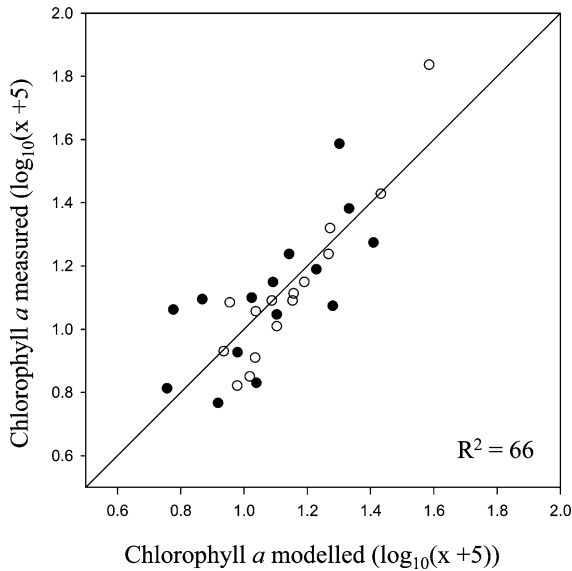


Figure 4. Regression modelling results (GLM) for chlorophyll *a* concentrations on artificial substrates. The transformation  $\log_{10}(\text{chlorophyll } a + 5)$  was used in the model and untransformed units are  $\text{mg chlorophyll } a \text{ m}^{-2}$ . Other details are as in Figure 1.

gradient of interest. For this study, the first criterion on which the indicators are judged is the  $R^2$  values of the regression models developed using Generalised Linear Modelling. However, there are

other features of indicators that should be taken into consideration. A good indicator should also have measured values spanning a relatively large range, to provide for the possibility of distinguishing intermediate levels of disturbance as well as reference vs. impacted sites. From a practical standpoint, obtaining measurements of the indicator must be feasible and yield usable results at the range of sites under consideration. For example, indicators needed to perform well for both cobble and sediment substrates in this study. Another important attribute is that there should be a clear conceptual understanding of how and why the indicator will change in response to disturbance. In the case of most of the measures of benthic metabolism, the observed response to changes in light and nutrient regimes associated with land-use change and riparian degradation were as expected: GPP,  $R_{24}$ , chlorophyll *a* on natural substrates, and  $\delta^{13}\text{C}$  values of plants generally increased with increasing percentage of total catchment area cleared and increasing nutrient and ion concentrations and decreased with increasing riparian vegetation cover.

Of the eight indicators of benthic metabolism evaluated in this study, GPP and  $R_{24}$  were the best overall indicators of ecosystem health. Both measures exhibited a range of values over two orders

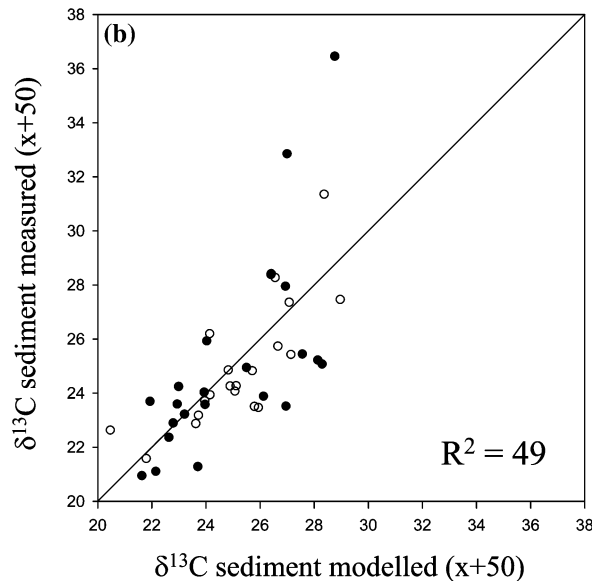
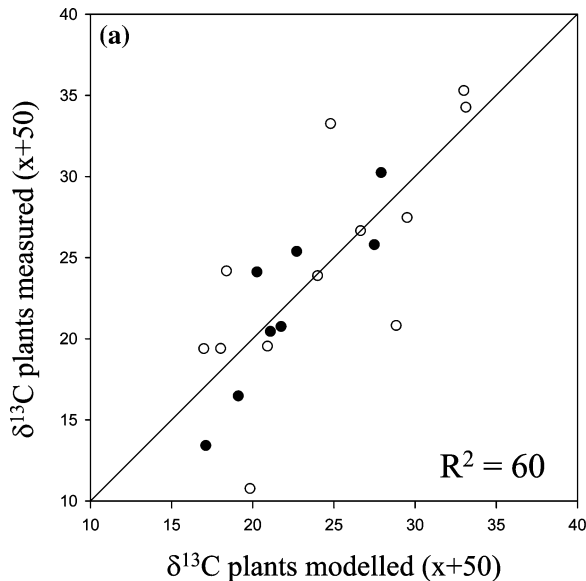


Figure 5. Regression modelling results (GLM) for  $\delta^{13}\text{C}$  values of aquatic plants (a) and sediment (b). The transformation  $\delta^{13}\text{C} + 50$  was used for both models and untransformed units are ‰. Other details are as in Figure 1.

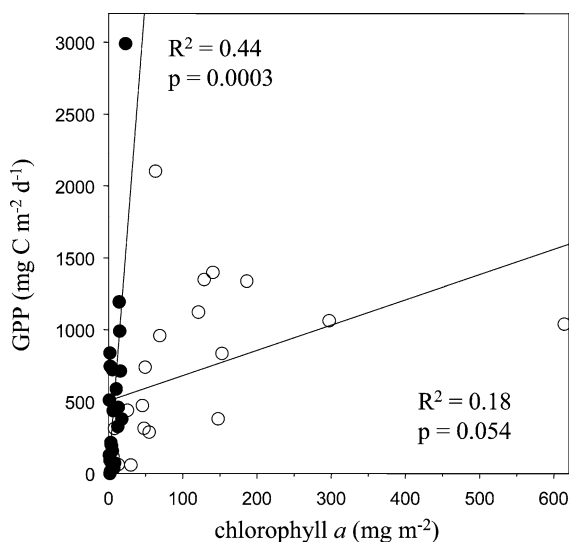


Figure 6. Relationships between gross primary production (GPP) and chlorophyll *a* concentrations on natural substrates. Results of regression analyses for cobble and sediment sites are shown with best fit lines. Symbols as in Figure 1.

of magnitude, and a high proportion of their variation could be explained by descriptors of the disturbance gradient, especially when cobble and sediment substrate sites were considered separately. Both reach scale and catchment scale factors could be considered important for these two

indicators since *Water and sediment chemistry* and *Riparian Conditions* were the categories of descriptors that explained most of the variation, and *Land-use* was important in the case of cobble  $R_{24}$ .

Algal growth on artificial substrates and stable isotopes of plants and sediment appeared to be moderately good indicators, with *Water and sediment chemistry* and *Land-use* explaining most of the variation in these indicators. Similar to GPP and  $R_{24}$ , both reach and catchment scale descriptors of the disturbance gradient were important for these three indicators. The model  $R^2$ 's were lower for these indicators than for GPP and  $R_{24}$ , but the more important limitation was the low number of sites for which data were successfully obtained for two of the three indicators. Sampling of aquatic plants was limited by the fact that they were present at fewer than half the sites. As mentioned in the Methods section, a variety of factors led to a relatively poor retrieval rate of 60% for the artificial substrates. Sediment samples for stable isotope analyses were collected for over 90% of the sites, but the  $\delta^{13}\text{C}$  values did not show as large a range in values as the plant samples and had a lower model  $R^2$  value.

With the exception of algal biomass for sediment sites and NDM for cobbles, NDM, P/R, and algal biomass on natural substrates were not ade-

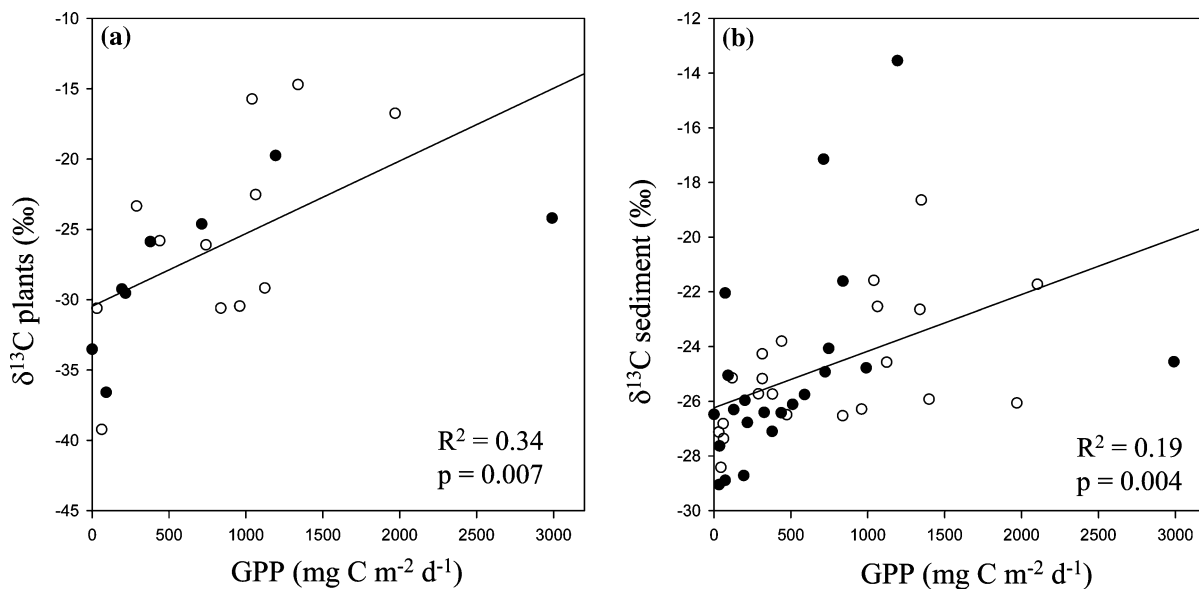


Figure 7. Relationships between  $\delta^{13}\text{C}$  values of aquatic plants (a) and sediment (b) and gross primary production (GPP). Results of regression analyses for all sites are shown with best fit lines. Symbols as in Figure 1.

quate indicators. The poor performance of NDM and P/R compared to GPP and  $R_{24}$  may be due to the fact that NDM and P/R are composites of GPP and  $R_{24}$ , and these two processes are likely to be affected by different aspects of the disturbance gradient. Because minimally impacted sites generally have intact riparian vegetation and substantial shading of the stream channel, these sites would be expected to have very low GPP and low  $R_{24}$ , yielding P/R ratios much lower than 1, and small, negative values of NDM. Both GPP and  $R_{24}$  are expected to increase with increasing catchment disturbance, but not necessarily in a way that leads to directional changes in NDM or P/R for these sites. For example, an increase in plant growth leading to P/R ratios exceeding 1 could be an indication of an impacted site. However, since disturbance may also increase sediment and organic matter input,  $R_{24}$  could increase independently of the increase in GPP, leading to disturbed sites with P/R less than 1.

#### *Comparison of benthic metabolism rates with other studies*

The range of sites in this study included catchments with very little clearing as well as predominately agricultural catchments, and riparian vegetation canopy cover levels of zero to almost 100%, so it is not surprising that values of GPP measured in this study (0.01 to 2990 mg C m<sup>-2</sup> d<sup>-1</sup>) nearly span the range of values reported in the literature. The lower end of the values for GPP measured in the current study compare well to the range of 20 to 1280 mg C m<sup>-2</sup> d<sup>-1</sup> for benthic chamber measurements in multiple reaches of four streams in three different biomes in North America (Bott et al., 1985, values taken only from stream reaches of orders 1 to 3 and units of oxygen were converted to carbon using a factor of 0.375 as described in the Methods). While a similar range of 20 to 710 mg C m<sup>-2</sup> d<sup>-1</sup> was reported using whole-stream open system measurements for forested streams in North America, the maximum value in the current study is less than half the value of 7500 mg C m<sup>-2</sup> d<sup>-1</sup> reported for a desert stream (Mulholland et al., 2001; values in units of oxygen also converted to carbon). Values of  $R_{24}$  from this study (10 to 2340 mg C m<sup>-2</sup> d<sup>-1</sup>) are similar to those reported by Bott et al. (1985, 70 to 1110 mg C m<sup>-2</sup> d<sup>-1</sup>) but span a moderately wider

range. Benthic chamber measurements made by Bunn et al. (1999) in forested streams of the Johnstone River catchment in north Queensland, the Northern jarrah forest, Western Australia, and the Mary River catchment, just north of the study area, fall at the lower end of the range of values of this study, with GPP ranging from 90 to 200 mg C m<sup>-2</sup> d<sup>-1</sup>, and  $R_{24}$  ranging from 170 to 380 mg C m<sup>-2</sup> d<sup>-1</sup>. When sites in the Mary River with varying amounts of grazing land-use are considered in addition to the forested sites, the maximum GPP and  $R_{24}$  values increase to 2100 and 1550 mg C m<sup>-2</sup> d<sup>-1</sup>, respectively (Bunn et al., 1999), but are still lower than the maximum values from this study. It is interesting to note that the slope, intercept, and  $R^2$  for the relationship between GPP and riparian canopy cover from this study (Fig. 2) are almost identical to that for reach level data from the 20 Mary River sites presented in Bunn et al. (1999).

#### *Surrogate measures of GPP*

None of the indirect measures of benthic metabolism proved to be adequate surrogates for GPP. Most of the relationships between individual indirect measures and GPP were not significant when explored using simple linear regression. Of those that were significant, the highest  $R^2$  was 44%. In general, these indicators all would be expected to respond to similar factors such as light, nutrients, stream velocity, etc. The lack of relationship is probably influenced by different factors in each situation, but one possibility is the different time scales over which the indicators respond. GPP and  $R_{24}$  are measured over 24 h and are influenced by conditions on that day, as well as the condition of substrate biofilm. Chlorophyll *a* content of biofilm on natural substrate likely reflects influences over the weeks to months during which the biofilm develops (4 weeks in the case of the artificial substrates) and is influenced by grazing and physical disturbance regimes. Similarly, material collected for stable isotope analysis integrates days to weeks for filamentous algae and even longer for aquatic macrophytes. Since indirect measures may be responding to different factors, and over different time scales, they appear to be complementary to direct measures, as opposed to serving as surrogate measures.

The lack of relationship between GPP and chlorophyll *a* on sediment and low  $R^2$  for cobbles is surprising considering that the substrates sampled for chlorophyll *a* were near where the chambers were deployed or actually in the chamber in the case of cobbles. Sites varied as to whether or not filamentous algae were present, and undoubtedly there were other less obvious differences in algal species across sites. Different types of algae exhibit different relationships between photosynthetic rate and chlorophyll *a* content (Krause-Jensen & Sand-Jensen, 1998). For example, sites dominated by benthic microalgae would be expected to have higher rates of GPP per mg of chlorophyll *a*, than sites dominated by filamentous algae. Even within the same species of unicellular algae, or aquatic macrophytes, variation in chlorophyll *a* concentrations have also been observed due to light availability (e.g. plants in low light environments producing additional chlorophyll *a* to maximise their ability to capture the available light) (Abal et al., 1994). This relationship between light availability and chlorophyll *a* concentrations is in contrast to the general trend that the total chlorophyll *a* of a streambed will increase as more light becomes available. It is also likely that differences in rates of invertebrate grazing between sites will have a large impact on the algae biomass present at a site, but might have a smaller influence on the primary production rates as this is predominantly controlled by light and nutrient availability (Rosemond et al., 1993).

The relationships between  $\delta^{13}\text{C}$  values and GPP were in the expected direction for both plants and sediment, with values increasing (becoming less negative) with increasing rates of GPP. However,  $R^2$  values of 34% and lower for the relationships for data from this study point to variation due to the influence of additional factors. The  $\delta^{13}\text{C}$  values of aquatic plants can be affected by changes in the rates of organic matter decomposition, respiration and water motion (Farquhar et al., 1989; France, 1995), so GPP is not expected to be the only influencing factor. In the case of sediment values,  $\delta^{13}\text{C}$  values are those of the organic carbon component of the sediment. Since sediment organic carbon could originate from multiple possible sources, a tight relationship with GPP would only be expected in streams where detritus from in-stream plant production dominated the organic

carbon pool. The relationships between  $\delta^{13}\text{C}$  values and GPP in this study were not tight enough to use plant and sediment samples as a surrogate for GPP measurements. It may be the case that  $\delta^{13}\text{C}$  values are more useful as independent indicators than they would be as surrogates because of the fact that  $\delta^{13}\text{C}$  values are influenced by multiple aspects of carbon cycling.

#### *Differences at sites with cobble vs. sediment benthic substrate*

Differences in the materials enclosed in chambers when deployed at sites dominated by cobbles compared to sites dominated by finer sediments suggest that is appropriate to keep the analyses of these two types of sites separate. In both types of sites, the chambers enclose all the photoautotrophs in the surface area under consideration since photosynthesis can only take place on the upper surfaces. However, chambers inserted into sediment substrates also enclose the microbial community in the sediment to the depth of insertion, which will contribute additional respiration. In contrast, when cobbles are inserted in the chambers, only metabolism of the microbial community associated with the cobble surface is being measured. As a result, higher rates of  $R_{24}$  are expected per square meter in sediment sites compared to cobble sites. The differential incorporation of subsurface microbial respiration may be one reason that the model explaining variation in NDM was weak for sediment sites but not for cobble sites.

## **Conclusions**

Stream ecosystem health monitoring has only recently begun to incorporate measures of ecosystem processes (Bunn et al., 1999; Bunn & Davies, 2000; Hill et al., 2000), despite the long history of the importance of these measures to stream ecology research and their demonstrated effectiveness in assessment of particular impacts on individual systems, such as heavy metal pollution (Crossey & La Point, 1988; Hill et al., 1997). Ecosystem process measures are effective indicators of stream ecosystem health in settings where responses of the processes to the disturbance of interest can be determined through an understanding of how factors associated

with disturbance influence the processes. This study demonstrates the effectiveness of using measures of benthic metabolism to detect impacts of a diffuse land-use disturbance gradient on stream ecosystem health in southeast Queensland. The same measures of ecosystem process may not work equally well in different settings, but a similar process of developing conceptual models, identifying features of reference and impacted sites, and evaluating process indicators should be applicable to other systems.

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