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Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream

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Abstract. Creightons Creek, a rural stream in southeastern Australia, has been severely degraded by large-scale sedimentation of sand in the streambed. Our paper highlights the use of whole-stream metabolism measurements, fluorescein diacetate hydrolysis studies, and in situ enzyme mapping to examine the effect of sediment instability on benthic and hyporheic metabolism across seasonal and flow variations in Creightons Creek. Median gross primary production (GPP) and ecosystem respiration (ER_{24}) rates, determined over a 20-mo period with the whole-stream single-station diurnal O_2 change method, ranged between 0 and 0.5 g O_2 m^{-2} d^{-1} and 0.6 and 3.7 g O_2 m^{-2} d^{-1}, respectively. These values gave photosynthesis/respiration (P/R) ratios between 0.00 and 0.41, indicative of a heterotrophic system. Creightons Creek was expected to support higher GPP because it has an open canopy, clear water, warm temperatures, and sufficient nutrients. However, this once-clay-bottomed stream now has an abrasive benthic layer of sand that moves continuously, even at low flows, and this layer has inhibited the growth of benthic primary producers (0–2 mg/m^2 of chlorophyll *a*). During high flows, when scour and abrasion from the bed movement were at a maximum, the highest relative enzyme activity was located in the hyporheic zone at a depth of 7 to 12 cm, where the sediment was more stable. During low flows, the highest enzyme activity occurred in the upper 4 cm of the sediment profile. Our study shows that the instability of the sediment bed is a major factor determining the rates and locations of metabolism.

Key words: sediment, stream metabolism, sediment stability, primary production, stream velocity, hyporheic zone.

Significant growth of benthic biofilms, filamentous algae, and macrophytes typically is expected in a small freshwater stream with a warm climate, an open canopy, clear running water, and high concentrations of nutrients. In these conditions, primary production rates can exceed ecosystem respiration (Grimm and Fisher 1984, Sinsabaugh 1997, Uehlinger et al. 2002). However, several studies (e.g., Grimm and Fisher 1984, Valett et al. 1994, Naegeli and Uehlinger 1997, Uehlinger 2000, Uehlinger et al. 2002) have found that the physical stability of the sediment is also an important factor controlling the establishment and growth of primary producers.

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Biofilms, algae, and macrophytes usually are restricted to stable substrata, which might include channel margins, backwater areas, and parafluvial sediments (Grimm and Fisher 1984, Naegeli and Uehlinger 1997). When sediments move during high-flow events, shear forces and abrasion by transported bed sediments severely damage or eliminate organisms living at the channel surface and in the top layers of sediment (Holmes et al. 1998, Uehlinger and Naegeli 1998). High flows damage the benthic primary producers more than the heterotrophic community in the hyporheic zone and cause an even more-pronounced heterotrophic state (Romani et al. 1998, Uehlinger and Naegeli 1998, Uehlinger 2000, Uehlinger et al. 2002). The instability of bed sediments also is related to substrate size; sand is less stable than clay-lined channels or gravel–cobble beds (Morisawa 1968). Streams with sand-bed sediments can have a surface layer that is in continuous motion even at low flow (Verdonschot 2001, Uehlinger et al. 2002).

Twenty percent of streams in southeastern Australia have been severely degraded by large-scale sedimentation of sand in the stream beds (Prosser et al. 2003). This sandy sediment is derived predominantly from massive catchment-scale erosion caused by anthropogenic activities, such as land clearing and agriculture, which might be compounded by bushfires (Davis and Finlayson 2000, Prosser et al. 2003). The influx of sediments into streams from such landuse practices and the resultant damaging effects have been well documented in stream ecosystems around the world (Quinn et al. 1997, Nerbonne and Vondracek 2001, Hecky et al. 2003, Wallbrink 2004, Rabeni et al. 2005). Large-scale sediment additions change the stream morphology, for example, by submerging pool and riffle sequences, and can leave an unstable, even, and relatively homogeneous streambed (Davis and Finlayson 2000, Bartley and Rutherfurd 2005).

The study stream, Creightons Creek, is expected to support high primary productivity because it has an open canopy, clear water, warm temperatures, and sufficient nutrient concentrations. However, because of excessive sedimentation of the streambed, this once-clay-bottomed stream now has an abrasive benthic layer of sand that moves continuously, even at low flow (Davis and Finlayson 2000). Our paper examines the influence of sediment instability on the rates and locations of gross primary production (GPP) and ecosystem respiration (ER_{24}) across seasonal and flow variations.

Methods

Study reach

Creightons Creek is located in southeastern Australia and has a catchment area of ~174 km^2. In the study area, the creek flows through an unconfined floodplain with an average channel width of 8 to 10 m. This small stream is spring fed and continues to flow in all but severe drought conditions. Long-term monthly rainfall at the nearby town of Euroa is at a minimum in February (32 mm) and maximum in June (76 mm). The mean daily maximum temperatures at Euroa are 12.3°C in July and 29.6°C in January (BOM 2006). The main land use in this rural catchment is cattle and sheep grazing. The riparian vegetation is predominantly sparse and discontinuous, consisting primarily of river red gums (*Eucalyptus camaldulensis*).

Creightons Creek has changed dramatically since the start of the 1900s. Originally, the channel contained deep pools and runs. However, an estimated 240,000 m^3 of sandy sediment, derived from erosion of the granite-dominated catchment, has settled on the streambed along a 30-km stretch of the creek (Davis and Finlayson 2000). The creeks in this region have distinctive elongated catchments, dominated by low relief and low gradients. Creightons Creek has one of the lowest hill-slope–channel connectivity values (~7%) recorded (Davis and Finlayson 2000). This low value means that efficiency of sediment transport through the stream network is very low because of low stream power.

Our study focused on 6 sites (each 100 m in length), each separated by ≥1 km along the heavily sedimented section of Creightons Creek (Table 1). These sites were associated with a rehabilitation project to reintroduce wood into the stream (see Bond and Lake 2005). Three of the 6 sites were treatment sites that had 4 large wooden structures (0.25 m × 15 m railway sleepers [ties]) added, and the remaining 3 were control sites with no experimental manipulations. For the measurements discussed here, no significant differences were detected between the treatment and control sites (nested repeated measures 1-way analysis of variance [ANOVA], $p > 0.05$), although the power to detect such differences, given the variability among sites, was very small (Atkinson 2007). Detecting differences between treatments was *not* the purpose of our study, but this data set forms part of a broader body of research into the effect of large wood additions on stream function, and this fact explains why treatment sites and control sites (no wood additions) had unequal numbers of piezometers installed and sediment cores taken (see *Surface and hyporheic water chemistry* section). No nearby unimpacted streams were available for comparative studies because of the large-scale degradation (Downes et al. 2006).

The 6 sites along Creightons Creek were sampled every 3 mo between January 2004 and August 2005. For every sampling trip, samples and measurements were taken at all sites on consecutive days, typically over a 1-wk period.

Flow and velocity measurements

Salt addition to the stream (Gordon et al. 2004) was used to quantify the flow and average velocity of the stream water at each site during the January to November 2004 sampling trips. On the other sampling dates, a current meter (Model CMC 20; Hydrological Services, Sydney, Australia) was used across a transect of the stream at each site ($n = 10$ points/transect) to determine flow and velocity. A more comprehensive survey of stream velocity and water depths at each site was conducted in October 2005 during high flow using the current meter, when multiple measurements of local velocity were taken randomly at each site ($n = 25$ measurements/100-m reach).

TABLE 1. Site coordinates along Creightons Creek. Sites are listed from upstream to downstream. The numbers in parentheses refer to the number of railway sleepers added to the study reach.

Site reference	Latitude	Longitude
Site 1—Railway (4)	36°47′22″S	145°28′25″E
Site 2—Drysdale (0)	36°45′19″S	145°26′08″E
Site 3—Geodetic (4)	36°44′50″S	145°25′51″E
Site 4—Tehans (4)	36°44′28″S	145°25′01″E
Site 5—Lords (0)	36°44′04″S	145°24′43″E
Site 6—Hills (0)	36°43′18″S	145°23′35″E

Particle-size distribution

Three sediment cores (0–12 cm) were taken using a polypropylene cylinder (3-cm diameter) from the thalweg at each site. Each core was dried (40°C for 48 h) and sieved through a series of 2.0-, 1.0-, 0.5-, and 0.15-mm-mesh sizes, and each fraction was weighed. The mass of the total sediment core and the individual masses of each size fraction were used to calculate the % mass of each size fraction to obtain a particle-size distribution for each site.

Surface and hyporheic water chemistry

Surface water-quality measurements at each site (pH, electrical conductivity, turbidity, dissolved O_2 [DO], and temperature) were taken using a Horiba Water Quality Checker U-10 (Horiba, Kyoto, Japan). Surface water samples were collected in 60-mL acid-washed polyethylene syringes from the thalweg, and hyporheic water was sampled from piezometers (Lee and Cherry 1978) installed at a sampling depth of 20 cm beneath the stream thalweg 2 h prior to sampling. Fifteen piezometers were installed at regular intervals throughout treatment sites, and 5 were installed in control sites. The piezometers were constructed from 1-m lengths of polyvinyl chloride (PVC) pipe with a nylon tube (0.5-cm diameter) fixed to the exterior. A fine mesh covered the base of the pipe and tube. The interstitial water was drawn up through the tube using a 60-mL polyethylene syringe. DO and temperature of the hyporheic water samples were determined immediately after slowly drawing a sample (to avoid air bubbles) into the syringe. The plunger was then carefully removed from the full syringe while the nozzle was blocked, and it was replaced by a YSI Model 55 Dissolved Oxygen Probe (Yellow Springs Instruments, Yellow Springs, Ohio), which was calibrated on site.

Three samples each of surface and hyporheic water were collected and analyzed for dissolved organic C (DOC), total P (TP), and total N (TN). Samples for DOC were filtered through Supor 200 (47-mm diameter, 0.2-μm pore size; Pall Corporation, Ann Arbor, Michigan) filters and acidified with 10-M HCl to a final $pH < 2$. DOC analyses were done with a Total Organic Carbon Analyzer (Model TOC-5000; Shimadzu, Kyoto, Japan). TP and TN concentrations were analyzed by flow-injection analysis (Quik Chem method 8000; Lachat Instruments, Loveland, Colorado) using an acid persulfate digestion (methods 5310B and 4500-PJ; APHA 2005). Compliance with the National Association of Testing Authorities (NATA; Australia) laboratory procedures and protocols was achieved by using standard reference materials and including blanks and duplicate samples in all assays. Upwelling and downwelling zones were determined from the vertical hydraulic gradient at each piezometer using a potentiomanometer (Winter et al. 1988).

Single-station open-system metabolism

DO sensors with attached data loggers (DO100; Greenspan Technology, Warwick, Queensland, Australia) were used to measure DO concentration and temperature in the water column every 5 min over an average deployment time of 40 h at each site. Photosynthetically active radiation also was logged every 5 min using light meters (Odyssey Data Recording Systems, Unshrouded Water Level Probe; Dataflow Systems, Christchurch, New Zealand) deployed beside the stream. Prior to deployment, the DO sensors were air calibrated together in a water-saturated environment for ≥ 2 h. The downloaded data were then corrected for deviations from 100% saturation during the air calibration. Equipment malfunction, caused by abrasion to the probe membrane leading to water penetration to the sensor, resulted in an occasional complete loss of data or poor R^2 values for the modeling process described next. Typically, 2 DO sensors were positioned at each site during each sampling trip (i.e., $n = 12$); however, the number of successful observations ranged from $n = 2$ to $n = 11$.

The diel variations in stream DO concentrations were modeled for each site to estimate GPP and ER_{24}. Kosinski (1984) critically evaluated a number of approaches used to extract these metabolic variables based on equation 1:

$$\frac{dC}{dt} = (P - R + KD), \quad [1]$$

where C is dissolved O_2 concentration (mg/L), P = rate of photosynthesis (mg L^{-1} d^{-1}), R = rate of respiration (mg L^{-1} d^{-1}), K = reaeration coefficient (d^{-1}), and D = O_2 saturation deficit/surplus (mg/L).

The approach taken in this work was based on the "daytime" regression method proposed by Kosinski (1984), where the photosynthesis term in equation 1 is replaced by AI^p, where A is a constant, I is the surface irradiance, and p is an exponent reflecting the ability of the primary producers to use the incident light (accounts for saturating photosynthesis). Equation 2, which is used in the data analysis, incorporates the temperature dependence of both reaeration (Kilpatrick et al. 1989) and respiration. A temperature dependence factor, θ, of 1.072 is commonly used to estimate respiration based on the assumption that respiration rate doubles for every 10°C temperature increase. In our study, respiration rate was calculated with θ as a parameter to be determined, but θ was constrained within the range 1.0 to 1.2.

$$\frac{\Delta[O_2]_i}{\Delta t} = AI_i^p - R(\theta^{(temp_i - temp_{av})}) + K(1.0241^{(temp_i - temp_{av})})D_i. \quad [2]$$

The parameters, A, K, p, R, and θ were derived from equation 2 using iterative numerical methods to minimize the difference between the modeling results and the measured DO concentrations using Model Maker 4.0 (AP Benson, Wallingford, UK). Estimates of daily GPP and ER_{24} were converted to g O_2 m^{-2} d^{-1} using the average depth of the stream.

Chlorophyll a

Sediment cores (15 from each treatment site and 5 from control sites) were taken from 0- to 12-cm depths within the sediments with a polypropylene cylinder (3-cm diameter). Surface (0–2 cm) and hyporheic (9–11 cm) sediments were removed from each core and analyzed for chlorophyll *a*. Algal samples also were scraped from 3-cm-diameter sections of the wood added at the treatment sites. The samples were stored in the dark on ice until extracted with 90% acetone. Chlorophyll *a* and pheophytin *a* concentrations were determined spectrophotometrically on a Hitachi UV-Vis (U-2000; Hitachi, Tokyo, Japan) at 665 to 750 nm with acidification (1-M HCl) (method 10200H; APHA 2005) within 7 d of sample collection. Core samples for chlorophyll *a* determination were not collected on the January 2004 field trip, and only surface chlorophyll *a* samples were taken during the May 2004 field trip.

Microbial metabolism

Fluorescein diacetate (FDA) hydrolysis and a novel enzyme-mapping device were used to determine the location of the microbial communities responsible for the stream metabolism. All chemicals were obtained from Sigma–Aldrich (St Louis, Missouri). Fluorescein diacetate hydrolysis was used to detect metabolically active zones in the surface and hyporheic sediment (Battin 1997). FDA is a nonfluorescent, nonpolar esterified compound that is hydrolyzed to fluorescein by cellular and extracellular enzymes produced in the matrix of the biofilm (Lundgren 1981, Chrzanowski et al. 1984, Battin 1997). All active cells should cleave the molecule because FDA is hydrolyzed by nonspecific esterases (Chrzanowski et al. 1984). Claret and Boulton (2003) first adapted the FDA hydrolysis method for use in Australian sand-bed streams. Samples of ~1 g of sediment were taken from each core (see *Chlorophyll* a section) for both surface and hyporheic depths at all 6 sites and put into acid-washed glass vials. Immediately, 3 mL of phosphate buffer (pH 7.6) and 0.1 mL of FDA (2 g/L) were added. Each vial was gently shaken and incubated at in situ field temperatures in the dark until a faint green color appeared (10–60 min). At this point, the reaction was stopped by adding 3 mL of acetone (Battin 1997), and the time was recorded. The samples were then stored on ice in the dark until they were frozen prior to analysis (within 6 h of collection). Analysis occurred within 7 d of sample collection. The samples were thawed and the absorbance was determined at 490 nm using a 1:1 mixture of acetone and the buffer as a reference. The sediment was dried at 105°C for 24 h to determine the dry mass of sediment used. Microbial hydrolytic activity was expressed as a rate of FDA hydrolyzed with the units: μmoles FDA g^{-1} dry mass h^{-1}.

An enzyme-mapping technique developed by Rogers and Apte (2004) was used to construct a depth profile of in situ relative enzyme activity in the sediments at submillimeter resolution. A rectangular filter paper (16 cm × 3 cm) loaded with naphthol AS-MX acetate ($C_{21}H_{19}NO_3$, 0.6 μmol/cm^2) was attached to a plastic ruler and inserted vertically into the sediment in the thalweg of the stream, perpendicular to the flow for 24 h. Eight filters were positioned randomly throughout 1 study reach per field trip. Enzymes in the sediment cleaved the acetate from the naphthol AS-MX, leaving an active site. The device was then removed from the sediment, and the filter paper was developed in a 30-mM solution of the azo dye, Fast Red TR, which binds to the active site and forms a red precipitate. The filter was scanned digitally at 200 dots per inch (dpi) using a conventional flat-bed scanner and converted to grayscale intensities using the program Scion Image for Windows (Beta 4.0.2, 2000; Scion Corporation, Frederick, Maryland). A calibration curve of grayscale intensities was prepared for a series of naphthol AS-MX loadings on filter paper, and this relationship was used to convert to moles of product formed per unit area over the 24-h

TABLE 2. Flow rates, stream velocities (mean ±1 SD), and number of days from a significant rainfall (>20 mm) event to the sampling date.

	Sampling date	Flow (ML/d)	Velocity (m/s)	Days after rainfall
Low flow	January 2004	2.1 ± 0.1	0.19 ± 0.08	72
	January 2005	2.0 ± 1.0	0.18 ± 0.03	50
	May 2004	5.0 ± 2.0	0.23 ± 0.04	161
	April 2005	2.6 ± 0.9	0.21 ± 0.06	55
	June 2005	4.3 ± 0.4	0.22 ± 0.08	116
High flow	August 2004	50 ± 10	0.42 ± 0.19	12
	August 2005	69 ± 3	0.42 ± 0.09	3
	November 2004	45 ± 7	0.34 ± 0.02	10

period (nmol naphthol AS-MX cm^{-2} d^{-1}) to yield relative enzyme activity.

Statistical analysis

Repeated-measures 1-way ANOVAs were used to compare stream water-chemistry values with hyporheic water-chemistry values (means of the hyporheic samples [5 or 15] collected at each site). Habitat type (stream/hyporheic) was used as the main between-subjects factor (with 6 site replicates for both stream and hyporheic), and the 8 sampling dates were used as the within-subjects factor. One-way ANOVA was used to determine if there was a seasonal trend in metabolism variables, and nested repeated-measures ANOVA was used to test for differences in hydrolytic activity and chlorophyll *a* concentrations between habitat types. These analyses were conducted using SYSTAT (version 11; Systat, San Jose, California).

Results

Flow and velocity

In January and May 2004, and January, April, and June 2005, flow was classified as low (or base) (≤10 ML/d). In August and November 2004 and August 2005, the creek was at a moderate/high flow (>10 ML/d) after significant rain events (Table 2). The creek dried between February and April 2004 because of extreme drought conditions. Velocities of the flowing stream were positively correlated with stream flow ($p < 0.005$, $F = 104$, $R^2 = 0.945$; Table 2). Similar stream velocities were found by Bond and Lake (2003) on the same stream.

Physicochemical water quality

Trends in stream and hyporheic DO, DOC, TN, TP, and temperature data were compared over the study period (Fig. 1A–E). DOC concentrations and temperature in the hyporheic zone were indistinguishable from those of the stream water ($p = 0.47$, $p = 0.07$, respectively) and varied according to seasonal and flow conditions (Fig. 1A, E). In all cases, DO was lower in the hyporheic zone than in the stream water ($p < 0.001$; Fig. 1B). However, even at low flow, hypoxia was localized but not prevalent, suggesting some degree of

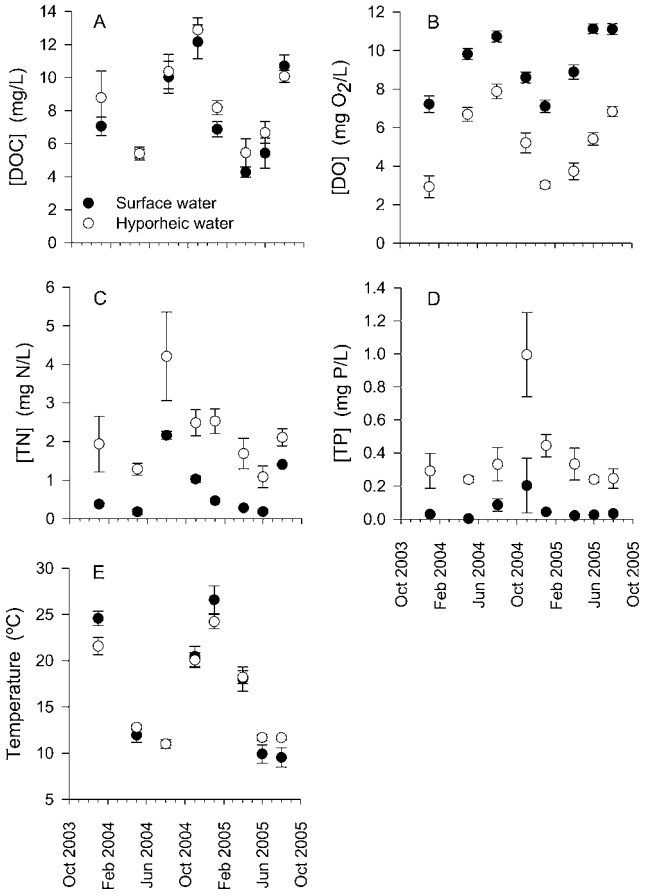

FIG. 1. Mean (±1 SD) dissolved organic C (DOC) (A), dissolved O_2 (DO) (B), total N (TN) (C), and total P (TP) (D) concentrations and water temperature (E) in hyporheic and surface water at 6 sites on Creightons Creek over the sampling period.

TABLE 3. Ranges of variables in measurements of stream metabolism in Creightons Creek determined using the single-station method. Median values for gross primary production (GPP), ecosystem respiration (ER_{24}), the ratio of photosynthesis to respiration (P/R), and the reaeration rate (K) and mean values for average stream temperature (T_{av}) are given in parentheses. θ = temperature dependence factor (found iteratively), ND = no data collected because of equipment malfunction.

Date	n	Flow (ML/d)	Mean depth (m)	T_{av} (°C)	GPP g O_2 m^{-2} d^{-1}	ER_{24} g O_2 m^{-2} d^{-1}	P/R	K (d^{-1})	θ	R^2 for models
January 2004	8	0.5–4.0	0.08	13–33 (21)	0–0.60 (0.15)	0.24–7.6 (0.98)	0.00–0.97 (0.09)	0–29 (13)	1.01–1.13	0.59–0.95
May 2004	4	3.6–4.5	0.10	7.6–17 (11)	0–0.086 (0.00)	0.10–2.2 (0.65)	0.00–0.11 (0.00)	2.6–12 (9.2)	1.00–1.17	0.58–0.94
August 2004	11	31–74	0.31	7.1–12 (9.2)	0–1.9 (0.49)	0.83–6.6 (3.7)	0.00–0.57 (0.20)	3.8–35 (16)	1.00–1.19	0.58–0.99
November 2004	2	42–48	0.25	15–20 (17)	0–0.13 (0.063)	0.98–1.1 (1.0)	0.00–0.13 (0.07)	0.00–1.1 (0.59)	1.00–1.08	0.56–0.89
January 2005	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
April 2005	8	1.2–3.0	0.09	14–21 (17)	0.01–0.54 (0.18)	0.22–4.1 (0.93)	0.00–0.34 (0.17)	2.9–20 (6.1)	1.00–1.2	0.94–0.99
June 2005	6	3.6–4.4	0.11	6.8–12 (9.1)	0.22–0.56 (0.36)	0.52–1.5 (0.83)	0.37–0.58 (0.41)	3.5–11 (7.5)	1.00–1.19	0.87–0.99
August 2005	3	68–71	0.37	8.7–11 (10)	0.19–2.0 (0.42)	1.8–3.4 (3.0)	0.06–0.58 (0.23)	17–20 (19)	1.00–1.19	0.82–0.91

interchange between the surface and interstitial waters. TN and TP concentrations were significantly higher in the hyporheic zone than in the surface water ($p = 0.003$, $p < 0.001$, respectively; Fig. 1C, D). The concentrations of these nutrients in the stream and hyporheic zone also increased with flow. Water-column TP concentrations were >0.02 mg P/L on each occasion, except for May 2004, when a very low mean concentration of 0.003 mg P/L was measured. Water-column TN concentrations were always >0.15 mg N/L. Hyporheic-zone TP and TN always were >0.2 mg P/L and 1.0 mg N/L, respectively.

Whole-stream metabolism

GPP, ER_{24}, and K for Creightons Creek were determined using the single-station method (Table 3, Fig. 2A–D). These 3 variables differed substantially among sites. The largest range in GPP occurred in August 2004 and August 2005 when measurements were taken 12 and 3 d after significant rainfall. High variability in August values probably occurred because 6 reaches were measured over 6 d during a period when stream metabolism was recovering rapidly following flooding. In all cases, GPP < ER_{24}, and P/R < 1. GPP and P/R did not differ significantly between high- and low-flow conditions ($p = 0.087$, $p = 0.57$, respectively; Fig. 2B, D). However, flow and the rate of ER_{24} were significantly positively related ($p < 0.005$, $R^2 = 0.20$). K values ranged between 0 and 35 per day over the study period (Table 3) and were highest in August 2004 and August 2005 because of an increase in stream turbulence from fast stream velocities during high-flow conditions.

Surface and hyporheic sediment samples were taken for chlorophyll *a* measurements at the same time as the open-system metabolism method was done (Table 4). Significantly higher concentrations of chlorophyll *a* were found at low flow during summer and autumn ($p < 0.001$) than at high flow in winter and spring. In

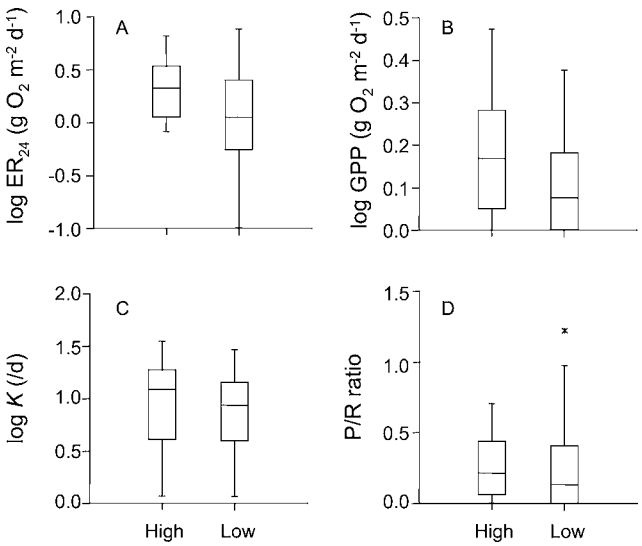

FIG. 2. Box-and-whisker plots for gross primary production (GPP) (A), ecosystem respiration (ER_{24}) (B), reaeration coefficient (K) (C), and the ratio of photosynthesis to respiration (P/R) (D) at high and low stream flow. Lines inside boxes are medians, ends of boxes are quartiles, and whiskers are the ranges of values.

TABLE 4. Chlorophyll *a* (chl *a*) and pheophytin *a* (pheo *a*) concentrations in surface (0–2 cm) and hyporheic sediments (9–11 cm). Unless otherwise indicated, $n = 60$. ND = no data collected.

Flow	Date/season	Sample	Chl *a* (mg/m^2)	Pheo *a* (mg/m^2)	Chl *a*:pheo *a*
Low	January 2004	Surface	ND	ND	ND
	summer	Hyporheic	ND	ND	ND
	January 2005	Surface	2 ± 2	4 ± 2	0.6
	summer	Hyporheic	1 ± 1	1 ± 2	0.4
	May 2004	Surface ($n = 40$)	2 ± 4	4 ± 5	0.6
	autumn	Hyporheic	ND	ND	ND
	April 2005	Surface	2 ± 4	5 ± 6	0.5
	autumn	Hyporheic	1 ± 2	2 ± 3	0.4
	June 2005	Surface	2 ± 4	5 ± 7	0.5
	winter	Hyporheic	0.4 ± 2	2 ± 3	0.2
High	August 2004	Surface ($n = 40$)	1 ± 1	1 ± 1	0.5
	winter	Hyporheic ($n = 40$)	0.3 ± 0.3	0.6 ± 0.3	0.5
	August 2005	Surface	0.1 ± 0.6	0.7 ± 0.8	0.2
	winter	Hyporheic	0.4 ± 1	1.4 ± 1.5	0.3
	November 2004	Surface	0.1 ± 0.4	0.4 ± 0.7	0.3
	spring	Hyporheic	0.2 ± 1	1 ± 1	0.2

all cases, some chlorophyll *a* was detected 10 cm below the surface in the hyporheic zone. The ratio of chlorophyll *a* to pheophytin *a* (chlorophyll decomposition product) was lower in the hyporheic zone than at the surface ($p = 0.001$).

A comparison of the relative amounts of chlorophyll *a* detected on the benthos, hyporheic zone, wood additions (railway sleepers), and stream water (Fig. 3), shows that the highest chlorophyll *a* concentrations were associated with the wood additions in both high- and low-flow conditions.

Benthic and hyporheic metabolism

Measurements of FDA hydrolysis at in situ temperatures were done on the surface and in hyporheic sediments (Table 5). Hydrolytic activity generally was higher at the sediment surface than at a depth of 10 cm, except in November 2004 during high flow. The surface:hyporheic hydrolytic activity ratio was significantly ($p = 0.039$) lower during high-flow conditions than during low-flow conditions.

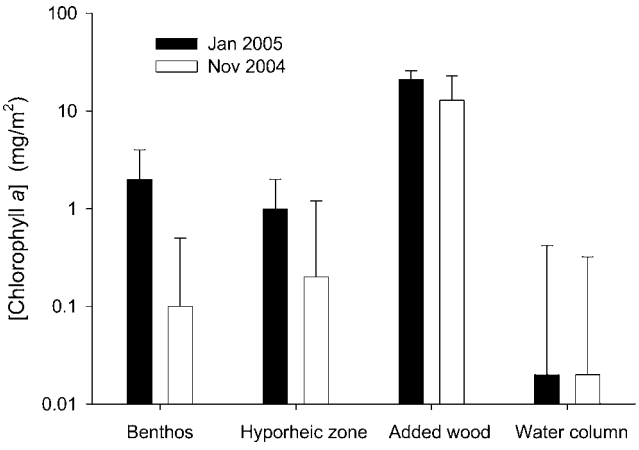

FIG. 3. Mean (+1 SD) chlorophyll *a* concentrations on different substrates, plotted on a logarithmic scale, for November 2004 (high flow) and January 2005 (low flow).

Under high-flow conditions when scour of the sand bed was high (Table 3), the highest enzymatic activity in the sediment occurred at depths between 7 and 12 cm (Fig. 4A). Under low-flow conditions, enzymatic activity was more evenly distributed throughout the 16-cm depth profile, but slightly more activity occurred in the top 4 cm of sediment (Fig. 4B).

Discussion

Algal biomass and ecosystem metabolism in Creightons Creek

The environmental conditions of Creightons Creek, such as an open canopy and clear, shallow water leading to good light availability at the benthos, a temperate climate and warm water temperatures, and a rural catchment yielding normally sufficient supplies of N and P, would typically favor growth of benthic biofilms, algae, and macrophytes. Despite these favorable conditions, the biomass of primary producers in Creightons Creek is very low. P limitation in the water column might have occurred in May 2004, but very low TP was not commonly observed.

Median GPP and ER_{24} rates ranged between 0 and 0.5 g O_2 m^{-2} d^{-1} and 0.6 and 3.7 g O_2 m^{-2} d^{-1}, respectively, giving P/R ratios between 0.00 and 0.41. Whole-stream metabolism variables for Creightons Creek are comparable with those in a selection of

TABLE 5. Summary of fluorescein diacetate (FDA) hydrolysis rates in surface (0–2 cm) and hyporheic sediments (9–11 cm). Unless otherwise indicated, $n = 60$. ND = data not collected.

Flow	Date/season	Sample	Hydrolytic activity (μmol FDA h^{-1} g^{-1})	Surface: hyporheic activity
Low	January 2004 summer	Surface	0.050 ± 0.007	1.7 ± 0.02
		Hyporheic	0.0300 ± 0.0002	
	January 2005 summer	Surface	0.019 ± 0.004	2.4 ± 0.4
		Hyporheic	0.008 ± 0.003	
	May 2004 autumn	Surface ($n = 40$)	0.037 ± 0.020	ND
		Hyporheic	ND	
	April 2005 autumn	Surface	0.026 ± 0.001	2.1 ± 0.6
		Hyporheic	0.01 ± 0.01	
	June 2005 winter	Surface	0.06 ± 0.04	1.8 ± 0.1
		Hyporheic	0.037 ± 0.001	
High	August 2004 winter	Surface ($n = 40$)	0.038 ± 0.03	1.6 ± 0.9
		Hyporheic ($n = 40$)	0.023 ± 0.01	
	November 2004 spring	Surface	0.016 ± 0.004	0.9 ± 0.4
		Hyporheic	0.017 ± 0.008	
	August 2005 winter	Surface	0.009 ± 0.004	1.4 ± 0.3
		Hyporheic	0.0070 ± 0.0001	

other systems that have similar catchment characteristics, e.g., sandy bottoms (GPP = 0.45–0.9, ER_{24} = 0.32–0.34, P/R = 1.16–1.25; Grimm and Fisher 1984), agricultural land use (GPP = 0.66–1.19, ER_{24} = 4–10, P/R = 0.18 ± 0.05; McTammany et al. 2007), or a temperate climate (GPP = 0.013–0.76, ER_{24} = 0.043–1.0, P/R = 0.42 [median]; Wilcock et al. 1998). GPP in Creightons Creek is relatively low, particularly in comparison to other agricultural streams with good light availability (McTammany et al. 2007), but it is comparable with the sand-bed Hassayampa River, Arizona (GPP = 0.0–0.29, ER_{24} = 1.33–1.65, P/R = 0–0.17), where Uehlinger et al. (2002) concluded that sediment instability had a detrimental effect on the metabolism of the river. Other studies have shown that GPP is positively correlated with photosynthetically active radiation, algal biomass, and nutrient concentrations (Young and Huryn 1996, McTammany et al. 2007). However, GPP in Creightons Creek was not significantly correlated with any of these variables.

Primary producers are notably lacking in Creightons Creek over a full range of seasons, as indicated by unexpectedly low concentrations of chlorophyll *a* (Creightons Creek: maximum = 2 mg/m^2; cf. Biggs 1995: low chlorophyll *a* in 16 streams in New Zealand = 2.1 mg/m^2; McTammany et al. 2007: chlorophyll ranging from 2.0 mg/m^2 in forested streams to 12 mg/m^2 in agricultural streams). The most plausible explanation for the low primary producer biomass in Creightons Creek is the continual motion of the sand bed, particularly in the uppermost 1 to 2 cm of sediment. Particle-size distributions were determined for the 6 sites along the heavily sedimented stretch of Creightons Creek (Fig. 5). The distributions were similar at all sites, although the downstream sites had slightly higher percentages of finer particles (<0.5 mm) than the most upstream site. The critical erosion velocity for particles <2 mm in diameter, which constitute 50 to 90% by mass of all surface sediment particles in Creightons Creek (Fig. 5), is ~0.20 m/s (based on the relationship of particle size to current velocity; Morisawa 1968, Allan 1995). A cumulative distribution plot for stream velocity shows that, under high-flow conditions, 88% of the wetted area is above the critical erosion velocity, and under low-flow conditions, 58% is above this threshold (Fig. 6). This movement of the sediments scours and buries photosynthetically active algal communities and biofilms in the streambed. Davis and Finlayson (2000) used scour chains in Creightons Creek and reported scour of 25 to 30 cm in small annual events, whereas scour of up to 5 cm occurred under baseflow conditions. The rapid and dynamic turnover of sediment is highlighted by the consistent occurrence of measurable amounts of chlorophyll *a* at depths of 10 cm (Table 4).

A comparison of chlorophyll *a* measured in the benthos, hyporheic zone, wood additions, and stream water shows that the highest chlorophyll *a* concentrations (hot spots for GPP) were associated with the most stable substrata (i.e., wood; Fig. 3). The establishment of primary producers on stable substrate in Creightons Creek strongly suggests that sediment instability, and not light, nutrients, or temperature, is the limiting factor inhibiting their development on the benthos. Biofilms attach readily and develop on wood in aquatic systems (Sinsabaugh et al. 1991, Tank and

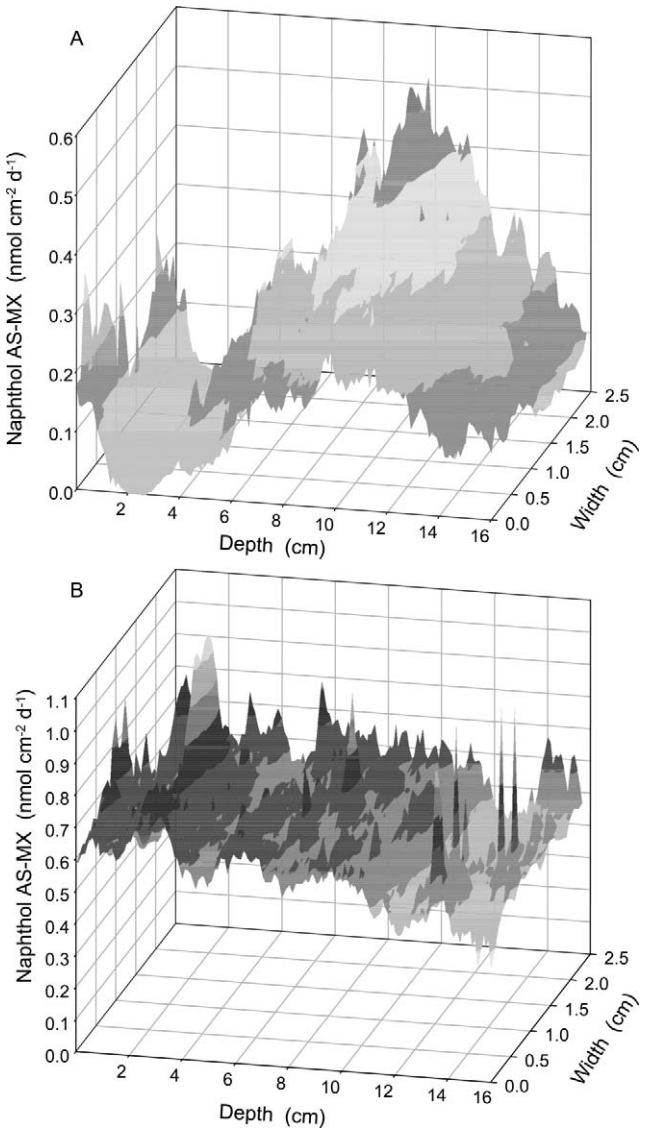

FIG. 4. Three-dimensional depth profiles (16 cm × 3 cm) comparing the sediment enzyme activity (measured as cleavage of naphthol AS-MX acetate) during high-flow (50 ML/d, winter; August 2004) (A) and low-flow (2 ML/d, summer; January 2005) (B) conditions.

Winterbourn 1995, Treadwell 2002). Scour pools up to 0.5 m deep developed around the wood additions. Slower stream velocities in the pools also would encourage biofilm growth on the wood surfaces. Stable large woody debris is a natural feature of many Australian lowland streams (Treadwell 2002), but it is very sparse in Creightons Creek because of burial by sand, snag removal, and loss of riparian vegetation. Note that GPP associated with biofilms on wood was insufficient to elevate reach-scale whole-stream GPP over respiration demands.

The instability of the benthic sediments is expected

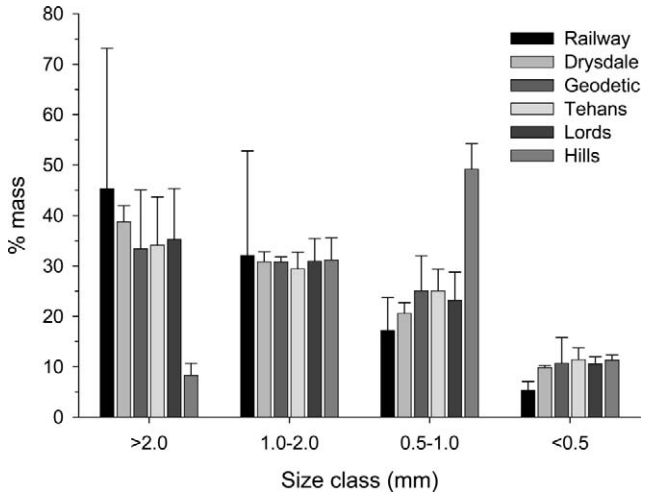

FIG. 5. Mean (+1 SD) percentage of particles in each size class in sediments collected from the thalweg (0–10-cm depth; $n = 3$) at each of the 6 sites along the stream. Sites are arranged in order from upstream to downstream (railway is the most upstream site).

to affect GPP more than ER_{24} because primary producers are largely restricted to lighted surfaces (Uehlinger and Naegeli 1998, Uehlinger et al. 2002). Creightons Creek fits this expectation. Creightons Creek is a heterotrophic stream ($P/R < 1$), where the energy required for ER_{24} comes from allochthonous sources of organic C. Hyporheic DOC concentrations were very similar to water-column DOC concentrations. This result suggests either that the hyporheic zone does not store DOC or that any stored DOC is metabolized rapidly (Fig. 1A). Therefore, metabolism in the sediments depends on the continuous supply of allochthonous organic C from the riparian zone or

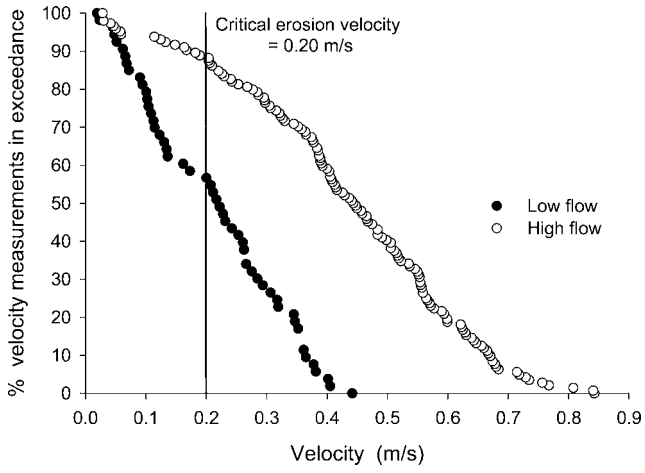

FIG. 6. Cumulative distribution plot comparing stream velocities in high flow ($n = 150$) and low flow ($n = 55$). Vertical line shows critical erosion velocity = 0.20 m/s.

from surface stream water. TN and TP concentrations were $\geq$2.5$\times$ higher in the hyporheic water than in the stream water on all sampling occasions, indicating that the hyporheic sediments trap and store nutrients. Algal detritus also is provided by the continuous turnover of sediment and downward transport of fine particulate organic matter through the porous sand sediment by vertical advection, exemplified by the small, but measurable, concentrations of chlorophyll *a* at depth. Significant concentrations of chlorophyll pigments also have been detected at depths of 5 to 10 cm in intertidal sand flats where horizontal currents ranged between 0 to 32 cm/s (Rusch et al. 2001) and up to 90 cm/s (Hedtkamp 2005).

The spatial distribution of ER_{24} was investigated using FDA hydrolysis and in situ enzyme mapping. In moderate/high-flow conditions, the highest relative enzyme activity was detected at a depth of 7 to 12 cm, presumably because the velocity of the water and the shear force exerted on the bed sediment caused greater scour and abrasive bed movement at the surface (Fig. 4A, B). The deeper sediments were seemingly less influenced by the high flows and had a better established and, therefore, more enzymatically active microbial community. In contrast, during low flow (January 2005; Fig. 4B), the highest enzyme activity occurred in the upper 4 cm of the sediment profile, although the low-flow depth profiles indicated less differentiation in enzymatic activity among depths than did the high-flow profiles. Less abrasion and smothering of biofilm and algae at the surface of the sediments from sand movement occurred during low-flow (and velocity) than during high-flow periods. The biofilm matrix itself also might stabilize the sandy sediment if low flows occur for long periods (O'Connor 1993). The hyporheic zone has low concentrations of DOC and localized hypoxia in summer (Fig. 1A), which might cause a decrease in aerobic hyporheic metabolism (Findlay et al. 2003, Vanderkruk 2004). A decrease in microbial activity with depth because of low DO has been observed in other freshwater sediments (Meyer and Edwards 1990, Triska et al. 1993, Claret and Boulton 2003). The differences between the low-flow (2 ML/d; Fig. 4A) and moderate/high-flow (50 ML/d; Fig. 4B) enzymatic activity profiles suggest that the depth of metabolic activity is dependent upon the interplay of substrate stability and supply of DO and DOC.

Ecological implications

The inability of biofilms to become properly established on the sediments is expected to adversely affect the fish and macroinvertebrate populations inhabiting Creightons Creek. The markedly low species richness and mean number of individuals in Creightons Creek (O'Connor and Lake 1994) can be explained by the combined effects of a restricted basal food resource (algae and biofilm) and reduction of habitat diversity, such as pools and fallen timber, from inundation by the sand. The wood additions (stable substrate) in Creightons Creek were colonized rapidly by algae within this otherwise strongly heterotrophic stream, and Bond et al. (2006) demonstrated that these hot spots of primary production were colonized quickly by large numbers of macroinvertebrates. An increase in the abundance of native fish species also was observed around the wood additions (Bond and Lake 2005). However, the wood additions did not generate a detectable difference in reach-scale rates of GPP and ER_{24}.

In conclusion, sand-bed streams can occur naturally, e.g., in semiarid southwestern North America (Grimm and Fisher 1984, Uehlinger et al. 2002). However, in southeastern Australia, sand is smothering >20% of the naturally clay-bottomed streams (Prosser et al. 2003). These sandy sediments are not natural but rather are caused by anthropogenically induced erosion that has occurred in many granitic catchments. The adverse effects of sediment instability on the stream function have been highlighted in our study, which identifies sediment instability as a primary stressor on the ecological health of Creightons Creek, especially under moderate to high flows. Our results also have important implications for understanding the biogeochemistry of sedimented streams and for assisting rehabilitation efforts.

Our paper highlights the utility of the FDA hydrolysis and enzyme-mapping techniques as tools for determining the location of metabolically significant microbial communities in freshwater sediments. Both FDA hydrolysis and enzyme mapping added additional insight into ecosystem functioning in this heavily sedimented stream. These techniques will not differentiate between aerobic and anaerobic microbial communities because esterase enzymes are ubiquitous (Battin 1997). Nevertheless, they provided understanding of the heterogeneity in the metabolism and distribution of active microbial communities at the millimeter scale in a relatively homogeneous sandy substrate.

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