
11 RIVER METABOLISM

11.1 INTRODUCTION

Photosynthesis, respiration, and the diffusion of oxygen across a river's surface combine to produce diurnal fluctuations in dissolved oxygen concentrations (Odum 1956). The photosynthetic production of oxygen is light dependent and so fluctuates diurnally. Oxygen diffusion into or from a river's surface is primarily a function of dissolved oxygen concentrations relative to saturation levels, and will also fluctuate diurnally in response to the photosynthetic mediated oxygen concentrations. Respiration by aquatic flora, fauna and microbes, however, continuously consumes dissolved oxygen. Collectively, these processes determine dissolved oxygen concentrations and are referred to as river metabolism.

Diurnal fluctuations and concentrations of dissolved oxygen are diagnostic of a river's trophic status. Oligotrophic rivers have oxygen concentrations typically close to saturation levels, with small diurnal fluctuations, whilst more productive, eutrophic rivers feature significant diurnal fluctuations that may range from near anoxia to super-saturation. Diurnal dissolved oxygen fluxes are indicative of river trophic status, and respond to eutrophication. To assess the impact of eutrophication on river oxygen dynamics, pre-disturbance conditions should be known to provide a reference for comparative purposes.

In this chapter, the metabolism of the Daly River and its tributaries is examined to:

- Provide baseline data for future monitoring,
- Gain an understanding of temporal and spatial patterns in river photosynthesis, respiration and oxygen exchange, and
- Provide an insight into the response of river metabolism to eutrophication.

11.2 METHODS

11.2.1 Study sites and measurement frequency

River metabolism was measured at seven sites in the Douglas Daly region (Figure 11.1, Table 11.1). Metabolism was measured at four sites (DR5, DG2, DG4 and HC3) approximately every month between June and October, whilst at the other sites metabolism was measured on 1-3 occasions. The Daly River is a 7th order stream, and the Douglas River a 6th order stream downstream of Hayes Creek. Hayes Creek is a 6th order stream and Middle Creek a 4th order stream.

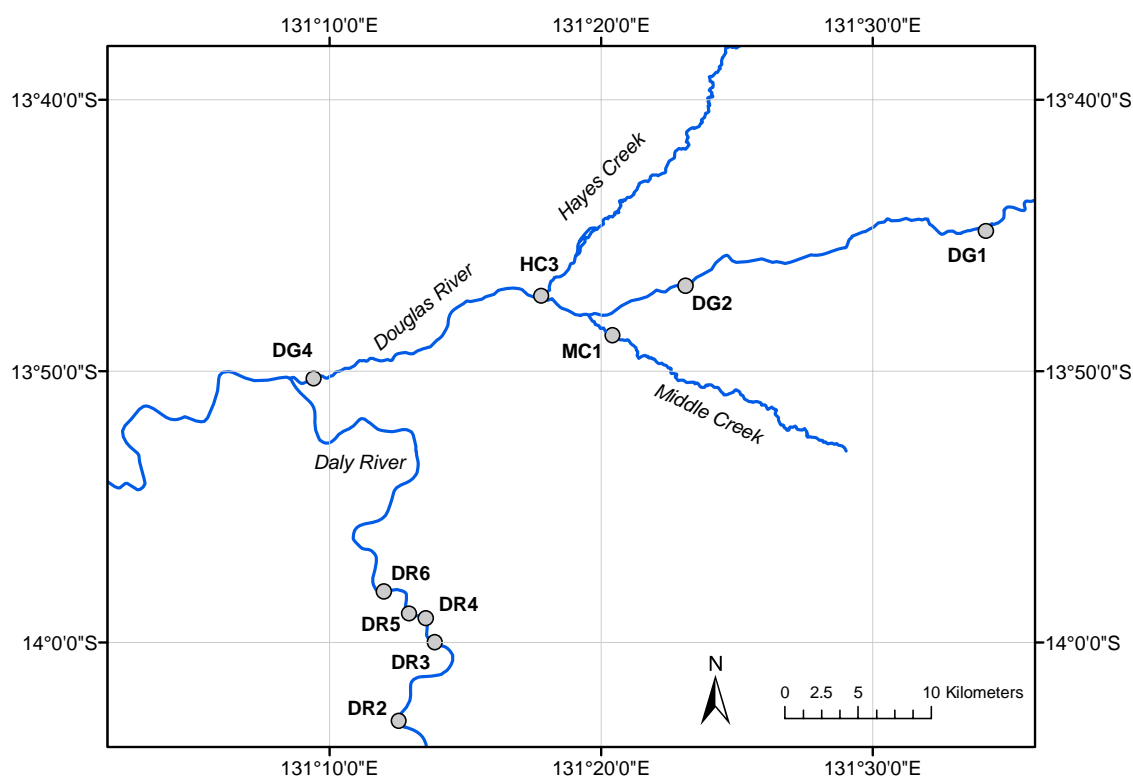


Figure 11-1 Douglas Daly Region sites

Table 11.1 Douglas Daly Region sites

<i>Site code</i>	<i>Site description</i>	<i>HYDSTRA site*</i>	<i>Measurement dates</i>
DR3	Daly River, Esplanade Conservation Area.	G8145385	Apr 14, Aug 17, Sep 14.
DR5	Daly River, Esplanade Conservation Area, 3.35 km downstream of DR5.	G8145708	May 10, Jun 16, Jul 4, Jul 28, Aug 8, Sep 9, Sep 27, Oct 25, Nov 8.
DG1	Douglas River, 1 km downstream of Butterfly Gorge.		Aug 8
DG2	Douglas River, 4 km upstream of Oolloo Rd crossing.	G8145422	May 10, Jun 16, Jul 4, Aug 8, Sep 9, Sep 27, Oct 25
DG4	Douglas River at Tipperary Road Crossing	G8140325	May 10, Jun 16, Jul 4, Aug 8, Sep 9, Sep 27, Oct 25
HC3	Hayes Creek, 20 m upstream of the confluence of the Douglas River	G8145712	Jul 4, Aug 8, Sep 9, Sep 27, Oct 25
MC	Middle Creek, 30 m downstream of Oolloo Rd crossing	G8145418	Aug 19, Sep 8.

* Department of Natural Resources, Environment and the Arts HYDSTRA water resource database sites.

River metabolism was also measured along a 360 km reach of the Katherine-Daly Rivers to examine broad longitudinal patterns (Fig. 11.2). One site (DR5) was located in the Daly Douglas region. Measurements of river metabolism were undertaken on July 28 and November 8. The Katherine River is a 6th order stream at KR1 and KR3.

Metabolism was measured during the seasonal recessional flow of the rivers and streams in the Daly river catchment (Fig. 11.3), with November measurements preceded by the first, albeit small, run-off events of the 2005/06 wet season.

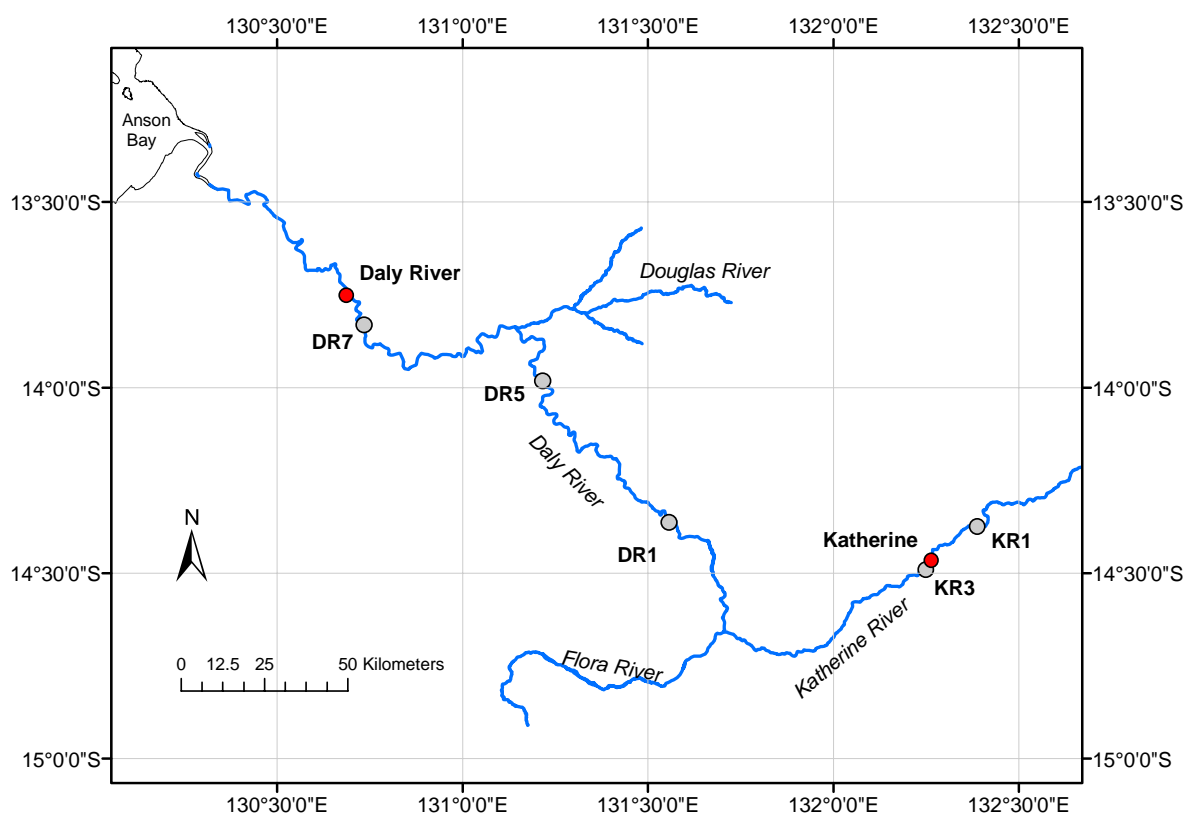


Figure 11-2 Katherine Daly River sites.

11.2.2 Diurnal measurements

Temperature, pH and dissolved oxygen (O₂) were measured every 10 minutes with a multi-parameter probe (Hydrolab DataSonde 4a, Austin, Texas) over periods of at least 30 hours. Each instrument was calibrated before and after deployment. Water samples were collected

for the analysis of alkalinity and chlorophyll *a* when the probe was deployed, and analysed by the methods outlined in Chapter 3. Other water quality parameters were measured at these sites, and are discussed in Chapter 3.

Average temperature, dissolved oxygen and pH measurements presented are for 24 hour periods. The diurnal variation in dissolved oxygen between its maximum daily value typically in the late afternoon, and daily minimum value at sunrise is referred to as the diurnal dissolved oxygen flux.

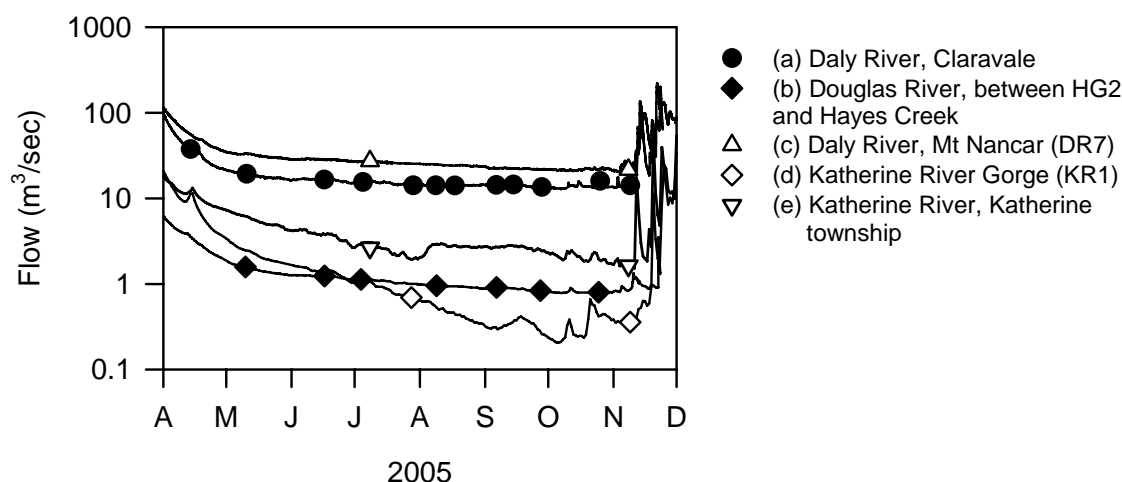


Figure 11-3 River flow and metabolism measurement dates for (a) Daly River at Claravale Crossing (G8140067) and sample dates for sites DR1 – DR6, (b) Douglas River (G8140063) and sample dates for DG2 and DG4, (c) Daly River at Mt Nancar (G8140040) and sample dates for DR7, (d) Katherine River at Katherine Gorge (G8140022) and sample dates for KR1, and (e) Katherine River at Katherine township (G8140001) and sample dates for KR3. Department of Natural Resources, Environment and the Arts HYDSTRA hydrographic sites are in parentheses.

Table 11.2 Katherine-Daly River sites

<i>Site label</i>	<i>Site description</i>	<i>HYDSTRA site*</i>	<i>River distance upstream of DR7</i>
KR1	Katherine River, near Helipad	G8140033	335.9 km
KR3	Katherine River, Low level bridge.	G8140014	312.8 km
DR1	Daly River, Claravale causeway.	G8145610	186 km
DR5	Daly River, Esplanade Reserve.	G8145708	103.5 km
DR7	Daly River, Mt Nancar.	G8140040	0 (10.6 km upstream of Daly River township crossing)

* Department of Natural Resources, Environment and the Arts HYDSTRA water resource database sites.

Incident photosynthetically active radiation (PAR) was recorded every 5 minutes in the Douglas Daly region with a LiCor (Lincoln, USA) meter and sensor, coincident with most measurements at site DR5. Recording was undertaken on the following dates: May 11, July 5, July 28-30, August 9-11, September 9, 15 and 28, and October 10.

11.2.3 Oxygen analysis

The rate of change of O₂ within the river reach was assumed to be due to: (i) photosynthetic production by primary producers, (ii) respiration by primary producers, fauna and microorganisms, and (iii) gas exchange across the water's surface. Analyses were undertaken as detailed by Webster et al. (2005).

11.2.4 Biomass Survey

In mid-August 2005, an estimate of the biomass and standing crop of primary producers, as chlorophyll *a*, was made along a 15.2 km reach of the Daly River upstream of site DR5. Within this reach, biomass and standing crop were determined for 10 km reaches upstream of sites DR3 and DR5 that correspond to the estimated daily travel distance for river flow. The inclusion of site DR3 permits a comparison of primary producer biomass determined by Webster et al. (2005) for the same reach of river in 2001 with the data collected in 2005.

The biomass and standing crop of primary producers were determined for the following: *Vallisneria nana*, *Chara*, *Spirogyra*, phytoplankton, and epibenthic algae on mobile sand, sessile sand and gravel. Mobile sand was determined by observations of the sand bed, its most obvious feature were "dunes of sand" and the movement of sand particles. Where flows were low, the sand had a firm, unbroken surface that was typically brown in colour due probably to diatoms.

Vallisneria nana was the dominant macrophyte at the time of sampling, with others (e.g. *Blyxia sp.*, *Ludwigia adscendens*, *Ceratopteris thalictroides*, *Ceratophyllum demersum*) present but in negligible amounts. Triplicate water samples were collected to determine the biomass of phytoplankton. To determine the biomass of sessile primary producers the area of river bed covered by each category was determined, and the biomass for each primary producer category estimated. Mobile sand was assumed to have negligible epibenthic algae.

The area of the river bed substrates was undertaken for the following categories: mobile sand, sessile sand and gravel. The area of each substrate was determined from a grid of 325 points along the river reach. The study reach was divided into sixty-five 250 m long sections, within which a randomly chosen transect perpendicular to the river bank was chosen and represented by 5 equidistant points. A substrate category was then assigned to each point, which was extrapolated to rectangular areas with average dimensions of 11 m width and 190 m length.

To determine the biomass of epibenthic algae, samples were collected from gravel and sessile sand. An upside-down 4.5 cm diameter Petri dish was pushed in the substrate, and a spatula slid underneath to remove the substrate. A larger 9 cm diameter Petri dish was used where the substrate comprised of large gravel material, which was scrapped of epibenthic algae.

Samples were stored on ice in the field, and then frozen. After thawing, the samples were ground with a mortar and pestle in a known volume of 90% acetone, and placed in an ultrasonicator for 30 minutes. These samples were then analysed by fluorometry for chlorophyll *a* (APHA 1998).

The biomass of *Chara* and *Vallisneria* along the river bank was assessed in 65 quadrats, each 2m long and extending 4m into the river. These were randomly located on either side of the river along 250m reaches, and assessed for the aerial cover of each plant expressed as a percentage of cover. On the river bed, 100 quadrats (0.25m²) were randomly sited and scored for the aerial cover of *Spirogyra*, *Chara* and *Vallisneria*.

To convert the *Vallisneria* and *Chara* scores to biomass, the aerial cover was scored for each plant for 15 quadrats, sampled destructively, dried at 60 °C, and then analysed for chlorophyll *a*. Biomass was determined from a linear regressions between aerial cover and biomass for *Chara* ($r^2=0.67$, $p<0.01$) and *Vallisneria* ($r^2=0.77$, $p<0.01$). *Spirogyra* was converted from aerial cover to biomass by applying the relationship determined by Townsend and Padovan (2005).

11.2.5 Canopy cover survey

Canopy cover over the rivers was assessed along a 10 km reach upstream of sites DR3, DR5, DG2, DG4 and HC3 in October 2005 using a convex, hemispherical densitometer (Lemmon 1957). At 1 km intervals, the average of four densitometer readings was taken from mid-channel, facing upstream and downstream and to the left and right banks. Where the river was braided (Douglas River, 25% of sites) readings were taken for each channel and averaged with a weighting for channel width.

11.3 RESULTS

11.3.1 Canopy cover, turbidity and incident PAR

Canopy cover over the Douglas River along 10 km reaches upstream of sites DG2 and DG4 averaged, respectively, 25% and 37%, whilst over Hayes Creek it averaged 57%. Riparian tree canopy cover did not extend over the middle of the Daly River channel.

The Daly River and its tributaries have clear waters over the dry season. Turbidity was low (average 2.0 NTU), with euphotic depths in the Daly River (average 7.4 m) that exceeded river depth. Incident Photosynthetically Active Radiation (PAR) in the Douglas Daly region

averaged 1420 $\mu\text{E}/\text{m}^2/\text{sec}$ between 09:00 and 17:00 hrs, and 1705 $\mu\text{E}/\text{m}^2/\text{sec}$ between 11:00 and 15:00 hours. The mid-point of these periods equates to solar noon.

11.3.2 Temperature, dissolved oxygen and pH in the Douglas Daly Region

Average daily water temperatures exhibited a marked seasonal pattern (Fig. 11.4) which mirrored atmospheric temperatures that reach a minimum in July. Over the dry season, water temperatures ranged between 24°C and 34 °C which equates to saturated O₂ concentrations of 8.4 mg/L and 7.1 mg/L respectively. Water temperatures were ≈ 2 °C higher in the Daly River in July and August compared with the Douglas River, possibly due to canopy cover over the Douglas River and its tributaries.

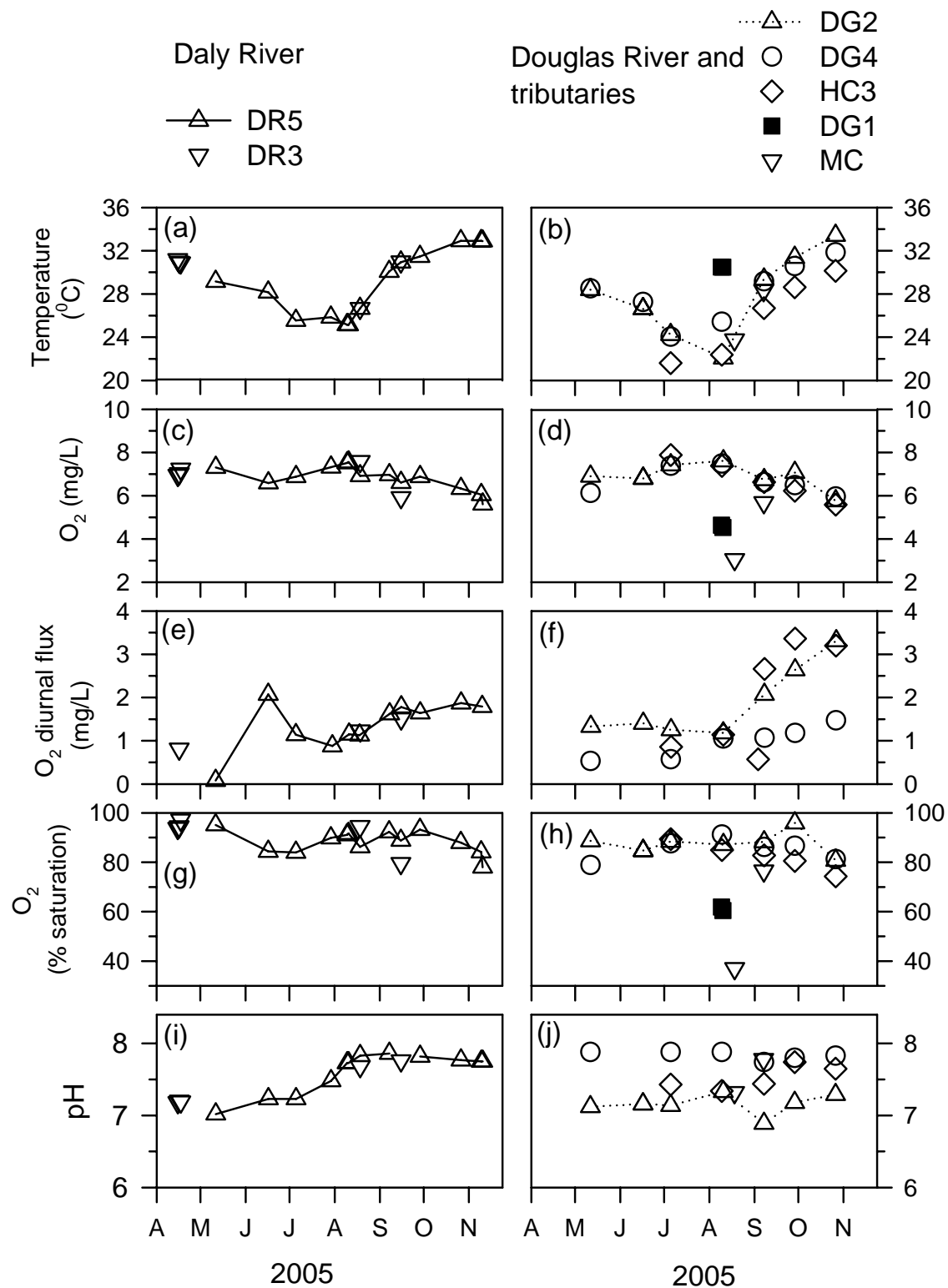


Figure 11-4 Douglas Daly region average daily water quality. (a) Daly River and (b) Douglas River and tributary water temperatures; (c) Daly and (d) Douglas River dissolved oxygen; (e) Daly and (f) Douglas River diurnal dissolved oxygen flux; (g) Daly and (h) Douglas River dissolved oxygen saturation; and (i) Daly and Douglas River pH. Diurnal O₂ fluxes for Middle Creek (5.2 mg/L in July, 14.8 mg/L in November) and DG1 (0.95 mg/L) are not shown.

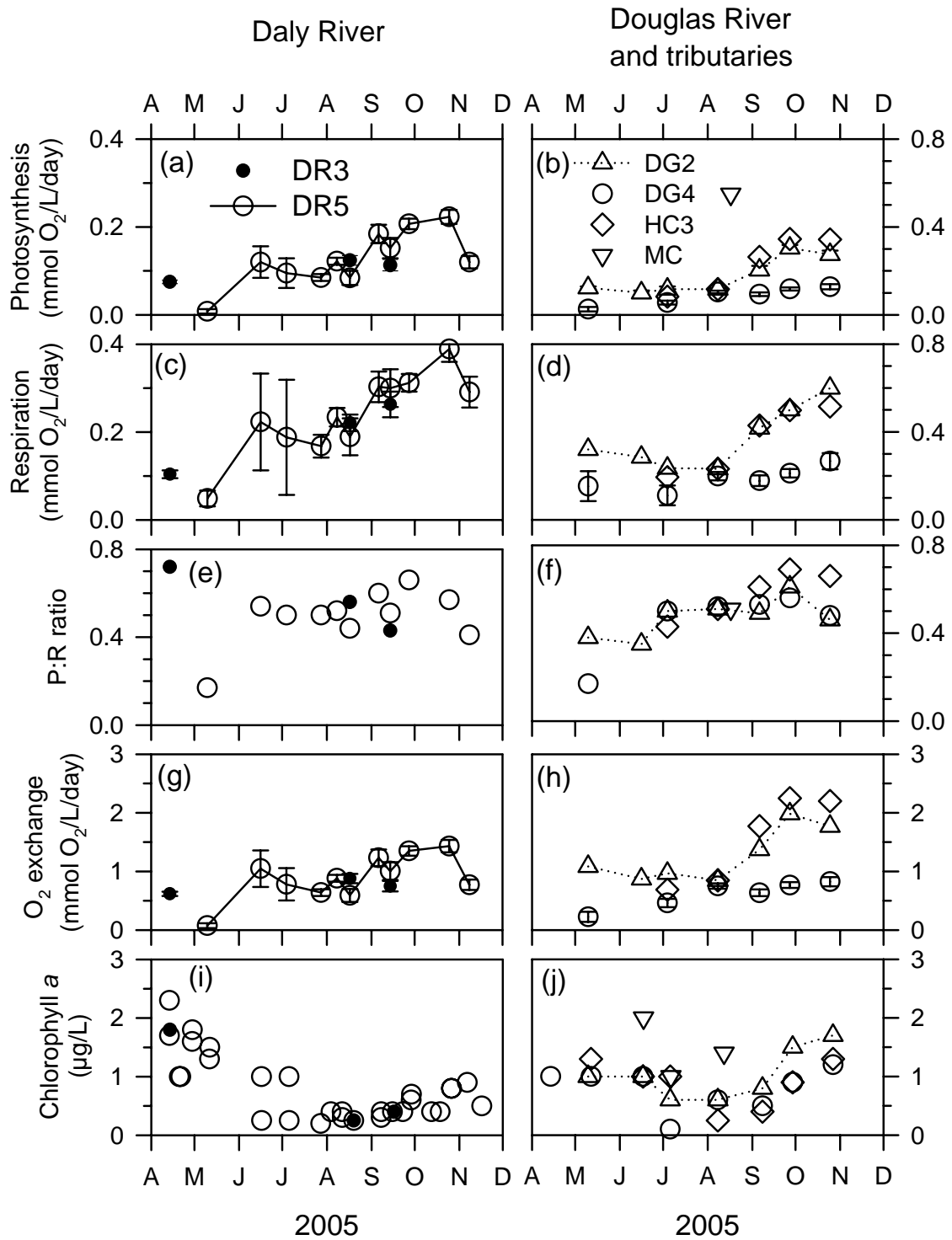


Figure 11-5 Douglas Daly region metabolism. (a) Daly River and (b) Douglas River and tributary (herein abbreviated to Douglas River) photosynthesis; (c) Daly and (d) Douglas River respiration; (e) Daly and (f) Douglas River P:R ratios (photosynthesis to respiration); (g) Daly and (h) Douglas River atmospheric oxygen input into the river; and (i) Daly and (j) Douglas River chlorophyll a. Note, Douglas River y-axis scale for plots (b), (d), (f) is double Daly River scale.

Douglas River temperatures at site DG1 were 5 °C warmer than at other sites (Fig. 11.4). The water quality at this site differed markedly from other sites due to the apparently substantial inflow of warm, hypoxic, acidic groundwater. O₂ concentrations at the site averaged 4.6 mg/L, whilst pH approximated 4.5.

In both the Daly and Douglas Rivers, the seasonal pattern of average daily O₂ concentrations (Fig. 11.4) comprised concentrations of 7-8 mg/L from May to mid-August, then a decline to 5-6 mg/L later in the dry season. Diurnal O₂ fluxes (Fig. 11.4) were 1-2 mg/L in the Daly River, and in the Douglas River 0.5-1.5 mg/L and 1-3 mg/L at sites DG4 and DG2 respectively. Hayes Creek O₂ fluxes were 1-3 mg/L. Average O₂ concentrations for Middle Creek were lower than for other Douglas Daly sites, with diurnal O₂ fluxes of 5 and 15 mg/L in August and September, and overnight concentrations of 1-2 mg/L. Flow in August was about 1 L/sec, and in September had ceased when water quality measurements were made in a small pool with substantial amounts of *Spirogyra*.

O₂ saturation levels were 80-100% at all sites except Middle Creek, where long periods of low oxygen concentrations during the night and early morning lowered average values (Fig. 11.4). In September, Middle Creek reached a maximum saturation level of 212% and showed a diurnal range from 1 mg/L to 16 mg/L. This occurred when the creek had ceased flowing and where measurements were taken in a small pool with abundant *Spirogyra*.

In the Daly River, pH increased from 7.0 to 7.8 between mid-May and mid-August, then remained largely unchanged (Fig. 11.4). In contrast, pH in the Douglas River catchment at sites DG4, DG2 and HC3 averaged 7.2, 7.8 and 7.5 respectively, without such a marked seasonal pattern (Fig. 11.4).

11.3.3 Photosynthesis, respiration and atmospheric oxygen exchange in the Douglas Daly region

Early in the dry season (April, May), rates of photosynthesis in both the Daly and Douglas Rivers were 0.01 - 0.1 mmol O₂/L/day (Fig. 11.5). From mid-August, rates increased in both rivers except at site DG4 where rates remained unchanged. At this time rates in the Daly River doubled, and in the Douglas River trebled.

Rates were highest in Hayes Creek (average 0.23 mmol O₂/L/day for common measurement dates) and the Douglas River at DG2 (average 0.19 mmol O₂/L/day). This was despite canopy cover over the mid-channel of these rivers. Rates were next highest in the Daly River (average 0.15 mmol/L/day) and Douglas River at DG4 (average 0.093 mmol O₂/L/day).

Respiration exhibited a similar temporal pattern to photosynthesis (Fig. 11.5), with photosynthesis to respiration (P:R) ratios approximating 0.5, and ranging from 0.2 to 0.7 (Fig. 11.5). Riverine oxygen concentrations were maintained by the diffusion of atmospheric O₂ into the rivers, with temporal patterns broadly similar to photosynthesis and respiration. Photosynthesis averaged 12% (range 10-13%) of total oxygen input (photosynthesis + atmospheric oxygen diffusion) to the Douglas and Daly Rivers. Respiration was higher, averaging 27% and ranging between 15% and 61%.

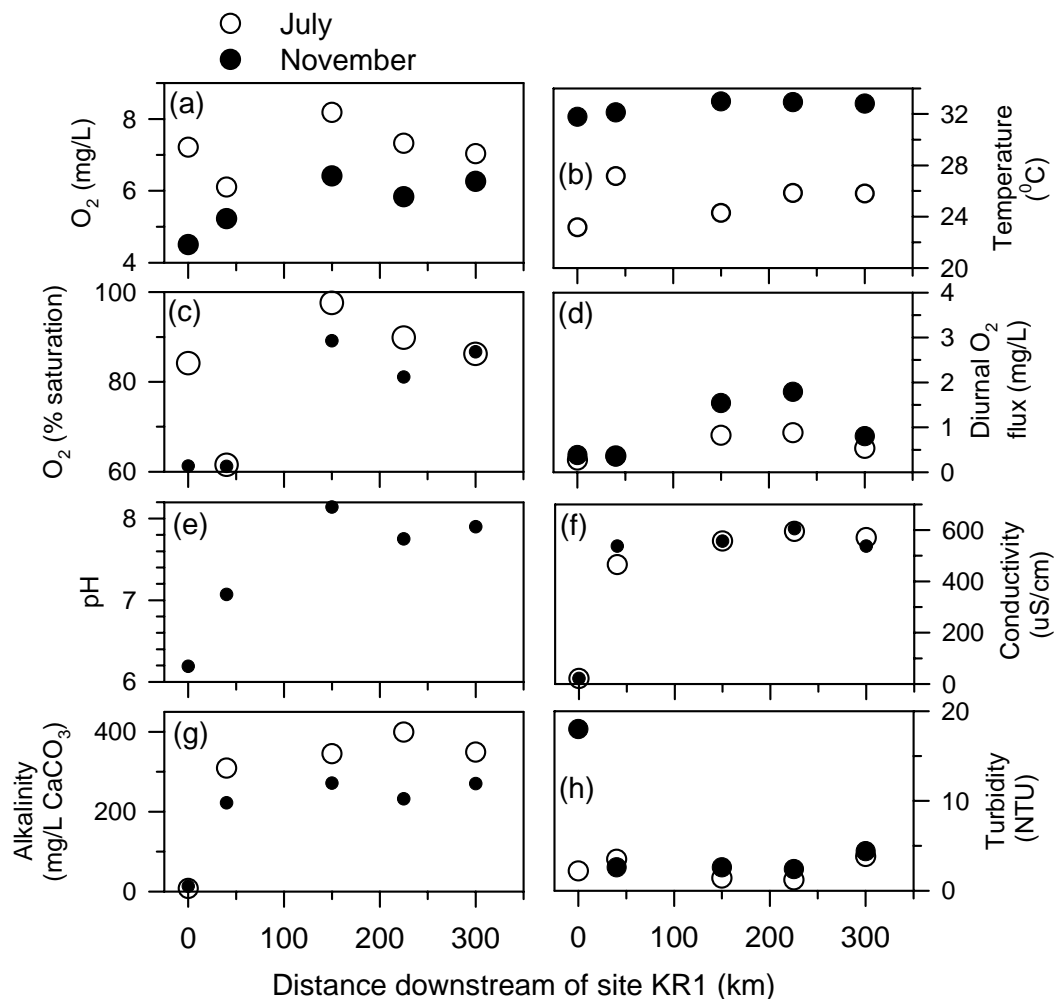


Figure 11-6 Katherine-Daly River water quality. (a) dissolved oxygen; (b) temperature; (c) dissolved oxygen saturation; (d) dissolved oxygen diurnal flux; (e) pH; (f) conductivity; (g) alkalinity, and (h) turbidity.

11.3.4 Chlorophyll *a* in the Daly and Douglas Rivers

Chlorophyll *a* concentrations in the Daly River declined from approximately 2 µg/L in April to 0.5 µg/L between May and July. Concentrations remained between 0.2 µg/L and 1 µg/L thereafter (Fig. 5i). The relatively high chlorophyll *a* concentrations during the wet-dry season

transition period were also reported by Webster et al. (2005) for this reach of the Daly River. Douglas River chlorophyll *a* concentrations (Fig. 11.5) had a similar range, however their seasonal pattern varied between sites. Concentrations however were uniformly high at the end of the dry season, in October and November.

11.3.5 Katherine-Daly River temperature, dissolved oxygen and pH

Water temperatures along the Katherine-Daly Rivers were 23-27 °C in July, and 31.8-32.8 °C in November (Fig. 11.6). O₂ concentrations were higher in July (≈7 mg/L, Fig. 11.6) than in November (5-6 mg/L). Saturation levels were 80-100% at the three sites in the Daly River, but as low as 60% at the upper two sites on the Katherine River. Diurnal fluxes were highest (1.5-2 mg/L; Fig. 11.6) in November in the middle reaches of the Daly River compared to other sites in both July and November (0.5-1 mg/L).

Water quality in the upper reaches of the Katherine River, at site KR1, is supplied from a Cretaceous sandstone aquifer. It is acidic with low conductivity and alkalinity (Fig. 11.6). Downstream, groundwater from the Tindal dolomite enters the river, increasing pH, alkalinity and conductivity. Turbidity was 1.2 – 4.4 NTU, with the exception of site KR1 in November which had a turbidity of 18 NTU due to storm runoff. Metabolism determinations at site KR3 may have been affected by Tindal aquifer inflow to the river.

11.3.6 Katherine-Daly River photosynthesis, respiration, atmospheric oxygen exchange and chlorophyll *a*

Photosynthesis in July was 0.023 – 0.095 mmol/L/day, with no marked longitudinal trend (Fig. 7a). The July and November photosynthetic rates were similar, being highest in the middle reaches of the Daly River at sites DR1 and DR5. This similarity between July and November contrasts with seasonal patterns in the Douglas River and at site DR5 where late dry season rates of photosynthesis are highest. This is probably due to the reduced light penetration caused by high turbidity, and possibly the removal of benthic algae from the rivers substrate associated with the first runoff events of the wet season. For example, the low photosynthetic rate of 0.008 mmol/L/day measured at KR1 coincided with a turbidity measurement of 18 NTU at the time of instrument deployment, and could have been higher during the period of water quality measurements.

Rates of respiration were generally higher than photosynthetic rates with the exception of site DR1 where the P:R ratio was 1.0 - 1.1 (Fig. 11.7). Photosynthesis constituted 11-13% of oxygen inputs to the river (photosynthesis + atmospheric exchange), whilst respiration

approximated 25% (excluding site KR1 in November where it was 146%). On average however photosynthesis + respiration + gas exchange must add to approximately zero. This is assuming the signs on all these terms are consistent with one another and that over 24 hours oxygen concentrations return to what they were at the beginning. It is possible the atmospheric exchange is over-estimated.

Chlorophyll *a* concentrations were ≈ 0.5 -1 $\mu\text{g/L}$ at all sites (11.7) excluding site KR1 where chlorophyll was 3.5 $\mu\text{g/L}$ in November which did not coincide with high photosynthetic rates however.

11.3.7 Biomass and standing crop of primary producers, August 2005.

A 15 km reach of the Daly River was surveyed to calculate biomass of primary producers. This reach comprised approximately equal portions of sand and gravel (Table 11.3) as included a small proportion of bedrock (<1%). These proportions concur with the survey undertaken in 2001 along a 17 km reach that overlapped with the 2005 reach (see Townsend and Padovan 2005). A noticeable change was that a small area (<0.5 km²) that had been recorded as gravel substrate in 2001 was now mobile sand due to the downstream advance of a large sand bed.

The biomass and standing crop of primary producers is summarized in Table 11.3. The biomass of river bed *Spirogyra* in August approximated 10 mg/m² which is almost a third of the 2001 maximum (Townsend and Padovan 2005). *Spirogyra* represented about one-third of the river's standing crop, similar to August 2001 (see Webster et al. 2005). *Chara* was recorded on the river bed, with densities (≈ 8 mg/m²) slightly lower than *Spirogyra*, and constituted 10% of the total standing crop. Whilst *Chara* was observed along the reach during the 2001 survey, its biomass was not determined.

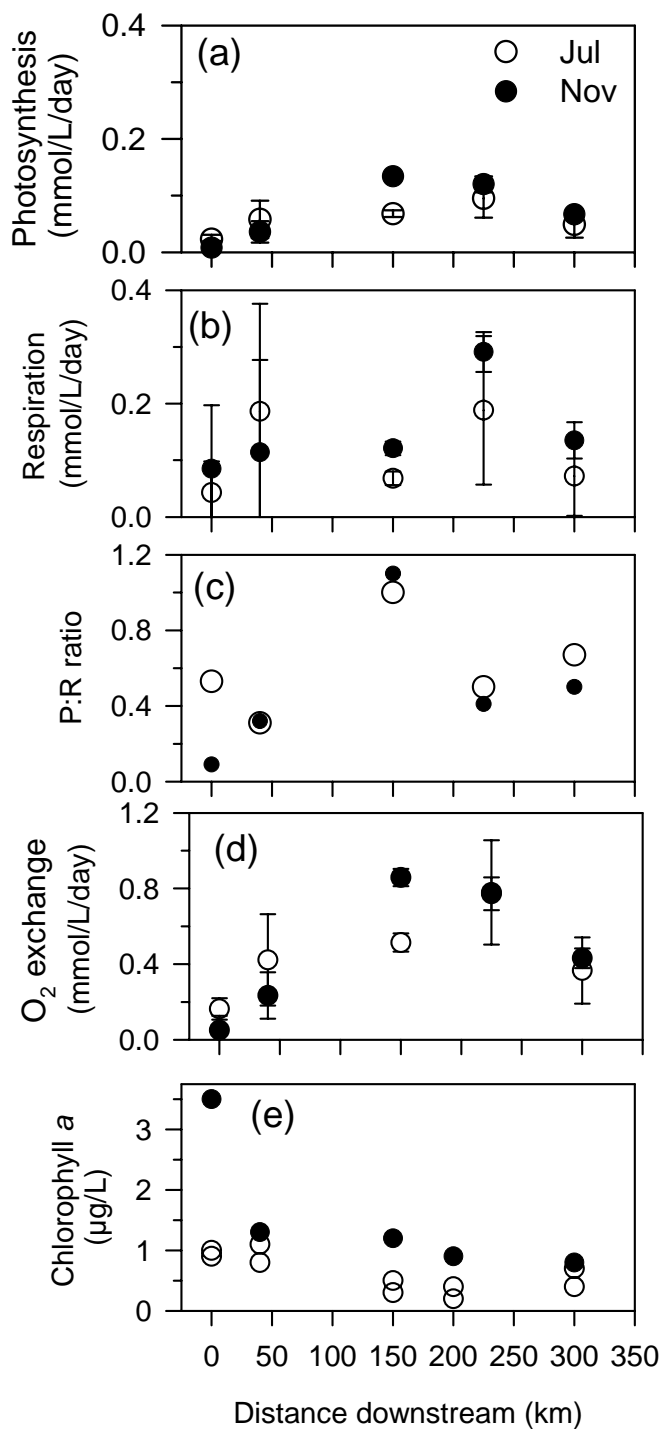


Figure 11-7 Katherine-Daly River metabolism. (a) photosynthesis; (b) respiration; (c) P:R ratio; (d) atmospheric oxygen exchange into the river; and (e) phytoplankton chlorophyll a.

The biomass of *Vallisneria*, which approximated 5 mg/m², equated to one-third of the 2002 recorded biomass (Webster et al. 2005) and constituted a small proportion of the total standing crop (≈2%). The reduced biomass of this macrophyte in 2005 concurs with a comparison of

Vallisneria spatial distribution recorded in 2001 and 2004 along the study reach of the Daly River. Large patches and linear beds of *Vallisneria* have disappeared over this period, increasing the frequency of 'absent' observations from 50% to 70% (Dostine, Department of Natural Resources, Environment and the Arts unpublished data). The assessment of primary producer biomass undertaken here does not include epiphytic algae, which is likely to be a relatively small proportion of the total standing crop based on the small standing crop of macrophytes.

The biomass of epibenthic algae on gravel was at least 3-4 times greater than other primary producers, including algae on sessile sand (Table 11.3). Due to its high biomass and the substantial area of suitable substrate, epibenthic algae constituted approximately half the August 2005 standing crop. Periphyton biomass on gravel in August 2005 (avg 32.8 mg/m², n=15, se=3.6) was approximately double that measured in August 2002 (Webster et al. 2005). On sand, epibenthic algae averaged 7.5 mg/m² (n=15, se = 1.9). Phytoplankton in the water column averaged 0.4 µg/L which is typical of the river at this time of year (Fig. 5i), and was proportionally the smallest contributor (1%) to the river's total standing crop.

Table 11.3 Biomass and standing crop of primary producers.

(a) River bed substrate area*

<i>River bed substrate</i>	<i>Total (ha)</i>	<i>Total (%)</i>	<i>DR5 (ha)</i>	<i>DR5 (%)</i>	<i>DR3 (ha)</i>	<i>DR3 (%)</i>
Sand, mobile	23.4	29	16.1	30	13.8	10
Sand, sessile	16.0	20	13.0	25	9.2	67
Sand, total	39.4	49	29.1	55	23.0	77
Gravel and rock	58.5	51	23.7	45	31.3	33
Total	81.2		52.8		54.3	

(b) Average biomass for each primary producer as chlorophyll *a*.

<i>Primary producer</i>	<i>Substrate</i>	<i>Total reach (mg/m²)</i>	<i>DR5 (mg/m²)</i>	<i>DR3 (mg/m²)</i>
Spirogyra	River bed	10.2	12.5	9.80
	River bank	7.96	9.30	9.16
Chara	River bed	8.41	7.96	7.81
	River bank	2.81	0.875	3.01
Vallisneria	River bed	5.71	6.57	4.15
Epibenthic microalgae	River bed, gravel	32.8	32.8	32.8
	River bed, sessile sand	7.52	7.52	7.52
Phytoplankton	Water column	0.388	0.388	0.388

(c) Standing crop of primary producers as chlorophyll *a*.

	<i>River substrate</i>	<i>Total reach (kg)</i>	<i>% of total reach</i>	<i>DR5 (kg)</i>	<i>% of DR5 reach</i>	<i>DR3 (kg)</i>	<i>% of DR3 reach</i>
Spirogyra	Bed	8.27	30.0	6.8	38.8	5.19	27.4
	Bank	0.121	0.4	0.093	0.5	0.09	0.5
	Total	8.39	30.4	7.89	39.3	5.28	28.1
Chara	Bed	2.28	8.3	0.475	2.7	1.60	8.5
	Bank	1.02	3.7	0.636	3.6	0.62	3.3
	Total	3.30	11.0	1.01	6.3	2.22	12.2
Vallisneria	Bed	0.695	2.5	0.525	3.0	0.33	1.7
Periphyton	Bed, gravel	13.7	49.6	7.79	44.5	10.2	53.9
	Bed, sand	1.2	4.3	0.98	5.6	0.693	3.7
Phytoplankton	Water column	0.315	1.1	0.21	1.2	0.21	1.1
Total		27.6		17.5		18.9	
Average		34.0 g/m ²		33.1 g/m ²		34.8 g/m ²	

* The total length of the reach was 15.2 km, starting upstream from DR5. The reaches upstream of DR3 and DR5 are for distances of 10 km. The DR5 and DR3 reaches overlap by 6.65 km.

11.4 DISCUSSION

The Daly River and its tributaries were heterotrophic during the 2005 dry season, with respiration exceeding photosynthesis at all sites with the exception of site DR1 which had a P:R ratio of ≈ 1 . Daly River heterotrophy was also reported by Webster et al. (2005) during the 2001 dry season at site DR3. Riverine heterotrophy is characteristic of most large, unpolluted rivers (Thorp and Delong 2002), and in the Daly River catchment extended to 4th order streams.

Rates of photosynthesis in the Douglas River and its tributaries were approximately double the rates measured in the Daly River, despite canopy cover over the Douglas River. Owing to the high incident PAR in the region, characteristic of the tropics, filtered light reaching the river bed could support photosynthesis as indicated by observations of macroalgal mats (e.g. *Spirogyra*, *Chara* and *Batrachospherium*). For example, if 80% of PAR was filtered by vegetation cover, then in the middle of the day (11:00 - 15:00 hrs) the PAR reaching the river's surface would approximate 350 $\mu\text{E}/\text{m}^2/\text{sec}$. Assuming an extinction coefficient of 0.75, PAR at 0.5 - 1.5 m depths would approximate 110-240 $\mu\text{E}/\text{m}^2/\text{sec}$, which is within the range of 100-400 $\mu\text{E}/\text{m}^2/\text{sec}$ for photo-saturation typical of benthic algae (Hill, 1996). The higher rates of photosynthesis in the Douglas River and its tributaries, compared to the Daly and Katherine Rivers, could be due to the greater availability of suitable substrate for epibenthic algae. The Daly River for instance has long reaches of mobile sand that are too unstable to maintain an epibenthic flora and development of a periphyton community. Whilst sand substrate is present in the Douglas River, it was not observed to be mobile.

Rates of photosynthesis and respiration tended to increase over the dry season. This pattern reflects the establishment and growth of primary producers during the dry season, notably macroalgae and the macrophyte *Vallisneria*. This seasonal pattern also occurred in 2001 at site DR3 (Webster et al. 2005). Photosynthesis was not matched by chlorophyll *a* concentrations in the water column. Indeed, chlorophyll was highest in the early dry season when photosynthesis was relatively low. Phytoplankton was a minor part of the river's standing crop in August 2005, and from the middle of the dry season in 2001. The higher rates of photosynthesis from August 2005 in the Daly River could be due to increased biomass of macrophytes as occurred in 2001 (Rea et al. 2002, Webster et al. 2005). Similar to 2001, the biomass of *Spirogyra* decreased in the later part of the dry season, though this may have been compensated by increased *Chara* (Townsend, pers. observation). The total standing crop of primary producers and photosynthetic rates in August 2001 and 2005 were similar, though the relative proportion of primary producers differed.

Nitrate concentration in the lower reaches of the Douglas River, downstream of site DG2 (Schult and Metcalfe 2006), were about 50 times higher than the upper reaches of the Douglas River, Hayes and Middle Creeks, and the Daly River. The high nitrate concentrations originate from groundwater inflow from the Tindal dolostone aquifer. This addition of nitrate however has not resulted in elevated rates of photosynthesis in the Douglas River, as DG4 rates were lower than other sites. This indicates primary production in the lower reaches of the Douglas River is unlikely to be nitrogen limited, as it has not increased photosynthesis.

The coupling of photosynthetic and respiration rates over the dry season in 2005 in the Douglas Daly region was also reported by Webster et al. (2005) for site DR3 in 2001. The results from this study, which provides a regional perspective, indicate that this coupling is characteristic of the Douglas and Daly Rivers. Webster et al. (2005) concluded the photosynthetic rate was many times greater than the rate of biomass accumulation of primary producers. This is consistent with primary production being dominated by phytoplankton, epibenthic algae and epiphytic algae which are grazed almost as quickly as they are grow. Algae have been shown to underpin river and wetland food webs in tropical rivers and wetlands (Douglas et al. 2005). Such a food pathway concurs with the algal-grazer model of riverine productivity proposed by Thorp and Delong (1994, 2002).

The oxygen content of the Daly River and its tributaries, which approximated 80-100% saturation, was maintained by atmospheric oxygen transfer into the river, rather than primary production. Oxygen is distributed through the water column by mixing processes driven by turbulence and diurnal convection that results from sensible heat loss at the river's surface. Vertical oxygen transfer to bottom waters however can be restricted by density stratification.

Along the fast flowing, shallow (<1.5 m) reaches of the Daly River and its tributaries, temperature profiles (Townsend, unpublished data) indicate the river is vertically mixed. Thermal stratification however has been measured in Daly and Katherine River pools 4-5 m deep, with concomitant vertical oxygen gradients (maximum 1.2 mg/L/m; Townsend et al. 2002).

The addition of nutrients to the Daly River and its tributaries is likely to increase primary production, initially through enhanced epibenthic and epiphytic algae, and possibly phytoplankton because these flora are fast growing. However, an increase in the biomass of primary producers may not be substantial because biomass accumulation is a small proportion of gross primary production. At site DR3 in 2001, Webster (2005) estimated this to be 4%. Consequently, nutrient addition and its impact on the biomass of primary producers may not be readily detected, or distinguished from inter-annual variations by monitoring programs. However, nutrient addition and subsequent increased river metabolism (photosynthesis and respiration rates) would be expected to be more sensitive than biomass monitoring. Predictive relationships between nutrient additions, primary production and river metabolism have not been established however, the ecological implications of additional nutrients to the Daly River from anthropogenic sources can be monitored by measuring river metabolism.

11.5 REFERENCES

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