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PRIMARY RESEARCH PAPER

Discharge-driven flood and seasonal patterns of phytoplankton biomass and composition of an Australian tropical savannah river

Simon A. Townsend · Michael M. Douglas

Abstract Discharge is a primary determinant of river phytoplankton, but its influence can be mediated by climate, water quality and catchment development. The relationship between discharge and phytoplankton over seasonal and flood temporal scales was examined for the Daly River in the Australian tropical savannah. Phytoplankton, water quality and hydrographic data were collected over the high-discharge wet season and lower-discharge dry season. Wet season main channel river conditions were unfavourable for phytoplankton growth. Floods, however, connected the main channel to off-channel water bodies that supplied phytoplankton, predominately *Cryptomonas*, to the river. Wet season phytoplankton biovolume and cell concentrations were higher than in the dry season and comprised the majority of the annual phytoplankton biomass load. High discharges served to both temporally connect the river to off-channel phytoplankton sources as well as dilute these sources. In the dry season, the Daly River was groundwater-fed and disconnected from off-channel phytoplankton sources and dominated by a potamoplanktonic population of *Cryptomonas* and *Peridinium*. River phytoplankton were determined by the seasonal discharge regime which drove water quality and underpinned a shift from highly productive, spatially extensive off-channel sources in the wet season to less productive more spatially confined in-channel sources in the dry season.

Keywords Potamoplankton · Water quality · *Cryptomonas* · *Peridinium* · Floodplain · Turbidity

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Introduction

Phytoplankton, especially in large lowland rivers, contribute to primary production (Oliver & Merrick, 2006), food webs (Thorp et al., 1998; Thorp & Delong, 2002; Delong, 2010), nutrient cycling and the downstream export of organic carbon (Descy & Gosselain, 1994). River phytoplankton originate from three sources: (1) self-sustaining river populations

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(potamoplankton, Reynolds, 1996), (2) benthic cells suspended into the water column and (3) cells from lentic sources, such as lakes and reservoirs (Allan & Castillo, 2007). Potamoplanktonic populations are sustained in hydraulic storage zones with sufficient resources and retention time for net growth to overcome losses to the main river channel (Descy & Gosselain, 1994; Reynolds, 2000).

Although retention time is a key controlling agent for river phytoplankton (Lucas et al., 2010), phytoplankton biomass is often related instead to discharge because transport times and the distances travelled by phytoplankton are often not known to calculate retention time. Phytoplankton biomass is typically inversely related to discharge and is river specific (Divina de Oliveira & Calherios, 2000; Allan & Castillo, 2007; Devercelli, 2010; Salmaso & Zignin, 2010; Mayora et al., 2013). High discharges reduce or deplete the supply of potamoplanktonic inocula to the main river channel by decreasing hydraulic storage retention times (Reynolds, 2000) and dilute phytoplankton in the main channel (Allan & Castillo, 2007). Moreover, high discharges typically have low water column irradiance for phytoplankton photosynthesis (e.g. Devercelli, 2010) which can further limit phytoplankton growth.

The inverse relationship between discharge and phytoplankton biomass is, however, not definitive. High discharges can be associated with increased phytoplankton concentrations, albeit temporally. Scouring can suspend benthic algae into the water column, whilst rising water levels can connect the river channel to lentic sources, notably floodplain lakes, and flush phytoplankton into a river (Lewis, 1988). The displacement of reservoir phytoplankton by floods can also increase river phytoplankton biomass (Lewis, 1988). Moreover, at low discharges, the primary controlling agent of river phytoplankton can shift from retention time to resource availability (Basu & Pick, 1997; Phlips et al., 2000; Sellers & Bukaveckas, 2003) or grazing (Caraco et al., 2006).

River discharge reflects climatic seasonality. Many tropical rivers have a predictable period of high discharge and floods (Hamilton et al., 2002; Lewis, 2008) referred to as the wet or rainy season, followed by a dry season characterized by low or no river discharge. Tropical perennial rivers lend themselves well to the study of discharge-based seasonality and more specifically phytoplankton–discharge

relationships. Most of Australia's tropical savannah rivers have near-natural discharge regimes and largely undeveloped catchments (Warfe et al., 2011), in contrast to many rivers globally which are impacted by catchment development, pollution, reservoirs, water extraction and channelization (Vörösmarty et al., 2010). The current near-natural state of most of Australia's tropical savannah rivers (Pusey et al., 2011) permits research into phytoplankton–discharge relationships to be conducted without confounding anthropogenic impacts, though these will increase as the region's water resources are further developed.

The Daly River is an example of an Australian tropical savannah river in a near-natural state with a perennial discharge regime. The primary aim of this research was to assess the hydrological and water quality drivers of the river's phytoplankton biomass and composition in relation to seasons and flood events. We hypothesize that phytoplankton biomass will be inversely related to discharge during flood events, though the relationship may be influenced by the river's connection to off-channel phytoplankton sources and vary among flood events. We further hypothesize that seasonal discharge regimes will underpin river phytoplankton composition and biomass.

The phytoplankton composition of rivers is not readily predicted, in part because a river's environmental conditions at the point of sample collection do not necessarily equate to the phytoplankton source waters (Reynolds, 1994). Nevertheless, small taxa which have high grow rates (r-selected taxa, sensu Pianka (1970)) to overcome downstream losses are favoured, for example, centric diatoms (Salmaso & Zignin, 2010). Some lowland rivers, however, with long retention times and low current speeds can have phytoplankton characteristic of lakes, for example, an extensive cyanobacterial bloom in an Australian inland river (Bowling & Baker, 1996). In this study, we primarily examined the phytoplankton of the Daly River during the high-discharge wet season and the wet-to-dry season transition. To provide a seasonal context, the phytoplankton were compared to the low-discharge dry season phytoplankton assemblage which was previously reported to be dominated by *Peridinium* (Townsend et al., 2012), though this may not be an annual phenomenon. We hypothesize that r-selected taxa will be dominant in the Daly River.

Additionally, we evaluate the application of two phytoplankton functional classifications to the Daly

River data. The functional classification of Kruk et al. (2010) is based on phytoplankton morphological traits, which select for particular habitat templates (Kruk & Segura, 2012). The second classification evaluated was proposed by Reynolds et al. (2002) and developed further by Borics et al. (2007) and Padisák et al. (2009), and is based on phytoplankton functional traits and environmental conditions. The two classifications were developed primarily for lakes, though the latter does include some river habitat templates and has been successfully applied to European rivers (Abonyi et al., 2012; Stanković et al., 2012). We assess whether the phytoplankton habitat templates of Padisák et al. (2009) and Kruk & Segura (2012) are applicable to the Daly River.

To place the Daly River's seasonal environmental conditions and phytoplankton biomass and composition into a broader global context, we compare the Daly River to the tropical and subtropical rivers of South America which also have an annual flood period. These rivers and their floodplain lakes have been a focus of phytoplankton research since the early 1970s (e.g. Schmidt, 1973), whilst comparatively less research has been published on the phytoplankton of the large tropical African and Asian rivers. Our research contributes to a broader understanding of the relationships between river phytoplankton biomass and composition and riverine environmental conditions through the study of an Australian tropical river which has hydrological and water quality characteristics that differ from some large South American rivers.

Methods

Climate, catchment and sample site description

The Daly River has a catchment area of $\sim$52,000 km^2 (Fig. 1a) with 6% of the natural vegetation cleared for intensive land-uses, principally agriculture and intensive cattle grazing (Schult & Townsend, 2012). The dominant land-use is cattle grazing in the savannah woodland, whereas conservation is second-ranked. The river's discharge regime is near-natural, with small reservoirs, and groundwater and river extractions currently having negligible impact (Schult & Townsend, 2012).

Rainfall is highly seasonal and typical of a tropical savannah climate. At the Katherine township (Fig. 1a), annual rainfall recorded at Bureau of Meteorology station 014902 has averaged 973 mm over the past 135 years, with 83% falling between December to March. Convective storms, monsoonal depressions and cyclones during these months can produce high wet-season river discharges and floods.

The Daly River is a perennial seventh-order river, based on 1:25,000 scale spatial information. The river is incised into an undulating landscape and comprises an alternating series of pools and runs, with a predominately gravel and sand riverbed. The river's seasonal discharge regime has four periods based on its water source (Fig. 2a; King et al., 2015). These periods are (1) the wet season when discharge is predominately surface runoff and interflow (January–March), (2) the wet-to-dry transition (April, May) when discharge shifts to groundwater dominance, (3) the dry season (June–October) when discharge is predominately groundwater-fed and (4) the dry-to-wet transition (November, December) when groundwater-fed discharge is diluted by episodic storm runoff events. These periods are not discrete though and vary between years in duration and timing, but describe different periods of the river's annual hydrograph.

Conductivity in the Daly River differentiates groundwater and surface water sources. Groundwater is supplied primarily from karst aquifers with conductivities exceeding 600 μS cm^{-1}, whereas surface water runoff has conductivities of less than 100 μS cm^{-1} (Townsend & Padovan, 2005). Perennial discharges occur in most sixth-order tributaries of the Daly River (Townsend et al., 2012), whereas intermittent streams which cease flowing during the dry and dry-to-wet transition seasons are common among lower- and middle-order watercourses (e.g. Townsend & Douglas, 2014).

The catchment's road network is sparse, with just four roads that lead to the Daly River along its 350 km length. The site chosen for the study, Banyan Farm (Fig. 1a; 130.668687°E, 13.714327°S), is the only site accessible by vehicle on a bitumen road during the wet season, except during major floods. The river, upstream of the sample site, is approximately 45–55 m wide between the lower river banks that contain dry season discharge, and generally more than twice this width between the upper banks which contain wet season discharge. Water quality, hydrographic and phytoplankton data were collected between 11 December 2009 and 21 September 2010 during the wet, wet-to-dry transition and dry seasons.
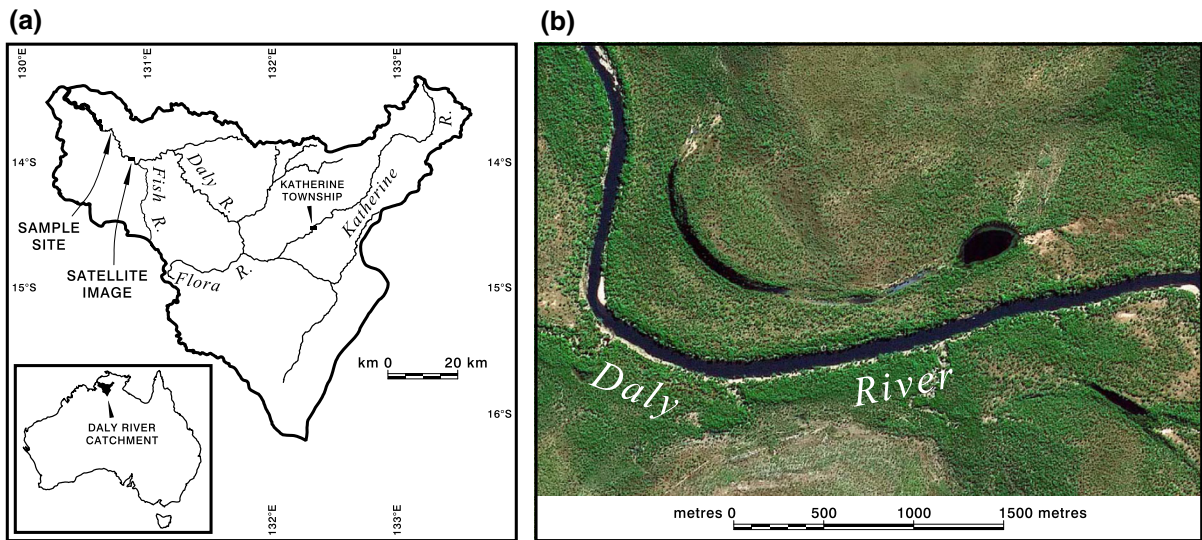
Fig. 1 **a** The Daly River catchment and Banyan Farm sample site, **b** an example of two off-channel lakes along paleochannels which were connected to the Daly River during the wet season

The riparian corridor of the Daly River and its major tributaries upstream of Banyan Farm features shallow perennial lakes, which are connected to the river during high wet-season discharges. The larger lakes are located in paleochannels (Fig. 1b) and are up to 3 km long and 200 m wide. Floods also produce numerous isolated small shallow pools. An area of 2010 km^2 in the middle of the catchment is prone to flooding, based on soil and vegetation data, and has shallow temporary wetlands that exist only in the wet season (Begg et al., 2001).

Hydrography, in situ measurements and sample collection and analysis

Discharge and depth (Z) data representative of the sample site were collected at the Mt Nancar hydrographic station, 19 km upstream of Banyan Farm (Fig. 1a). The 2010 wet season maximum daily discharge (1690 m^3 s^{-1}; Fig. 2a) was lower than the 37-year median (2015 m^3 s^{-1}) and highest recorded (5900 m^3 s^{-1}) maximum daily discharges, and had a recurrence interval of 1.7 years.

Water samples were collected and water quality measured 2 m from the river bank approximately every second day between 11 December and 13 April, then twice a week until 22 July, followed by fortnightly until 21 September. Chlorophyll a (Chl a) water samples were filtered through a Whatman GF/

C glass-fibre filter within half an hour of collection then frozen for later analysis. Temperature, pH and conductivity were measured with a Quanta multi-parameter probe (Hach Hydromet, Loveland, Colorado) and turbidity using a Hach Hydromet meter (model 2100P).

Water quality measurements and samples for soluble nutrients, colour, Chl a and phytoplankton (Fig. 2b) were also taken from a boat in the middle of the river weekly between mid-January and mid-April, then approximately fortnightly until 21 September. The nutrient and colour water samples were filtered immediately after collection through 0.45 and 0.22 μm membranes, respectively. Current speed was measured from an anchored boat with hand-held SonTek FlowTracker Acoustic Doppler Velocimeter (Xylem Water Solutions, California) at a depth of 10 cm from the surface and averaged over 40 s.

Profiles of photosynthetically available radiation (PAR) were measured from the boat with a LI-192 underwater quantum sensor (LI-COR, Lincoln, Nebraska). The attenuation coefficient for each profile was calculated from a regression of the natural log-transformed PAR and depth, and is expressed as the euphotic depth (Z_{eu}), which is the depth to which 1% of PAR at the surface penetrates below the water's surface. Ratios of Z_{eu} to river depth (Z_{eu}:Z) were calculated using the depths recorded at the Mt Nancar hydrographic station.

Fig. 2 Daly River discharge, water quality and phytoplankton for the dry-to-wet (which preceded the wet season and is not labelled), wet, wet-to-dry transition and dry seasons. **a** Daily discharge, numbered flood events and conductivity, **b** depth and taxa richness which equate to phytoplankton sample dates, **c** measured and predicted Z_{eu}:Z ratios, where Z_{eu} is the euphotic depth and Z river depth and **d** biovolume relative abundance of Morphologically Based Functional Group (MBFG) V (Kruk et al., 2010), *Cryptomonas* sp. and *Peridinium inconspicuum*. Water quality and phytoplankton data were collected at Banyan Farm, and depth and flow data at Mt Nancar hydrographic station (GS8140040). Measured ratios were determined from field data, and the predicted ratios from a linear regression of Z_{eu} and turbidity (see Fig. 4b)
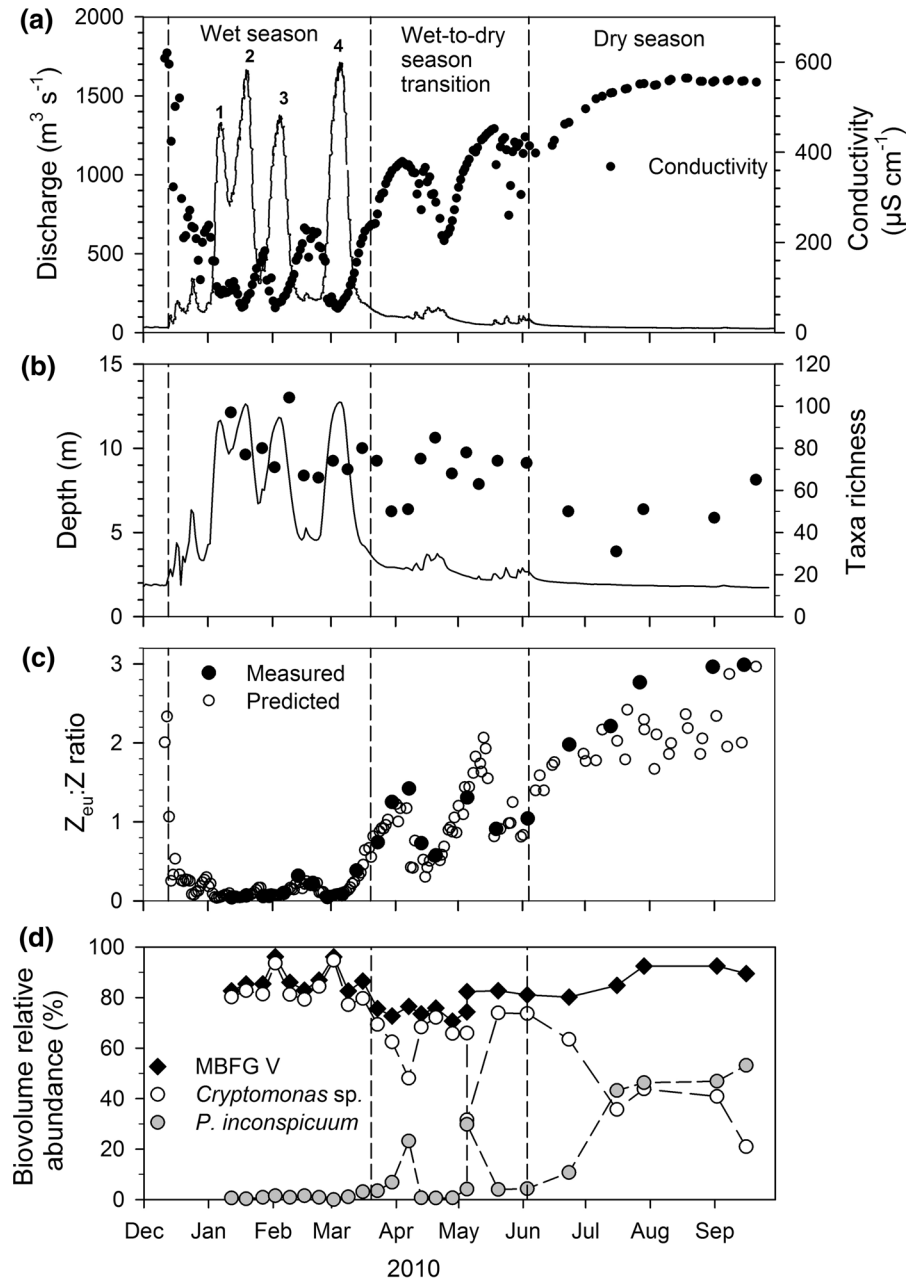
Water samples were analyzed using standard methods (American Public Health Association, 1998) for nitrite and nitrate (method 4500-NO$_3$–F), ammonium (method 4500 D), soluble reactive phosphorus (SRP, method 4500-P F) and fluorometry for Chl *a* (10200-H 3) after ultra-sonication in 90% acetone and acidification. Detection limits were 1 µg l^{-1} for the nutrients and 0.5 µg l^{-1} for Chl *a*. Colour produced by humic substances (Cuthbert &

del Giorgio, 1992) was measured as gilvin, which is absorbance at 440 nm relative to a distilled water blank (Kirk, 1976).

Phytoplankton enumeration and identification

Duplicate samples were collected for phytoplankton identification and enumeration. Two subsamples were taken from each sample. One subsample was

preserved in Lugol's iodine and concentrated by sedimentation, and all non-diatom taxa and total diatom cells were counted using a Lund cell on a Zeiss Axioskop microscope at ×400 magnification. Forty transects across the cell were examined during each count, ensuring that 150 or more individuals of the 5 most frequently occurring taxa were enumerated, giving a counting precision of ±20% or better for these taxa. The total number of cells and units counted per sample exceeded 1000. Non-diatom taxa were identified to species level, though the species could not always be identified.

The second subsample was preserved in ethanol after sedimentation for further diatom identification and enumeration. The sample was concentrated and treated with dilute HCl and H_2O_2 (Townsend & Gell, 2005), and 300 valves were counted at ×1000 magnification. The diatom *Urosolenia,* however, was enumerated using the method for non-diatomaceous phytoplankton because their fragile frustules were destroyed by the digestion process. Diatoms were also identified to species level. The diatom and non-diatom data were then pooled for each sample, and taxa cell concentrations of the two duplicate samples averaged. Phytoplankton biovolumes were calculated using standard geometric formulae (Hillebrand et al., 1999). Taxa were assigned a Morphologically Based Functional Group (MBFG) using the dichotomous key of Kruk et al. (2010).

Data analyses

Analyses were performed to compare wet, wet-to-dry transition and dry season variables, and test relationships between discharge and dependent variables at seasonal and flood temporal scales. Statistical analyses were performed using SigmaPlot version 12.5 (Systat Software, San Jose, CA).

Linear regressions were undertaken for the independent variable discharge and dependent variables Chl *a* and biovolume concentration data for each season and included a test of the power to detect a difference at the 5% level when one existed. Regression analyses were also performed for individual flood event discharge and Chl *a* concentrations and the equality of the regression gradients tested according to Zar (1974). Regression coefficients of determination and statistical significance were not increased by log_{10} transformation of discharge. Stepwise linear

regressions tested the dependence of Z_{eu} on the independent variables colour and turbidity and also tested the dependence of the relative abundance of two phytoplankton taxa on the following twelve exploratory variables: discharge, depth, current speed, conductivity, pH, NO_3, NH_4, SRP, molar soluble N:P ratio, temperature, Z_{eu} and Z_{eu}:Z ratio.

Multiple comparisons for several water quality variables were conducted by the non-parametric Kruskal–Wallis ANOVA on ranks with Dunn's multiple comparisons when the data were not normally distributed with equal variance. Otherwise, parametric ANOVAs and Student's *t* tests were conducted.

The PRIMER 6.1.2 software package (Clarke & Gorley, 2006) was used to undertake multivariate analyses on environmental and phytoplankton data. A principal component analysis (PCA) was conducted on environmental data for the 25 phytoplankton sample dates for the twelve variables used for the stepwise linear regression analyses. The data were first standardized, due to the non-normal distribution of some variables and different ranges, to values between 0 and 1, $X_{standardized} = (X - X_{min})/(X_{max} - X_{min})$.

Multivariate analyses of phytoplankton biovolume relative abundance data were performed, after square root transformation to down-weight frequently occurring taxa, although this had little impact on the analysis due to the dominance of a few taxa. Nonmetric MDS ordinations were performed on a Bray–Curtis similarity matrix. Tests for taxa that differentiated between seasons were undertaken using the SIMPER algorithm (Clarke & Warick, 2001). The BIOENV algorithm, which applies Spearman's rank correlations, was applied to determine the environmental variables that best explained the phytoplankton non-metric MDS ordination. PRIMER was also used to compute the Shannon–Wiener (log_2) diversity (H') and Pielou's evenness indices using cell concentration data. Taxa richness and biodiversity indices are expressed as means and standard errors.

Loads of phytoplankton biomass and Chl *a* were calculated as the product of discharge at Mt Nancar hydrographic station and biomass and Chl *a* concentration at Banyan Farm. Phytoplankton biovolume was converted to biomass assuming a density of 1.050 kg m^{-3}, which is a typical non-diatom phytoplankton density (Reynolds, 2006). For the purposes of calculating an annual load, the Chl *a* concentration measured on the last sample date, 21 September, was

assumed to be representative of the remaining period to 10 December, which is reasonable based on the similarity of Daly River Chl a concentrations in September, October and November 2000 (Townsend et al., 2012).

Results

Hydrography and water quality

The first major runoff event occurred in mid-December, marking the commencement of the wet season and was followed by four major flood events (Fig. 2a) of 12–24 days duration (Table 1) with a maximum depth of 12.7 m (Fig. 2b). The transition from surface to groundwater dominant discharge, traced by an increase in conductivity (Fig. 2a), was interrupted by a large storm runoff event on April 21 and smaller ones in late May which temporarily lowered river conductivity, but not to wet season levels. From early June, groundwater dominated discharge based on the consistently high conductivity (Fig. 2a).

Current speeds during the wet season averaged 0.98 ± 0.13 m s^{-1} and then decreased to averages of 0.27 ± 0.020 and 0.14 ± 0.050 m s^{-1} during the wet-to-dry and dry seasons, respectively. These averages equate to retention times of 2.9, 10.5 and 15.8 days during the wet, wet-to-dry and dry seasons, respectively, over the 245 km reach between the Banyan Farm sample site and the Flora and Katherine River junction, which marks the start of the Daly River (Fig. 1a) and are indicative of relative seasonal retention times. Water temperatures were warm

(Fig. 3a), between 23.1 and 32.4°C. The river's pH during the wet season approximated neutral conditions (Fig. 3b), but increased to reach 8.5 in September as alkaline karst groundwater supplied a greater proportion of river discharge.

Wet season turbidity and colour were high and Z_{eu} low (Fig. 3c, d, e) compared to the wet-to-dry transition and dry seasons. Z_{eu} declined rapidly with increased turbidity from 5 to 35 NTU (Fig. 4a). A stepwise multiple linear regression of log$_{10}$-transformed data revealed that turbidity best explained euphotic depth (Fig. 4b), whereas colour's contribution to the regression was negligible ($r^2 = 0.005$; $P = 0.047$). For most of the wet season, Z_{eu} was a small proportion (average 21%) of the river's depth (Fig. 2c). During the wet-to-dry transition, however, Z_{eu} approximated the river's depth, whilst over the dry season Z_{eu} exceeded the river's depth (Fig. 2c). Nitrate and ammonium concentrations declined between the three seasons, whilst SRP concentrations did not differ significantly (Fig. 3f, g, h). Nitrite-N concentrations were consistently low (<3 µg l^{-1}). Molar soluble N:P ratios reflected nitrate concentrations due to the low SRP concentration range and were generally more than tenfold higher in the wet season than the dry season (Fig. 3i). Silicon concentrations are high in the Daly River (~ 10 mg l^{-1}; Department of Environment and Natural Resources (DENR) unpublished wet season data, Townsend et al., 2012) compared to concentrations that limit diatom growth, which have an upper limit of 0.5 mg l^{-1} (Reynolds, 2006).

Ordination of a principal component analysis of standardized environmental data (Fig. 5) revealed that the first PCA axis explained 69% of variation and was

Table 1 Daly River 2010 flood duration, chlorophyll a concentration and linear regression statistics for flood data. See Fig. 2 for flood hydrographs

Flood	Flood duration (days)			Chl a concentration (µg l^{-1}). Average and standard error of the mean and number of data in parentheses		Linear regression r[b]		
	Rise	Fall	Total	Rise	Fall	Rise	Fall	Combined
1	7.9	4.4	12.3	1.5 ± 0.2 (6)	1.7 ± 0.1 (3)	0.02	0.34	0.02
2	7.7	6.3	14.0	0.8 ± 0.2 (10)[a]	1.8 ± 0.2 (8)[a]	0.19	0.66[b]	0.61[b]
3	9.8	12.2	22.0	0.9 ± 0.3 (9)[a]	2.1 ± 0.3 (6)[a]	0.64[b]	0.59[b]	0.61[b]
4	9.6	13.9	23.5	0.8 ± 0.1 (15)[a]	2.6 ± 0.4 (16)[a]	0.56[b]	0.31[b]	0.45[b]

[a] Rising and falling limb concentrations different at the 5% significance level, t test

[b] Regression slope different from zero at the 5% significance level. All regression gradients were negative

Fig. 3 Box plots of water quality for the wet (W), wet-to-dry transition (WD) and dry (D) seasons. The seasons are shown in Fig. 2. **a** Temperature, **b** pH, **c** turbidity, **d** colour, **e** euphotic depth, **f** nitrate, **g** ammonium, **h** soluble reactive phosphorus (SRP) and **i** soluble molar N:P ratio. Parametric ANOVAs with Tukey's multiple comparisons or Kruskal–Wallis ANOVAs on ranks with Dunn's multiple comparisons were performed to test hypotheses of equality between seasons. *Statistically significant difference ($P < 0.05$) between consecutive seasons. The box plots show 5th, 10th, 25th, 50th, 75th, 90th and 95th ‰, except when percentile values overlap
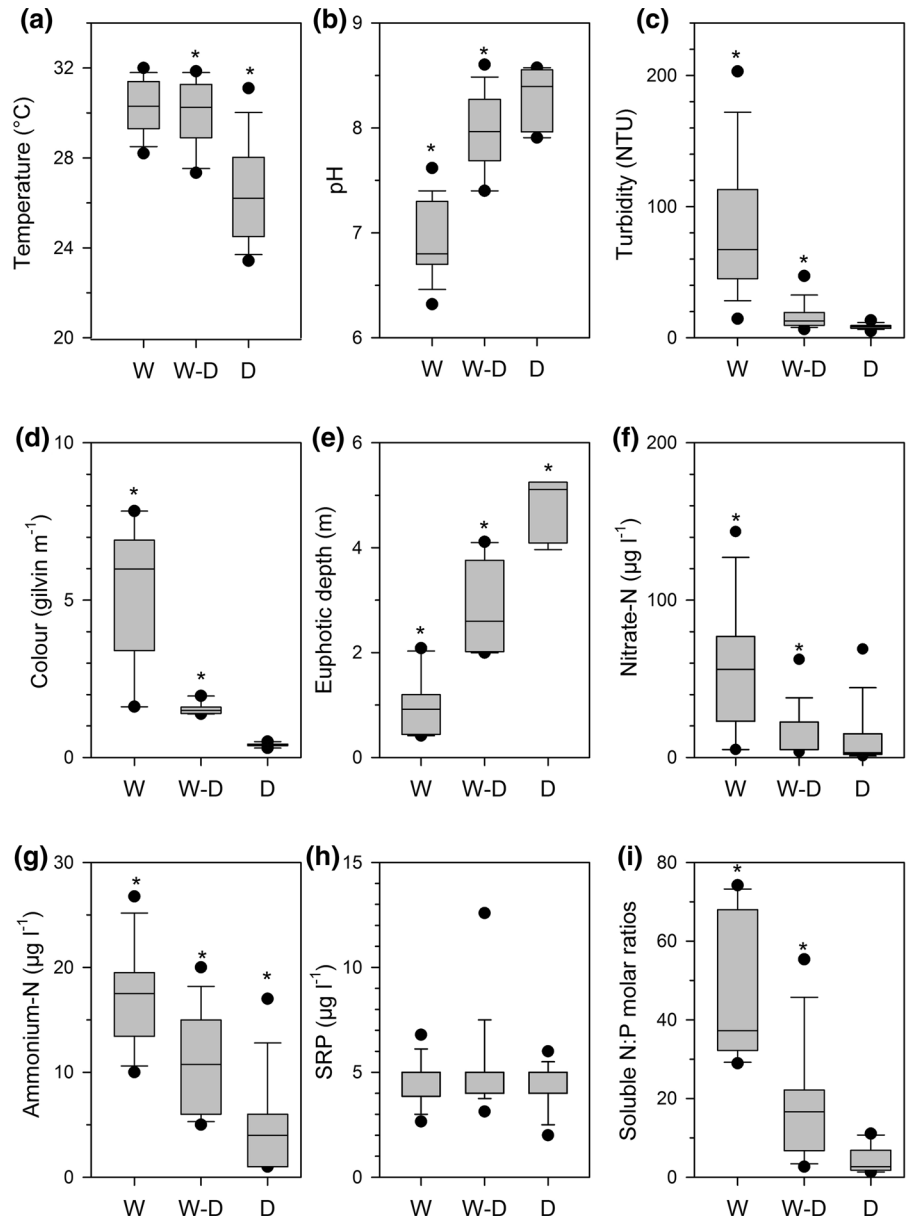

correlated with ionic chemistry (conductivity, $r = 0.40$; pH $r = 0.29$), water clarity (Z_{eu}, $r = 0.38$; Z_{eu}:Z, $r = 0.33$) and river hydrography (depth, $r = -0.38$; current speed, $r = -0.35$; discharge $= -0.30$). The second axis explained an additional 12% of the variation and was correlated with nitrate ($r = -0.48$), discharge ($r = -0.44$) and temperature ($r = -0.43$). Discharge underpinned the seasonal pattern of environmental data in ordination space and was significantly correlated (Spearman's rank tests, $P < 0.001$ except temperature) to

conductivity ($r = -0.97$), Z_{eu} ($r = -0.92$), pH ($r = -0.82$), nitrate ($r = 0.77$), N:P ratio ($r = 0.69$) and temperature ($r = 0.49$; $P = 0.01$).

Phytoplankton concentrations and loads

Wet season Chl *a* concentrations were two-thirds lower than wet-to-dry and dry season concentrations, whereas wet season biovolume and cell concentrations were 2–3-fold higher (Fig. 6). The annual load of Chl *a* and phytoplankton biomass was dominated by the
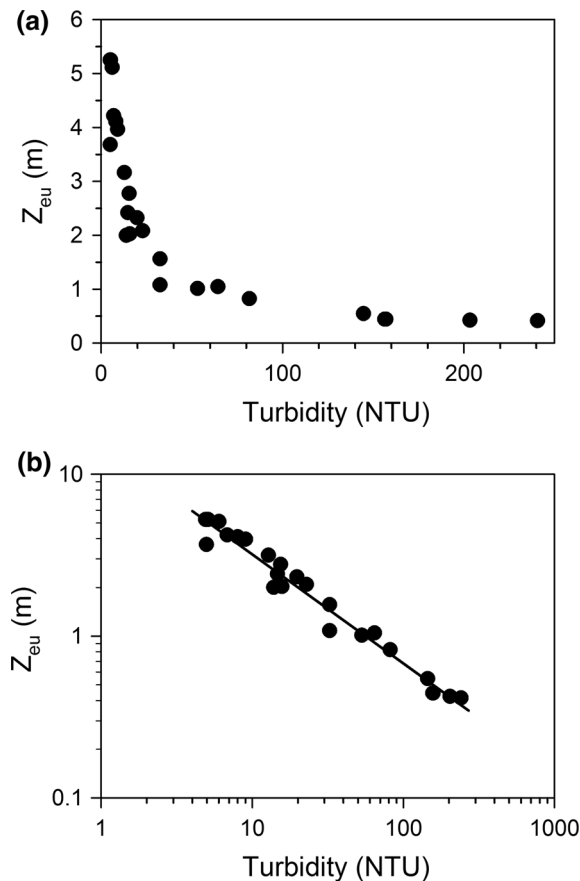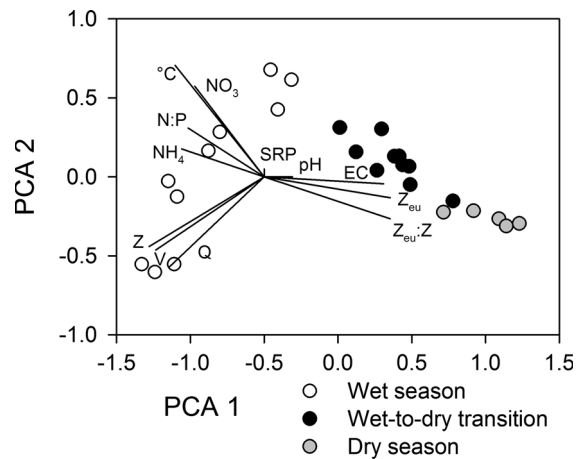
Fig. 4 Daly River Banyan Farm **a** turbidity and euphotic depth (Z_{eu}) scatter plot, and **b** $\log_{10}$ transformed scatter plot of turbidity and euphotic depth, and linear regression (with standard errors of coefficients): $\mathrm{Log}_{10}(Z_{eu}) = 1.179 \pm 0.037 - 0.674 \pm 0.024$ $\log_{10}$(turbidity); $n = 23$; $r^2 = 0.974$; $P < 0.001$

Fig. 5 Principal component analysis of standardized environmental variables for the wet, wet-to-dry and dry seasons, Jan. 2010–Sept. 2010, Daly River at Banyan Farm. *Variables* discharge (Q), velocity (V), depth (Z), conductivity (EC), pH, nitrate (NO_3), ammonium (NH_4), soluble reactive phosphorus (SRP), temperature (°C), euphotic depth (Z_{eu}) and Z_{eu}:Z ratio

wet season (14 December–20 March) contribution, which comprised 75% of the Chl *a* load (8.3 tons) and 92% of the phytoplankton biomass load (920 tons), due to the 13-fold higher discharge volume of the wet season compared to the remainder of the year and similarity of seasonal phytoplankton biomass and Chl *a* concentrations.

Chl *a* concentrations and discharge were inversely but poorly related during the wet season ($n = 91$, $r^2 = 0.16$, $P < 0.01$) and not significantly related during the wet-to-dry ($n = 70$, $r^2 = 0.05$, $P = 0.06$) or dry seasons ($n = 15$, $r^2 = 0.20$, $P = 0.09$). Linear regressions of seasonal biovolume and discharge wet were not significant, though a wet season relationship ($n = 10$, $r^2 = 0.35$; $P = 0.07$) may exist because the

power of the analysis was low, increasing the likelihood of a type II error (acceptance of a false hypothesis).

Statistically significant Chl *a* versus discharge relationships were identified for 3 of the 4 floods (Table 1). Chl *a* concentrations over the falling limb of floods 2, 3 and 4 were at least double concentrations measured over the rising limb. Additionally, Chl *a* concentrations were inversely and linearly related to flood discharge (Table 1) for rising and falling limbs and combined data for each of floods 2–4. Chl *a* concentrations of floods 3 and 4 decreased 52 and 48%, respectively, when discharges increased 3-fold from 400 to 1200 m^3 s^{-1}. The discharge-Chl *a* linear regressions for floods 2–4 were similar, with no differences ($P > 0.05$) between the regression slopes. A quasi-hysteresis effect was evident for floods 2–4 (Fig. 7), though concentrations did not return to initial concentrations. The first flood, however, did not show these patterns (Table 1).

Phytoplankton composition, diversity and temporal pattern

A total of 272 taxa were identified. Almost 70% of taxa were diatoms (Fig. 8). Next ranked were Chlorophyta and Cyanobacteria, whereas Euglenophyta, Chrysophyta, Cryptophyta and Pyrrophyta each

Fig. 6 Box plots of Daly River **a** chlorophyll *a* (Chl *a*), **b** phytoplankton biovolume concentration, **c** phytoplankton cell concentration and **d** phytoplankton Chl *a* content calculated from Chl *a* and biovolume concentration data for the wet (W), wet-to-dry transition (WD) and dry (D) seasons. The seasons are shown in Fig. 2. The box plots show 5th, 10th, 25th, 50th, 75th, 90th and 95th ‰, except when percentile values overlap


Season (W wet; W-D wet-to-dry transition; D dry season)
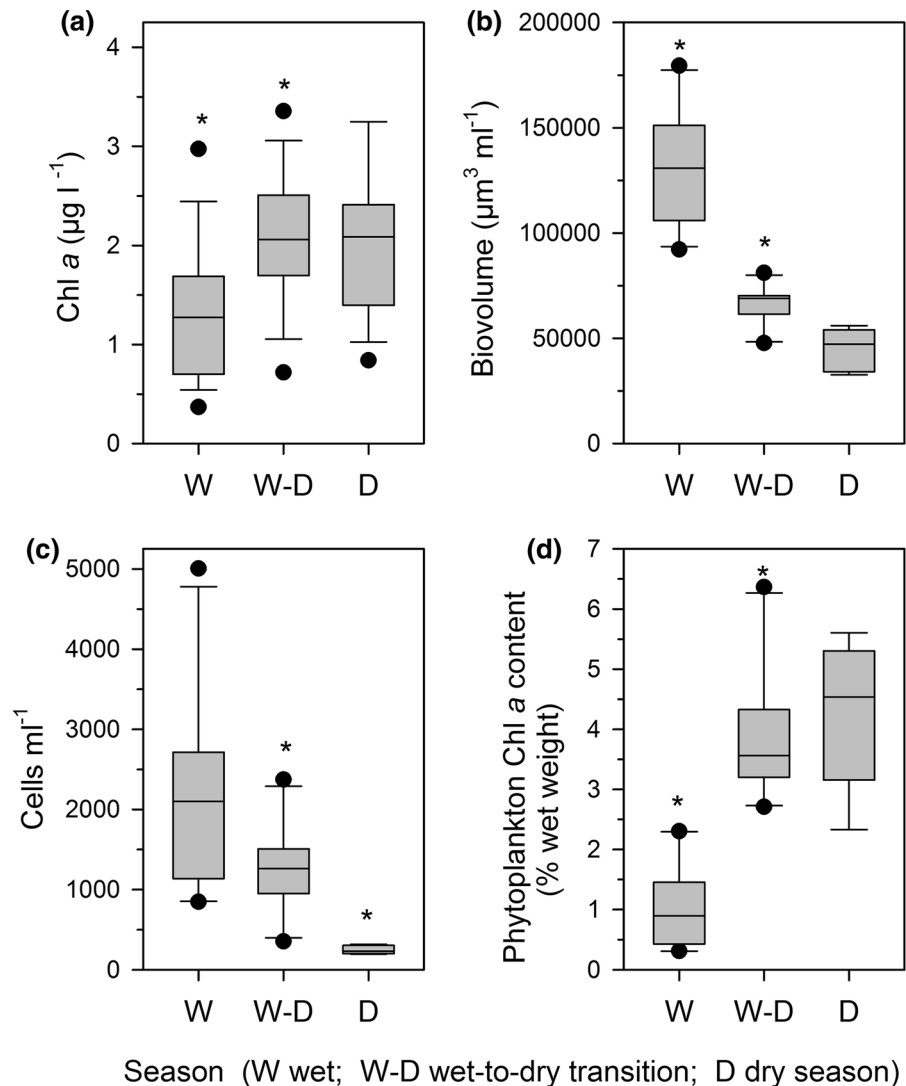
comprised less than 2% of the total. Nearly, all diatom taxa (∼90%) were benthic based on a previous survey of the river's substrata (Townsend & Gell, 2005), whilst the remainder were facultative planktonic (e.g. *Aulacoseira, Fragilaria, Synedra* and *Tabularia*) excluding planktonic *Urosolenia*. Non-diatomaceous taxa were predominately planktonic (e.g. *Ankistrodesmus, Cosmarium, Cryptomonas, Euglena, Peridinium, Scenedesmus, Trachelomonas*), excluding *Mougeotia*. Most taxa occurred infrequently, with half recorded on three or fewer of the 25 sample dates.

Taxa richness was not evenly distributed among seasons (Fig. 8). The number of taxa per sample was similar during the wet (79 ± 4; $n = 10$) and wet-to-dry transition (69 ± 4; $n = 10$) seasons and higher than the dry season (49 ± 5; $n = 25$; ANOVA; $P < 0.001$; pair-wise comparisons $P < 0.01$). The number of taxa exclusive to the wet and wet-to-dry transition seasons totaled 160 (Fig. 8), but occurred infrequently, and exceeded by sixfold the number of taxa occurring only during the dry season. One-third of taxa were common to each of the three seasons.

Shannon–Wiener diversity indices were higher (ANOVA $P < 0.01$; Tukey multiple comparisons $P < 0.05$) for both the dry (2.34 ± 0.15 bits ind^{-1}) and wet-to-dry seasons (2.17 ± 0.15 bits ind^{-1}) than the wet season (1.61 ± 0.15 bits ind^{-1}). This was due partly to the more even distribution of taxa (ANOVA
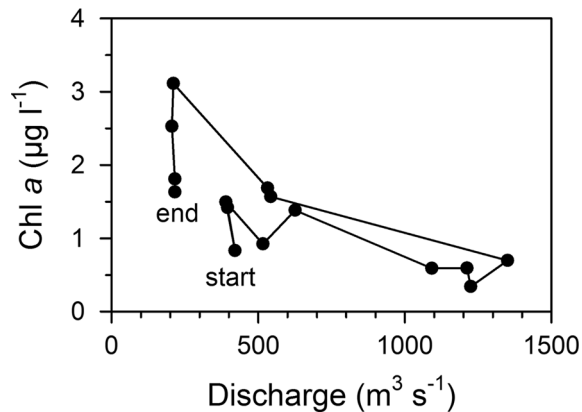
Fig. 7 An example of the quasi-hysteresis relationship between discharge and chlorophyll *a* concentration. Flood 3. See Fig. 2 for flood hydrograph and Table 1 for flood duration and chlorophyll *a* concentration data

$P < 0.01$; Tukey multiple comparisons $P < 0.05$) of the dry (evenness 0.42 ± 0.030) and wet-to-dry seasons (0.36 ± 0.024) than the wet season (0.26 ± 0.028).

The river's phytoplankton biovolume was dominated by Cryptophyta and Pyrrophyta (Fig. 8), while Chlorophyta, Cyanobacteria, Euglenophyta and diatoms (Bacillariophyceae) comprised 1–14% of the total seasonal biovolume. Taxa that belonged to MBFG V, which comprises unicellular flagellates with representative taxa from Cryptophyceae, Dinophyceae, Euglenophyceae, Volvocales and Chlorococcales (Kruk et al., 2010), dominated the phytoplankton biovolume assemblage (average $83 \pm 1.4\%$; Table 2; Fig. 2d). *Cryptomonas* sp. was dominant during the wet season. During the wet-to-dry and dry seasons, *Cryptomonas* sp. abundances decreased but were matched by increased *Peridinium inconspicuum* Lemmermann abundances to maintain approximately 80% of phytoplankton biovolume (Fig. 2d). MBFGs I, IV, VI and VII comprised almost all of the remaining phytoplankton assemblages (Table 2).

A non-metric MDS plot of Bray–Curtis similarity matrices of biovolume relative abundance (Fig. 9) showed statistically significant separation of seasonal phytoplankton assemblages (ANOSIM multiple comparisons; global $R = 0.41$, $P = 0.001$; season pairwise comparisons $R = 0.40$–0.50, $P < 0.002$). SIMPER analysis identified that *Aphanocapsa* sp. contributed most to total dissimilarity between the seasons, contributing between 12.6 and 15.0%, whilst

Peridinium inconspicuum, *Cryptomonas* sp. and a small unidentified chlorophyte contributed collectively an additional 10.8–15.6% dissimilarity.

The Bray–Curtis matrix of biovolume relative abundance data was best explained by temperature and Z_{eu} (BIOENV; $\rho = 0.62$, $P = 0.001$). Stepwise linear regression analyses also revealed that light was a significant explanatory environmental variable, though not temperature. Z_{eu} explained 83% of *Cryptomonas* sp. relative abundances ($P < 0.001$), whereas $Z_{eu}{:}Z$ explained 76% *Peridinium inconspicuum* relative abundances ($P < 0.001$). No other variables were selected.

Discussion

A comparison of Daly River and large South American River hydrology and water quality

Over the 2010 wet season, the Daly River experienced floods of short duration (2–4 weeks; Table 1) consistent with other Australian tropical savannah rivers (see Petheram et al., 2008). This contrasts with some large, high-order South American rivers which can have a single annual flood of 4–16 weeks duration that rise and fall slowly, for example, the Orinoco River (Lewis, 1988; Paraná River García de Emiliani, 1997; Izaguirre et al., 2001; Unrein, 2002; Mayora et al., 2013), Baía River (Train & Rodrigues, 1998), Paraguay River (Divina de Oliveira & Calherios, 2000) and Amazon River and its high-order tributaries (Meade et al., 1991). The greater catchment area of the South American rivers, 10–100-fold more than the Daly River, partly accounts for the different flood regimes. Floods of short duration will produce equally short connection periods to floodplain water bodies compared to the above listed rivers, as well as periods of disconnection favourable for phytoplankton growth that can later supply the river when flood connection is resumed.

The depth of Daly River flood events also contrasted with some large South American rivers. During flood events, the Daly River increased 10 m in depth, whereas during most of the South American river studies listed above, excluding the Amazon River, river depth increased only up to 3 m because floodwaters spilled onto extensive floodplains. River depth has implications for phytoplankton primary
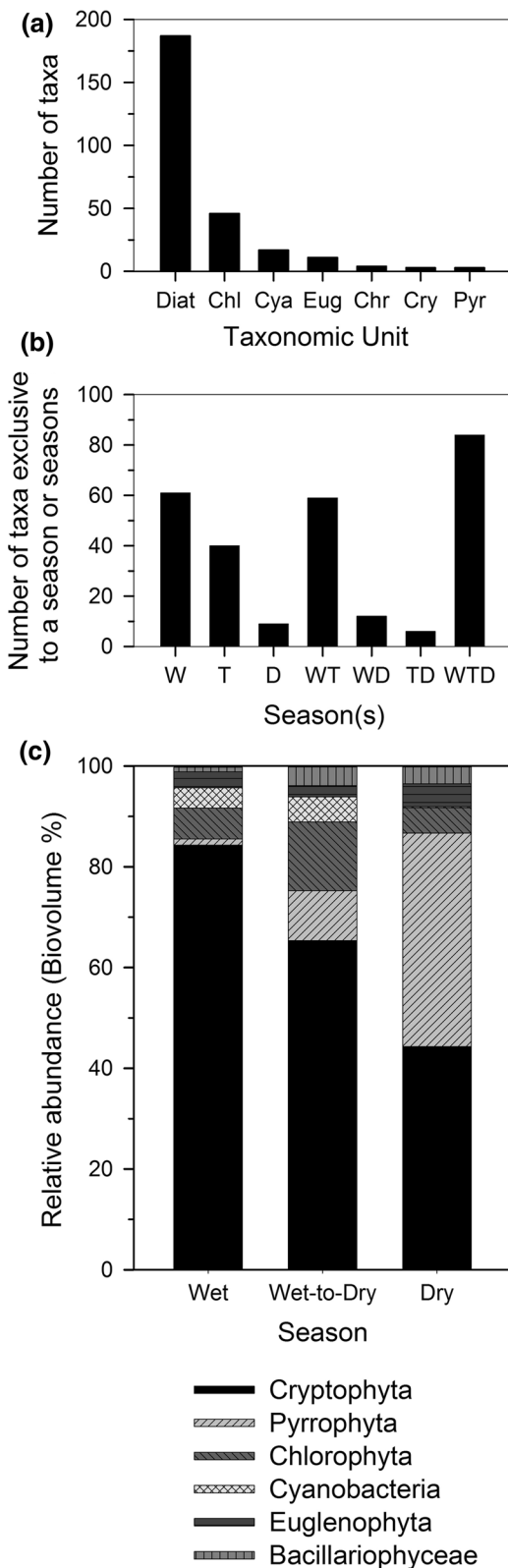
production because in a highly turbid, deep river such as the Daly River (Fig. 2), the euphotic depth was a small proportion of the river's depth. Additionally, the Daly River had a 100-fold discharge range, compared to, for example, the middle Paraná River which had a threefold range (Devercelli, 2010).

The highly seasonal flow regime of the Daly River underpinned the river's seasonal pattern of water quality, in common with other studies (e.g. Bortolini et al., 2016b). Discharge at a seasonal temporal scale drove water clarity, ionic chemistry and nitrate concentrations. Low water clarity during floods and higher clarity during the low discharge period are characteristic of South American tropical and sub-tropical rivers (Lewis, 1988; Divina de Oliveira & Calherios, 2000; Zalocar de Domitrovic, 2002; Bortolini et al., 2016b). Daly River floods had similar water clarity to the South American rivers considered above, but higher clarity during the low discharge dry season. For example, the Orinoco River due to high concentrations of dissolved organic matter (Lewis, 1988) and the Paraná (Unrein, 2002) and Paraguay Rivers (Zalocar de Domitrovic, 2002) due to high suspended solid concentrations had water clarities ($Z_{eu} < 1$ m) at least fourfold lower than the Daly River during the dry season. In 2000, a Z_{eu} of 12 m was measured in a tributary of the Daly River (Townsend et al., 2012), reflecting the low turbidity of the karst groundwater source.

Daly River SRP and dry season soluble nitrogen concentrations were generally similar (Train & Rodrigues, 1998; Soares et al., 2007) or lower (Unrein, 2002; Devercelli, 2006) than the large South American Rivers. Wet season soluble nitrogen concentrations, however, did not reach the high concentrations of the Paraná River which had exceeded 1 mg l^{-1} (Devercelli, 2010).

Phytoplankton concentrations

The biovolume and Chl *a* concentrations in the Daly River were either similar (Divina de Oliveira &

Table 2 Morphologically based functional group (MBFG) taxa for the Daly River and their relative abundance for the wet (W), wet-to-dry transition (WD) and dry (D) seasons

MBFG[a]	MBFG description[a]	Average relative biovolume abundance (%)			Common taxa according to season
		Wet	Wet-to-dry	Dry	
I	Small organisms, with high surface to volume ratios	3.6	3.6	3.1	Unidentified small spherical chlorophyte (possibly a chlorococcalean; W, WD, D)
II	Small flagellated organisms with siliceous exoskeletal structures	0.2	<0.1	0.0	*Dinobryon* sp. (W)
III	Large filaments with aerotopes	0.1	1.2	<0.1	*Phormidium* sp.(WD)
IV	Organisms of medium size lacking specialized traits	1.7	9.4	1.2	*Ankistrodesmus* spp. (WD), *Chlorella* sp. (WD), *Scenedesmus quadricauda* (Turpin) Brébisson (WD), *Scenedesmus quadrispina* Chodat (WD), Desmidiaceae spp. (W,WD)
V	Unicellular flagellates of medium to large size	89.7	78.3	92.1	*Cryptomonas* sp. (W, WD, D), *Euglena* spp. (W, WD, D), *Peridinium inconspicuum*, (WD, D), *Pyramimonas* (W, WD, D), *Strombomonas* (W), *Trachelomonas* sp. (D)
VI	Non-flagellated organisms with siliceous exoskeletons	0.9	3.9	3.5	*Gomphonema affine* Kützing (W, WD, D), *Nitzschia agnita* Hustedt (WD, D), *Nitzschia pusilla* Grunow (D), *Nitzschia sociabilis* Hustedt (WD, D), *Synedra ulna* (Nitzsch) Ehrenberg (W, WD, D), *Tryblionella levidensis* W. Smith (D)
VII	Large mucilaginous colonies	3.8	3.7	0.2	*Aphanocapsa* (W, WD)

[a] Kruk et al. (2010)
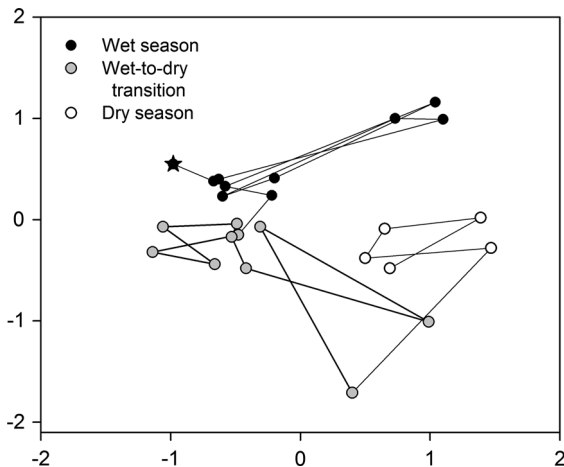
Fig. 9 Non-metric multidimensional scaling ordination (stress = 0.12) of phytoplankton biovolume relative abundances for the Daly River at Banyan Farm. The first sample is represented by a *black star* and the line joins consecutive sample dates between mid-January 2010 and 21 September 2010. The seasons are shown in Fig. 2

Calherios, 2000; Zalocar de Domitrovic, 2002) or lower than large South American rivers (Izaguirre et al., 2001; Soares et al., 2007). Compared to most European (see Salmaso & Zignin, 2010) and North American rivers (see Dodds et al., 1998), Daly River Chl *a* concentrations were low. Dry season Chl *a* concentrations measured during 2010 were similar to concentrations in previous years (Webster et al., 2005; Townsend et al., 2011; Schult & Townsend, 2012; Townsend et al., 2012) which suggests no major inter-annual variation of dry season phytoplankton biomass.

In common with many rivers, Daly River Chl *a* concentrations tended to be lower during high discharges, though wet season concentrations were not overall substantially lower than dry season values. Wet season biovolume and cell concentrations, however, exceeded dry season values, which contrasts with other studies (e.g. García de Emiliani, 1997) and implies the Chl *a* content of phytoplankton were lowest in the wet season (Fig. 6d). Moreover, the higher wet season biovolume concentrations demonstrate that a high-discharge wet season can supply substantial phytoplankton concentrations that exceed low-discharge concentrations.

Phytoplankton sources

Phytoplankton during the wet and wet-to-dry seasons probably originated from sources external to the river's main channel. The maintenance of a sustainable potamoplanktonic population in the main river channel was unlikely due to short retention times, low $Z_{eu}:Z$ ratios and low SRP concentrations. Moreover, fluctuating water levels would have reduced the longevity of hydraulic storage zones for potamoplanktonic growth. The suspension of riverbed benthic algae was an improbable source of phytoplankton because the first flushes in December would have suspended and transported these algae downstream, and subsequent riverbed scouring and low benthic PAR prevented algal regrowth.

Other possible sources of river phytoplankton were low-order streams and lentic water bodies. Although headwater streams in the Daly catchment experience frequent wet season storm disturbances, benthic algae exhibit substantial resilience (Townsend & Douglas, 2014) and could have supplied phytoplankton to the Daly River. The benthic algae, however, were dominated by filamentous chlorophytes which made a negligible contribution to the river's phytoplankton at Banyan Farm, which suggests that headwater streams were not a significant source of phytoplankton.

The most likely sources of wet season phytoplankton were off-channel lakes and pools on the river's floodplain, in particular those located along paleochannels (Fig. 1b). The flooded, mainly terrestrial, area upstream of the sample site can be substantial. Jardine et al. (2012) identified an area of frequent flood inundation of approximately 200 km^2 based on satellite imagery, whereas Begg et al. (2001) identified a tenfold greater area prone to flooding. During the wet season, and to a lesser extent the wet-to-dry transition, lentic water bodies were connected to the river's drainage system and probably supplied phytoplankton to the main river channel. The high wet season biovolume and cell concentrations, compared to the dry season, indicated that off-channel lakes were highly productive.

The influence of floodplain lakes on river phytoplankton has been widely reported for large South American rivers (e.g. Orinoco River Lewis, 1988; Paraguay River Divina de Oliveira & Calherios, 2000; Parana River Devercelli, 2006, 2010). The first flush of South American floodplain lakes into rivers can produce high Chl a concentrations in the main river channel (Lewis, 1988; Devercelli, 2006). This may also account for the relatively high Daly River Chl a concentrations during the rising limb of the first flood compared to the subsequent floods, and is supported by records of high Chl a concentrations found in regional lentic water bodies during the dry season (10–20 µg l^{-1}; Hart & McGregor, 1980; Townsend & Edwards, 2003; Townsend, 2006).

Chl a concentrations for floods 2–4 exhibited an inverse relationship with discharge, consistent with dilution, though the effect was less than proportional to increased discharge. Flood waters and catchment inflows to floodplain water bodies probably diluted lentic phytoplankton and flushed them into the main channel, thereby accounting for the relatively low Chl a concentrations of the rising limb of floods 2–4. The higher Chl a concentrations over the falling limb of these floods suggest the growth of lentic phytoplankton during the latter phases of river connection and their export to the Daly River. Hysteresis of Chl a concentrations has been observed for a small floodplain outlet (Ahearn et al., 2006) but not for a main river channel which integrates phytoplankton from multiple sources. Lentic phytoplankton growth could have been enhanced by the high nitrate concentrations of main channel inflows and increased water clarity due to sedimentation of suspended material, but required retention times sufficient for net phytoplankton growth. During the wet season, floodplain waterbodies in the region can have Chl a concentrations of up to 10 µg l^{-1} (Hart & McGregor, 1980), which is at least threefold higher than the Daly River concentrations.

The source of phytoplankton during the dry season was most likely the main channel of the Daly River because the river was disconnected from floodplain water bodies and many low- and middle-order tributaries had ceased flowing (e.g. Townsend & Douglas 2014). Moreover, approximately half of the river's dry season discharge at Banyan Farm originated from the direct input of groundwater to the river approximately (Tickell, 2011). Within the main channel of the Daly River, the most likely sites of sustained potamoplanktonic growth were hydraulic storage zones (see Reynolds, 1994) such as shallow (<0.5 m) side-arms (Townsend et al., 2012) and deep pools of up to 10 m depth and 2–3 km long (DENR, unpublished data).

Phytoplankton and chlorophyll *a* loads

The high wet season loads of Chl *a* and phytoplankton, compared to the remainder of the year, indicate the significant off-channel supply of phytoplankton to the Daly River and suggest that wet season phytoplankton productivity was higher than the dry season. High floodplain Chl *a* loads have also been calculated for the Orinoco River in South America (Lewis, 1988).

Phytoplankton suspended in the Daly River main channel during the wet season, under dark conditions, may have remained viable for 1–2 days based on a study of Lewis (1988) and probably inoculated downstream off-channel water bodies, notably the river's extensive lowland floodplains. Moreover, the phytoplankton may have contributed to floodplain's food web (e.g. Lewis et al., 2001) and provided a nutrient and energy subsidy from middle reach water bodies to the lowland floodplain. Phytoplankton in the main channel and riparian lentic water bodies may have also been prey for drifting fish larvae. Upon reaching brackish waters of the estuary, the phytoplankton probably provided a labile source of dissolved organic carbon for microbial metabolism (Guenet et al., 2010).

Phytoplankton composition and diversity

Discharge probably drove the shift from *Cryptomonas* domination of the Daly River's phytoplankton assemblage in the wet season to *Peridinium* and *Cryptomonas* domination in the dry season. The river's light climate was identified as a prime water quality driver underpinning the shift, with Z_{eu} increasing 13-fold. *Peridinium inconspicuum* appears to have been favoured by the high light and low soluble nutrient concentration environment. During the dry season, however, Daly River phytoplankton reached maximum primary production at 25–50% of incident surface PAR (Robson et al., 2010), indicating light was not limiting phytoplankton biomass. Moreover, average water column PAR approximates saturation rates due to the high incident PAR of the tropical latitude, high water clarity and shallow depth (Townsend et al., 2012).

Dry season nutrient limitation studies by Ganf & Rea (2007) and Robson et al. (2010) provide experimental evidence that dry season phytoplankton were nutrient limited. Whilst this is supported by the low soluble nutrient concentrations, notably nitrogen relative to phosphorus, these concentrations alone do not substantiate nutrient limitation because the low concentrations could have resulted from rapid phytoplankton uptake (Dodds, 2003). Nevertheless, based on experimental evidence and high water column PAR, the shift from wet season PAR limitation to dry season nutrient limitation, within the constraints of the river's hydraulic environment, probably limited phytoplankton biomass and drove taxa selection that resulted in *Peridinium* dominance.

Small flagellates, such as *Cryptomonas* and *Peridinium,* dominate in the Daly River, are r-selected taxa (sensu Pianka, 1970) based on their morphology and capable of efficient resource acquisition and rapid growth. Mobility can support efficient nutrient acquisition, limit grazing losses and reduce losses due to sinking (Kruk et al., 2010) and possibly hydraulic flushing. *Cryptomonas* can sustain viable populations in floodplain water bodies during river connection despite periodic dilution (Divina de Oliveira & Calherios, 2000; Devercelli, 2010) and is common in rivers with floodplains (Lewis, 1988; García de Emiliani, 1997; Train & Rodrigues, 1998; Divina de Oliveira & Calherios, 2000; Zalocar de Domitrovic, 2002; Townsend, 2006) but seems to have been in relatively high abundance in the Daly River. The occurrence of *Aphanocapsa* during the wet and wet-to-dry seasons and the chlorophytes *Ankistrodesmus*, *Scenedesmus* and *Chlorella* during the wet-to-dry season may be indicative of eutrophic lentic off-channel sources (see Padisák et al., 2009; Bortolini et al., 2016b).

The dominance of the Daly River's phytoplankton assemblage in the dry season by *Peridinium,* notably *Peridinium inconspicuum,* also occurred in 2000 (Townsend et al., 2012) which suggests the plankton may be dominant annually. *Peridinium* is common to the region's lentic water bodies (Townsend & Luongvan, 1998; Townsend, 2001, 2006) which have high water clarity ($Z_{eu} > 3.5$ m) and low nutrient concentrations (soluble $P < 10$ µg l^{-1}; NO$_3$–N < 20 µg l^{-1}) similar to the Daly River. The genus *Peridinium* is more commonly associated with stratified lake environments (Reynolds et al., 2002) but has also been reported in subtropical Paraná River (Train & Rodrigues, 1998) and South American floodplain lakes during connection to the main river channel (Huszar & Reynolds, 1997; Bortolini et al., 2016a), suggesting a range of environmental preferences for *Peridinium* species.

This evaluation of whether the Daly River's environmental conditions conform to the phytoplankton habitat templates of Kruk & Segura (2012) and codons of Padiśak et al. (2009) is limited to the extent that the environmental data collected at Banyan Farm were representative of the environmental conditions that sustained the river's phytoplankton. The environmental variables that best explained the MBFG Group V (unicellular flagellates; Kruk & Segura, 2012) were light attenuation ($Z_{eu} > 1.18$ m), temperature (<20°C), total nitrogen (<2800 μg l^{-1}) and zooplankton. During the dry season, the Daly River's Z_{eu} met the Group V criterion. Wet season river Z_{eu} values, however, were lower than the criterion but these were unlikely to be indicative of floodplain water bodies and instead higher Z_{eu} values were probably due to sedimentation of suspended material (e.g. Moreira-Turcq et al., 2004). Additionally, floodplain lentic $Z_{eu}:Z$ ratios were probably substantially greater than the river due to the relatively shallow depth of the lentic waterbodies (see Izaguirre et al., 2001; Unrein, 2002). Total nitrogen concentrations concur with the Group V threshold. In the wet season, concentrations are less than 600 μg l^{-1} (unpublished data, DENR) and less than 120 μg l^{-1} in the dry season (Townsend et al., 2012). Daly River temperatures exceeded the Group V 20°C criterion, but were nevertheless typical of regional lentic and lotic water bodies (22–37°C; Townsend et al., 1997; Townsend, 2006; Townsend & Douglas, 2014). Thus, nitrogen and dry season Z_{eu} data supported the Group V habitat template. Temperature a major variable in the habitat dichotomous key of Kruk & Segura (2012), however, may be overstated in defining Group V because flagellates are abundant in the warm lentic water bodies in the region (Townsend & Luong-van, 1998; Townsend, 2001, 2006).

The functional group classification of Padisák et al. (2009) nominates six river codon habitat templates. These are macrophyte epiphytes (T_C, T_D), epilithic diatoms (T_B), highly eutrophic waters (W_o), low-gradient, shallow, mixed enriched rivers (J) and shallow turbid waters (D). The environmental conditions of the Daly River during the dry season, when the river had high water clarity and low nutrient concentrations, did not readily conform to these codons. The Daly River was not dominated by macrophytes, though *Vallisneria* and charophytes are present in the river's middle reach (Townsend et al., 2017), nor

was it nutrient enriched. Rivers with low turbidity (<5 NTU), low nutrient concentrations (<100 μg l^{-1} total nitrogen, <10 μg l^{-1} total phosphorus) and moderate current speeds (0.1–0.2 m s^{-1}), such as the Daly River during the dry season are not well represented by a codon habitat template, which may reflect their global rarity and/or limited research effort.

The higher wet season species richness of the Daly River, compared to the dry season, probably reflected the greater diversity of habitat sources contributing phytoplankton to the river and was mainly due to vagrant or infrequently occurring taxa. The relatively high wet season richness of the Daly River is consistent with some South American rivers (e.g. García de Emiliani, 1997), though phytoplankton richness during the high discharges of the rainy season can be lower than the dry season (Soares et al., 2007). Daly River diatoms had a high species richness, but low relative abundance compared to other rivers (Rojo et al., 1994).

In conclusion, the seasonal pattern of discharge drove changes in water quality and temporal changes in the Daly River's phytoplankton biomass and composition. Wet season main channel river conditions were unsuitable for the growth of a sustainable phytoplankton population; however, high discharges probably connected the main channel to riparian and other off-channel water bodies which supplied phytoplankton to the main channel. On an individual flood temporal scale, however, floods late in the wet season diluted, though not proportionally, the phytoplankton concentration of the main channel and by inference the off-channel sources. High discharges served to both connect the river to off-channel phytoplankton sources as well as dilute these sources. The river transported a greater phytoplankton load over the wet season than the dry season, despite the 75% shorter duration, which indicated high catchment wet season phytoplankton productivity. We surmise that Daly River phytoplankton originated from two seasonally dependent, but temporally and spatially disconnected sources. River phytoplankton shifted from highly productive, spatially extensive off-channel sources in the wet season to less productive, spatially confined in-channel sources in the dry season.

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