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River regulation alters drivers of primary productivity along a
tropical river-estuary system

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Abstract

Worldwide, rivers continue to be dammed to supply water for humans. The resulting regulation of downstream flow impacts on biogeochemical and physical processes, potentially affecting river and estuarine productivity. Our study tested the hypothesis that primary production in the downstream freshwater reaches of a dammed river was less limited by light and nutrients, relative to downstream estuarine primary production. In a tropical dryland Australian river-estuary, we found that water column primary productivity was highest in freshwater sites which had lowest light attenuation. Nitrogen may also have limited primary productivity. Below the freshwater zone was a region of macrotidal mixing with high concentrations of suspended soil particles, nutrients and chlorophyll *a*, and lower but variable primary productivity rates. Light controlled productivity, but the algal cells may also have been osmotically stressed, due to increasing salinity. Further downstream in the estuary, primary productivity was lower than the freshwater reaches and light availability appears to be a factor. Therefore the reduced magnitude of peak flow events due to flow regulation, and the resulting decrease in nutrient export, is likely to be negatively impacting estuarine primary production. This has implications for future development of dams where rivers have highly seasonal flow.

Additional keywords: water quality; nutrients, light, Ord River, river regulation

Introduction

Throughout the world, approximately 3% of the land surface is now covered with artificial lakes and reservoirs (Gleick 1999). About 300 large dams (>15 m deep) are currently built every year, mostly in developing countries (Tockner and Stanford 2002). These dams provide water resources for human needs including irrigation, flood control, drinking water supplies and hydroelectric power. Impoundment of water affects not just the hydrology, but also a range of biogeochemical processes, with flow-on effects on primary productivity and food webs downstream (e.g. Ahearn *et al.* 2005; Bosch 2008).

Much of the research on the effects of water impoundments on ecosystems downstream has focussed on temperate areas of the world which typically receive modest and more regular rainfall in the winter months. The effect of water impoundments in tropical areas is less well understood. The tropics are characterized by major seasonal rainfall shifts with high volumes of rain falling in summer months. These events result in large areas becoming flooded with a resultant fuelling of terrestrial and aquatic primary productivity, and increased biomass of biota and spawning of fish species (Junk *et al.* 1989; Lewis *et al.* 2000). As a result allochthonous inputs to the system are an important supplement to autochthonous sources.

Flow regulation caused by water impoundment can also have substantial impacts on river and estuarine functioning. Allochthonous inputs typically decrease with less flooding affecting both freshwater and estuarine productivity. Gillanders and Kingsford (2002) in a review on the effects of freshwater flow in estuarine habitats identified links between flow, primary and secondary production. Additionally, studies have shown that the magnitude of freshwater flow, or rainfall as a proxy measure, is correlated with estuarine fish and crustacean catches (Vance *et al.* 1985; Robins *et al.* 2005), although the underlying mechanisms are poorly understood. Physiological responses to salinity changes has been proposed as one mechanism (Baptista *et al.* 2010).

Tropical Australia remains one of the few regions in the world where there are still significant numbers of rivers and estuaries that have not been subjected to flow regulation or water abstraction. These rivers convey ~70% of Australia's freshwater runoff (Hamilton and Gehrke 2005). The most common river type in the Australian tropics has highly intermittent summer flow (Kennard *et al.* 2010). These rivers, henceforth referred to as tropical dryland rivers, have infrequent, but major, rainfall events causing extensive flooding. They are typically turbid, and may have little or no flow in the dry season, reducing to a series of disconnected waterholes. There is increasing pressure to exploit these water supplies for human uses, including water impoundment for irrigation. However, there are still critical knowledge gaps including an understanding of the hydrological, biogeochemical and ecological linkages at landscape scales (Hamilton and Gehrke 2005).

This study therefore tested the hypothesis that the drivers of primary production changed across the freshwater-estuarine continuum in response to damming of a tropical dryland river. Specifically, in the freshwater reaches, light availability was hypothesized to be high relative to further downstream where the tidal influence increases turbidity. Additionally, nutrients were predicted to be less limiting in the freshwater zone downstream of the dam wall than further downstream in the estuary.

Methods

Site Description

The Ord River flows from Lake Argyle in the east Kimberly region of Western Australia (Fig. 1). The dam creating Lake Argyle was built in 1972. The lake has a surface area of 1000 km² and a capacity of 10,763,000 ML, draining 46,100 km² of catchment. It was created to provide water for irrigation and hydroelectric power. Approximately 45 km below Lake Argyle is the Kununurra Diversion Dam (KDD), a much smaller dam (90,000 ML). It was completed in 1963 and was designed to divert water into the nearby irrigation area. From the KDD, the lower Ord River extends 160 km, flowing into Cambridge Gulf. There is a constant baseflow of water from the KDD. The Dunham River enters the Ord River just below KDD and only flows during wet season flow events. The Ord River is freshwater and uni-directional in flow from the KDD to Carlton Crossing (between Sites 2 and 3, Fig. 1).

The freshwater zone of the river is relatively shallow, being a few metres at the deepest sections. The riverbed is dominated by gravel and sand with patches of aquatic macrophytes, such as *Vallisneria*, and rocky areas. The rocky areas were covered with a thick mat of attached algae. Below this is the freshwater tidal zone (down to Site 5) and the water level rises and falls with the tide. The substrate is silty sand and gravel, with muddy river banks exposed at low tide. Below Site 5 is the estuarine zone which, due to the macrotidal nature of the estuary, is vigorously mixed and has a soft muddy substrate. The tides in the estuary are asymmetric, with water moving upstream more quickly than downstream. The Ord River flows into Cambridge Gulf, a pristine coastal region with one of the largest tidal amplitudes (6 m at the mouth) in the world (Wright *et al.* 1973; Wolanski *et al.* 2001).

Regular water quality monitoring

Regular water quality sampling was conducted monthly at 8 sites (Sites 3, 4, 5, 6, 7, 8, 10, 11) within the tidal estuary from 2002 to 2007 (Fig. 1). Surface water column readings of temperature, conductivity, dissolved oxygen, turbidity and pH were obtained at each site using a datalogger (Hydrolab, Castle Hill, Australia), along with Secchi depth measurements. The water column was well mixed, based on profiles of temperature and oxygen undertaken with dataloggers. Sample collection commenced at the most downstream site (Site 11) on or near high tide on a neap tide cycle and an upstream transect was done. Two 1-L water samples were collected at 0.5 m depth at the sites listed above in lower Ord River and estuary. Water samples were stored on ice in the field, and then at 4°C, and analyzed within 24 h of collection. Subsamples for dissolved nutrients were filtered through 0.45-µm membrane filters, and known volumes of samples were filtered onto pre-weighed filters, dried at 60°C, then weighed for suspended solids. For chlorophyll *a* analyses, known volumes of water were filtered onto glass fibre filters (Whatman GF/F, Kent, UK) for subsequent extraction and measurement. Samples were analyzed for total nitrogen (TN), phosphorus (TP), total suspended solids (TSS), nitrate+nitrite (NO₂/NO₃), ammonia (NH₃), silicate (Si), filterable reactive P (FRP), dissolved organic N (DON) and P (DOP), and chlorophyll *a*, using standard methods (APHA 2005). River flow, in m³ s⁻¹ was measured constantly at a gauging station at Tarrara Bar (Fig. 1) throughout the study.

150

151 *Algal studies*

152 In August 2006 and February 2007, sampling trips to quantify algal biomass, species
153 composition and productivity were undertaken to the Ord River. These trips were
154 chosen to contrast wet and dry seasons and involved measurements of primary
155 productivity, using ^{13}C -uptake incubations, ^{15}N -uptake by algae, and algal species
156 biomass and composition, using pigment analysis. On the first trip, nutrient algal
157 bioassays were also conducted. Three sites spanning the river-estuary system were
158 studied on the first trip (Sites 2, 6, 9), and four sites on the second trip (Sites 1, 2, 6, 9)
159 (Fig. 1). During these trips, water quality sampling and datalogger profiling was also
160 conducted using the same protocols outlined above.

161

162 Pigment analyses

163 Surface water was also collected at each site for algal pigment analysis to estimate
164 algal community composition and concentration. A known volume of sample water
165 was filtered through a 47-mm glass fibre filter (Whatman GF/F) and the filter then
166 stored in a vial in liquid N until analysis. To extract the pigments, filters were
167 sonicated in acetone, stored at 4°C for 15 h, diluted 1:10 with water and re-sonicated,
168 then centrifuged to remove the glass fibres.

169

170 Sediment samples were also collected on the river edge at each site for algal pigment
171 analysis. Sediment samples were collected using a cut-off syringe and the top cm
172 sliced off. This was then homogenised and a sub-sample transferred into cryovials.
173 These were stored in liquid N until analysed. Thawed samples were weighed,
174 sonicated in acetone, stored at 4°C for 15 h, then samples were centrifuged. The
175 supernatant was kept aside and the sediment re-extracted with a resting time of 3-4 h
176 before repeating centrifugation. The extract was added to the first extract, diluted by
177 10% with water, and made up to a set volume with acetone.

178

179 The final extract of all samples was filtered through a 0.2- μm membrane filter
180 (Whatman, anatop) prior to analysis by high performance liquid chromatography
181 (HPLC) system (Waters – Alliance, Milford, Massachusetts, USA), comprising a
182 2695XE separations module with column heater and refrigerated autosampler and a

2996 photo-diode array detector. Immediately prior to injection, the sample extract was mixed with a buffer solution (90:10 28 mM tetrabutyl ammonium acetate, pH 6.5: methanol) within the sample loop. After injection, pigments were separated using a Zorbax Eclipse XDB-C8 stainless steel 150 mm x 4.6 mm ID column with 3.5 μ m particle size (Agilent Technologies, Santa Clara, California, USA) and a binary gradient system with an elevated column temperature following a modified version of the Van Heukelem and Thomas (2001) method. The flow rate was 1.1 mL min⁻¹ and the column temperature was 55°C. The separated pigments were detected at 436 nm and identified against standard spectra using Waters Empower software (Milford, Massachusetts, USA). Concentrations of chlorophyll a, chlorophyll b and β , β -carotene in sample chromatograms were determined from Sigma (USA) standards, while all other pigment concentrations were determined from standards (DHI, Denmark).

Primary productivity and N uptake

Water samples collected below the surface were kept in buckets until ¹³C-uptake incubations were conducted. Acid-washed polycarbonate bottles (500 ml) were filled with water collected from each site. Triplicate bottles from each bucket were incubated at one of five light levels: 0, 5, 14, 50 and 100% of surface light using shade bags of appropriate light attenuation. ¹³C-sodium bicarbonate (¹³C 99%, Cambridge Isotope Laboratories, Andover, Massachusetts) was added to bottles at a concentration of 1.42 mM bicarbonate. This equated to between 30 and 60% enrichment of the total bicarbonate concentration.

Incubators for the bottles were large plastic bins with continuously flowing river water to ensure that the ambient water temperature was maintained. The temperature was logged throughout the incubations. The bottles were placed in full sunlight and incubated either side of local apparent noon (when the sun was highest in the sky) for 2 to 3 h. Known volumes of water from the bottles were filtered onto precombusted glass fibre (Whatman GF/F) filters. Filters were frozen until returned to the laboratory. Filters were then dried at 60°C for 24 h before being analysed for ¹³C/¹²C isotope ratio and %carbon on a mass spectrometer (GV Isoprime, Manchester, UK).

A water sample was also collected at each site for alkalinity measurements. Water samples were kept in filled bottles on ice until analysed in the laboratory by titration (APHA 2005). Alkalinity, pH, water temperature and conductivity values were used to determine the bicarbonate concentrations in the water. Secchi depth readings were converted to euphotic depth values using a multiplier of 1.7 (Chapra 1997).

Maximum rates of productivity ($P_{\max}$, $\text{mg C m}^{-3} \text{ h}^{-1}$) were determined based on the surface rates, as this is where the highest rates were measured. Water column areal productivity ($\text{mg C m}^{-2} \text{ d}^{-1}$) was calculated by integrating primary productivity through the water column based on the ^{13}C -bicarbonate incubation data, alkalinity measurements and Secchi depths. A rain event while sampling Site 2 in February 2007 resulted in high light attenuation and hence, low depth-integrated primary productivity. Hence primary productivity rates were also calculated based on a more typical Secchi depth of 94 cm. Additionally, particulate carbon concentrations at Site 6 were high (6.2 mg C L^{-1}) due to the presence of high concentrations of non-algal carbon. To calculate primary productivity rates at Site 6, algal carbon was calculated for this site based on a comparison of carbon:chlorophyll ratios across the other sites. The correlation (R^2) between carbon and chlorophyll was 0.74. The carbon concentrations used were based on mass spectrometer analyses outlined above.

For ^{15}N -uptake experiments, a similar protocol and the same sites were used, but bottles were spiked with one of three sources of N: NH_3 , NO_3 or urea, rather than bicarbonate (Glibert *et al.* 1991). These N sources were added to be ~10% of the ambient concentration of each nutrient in the water. Bottles were incubated in the bins with flow-through water in full sunlight for 1 h, then water was filtered onto pre-combusted filters and processed using the same protocol as for ^{13}C -filters. Filters were analysed for $^{15}\text{N}/^{14}\text{N}$ ratios and %N. One site, Site 6, had very high PN concentrations which were not commensurate with high chlorophyll *a* concentrations. Therefore, calculation of biomass-specific uptake rates would have resulted in falsely high rates at this site. For consistency, non-biomass specific uptake rates (v) were calculated using the equations of Dugdale and Goering (1967). Water samples from the sites for urea analysis were also filtered through $0.45\text{-}\mu\text{m}$ membrane filters and analysed using the diacetyl monoxime method (Rahmatullah and Boyde 1980).

A Yeo-Kal logger (Brookvale, NSW, Australia), which measured time series of oxygen concentration and temperature, was deployed for 5.5 days a small distance downstream from Site 2 during August 2006 and February 2007. The collected data were used to estimate whole system photosynthesis rates using a form of the diurnal curve method applied by Webster *et al.* (2005) to similar measurements in the Daly River. It assumed a water depth of 1 m based on in situ measurements, and the same photosynthetic ratio (oxygen production:carbon dioxide utilisation) was used as previously outlined by Webster *et al.* (2005). Like the more traditional diurnal curve method, described for example by Chapra (1997), the modified method infers photosynthesis rates from measured changes in oxygen concentration. However, the modified method is based on an analysis of rates of change of oxygen concentrations, rather than on the concentrations themselves. The approach allows the estimation of calculation uncertainty.

Algal nutrient bioassays

In the first sampling trip, surface water samples were collected at the three sites for algal nutrient bioassays. The assays involved pouring water into polycarbonate bottles with four treatments: control, N, P and N+P addition. There were three replicate bottles of each treatment. Sodium nitrate was added as the N treatment; potassium dihydrogen phosphate was added as the P treatment. The ambient NO_3 concentration was assumed to be 0.1 mg L^{-1} and the ambient FRP concentration was assumed to be 0.01 mg L^{-1} , and nutrients were added at ten times ambient concentrations. Bottles were incubated in plastic bins with flow-through river water under ambient light conditions for 24 h. Bottles were then stored in the dark for at least 20 min prior to reading the photosynthetic yield response using a PHYTOPAM (Heinz Walz GmbH, Effeltrich, Germany) (Ganf and Rea 2007). Two readings were taken from each bottle.

Data analysis

Correlations between chlorophyll *a* concentrations and variables potentially affecting it (Secchi depth, TSS, turbidity, DON, NO_2/NO_3 , NH_3 , DOP, FRP and Si) were undertaken within the three zones of the system: freshwater (Sites 3, 4, 5), transition (Sites 6, 7) and estuary (Sites 8, 10, 11) using the long-term dataset. Data were first

tested for normality and a Spearman Rank Correlation was undertaken using SAS Software (SAS Institute Inc.). For the algal nutrient bioassays, data were analysed for normality, then statistical differences between treatments were tested with an unpaired t-test using SAS software.

Results

During the study, flow rates at Tarrara Bar were less than $100 \text{ m}^3 \text{ s}^{-1}$ throughout most of the year (Fig. 2). Peak flow occurred in summer with late summer 2006 (February/March) having the highest peak. Between August 2006 and February 2007, when sampling trips occurred which focussed on algal variables, the summer flow peak was small relative to most other years of the study.

Physico-chemical variables – long term dataset

The physico-chemical variables were examined based on their potential to control of algal production in the system. The water temperatures, based on monthly transect data across 5 y in the lower Ord River and estuary, were similar among sites (27 to 28°C) (Table 1). There was also little difference in temperature throughout the year with a standard deviation across sites of $\sim 4^\circ\text{C}$. The two upstream sites (Sites 3, 4) were freshwater (150 to $165 \mu\text{S m}^{-1}$) with the saltwater intrusion measurable at Site 6 ($990 \pm 1472 \mu\text{S m}^{-1}$). The downstream sites, Sites 10 and 11, had the highest salinity water. Dissolved oxygen and pH tended to be highest at the freshwater sites. Turbidity was highest, but highly variable, at Site 7.

Total and dissolved organic N and P, Si, and chlorophyll *a* concentrations all peaked at the same site as turbidity, i.e. Site 7 (Table 2). Secchi depths were also lowest at this site (0.2 m). The calculated euphotic depth, based on the Secchi depth (Chapra 1997) was 0.34 m. In contrast, dissolved inorganic N (DIN) and FRP concentrations were lowest in the freshwater sites, and the calculated euphotic depth was highest, i.e. 6.2 m. The mean molar TN:TP ratios were within the range of the Redfield ratio (1958) in the freshwater sites (7:1 – 24:1), lower than Redfield in the transition zone (6:1 – 7:1), and close to Redfield in the estuary (10:1 – 16:1). DIN:FRP ratios in the freshwater sites were between 9:1 and 13:1 (Table 2). Below Site 7, ratios increased to $\sim 18:1$ and remained constant throughout the estuarine sites. Chlorophyll *a*

concentrations in the freshwater were 2 to 4 mg m⁻³, increasing to 7 mg m⁻³ in the transition zone, decreasing again to 2 to 3 mg m⁻³ in the estuarine zone.

The proportion of different N and P fractions varied considerably down the river-estuary system (Fig. 3). At the freshwater Sites 3, 4 and 5, DON was the dominant N fraction, whilst DOP and DIP were the dominant P fractions. At the transition Sites 6 and 7, particulate N (PN) was the dominant N fraction, while particulate P (PP) was the dominant P fraction. Further downstream in the estuary, DIN, DIP and PP were the dominant fractions.

In the freshwater zone (Sites 3, 4, 5), chlorophyll *a* concentrations were significantly correlated with NH₃, NO₂/NO₃ and turbidity ($R^2 = 0.33$, $P < 0.05$, $R^2 = 0.52$, $P < 0.005$, and $R^2 = 0.47$, $P < 0.005$ respectively). In the transition zone (Sites 6, 7), where salinity was increasing and turbidity was high, chlorophyll *a* concentrations were only correlated with temperature ($R^2 = 0.36$, $P < 0.05$). In the estuarine zone (8, 10, 11), where salinity was high, chlorophyll *a* concentrations only correlated with NH₃, but it was a negative correlation ($R^2 = -0.32$, $P < 0.05$).

Algal studies

Algal primary production and species composition (using HPLC pigments) was examined in more detail during two intensive sampling trips. There were some differences in nutrient and chlorophyll *a* concentrations, and physical variables between August 2006 and February 2007 sampling trips, but differences were not consistent (Table 3, Fig. 4). Site 6 showed the greatest variability with nutrients, conductivity and turbidity being higher on the first sampling trip. These values were also similar to those measured during the long-term water quality monitoring program, although temperatures were lower in August and higher in February than the mean of the long-term dataset (cf. Tables 1, 2). Consistent with the long-term dataset, total nutrients were typically highest at Site 6.

Chlorophyll *a* concentrations in the water column ranged from 0.8 to 4.5 mg m⁻³ with highest concentrations at the transition zone, Site 6, and lowest values at the estuary site (Site 9) (Fig. 4). Pigments which relate specifically to an algal class are termed marker pigments (Jeffrey and Vesk 1997; Jeffrey and Wright 2006). The marker

pigment, fucoxanthin, indicative of diatoms, was dominant at all sites in August 2006, representing 21% of the chlorophyll *a* concentrations at the freshwater sites (Sites 1 and 2) to 39 % at the transition site (Site 6). Chlorophytes (as indicated by the marker pigments, lutein and chlorophyll *b*) and dinoflagellates (peridinin) were only observed at the freshwater sites, while cyanophytes (zeaxanthin) were present at all sites and cryptophytes (alloxanthin) were at all sites except the transition site.

By comparison, in February 2007, diatoms only dominated the biomass (fucoxanthin being a high proportion of the chlorophyll *a* concentration) at the estuary site (Fig. 4). The biomass at the freshwater sites (Sites 1, 2) was dominated by cyanophytes (zeaxanthin) and chlorophytes (lutein and chlorophyll *b*), while at the transition site (Site 6) the biomass was dominated by chlorophytes. Cryptophytes (alloxanthin) were present at all sites and dinoflagellates (peridinin) were present only at the estuarine site (Site 9). Cyanophytes were present at all sites.

Sediment chlorophyll *a* concentrations were higher at the freshwater sites (Sites 1, 2) than the downstream sites (Sites 6, 9) (Fig. 4). During both sampling periods, benthic algal biomass was dominated by diatoms at all sites, except one of the freshwater sites (Site 1) in February 2007. At this site, there were chlorophytes (lutein and chlorophyll *b*), cyanophytes (zeaxanthin), cryptophytes (alloxanthin) and dinoflagellates (peridinin) present, as well as diatoms. Chlorophytes and cyanophytes were at both the freshwater and estuarine sites, and cryptophytes were only at the freshwater site only. At the estuarine site (Site 9), in February 2007, diatoms dominated the benthic algal biomass. The transition site (Site 6) was similar to the estuarine site with the exception that dinoflagellates were contributing to the benthic algal biomass.

Depth-integrated primary productivity rates in the water column, as measured by ^{13}C -uptake, were highest in the freshwater sites, Sites 1 and 2 (5.6 to 7.5 mg C m⁻² h⁻¹) (Table 3). There was little measureable integrated primary productivity at Site 6 due to the high light attenuation, i.e. 4 to 11 cm in the first sampling trip. On the February 2007 trip, light attenuation was not as high at Site 6, but had increased at Site 9, resulting in higher integrated primary productivity at Site 6 and lower values at Site 9.

Maximum rates of primary productivity ($P_{\max}$), which were typically rates at the surface, were typically higher at freshwater sites (Table 3). The whole-system photosynthesis, which includes benthic algal and macrophyte photosynthesis, as measured by the diurnal curve method for oxygen at Site 2, in the freshwater zone of the river, was 435 and 375 mg C m⁻² d⁻¹ in August 2006 and February 2007 respectively. Non-biomass specific uptake (v h⁻¹) of NH₃, NO₃ and urea by phytoplankton was compared on both sampling occasions (Fig. 5). Uptake was higher overall on the second trip, and freshwater sites had higher uptake than downstream sites. Urea uptake was a major source of N for phytoplankton compared with NH₃ and NO₃.

In the algal nutrient bioassays in August 2006, phytoplankton did not respond to nutrient additions after 24 h, as measured by photosynthetic yield, at sites 2 and 6, but did respond to N, P and N+P additions at site 9 (Fig. 6). The yield values for the control treatment were lowest at site 6 and highest at Site 2. At the time the algal bioassays were undertaken, FRP and available N (NH₃, NO₂/NO₃, urea) concentrations were 0.008 and 0.032 mg L⁻¹ respectively at site 2, 0.023 and 0.177 mg L⁻¹ respectively at Site 6, and 0.019 and 0.132 mg L⁻¹ at Site 9.

Discussion

Freshwater zone

Our study found that the freshwater zone of the regulated Ord River system had the highest water column primary productivity. Light penetration was typically to the bottom of the water column suggesting that light was not a key limiting factor for growth. Analysis of the long-term dataset showed that chlorophyll *a* concentrations were correlated with NO₂/NO₃ and NH₃, suggesting that N was limiting growth. Additionally, the algal studies identified urea as an important source of DON for phytoplankton growth (Berman and Bronk 2003). The role of urea as an N source for algae is rarely studied in freshwater systems. Urea is produced from the breakdown of the large pool of DON.

Water residence time was likely to be a key constraint to algal biomass accumulation, at least in the water column. During the August field survey, the residence time for

flow discharged from the KDD to reach Site 2 is estimated to have been 1.8 d with an estimated time to reach the estuary of 4.5 d. The phytoplankton community was not dominated by any one group, being a mixture of diatoms, cyanobacteria, green algae and cryptophytes. Groups such as diatoms and green algae are capable of rapid growth. However, even with maximum doubling times for freshwater phytoplankton of $\sim 1 \text{ d}^{-1}$, and more typical doubling times of 0.5 d^{-1} (Reynolds 2006), water residence time is still likely to be limiting. Another factor that may control primary production is grazing, but this was not the focus of this study.

It appears that phytoplankton were not the main source of primary productivity in the freshwater zone since whole-system rates were considerably higher than phytoplankton rates. This is consistent with the observed presence of beds of macrophytes and algal-covered rocky areas throughout the freshwater zone. There are few studies of primary productivity in non-eutrophic tropical rivers for comparison with this study. In the Daly River, a clear perennially flowing river in tropical Australia, whole-system rates of photosynthesis, measured using oxygen fluxes, were higher, i.e. 200 - 4800 compared with 375 - 435 $\text{mg C m}^{-2} \text{ d}^{-1}$ in our study (Webster *et al.* 2005). However, these authors surmised that nutrient limitation caused most of the photosynthesis to result in the production of dissolved organic carbon, rather than the growth of primary producer biomass. It is possible that similar mechanisms may be operating in the Ord River.

A more recent study of phytoplankton production in the Daly River, using the same ^{13}C -uptake technique, also found rates were somewhat higher than our study, i.e. 60 to 180 compared with 60 to 75 $\text{mg C m}^{-2} \text{ d}^{-1}$ (M. Burford, unpubl data). Higher phytoplankton productivity (168 to 290 $\text{mg C m}^{-2} \text{ d}^{-1}$) was also measured in an unregulated dryland river in central Australia during a no-flow period (Burford *et al.* 2008a) but rates were similar to the unregulated Flinders River in tropical Australia, i.e. 66 to 121 $\text{mg C m}^{-2} \text{ d}^{-1}$ (M. Burford, unpubl data). These dryland rivers have highly intermittent flow, comparable with the flow regime of the Ord River prior to damming (Petitt *et al.* 2001; Kennard *et al.* 2010). Therefore, there was no evidence that regulation changed primary production rates in the water column.

There are two counteracting factors that impact on nutrient concentrations and light attenuation in the river downstream of the dam. Lake Argyle is gradually becoming filled with sedimented material (Dixon and Palmer 2009), reducing the transport of suspended sediments and associated nutrients downstream. Counteracting this, the deeper anoxic waters of the Lake Argyle and the KDD may be providing a zone for remineralisation of particulate nutrients, potentially increasing dissolved nutrient concentrations downstream (Friedl and Wüest 2002). Additionally, the irrigation scheme discharges dissolved nutrients into drains that flow into the lower Ord River above Tarrara Bar (Parslow *et al.* 2003). The combination of these factors is likely to explain why there are measureable concentrations of NO_2/NO_3 , NH_3 and FRP in the freshwater zone of the lower Ord.

Transition zone

Further downstream, below Site 5, the freshwater reached the marine waters and the macrotides caused mixing of salt and other materials. The turbidity, TSS and nutrient concentrations in the water column in this zone were much higher than either upstream or downstream, and highly variable. There was resuspension and settling associated with tidal changes in water velocity and shear stress. Studies have shown that the high degree of tidal pumping of sediment in the system has made it geomorphologically unstable and is resulting in a high level of siltation (Wolanski *et al.* 2001; Wolanski 2006). The proportion of dissolved inorganic nutrients increased relative to upstream, suggesting that remineralisation processes were important. Numerical modelling confirms that the remineralisation of trapped particulate nutrients occurs in the tidal pulsing zone (Parslow *et al.* 2003; Robson *et al.* 2008).

Despite the relatively high nutrient concentrations, depth-integrated primary productivity in the water column was lower than upstream. This was, in large part, the result of high light attenuation since primary productivity was higher when turbidity was lower. P_{max} and algal group composition varied considerably between the two sampling occasions. When salinity was lowest, the algal group composition reflected the mixed freshwater community, and when salinity was higher, the community reflected a diatom-dominated estuarine community. Additionally, in this zone the long-term chlorophyll *a* concentrations were highly variable. The macrotidal nature of this zone is an unfavourable (high salinity-gradient and highly turbid)

environment and likely to periodically compromise algal growth. This is substantiated by the low photosynthetic yield in the phytoplankton community in this zone, and the lack of capacity to respond to nutrient additions in algal bioassays. Other studies have shown that increased salinity can limit growth of freshwater species (e.g. Robson and Hamilton 2003; Roubex *et al.* 2008). Sediment chlorophyll *a* concentrations were also low, likely due to low light availability, and the high tidal energy continually depositing and scouring sediments on the water's edge.

Estuarine zone

Further into the estuary, light attenuation decreased. This resulted in primary productivity rates intermediate between the freshwater and transition zones, although chlorophyll *a* concentrations were lower than upstream. Rates of maximum primary production ($P_{\max}$) were similar to those measured in another tropical Australian estuary, Darwin Harbour (Burford *et al.* 2008b), but chlorophyll *a* concentrations were higher. $P_{\max}$ was lower than those measured in the Fly River delta and a tropical Indian estuary (Robertson *et al.* 1993; Sarma *et al.* 2009). Light availability is likely to have limited primary productivity as $P_{\max}$ was as high as in the freshwater reaches in February 2007. Analysis of the long-term dataset showed a negative correlation between chlorophyll *a* concentrations and NH_3 . However, in the algal bioassay conducted in August 2006, phytoplankton responded to N and P. This is surprising as the DIN concentrations, and particularly NO_3 , were relatively high, i.e. 0.132 mg L^{-1} .

The ^{15}N -uptake experiments also showed that NH_3 was a preferred source of N, compared with NO_3 . Additionally, urea provided an important source of N for phytoplankton growth requirements. Some studies have shown the importance of urea in estuaries (Twomey *et al.* 2005; Torres-Valdes and Purdie 2006). Diatoms dominated both the water column and sediment, consistent with other estuarine studies (Biswas *et al.* 2010; Gameiro and Brotas 2010). Studies of estuaries downstream of dammed rivers have found a reduction in Si concentrations, affecting diatom productivity (Li *et al.* 2007). However, in our study, Si did not appear to be a limiting factor for diatoms as the proportion of diatoms was higher in the estuary than upstream despite lower Si concentrations. Additionally, concentrations were not sufficiently low to be considered limiting for diatoms (Egge and Aske 1992).

Implications

Much of tropical northern Australia has rivers with highly intermittent flow (Leigh and Sheldon 2008; Kennard *et al.* 2010). Prior to damming, the lower Ord River also had highly intermittent flow, consistent with the adjacent river systems (Doupé and Petitt 2002). During the wet season, the highly episodic rainfall, often induced by cyclonic weather conditions, caused major flooding. During the dry season, the river became a series of pools. Nutrient loads were likely to be higher in the wet season, but lower in the dry season. However, damming of the Ord River has fundamentally changed the river flow regime such that it is now similar to tropical rivers with a baseflow throughout the year, and less wet season flow. Leigh and Sheldon (2008) have proposed that flow permanence and regularity in ‘tropical’ river types, flow variability and absence in ‘dryland’ river types, and wet-dry seasonality in both river types are the key hydrological drivers maintaining and explaining ecological function and biodiversity in unregulated rivers in Australia’s wet-dry tropics. Indeed, other studies of the Ord River have shown that riparian vegetation dynamics and in-stream fauna have been affected by regulation (Doupé and Petitt 2002).

The reduction in large flow events in the Ord River post-damming has increased tidal pulsing and reduced wet season flows. This causes siltation in the transition zone, and in the longer term will further reduce freshwater flows to the estuary (Wolanski *et al.* 2001; Wolanski 2006). The net effect is likely to be reduced transport of nutrients and particulate matter to the estuary, and a corresponding decrease in primary production. Phytoplankton species composition is also likely to be affected, with studies showing that phytoplankton functional groups in estuaries are affected by flushing times (Costa *et al.* 2009). These factors will have flow-on effects on higher trophic levels. A study comparing juvenile estuarine penaeid prawns in the Ord River estuary with adjacent unregulated rivers found that abundance was lower in the Ord system (Kenyon *et al.* 2004). Other studies have found that the magnitude of flow affects estuarine primary production (Mallin *et al.* 1993; Gillanders and Kingsford 2002). Additionally, flow has been correlated with catches of a range of crustacean and fish species (Vance *et al.* 1985; Robins *et al.* 2005; Baptista *et al.* 2010).

Our research has implications for the future development of water resources of dryland rivers. Much of the focus on the effect of flow regulation has been on the

552 rivers with little understanding of the effect on estuaries. However, by undertaking
553 studies that span the river-estuary continuum, the effect of flow regulation on algal
554 productivity across this continuum can be determined. Regulated flow, and the
555 associated reduction in suspended sediments and increase in dry-season nutrient
556 availability, is likely to favour primary producers in the freshwater zone. However, in
557 the estuary, reduced flooding will result in less nutrients being transported into the
558 estuary, and is likely to reduce estuarine primary production. Our understanding of
559 future impacts of flow regulation on regulated rivers is confounded by the overlaying
560 climate change effects on flow which are, as yet, poorly modelled for northern
561 Australia. However, any reduction in flow is likely to exacerbate a decline in estuarine
562 productivity.

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Figure Legend

Figure 1: Map of the lower Ord River-estuary system, including regular monitoring sites (Sites 3, 4, 5, 6, 7, 8, 10, 11) and sites sampled for algal variables in August 2006 (Sites 2, 6, 9) and February 2007 (Sites 1, 2, 6, 9).

Figure 2. Flow hydrograph at Tarrara Bar ($\text{m}^3 \text{s}^{-1}$) during the study from 2002 to 2007.

Arrows denote dates for two sampling trips to measure algal variables.

Figure 3: Mean percentage of (a) N and (b) P fractions in the water column at sampling sites over five years.

Figure 4: Chlorophyll *a* concentrations, and proportions of biomarker pigments in (a, c) water column (mg m^{-3}) and (b, d) sediment ($\mu\text{g g}^{-1} \text{ww}$) samples collected from three sites in the Ord River-estuary system in August 2006 and four sites in February 2007. Pigments are Chl-*a* (chlorophyll *a*); Perid (peridinin); Fuco (fucoxanthin); Hex-fuco (19'-hexanoyloxyfucoxanthin); Allo (alloxanthin); Zea (zeaxanthin); Lut (lutein); Chl *b* (chlorophyll *b*).

Figure 5: Mean (+ SD) non-biomass specific uptake (v h^{-1}) of NH_3 , NO_3 and urea ($\pm$ SD) by phytoplankton at the algal sampling sites on two sampling occasions in August 2006 and February 2007.

Figure 6: Mean (+ SD) photosynthetic yield measurements for surface water samples incubated for 24 h with the following treatments: control, N, P, N+P addition ($n = 3$) for the first sampling occasion in August 2006. * $P < 0.05$

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Table 1: Mean (SD) values for physico-chemical variables at eight sites along the lower Ord River and estuary from February 2002 to February 2007. DO = dissolved oxygen, TSS = total suspended solids.

Site	Temperature (°C) n = 43	Conductivity ($\mu\text{S m}^{-1}$) n = 63	DO (mg L^{-1}) n = 43	Turbidity (NTU) n = 50	pH n = 52	Secchi (m) n = 25	TSS (mg L^{-1}) n = 40
3	27.5 (3.9)	150 (33)	7.78 (0.99)	59 (194)	8.12 (0.25)	1.1 (0.4)	12.7 (16.2)
4	28.0 (3.8)	165 (42)	7.84 (0.76)	48 (146)	8.13 (0.25)	1.0 (0.5)	18.7 (17.0)
5	27.5 (4.1)	239 (123)	7.45 (0.91)	210 (286)	8.13 (0.26)	0.5 (0.3)	293.5 (409.8)
6	27.7 (4.2)	990 (1472)	7.15 (0.98)	482 (422)	8.14 (0.27)	0.3 (0.4)	625.0 (728.3)
7	27.2 (4.1)	5044 (5087)	6.89 (0.93)	672 (499)	8.06 (0.26)	0.2 (0.6)	1094.8 (1727.9)
8	27.5 (3.8)	20195 (7542)	6.41 (0.71)	287 (260)	7.89 (0.21)	0.2 (0.2)	205.5 (249.3)
10	27.6 (3.6)	24101 (6962)	6.27 (0.65)	229 (259)	7.79 (0.34)	0.3 (0.2)	108.0 (82.3)
11	27.8 (3.5)	23213 (7040)	6.28 (0.68)	177 (246)	7.81 (0.27)	0.5 (0.4)	79.4 (74.0)

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Table 2: Mean (SD) nutrient and chlorophyll *a* (mg m^{-3}) concentrations and Secchi readings (m) at eight sites along the Ord River system from monthly sampling between February 2002 to February 2007. Bold numbering denotes the site with the highest mean concentration of each variable, and in the case of Secchi refers to the lowest depth. NH_3 = ammonia, DON = dissolved organic N, NO_2/NO_3 = nitrate, FRP = filterable reactive P, DOP = dissolved organic P, Si = silicate, Chl *a* = chlorophyll *a*.

Site	TN n = 40	NH_3 n = 40	DON n = 40	NO_2/NO_3 n = 40	TP n = 40	DOP n = 40	FRP n = 40	Si n = 30	Chl <i>a</i> n = 40
3	0.208 (0.138)	0.019 (0.009)	0.137 (0.094)	0.029 (0.046)	0.019 (0.010)	0.006 (0.002)	0.008 (0.003)	7.71 (1.03)	3 (3)
4	0.193 (0.098)	0.022 (0.013)	0.127 (0.077)	0.026 (0.031)	0.024 (0.018)	0.008 (0.011)	0.009 (0.004)	7.75 (1.07)	2 (2)
5	0.282 (0.183)	0.027 (0.015)	0.145 (0.099)	0.035 (0.044)	0.088 (0.010)	0.008 (0.006)	0.013 (0.007)	7.81 (0.92)	4 (4)
6	0.531 (0.422)	0.028 (0.014)	0.172 (0.159)	0.055 (0.051)	0.202 (0.218)	0.012 (0.024)	0.020 (0.009)	7.55 (1.10)	6 (10)
7	0.908 (0.737)	0.031 (0.018)	0.239 (0.306)	0.117 (0.082)	0.290 (0.273)	0.026 (0.078)	0.026 (0.010)	6.55 (1.43)	7 (12)
8	0.385 (0.234)	0.034 (0.033)	0.091 (0.109)	0.138 (0.052)	0.083 (0.078)	0.007 (0.009)	0.022 (0.007)	3.47 (1.54)	3 (4)
10	0.291 (0.131)	0.040 (0.034)	0.092 (0.089)	0.122 (0.039)	0.050 (0.027)	0.007 (0.008)	0.020 (0.006)	2.55 (1.14)	2 (2)
11	0.301 (0.137)	0.043 (0.034)	0.078 (0.078)	0.122 (0.046)	0.041 (0.027)	0.007 (0.007)	0.021 (0.006)	2.68 (1.15)	3 (4)

Table 3: Nutrient concentrations (mg L^{-1}), physical variables and primary production measures (P_{max} : $\text{mg C m}^{-3} \text{ h}^{-1}$, Int. pp: $\text{mg C m}^{-2} \text{ d}^{-1}$) at the four intensively sampled sites along the Ord River in August 2006 and February 2007. nd = not determined. NH_3 = ammonia, DON = dissolved organic N, NO_2/NO_3 = nitrate, FRP = filterable reactive P, DOP = dissolved organic P, Temp = temperature, Cond. = conductivity, Turb = turbidity, Int. pp = depth integrated primary productivity.

Site	Date	DON	urea	NH_3	NO_2/NO_3	DOP	FRP	Secchi (m)	Temp. ($^{\circ}\text{C}$)	Cond. ($\mu\text{S m}^{-1}$)	Turb. (NTU)	P_{max}	Int pp
1	Aug'06	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
	Feb'07	0.11	0.011	0.010	0.016	0.006	0.008	0.94	31.9	260	12	12.61 (0.14)	61.5 (5.9)
2	Aug'06	nd	0.002	0.030	<0.010	nd	0.008	0.93	25.3	278	nd	10.25 (1.04)	74.8 (14.5)
	Feb'07	0.17	0.013	0.020	0.044	0.006	0.011	0.09	32.9	240	8	17.34 (1.76)	74.3 (18.9)
6	Aug'06	0.14	0.002	0.025	0.150	0.006	0.023	0.04	25.9	1096	1400	7.56 (2.20)	nd
	Feb'07	0.18	0.010	0.022	0.028	0.027	0.008	0.10	32.7	320	170	0.24 (0.16)	0.1 (0.1)
9	Aug'06	0.09	0.004	0.013	0.115	<0.005	0.019	0.42	24.8	4450	1000	4.01 (0.38)	10.9 (1.3)
	Feb'07	0.17	0.030	0.025	0.210	0.009	0.022	0.04	31.7	4230	370	16.34 (1.06)	1.8 (0.6)

Figure 1

Figure 2.

Figure 3.

Figure 4

Figure 5

Figure 6