Hydrobiologia (2006) 556:163–179
DOI 10.1007/s10750-005-0885-y

Primary Research Paper

Hydraulic phases, persistent stratification, and phytoplankton in a tropical floodplain lake (Mary River, northern Australia)

Simon Anthony Townsend

Department of Infrastructure, Planning and Environment, Northern Territory Government, PO Box 30, Palmerston, NT 0831, Australia (Tel.: 61 8 8999 3413; Fax: 61 8 8999 4445; E-mail: simon.townsend@nt.gov.au)

Received 29 July 2004; in revised form 2 July 2005; accepted 22 July 2005

Key words: algae, tropics, nitrogen, phosphorus, functional groups, diatoms, oxygen

Abstract

The Mary River, in the Australian wet/dry tropics, flows seasonally. When the river ceases flowing in the dry season, a series of isolated lakes remain along the river's main floodplain channel. The limnology of a channel lake, which is 14 km long and 6-9 m deep in the dry season, was examined between April and December 2000. Four hydraulic phases were identified, these being (1) riverine (April), (2) riverine to lake transition (May), (3) lake (June–late-November), and (4) lake to riverine transition (late-November–December). These phases differ with respect to their duration and flow direction from lakes located on tropical floodplains of perennially flowing rivers. Despite the variable hydraulic conditions, the main channel remained thermally stratified, with only infrequent and short-lived deep mixing events, and sufficient light for photosynthesis in the diurnal mixed layer. During the period of isolation and in contrast to floodplain lakes in tropical South America, the depth of the Mary River channel lake always exceeded, by at least 2-fold, the depth of the diurnal mixed layer. The water quality (conductivity, dissolved oxygen, pH, Si and water clarity) and phytoplankton assemblage of the channel lake was primarily driven by its hydraulics, though this was not evident for the channel's nutrient concentrations. Dissolved oxygen concentrations during lentic conditions were double values during the riverine and transition phases. This was attributed to the cessation of inflowing waters with a high biological oxygen demand, and enhanced photosynthetic activity of higher concentrations of phytoplankton retained under lentic conditions. The channel's phytoplankton assemblage reflected the channel's hydraulics, with the most common phytoplankton throughout the study period belonging to functional groups L_o (*Peridinium inconspicuum*), W1 (euglenoids), W2 (*Trachelmonas*) and Y (*Cryptopmonas, Rhodomonas*), with groups A (*Acanthoceras*) and D (*Nitzschia agnita, Synedra alna*) prominent during the lentic phase. Despite persistent stratification under lentic conditions, there was no clear evidence of autogenic succession or domination by any single phytoplankton functional group.

Introduction

Floodplain lakes are the most common lentic water bodies in the tropics, in contrast to temperate latitudes where lakes are predominately of glacial origin (Lewis, 2000). For example, there are an estimated 8000 lakes in the floodplain of the Amazon and Solimões Rivers (Melack, 1984), 2300 lakes on the lower Orinoco River floodplain in Venezuela (Hamilton & Lewis, 1990), and at least 1500 lakes on the Sepik-Ramu floodplain in Papua New Guinea (Vyvernam, 1994). Despite their large number and inherent vulnerability to degradation (Lewis, 2000), limnological research of tropical floodplain lakes is recent compared to large, deep tropical lakes (see Talling & Lemoalle, 1998).

Tropical floodplain lakes are typically shallow, with a wide range of shapes: circular, elongated, crescent-like and dendritic. Another defining characteristic is their seasonal and generally predictable hydrological cycle underpinned by annual flooding (Hamilton et al., 2002). This cycle can range from isolated, very shallow or even desiccated water bodies during the dry season, to much deeper water bodies inundated by a major river, local runoff and precipitation (Hamilton & Lewis, 1990; Lesack & Melack, 1995). During flooding, a lake's dimensions can increase orders of magnitude in volume and surface area (Lesack & Melack, 1995), to become indistinguishable from waters inundating the floodplain.

The flood pulse is a primary driver of the ecology of floodplain lakes, as well as their aquatic/terrestrial zones (Junk et al., 1989). The variable hydraulic conditions imposed by the flood pulse on floodplain lakes underpin a pronounced seasonal response in phytoplankton composition (García de Emiliani, 1993; Huszar & Reynolds, 1997; Ibañez, 1998; De Oliveira & Calherios, 2000). The amplitude of the flood pulse and the period of lake isolation vary amongst tropical floodplain lakes, depending on the floodplain's geomorphology and hydrology, and more broadly the river's catchment area and its climate. Lakes with a large seasonal depth range (≈10 m), tend to have shorter periods of hydraulic isolation owing to their relatively long period of filling and draining (e.g., Amazon Basin lakes), compared with lakes with a smaller depth range (≈2–3 m, e.g., Orinoco floodplain lakes). Phytoplankton dynamics in tropical floodplain lakes are likely to be just as variable as their seasonal patterns of flooding and isolation, though still founded on the same primary ecological drivers.

The Mary River is one of several major rivers in the Australian wet/dry tropics that annually inundate a coastal floodplain (Finlayson et al., 1988). In the dry season, many of these rivers cease flowing, with some reducing to one or several floodplain lakes along the main river channel. These lakes are the first to receive river inflow at the beginning of the wet season, and the last to receive riverine and floodplain inflows at the end of the wet season. This lake typology does not occur by definition on the perennially flowing rivers of South America (see Hamilton & Lewis, 1990; Sippel et al., 1992).

In this paper, the limnology of a lake along the main channel of the Mary River is examined over a range of hydraulic conditions. The study focuses on the physical and chemical limnology of the lake, and its influence on the lake's phytoplankton assemblage.

Site description

The Mary River (Fig. 1) drains a catchment area of 8062 km^2, comprising mainly savanna woodland in the upper catchment with negligible clearing of the native vegetation. The catchment is sparsely populated, with no townships and about 200 residents. Land-use above the floodplain is mainly low intensity cattle grazing, defense training and conservation. The river's coastal floodplain area is approximately 480 km^2 upstream of the tidal creeks, and is vegetated mainly by grasses, sedges and *Melaleuca* woodland with some stands of the weed *Mimosa pigra* and introduced pastoral plants. The lakes support nature based tourism and are popular for recreational fishing, whilst the floodplain is grazed by cattle during the dry season, with some areas managed for nature conservation.

Flow in the Mary River reflects the marked seasonal distribution of rainfall characteristic of a wet/dry tropical climate. Annual rainfall at Darwin, 75 km west of the Mary River floodplain, averages 1714 mm, with 64% of rain falling between January and March, 97% between October and April, and negligible amounts between May and September. The river typically commences flow in December, inundating the floodplain by over-bank flow between January and March during most wet seasons, followed by seasonal recession flow until at least May. As the river recedes, floodplain waters drain into the main river channel, or flow along alternative routes to estuarine creeks, or become trapped in depressions.

When the Mary River ceases flowing, a series of isolated lakes remain in the river channel, known locally as billabongs. The largest lake is the main channel of the Mary River (Fig. 1) which is 14 km long, 75–100 m wide and typically 6 m deep at the end of the dry season. The channel is fringed by

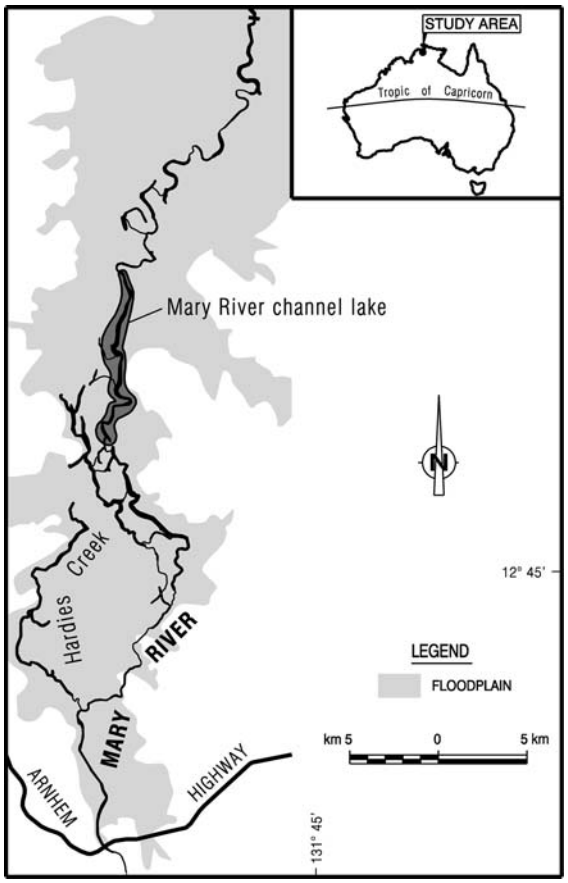


Figure 1. Mary River channel lake, on the Mary River floodplain, in the Australian wet/dry tropics. The lake is bounded by heavy shading to highlight its position.

lotus lily (*Nelumbo nucifera*) protruding 1-2 m from the bank. Riparian vegetation along the upper half of the channel is dominated by *Melaleuca* trees, *Barringtonia* freshwater mangrove and monsoon vine forest. Vegetation along the lower half of the channel is mainly grasses.

Methods

Water sample and field data collection

Between April 5 and December 20, 2000, water samples were collected on average every 3 weeks from five sites along the length of the Mary River channel (Fig. 2). These sites were equidistant from adjacent sites and the channel's inlet and outlet. Two depth integrated samples were collected at each site using a hose with a one-way valve; a 0–2 m sample that approximated the depth of the diurnal mixed layer, and a water column sample.

The samples were analyzed by standard methods (APHA, 1998) for the following parameters: total phosphorus (TP), filterable reactive phosphorus (FRP), silicon, nitrate, nitrite, ammonia, total Kjeldahl nitrogen (TKN), alkalinity and chlorophyll *a*. Samples were also analyzed for gilvin, a quantitative measure of colour (Cuthbert & del Giorgio, 1992) by spectrophotometric measurement of absorption at 440 nm of a filtered sample. Samples for gilvin and soluble nutrients were filtered in the field through a 0.45 μm pore size membrane. Nitrite will not be discussed further because its concentrations were always below the detection limit of 1 $\mu g\ l^{-1}$.

A composite of the five 0–2 m integrated samples was collected for the identification and

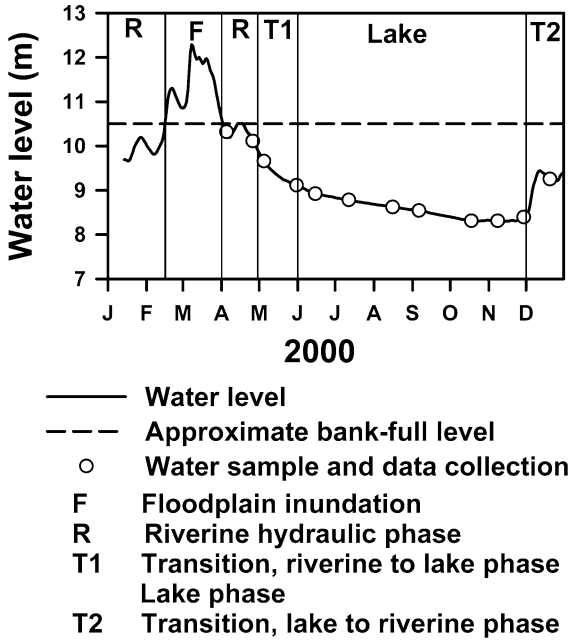


Figure 2. Water level of the main channel of the Mary River, with hydraulic phases shown and water sample collection dates. The dotted line approximates the height of over-bank flow.

enumeration of phytoplankton and preserved with Lugol's iodine solution. The primary taxonomic references used were Prescott (1978), Ling & Tyler (1986), Day et al. (1995), Gell et al. (1999), Sonneman et al. (1999) and Ling & Tyler (2000). A 1 l sample was concentrated 50 times by sedimentation. At least 150 phytoplankton units (single cells, filaments or colonies) of the dominant taxa were counted in a Lund cell to ensure the error ($p \leq 0.05$) was less than $\pm 16\%$ (Lund et al., 1958). Counting also included the number of cells in each filament or colony, permitting phytoplankton concentration to be expressed as cells ml^{-1}. Other taxa were counted to obtain an accuracy of $\pm 20\%$, excluding infrequently occurring phytoplankton which were enumerated from a scan of half the Lund cell. A total of between 870 and 4960 units were counted for each sample. Cell volumes were determined using standard geometric formulae, without correction for cell vacuole volume which may result in the over-estimation of the biovolume of some diatoms. The phytoplankton composition of the lake was evaluated according to the functional groups defined by Reynolds et al. (2002).

At each site, profiles of dissolved oxygen, temperature, pH and conductivity were measured with a multi-parameter probe at 0.5 m depth intervals, and in the same sequence during each survey between 9:00 and 15:00 h. Profiles of photosynthetically active radiation (PAR) were measured with a 'Licor 188B.'

The lake's water level was recorded daily at a hydrographic station located mid-way along the channel. Between mid-May and mid-November a pontoon was deployed 15 m from the channel's bank adjacent to the hydrographic station. Below the pontoon a thermistor chain measured temperatures every half hour at depths of 0.1, 0.5, 1, 1.5, 2, 3, 4, 5 and 6 m, with the deepest thermistor located 2–3 m above the deepest point in the channel. Above the pontoon, at a height of 2 m, wind speed and direction were recorded every 10 min.

The Australian Bureau of Meteorology supplied other meteorological data. Minimum and maximum daily air temperatures, as well as half hour readings of solar radiation (290–5000 nm), were provided for Darwin Airport, 75 km west of the Mary River channel. This meteorological station is only 1 km from the coastline, whereas the Mary River channel is 70 km inland. Because the range of daily air temperatures increases with distance inland, Darwin Airport temperatures have been corrected by 2 °C to provide a better estimate of daily minimum and maximum air temperatures at the Mary River channel.

Calculations

The attenuation of light was calculated from a linear regression of the natural log transformed PAR against depth, and is expressed as the euphotic depth, which is defined as the depth to which 1% of incident light penetrates.

The light profile through the water column, for half hour increments and for each day, was determined using light attenuation and radiation data. Solar radiation measured at Darwin Airport was converted to PAR by the following:

$$\mathrm{PAR}(\mu\mathrm{M\,m^{-2}s^{-1}}) = 0.95 \times 0.45 \times 4.57(\mathrm{W\,m^{-2}}),$$

where 0.95 corrects for the proportion of incident light reflected at the lake's surface; 0.45 is the proportion of solar radiation that is PAR; and $1\ \mathrm{W} = 4.57\ \mu\mathrm{M\ m^{-2}\ s^{-1}}$.

PAR transmitted through the water column, at 0.25 m depth intervals, was computed by:

$$I = I_0 e^{-kz}$$

where, I is PAR; k is the attenuation coefficient for the survey date or was interpolated linearly between sample dates; z is depth; I_0 is PAR at the surface. These computations agreed well with measured PAR intensities ($r^2 = 0.96$; $p < 0.01$).

To gain an insight into the availability of light for photosynthesis in the diurnal mixed layer, the depth of PAR intensities for compensation (defined as no net photosynthetic production) and photosynthetic saturation were determined for the period 10:00–16:00 h, and the daily average calculated. Compensation and saturation intensities of 5 μM m^{-2} s^{-1} and 100 μM m^{-2} s^{-1} were selected (see Kirk, 1983; Reynolds, 1984), and are likely to be conservative and under-estimate actual saturation intensities and over-estimate compensation intensities.

The stability of stratification is the minimum amount of work required to mix a water body assuming heat is conserved. This was calculated according to Idso (1973), using both thermistor and profile data for the study period.

$$\text{Stability (MJ m}^{-2}\text{), S} = g a_0^{-1} \int_0^{Zm} (z - z*) a_z (\rho_z - \rho) \mathrm{d}z$$

where g is the acceleration due to gravity; a_0 is the lake's surface area; z is depth; z_m is the maximum depth; a_z is the lake's area at depth z, z* the depth of the mean density of the stratified lake; ρ is the lake's mean water density; ρ_z is the density of water at depth z.

Temporal patterns in phytoplankton composition of the lake were examined by multivariate analysis using the PATN software package (Belbin, 1993). Bray–Curtis measures of sample similarity were analyzed by classification using the FUSE routine and the UPGMA option to produce a dendrogram of sample composition similarity.

Results

Hydrography of the main channel of the Mary River

Flow through the Mary River channel in 2000 was similar to other years and can be separated into several hydraulic phases (Fig. 2). Between mid-February and mid-April, the Mary River inundated its floodplain. When the flood waters receded, a riverine phase followed when the Mary River was contained within its banks. Over May, flow through the channel gradually reduced, constituting a transition from riverine to lake conditions.

The channel then became hydraulically isolated to become a floodplain lake. Its water level declined 1.2 m due to evapo-transpiration losses exceeding rainfall interception. In late-November the Mary River resumed flow and entered the channel lake, to fill the water body over an estimated 2–3 days, then continued to flow downstream to enter the next floodplain lake. This phase constituted a transition from lake to riverine conditions, and is probably the shortest phase before riverine conditions return, followed by floodplain inundation.

Wind and solar radiation

The transfer of wind energy to a water's surface is a function of both wind speed and fetch. Wind speeds over the channel exhibited a predictable diurnal pattern (Fig. 3), typical of the coastal zone. Overnight wind speeds were low, averaging 0.5 m s^{-1} between 21:00 h and 07:30 h. After sunrise, wind speeds increased steadily to reach a maximum of 3 m s^{-1} at mid-day, then declined during the months of May and June. However, from July onwards an afternoon sea breeze prevailed until about 20:00 h with speeds reaching 5 m s^{-1} (Fig. 3).

Winds were predominately from the south-east between May and July and perpendicular to the Mary River channel. Consequently, the lake's fetch during these months was no greater than its width. Later in the year, daytime wind direction shifted to a southerly or westerly orientation. The length of the lake's fetch increased during these months along portions of its length, depending on the lake's orientation and the shelter provided by riparian vegetation.

Temperature and oxygen stratification

The Mary River channel was thermally stratified throughout most of the dry season, with a

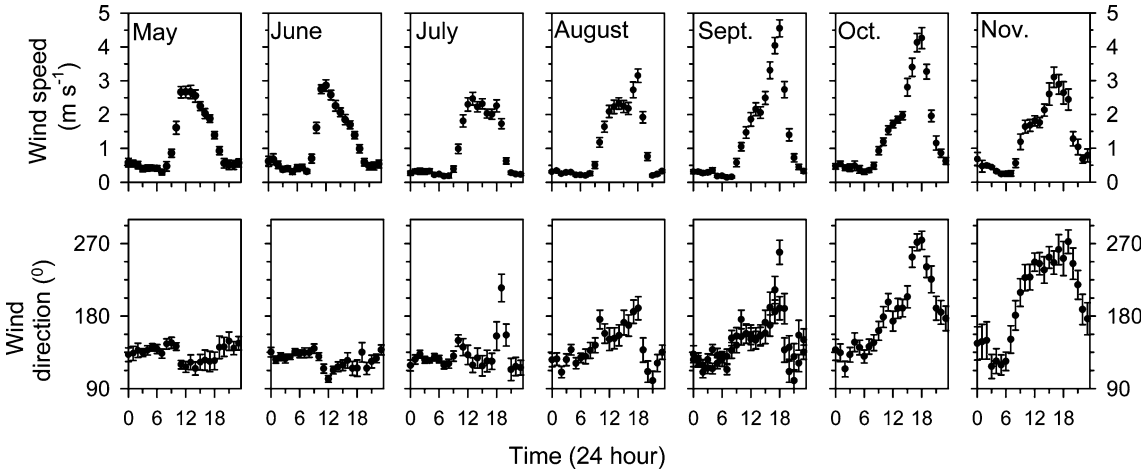


Figure 3. Average and standard error of half-hourly wind speed and direction for each month, mid-way along the Mary River channel lake.

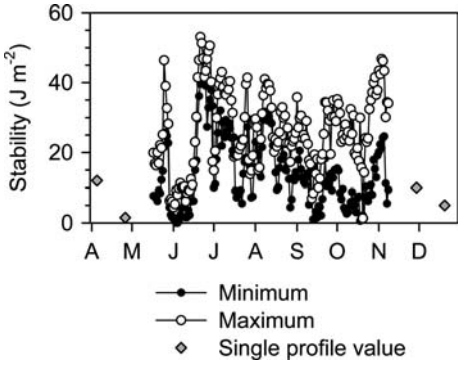
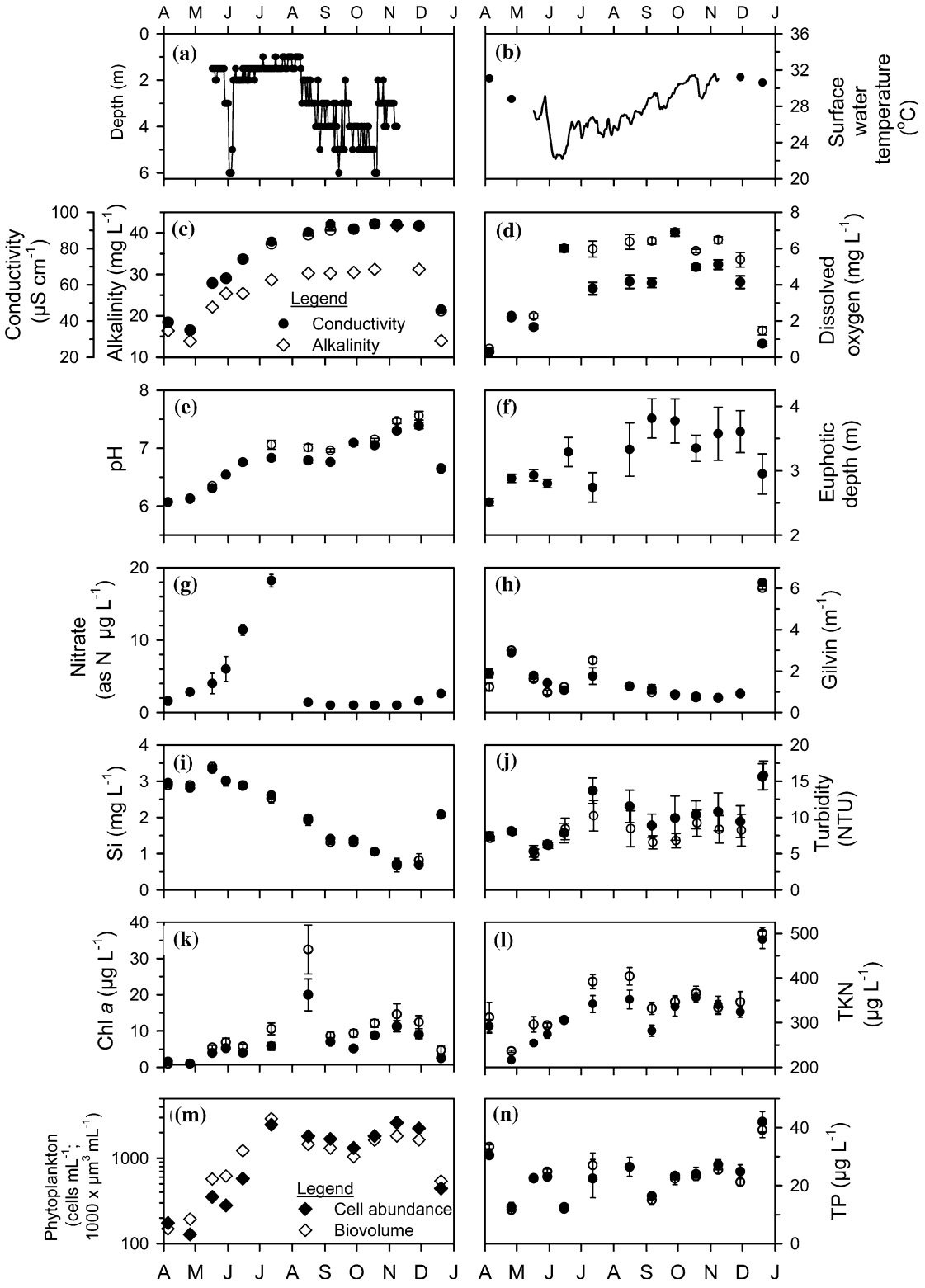


Figure 4. Daily minimum and maximum stability of stratification during the period of thermistor data collection (mid-May to mid-November, 2000), and single daytime temperature profiles (April, November, December).

pronounced diurnal cycle (Fig. 4). Heat gain during daylight hours produced an afternoon stability maximum between 15:00 and 18:00 h. Despite the relatively strong afternoon sea breeze, the lake remained stratified owing to the buoyant resistance of the surface waters. After sunset, superficial heat loss and subsequent convective mixing produced isothermal conditions to an average depth of 2.8 m (Fig. 5a), reducing the stability of stratification to approximately half the daytime maximum. Weak overnight winds would have transferred negligible energy to the lake for vertical mixis. Despite persistent stratification, temperatures below the diurnal mixed layer increased from a minimum of 22 °C in June to 30 °C in November. The significance of this heat transfer to the bottom waters was to reduce the vertical density gradient and stability of stratification.

Three periods (June 1–5, Sept. 13–14, Oct. 18–21; Fig. 4) of deep nocturnal vertical mixing, to at least 6 m depth and possibly holomixis, have been identified during the period of thermistor data collection. These events coincided with low air temperatures. Deep mixing in early June coincided with a fall in overnight temperatures from a minimum air temperature of 22.1 °C on May 28, when surface water temperatures were 28 °C, to a minimum air temperature of 10.5 °C on June 3. Between June 1 and 5, the lake's average temperature cooled 4.9 °C, which equaled half the annual temperature range (Fig. 5b). The September period of deep nocturnal mixing coincided with a 5 °C fall in the overnight minimum air temperature to 18 °C. In October, deep mixing coincided with low air temperatures during the day (maximum 26.7 °C compared to 35 °C during the preceding

Figure 5. Water chemistry of the main channel of the Mary River. Average water chemistry, with standard error, shown for most parameters. Open and closed circles represent, respectively, values for the 0–2 m and profile integrated water samples. (a) Depth of diurnal mixed layer, (b) average daily surface water temperature (measured by thermistor), (c) conductivity and alkalinity, (d) dissolved oxygen, (e) pH, (f) euphotic depth, (g) nitrate, (h) gilvin, (i) silicon, (j) turbidity, (k) chlorophyll *a*, (l) total Kjeldahl nitrogen, (m) phytoplankton cell and biovolume concentration, and (n) total phosphorus.


A M J J A S O N D J
(a)
Depth (m)
(b)
Surface water temperature (°C)
(c)
Conductivity (µS cm⁻¹)
Alkalinity (mg L⁻¹)
Legend
Conductivity
Alkalinity
(d)
Dissolved oxygen (mg L⁻¹)
(e)
pH
(f)
Euphotic depth (m)
(g)
Nitrate (as N µg L⁻¹)
(h)
Gilvin (m⁻¹)
(i)
Si (mg L⁻¹)
(j)
Turbidity (NTU)
(k)
Chl a (µg L⁻¹)
(l)
TKN (µg L⁻¹)
(m)
Phytoplankton (cells mL⁻¹; 1000 x µm³ mL⁻¹)
Legend
Cell abundance
Biovolume
(n)
TP (µg L⁻¹)

days) and overnight (minimum 17.0 °C compared to 22 °C during the preceding days).

Stratification and mixing in April, late-November and December, when thermistor data were not collected, can only be inferred from four daytime profiles. On each date (April 5 and 26, November 29 and December 20) the channel was weakly stratified, with a diurnal mixed layer estimated to be 3 m deep based on the depth of the thermocline.

Oxygen concentrations in April and May were less than 2 mg l^{-1} (Figs. 5d and 6), then more than doubled under lentic conditions when average concentrations in the upper 2 m fluctuated between 5 and 6 mg l^{-1} or 70–91% saturation. Dissolved oxygen through the water column reflected the channel's thermal stratification, with a near uniform vertical oxygen gradient without any pronounced oxycline. Notable also was the maintenance of oxic conditions (0.5–1 mg l^{-1}) near the lake's sediments.

Water chemistry

The water chemistry of the Mary River channel can be separated into four phases, that broadly align with the channel's hydraulics: (1) riverine or through-flow conditions (April), (2) a transition from riverine to lentic (lake) conditions (May), (3) hydraulic isolation (June–late-November) and (4) lake to riverine transition including filling (late-November–December). These phases were reflected by the channel's conductivity, with the lowest values (35-45 μS cm^{-1}) recorded during flow-through conditions in April and riverine inflow later in the year (Fig. 5c). Conductivity increased over the transition from riverine to lentic conditions due to evapo-transpiration, reaching a maximum of 92 μS cm^{-1}.

In April, during through-flow, conductivity was less than 40 μS cm^{-1}, pH 6.1 and poorly buffered (alkalinity 30 mg l^{-1} (as $CaCO_3$)), and dissolved oxygen less than 2 mg l^{-1} (Fig. 5). Soluble nitrogen and phosphorus concentrations were low, being 1–4 μg l^{-1} of NO_3–N (Fig. 5g), and less than 10 μg l^{-1} NH_3–N, whilst FRP averaged 2 μg l^{-1}. The euphotic depth of the channel averaged 2.8 m (Fig. 5f).

During the transition phase in May, flow-through the channel gradually reduced to zero. The most notable changes in water chemistry were an almost doubling of conductivity, increased pH, and higher concentrations of dissolved oxygen and nitrate (Fig. 5). FRP concentrations throughout the study approximated 2 μg l^{-1}, except in early May when they averaged 8 μg l^{-1}.

Under lentic conditions, high nitrate concentrations in mid-June and mid-July (Fig. 5g) were accompanied by ammonia concentrations of up to 25 μg l^{-1}. In mid-August, however, nitrate concentrations had decreased to an average of 1.4 μg l^{-1}, whilst ammonia concentrations were less than 10 μg l^{-1}. Both forms of soluble nitrogen then remained at these levels (< 3 μg l^{-1} NO_3–N, ≤ 10 μg l^{-1} NH_3–N) until the lake–riverine transition phase. Silicon concentrations declined, at an almost uniform rate, from 4.6 mg l^{-1} in June to 1.0 mg l^{-1} in November (Fig. 5i). The lake's pH continued to rise during this period, though at a slower rate, to reach a maximum of 7.6 (Fig. 5e). Under lentic conditions water clarity improved

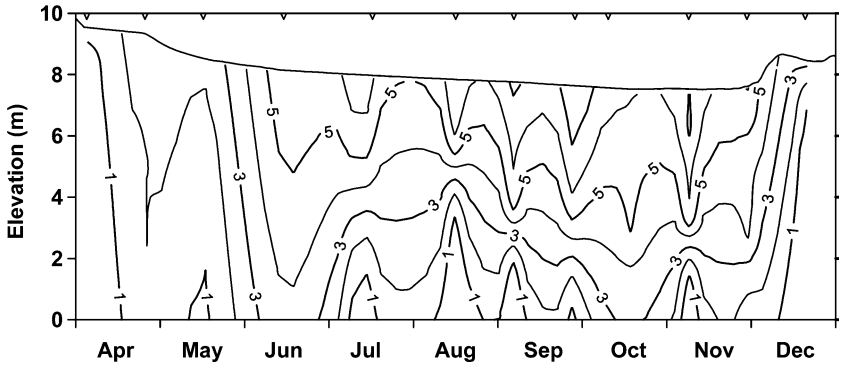


Figure 6. Dissolved oxygen isopleths (mg l^{-1}) mid-way along the Mary River channel lake. Profile dates are indicated on the upper *x*-axis.

marginally, due to reduced colour whilst turbidity remained largely unchanged (Fig. 5).

Following the inflow of the Mary River into the channel lake in late-November, conductivity, alkalinity and dissolved oxygen halved, pH decreased 0.8 units, and the euphotic depth decreased due to increased turbidity and colour (Fig. 5). Although total phosphorus and total Kjeldahl nitrogen almost doubled, FRP and nitrate concentrations remained low (<3 $\mu g\ l^{-1}$).

Concentrations of total nitrogen and phosphorus fluctuated at least two-fold, and tended to follow the same seasonal trend (Fig. 5). The soluble forms of both nutrients were generally a minor fraction ($< 10\%$) of the total nutrient concentration.

Phytoplankton are exposed to a light regime that is a function of the incident radiation, light attenuation, and the ratio of the mixed and euphotic depths. In the Mary River channel, light intensities in the mixed layer exceeded the compensation intensity on 85% of days (Fig. 7). Moreover, light intensity within the mixed layer exceeded the saturation intensity for photosynthesis during 4 out of 10 days (Fig. 7). These calculations indicate adequate light for photosynthesis by phytoplankton in the diurnal mixed layer.

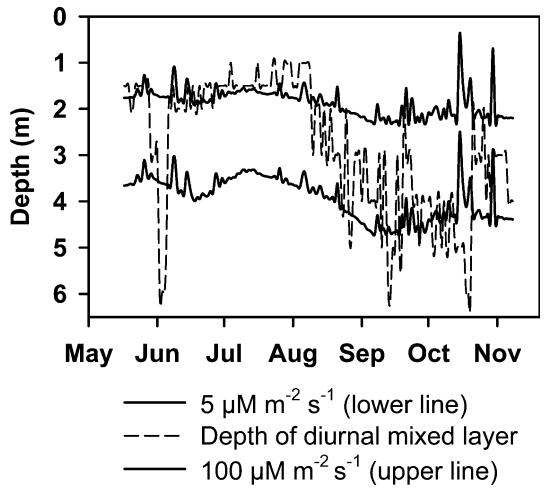


Figure 7. The depth of photosynthetically active radiation (PAR) that approximates compensation (5 μM m^{-2} s^{-1}; photosynthetic and respiration activity equal) and light saturation intensities in the diurnal mixed layer of the Mary River channel lake. Solar noon approximated 13:00 h.

Phytoplankton

Average chlorophyll *a* concentrations for each sample date varied between 1.0 and 32 $\mu g\ l^{-1}$ in the upper 2 m of the lake (Fig. 5k), being lowest under riverine conditions and averaging 13 $\mu g\ l^{-1}$ under lake conditions. The relatively high concentrations measured in August (32 $\mu g\ l^{-1}$) are considered atypical when compared to 1996 chlorophyll *a* data reported by Powell & Townsend (1997). Chlorophyll *a* concentrations in the upper 2 m of the lake were approximately 40% higher than in the water column sample, indicating higher phytoplankton concentrations in the diurnal mixed layer. The chlorophyll *a* content of phytoplankton was 0.2–1.4% of freshweight biomass (assuming 1 cm^3 = 1 g) and averaged 0.58%, within the range reported by Vörös & Padisák (1991) for shallow European lakes.

A total of 100 taxa were identified, with chlorophyll *a*, total cell and biovolume concentrations that ranged over at least one order of magnitude (Fig. 5m), whilst some individual taxa ranged over 3 orders of magnitude. Multivariate analysis of the phytoplankton biovolume data, presented as a dendrogram (Fig. 8), reveals major groups that coincide broadly with the lake's hydraulic phases. A similar dendrogram was produced using cell concentration data.

The two April dates constitute one group, coinciding with flow through the channel, and are distinguished from the other sample dates by their low cell and biovolume concentrations, abundance of *Anabaena* cells, and relatively high biovolume concentrations of *Euglena* and *Navicula* (Table 1). The dissimilarity between the two April dates is attributed to species being present on only one of the two sample dates. For example, *Mougeotia* and *Phacus longicauda* each constituted about 20% of the biovolume concentration on April 26, but were absent on April 5. Conversely, colonies of *Volvox* were present only on April 5.

The May, June and December assemblages constituted the second group, with the May and December assemblages coinciding with transition periods. The June assemblage, however, occurred under lentic conditions and 10 days after a deep mixing period and closely resembled the pre-mixis assemblage. Overall, the group is distinguished by their high biovolume concentrations of

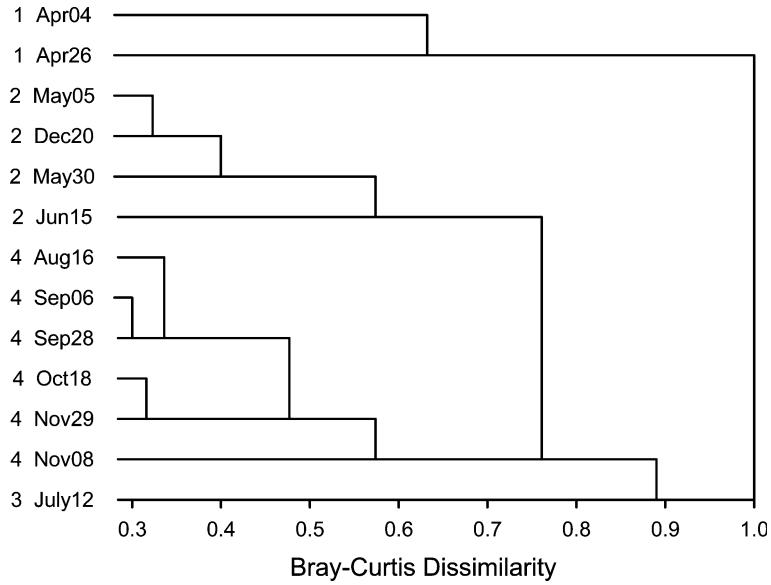


Figure 8. Dendrogram of UPGMA classification of phytoplankton assemblages based on Bray–Curtis measure of dissimilarity and biovolume concentrations. The alphanumeric code on the *Y*-axis indicates the dendrogram group and sample date in 2000. Group 1: riverine; Group 2: transition (May: riverine to lake; December: lake to riverine) and early-lake phase; Group 3: mid-July when the lake's phytoplankton biovolume was dominated by *Acanthoceras*; Group 4: lake phase.

Cryptomonas and *Rhodomonas* sp. (Table 1). In common with group 1, *Cryptomonas* sp., *Chroomonas acuta*, and *Euglena* sp. were present in high concentrations, whilst the diatom population remained low (Fig. 9). The June assemblage differed from the May and December transition assemblages in the concentration of taxa, rather than taxa present.

Between July and November the composition of the lake's phytoplankton developed almost chronologically (Fig. 8), based on their similarity. The third group is represented by phytoplankton collected on a single date (July 12) when *Acanthoceras* sp. (formerly *Attheya*) dominated the phytoplankton population (76% of total biovolume concentrations; Fig. 9). This was the only occasion a single taxon was dominant. The concentration of *Acanthoceras* then declined 3 orders of magnitude over the following 4 months.

The fourth phytoplankton group also coincided with the lentic conditions, and was represented by phytoplankton collected between August and November when *Nitzschia agnita* was the most frequently occurring taxa (8–42% of total biovolume, 63–97% of diatoms cells; Fig. 9). Although their abundance was relatively low, *Synedra ulna* constituted between 7 and 42% of the lake's phytoplankton biovolume (Fig. 9), and up to 79% of the diatom biovolume. Between November 8 and 29, the proportion of diatoms halved, from 71 to 35% biovolume, with an unidentified spherical (diameter 10 μm) chlorophyte (24% of total biovolume) and *Peridinium inconspicuum* (10% of total biovolume) being most numerous at the end of November. *Cryptomonas* sp. and *Rhodomonas* sp. were present through this period, representing up to 34 and 13% of the phytoplankton biomass, respectively.

Several taxa were present throughout the dry season, in usually low concentrations. These were *Euglena* spp., *Trachelomonas* spp., *Strombomonas* sp., *Peridinium* spp. (notably *P. inconspicuum*), *Chroomonas acuta*, *Rhodomonas* sp., *Cryptomonas* sp., and an unidentified spherical chlorophyte.

Discussion

Hydraulic phases

Lakes located on tropical floodplains are usually connected to the main river by a single channel and feature a marked seasonal pattern of water

Table 1. Phytoplankton assemblages within dendrogram groups (see Fig. 8)

Dendrogram group and hydraulic phase	1	2	3	4
	Riverine	Transition, riverine to lake (May) and early lake phase (June)	Lake (I)	Lake (II)
Sample months	April	May, June, December	July	Aug.–Nov.
Cell abundance (cells ml^{-1})	126–169	279–575	2450	1310–2590
Diatom abundance (cells ml^{-1})	3–4	5–25	1560	341–1560
Biovolume ($1000 \times \mu m^3$ ml^{-1})	160–220	191–730	5280	1580–3050
Diatom biovolume (μm^3 ml^{-1})	18	11–97	4050	490–2100
Numerically abundant taxa (%)	*Anabaena* sp. (10–13%), *Chroomonas acuta* (10–13%), *Cryptomonas sp.* (3–8%), *Scenedesmus* (3–12%), *Euglena* (2%)	Unidentified spherical chlorophyte (1–9%), *Chroomonas acuta* (1–36%), *Rhodomonas* (1–9%), *Cryptomonas* spp. (1–52%), *Peridinium inconspicuum* (1–19%), *Euglena* (1–12%)	*Acanthoceras* sp. (62%), *Sphaerocystis* (8%), *Dinobryon* (7%), *P. inconspicuum* (6%)	*Acanthoceras* sp. (< 1–5%), *Nitzschia agnita* (11–62%), *Synedra ulna* (1–7%), *Cryptomonas* sp. (1–17%), *Rhodomonas* sp. (< 1–3%), Unidentified chlorophyte (2–34%), *Trachelomonas* (1–3%), *P. inconspicuum* (3–6%), *Euglena* (1–3%)
Biovolume	*Euglena* (12–17%), *Phacus* (1–19%), *Cryptomonas* sp. (4–23%), *Rhodomonas*, (0–12%), *Navicula cryptocephala* (7–10%)	*Euglena* (1–20%), *Phacus* (0.9–6.5%), *Cryptomonas* spp. (1–38%), *Rhodomonas* (1–35%), *Chroomonas acuta* (< 1–2%), *P. inconspicuum* (1–18%)	*Acanthoceras* sp. (76%), *Rhodomonas* (5%), *P. inconspicuum* (4%)	*Acanthoceras* sp. (< 1–14%), *Nitzschia agnita* (8–42%), *Synedra ulna* (7–42%), *Cryptomonas* sp. (2–34%), *Rhodomonas* sp. (1–13%), unidentified spherical chlorophyte (1–15%), *Trachelomonas* (3–7%), *P. inconspicuum* (3–7%), *Euglena* (6–18%), *Phacus* (0–1.6%)

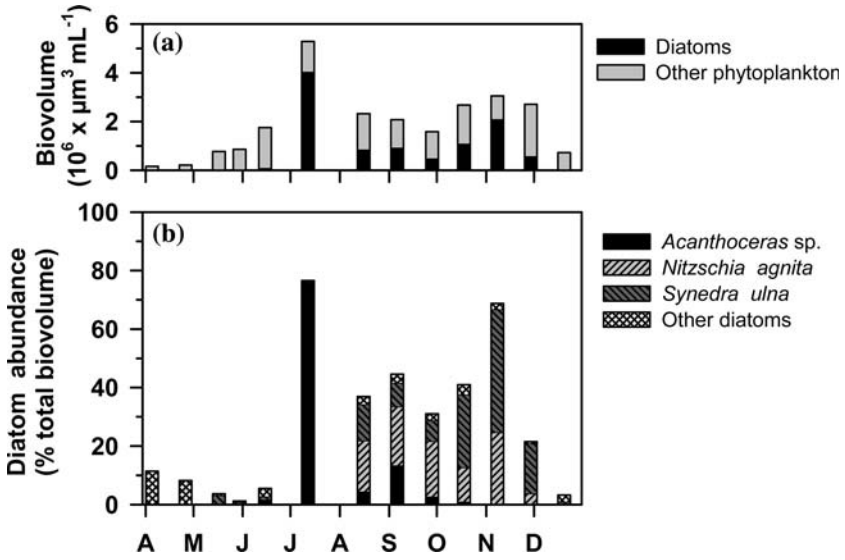


Figure 9. (a) Diatom and other phytoplankton concentrations in the Mary River channel lake, and (b) the proportion of *Acanthoceras*, *Nitzschia agnita*, *Syendra ulna* and other diatoms of total phytoplankton biovolume.

level. These hydraulic phases are broadly: (1) rising water level when river water flows into and fills a lake, (2) high water levels, (3) falling water levels, and (4) low water levels when the lake is effectively isolated from the main river. At high water, river water may flow through a lake (e.g., Lake Tineo; Hamilton & Lewis, 1987) or be stored within the lake's confines (e.g., Batata Lake; Huszar & Reynolds, 1997).

The Mary River channel lake also experienced these phases, though with some variations. The channel's falling (riverine) phase was caused by a reduction in river water flowing into the channel lake, rather than water flowing out of the lake which occurs when lakes are located on the floodplain. Moreover, the isolation (lake) phase of the Mary River floodplain channel lake is determined by the cessation and resumption of river flow, rather than the relative water levels between the main river and the floodplain lake. Additionally, the high water phase of the Mary River describes flow confined within the river's banks, as well as an additional fifth phase defined by overbank flow and inundation of the floodplain.

The duration of the hydraulic phases of the Mary River channel differs from that reported for South American tropical floodplain lakes. Most significantly, the Mary River channel lake experiences a longer period of hydraulic isolation (see Hamilton & Lewis, 1987; Vásquez, 1992; Lesack & Melack, 1995; Huszar & Reynolds, 1997; Ibañez, 1998; Hamilton et al., 2002). The South American lakes are isolated for periods of up to 3–4 months, at least half the period for the Mary River channel lake and other channel lakes on the Mary River floodplain and in the region with seasonally flowing rivers.

Stratification and mixing

Thermal stratification in tropical lakes tends to be longer, but less stable, than higher latitude lakes (Lewis, 2000). Nevertheless, tropical lakes are predominantly warm monomictic (Lewis, 2000), experiencing holomixis during the hemispheric winter, similar to middle latitude lakes, though mixis can occur at other times of the year (see Townsend, 1998). The predominantly warm monomictic regime of tropical lakes, and their range of mixing behaviours, has been most frequently reported for moderate to large lakes (see Talling & Lemoalle, 1998), whilst the thermal behaviour of tropical floodplain lakes are less frequently reported despite their abundance.

Forces operating at different temporal scales drove the mixing regime of the Mary River channel lake. Hydrodynamics in the lake's horizontal plane were dominated by a highly seasonal pattern

of through-flow. Vertical mixing, in contrast, was dominated by a diurnal pattern of stratification and mixing (see Imberger, 1985) that is also known as atelomixis (see Barbosa & Padisák, 2002). Holomixis was short-lived (hours to days) and infrequent in the channel lake, and likely to be most frequent in the dry season (June–August), in common with other albeit deeper and larger water bodies in the region (see Townsend, 1998).

The influence of wind induced mixing was mediated by the lake's short fetch and shelter by riparian vegetation, as well as a water level 1–2 m below the floodplain. Deep mixing events were driven by convective cooling, though strong winds in some years may also produce holomixis. Significantly, the depth of Mary River channel lake exceeded the depth of diurnal mixis. This contrasts with some Amazonian and other South American floodplain lakes which tend to reduce to a depth less than the diurnal mixed layer and so experience holomixis daily (e.g., MacIntyre & Melack, 1988; Huszar & Reynolds, 1997).

Deep mixing events attain their ecological significance by modifying the physical environment. Planktonic strategies to remain in the euphotic zone, such as buoyancy and motility, are no longer advantageous. Additionally, phytoplankton are exposed to a more variable light climate, as they are transported through the water column. Deep mixing will also affect a lake's chemistry, through the transport of hypolimnetic waters that can be anoxic and nutrient enriched, to the surface and dilution of deeper waters with oxic, often nutrient depleted, surface waters. In the Mary River channel lake, deep mixing events were too short to induce a major shift in phytoplankton assemblage, similar to a nearby reservoir (see Townsend, 2001). The deep mixing events in the Mary River channel lake did, however, oxygenate the bottom waters.

Hypolimnetic deoxygenation is rapid in warm tropical waters owing to the increased microbial activity and reduced oxygen solubility, even in lakes of low trophic state (Townsend, 1999). Despite the persistent stratification and warm temperatures of the Mary River lake, its hypolimnion remained oxic in contrast to deeper water bodies in the region (see Townsend, 1999) and other tropical floodplain lakes (see Melack & Fisher, 1983). Eddy diffusion is the most probable mechanism for the maintenance of hypolimnetic oxia. This explanation is supported by the increase in hypolimnetic temperatures, as eddy diffusion of oxygen would have been accompanied by the transport of heat. By maintaining an oxygenated hypolimnion, conditions were less favourable for nitrogen and phosphorus release from the sediments. Deep mixing did not result in prolonged nutrient enrichment of the lake's surface waters, further mediating the ecological significance of these events in the channel lake.

Water chemistry and phytoplankton biomass

Dissolved oxygen concentrations in the Mary River channel were low during the through-flow and filling periods (0.5–2 mg l^{-1}), and highest during hydraulic isolation (4-7 mg l^{-1}). This seasonal pattern of oxygen concentrations concurs with the pattern reported for this channel lake and others on the Mary River floodplain (Powell & Townsend, 1997; Townsend & Edwards, 2003). The sharp reduction in the lake's oxygen concentration following the inflow of the Mary River at the beginning of the wet season is common to tropical floodplain lakes (e.g., Vásquez, 1992), sometimes causing extensive fish kills generally attributed to hypoxia (Calheiros & Hamilton, 1998; Townsend & Edwards, 2003).

The relatively high lentic concentrations of dissolved oxygen in the main channel of the Mary River were probably due to enhanced photosynthetic activity, as indicated by a rise in pH, and possibly the cessation of riverine inflow with a high oxygen demand. The doubling of chlorophyll *a* concentrations suggest phytoplankton contributed to elevated photosynthetic production of oxygen. Submerged macrophytes would have also contributed, though this is likely to be minor owing to their relatively small biomass (pers. obs.). The higher phytoplankton biomass during hydraulic isolation, compared to riverine conditions, is best explained by the retention of phytoplankton under lentic conditions when the flushing effect of river flow is absent, rather than nutrient availability which was similar under riverine and lentic conditions. The seasonal pattern of dissolved oxygen in the river channel is underpinned by its hydraulic state, and in turn its effect on phytoplankton biomass and production of oxygen.

Under lentic conditions, the low FRP and nitrate concentrations suggests that either N or P may limit the lake's phytoplankton biomass, being less than saturation concentrations (3–6 P $\mu g\ l^{-1}$; 100 N $\mu g\ l^{-1}$; Reynolds, 1997) that commonly limit phytoplankton growth. Bioassay experiments, conducted in September 1999 when nutrient concentrations were similar to 2000 (Webber, 2000), found P to limit the lake's phytoplankton biomass. However, as has been shown for other Mary River floodplain lakes (Webber, 2000), nitrogen may also limit biomass, or the limiting nutrient may alternate between N and P over time.

The trophic classification of waters is often problematic, being dependent on the classification scheme. Under lake conditions (June–late-November), the average chlorophyll *a* concentration (13 $\mu g\ l^{-1}$) of the Mary River channel concurs with a eutrophic classification based on USEPA (1974; eutrophic $>12\ \mu g\ l^{-1}$) and OECD (1982; eutrophic $>8\ \mu g\ l^{-1}$) schemes. However, Huszar et al. (1997) caution against the application of temperate derived trophic classifications schemes to tropical waters. Eutrophic waters typically comprise a significant proportion, if not domination, by Cyanobacteria which in the Mary River channel lake constituted less than 1% of phytoplankton biomass, thereby indicating a lower trophic classification than eutrophy. Based on 1996 data, the channel lake would have been classified mesotrophic. The trophic state of the Mary River channel is probably best described as mesotrophic or meso-eutrophic.

Phytoplankton

To further our understanding and prediction of phytoplankton distribution and dynamics, functional groups of taxa which respond similarly to a single set of environmental conditions are being developed (Reynolds et al., 2002). Individual members of a group have similar morphological, physiological and ecological traits, though each member may not always be present owing to the stochastic nature of colonization, notably the inocula available (Reynolds et al., 2002). The phytoplankton main functional groups present in the Mary River channel lake, during each hydraulic phase, are presented in Table 2.

Under riverine conditions, the W1 group (principally euglenoids) was most common, then group Y (mainly *Cryptomonas*), but collectively these groups comprised only 47% of the total biovolume. *Crpytomonas* are small, r-selected plankton based on their morphology (see Reynolds, 1997), with replication rates likely to compensate population losses swept downstream. Groups W1, L_o (*Peridinium*) and W2 (*Trachelmonas*) are atypical of fast flowing rivers, but may have originated from slow moving, floodplain waters or backwaters of the river system. The phytoplankton assemblage in the river channel probably originated from a number of sources, precluding the domination of any one function group. Functional groups Y and L_o have also been reported to be prominent in a Brazilian floodplain lake (Huszar & Reynolds, 1997).

Table 2. Most common phytoplankton functional groups (see Reynolds et al., 2002), based on their average percentage contribution to the total biovolume concentration for each hydraulic phase

Functional group (rows) and hydraulic phase	Riverine	Transition, riverine to lake (May) and early-lake phase (June)	Lake (July)	Lake (Aug.–Nov.)
W1, *Euglena*, *Phacus*	26	15	2.8	9.6
W2, *Trachelmonas*	4.4	7.5	1.7	5.1
L_o, *Peridinium*	4.9	14	7.3	8.6
Y, *Cryptomonas*, *Rhodomonas*	20 (6)	46 (25)	8.4 (5.2)	25 (6.5)
A, *Acanthoceras* sp.	0	0.4	76	3.7
D, *Synedra*, *Nitzschia*	0.3	1.3	0.3	35
Percentage total	55.6	84.2	96.2	87

The percentage contribution of *Rhodomonas* to the total biovolume concentration is shown in parentheses.

Cryptomonas was accompanied by *Rhodomonas* throughout the 9 month study period (Table 2). The two genera are closely related taxonomically, both being crytophytes. *Rhodomonas* is a single cell flagellate with similar morphology and biovolume range (5–8000 μm^3 in the Mary River channel) to *Cryptomonas* (2500 um^3), and adapted to a wide range of habitats. Olrik (1994) identifies the two genera as having traits that are transitional between colonizers (C-species), disturbance-tolerant (R-species) and stress-tolerant (S-species). In this paper, *Rhodomonas* is placed in the Y functional group, and is tentatively recommended for inclusion in the group. The different pigment contents of the two genera, however, may result in the selective advantage of one over the other in some waters.

The dominant group during the transition phases was group Y. The multivariate analysis places the lentic assemblage following the early June short mixing event amongst the transition group, indicating this event did not impose significant selection pressure on the lake's phytoplankton.

The most marked change in the lake's phytoplankton composition occurred in mid-July, when *Acanthoceras* dominated the lake's biovolume. This genus has a similar morphology to *Urosolenia*, a member of functional group A, being distinguished by two spines on each end of its broad flattened frustule. The habitat description for functional group A (clear, often well mixed and base poor; Reynolds et al., 2002) concurs with the Mary River channel. The short-lived dominance of *Acanthoceras* sp. in the Mary River channel is difficult to explain, though its demise may have been associated with the more than 10-fold reduction in nitrate concentrations (Fig. 5g), possibly inferring a high N half-saturation rate for *Acanthoceras* growth relative to other phytoplankton in the channel lake, though group A is described by Reynolds et al. (2002) as being tolerant of low nutrient levels. *Urosolenia* is infrequently reported in the literature, but was accompanied by other diatoms and mainly small chlorophytes in a floodplain lake studied by Huszar & Reynolds (1997).

The dominance of *Acanthoceras* was replaced by *Nitzschia agnita* and *Synedra ulna*, though taxa belonging to groups L_o, W1, W2 and Y constituted a substantial proportion of the phytoplankton biovolume (Table 2). The morphology of *Synedra ulna* is almost the same as *Synedra acus*, a member of functional group D together with *Nitzschia*, and found in shallow, enriched waters (Reynolds et al., 2002). *Nitzschia* has also been reported to be prominent during low water levels in a tropical floodplain lake on the Solimões River by Ibañez (1998).

The Mary River channel lake exhibited stable thermal stratification during the period of hydraulic isolation, with adequate light for photosynthesis in the diurnal mixed layer. Such conditions, considered alone, favour the autogenic succession of phytoplankton, which is driven by the activity of pelagic organisms themselves (see Reynolds, 1988), and contrasts with the continuously changing environment of some tropical floodplain lakes (e.g., Huszar & Reynolds, 1997; De Oliveira & Calherios, 2000). There is no clear evidence, however, of autogenic succession in the Mary River channel lake during hydraulic isolation, nor the dominance by a phytoplankton functional group, not with standing the occasional dominance by *Acanthoceras*, and functional group D. Composite sampling may have masked lentic planktonic succession if the water body, instead of being homogenous, featured spatially defined phytoplankton populations over the lake's 14 km length that were influenced by localized nutrient dynamics and grazing pressures.

Competition experiments suggest that diatoms are good competitors for phosphorus, being superior to Chlorophyaceae and Cyanobacteria, but as nitrogen competitors diatoms are subordinate to cyanobacteria (Sommer, 1989). This competitive advantage probably favoured their prominence in the Mary River channel lake during lentic conditions, when Si concentrations were high and unlikely to limit diatom growth. Equally important was the favourable physical environment to diatoms, the diurnal mixed layer was apparently sufficiently turbulent to maintain a suspended diatom population that compensated sedimentation losses. Diatoms, however, did not continually dominate the channel lake's phytoplankton. Periodic enrichment of the lake, possibly by disturbance of the littoral environment by power boats, could have produced a variable nutrient supply that has prevented the long-term domination by diatoms.

Conclusion

Similar to other tropical floodplain lakes, the limnology of the Mary River channel lake is driven, on a seasonal time scale, by the channel's hydraulics. Four phases were identified: (1) riverine (April), (2) riverine to lake transition (May), (3) lake (June–late-November), and (4) lake to riverine transition (late-November–December). A fifth phase, over-bank flow and floodplain inundation was recognized but not studied. These channel lake phases differ from lakes located on a floodplain with respect to phase duration and flow direction. The water chemistry (conductivity, dissolved oxygen, pH, Si and water clarity) and phytoplankton assemblages of the Mary River channel lake were underpinned by the channel's hydraulics, though this was not evident for the channel's nutrients. A diurnal cycle of heat gain and loss, rather than a seasonal cycle, drove thermal stratification with infrequent and short-lived deep mixing events. Despite the lake's persistent stratification, the hypolimnion remained oxic. Phytoplankton autogenic succession during lentic conditions was not apparent, even though physical conditions were stable. The most common phytoplankton throughout the study period belonged functional groups L_o (*Peridinium inconspicuum)*, W1 (euglenoids), W2 (*Trachelomonas*) and Y (*Cryptomonas, Rhodomonas*), with groups A (*Acanthoceras*) and D (*Nitzschia agnita, Synedra ulna*) prominent during the lentic phase.

Acknowledgements

This research was supported by the Australian Government's Natural Heritage Trust and the Northern Territory Government. The many hours of phytoplankton identification and enumeration was patiently undertaken by Gosia Przybylska, and field work ably lead by Cyrus Edwards. Reviews by two anonymous referees and Associate Editor, Judith Padisák, improved the manuscript.

References

APHA, 1998. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, American Water Works Association and Water Environment Federation. United Book Press, Maryland.

Barbosa, F. A. R. & J. Padisák, 2002. The forgotten lake stratification pattern of atelomixis, and its ecological importance. Verhandlungen der internationalen vereinigung für theroetische and angwandte limnologie 28: 1385–1395.

Belbin, L., 1993. PATN – Pattern Analysis Package. Commonwealth Scientific and Industrial Research Organization, Canberra.

Calheiros, D. E. & S. K. Hamilton, 1998. Limnological conditions associated with natural fish kills in the Pantanal wetland of Brazil. Verhandlungen der internationalen vereinigung für theroetische and angwandte limnologie 26: 2189–2193.

Cuthbert, I. D. & P. del Giorgio, 1992. Toward a standard method of measuring colour in freshwater. Limnology and Oceanography 37: 1319–1326.

Day, S. A., R. P. Wickham, T. J. Entwistle & P. A. Tyler, 1995. Bibliographic Checklist of Non-Marine Algae in Australia. Australian Biological Resources Study, Canberra.

De Oliveira, M. D. & D. F. Calherios, 2000. Flood pulse influence on phytoplankton communities of the south Pantanal floodplain, Brazil. Hydrobiologia 427: 101–112.

Finlayson, C. M., B. J. Bailey, W. J. Freeland & M. R. Flemming, 1988. Wetlands of the Northern Territory. In A. J. McComb & P. S. Lake (eds), Thc conservation of Australian wetlands. Surrey Beatty and Sons, Sydney; 103–126.

de García Emiliani, M. O., 1993. Seasonal succession of phytoplankton in a lake of the Paraná River floodplain, Argentina. Hydrobiologia 264: 101–114.

Gell, P. A., J. A. Sonneman, M. A. Reid, M. A. Illman & A. J. Sincock, 1999. An Illustrated Key to Common Diatom Genera from Southern Australia. Cooperative Research Centre for Freshwater Ecology, Thurgoona (Australia).

Hamilton, S. K. & W. M. Lewis, 1987. Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela. Limnology and Oceanography 32: 1277–1290.

Hamilton, S. K. & W. M. Lewis, 1990. Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain, Venezuela. Archiv für Hydrobiologie 119: 393–425.

Hamilton, S. K., S. J. Sippel & J. M. Melack, 2002. Comparison of inundation patterns among South American floodplains. Journal of Geophysical Research 107: 8038–8052.

Huszar, V. L. M. & C. S. Reynolds, 1997. Phytoplankton periodicity and sequences of dominance in an Amazonian flood-plain lake (Lago Batata, Pará, Brazil): responses to gradual environmental change. Hydrobiologia 346: 169–181.

Huszar, V. L. M., L. H. S. Silva, P. Domingos, M. Marinho & S. Melo, 1997. Phytoplankton species composition is more sensitive than OECD criteria to the trophic status of three Brazilian tropical lakes. Hydrobiologia 369/370: 59–71.

Ibañez, M., 1998. Phytoplankton composition and abundance of a central Amazonian floodplain lake. Hydrobiologia 362: 79–83.

Idso, S. B., 1973. On the concept of lake stability. Limnology and Oceanography 18: 681–683.

Imberger, J., 1985. The diurnal mixed layer. Limnology and Oceanography 30: 737–770.

Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river-floodplain systems. In Dodge, D. P. (ed.), Proceedings of the International Large River Symposium. Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences 106: 110–127.

Kirk, J. T. O., 1983. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, Melbourne.

Lesack, L. F. & J. M. Melack, 1995. Flooding hydrology and mixture dynamics of lake water derived from multiple sources in an Amazon floodplain lake. Water Resources Research 31: 329–345.

Lewis, W. M., 2000. Basis for the protection and management of tropical lakes. Lakes & Reservoirs Research: and Management 5: 34–48.

Ling, H. U. & P. A. Tyler, 1986. A Limnological Survey of the Alligator Rivers Region Part II: Freshwater Algae, Exclusive of Diatoms. Australian Government Publishing Service, Canberra.

Ling, H. U. & P. A. Tyler, 2000. Australian Freshwater Algae (Exclusive of Diatoms). Stuttgart, J. Cramer, .

Lund, J. W. G., C. Kipling & E. D. Le Cren, 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143–170.

MacIntyre, S. & J. M. Melack, 1988. Frequency and depth of vertical mixing in an Amazon floodplain lake (L. Calado, Brazil). Verhandlungen der internationalen vereinigung für theroetische and angwandte limnologie 23: 80–85.

Melack, J. M., 1984. Amazon floodplain lakes: shape, fetch and stratification. Verhandlungen der internationalen vereinigung für theroetische and angwandte limnologie 22: 1278–1282.

Melack, J. M. & T. R. Fisher, 1983. Diel oxygen variations and their ecological implications in Amazon floodplain lakes. Archiv für Hydrobiologie 98: 422–442.

OECD, 1982. Eutrophication of Waters: Monitoring, Assessment and Control. OECD, Paris.

Olrik, K., 1994. Phytoplankton Ecology: Determining Factors for the Distribution of Phytoplankton in Freshwater and the Sea. Danish Environmental Protection Agency, Denmark.

Powell, L. & S. A. Townsend, 1997. A Survey of Water Quality in the Billabongs of the Mary River Floodplain: A Report for the Community. Northern Territory Department of Lands, Planning and Environment, Darwin.

Prescott, G. W., 1978. How to Know the Freshwater Algae. W. C. Brown Company, Duduque (USA).

Reynolds, C. S., 1984. The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge.

Reynolds, C. S., 1988. The concept of ecological succession applied to seasonal periodicity of freshwater phytoplankton. Verhandlungen der internationalen vereinigung für theroetische and angwandte limnologie 23: 683–691.

Reynolds, C. S., 1997. Vegetation Processes in the Pelagic: A Model for Ecosystem Theory. Ecology Institute, Oldendorf.

Reynolds, C. S., V. Huszar, C. Kruk, L. Naselli-Flores & S. Melo, 2002. Towards a functional classification of the freshwater phytoplankton. Journal of Plankton Research 24: 417–428.

Sippel, S. J., S. K. Hamilton & J. M. Melack, 1992. Inundation area and morphometry of lakes on the Amazon River floodplain, Brazil. Archiv für Hydrobiologie 123: 385–400.

Sommer, U., 1989. The role of competition for resources in phytoplankton succession. In Sommer, U. (ed.), Plankton Ecology: Succession in Plankton Communities. Springer-Verlag, Berlin: 57–106.

Sonneman, J. A., A. Sincock, J. Fluin, M. Reid, P. Newall, J. Tiby & P. Gell, 1999. An Illustrated Guide to Common Stream Diatom Species from Temperate Australia. Cooperative Research Centre for Freshwater Ecology, Thurgoona (Australia).

Talling, J. F. & J. Lemoalle, 1998. Ecological Dynamics of Tropical Inland Waters. Cambridge University Press, Cambridge.

Townsend, S. A., 1998. The influence of retention time and wind exposure on stratification and mixing in two tropical Australian reservoirs. Archiv für Hydrobiologie 141: 353–371.

Townsend, S. A., 1999. The seasonal pattern of dissolved oxygen, and hypolimnetic deoxygenation, in two tropical Australian reservoirs. Lakes & Reservoirs: Research and Management 4: 41–53.

Townsend, S. A., 2001. Perennial domination of phytoplankton by *Botryococcus* and *Peridinium* in a discontinuously polymictic reservoir (tropical Australia). Archiv für Hydrobiologie 151: 529–548.

Townsend, S. A. & C. A. Edwards, 2003. A fish kill event, hypoxia and other limnological impacts associated with early wet season flow into a lake on the Mary River floodplain, tropical northern Australia. Lakes & Reservoirs: Research and Management 8: 169–179.

USEPA, 1974. An Approach to a Relative Trophic Index System for Classifying Lakes and Reservoirs. U.S. Environmental Protection Agency, Washington.

Vásquez, E., 1992. Temperature and dissolved oxygen in lakes of the Lower Orinoco River floodplain (Venezuela). Revue d'hydrobiologie Tropicale 25: 23–33.

Vörös, L. & J. Padisák, 1991. Phytoplankton biomass and chlorophyll-*a* in some shallow lakes in central Europe. Hydrobiologia 215: 111–119.

Vyvernam, W., 1994. Limnological features of lakes on the Sepik-Ramu floodplain, Papua New Guinea. Australian Journal of Marine and Freshwater Research 45: 1209–1224.

Webber, E. J., 2000. Response of Mary River Phytoplankton to Nitrogen and Phosphorus Enrichment. Honors Thesis. Northern Territory University, Darwin.