

ENVIRONMENTAL GRADIENTS ALONG A LOWLAND WEIR POOL IN THE
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ABSTRACT

The 60-km-long pool created by the Mildura weir exhibits pronounced physical, chemical and biological gradients along its length. As the river deepens and widens downstream along the weir pool, the flow velocity decreases and the potential for thermal stratification (intensity and duration of stratification) increases. Most nutrient concentrations (TN, NO_x, FRP) as well as the euphotic depth increased in the downstream direction whereas TP and turbidity decreased. The increase in bioavailable nutrients co-occurred with an increase in electrical conductivity suggesting the presence of relatively more saline groundwater inflows to the weir pool.

Throughout the summer (12 December 2003–18 March 2004), with the exception of 8 days, the water column throughout the weir pool mixed completely on a diurnal basis in the deeper sections and was continuously mixed in the shallower upstream sections. This mixing substantially reduced the mean irradiance experienced by the phytoplankton near the weir. Maximum cyanobacteria concentrations were observed in the mid-weir pool where the range of conditions was most suitable. Diatom abundance increased along the most downstream 20 km of the pool where the water column was deeper and slower flowing yet still mixed completely on a diurnal basis. Peaks in cyanobacteria biomass are not expected in the lower weir pool until lower discharges promote persistent thermal stratification and increase the mean irradiance in the surface mixed layer. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: cyanobacteria; weir pool; nutrients; phytoplankton; flow velocity; thermal stratification; River Murray

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INTRODUCTION

Toxic cyanobacteria blooms pose a risk to human and animal health in rivers around the world. Toxic blooms have been reported in diverse regions such as California (CRWQCB, 2009), Spain (Moreno *et al.*, 2004), Portugal (Vasconcelos *et al.*, 1996), Germany (Fromme *et al.*, 2000) and China (Ueno *et al.*, 1996). Cyanobacteria blooms are a persistent problem in many Murray-Darling Basin (MDB) rivers in Australia, including the River Murray (Murray-Darling Basin Authority, 2010), and blooms are also often observed in range of rivers spanning the continent such as the Fitzroy (Queensland), the Swan and Canning rivers (Western Australia) and the Hawkesbury River (New South Wales). A common observation is that slower flowing lowland rivers are particularly susceptible to cyanobacteria blooms. Developing an improved understanding of the processes by which flow influences cyanobacteria blooms in rivers will contribute to better management of these resources.

Sherman *et al.* (1998) showed that flow exerted a primary control on river stratification and exerted a controlling influence on phytoplankton population dynamics in a weir pool on the lower Murrumbidgee River. Periods of persistent thermal stratification can create a favourable light environment for positively buoyant cyanobacteria capable of maintaining their position within the surface layer (Humphries and Lyne, 1988; Sherman *et al.*, 1994) provided the ratio of mixing depth to euphotic zone is substantially <3 (Lewis, 1978; Sherman *et al.*, 1998; Bormans *et al.*, 2005). As discharge decreases, the production of turbulent kinetic energy (TKE) at the bottom of the water column decreases (Bormans and Webster, 1998) and the water residence time increases. The decreased mixing energy facilitates the development of persistent stratification, and the increased residence time allows for greater cyanobacteria population growth. The destruction of thermal stratification on at least a diurnal basis is believed to reduce the likelihood of cyanobacteria blooms (>15000 cells mL⁻¹ or 2 mm³ L⁻¹) (Webster *et al.*, 2000).

The River Murray is naturally prone to blooms because of its low bed slope and periods of low flow (Sullivan *et al.*, 1988). In the lowland sections of the river, the construction

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of 13 low-level weirs has exacerbated the problem by altering the natural hydraulic regime (Walker and Thoms, 1993). The immediate effect of the standard operation of these weirs is to deepen and stabilize the water column (Walker and Thoms, 1993), promoting the development of thermal stratification and the growth of cyanobacteria blooms (Webster *et al.*, 1996).

By producing a backwater, weirs create a velocity gradient along the weir pool due to changes in channel dimensions—typically increases in channel mean width and mean depth in the downstream direction. Upstream of the weir pool, where the river is free flowing, uniform flow conditions of approximately constant depth and velocity prevail. Within the weir pool, there is a transition from high to low flow velocities in the downstream direction (McCarthy *et al.*, 2004b; Walker and Thoms, 1993). Kimmel *et al.* (1990) suggest that the growth of phytoplankton will change from light limited in the upper reaches to nutrient limited closer to the regulatory structure as increasing residence time creates lake-like conditions. This model has been supported in Herrington Lake on the Ohio River (Bukaveckas and Crain, 2002) and may be applicable to weir pools along the River Murray.

In the presence of persistent thermal stratification, the engineering design of a weir influences the residence time of phytoplankton within the weir pool as well. Along the Murrumbidgee River, 'undershot' weirs discharge water from a gate located at the bottom of the river (Sherman *et al.*, 1998). An 'undershot' design can cause the release of water from below the thermocline and can lead to almost indefinite water residence times in the surface layer of the water column. In contrast, all of the 13 low-level weirs on the River Murray are overflow weirs and release water from the surface layer of the water column. In this case, the surface layer may be preferentially skimmed off with the result that the residence time is shorter than would be experienced for a well-mixed water column.

Within the 60-km-weir pool created by the Mildura weir, cyanobacteria blooms are common (e.g. Scholz, 2003), and large-scale transformations (50–60 km) of the phytoplankton community (i.e. increase in cyanobacteria, decrease in diatoms) have been documented (McCarthy *et al.*, 2004b). When observed at a coarse spatial resolution, the environmental gradients appear uniform from the free-flowing section of river upstream of the weir pool to the weir. However, gradients that appear uniform at a large scale may be discontinuous at finer resolution (cf. Duarte and Kalff, 1990; Jean and Bouchard, 1993). The objective of the present study was to explore the nature of the physical and chemical gradients and their influence on the phytoplankton at a smaller spatial scale (10 km intervals). It was anticipated that this spatial resolution will allow delineation of important processes that drive cyanobacteria dynamics in lowland river weir pools.

MATERIALS AND METHODS

Site description

The MDB covers over 1 million km² (approximately 14% of Australia's total area) across five states and territories in south-eastern Australia (Crabb, 1997). The major river of the MDB, the River Murray, flows 2530 km from the south-eastern highlands, through the southern MDB, to the sea at Goolwa. The River Murray is heavily regulated with five barrages near the river mouth, 13 low-level weirs, a high-level weir (Yarrawonga weir) and Hume dam that combine to store and transport water to townships and irrigation districts along the river (Walker, 1985).

The study focused on a 66-km reach of the River Murray upstream of Mildura weir (Lock and Weir 11, 34°10'32.5" S, 142°09'54" E). The weir is located within the Mallee Tract of the River Murray in the southern MDB, 886 river kilometres upstream (average mean thread distance, AMTD km) from the Murray mouth (Figure 1). Constructed in 1927 to facilitate river navigation, the weir is now primarily operated for domestic, irrigation and recreation purposes (Crabb, 1997). The weir pool has a volume of 36600 ML at full supply and, under normal operating conditions, is maintained at ±5 cm of full supply level. The influence of the weir extends for approximately 60 km upstream.

The study reach consisted of six sites within the Mildura weir pool (AMTD 886–936 km) and a seventh site in the free-flowing section upstream of the weir pool (AMTD 952 km). The river channel has a near-rectangular cross-section and low bed slope (1:20000) and is inset within a large trench cut into ancient lake and marine sediments (Thoms *et al.*, 2000). Along its length, the weir pool deepens from 2.1 m to 7.4 m and widens from 110 m to 148 m, increasing the channel cross-sectional area from 231 m² to 1094 m² (Figure 1, Table I).

The summer irrigation season extends from December to April. Inflows exhibit particularly high interannual variability during the first two months of the season with the mean discharge from 1990 to 2004 being approximately double the median discharge (Figure 2). Inflows are much more consistent during the latter part of the irrigation season (February onwards). During the study period (2003–2004), inflow was similar to median inflow conditions except for January 2004 when inflow was approximately 35% greater than the historical median. During the irrigation season, about 1000 ML day⁻¹ is withdrawn from the weir pool, and the discharge over the weir is generally between 3500 and 5000 ML day⁻¹ with slight peaks late in the week (Wednesday–Friday) to satisfy weekend irrigation demands. The location of major irrigation pumps along the weir pool, First Mildura Irrigation Trust (FMIT), Sunraysia Rural Water Authority (SRWA) and Lower Murray Water (LMW), are shown in Figure 1.

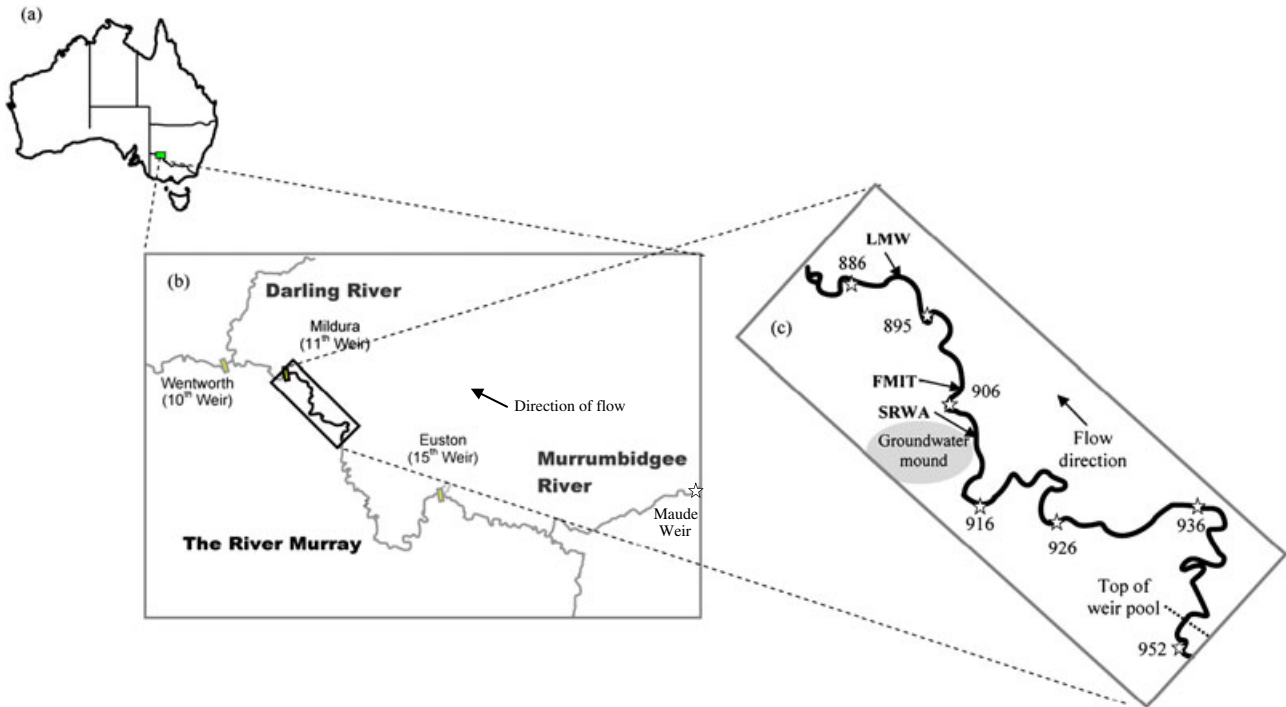


Figure 1. Location of study sites (stars) on the River Murray within (a) south-eastern Australia, (b) the Mallee Tract and (c) the Mildura weir pool. Numbers denote the site average mean thread distance (AMTD, the distance in km of a site from the mouth of the river). Also shown on (b) is the location of Maude weir on the Murrumbidgee River (star) and on (c) groundwater mound (grey area) and the location of major irrigation pumps, First Mildura Irrigation Trust (FMIT), Sunraysia Rural Water Authority (SRWA) and Lower Murray Water (LMW)

Field sampling

The field sampling was conducted at the seven sites (Table I) between 11 December 2003 and 18 March 2004. Routine sampling included *in situ* measurement of water column irradiance, temperature, flow velocity, pH, electrical conductivity, dissolved oxygen and turbidity and collection of water samples for nutrient and cyanobacteria analyses.

Flow velocity

Mid-stream vertical flow velocity profiles (0.5 m depth intervals) were measured weekly at each site using a portable

flow meter (FLO-MATE™ 2000, Marsh-McBirney, Inc., Frederick, MD, USA).

Temperature

At each site, temperature loggers (Stowaway Tidbit™, ONSET Computer Corporation, Bourne, MA, USA) were installed at the top and bottom of the water column and recorded water temperature (0.2°C resolution) at hourly intervals for the duration of the study. Top and bottom temperature logger data (2003–2004) were used to determine the duration and strength (temperature difference) of

Table I. Summary of study sites

AMTD(km)	Name	Distance from weir(km)	Physical dimensions			Location	
			Depth(m)	Width(m)	Area(m ²)	Latitude	Longitude
886	Mildura weir	0	7.4	148	1094	34° 11' 03"	142° 10' 03"
895	Bruce's Bend	9	7.7	136	1047	34° 12' 27"	142° 13' 43"
906	Psyche Bend	20	5.5	139	765	34° 16' 14"	142° 14' 54"
916	Bonnie Doone	30	5.1	130	663	34° 17' 54"	142° 16' 08"
926	Karadoc	40	3.8	137	521	34° 19' 50"	142° 18' 19"
936	Mallee Cliffs	50	3.8	117	445	34° 20' 32"	142° 23' 49"
952	Iraak	66	2.1	110	231	34° 24' 34"	142° 21' 10"

River width is mean width of 10km river section upstream of site taken from McCarthy *et al.* (2004b).

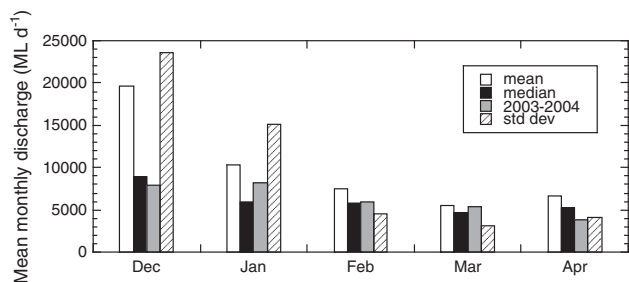


Figure 2. Monthly irrigation season inflows (mean, median and standard deviation) to Mildura weir pool during 1990–2004 compared to flows during the 2003–2004 study period (data courtesy of Murray-Darling Basin Authority)

diurnal stratification. A top–bottom temperature change of $<0.2^{\circ}\text{C}$ (logger resolution) was assumed to indicate complete mixing of the water column.

Irradiance

Downwelling PAR was measured weekly at each site using a LI-COR quantameter (LI-1000, LI-COR Biosciences, Lincoln, NE, USA) equipped with cosine-corrected LI-COR underwater (LI-192SA) and surface flat-plate quantum sensors (LI-190SA). Simultaneous measurements of underwater and surface downwelling irradiance were taken at 0.1 m depth intervals (to a depth of 2 m, unless the water column was shallower). Euphotic depth (Z_{eu}) was determined in mid-channel as the depth to which 1% of surface irradiance penetrated.

Nutrients

At each site, three independent water samples were taken across the river at 25%, 50% and 75% of the river width. Nutrients were analysed fortnightly, and cyanobacteria were analysed weekly until 20 January 2004, thereafter fortnightly. At each point across the river, vertically integrated samples were taken using a 12-V submersible pump (positioned in a shallow bucket to prevent benthic sediment contamination) attached to a 10-m opaque Nylflex Waterflex garden hose (internal diameter 20 mm). The sampler was lowered and raised through the water column with the water sample collected in a 25-L container. From this sample, a 200-mL unfiltered sub-sample was taken for total nitrogen (TN) and total phosphorus (TP) determinations. TN was determined colorimetrically after its reduction to nitrate using a cadmium column after pre-digestion in $\text{NaOH-K}_2\text{S}_2\text{O}_8$ and oxidation to nitrate and TP by pre-digestion in $\text{NaOH-K}_2\text{S}_2\text{O}_8$ and oxidation to orthophosphate (APHA, 1995).

One 10-mL aliquot of 0.2- μm filtered water was taken for determination of nitrate and nitrite expressed as oxides of nitrogen (NO_x) and 'soluble' phosphorus as filterable reactive

phosphorus (FRP). NO_x and FRP were determined colorimetrically using standard methods (APHA, 1995) and are assumed to be bioavailable to the phytoplankton. All nutrient samples were analysed at the NATA-certified MDFRC Chemical Laboratory (Albury). Note that ammonia was not determined in this project but six weekly measurements at the weir during 2001–2003 averaged 4.8 ± 0.3 (s.d.) $\mu\text{g NH}_3\text{-NL}^{-1}$ and the ratio of NH_3 to NO_x was 0.63 ± 0.03 (McCarthy *et al.*, 2004b).

Cyanobacteria

A 200-mL sub-sample was taken and preserved in Lugol's iodine solution (2 mL) for the determination of cyanobacteria cell concentrations. Samples were first concentrated by sedimentation for 1 week, and then cyanobacteria were identified to genera at $400\times$ magnification (potentially toxic taxa to species) and enumerated at $200\times$ magnification by examining a minimum of 10% of a Lund cell (0.55 mL). Cell concentrations were converted to mean depth-integrated biovolume using standard formulas for Australian taxa (NRMMC, 2005). Area-weighted phytoplankton populations were calculated as the product of the mean biovolume and local channel cross-sectional area. Cyanobacteria sample analysis was conducted at the NATA-certified WSL Consultants Laboratory (Richmond).

Physico-chemical profiles

Mid-stream at each site, one vertical physico-chemistry profile (1-m interval) of pH, electrical conductivity (μScm^{-1} at 25°C), dissolved oxygen (mgL^{-1}), temperature ($^{\circ}\text{C}$) and turbidity (nephelometric turbidity unit, NTU) was obtained weekly using a HORIBA U-10 multi-probe (Australian Scientific Ltd, Kotara, NSW, Australia).

Fluorescence profiles

On 5 February 2004, *in situ* vertical profiles of chlorophyll fluorescence were measured at 103 locations along the middle of the weir pool (approximately every 600 m) using a submersible fluorescence profiler (FluoroProbe, bbe Moldaenke, Kronshagen, Germany) configured to discriminate between functional groups of phytoplankton (diatoms, green algae, cyanobacteria and cryptomonads) based on the relative abundance of ancillary photosynthetic pigments.

Supplemental thermistor chain and meteorological monitoring

Supplemental monitoring was conducted during January and February 2005 to further resolve the surface layer dynamics at a pontoon moored in the centre of the channel near the weir at AMTD 886 km. This monitoring consisted of the deployment of a meteorological station (Kipp & Zonen

CM11 and CG2 radiometers, Vaisala HMD30UYB air temperature and relative humidity, Vaisala WAV-15, WAA-15 wind direction and speed) and high precision thermistor chain (18 thermistors, $\pm 0.015^\circ\text{C}$ accuracy, 0.007°C resolution). All instruments were sampled every 10s and logged as 10-min averages.

Surface mixed-layer depth

The active surface mixing layer depth, Z_{mix} , is defined here as the depth to the thermistor with a 10-min mean temperature at least 0.05°C colder than that of the thermistors above it (Sherman *et al.*, 1998). During 2003, this criterion for Z_{mix} has been shown to correspond well to gradients in parameters such as dissolved oxygen and unquenched chlorophyll fluorescence (Sherman *et al.*, 2000) and can be considered the lower boundary of active turbulent mixing at the time of measurement. On a diurnal basis, the maximum observed Z_{mix} is the depth to which the surface layer phytoplankton population is homogeneously redistributed and largely determines the light dose received by the phytoplankton. In persistently stratified systems such as lakes and reservoirs where bottom-generated turbulence does not reach the surface layer, Z_{mix} typically occurs shortly before sunrise.

Discharge

Mean daily discharge data were obtained from the Murray-Darling Basin Authority (MDBA) gauging stations located at Colignan (AMTD 985 km) and at the Mildura weir (AMTD 886 km).

Statistical analysis

Normally distributed (determined by Shapiro–Wilk normality test, $\alpha=0.05$) physical and chemical data (subjects) were compared between sites (between-subject factor) using one-way repeated measures analysis of variances (RM

ANOVAs) to account for repeated measures over time (within-subject factor). The RM ANOVA may indicate a significant treatment effect on its own, but the treatment effect may be influenced by time, indicated by the significant interaction term (sites \times time). A significant interaction term specifies that the treatment has a significant effect but the magnitude of the effect varies over time. All statistical analyses were conducted using SYSTAT[®] Version 11 (SYSTAT, Inc., USA).

RESULTS

Hydrology and hydraulics

Mean daily discharge upstream of the weir pool (AMTD 985 km) and at the Mildura weir (AMTD 886 km) was uncharacteristically high in January during the sampling period (Figure 3a) but otherwise fairly representative of median conditions in the weir pool. Discharges remained above 5500MLday^{-1} between 5 December 2003 and 30 January 2004 before dropping slightly to 4000MLday^{-1} between 30 January 2004 and 21 March 2004.

The mean mid-channel flow velocity decreased from the upstream end of the weir pool (AMTD 952) to the weir (AMTD 886) as the channel cross-sectional area increased due to increasing river mean depth and mean width (Table I, Figure 3b). As well, the vertical flow velocity gradient weakened along the weir pool, especially at the upstream end (886 AMTD Figure 4). Assuming a representative mean velocity of $0.15\text{--}0.2\text{ms}^{-1}$ gives an approximate travel time of 4–5 days for water to pass along the entire weir pool.

Thermal stratification

The temperature difference, ΔT , between the top and bottom of the water column increased downstream towards the weir (Figure 5) as the flow velocity decreased. Diurnal

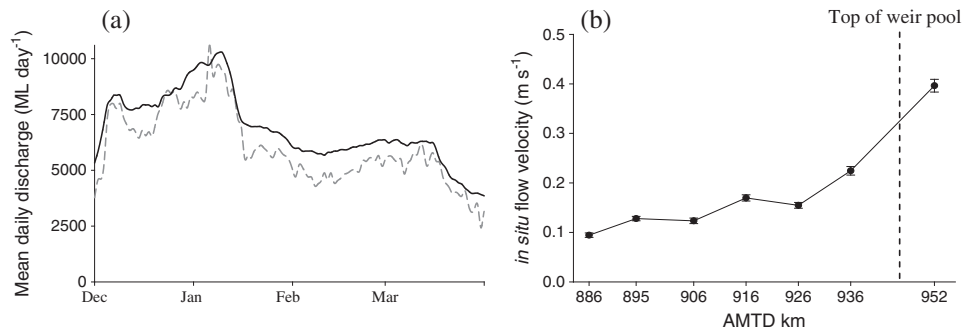


Figure 3. (a) Mean daily discharge upstream of weir pool (AMTD 985 km, black) and at Mildura weir (AMTD 886 km, grey dashed) gauging stations over with sampling period (December 2003–March 2004) and (b) mean (\pm standard error) *in situ* flow velocity from time-averaged vertical profiles within (AMTD 886–936 km) and upstream (AMTD 952 km) of the Mildura weir pool over December 2003 and March 2004.

Vertical dashed line denotes the upstream end of the weir pool

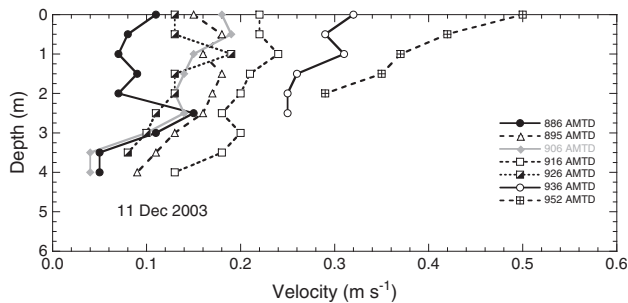


Figure 4. Flow velocity vertical profiles measured at the seven sites on 11 December 2003

stratification, indicated by $\Delta T > 0$, was stronger (bigger ΔT) and lasted longer as the water approached the weir. For the majority of the sampling period, all sites were completely mixed during the night (0100–0800h). However, between AMTD 906 and 886 km, conditions allowed the water column to persistently stratify for brief periods (e.g. 8 days over the sampling period at AMTD 886 km).

Immediately following sunrise, increasing solar radiation would heat the surface waters compared to the bottom waters. The thermal stratification continued to build until 1500–1630 h at which time the maximum daily temperature differential, ΔT , would be achieved. ΔT increased from AMTD 952 km (0.74°C) through to the weir (6.37°C). After this time, the water column would begin to destratify taking approximately 10–13.5 h to completely mix.

The pattern of diurnal thermal stratification created by averaging all temperature difference data for each 10-min period during a day is shown in Figure 6. Stratification commenced shortly after 0800 and peaked between 1500 and 1630. Thermal stratification was minimal at the two most upstream sites (AMTD 936 and 956 km) where the water column was shallow ($<4\text{ m}$) and flow velocity was $>0.2\text{ ms}^{-1}$. Maximum ΔT ranged from 0.7 to 1°C at the middle three sites (AMTD 906–926 km), where the water column was 3.8–5.5 m deep and mean flow velocities were in the range of $0.12\text{--}0.17\text{ ms}^{-1}$, and increased again to nearly 2°C along the final 10 km of the weir pool (sites AMTD 886–895 km) where the depth increased to $>7.5\text{ m}$. The sampling site at AMTD 906 km appears to be in a transitional zone between the middle and lower weir pool sections as it exhibits a maximum temperature change similar to that of the middle weir pool but a duration of stratification more similar to that in the lower weir pool.

Light environment and surface mixed-layer dynamics

Turbidity remained relatively constant between AMTD 952 km ($31.6 \pm 1.5\text{ NTU}$) and AMTD 906 km ($30.5 \pm 0.9\text{ NTU}$) before dropping significantly to the weir (AMTD 886 km,

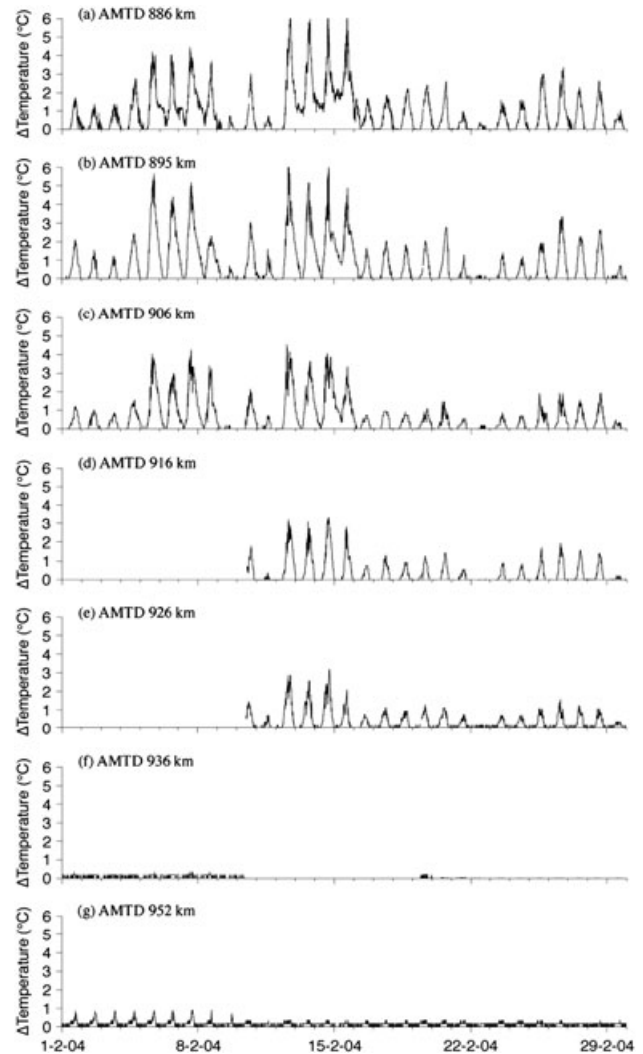


Figure 5. (a–g) Temperature difference between top and bottom temperature loggers located within (AMTD 886–936 km) and upstream (AMTD 952 km) of Mildura weir pool during February 2004. Mean discharge during this period was 5000 ML day^{-1}

$25.6 \pm 0.7\text{ NTU}$), but the magnitude of differences between the sites varied over time (Figure 7b, Table II). The decline in turbidity reflected the enhanced settling of suspended particles as flow velocity decreased and stratification increased along the weir pool. This is consistent with the theory of Condie and Bormans (1997) and similar observations in a nearby (ca. 200 km upstream) Murrumbidgee River weir pool by Sherman *et al.* (1998). The sedimentation of suspended particles facilitated an increase in light penetration with euphotic depth (Z_{eu}) from AMTD 952 km ($1.72 \pm 0.066\text{ m}$) to AMTD 886 km ($2.17 \pm 0.099\text{ m}$) (Figure 7d).

The light climate experienced by phytoplankton is a function not only of the depth of the euphotic zone, Z_{eu} , but also the amount of time spent by the phytoplankton in this well-lit environment. The phytoplankton population within the

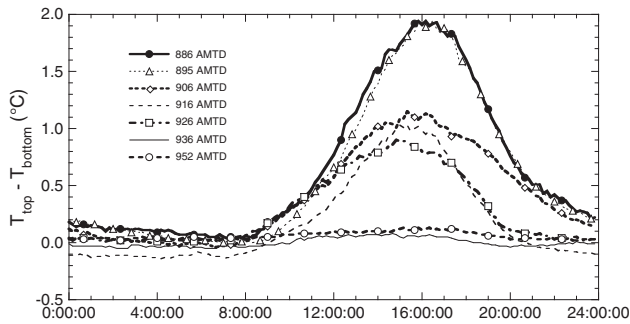


Figure 6. Mean diurnal water column temperature differences (top-bottom) at the seven sampling sites created by averaging all data collected from December 2003 through March 2004

actively mixing surface layer (SML), i.e. within a distance Z_{mix} of the water surface, is continuously redistributed throughout the SML and its growth depends upon the level of light within the SML. Light availability within the SML is conveniently represented in terms of the ratio of the SML depth to euphotic depth, $Z_{mix}:Z_{eu}$. Mildura weir pool experiences a typical summer irradiance of 307 W m^{-2} which provides daily SML photon doses (PAR) of 4 and $12 \text{ mol quantum}^{-2} \text{ day}^{-1}$ for $Z_{mix}:Z_{eu}=3$ and 1, respectively. Photon doses of ca. $4 \text{ mol quantum}^{-2} \text{ day}^{-1}$ are associated with light limitation of *Anabaena* growth rate both in similar environmental conditions (Sherman *et al.*, 1998) and in laboratory cultures (Green, 2001).

The maximum Z_{mix} during a day typically occurs just before sunrise in persistently stratified systems but can occur at other times depending on the supply of TKE available for mixing out the potential energy (PE) of the stratification. When the water column mixes completely, the maximum surface mixing layer depth Z_{mix} is equal to the water column depth on that day. This condition prevailed everywhere during the study period with exception of a few days at the site closest to the weir. At the shallow, continuously mixed section upstream of the weir pool (AMTD 952 km), $Z_{mix}:Z_{eu}$ was approximately one (1.28 ± 0.10). Moving downstream, Z_{mix} increased at a greater rate than Z_{eu} because of the increasing depth of the water column. $Z_{mix}:Z_{eu}$ increased from 2.09 ± 0.10 (AMTD 936 km) to 3.90 ± 0.26 (AMTD 895 km) before declining slightly to 3.48 ± 0.20 at the weir.

For the infrequent periods of persistent stratification in the lower weir pool, thermistor chain data collected near the weir (AMTD 886 km) between 10 January and 28 February 2005 provided more detail regarding the dynamics of Z_{mix} . Persistent stratification occurred on 8 days out of 33 days sampled; discharge was between 4900 and 6000 ML day^{-1} and the weather was hot and calm. The mean and median values of Z_{mix} were both 2.6 m which gives a typical $Z_{mix}:Z_{eu}$ value of about 1.3, assuming the optical properties of the water column are similar to those measured during 2003–2004. A value of $Z_{mix}:Z_{eu}=1.3$ would be expected to

support cyanobacteria blooms provided there was ample residence time. This value is similar to that at the upstream end of the weir pool; however, the local residence time will be somewhat longer closer to the weir due to the lower flow velocity.

Nutrients

Depth-integrated TN concentrations varied between 380 and $805 \mu\text{g NL}^{-1}$, and TP concentrations varied from 38 to $76 \mu\text{g PL}^{-1}$ over the sampling period. Concentrations of highly bioavailable nutrients ranged from <2 (minimum level of detection) to $18 \mu\text{g NL}^{-1}$ for oxides of nitrogen (NO_x) and from 4 to $26 \mu\text{g PL}^{-1}$ for FRP.

Statistically significant declines in TP, attributed to the increased sedimentation of phosphorus bound to suspended particles (McCarthy *et al.*, 2004b), were observed along the entire weir pool from AMTD 952 km ($49.0 \pm 1.29 \mu\text{g PL}^{-1}$) to AMTD 886 km ($44.2 \pm 0.73 \mu\text{g NL}^{-1}$). TP at each site responded differently over time (Table II) as was the case with turbidity.

In contrast to TP, no decrease in TN concentration between AMTD 952 km ($482.5 \pm 11.71 \mu\text{g NL}^{-1}$) and AMTD 886 km ($483.0 \pm 12.91 \mu\text{g NL}^{-1}$) was observed (Figure 7a) even though sedimentation of TN within the weir pool was expected (McCarthy *et al.*, 2004b). In fact, TN increased at a rate of $0.392 \mu\text{g NL}^{-1} \text{ km}^{-1}$ from AMTD 916 km ($481.0 \pm 10.30 \mu\text{g NL}^{-1}$) to AMTD 895 km ($489.6 \pm 15.91 \mu\text{g NL}^{-1}$) (Figure 7a, Table II). Because nutrient release or remobilization from the sediments is doubtful due to persistent oxic conditions and low flow velocities, another source of nitrogen is likely. N_2 fixation at an estimated rate of $6.1 \times 10^{-10} \text{ mg-N cell}^{-1} \text{ day}^{-1}$ (normalized for mean N_2 taxa, $4712 \text{ cells mL}^{-1}$ and assuming a travel time of 3 days along the reach) is one possible explanation for this increase (Sherman *et al.*, 1998). Another possibility is inflow of nitrogen-enriched groundwater.

There were statistically significant increases in NO_x and FRP between AMTD 952 km (NO_x $7.1 \pm 0.39 \mu\text{g NL}^{-1}$, FRP $7.2 \pm 0.34 \mu\text{g PL}^{-1}$) and the weir (NO_x $9.8 \pm 0.64 \mu\text{g NL}^{-1}$, FRP $10.3 \pm 0.85 \mu\text{g PL}^{-1}$) (Figure 7a,c; Table II). The percentage of bioavailable nutrients to total nutrients, $\text{NO}_x:\text{TN}$ and FRP:TP also increased downstream along the river from AMTD 952 km ($\text{NO}_x:\text{TN}$, 1.44 ± 0.09 ; FRP:TP, 13.98 ± 0.69) to the weir ($\text{NO}_x:\text{TN}$, 1.92 ± 0.12 ; FRP:TP, 23.55 ± 1.96) (Table II).

The increases in NO_x and FRP were most pronounced from AMTD 916 km to the weir (AMTD 886 km), and the proportion of bioavailable nutrients reflected this ($\text{NO}_x:\text{TN}$, $1.2 \rightarrow 1.8\%$; FRP:TP, $16.3 \rightarrow 23.3\%$). This section of river exhibited large increases in EC compared to a more gradual increase in EC over the length of the weir pool (Figure 7f). The bioavailable nutrient and EC increases suggest inflows

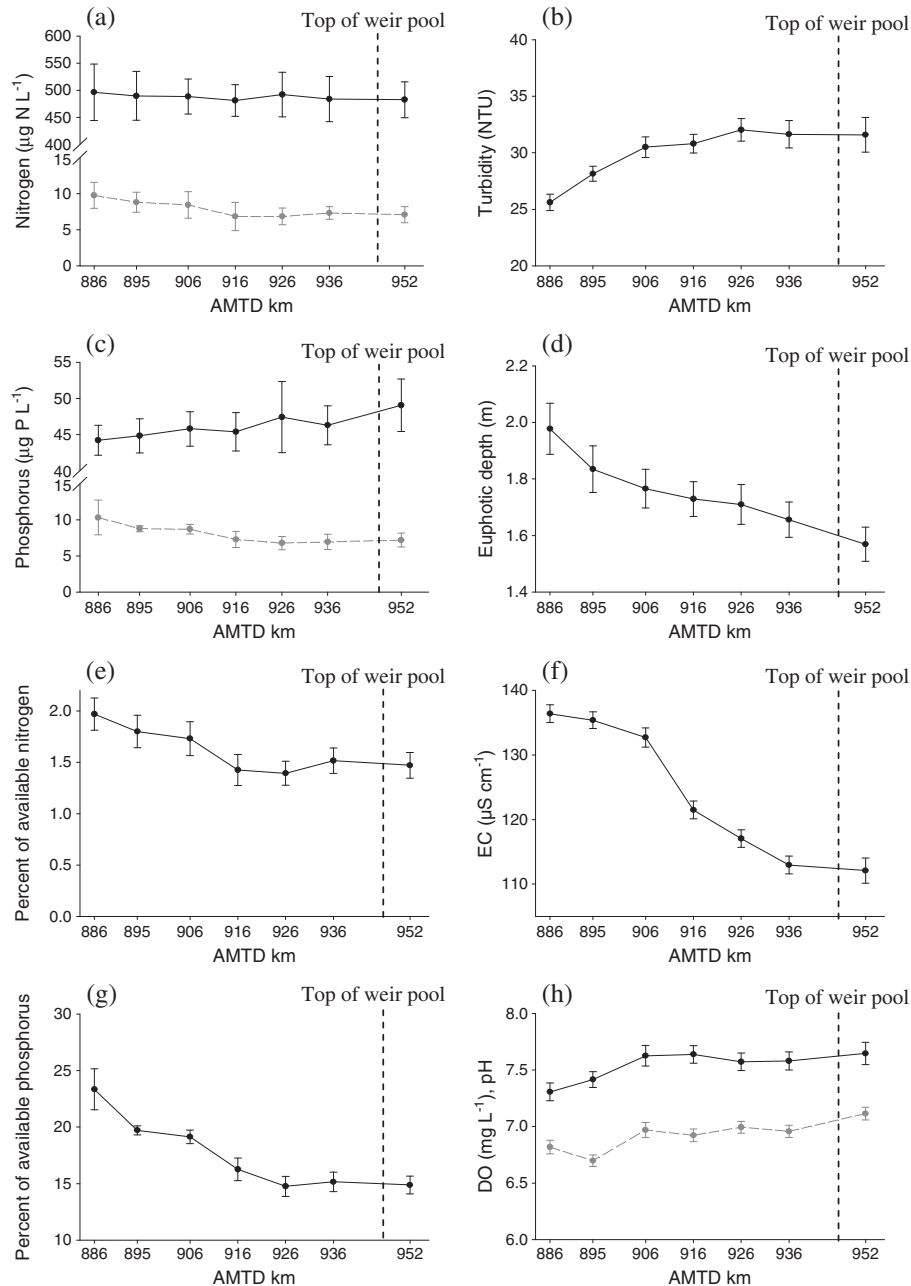


Figure 7. Longitudinal gradients in mean (\pm standard error): (a) total nitrogen (black) and oxides of nitrogen (grey dashed), (b) turbidity, (c) total phosphorus (black) and filterable reactive phosphorus (grey dashed), (d) euphotic depth, (e) filterable reactive phosphorus, (f) electrical conductivity, (g) oxides of nitrogen, (h) dissolved oxygen (black) and pH (grey dashed), in Mildura weir pool between December 2003 and March 2004. Vertical dashed line denotes the upstream end of the weir pool

from the N-enriched and P-enriched saline groundwater mound associated with the nearby Red Cliffs Irrigation District (McCarthy *et al.*, 2004a; Mackay *et al.*, 1988).

Cyanobacteria population composition

The cyanobacteria community within the study reach between December 2003 and March 2004 consisted of 15

genera, three of which are known to contain potentially toxic species (*Anabaena*, *Microcystis* and *Planktolyngbya*) with further identification revealing seven potentially toxic species. All sites were dominated by the potentially toxic *Anabaena* (74.1% of mean overall cyanobacteria biovolume) (*Anabaena circinalis*, 48.8%; *Anabaena flos-aquae*, 3.4%) and the non-toxic *Aphanizomenon* (23.1%) and *Aphanocapsa* (1.0%) (Table III). Other genera observed

Table II. Mean (±standard error) properties along Mildura weir pool. Also shown are the results of one-way repeated measures analysis of variance (RM ANOVA) of longitudinal trends. Significant interaction between the influence of site and time on each parameter indicated by *

Parameter	AMTD km						RM ANOVA				
	886	895	906	916	926	936	952	F	p	n	Interaction
Light and mixing dynamics											
Turbidity (NTU)	25.6 (±0.66)	28.1 (±0.66)	30.5 (±0.88)	30.8 (±0.79)	32.0 (±0.96)	31.6 (±1.16)	31.6 (±1.45)	16.54	<0.05	7	*
Z _{eu} (m)	1.98 (±0.09)	1.83 (±0.08)	1.77 (±0.07)	1.73 (±0.06)	1.71 (±0.07)	1.66 (±0.06)	1.57 (±0.06)	69.38	<0.001	7	
Z _{mix} :Z _{eu}	3.48 (±0.20)	3.90 (±0.26)	2.94 (±0.18)	2.74 (±0.11)	2.05 (±0.11)	2.09 (±0.10)	1.28 (±0.10)	-	-	-	-
Nutrient dynamics											
TN (µgNL ⁻¹)	496.5 (±52.11)	489.6 (±45.00)	488.5 (±32.31)	481.3 (±29.13)	492.1 (±41.35)	483.8 (±41.49)	482.5 (±33.11)	1.33	0.30	7	
NO _x (µgNL ⁻¹)	9.8 (±1.81)	8.8 (±1.40)	8.5 (±1.85)	6.9 (±1.95)	6.9 (±1.16)	7.3 (±0.88)	7.1 (±1.11)	12.75	<0.01	7	*
TP (µgPL ⁻¹)	44.2 (±2.07)	44.8 (±2.36)	45.8 (±2.38)	45.4 (±2.65)	47.4 (±4.92)	46.3 (±2.70)	49.0 (±3.64)	13.85	<0.05	7	*
FRP (µgPL ⁻¹)	10.3 (±2.40)	8.8 (±0.42)	8.7 (±0.67)	7.3 (±1.12)	6.8 (±0.92)	7.0 (±1.06)	7.2 (±0.95)	19.71	<0.001	7	*
NO _x :TN (%)	1.76 (±0.16)	1.56 (±0.16)	1.58 (±0.16)	1.20 (±0.15)	1.19 (±0.12)	1.32 (±0.12)	1.26 (±0.12)	11.26	<0.05	7	*
FRP:TP (%)	23.34 (±1.80)	19.71 (±0.39)	19.14 (±0.59)	16.25 (±0.99)	14.76 (±0.89)	15.15 (±0.87)	14.88 (±0.79)	35.93	<0.001	7	
Physico-chemistry dynamics											
EC (µS cm ⁻¹)	136 (±1.4)	135 (±1.3)	133 (±1.5)	121 (±1.4)	117 (±1.3)	113 (±1.4)	112 (±2.0)	76.13	<0.01	7	*
DO (mg L ⁻¹)	7.31 (±0.07)	7.42 (±0.07)	7.63 (±0.09)	7.64 (±0.08)	7.57 (±0.08)	7.58 (±0.08)	7.65 (±0.10)	4.51	0.87	7	
pH	6.82 (±0.06)	6.70 (±0.05)	6.97 (±0.07)	6.92 (±0.06)	6.99 (±0.05)	6.96 (±0.05)	7.11 (±0.06)	9.54	<0.05	7	*

at all sites, but less common, included *Planktolyngbya* (0.6%), *Snowella* (0.3%), *Phormidium* (0.2%) and *Oscillatoria* (0.2%). The cyanobacteria community infrequently (<0.1%, Table III) consisted of *Pseudanabaena*, *Microcystis*, *Merismopedia*, *Cyanodictyon*, *Geitlerinema*, *Nostoc*, *Phormidium*, *Oscillatoria*, *Spirulina* and *Planktothrix*.

The community structure of cyanobacteria varied from upstream of the weir pool (AMTD 952 km) to the weir (AMTD 886 km) (Table III). The percentage of total biovolume for *Anabaena* decreased from 79.4% at AMTD 952 km to 64.6% at the weir. In contrast, the relative contribution for the other dominant genera increased from AMTD 952 km to the weir (AMTD 886 km), i.e. *Aphanizomenon* (19.6→28.9%), *Aphanocapsa* (0.5→1.6%) and *Planktolyngbya* (0.4→1.8%). The diversity of cyanobacteria taxa also increased from AMTD 952 km (8 genera) to AMTD 886 km (11 genera).

Depth-integrated cyanobacteria biovolumes ranged from 0.067 mm³L⁻¹ (AMTD 895 km, 18 February 2004) to 1.97 mm³L⁻¹ (AMTD 926 km, 6 January 2004) with all samples containing maximum biovolumes less than bloom levels (e.g. 2 mm³L⁻¹). Dominant taxa reached maximum concentrations of 1.85 mm³L⁻¹ for *Anabaena* (AMTD 926 km, 20 January 2004), 0.54 mm³L⁻¹ for *Aphanizomenon* (AMTD 906 km, 6 January 2004) and 0.028 mm³L⁻¹ for *Aphanocapsa* (AMTD 906 km, 2 March 2004).

Mean (averaged over all sampling trips for each site) cyanobacteria biovolumes increased from AMTD 952 km (0.61±0.058 mm³L⁻¹) to AMTD 926 km (0.79±0.090 mm³L⁻¹) before levelling off to AMTD 906 km then declining to the weir (0.34±0.032 mm³L⁻¹) (Figure 8). *Anabaena* biovolumes mirrored the trend of total biovolumes, increasing between AMTD 952 km (0.50±0.050 mm³L⁻¹) and AMTD 926 km (0.65±0.090 mm³L⁻¹) before levelling off to AMTD 906 km (0.62±0.046 mm³L⁻¹) and then declining to the weir (0.24±0.029 mm³L⁻¹). Similar trends were observed for both *Aphanizomenon* and *Aphanocapsa* which increased from upstream of the weir pool at AMTD 952 km (*Aphanizomenon*, 0.10±0.020 mm³L⁻¹; *Aphanocapsa*, 0.002±0.0005 mm³L⁻¹) to AMTD 906 km (*Aphanizomenon*, 0.16±0.030 mm³L⁻¹; *Aphanocapsa*, 0.006±0.001 mm³L⁻¹) then declined steadily to the weir (*Aphanizomenon*, 0.09±0.012 mm³L⁻¹; *Aphanocapsa*, 0.004±0.001 mm³L⁻¹). For the remaining taxa mean, depth-integrated biovolumes remained <0.01 mm³L⁻¹ at all sites.

When cyanobacteria biomass is viewed in areal terms (i.e. integrating over the water depth) for a typical discharge (5000 ML day⁻¹), water column biovolumes of the three dominant taxa, *Anabaena*, *Aphanizomenon* and *Aphanocapsa*, increase steadily where Z_{mix}:Z_{eu} <3 to peaks at AMTD 896–906 km (*Anabaena*, 3410 mm³m⁻²; *Aphanizomenon*, 924 mm³m⁻² and *Aphanocapsa*, 46 mm³m⁻²), before declining to the weir (as Z_{mix}:Z_{eu} remains >3) (Figure 9).

Table III. Mean contribution (by percentage biovolume) of cyanobacteria genera within (AMTD 886–936 km) and upstream (AMTD 952 km) of the Mildura weir pool between December 2003 and March 2004. Potentially toxic genera and species identified by *

Genus species	AMTD km							Mean
	886	895	906	916	926	936	952	
* <i>Anabaena</i>	64.6	72.5	75.1	75.2	76.7	74.7	79.4	74.0
* <i>A. circinalis</i>	54.5	54.5	51.3	47.3	41.4	44.2	48.4	48.8
* <i>A. flos-aquae</i>	1.9	2.6	4.7	3.4	3.6	3.7	3.7	3.4
* <i>A. spiroides f. spiroides</i>	1.3	2.9	2.1	0.5	4.1	1.0	1.8	2.0
* <i>A. torulosa</i>	0.4	1.4	0.1	0.1	0.3	0.3	0.2	0.4
<i>Aphanizomenon</i>	28.9	23.1	22.3	23.0	21.2	23.8	19.6	23.1
<i>Aphanocapsa</i>	1.6	1.6	1.3	0.8	1.0	0.6	0.5	1.0
<i>Cyanodictyon</i>				0.002				0.0004
<i>Geitlerinema</i>			0.05					0.01
<i>Merismopedia</i>			0.03	0.01		0.4	0.06	0.08
* <i>Microcystis</i>	0.1	0.2	0.1	0.00	0.4	0.0	0.0	0.1
* <i>M. aeruginosa</i>	0.7	0.0	0.2	0.2	0.1	0.0	0.0	0.2
* <i>M. aeruginosa f. flos-aqua</i>					0.3			0.05
<i>Nostoc</i>					0.1			0.01
<i>Oscillatoria</i>		1.3						0.2
<i>Phormidium</i>	2.5							0.3
* <i>Planktolyngbya</i>	1.8	0.7	0.5	0.4	0.3	0.4	0.4	0.6
* <i>Planktolyngbya subtilis</i>	1.8	0.7	0.5	0.4	0.3	0.4	0.4	0.6
<i>Planktothrix</i>					0.1			0.02
<i>Pseudanabaena</i>	0.2	0.1	0.1	0.2	0.1	0.01	0.02	0.1
<i>Snowella</i>	0.3	0.6	0.6	0.4	0.2	0.04	0.02	0.3
<i>Spirulina</i>	0.09							0.01
Total genera	11	8	9	8	9	8	8	15

Phytoplankton distribution

The mean water column chlorophyll fluorescence of the three dominant phytoplankton groups along the length of the weir pool measured on 5 February 2004 is shown in Figure 10. Green algae accounted for more than 50% of the measured fluorescence throughout the weir pool. Cyanobacteria were the second most prevalent functional group followed by diatoms.

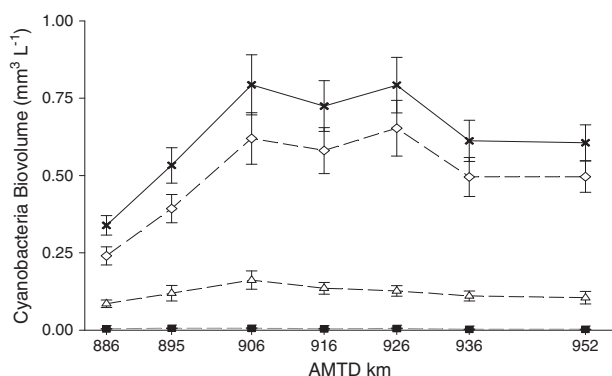


Figure 8. Mean biovolume for total cyanobacteria (crosses), *Anabaena* (diamonds), *Aphanizomenon* (triangles) and *Aphanocapsa* (squares) within (AMTD 886–936 km) and upstream (AMTD 952 km) of the Mildura weir pool between December 2003 and March 2004

The relative distribution of the three functional groups changed along the weir pool. Green algae were observed to decrease steadily along the weir pool, albeit by only a very small amount. Cyanobacteria increased steadily from the upstream end to AMTD 900 km but then decreased steadily to the weir. Diatom concentrations were unchanged from upstream to AMTD 920 km and then increased steadily to the weir—an unexpected observation that we discuss further in the next section.

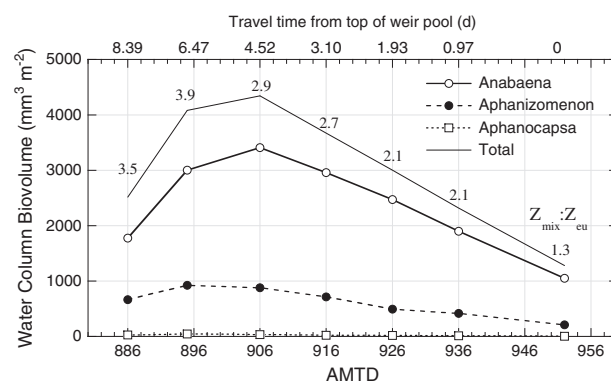


Figure 9. Average areal cyanobacteria biomass during December 2003–March 2004 for dominant species along Mildura weir pool. Top axis is travel time from upstream end of weir pool assuming discharge of 5000 ML day⁻¹. Numbers in italics denote $Z_{mix}:Z_{eu}$

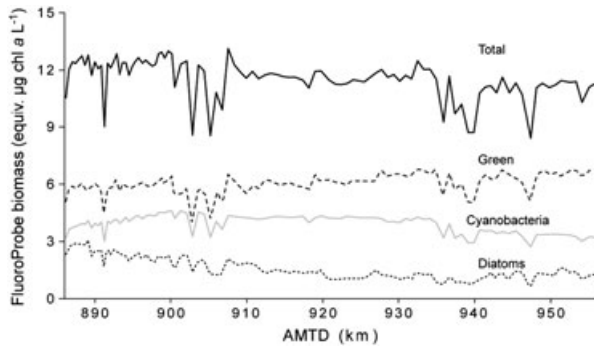


Figure 10. Longitudinal FluoroProbe profile of mean phytoplankton biomass along Mildura weir pool on the 4–5 February 2004. Phytoplankton groups are total (solid), greens (long dash), cyanobacteria (grey) and diatoms (short dash)

DISCUSSION

Thermal stratification

Barriers to flow in lowland rivers, such as Mildura weir, produce a transition from higher to lower flow velocities as the water column deepens from the upstream end of the backwater to the weir structure. Along the velocity gradient produced by Mildura weir, the physical and chemical environments progressively change, and these changes impact the ecological functioning of the River Murray. As flow velocity decreases, less turbulence is generated by friction along the channel bottom and the water column becomes less well mixed. This is accompanied by decreased resuspension of bottom sediment and facilitates the establishment of thermal stratification—both stronger and of longer duration—which increases sedimentary losses of particulate matter including diatoms. Increased sedimentation improves light transmission and the euphotic depth increases, which in turn increases the volume of habitat potentially suitable for primary production. Ultimately, the flow velocity may decrease sufficiently to allow persistent thermal stratification to develop and we would expect this to provide a competitive advantage to buoyant or motile phytoplankton, especially cyanobacteria that can maintain their position within the euphotic zone.

Dominance by buoyant, nitrogen-fixing cyanobacteria is expected in weir pools with $Z_{\text{mix}}:Z_{\text{eu}} < \text{c.a. } 3$, low concentrations of bioavailable dissolved inorganic nitrogen, and there is ample residence time (roughly 14 days) to allow the cyanobacteria population to grow and competing species to settle out of the water column (Sherman *et al.*, 1998). More nutrient replete water columns with similar thermal stability, i.e. $Z_{\text{mix}}:Z_{\text{eu}}$, may support different functional groups of phytoplankton such as dinoflagellates (Whittington *et al.*, 2000).

During our study in the Mildura weir pool, discharge was in the range typical of summer and autumn conditions. Flow

velocity dropped by more than half (from 0.4 to 0.15 ms^{-1}) along the upstream section of the weir pool (from AMTD 952 km to AMTD 926 km) before decreasing more gradually to 0.09 ms^{-1} along the remainder of the weir pool. Upstream of AMTD 936 km, flow velocity was $>0.2 \text{ms}^{-1}$ and the water column was always well mixed. This is consistent with the observations of Bormans and Webster (1999) who suggested that a critical flow velocity of 0.2 ms^{-1} was sufficient to maintain well-mixed conditions in a number of weir pools along the River Murray. Between AMTD 906 and 926 km, stratification developed diurnally but complete mixing of the water column occurred each night. Only at the most downstream three sites (AMTD 886, 895 and 906 km) was persistent stratification ever observed and this occurred only during a few days in February 2004 (Figure 5) when discharge over the weir was approximately 4600 ML day^{-1} and the weather was particularly hot with air temperatures in excess of 36°C. The reach between AMTD 895 and 906 km only failed to mix completely on one night (14–15 February 2004) during the entire study period.

We can predict a location along the weir pool downstream, of which we expect thermal stratification to persist for more than 24 h (i.e. the water column does not mix completely) following Bormans and Webster (1997). They proposed a river mixing parameter, R , that compares the rate of change of TKE introduced by bottom stress to the rate of change of PE added to the water column by the surface heat and radiation fluxes. Following Bormans and Webster (1997) we have

$$R = \frac{e \frac{\partial}{\partial t} \text{TKE}}{\frac{\partial}{\partial t} \text{PE}} \quad (1)$$

$$\frac{\partial}{\partial t} \text{PE} = \frac{\alpha g H}{2 C_p} \left(Q_{\text{net}} - \frac{2 Q_{\text{sw}}}{h H} \right) \quad (2)$$

$$\frac{\partial}{\partial t} \text{TKE} = C_d r U^3 \quad (3)$$

where Q_{net} is the net water surface heat flux (W m^{-2}), Q_{sw} is the net shortwave radiation (W m^{-2}), H is the depth of the water column (m), U is the mean flow velocity (ms^{-1}), η is the attenuation coefficient (m^{-1}), ρ is the density of the water (997.3kg m^{-3}), α is the coefficient of thermal expansion ($0.00025 \text{ } ^\circ\text{C}^{-1}$), C_p is the heat capacity of water ($4180 \text{ J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$), C_d is the drag coefficient for bottom friction (assumed to be 0.0025) and ε is the mixing efficiency of the TKE (0.004). For $R > 1$, the water column is expected to be completely mixed. For $R < 1$, the development of

thermal stratification is possible. The parameter R is not applicable at night when the net heat flux is negative and the surface layer deepens due to penetrative convection. Under typical conditions at the weir pool (mean daily wind speed 1.3 ms^{-1} , range $1\text{--}2 \text{ ms}^{-1}$, data not shown), it is not necessary to incorporate a wind speed term in Equation (3) because the contribution of wind stirring to water column mixing is negligible compared to the contributions from bottom friction and penetrative convection.

We computed R on an hourly basis between 0800 and 1800 h using the mean values of Q_{net} and Q_{sw} measured during January–February 2005, assuming a water temperature of 24°C and using linearly interpolated values of attenuation and water depth between the seven measurement sites. The predicted location of the transition to continuously well-mixed water column ($R=1$) is shown in Figure 11 for the typical summer range of discharge ($4000\text{--}10000 \text{ ML day}^{-1}$) through the weir pool. As discharge through the weir pool, Q , decreases, the mean water column flow velocity decreases as does the supply of TKE available to mix the water column and the transition between always-mixed and potentially stratified conditions moves upstream as expected. As solar heating intensifies during the middle of the day, the transition location moves farther upstream as the supply of PE (Equation (2)) increases relative to the available TKE. After solar noon (roughly 1300 h in Figure 11), the supply of PE steadily diminishes as the water column begins to cool at the surface and the transition moves downstream again.

Downstream of AMTD 909 km, the flow velocity is never sufficient to guarantee continuous mixing even at a flow of $10000 \text{ ML day}^{-1}$. Under low flow conditions ($\sim 4500 \text{ ML day}^{-1}$), this location moves upstream to roughly AMTD 925 km. This result is consistent with the diurnal stratification observed along the weir pool during February 2004 (Figure 5, mean discharge $\sim 5000 \text{ ML day}^{-1}$)—all sites from

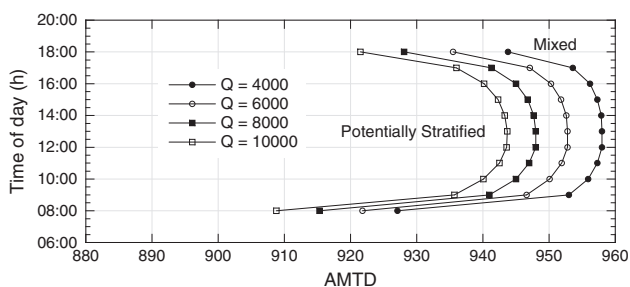


Figure 11. Hourly location of the predicted transition from a potentially stratified to continuously mixed water column in Mildura weir pool for the typical range of summer discharges, Q . If the intersection of AMTD and time is to the left of the curve for a specific discharge, there is the potential for the water column to thermally stratify when exposed to the mean meteorological conditions measured at the weir pool during January–February 2005

AMTD 886 to 926 km stratified diurnally and sites AMTD 936 and 952 km were continuously mixed.

In accordance with both observations and predictions of stratification potential, both turbidity and TP decline progressively along the diurnally stratified section of the weir pool (AMTD 886–926 km), indicating a loss of particulate matter from the water column. This behaviour is qualitatively similar to that observed by Sherman *et al.* (1998) in Maude weir on the Murrumbidgee River—which joins the River Murray 185 km upstream of Mildura weir pool—in which the suspended sediment load consists $>80\%$ of particles $<1 \mu\text{m}$ in diameter and which contain 3.5 times as much phosphorus (per unit mass) as particles $>2 \mu\text{m}$ (Olley *et al.*, 1995). We can calculate the effective settling velocity, w , of the lost particulate phosphorus, $\text{PP} = \text{TP} - \text{FRP}$, as $w = (\Delta\text{PP} H) / (\text{PP}_0 \Delta t)$, where ΔPP is the observed decrease in PP concentration from its initial value at the upstream end of the weir pool, PP_0 , through a water column of mean depth H over a time interval Δt (Sherman *et al.*, 1998). Assuming $H = 5 \text{ m}$ and using the mean travel time of 6.5 days, we estimate a particle settling velocity of 0.075 m day^{-1} . This is greater than the value of 0.062 m day^{-1} observed by Sherman *et al.* (1998) in Maude weir pool and suggests that the particle-bound phosphorus has a somewhat larger particle size in Mildura weir pool. The rate of decrease in turbidity increases with the strength and duration of thermal stratification and the increasing local residence time such that the most rapid increase in euphotic depth occurs closest to the weir.

The role of light

Of greater relevance to the composition of the phytoplankton population is the overall availability of light in the mixed layer as reflected in the ratio $Z_{\text{mix}}:Z_{\text{eu}}$, which governs the mean light intensity experienced by a phytoplankton cell as it moves through the mixed layer. The value of $Z_{\text{mix}}:Z_{\text{eu}}$ increased from 1.28 at the upstream end of the weir pool to 3.5 at the weir (Table II) because persistent thermal stratification, which would have reduced Z_{mix} , was seldom able to become established. Instead, Z_{mix} was simply the depth of the water column for the vast majority of the time and it increased more rapidly than Z_{eu} so that $Z_{\text{mix}}:Z_{\text{eu}}$ continued to increase along the weir pool producing an environment less favourable to buoyant cyanobacteria than to other taxa. In impoundments on rivers such as the Fitzroy River (Queensland), changes in the light climate strongly regulate phytoplankton community composition over summer (Bormans *et al.*, 2005).

It has been shown for the Darling and Murrumbidgee rivers—major tributaries to the River Murray—that *Anabaena* and *Aulacoseira* are the most common species of phytoplankton and that *Anabaena* usually dominates the

population when $Z_{\text{mix}}:Z_{\text{eu}}$ is close to 1 and *Aulacoseira* dominates when $Z_{\text{mix}}:Z_{\text{eu}}$ is about 3 or greater because of their differing light requirements (Sherman *et al.*, 1998). Although we have only collected data on cyanobacteria abundance for Mildura weir pool, it is known that *Aulacoseira* is the dominant phytoplankton species in this part of the River Murray (Bormans and Webster, 1999), and we should expect similar phytoplankton population dynamics to apply. The observed changes in $Z_{\text{mix}}:Z_{\text{eu}}$ and areal *Anabaena* biomass along the weir pool (Figure 9) are consistent with the $Z_{\text{mix}}:Z_{\text{eu}} > 3$ threshold. The progressive decline in cyanobacteria fluorescence and increase in diatom fluorescence shown in Figure 10 provide further support. However, we must still explain the increase in diatom concentration over the lower half of the weir pool as the mean light intensities upstream of AMTD 920 km are not expected to inhibit the growth of *Aulacoseira*.

The role of residence time

Another important difference between our observations and those of Sherman *et al.* (1998) relates to residence times experienced by phytoplankton in weir pools, and hence their opportunity to grow. Because Mildura weir pool mixes diurnally, the residence time of phytoplankton in the euphotic zone will be close to the conventional hydraulic residence time (=volume/discharge) which ranges from 3 to 7 days. Furthermore, Mildura weir is an overflow weir—all water is released from the surface layer—so that during diurnal stratification the residence time in the euphotic zone may be somewhat less. In contrast, Maude weir, on the lower Murrumbidgee River, released water at much lower rates and from below the surface layer. The bottom releases at Maude weir allowed for much longer surface layer residence times of ca. 80 days, and Sherman *et al.* (1998) suggested a residence time of 14 days was required for the development of nuisance *Anabaena* blooms.

The role of nutrients

The longitudinal distributions of NO_x and FRP appear unrelated to the changes in the flow velocity and patterns of thermal stratification within the weir pool. Throughout the weir pool, the molar $\text{NO}_x\text{-N}:\text{FRP-P}$ ratio is within a few percent of 0.45 whereas the molar $\text{TN}:\text{TP}$ ratio increases from 4.4 upstream to 5 at the weir. Both ratios suggest severe nitrogen limitation of the phytoplankton population. The concurrent increases in bioavailable nutrients and conductivity between AMTD 916 km and AMTD 906 km strongly suggest an inflow of nutrient-enriched saline groundwater from the raised groundwater mound of the nearby Red Cliffs Irrigation District (McCarthy *et al.*, 2004a; Mackay *et al.*, 1988). Leaching of inorganic fertilizers (nitrate and phosphate) to the groundwater has been

identified as a 'significant potential contributor' of nutrients to the River Murray within this region (SMEC, 2001).

The inferred groundwater-supplied increase in bioavailable nutrients may have significant implications for phytoplankton, by supporting larger populations and altering nitrogen to phosphorus ratios. The very low concentrations of inorganic nitrogen may constrain the growth of low-light tolerant species such as *Aulacoseira* which might otherwise be able to compete more successfully with the nitrogen-fixing *Anabaena*. Given that sediment nutrient release in the weir pool is uncommon (Murray-Darling Freshwater Research Centre, unpublished data), controlling inflows of nutrient-enriched groundwater through better farm practices or interception schemes may impact phytoplankton populations within the Mildura weir pool. Groundwater interception schemes have limited the inflow of groundwater within other sections of the weir pool (cf. near AMTD 936 km) (McCarthy *et al.*, 2004a) and may be useful in this section.

The increase in diatom abundance as the weir is approached may appear somewhat surprising given that slower flows and stronger thermal stratification could be expected to facilitate their loss by sedimentation. Apparently, the diurnal mixing is sufficient to keep enough of the population suspended to facilitate their growth. The time-dependent concentration, $C(t)$, of particles with initial concentration C_0 and sinking velocity, w , as they sediment out of a quiescent water column of depth, H , is simply $C(t) = C_0[1 - (w/H)t]$; for an actively mixing water column, the concentration decreases exponentially, $C(t) = C_0 e^{-(wH/t)}$ (Bormans *et al.*, 2005). Assuming a sinking velocity of 0.95 m day^{-1} (Sherman *et al.*, 1998), it would take 6.6 days for the 90% of the diatom population to sink out of a quiescent, persistently stratified water column. This time increases to approximately 17 days in a continuously mixing water column. Expressed as a specific loss rate, the sedimentation of diatoms would be in the range from 0.15 day^{-1} (mixed) to 0.35 day^{-1} (stratified) in the 5–7 m deep section of the weir pool. The increase in diatom biomass (Figure 9) between AMTD 886 and 916 suggests a net specific growth rate of 0.14 day^{-1} which, after allowance for the sinking losses, gives a specific growth rate of $0.29\text{--}0.59 \text{ day}^{-1}$. This is within the range of field and laboratory observations reported in Bormans and Webster (1999) for *Aulacoseira granulata*, the dominant taxa in rivers of the MDB.

The changes in cyanobacteria biomass and composition (Figure 9) along the weir pool certainly reflect the influences of residence time and light availability. Despite a continuing increase in NO_x and FRP from AMTD 916 to AMTD 886, the cyanobacteria population has declined consistent with the decreasing mean light intensity in the water column. It is also possible that the introduction of bioavailable nutrients downstream of AMTD 916 km has contributed to the

increase in diatom biomass. Between site AMTD 916 km and the weir, our nutrient measurements showed small increases in the concentrations of FRP (from 7 to 10 $\mu\text{g-PL}^{-1}$) and NO_x (from 7 to 10 $\mu\text{g-NL}^{-1}$) coincident with an increase in electrical conductivity implying that relatively nutrient-enriched groundwater was entering the weir pool between AMTD 906 and 916 km. Furthermore, the riparian groundwater upstream of Mildura weir (~AMTD 976 km) is known to be enriched in nitrate and silica relative to the river (Lamontagne *et al.*, 2002, 2006), and it is not unreasonable to assume that similar conditions apply closer to Mildura weir given the similar hydrogeology and land use practices along the river. Our hypothesis is also consistent with data (not shown) collected by the Murray-Darling Basin Authority that show an increase since the year 2000 in silica concentration between AMTD 1120 km and Mildura weir.

Implications for cyanobacteria

The environmental gradients imposed by the Mildura weir might be expected to increasingly favour cyanobacteria growth downstream along the Mildura weir pool by increasing thermal stratification potential, light availability and residence time. However, at moderate (4000–5500 ML day^{-1}) or larger discharges, the entire weir pool mixes on at least a diurnal and often a continuous basis, and $Z_{\text{mix}}:Z_{\text{eu}}$ is less suitable for cyanobacteria growth close to the weir. Under this flow regime, the range of conditions more suitable for cyanobacteria (namely $Z_{\text{mix}}:Z_{\text{eu}} < 2$ and diurnal stratification) is located mid-weir pool, as predicted by Kimmel *et al.* (1990). The light limitation of cyanobacteria, not nutrient limitation predicted by Kimmel *et al.* (1990), closer to the weir outweighs the advantages of stronger diurnal thermal stratification and increased bioavailable nutrients.

It is not until discharges over the Mildura weir decline sufficiently for persistent thermal stratification to develop over extended periods that we expect a shift favouring cyanobacteria to the most downstream 20 km of the weir pool (AMTD 886–906 km) from mid-weir pool. The two-layer system created during these periods of persistent thermal stratification will greatly reduce turbulent mixing, thereby decreasing turbidity, deepening the euphotic depth and decreasing the surface mixed-layer depth. This will result in $Z_{\text{mix}}:Z_{\text{eu}} \approx 1$, which favours buoyant cyanobacteria capable of maintaining their position within the surface layer (Humphries and Lyne, 1988; Sherman *et al.*, 1994). Should discharge be less than ca. 3000 ML day^{-1} for extended periods (>14 days), cyanobacteria blooms are expected to develop over the lower 20 km of the weir pool (Sherman *et al.*, 1998), particularly given the increase in bioavailable nutrients downstream of the saline groundwater inflows.

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