REGULATED RIVERS: RESEARCH & MANAGEMENT
Regul. Rivers: Res. Mgmt. **16**: 327–344 (2000)

ADVECTION, GROWTH AND NUTRIENT STATUS OF PHYTOPLANKTON POPULATIONS IN THE LOWER RIVER MURRAY, SOUTH AUSTRALIA

PETER D. BAKER[a,*], JUSTIN D. BROOKES[a,b], MICHAEL D. BURCH[a], HOLGER R. MAIER[c] AND GEORGE G. GANF[b]

[a] *Cooperative Research Centre for Water Quality and Treatment, Private Mail Bag 3, Salisbury, South Australia 5108, Australia*
[b] *Department of Environmental Biology, The University of Adelaide, Adelaide, South Australia 5005, Australia*
[c] *Department of Civil and Environmental Engineering, The University of Adelaide, Adelaide, South Australia 5005, Australia*

ABSTRACT

To investigate the link between river flow, nutrient availability and development of algal blooms, growth rates of the major phytoplankton species were examined *in situ* in the lower River Murray, South Australia over the 1994/1995 summer. Eight sites were selected over a 54 km reach between Lock 1 and Nildottie and growth rates estimated by monitoring mean cell density in time-aligned 'parcels' of water as they travelled downstream. Discharge at Lock 1 during the period of study (3000–5000 ML day^{-1}) typified summer entitlement flows to South Australia. A large, shallow floodplain lake (lagoon), with an hydraulic connection to the river, supported a large population of cyanobacteria in summer, but inputs to the main channel did not substantially affect the abundance and composition of river phytoplankton. Mean net growth rates of *Anabaena circinalis* and *A. flos-aquae* f. *flos-aquae* were 0.132 and 0.176 day^{-1}, respectively, although individual rates varied from positive to negative. In contrast, the mean growth rate of the filamentous diatom *Aulacoseira granulata* was -0.15 day^{-1}, reflecting a decrease in population size with advection downstream. Mean cell densities of the three species did not exceed 5000 cells mL^{-1} throughout the study. Growth bioassays conducted in the laboratory indicated that nitrogen was often the nutrient limiting algal growth, although it was not established whether nitrogen was limiting *in situ*. A conceptual model is presented, linking these findings with those of other work on the lower River Murray, to summarize the physical and chemical environmental factors governing the abundance of cyanobacteria in this reach of the river. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: cyanobacteria; phytoplankton; *Anabaena*; *Aulacoseira*; riverine ecology; growth rate; nutrients; River Murray

INTRODUCTION

Cyanobacteria, particularly species of *Anabaena*, are a common component of summer phytoplankton in semi-arid lowland rivers of the Murray–Darling Basin, in south-eastern Australia (Baker *et al.*, 1993). Under certain environmental conditions, rapid growth of cyanobacteria may occur, resulting in the development of extensive blooms. The most significant occurrence in the Murray–Darling Basin was a bloom of *Anabaena circinalis* that stretched over 1000 km of the Darling–Barwon River in 1991 (Bowling and Baker, 1996). The occurrence of blooms of *A. circinalis* in rivers is of concern to water managers and consumers, because the production of saxitoxin group toxins and taste and odour metabolites can compromise the quality of water used for public water supply, agriculture and recreation.

The River Murray rises in the Snowy Mountains in the eastern highlands and flows in a general westerly direction for 2560 km, entering the ocean via Lake Alexandrina in South Australia. It receives water from numerous tributaries within the Murray–Darling Basin, including the highly turbid Darling River, which accounts for nearly 10% of the long term average discharge of the system (Walker and Thoms, 1993). The lower River Murray, below the Darling River confluence (Figure 1), meanders for 830 km through a semi-arid lowland region and has a gradient of less than 50 mm km^{-1}. Flow is highly

* Correspondence to: Cooperative Research Centre for Water Quality and Treatment, Private Mail Bag 3, Salisbury, 5108, Australia.

Received 3 June 1999
Accepted 15 September 1999

Copyright © 2000 John Wiley & Sons, Ltd.

regulated by a series of ten low level weirs, which stabilize water levels for irrigation, navigation and domestic water supply to the city of Adelaide and several country centres.

Under the Murray–Darling Basin Agreement, South Australia receives a minimum annual water allocation of 1850 GL (entitlement flow) to satisfy community demands, which is about 42% less than natural flow conditions (Jacobs, 1989). The combination of gentle gradient, low summer flows and highly regulated river management has resulted in the river resembling a string of inter-connected lakes (Walker

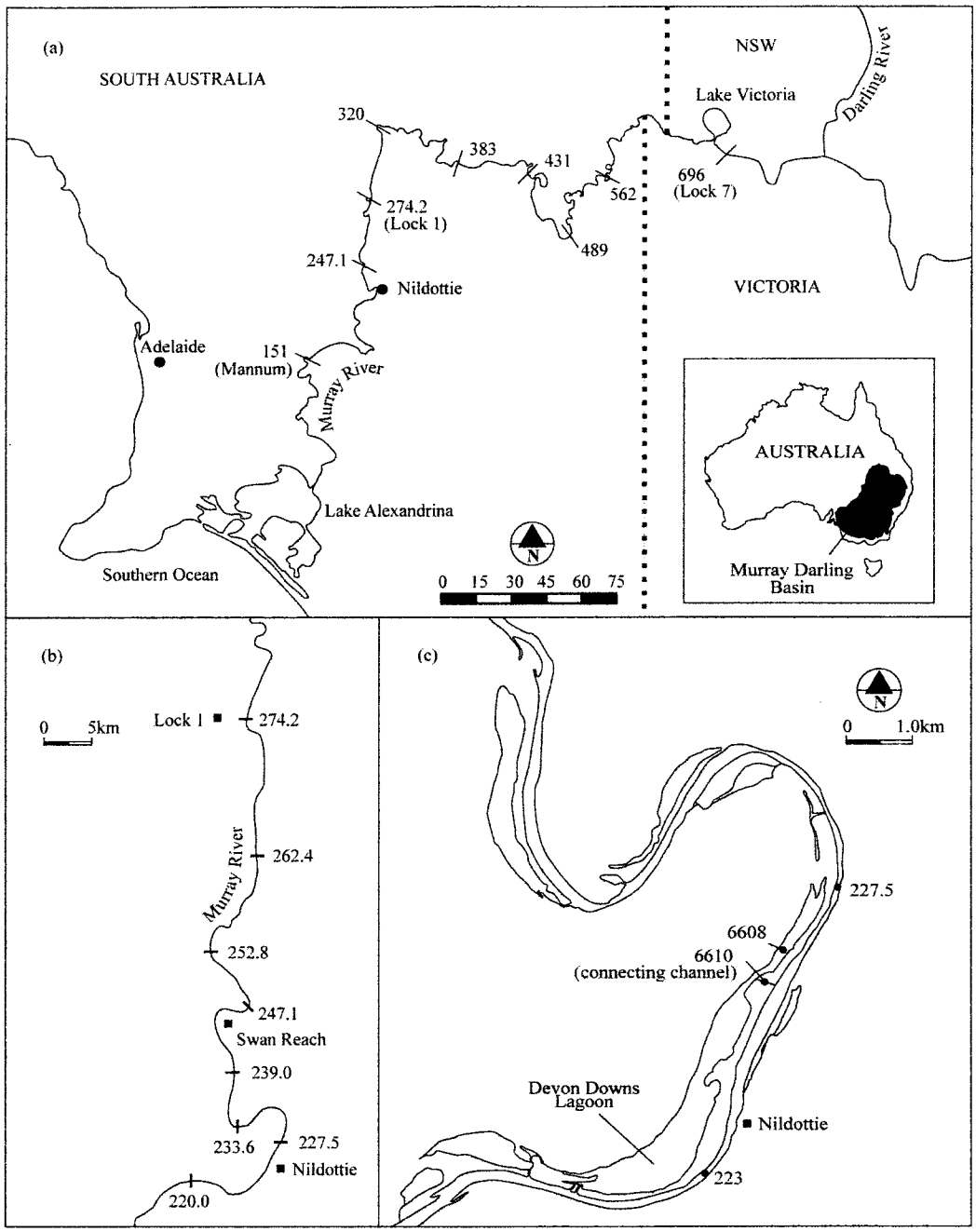

Figure 1. The lower River Murray, indicating sampling sites (a) from Lock 7 (AMTD 696 km) to Mannum (AMTD 151 km); (b) from Lock 1 (AMTD 274.2 km) to Nildottie (AMTD 220.0 km); and (c) Devon Downs Lagoon, Nildottie

Copyright © 2000 John Wiley & Sons, Ltd.

and Thoms, 1993). Historically, these conditions have often led to elevated numbers of *Anabaena* spp. in the lower River Murray (Burch *et al*., 1994) and flow has been identified as a major variable that determines the onset and duration of *Anabaena* growth (Maier *et al*., 1998).

A similar relationship between flow and cyanobacterial growth has been demonstrated at Maude Weir, on the Murrumbidgee River in New South Wales. In the weir pool at Maude, low discharge (< 500 ML day^{-1}) and selective withdrawal at the bottom by underflow weirs extended the retention time of water in the stratified surface layer (Sherman *et al*., 1998). Bloom formation of the filamentous cyanobacterium *A. circinalis* resulted when these conditions persisted for more than 2 weeks.

In contrast to the Maude weir pool, the reach of the River Murray near Nildottie, South Australia is generally not conducive to the development of sustained cyanobacterial blooms. This is because the combination of river discharge and high winds generally prevents the formation of persistent thermal stratification (Bormans *et al*., 1997). In addition, the weir pools of the lower River Murray are influenced by overflow weirs and retention times may differ from those in the Murrumbidgee River. Buoyant cyanobacteria are unlikely to be retained for extended periods in the surface layers of overflow weir pools and the time available for growth of the resident phytoplankton community would be less.

The aim of this study was to estimate growth rates *in situ* of the major phytoplankton species in the main channel of the lower River Murray, downstream of Lock 1, by monitoring changes in cell density of populations as they migrate downstream. This technique is considered to provide a more realistic estimate of growth rates for phytoplankton populations in the lower River Murray than would be determined by continuous sampling at the same weir pool site. Features of the physical and chemical environment which may promote cyanobacterial growth were also examined.

The concept of tracking a water 'parcel' downstream to estimate growth and loss rates of phytoplankton has previously been attempted in large rivers, with considerable success; in the River Lot, France (Capblancq and Decamps, 1978), in the lower River Wye, UK (Jones, 1984), in the River Bure, UK (Moss *et al*., 1989) and in the River Rhine, Germany (de Ruyter van Steveninck *et al*., 1992). In order to estimate growth of phytoplankton in a flowing body of water, it is necessary to make certain assumptions regarding the movement of suspended particles in relation to the rate of stream flow, the uniformity of flow and the dispersion of particles within the transporting medium. There is however, evidence that zones of hydraulic retention may delay the downstream movement of phytoplankton and support additional growth (Reynolds *et al*., 1991; Reynolds and Glaister, 1993; Reynolds, 1994).

In addition to in-channel growth of phytoplankton, inputs of phytoplankton may enter the river from tributaries and/or adjacent wetlands connected to the main channel. A feature of the lower River Murray, is the extensive floodplain which ranges in width from 2 to 10 km and hosts a network of permanent and temporary wetlands. The wetlands adjacent to the study area in the Gorge Section of the river are typically elongated 'channel margin swales' (or lagoons), connected to the river by a single channel except during overbank flows (Walker and Thoms, 1993). Certain lagoons adjacent to the main river channel harbour significant populations of cyanobacteria in summer (Baker, 1999) and may be a source of recruitment for river populations via a permanent hydraulic connection (Burch *et al*., 1994). A further aim of our study was to examine the relative contribution of seasonal cyanobacterial populations in floodplain wetlands of the lower River Murray to that in the main river channel.

METHODS

Phytoplankton advection 'model' for the lower River Murray

Estimation of phytoplankton growth rates in the main channel of the River Murray was based upon the assumption that the downstream movement of suspended particles is governed by the rate of flow of the bulk medium. A further assumption was that the predominant source of recruitment of cells along the river was from upstream. The first assumption was examined by 'tracking' an identifiable population of *A. circinalis* as it migrated downstream from Lock 7 to Mannum (544 km by river) between October 1994

Copyright © 2000 John Wiley & Sons, Ltd.

and January 1995. The dates of initial detection of *A. circinalis* at nine sites sampled weekly, were compared with the dates predicted by the rate of river flow. The location of these sites are shown in Figure 1a and are identified by their distance in river kilometres from the mouth of the River Murray in South Australia, hereafter termed the average mean thread distances (AMTD), in keeping with terminology used in the River Murray Hydraulic Model (RMHM) (Water Studies, 1992). The detection limit for the analysis was one cell per 50 mL of sample, based on a microscopic examination of pre-concentrated sample ($10\times$) in five separate counting chambers of 1 mL nominal volume.

Phytoplankton sampling

Phytoplankton populations were monitored at eight sites weekly or twice weekly, during the 1994/1995 summer along a 54 km reach of the lower River Murray between Lock 1 (AMTD 274.2 km) and Nildottie (AMTD 220.0 km), South Australia. The study sites were selected to ensure a 'parcel' of water departing from Lock 1 could be sampled on more than one occasion before reaching Nildottie, given a sampling interval of 3–4 days. The eight sites (Figure 1b) coincided with cross-sections surveyed for the RMHM and are identified by their AMTD.

Three independent water column samples (0–3 m depth) were collected midstream approximately 10–20 m apart at each site with a rigid plastic hosepipe (internal diameter 40 mm). One litre samples were returned to the laboratory and a 100 mL subsample from each was preserved in Lugols iodine solution (1 mL), concentrated by sedimentation and examined microscopically in Sedgwick Rafter counting chambers for species identification and enumeration. A minimum count of 100 trichomes gave an expected error of $\pm 20\%$ for the 95% confidence limit (Lund *et al.*, 1958).

Calculation of mean travel times

The RMHM was used to calculate the flow, river level, cross-sectional area and mean stream velocity daily at each sampling site during the study period. 'Parcels' of water were tracked by estimating the mean transport time of water, calculated from the mean stream velocities at each site and the distance between sites in accordance with the following equation:

$$T_{C1\rightarrow C2} = 1/2(V_{C1} + V_{C2})/(S_{C1\rightarrow C2}) \quad (1)$$

where $T_{C1\rightarrow C2}$ is the travel time (days) between cross-section 1 (C1) and cross-section 2 (C2); V_{C1} and V_{C2} are the mean stream velocities (km day^{-1}) at cross sections 1 and 2, respectively; and $S_{C1\rightarrow C2}$ is the distance (km) between cross-sections 1 and 2.

Calculation of phytoplankton growth rates

Phytoplankton growth rates were calculated from mean cell densities of selected species in time-aligned 'parcels' of water as they travelled downstream between Lock 1 and Nildottie. The position of a 'parcel' of water, identified by its initial sampling date at Lock 1 (AMTD 274.2 km), was determined at subsequent sampling dates by calculation of mean travel times. In some instances, the predicted location of a particular 'parcel' of water did not exactly coincide with the sampling locations. In these cases the sampling site closest to the predicted location was used. The sampling program allowed the same 'parcel' of water to be sampled up to four times over the estimated 7–10 days travel time between Lock 1 and Nildottie. Net exponential growth rates *in situ* were calculated from the differences in cell counts between time aligned pairs of downstream and upstream samples collected on successive sampling occasions.

Contribution of cyanobacteria from a floodplain wetland

Devon Downs Lagoon, a large permanent wetland near Nildottie (Figure 1c), was chosen as a suitable site to monitor advection and recruitment of cyanobacteria from a source other than the river upstream. This lagoon has a history of cyanobacterial blooms and was the site of complementary studies examining the influence of wind and water levels on the exchange of lagoon and river water (Webster *et al.*, 1997a)

Copyright © 2000 John Wiley & Sons, Ltd.

and aspects of the life history and ecology of *A. circinalis* (Baker, 1999). The lagoon has a surface area of 2.7 km^2, a volume of 1.3×10^3 ML and an average depth of 0.5 m during normal summer flows of about 3000–5000 ML day^{-1} at Lock 1 (~ 0.05–0.08 m s^{-1}). It is connected to the river by a narrow man-made channel toward the northern end, approximately 400 m long, 7 m wide and 1–2 m deep. Other inlet/outlets to the river at the southern end of the lagoon are not connected during normal summer flows.

The cross-sectional profile of the northern inlet/outlet channel was surveyed at a site approximately 10 m upstream of its confluence with the river. Water velocity, depth and temperature were logged at 16 min intervals using an ultrasonic doppler velocity meter (Starflow Model 6525B) positioned at the bottom of the channel. This data was used to monitor directional flow into and out of Devon Downs Lagoon from 19 December 1995 to 20 March 1996.

Hosepipe samples (0–3m) were collected twice weekly for phytoplankton analysis at the midpoint of the lagoon channel (Site 6610) and in the river immediately upstream (AMTD 227.5 km) and downstream (AMTD 223.0 km) of the lagoon channel (Figure 1c). A surface sample was also collected from Site 6608 in the lagoon. Daily flows in the river at Nildottie were calculated from discharge at Lock 1 and the RMHM, using river cross-sectional profiles at AMTD 227.5 km. The downstream site was positioned to allow a sufficient distance (3 km) for dispersion and mixing of lagoon and river phytoplankton, but the travel time between the upstream and downstream sites was considered sufficiently short to minimize the effect of in-channel growth.

Cell densities at the downstream site in the river (AMTD 223 km) were predicted from the contribution of flow from the lagoon to the river and the cell densities of cyanobacteria in the Devon Downs outlet channel and in the river at the upstream site (AMTD 227.5 km) on the same day. Student's *t* test was used to statistically examine differences in cell densities in the river upstream and downstream of the lagoon outlet.

Nutrient availability for growth

Nutrient concentrations were determined in samples collected at each of the eight river sites between Lock 1 and Nildottie on 6 February 1995. Three independent samples were collected at each site with a 3 m hosepipe and transported on ice to the laboratory on the day of collection. Concentrations of total phosphorus, filterable reactive phosphorus (0.45 μm), oxidized nitrogen (nitrate + nitrite), ammonia nitrogen and total Kjeldahl nitrogen (TKN) were determined by standard laboratory methods (Anon., 1995).

Additional sampling for nutrient analysis was undertaken on 6–7 March 1996 at five river sites and one wetland site (Devon Downs Lagoon) along a 204 km reach of the lower River Murray between AMTD 431 and 227.5 km. Growth bioassays were also undertaken to determine whether nutrients were limiting phytoplankton growth and to assess the availability of nutrients for growth.

Bioassays were conducted by enrichment of replicate hosepipe samples ($n = 3$) of river water from each site with either 100 μM $NaNO_3$ (+N), 100 μM K_2HPO_4 (+P) or 100 μM $NaNO_3$ and K_2HPO_4 (+N and +P). The control flasks had no nutrients added. Flasks were incubated at 25°C, at an irradiance of 120 μmol m^{-2} s^{-1} on a 12:12 h light:dark cycle. Phytoplankton biomass, estimated from DCMU-sensitive chlorophyll fluorescence, was measured on day 0 (initial) and day 5 using a fluorometer (Turner Model 111) following addition of 10 μM DCMU (Wood and Oliver, 1995). Single factor ANOVA and Dunnet's *post hoc* test were performed to determine whether biomass had increased following incubation, relative to the day 0 treatment and the control.

RESULTS

Phytoplankton advection 'model' for the lower River Murray

An *A. circinalis* population, initially detected in the River Murray on 14 October 1994 at the furthest site upstream (Lock 7, AMTD 696 km), was monitored as it migrated down river to Mannum (AMTD

Copyright © 2000 John Wiley & Sons, Ltd.

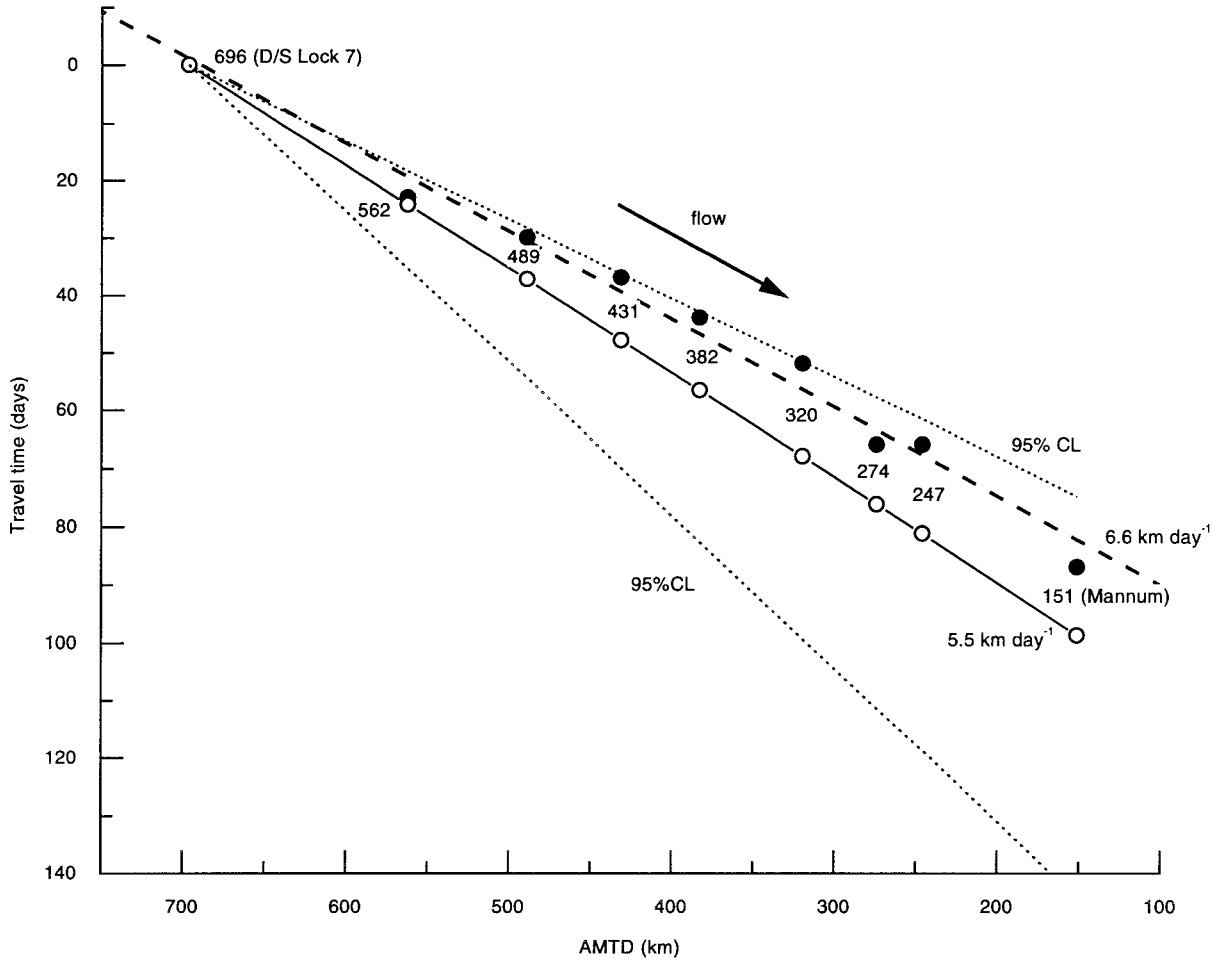

Figure 2. Phytoplankton advection model for the River Murray. Detection of a population of *A. circinalis* at successive sampling sites between Lock 7 and Mannum (black circles) and the calculated rate of advection of 6.6 km day^{-1} (dashed line, $r = 0.99$, $p < 0.0001$), that falls within the standard error and derived 95% confidence limits (dotted lines) of the mean bulk flow of 5.5 km day^{-1} ($n = 21$, open circles) along the same reach and over the same time period

151 km). The sequential pattern of detection of *A. circinalis* at successive river sites was consistent with the advection downstream of a population 'front' (Figure 2). The distances (km) from Lock 7 to each site, and the time taken (days) before *A. circinalis* was detected at each site, were linearly correlated ($r = 0.99$, $p < 0.0001$). The slope of the regression was 6.6, indicating an advection velocity of 6.6 km day^{-1} or 0.075 m s^{-1}.

The mean stream velocity (and standard error) along this section of river was also calculated from cross-sectional areas at 21 sites and from the initial discharge at Lock 7 on 14 October, 1994 of 5123 ML day^{-1}, using the RMHM. The rate of *A. circinalis* migration downstream was found to be within the 95% confidence interval of the mean stream velocity (Figure 2). This supports our assumption that phytoplankton move laterally at the same rate as the suspending water medium. We therefore concluded that phytoplankton populations could be tracked as they moved downstream and relative community changes could be examined.

Copyright © 2000 John Wiley & Sons, Ltd.

Phytoplankton advection and growth

Stream velocities at each of the eight sites between Lock 1 and Nildottie, averaged over the sampling period ranged from 0.040 to 0.108 m s^{-1} (Figure 3). These values and the distance between sites were then used to estimate travel times and the position of 'parcels' of water along the river.

Phytoplankton species present at each of the eight sites included the filamentous cyanobacteria *A. circinalis* Rabenhorst, *A. flos-aquae* f. *flos-aquae* (Lyngb.) Komàrek, *A. spiroides* f. *spiroides* (Elenk.) Komàrek, *A. spiroides* var. *tumida* Nygaard, *A. aphanizomenoides* Forti, *A. planctonica* Brunnthaler, *Aphanizomenon issatschenkoi* (Usacev) Proškina-Lavrenko, *Anabaenopsis elenkinii* Miller, *Cylindrospermopsis raciborskii* (Wolosz.) Seenaya & Subba Raju, *Planktothrix perornata* var. *attenuata* (Skuja) Anagnostidis & Komàrek, *Pseudanabaena* sp., the filamentous centric diatom *Aulacoseira granulata* (Ehr.) Simonson and the filamentous green algae *Planctonema lauterbornii* Schmidle and *Chlorhormidium* sp. Three of these species were investigated in detail; two cyanobacteria (*A. circinalis* and *A. flos-aquae* f. *flos-aquae*) and the diatom *A. granulata*. Population changes and growth of these species were examined in 17 separate phytoplankton communities by tracking 'parcels' of water leaving Lock 1 and repeatedly sampling the 'parcel' of water as it flowed downstream (Figure 4).

Net growth rates were determined from pairs of counts of each species in successive samples from each of the 17 phytoplankton communities. As some communities were sampled more than twice, this amounted to the calculation of 28 separate growth rates for each species. Of the 28 measurements, 20 were positive and eight negative for *A. circinalis*, 22 were positive and six negative for *A. flos-aquae* f.

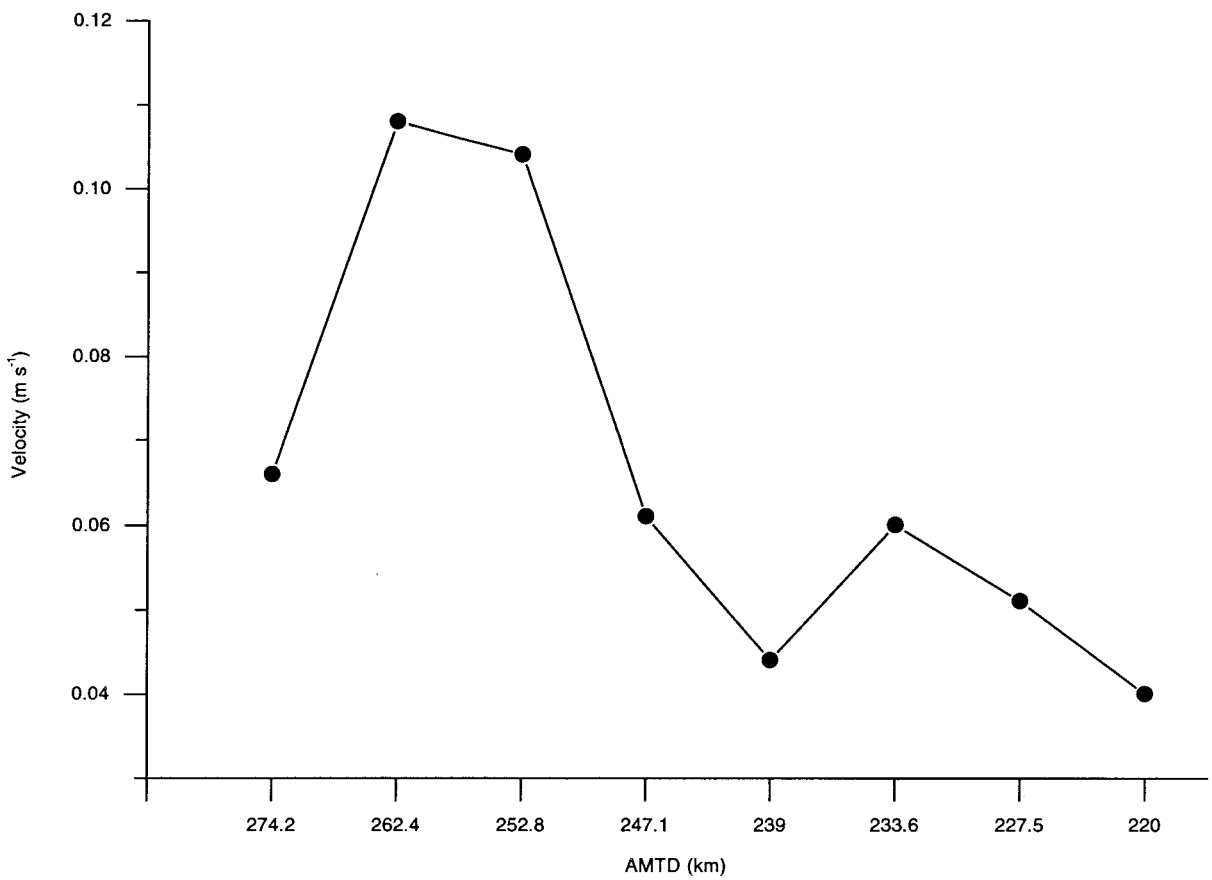

Figure 3. Stream velocities averaged over the sampling period (1994/1995) at each cross-section sampling site between Lock 1 and Nildottie

Copyright © 2000 John Wiley & Sons, Ltd.

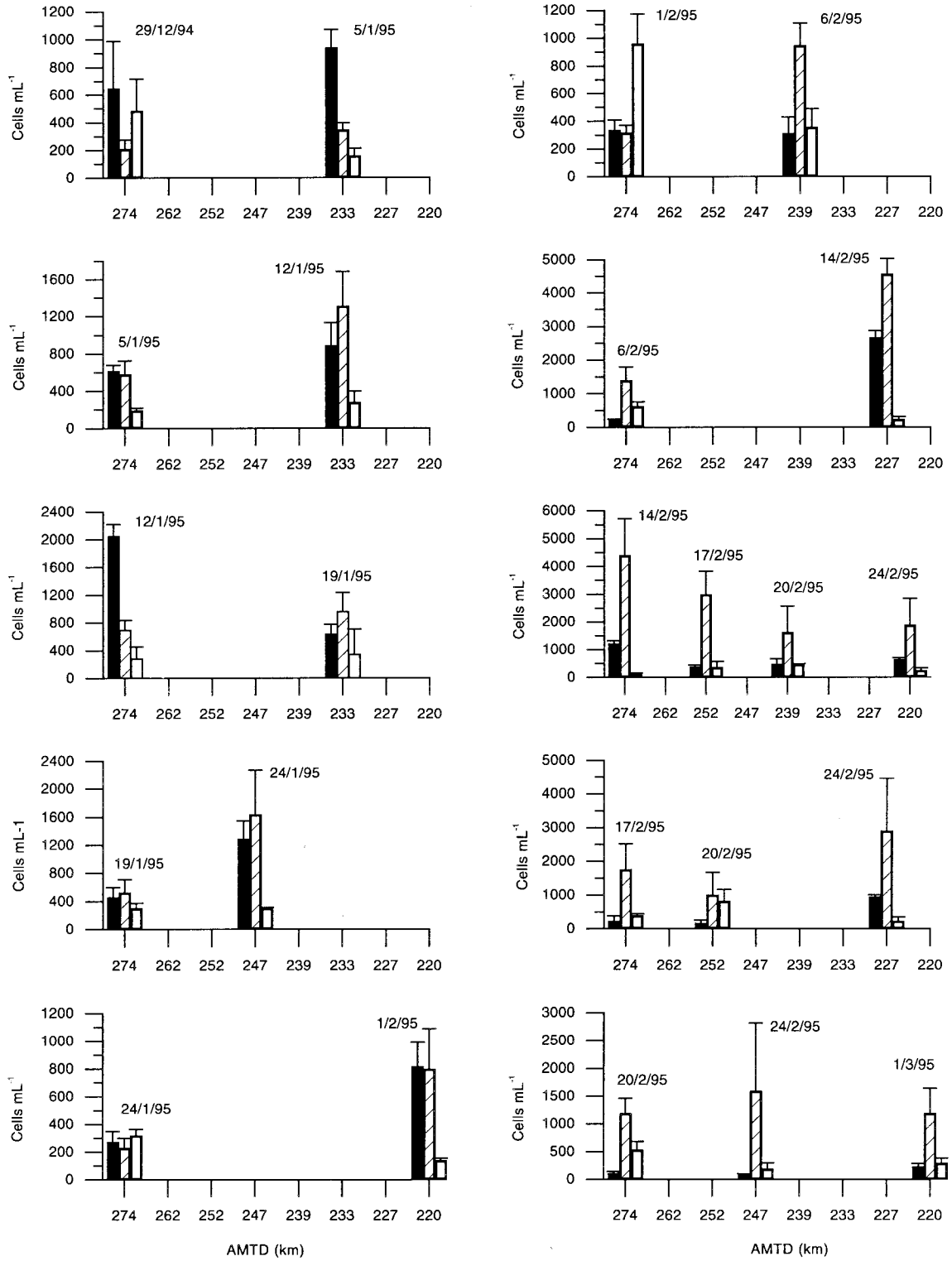

Figure 4. Changes in cell density of the dominant phytoplankton species in parcels of water tracked as they move downstream from Lock 1 (AMTD 274.2) to Nildottie (AMTD 220.0). Each figure indicates the cell density (mean $\pm$ S.D., $n = 3$) of the starting populations at Lock 1 and of the same population on subsequent dates and distances downstream. *A. circinalis* (black columns), *A. flos-aquae* f. *flos-aquae* (hatched columns) and *A. granulata* (white columns)

Copyright © 2000 John Wiley & Sons, Ltd.

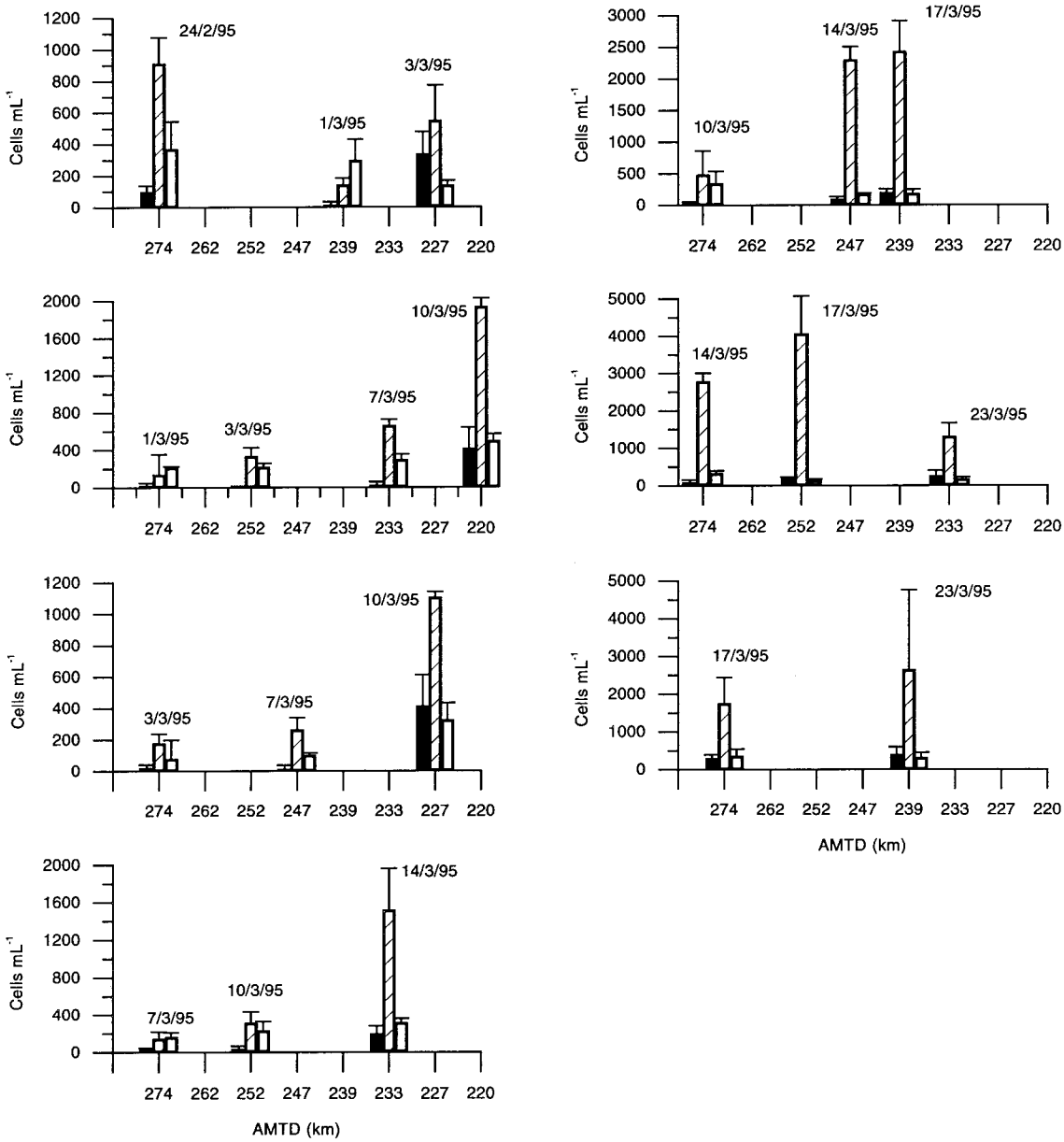

Figure 4 (*Continued*)

flos-aquae and 15 positive and 13 negative for *A. granulata* (Table I). A mean growth rate of 0.176 ($\pm$0.436) day^{-1} was calculated for *A. circinalis*, while that for *A. flos-aquae* f. *flos-aquae* was 0.132 ($\pm$0.233) day^{-1}. In contrast, *A. granulata* had a mean negative growth rate of $-$0.015 ($\pm$0.184) day^{-1}. Extrapolation of these mean growth rates suggests that the population size of *A. granulata* would decrease by 50% after a travel time of 46 days, while populations of *A. circinalis* would double in size about every 4 days and *A. flos-aquae* f. *flos-aquae* every 5 days.

Although relatively high growth rates were sometimes recorded for all species, these did not translate into high cell densities. *A. flos-aquae* f. *flos-aquae* was the most abundant species with a maximum cell density of 4560 cells mL^{-1}. The maximum concentration of *A. circinalis* was 2670 cells mL^{-1} and concentration of *A. granulata* was always less than 1000 cells mL^{-1}.

Copyright © 2000 John Wiley & Sons, Ltd.

Table I. Mean net growth rates of phytoplankton species in the River Murray, Lock 1 (AMTD 274.2 km) to Nildottie (AMTD 220.0 km), from December 1994 to March 1995[a]

Species	Cell density (cells mL^{-1})		Number of growth rates		Mean growth rate	Doubling time
	Maximum	Mean	Positive	Negative	(day^{-1})	(days)
Anabaena circinalis	2670	500	20	8	0.176 ($\pm$0.436)	4.0
Anabaena flos-aquae	4560	800	22	6	0.132 ($\pm$0.233)	5.2
Aulacoseira granulata	960	700	15	13	−0.015 ($\pm$0.184)	−58.7

[a] Standard deviations are shown in parentheses.

Contribution of cyanobacteria from backwaters

Daily river flows at Lock 1 ranged from 2850 to 9910 ML day^{-1} (stream velocity $\sim$0.05–0.16 m s^{-1}) during the period of study and flow was mostly exiting the lagoon during that time period. The average daily outflow measured at the channel was 135 ML day^{-1} ($\sim$0.2 m s^{-1}); however flow fluctuated dielly, with peak outflows during the day and minimum outflows (or occasional inflows) during the night. Further details of the diurnal flow pattern is provided by Webster *et al.* (1997a,b). The average contribution of water originating from Devon Downs Lagoon channel to river flow at Nildottie was approximately 2.8%, although lagoon water contributed up to 5.3% of total river flow on some days. The average retention time of water in the lagoon was approximately 9 days; however, water level displayed negligible fluctuation. As no other surface inputs occurred during the study period, the net movement of surface water out of the lagoon was probably replenished from a groundwater connection (Webster *et al.*, 1997a).

Cyanobacterial cell densities in Devon Downs Lagoon and the daily average flow out of the lagoon to the river were used to select the optimum sampling days to assess the maximum contribution of Devon Downs Lagoon to the abundance and composition of cyanobacteria in the river. Five occasions were selected on which the average daily outflow exceeded 130 ML day^{-1} and total cyanobacteria in the lagoon (Site 6608) ranged from 8×10^4 to 3.6×10^5 cells mL^{-1} (Table II). Total cyanobacteria in the river at the sampling site upstream of the lagoon channel (AMTD 227.5 km) did not exceed 6×10^3 cells mL^{-1} on these five dates.

The predictions of cell densities at the downstream site (AMTD 223 km), based on proportional flows and cyanobacterial cell densities in the river upstream (AMTD 227.5 km) and exiting the lagoon, were compared with the observed cell densities for each of the five sampling dates (29 December, 16 January, 8 February, 12 February, 29 February). The results indicated that cell density recorded at the downstream site was generally less than that predicted (Table II). The composition of cyanobacteria between upstream and downstream sites was also similar, being dominated by *A. flos-aquae* f. *flos-aquae*, *A. aphanizomenoides* and *A. circinalis*. Overall, there was no discernible influence of the lagoon outflow on cell numbers in the river on the indicated dates (Student's t test; $t_4 < 2.776$; $p > 0.05$).

Nutrient availability for growth

Filterable nitrogen and filterable phosphorus were not detected in most samples collected between Lock 1 and Nildottie on 6 February 1995, for minimum detection levels of 0.010 and 0.005 mg L^{-1}, respectively. The total phosphorus concentration ranged from 0.039 to 0.061 mg L^{-1} and total nitrogen concentration ranged from 0.45 to 0.54 mg L^{-1} (Table III). Nutrient analyses of river samples collected the following summer (6–7 March 1996) revealed similar nutrient concentrations (Table III). FRP and NO_x were near to or below the limit of detection in both the main channel (AMTD 431 to 227.5 km) and in Devon Downs Lagoon adjacent to Nildottie. All FRP concentrations were less than 0.007 mg L^{-1}; values at which growth is considered to be P-limited (Sas, 1989). Total P at each site ranged from 0.062 to 0.070 mg L^{-1} in the river, but was 0.131 mg L^{-1} in Devon Downs Lagoon, while total N ranged from 0.81 to 0.90 mg L^{-1} in the river and was 1.30 mg L^{-1} in the lagoon.

Copyright © 2000 John Wiley & Sons, Ltd.

Table II. Contribution of cyanobacteria in outflows from Devon Downs Lagoon to the main channel of the River Murray at Nildottie on selected days, 1995/1996

Date	River flow	Mean lagoon outflow	Dominant species	Mean cell abundance (cells mL^{-1})				
	(ML day^{-1})	(ML day^{-1})		River U/S 227.5	Lagoon 6608	Lagoon outlet 6610	River D/S 223.0 (observed)	River D/S 223.0 (predicted)
29/12/95[b]	4906	161	*Anabaena flos-aquae*	780	336 790	71 090	1480	3010
			Anabaena aphanizomenoides	680	9150	1810	135	720
			Anabaena circinalis	3435	3930	1515	350	3370
			Total cyanobacteria	4440	362 300	77 230	2210	6750
16/1/96	2878	162	*Anabaena flos-aquae*	770 (276)	18 460	18 940 (7194)	1710 (730)	1740
			Anabaena aphanizomenoides	930 (128)	153 850	26 580 (6157)	1320 (87)	2300
			Anabaena circinalis	2660 (655)	2270	2030 (1016)	1840 (1735)	2630
			Aphanizomenon	940 (38)	5680	5095 (2847)	850 (371)	1160
			Total cyanobacteria	5790 (407)	202 260	57 360 (15 301)	6400 (2087)	8540
8/2/96	3426	131	*Anabaena flos-aquae*	1010 (490)	24 740	2920 (123)	1480 (213)	1080
			Anabaena aphanizomenoides	1295 (568)	37 180	28 350 (10 753)	1250 (166)	2290
			Anabaena circinalis	1775 (438)	1050	690 (68)	1000 (351)	1730
			Total cyanobacteria	5210 (636)	96 330	34 390 (11180)	5720 (845)	6280
12/2/96	3426	170	*Anabaena flos-aquae*	640 (100)	44 770	6120 (552)	400 (35)	900
			Anabaena aphanizomenoides	1380 (74)	31 040	9720 (775)	N/A	1770
			Total cyanobacteria	3540 (70)	84 470	17 550 (1316)	2840 (269)	4200
29/2/96	9606	155	*Anabaena flos-aquae*	480 (76)	229 400	6210 (1338)	570 (59)	570
			Anabaena aphanizomenoides	770 (89)	54 550	2150 (45)	620 (56)	790
			Cylindrospermopsis	1535 (100)	1380	700 (102)	1440 (205)	1520
			Total cyanobacteria	4240 (237)	294 130	10 770 (1384)	4360 (284)	4340

[a] Standard deviations are shown in parentheses.
[b] No replicates collected on 29 December 1995; U/S, upstream; D/S, downstream.

Copyright © 2000 John Wiley & Sons, Ltd.

Table III. Mean nutrient concentrations at sites in the lower River Murray and in Devon Downs Lagoon, 6 February 1995 and 6–7 March 1996[a]

Site AMTD (km)	Sampling date	FRP (mg L^{-1})	Total P (mg L^{-1})	NO_x-N (mg L^{-1})	NH_3-N (mg L^{-1})	TKN (mg L^{-1})
431	1996	<0.005	0.063 (0.005)	0.013 (0.006)	0.010 (0.001)	0.860 (0.115)
383	1996	<0.005	0.066 (0.002)	0.020 (0)	0.020 (0.010)	0.850 (0.095)
320	1996	<0.005	0.066 (0.002)	0.013 (0.006)	0.008 (0.002)	0.880 (0.121)
274.2	1996	<0.005	0.070 (0.006)	<0.010	0.008 (0.004)	0.893 (0.091)
	1995	<0.005	0.039 (0.002)	<0.010	0.008 (0.003)	0.440 (0.057)
262.4	1995	<0.005	0.05 (0.006)	<0.01	<0.005	0.520 (0.052)
252.8	1995	<0.005	0.051 (0.002)	<0.01	0.014 (0.003)	0.493 (0.042)
247.1	1995	<0.005	0.045 (0.005)	<0.01	0.012 (0.010)	0.473 (0.050)
239.0	1995	0.011 (0.010)	0.061 (0.027)	<0.01	0.014 (0.004)	0.527 (0.132)
233.6	1995	<0.005	0.050 (0.005)	<0.01	0.009 (0.002)	0.437 (0.057)
227.5	1996	<0.005	0.062 (0.002)	0.010 (0)	0.020 (0.020)	0.787 (0.091)
	1995	<0.005	0.054 (0.004)	<0.010	0.013 (0.011)	0.510 (0.010)
220.0	1995	<0.005	0.050 (0.009)	<0.01	0.013 (0.004)	0.510 (0.030)
Devon Downs Lagoon	1996	0.006 (0.001)	0.131 (0.011)	<0.010	0.006 (0.001)	1.30 (0.173)

[a] Standard deviations are shown in parentheses.

Nutrient limitation in phytoplankton samples collected on 6–7 March 1996 was also detected by nutrient bioassays (Figure 5). In all samples collected from river sites and from Devon Downs Lagoon, some growth occurred in bioassays with nitrogen addition only, but significant growth occurred with addition of both nitrogen and phosphorus. The phosphorus treated samples did not show any growth, presumably because they were nitrogen limited. Growth assays were performed on numerous other occasions between January 1995 and April 1996 at lower River Murray sites. Both nitrogen limitation and co-limitation of N and P was regularly detected, but N was always more limiting than P.

The amount of phosphorus required to support the observed increases in chlorophyll concentration over five days in the nitrogen addition treatments (March 6–7 sampling) was estimated using a chlorophyll:phosphorus ratio of 1:1 (Reynolds, 1992) and expressed as a percentage of the total non-chlorophyll phosphorus fraction. Between 8 and 78% of the P in the non-chlorophyll bearing particulate fraction was estimated to be bioavailable (Table IV). In contrast, the total nitrogen in that fraction was essentially unavailable for growth, as indicated by the low growth in the phosphorus addition treatments.

Copyright © 2000 John Wiley & Sons, Ltd.

DISCUSSION

The major objective of this study was to estimate growth rates *in situ* of the major planktonic species of cyanobacteria in the lower River Murray to determine whether the main channel supported growth under the existing physical and chemical conditions. The principal assumption in the determination of *in situ* growth was that the downstream migration of phytoplankton cells is governed by the rate of flow of the

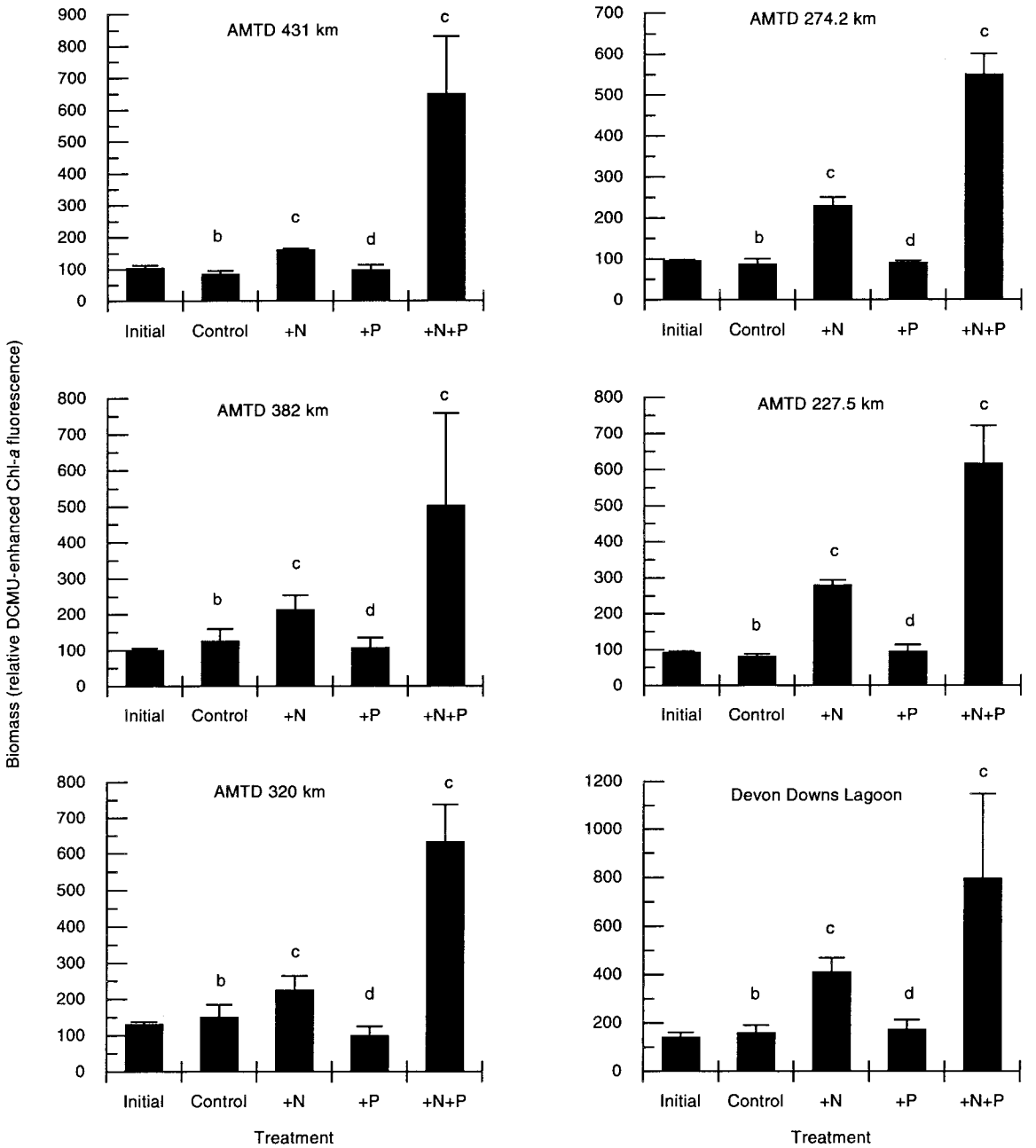

Figure 5. Growth bioassays, measured as DCMU-sensitive chlorophyll fluorescence of phytoplankton sampled from lower River Murray sites and enriched with nitrogen, phosphorous or nitrogen and phosphorous. a, Control is significantly different from the initial ($t = 0$); b, control is not significantly different from the initial; c, nutrient spike treatment is significantly different from the control ($t = 5$ days); d, nutrient treatment is not signficantly different from the control

Copyright © 2000 John Wiley & Sons, Ltd.

Table IV. Estimates from bioassay experiments of the bioavailable fraction of total phosphorus in the non-chlorophyll bearing fraction, required to support the observed growth of phytoplankton, upon the addition of nitrogen

Site AMTD (km)	Relative change in chlorophyll concentration ($\mu g\ L^{-1}$)	P incorporated into new growth (Chl:P = 1:1) ($\mu g\ L^{-1}$)	Total P in the non-Chl bearing total P fraction ($\mu g\ L^{-1}$)	% of total P which is bioavailable
431	3.7	3.7	44	8
383	19.6	19.6	49	40
320	16	16	46	35
274.2	23.3	23.3	48	49
227.5	32	32	41	78
Devon Downs Lagoon	61	61	84	73

water medium. It was important to provide evidence to support this assumption, so that growth of a discrete population could be measured by tracking its progress downstream from the known stream velocity. Although no direct measurement of cell migration was obtained, the detection of an apparent population 'front' of *A. circinalis* on a broader spatial scale moving downstream from Lock 7 to Mannum provided a suitable phytoplankton advection 'model'. This indicated with a statistically acceptable level of confidence that cyanobacterial cells were transported along the river, at approximately the same rate as the suspending medium. It is possible that a change in chemical and physical character of the river associated with the source water could promote growth of *A. circinalis* at successive sampling sites by initiating processes such as the germination of akinetes. However, there was no indication at the time of any appreciable change in flow or water quality.

Both negative and positive growth rates were measured *in situ* for two species of cyanobacteria and for a filamentous centric diatom. Although some estimations were based on very low cell counts, the mean growth rates of *A. circinalis* and *A. flos-aquae* f. *flos-aquae* were positive, while that of the diatom *A. granulata* was negative. *A. granulata* is a negatively buoyant species and growth is favoured by high turbulence and a well mixed water-column (Hötzel and Croome, 1996). At low flows, *A. granulata* will tend to drop out of suspension from the photic zone and growth cannot be sustained. The mean negative growth rates obtained for *A. granulata* in this study and evidence of thermal stratification in the lower River Murray at flows of around 4000 ML day^{-1} (Bormans *et al.*, 1997) support this argument. A model developed by Bormans and Webster (1994) to simulate temporal and spatial variability of *A. granulata* concentrations in the middle reaches of the River Murray also suggests that silica limitation at low flows reduces the specific growth rate below the rate of loss through sinking.

The mean positive growth rates of *A. circinalis* and *A. flos-aquae* f. *flos-aquae* indicated that environmental conditions during summer were more favourable for buoyant cyanobacteria than for diatoms and possibly other phytoplankton groups. The buoyancy of *Anabaena* increases its light harvesting potential in the turbid and periodically stratified waters of the River Murray, which is reflected by the higher growth rates. Changes in population size due to the buoyancy of *A. circinalis* and sinking of *A. granulata* during low flow has also been clearly demonstrated in the Maude weir pool of the Murrumbidgee River (Sherman *et al.*, 1998).

In situ growth rates of *A. circinalis* in our study were appreciably less than that previously recorded in culture under optimum conditions of light and nutrients. A maximum growth rate of 0.67 day^{-1} (± 0.03) and a mean doubling time of about 1.0 day (Velzeboer *et al.*, 1998) and a minimum doubling time of about 1.4 days (Winder and Cheng, 1995) have been recorded for Australian strains of *A. circinalis*. The relatively low net growth rates and low yields of cyanobacterial biomass (< 5000 cells mL^{-1}) that were observed during the study period might be attributable to a number of factors, including nutrient limitation, intermittent periods of thermal instability and loss processes such as grazing, sedimentation and washout. Nutrient analyses and bioassays conducted in our study indicated that both nitrogen and

Copyright © 2000 John Wiley & Sons, Ltd.

phosphorus limitation were contributing factors to low algal biomass, while the physical features specific to this reach of the river during the 1996 summer were not conducive to the development of cyanobacterial blooms (Bormans *et al*., 1997). The residence time of < 10 days between Lock 1 and Nildottie was insufficient for large increases in biomass; however, the low biomass at Lock 1 was also indicative of poor growth in the upstream phytoplankton community.

Hydraulic retention zones or 'dead zones' in rivers have been suggested as areas where the downstream movement of phytoplankton is delayed sufficiently to allow additional growth, thereby increasing the net growth rate of phytoplankton along a reach of river (Reynolds *et al*., 1991; Reynolds and Glaister, 1993; Reynolds, 1994). Existence of such zones are dependent upon the sinuosity and gradient of the river channel and may be indicated by lower stream velocities and relatively higher phytoplankton biomass. Although, 'dead zones' may have considerable effect on local instream phytoplankton growth, it was necessary in this study to assume that flow was uniform in order to calculate water travel times and growth along a large river reach. A surface scum of cyanobacteria was observed on one occasion during the study period at Nildottie, but average stream velocity at this site (AMTD 227.5; refer to Figure 3) was not particularly low compared with others and the presence of scum could be due to the wind shelter afforded by high limestone cliffs in this region.

Estimates of inputs of cyanobacteria from Devon Downs Lagoon to the main channel of the river were made during midsummer when entitlement flows of about 4000 ML day^{-1} prevailed. Mean flow out of the lagoon gauged at the channel entrance of 135 ML day^{-1} was predominately wind driven (Webster *et al*., 1997a) and did not reflect an hydraulic gradient. When the resident population of total cyanobacteria in the lagoon was less than 4×10^5 cells mL^{-1}, the advection of cyanobacteria to the river had no significant effect on phytoplankton abundance or species composition downstream. Although it is possible that permanently connected wetlands such as Devon Downs Lagoon act as a source of recruitment for river cyanobacteria, we conclude that the size of the inoculum during the study was insufficient to influence the estimated cell densities of key species in the main channel. However, cyanobacterial populations may contribute significantly to river populations under certain hydrologic conditions. A similar mechanism has been suggested for the River Bure (UK), where adjacent, connected Broads (shallow lakes) act as nurseries for phytoplankton and provide a significant inoculum to the main river channel (Moss *et al*., 1989). Evidence has been obtained from ground and aerial surveys of the lower River Murray (P. Baker and M. Burch, unpublished data) to indicate significant advection of cyanobacteria from large lagoons into the main channel following a rapid drop in water level. Such events are likely when typical peak flows in spring are delayed to midsummer and the recession of floodwaters from wetlands occurs after cyanobacterial populations are well established.

The observed net growth rates of *Anabaena* in the lower River Murray might suggest that growth was limited by either the concentration of nutrients and/or the rate of supply of nutrients. Soluble inorganic nitrogen (oxidized N and ammonia) and filterable reactive phosphorus were all approaching or below the limit of detection in nutrient analyses. Total phosphorus was generally < 0.1 mg L^{-1} and bioassays revealed that 8–78% of this fraction was bio-available. In a previous study, desorbable and bioavailable phosphorus in the Murray and Darling Rivers was estimated to be between 18 and 48% of the total phosphorus (Oliver *et al*., 1993). In contrast, total nitrogen in the river was generally unavailable for growth and nitrogen was the element which became limiting and inhibited growth in bioassays. Interestingly, *Anabaena* is a nitrogen fixing cyanobacterium and presumably should not be nitrogen limited.

The N-limitation observed in this study contributes to the increasing amount of evidence which conflicts with the paradigm that temperate freshwaters are predominately phosphorus limited (Hecky and Kilham, 1988). In a review of North American lake studies, Elser *et al*. (1990) found that nitrogen was limiting just as often as phosphorus, while Wood and Oliver (1995) detected N-limitation in the Murrumbidgee River using a rapid active fluorometry 'NIFT' assay.

We suggest that although phosphorus may ultimately limit biomass, low nitrogen concentrations in the River Murray favour the heterocystic nitrogen-fixing species such as *A. circinalis* and *A. flos-aquae* f. *flos-aquae* and are unfavourable for the non-nitrogen-fixing species such as *Microcystis aeruginosa*. The

Copyright © 2000 John Wiley & Sons, Ltd.

physical conditions in the lower River Murray during summer were similar to those that are known to favour growth of *Microcystis* (Ganf, 1974; Köhler, 1992), but populations of *M. aeruginosa* did not become established during the period of study. The combination of physical and chemical conditions produced a habitat which presumably favoured the growth of *Anabaena* in preference to non-nitrogen-fixing cyanobacteria, albeit at sub-optimum conditions.

During the study period, most of the water in the lower River Murray was sourced from the upper Murray and its tributaries, which historically have lower nutrient loads than the other major tributary, the Darling River. Water sourced from the Darling River has a higher phosphorus load (Shafron *et al.*, 1990), which could feasibly sustain a higher cyanobacterial biomass during periods when the Darling River contributes a higher proportion of flow. In the summer of 1996/1997, a higher contribution of Darling River water resulted in elevated levels of both N and P in the lower River Murray and the occurrence of the non-nitrogen-fixing cyanobacterium *Planktothrix perornata* var. *attenuata* was found in relatively high abundance (Baker, 1999). Generally, however, higher turbidities in the lower Murray associated with high inputs of Darling River water can restrict the euphotic zone to approximately 0.5 m, thus mitigating the effects of increased nutrient concentrations. An additional explanation for nutrient limitation in the lower River Murray in 1994/1995 and 1995/1996 was the lack of overbank flows attributable to the low winter/spring flows from the headwaters. This would have reduced the nutrient input from the floodplain to the river channel during recession of floodwaters.

A conceptual model has been developed (Figure 6), based on the findings of this study and a study by Bormans *et al.* (1997) along the same river reach in 1996, to summarize the physical and chemical environmental factors governing the abundance of cyanobacteria in the lower River Murray. Bormans *et al.* (1997) found that wind strength was a dominant variable affecting the degree of temperature stratification, given low flow conditions in summer. By applying this modelled relationship to a historical dataset of river phytoplankton, they concluded that the combination of these conditions was critical to the development of sustained cyanobacterial blooms. On the basis of this work, we rank flow as the primary factor affecting the development of cyanobacterial populations. High flow (>10000 ML day^{-1}) results in high turbulence and species such as the negatively buoyant diatom *A. granulata* are favoured. When

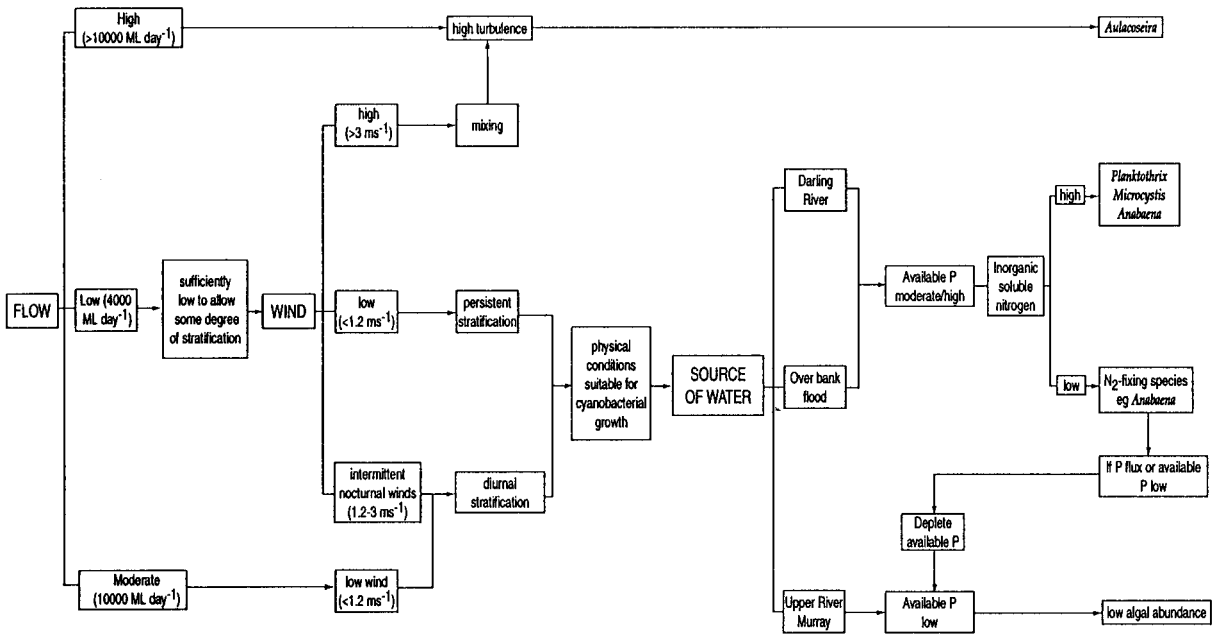

Figure 6. Conceptual model of the physical and environmental factors governing cyanobacterial abundance in the lower River Murray

Copyright © 2000 John Wiley & Sons, Ltd.

flow is moderate (ca. 10000 ML day^{-1}), diurnal stratification may occur if wind strength is low (< 1.2 m s^{-1}). During periods of low flow, equivalent to summer entitlement flows (4000 ML day^{-1}), within stream turbulence is sufficiently low to allow some degree of thermal stratification, provided that wind strength is low to moderate (< 3 m s^{-1}). Persistent stratification may result when the wind speed is < 1.2 m s^{-1} (and flow is low), while diurnal stratification is more likely at wind speeds between 1.2 and 3 m s^{-1}. Irrespective of flow, high wind strength (> 3 m s^{-1}) will disrupt thermal stratification and result in a mixed water column. Evidence collected from the two studies indicates that both diurnal and persistent stratification provide the physical conditions suitable for the development of cyanobacterial populations in the lower River Murray. These findings differ from those based on studies of the Maude weir pool, whereby periods of diurnal stratification lead to the dominance of the diatom *A. granulata* (Webster *et al*., 1997b).

The source of water is the other environmental factor which is considered to be significant in the composition and abundance of phytoplankton in the lower River Murray. If water is sourced from the Darling River, or if overbank flooding has occurred during the high spring flows originating from the upper River Murray, phosphorus concentrations in the river may be elevated. The availability of nitrogen will then determine which species are present. High soluble inorganic nitrogen availability will favour cyanobacterial genera such as *Microcystis* and *Planktothrix* and other phytoplankton. However, if this nitrogen fraction is low, the nitrogen fixing genera, such as *Anabaena*, *Aphanizomenon*, *Anabaenopsis* and *Cylindrospermopsis* will be favoured. When flow has originated from the upper River Murray and flow has remained within the main channel, then available phosphorus will be low and phytoplankton abundance will also remain low.

ACKNOWLEDGEMENTS

This study formed part of a larger research effort supported by the National River Health Program to examine the ecology of bloom-forming cyanobacteria in Australian rivers. Funding was provided by the Land and Water Resources Research and Development Corporation under the National River Health Program and the Co-operative Research Centre for Water Quality and Treatment. This study was extremely labour intensive in terms of sampling and sample analysis and the authors wish to acknowledge the technical assistance provided at various stages by Karan Smith, Renate Velzeboer, Mira Orlovic, Jo Dean, Jan Dearden, Dean Newman, Chris Blake and Peter Hockley. Advice on River Murray Operations was provided by SA Water officers Brenton Erdmann, Phil Pfieffer, Peter Stace, David Bain and Jack Belsham, while advice on the River Murray Hydraulic Model was provided by Stuart Blanch from the University of Adelaide, Departments of Zoology and Botany.

REFERENCES

Anon. 1995. *Standard Methods for the Examination of Water and Wastewater*, 19th edition, American Public Health Association, Washington DC.

Baker, P.D. 1999. The role of akinetes in the development of cyanobacterial populations in the lower Murray River, *Aquat. Conserv.: Mar. Freshwater Res.*, **50**(3), 265–279.

Baker, P.D., Humpage, A.R., and Steffensen, D.A. 1993. Cyanobacterial blooms in the Murray–Darling Basin: their taxonomy and toxicity, *Research Report No. 8/93*, Australian Centre for Water Quality Research.

Bormans, M. and Webster, I.T. 1994. Effects of flow on algal growth in well mixed rivers, in *Proceedings of Environmental Flows Seminar*, *Canberra*, *25–26 August*, *1994*, Australian Water and Wastewater Association, pp. 29–35.

Bormans, M., Maier, H.R., Burch, M.D., and Baker, P.D. 1997. Temperature stratification in the lower River Murray, Australia: implication for cyanobacterial bloom development, *Aquat. Conserv.: Mar. Freshwater Res.*, **48**(7), 647–654.

Bowling, L.C. and Baker, P.D. 1996. Major cyanobacterial bloom in the Barwon-Darling River, Australia, in 1991, and underlying limnological conditions, *Aquat. Conserv.: Mar. Freshwater Res.*, **47**(4), 643–657.

Burch, M.D., Baker. P.D., Steffensen, D.A., Bursill, D.B., Bain, D.B., Ganf, G.G., and Brookes, J.D. 1994. Critical flow and blooms of the cyanobacterium *Anabaena circinalis* in the River Murray, South Australia, in *Proceedings of Environmental Flows Seminar*, *Canberra*, *25–26 August 1994*, Australian Water and Wastewater Association, pp. 44–51.

Copyright © 2000 John Wiley & Sons, Ltd.

Capblancq, J. and Decamps, H. 1978. Dynamics of the phytoplankton in the River Lot, *Verh. Int. Verein. Limnol.*, **20**, 1479–1484.
de Ruyter van Steveninck, Admiraal, W., Breebaart, L., Tubbing, G.M.J., and van Zanten, B. 1992. Plankton in the River Rhine: structural and functional changes observed during transport downstream, *J. Plankton Res.*, **14**, 1351–1368.
Elser, J.J., Marzolf, E.R., and Goldman, C.R. 1990, Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments, *Can. J. Fish. Aquat. Sci.*, **47**, 1468–1477.
Ganf, G.G. 1974. Diurnal mixing and the vertical distribution of phytoplankton in a shallow equatorial lake (Lake George, Uganda), *J. Ecol.*, **62**, 611–629.
Hecky, R.E. and Kilham, P. 1988. Nutrient enrichment of phytoplankton in freshwater and marine environments: a review of recent evidence of the effects of enrichment, *Limnol. Oceanogr.*, **33**(4), 796–822.
Hötzel, G. and Croome, R. 1996. Population dynamics of *Aulacoseira granulata* (EHR.) SIMONSON (Bacillariophyceae, Centrales), the dominant alga in the Murray River, Australia, *Arch. Hydrobiol.*, **136**(2), 191–215.
Jacobs, T. 1989. Regulation of the Murray–Darling river system, in Lawrence, B. (Ed.), *Proceedings of the Native Fish Management Workshop*, Murray–Darling Basin Commission, Canberra, pp. 55–96.
Jones, F.H. 1984. The dynamics of suspended algal populations in the lower Wye catchment, *Water Res.*, **18**, 25–35.
Köhler, J. 1992. Influence of turbulent mixing on growth and primary production of *Microcystis aeruginosa* in the hypertrophic Bautzen Reservoir, *Arch. Hydrobiol.*, **123**(4), 413–429.
Lund, J.W.G., Kipling, C., and Le Cren, E.D. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting, *Hydrobiologia*, **11**, 143–170.
Maier, H.R., Dandy, G.C., and Burch, M.D. 1998. Use of artificial neural networks for modelling cyanobacteria *Anabaena* spp. in the River Murray, South Australia, *Ecol. Model.*, **105**(2/3), 257–272.
Moss, B., Booker, I., Balls, H., and Manson, K. 1989. Phytoplankton distribution in a floodplain lake and river system. I. Hydrology, nutrient sources and phytoplankton biomass, *J. Plankton Res.*, **11**, 813–838.
Oliver, R.L., Hart, B.T., Douglas, G.B., and Beckett, R. 1993. Phosphorus speciation in the Murray and Darling Rivers, *Water, Official J. Austr. Water Wastewater Assoc.*, **20**, 24–29.
Reynolds, C.S. 1992. Eutrophication and the management of planktonic algae: what Vollenveider couldnt tell us, in Jones, J.G. and Sutcliffe, D.W. (Eds), *Eutrophication: Research and Application to Water Supply*, Freshwater Biological Association, Ambleside, UK.
Reynolds, C.S. 1994. The long, the short and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers, *Hydrobiologia*, **289**, 9–21.
Reynolds, C.S., Carling, P.A., and Beven, K. 1991. Flow in river channels, new insights into hydraulic retention, *Arch. Hydrobiol.*, **121**, 171–179.
Reynolds, C.S. and Glaister, M.S. 1993. Spatial and temporal changes in phytoplankton abundance in the upper and middle reaches of the River Severn, *Arch. Hydrobiol. (Supplementband)*, **101**, 1–22.
Sas, H. 1989. *Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations*, Academia Verlag Richarz, Sankt Augustin.
Shafron, M., Croome, R. and Rolls, J. 1990. Water quality, in Mackay, N.J. and Eastburn, D. (Eds), *The Murray*, Murray–Darling Basin Commission, Canberra, pp. 147–166.
Sherman, B.S., Webster, I.T., Jones, G.J., and Oliver, R.L. 1998. Transitions between *Aulacoseira* and *Anabaena* dominance in a turbid river weir pool, *Limnol. Oceanogr.*, **43**(8), 1902–1913.
Velzeboer, R.M.A., Baker, P.D., and Rositano, J. 1998. Characterisation of saxitoxins produced by the cyanobacterial genus *Anabaena* in Australia, *Research Report No. 135*, Urban Water Research Association of Australia.
Walker, K.F. and Thoms, M. 1993. Environmental effects of flow regulation on the River Murray, South Australia, *Regul. Rivers: Res. Mgmt*, **8**, 103–119.
Water Studies Pty. Ltd. 1992. *River Murray Flow Model*, Vols 1, 2 and 3. Engineering and Water Supply Department of South Australia. EWS 92/12.
Webster, I.T., Maier, H.R., Baker, P.D., and Burch, M.D. 1997a. Influence of wind on water levels and lagoon–river exchange in the River Murray, Australia, *Aquat. Conserv.: Mar. Freshwater Res.*, **48**(6), 541–550.
Webster, I.T., Sherman, B.S., and Jones, G.J. 1997b. Flow, stratification, and the growth of phytoplankton in a river impoundment, *Verh. Int. Verein. Limnol.*, **26**, 641–644.
Winder, J.A. and Cheng, D.M.H. 1995. Quantification of factors controlling the development of *Anabaena circinalis* blooms, *Research Report No. 88*, Urban Water Research Association of Australia.
Wood, M.D. and Oliver, R.L. 1995. Fluorescence transients in response to nutrient enrichment of nitrogen- and phosphorus-limited *Microcystis aeruginosa* cultures and natural phytoplankton populations: a measure of nutrient limitation, *Austr. J. Plant Physiol.*, **22**, 331–340.

Copyright © 2000 John Wiley & Sons, Ltd.