Literature Review: Nutrient cycling and phytoplankton communities of the Lower River Murray, Lower Lakes and Coorong

Report to:

Department of Environment and Heritage, the Government of South Australia

Kane Aldridge, Alex Payne and Justin Brookes

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THE UNIVERSITY OF ADELAIDE AUSTRALIA

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Introduction

The Lower River Murray, Lower Lakes (Lake Alexandrina and Lake Albert) and Coorong contain a high biodiversity and are ecologically important for South Australia and indeed the entire Murray-Darling Basin. In addition, the region is a source of domestic water for much of South Australia; a source of water for irrigated agriculture; supports a substantial fishery; provides recreational pursuits, and has a high cultural and aesthetic value. The Lower Lakes are large (over 750 km^2), shallow (maximum depth of 4.1 m), connected, terminal lakes of the Murray-Darling Basin (Figure 1), Australia's largest drainage basin (1,063,000 km^2). Together with the Coorong, an estuarine-hypersaline coastal lagoon, the Lower Lakes were declared a *Wetland of International Importance* in 1985 under the Ramsar Convention. The recognition of the region as a '*Wetland of International Importance'* is due to the abundant and diverse ecological communities within the region, which are a result of a high habitat diversity created largely by the salinity gradient that exists. The region is an important refuge for a number of threatened freshwater fish species; an important feeding habitat for waterbirds; and an important source of water and resources to the near shore environment (Cook *et al.* 2008).

The River Murray, one of the world's longest rivers, carries the largest and most constant flow of water to the region. The Darling River also contributes significant flow, although this is more variable and carries high loads of fine particles, resulting in extremely high turbidity. Although several local streams discharge into the Lower River Murray and Lake Alexandrina, their overall contribution to total annual flow are only considered to be significant during periods of low River Murray inputs (Anon 2007). Extraction of water upstream for irrigation and human use has severely reduced the amount of water passing into and through the Lower Lakes. Consumptive water use within the Murray-Darling Basin has reduced average stream-flow through the Murray Mouth from 12,233 GL/yr to 4733 GL/yr, a 61% reduction (CSIRO 2008). This has dramatically influenced the principal factors driving the ecosystems of the region: discharge, water level regime and salinity regime.

From September 2001 until the end of this study the Murray-Darling Basin experienced severe rainfall deficiencies, the second driest seven-year period in its recorded history (MDBC 2008). This combined with the over-allocation of water within the Murray-Darling Basin, has resulted in a dramatic reduction in inflows to the Lower Lakes and gradual but unprecedented water level drawdown. From August 2006 to August 2009, water levels fell in the Lower Lakes from average levels of 0.75 m AHD to -0.75 m AHD, resulting in the intrusion of saline water into the lakes (Aldridge *et al*. 2009).

Given the ecological and socio-economic importance of the region, it is surprising that very little is known about the biogeochemistry and phytoplankton dynamics. In general, studies of biogeochemistry and phytoplankton in the region have been short-term and therefore provide little information on the key drivers of change over longer temporal scales. This review brings together information that is available on nutrient dynamics and phytoplankton communities for the region with a description of the key drivers that have been identified. Since very is little known about the impacts of many parameters on nutrient dynamics and phytoplankton communities in the region, a description of important drivers identified in the broader scientific literature are included. In addition, general descriptions of nutrient cycling and phytoplankton are provided in Appendix 1 and Appendix 2.

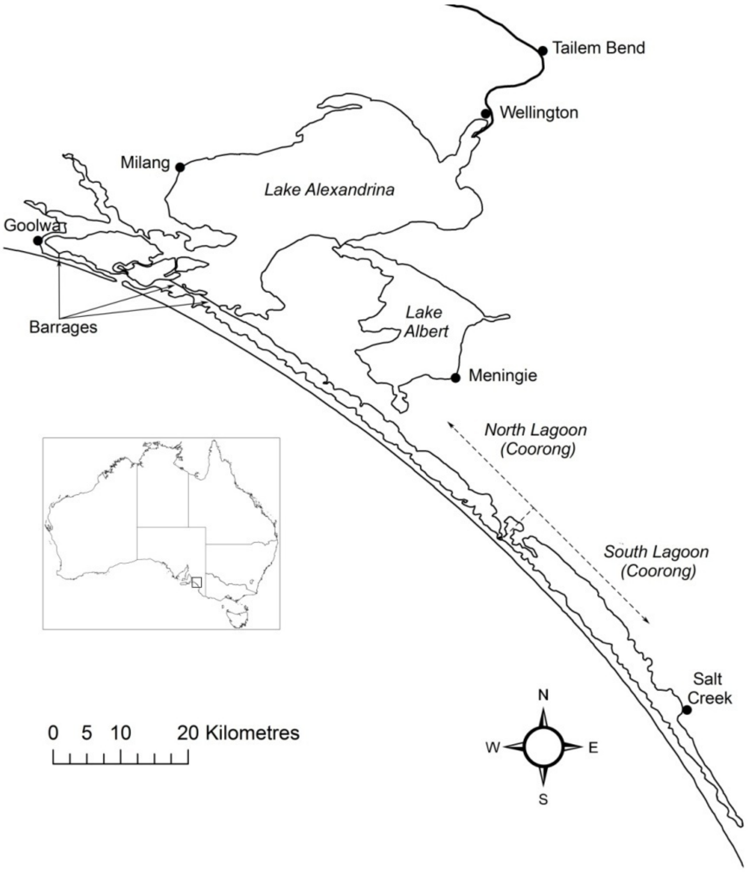


Figure 1. Map of the Lower River Murray, Lake Alexandrina, Lake Albert and the Coorong.

Nutrient dynamics in the Lower River Murray, Lower Lakes, Coorong and Murray Mouth

Background

Nutrients are essential components of all living organisms. They are substances that are metabolised by organisms to give energy and build tissue (Wetzel 2001). They can be divided into macronutrients and micronutrients, providing an indication of the amount necessary for the growth of biota. Macronutrients include carbon (C), hydrogen (H), oxygen (O), nitrogen (N), and phosphorus (P), and lesser amounts of sulfur (S), potassium (K), magnesium (Mg), and calcium (Ca). C, H and O are always present in great abundance with the remaining macronutrients consisting of approximately 0.1% of the organic matter in aquatic systems (Wetzel 2001). Of these, P and N are often the nutrients that limit the growth of biota with the remainder usually in amounts that exceed the requirements of autotrophic organisms (Kalff 2002). Thus, N and P often determine the total autotrophic biomass within aquatic systems (Shafron *et al*. 1990; Kalff 2002) and so shape the structure of these ecosystems. The probability of primary N limitation of phytoplankton is greatest when N:P supply molar ratios are well below algal demand molar ratio of approximately 16:1. The reverse is true for P limitation with a molar ratio of greater than 16:1 providing some indication of P limitation (Kalff 2002).

Detailed description of the processes involved in N and P cycling are provided in Appendix 1.

Lower River Murray

Despite its importance there have been few studies on nutrient dynamics in the Lower River Murray. While there have recently been some reviews of historical data (Aldridge *et al*. 2007; Hipsey *et al*. 2009) that has been collected for human water supply purposes, there have been no attempts to develop a nutrient budget for the region and only one study of internal nutrient cycling, which was a short-term study (Brookes *et al*. 2008). The information that has been generated highlights the importance of land-use and flow regime on nutrient dynamics.

Land-use as a historical driver of nutrient concentrations

The removal of native vegetation and replacement with agriculture, industry and urban areas has resulted in an increase in the inputs of nutrients to water bodies. This enhanced input, of otherwise limiting nutrients, has lead to the artificial eutrophication of many freshwater systems (Moss 1988; Oliver and Ganf 2000; Reynolds 1984; Vollenweider 1968). Eutrophication caused by human activities can occur rapidly and has disturbed the natural nutrient balance of freshwater systems (e.g. Golterman 1995; Reynolds 1984; Vollenweider 1968). A majority of the increased inputs of phosphorus come from the terrestrial environment. Inorganic phosphate is a major component of many fertilisers and much of the phosphorus that is not used by the fertilised crops is passed through soil profiles and into streams and rivers (Kalff 2002). In agricultural regions, fertiliser use is also a major source of nitrogen. Others major sources of nitrogen and phosphorus include detergents, sewage, stormwater, agricultural effluent and fixation by microbes for nitrogen.

The River Murray contains multiple land-uses within its catchment and consequently, receives a myriad of pollutants from point sources, such as effluent pipes and drains and from diffuse sources, such as run-off, sub-surface seepage and tributaries (Shafron *et al.* 1990). The main types of discharges to River Murray that are likely to influence nutrient concentrations include: irrigation drainage, stormwater, domestic sewage, water treatment plant wastes, domestic grey-water, river vessel wastes and groundwater.

From a review of available data and a field survey, Aldridge *et al*. (2007) observed an increase in nutrient loads and an increase in nutrient concentrations along the lower River Murray. It suggested that either diffuse sources of nutrients or a large number of small point sources of nutrients may be contributing significantly to the Lower River Murray nutrient load (Aldridge *et al*. 2007). To investigate these trends further, three potentially significant point sources of nutrients to the River Murray were investigated; a Houseboat Marina; a Wetland; and an Irrigation Pump Outlet from land used for dairy farming. Poorer water quality (including elevated nutrient concentrations and low dissolved oxygen levels) was evident within the three studied land-uses (Aldridge *et al*. 2007). However, only the Irrigation Pump Outlet appeared to have a significant impact on the water quality within the river. The impact of the Irrigation Pump Outlet was more evident at the bottom of the water column than surface waters. The results suggested that the increasing nutrient loads and concentrations along the lower River Murray may have been associated with increased loads from the Lower Murray flood irrigation drainage channels. Flood irrigation practises results in irrigation returns (IR) to the river, a number of which were monitored in 2005-2008 as part of an EPA LMRIA environmental monitoring and rehabilitation project (Mosley and Fleming 2008). It was found total outflows from irrigation returns to the River Murray were less than 0.5 GL in 2008, which is <0.1% of the flow over Lock 1. However, high concentrations of nutrients in the returns are potentially an important source of nutrients into the river (Mosley and Fleming 2008).

Flow regime as a driver of nutrient dynamics

Flow regime plays a major role in determining nutrient concentrations in water bodies, which ultimately structures biological communities. High flows reduce the likelihood of stratification (Bormans *et al*., 1997)and deoxygenation of the water column therefore reducing nutrient flux from the sediments to the water column. In addition, with increased rainfall in the surrounding catchment, nutrients associated with sediments are passed downstream and into streams and rivers. The movement of large amounts of sediment during storms is particularly significant (Shafron *et al*. 1990). Nitrogen and phosphorus concentrations in the River Murray are highest during winter-spring when flows are greatest. Nutrients enter the River Murray through tributaries, run-off and resuspension of sediments (Shafron *et al*. 1990).

Under low flow conditions, the external nutrient inputs are reduced and sediments are deposited on the river bed. The River Murray, like many rivers throughout the world, is highly regulated meaning that the river is made up of a series of relatively stable weir pools with very little water level fluctuation (Jacobs 1990). This creates conditions ideal for the development of thermal stratification, which has important implications for nutrient dynamics within water bodies.

Under periods of low flow, soluble nutrients may be released from sediments due to stratification and the development of anoxic conditions within the sediment. Brookes *et al*. (2008) undertook sediment incubation experiments to determine the potential for release of nutrients (nitrogen and phosphorus) and metals (iron and manganese) from the sediments in the lower River Murray under anoxic sediment conditions, which could occur as a result of the drought and low river flow. The experiments demonstrated that there is significant capacity for release of the nutrients (nitrogen and phosphorus) and the redox-sensitive metal manganese into the water column. Four sites were investigated for sediment release capacity: Wellington, Tailem Bend, Murray Bridge and Nildottie. All sites showed significant release of the nutrients nitrogen and phosphorus. A significant feature of the results was the very high release rates found for ammonium (NH_4). Rates ranged from 220 mg/m^2/day at Nildottie down to 20 mg/m^2/day at Wellington. Nitrogen flux rates were approximately 3 times higher at Nildottie than the three other lower River sites which all had similar rates. Total phosphorus (TP) release rates were in the range 1-10 mg/m^2/day. Wellington also showed the highest release rates for phosphorus and sediment oxygen demand (SOD), which were thought to be related to higher sediment organic loadings at this location.

Soluble iron release was not detected from the sediments at any of the sites, whereas significant manganese release occurred at all sites. The greatest manganese flux rates occurred at Murray Bridge followed by Wellington and Tailem Bend, while rates at Nildottie were considerably lower. The modelled calculations show that the manganese concentration at Murray Bridge could theoretically reach up to 60 mg/L in a 5 m water column after 10 days of anoxic conditions in the sediments. Other sites show proportionately lower potential concentrations, but could still have relatively high manganese in the water column under anoxic conditions. Modelled calculations showed that concentrations of manganese at Wellington could be up to 15 mg/L in a 15 m deep water column and up to 30 mg/L at Tailem Bend in a 5 m deep water column.

The significance of this is that under very low flow the river can become persistently thermally stratified for varying periods, which results in oxygen depletion both in the sediments and water adjacent to the sediments allowing these contaminants to be released into the water. Nutrients can then be available for algal growth. Manganese is problematic for potable water supply as it oxidises upon exiting customers tap and causes dirty water.

When outputs (outflows, evapotranspiration) of water exceeds inputs (inflows, rainfall), sediments of water bodies may become dry, including those on the edges of lakes with seasonally fluctuating water levels. The inundation of previously dry sediments, causes leaching of nutrients from dead organic matter (Baldwin and Mitchell 2000) resulting in an enhanced flux of nutrients downstream. The increased flow in water bodies may also result in sediment being resuspended from the sediment surface. This may increase the turbidity of the water body and expose anoxic sediments to the water column and so result in a release of nutrients from the sediments.

Recent condition

Recent water quality data that is available for the Lower River Murray has been reviewed by Hipsey *et al*. (2009) as part of the validation of a three-dimensional hydrodynamic-biogeochemical model for the region. They found that changes in water quality in the river during the past decade strongly reflect changes in inputs, and thus were dominated by the dramatic reduction in flow reaching Lock 1 (Hipsey *et al*. 2009). Several elements were positively associated with flow including iron, aluminium, manganese, phosphorus and surface samples of dissolved organic carbon. The positive relationship with flow indicates increased inputs from upstream through mobilisation from the catchment. Historically there has been more variation between years than between sites, but these strong seasonal variations have not been noticed during the recent drought years and particularly in the modelling study period ranging between 2007 and 2009. As water passed downstream from Lock 1, several parameter concentrations also varied through internal processes, or additional sources, including filterable reactive phosphorus (FRP), oxidised nitrogen (NO_x), sulfate and conductivity (Hipsey *et al*. 2009). These increased downstream, perhaps reflecting evapo-concentration, contributions due to internal biogeochemical cycling and/or additional inputs, such as those from irrigation returns.

Lower Lakes

As for the Lower River Murray, there have been very few comprehensive studies of nutrient dynamics within the Lower Lakes. More recently Cook *et al*. (2008) and Aldridge *et al*. (2009) have inferred changes in nutrient dynamics from nutrient concentrations, but there remains a lack of knowledge on internal flux rates and factors controlling the flux rates. As with the Lower River Murray, land-use and flow regime have been identified as important factors controlling nutrient loads delivered and retained in the Lower Lakes.

Eutrophication

Paleolimnological studies have demonstrated that nutrient inputs from upstream have increased following European settlement (Herzeg *et al.* 2001; Fluin *et al.* 2007). This was believed to be a result of the development of the agriculture industry within the basin (Herzeg *et al.* 2001; Fluin *et al.* 2007). Indeed, the Lower Lakes are now considered to be eutrophic (Geddes 1984a), which is supported by the regular occurrence of algal blooms (Baker 2000). However, most nutrients in the Lower Lakes are not in bio-available forms, thus influencing phytoplankton growth (Geddes 1984a). Cook *et al.* (2008) found that the lakes assimilated inputs of inorganic nutrients from the Lower River Murray rapidly and exported them to the Coorong in organic forms.

Flow as a historical driver nutrient dynamics

Cook *et al*. (2008) investigated elemental concentrations in the Lower Lakes and at Tailem Bend in order to develop a nutrient budget for the Lower Lakes for the period 1979 and 1997. It was found that inorganic nutrients (NO_x, FRP and Si) and TP concentrations were generally highest in the lower River Murray and decreased markedly within the Lower Lakes, particularly for NO_x and FRP (Cook *et al*. 2008). This was because the Lower Lakes were a sink for NO_x, FRP and Si with a net retention occurring virtually every year. Highest absolute retention rates generally occurred in the highest flow years, whilst lowest absolute retention rates occurred in the lowest flow years. There were no strong relationships between nutrient concentrations and discharge into the Lower Lakes. In contrast to total phosphorus (TP) and the inorganic nutrients, total Kjeldahl nitrogen (TKN) concentrations were consistently highest in the Lower Lakes, presumably due to higher algal biomass. In addition, TKN was positively associated with flow. A drought-breaking inflow in late 1983 through to 1984 resulted in some of the highest persistent concentrations of all inorganic nutrients and TP in the lower River Murray, which was also reflected in the Lower Lakes. Concentrations of Si and FRP remained elevated in the Lower Lakes for several years after this inflow event. NO_x, by contrast, was rapidly removed from the water column, becoming undetectable within approximately 1 year. The years 1989 to 1993 had consistently high flows, but elevated inorganic nutrient concentrations within the lake were only observed in 1990. NH_4 was not analysed on a routine basis, however, the limited data set available suggests it was generally below the inimal limit of detection in the Lower Lakes and comprised a variable fraction of inorganic nitrogen (generally insignificant, but up to 50%).

Salinity as a driver of nutrient dynamics and recent condition

During periods of low-flow, water quality of the lakes is strongly influenced by internal biogeochemical processes, which have major implications for the functioning of the ecosystem. Recent monitoring of water quality within the Lower Lakes during a period of rapid water level drawdown and subsequent salinisation showed that nutrient concentrations in the Lower Lakes have increased (Aldridge *et al*. 2009). Seawater leakage from the barrages resulted in the formation of permanent density stratification leading to anoxia rapidly developing in the hypolimnion. As a result, soluble nutrient concentrations (NH_4 and FRP) concentrations increased in Goolwa Channel where stratification was present.

Phosphate (PO_4) comprised between 1.4 (January 2007) and 14.6% (July 2007) of TP with variation in TP concentrations associated with changes in PO_4 concentration. Although, there was no large change in PO_4 concentrations across the system as a whole during the study period, PO_4 concentrations increased in Goolwa Channel where the salinity increase and subsequent oxygen depletion was most evident. Under oxic conditions PO_4 is adsorbed to Fe in sediments (Boström *et al.* 1988) (see Figure 2). However, the input of sulfate (associated with saline water) combined with oxygen depletion in the sediments is thought to increase the flux of PO_4 from sediments to the water column due to sulfate reduction (requires sulfate pool and anoxic conditions). This leads to the production of Fe-S compounds and the displacement of PO_4 from the sediment pool (Wetzel 2001) (see Figure 2).

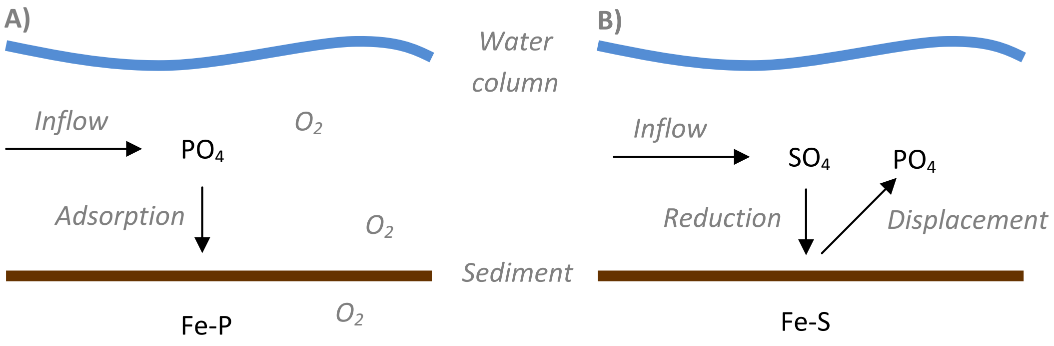


Figure 2. Conceptual model of phosphate (PO_4) release from sediments, associated with sulfate (SO_4) reduction. A) shows the adsorption of phosphorus (P) to iron (Fe) in the sediments under well mixed oxic conditions with low salinity (low sulfate). B) shows the dissociation iron bound phosphorus due to the binding of sulfur to iron (under stratified, anoxic conditions with high salinity (high sulfate).

Average lake concentrations of NH_4-N increased rapidly during the study period, although there was considerable variation in concentrations ranging from 0.8 mg/L in Goolwa to 0.3 mg/L at Clayton in April 2008. While the increase in NH_4-N concentrations were correlated with salinity, a number of processes are likely to have been involved in this increase, including:

- Displacement of NH_4 from sediment exchange sites by cation exchange due to increased levels of cations (salts) (Rysgaard *et al.* 1999; Baldwin *et al.* 2006; Laverman *et al.* 2007)
- Reduced nitrification rates under anoxic conditions (higher NH_4 concentrations were observed in the hypolimnion than the epilimnion at Goolwa during periods of stratification)
- Increased decomposition rates in sediment exposed to the atmosphere during the drawdown (Sah *et al.* 1989; Mitchell and Baldwin 1999; Baldwin and Mitchell 2000; Baldwin *et al.* 2005). In this case, occasional reflooding of sediments by rainfall, seasonal increase in water level, or wind-driven hydrodynamic processes would be required to transport the remineralised NH_4 to the water column.

There was also a general increase in average total nitrogen (TN) concentrations in the lakes through the study period with differences in TN closely related to suspended material which also increased.

This was thought to result from increased resuspension of finer sediments towards the centre of the lakes (Aldridge *et al*. 2009) as water level dropped and these finer sediments have become exposed to increased wave activity. Dissolved inorganic nitrogen (NO_x plus NH_4) consisted of approximately 6.7% of TN, however, this proportion increased through the study period from 3.1 to 14.8%.

Aldridge *et al*. (2009) also found that drying-reflooding cycles can have important implications for nutrient dynamics in the Lower Lakes. The flux of NH_4 from sediments of Lake Alexandrina was far greater than those observed elsewhere (Baldwin *et al.* 2005). This flux was enhanced by a drying-reflooding cycle, most likely due to cell lysis, with nutrients leached from cells upon re-inundation (Baldwin and Mitchell 2000). A possible explanation of the extremely high NH_4 flux is that since flow regulation, Lake Alexandrina has essentially acted as a terminal system to the River Murray acting as a depositional zone of nutrients and sediments. The large initial flux of NH_4 would be expected to result in an increase in autotrophic or heterotrophic productivity. However, this may be offset by the increased affinity of sediments for phosphorus unless significant external inputs of phosphorus are supplied. Increased assimilation of nutrients by the heterotrophic microbial community may result in the development of anoxic conditions (Baldwin and Mitchell 2000). Similarly, an increase in the available nutrient pool may increase the standing biomass of phytoplankton since the maximum carrying capacity of phytoplankton will ultimately be limited by nutrient availability (Dillon and Rigler 1974).

Coorong and Murray Mouth

As for the Lower River Murray and Lower Lakes, there have been very few comprehensive studies of nutrient dynamics within the Coorong, despite the ecological significance of the region. Recently Ford (2007) inferred changes in nutrient dynamics from nutrient concentrations, but there remains a lack of knowledge on internal flux rates and factors controlling the flux rates. In common with the Lower River Murray, land-use and flow regime have been identified as important factors controlling nutrient loads delivered and retained in the Lower Lakes.

Salinity as a driver of nutrient dynamics and recent condition

Ford (2007) analysed historical water quality data collected at multiple stations along the Coorong between 1997 and 2003 to develop an understanding of the major biogeochemical processes controlling the availability of nutrients and pelagic primary production. Many of the biogeochemical processes where strongly related to the salinity gradient that exists within the Coorong, with salinity increasing southward and varying seasonally (Ford 2007). It was found that during the study period concentrations of particulate nitrogen and phosphorus were high, due to high phytoplankton biomass but also detrital material. Similarly, concentrations of dissolved organic nitrogen and phosphorus increased southwards along the Coorong faster than the salinity increase indicating that there are sources of these materials in the southern lagoon. In contrast to the relatively high concentrations of nutrients embodied in organic forms, the concentrations of bioavailable forms (ammonium, nitrate, and phosphate) were low. Ford (2007) suggested that there exists tight cycling of nutrients between the organic and inorganic forms, or that the system is either light or nutrient limited and the rate of biomass production is much less than the theoretical maximum.

Haese *et al*. (2009) studied internal processes in the Coorong and found that the limited availability of dissolved inorganic nitrogen for primary production is principally controlled by the production of dissolved organic matter. Confirming Ford (2009), Haese *et al*. (2009) observed that the dissolved organic matter builds up to very high concentrations, suggesting that it is not bioavailable (not broken down readily). Importantly, benthic ammonium and phosphate fluxes were insignificant in the winter and summer, demonstrating that the shallow lagoon margins efficiently transform bioavailable ammonium and retain phosphorous. Ford (2007) suggested that low phosphate concentrations could be explained by co-precipitation of phosphate with calcite, which occurs in hypersaline environments. Benthic primary production was very high along the inundated shallow lagoon margins in the winter and in the summer (Haese *et al*. 2009), suggesting high demand for inorganic nutrients and possibly explaining the low inorganic nutrient flux rates and water column concentrations. Although Haese *et al*. (2009) did not study sediments at greater water depth, they suggested that it is likely that deeper lagoon areas accumulate much detrital biomass and release dissolved nutrients at much greater rate than measured along the shallow margins.

Additional potential drivers of nutrient dynamics

Sediments are a major store of nutrients within aquatic ecosystems (Marsden 1989; Martinova 1993; Søndergaard *et al.* 1993). Nutrients may be released from sediments through a number of processes, including release from decaying organic material and desorption from sediment particles. Under periods of low River Murray inflows, the flux of nutrients from the sediment have been shown to be important in controlling nutrient concentrations in the River Murray (Brookes *et al*. 2008), the Lower Lakes (Aldridge *et al*. 2009) and the Coorong (Haese *et al*. 2009). Since these flux rates are influenced by a variety of factors, not all of have been investigated for the Lower River Murray, Lower Lakes and Coorong. Therefore, it was necessary to provide information on all important factors that have been identified by the scientific literature.

Redox potential, oxygen and the cycling of iron and sulfur

It has been well documented that differences in the reduction-oxidation (redox) potential of sediments may influence the ability of sediments to adsorb and desorb phosphorus (Boon and Sorrell 1991; Jaynes and Carpenter 1986; Mortimer 1941; Mortimer 1942; Spiro and Stigliani 1996; Webster *et al.* unpublished). Redox potential is a measure of the transfer of electrons of a particular system, with reduction involving a gain of electrons and oxidation involving loss of electrons. (Hutchinson 1957; Ruttner 1963; Stumm and Morgan 1970; Ponnamperuma 1972; Spiro and Stigliani 1996). Both processes occur simultaneously and cannot occur without the other. Redox potential is an indicator of aerobic or anaerobic sediment conditions: a positive redox potential signifies a high content of oxidants (aerobic/oxidising conditions), while a negative redox potential signifies a high content of reductants (anaerobic/reducing conditions) (Hutchinson 1957; Ruttner 1963; Stumm and Morgan 1970; Ponnamperuma 1972; Spiro and Stigliani 1996). While there are several oxidants that influence redox potential, oxygen is the most powerful and therefore, has the largest influence on redox potential (Spiro and Stigliani 1996). Redox potential is important for the transfer of phosphorus as it reflects the solubility of mineral ions, primarily iron and manganese, to which nutrients bind on the sediment surface (Mortimer 1941; Mortimer 1942; Oliver 1993; Webster *et al.* 2001).

Iron is the most important binding mineral for phosphorus. Under oxidised conditions, orthophosphates (PO_4^3) strongly adsorb to sediments due to the oxidation of ferrous sulphides into amorphous ferric oxyhydroxides, which have a high affinity for phosphorus (Baldwin 1996; De Groot and Fabre 1993; De Groot and Van Wijck 1993). This oxidised surface layer may also prevent diffusion of phosphorus and reduced mineral ions from deeper sediments (Hutchinson 1957; Moss 1988), including those from the decomposition of sedimented organic particles. If oxygen levels are depleted within the sediment, iron oxyhydroxides are reduced, causing the dissolution of iron and phosphate from the sediment surface. Release of phosphorus from reduced sediments has been shown to be far greater than from oxidised sediments in many lakes throughout the world (Jensen and Andersen 1992; Lennox 1984; Marsden 1989; Mortimer 1941; Mortimer 1942; Sondergaard *et al.* 1993; Stephen *et al.* 1997). With lowered redox potentials alternative electron acceptors are used for the mineralization of organic matter, resulting in the production of reduced products affecting phosphorus cycling in lakes in various ways (Bostrom *et al*. 1988). For example, the ability of sediments to adsorb nutrients may be influenced by the sulfur cycle. If sulfate is readily available in the water column and anaerobic conditions prevail, sulfate reduction can occur, leading to the production of Fe-S compounds (Wetzel 2001). This may result in the displacement of PO_4 bound to mineral ions result in the release of PO_4 from the sediment pool (Wetzel 2001) as was observed in Goolwa Channel during a period of salinisation and water level drawdown (Aldridge *et al*. 2009)

pH

pH has not been found to be a significant driver of change in the Lower River Murray, Lower Lakes or Coorong. This is perhaps largely due to the fact that most studies have been conducted within a relatively narrow pH range. However, pH is known to effect nutrient dynamics in a number of complex and contrasting ways but the influence of pH on nutrient dynamics has received less attention than that of redox potential, as its influence is considered to be less significant. In particular, there appears to be little information available on the influence of pH on nitrogen dynamics. Jensen and Andersen (1992) demonstrated that in aerobic sediment from four Danish lakes water temperature and background nitrate concentrations were more important in controlling phosphorus dynamics than pH. In fact, temperature and nitrate were considered to be important factors in all four lakes, but pH was only important in one lake. However, this study was conducted at pH values of 7.5 -10. pH values of this magnitude are relevant to the region with pH values of greater than 8 considered normal and pH values of up to 9.5 being observed during periods of low River Murray inflow (Cook *et al*. 2008).

Increased pH decreases the phosphorus binding capacity of iron and aluminium compounds, primarily due to ligand exchange reactions in which hydroxide ions replace orthophosphate (Lijklema 1977; Bostrom *et al*. 1988). In, contrast in calcareous lakes, particularly shallow lakes, increased pH may result in the precipitation of $CaCO_3$, with phosphorus co-precipitated or adsorbed to the precipitate (Otsuki and Wetzel 1972; Gunatilaka 1982). Gomez (1999) found that in coastal lagoons under oxic conditions when pH was decreased to 6, calcium bound phosphate was mobilised due to dissolution of this fraction and the liberated phosphate became iron-bound, which may be desorbed if conditions become anoxic.

Acidification may lead to oligotrophication through water column nutrient depletion. This may occur due to the inhibition of decomposition and the release of nutrients. In Scandinavian Lakes it has been found that low pH caused a loss of macrophytes, which were replaced by the moss *Sphagnum* (Hendrey and Vertucci 1980). *Sphagnum* forms a benthic mat that may prevent efficient recycling of nutrients from the sediments. In addition, aluminium may precipitate out phosphorus from the water column and bind it in the sediments in a form which is not sensitive to redox changes (Kopacek *et al*. 2000). Furthermore, acidification can result in a mobilization of magnesium, iron and aluminium to toxic levels, prevent nitrification by inhibiting nitrifying bacteria and depress the availability of phosphorus which precipitates with iron oxides.

Organic carbon

While there have been no direct studies on the influence organic carbon on nutrient dynamics in the region, higher nutrient flux rates from sediments have been observed in sediments containing greater amounts of organic matter (carbon) from both the Lower River Murray (Brookes *et al*. 2008) and Lower Lakes (Aldridge *et al*. 2009). Organic carbon occurs as both living and dead organic matter, the latter usually being split into dissolved and particulate organic carbon (matter) (Wetzel 2001). It is a crucial energy and food source in aquatic ecosystems. However, when excess bioavailable carbon is supplied to lakes the decomposition of organic material may indirectly influence nutrient dynamics through the development of anoxic conditions (Wallace 2006). As the loads of organic matter are increased, the rate of decomposition and the consumption of oxygen for respiration also increase. Consequently, oxygen levels in sediments may fall, resulting in nutrient release from sediments (Wallace 2006). In addition, nutrients are directly released from organic matter as they are decomposed. These nutrients may then be recycled back into the system, taken up by heterotrophic or autotrophic microbial communities (Wetzel 2001). From there nutrients are available to higher trophic levels or are returned to the dead organic matter compartment (Wetzel 2001).

Stratification

As discussed above, stratification has been shown to be an important driver of internal nutrient dynamics during periods of low inflow in the River Murray (Brookes *et al*. 2008) and Lower Lakes (Aldridge *et al*. 2009). Thermal stratification develops when a stable water body is heated from above by solar radiation (Wetzel 2001). As the light passes through the water column its energy is sequentially absorbed and the water is heated. The more light that is absorbed the less light passes down the water column and so there is disproportionate heating of the epilimnion and hypolimnion. Consequently, the water in the epilimnion is less dense than that of the hypolimnion and this buoyancy prevents mixing of the two layers and isolates the hypolimnion from the atmosphere preventing gas exchange with the hypolimnion (Wetzel 2001). Since there is no supply of oxygen from the atmosphere, much of the oxygen may be used during the respiration of organic material that has settled on the bottom of the river or lake (Wetzel 2001). This may reduce oxygen levels to below the tolerance threshold of many organisms. In addition, there is a reduction in the redox potential and so nutrients are released from the sediments into the overlying water column.

Sediment resuspension

Resupsenion is likely to play an important role in diurnal cycles of nutrient dynamics in the Lower Lakes in Coorong due to their shallow nature. However, no one has investigated the role of sediment resuspension. The resuspension of deposited sediments by wave activity plays an important role in structuring lake ecosystems, particularly in shallow lakes. Sediment resuspension may influence primary and secondary productivity of an ecosystem by influencing nutrient availability. Particulate nutrients may increase due to resuspension since high concentrations of particulate nutrients are found within the sediments. Depending on the particular properties of the lake water and sediment, resuspension may either increase, decrease or have no effect on the dissolved nutrient concentration (Andersen 1974; De Groot 1981; Peters and Cattaneo 1984). In many cases, resuspension is likely to lead to release of dissolved nutrients. There are a number of alternative mechanisms for this including a release of PO_4 from the porewater and increased mineralisation of organic matter due to the oxic conditions occurring during resuspension (Sondergaard *et al.* 1992). The extent of resuspension will depend upon wind, sediment character, water depth, lake bathymetry and the presence of macrophytes.

Salinity

As discussed previously, salinity has been shown to be an important driver of internal nutrient flux rates in the Coorong and Lower Lakes. There is a general consensus of increasing ammonium concentrations due to increasing salinity levels resulting in increased competition of ammonium ions with other cations for binding sites of sediment (Baldwin *et al.* 2006; Laverman *et al.* 2007; Rysgaard *et al.* 1999). This has been shown to reduce nitrification through reduced sediment ammonium concentrations and inhibitory effects on nitrifying bacteria (Rysgaard *et al.* 1999). Similarly, reduced denitrification rates have been observed with increasing salinity (Rysgaard *et al.* 1999), although denitrification is considered to be greater in marine than freshwater (Seitzinger 1988), both due to differences in nitrate availability rather than salinity itself. In addition, nitrate reduction has been shown to increase with salinity due to increased mobilisation of organic matter and nitrogen fixation by planktonic organisms is generally greater in freshwater, but this is generally regulated by nutrient status of the water body rather than salinity (Howarth *et al.* 1988).

Baldwin *et al.* (2006) found decreased phosphorus concentrations with increasing salinity due to increased solubilisation of iron and precipitation of PO_4 with iron. In the study of Baldwin *et al.* (2006) only sodium chloride was used as a source of salinity. However, in reality part of an increase in salinity is likely to be a result of increased sulfate concentrations. As discussed above, this has implications for phosphorus cycling. Under anaerobic conditions, sulfate reduction can occur, leading to the production of Fe-S compounds and the release of PO_4 from the sediment pool (Wetzel 2001). Many of the biogeochemical processes involved in nitrogen cycling occur in the sediments and are also affected by the higher sulfide concentrations under elevated salinities. Both nitrification and denitrification are inhibited, while dissimilatory nitrate reduction to ammonium (DNRA) and nitrogen fixation are stimulated by sulfide (Ford 2007). Consequently high salinity waters will favour a high ammonium:nitrate ratio in the water column and an increase in organic nitrogen stored in detrital material, while low salinity waters are more likely to be dominated by nitrate and have significant losses of bioavailable nitrogen through denitrification (Ford 2007).

These biogeochemical processes are further complicated by changes in physical conditions as a result of salinisation. For example, increasing salinity can alter light penetration through salt induced aggregation and flocculation of suspended material (Grace *et al.* 1997a) and so increase pelagic and benthic productivity and demand for nutrients. Furthermore, increased ionic strength can lead to salinity stratification (Nielsen *et al.* 2003), reducing oxygen penetration into sediments shifting biogeochemical cycling from aerobic to anaerobic processes (Donnelly *et al.* 1997), which as discussed above, is known to have a major effect on nutrient fluxes from sediments.

Water level and drying-reflooding cycles

Changes in water level and subsequent drying-wetting cycles have major implications for the biogeochemistry of inland water, particularly in the variable climates. These cycles occur on a wide range of temporal scales from daily (tidal influence), to seasonal and beyond (related to magnitude of inflows). Much of our knowledge on these impacts of drying and wetting have been found in floodplains and wetlands.

The major effects of drying of previously inundated sediments are to the mineralogy and microbial ecology, both of which respond to increasing oxygen concentrations within the sediment (Baldwin and Mitchell 2000). As water levels fall, the oxygen penetration depth within sediments will increase. This is initially due to increased delivery of oxygen rich water to the sediments. As sediments begin to dry oxygen penetration will continue to increase due to contact with the atmosphere and finally through the development of cracks accompanying the loss of moisture. The increasing oxygen concentrations will influence the mineralogy by causing the oxidation of reduced mineral phases (Baldwin and Mitchell 2000). The most notable change that influences nutrient cycling is the oxidation of ferrous sulfides into amorphous ferric oxyhydroxides which have a high affinity for phosphorus (De Groot and Van Wijck 1993). This is thought to be responsible for the increase in affinity for phosphorus of aerated sediments (De Groot and Fabre 1993; Baldwin 1996). However, as drying continues, the affinity of sediments for phosphorus has been shown to reduce due to oxyhydroxides becoming crystalline (Lijklema 1980), reducing the number of phosphorus binding sites (Sah *et al.* 1989; Qiu and McComb 1994; Baldwin 1996).

The penetration of oxygen into inundated sediments during drying will also influence nutrient cycling by altering the microbial composition and activity (Baldwin and Mitchell 2000). Initially, the expansion of the oxygen penetration depth may allow aerobic and anaerobic nutrient cycling processes to occur concurrently (Baldwin and Mitchell 2000). These process rates may be enhanced by the coupling of processes such as nitrification and denitrification, with denitrification rates enhanced by the presence of nitrification through the provision of nitrate (Knowles 1982). As oxidation continues however, obligate anaerobic heterotrophs will be killed or form resting stages (Lynch and Hobbie 1988), thus reducing the rate of the processes that they carry out. Furthermore, the loss of moisture from the soil as sediments continue to dry will result in a further decrease in bacterial biomass and activity (De Groot and Van Wijck 1993) and extreme drying will result in high bacterial mortality and cell lysis (West *et al.* 1988; Qiu and McComb 1994).

Upon re-inundation lysed cells may leach nutrients resulting in the flux of large amounts of nutrients into the porewater and overlying water column (Sah *et al.* 1989; Mitchell and Baldwin 1999; Baldwin and Mitchell 2000; Baldwin *et al.* 2005). This is thought to result in increased rates of microbial activity, including rates of nitrification and denitrification (Baldwin and Mitchell 2000) if microbial communities have survived the desiccation processes. Denitrifying bacteria are predominately facultative anaerobes (Knowles 1982) and so drying-reflooding cycles have been shown not to reduce denitrification rates (Kern *et al.* 1996). However, if obligate anaerobes are dominant then rates of microbial processes will presumably be lower upon re-inundation than prior to drying.

Recently, Aldridge *et al*. (2009) investigated the influence of dyring-reflooding cycles on sediments of Lake Alexandrina. They compared coarser sediments that are found largely on the peripheral of the lake (many of which are now exposed) to finer sediments found in the centre of the lake (most of which is still inundated, but some is now exposed). They found that drying-reflooding cycles enhanced the short-term flux of nutrients from the sediment and the nutrient flux from finer sediments, particularly ammonium, was far greater from finer sediments than coarser sediments of Lake Alexandrina (Aldridge *et al*. 2009). However, the longer term response of sediment nutrient flux to complete dyring and the impacts of partial drying is no understood in the region.

Interactions with benthic invertebrates

The roles of various benthic invertebrates in controlling nutrient flux rates in the region have not been investigated. Heterotrophic microorganisms play direct and indirect roles in phosphorus adsorption and desorption from sediments. Indirectly, microorganisms may alter the redox potential of the sediments and so affect their phosphorus sorption capacity. Heterotrophic microorganisms use dissolved oxygen, nitrate (NO_3), SO_4^2, Fe as electron acceptors during the oxidation of organic matter and so are themselves reduced (Wetzel 2001). Consequently, the ions become soluble and are released into the water column, along with the phosphorus to which they were bound. In addition, microbial respiration and the decay of organic matter can result in the direct release of phosphorus into the interstitial water, which can then diffuse into the overlying water column (Kalff 2002). This phosphorus is organic or colloidal polyphosphate phosphorus. Alternatively, oxygen production by benthic autotrophs may maintain oxic conditions within the sediment and so promote phosphorus adsorption.

Benthic macroinvertebrates can also promote phosphorus release and uptake into the sediments. Burrowing, filtering, feeding and excreting activity at the sediment-water interface can increase the amount of phosphorus released from oxic sediments by disturbing the oxic layer of sediments (Kalff 2002). This process is known as bioturbation. In addition, macroinvertebrate activity can also increase the dissolved oxygen flux to the sediments, thus increasing the phosphorus adsorbing capacity (Kalff 2002).

Interaction with phytoplankton and macrophytes

The roles of phytoplankton and macrophytes in controlling nutrient flux rates in the region have not been investigated. Phytoplankton and macrophytes access nutrients from the water column, converting them to organic forms that may be transferred up the food chain. Phytoplankton and macrophytes compete for nutrients and so increase overall demand for nutrients. Although sorption is controlled by redox potential, changes in water and sediment concentrations are restricted by the equilibrium that exists between pore-water and water column concentrations. If water column concentrations are reduced by phytoplankton growth under oxic conditions then there is an upward flux of phosphorus from pore-water (unbound) to the water column. However, there is no flux of phosphorus attached to the sediment. If nutrients in the water column are depleted under anoxic conditions, nutrients are desorbed from the sediments into the pore-water (Kalff 2002). Since the pore-water and water column are in equilibrium there would be an enhanced flux of nutrients into the hypolimnion, which is sufficient to enhance phytoplankton growth (Webster *et al.* 2001).

Macrophytes also influence nutrient dynamics indirectly. The roots and rhizomes of macrophytes often have to tolerate anoxic and reducing sediments (Brix *et al.* 1992; Carpenter *et al.* 1983; Chabbi *et al.* 2000; Chen and Barko 1988; Flessa 1994; Sorrell 1994; White and Ganf 1998). Under these conditions there is a limited supply of oxygen (Sculthorpe 1967; Sorrell 1994; White and Ganf 1998; White and Ganf unpublished) available to meet the metabolic oxygen demand of the below ground biomass. Consequently, macrophytes have evolved adaptive mechanisms to internally transport air (oxygen) from the shoot system. Some oxygen is eventually released into the surrounding sediment (Boon and Sorrell 1991; Brix *et al.* 1992; Carpenter *et al.* 1983; Carpenter and Lodge 1986; Chabbi *et al.* 2000; Chen and Barko 1988; Flessa 1994; Jaynes and Carpenter 1986; Sorrell 1994; Wigand *et al.* 1997). This release of oxygen may increase the redox potential of the surrounding sediment and increase the capacity of sediments to store nutrients (Boon and Sorrell 1991; Carpenter *et al.* 1983; Chen and Barko 1988; Christensen *et al.* 1994; Flessa 1994; Jaynes and Carpenter 1986; Wigand *et al.* 1997; Aldridge and Ganf 2003). Macrophytes also reduce the release of nutrients from sediments by reducing porewater concentrations and so reducing diffusion rates; and by preventing resuspension of oxic surface layer of sediments that the inhibits the movement of nutrients from underlying anoxic sediments into the water column (Sondergaard *et al*. 1992).

Phytoplankton

Background

Plankton can be considered to be plants and animals adapted to suspension in the sea or in fresh waters, which is liable to passive movement by wind and current (Reynolds 1984). Phytoplankton of freshwater environments include representatives of several groups of algae and bacteria, as well as the infective stages of certain actinomycetes and fungi (Reynolds 1984). However, phytoplankton are generally considered to be photosynthetic algae and bacteria (Reynolds 1984). Phytoplankton make a large contribution to the total primary productivity of freshwater and marine ecosystems and so are important energy sources for these foodwebs (Wetzel 2001).

Phytoplankton have no or limited powers of locomotion and are therefore more or less subject to the distribution by water movements (Wetzel 2001). Certain planktonic algae move by means of flagella or possess various mechanisms that alter their buoyancy (Wetzel 2001). Phytoplankton are largely restricted to lentic waters and large rivers with relatively low current velocities and are rapidly fragmented or killed by abrasion of turbulence in fast flowing environments (Wetzel 2001).

Phytoplankton consist of a diverse range of species from a number of distantly related phylogenetic groups. A selection of the more common phylogenetic groups found in the Lower River Murray, Lower Lakes and Coorong including:

- Cyanophyta (cyanobacteria or blue-geen algae)
- Chlorophyta (green-algae)
- Bacillariophyta (diatoms)
- Euglenophyta
- Dinophyceae (dinoflagellates)

Detailed description of the phytoplankton groups are provided in Appendix 2.

Phytoplankton in the Lower River Murray, Lower Lakes, Coorong and Murray Mouth

Lower River Murray

Despite the occurrence of algal blooms within the Murray-Darling River and their importance as a carbon supply for the Murray River (Oliver and Merrick 2006), there have been few detailed studies of phytoplankton in the Lower River Murray. Of the information that has been collected, much of it has focussed on only problematic species. Of greatest concern are those species that are toxic, including:

- *Anabaena circinalis*
- *Anabaena smithii*
- *Aphanizomenon ovalisporum*

- *Cylindrospermopsis raciborskii*
- *Gymnodinium*
- *Microcystis aeruginosa*
- *Nodularia spumigena*
- *Prorocentrum*
- *Protoperidinium*
- *Planktolyngbya subtilis* – although generally considered non toxic it is suspected of toxicity

Flow as the primary driver of phytoplankton communities

Flow is a major factor determining the phytoplankton abundance and species composition in Australian lowland rivers (Burch *et al*. 1994; Hotzel and Croome 1994; Sherman *et al.* 1998). This is due to some species being reliant upon flow for movement through the water column, without which they would settle to the sediment where they would be unable to access light for photosynthesis. In comparison, others are motile and under low flow conditions are able to move from the sediment (to access nutrients) to the surface of the water column (to access light).

In the River Murray at Morgan there was a transition between the dominant species *Aulacoseira granulata* and *Anabaena* spp. which was highly dependent on flow. During periods of high flow (>10,000 ML day^{-1}) the diatom *Aulacoseira granulata* dominates. At low flows *Aulacoseira* tends to sediment out of the photic zone and growth cannot be sustained (Condie and Bormans 1997). The incidence of *Anabaena* spp. has been observed to be restricted to daily flows less than 6000 ML day^{-1} (Burch *et al*. 1994) which coincides with periods of stratification (Bormans and Webster 1997; Bormans *et al*. 1997).

When flow is moderate (ca. 10,000 ML d^{-1}), diurnal stratification occurs if wind strength is low (<1.2 ms^{-1}). During periods of low flow, equivalent to summer entitlement flows (4,000 ML d^{-1}), turbulence is sufficiently low to allow some degree of thermal stratification, provided that wind strength is low to moderate (<3 ms^{-1}). Persistent stratification may result when wind speed is <1.2 ms^{-1} (and flow is low), while diurnal stratification is more likely at wind speeds between 1.2 – 3 ms^{-1}. Irrespective of flow, high wind speed (>3 ms^{-1}) will disrupt thermal stratification and result in a mixed water column.

On some occasions relatively high concentrations of *Anabaena* were observed during high but receding flow. It is believed that these populations originated in lagoons adjacent to the main river channel but with a hydraulic connection (Burch *et al*. 1994; Webster *et al.* 1997; Baker *et al*. 2000). The wetland lagoons are shallow, provide a good habitat for cyanobacteria and often record higher cyanobacterial numbers than the main river channel. As the river hydrograph recedes, the wetlands drain back into the main river channel and may contaminate the river with cyanobacteria.

Nutrient limitation

During the summer of 1995/1996 nutrient growth bioassays and FDA-conversion bioassays (Brookes *et al*. 2000) revealed nitrogen limitation on several occasions in the lower River Murray and the nitrogen present was essentially unavailable for growth. In contrast, phosphorus limitation was detected on only one occasion and between 8 and 70% of the total phosphorus was bioavailable (Baker *et al*. 2000). It is likely that although phosphorus may ultimately limit total phytoplankton biomass, low nitrogen concentrations in the River Murray favour heterocystic nitrogen-fixing species such as *Anabaena circinalis* and *Anabaena flos-aquae* while limiting the growth capacity of non-nitrogen fixing species such as *Microcystis aeruginosa*. Physical conditions in the lower River Murray during summer are similar to those that favour growth of *Microcystis* (Ganf 1974), but populations of *Microcystis* did not become established during the study period nor in any other year for which there are records (Brookes *et al*. 2000). The particular combination of physical and chemical conditions presumably favoured the growth of *Anabaena* in preference to non-nitrogen fixing cyanobacteria, albeit at sub-optimum conditions.

In the summer of 1995/96 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 (Shafron *et al*. 1990). In the summer of 1996/97, a higher contribution of Darling River water resulted in elevated levels of both nitrogen and phosphorus in the lower River Murray and consequently the non-nitrogen fixing cyanobacterium *Planktothrix perornata* was found in relatively high abundance (Baker 1999). Indeed, *Planktothrix* is an indicator of turbid, mixed layers according to the classifications system of Reynolds (2002).

Recent condition

Hipsey *et al*. (2009) reviewed recent phytoplankton data from the Lower River Murray. From the limited data that was available, it was apparent that there were strong seasonal changes in phytoplankton abundance, with chlorophyll concentrations peaking in summer in the river. However, there were no apparent changes in chlorophyll concentrations between 1998 and 2008. Cyanobacterial concentrations on the other hand, appear to have increased and were particularly high in the summer of 2007/08. A better temporal coverage of analyses was conducted for a large number of individual algal groups that are of concern to SA Water in the River Murray (e.g., *Anabaena circinalis*, *Aphanizomenon* spp. and *Cylindrospermopsis raciborskii*). No clear spatial patterns are evident for these algae, although highest values were observed in summer months, particularly in the summer of 2007/08 for *Aphanizomenon* and *C. raciborskii*. There appeared to be a general increase in concentrations of all 3 species during the observation period, as well as for the chlorophyte *Ankistrodesmus*. Cell counts for the diatom *Aulacoseira* were patchy in time and space, so temporal and spatial trends are unclear. However, the available data does not indicate the same long-term increasing trend. In contrast to the annual patterns of the high cyanobacteria concentrations in summer, higher cell counts for *Aulacoseira* tended to appear in the spring.

Lower Lakes

Although our limnological understanding of the Lower Lakes is generally poor, it is a historically important site, as it was the site of the first detailed scientific account of toxic cyanobacteria (Francis 1978; Codd *et al*. 1994). However, there have been few studies on the composition of the phytoplankton community and the important drivers.

Nutrients and turbidity as drivers of phytoplankton communities

Paleolimnological studies have demonstrated that following European settlement the diatom community has changed, reflecting the altered salinity regime and increased nutrient inputs from upstream agriculture (Fluin *et al.* 2007). Geddes (1984a) concluded that the total phosphorus (TP) and Total Kjeldahl nitrogen (TKN) levels placed Lake Alexandrina in the eutrophic-hypereutrophic category of Vollenweider (1968) and places Lake Alexandrina in the eutrophic category for Australian waters (Walker and Hillman 1977). Despite the eutrophic- hypereutrophic status, Geddes (1984a) suggested that Lake Alexandrina was a marginal environment for phytoplankton growth, primarily due to the highly turbid environment (mean value of 92.7 NTU in 1963-1978). Within Lake Alexandrina turbidity is recognised as one of the key factors determining phytoplankton community structure (Geddes 1984a, 1988, Baker 2000). Geddes (1984a) also proposed that the availability of nutrients for phytoplankton growth could be the limiting factor at certain times of the year. Although the TKN and TP levels were high, levels of NOx and FRP were low, suggesting that most nutrients are in particulate form and biologically unavailable.

The filamentous green algae *Planctonema lauterbornii* accounted for more than 95% of algal cells in Lake Alexandrina from 1975 to 1978. The dominance of P*. lauterbornii* in Lake Alexandrina during this period is attributed to high turbidity, low light availability and high nitrogen and phosphorus levels (Geddes 1988, Baker 2000). Conversely, moderate to low nutrients, low turbidity and high light availability promote the growth of cyanobacteria, in particular *Nodularia spumigenia*, *Anabaena* spp. and *Aphanizomenon* spp (Baker 2000). Baker (2000) reported that the occurrence of *N. spumigenia* in the summer /autumn of 1990/91 and 1995 was associated with low flow (<10000ML/day), moderate turbidity (<50NTU), low conductivity (400EC-1100EC) and variable nutrient concentrations.

Cyanobacterial blooms have regularly occurred in Lake Alexandrina and Lake Albert between 1990 and 1995 during extended periods of low flow, low turbidity and low turbulence (P. Baker, Australian Water Quality Centre, *personal communication*). Lake Alexandrina and Lake Albert have been experiencing blooms (>15 000cells/mL) of picocyanobacteria (*Aphanocapsa* spp, *Planktolyngbya* spp., *Aphanizomenon* spp. and *Pseudanabaena* spp.) regularly between August 2008 and September 2009 (see recent condition described below). In addition, the first recorded bloom of *Cylindrospermopsis raciborskii* occurred in the Lower Lakes in 2006 (Cook *et al*. 2008).

Recent condition of the Lower Lakes

From January 2007 until present a detailed water quality monitoring project has been conducted by the University of Adelaide (Kane Aldridge, Justin Brookes, Dominic Skinner and Alex Payne). This project has been funded by Land and Water Australia, the South Australian Murray-Darling Basin Natural Research Management Board and the South Australian Environmental Protection Authority.

As part of this project, samples have been collected for algal identification. During each sampling trip, integrated water samples were collected and immediately preserved in lugol's iodine and full algal identification and counts were conducted by the Australian Water Quality Centre. Samples have been analysed from a total of 10 sites in the Lower Lakes. For the purposes of this study, data is presented from sites that had the most comprehensive data-set, which appropriately represented Goolwa Channel ("Goolwa"), Lake Alexandrina ("Lake Alexandrina Middle"), Pomanda Embayment

("Lake Alexandrina Opening") and Lake Albert ("Lake Albert Middle"). Overall, there were a wide range of phytoplankton species present in the Lower Lakes, including species from six phylogenetic groups (Cyanobacteria, Chlorophyta, Bacillariophyta, Cryptophyta, Euglenophyta and Dinophyceae) and over 50 genera (Table 1).

The study period was a period of rapid change in the Lower Lakes, with changes to a number of parameters that influence phytoplankton communities including; decreased water level; increased salinity; increased prevalence of salinity stratification in Goolwa channel; increased dissolved inorganic nutrient concentrations, particularly in Goolwa channel; and increased suspended solids (Aldridge *et al*. 2009). All of these concurrent changes have contrasting effects on phytoplankton communities and as a result the species response to any one variable was difficult to detect. Overall, at the species/genus level, phytoplankton communities were highly unpredictable as seen in Figure 3.

Table 1. Genera and group list for the Lower Lakes, January 2007 to June 2009. For the main bodies of Lake Alexandrina and Lake Albert the dominant genera highlighted in bold-black, For Goolwa channel the dominant genera highlighted in bold-grey.

Phylogenetic group	Genera
Cyanobacteria	*Anabaena, Anabaenopsis,* ***Aphanizomenon*****,** ***Aphanocapsa****, Chroococcus, Coelosphaerium, Cylindrospermopsis, Geitlerinema, Merismopedia, Microcystis,* ***Nodularia****, Phormidium,* ***Planktolyngbya*****,** ***Pseudanabaena****, Pseudanabaena*,* ***Synechococcus****, Synechococcus*,* ***Synechocystis****, Trichodesmium*
Chlorophyta	***Ankistrodesmus****, Ankyra ,Aulacoseira, Chlamydomonas,* ***Chlorella****, Chodatella, Closteriopsis, Closterium, Crucigenia, Dictyosphaerium, Kirchneriella, Micrasterias, Monoraphidium, Nephrocytium, Oocystis, Pediastrum, Planctonema, Scenedesmus, Schroedaria, Staurastrum, Tetraedron, Tetrastrum*
Bacillariophyta	***Cyclotella****, Licmophora, Navicula, Nitzschia, Staurosira, Synedra*
Cryptophyta	*Chroomonas,* Cryptomonadaceae species, *Cryptomonas,* Cryptophyceae species
Euglenophyta	*Euglena*
Dinophyceae	*Glenodinium, Gymnodinium, Katodinium, Prorocentrum, Protoperidinium*

** denotes genus morphological similar to that listed*

In order to assess the current condition of the Lower Lakes phytoplankton community, a number of approaches were tested, not all of which were possible due to lack of available information on the species present within the Lower Lakes. A description of each approach attempted is provided since it provides useful information on knowledge gaps for the region and phytoplankton ecology in general.

The problems associated with an extremely high level of variability found within phytoplankton communities and a high level of unpredictability at a species level has led scientist to classify species into functional groups. The aim of this approach is to allow predictions of which functional groups are likely to dominate under particular conditions, rather than which species, which has proven difficult. This approach was first developed by Reynolds (1997).

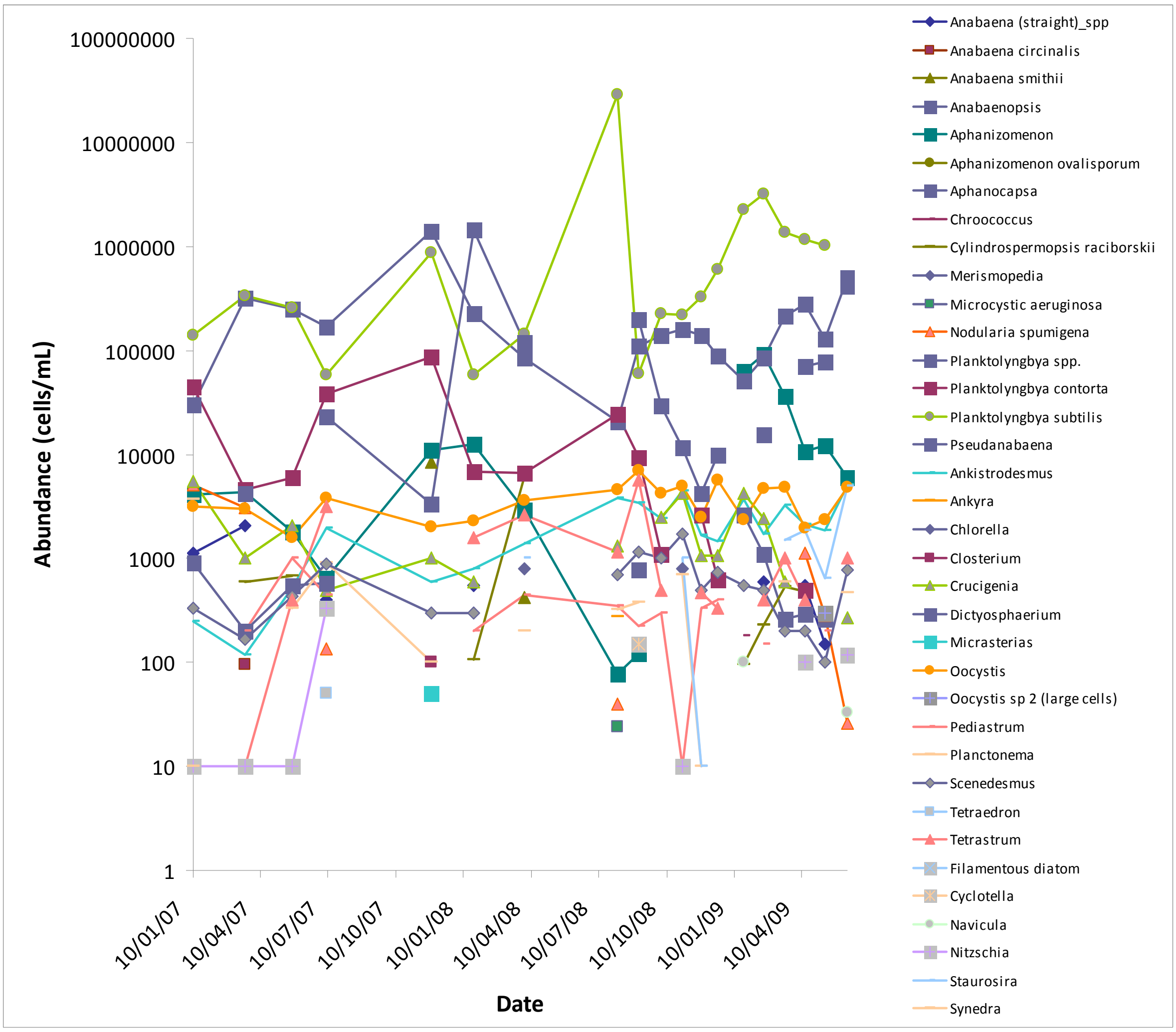


Figure 3. Phytoplankton abundance in Lake Alexandrina, January 2007 to June 2009.

Attempts were made to classify all species currently found in the Lower Lakes into the functional groups of Reynolds (2002) (See Table 2 for classification and Table 3 for application of the functional group approach to the Lower Lakes). This has potential to be a powerful tool for the Lower Lakes as it not only provides an indication of the condition of the phytoplankton community but may also be used to indicate the overall condition of the Lower Lakes ecosystem. Unfortunately, with our current knowledge only half of the species could be classified into such a table.

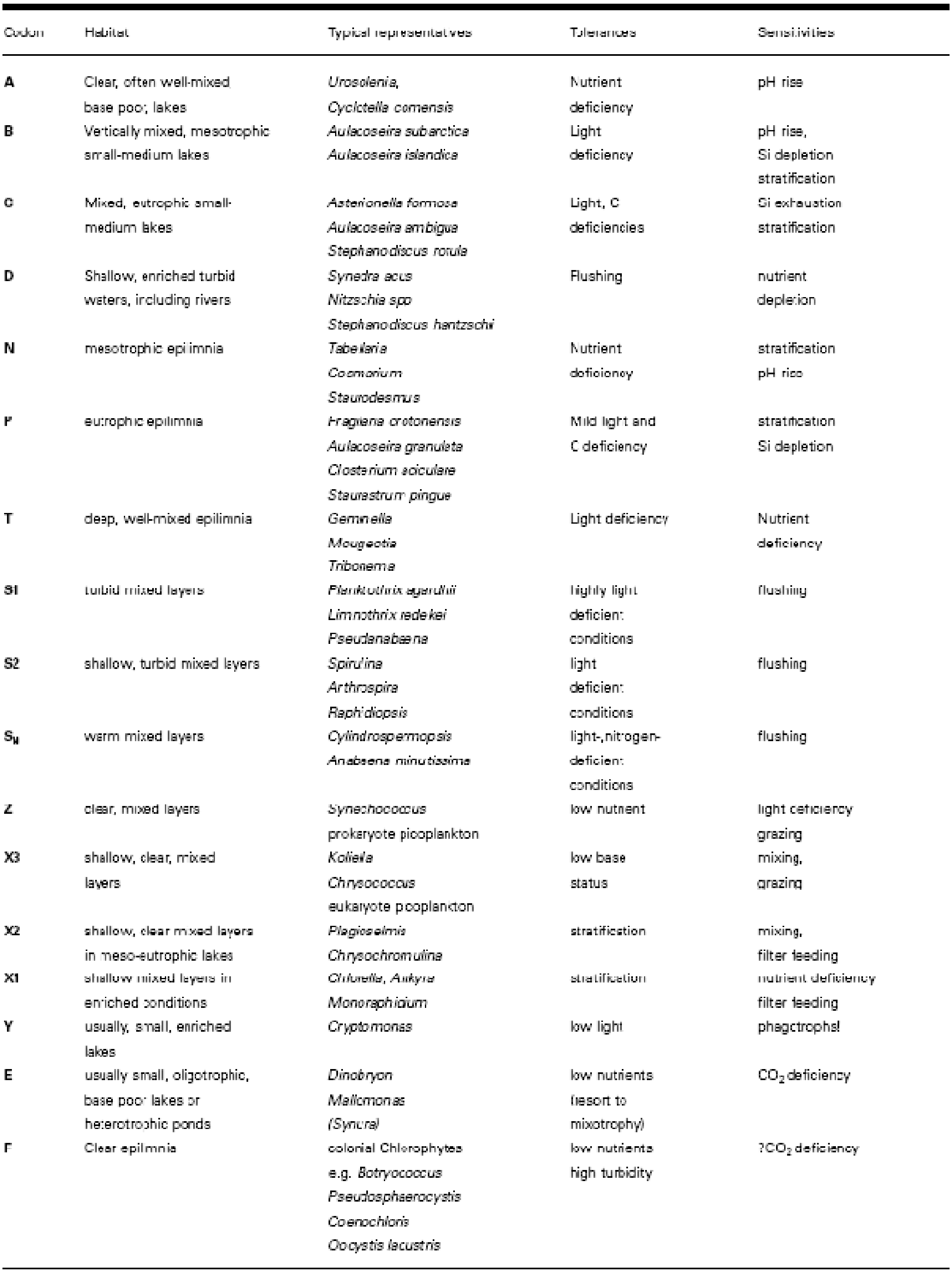
It is important to note that this application is mainly relevant to the species level. Information was only available at the genera level and so must be used with caution. Nevertheless, the dominant genera in the Lower Lakes that have been classified by Reynolds (2002), are:

- Lake Alexandrina and Lake Albert
    - *Aphanizomenon* – Habitat: Dinitrogen-fixing Nostocaleans (tolerant of low nitrogen, sensitive to mixing and poor light)
    - *Aphanocapsa* – Habitat: short, nutrient-rich columns (sensitive to deep mixing)
    - *Pseudoanabaena* – Habitat: turbid, mixed layers (tolerant of highly light deficient conditions, sensitive to flushing)
- Goolwa channel
    - *Synechococcus* – Habitat: clear, mixed layers (tolerant of low nutrients, sensitive to light deficiency and grazing)
    - *Chlorella* – Habitat: shallow mixed layers in enriched conditions (tolerant of stratification, sensitive to nutrient deficiency and filter feeding)
    - *Cyclotella* – Habitat: clear, often well mixed, base poor lakes (tolerant of nutrient deficiency, sensitive to pH rise)

Some of the indications of this classification system fit reasonably well for the Lower lakes. For Lake Alexandrina and Lake Albert, the presence of *Pseudoanabaena* suggests turbid, mixed layers and it is sensitive to flushing which has not occurred during the study period. In contrast, the presence of *Aphanizomenon* suggests low nitrogen conditions whereas the presence of *Aphanocapsa* suggests nutrient rich conditions. Similar findings were observed for Goolwa channel with the indicator species suggesting well mixed conditions, or at least well mixed layers. However, there was a near permanent presence of salinity stratification at Goolwa during the study period (Aldridge *et al*. 2009). However, the indicator species also suggest clear conditions, which was the case in Goolwa channel. These species also suggest an absence of predators (zooplankton and filter feeders) and nutrient limitation in Goolwa channel during the study period.

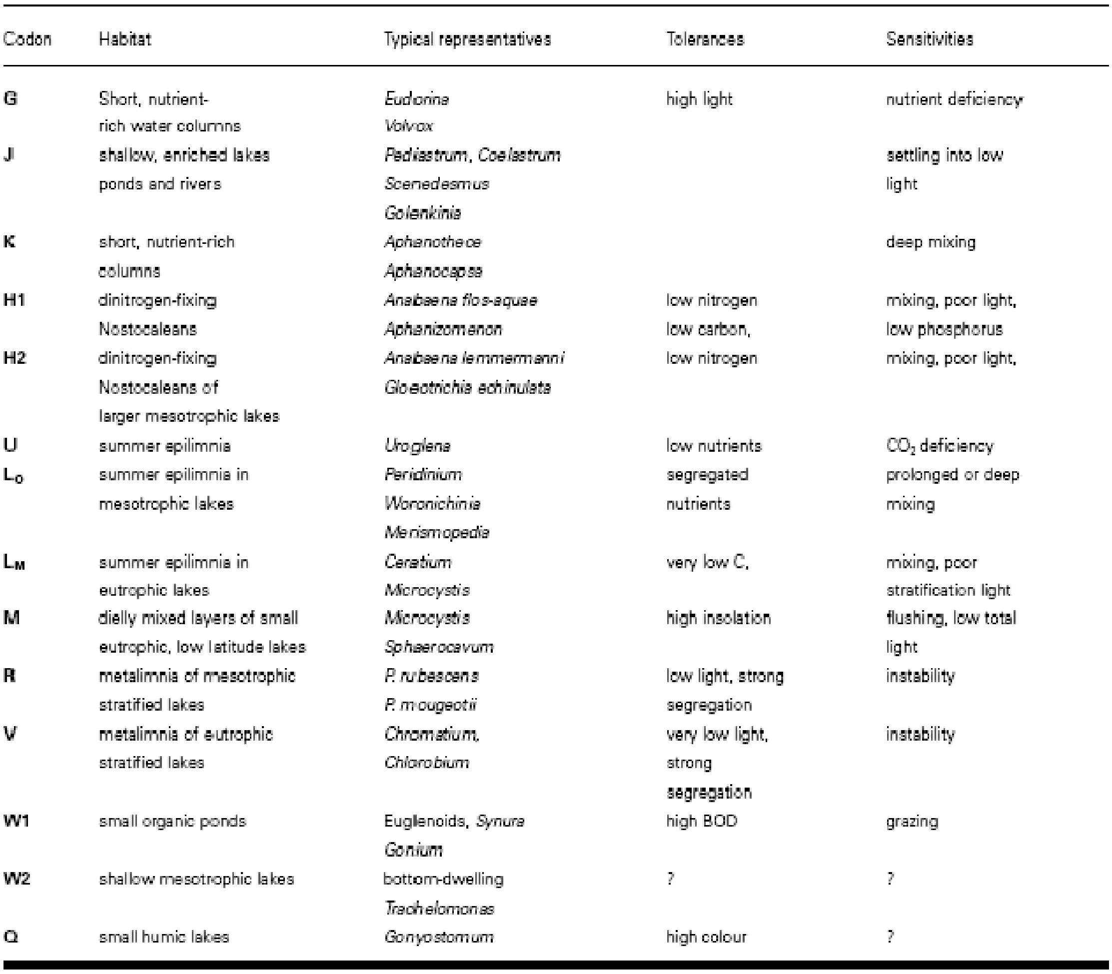
It appears that the classification system may be a suitable approach to investigate in the future to provide an indication of lake condition and status of the phytoplankton community.

Table 2. Trait-separated functional groups of phytoplankton (from Reynolds, 2002)



Codon	Habitat	Typical representatives	Tolerances	Sensitivities
A	Clear, often well-mixed base poor lakes	*Urosolenia,* *Cyclotella comensis*	Nutrient deficiency	pH rise
B	Vertically mixed, mesotrophic small-medium lakes	*Aulacoseira subarctica* *Aulacoseira islandica*	Light deficiency	pH rise, Si depletion stratification
C	Mixed, eutrophic small-medium lakes	*Asterionella formosa* *Aulacoseira ambigua* *Stephanodiscus rotula*	Light, C deficiencies	Si exhaustion stratification
D	Shallow, enriched turbid waters, including rivers	*Synedra acus* *Nitzschia spp* *Stephanodiscus hantzschii*	Flushing	nutrient depletion
N	mesotrophic epilimnia	*Tabellaria* *Cosmarium* *Staurodesmus*	Nutrient deficiency	stratification pH rise
P	eutrophic epilimnia	*Fragilaria crotonensis* *Aulacoseira granulata* *Closterium aciculare* *Staurastrum pingue*	Mild light and C deficiency	stratification Si depletion
T	deep, well-mixed epilimnia	*Geminella* *Mougeotia* *Tribonema*	Light deficiency	Nutrient deficiency
S1	turbid mixed layers	*Planktothrix agardhii* *Limnothrix redekei* *Pseudanabaena*	highly light deficient conditions	flushing
S2	shallow, turbid mixed layers	*Spirulina* *Arthrospira* *Raphidiopsis*	light deficient conditions	flushing
S_N	warm mixed layers	*Cylindrospermopsis* *Anabaena minutissima*	light-, nitrogen-deficient conditions	flushing
Z	clear, mixed layers	*Synechococcus* prokaryote picoplankton	low nutrient	light deficiency grazing
X3	shallow, clear, mixed layers	*Koliella* *Chrysococcus* eukaryote picoplankton	low base status	mixing, grazing
X2	shallow, clear mixed layers in meso-eutrophic lakes	*Plagioselmis* *Chrysochromulina*	stratification	mixing, filter feeding
X1	shallow mixed layers in enriched conditions	*Chlorella, Ankyra* *Monoraphidium*	stratification	nutrient deficiency filter feeding
Y	usually, small, enriched lakes	*Cryptomonas*	low light	phagotrophs!
E	usually small, oligotrophic, base poor lakes or heterotrophic ponds	*Dinobryon* *Mallomonas* *(Synura)*	low nutrients (resort to mixotrophy)	CO_2 deficiency
F	Clear epilimnia	colonial Chlorophytes e.g. *Botryococcus* *Pseudosphaerocystis* *Coenochloris* *Oocystis lacustris*	low nutrients high turbidity	?CO_2 deficiency

Table 3 continued



Codon	Habitat	Typical representatives	Tolerances	Sensitivities
G	Short, nutrient-rich water columns	*Eudorina* *Volvox*	high light	nutrient deficiency
J	shallow, enriched lakes ponds and rivers	*Pediastrum*, *Coelastrum* *Scenedesmus* *Golenkinia*		settling into low light
K	short, nutrient-rich columns	*Aphanothece* *Aphanocapsa*		deep mixing
H1	dinitrogen-fixing Nostocaleans	*Anabaena flos-aquae* *Aphanizomenon*	low nitrogen low carbon,	mixing, poor light, low phosphorus
H2	dinitrogen-fixing Nostocaleans of larger mesotrophic lakes	*Anabaena lemmermanni* *Gloeotrichia echinulata*	low nitrogen	mixing, poor light,
U	summer epilimnia	*Uroglena*	low nutrients	CO_2 deficiency
$\mathbf{L_O}$	summer epilimnia in mesotrophic lakes	*Peridinium* *Woronichinia* *Merismopedia*	segregated nutrients	prolonged or deep mixing
$\mathbf{L_M}$	summer epilimnia in eutrophic lakes	*Ceratium* *Microcystis*	very low C,	mixing, poor stratification light
M	dielly mixed layers of small eutrophic, low latitude lakes	*Microcystis* *Sphaerocavum*	high insolation	flushing, low total light
R	metalimnia of mesotrophic stratified lakes	*P. rubescens* *P. mougeotii*	low light, strong segregation	instability
V	metalimnia of eutrophic stratified lakes	*Chromatium*, *Chlorobium*	very low light, strong segregation	instability
W1	small organic ponds	Euglenoids, *Synura* *Gonium*	high BOD	grazing
W2	shallow mesotrophic lakes	bottom-dwelling *Trachelomonas*	?	?
Q	small humic lakes	*Gonyostomum*	high colour	?

Table 3. Trait based functional groups of phytoplankton genera for the Lower Lakes, January 2007 to June 2009. For the main bodies of Lake Alexandrina and Lake Albert the dominant genera highlighted in bold-black. For Goolwa channel the dominant genera highlighted in bold-grey. Note that the trait-based approach is generally relevant to the species level.

Phylogenetic group	Genera	Codon	Indicator species	Habitat	Tolerance	Sensitivity
Cyanobacteria	*Anabaena*	S_N	*Anabaena minutissimaa*	Warm mixed layers	Light, nitrogen deficient conditions	Flushing
		H1	*Anabaena flos-aquae*	Dinitrogen-fixing Nostocaleans	Low nitrogen, low carbon	Mixing, poor light
		H2	*Anabaena lemmemnanni*	Dinitrogen-fixing Nostocaleans of larger mesotrophic lakes	Low nitrogen	Mixing, poor light
	Anabaenopsis	Information not available				
	Aphanizomenon	H1	*Aphanizomenon spp*	Dinitrogen-fixing Nostocaleans	Low nitorgen, low carbon	Mixing, poor light
	Aphanocapsa	K	*Aphanocapsa spp*	Short, nutrient-rich columns	---	Deep mixing
	Chroococcus	Information not available				
	Coelosphaerium	Information not available				
	Cylindrospermopsis	S_N	*Cylindrospermopsis spp*	Warm mixed layers	Light, nitrogen deficient conditions	Flushing
	Geitlerinema	Information not available				
	Merismopedia	L_O	*Merismopedia spp*	Summer epilimnia in mesotrophic lakes	Segregated nutrients	Prolonged or deep mixing
	Microcystis	L_M	*Microcystis spp*	Summer epilimnia in eutrophic lakes	Very low carbon	Mixing, poor stratification, light
		M	*Microcystis spp*	Dielly mixed layers of small eutrophic, low latitude lakes	High insolation	Flushing, low total light

	Nodularia	Information not available				
	Phormidium	Information not available				
	Planktolyngbya	Information not available				
	Pseudanabaena	S1	*Pseudanabaena spp*	Turbid, mixed layers	Highly light deficient conditions	Flushing
	Synechococcus	Z	*Synechococcus spp*	Clear, mixed layers	Low nutrient	Light deficiency, grazing
	Synechocystis	Information not available				
	Trichodesmium	Information not available				
Chlorophyta	***Ankistrodesmus***	Information not available				
	Ankyra	X1	*Ankyra spp*	Shallow mixed layers in enriched conditions	Stratification	Nutrient deficiency, filter feeding
	Aulacoseira	B	*Aulacoseira subarctica and islandica*	Vertically mixed, mesotrophic small-medium lakes	Light deficiency	pH rise, Si depletion
		C	*Aulacoseira ambigua*	Mixed, eutrophic small-medium lakes	Light, C deficiency	Si exhaustion, stratification
		P	*Aulacoseira granulata*	Eutrophic epilimnia	Mild light and C deficiency	Stratification, Si depletion
	Chlamydomonas	Information not available				
	Chlorella	X1	*Chlorella spp*	Shallow mixed layers in enriched conditions	Stratification	Nutrient deficiency, filter feeding
	Chodatella	Information not available				

	Closteriopsis	Information not available				
	Closterium	P	*Closterium aciculare*	Eutrophic epilimnia	Mild light and C deficiency	Stratification, Si depletion
	Crucigenia	Information not available				
	Dictyosphaerium	Information not available				
	Kirchneriella	Information not available				
	Micrasterias	Information not available				
	Monoraphidium	X1	*Monoraphidium spp*	Shallow mixed layers in enriched conditions	Stratification	Nutrient deficiency, filter feeding
	Nephrocytium	Information not available				
	Oocystis	F	*Oocystis lacustins*	Clear epilimnia	Low nutrients, high turbidity	?CO2 deficiency
	Pediastrum	J	*Pediastrum spp*	Shallow, enriched lakes, ponds and rivers		Settling into low light
	Planctonema	Information not available				
	Scenedesmus	J	*Scenedesmus spp*	Shallow, enriched lakes, ponds and rivers		Settling into low light
	Schroedaria	Information not available				
	Staurastrum	P	*Staurastrum pingue*	Eutrophic epilimnia	Mild light and C deficiency	Stratification, Si depletion
	Tetraedron	Information not available				
	Tetrastrum	Information not available				
Bacillariophyta	***Cyclotella***	A	*Cyclotella comensis*	Clear, often well mixed, base poor lakes	Nutrient deficiency	pH rise
	Licmophora	Information not available				
	Navicula	Information not available				

	Nitzschia	Information not available				
	Staurosira	Information not available				
	Synedra	D	*Synedra acus*	Shallow, enriched, turbid waters, including rivers	Flushing	Nutrient depletion
Cryptophyta	*Chroomonas*	Information not available				
	Cryptomonas	Y	*Cryptomonas spp*	Usually, small, enriched lakes	Low light	Phagotrophal
Euglenophyta	*Euglena*	W1	Euglenoids	Small organic ponds	High BOD	Grazing
Dinophyceae	*Glenodinium*	Information not available				
	Gymnodinium	Information not available				
	Katodinium	Information not available				
	Prorocentrum	Information not available				
	Protoperidinium	Information not available				

There is very little information available on what a healthy or acceptable phytoplankton community consists of since the majority of species are fairly cosmopolitan. In order to assess the current condition of the phytoplankton community in the Lower Lakes, a ‘healthy’ condition was considered to be one that contains a large number of species that are able to be consumed by zooplankton. This will allow carbon fixed by phytoplankton photosynthesis to be carried up through the food chain. There are a number of factors which influence the ability of zooplankton to consume phytoplankton, including the toxicity of the phytoplankton, whether they form colonies or are solitary and the maximum dimensions of the phytoplankton. An attempt was made to identify each of these characteristics for each of the phytoplankton genera observed in the Lower Lakes to determine which are likely to be available for consumption by zooplankton. The maximum unit size was matched against maximum consumable size of zooplankton species that have been observed in the Lower Lakes as reported by Geddes (1984). These maximum unit size were either found directly in the literature or calculated from equations developed by Kobayashi (1991), based on zooplankton size. This approach is outlined in Table 4, showing the likelihood that particular example genera may be consumed by zooplankton of the Lower Lakes.

Table 4. Example table of likely prey genera of zooplankton in the Lower Lakes. Green indicates characteristics that will favour the phytoplankton species being a food source for zooplankton, red indicates characteristics that will disfavour the phytoplankton species being a food source for zooplankton and teal is an intermediate characteristic.

Genera	Toxic?	Colonial or solitary	Maximum unit size	Resultant likelihood of being zooplankton prey
A	Yes	Colonial	Small	Highly unlikely
B	No	Solitary	Small	Highly likely
C	No	Colonial or solitary	Intermediate	Likely

Unfortunately, this approach was not able to be completed since there was insufficient information available for each of these characteristics for phytoplankton found within the Lower Lakes. For example, samples identified by Australian Water Quality Centre were only resolved to the genus level, but the maximum unit size was found to be highly variable within particular genera. In addition, it was found that additional factors are important in determining whether phytoplankton can be consumed by zooplankton, including their motility, digestibility and nutritional value.

The approach that proved to be most useful to assess the current condition of the Lower Lakes was to assess the species and phylogenetic group diversity that currently exists within the Lower Lakes. The assumption was made that a high level of diversity will provide a diversity of food sources for the zooplankton community. However, consideration was also given to the dominant groups of algae found within the Lower Lakes. Dominance of Cyanobacteria is not considered to reflect a healthy lake condition. Indeed, Cyanobacteria are not preferred food sources for many Australian zooplankton (Izmail, unpublished).

During the study period, at Pomanda Embayment the number of species observed varied between 19 and 11, with lowest values occurring in spring 2008 (Figure 4). The number of phylogenetic groups varied between 2 and 4 (Figure 4), with the community dominated by Cyanobacteria (Figure 5). Phytoplankton abundance was very high. Chlorophyta were relatively abundant and Bacillariophyta and Cryptophyta were present at different times but in relatively low abundances.

A similar pattern was observed for Lake Alexandrina Middle with extremely high phytoplankton abundance and lowest species number occurring during spring-summer (Figure 6 and Figure 7). There was a general increase in Cyanobacteria and Cryptophyta through the study period with the community dominated by Cyanobacteria throughout and Chlorophyta were relatively abundant (Figure 7).

The number of species observed in Lake Albert were lower than that of Pomanda Embayment and Lake Alexandrina Middle with lowest numbers of 10 observed in summer 2009 (Figure 8). Cyanobacteria were dominant and have remained relatively stable through the study period (Figure 9). Chlorophyta and Bacillariophyta have appeared to increase during the study period, particularly Bacillariophyta during 2009.

At Point Sturt, the number of phytoplankton species appears to have decreased during the study period although there has been considerable seasonal variation (Figure 1). However, abundances of Cyanobacteria, Chlorophyta and Bacillariophyta have increased, with Cyanobacteria dominant (Figure 11). The decrease in the number of species appears to be more pronounced in Goolwa Channel with only four phytoplankton species observed in June 2009, which were from 3 phylogenetic groups (Figure 12). Although Cyanobacteria were the dominant group early in the study period, by April 2009 Chlorophyta had become dominant (Figure 13). There were also increases in the abundance of Bacillariophyta and Dinoflagellates.

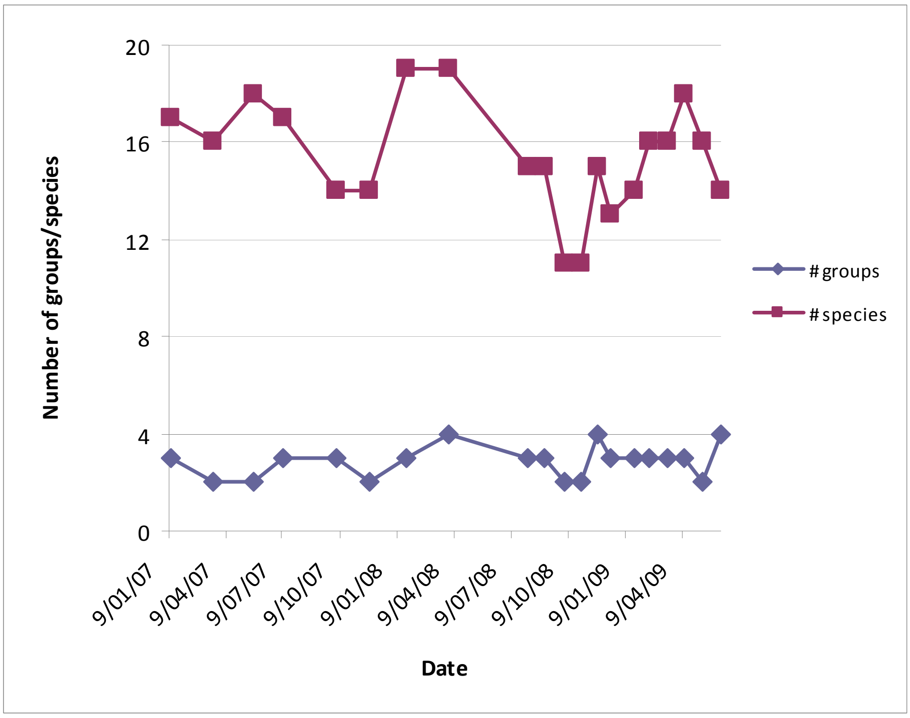


Figure 4. Phytoplankton phylogenetic group and species diversity at Pomanda Embayment, January 2007 to June 2009.

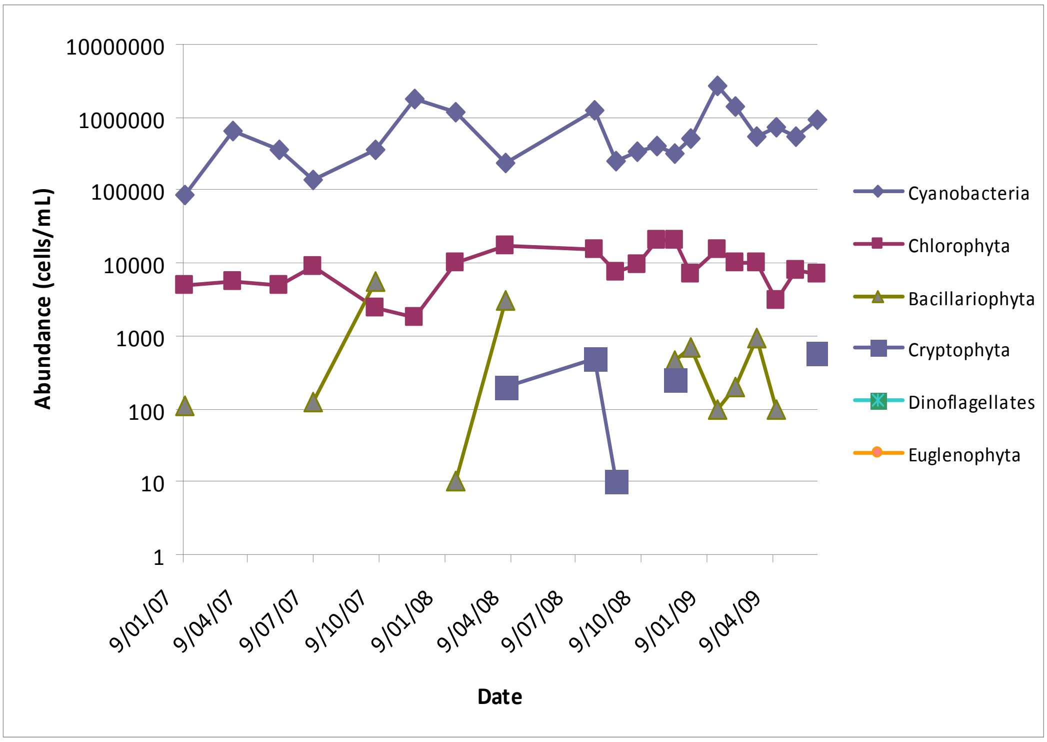


Figure 5. Abundance of phytoplankton phylogenetic groups at Pomanda Embayment, January 2007 to June 2009.

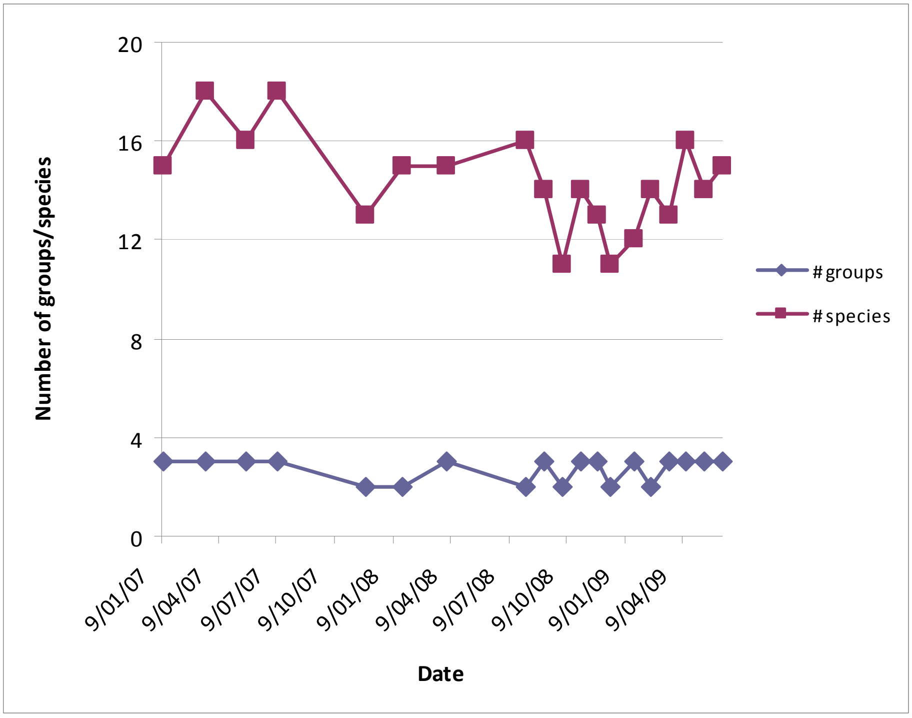


Figure 6. Phytoplankton phylogenetic group and species diversity at Lake Alexandrina Middle, January 2007 to June 2009.

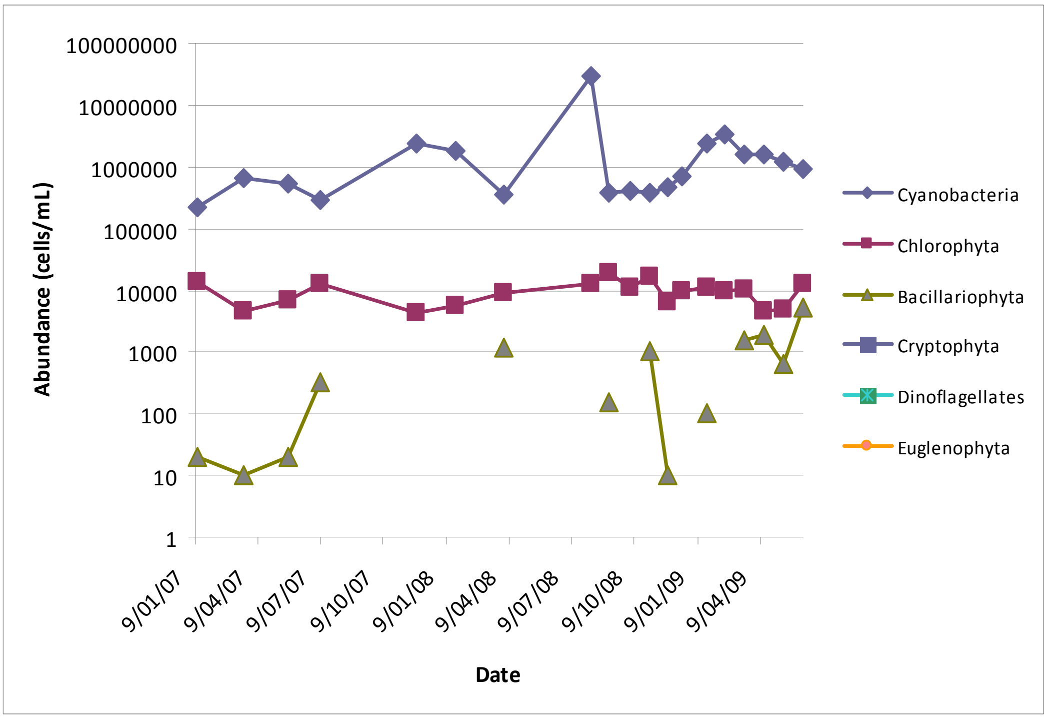


Figure 7. Abundance of phytoplankton phylogenetic groups at Lake Alexandrina Middle, January 2007 to June 2009.

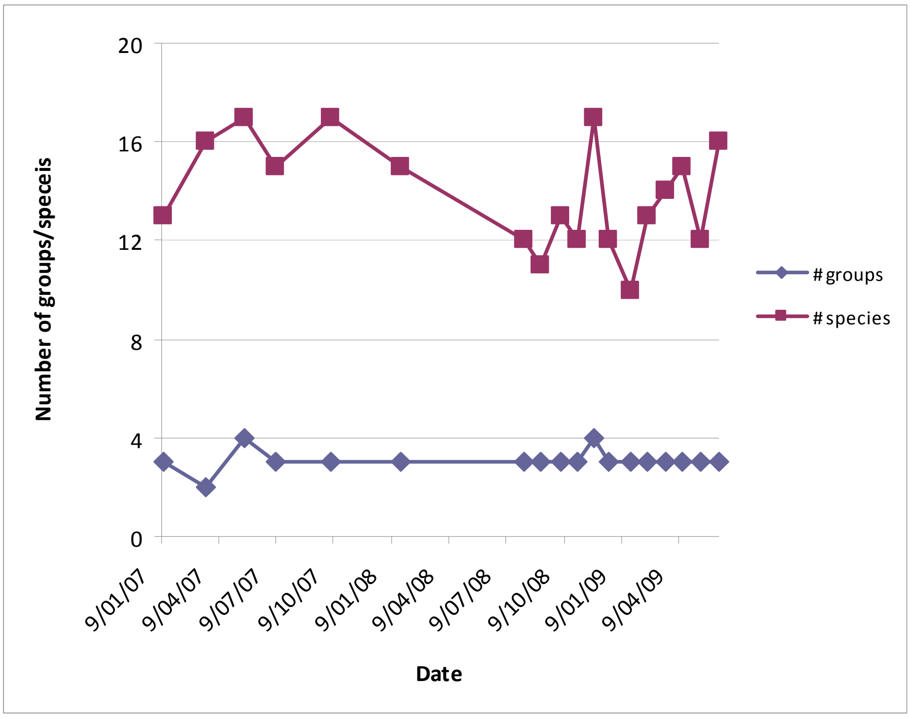


Figure 8. Phytoplankton phylogenetic group and species diversity at Lake Albert Middle, January 2007 to June 2009.

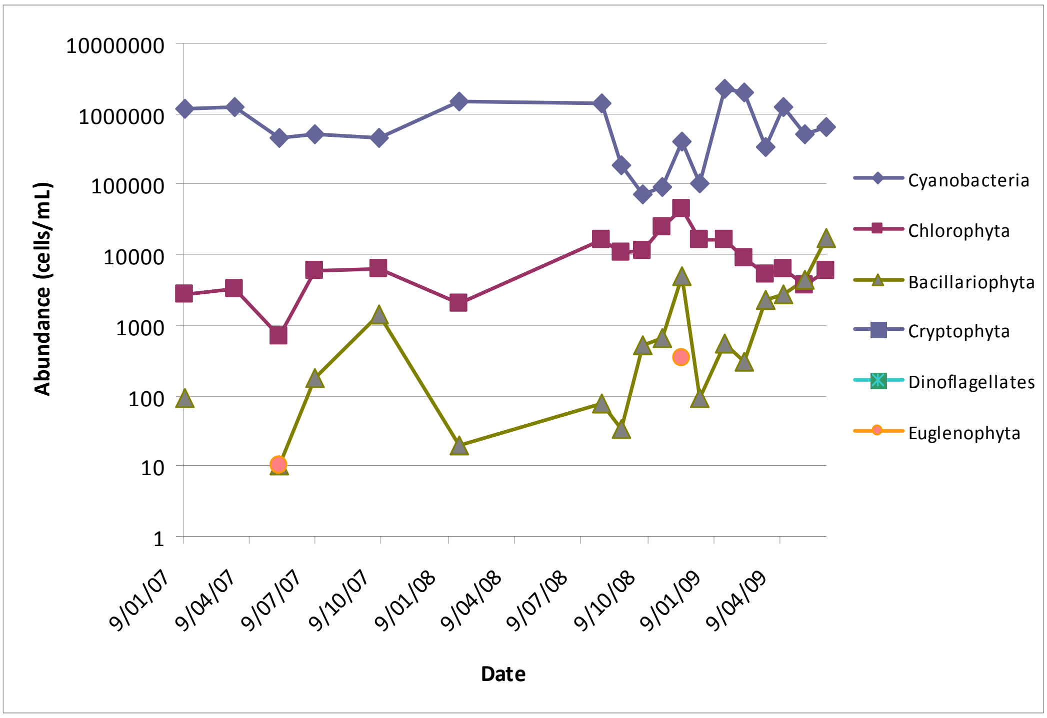


Figure 9. Abundance of phytoplankton phylogenetic groups at Lake Albert Middle, January 2007 to June 2009.

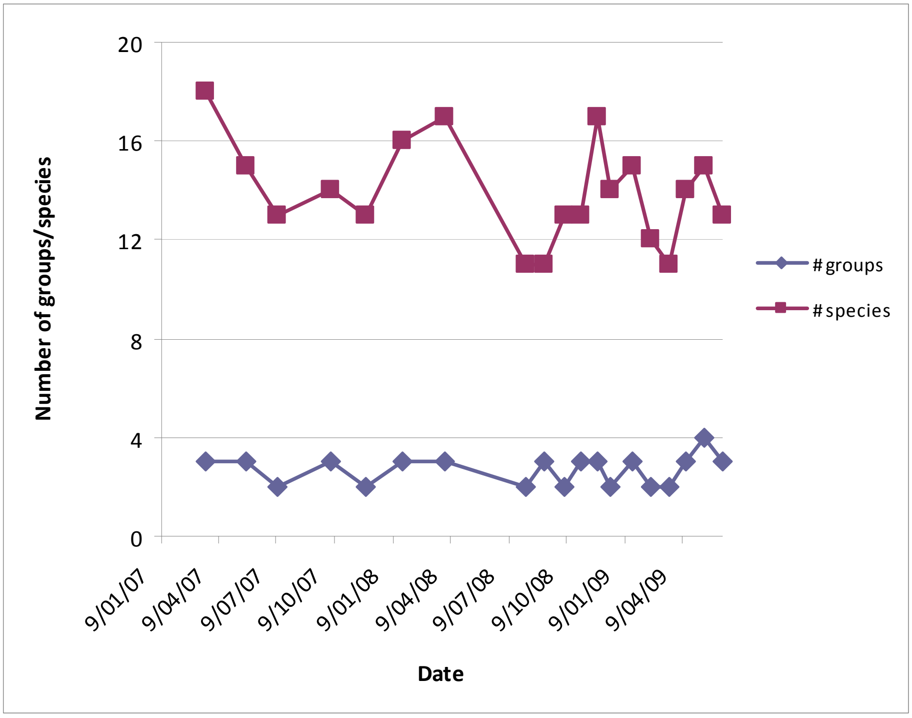


Figure 10. Phytoplankton phylogenetic group and species diversity at Point Sturt, January 2007 to June 2009.

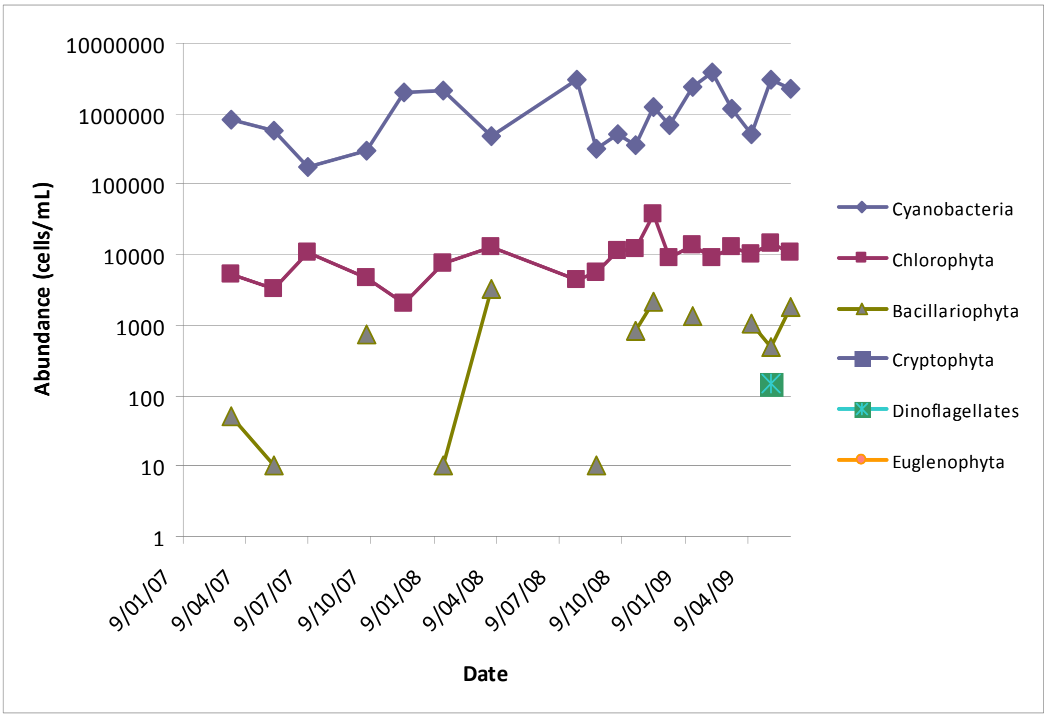


Figure 11. Abundance of phytoplankton phylogenetic groups at Point Sturt, January 2007 to June 2009.

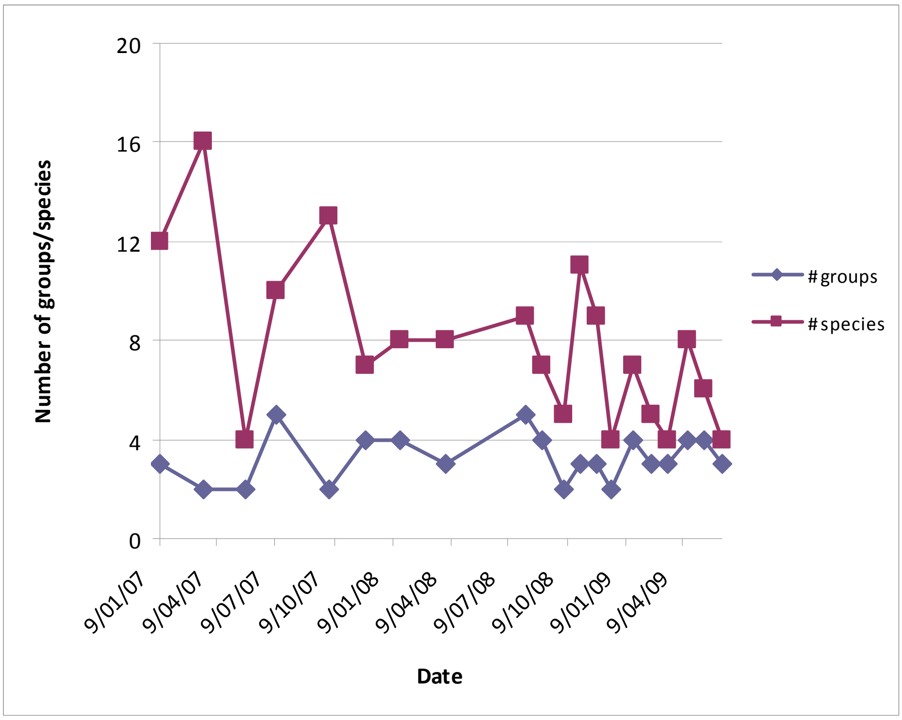


Figure 12. Phytoplankton phylogenetic group and species diversity at Goolwa Barrage, January 2007 to June 2009.

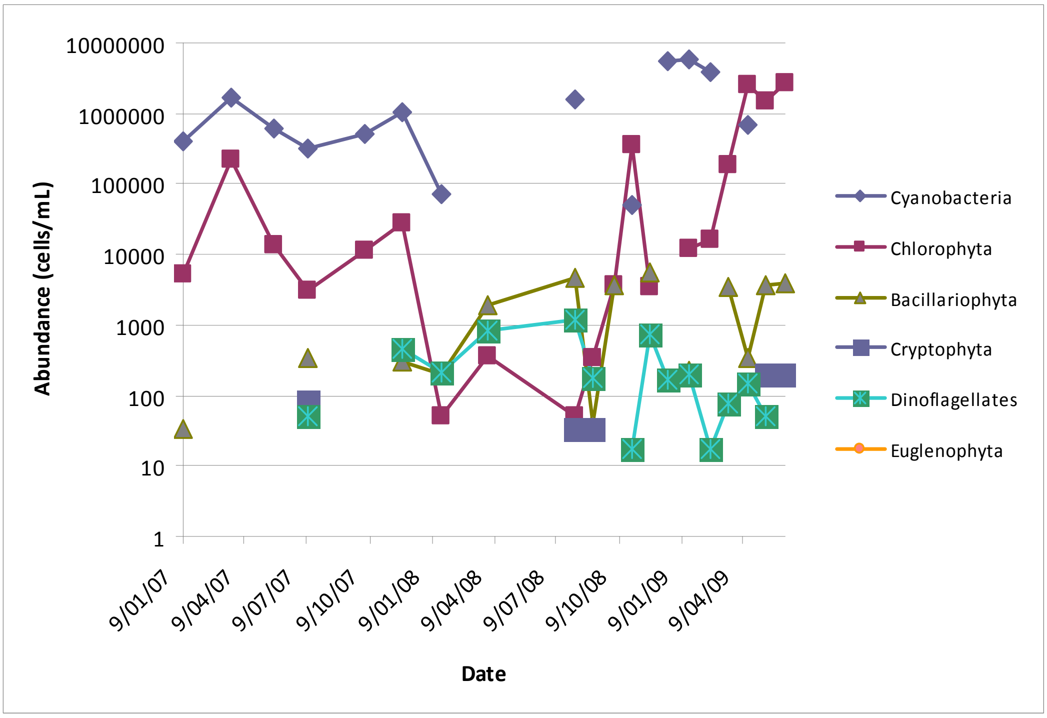


Figure 13. Abundance of phytoplankton phylogenetic groups at Goolwa Barrage, January 2007 to June 2009.

To determine the key drivers of changes in the phytoplankton community composition (species/genera and phytoplankton groups) during this period of extremely low inflow, further in depth multivariate statistical analysis was required. This was done in order to determine the response of phytoplankton community composition to a number of concurrently changing environmental parameters. Ordinations were carried out using PC-Ord with a main matrix containing cell numbers of each group or species/genera at each site for each sampling trip and this was overlain with a second matrix containing the same data-set as well as salinity, temperature, pH, dissolved oxygen, total suspended solids, total phosphorus and total nitrogen.

For phytoplankton groups, a successful one-dimensional NMS ordinations (Sorensen) was achieved with a stress level of less than 16. Greatest separation was associated with Goolwa, with increasing Chlorophyta and Dinophyta and decreasing Cyanophyta at Goolwa on many occasions (Figure 14). However, this was not always the case with the Goolwa phytoplankton community often closely associated with other sites, but this was not related to seasonality. No physico-chemical parameters were found to be important in controlling the distribution of phytoplankton groups (Figure 14).

Successful two-dimensional NMS ordinations (Sorensen) were also conducted on individual phytoplankton genera, with stress levels of less than 16. An initial ordination was conducted to determine key drivers of change across all sites. It was found the community in Lake Alexandrina Opening, Lake Alexandrina Middle, Lake Albert Middle and Points were closely associated within one general community group with no major diversions from this group during the drawdown and salinisation period (Figure 15). While the Goolwa phytoplankton community was initially part of this group by January 2008 the Goolwa community began to diverge, initially indicated by increasing *Prorocentrum*. For the remaining study period the Goolwa channel displayed a wide distribution along both axis. By the end of the study period (January 2009 – June 2009) the Goolwa community had seemed to reach more of an equilibrium with the community strongly associated with increasing salinity and decreasing dissolved oxygen (due to oxygen depletion of the hypolimnion in Goolwa channel). *Cyclotella* was closely associated with increasing salinity suggesting it may be a good indicator species of these changes.

Since the Goolwa phytoplankton community displayed such large seasonal variation a separate ordination was conducted on this community alone since different factors may be contributing to changes at this reduced spatial scale. It was found that in addition to salinity, pH was a major factor resulting in changes in the phytoplankton community at Goolwa between 2007 and 2009 (Figure 16). However, it is thought that this was not a causal relationship but instead associated with the inputs of lower saline water that also has a lower pH via the barrages. This was not thought to be related to release of acid from acid sulphate soils since no change in alkalinity was detected during this period (Aldridge *et al*. 2009). *Synechococcus* appeared to be a good indicator genera of increasing salinity and decreasing pH during this period.

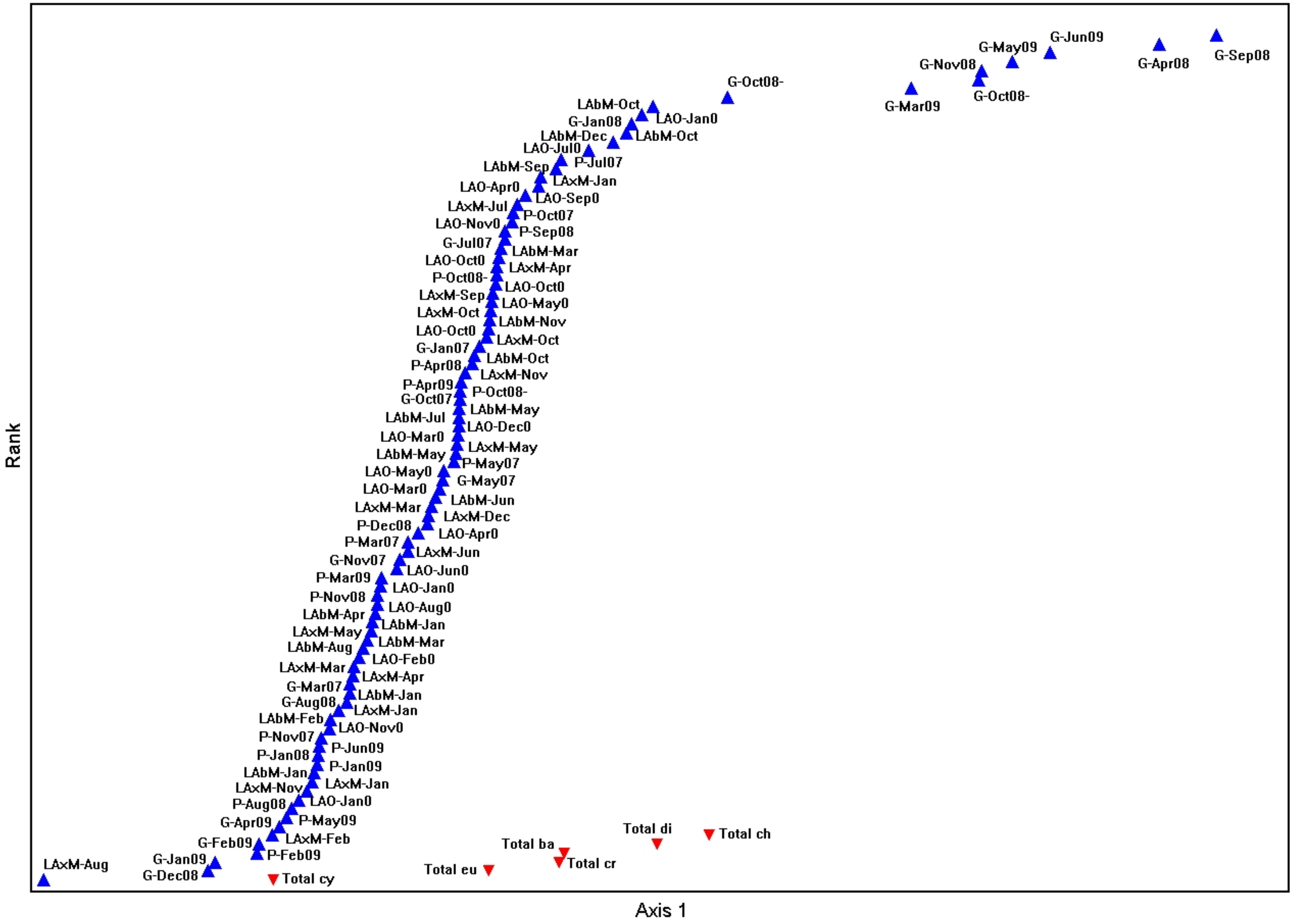


Figure 14. One-dimensional NMS Ordination (Sorensen) of changes in Lower Lakes phytoplankton community 2007-2009. Drivers of change in the phytoplankton community (indicator groups) shown as red triangles; total cy (Cyanophyta), total eu (Euglenophyta), total cr (Cryptophyta), total ba (Bacillariophyta), total di (Dinophyceae) and total ch (Chlorophyta). LAO represents Lake Alexandrina Opening, LAxM represents Lake Alexandrina Middle, P represents Points, LAbM represents Lake Albert Middle and G represents Goolwa.

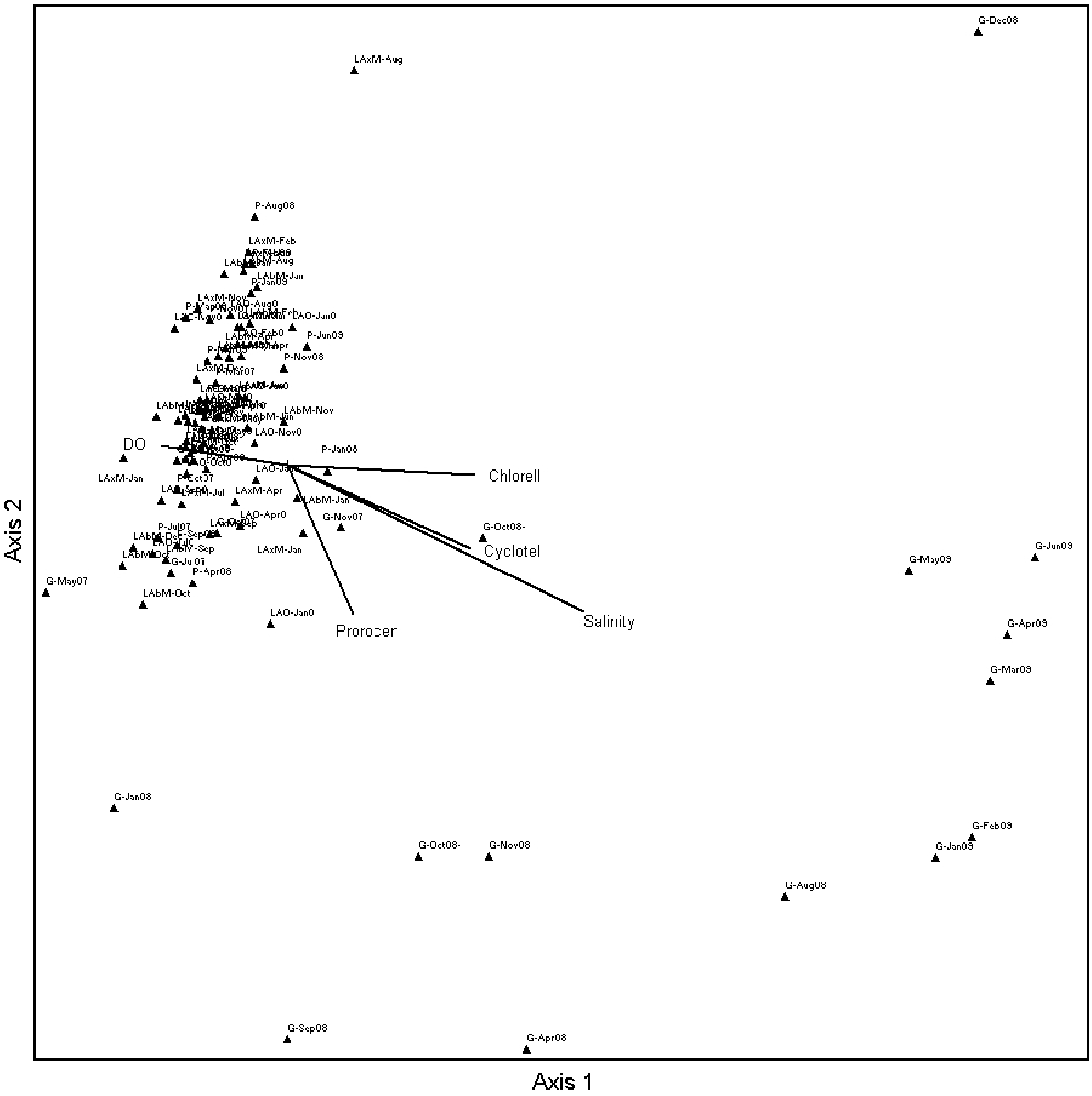


Figure 15. NMS Ordination (Sorensen) of changes in Lower Lakes phytoplankton community 2007-2009. Vectors show major drivers of change in the phytoplankton community, including salinity and DO (dissolved oxygen) and indicator genera of changes; Prorocen (*Prorocentrum*), Chlorell (*Chlorella*) and Cyclotel (*Cyclotella*). LAO represents Lake Alexandrina Opening, LAxM represents Lake Alexandrina Middle, P represents Points, LAbM represents Lake Albert Middle and G represents Goolwa. r^2 cut-off value of 0.64 for salinity, 0.39 for *Cyclotella*, 0.36 for *Chlorella,* 0.32 for *Prorocentrum* and 0.25 for dissolved oxygen. All other r^2 cut-off values between 0.2 and 0.25.

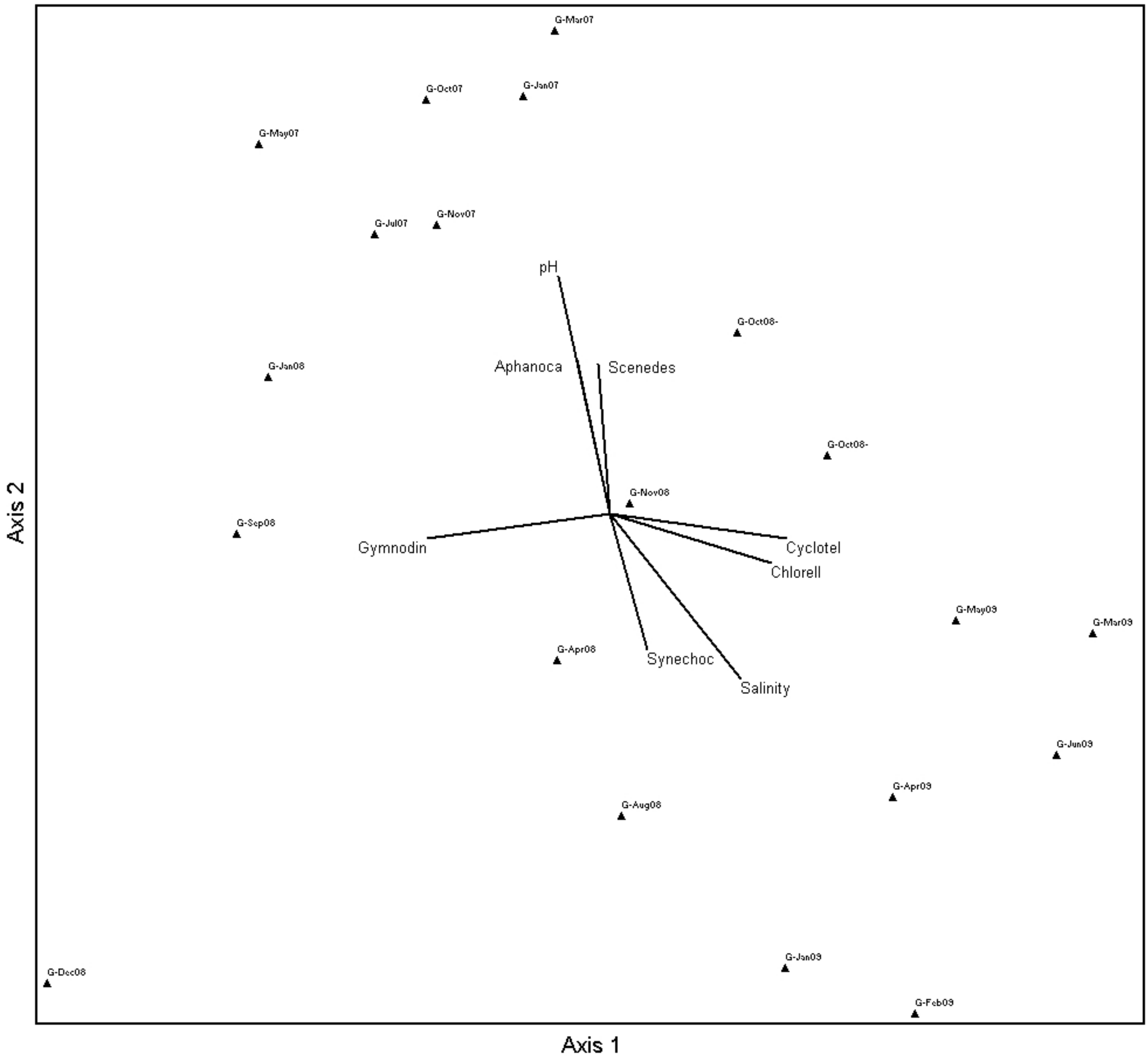


Figure 16. NMS Ordination (Sorensen) of changes in Goolwa phytoplankton community 2007-2009. Vectors show major drivers of change in the phytoplankton community, including salinity and pH and indicator genera of changes; Scenedes (*Scenedesmus*), Synechoc (*Synechococcus*) Chlorell (*Chlorella*), Cyclotel (*Cyclotella*), Aphanoca (*Aphanocapsa*) and Gymnodi (*Gymnodinium*). G represents Goolwa. r^2 cut-off value of 0.46 for pH, 0.40 for salinity, 0.35 for *Gymnodinium*, 0.34 for *Cyclotella*, 0.32 for *Chlorella,* 0.30 for *Aphanocapsa*, 0.28 for *Scenedesmus* and 0.26 for *Synechococcus*.

Given the current information that is available for the region a healthy or acceptable phytoplankton community may be considered one that has low-moderate biomass and a diverse mixture of phytoplankton groups and species. The extremely high abundance of phytoplankton and the dominance of Cyanobacteria in the Lower Lakes suggest that the condition of the Lower Lakes phytoplankton community is poor. The community that is becoming established at Goolwa Barrages appears to be unique within the Lower Lakes. At Goolwa Barrage there has been a dramatic loss in the number of species, presumably due to saline intrusions near the barrages (Aldridge *et al*. 2009), resulting in the loss of freshwater phytoplankton species. The dominance of Chlorophyta over Cyanobacteria in the Goolwa channel may also be a result of the high salinities observed in this region, with freshwater Cyanobacteria replaced by estuarine Chlorophyta. In addition, it may be due to reduced grazing pressure on green algae due to salinisation (loss of zooplankton community), however, this was not able to be assessed with the current data-base.

Coorong and Murray Mouth

While there are some observations of phytoplankton communities within the Coorong, no one has carried out a comprehensive assessment of the drivers of phytoplankton community. A comparison of the information that is available suggests that the composition of the phytoplankton community in the Coorong appears to be heavily dependent on freshwater inflows from the River Murray (Geddes 1987, 2005, Geddes and Butler 1984; Brookes 2002; Geddes and Francis 2008).

Flow as the primary driver of phytoplankton communities

The importance of River Murray inflows to the phytoplankton community of the Coorong is due to the input of freshwater species from the Lower Lakes and impacts on salinity levels and hydrodynamic conditions. Geddes (1987) and Geddes and Butler (1984) reported that diatoms and flagellates were the dominant phytoplankton species in the North Lagoon, with chlorophyll a levels increasing in a north-south direction (low-high salinity). Geddes and Butler (1984) conducted their analysis when there was no flow from the River Murray, whilst Geddes (1987) conducted experiments during a period of high flow from the River Murray (1983-1984 mean flow of approximately 800GL/month). At times of high flow *Planktonema lauterbornii* was the dominant phytoplankton at sites closest to the barrages, presumably from Lake Alexandrina water, but as flows slowed, diatoms and flagellates became dominant again (Geddes 1987).

After a small release in 2004 of Lake Alexandrina water into the Coorong (approximately 30-40GL over 15 days), Geddes (2005) reported abundant numbers of freshwater phytoplankton (*Aphanocapsa*, *Monoraphidium*, *Crucigenia*, *Planktonema*, *Oocystis* and *Planktolyngyba*) from samples at Tauwitchere Barrage and Pelican Point. The number of freshwater phytoplankton decreased with distance from the outflow, resulting in the aforementioned phytoplankton believed to be flushed in from Lake Alexandrina. There were very high numbers of the green algae *Nannochloris* at Mark Point with proportionally few other species (Geddes 2005).

A study at Pelican Point was undertaken by Geddes and Francis (2008) in March 2005, after a 200 day closure of the barrages. At this time the Coorong was operating as a marine coastal lagoon and under marine influence. The observed phytoplankton community was dominated by diatoms, as seen by Geddes and Butler (1984). There were two predominant diatoms, *Chaetoceros* and *Asterionella,* making up approximately 56.6 and 33.3% respectively (collectively 89.9%) of the total cell number. According to the classification system of Reynolds (2002), *Asterionella* may be an indicator of mixed and eutrophic conditions.

Geddes and Tanner (2007) studied the phytoplankton at eight different sites in the Murray Mouth and North Lagoon on three different occasions in 2004/2005. Overall, the phytoplankton community was dominated by the green algae *Nannochloris*, particularly in the southern sites where cell numbers were in excess of 1million cells/mL. There was also the strong presence of a few diatom and dinoflagellate genera, namely *Chaetoceros*, *Nitzchia*, *Asterionella* and *Gymnodinium*. According to the classification system of Reynolds (2002), *Nitzchia* may be an indicator of shallow, enriched turbid waters. The presence of *Nannochloris* right up to Barkers Knoll in November 2004 is believed to be as a result of water from the south (more saline water) moving north and out of the Murray Mouth (Geddes and Tanner 2007). No cyanobacteria were seen by Geddes and Tanner (2007), but a few genera were observed by Geddes and Francis (2008). No freshwater phytoplankton species were observed by Geddes and Tanner (2007) in 2004/2005.

Recent condition

In December 2007, phytoplankton samples were collected along the salinity gradient of the Coorong (Rod Oliver, CSIRO, unpublished). In the sites closest to the Murray Mouth the phytoplankton community appears to be limited to three genera, one green algae recorded as Chlorococcales (believed to be *Nannochloris* as it belongs to the chlorococcales family and has been observed in high numbers in previous studies), one diatom genera, *Chaetoceros* and a cryptomonad, *Chryptomonas*. The phytoplankton community of sites in the south of the North Lagoon and the South Lagoon become dominated by green algae and in particular the aforementioned Chlorococcales, with cell numbers exceeding 500,000 cells/mL (Rod Oliver, CSIRO, unpublished).

Nayar and Loo (2009) studied changes in phytoplankton and phytobenthic productivity along the salinity gradient in the Coorong. It was found that phytoplankton productivity only makes a small contribution to the overall productivity of the system, with greatest contribution made in the Southern Lagoon. Nayar and Loo (2009) presented hypotheses for the low phytoplankton productivity in the Coorong including stratification-induced light limitation and nutrient limitation due to low River Murray inflows.

Additional potential drivers of phytoplankton communities

There are a number of factors that are known to be important drivers of phytoplankton community composition and productivity, that have not necessarily been determined by investigations for the region. Many of these are closely associated with river inflows.

Turbidity and light

Turbidity is a measure of water clarity that results from the presence of suspended particles, including inorganic and organic material (plankton and detritus). It usually consists of inorganic particles originating from erosion of soil from the catchment and from resuspension of the bottom sediment (Nolen *et al*. 1985). These particles may reduce underwater light availability. A key factor that contributes to species composition of a phytoplankton community is the light gradient. The light gradient is partly created by light absorption by the phytoplankton species themselves.

In many Australian waters, turbidity is high and Lake Alexandrina and Lake Albert have particularly high turbidity (since European settlement). Under such conditions, light availability may be the major factor controlling algal growth by limiting photosynthetic activity (Talling 1971; Ganf 1980), although it is difficult to separate the effects of physical and chemical factors in controlling the phytoplankton community (Jones 1977). Indeed, turbidity is known to be an important driver of the phytoplankton community in the Lower Lakes, as previously discussed. In eutrophic and turbid lakes, the dominant algae are often forms that can maintain themselves within the euphotic zone especially vacuolated cyanophytes, large dinoflagellates and motile green algae, or low-light-adapted forms, particularly diatoms (Wetzel 2001; Reynolds 1997). Turbidity can have a positive effect on cyanobacteria since they are able to utilize low levels of light (Reynolds 1987).

Nutrients

Nutrients are substances that can be metabolised by organisms, including phytoplankton, to give energy and build tissue (Wetzel 2001). Nutrients play an important role in controlling the overall productivity of phytoplankton communities, with phosphorus and nitrogen often limiting growth (Kalff 2002). Thus, nitrogen and phosphorus often determine the total autotrophic biomass within aquatic systems (Shafron *et al*. 1990; Kalff 2002) and so shape the structure of these ecosystems. The probability of primary nitrogen limitation of phytoplankton is greatest when N:P supply molar ratios are well below the algal demand molar ratio of approximately 16:1. The reverse is true for phosphorus limitation with a molar ratio of greater than 16:1 providing some indication of phosphorus limitation (Kalff 2002).

Algal species differ in specific nutrient requirements and optimal ratios of N:P. Thus, in a multi-species algal community, growth rates among different species are likely to be limited by different resources, including differing nutrients. Many cyanobacteria are able to fix atmospheric nitrogen when other sources of nitrogen are limited. Total phosphorus concentrations have been found to have a strong positive relationship with total phytoplankton biomass (chlorophyll a) (Dillon and Rigler 1974). If favourable hydrodynamic conditions prevail, excessive nutrient concentrations can allow excessive growth of phytoplankton, with the occurrence of 'algal blooms'. However, the levels of TN or TP are not always a good representation of actual nutrient levels available for algal use (Geddes 1984a). Many forms of nitrogen and phosphorus are inorganic and often adhered to sediment in the water column (Geddes 1988).

Despite the known importance of nutrients as drivers of phytoplankton communities there have been few investigations on the influence of nutrients within the lower River Murray, Lower Lakes and Coorong.

Mixing regime

In many aquatic environments, phytoplankton species are not thoroughly mixed but slowly drift through the water column, often passively by turbulent diffusion and sinking and sometimes also actively by means of flagellae or buoyancy regulation (Reynolds 1984, 1997). The implications of slow mixing processes for phytoplankton competition are not well understood. However, field data and experiments clearly demonstrate that the intensity of mixing has a major impact on phytoplankton bloom development and on the species composition of phytoplankton communities (Eppley *et al*. 1978; Reynolds *et al*. 1983; Viner and Kemp 1983; Cloern 1991; Visser *et al*. 1996; Berman and Shteinman 1998). Mixing influences the summer succession of phytoplankton by favouring certain groups due to the different nutrient and light conditions (Olrik 1981; Padisak *et al*. 1988).

Moreover, mixing through a light gradient in the water column affects phytoplankton growth because mixing processes largely determine the light conditions experienced by the phytoplankton. Huisman *et al*. (1999) discovered the existence of a “critical turbulence” in planktonic systems that are not well mixed. If vertical mixing rates exceed this critical turbulence, the phytoplankton species are relatively well mixed and dense phytoplankton blooms can develop, only if the mixed water column is shallow. However, if vertical mixing rates are less than the critical turbulence, blooms develop in a completely different manner. In this case, phytoplankton growth rates exceed the vertical mixing rates, the phytoplankton populations aggregate in the upper water column, and dense phytoplankton blooms can develop irrespective of water column depth (Huisman *et al*. 1999).

Not only are water movements important in the physical movement of phytoplankton into and out of the photic zone but they also play a vital role in the transport of mineralised matter from lower depths and from the littoral regions to the open water. For these reasons, the degree of turbulence and water movement are critical in the regulation of phytoplankton frequency and production (Wetzel 2001).

Thermal stratification develops when a stable water body is heated by solar radiation (Wetzel 2001) with a disproportionate heating of the epilimnion and hypolimnion. As a result, the water in the hypolimnion is more dense than that of the epilimnion, preventing exchange between the hypolimnion and the atmosphere (Wetzel 2001). Thermally stratified water bodies favour gas–vacuolated cyanobacteria which are able to actively maintain their buoyancy and position in the water column, unlike many other phytoplankton that rely on turbulence to keep them in the photic zone (Reynolds 1984).

Flow in the River Murray is highly regulated, with the Lower River Murray now consisting of a series of weir pools with little water level fluctuation (Close 1990; Jacobs 1990). This lack of water level fluctuation promotes the development of thermal stratification. Persistently thermally stratified conditions can result in oxygen depletion both in the sediments and water adjacent to the sediments allowing nutrients to be released into the water. There is potential for these nutrients to be mixed into the water column and stimulate algal growth (Brookes *et al*. 2008). Due to the increased nutrient loads, water bodies can support greater primary production (Dillon and Rigler 1974). If favourable environmental conditions prevail, then the increased nutrient loads can support large standing crops of often undesirable cyanobacterial populations. As discussed previously, the importance of mixing regime to phytoplankton communities of the River Murray has been shown. However, while mixing regime is also considered important for the Coorong and Lower Lakes, this has not been investigated in any detail.

Salinity

Plants and animals have developed a range of physiological mechanisms and adaptations to maintain the necessary balance of water and dissolved ions in cells and tissues. Due to physiological effects of salinity on individual species, the impacts of salinity are reflected in the phytoplankton community composition as some species are disadvantaged whilst others favoured by new chemical environments. Because phytoplankton have short generation times, they respond quickly to environmental changes in the chemical environment.

The distribution of phytoplankton along estuary gradients tends to favour cyanobacteria and chlorophytes in brackish waters (Nakanishi and Monsi 1965; Muylaert and Sabbe 1999), and dinoflagellates and diatoms at mid-to-high salinities (10 ppt (10000 mgL^{-1}; Kies 1997)). Species diversity is known to be lowest at approximately 5 ppt (5000 mgL^{-1}), the approximate lethal limit for many phytoplankton in estuaries (Rijstenbil 1898). High salinity is lethal to freshwater plants and animals because the cells of the organism have either a lack of water or an excess of ions (or have both) that can result in a range of toxic effects. The ability of an animal species to maintain (regulate) the optimal internal osmotic concentration against external gradients determines the salinity tolerance of the species. Hart *et al*. (1991) and Nielsen *et al*. (2003) reviewed the salinity tolerances of Australian freshwater biota and found that there was only sparse information for phytoplankton. In general, it was found that a majority of freshwater algae were not tolerant of increases in salinity with the majority not able to survive above salinities of 10000 mgL^{-1} (Nielsen *et al*. 2003). In general, diatoms decrease in abundance and diversity with increasing salinity. Those species that are able to survive in a broad range of salinities undergo morphological and physiological changes in order to tolerate the changes in salinity. In addition, some species produce resting cysts to allow survival in high salinities (Nielsen *et al*. 2003).

The effect of salinity on freshwater cyanobacteria appears to be similar to that of freshwater algae. Moore *et al*. (1985) found that sodium chloride concentrations up to 5800 mg L^{-1} had no long-term effects on the growth of three freshwater Cyanobacteria, which were able to adapt rapidly to changes in salinity. Furthermore, Reed *et al*. (1984) found that 48 strains of Cyanobacteria, representing 13 genera, were all able to compensate for osmotic stress up to 14 500 mg L^{-1} sodium chloride. Stulp and Stam (1984) studied the salt response of 21 strains of the cyanobacterium *Anabaena*. They found that 15 of 21 strains grew best in fresh water and three grew as well at 17000 mg L^{-1} sodium chloride. All strains recovered from exposure to 7000 mg L^{-1} sodium chloride. These results suggest that the temporal pattern of any salinity changes may be as important as the absolute changes. Bacteria will probably be less affected by low-level and constant salinity changes that allow time for them to adapt than to highly variable salinity changes. Seasonal timing of salt increases may also matter, as an increase in bacterial salt tolerance with increasing temperature has also been reported (Atlas and Bartha 1981).

One of the major impacts of changes in salinity on phytoplankton communities is likely to be linked to changes in the physical and chemical environment. Salinity may induce the aggregation and flocculation of suspended material, thus increasing light availability, which as discussed previously will impact upon the phytoplankton community. Similarly, the input of saline water may result in salinity stratification, preventing mixing of the water column, which is also know to be important for phytoplankton communities (see above). Also, salinity may have a number of impacts on nutrient availability (see nutrient dynamics section), which is also important for phytoplankton communities (see above).

It is likely that the observed response of the phytoplankton community in the Coorong is related to changes in salinity, with low inflows increasing salinities above thresholds of many phytoplankton species. This document has also identified that under extremely low River Murray inflows, increased salinity in the Lower Lakes has resulted in a large shift in the phytoplankton community composition. A similar response would be likely in the Lower River Murray, although this has not been investigated since salinities have not approached those levels in recent times.

pH and acidification

pH has not been found to be a significant driver of change in the phytoplankton communites of the Lower River Murray, Lower Lakes or Coorong. This is perhaps largely due to the fact that most studies have been conducted within a relatively short pH range.

However, acidification is known to alter the structure of the phytoplankton communities on several levels i.e. species richness, species composition and dominance. Geelen and Leuven (1986) conducted a review of the impact of acidification on phytoplankton and zooplankton communities and concluded that phytoplankton species composition changes and richness decreases at low pH. However, there was a considerable difference in the response between lakes from around the world. The first striking aspect is that with decreasing pH the number of species of Chlorophyta, Bacillariophyceae and Cyanophyta becomes reduced (Geelen and Leuven 1986). In some oligotrophic acidified water, blue-green microalgae become dominant or have an increased biomass (Conway and Hendrey 1982; Findlay and Kasian 1990). In acidified natural waters there is a decrease in number of microalgal species, and a shift in dominance from diatoms to filamentous green microalgae (Marker and Willoughby 1988).

Lakes with pH values < 5.0 display a homogeneous and limited phytoplankton composition consisting of about ten species (Geelen and Leuven 1986). The greatest changes in composition were found in the pH interval 5-6.2. Many species found in circumneutral waters are absent or rare in acidic lakes. It is evident that not only the pH, but also some other environmental factors are responsible for the structural and functional changes in acidifying systems. Decreased nutrient availability, changes in trophic relationships between primary and secondary producers and altered predator-prey systems may contribute to the simplification of acidifying aquatic ecosystems. Unfortunately, the importance of the key factors involved, and the mechanism of acidification processes are not fully understood (Geelen and Leuven 1986).

Predation

Under certain conditions, grazing of phytoplankton can have a significant effect on the algal community. Predation by metazoan animals, more specifically the microcrustacea, can heavily contribute to seasonal succession of phytoplankton. Selective pressures on phytoplankton species composition are highly variable seasonally and spatially within lakes and rivers. As temperatures of temperate waters increase, feeding and reproduction of zooplankton increase greatly (Wetzel 2001)

The grazing of zooplankton has been observed to have both negative and positive effects on the algal population (Crumpton and Wetzel 1982). In some cases, grazing of phytoplankton by zooplankton is so heavy that the algal population decreases. In other cases, nutrient regeneration caused by zooplankton grazing, promoting algal growth can potentially offset the negative effects of grazing mortality (Elser *et al*. 1987).

Within the grazing zooplankton, a degree of size and species selectivity occurs. Consequently, a competitive advantage arises by the less effectively grazed algal species which are often larger and less edible (Wetzel 2001). Because of this selectivity within zooplankton, if grazing is heavy, algal succession can be altered even in optimal physical and nutrient levels. Similarly, if invertebrates and fish show size selective feeding on zooplankton they can indirectly alter algal succession (Wetzel 2001). Although predation of phytoplankton has not been investigated directly within the region, Geddes (1984b) hypothesised that zooplankton predation was an important factor controlling the phytoplankton community of the Lower Lakes. Within the Lower Lakes there exist no open water planktivorous fish, and the littoral planktivorous species that do exist don't seem to have a significant effect on the overall zooplankton community (Geddes 1984b). This is thought to result in high predation rates of zooplankton on the phytoplankton community.

Predation of zooplankton can be altered or inhibited by some phytoplankton that contain toxic organic substances. Kurmayer and Juttner (1999) found that the cyanobacterium *Planktothrix,* which contains microcystins and other toxins, are complete feeding deterrents for *Daphnia* and other zooplankton. This is supported by recent unpublished studies by Azma Ismail at The University of Adelaide, who looked at the food preferences (phytoplankton) of zooplankton in Myponga and South Para Reservoirs, South Australia. It was found that larger species of zooplankton are more efficient grazers and high ingestion efficiency occurs at small cell sizes of algae (chlorophyta). It was also found that toxic cyanobacteria were not a preferred food source of zooplankton (Ismail, unpublished).

Macrophytes and alternative ecosystem states

It is believed that an ecosystem can exist in a number of alternative states for a given range of environmental conditions (Scheffer 1990). A gradual change in condition may initially result in little change in the ecosystem state, but this is eventually interrupted by a sudden drastic switch to a contrasting state (Scheffer *et al.* 2001). The most quoted example of the switch in ecosystem states is in shallow lakes, where a switch from a clear, macrophyte dominated state to turbid, phytoplankton dominated state occurs with the onset of eutrophication (Scheffer *et al.* 1993).

Macrophyte dominant communities are considered healthy since they are associated with clear water and the macrophytes provide habitat and food for a diverse range of aquatic organisms (Scheffer *et al.* 1993). On the other hand, dominant phytoplankton communities in shallow lakes are considered unhealthy as they are often associated with highly turbid water and provide little habitat for other aquatic organisms (Scheffer *et al.* 1993). When coupled with inappropriate management of the flow regime of freshwater systems (increased residence time), increased nutrient inputs can result in the development of cyanobacterial blooms that are toxic to aquatic organisms, domestic stock and humans (Harris 1994).

The mechanism for the switch between clear and turbid states is centred on the interaction between submerged vegetation and turbidity (Scheffer *et al*. 1993). Submerged macrophytes reduce turbidity and phytoplankton growth by reducing the resuspension of sediments; reducing water column nutrient concentrations; and the provision of habitat for planktivores (Scheffer *et al.* 1993). In contrast, high turbidity reduces the growth of submerged macrophytes due to reduced light availability, thus reducing photosynthesis and growth of macrophytes (Scheffer *et al*. 1993).

As nutrient concentrations are increased through eutrophication, a gradual increase in turbidity (phytoplankton growth) may be observed, but the system still remains in a clear water state (Scheffer *et al.* 1993). However, as turbidity increases macrophytes will receive less light and therefore be placed under stress, making the ecosystem more vulnerable or less resilient to perturbations (eg. Large input of turbid water). The hysteresis period ends with a catastrophic transition to a turbid state that often accompanies a perturbation that the pristine macrophyte dominated community would have been unable to resist (Scheffer *et al.* 1993).

In a similar way, the return to a macrophyte dominated state is not immediate following a reduction in external nutrient loads. In many cases, no improvements in phytoplankton concentration or macrophyte abundance are observed for 10-20 years following significant reductions in external nutrient loads (Jeppesen *et al.* 2005). It is believed that a perturbation is often required to cause the sudden shift in ecosystem states (Scheffer *et al.* 2001). This may include a period of particularly low turbidity or biomanipulation of the ecosystem to increase grazing rates upon phytoplankton. These perturbations need to be large enough to allow for the establishment of the macrophyte community. The reason for the hysteresis effect of restoration programs is thought to be a result of the large pool of nutrients released from sediments of eutrophic waterbodies.

Summary

Nutrient dynamics and phytoplankton communities of the Lower River Murray, Lower Lakes and Coorong are closely associated with River Murray inflows, as indicated by Figure 17 and Figure 18 which highlight some of the important processes. Changes in inflows influence *in situ* conditions including the physical and chemical conditions that control nutrient cycling and phytoplankton growth. Under high River Murray inflows, nutrients are primarily brought in from the upstream catchment as well as from return flows from the inundation of previously dry floodplains and wetlands, which results in the release of nutrients (Figure 17). The increased delivery of nutrients stimulates phytoplankton productivity in the Lower River Murray and mixed water column favours diatoms over cyanobacteria. Lower River Murray phytoplankton are predated by zooplankton and are also passed downstream acting as inoculums for the phytoplankton community in the Lower Lakes. In the Lower Lakes, high turbidities that result from inflows with high suspended solid loads as moblisation from wind-driven resuspension reduces the predation of zooplankton by fish, thus increase predation of phytoplankton by zooplankton. The flow of water across the barrages to the Coorong transports both nutrients and phytoplankton. In the Coorong these may be consumed by zooplankton or if transported to areas beyond their salinity tolerance may die and be consumed by benthic infauna. The salinity gradient in the Coorong created by inputs of freshwater from the Lower Lakes creates a diversity of habitats for different phytoplankton communities to exist.

In comparison, under low inflows there is reduced inputs of nutrients from the catchment, low external inputs of suspended solids and reduced mixing (Figure 18). This increases water clarity of the Lower River Murray and Lower Lakes, thus allowing for high rates of primary production. However, reduced mixing in the Lower River Murray results in stratification, which has two major impacts on the phytoplankton community. Firstly, it results in the release of bioavailable nutrients from sediment due to deoxygenation of the sediments and thus increases phytoplankton productivity. Secondly, it favours the growth of motile cyanobacteria that are able to move through the water column and access light from the surface and nutrients from the hypolimnion. Since cyanobacteria are considered a poor source of food for zooplankton there is limited predation of the phytoplankton by zooplankton. The high levels of cyanobacteria in the Lower River Murray act as inoculums for the phytoplankton community in the Lower Lakes, which again are not consumed at a great rate by zooplankton. Under extreme lows that currently exist, salinity inputs via the barrages results in salinity stratification in Goolwa channel and subsequent release of nutrients from the sediments. Due to high levels of mixing in the Lower Lakes, both the salinity and nutrients are mixed through the lakes, maintaining high productivity but exceeding the salinity tolerance of freshwater species. Due to no flows of water across the barrages to the Coorong there are no flows of water, resources of phytoplankton from the Lower lakes to the Coorong. Instead inflows from the Southern Ocean bring in salt and phytoplankton, with salt accumulating and salinities exceeding the tolerances of many freshwater and estuarine species. Instead of passing to the zooplankton these phytoplankton are consumed by benthic infauna.

Knowledge gaps to assist managers set research priorities

Despite the importance of the water quality of the Lower River Murray to South Australia for environmental, social and economic purposes, there is very little information available on nutrient dynamics and phytoplankton communities for the region. The worked carried out in recent years through the CLLAMMecology program has been able to develop a basic understanding of how the system functions under low flows. While this information can be used to predict a possible response to increased flows, these hypotheses remain untested. For example, much of the information generated by Cook *et al.* (2008) and Aldridge *et al*. (2009) details changes in nutrient concentrations in the lake under different flow conditions. While a number of important observations were made on likely causes of the changes, these remain untested experimentally, with few studies of internal nutrient dynamics and phytoplankton communities conducted for the region. An in depth understanding of how internal nutrient dynamics and phytoplankton assemblages change under different conditions is required, particularly for the influence of salinity, water level, water regime and the interactions between them.

Monitoring of nutrients and phytoplankton assemblages play an important role in this by allowing an understanding of the overall response to changes in management and climatic conditions. However, it is important that monitoring is conducted on the long-term to allow the provision of adequate data-sets to assess the overall response of nutrients and phytoplankton to changes in water regime. In addition, long-term monitoring provides data for the calibration and validation of models such as ELCOM-CAEDYM, thus increasing the reliability of outputs.

However, in order to manipulate the system to achieve the greatest ecological benefit a detailed understanding of the mechanisms behind observed response is required. This can be achieved through targeted scientific research. Broad scientific questions that will contribute to the future management of the region include:

- What is the flow of resources (nutrients, phytoplankton etc.) between sites under different water regimes? What is the impact upon downstream ecosystems under high flows? What role do return-flows from floodplain inundation have on the productivity of the whole system?
- What contribution do external nutrient sources and internal nutrient cycling make to the nutrient budget under different flow regimes? What are the implications of internal and external nutrient supplies for ecosystem productivity?
- How do River Murray inflows alter phytoplankton community structure and productivity? How do inflows stimulate productivity and the flow of energy through foodwebs? What are the mechanisms? Is it the provision of nutrients, phytoplankton or detritus?
- What phytoplankton are preferred food sources for zooplankton? What conditions stimulate these phytoplankton communities?
- What is the optimal water regime (flow, water level, salinity) to maintain a productive and diverse phytoplankton community? What is the optimal water regime (flow, water level, salinity) to maintain populations of phytoplankton that are preferred food sources for zooplankton?
- Are certain processes or phytoplankton species/groups/assemblages good indicators of the overall condition of the region?
- What are the interactions between nutrient supply, turbidity, phytoplankton and macrophytes? What are the implications for biodiversity and ecosystem resistance and resilience?

Addressing these questions will provide information that will assist the management of the region considerably by identifying the mechanisms responsible for observed changes. This information will be able to be used for making predictions about likely response to climate change.

Currently, there exists a divide between the knowledge of biogeochemistry and ecology of the region and to add value to this information this must be addressed. Both nutrient dynamics and phytoplankton productivity are essential drivers of the foodwebs of the region. Scientific investigations should consider this role in detail in order to provide the information required for the future management of the region.

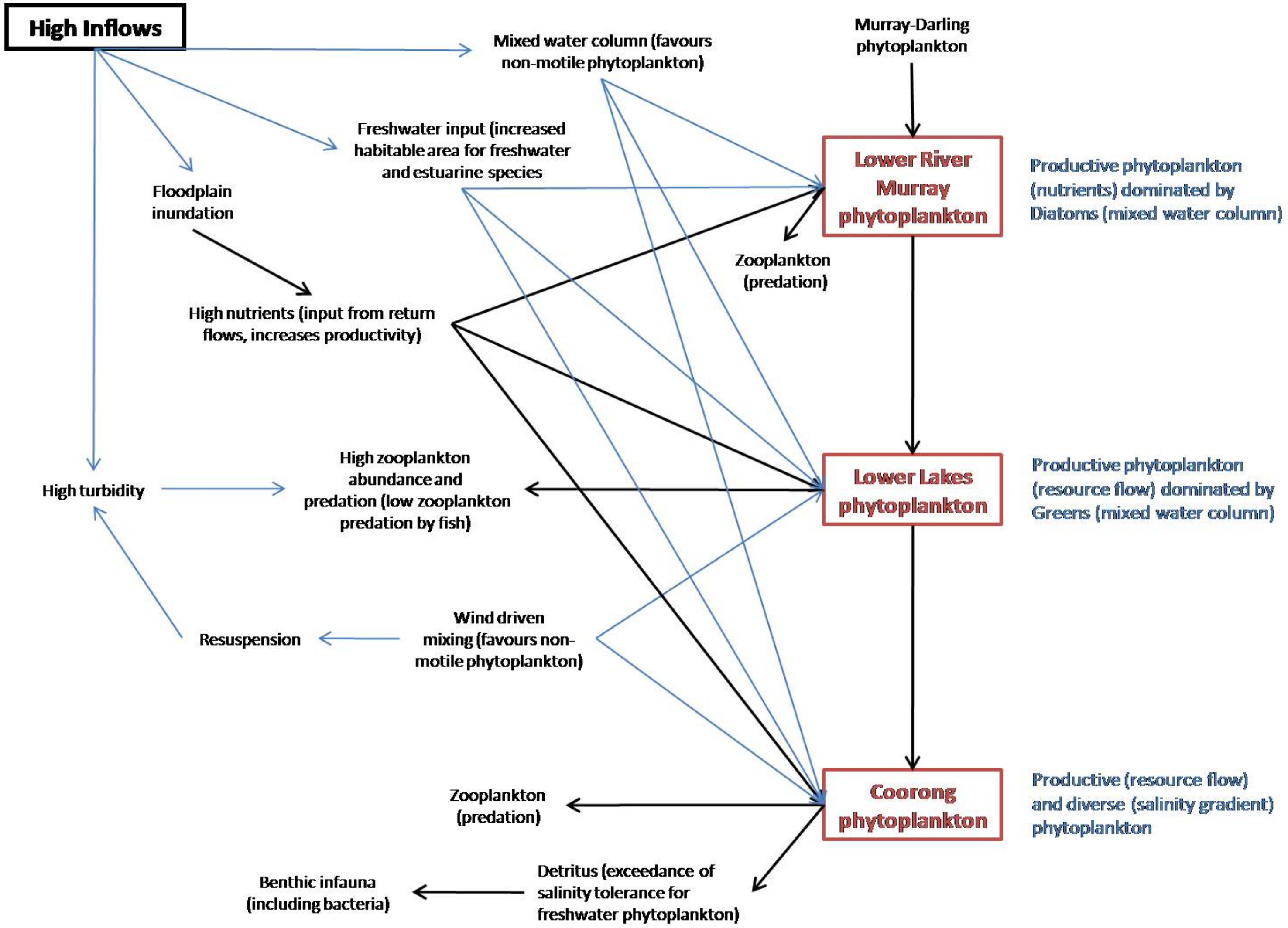


Figure 17. Conceptual diagram of nutrient dynamics and phytoplankton community in the Lower River Murray, Lower Lakes and Coorong under high flows. Black lines denote energy transfer, blue lines denote key drivers.

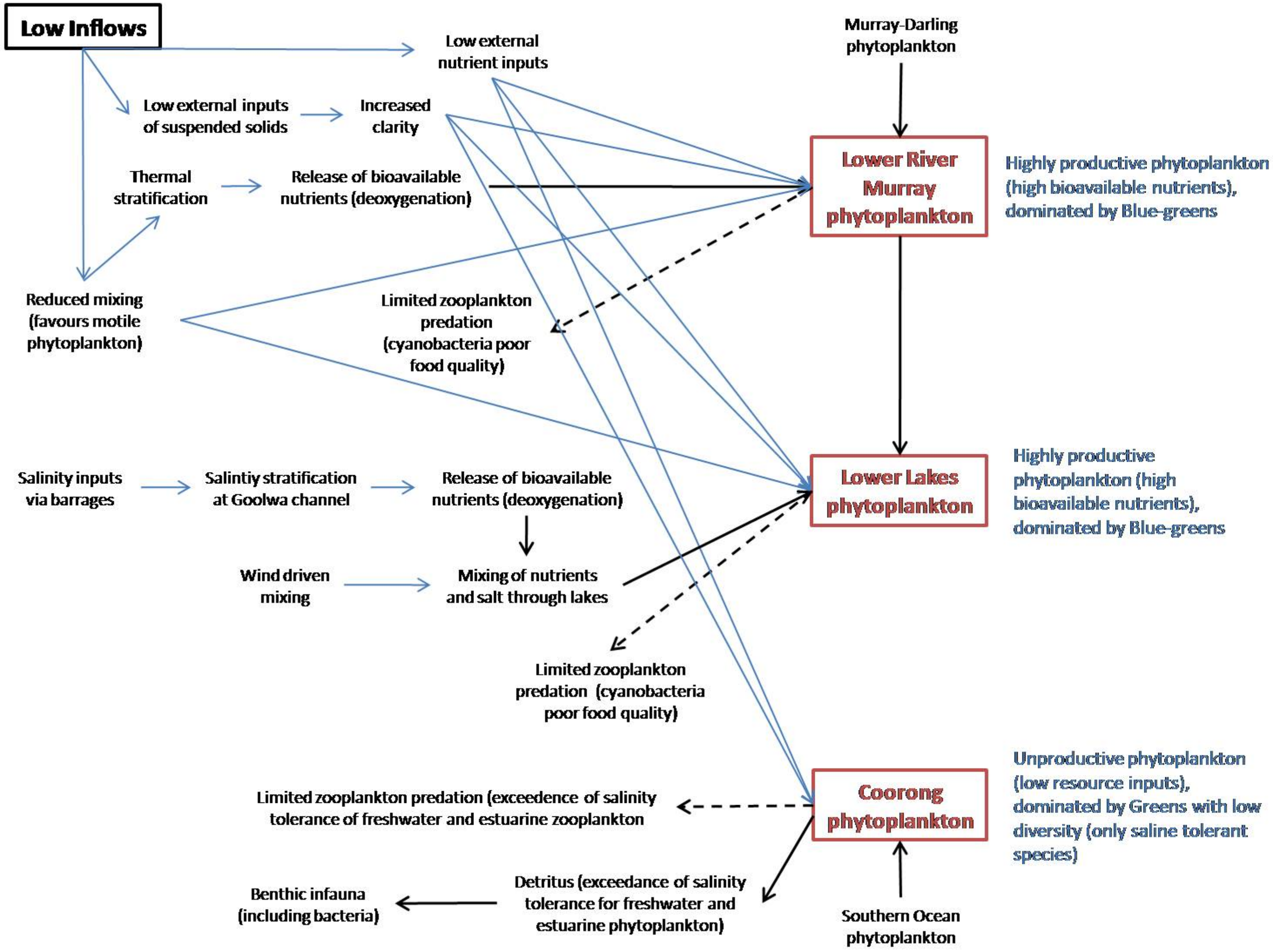


Figure 18. Conceptual diagram of nutrient dynamics and phytoplankton community in the Lower River Murray, Lower Lakes and Coorong under low flows. Black lines denote energy transfer, blue lines denote key drivers.

Appendix 1 – Background information for Nutrient cycling

Nitrogen

As with all nutrients, the nitrogen cycle in aquatic systems is complex, with continuous cycling between sediments, dead organic matter, the water column and the various components of the aquatic food-web. External sources of nitrogen into aquatic systems include the surrounding catchment, groundwater inputs and the atmosphere, which supplies nitrogen gas (N_2) (Wetzel 2001). Nitrogen also occurs in various oxidised and reduced forms with the amounts of each form available often regulating riverine productivity (Shafron *et al*. 1990).

The total nitrogen (TN) loads of rivers draining undisturbed forests consist of mostly organic N, with the TN load and fraction of nitrate (NO_3) increasing with human disturbance (Kalff 2002). Indeed, in oligotrophic waters dissolved organic nitrogen (DON) dominates the total dissolved nitrogen pool. Dissolved inorganic nitrogen (DIN) concentrations are often higher in winter than summer because in winter there are low photosynthetic rates in comparison to supply rates with most annual runoff occurring during winter (Kalff 2002).

Nitrogen fixation

Nitrogen fixation is an enzyme-catalysed process, through which N_2 is converted to ammonium (NH_4) and organic forms of nitrogen (Kalff 2002). The process is limited to prokaryotic organisms, including some blue-green algae, cyanobacteria and bacteria (Wetzel 2001). However, eukaryotic plants can form symbiotic relationships with nitrogen fixers, allowing the plants to obtain a portion of the atmospheric N_2.

A majority of the nitrogen in terrestrial systems is retained or denitrified and so there is only modest nitrogen export to aquatic systems (Kalff 2002). Consequently, substantial planktonic N-fixation occurs within rivers, lakes and wetlands. In many cases, receiving water has a low N:P supply ratio relative to demand ratio of algae and so N-fixation can prevent N-limitation and promote further growth (Kalff 2002). Nitrogen fixing cyanobacteria require light energy to reduce N_2 to organic nitrogen of the protoplasm. It is an energetically expensive process and so when light irradiance is low, or nitrogen is readily available as NH_4 or nitrite/nitrate (NO_2/NO_3, mutually expressed as NO_X), then nitrogen fixation ceases (Kalff 2002). Fixed nitrogen is cycled through the system by leakage of nitrogen from the cells, ammonification following death of the organisms or animal predation on N-fixing organisms (Wetzel 2001).

Ammonification

In water ammonium is primarily present as NH_4, but may also occur as NH_4OH, which is highly toxic to many organisms (Wetzel 2001). The proportions of NH_4 to NH_4OH are governed by temperature and pH, with the relative proportions of NH_4OH increasing with pH (Wetzel 2001).

Much of the NH_4 that occurs in aquatic ecosystems arises as the primary end-product of the decomposition of particulate and dissolved dead organic matter by heterotrophic bacteria. This process involves the deamination of proteins, amino acids, urea and other nitrogenous organic compounds (Wetzel 2001). Although intermediate nitrogen compounds are formed in the progressive degradation of organic material, they rarely accumulate because deamination by bacteria proceeds rapidly, eventually releasing NH_4 (Wetzel 2001).

The hypolimnia of aquatic systems contain elevated DIN concentrations due to diffusion of NH_4 from decomposition of organic material within the sediments. Since there is low net uptake of nitrogen in the aphotic zone, hypolimnetic NH_4 concentrations increase over time. However, during storms large quantities of hypolimnetic NH_4 and other nutrients may be returned to the epilimnia with entrainment of hypolimnetic water (Kalff 2002). Sediments contain a large percentage of the NH_4 because it strongly adsorbs to particulate and colloidal particles (Kalff 2002). However, with the loss of the oxidised microzone at the sediment-water interface under anoxic conditions, the adsorptive capacity of the sediments is greatly reduced and a marked release of NH_4 may occur to the overlying water column (Wetzel 2001).

Nitrate assimilation

The energy necessary to assimilate nitrogen is lowest for NH_4-N and increases for NO_3-N and N_2-N for N_2 fixing cyanobacteria (Wetzel 2001). Consequently NH_4 is an energy-efficient source of nitrogen. On the other hand NO_3 must be reduced to NH_4 before it can be assimilated by plants (Wetzel 2001). Upon reduction to NH_4, it may be incorporated into the microbial/algal protoplasm with the whole process known as nitrate assimilation (Kalff 2002). From here, the nitrogen may be passed through the food-web.

Nitrification

Nitrification is the biological oxidation of organic and inorganic nitrogenous compounds from a reduced state, which begins with the conversion of NH_4 to NO_2, which then proceeds further to NO_3, which may then partake in denitrification reactions (Kalff 2002; Wetzel 2001). It is catalysed by a variety of microorganisms that obtain energy for metabolism and results in high NO_X:NH_4 ratios in well-oxygenated epilimnion of unpolluted clear-water lakes (Kalff 2002).

The rate of nitrification is mainly a function of the NH_4 (or NO_2) pool, dissolved oxygen supply rate, carbon dioxide (CO_2) availability, water temperature and pH. The major site of nitrification is the interface between oxic and anoxic waters/sediments because the anoxic zone has a high NH_4 supply rate, resulting from ammonification within sediments (Wetzel 2001). Nitrification has a large demand upon dissolved oxygen within the hypolimnion and nitrification may cease under anoxic conditions (Kalff 2002). Carbon dioxide is important because nitrifying microbes are chemoautotrophs, which reduce CO_2 into organic carbon with energy supplied from oxidation of NH_4 (Kalff 2002).

Denitrification

Denitrification is closely coupled with nitrification. Denitrification is a bacterially mediated process of reducing oxidised nitrogen anions (NO_X), with the concomitant oxidation of organic matter. Oxidised nitrogen is firstly reduced to nitrous oxides (NO, N_2O) and then to N_2 gas (Wetzel 2001). If not refixed, N_2O and N_2 may be released back into the atmosphere. Denitrification is carried out by many heterotrophic facultative anaerobic bacteria and fungi at the oxic-anoxic interface in lakes and rivers, where microbes use nitrogen oxides as an alternative terminal electron acceptor to oxygen (Kalff 2002; Wetzel 2001).

Denitrification occurs in anaerobic environments and rates are enhanced in shallow, warm water bodies. The presence of aquatic macrophytes promotes denitrification by enhancing the sedimentation of organic material (Kalff 2002). Emergent macrophyte stems also act as conduits for the upward flux of N_2 and N_2O from the root zone to atmosphere (Kalff 2002). In addition, macrophytes inadvertently release oxygen from their roots into the surrounding sediments, which allows linked nitrification-denitrification in the surrounding sediments (Kalff 2002).

Phosphorus

Phosphorus cycling in the aquatic environment is complex due to the transformation of phosphorus between organic and inorganic fractions in both soluble and insoluble forms. More than 90% of the phosphorus in freshwater ecosystems consists as organic P, as organic phosphates and cellular constituents in the biota and adsorbed to inorganic and dead particulate organic materials (Wetzel 2001). Dissolved inorganic phosphate, more commonly referred to as orthophosphate or filterable reactive phosphorus, is the most biologically available form of P, which is derived from the breakdown of dissolved organic phosphorus and also release from sediments by biochemical processes (Shafron *et al*. 1990). In freshwater ecosystems, phosphorus is generally considered to be more often limiting for primary production than N, particularly in oligotrophic waters at mid-latitude (Kalff 2002). This, along with the closed nature of the phosphorus cycle (no fixation from the atmosphere) mean that many management strategies of eutrophication have focussed on reducing phosphorus loads.

Phosphorus inputs

Phosphorus enters aquatic systems from the terrestrial environment and from direct atmospheric deposition on the water surface (Kalff 2002). Contributions from the catchment normally dominate total inputs except where catchments are very small and composed of soils with low phosphorus concentrations (Kalff 2002). Phosphorus demand is typically high relative to supply and so phosphorus retention with streams and rivers is high with little released into receiving waters of vegetated catchments (Kalff 2002). Phosphorus is released primarily in the dissolved organic form, supplemented by organic phosphorus associated with terrestrial sediment particles (Kalff 2002). In poorly vegetated catchments, such as crop-growing areas, phosphorus is usually released while sorbed to soil particles, especially during storm run-off periods (Kalff 2002).

Biological utilisation and recycling

Biological uptake of phosphorus by algae, cyanobacteria, bacteria and larger aquatic plants generally follows Michaelis-Menten kinetics, often at rates more rapid that what is used for growth (Wetzel

2001). Consequently, cells can often accumulate phosphorus. The rates of phosphorus uptake are closely correlated with the metabolism of the dominant organisms, which may be determined by the levels of incident light as well as the extent of detrital accumulation (Wetzel 2001). eg. phosphorus uptake is primarily associated with attached and planktonic algae in low shaded environments. Uptake by macrophytes, particularly rooted vascular plants, is generally much less than by attached algae and other microbes (Wetzel 2001). Average planktonic algal abundance has been positively correlated to total phosphorus (TP) concentrations of streams, rivers and lakes (Dillon and Rigler 1974).

Phosphorus can be released from biota by excretion in inorganic and organic forms from living microbiota or as the organisms senesce, die and lyse. The dissolved organic phosphorus compounds are utilised enzymatically more slowly than dissolved inorganic phosphorus. Consequently, there is an accumulation of phosphorus compounds with higher molecular weights and these compounds are exported downstream for subsequent utilisation (Wetzel 2001).

Appendix 2 – Background information for phytoplankton

Cyanophyta

Cyanophyta, or cyanobacteria, are a form of bacteria (prokaryotic) which lack a typical membrane-bound nuclei, but instead contain chromatin bodies. All cyanobacteria lack chlorophyll *b* but are able to store excess energy from photosynthesis as glycogen and glycoproteins. Reproduction is by fission but in some filamentous species akinetes function as dormant reproductive cells. Some cyanobactera form colonies, although the colonial organisation is very simple, with the branched trichome being the most complex organisation known (Prescott 1962)

Some species are able to fix atmospheric nitrogen when other sources of nitrogen, like ammonium and nitrate are deficient, providing them with a large ecological advantage. This is observed in species with specialised cells called heterocysts (eg. species of the genera *Anabaena, Aphanizomenon, Cylindrospermopsis, Nodularia* and *Nostoc*) (Chorus and Bartrum 1999). These nitrogen fixing cyanobacteria are usually promoted by surface warming, good light levels and adequate nutrient supplies.

Some cyanobacteria produce toxic substances which can be harmful to domestic stock and humans. This is particularly problematic when toxic cyanobacteria 'bloom' and form a surface scum through the flotation of buoyant colonies (Reynolds 1997). There are three main classes of toxins:

- Hepatotoxic microsystins - They acutely attack the digestive tract of consumers causing pneumonia like symptoms and sickness in humans. Microcystins have been found in a range of cyanobacterial species, not just from *Mycrocystis*. *Nodularia spumigena,* a common trouble species to the Lower Lakes produces a toxic chemical called nodularin, which has similar hepatotoxic effects to micocystins, through the inhibition of protein phosphatises.
- Neurotoxic anatoxins - principally produced by the nostocalean genera (*Anabaena* and *Aphanizomenon*).
- Lipopolysaccharides - These have been associated with sublethal skin irritations after contact with cumulative chronic consequences upon frequent exposure. Seen in some species of *Gloeotrichia and Planktolyngbya*, with the latter currently one of the dominant genera of the Lower Lakes.

Chlorophyta

Chlorophyta are a diverse group of eukaryotic algae that are characterised by grass-green chloroplasts. Cells contain a wide range of chloroplasts ranging from one to many. The green algae contain both chlorophyll *a* and *b* as their photosynthetic pigment. Excess energy from photosynthesis is stored as starch. The cell wall is composed of cellulose and pectic compounds.

Bacillariophyta

Diatoms are distinctive in that their cell wall is impregnated with silica. They all have two distinct halves (valves) and are never flagellate (Reynolds 1984). Diatoms tend to dominate in well mixed, and often cold environments (Reynolds 1997). Chloroplast colours are usually yellow-brown in planktonic species and dark brown in sessile and mud living forms. These colours result from the masking of the chlorophylls present by the xanthophyll pigments. Reserve substances include lipid, volutin globules and leucosin in concentrated solution (Boney 1975).

Euglenophyta

Euglena are unicellular protists that are generally found in freshwater, although they are also common in estuaries. They have a gullet and complex vacuolar system, allowing them to consume substances by phagocytosis. They can therefore be autotrophic or heterotrophic (Prescott 1962). Both colourless and pigmented species are known, depending on their degree of autotrophy/heterotrophy. They contain flagella, usually two per cell, which arise from an anterior opening. Chloroplasts are numerous and of various shapes and the food reserve is a starch-like polysaccharide, paramylon (Reynolds 1984).

Dinophyceae

The dinoflagellates are widely distributed in marine, estuarine and freshwater environments, although the majority are marine. They are mostly unicellular and autotrophic, but some colourless parasitic species are known. Chloroplasts of dinoflagellates are yellow-green or yellow-brown in colour and starch and oils are the principal reserve substances (Boney 1975). Some types have a thin wall, while others possess a thick cellulose cell wall with precise patterning of plates. These are referred to as ‘armoured’ dinoflagellates

Dinoflagellates can actively control their position in the water column. The cells bear two flagella, one longitudinal and the other transverse. Vibration of the longitudinal flagellum pushes water away and the transverse flagellum causing cell rotation and forward motion. Their motility allows them to dominate stratified lakes with segregated resources (light in surface waters, nutrients in bottom waters) and they are able to survive at both high and low nutrient and light conditions. In typically mesotrophic to eutrophic lakes some large celled genera, like *Ceratium* and *Peridinium* can form a very large biomass. In these environments they compete with bloom forming cyanobacteria, or may precede, or more commonly succeed them (Reynolds 1997).

Some species are toxic, producing saxitoxins and gonyuatoxins. These have commonly been associated with Paralytic Shellfish Poisoning which is a large concern to many fisheries (See http://www.issg.org/database/species/ecology.asp?si=645&fr=1&sts=&lang=EN).

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