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Full Length Research Paper

Seasonal examination of phytoplankton abundance and assemblages in Myall Lake and Bombah Broadwater, New South Wales, Australia

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The Myall Lakes are a series of interconnected, shallow and poorly flushed coastal lakes located within the Myall Lakes National Park in NSW, Australia. The following field study aims to uncover patterns in temporal variability in water quality and phytoplankton abundance, diversity and assemblage structure, in the upper and lower water bodies of the Myall Lakes system. The result showed that the two lakes differ greatly in their catchment to lake area ratios, freshwater inputs, degree of saline intrusion, light attenuation and submerged macrophyte biomass. The broadwater, which receives large inputs of freshwater from the catchment, and is influenced by saline inputs from the Port Stephen's estuary, exhibited highly variable water quality and dissolved nutrient concentrations, and phytoplankton assemblages with much temporal variation in taxa present, biovolume, cell size and abundance, and taxonomic diversity. In contrast, the upper lake, Myall Lake, shows much greater stability in water chemistry and nutrient availability; the phytoplankton community is diverse, with relatively low and constant biovolume, and is dominated year-round by small-celled cyanobacteria. Differences in phytoplankton between the two lakes were greatest during the autumn and winter, and least during the summer, when the phytoplankton assemblages in both lakes were dominated by similar cyanophyte taxa.

Key words: Seasonal variation, phytoplankton abundance and assemblages, Myall Lake and Bomba Broadwater.

INTRODUCTION

Concentrations of available nitrogen and phosphorus in aquatic ecosystems represent contributions from both autochthonous and allochthonous sources. In river estuaries, it is allochthonous sources of nutrients that are generally most responsible for the supply of nitrogen and phosphorus to aquatic primary producers. Catchment activities have a major impact on the export of nutrients to rivers, lakes and estuaries. Deforestation, agricultural practices (fertilisers and land clearing), urban developments, industry and stormwater run-off lead to the accumulation of nutrients and sediments in poorly flushed water bodies (Entry and Emmingham, 1996; Mander et al., 1997; Jorgensen et al., 2000; Edward et al., 2003). Activities in the catchment also impact on the N:P ratios found in lakes and streams, with forested watersheds contributing to very high TN:TP ratios in lakes (Barbanti et al., 1995).

In general, Australia's freshwater, marine and estuarine systems are lower in nutrients than European and North American systems, partly due to lower rates of atmospheric deposition of N, and partly because Australian catchments, by comparison, are less disturbed

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(Harris, 2001). Pristine catchments in Australia generally export low amounts of N and P; the nitrogen appears largely as dissolved organic nitrogen (DON) and is sourced from decaying vegetative matter (Harris, 2001). When catchments are anthropogenically modified, there is a shift from catchment inputs of largely DON to largely dissolved inorganic nitrogen (DIN) (Harris, 2001).

Oligotrophic (low nutrient) waters exhibit greater clarity than eutrophic (nutrient rich) systems (Flindt et al., 1999). Macrophytes tend to dominate in oligotrophic waters, while eutrophic systems are typically dominated by phytoplankton which rapidly uptake available nutrients and thus suppress the development of macrophytes that require a high light regime (Casanova et al., 1997; Flindt et al., 1999; Asaeda et al., 2001; Asaeda et al., 2007). An increase in nutrient loading, coupled with an increase in water temperature, can result in a rapid shift from a macrophyte-dominated system to a phytoplankton-dominated system (Asaeda and van Bon, 1997; Asaeda et al., 2001).

In anthropogenically-modified catchments, excessive amounts of nutrients and sediments may enter coastal waterbodies via rivers and creeks. Nutrient enrichment may result in the development of blooms through the rapid growth of opportunistic phytoplankton (largely cyanobacteria, chlorophytes and diatoms) and macrophytes (Codd, 2000; Menedez and Comin, 2000). The outcome of enhanced sediment loads is an increase in turbidity that can alter autotrophic assemblages (as light levels decline) and restrict macrophyte growth (Asaeda et al., 2001). Competition for available nutrients and light influence those taxonomic groups that dominate at a given time (Carr et al., 1997; Flindt et al., 1999).

The following field study aims to uncover patterns in temporal variability in water quality and phytoplankton abundance, diversity and assemblage structure, in the upper and lower water bodies of the Myall Lakes system. It includes a consistent sampling approach and greater spatial and temporal replication than in previous studies. It allows a more rigorous statistical analysis of data, including multivariate analysis of phytoplankton community structure and the identification of those taxa contributing most to observed temporal and spatial differences in phytoplankton assemblages.

MATERIALS AND METHODS

Study site

The Myall Lakes system is composed of an interconnected chain of four shallow Lakes located within the Myall Lakes National Park. The upper lake, Myall Lake, is the largest lake at 63 km^2, but has a small catchment (226 km^2) in relation to lake area; the lake to catchment area ratio is < 4:1. The average lake depth is 2.85 m and maximum depth is ~5 m (Dasey et al., 2005). Myall Lake exhibits high water clarity and is the most pristine of the four lakes (DIPNR, 2004). It is connected via a narrow channel to Boolambayte Lake, which is directly connected to another small lake, Two-Mile Lake, before opening into Bombah Broadwater. This water body is often referred to in this thesis, and in DIPNR (2004), as Bombah Broadwater. Bombah Broadwater is the second largest lake (23 km^2) in the Myall Lakes system, and has a large catchment area of 465 km^2 (ratio of catchment to lake area is 20.1). The catchment drains largely via the Upper Myall River into Bombah Broadwater. Other inputs include saline water from the Port Stephen's estuary which enters the lake via the Lower Myall River, a long (24 km) and narrow watercourse. The approximate flushing times of water in Bombah Broadwater and in Myall Lake are about 65 days and 540 days, respectively (Sanderson, unpubl data). For the most part, fluctuations in water depth are associated with rainfall events rather than tidal influence (Atkinson et al., 1981). Mean annual precipitation is ~1300 mm (DIPNR, 2004). Between lake differences in catchment runoff, coupled with their physical separation (i.e. two lakes located between them), leads to considerable differences in lake water chemistry and productivity.

Field sampling and variables measured

This field study involved sampling in the two largest lakes in the Myall Lakes system, Myall Lake and Bombah Broadwater (Figure 1), which are indirectly connected by a series of two smaller lakes which total about 10 km in length. Samples of phytoplankton and dissolved inorganic nutrients, and associated water quality data, were collected from six randomly selected areas in Bombah Broadwater and in Myall Lake during each of four Austral seasons (autumn, winter, spring, summer) over the period April 2003 to January 2004. As Bombah Broadwater is known to experience greater environmental fluctuations than Myall Lake, due largely to tidal influences and irregular riverine inputs, it was sampled twice per season. The times of collection are shown in the plot of rainfall data (Figure 2).

Water quality variables were measured using a Yeo-Kal 611 water quality analyser. Nutrient, chlorophyll a and phytoplankton cell samples were collected from a depth of 0-1 m using a Perspex pole sampler (1.5 m long, 60 mm diameter), which was then emptied into a twice-rinsed receiving container. Nutrient samples (25 ml) and chlorophyll a were analysed and measured using spectrophotometer.

Phytoplankton cell samples (250 ml) were preserved with 1 ml acid Lugols solution and stored in the dark for up to 4 weeks. Algal cells in 100 ml subsamples were left to settle in graduated cylinders in the dark for 48 h, after which 90 ml from the top layer of each sample was pipetted out and the remainder (10 ml) transferred to an amber glass vial which was then stored in the dark at room temperature. Phytoplankton cells were counted using the Lund Cell. Identification of cells was to genus level, and where possible, species level. Biovolume for each set of 6 samples was calculated from 25 randomly selected cells per taxa, and was based on geometric assignation (Sicko-Goad et al., 1977; Kononen et al., 1984; Hillebrand et al., 1999; Sun and Liu, 2003).

Data analysis

Univariate ANOVA (GMAV v5, University of Sydney) was used to detect significant seasonal differences in the following variables: total cell abundance, abundance of major classes, taxonomic richness, Shannon-Wiener Diversity Index (H′), chlorophyll a, chl a/cell and cell biovolume. Time was nested in season for the Bombah Broadwater dataset. Cochran's test was used to test for homogeneity of variances. Where the variances differed significantly, data were transformed using ln(x+1) to improve homogeneity and thereby reduce the chance of a Type I error (Irwin et al., 2006). When significant seasonal effects were observed, post hoc SNK (Student-Newman-Keuls) tests were carried out to detect how seasons differed. Non-metric multivariate statistics, using PRIMER v.5.2.7, were used to produce nMDS plots for examination of patterns in phytoplankton assemblages

Figure 1. Map of the Myall Lakes and catchment. Adapted from DLWC (2004).

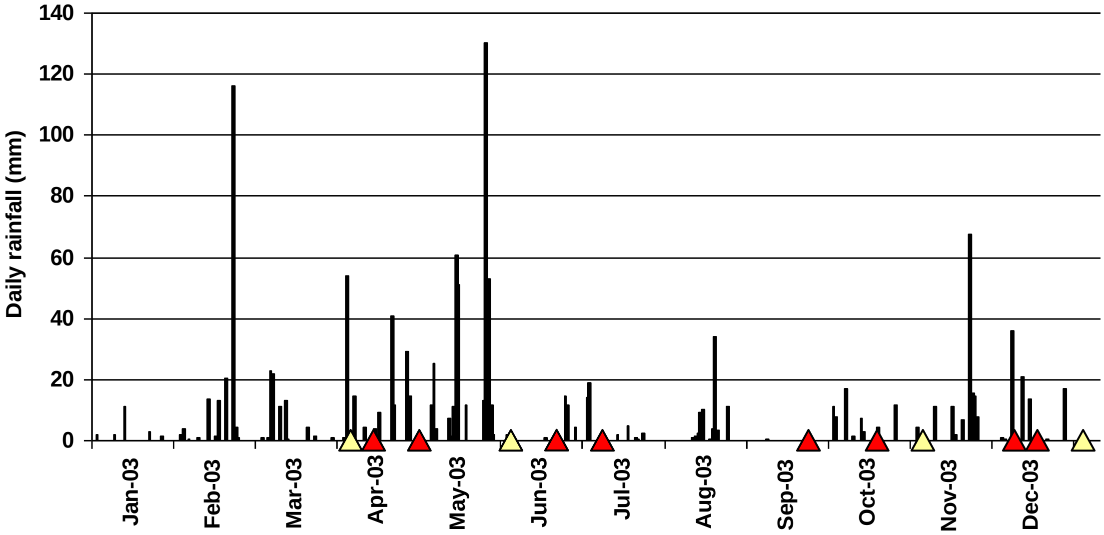

Figure 2. Rainfall (mm) recorded daily during 2003, as measured at Bulahdelah (data from Bureau of Meteorology, Australia). Triangles indicate times of sampling in Myall Lake (yellow) and Bombah Broadwater (red).

between seasons and between lakes. Significant differences in assemblage structure, and species contributing to the similarities or dissimilarities observed, were determined using the Analysis of Similarities (ANOSIM) and Similarity of Percentage (SIMPER) procedure. The Shannon-Wiener species diversity index, which increases as the species number (richness) and the equitability of species abundance increases, was also determined using PRIMER.

RESULTS

Rainfall and water chemistry

Sampling commenced in early April 2003 after a rainfall event. Frequent rain events (max 130 mm in a single

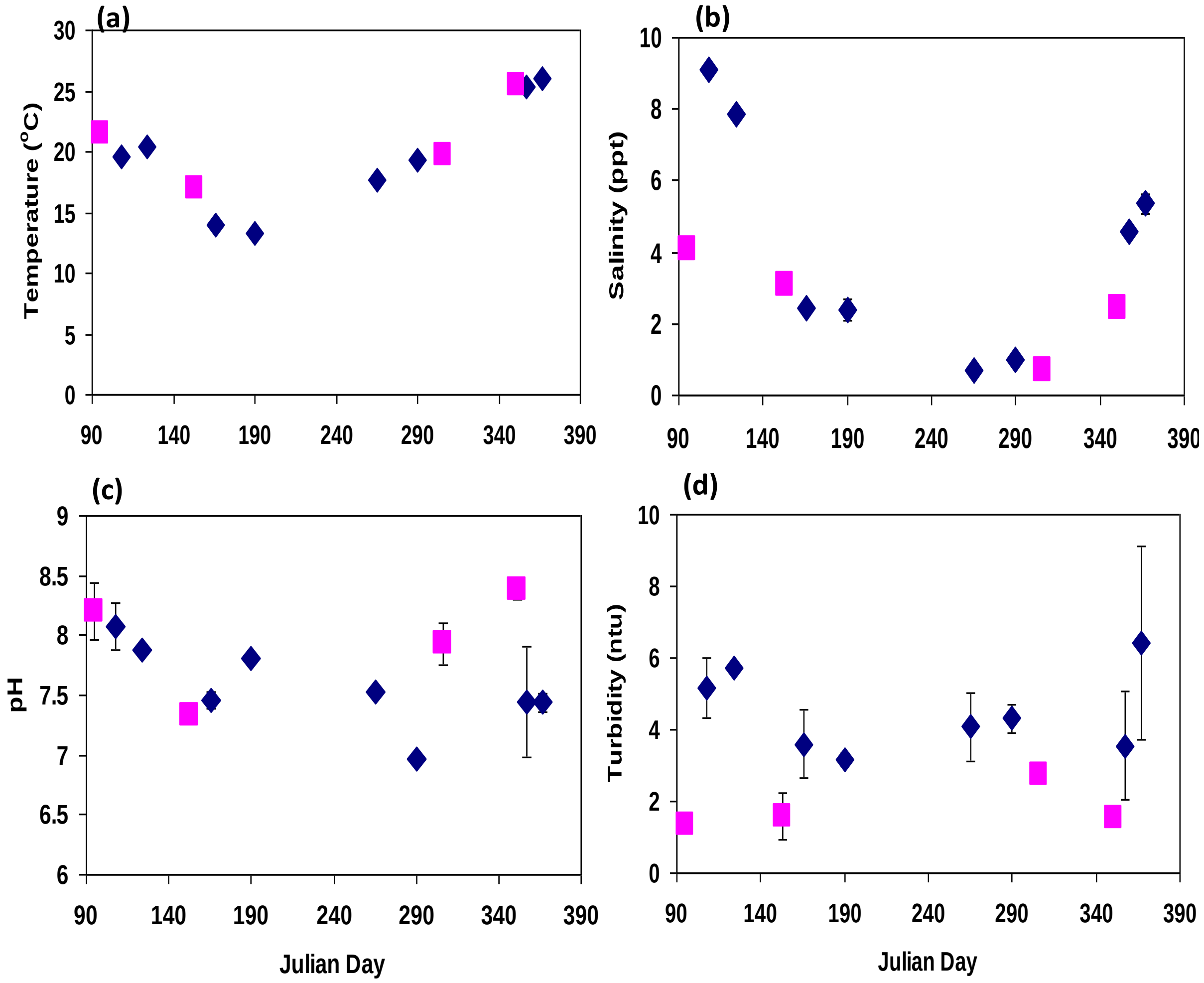

Figure 3. Water quality variables at 0-1 m depth in Myall Lake (ML) and Bombah Broadwater (BB) for all sampling periods (mean + SE, n = 6). (a) Temperature, (b) Salinity (c) pH and (d) Turbidity. Julian Days start on 1 Jan 2003. Raw data provided by Donna Cohen.

day) continued until late May 2003 (Figure 3). Both winter and spring periods (June to September) were relatively dry seasons. They were followed by an increase in rainfall frequency and intensity during the last few months in 2003. About 1300 mm of rain fell in 2003; this amount and the seasonal trends in rainfall are typical for the Myall Lakes area (DIPNR, 2004).

Figure 4a to d shows water quality values (salinity, temperature, pH and turbidity) during all sampling occasions. Observations of salinity in Myall Lake were between 0.7 and 3.1 ppt while Bombah Broadwater exhibited a broader salinity range of 0.7 and 9.1 ppt (Figure 4a), which reflected seawater intrusion from the Port Stephens Estuary via the Lower Myall River. Water temperature in the lakes varied seasonally, with values ranging from 13 - 26°C (Figure 4b).

During the cooler months, pH was reduced in both lakes, presumably due to temperature-related decrease in primary productivity. The pH was much higher in Myall Lake, which supports large and extensive meadows of charophytes (Chara, Nitella). Although turbidity levels in both lakes were low (< 9 NTU) at all times of sampling, Bombah Broadwater showed higher and more variable turbidity than Myall Lake (mean values of 1.5-3 NTU) (Figure 4d).

Dissolved inorganic nutrient concentrations in the water column (ammonia, oxides of nitrogen, and soluble reactive phosphorus) varied over the seasons, especially in Bombah Broadwater where the highest DIN concentrations (ammonia plus NOx) were observed in winter (Figure 5). In both lakes (Myall Lake and Bombah Broadwater), available phosphate (orthophosphate) levels were below 5 mg/L on all sampling occasions, and were particularly low (≤ 1 mg/L) in Myall Lake (Figure 5c). In Bombah Broadwater, the dissolved nitrogen to phosphate (N:P) ratios were significantly higher in winter (50-160) than in other seasons (Figure 5d). The ratios in Myall Lake were only slightly higher in winter

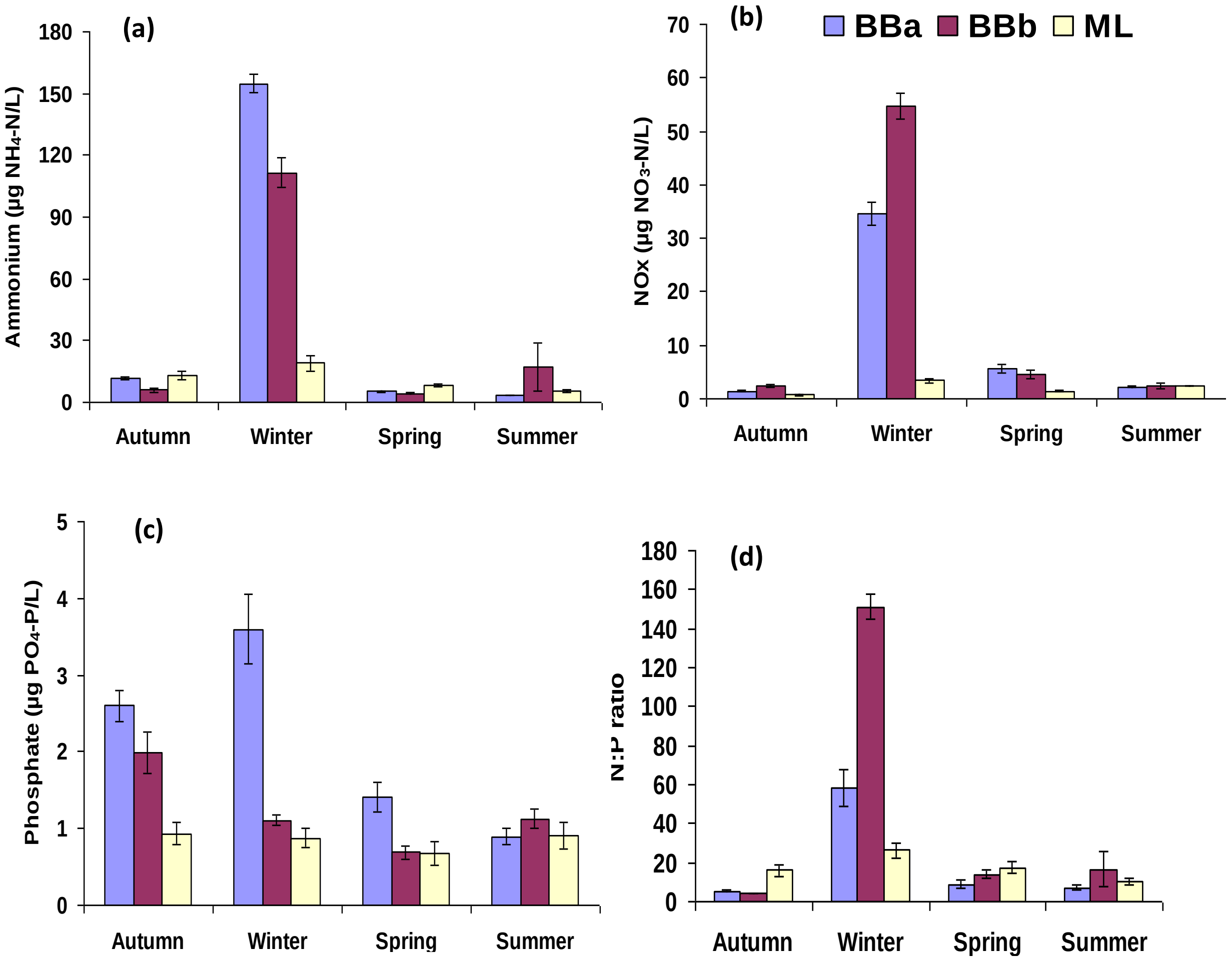

Figure 4. Water column dissolved inorganic nutrient concentrations (mean ± SE, n = 6) in Myall Lake (ML) and Bombah Broadwater (BB): (a) ammonia, (b) NOx, (c) orthophosphate and d) N:P ratio (dissolved nutrients only), with dashed line indicating the generally preferred upper limit for cyanophyte growth. Bombah Broadwater was sampled twice per season. Raw data provided by Donna Cohen.

(~25). At all other sampling times, mean N:P ratios were < 20 in both lakes (Figure 5d).

Phytoplankton seasonal trends

Abundance and diversity

A total of 35 phytoplankton genera were identified in the 72 samples collected (Table 1). The number of genera observed ranged from autumn/winter lows of 7 and 9 genera to more diverse summer assemblages of 19 and 20 genera in Bombah Broadwater and Myall Lake, respectively. Nine genera were observed in either Bombah Broadwater or Myall Lake but not both. Cyanophyceae, Chlorophyceae, Bacillariophyceae and Dinophyceae were the dominant classes. Only one taxon, Merismopedia, was considered 'very abundant' (>10,000 cells/mL) in summer, in both Myall Lake and Bombah Broadwater, and was likewise very abundant in spring in Myall Lake. The only two common and abundant taxa (up to 10,000 cells/mL) that were observed in both lakes included *Chroococcus* and *Coelasphaerium*.*Microspora* and *Gymnodinium* were common only in Bombah Broadwater while *Aphanocapsa* and *Gleocystis* were common and abundant, respectively, in Myall Lake. The remaining 28 genera were uncommon in either one or both of the lakes.

In autumn, winter and spring, ANOVA and SNK tests showed total cell abundance was markedly lower in Bombah Broadwater than in Myall Lake; summer cell densities exceeded 25,000 cells/mL, in both lakes (Figure 6a). In each lake, ANOVAs found significant differences in cell abundance between seasons but no significant difference with the factor 'time' (nested within season) for Bombah Broadwater (Table 2).

Cyanophyceae abundance differed significantly with season in both lakes and although rarely observed in

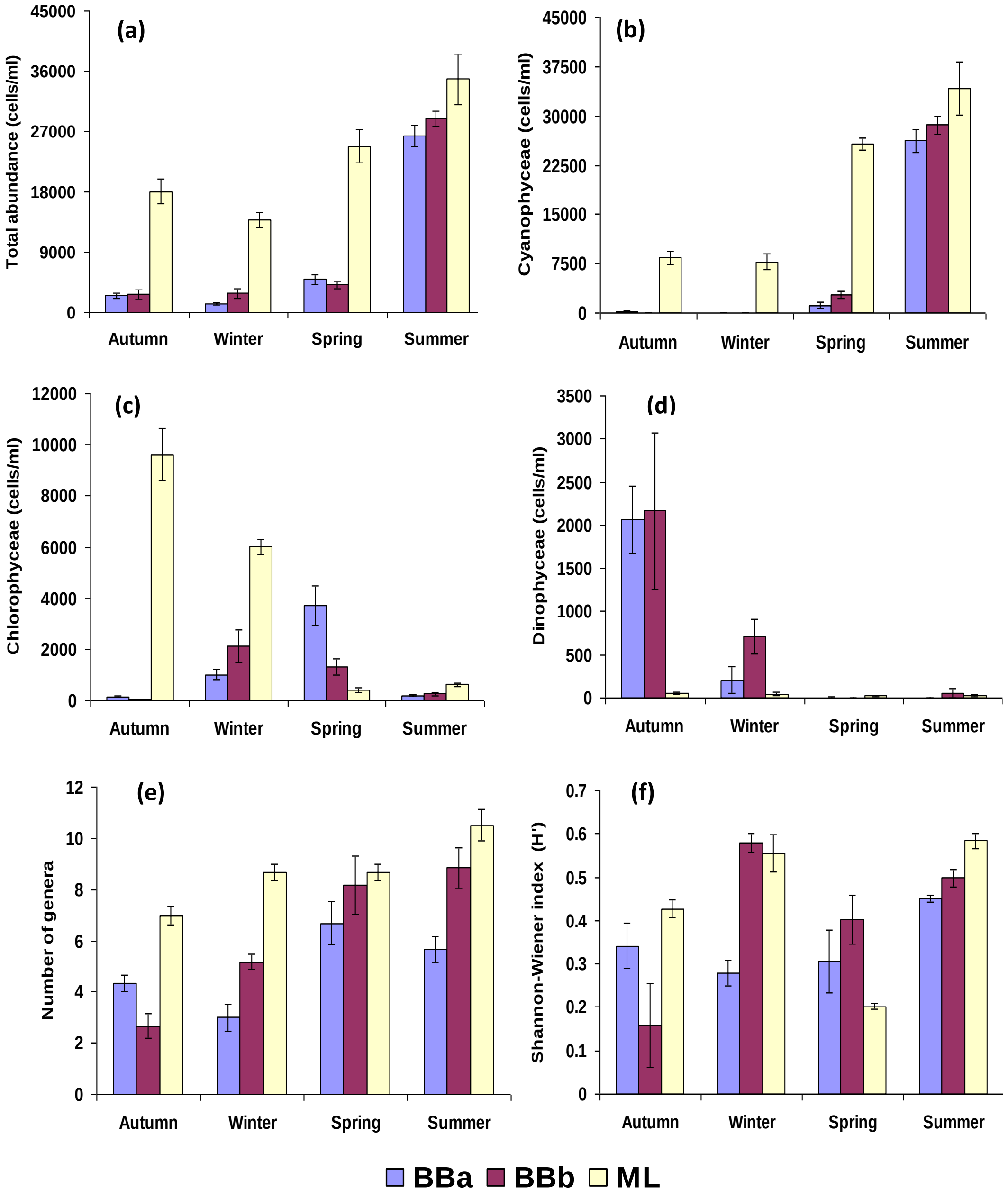

Figure 5. Phytoplankton abundance: a) total cells, b) Chlorophyceae, c) Cyano-phyceae, d) Dinophyceae, and diversity measures: e) taxonomic richness and f) Shannon-Wiener Index (mean ±SE, n=6).

autumn and winter in Bombah Broadwater, Cyanophyceae was clearly the dominant class in both lakes during the summer of 2003 (Table 1, Figure 6b). In Bombah Broadwater, significant differences over shorter temporal scales (weeks) were apparent for both Cyanophyceae and Chlorophyceae.

The abundance of Chlorophyceae varied significantly with season only in Myall Lake (Table 2), where high numbers of *Gloeocystis* were observed in autumn and winter (5000 to 10,000 cells/mL). Dinophyceae were very uncommon in Myall Lake on all sampling occasions but were found in abundance in Bombah Broadwater (about 2000 *Gymnodinium* per mL), at both sampling times during autumn (Figure 6d).

Although more genera were observed in Bombah Broadwater samples collected in spring and summer than in autumn and winter (Table 1), ANOVA showed that neither taxonomic richness nor diversity (Shannon-Wiener Index) differed significantly between seasons (Table 1, Figure 6e,f). Interestingly, there was a significant difference at smaller temporal scales (time within season). In contrast, Myall Lake phytoplankton

Table 1. Phytoplankton taxa observed and their abundance level in autumn (Au), winter (W), spring (Sp) and summer (Su): Abundance: uncommon (U), common (C), abundant (A) and very abundant (VA). Observations are based on 12 samples per season in Bombah Broadwater and 6 samples per season in Myall Lake.

Class	Genus	Broadwater (N=48)				Myall Lake (N=24)			
		Au	W	Sp	Su	Au	W	Sp	Su
Cyanophyceae	*Anabaena*				U				
	Aphanocapsa				U		C	C	C
	Chroococcus				C		U	A	A
	Coelasphaerium			U	A	C	C	A	A
	Gloeocapsa	U		U		U		U	U
	Merismopedia			U	VA	C	C	VA	VA
Chlorophyceae	*Chlamydomonas*				U	U	U	U	U
	Chodatella				U	U	U	U	U
	Coelastrum								U
	Cosmarium		U		U	U	U	U	U
	Dispora				U				U
	Franceia			U					U
	Gloeocystis			U	A	A			U
	Gleokinina							U	U
	Gloeoactinium		U						
	Microspora	U	U	C	U	U			U
	Palmella				U			U	U
	Scenedesmus			U	U	U	U	U	U
	Strombomonas			U	U				
	Tetraspora	U				U	U		
	Trachelomonas	U							
	Volvox	U	U	U	U	U		U	
Bacillariophyceae	*Amphora*		U						
	Coconeis	U		U	U			U	U
	Cyclotella			U					
	Fallacia			U					U
	Gomphonema			U				U	
	Gyrosigma				U			U	
	Navicula	U		U	U				
	Planothidium				U			U	
	Synedra			U				U	
Dinophyceae	*Gymnodinium*	C	U	U	U	U	U	U	U
Crysophyceae	*Chroomonas*		U	U					
Euglenophyceae	*Euglena*	U			U			U	
	# of genera	9	7	17	19	13	12	18	20

Very abundant (VA) > 10,000 cells/ml; Abundant (A) 5001 – 10,000 cells/ml; Common (C) 1000 – 5000 cells/ml; Uncommon or rare (U) < 1000 cells/ml.

showed significantly higher phytoplankton diversity in summer than in spring and autumn.

Chlorophyll a, chl a /cell and biovolume

Chlorophyll a concentrations were greater and more variable in Bombah Broadwater (mean values of 2 to 11 µg/L) than in Myall Lake (< 3 µg/L), however, both showed significant differences in concentration with season (Figure 7a, Table 3), with the highest mean chlorophyll a values in autumn and winter. Significant short temporal differences (time within season) were also observed for Bombah Broadwater.

Chlorophyll a content per cell was highly variable with season in Bombah Broadwater and reflected the dominance of large dinoflagellates (*Gymnodinium*) in

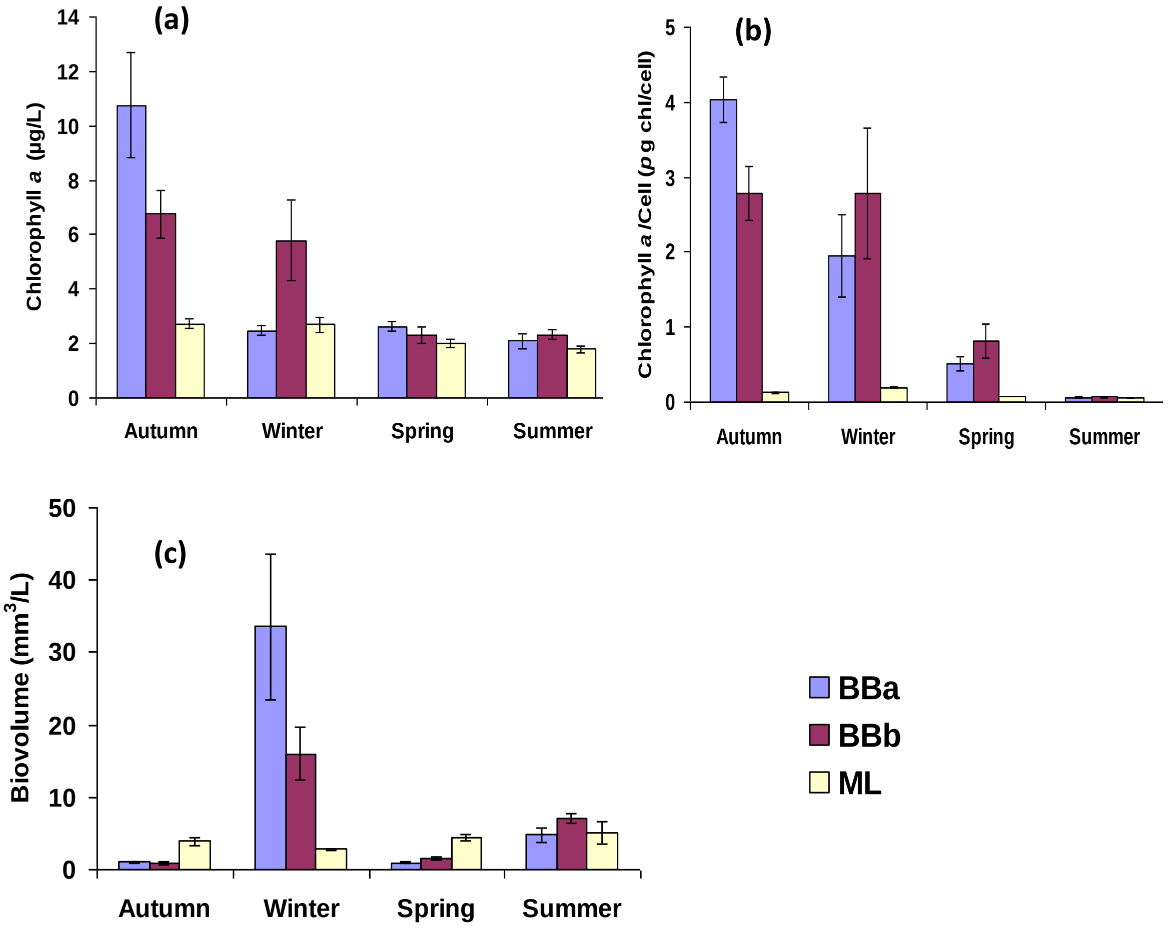

Figure 6. Seasonal measures of chlorophyll a, chlorophyll a/cell and biovolume (mean ± SE; n = 6). ML = Myall Lake, BBa = Bombah Broadwater first sampling occasion and BBb = Bombah Broadwater second sampling occasion.

autumn, abundant *Gymnodinium, Cosmarium* and *Gloeoactinium* in winter, followed by the dominance of Microspora in spring, and small-celled cyanobacteria (*Coelasphaerium* and *Merismopedia*) in summer (Tables 1 and 3). Myall Lake chl a/cell values were less variable but significantly different with season; Chlorophytes (Gloeocystis) and cyanophytes dominated in autumn and winter, while cyanophytes (several species) comprised >95% of the cells in spring and summer.

Biovolume showed significant seasonal differences in Bombah Broadwater but not at shorter temporal scales (weeks) (Table 3). Cell biovolume in Bombah Broadwater was significantly higher in winter (mostly due to large-celled Gloeoactinium) than in all other seasons; in Myall Lake, biovolume remained relatively constant across seasons (Tables 1 and 3).

There were strong seasonal differences in therelationships between biovolume and chlorophyll a in Bombah Broadwater, which reflects major changes in dominant taxa over the study period (Figure 8). High chlorophyll a content per biovolume on both sampling dates in autumn was due to the dominance of large-celled dinoflagellates (>70% of all cells) (Table 4). Also of interest is the wide range in biovolume of phytoplankton samples collected during winter (5 to 68 mm3/L); the abundance of Gloeoactinium (large-celled taxa) was largely responsible for this variation. In contrast, Myall Lake showed much overlap between seasons (due to similar dominant taxa year-round), and narrower ranges in both chlorophyll (1.5 to 4 µg/L) and biovolume (2 to mm^3/L). Overlap between lakes occurred only during spring and summer, when phytoplankton assemblages were dominated by the same small-celled cyanophyte taxa (Table 4).

Phytoplankton assemblages and dominant taxa

The three most numerous taxa and their percentage contribution to the abundance of phytoplankton in each of the 12 sample sets are shown in Table 4. Compared to Myall Lake, Bombah Broadwater shows greater diversity in taxa which contribute >10% to total cell abundance (N=10 genera). Although percentage contribution varies

Table 2. Mean squares and their significance values derived from ANOVA of chlorophyll *a*, chlorophyll/cell and biovolume. All datasets were Log_e (n+1) transformed. ML = Myall Lake, BB = Bombah Broadwater (random factor Time nested within Season). Bolded SNK results are shown where significantly different. A=autumn, W=winter, S=summer and Sp=spring, * = p<0.05; ** = p<0.01; *** = p<0.001.

Lake	Sources of variation	df	Total cells	Cyanophyceae	Chlorophyceae	Dinophyceae	Taxonomic richness	Shannon-Wiener Index (H')
BB	Season	3	19.56** S>Sp>A,W	241.86* S,Sp>A>W	46.90ns	142.93*** A,W>S,Sp	50.91^{ns}	0.11^{ns}
	Time (Season)	4	0.34^{ns}	24.92*** Bba>BBb	10.06*** Bba>BBb	2.87^{ns}	14.81** Bba>BBb	0.11** Bba>BBb
	Residual	40	0.29	1.23	0.98	2.46	0.02	0.02
ML	Season	3	0.98*** S,Sp>A,W	3.58*** S,Sp>A,W	14.57*** A>W>S>Sp	1.68^{ns}	12.26*** S>W,Sp>A	0.18*** S,W>A>Sp
	Residual	20	0.06	0.08	0.11	3.14	1.11	0.00

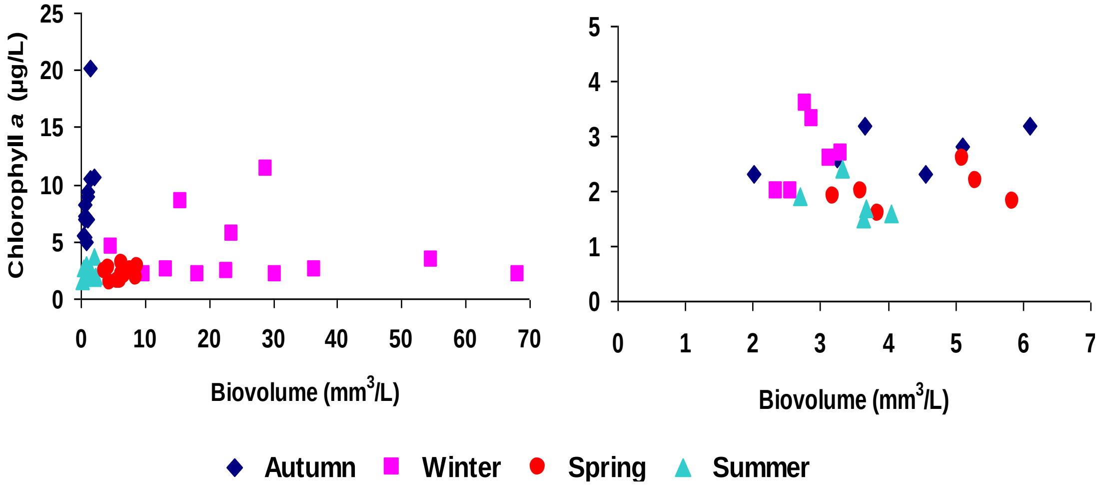

Figure 7. Seasonal patterns in chlorophyll a – biovolume relationships for a) Bombah Broadwater (sampled twice per season) and b) Myall Lake (omitted 1 outlier with biovolume 13 mm3/L).

Table 3. Mean squares and their significance values derived from ANOVA of ln(n+1) transformed chlorophyll *a*, chlorophyll *a* /cell and biovolume data. * = p<0.05; ** = p<0.01; *** = p<0.001. ML = Myall Lake, BB = Bombah Broadwater. Bolded SNK results show how treatments were significantly different.

Lake	Source of variation	df	Chl a	Chl a/cell	Biovolume
BB	Season	3	3.03* A>W,S,Sp	4.67** A,W>Sp>S	16.37** W>S>Sp,A
	Time (Season)	4	0.35** Bba>BBb	0.13^{ns}	0.66^{ns}
	Residual	40	0.090	0.070	0.12
ML	Season	3	0.12** A,W>S,Sp	0.02** W>A>Sp,S	0.16^{ns}
	Residual	20	0.02	0.0004	0.09

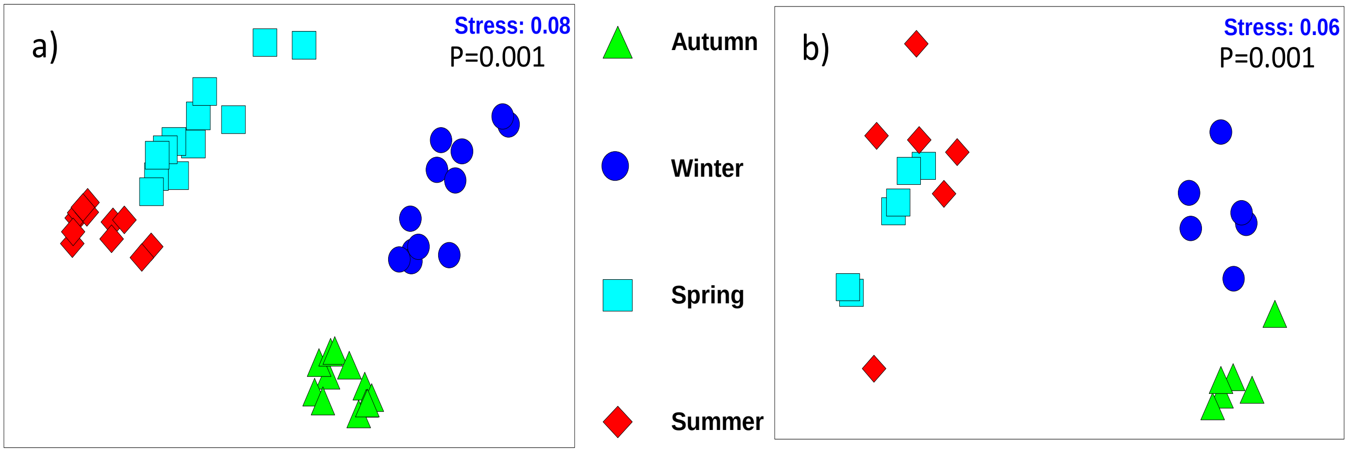

Figure 8. Non-metric multi-dimensional scaling plots of phytoplankton assemblages in each of four seasons in a) Bombah Broadwater and b) Myall Lake.

with season, Myall Lake shows only four dominant taxa during the study, with the same three dominant taxa in autumn and winter, and a slightly different combination of dominant taxa in spring and summer.

When the phytoplankton assemblage data for each lake was subjected to nMDS ordination, clear seasonal separation was evident in species assemblages in both lakes, with a tighter grouping of points in Bombah Broadwater (Figure 8). In each lake, spring and summer assemblages appear to be the most similar.

Myall Lake phytoplankton assemblages within sample sets were more similar to each other than those collected in Bombah Broadwater, except during summer (Table 5). The greatest variability among phytoplankton samples (i.e. low % similarity) was observed in Bombah Broadwater during spring, when salinity levels were very low (1 to 2 ppt) and Chlorophyceae were numerically dominant.

Non-metric multi-dimensional scaling (nMDS) ordination plots of phytoplankton assemblages between lakes, and times within season for Bombah Broadwater, are shown for each season in Figure 8. Phytoplankton assemblages in the two lakes show clear separation in autumn and winter; at these times, none of the three most dominant taxa were the same (Table 4); in spring, two of the dominant taxa were shared, and in summer, the three most dominant taxa were the same in both lakes, and at both sampling times (1 week apart) in Bombah Broadwater. Although assemblages were more similar in spring, both between lakes and between times within seasons, the assemblages remainedsignificantly different.

Table 4. The three most numerous taxa (%) in each lake and season. ML = Myall Lake, BBa = Bombah Broadwater first sampling occasion and BBb = Bombah Broadwater second sampling occasion. N=6 samples per sampling occasion.

Season	BBa (%)	BBb (%)	ML (%)
Autumn	*Gymnodinium* (71)	*Gymnodinium* (94)	*Gloeocystis*(49)
	Gloeocapsa (10)	*Volvox* (2)	*Coelasphaerium* (33)
	Microspora (5)	*Euglena* (1)	*Merismopedia* (13)
Winter	*Gloeoactinium* (86)	*Cosmarium* (42)	*Gloeocystis* (40)
	Chroomonas (6)	*Gymnodinium* (26)	*Coelasphaerium* (25)
	Gymnodinium (5)	*Gloeoactinium* (16)	*Merismopedia* (16)
Spring	*Microspora* (68)	*Microspora* (26)	*Merismopedia* (41)
	Merismopedi a (12)	*Coelasphaerium* (32)	*Coelasphaerium* (25)
	Coelasphaerium (11)	*Merismopedia* (22)	*Chroococcus* (24)
Summer	*Merismopedia* (40)	*Merismopedia* (47)	*Merismopedia* (46)
	Coelasphaerium (35)	*Coelasphaerium* (37)	*Chroococcus* (27)
	Chroococcus (24)	*Chroococcus* (11)	*Coelasphaerium* (16)

Table 5. The percent similarity of phytoplankton taxa observed in each set of 6 samples. ML = Myall Lake, BBa = Bombah Broadwater first sampling occasion and BBb = Bombah Broadwater second sampling occasion.

Season	% Similarity of taxa within sample sets		
	BBa	BBb	ML
Autumn	78	77	87
Winter	75	75	85
Spring	58	65	83
Summer	81	87	77

Overall stress values of ordinations were below 0.1 in all plots, indicating that the plots are reliable in representing the differences in species assemblages between sample sets.

ANOSIM pairwise tests showed significant differences between all pairs of assemblages (P < 0.5), except for the comparison of the two Bombah Broadwater sampling times in spring (Table 6). The percentage dissimilarity between the lakes was higher in autumn and winter (89 to 96%) than in spring (59 and 76%) and summer (30 and 36%). SIMPER results indicated that the species contributing most to the dissimilarity between lakes during both winter and autumn were Gloeocystis, Coelasphaerium, and Merismopedia (Table 6). Taxa contributing most to the dissimilarity between lakes in spring were Chroococcus, Microspora and Merismopedia and in summer, they were Aphanocapsa, Palmella and Anabaena.

DISCUSSION

Factors affecting phytoplankton cell abundance

This study examined temporal variation in water chemistry and phytoplankton in the upper and lower water bodies of the Myall Lakes system. It offers a more consistent sampling approach and greater sample replication than in previous studies, and statistically confirms some of the trends observed by Ryan (2002) and DIPNR (2004).

Water quality and nutrient concentrations in both lakes fell within the ranges observed in the two previous years (DIPNR, 2004) and reflect freshwater inputs and saline intrusion from the Upper and Lower Myall River. As expected, there were highly variable physico-chemical conditions in Bombah Broadwater (within and between seasons) compared to Myall Lake, which consistently

Table 6. ANOSIM Pairwise tests and SIMPER dissimilarity results. Bolded genera are more numerous in the 1st of the pairs. ML = Myall Lake, BBa = Bombah Broadwater first sampling set and BBb = Bombah Broadwater second sampling set.

ANOSIM Pairwise test			Dissimilarity from SIMPER results	
Pair	**Global R Stat**	**Sig. Level (%)**	**Dissim (%)**	**Three taxa most responsible for dissimilarity pair**
Autumn				
BbavsBBb	0.906	0.2	42	*Gloecapsa* 31%, *Microspora* 21%, *Gymnodinium* 16%
Bbavs ML	1	0.2	93	*Gloeocystis* 22%, *Coelasphaerium* 20%, *Merismopedia* 16%
BBbvs ML	1	0.2	94	*Gloeocystis* 24%, *Coelasphaerium* 22%, *Merismopedia* 18%
Winter				
BbavsBBb	0.987	0.2	53	*Cosmarium* 37%, *Gymnodinium* 24%, *Gloeoactinium* 13%
Bbavs ML	1	0.2	96	*Gloeocystis* 20%, *Coelasphaerium* 17%, *Merismopedia* 15%
BBbvs ML	1	0.2	89	*Gloeocystis* 16%, *Coelasphaerium* 16%, *Merismopedia* 145
Spring				
BbavsBBb	0.198	5.0	45	*Coelasphaerium* 17%, *Merismopedia* 14%, *Chroococcus* 13%
Bbavs ML	0.958	0.2	76	*Chroococcus* 19%, *Microspora* 16%, *Merismopedia* 14%
BBbvs ML	0.902	0.2	59	*Chroococcus* 16%, *Microspora* 14%, *Merismopedia* 13%
Summer				
BbavsBBb	0.407	0.4	21	*Anabaena* 37%, *Gymnodinium* 8%, *Scenedesmus* 7%
Bbavs ML	0.726	0.4	30	*Aphanocapsa* 26%, *Palmella* 11%, *Gloeothece* 7%
BBbvs ML	0.872	0.2	36	*Aphanocapsa* 18%, *Palmella* 19%, *Anabaena* 13%

showed low nutrient concentrations and little change following rain events. Not surprisingly, dramatic changes in water chemistry in Bombah Broadwater lead to much greater temporal variation in phytoplankton abundance and to a more pronounced succession of phytoplankton taxa than in Myall Lake, which was consistently numerically dominated by nutrient-efficient, small-celled cyanobacteria.

The current study found that large-celled chlorophytes (Gloeoactinium, Cosmarium) dominated in Bombah Broadwater during winter when dissolved N and P concentrations were high and N:P weight ratios exceeded 60. It is common for phytoplankton community structure to exhibit dominance by large-celled taxa when nutrient availability is increased (Irwin et al., 2006). Bulgakov and Levich (1999) reported stimulation of Chlorophyceae growth and dominance when N:P weight ratios were in the range of 20 to 50; a reduction in N:P to 5 to 10 lead to a community dominated by Cyanophyceae. N:P ratios in the both lakes of the Myall Lakes system were < 20 and often < 10 during most sampling occasions. Studies by Nikulina (2003) and Ornolfsdottir et al. (2004b) show nutrient-related changes in the phytoplankton communities of shallow waters in the Gulf of Finland; cyanobacteria dominated when available nutrients were depleted and N:P ratios were low. In some Northern Hemisphere temperate lakes, phytoplankton assemblage structure changes with Total Phosphorous (TP) concentrations; cyanobacteria dominate in water bodies at intermediate TP levels (0.1-0.5 mg/L), green algae dominate at hypertrophic levels (>0.5 mg/L), and a mixed community dominates at TP levels < 0.1 mg/L (Jeppesen et al., 1999).

Factors can cause shifts and changes in the abundance and distribution of phytoplankton species are: variations in salinity, nutrients, physical mixing, temperature, grazing and other biological and chemical properties (Pickney et al., 1999; Qian et al., 2003). In the Myall Lakes, it appears that the level of nutrients available and the relative amounts of key macronutrients (N and P), as well as variations in salinity (Bombah Broadwater only) may be the main factors impacting on phytoplankton growth and community structure. Zooplankton grazing control is low, especially in Myall Lake. Previous study reported low zooplankton densities (mostly early stage copepods) in both lakes, and her measured rates of grazing were in the low end of ranges reported for Australian and Northern Hemisphere coastal waters. It is uncertain the degree to which temperature is a controlling factor in the Myall Lakes; cooler winter temperatures are likely to limit phytoplankton growth rates and may also restrict the growth of some taxa.

Phytoplankton diversity

Taxonomic richness was generally higher in Myall Lake than in Bombah Broadwater, with both showing thehighest diversity during the warmer months. Significant differences between seasons (Myall Lake) and between times within seasons (Bombah Broadwater) reflect the ability of phytoplankton to respond to changes in structural stability and the periods of disturbance (Holzmann, 1993; Weithoff et al., 2001). Although the composition of phytoplankton in Bombah Broadwater changed greatly from sampling time to sampling time, it did not significantly affect taxonomic richness or the Shannon-Wiener diversity index. This is largely because phytoplankton samples taken within Bombah Broadwater showed higher variability in diversity at any one time than those collected within Myall Lake, which is a much more uniform environment. Diversity is not a reliable bioindicator for detecting changing conditions in Bombah Broadwater, except during bloom periods when diversity measures are relatively insensitive to rare species (Sager and Hasler, 1969). Myall Lake is larger than Bombah Broadwater but is more uniform in water chemistry and biota. The high similarity in taxonomic diversity among samples probably indicates stable or equilibrium lake conditions, with competition between species being the most likely cause of changes in species composition (Weithoff et al., 2001).

Phytoplankton biomass (chl a content, chl/cell and biovolume)

Chlorophyll a concentrations were low and changed little with season in Myall Lake. As catchment inputs are very low for this lake, nutrient availability is highly dependent on nutrient regeneration processes (for example decay of biota, sediment fluxes). Bombah Broadwater exhibited significantly higher and more variable chl concentrations in autumn and winter, the seasons during which there was the greatest rainfall. Wilson (2003) also detected an increase in chlorophyll a and cell counts of phytoplankton in Bombah Broadwater following a major rainfall event. Qian et al. (2003) showed that freshwater flows are a major controlling factor in the temporal variation and distribution of chlorophyll a. Water bodies which receive sustained freshwater inflow generally have higher nutrient loads and, as a consequence, elevated chlorophyll a levels (Grange and Allanson, 1995). However, decreases in chlorophyll a during warmer months are commonly found (Grange and Allanson, 1995; Gaevskii et al., 2000; Polat, 2002; Qian et al., 2003).

Chlorophyll a was not positively correlated with either phytoplankton abundance or biovolume and so is not considered a good indicator of biomass in this system. This effect is probably due to the broad range of phytoplankton sizes and types (dinoflagellates, green algae, cyanophytes) that dominate at different times, and to their taxa-specific patterns in chlorophyll a production.

Although concentrations of chl a and chl a per cell followed similar seasonal patterns in both lakes, chl/cell was more variable in Bombah Broadwater due to greater temporal variation in both phytoplankton types present and in cell size of common species. The highest concentration of chl a/cell was observed in autumn in Bombah Broadwater due to the dominance of large-celled dinoflagellates. Low chl a/cell values were typical in summer when numerous small-celled taxa (cyanobacteria) dominated both lakes. This pattern is commonly found when cell size varies greatly from season to season (Polat, 2002) and increases the importance of examining samples for phytoplankton composition and cell size, as well as chlorophyll a concentration.

Biovolume (3 mm/L) is a more reliable, but more time consuming, measure of biomass than chlorophyll a concentration. Variability in the chlorophyll-biovolume relationship depends on the life form of the predominant group and their average cell size (Abbots et al., 1984; Li, 1994; Felip and Catalan, 2000). Biovolume varied temporally in Bombah Broadwater (up to 68 mm^3/L) but not in Myall Lake (2 to 6 mm^3/L). This reflects large seasonal changes in Bombah Broadwater and the dominance of large-celled taxa during the winter, compared to the small-celled cyanophytes that dominated in Myall Lake throughout the year. As a result, there was no seasonal pattern in the biovolume-chlorophyll relationship in Myall Lake. Because of changes in phytoplankton groups that contribute most to the biovolume measured, the distribution of chlorophyll a and biovolume do not always match (Felip and Catalan, 2000).

Phytoplankton assemblages and dominant taxa

Phytoplankton communities are assembled based on the particular environmental conditions that influence the relative success of individual organisms present in the community (Reynolds, 1998). Bombah Broadwater showed the greatest seasonal changes in phytoplankton assemblages, which appear to be due to the temporal variability in two factors: nutrient inputs from the catchment and salinity. In many estuaries, it is the loadings of nutrients, in particular nitrate and ammonium, that most influence the growth rate and community composition of phytoplankton (Pickney et al., 1999).

Lake assemblages were most similar to each other in summer when the dominant taxa were shared (Merismopedia, Coelasphaerium and Chroococcus). All of these taxa are cyanophytes which are tolerant of a wide range in salinity and tend to exhibit growth optimums at high temperatures (Robarts and Zohary, 1987).As in this study, DIPNR (2004) and Ryan (2002) found that Cyanophyceae were abundant and dominant in Myall Lake and Bombah Broadwater during the warmer months. But during summer, dissolved nutrient concentrations (N and P) in both lakes were low, and the N:P ratio was ≤ 20. Poor nutrient conditions, especially low P levels, are unlikely to have inhibited the growth of cyanophytes as they are known to be highly efficient in utilising orthophosphates when in low concentration (Vuorio et al., 2005). Cyanophytes also prefer neutral to alkaline waters and tend to dominate at high pH, possibly due to the use of bicarbonate ion as a carbon source (Paerl, 1988a; Temporenas et al., 2000).

The size of numerically dominant phytoplankton can vary for a number of reasons, many of which are outlined in Beardall and Redden (2007). Factors that contribute to observed patterns in cell size are nutrient availability and uptake rates, photosynthetic rate, cell sinking rates and buoyancy mechanisms, water column mixing and the impact of grazers. It is well known that when nutrients are highly available, large cells tend to dominate; as nutrients become depleted, they are succeeded by nutrient-efficient, small-celled taxa (Tremblay et al., 1997).

Conclusion

Bombah Broadwater exhibits greater temporal variation in physico-chemical variables (water quality and available nutrients) and in phytoplankton cell abundance, biomass and composition. Dinoflagellates and Chlorophyceae are most abundant in autumn and winter and Cyanophyceae in spring and summer. In contrast, Myall Lake is much less disturbed and shows low temporal and spatial variation in water chemistry and in phytoplankton biomass and assemblage structure. Cyanophyceae dominate year-round in Myall Lake while Chorophyceae appear in large numbers in autumn and winter. The lake system appears to be mesotrophic, with nutrients in Bombah Broadwater being derived largely from the catchment. In contrast, phytoplankton growth in Myall Lake is much more dependent on nutrients generated by internal recycling processes (Dasey et al., 2005).

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