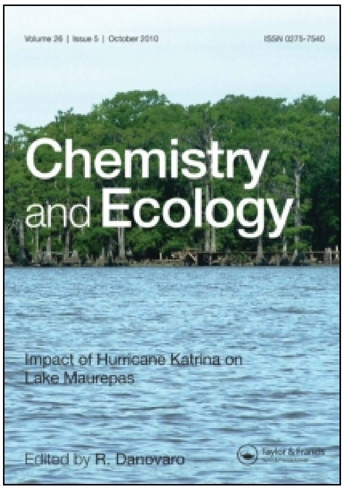


Chemistry and Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

Biomass dynamics of charophyte-dominated submerged macrophyte communities in Myall Lake, NSW, Australia

D. Shilla[a]; J. Dativa[a]
[a] Graduate School of Science and Engineering, Department of Environmental Science and Human Engineering, Saitama University, Saitama-shi, Japan

To cite this Article Shilla, D. and Dativa, J.(2008) 'Biomass dynamics of charophyte-dominated submerged macrophyte communities in Myall Lake, NSW, Australia', Chemistry and Ecology, 24: 5, 367 — 377

To link to this Article: DOI: 10.1080/02757540802351185

URL: http://dx.doi.org/10.1080/02757540802351185

Chemistry and Ecology
Vol. 24, No. 5, October 2008, 367–377

RESEARCH ARTICLE

Biomass dynamics of charophyte-dominated submerged macrophyte communities in Myall Lake, NSW, Australia

D. Shilla* and J. Dativa

Saitama University, Graduate School of Science and Engineering, Department of Environmental Science and Human Engineering, Saitama-shi, Japan

(*Received 7 January 2008; final version received 17 July 2008*)

The dynamics of submerged macrophytes were studied in a large and shallow near-pristine lake in New South Wales, Australia. The objectives were to investigate the seasonal dynamics in biomass of *Chara fibrosa*, *Nitella hyalina* and *Najas marina* both in time and space, and to characterise the underlying relationship between the plant biomass and both the gyttja and water depths. Charophytes were most densely grown in the north-east bays of the lake compared to the north-west bays. Average biomass of *Chara fibrosa* was highest at the north-east bays of this lake (e.g. 210 g d.w m^{-2}) followed by north-west bays (e.g. 148 g d.w/m^2), South-west bays (e.g. 60 g d.w/m^2) and lastly central deep area of the lake (e.g. 31 g d./m^2). A similar trend was displayed by *Nitella hyalina* biomass where at the north-east bays the biomass was the highest (e.g. 167 g d.w m^{-2}) followed by north-west bays (e.g. 128 g d.w/m^2), south-west bays (e.g. 38 g d.w/m^2) and central deep area of the lake (e.g. 23 g d.w/m^2). During the summer season the maximum total biomass of charophytes at Corrigans bay was recorded (e.g. 300 g d.w/m^2), mostly being dominated by *Nitella hyalina*. Total biomass of charophyte was reduced during the winter season (e.g. 50 g d.w m^{-2}). *Najas marina* biomass remained low both in time and space except in May at Bibby harbour and Shelly beach where its biomass peaked (e.g. 276 and 175 g d.w m^{-2} respectively). Gyttja depth showed a positive relationship with total charophyte biomass ($r^2 = 0.70$; $p < 0.01$) and it seemed to favour the growth of charophytes at the expense of other submerged macrophytes, e.g. *Myriophyllum* sp. and *Vallisneria* sp. Water depth displayed a negative relationship with total charophyte biomass ($r^2 = -0.94$; $p < 0.01$). Both *Chara fibrosa* and *Nitella hyalina* correlated positively with gyttja depth ($r^2_{\text{Chara-gyttja)}} = 0.69$, $r^2_{\text{Nitella-gytja)}} = 0.65$; $p < 0.01$) and negatively with water depth ($r^2_{\text{Chara-depth}} = -0.94$, $r^2_{\text{Nitella-depth}} = -0.93$; $p < 0.01$). *Najas marina* correlated positively only with water depth ($r^2 = 0.67$, $p < 0.01$).

Keywords: biomass; charophytes; gyttja; seasonal changes; submerged macrophytes

1. Introduction

Many studies have documented that charophytes are fast colonisers of shallow lakes [1–4], and that they can grow successfully under competition pressure with other macrophytes [5,6]. This success of charophyte colonisation in shallow lakes at the expense of other macrophytes, has been associated with their ability to develop a high biomass [5,6], ability to store large amounts

---

*Corresponding author. Email: dshilla@yahoo.com

ISSN 0275-7540 print/ISSN 1029-0370 online

DOI: 10.1080/02757540802351185
http://www.informaworld.com

of nutrients [7] and their ability to act as a nutrient sink, decreasing the availability of nutrients for phytoplankton and epiphyton [8].

Water depth is a critical factor affecting the biomass and spatial distribution of submerged macrophytes in shallow aquatic systems [9–12]. Changes in water level have been known to cause yearly fluctuations in aerial coverage of submerged macrophytes in shallow lakes, which in turn affect its biomass [6]. Submerged macrophyte distribution in lakes is limited by turbulence near shore [13] as well as light conditions especially in deeper waters [14]. Moreover, bottom lake substrate upon which macrophytes grow is a very important factor affecting their colonisation ability especially for rooted macrophytes. Most submerged macrophytes are able to take up nutrients from the sediment which enables them to grow even when nutrient concentrations in the water column are very low [15].

Water quality is important for the growth of charophytes. Charophytes (*Chara fibrosa* and *Nitella hyalina*) and *Najas marina* for example, require brackish or highly alkaline rather than acidic waters in order to flourish. Species differ in their tolerance to salinity and in their requirement for calcium ions [16]. Most charophytes cannot grow in water that is permanently very turbid and high in nutrients, but some can photosynthesise at low light intensities, or can survive periods of turbid water [17]. For species adapted to clear water, turbid water phases or inflows which temporarily reduce light penetration have an adverse effect on growth, biomass and hence abundance [18]. Charophytes have been recorded at depths of up to 27 m in clear water lakes but more commonly grows in shallow waters from a few to 1 or 2 metres deep. In Myall Lake, high temperatures during summer periods are responsible for the die-back of these macrophytes while near the lake shore, high turbidity due to dynamic conditions caused by wave actions and boating activities, hinder the growth of the macrophytes. Here, we report on the results of the seasonal biomass dynamics of *Chara fibrosa*, *Nitella hyalina* and *Najas marina* evaluating the effects of water depths, gyttja depths and other environmental parameters affecting the biomass of macrophytes growing in Myall Lake.

2. Material and methods

2.1. *Study area*

Myall Lake is the largest and most poorly flushed of the four connected coastal Lakes in a largely forested catchment in temperate east Australia. It is situated 75 km north of Newcastle on the central coast of New South Wales, Australia (152° 20′ E, 32° 25′ S). The average depth of the lake is about 2 m, the deepest part being 4.1 m. A series of shallow bays are located in the eastern and northern coastlines (Figure 1). Most of the lake is covered with organic mud (gyttja) (about 1 m deep) except for small areas near the shore. It has a surface area of 62.8 km^2, being characterised by salinity <2 ppt, very low catchment runoff, high water clarity, and low plankton biomass [19,20]. Salinity levels vary from almost fresh water at the northern shore of Myall Lake to brackish at the Bombah Broadwater. The main input of freshwater comes from the upper Myall River and the Boolambyte creek. Other inputs of freshwater are groundwater drainage from the sand mass on the eastern shore with annual total discharge slightly less than that of the upper Myall River and the rain fall upon the lake surfaces. Most of the groundwater aquifers beneath Myall Lakes National Park (MLNP) are characterised by the dominance of Na-Cl and Na-Mg-Cl ion pair which also indicates strong influence of seawater [21].

Although the river entrance is permanently open, tidal response within the lakes is severely attenuated due to the limited hydraulic conveyance. Tide stage attenuation along the lower Myall river is relatively uniform with a mean spring tidal range of 1.35 m at the entrance diminishing to 0.03 m at the Broadwater, the southernmost lake of the Myall system which also includes

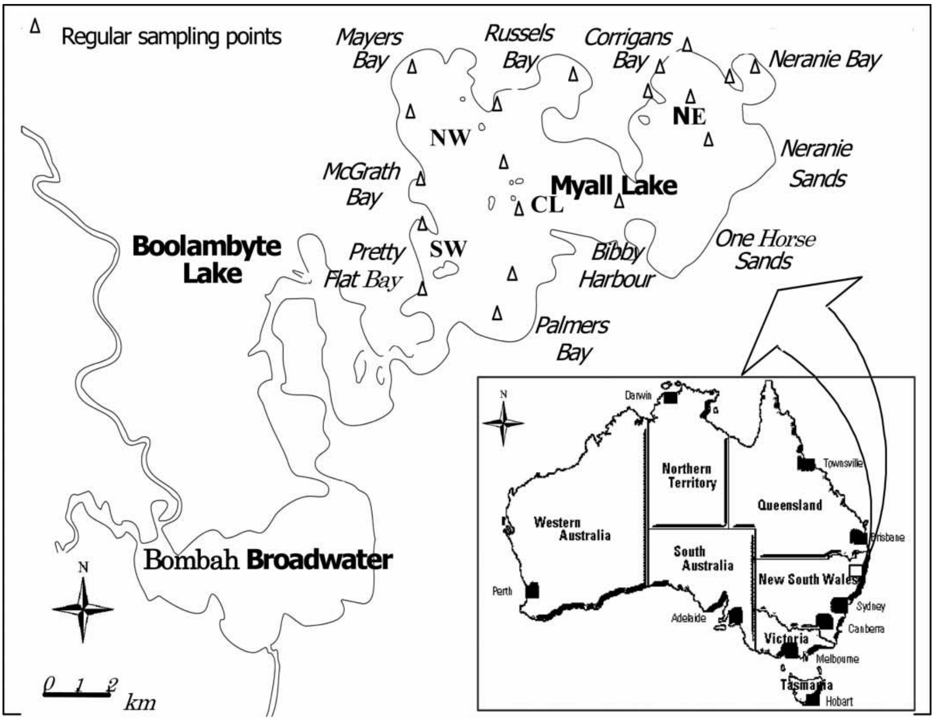


Figure 1. Location map of Myall Lake and other connected lakes showing sampling points.

Boolambayte Lake and Myall Lake. As a consequence, most of the nutrients that enter via rainfall events in the Myall catchment are wholly processed in the lakes, as exports to the estuary are fairly small [22]. During sustained periods of dry weather, the concentration of nutrients in Myall Lake is bound to be a consequence of internal recycling and processing [23,24]. Mean total phosphorus, soluble reactive phosphorus (SRP) and total nitrogen (TN) have been reported for Myall Lake waters ranging between 0.01–0.03, 0.01–0.016 and 0.70–>1.00 mg/l, respectively [22]. Water residence time has been estimated between 400 to 800 days [25]. The lake suffered from blue green algae bloom April 1999 to April 2000 [25,26].

The mean annual rainfall for Myall Lake is 1328 mm with wetter months occurring in late summer and early autumn with mean monthly rainfall of 100 mm [27]. The mean monthly maximum temperatures range from 27 °C in summer to 17 °C in winter with minimums of 15 °C and 3 °C, respectively. Most of the lake is covered by three predominant macrophytes, namely *Chara fibrosa*, *Nitella hyalina* and *Najas marina* except in shallower shores. Other plant species which are found in Myall Lake include *Myriophyllum salsugineum*, *Vallisneria gigantea*, *Ruppia megacarpa*, *Potamogeton perfoliatus* and other green filamentous macroalgae assemblages.

The Myall Lakes were considered pristine until harmful algal blooms (*Anabaena* sp. and *Microcystis* sp.) were reported in April 1999. Monitoring and other studies were undertaken from 1999 to 2002 to determine the likely cause of the blue green algal blooms and assess the health status of the lake. This included studies of water quality, nutrients, phytoplankton, macroalgae, and sediments [19]. The results showed large variation in ecological characteristics between wet and dry periods, and among interconnected lakes. The most southern lake, for example had the highest nutrient load, variable salinity, turbidity, and harmful algal blooms associated with freshwater inflows. At the other extreme, the most northern lake received low nutrient loads, had stable salinity, good water clarity, and extensive seasonal growth of Charophytes. It is difficult to assess the health of

Table 1. Ranges of basic limnological variables and nutrient concentration from water samples collected in the field from Myall Lake, Australia. Values are the mean of 90 samples; the values in parentheses are standard deviations (SD).

Parameter	Minimum	Maximum	Mean (SD)
pH	6.51	9.58	8.30 (0.62)
Conductivity (mS/cm)	0.5	5.7	3.37 (1.92)
ORP (mVolt)	184.15	420.0	272.25 (35.73)
Dissolved O_2 (mg/l)	5.30	13.10	9.47 (2.01)
Temperature (°C)	12.70	30.00	21.37 (4.82)
Salinity (ppt)	0.20	3.09	1.15 (0.97)
Turbidity (NTU)	0	68.30	4.57 (1.97)
Water TP ($\mu g\, l^{-1}$)	10	60	48.35 (15.68)
Water SRP ($\mu g\, l^{-1}$)	1.02	4.05	2.15 (0.86)

Myall Lakes within current paradigms of eutrophication due to the simultaneous occurrence of eutrophic and oligotrophic conditions. Sampling campaigns were conducted at 4–5 week intervals from August 2003 to May 2005 for biomass, sediment and water sample collection.

2.2. *Biomass sampling*

Submerged plants were sampled regularly at an interval of one month at 10 locations on the lake. Three locations were at the extreme locations of the lake, namely the north-east (a relatively wind protected site), north-west (a relatively wind exposed site) and south-west. An additional location (namely, central deep area of the lake, CL) was chosen at the central deeper area of the lake (Figure 1). Plants (10 replicates) were collected using a 30 cm wide rake, scraping for a distance of 1 to 2 m. Samples were washed, sorted into species and were then dried in an air-forced oven (50 °C) until a constant weight was obtained. The final densities of macrophytes were calculated taking into account the variation on the bottom area sampled.

Water and gyttja depths were measured onsite using a calibrated plastic rod. Gyttja depth was measure by penetrating a calibrated plastic rod into the gyttja layer until it reached the hard sediment. The difference between the lake's bottom surface and the depth of the hard sediment layer was recorded as the gyttja depth. At the same time, in situ measurement of water temperature, light intensity (at different depths), dissolved oxygen concentration, pH, salinity, conductivity and turbidity of water were recorded using a water quality monitor (HORIBA U21XD, KOREA) (Table 1).

The variation coefficient (maximum biomass: minimum biomass) of the biomass values (g d.w m^{-2}) was used to assess the temporal stability of biomass at the sampling sites [4,28]. Analysis of variance (ANOVA) was used to check the existence of differences in biomass between sites and species. Correlation analysis was run to check for the relationship between water depth and gyttja depth with biomass. All statistical analyses were performed using SPSS software version 11.

3. Results

3.1. *Comparison of biomass across sampling sites*

Charophyte biomass showed reasonable stability (low ratio of maximum to minimum biomass) except for *Chara fibrosa* from south-west bays at south-western bay (SW) and *Nitella hyalina* from north-east bays at north-eastern bay (NE, Table 3). The lake was dominated by a charophyte community of the species *Chara fibrosa* and *Nitella hyalina*, and only a small biomass of *Najas*

Table 2. Mean ($n = 90$) biomass of charophytes at different sampling locations of the lake. The numbers in parentheses are standard deviations. *C. fibrosa*, *N. hyalina* and *N. marina* are the separate biomasses of *Chara fibrosa*, *Nitella hyalina* and *Najas marina*, respectively.

Sites	*C. fibrosa* (g d.w m^{-2})	*N. hyalina* (g d.w m^{-2})	*N. marina* (g d.w m^{-2})	k-value (m^{-1})	W. depth (m)	G. depth (m)
NE	209.52 (62.16)	166.62 (52.71)	9.60 (4.01)	2.15	0.77 (0.24)	1.92 (0.62)
NW	147.88 (68.18)	128.36 (67.20)	20.25 (10.54)	1.38	0.84 (0.26)	1.87 (0.60)
SW	59.81 (28.04)	38.37 (21.28)	52.92 (14.25)	1.39	2.8 (0.91)	1.39 (0.43)
CL	31.17 (14.75)	22.70 (11.37)	3.21 (1.68)	0.27	4.26 (1.39)	2.4 (0.63)

Site (NE) = north-eastern bays, (NW) = north-west bays; (SW) = south-west bays and (CL) = Central deep area of the lake; w.depth = water depth and g. depth = gyttja depth. Difference in biomass tested by ANOVA across sites were significant at $p < 0.0001$.

marina was recorded throughout the sampling campaigns except in February 2004 at the south-western bay (SW) and May 2004 at the deep central part of the lake (CL) where significantly higher biomass was recorded (Table 2).

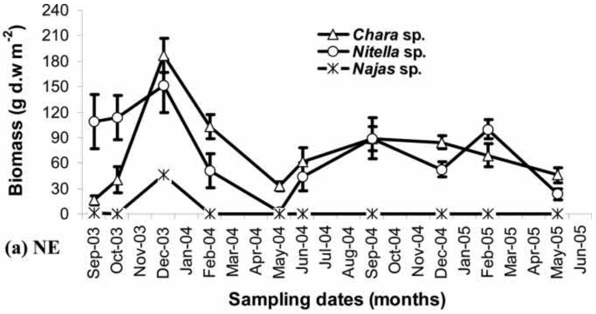
The mean biomass of charophytes differed across sampling sites. The mean biomasses (gram dry weight per meter squared) of *Chara fibrosa* (209.52 g d.w. m^2) and *Nitella hyalina* (166.62 g d.w. m^2) at the north-east bays were significantly higher than that from the remaining sites (Table 2). *Najas marina* mean biomass was highest at the central part of the Lake. The maximum biomasses were reached either in summer (December) for charophytes or autumn (May) for *Najas marina* (Figure 3a, b and c).

Macrophyte biomass was significantly higher during the summer season (December 2003 and February, 2005) than the rest of the seasons. At north-eastern bay (NE), the peak charophytes biomass was recorded on December and February for the years 2003 and 2005, respectively whereas in June 2004 and August 2005, the minimum biomass was recorded (Figure 2a). For north-west bay (NW), winter biomass (September 2004) was low whereas peak charophyte biomass was recorded in summer (February 2005, Figure 2b). South-west bay (SW) showed a similar pattern whereby peak biomass of charophytes were recorded on summer (December) of the years 2003 and 2004, respectively (Figure 2c). At the deep central area of the lake, the peak biomass of the *Chara fibrosa* was recorded during autumn season (May) of 2004. Charophyte biomass for the rest of the seasons at central deep area remained low (Figure 2d).

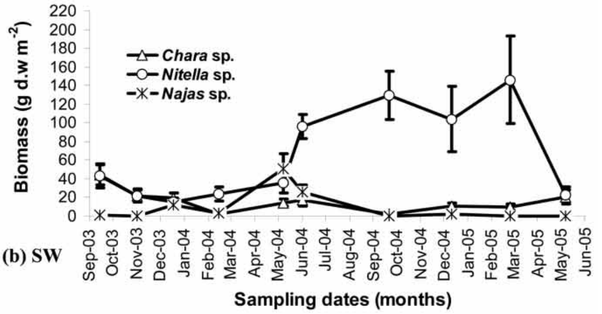
Table 3. Mean ($n = 90$) biomass, range and stability (maximum biomass/minimum biomass ratio) of the three aquatic macrophytes at five sampling sites. NE represents north-eastern bays; NW is north-west bays; SW is south-west bays and CL is central deep area of the lake.

Site	Species	Mean (g d.w m^{-2})	Range (g d.w m^{-2})	MaxB:MinB*
NE	*C. fibrosa*	77.64	16.38–186.68	11.40
NW	*C. fibrosa*	9.71	1.04–21.54	20.71
SW	*C. fibrosa*	40.89	2.91–105.14	36.15
CL	*C. fibrosa*	9.09	4.06–18.81	4.64
NE	*N. hyalina*	38.95	0.85–74.34	87.53
NW	*N. hyalina*	30.10	11.42–52.94	4.64
SW	*N. hyalina*	18.88	4.53–37.64	8.30
CL	*N. hyalina*	22.86	2.46–54.33	22.10
NE	*N. marina*	7.92	0.93–46.53	49.46
NW	*N. marina*	12.72	1.47–50.73	34.47
SW	*N. marina*	2.74	6.77–12.39	1.83
CL	*N. marina*	114.53	15.14–551.32	36.41

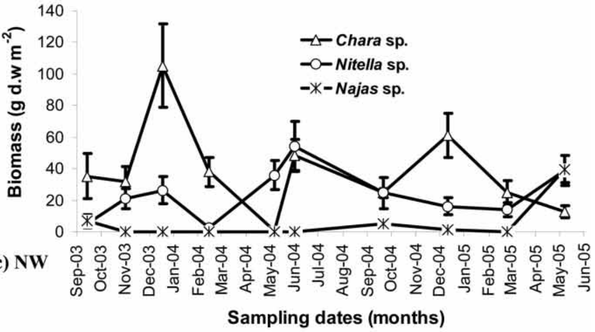
*MaxB:MinB = Ratio of the maximum biomass to the minimum biomass.



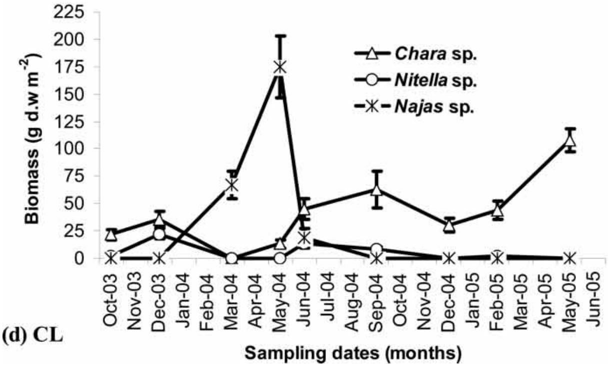
(a) NE



(b) SW



(c) NW



(d) CL

Figure 2. Seasonal changes in dry-weight biomass of *Chara fibrosa*, *Nitella hyalina* and *Najas marina* at (a) north-eastern bays (NE), (b) north-western bays (NW), (c) south-western bays (SW), and (d) deep central (CL) part of the Myall Lake.

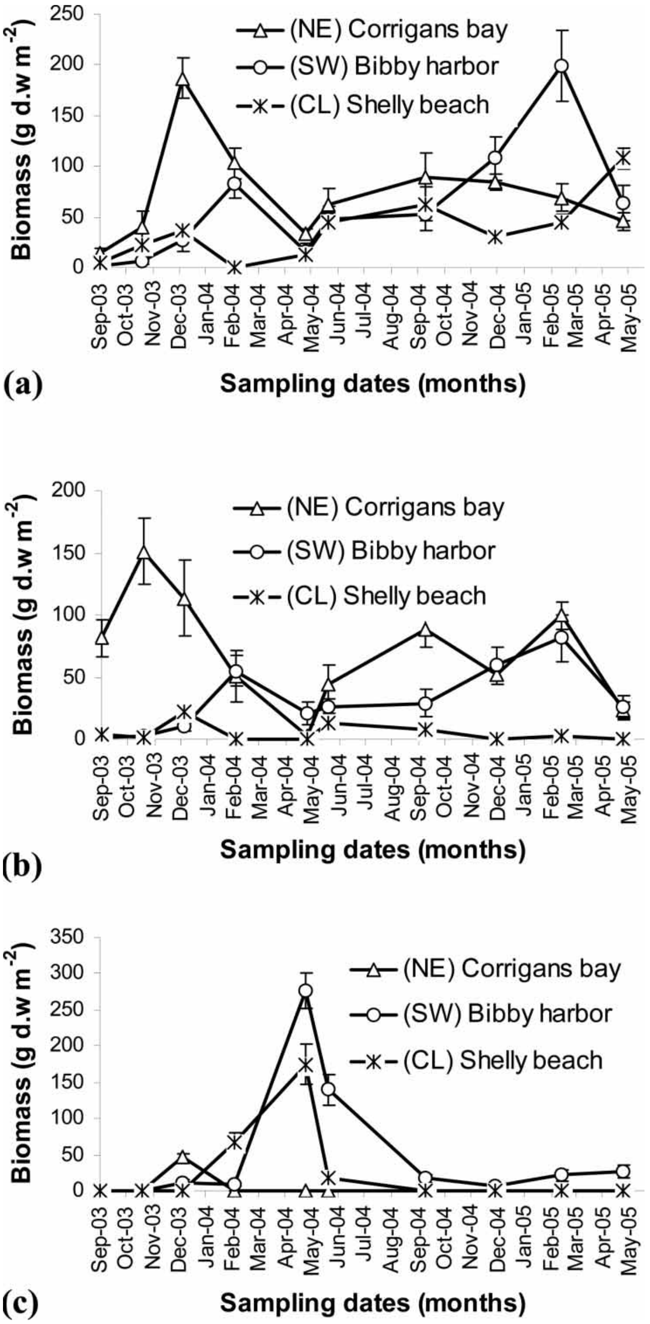


Figure 3. Seasonal changes in dry-weight biomass of (a) *Chara fibrosa*, (b) *Nitella hyalina* and (c) *Najas marina* at three sampling points of Myall Lake.

The biomass of *Najas marina* recorded throughout this study was significantly low for all seasons except at south-western bay (SW) and central deep area of the lake (CL) where the biomass was significantly higher during the autumn season (Figure 3c). The most obvious changes observed during this study were therefore the large annual change in the area covered by charophytes (*Chara fibrosa* and *Nitella hyalina*), which underwent a large summer bloom and winter die-back in most areas of the lake. These species were observed to grow vigorously from seed (presumably) in early spring to mature plants in summer season and over winter. In conjunction with the summer bloom of the charophytes, *Najas marina* on the other hand underwent a large autumn increase and winter die-back in the study period.

3.2. *Relationship between water and gyttja depths to the macrophytes biomass*

The biomass of submerged macrophytes was low when the water depth was greatest and vice versa, displaying an inverse relationship with water depth. *Chara fibrosa* and *Nitella hyalina* biomass correlated negatively with water depth ($r^2_{\text{nit-water depth}} = -0.93$, $r^2_{\text{chara-water depth}} = -0.94$). The exception was with *Najas marina* where a significant positive correlation between water depth and its biomass was observed ($r^2 = 0.67$, $p = 0.000$). Multiple regression analysis considering water depth, gyttja depth, turbidity, dissolved oxygen and light parameters retained water depth and gyttja depth as significant predictor variables, with the model explaining 52% of the variation in mean macrophytes biomass ($r^2 = 0.52$, $p < 0.001$). Gyttja depth displayed a positive relationship with charophytes biomass ($r^2_{\text{chara-gyttja depth}} = 0.69$, $r^2_{\text{Nitella-gyttja-depth}} = 0.65$; $p = 0.000$). There was no correlation between gyttja depth and the biomass of *Najas marina*.

3.3. *Effect of vegetation on attenuation coefficient*

The light intensity distribution normalised by the global radiation at each depth gives k values which show variation with biomass density. At CL (central deep area of the lake) there was biomass only around the bottom while at NE (north-east bays), NW (north-west bays) and SW (south-west bays) macrophytes grew up to 50 cm below the water surface. The light attenuation was larger inside the plant foliage although it wasn't much without plants.

Table 2 shows the relationship between the light attenuation coefficient, k, and the plant biomass at 1 m depth per square metre. Here the light attenuation coefficient was defined by $I/I_0 = exp(-kz)$, where I is the light intensity at depth z, and I_0 is the global light intensity. The light attenuation coefficient saturates at biomass values greater that 100 gm^{-2} beyond which, the light was not affected with higher biomass.

4. Discussion

Charophytes (*Chara fibrosa*, *Nitella hyaline*) and *Najas marina* were the most dominant macrophytes species growing there during the study period. During the decay period, charophytes decomposed into gyttja by releasing a mucous-like substance. *Najas marina* too, is likely to contribute some organic matter towards the gyttja layer during the decomposition process. The gyttja layer was about 1.87 m in thickness inside the bays along the western shores, whereas it was more than 2.4 m thick in the central deeper zones. Investigation in the field showed that no plants other than charophytes (*C. fibrosa* and *N. hyalina*) and *N. marina* grew on the surface of gyttja, thus reducing the lake biodiversity. This may have been attributed to the high content of hydrogen sulphide formed in gyttja under anoxic conditions [29].

The macrophytes biomass at the western bays of Myall lake was low (e.g. Table 2), compared to the biomass of charophytes reported in other studies [30–32]. The vegetation and lakebed in this locality continuously experienced strong current action under high wind conditions. With a steep shore with a slope of about 0.15, the shallow bottom was composed of rocks extending to about 3 m. A small amount of gyttja of about 1.39 m thick was found to have accumulated on the gnarled crests of the rock. The less accumulation of gyttja and subsequently less macrophytes biomass may apparently be due to strong wave action. Therefore, even if gyttja was produced by charophytes and *Najas marina*, it seemed to be washed away easily under strong wave action. Gyttja is of paramount importance when it comes to growth of charophytes because due to their pseudo-roots, the substrate is easily penetrated thereby supporting the plant, and at the same time serving it for nutrition purposes. Nutrients at this site has been reported to be low [29], and this could be the reason for the low biomass compared to north-eastern bays.

Although the charophytes biomass showed reasonable stability with few exceptions, ratios of the maximum/minimum biomass show association with nutrient availability. The observed patterns may have resulted mostly from the variability of biomass at sites with differing nutrients conditions which reflect both the beneficial effects (availability) and the detrimental effects (toxicity) of nutrients along the year. Very high concentrations of nitrogen, for example, have been found to cause toxic effects on plants, thus limiting the biomass development [33]. The described relationships and patterns of variation may be used to assess the global nutrient disturbance level of areas in aquatic ecosystems. Validation of the observed patterns for other geographical areas and other macrophyte species may provide a general valuable tool to assess the anthropogenic nutrient disturbance in aquatic ecosystems.

The north-eastern bays were relatively calm compared to western bays. Because the charophyte biomass was large (Table 2) compared to biomasses reported in other studies, e.g. Pereyra-Ramos [31], Królikowska [32] and Kufel and Kufel [34], gyttja production seemed to be higher (about 1.92 m thick) in these bays relative to south western bays. However, water depth was about 1 m inside the bays, and the effects of wave action could be expected in case of storms. Under such circumstances, gyttja that was produced will be washed away despite the large production. Although a map of the original bed morphology of the Myall Lake was not available to us, the gyttja depth supposedly corresponds to the depth until the original ground surface. Even though the relationship between macrophytes and nutrient levels is complex [35], high nutrients levels, both in sediment and water column have been recorded at this site [29,36]. Nutrients have been shown to have effects on the biomass of macrophytes [34]. At the deeper central area of the lake, on the other hand, gyttja has accumulated more than 2.4 m in thickness, without being disturbed. This suggests that seasonal wind-induced drifting and movement under gravitation over a steadily sloping bottom, play an important role in determining the deposition and thickness of gyttja as well as the distribution of macrophytes in the central deep area of the lake (A. Redden, unpubl.). Although charophytes and *Najas marina* biomass was relatively smaller in this site, the gyttja depth correlated well with total plant biomass. The light factor could be the reason for the reduced macrophytes biomass in the central area of the lake. In spite of high increasing rate with low biomass, the light attenuation coefficient saturated at values greater than 100 gm^{-2}. As the density of macrophytes increased above 100 gm^{-2}, the light was not much affected with higher biomasses than this. At multi-species locations, negative correlation between charophyte biomass and other species suggested competition for light. The light attenuation was substantially larger inside the plant foliage while it was less without plants. Light availability is the major factor in the regulation of growth and competition among macrophytes. Light attenuation rapidly limits macrophyte growth and growth usually ceases between 1–3% of full sunlight [6,34,37]. Considerable photosynthetic, respiratory and temperature adaptations are found among the macrophytes in order to tolerate low light conditions. Light availability has been reported as a significant factor determining competitive success of macrophyte species [6,34].

The biomass values found in literature vary considerably and are probably related to specific characteristics and environmental conditions, though many are within the range recorded here. The water depth at central deep area in this study was significantly greater than the rest of the bays. Schwarz et al. [18] demonstrated in their study that the increase in magnitude of charophyte biomass was low when the water depth was high and that there was a considerable lag between the onset of biomass increase at different depths. They further stressed that biomass at a depth of 20 m was reduced to zero. Fernández-Alaez et al. [4] and Blindow et al. [38] in their studies reported an increasing biomass of macrophytes when the water depth was shallow, but decreased when the water depth was at maximum. The less biomass recorded at the central deep area of the lake in this study may be attributed to the water depth. The negative correlation between water depth and charophyte biomass means that water depth has a profound effect on the growth of charophytes, probably due to light limitation at such depths. Positive correlation between charophyte biomass and gyttja thickness suggested that physical processes play an important role in deposition of gyttja. *Najas marina* however, correlated positively with water depth due to its growth nature, as it grows in tall stands, nearly reaching the surface of the water.

References

[1] I. Blindow and M.J.M. Hootsmans, *Allelopathy effects from* Chara *spp. on two species of unicellular green algae*, in *Lake Veluwe: A macophyte dominated system under eutrophication stress*, M.J.M. Hootsmans and J. Vermaat, eds., Kluwer Academic Publishers, Dordrecht, 1991, pp. 158–174.

[2] J. Simons, M. Ohm, R. Daalder et al., *Restoration of Botshol (The Netherlands) by reduction of external nutrient load: recovery of a characean community dominated by* Chara connivens, *Hydrobiologia* 275/276 (1994), pp. 243–253.

[3] B. Beltman and C. Allegrini, *Restoration of lost aquatic plant communities: new habitats for* Chara, Neth. J. Aquat. Ecol. 30 (1997), pp. 331–337.

[4] M. Fernández-Alaez, C. Fernández-Alaez, and S. Rodríguez, *Seasonal changes in biomass of charophytes in shallow lakes in the northwest of Spain*, Aquat. Bot. 72 (2002), pp. 335–348.

[5] I. Blindow, *Interactions between submerged macrophytes and macroalgae in shallow lakes*, Ph.D. Thesis, Lund University Sweden, 1991, pp. 1–111.

[6] I. Blindow, *Long and short term dynamics of submerged macrophytes in two shallow eutrophic lakes*, Freshwater Biol. 28 (1992), pp. 15–27.

[7] L. Kufel and T. Ozimek, *Can* Chara *control phosphorus cycling in Lake Luknajno (Poland)? Hydrobiologia* 275/276 (1994), pp. 277–283.

[8] I. Blindow, A. Hargeby, and G. Andersson, *Alternative stable state in shallow lakes: What causes a shift?* in *The Structuring Role of Submerged Macrophytes in Lakes*, E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, eds., Springer, New York, 1998, pp. 353–360.

[9] M. Wallsten and P.O. Forsgren, *The effects of increased water levels on aquatic macrophytes*, J. Aquat. Plant Manage. 27 (1989), pp. 32–37.

[10] A. Kowalczewski and T. Ozimek, *Further long-term changes in the submerged macrophyte vegetation of the eutrophic Lake Mikolajskie (north Poland)*, Aquat. Bot. 46 (1993), pp. 341–345.

[11] S. Gafny and A. Gasith, *Spatially and temporally sporadic appearance of macrophytes in the littoral zone of Lake Kinneret, Israel: Taking advantage of a window of opportunity*, Aquat. Bot. 62 (1999), pp. 249–267.

[12] K.E. Havens, B. Sharfstein, M.A. Brady et al., *Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA*, Aquat. Bot. 78 (2004), pp. 67–82.

[13] P.A. Chambers and J. Kalff, *Light and nutrients in the control of aquatic plant community structure*, J. Ecol. 75 (1987), pp. 611–619.

[14] P.A. Chambers and J. Kalff, *Depth distribution and biomass of submerged aquatic macrophytes communities in relation to sechi depth*, Can. J. Fish. Aquat. Sci. 42 (1985), pp. 701–709.

[15] J.W. Barko and W.F. James, *Effects of submerged aquatic macrophytes on nutrient dynamics, sedimentation and resuspension*, in *The Structuring Role of Submerged Macrophytes in Lakes*, E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, eds., Springer, New York, 1998, pp. 197–214.

[16] A. Garcia, *Charophytes flora of south-western South Australia and south-western Victoria: Systematics, distribution and ecology*, Aus. J. Bot. 47 (1999), pp. 407–426.

[17] M.T. Cassanova and M.A. Brock, *Charophyte occurance, seed banks and establishment in farm dams in New South Wales*, Aus. J. Bot. 47 (1999), pp. 437–444.

[18] A. Schwarz, I. Hawes, and C. Howard-Williams, *Mechanisms underlying the decline and recovery of a characean community in fluctuating light in a large oligotrophic lake*, Aus. J. Bot. 47 (1999), pp. 325–336.

[19] J.R. Wilson and M.W. Dasey, *Harmful algal blooms in a pristine coastal lake in eastern Australia: Understanding temporal and spatial variations*, Department of Land and Water Conservation, Newcastle, Australia, 2004, pp. 1–19.

[20] J. Wilson, *The effect of runoff event on the ecology and chemistry of Myall Lakes: Changes in water quality, nutrients and phytoplankton assemblages*, Department of Infrastructure, Planning and Natural resources. Centre for Natural Resources, Parramatta, 2004, pp. 1–38.

[21] DIPNR, 2004. Natural Resource Management $436.5 Million Boost, Media Release – Ministers Office, Sydney.

[22] G.P. Harris, *Comparison of the biogeochemistry of lakes and estuaries: ecosystem processes, functional groups, hysteresis effects and interaction between macro and microbiology*, Marine Freshwater Res. 50 (1999), pp. 791–811.

[23] T.D. Waite, *Principles of Water Quality*, Academic Press, Orlando, 1984.

[24] B.G. Sanderson, T. Asaeda, L. Rajapakse, and A.M. Redden, *Mechanisms affecting biomass and distribution of Charophytes and Najas marina in Myall Lake, New South Wales, Australia*, Hydrobiologia 608 (2008), pp. 99–119.

[25] D. Palmer, D.J. Fredericks, C. Smith, and D.T. Heggie, *Nutrients from sediments*, Australian Geological Survey Organisation (AGSO) Research Newsletter No. 33, 2000.

[26] D. Palmer, D.J. Fredericks, C. Smith, G. Logan, and D.T. Heggie, *Benthic Nutrient Fluxes in Bombah Broadwater, Myall Lakes*, Australian Geological Survey Organisation, Professional opinion, No. 2000/33, 2000.

[27] G. Atkinson, M. Hutchings, P. Johnson, W.D. Johnson, and M.D. Melville, *An ecological investigation of the Myall Lakes region*, Aus. J. Ecol. 6 (1981), pp. 299–327.

[28] B. Moss and D.F. Westlake, *Community stability*, in *The Functioning of Freshwater Ecosystems*, E.D. Le Cren and R.H. Lowe-MacConnell, eds., Cambridge University Press, New York, 1980, pp. 206–208.

[29] D. Shilla, T. Asaeda, T. Fujino, and B. Sanderson, *Decomposition of dominant submerged macrophytes: implications for nutrient release in Myall Lake, NSW, Australia*, Wetlands Ecol. Manage. 14 (2006), pp. 427–433.

[30] S. Bernatowicz and J. Radziej, *Annual macrophyte production in the complex of Lake Mamry*, Pol. Arch. Hydrobiol. 12 (1964), pp. 307–348.

[31] E. Pereyra-Ramos, *The ecological role of Characeae in the lake littoral*, Ekol. Pol. 29 (1981), pp. 167–209.

[32] J. Królikowska, *Eutrophication processes in a shallow, macrophyte-dominated lake-species differentiation, biomass and the distribution of submerged macrophytes in Lake Luknajno (Poland)*, Hydrobiologia 342/343 (1997), pp. 411–416.

[33] S. Cabaço, R. Machása, and R. Santos, *Biomass-density relationships of the seagrass* Zostera noltii: *A tool for monitoring anthropogenic nutrient disturbance*, Estuar. Coast. Mar. Sci. 74 (2007), pp. 557–564.

[34] L. Kufel and I. Kufel, *Chara beds acting as nutrient sinks in shallow lakes - a review*, Aquat. Bot. 72 (2002), pp. 249–260.

[35] M. Sondergaard, E. Jeppesen, and K. Christofferson, eds, *The Structuring Role of Submerged Macrophytes*, Springer-Verlag, New York, 1997.

[36] K. Siong and T. Asaeda, *Does calcite encrustation in Chara provide a phosphorus nutrient sink?* J. Environ. Qual. 35 (2006), pp. 490–494.

[37] I. Dampska, *Charophyta-stoneworts. Freshwater flora of Poland*, Vol, 13, PWN, Warsaw, 1964, 126 pp.

[38] I. Blindow, A. Hargeby, and G. Andersson, *Seasonal changes of mechanisms maintaining clear water in a shallow lake with abundant Chara vegetation*, Aquat. Bot. 72 (2002), pp. 315–334.