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Macroinfauna Dynamics and Sediment Parameters of a Subtropical Estuarine Lake—Coomabah Lake (Southern Moreton Bay, Australia)

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ABSTRACT

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The distribution, composition, density, and biomass of benthic macrofauna within estuarine environments typically exhibit significant variations attributable to heterogeneity in and interactions between physical, biological, and chemical processes. The spatial and temporal dynamics of benthic macroinfauna assemblages and physicochemical sediment parameters within the intertidal mudflats of a subtropical estuarine lake (Coomabah Lake, Southern Moreton Bay) were studied at four sites from August 2006 to April 2007. No significant seasonal changes were observed at any site for all physical sediment parameters. The northern sample sites were characterised by fine- to medium-grained to moderately to poorly sorted sediments and the southern sample sites by fine-grained to moderately well to well-sorted. A total of 1029 individuals representing species from three orders, including deposit feeding and filter feeding macroinfaunal groups, were collected. The highest combined species densities occurred in the fine-grained southern sites, with the greatest combined species density occurring at Site 4 during winter. Amphipods (*Victoriopsis australiensis*) and polychaete worms (*Simplisetia aequisetis*) dominated the lake-wide faunal community with *V. australiensis*, representing 49% of the total retrieved macroinfauna. Significant correlations between mean macroinfauna densities, biomass_{DW}, sediment parameters, and seasonal maximum monthly temperatures were identified during the study. Seasonal trends in combined site densities were observed at each of the lake sites, with the highest combined density occurring during winter. Spatial and temporal variations might also be partially explained by the predation pressures of fish and migratory wading birds within the lake, with the seasonal presence of migratory wading birds coinciding with the minimum observed macroinfauna densities at each sample site.

ADDITIONAL INDEX WORDS: Population dynamics, intertidal sediments, predation.

INTRODUCTION

Despite ever-changing physical and chemical conditions, estuaries are characterised by high primary productivity (Alongi, 1998; Heip *et al.*, 1995; Kennish, 2002) and concentrations of organic matter (Cifuentes, 1991; Dunn *et al.*, 2008). Consequently, estuarine sediments often support high abundances and biomasses of benthic macrofauna (Moreira, Aldea, and Troncoso, 2010; Snelgrove, 1999), which provide vital food for many crustacean, fish, and shorebird species (Wolff, 1987; Ysebaert *et al.*, 2005). As a result, intertidal habitats are of high conservation value (Fujii, 2007; Kennish, 2002) and often function as nursery grounds for important recreational and commercial fish species (Gray, McElligott, and Chick, 1996; Ysebaert *et al.*, 2005).

The distribution, composition, density, and biomass of benthic macrofauna within estuarine environments typically exhibit significant variations attributable to the heterogeneity in and interactions between physical, biological, and chemical processes. To date, extensive efforts have been made to investigate macrofauna community dynamics and the role of influencing variables, such as hydrodynamic conditions, water depth, sediment composition, temperature, biogeochemical conditions, productivity and primary producer community structure, water column conditions, predator-prey relationships, and anthropogenic disturbances (*e.g.*, Arvanitidis *et al.*, 1999; Jones, Watson-Russell, and Murray, 1986; Kanaya and Kikuchi, 2008; McKindsey, Archambault, and Simard, 2012; Rossi, Castelli, and Lardicci, 2006; Ysebaert *et al.*, 2002, 2003). Furthermore, investigations regarding temporal variations of benthic macrofauna are also of great interest (*e.g.*, Cheng, 1995; Cheng and Chang, 1999; Jones, 1987; Kanaya, Suzuki, and Kikuchi, 2011; Morrissey *et al.*, 1992; Sánchez-Moyano, García-Asencio, and García-Gómez, 2010; Ysebaert and Herman, 2002).

Because of their importance to estuarine food web dynamics and biogeochemical processes (Kristensen, 2000; Welsh, 2003),

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benthic macroinfauna are regarded as a key feature in estuarine monitoring programmes (Ysebaert and Herman, 2002). Through their feeding, burrow construction, bioturbation, and burrow irrigation activities, infauna can influence rates of organic matter inputs to the sediment, the vertical distribution of sedimentary organic matter, rates and pathways of organic matter mineralisation, and the fluxes of the regenerated dissolved nutrients back to the overlying water (Dunn *et al.*, 2009, 2012; Jordan *et al.*, 2009; Welsh, 2003). The extent of these influences depends on the functional groups of animals present and their abundance, biomass density, population dynamics, and individual size (Kristensen, 2000; Welsh, 2003). Therefore, investigations regarding macroinfauna community structure and dynamics are important when formulating models and quantitative predictions about the functioning of soft-bottom marine systems.

The present study investigated the spatial and temporal dynamics of benthic macroinfauna assemblages along with physicochemical sediment parameters within the intertidal mudflats of a subtropical estuarine lake of conservation significance. This work is intended to provide an initial assessment of the benthic macroinfauna assemblages in conjunction with physicochemical sediment and environmental parameters in an attempt to identify relationships and spatial and temporal variations within Coombabah Lake.

METHODS AND MATERIALS

Site Description

Coombabah Lake (27°54'33" S, 153°21'07" E) is a subtropical, semiurbanised estuarine lake, which is part of Coombabah Creek, located in SE Queensland (Gold Coast, Australia) (Figure 1). The lake covers an area of approximately 2 km²; however, despite its modest dimensions, the lake and intertidal surrounds are recognised as a wetland of significant importance under the Convention on Wetlands as part of the Moreton Bay Ramsar wetland (www.ramsar.org/index_list.htm). The site is also an important migratory bird habitat and is listed under the China–Australia Migratory Bird Agreement (1974) and Japan–Australia Migratory Bird Agreement (1986). Furthermore, the lake is a protected fish habitat area (Fisheries Act 1994) and provides a nursery for commercially and recreationally important fish, prawn and crab species. The lake is open to the Gold Coast Broadwater (a barrier island lagoon), through Coombabah Creek, and is subject to a mixed semidiurnal tidal regime with salinity ranging from ~10 to 33 (Ali, Lemckert, and Dunn, 2010). The tidal and hydrodynamic conditions characteristics of the lake are described by Knight *et al.* (2008), Ali, Zhang, and Lemckert (2009), and Ali, Lemckert, and Dunn (2010). Annual rainfall for the region is approximately 1400 mm, with intense rainfall events common throughout the summer period. The minimum and maximum mean daily temperatures range from 9.2 to 28.5°C during July and January, respectively.

With the exception of shallow channels, Coombabah Lake is characterised by a relatively flat bathymetry, with water depths of 0 to ~1 m at low water. During periods of low water, large portions of the lake sediments become exposed, which are characterised by mostly fine sediments away from the major drainage channels (Dunn *et al.*, 2008).

The lake supports a mangrove dominated fringing flora, with *Casuarina* sp. and *Melaleuca* sp. on areas above the high-tide mark. Grey mangroves (*Avicennia marina*) form dense stands in low-lying areas connected to the lake in addition to *Ceriops tagal*, *Aegiceras corniculatum*, *Bruguiera gymnorhiza*, and *Rhizophora stylosa* found in fringing mangrove stands. The lake edge–mangrove interface is ~20 km in length, with mangroves extending landward between ~5 and 700 m (commonly ~400 m).

Sample Collection

Sediment samples were collected from four sampling sites within Coombabah Lake to determine macroinfauna abundance and biogeochemical properties, representing four regions of different surface sediment particle size distributions, organic matter sources, and hydrological features of the lake (see Dunn *et al.*, 2012) (Figure 1). Six undisturbed sediment cores were collected during low water exposure from each of the four sites during consecutive seasons (winter [August] and spring [November] 2006; summer [January] and autumn [April] 2007) using sediment cores (plexiglass; 20 cm internal diameter × 33 cm length) for the determination of macroinfauna populations at each site during each season (*i.e.* total $n = 96$). Following collection, the sediment cores were transported to a constant temperature laboratory before being placed within a 220-L holding tank containing aerated site water, maintained under seasonal temperatures. Three additional sediment cores (PVC; 50 mm internal diameter × 400 mm length) were also collected at each of the four sites during each of the four seasons (*i.e.* total $n = 48$) for the determination of physical and biogeochemical parameters. Following collection these cores were immediately sliced into six depth horizons (0–1, 1–2, 2–4, 4–6, 6–10, and 10–15 cm) for determination of density, porosity, grain size distribution, organic matter content (LOI₅₅₀), bioavailable ammonium (NH₄⁺_{bio}; porewater + exchangeable NH₄⁺), and bioavailable phosphate (PO₄³⁻_{bio}; porewater + exchangeable PO₄³⁻) concentrations. Subsamples of each depth horizon for the determination of NH₄⁺_{bio} and PO₄³⁻_{bio} were immediately transferred to sample tubes containing 1 M KCl and 1 M MgCl₂, respectively, and stored at <4°C in the field. All samples were returned to the laboratory within 2 hours of collection and stored at –20°C until analysis.

Sediment Analyses

Sediment wet-bulk density and water content were determined according to methods outlined by Percival and Lindsay (1997). Organic matter content (LOI₅₅₀) was determined and calculated according to Heiri, Lotter, and Lemcke (2001). The dry sieving technique was used to determine the contribution of very coarse sand (1000–2000 µm), coarse sand (500–1000 µm), medium coarse sand (250–500 µm), fine sand (125–250 µm), very fine sand (63–125 µm), and mud (<63 µm) grain size fractions. The method of Folk (1968) was used to quantify the sorting characteristics of sediments. Grain size of sediments was recorded using the standard phi unit (ϕ). A cumulative frequency plot of grain size (ϕ) was used to measure the mean (M_z) and sorting characteristic (σ_I) graphically given by

Figure 1. Location of sampling sites within Coombabah Lake (a). Insert shows location of the study area in Australia (b) and southern Moreton Bay (c).

$$M_z = \frac{(\phi_{16} + \phi_{50} + \phi_{84})}{3} \quad (1)$$

$$\sigma_I = \frac{(\phi_{84} - \phi_{16})}{4} + \frac{(\phi_{95} - \phi_5)}{6.6}, \quad (2)$$

where M_z is the graphical mean, σ_I is the sorting value (Inclusive Graphic Standard Deviation), and ϕ_x is the grain size at the $x\%$ value on the cumulative frequency curve (Folk, 1968).

Descriptive terms of Folk (1968) were used to characterise M_z as calculated from Equation 1, including very coarse grained ($-1.0-0.0 \phi$), coarse grained ($0.0-1.0 \phi$), medium grained ($1.0-2.0 \phi$), fine grained ($2.0-3.0 \phi$), very fine grained ($3.0-4.0 \phi$), and coarse silt ($4.0-5.0 \phi$).

The sorting scale of Folk (1968) is used to characterise the sorting value σ_I as calculated from Equation 2: very well sorted ($\sigma_I < 0.35$), well sorted ($\sigma_I = 0.35-0.5$), moderately well sorted ($\sigma_I = 0.5-0.7$), moderately sorted ($\sigma_I = 0.7-1.0$), poorly sorted ($\sigma_I = 1.0-2.0$), very poorly sorted ($\sigma_I = 2.0-4.0$), and extremely poorly sorted ($\sigma_I > 4.0$).

Prior to nutrient analyses all laboratory glass- and plastic-ware were cleaned by soaking in 10% (v/v) HCl (>48 h) then rinsed three times with deionised water (Milli-Q; 18 MΩ cm).

All reagents were of analytical grade purity, and all water used during dilutions was deionised water. Sediment NH_4^+ and PO_4^{3-} concentrations were determined by extracting aliquots of the homogenised sediment with 1 M KCl and 1 M MgCl_2 , respectively, by shaking. Following extraction, samples were centrifuged and the supernatant filtered (GF/F membrane, 47-mm internal diameter, Millipore) before spectrophotometric analysis at 640 nm using the phenate method for NH_4^+ concentrations and as molybdate reactive phosphorous (690 nm) for PO_4^{3-} concentrations (APHA, 1998).

Benthic Macroinfauna Analyses

Sediment cores placed in holding tanks were removed and the entire sediment core (20 cm internal diameter $\times$ 30 cm length) was sieved (250- μm stainless steel mesh) for the collection and identification of benthic macroinfauna species. Evaluation of the depth occurrences of the burrowing macroinfauna showed that more than 90% of the benthic infauna was concentrated in the top 0–10 cm interval in all cores sampled. Recovered macroinfauna were rinsed with freshwater to remove any adhering sediment or detritus and were preserved in 70% ethanol. Specimen identification (species level) and counts were performed under a low powered microscope. Dry weight (biomass_{DW}) was determined after drying at 80°C for 48

h and reported as $g\ m^{-2}$. Shannon diversity index (H') was calculated according to Lee (1999).

Environmental Data

Regional air temperature ($^{\circ}C$) and rainfall (mm) data obtained from the Australian Bureau of Meteorology automated Gold Coast weather station (Gold Coast Seaway, station number: 040764) were used as a complementary environmental characterisation of the study area. Previous hydrological measurements within the lake (data not shown) indicate that the approximate duration of sediment exposure per tidal cycle at Sites 1, 2, 3, and 4 was approximately 4, 3, 3, and 2 hours, respectively.

Statistical Analyses

Sediment parameter values for each sample depth horizon across the 15-cm depth profile are reported as mean values $\pm$ standard deviation (SD) from the triplicate cores for each site during each seasonal sampling event. Spatial and temporal variations (between site and/or season) were assessed using analysis of variance (ANOVAs), including Tukey's HSD or Games-Howell *post hoc* analysis. Prior to the analysis, the homogeneity of variance was evaluated using the Levene test, and, when violated, nonparametric analyses were performed. Pearson correlations (two-tailed; $\alpha = 0.05$) were used to assess and identify relationships between physicochemical sediment conditions (sample depth: 0–15 cm), environmental parameters, and benthic macroinfauna communities sampled (sample depth: 0–30 cm). Analyses were performed using SPSS Windows (SPSS, Inc., version 11.5.0). The infaunal assemblages and sediment characteristics at the sample sites were analysed using the PRIMER software package from the Plymouth Marine Laboratory (Clarke and Warwick, 2001).

RESULTS

Physicochemical Sediment Parameters

Daily temperature and rainfall data for the sampled period is shown in Figure 2. During the seasonal sampling events, regional temperatures ranged from $8^{\circ}C$ (August) to $34.5^{\circ}C$ (January). The maximum monthly rainfall occurred during November 2006 (122 mm).

No significant seasonal differences were observed at any site for all physical sediment parameters. Annual mean values of the sediment parameters with depth at each sampling site are shown in Table 1. Mean sediment wet-bulk densities ranged between 1.5 ± 0.1 (Site 4) to $2.0 \pm 0.1\ g\ cm^{-3}$ (Site 1) but were relatively consistent at each site with increasing depth. No significant difference was observed between sites. Water content throughout the sampled sediment profiles at all sites ranged from 20.4 to 69.6% and generally decreased with increasing sediment depth (Table 1). Water content significantly differed between all sample sites ($p < 0.001$, $\alpha = 0.05$), with the exception of Site 2 compared to Site 3.

Mean grain size and sorting of sediments are presented in Table 1. The mean grain size ranged between very fine grained (Site 4, 0–1 cm and 1–2 cm depths) and coarse grained (Site 2, 10–15 cm depth). Northern sediments located toward the marine entrance of the lake (Sites 1 and 2) were typically described as fine- to medium-grained to moderately to poorly

Figure 2. Daily recordings of air temperature (minimum and maximum) and rainfall in the southern Moreton Bay region (Australian Bureau of Meteorology weather station, Gold Coast Seaway, station number: 040764).

sorted sediments. In comparison, the southern sample sites are typically described as fine-grained to well to moderately well sorted. Sediment at the northern Sites 1 and 2 was significantly different in mean grain size compared to the southern Sites 3 and 4. For example, mean grain sizes throughout the sample profiles at Site 1 were significantly greater than Site 4 ($p = 0.002$, $\alpha = 0.05$), and Site 2 was significantly greater than Site 3 ($p = 0.004$, $\alpha = 0.05$) and Site 4 ($p = 0.002$, $\alpha = 0.05$). At a depth of ~ 10 cm, a patchy horizon of mollusc shells was present in the sediments at Sites 1 and 2.

Lake sediments were characterised by high organic matter contents with mean LOI_{550} values ranging from $1.21 \pm 0.45\%$ (Site 1, 1–2 cm depth, summer) to $9.57 \pm 6.53\%$ (Site 3, 10–15 cm depth, winter) (Figure 3). LOI_{550} values within the southern sites (3 and 4) were greater than the northern sites (1 and 2). Specifically, LOI_{550} values at Site 3 was significantly greater than Sites 1 ($p < 0.001$, $\alpha = 0.05$) and 2 ($p = 0.001$, $\alpha = 0.05$) values. Additionally Site 4 values were significantly greater than Site 1 ($p < 0.001$, $\alpha = 0.05$) and Site 2 ($p = 0.003$, $\alpha = 0.05$) values. Maximum LOI_{550} contents within Site 3 and 4 sediments occurred during winter and within Site 1 and 2 sediments during autumn and spring, respectively.

PO_4^{3-} concentrations ranged between 1.8 ± 0.4 to $21.0 \pm 8.1\ nmol\ g^{-1}$ dry wt (Figure 4) and showed no significant difference between sample sites. Furthermore, no significant seasonal differences were observed. Additionally, NH_4^{+} concentrations ranged from 13.2 ± 3.6 to $524.0 \pm 26.0\ nmol\ g^{-1}$ dry wt (Figure 5) and significantly changed between sites and seasons ($p < 0.001$, $\alpha = 0.05$) during the study. Site 4 concentrations were significantly greater than Site 1 ($p < 0.001$, $\alpha = 0.05$) and Site 2 ($p = 0.001$, $\alpha = 0.05$), respectively. Maximal NH_4^{+} concentrations at all sites throughout the lake occurred during the summer and autumn sampling periods.

Macroinfauna Dynamics

Over the course of the sampling programme, 1029 macroinfauna individuals were collected and identified, including six species from three orders representing deposit-feeding and filter-feeding macroinfaunal groups. Macrofauna abun-

Table 1. Annual averaged depth profiles of sediment parameters at each site (mean values $\pm$ standard deviation; $n = 12$ [three replicates $\times$ four seasons]).

Site	Depth (cm)	Wet-Bulk Density (g cm^{-3})	Water Content (%)	Graphic Mean Grain Size		Inclusive Graphic Standard Deviation	
				ϕ	Description	σ_1	Sorting
1	0–1	1.9 ± 0.1	27.4 ± 4.8	2.7	Fine grained	0.91	Moderately sorted
	1–2	1.9 ± 0.1	23.7 ± 1.8	2.7	Fine grained	0.94	Moderately sorted
	2–4	1.9 ± 0.1	22.8 ± 1.7	2.6	Fine grained	0.85	Moderately sorted
	4–6	2.0 ± 0.1	23.7 ± 1.9	2.6	Fine grained	0.89	Moderately sorted
	6–10	2.0 ± 0.1	23.6 ± 2.0	2.6	Fine grained	0.92	Moderately sorted
	10–15	2.0 ± 0.1	24.9 ± 2.5	2.4	Fine grained	0.72	Moderately sorted
2	0–1	1.6 ± 0.2	47.3 ± 13.3	2.0	Medium grained	1.45	Poorly sorted
	1–2	1.6 ± 0.3	42.7 ± 12.7	1.6	Medium grained	1.61	Poorly sorted
	2–4	1.6 ± 0.2	40.7 ± 10.7	1.2	Medium grained	1.81	Poorly sorted
	4–6	1.7 ± 0.2	37.6 ± 9.1	1.3	Medium grained	1.91	Poorly sorted
	6–10	1.8 ± 0.2	33.0 ± 7.3	1.1	Medium grained	2.03	Very poorly sorted
	10–15	1.8 ± 0.2	33.8 ± 7.3	0.4	Coarse grained	1.81	Poorly sorted
3	0–1	1.6 ± 0.1	45.8 ± 4.13	2.9	Fine grained	0.83	Moderately well sorted
	1–2	1.6 ± 0.1	43.4 ± 5.6	2.8	Fine grained	0.86	Moderately well sorted
	2–4	1.6 ± 0.1	41.7 ± 5.4	2.6	Fine grained	0.83	Moderately well sorted
	4–6	1.7 ± 0.1	38.6 ± 2.9	2.6	Fine grained	0.89	Moderately well sorted
	6–10	1.7 ± 0.1	39.1 ± 2.2	2.6	Fine grained	0.93	Moderately well sorted
	10–15	1.7 ± 0.1	40.3 ± 6.9	2.5	Fine grained	0.90	Moderately well sorted
4	0–1	1.4 ± 0.1	59.5 ± 6.3	3.0	Very fine grained	0.69	Well sorted
	1–2	1.5 ± 0.1	55.2 ± 5.2	3.0	Very fine grained	0.77	Moderately sorted
	2–4	1.5 ± 0.1	53.6 ± 4.0	2.8	Fine grained	0.66	Well sorted
	4–6	1.5 ± 0.1	52.3 ± 3.8	2.8	Fine grained	0.71	Well sorted
	6–10	1.5 ± 0.1	48.6 ± 3.9	2.9	Fine grained	0.80	Moderately sorted
	10–15	1.6 ± 0.1	43.2 ± 3.1	2.9	Fine grained	0.75	Moderately sorted

dance demonstrated significant spatial and temporal variations with the greatest combined seasonal abundances reported at the fine-grained Site 4 ($p < 0.001$, $\alpha = 0.05$) and the greatest abundances across the lake recorded during winter (< 0.001 , $\alpha = 0.05$). Seasonal trends in total site densities were observed at each of the four sites with temporal changes in macroinfauna densities characterised by a trending decline from winter through to autumn (Figure 6). The combined mean site densities were significantly correlated (negatively) with seasonal maximum monthly temperatures ($r = -0.625$, $p = 0.010$, $n = 16$). Mean combined densities ranged between 74.3 ± 74.5 ind. m^{-2} (Site 1, spring) and 955.5 ± 624.8 ind. m^{-2} (Site 4, winter; Figure 6). *Victoriopisa australiensis* (amphipods) followed by *Simplisia aequisetis* (polychaete worms) were the most numerically dominant species collected (Figure 6). *S. aequisetis* was the greatest contributor to the burrowing faunal assemblages at Sites 1, 2, and 3, accounting for 60%, 87%, and 64% of the total individuals collected, respectively (Figure 6). *V. australiensis* accounted for 92% of all the total collected burrowing macrofauna at Site 4. The contribution of *V. australiensis* to mean densities decreased from the southern fine grained sites (Sites 3 and 4) in comparison to the northern fine to medium grained sites (Sites 1 and 2). Overall, *V. australiensis* represents 49% of the total retrieved macroinfauna across the four sites and four seasons sampled. No single species was recorded simultaneously at all four sites during any of seasonal sampling periods; however, *V. australiensis*, *S. aequisetis*, and *H. cordiformis* were recorded at all four sites during one or more seasons (Table 2). *S. aequisetis* demonstrated a seasonal pattern, with increased densities typically occurring during winter and spring.

Mean site biomass_{DW} ranged between 0.16 ± 0.15 g m^{-2} (Site 1, summer) and 10.44 ± 11.69 (Site 1, winter; Figure 6). Combined biomass_{DW} at Sites 1 and 2 were 91.5 g m^{-2} and 89.0 g m^{-2} , respectively, compared to 18.0 g m^{-2} and 32.6 g m^{-2} for Sites 3 and 4, respectively. *V. australiensis* contributed greatest to Sites 3 and 4 biomass_{DW}. The greatest contribution to biomass_{DW} by *S. aequisetis* occurred at Site 3 (50%). Representing just 20% and 3% of the mean biomass at Sites 1 and 2, *H. Cordiformis* accounted for 61% and 82% of the recorded biomass_{DW} at these sites, respectively.

Site 1 demonstrated the greatest seasonal Shannon diversity index values with increased values during winter (1.82) and autumn (1.74). Seasonal lake-wide diversity values ranged between 1.12 (spring) and 1.48 (autumn) with an annual mean value of 1.3 ± 0.16 .

Relationships between Sediment Parameters and Macroinfauna Dynamics

Correlations between depth-averaged physicochemical sediment parameters are shown in Table 3. Significant correlations were observed between sediment parameters and macroinfauna mean density and biomass_{DW}. The combined density of macroinfauna was significantly correlated with seasonal depth-averaged sediment density ($r = -0.636$, $p = 0.008$, $n = 16$), porosity ($r = 0.570$, $p = 0.21$, $n = 16$), and organic matter content (LOI₅₅₀; $r = 0.755$, $p = 0.001$, $n = 16$). Mean densities of *V. australiensis* significantly correlated with mean $\text{NH}_4^+_{\text{bio}}$ (0–4 cm; $r = 0.505$, $p = 0.046$, $n = 16$), mean $\text{PO}_4^{3-}_{\text{bio}}$ ($r = 0.714$, $p = 0.002$, $n = 16$), and LOI₅₅₀ ($r = 0.682$, $p = 0.004$, $n = 16$). Additionally, mean density *S. Aequisetis* also significantly correlated with $\text{NH}_4^+_{\text{bio}}$ (0–4 cm; $r = -0.499$, $p = 0.049$, $n = 16$) (Table 4). Furthermore, *V. australiensis* biomass_{DW} significantly correlated $\text{NH}_4^+_{\text{bio}}$ (0–4 cm; $r = -0.508$, $p = 0.045$, $n = 16$),

Figure 3. Seasonal depth profiles of sediment LOI_{550} contents at each sampling site within Coombabah Lake. Data are mean values, and error bars show the standard deviation of the mean rate ($n = 3$).

mean PO_4^{3-} ($r = 0.684$, $p = 0.003$, $n = 16$), and LOI_{550} ($r = 0.552$, $p = 0.027$, $n = 16$). Mean biomass $_{\text{DW}}$ of *H. cordiformis* also significantly correlated with LOI_{550} values ($r = -0.505$, $p = 0.046$, $n = 16$, Table 4).

DISCUSSION

The northern sample sites (Sites 1 and 2) were characterised by fine to medium grained to moderately to poorly sorted sediments and the southern sample sites (Sites 3 and 4) by fine grained to moderately well to well-sorted sediments, as a result of the hydrodynamic regime and settling behaviour of sediment particles (Dronkers, 1986; van Leussen, 1999). The tidal regime of the lake and Coombabah Creek indicates pumping of sand-dominated sediments from the downstream marine entrance landward into the northern areas of the lake (Ali, Zhang, and Lemckert, 2009; Dunn *et al.*, 2007a).

Nutrient concentrations measured during this study were comparable to surface sediment concentrations measured previously within the lake (Dunn *et al.*, 2007b). Spatial and temporal differences in sedimentary inorganic nutrient concentrations throughout the lake are attributable to variations in sediment grain size, organic matter remineralisation, and external nutrient inputs. Sediment organic matter contents

Figure 4. Seasonal depth profiles of sediment PO_4^{3-} concentrations at each sampling site. Data are mean values, and error bars show the standard deviation of the mean rate ($n = 3$).

were greater within the southern lake fine-grained to moderately well to well-sorted sediments compared to the northern fine to medium grained to moderately to poorly sorted sediments. Organic matter content within the lake corresponded to the well-established and commonly observed correlation of increased organic matter with reducing sediment grain size (*e.g.*, Dankers and Beukema, 1983; Dunn *et al.*, 2008; Schrijvers, Van Gansbeke, and Vincx, 1995).

During a previous stable isotope and lipid biomarker study, Dunn *et al.* (2008) identified a greater contribution of autochthonous and labile organic matter to the sedimentary organic matter pool in the northern (marine entrance) sediments compared to the more allochthonous sourced organic matter of the southern region of the lake. Dunn *et al.* (2008) also observed that lower C/N ratios within the lake corresponded to regions of increased concentrations of chlorophyll-*a* and phaeopigment concentrations, with significant negative correlations occurring between chlorophyll-*a* and phaeopigment concentrations and C/N ratios, reflecting the influence of the low C/N ratio microalgal biomass and bacterial communities. In addition to stimulating microbial metabolism, sediment oxygen demand and nutrient regeneration (Ferguson, Eyre, and Gay, 2003; Slomp *et al.*, 1993), sedimentary organic matter is a major food source for benthic infauna (Cheng and Chang, 1999; Spilmont *et al.*, 2009) despite its often refractory nature

Figure 5. Seasonal depth profiles of sediment $\text{NH}_4^+_{\text{bio}}$ concentrations at each sampling site. Data are mean values, and error bars show the standard deviation of the mean rate ($n = 3$).

(Cheng, 1995). Variations in the delivery and bioavailability of organic matter and regenerated nutrients, therefore, might influence benthic infauna population dynamics (Cheng and Chang, 1999; Ponti, Casselli, and Abbiati, 2010; Sánchez-Moyano, García-Asencio, and García-Gómez, 2010). During this study, increases in the combined macroinfauna density were observed to significantly correlate ($r = 0.755$, $p = 0.001$, $n = 16$) with increased sediment organic matter content (food supply) within the surface sediments of Coombabah Lake, indicating that sediment column organic matter content was a factor influencing the combined macrofauna population dynamics of Coombabah Lake on a relatively small spatial scale (e.g., ~500 m). The significant correlation was influenced by the increased contribution of *V. australiensis* to overall densities in the fine-grained southern sites characterised by increased contents of organic matter. Additionally, significant correlations between *V. australiensis* density and mean $\text{NH}_4^+_{\text{bio}}$ and $\text{PO}_4^{3-}_{\text{bio}}$ concentrations were also identified (Table 4). The findings of the study illustrate associations between *V. australiensis* densities, LOI_{550} , $\text{NH}_4^+_{\text{bio}}$, and $\text{PO}_4^{3-}_{\text{bio}}$ concentrations within Coombabah Lake, which themselves share significant correlations (Table 3). Additionally, significant correlations were also observed between LOI_{550} content and mean biomass_{DW} of *V. australiensis* ($r = 0.552$, $p = 0.027$, $n = 16$), again reflecting the importance of organic matter content–food supply to the deposit feeding species. Previously several studies have also established sediment characteristics as significant factors influencing the distribution of macroinfauna species in estuarine and coastal waters (e.g., Cheng and Chang, 1999; Kanaya and Kikuchi, 2008; Ysebaert *et al.*, 2002, 2003).

Although the sample sites were paucispecific, the lake included species commonly observed in intertidal surface sediments along the coastline of eastern Australia (e.g., Hirst, 2004; Ruella, 1975). Recorded densities are similar to those previously reported within the intertidal lake and surrounding environments (Dunn *et al.*, 2009; GHD, 2003) and those reported in other shallow intertidal sediments (Kanaya and

Figure 6. Burrowing macroinfaunal dynamics, including (a) mean density, (b) species contributions to mean density, (c) total biomass_{DW}, and (d) species contribution to total biomass_{DW}.

Table 2. Density (ind. m^{-2}) and biomass_{DW} (g m^{-2}) of Coombabah Lake macroinfauna species (mean values $\pm$ standard deviation or single recorded density where $n = 1$).

		Species (Family)					
		Deposit Feeder					Filter Feeder
Site	Season ^a	<i>Victoriopisa australiensis</i> (Melitidae)	<i>Simplisetia aequisetis</i> (Nereididae)	<i>Heloccius cordiformis</i> (Ocypodidae)	<i>Penaeus plebejus</i> (Penaeidae)	<i>Clorida depressa</i> (Squillidae)	<i>Pitar affinis</i> (Veneridae)
Density (ind. m ⁻²)							
1	W	79.6 ± 22.5	95.6 ± 31.9	57.3 ± 14.2	—	—	31.85 ± 0.0
1	Sp	63.7	159.3 ± 45.0	63.7	—	31.9	—
1	Su	—	106.2 ± 71.7	—	—	—	—
1	A	—	47.8	53.0 ± 18.4	31.9	31.9	—
2	W	76.4 ± 48.3	503.2 ± 615.4	31.9	—	—	—
2	Sp	79.3 ± 22.5	498.9 ± 477.9	—	—	—	—
2	Su	47.8 ± 22.5	108.9 ± 62.1	39.8 ± 15.9	—	—	—
2	A	42.5 ± 18.4	159.3 ± 140.0	63.7	31.9	—	—
3	W	339.7 ± 109.7	472.4 ± 299.7	31.9 ± 0.0	—	—	—
3	Sp	119.4 ± 18.4	210.2 ± 26.0	31.9	—	—	—
3	Su	63.7 ± 45.0	146.5 ± 73.3	—	—	—	—
3	A	66.3 ± 66.3	172.0 ± 102.2	—	—	—	—
4	W	897.1 ± 560.2	42.5 ± 75.8	31.9	—	—	—
4	Sp	440.6 ± 68.1	71.7 ± 18.4	—	—	—	—
4	Su	254.8 ± 146.6	127.4	31.9 ± 0.0	—	—	—
4	A	414.0 ± 122.5	31.9	31.9 ± 0.0	—	—	—
Biomass _{DW} (g m ⁻²)							
1	W	0.87 ± 1.21	0.47 ± 0.60	5.81 ± 4.68	—	—	15.22 ± 8.70
1	Sp	0.81	0.18 ± 0.11	8.21	—	0.05	—
1	Su	—	0.14 ± 0.15	—	—	—	—
1	A	—	0.09	4.96 ± 4.25	0.08	0.02	—
2	W	0.27 ± 0.34	0.58 ± 0.42	0.51	—	—	—
2	Sp	0.11 ± 0.12	0.81 ± 0.70	—	—	—	—
2	Su	0.06 ± 0.03	0.73 ± 1.36	7.41 ± 4.49	—	—	—
2	A	0.09 ± 0.05	0.27 ± 0.26	42.7	0.07	—	—
3	W	0.35 ± 0.14	0.44 ± 0.31	0.29 ± 0.38	—	—	—
3	Sp	0.15 ± 0.11	0.28 ± 0.17	4.87	—	—	—
3	Su	0.07 ± 0.04	0.17 ± 0.10	—	—	—	—
3	A	0.16 ± 0.05	0.77 ± 1.32	—	—	—	—
4	W	1.14 ± 0.53	0.07 ± 0.03	0.62	—	—	—
4	Sp	1.03 ± 0.27	0.16 ± 0.10	—	—	—	—
4	Su	0.49 ± 0.41	0.44	0.95 ± 1.02	—	—	—
4	A	0.78 ± 0.28	0.10	2.50 ± 0.82	—	—	—

^a W, Sp, Su, and A represents winter, spring, summer, and autumn, respectivelyTable 3. Pearson correlation coefficients between mean annual sediment parameter values for each sediment depth horizon ($n = 24$ [six sample horizons $\times$ four seasons]).

	Water content (%)	<63 μm (%)	>250 μm	LOI ₅₅₀ (%)	NH ₄ ⁺ _{bio} (nmol g ⁻¹ dry wt.)	PO ₄ ³⁻ _{bio} (nmol g ⁻¹ dry wt.)
Wet-bulk density						
<i>r</i>	-0.995**	-0.205	-0.442*	-0.921**	-0.554**	-0.161
<i>p</i>	0.000	0.337	0.030	0.000	0.005	0.453
Water content						
<i>r</i>		0.226	-0.446*	0.905**	0.586**	0.188
<i>p</i>		0.287	0.029	0.000	0.003	0.379
<63 μm						
<i>r</i>			-0.713**	0.225	0.361	-0.057
<i>p</i>			0.000	0.290	0.083	0.792
>250 μm						
<i>r</i>				0.458*	-0.403	-0.036
<i>p</i>				0.024	0.051	0.868
LOI ₅₅₀						
<i>r</i>					0.573**	0.224
<i>p</i>					0.003	0.292
NH ₄ ⁺ _{bio}						
<i>r</i>						0.637**
<i>p</i>						0.001

* Correlation significant at the 0.05 level [two-tailed].

** Correlation significant at the 0.01 level [two-tailed].

Table 4. Species-specific Pearson correlation coefficients between mean density and depth-averaged (0–4 cm and 0–15 cm) mean sediment nutrient concentrations and mean LOI_{550} content and biomass_{DW} and depth-averaged (0–4 cm and 0–15 cm) mean sediment nutrient concentrations and mean LOI_{550} content ($n = 16$ [four sites $\times$ four seasons]).

	NH ₄ ⁺ _{bio} (0–4 cm), nmol g ^{−1} dry wt.	NH ₄ ⁺ _{bio} (0–15 cm), nmol g ^{−1} dry wt.	PO ₄ ^{3−} _{bio} (0–4 cm), nmol g ^{−1} dry wt.	PO ₄ ^{3−} _{bio} (0–15 cm), nmol g ^{−1} dry wt.	LOI ₅₅₀ (0–15 cm), %
Mean density (ind. m ^{−2})					
<i>V. australiensis</i>					
<i>r</i>	0.505*	0.282	0.322	0.714**	0.682**
<i>p</i>	0.046	0.290	0.224	0.002	0.004
<i>S. aequisetis</i>					
<i>r</i>	−0.499*	−0.451	−0.245	−0.311	0.243
<i>p</i>	0.049	0.077	0.359	0.242	0.365
<i>H. cordiformis</i>					
<i>r</i>	−0.153	0.030	−0.051	0.120	−0.342
<i>p</i>	0.571	0.912	0.852	0.659	0.195
<i>P. plebejus</i>					
<i>r</i>	0.113	0.184	−0.061	0.470	0.427
<i>p</i>	0.676	0.495	0.822	0.066	0.099
<i>C. depressa</i>					
<i>r</i>	0.109	−0.132	−0.079	0.080	0.478
<i>p</i>	0.688	0.625	0.772	0.768	0.061
<i>P. affinis</i>					
<i>r</i>	0.109	−0.132	0.080	−0.079	−0.478
<i>p</i>	0.688	0.625	0.768	0.772	0.061
Mean biomass _{DW} (g m ^{−2})					
<i>V. australiensis</i>					
<i>r</i>	0.508*	0.238	0.373	0.684**	0.552*
<i>p</i>	0.045	0.375	0.154	0.003	0.027
<i>S. aequisetis</i>					
<i>r</i>	−0.482	−0.250	−0.263	−0.327	0.146
<i>p</i>	0.059	0.351	0.325	0.217	0.589
<i>H. cordiformis</i>					
<i>r</i>	−0.328	0.074	0.054	0.051	−0.505*
<i>p</i>	0.215	0.786	0.844	0.852	0.046
<i>P. plebejus</i>					
<i>r</i>	0.059	0.182	0.440	−0.057	0.421
<i>p</i>	0.828	0.500	0.088	0.833	0.104
<i>C. depressa</i>					
<i>r</i>	0.166	0.448	0.494	−0.064	0.426
<i>p</i>	0.539	−0.309	0.052	0.813	0.100
<i>P. affinis</i>					
<i>r</i>	−0.323	−0.309	0.494	−0.106	0.328
<i>p</i>	0.233	0.244	0.052	0.697	0.215

* Correlation significant at the 0.05 level (two-tailed).

** Correlation significant at the 0.01 level (two-tailed).

Kikuchi, 2008; Kanaya, Suzuki, and Kikuchi, 2011; Mucha, Vasconcelos, and Bordalo, 2004).

Species present demonstrated temporal variations with low abundance during summer conditions and significantly greater abundance during winter conditions, with mean site densities significantly correlating (negatively) with seasonal maximum monthly temperatures ($r = -0.625$, $p = 0.010$, $n = 16$). In addition to abundances, seasonal shifts in community structures were also observed. This finding suggests that seasonal temperature variation plays a potentially key role in the overall temporal macrofauna population dynamics of Coombabah Lake. Temporal evolutions observed within the lake have also

been reported in temperate (*e.g.*, Ysebaert and Herman, 2002) and subtropical intertidal environments (*e.g.*, Chang, 1995; Da Cunha Lana and Guiss, 1991; Fonseca and Netto, 2006). The temporal variations observed within Coombabah Lake, however, are in contrast to those recorded in some other studies within Australian intertidal systems that reported no significant seasonal trends (Dittman, 2002; Jones, Watson-Russell, and Murray, 1986; Rainer, 1981). In many cases, intra-annual trends in macrofauna dynamics are attributable to patterns of species recruitment, water column and sediment conditions, competition, and predation stresses (Moreira, Aldea, and Troncoso, 2010). These facts could help explain the lower

values of density observed during summer in Coombabah Lake, with recruitment potentially occurring during autumn, together with an increase in food supply (organic matter) leading to maximum macroinfauna densities during winter. This could be especially true for Site 3 and Site 4 where maximum LOI_{550} values, representing a food supply, occurred during winter.

Predation is most often presumed to be an important organising force of soft-sediment community structures (Bell, 1980; Brey, 1991). Furthermore, a feature of soft sediments is that any epibenthic predator feeding on the infauna is almost bound to cause a significant disturbance to the substrate (Glassom and Branch, 1997), potentially further influencing infauna dynamics. Macroinfauna within Coombabah Lake provides food sources for commercially and recreationally important fish and migratory wading bird species. Predation pressures presumably include resident species, *Sillago ciliata* (whiting) and *Platycephalus fuscus* (dusky flathead), which would typically feed in sandier sediments (northern region), and *Acanthopagrus australis* (bream) and *Mugil cephalus* (mullet), which generally feed in more mud-dominated sediments (GHD, 2003). Intertidal regions and sand/mud flats are also important feeding grounds for shorebirds, which are attracted to prey such as infaunal polychaetes and amphipods (Evans *et al.*, 1998). In addition to resident shorebirds, the lake often serves as an important bird-staging area along avian migratory routes as an important declared migratory bird habitat. Migratory wading birds arriving from Europe and Asia during October (spring) to May (autumn) tend to roost in close proximity to surrounding feeding grounds and move out to feed on the tidal flats, often in hundreds (Dunn, personal observation), during ebb tides. Increased predation pressures resulting from the presence of migratory wading birds within the lake coincide with the minimum observed macroinfauna densities within the lake during summer. Avian predation resulting in reduced densities of prey species in intertidal soft-sediment environments has been demonstrated by many studies (*e.g.*, Evans *et al.*, 1998; Hulscher, 1982; Quammen, 1981; Rosa *et al.*, 2008; Zwarts and Blomert, 1992). This observation suggests that avian predation is potentially a key factor influencing the temporal macrofauna population dynamics of Coombabah Lake.

CONCLUSION

In conclusion, this study investigated physicochemical sediment characteristics and macroinfauna dynamics within the sediments of Coombabah Lake. Seasonal sampling events indicated that physical sediment parameters demonstrated spatial variations but little seasonal variability in comparison to nutrient and organic matter concentrations. Spatial and temporal variations of the deposit-feeding and filter-feeding macroinfauna populations were observed according to sediment condition and sample season. Variations in the physicochemical surface parameters within the subtropical lake provide macroinfauna with different habitats that resulted in the coexistence of infauna with different habitat selectivity within a relatively small scale (*e.g.*, approximately 500 m). During the study the highest combined species densities occurred in the southern fine-

grained to moderately well to well-sorted sediments (Sites 3 and 4). Variations of mean macroinfauna density and biomass_{DW} within the lake significantly correlated to nutrient and organic matter content. Strong temporal trends in total site densities were observed at each of the lake sites with significantly greater abundances and biomass observed during the winter.

The temporal variation of lake macroinfauna observed during this study showed trends that are hypothesised to be related to changing biotic and abiotic factors, including meteorological conditions, organic matter supply, patterns of species recruitment, and predation stresses. Specifically, the presence of migratory wading birds (October to May) within Coombabah Lake coincided with the minimum observed macroinfauna densities. In addition to interannual variations, biotic and abiotic factors would presumably determine long-term (intraannual) variations of macroinfauna assemblages throughout Coombabah Lake.

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