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Spatial patterns and diversity of foraminifera from an intermittently closed and open lagoon, Smiths Lake, Australia

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ABSTRACT

Foraminifera represent an important tool for assessing and monitoring the past, present and future relative health of marine systems, but this is only possible where baseline assemblage characteristics have been previously established. This type of baseline data is currently lacking for intermittently closed and open lakes or lagoons (ICOLL). ICOLLs are estuarine environments that are isolated from the open ocean for much of the time, but are subject to distinct periods of tidal exchange and large fluctuations in hydrodynamic factors when the barrier that isolates the ICOLL is opened to the sea. This study provides new data on diversity and distribution of foraminifera from Smiths Lake, an ICOLL on the Australian eastern coastline. Environmental parameters were measured to identify potential abiotic controls on the distribution and relative abundance of assemblages and individual taxa. Results indicate that, whilst the Smiths Lake assemblage is largely similar to foraminifera assemblages found in estuaries consistently open to the sea, it can be differentiated based upon lower species richness and a lack of calcareous taxa, even in the seaward parts of the lagoon. Parameters associated with depth, including sediment grain size and nutrient supply, are identified as significant controls on both assemblage distribution and the relative abundance of common taxa in Smiths Lake. ICOLLs are considered extremely sensitive to anthropogenic activities and these results represent an important potential tool in ICOLL management.

1. Introduction

Intermittently closed and open lakes or lagoons (ICOLLs) is a term used to describe both saline coastal lagoons and barrier type estuaries where low freshwater inflow leads to sand barrier formation across the estuary entrance, preventing exchange with the open ocean (Roy et al., 2001; Dye and Barros, 2005; Dye, 2005; Jones and West, 2005; Haines et al., 2006; Everett et al., 2007). This differs from the majority of 'true' coastal lagoons and saline lakes, which are either permanently or frequently connected to the open ocean (Haines et al., 2006). The opening and closing of ICOLLs is highly stochastic, with the timing, frequency of entrance opening, and length of time the estuary is open to the sea influenced by: catchment size; rainfall; evaporation; the size of the barrier; the number of fluvial inputs into the system; marine currents; wave activity; weather patterns and the size of the initial breakout (Roy et al., 2001; Everett et al., 2007). ICOLLs only sporadically reach a steady state (Roy et al., 2001; Everett et al., 2007), as the transition between open and closed phases results in large fluctuations in hydrodynamic factors, particularly salinity. When the entrance is closed (which under natural conditions is the majority of the time), ICOLLs can be regarded as terminal lakes (Haines et al., 2006). All freshwater inputs from the catchment are retained and salinity levels may decrease. Where freshwater input is extremely low, evapotranspiration may exceed catchment runoff, creating hypersaline conditions. When the entrance is open, freshwater input is able to drain and tidal exchange brings marine waters into the system.

ICOLLs are confined to temperate micro-tidal coasts where annual rainfall is intermittent (Gale et al., 2006). Whilst found in Brazil (Suzuki et al., 1998), Mexico (Lankford, 1976), New Zealand (Kirk and Lauder, 2000), South Africa (where they are referred to as Temporally Open/Closed Estuaries – Perissinotto et al., 2000; Froneman, 2004; Stretch and Parkinson, 2006), and the United States (Elwany et al., 1998), the term ICOLL is generally used to describe systems along the south-eastern Australian coastline (Roy et al., 2001). ICOLLs are common in this region, particularly in New South Wales, where approximately half of all estuaries are ICOLLs (Haines et al., 2006).

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Because of their intermittent connection to the open ocean, ICOLLs are considered to be extremely sensitive to anthropogenic activities (Boyd et al., 1992). In their 'terminal lake' phase, all inputs are retained in the ICOLL, including any pollutants transported into the system either via surface runoff or through fluvial inputs (Webster and Harris, 2004). Even when open, tidal exchange may still be restricted, and flushing of the system limited (Haines et al., 2006). Additionally, many ICOLLs are artificially opened to the sea by local regulators when they reach a predefined mean water level (Everett et al., 2007). Because of this, many ICOLLs that would naturally remain closed for long periods of time instead frequently experience sustained periods of contact with the open ocean. Despite their sensitivity, ICOLLs have received little consideration in estuarine management strategies, likely due to their generally small size and distance from major urban centres (Haines et al., 2006). Many ICOLLs have not been included as part of assessments of the approximately 800 estuarine systems that have been classified throughout Australia (Bucher and Saenger, 1991; Boyd et al., 1992; Harris et al., 2002).

Previous work has demonstrated that foraminifera represent an important proxy for assessing and monitoring the past, present and future relative health of marginal marine systems (Armynot du Chatelet et al., 2004). Where modern baseline taxonomic composition and ecological distribution can be established, and is then combined with down-core assemblages, the possibility exists to reconstruct historical trends (Culver et al., 2012), identify the repercussions of anthropogenic activities, and monitor the effectiveness of any attempted remediation (Debenay et al., 2000). Given that many ICOLLs are unquestionably anthropogenically impacted (through artificial opening), foraminifera represent an important potential tool for ICOLL management. Their application is limited however, until baseline ecological studies have been undertaken.

Work on foraminifera from coastal lagoons either open or closed (e.g. Cann et al., 2000; Debenay et al., 2000, 2001; Revets, 2000; Debenay et al., 2001; Cearreta et al., 2002) is lacking when compared with other types of estuarine systems. Given that ICOLLs are concentrated in south-eastern Australia, this lacuna is likely a reflection of the lack of work on Australian foraminifera generally. Published studies have described foraminifera from <4% of Australian estuaries (McKenzie, 1962; Albani, 1968a, 1968b, 1979; Johnson and Albani, 1973; Collins, 1974, Michie, 1987, Albani and Johnson, 1976, Quilty, 1977; Bell, 1978, 1995, 1996; Apthorpe, 1980; Yassini and Jones, 1989; Bell and Drury, 1992; Cotter, 1996; List, 1996; Cann et al., 2000; Revets, 2000; Clarke et al., 2001; Haslett, 2001; Wang and Chappell, 2001; Horton et al., 2003; Strotz, 2003; Woodroffe et al., 2005; Quilty and Hosie, 2006; Haslett, 2007; Haslett et al., 2010; Nash et al., 2010; Callard et al., 2011; Strotz, 2012; Schröder-Adams et al., 2014). Foraminifera have been documented from another ICOLL from New South Wales, Coila Lake (Strotz, 2003), but that study was neither comprehensive nor detailed. Because of this lack of previous work, it is currently unclear what constitutes an ICOLL foraminifera assemblage, precluding the use of foraminifera as environmental proxies in ICOLLs.

This study seeks to resolve this information gap by providing new primary data on foraminifera ecology from a little studied estuary type and to test the following hypothesis: the foraminiferal assemblage present in an ICOLL is distinct from foraminifera assemblages found in open estuarine systems. If upheld, this may mean that the extensive body of existing work on foraminifera from open estuaries may not be directly applicable to ICOLLs. There is some justification for suggesting ICOLL biotas are exceptional, as it has been established that the presence of species within an ICOLL, even locally common taxa, is unpredictable because species can only gain entry during a brief open phase (Robinson et al., 1983; Roy et al., 2001). The proposed hypothesis is tested by documenting the distribution and diversity of foraminifera from Smiths Lake, an ICOLL located on the north coast of New South Wales. Potential controls on species distribution and abundance are identified through comparison with selected hydrological parameters. The foraminifera biota from Smiths Lake is compared with previous studies of foraminifera from open estuaries to determine if a distinct ICOLL foraminifera biota exists.

2. Materials and methods

2.1. Study area

Smiths Lake is located approximately 280 km north of Sydney (Fig. 1). It is a coastal lagoon with a fluctuating surface area of 9.5–9.8 km^2 and a catchment area of 33 km^2 (Everett et al., 2007). Freshwater input into the system is limited (Gale et al., 2006), confined to small creeks, predominately Wamwarra and Tarbuck Creeks (Webb, Mckeon and Associates, 2008, Fig. 1), and rainfall runoff from the immediate periphery of the system. There is no marked seasonality to rainfall volumes and, for the period 1980–2014, mean annual rainfall was 1460 mm. The coastline is wave-dominated, and ocean tides are semi-diurnal and micro-tidal (spring tidal range < 2 m). Prevailing winds are from the north-east in summer and west and south-west in winter. Winds are generally 10–20 km/h but localised thunderstorms can create gusts over 100 km/h. Best estimates suggest currents of up to 0.5 m/s could be generated during prolonged storm conditions (Webb, Mckeon and Associates, 2008), and all wave activity in the lagoon during closed phases are wind waves.

A large barrier beach, 200 m in width at its narrowest point and created by longshore sand transport (Roy, 1984), closes the lake off from the sea the majority of the time. Tidal flows are completely blocked when the lagoon is closed (Webb, Mckeon and Associates, 2008). Heavy rains in the catchment would ultimately lead to a freshwater discharge strong enough to breach the sandbar (Bird, 1967). In recent times this no longer occurs, as the lake has been opened artificially every 1.5 years since 1932 to prevent flooding of the catchment and to ensure good fish stocks (Robinson et al., 1983; Everett et al., 2007). Whilst opening of Smiths Lake is infrequent when compared with other ICOLLs, which are opened multiple times per annum or kept permanently open to the sea through construction of training walls (Dye and Barros, 2005), it is estimated to be twice as frequent as natural openings would occur (Webb, Mckeon and Associates, 2008). The lake is tidal following a breakout event, although the tidal range is only 10% of the ocean tide range. Tidal velocities during breakout events are imperceptible except in the entrance area, and tidal flows into and out of the lagoon average less than 3% of the lagoon volume (Webb, Mckeon and Associates, 2001). Within 2–3 months after a breakout, the lagoon entrance is completely blocked (Gale et al., 2006).

The eastern or seaward side of the lagoon is dominated by an extensive shallow flood-tide delta that consists of well-sorted, light-coloured quartz sand, deposited by ocean waves and tidal flows at times when the barrier beach is opened to the sea. This delta is the only part of the lagoon subject to significant sediment transport (Gale et al., 2011). The western side of the lake consists of a low energy basin-style setting, approximately twice the size of the eastern section (Fig. 1). Around the lagoon foreshore, to a depth of approximately 2 m, sediments consist of reworked coastal sands, deposited during the last interglacial, combined with fluvial sands and gravels from Wamwarra and Tarbuck Creeks (Gale et al., 2011). Deeper areas (below 2 m) are dominated by fluvial muds (Robinson et al., 1983). The total fluvial sediment load entering the lagoon is estimated to be 3000 m^3/yr (Webb, Mckeon and Associates, 2001). Concentrations of total organic carbon, nitrogen and phosphorous

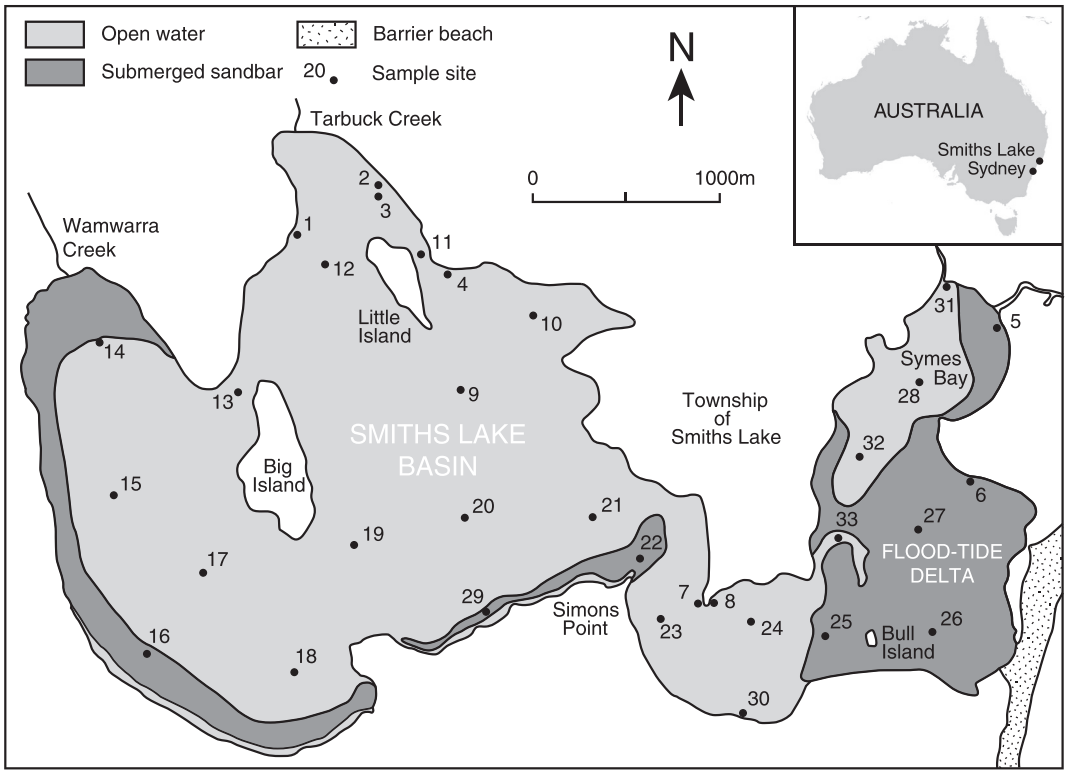

Fig. 1. Map of Smiths Lake. Upper right inset shows location of Smiths Lake on the eastern Australian coastline. Dark grey areas indicate submerged sandbars.

levels in the sediments are all low (Webb, Mckeon and Associates, 2001), and Smiths Lake is considered predominately oligotrophic (Smith and Heggie, 2003). Chlorophyll a and turbidity levels in Smiths Lake are well below the mean for the region and relative water quality in the lagoon is classified as 'good' (Roper et al., 2011). Seagrasses fringe almost the entire periphery of the lagoon, and the low sediment input and nutrient levels allow for extensive seagrass beds at depths of 3.5–4 m (Robinson et al., 1983; Gale et al., 2011).

The catchment consists predominately of state forest and is relatively uninhabited, with approximately 1100 people living in the catchment area (Everett et al., 2007). Agriculture is largely absent from the catchment. Whilst no ICOLL in New South Wales can be considered 'pristine', the small population, lack of agriculture and infrequent openings indicates Smiths Lake is one of the better representatives of an undisturbed ICOLL system.

2.2. Data collection

Sediment samples and environmental data were collected in April, 2003. At the time of collection, the lake was closed to the ocean. The previous opening prior to sampling was June 2002 (Everett et al., 2007). According to the Australian Bureau of Meterology, rainfall for the period January–April 2003 (639 mm) was similar to the mean rainfall volumes for the same period (571 mm). Thirty three sites were sampled, selected to represent the range of environments present in the lagoon. None of the chosen sites are subject to tidal exposure when the lagoon is closed, but sites located on sandbars (Fig. 1) would be exposed when the barrier is breached. Sediment was collected either by hand from the shoreline, or using a standard Van Veen style grab sampler lowered from a small boat. Because the generally muddy nature of the substrate resulted in the grab sampler returning 'undisturbed' blocks of sediment, the top 1 cm of sediment was collected for all samples (as per recommendations of Scott et al., 2001). Sediment was placed into 100-ml vials, and treated with buffered ethanol to preserve foraminifer protoplasm for staining upon return to the shore.

Six environmental parameters; electrical conductivity (mS/cm), dissolved oxygen (mg/L), pH, oxidation reduction (redox) potential (mV), depth (m) and temperature (°C), were measured to evaluate abiotic controls on species distribution. These hydrological parameters were chosen as they have been previously demonstrated to influence foraminiferal diversity and abundance (e.g. Murray, 1973; Boltovskoy and Wright, 1976; Haynes, 1981; Boltovskoy et al., 1991; Murray, 2001; Strotz, 2012). Conductivity results were converted to salinity (in ppt) using the method outlined in Rice et al. (2012). Measurements were collected at the sediment–water interface using a Hydrolab 4 datasonde. Multiple readings for all parameters (excluding depth) were taken over a one-month period at varying times of day. The mean of these results was then used, to account for potential variations in values due to fluctuations in ambient atmospheric temperatures and diurnal cycles. Results were visualised as contour maps created using Surfer version 8.04 (Fig. 2) and values are presented in Appendix A.

Importantly, these data are not presumed to reflect the 'absolute' mean value for any of the measured parameters in Smiths Lake (except depth), given conditions within the lake can vary dramatically depending upon time of year or due to an anomalous event, such as extremely high rainfall or the opening of the barrier beach (Robinson et al., 1983; Roy et al., 2001). They are presumed however, to represent the relative difference between sites, differentiating, for example, sites where oxygen concentrations are low relative to the rest of the lagoon.

Sediment samples were treated, at the time of collection, with rose Bengal stain to ascertain whether the foraminifera tests

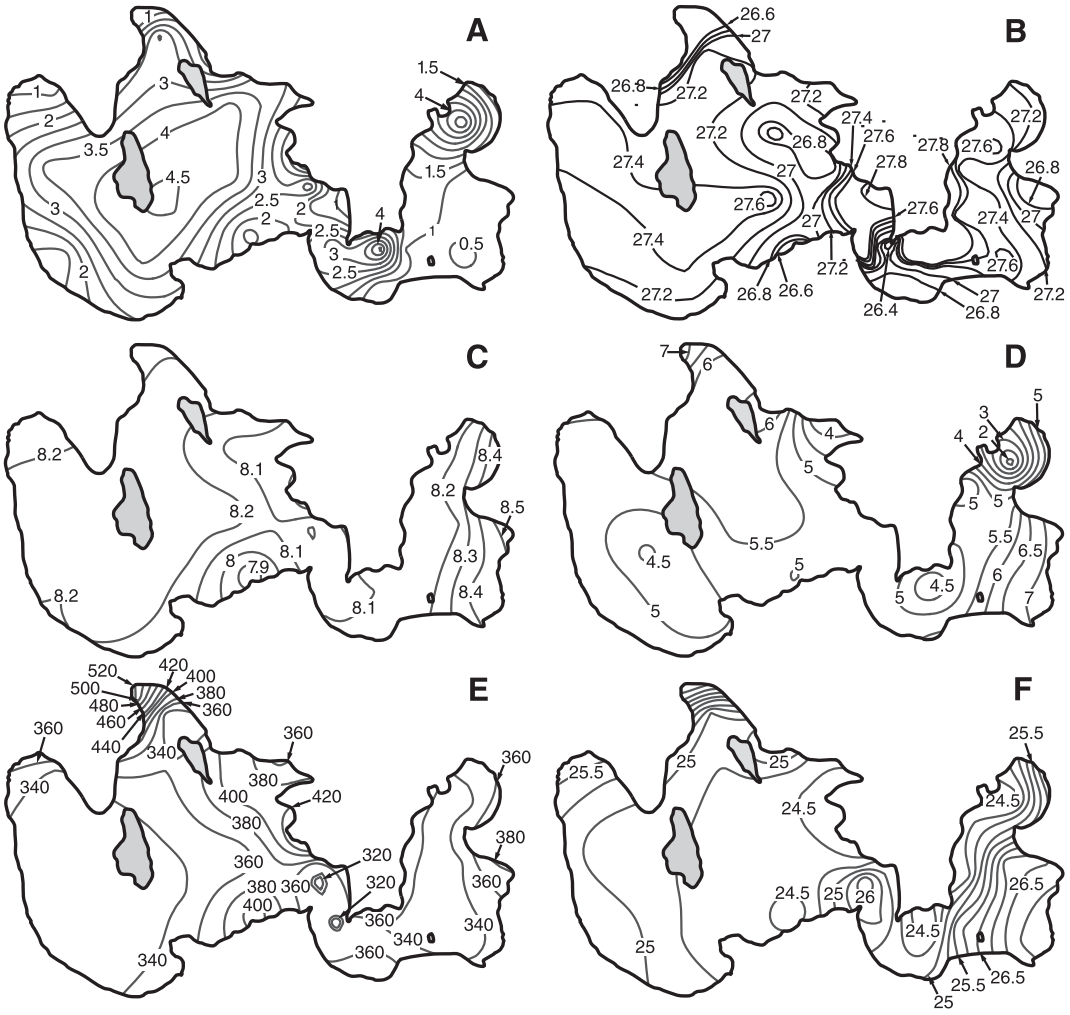

Fig. 2. Contour maps for the six measured environmental parameters. With the exception of depth (A), all contour values represent the mean of measured values. A. Depth (metres); B. Salinity (ppt); C. pH; D. Dissolved Oxygen (mg/L); E. Oxidation Reduction Potential (mV); F. Temperature (°C). Measured values used for contour maps are provided in Appendix A. For Fig. 2A (depth), both Big and Little Islands (Fig. 1) are very steep sided. The contour lines that appear to intersect these islands actually wrap around them, but are obscured by the scale of the contours (drawn at 0.5 m intervals).

recovered represented either live or dead individuals. Sample processing followed the methods described by Scott et al. (2001). Samples were washed through a 63 μm sieve and allowed to air dry in ambient conditions (<25 °C). Foraminifera were concentrated using sodium polytungstate separation (Strotz, 2012). Following floatation, samples were split with a microsplitter, into representative sub-samples for counting. Three hundred individuals were then picked from each sample, unless that proved impossible due to insufficient available specimens. It has been previously demonstrated that counts larger than 300 do not improve accuracy (Scott et al., 2001). The number of specimens recovered from each sample is listed in Appendix B. Sample SML6 did not yield any foraminifera and was not included as part of any analyses.

Foraminifera were considered 'alive' even if only the last few chambers were stained by the rose Bengal stain. Even so, because of the low yield of stained ('live') foraminifera (<10%), all analyses and discussions herein of foraminifera are based upon total assemblages, using the methodology developed by Scott and Medioli (1980). Comparisons of the total assemblage with the stained component in previous estuarine studies have demonstrated they are effectively interchangeable (Hayward, 1982; Hayward et al., 1999; Southall et al., 2006). Taxa were identified to species level using a stereo microscope and photomicrographs of representative specimens were taken using a JEOL-JSM 840 scanning electron microscope.

2.3. Analysis

All foraminifera counts were first converted to relative abundances (Appendix B). To remove variance–mean relationships and any potential overemphasis on rare or abundant taxa, unless otherwise indicated, all analyses of species abundance data was performed using log transformed (ln x+1) values, as per the recommendations of Patterson et al. (2005). Because environmental data ranged several orders of magnitude across the six measured parameters, these data were standardized (subtraction of the mean followed by division by the standard deviation) for all analyses.

Box and whisker plots were produced based upon the Tukey method (interquartile range (IQR); whiskers = ± 1.5*IQR). Assemblages were initially identified using Q-mode cluster analysis, based upon Bray–Curtis dissimilarity ($BCij = \frac{2Cij}{Si+Sj}$) and unweighted paired-group average linking. Bray–Curtis dissimilarity (Bray and Curtis, 1957) has been used successfully to discriminate foraminifera assemblages in previous studies (e.g. Debenay and Payri,

2010; Narayan and Pandolfi, 2010). Analysis of similarities (ANOSIM), also using Bray–Curtis dissimilarity, was employed as a post-hoc test to establish whether proposed assemblages are significantly different from each other. Similarity percentage analysis (SIMPER) was used to identify which taxa contribute most to between-assemblage differences.

Diversity index calculations used only relative abundance data (i.e data was not log transformed prior to calculations). The calculated indices, Fisher-α, Shannon H, and Dominance (sample max p_i – the relative abundance of the most abundant taxon in that sample), were chosen following the recommendations of Hayek and Buzas (2013). The only exception is that Fisher-α is preferred herein to strict diversity, as it accounts for differing sample sizes (Hayward et al., 1999).

To assess the influence of the measured environmental parameters on assemblage/taxon distribution, canonical correspondence analysis (CCA) was used. Input for the CCA consisted of all species abundance data and environmental data. As an additional method to identify the influence of the measured environmental parameters on species distribution and diversity, stepwise multiple linear regression (SMLR), using a backward elimination model, was used. A backward elimination model starts with all independent predictor variables included in the model and variables are then eliminated using a chosen comparison criterion until combined explanatory power no longer increases or partial correlation coefficients become insignificant. For this study, the comparison criterion was akaike information criterion (AIC) scores. SMLR is considered a robust multivariate analysis technique as it reduces the likelihood of over-fitted data (Hair et al., 2009). A Shapiro–Wilk test confirmed that all data were normally distributed prior to analysis. The six measured environmental parameters were used as predictor variables and either species abundance data or diversity measures were the response variables. SMLR was performed for each taxon individually, but only for those taxa where overall relative abundance is greater than 5%. Generated models were only considered statistically significant where p-values indicated significance ($p < 0.05$), AIC Δi (the difference between initial and final AIC scores) was less than 10 (Burnham and Anderson, 2004), and the adjusted r^2 (r'^2) value was greater than 0.5 (Patterson et al., 2005). Non-linear functions were fitted for statistically significant models and their individual constituent predictors, where a valid model had more than one predictor, using CurveExpert 2.0.4 (http://curveexpert.webhop.biz). This program solves non-linear regressions using the Levenberg–Marquardt method and then automatically selects the best fitting function, based upon the strength of the correlation between observed values and the fitted curve.

Diversity index calculations, Q-mode cluster analysis, ANOSIM, and SIMPER were all performed using PAST 2.17c (Hammer et al., 2001). R 3.1.1 (R Development Core Team, 2010) was used to create box and whisker plots, to perform CCA (Oksanen et al., 2011) and to carry out SMLR (Venables and Ripley, 2002).

3. Results

3.1. Foraminifera diversity and distribution

Seventeen species of foraminifera were identified in Smiths Lake (Appendix B). Electron micrographs of representative foraminifera are displayed in Fig. 3. One new species was identified (*Pseudoclavulina skeletori* sp. nov.). A description of this taxon (and other selected taxa) is provided in Appendix C. All other species present throughout the lake are found in other estuaries along the New South Wales coastline (Albani, 1968a, 1968b, 1979; Yassini and Jones, 1989; Yassini and Jones, 1995; Cotter, 1996; List, 1996; Strotz, 2003, 2012; Schröder-Adams et al., 2014). Inner shelf taxa such as *Elphidium hispidulum* Cushman and *Cornuspira* sp. (Hayward et al., 1997, 1999) occur rarely (Appendix B) and no specimens of planktic species were found. Fisher-α, Shannon-H and dominance values, along with the mean values and standard deviation for these diversity measures are presented in Table 1. Values vary by an order of magnitude for Fisher-α ($\alpha_{max} = 3.56$, $\alpha_{min} = 0.35$) and by two orders of magnitude for Shannon-H, ($H_{max} = 1.85$; $H_{min} = 0.03$) throughout the lagoon. Dominance levels range between 27.51% and 99.56%. Generally, evenness and species richness are correlated; those sites with the lowest α values also have the highest levels of dominance.

Agglutinated taxa (those foraminifera with an arenaceous test composed of particles sourced from the surrounding sediment) make up just under 87% of the total biota. Four species: *Rhumblerella australis* (Collins) (34.87%); *Ammobaculites exiguus* Cushman and Brönnimann (19.88%); *Miliammina fusca* (Brady) (16.76%) and *Ammonia aoteana* (Finlay) (10.58%) make up approximately 82% of the biota. Of these four taxa, only *A. aoteana* has a calcium carbonate test. Two of these taxa (*M. fusca* and *A. exiguus*) possess test architectures that are subject to preferential destruction (Goldstein and Watkins, 1999). The high relative abundance of these two taxa suggests that taphonomic effects in Smiths Lake are negligible. Both *Simobaculites barwonensis* (Collins) (max $p_i = 51.33\%$) and *Elphidium excavatum clavatum* (Cushman) (max $p_i = 24.49\%$) are common at selected sites. All remaining taxa are rare. The relative abundance of individual species (both common and rare) is highly variable from site to site, resulting in low means and broad interquartile ranges for dominant taxa, and numerous outliers for all taxa (Fig. 4).

Based upon Q-mode cluster analysis, two assemblages are established, designated Assemblage 1 and Assemblage 2 (Fig. 5). ANOSIM indicates a statistically significant difference between these two assemblages (p-value = 0.0001). The spatial distribution of the two assemblages in the lagoon is presented in Fig. 6. SIMPER analysis identifies that *R. australis* (21.91%); *A. exiguus* (18.29%); *M. fusca* (Brady) (17.39%) and *A. aoteana* (11.66%) are the primary contributors to the dissimilarity between the two assemblages.

Assemblage 1 (A1) is confined to the deeper parts of the basin that makes up the western and central parts of the lagoon (Fig. 6). With the exception of SML11, all sites assigned to A1 are at locations where water depth is greater than 3 m and where sediments consist of fine silts and muds. The assemblage is dominated by two species, *R. australis* (mean relative abundance A1 = 79.38%) and *A. aoteana* (mean relative abundance A1 = 16.18%). Their combined relative abundance is never <73%. *Rhumblerella australis* is consistently the dominant of the two taxa, with a high median and relatively narrow IQR compared to its IQR for the lagoon overall (Fig. 4). Whilst 10 of the 17 species present in Smiths Lake occur at A1 sites, at almost half of A1 sites *R. australis* and *A. aoteana* are the only two species present, and at a number of sites the biota is virtually monospecific (relative abundance of *R. australis* > 95%). At selected A1 sites, other taxa may exceed 5% relative abundance, but mean relative abundance of all other taxa within A1 is <2%. Mean values for A1 Fisher-α and Shannon H are both less than the overall lagoon mean values ($\alpha_{A1mean} = 0.75$; $H_{A1mean} = 0.44$) and mean A1 dominance is essentially identical to the mean relative abundance of *R. australis* (A1 mean $P_i = 78.59\%$).

Assemblage 2 (A2) is concentrated in shallow areas around the edges of the western basin and the seaward part of the lagoon, east of Simons Point (Fig. 6). Sediments at these locations consist mostly of quartz sands. Like A1, two taxa dominate the assemblage, *A. exiguus* (36.86%) and *M. fusca* (23.95%). Neither of these two taxa is consistently dominant within A2, nor are they concentrated spatially. Whilst these two taxa have higher medians within A2

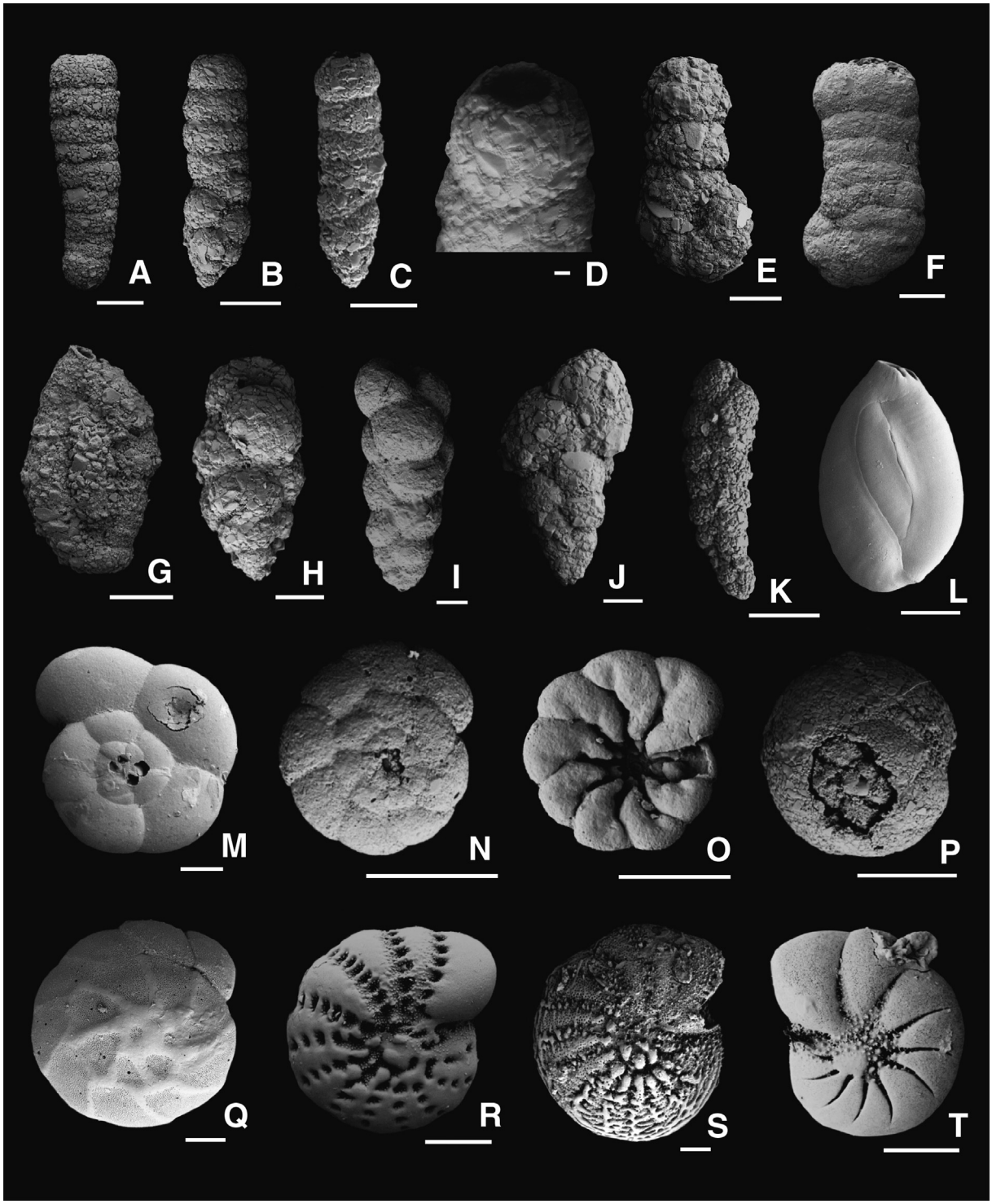

Fig. 3. Foraminifera from Smiths Lake. All scale bars equal 100 μm. A. *Scherochorella barwonensis* (Collins) B. *Pseudoclavulina skeletori* sp. nov. C. *Pseudoclavulina skeletori* sp. nov. D. *Pseudoclavulina skeletori* sp. nov. (aperture view) E. *Ammobaculites exiguus* Cushman and Bronnimann F. *Simobaculites barwonensis* Collins G. *Miliammina fusca* (Brady) H. *Rhumblerella australis* (Collins) I. *Rhumblerella australis* (Collins) J. *Textularia agglutinans* K. *Spiroplectammina earlandi* (Parker) L. *Quinqueloculina seminula* (Linnaeus) M. *Trochammina inflata* (Montagu) N. *Paratrochammina bartrami* (Hedley, Hurdle and Burdett) O. *Paratrochammina bartrami* (Hedley, Hurdle and Burdett) P. *Trochammina sp.* indet Q. *Ammonia aoteana* (Finlay) R. *Elphidium excavatum clavatum* (Cushman) S. *Elphidium hispidulum* (Cushman) T. *Haynesina depressula* (Walker and Jacob).

than for the lagoon overall, the IQR and whiskers for both taxa remains broad (Fig. 4). Other important constituents of the biota include *Scherochorella barwonensis* (13.6%) and *Simobaculites barwonensis* (7.18%). All remaining taxa are rare. Mean values for A2 Fisher-α and Shannon H are both greater than the overall lagoon mean value ($\alpha_{A2mean} = 1.71$; $H_{A2mean} = 1.2$). Mean A2 dominance is less than the overall lagoon average (A2 mean $P_i = 52.93\%$).

Two sites, SML26 and SML31 remain unassigned to either assemblage. The two sites bear little resemblance to other sites (~30% similarity – Fig. 5), and do not resemble each other. SML26 is

Table 1
Diversity indices for Smiths Lake: Fisher-α; Shannon H; Dominance (Max pi).

Site	α	H	Max p_i
SML1	1.71	1.19	43.00
SML2	2.05	1.09	57.33
SML3	1.40	1.08	57.67
SML4	1.40	1.22	53.46
SML5	1.40	1.13	49.74
SML7	2.77	1.52	46.33
SML8	1.71	1.22	58.16
SML9	0.35	0.61	69.67
SML10	0.83	0.68	65.34
SML11	2.05	0.92	73.00
SML12	0.83	0.30	93.33
SML13	1.40	0.43	91.26
SML14	0.83	0.74	74.13
SML15	0.58	0.08	98.67
SML16	1.40	1.28	40.69
SML17	0.58	0.08	98.66
SML18	0.35	0.26	92.67
SML19	0.35	0.57	74.00
SML20	0.58	0.71	58.00
SML21	0.58	0.51	82.34
SML22	2.77	1.79	27.51
SML23	0.35	0.16	96.33
SML24	1.11	0.55	86.66
SML25	3.56	1.81	33.56
SML26	0.58	0.42	88.37
SML27	0.83	0.84	53.00
SML28	0.83	0.53	85.33
SML29	2.77	1.85	33.33
SML30	1.11	0.81	72.32
SML31	0.35	0.03	99.56
SML32	1.11	1.25	51.33
SML33	1.40	0.98	62.98
Mean	1.25	0.83	67.74
StDev	0.83	0.51	21.42

located proximal to the barrier beach. Only 43 specimens were recovered from SML26 and almost all of these are *Paratrochammina bartrami* Hedley, Hurdle and Burdett (relative abundance = 88.37%). Whilst a site with so few specimens often would be removed from q-mode cluster analysis, its removal was found to have no effect on the dendrogram, so it was retained for completeness. SML31 is located on the northern edge of Symes Bay. The SML31 biota is virtually monospecific, composed almost entirely of *M. fusca* (99.56%).

3.2. CCA and SMLR

For CCA, the total inertia (sum total of all unconstrained eigenvalues) is 1.795, with the sum of all constrained eigenvalues = 0.634. Thus, the environmental factors included explain 35.32% of the variation in the dataset. Eigenvalues for axis 1 (0.327) and axis 2 (0.139) explain 18% and 8% of the total variation respectively, and 74% of the variation explained by the included environmental factors. The species–environment correlations of axis 1 and 2 is evidence supporting an association between the species and environmental matrices (axis 1 = 0.88; axis 2 = 0.71). Ordination of the CCA constrained by measured environmental factors is presented for sample sites in Fig. 7A, and for species in Fig. 7B.

CCA results indicate sites assigned to A1 are strongly and positively associated with water depth (high axis 1 values – Fig 7A). Sites assigned to A2 are generally negatively associated with water depth (negative values on Axis 1) and positively with temperature. Whilst individual A2 sites may correlate positively with the remaining environmental factors, no other factors can be correlated

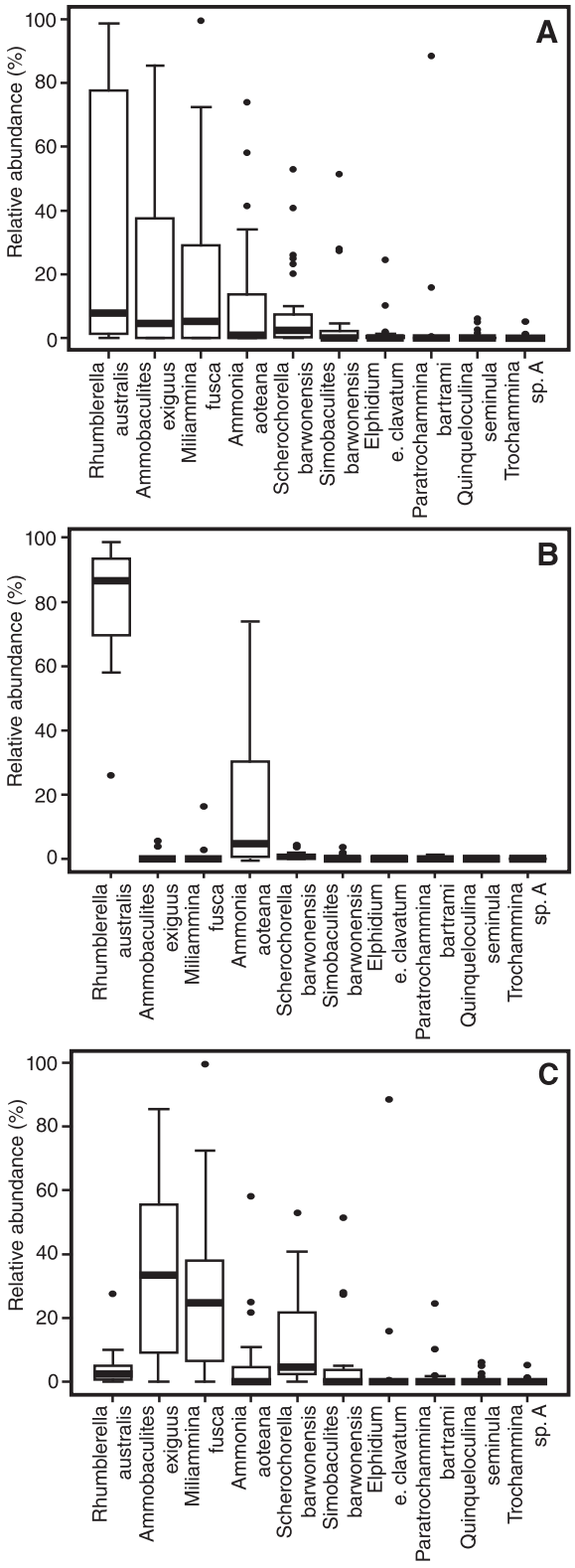

Fig. 4. Box plots for: A. Total assemblage; B. Assemblage 1; C. Assemblage 2. Assemblages are based upon q-mode cluster analysis (Fig. 5). Only taxa with a relative abundace of >5% at 1 or more sites are included in these plots.

with the assemblage as a whole. Species associated with deeper water include *R. australis*, *A. aoteana* and *E. excavatum clavatum* (Fig. 7B). *Simobaculites barwonensis* is associated with increasing

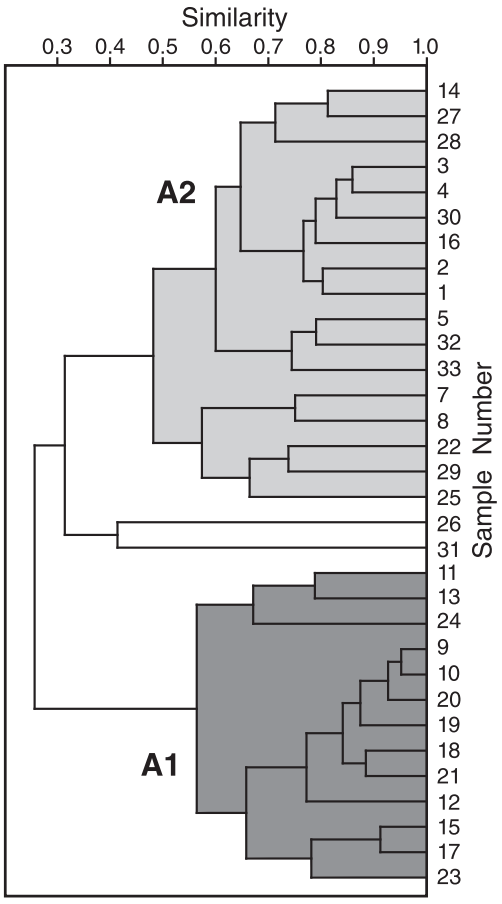

Fig. 5. Q-mode cluster analysis dendrogram for Smiths Lake based upon Bray–Curtis similarity index. Assemblage 1 (A1) in dark grey, Assemblage 2 (A2) in light grey.

pH. *Quinqueloculina seminula* is not correlated with any of the included environmental factors. All other species with a relative abundance >5% at one or more sites are correlated with shallow water and increasing temperature.

SMLR confirms that the majority of relationships between species and included environmental factors are not statistically significant (Table 2). Only two associations meet the requirements to be considered valid correlations. *Rhumblerella australis* is correlated with both depth (increasing) and dissolved oxygen (decreasing). *Miliammina fusca* is correlated with decreasing depth. CurveExpert identified a rational function ($y = \frac{a+bx}{1+cx+dx^2}$) as the best fitted result for all valid correlations (Fig. 8). The correlation between observed values and the fitted rational function for *R. australis* is 0.606 and for *M. fusca* is 0.801. If only depth is considered in comparison to the proportion of *R. australis*, the goodness-of-fit increases (0.874), and where only dissolved oxygen is considered, the goodness-of-fit is 0.399.

4. Discussion

The foraminifera assemblage from Smiths Lake is broadly similar to that found in open estuaries (those permanently or frequently connected to the open ocean), despite the distinct physio-chemical conditions present in ICOLLs (Roy et al., 2001). The dominance of agglutinated taxa and *Ammonia* in Smiths Lake is consistent with many previously described foraminifera assemblages from open estuarine systems in both Australia (e.g. Albani, 1968a; 1968b, 1979; Yassini and Jones, 1989; Yassini and Jones, 1995; Cotter, 1996; Strotz, 2003, 2012; Nash et al., 2010; Strotz, 2012) and internationally (e.g. Scott et al., 1980; Goldstein, 1988; Patterson, 1990; Hayward et al., 1999; Murray, 2013). The high relative abundance of a small number of taxa, irrespective of overall diversity, is consistent with previous estuarine foraminifera studies (Murray, 2013). The spatial distribution of the two assemblages within the lagoon, with a duospecific assemblage in deeper water and a more diverse shallow water assemblage, is consistent with previous studies (Strotz, 2012). Depth (and the environmental parameters associated with depth) as an important control on the distribution of both foraminifera assemblages and the abundance of key taxa that dominate the overall assemblage is consistent with previous studies (e.g. Haynes, 1981; Cann et al., 1988; Hayward et al., 1999). This all would seem to suggest there is little that is distinct about ICOLL foraminifera assemblages compared with typical estuarine assemblages.

Distinct differences do exist between Smiths Lake and open estuaries of similar size when comparing species richness. Whilst species richness, for all biota, is generally lower in estuarine settings when compared with coastal and oceanic environments (Day et al., 1989; Attrill and Rundle, 2002), species richness in Smiths Lake is considerably less than previous studies of estuarine foraminifera from open coastal lagoons (Phelger, 1965; Debenay et al., 2001; Revets, 2000; Albani et al., 2007) and other estuary types (e.g. Murray, 1968; Alve and Murray, 1999; Hayward et al., 1999; Sen Gupta, 1999; Murray, 2006; Culver et al., 2012), where sometimes 100 + taxa have been recorded for a single estuary. This is not a regional issue, as nearby open estuaries have much higher foraminifera species richness than Smiths Lake (Albani, 1968b, 1979; Yassini and Jones, 1989; Strotz, 2012). By contrast, levels of foraminifera species richness found in closed coastal lagoons and previously studied ICOLLs are similar to Smiths Lake (Cearreta et al., 2002; Strotz, 2003; Frontalini et al., 2010). Comparatively low levels of species richness have been recorded for ICOLL macrofaunas as well (Dye and Barros, 2005).

Smiths Lake lacks the diverse, predominantly calcareous foraminifera assemblage that commonly occurs in the most seaward part of estuarine systems, where oceanic influence (and salinity) is greatest. This assemblage is characteristically a concentration of much of the foraminifera species richness for an estuary (Yassini and Jones, 1989; Strotz, 2012). In fact, few foraminifera of any kind are found on the flood-tide delta immediately adjacent to the barrier, where the diverse calcareous assemblage would be expected to occur. The lack of specimens on the delta may be because this is the only area of Smiths Lake subject to notable sediment transport (Gale et al., 2011). However, the complete absence of a diverse calcareous seaward assemblage, as well as the reduced species richness and lack of calcareous taxa throughout the lagoon (<13% of total assemblage), is more likely due to limited exchange with the open ocean and the associated reduction in salinity (Fig. 2). Increasing isolation from open ocean conditions has been demonstrated to alter the structure of benthic assemblages, leading to a decrease in diversity and changes in species dominance (Teske and Wooldridge, 2001; Dye and Barros, 2005; Nash et al., 2010). ICOLL Biological communities are euryhaline, due to the fluctuations in salinity associated with alternation between 'open' and 'closed' phases (Haines et al., 2006). Euryhaline communities are generally lower in diversity than equivalent open estuary euryhaline/stenohaline communities or stenohaline marine communities (Whitfield et al., 2012), and are typically comprised of fewer species in higher abundance (Haines et al., 2006). Both of these observations are consistent with the foraminifera assemblage from Smiths Lake.

Results for CCA indicate that 35.32% of the variation in species

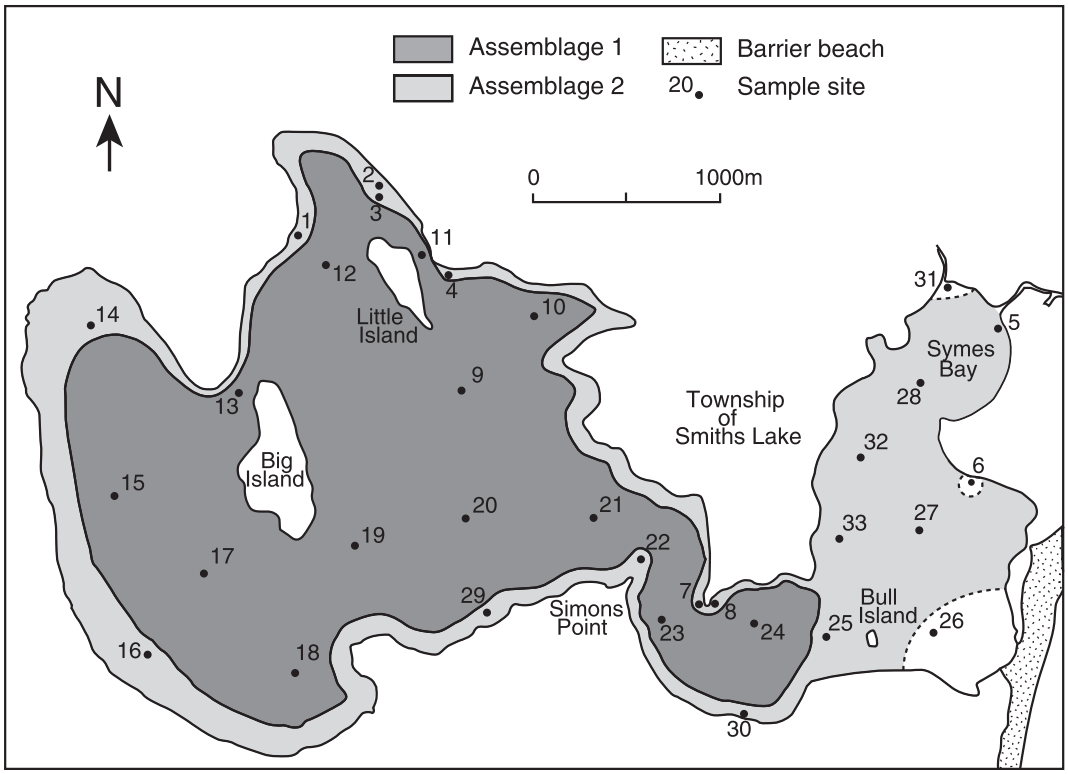

Fig. 6. Distribution of assemblages identified by q-mode cluster analysis in Smiths Lake. In areas where no sample has been collected, extrapolation of assemblage is based upon the nature of the physical environment and composition of the biota at the nearest sample site. Assemblage 1 in dark grey. Assemblage 2 in light grey. Dashed lines used to indicate areas not assigned to either assemblage.

abundance is explained by the measured environmental variables. This result is consistent with other studies that utilised similar methods (Cleary and Renema, 2007). This means that only approximately one third of the variation is explained by environmental parameters that have been previously been identified as either significant controls on species abundance (e.g. Murray, 1973; Boltovskoy and Wright, 1976; Haynes, 1981; Boltovskoy et al., 1991; Murray, 2001; Strotz, 2012) or proxies for significant controls (Bell and Edwards, 1980; Murray, 2006). At least some of the unexplained variation can likely be attributed to biotic interactions, including food availability, predator frequency and parasites (Cleary and Renema, 2007). Even though the measured environmental parameters are mean values, the measurements used in the analysis still represent a limited period of time, and some of the unexplained variation may be due to taxa responding to longer term fluctuations in these parameters. The inability to relate rare species to environmental parameters (due to a lack of statistical power) is also likely a factor. Previous work indicates that some component of local recruitment and survivorship of species, and thus relative abundance, is inherently stochastic (Newbery et al., 1996; Nekola and White, 1999). These explanations also likely account for why only two taxa yield statistically valid models through SMLR.

Despite the moderate level of explanatory power, CCA does suggest depth as an important control on species and assemblage distribution in Smiths Lake (Fig. 7). The results of SMLR also establish depth as an important control on abundance of *M. fusca* and of *R. australis* in Smiths Lake (Table 2). Depth as an ecological control on assemblage distribution is consistent with previous studies of estuarine foraminifera (Hayward et al., 1999; Strotz, 2012), but the lack of correlation with all other measured hydrological parameters, particularly salinity, is not. In open estuaries, the distinct horizontal salinity gradient (with salinity generally decreasing away from the estuary mouth) results in noticeable changes in foraminifera assemblage composition across the estuary (Yassini and Jones, 1995; Murray, 2006; Quilty and Hosie, 2006; Strotz, 2012). The lack of correlation with parameters other than depth in Smiths Lake is perhaps expected, given Smiths Lake is well mixed when closed off from the ocean (Gale et al., 2011), with little difference in the measured hydrological parameters across the lagoon (Fig. 2).

It is important to note that depth is a proxy for a collection of abiotic and biotic parameters and is unlikely to be strictly a control in and of itself (Hayward et al., 1999). Parameters represented by depth include water movement, sediment grain size, light penetration, organic matter (Murray, 2006) and vegetation cover (Bell and Edwards, 1980). Sediment grain size and organic matter are likely the most important of these in Smiths Lake. This is because the other parameters controlled by depth are largely inapplicable in Smiths Lake. Water movement is limited and episodic, only occurring during open phases (3 months out of every 18 months). Entrainment of sediment by water movement only occurs around the flood-tide delta, meaning water movement would have little impact on Assemblage 1 or 2. High water clarity (Roper et al., 2011) allows light to penetrate to the deepest parts of the lagoon. Aquatic macrophytes are broadly distributed throughout all parts of the lake (Robinson et al., 1983) and are found down to depths of ~4 m.

Sediment grain size has been previously identified as a primary control on foraminifera species richness and abundance in estuarine environments (Armynot du Châtelet et al., 2009). Results for Smiths Lake further reinforce the importance of grain size, with Assemblage 1 and 2 both restricted to different sediment types. Assemblage 1 is found exclusively on fine silts and muds. Assemblage 2 is found where sediments consist of quartz sands (with the exception of SML28, which is discussed below). Previous work has

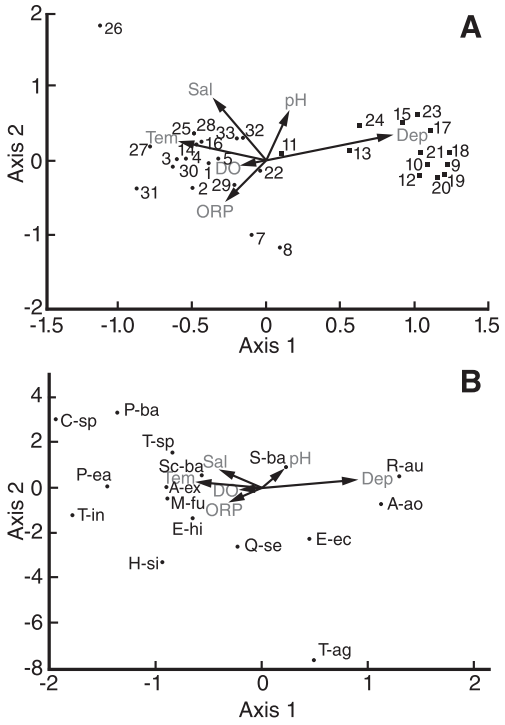

Fig. 7. Ordination based upon CCA for: A. sample sites; B. species. 1st and 2nd axis illustrated. Assemblage 1 sites indicated by solid squares. Assemblage 2 sites indicated by solid circles. Arrows represent measured environmental parameters. Dep – Depth; ORP – Oxidation Reduction Potential; DO – Dissolved Oxygen; Tem – Temperature; Sal – Salinity. Abbreviations for species: A-ao – *Ammonia aoteana*; A-ex – *Ammobaculites exiguus*; C-sp – *Cornuspira* sp.; E-ec – Elphidium *excavatum clavatum*; E-hi – *Elphidium hispidulum*; H-si – *Haynesina simplex*; M-fu – *Miliammina fusca*; P-ba – *Paratrochammina bartrami*; P-ea – *Palustrella earlandi*; Q-se – *Quinqueloculina seminula*; R-au – *Rhumblerella australis*; S-ba – *Simobaculites barwonensis*; Sc-ba – *Scherochorella barwonensis*; T-ag – *Textularia agglutinans*; T-in – *Trochammina inflata*; T-sp. – *Trochammina* sp.

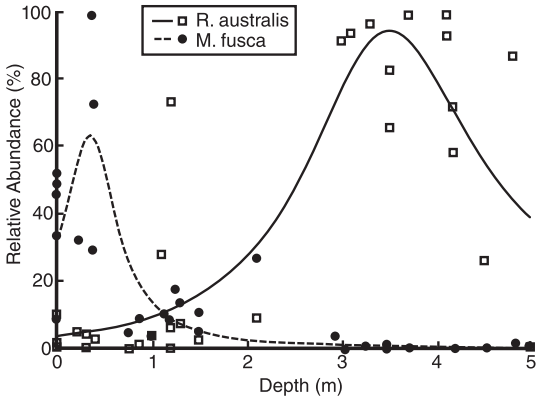

Fig. 8. Relationship between abundance and depth for two taxa where SMLR indicates a significant relationship. Lines represent fits to observed data based upon a rational function.

identified a link between grain size and diversity, but results are somewhat contradictory. Some studies demonstrate decreasing foraminifera diversity (Debenay et al., 2001; Armynot du Châtelet et al., 2009) with increasing grain size, whilst in others the opposite is true (Diz et al., 2004). Smiths Lake parallels the results of Diz et al. (2004) with diversity higher for Assemblage 2.

Like grain size, previous studies have noted a link between foraminifera distribution and nutrient supply (in the form of organic matter), but with conflicting results. Increased species richness has been associated with both low (Setty, 1976; Schafer et al., 1991, 1995; Armynot du Châtelet et al., 2004) and high (Bandy et al., 1964a, 1964b, 1965; Cearreta, 1988; Debenay et al., 2001) levels of organic matter. More recently Armynot du Châtelet et al. (2009) attempted to resolve this inconsistency and identified decreasing species richness with increasing organic matter. In Smiths Lake, nutrient supply increases marginally with depth (Everett et al., 2007 unpublished results). Thus, the results for Smiths Lake align with the findings of Armynot du Châtelet et al. (2009), as species richness for Assemblage 1, located in the deepest parts of the lagoon, is lower than for Assemblage 2. Because Smiths Lake is considered predominately oligotrophic, (Smith and Heggie, 2003) overall species richness should be higher than comparable systems where organic matter is high. As species richness is much lower than nearby eutrophic, but open, estuaries (Yassini and Jones, 1989; Strotz, 2012) this further reinforces the importance of limited exchange with the open ocean as a control on species richness in Smiths Lake.

The fitted rational function indicates peak abundance at specific depths for both *M. fusca* and *R. australis* (Fig. 8). The correlation is not 100% (goodness-of-fit <1.0) meaning environmental factors associated with depth are an important, but not exclusive control for either species. For example, at SML31, the high relative abundance of *M. fusca* (Appendix B) is likely due to the close proximity of an unnamed creek and the associated freshwater input from that

Table 2
Results of stepwise multiple linear regression (SMLR) for taxa with overall relative abundance >5% and diversity indicies. Predictor variables are measured environmental parameters. D – Depth; S – Salinity; DO – Dissolved Oxygen; T – Temperature; ORP – Oxidation reduction potential. FO (%) is the frequency of occurrence and represents the percentage of sampled sites where that taxon was found. Species in bold represent statistically significant correlations.

Taxon	FO (%)	Predictors	p-value	AIC Δi	R-Sq	Adj. R-Sq
Ammobaculites exiguus	59.4	D + S + DO + pH	0.0002	1.91	0.54	0.47
Ammonia aoteana	59.4	S	0.007	6.58	0.22	0.19
Elphidium excavatum clavatum	31.3	D + S	0.0002	5.85	0.44	0.4
Elphidium hispidulum	18.8	pH + T	0.003	4.95	0.33	0.28
Miliammina fusca	**68.8**	**D**	**1E-11**	**9.18**	**0.78**	**0.78**
Palustrella earlandi	25.0	S + pH + ORP + T	0.02	2.23	0.33	0.23
Paratrochammina bartrami	12.5	ORP + T	0.03	7.36	0.21	0.15
Quinqueloculina seminula	12.5	D + T	0.002	7.29	0.34	0.3
Rhumblerella australis	**87.5**	**D + DO**	**2E−08**	**4.29**	**0.7**	**0.68**
Scherochorella barwonensis	75.0	D + S + DO + pH	0.001	2.04	0.48	0.4
Trochammina inflata	12.5	ORP	0.02	6.54	0.16	0.13
Fisher α	NA	D + pH	0.0002	7.07	0.45	0.41
Shannon H	NA	D + pH	0.0002	7.01	0.45	0.41
Dominance	NA	D + pH	0.001	6.32	0.37	0.32

creek, as *M. fusca* has been shown to be tolerant of low salinity (Hayward et al., 1999). The peak abundance results associated with depth are significant however, as it means both taxa can be used as proxies for palaeo-depth in the sedimentary record. For *M. fusca*, peak depth is approximately 0.4 m, and below 3 m almost no *M. fusca* is found. *Miliammina fusca* is a common constitutent of shallow-water/marsh biotas around the globe (e.g. Jennings and Nelson, 1992; Scott et al., 1996; Hayward et al., 1999; Sen Gupta, 1999) and previous studies have identified peak abundance at a similar depth to this study (Horton, 1999; Wang and Chappell, 2001; Horton et al., 2003). For *R. australis*, peak depth is approximately 3.5 m. *Rhumblerella australis* has been previously reported from a range of settings, from estuaries and coastal lagoons to the continental shelf (Loeblich and Tappan, 1994; Yassini and Jones, 1995; Schröder-Adams et al., 2014). This indicates that *R. australis* must be able to persist at greater depths than identified in this study. The peak depth of 3.5 m is therefore best thought of as the lower bound of *R. australis*' peak depth. Results of SMLR indicate that dissolved oxygen is also an important control on *R. australis* abundance. Whilst the goodness-of-fit for the best fitting function (rational) is poor (0.399), site SML28 (Fig. 1) reveals a potential dissolved oxygen threshold for *R. australis*. Located at the deepest part of the lagoon (5 m depth), SML28 is typical, in terms of environment, of sites assigned to Assemblage 1. *Rhumblerella australis* is absent from the site however (Appendix B), and the site is assigned to A2 due to the high relative abundance of *A. exiguus* ($P_i = 85.33\%$). Dissolved oxygen levels at SML28 are lower than anywhere else in the lagoon (Fig. 2). Dissolved oxygen tolerance levels for *R. australis* have not been previously published, but the lack of *R. australis* at SML28 indicates that this taxon cannot tolerate levels as low as 1.67 mg/L. Although SMLR does not conclusively demonstrate correlation between any of the measured environmental parameters and abundance of *A. exiguus*, the high abundance of *A. exiguus* at SML28 indicates that it is tolerant of low oxygen conditions. Previous work has identified *A. exiguus* is able thrive in a wide variety of environments, including those where oxygen levels are low (Hayward and Hollis, 1994; Hayward et al., 1999)

5. Conclusions

The foraminifera assemblage found in Smiths Lake and the foraminifera assemblage found in open estuaries are broadly similar. At the same time, differences are identified, highlighting the importance that reduced salinity levels have in structuring the biota. These differences include:

a) Lower species richness than comparable open estuarine systems, even when compared with open systems that are eutrophic.
b) A lack of calcareous taxa, including the 'high' diversity calcareous assemblage in the seaward part of the estuary observed in open estuarine systems.
c) Whilst salinity is an important limiting factor on the overall assemblage composition, parameters associated with depth (sediment grain size and nutrient supply) are the most significant controls on both assemblage distribution within the lagoon and the distribution of the most common taxa.
d) Whilst abiotic environmental parameters previously identified as controls on foraminifera species distribution are important, biotic controls and stochastic processes also play a significant role.

Given that Smiths Lake is one of the best available representatives of an archetypal ICOLL, these characteristics are proposed as typical of an ICOLL foraminifera community. Individually none of these characteristics are exclusive to ICOLLs, but combined they are distinct from a typical open estuary foraminifera assemblage.

The palaeoecological interpretation of fossil foraminifera biotas, and using these interpretations to interpret the relative health of marginal marine systems, is dependent upon our understanding of the ecological processes that influence extant foraminifera communities. These results for Smiths Lake are an important component of that understanding, both expanding our knowledge of foraminifera ecology from a rarely studied environmental setting and providing new baseline data that can be used to reconstruct historical trends in ICOLLs and other marginal marine systems.

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Appendices. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2015.07.048.

References

Albani, A.D., 1968a. Recent Foraminiferida from Port Hacking, new South Wales. Contributions Cushman Found. Foraminifer. Res. 19, 85–119.
Albani, A.D., 1968b. Recent Foraminiferida of the Central Coast of New South Wales, vol. 1. Australian Marine Sciences Association, p. 37.
Albani, A.D., 1979. Recent Shallow Water Foraminiferida from New South Wales, vol. 3. Australian Marine Sciences Association, p. 57.
Albani, A., Barbero, R.S., Donnici, S., 2007. Foraminifera as ecological indicators in the Lagoon of Venice, Italy. Ecol. Indic. 7, 239–253.
Albani, A.D., Johnson, K.R., 1976. Resolution of foraminiferal biotopes in Broken Bay, New South Wales. J. Geol. Soc. Aust. 22, 435–446.
Alve, E., Murray, J.W., 1999. Marginal marine environments of the Skagerrak and Kattegat: a baseline study of living (stained) benthic foraminiferal ecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 146, 171–193.
Apthorpe, M., 1980. Foraminiferal distribution in the estuarine Gippsland lakes system, Victoria. Proc. R. Soc. Vic. 91, 207–232.
Armynot du Chatelet, E., Debenay, J.P., Soulard, R., 2004. Foraminiferal proxies for pollution monitoring in moderately polluted harbors. Environ. Pollut. 127, 27–40.
Armynot du Chatelet, E., Bout-Roumazeilles, V., Riboulleau, A., Trentesaux, A., 2009. Sediment (grain size and clay mineralogy) and organic matter quality control on living benthic foraminifera. Rev. micropaléontologie 52, 75–84.
Attrill, M.J., Rundle, S.D., 2002. Ecotone or Ecocline: ecological Boundaries in estuaries. Estuar. Coast. Shelf Sci. 55, 929–936.
Bandy, O.L., Ingle, J.C., Resig, J.M., 1964a. Foraminifera, Los Angeles county outfall area, California. Limnol. Oceanogr. 9, 124–137.
Bandy, O.L., Ingle, J.C., Resig, J.M., 1964b. Foraminiferal trends, Laguna Beach outfall area, California. Limnol. Oceanogr. 9, 112–123.
Bandy, O.L., Ingle, J.C., Resig, J.M., 1965. Foraminiferal trends, Hyperion outfall, California. Limnol. Oceanogr. 10, 314–332.
Bell, F.C., Edwards, A.R., 1980. An Environmental Inventory of Estuaries and Coastal Lagoons in New South Wales. Total Environment Centre, Sydney, p. 187.
Bell, K.N., 1978. Recent foraminifera from Limeburners Bay, Victoria. Vic. Nat. 95, 133–136.
Bell, K.N., 1995. Foraminiferans from Lake Connewarre, Victoria. Vic. Nat. 122, 228–233.
Bell, K.N., 1996. Foraminiferan faunas of the Tamar River and Port Dalrymple, Tasmania: a preliminary survey. Rec. Queen Vic. Mus. 102, 1–25.
Bell, K.N., Drury, S.R., 1992. The foraminiferal fauna of Mallacoota inlet, east Gippsland, Victoria. Vic. Nat. 109, 7–16.
Bird, E.C.F., 1967. Depositional Features in estuaries and lagoons on the south coast of new South Wales. Aust. Geogr. Stud. 5, 113–124.
Boltovskoy, E., Wright, R., 1976. Recent Foraminifera. Junk, The Hague, p. 515.
Boltovskoy, E., Scott, D.B., Medioli, F.S., 1991. Morphological variations of benthic foraminiferal tests in response to changes in ecological parameters: a review. J. Paleontology 65, 175–185.
Boyd, R., Dalrymple, R., Zaitlin, B.A., 1992. Classification of clastic coastal depositional environments. Sediment. Geol. 80, 139–150.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325–349.
Bucher, D., Saenger, P., 1991. An Inventory of australian estuaries and Enclosed Marine waters: an Overview of results. Aust. Geogr. Stud. 29, 370–381.
Burnham, K.P., Anderson, D.R., 2004. Multimodel Inference: understanding AIC and BIC in model Selection. Sociol. Methods Res. 33, 261–304.
Callard, S.L., Gehrels, W.R., Morrison, B.V., Grenfell, H.R., 2011. Suitability of salt-marsh foraminifera as proxy indicators of sea level in Tasmania. Mar. Micropaleontol. 79, 121–131.
Cann, J.H., Bourman, R.P., Barnett, E.J., 2000. Holocene foraminifera as indicators of relative estuarine-lagoonal and oceanic influences in estuarine sediments of the River Murray, South Australia. Quatern. Res. 53, 378–391.
Cann, J.H., Belperio, A.P., Gostin, V.A., Murray-Wallace, C.V., 1988. Sea-level history, 45,000 to 30,000 yr BP, inferred from benthic foraminifera, Gulf St. Vincent, South Australia. Quatern. Res. 29, 153–175.
Cearreta, A., 1988. Distribution and ecology of benthic foraminifera in the Santona estuary. Spain. Rev. Espanola Paleontol. 3, 23–38.
Cearreta, A., Alday, M., Conceicao, F.M., Andrade, C., Cruces, A., 2002. Modern foraminiferal record of alternating open and restricted environmental conditions in the Santo Andre lagoon, SW Portugal. Hydrobiologia 475, 21–27.
Clarke, J.D.A., Bone, Y., Cann, J.H., Davies, M., Macphail, M.K., Wells, F., 2001. Post-glacial biota from the inner part of southwest Joseph Bonaparte Gulf. Aust. J. Earth Sci. 48, 63–79.
Cleary, D.F.R., Renema, W., 2007. Relating species traits of Foraminifera to environmental variables in the Spermonde Archipelago, Indonesia. Mar. Ecol. Prog. Ser. 334, 73–82.
Collins, A.C., 1974. Port Phillip Survey 1957–1963 Foraminiferida. Memoirs of the National Museum of Victoria 35, 1–62.
Cotter, K.L., 1996. Benthic foraminiferal assemblages in the Clyde River estuary, Batemans Bay, NSW. Proc. Linn. Soc. N. S. W. 116, 193–208.
Culver, S.J., Mallinson, D.J., Corbett, D.R., Leorri, E., Rouf, A.A., Shazili, N.A.M., Yaacob, R., Whittaker, J.E., Buzas, M.A., Parham, P.R., 2012. Distribution of foraminifera in the Seitu estuary and lagoon, Terengganu, Malaysia. J. Foraminifer. Res. 42, 109–133.
Day, J.W., Hall, C.A.S., Kemp, W.M., Yanez-Arancibia, A., 1989. Estuarine Ecology. John Wiley and Sons, New York, p. 576.
Debenay, J.P., Payri, C.E., 2010. Epiphytic foraminiferal assemblages on macroalgae in reefal environments of New Caledonia. J. Foraminifer. Res. 40, 36–60.
Debenay, J.-P., Guillou, J.-J., Redois, F., Geslin, E., 2000. Distribution trends of foraminiferal assemblages in Paralic environments. Environ. Micropaleontol. 15, 39–67. Springer US.
Debenay, J.-P., Geslin, E., Eichler, B.B., Duleba, W., Sylvestre, F., Eichler, P., 2001. Foraminiferal assemblages in a hypersaline lagoon, Araruama (RJ) Brazil. J. Foraminifer. Res. 31, 133–151.
Diz, P., Francés, G., Costas, S., Souto, C., Alejo, I., 2004. Distribution of benthic foraminifera in coarse sediment, Ría de Vigo, NW Iberian margin. J. Foraminifer. Res. 34, 258–275.
Dye, A.H., 2005. Meiobenthos in intermittently open/closed coastal lakes in New South Wales: spatial and temporal patterns in densities of major taxa. Mar. Freshw. Res. 56, 1055–1067.
Dye, A.H., Barros, F., 2005. Spatial patterns of macrofaunal assemblages in intermittently closed/open coastal lakes in New South Wales, Australia. Estuar. Coast. Shelf Sci. 64, 357–371.
Elwany, M.H.S., Flick, R., Aijaz, S., 1998. Opening and closure of a marginal Southern California lagoon inlet. Estuaries 21, 246–254.
Everett, J.D., Baird, M.E., Suthers, I.M., 2007. Nutrient and plankton dynamics in an intermittently closed/open lagoon, Smiths Lake, south-eastern Australia: an ecological model. Estuar. Coast. Shelf Sci. 72, 690–702.
Froneman, P.W., 2004. Food web dynamics in a temperate temporarily open/closed estuary (South Africa). Estuar. Coast. Shelf Sci. 59, 87–95.
Frontalini, F., Coccioni, R., Bucci, C., 2010. Benthic foraminiferal assemblages and trace element contents from the lagoons of Orbetello and Lesina. Environ. Monit. Assess. 170, 245–260.
Gale, E., Pattiaratchi, C., Ranasinghe, R., 2006. Vertical mixing processes in Intermittently Closed and Open Lakes and Lagoons, and the dissolved oxygen response. Estuar. Coast. Shelf Sci. 69, 205–216.
Gale, E., Ward, M., Haines, P., 2011. Coastal Zone Management Plan for Smiths Lake Estuary. BMT WBM Report for Great Lakes Council, New South Wales, Australia, p. 102.
Goldstein, S.T., 1988. Foraminifera of relict salt marsh deposits, St. Catherines Island, Georgia: taphonomic implications. Palaios 3, 327–334.
Goldstein, S.T., Watkins, G.T., 1999. Taphonomy of salt marsh foraminifera: an example from coastal Georgia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 149, 103–114.
Haines, P.E., Tomlinson, R.B., Thom, B.G., 2006. Morphometric assessment of intermittently open/closed coastal lagoons in New South Wales, Australia. Estuar. Coast. Shelf Sci. 67, 321–332.
Hair, J.F., Anderson, R.E., Tatham, R.L., Black, W.C., 2009. Multivariate Data Analysis, seventh ed. Prentice Hall, Upper Saddle River, p. 816.
Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological Statistics software package for education and data analysis. Palaeontol. Electron. 4, 9.
Harris, P.T., Heap, A.D., Bryce, S.M., Porter-Smith, R., Ryan, D.A., Heggie, D.T., 2002. Classification of Australian clastic coastal depositional environments based upon a quantitative analysis of wave, tidal, and river power. J. Sediment. Res. 72, 858–870.
Haslett, S.K., 2001. The palaeoenvironmental implications of the distribution of intertidal foraminifera in a tropical Australian estuary: a reconnaissance study. Aust. Geogr. Stud. 39, 67–74.
Haslett, S.K., 2007. The distribution of foraminifera in surface sediments of the Clyde River Estuary and Bateman's Bay (New South Wales, Australia). Rev. Española Micropaleontol. 39, 63–70.
Haslett, S.K., Davies-Burrows, R., Panayotou, K., Jones, B.G., Woodroffe, C.D., 2010. Holocene evolution of the Minnamurra River estuary, southeast Australia: foraminiferal evidence. Z. für Geomorphol. 54 (Suppl. 3), 79–98.
Hayek, L.-A.C., Buzas, M.A., 2013. On the proper and efficient use of diversity measures with individual field samples. J. Foraminifer. Res. 43, 305–313.
Haynes, J.R., 1981. Foraminifera. Macmillan Publishing, London, p. 433.
Hayward, B.W., 1982. Associations of benthic foraminifera (Protozoa: Sarcodina) of inner shelf sediments around the Cavalli Islands, north-east New Zealand. N. Z. J. Mar. Freshw. Res. 16, 27–56.
Hayward, B.W., Hollis, C.J., 1994. Brackish foraminifera in New Zealand: a taxonomic and ecologic review. Micropaleontology 40, 185–222.
Hayward, B.W., Hollis, C.J., Grenfell, H.R., 1997. Recent Elphidiidae (Foraminiferida) of the South-west Pacific and Fossil Elphidiidae of New Zealand, vol. 16. Institute of Geological and Nuclear Sciences, Lower Hutt, p. 166.
Hayward, B.W., Grenfell, H.R., Reid, C.M., Hayward, K.A., 1999. Recent New Zealand shallow-water benthic foraminifera: taxonomy, ecologic distribution, biogeography, and use in paleoenvironmental assessment. Inst. Geol. Nucl. Sci. Monogr. 21, 1–258.
Horton, B.P., 1999. The distribution of contemporary intertidal foraminifera at Cowpen Marsh, Tees Estuary, UK: implications for studies of Holocene sea-level changes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 149, 127–149.
Horton, B.P., Larcombe, P., Woodroffe, S.A., Whittaker, J.E., Wright, M.R., Wynn, C., 2003. Contemporary foraminiferal distributions of a mangrove environment, Great Barrier Reef coastline, Australia: implications for sea-level reconstructions. Mar. Geol. 198, 225–243.
Jennings, A.E., Nelson, A.R., 1992. Foraminiferal assemblage zones in Oregon tidal marshes; relation to marsh floral zones and sea level. J. Foraminifer. Res. 22, 13–29.
Johnson, K.R., Albani, A.D., 1973. Biotopes of recent benthonic foraminifera in Pitt water, Broken Bay, N.S.W. (Australia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 14, 265–276.
Jones, M.V., West, R.J., 2005. Spatial and temporal variability of seagrass fishes in intermittently closed and open coastal lakes in southeastern Australia. Estuar. Coast. Shelf Sci. 64, 277–288.
Kirk, R.M., Lauder, G.A., 2000. Significant Coastal Lagoon Systems in the South Island, New Zealand: Coastal Processes and Lagoon Mouth Closure, vol. 146. Dept. of Conservation, p. 47.
Lankford, R.R., 1976. Coastal lagoons of Mexico, their origin and classification. In: Wiley, M. (Ed.), Estuarine Processes. Academic Press, New York, pp. 188–215.
Loeblich, J., Tappan, H., 1994. Foraminifera of the Sahul shelf and Timor sea. Cushman foundation for foraminiferal research. Spec. Publ. 31, 1–663.
List, K., 1996. Relationships between Sediment Type and the Recent Benthic Foraminifera of Lake Conjola. Centre for Marine Science, Technical Contribution, NSW, Australia, pp. 1–34.
Mckenzie, K.G., 1962. A record of foraminifera from Oyster Harbour near Albany, Western Australia. J. R. Soc. West. Aust. 45, 117–132.
Michie, M.G., 1987. Distribution of foraminifera in a macrotidal tropical estuary: Port Darwin, Northern Territory of Australia. Australian Journal of Marine and Freshwater Research 38, 249–259.
Murray, J.W., 1968. Living foraminifers of lagoons and estuaries. Micropaleontology 14, 435–455.
Murray, J.W., 1973. Distribution and Ecology of Living Benthic Foraminiferids. Heinemann Educational, London, p. 274.
Murray, J.W., 2001. The niche of benthic foraminifera, critical thresholds and proxies. Mar. Micropaleontol. 41, 1–7.
Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Cambridge, p. 440.
Murray, J.W., 2013. Living benthic foraminifera: biogeographical distributions and the significance of rare morphospecies. J. Micropalaeontology 32, 1–58.
Narayan, Y.R., Pandolfi, J.M., 2010. Benthic foraminiferal assemblages from Moreton Bay, South-East Queensland, Australia: application in monitoring water and substrate quality in subtropical estuarine environments. Mar. Pollut. Bull. 60, 2062–2078.
Nash, G.J., Binnie, M.N., Cann, J.H., 2010. Distribution of foraminifera and ostracods in the Onkaparinga estuary, South Australia. Aust. J. Earth Sci. 57, 901–910.
Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. J. Biogeogr. 26, 867–878.
Newbery, D.M., Campbell, E.J.F., Proctor, J., Still, M.J., 1996. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. Vegetatio 122, 193–220.
Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2011. Vegan: Community Ecology Package, p. 190. https://github.com/vegandevs/vegan.
Patterson, R.T., 1990. Intertidal benthic foraminiferal biofacies on the Fraser River Delta, British Columbia: modern distribution and paleoecological importance. Micropaleontology 36, 229–244.
Patterson, R.T., Dalby, A.P., Roe, H.M., Guilbault, J.-P., Hutchinson, I., Clague, J.J., 2005. Relative utility of foraminifera, diatoms and macrophytes as high resolution indicators of paleo-sea level in coastal British Columbia, Canada. Quat. Sci. Rev.

24, 2002–2014.
Perissinotto, R., Walker, D.R., Webb, P., Wooldridge, T.H., Bally, R., 2000. Relationships between zoo- and phytoplankton in a warm-temperate, semi-permanently closed estuary, South Africa. Estuar. Coast. Shelf Sci. 51, 1–11.
Phleger, F.B., 1965. Patterns of living marsh foraminifera in south Texas coastal lagoons. Bol. la Soc. Geol. Mex. 28, 1–44.
Quilty, P.G., 1977. Foraminifera of Hardy inlet, southwestern Australia. J.R. Soc.West. Aust. 59, 79–90.
Quilty, P.G., Hosie, G., 2006. Modern foraminifera, Swan River estuary, Western Australia: distribution and controlling factors. J. Foraminifer. Res. 36, 291–314.
R Development Core Team, 2010. R: a Languge and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Revets, S.A., 2000. Foraminifera of Leschenault inlet. J. R. Soc. West. Aust. 83, 365–375.
Rice, E.W., Baird, R.B., Eaton, A.D., Clesceri, L.S., 2012. Standard Methods for the Examination of Water and Wastewater 22nd Edition. American Public Health Association, American Water Works Association, Water Environment Federation, p. 1496.
Robinson, K.I.M., Gibbs, P.J., Barclay, J.B., May, J.L., 1983. Estuarine flora and fauna of smiths Lake, new South Wales. Proc. Linn. Soc. N. S. W. 107, 19–34.
Roper, T., Creese, B., Scanes, P., Stephens, K., Williams, R., Dela-Cruz, J., Coade, G., Coates, B., Fraser, M., 2011. Assessing the Condition of Estuaries and Coastal Lake Ecosystems in NSW. Estuaries and Coastal Lakes Technical Report Series, Sydney, p. 270.
Roy, P.S., 1984. New South Wales estuaries: their origin and evolution. In: Thom, B.G. (Ed.), Coastal Geomorphology in Australia. Academic Press Australia, North Ryde, pp. 99–121.
Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of south-east australian estuaries. Estuar. Coast. Shelf Sci. 53, 351–384.
Schafer, C.T., Collins, E.S., Smith, J.N., 1991. Relationship of foraminifera and thecamoebian distributions sediments contaminated by pulp mill effluent: Saguenay Fjord, Quebec, Canada. Micropaleontology 17, 255–283.
Schafer, C.T., Winters, G.V., Scott, D.B., Pocklington, P., Cole, F.E., Honig, C., 1995. Survey of living foraminifera and polychaete populations at some Canadian aquaculture sites: potential for impact mapping and monitoring. J. Foraminifer. Res. 25, 236–259.
Schröder-Adams, C.J., Boyd, R.L., Tran, T., 2014. Estuarine foraminiferal biofacies pattern compared to the brackish ichnofacies model: Port Stephens, southeast Australia. Estuar. Coast. Shelf Sci. 139, 78–87.
Scott, D.B., Medioli, F.S., 1980. Living vs. total foraminiferal populations: their relative usefulness in paleoecology. J. Paleontology 54, 814–831.
Scott, D.B., Medioli, F.S., Schafer, C.T., 2001. Monitoring in Coastal Environments Using Foraminifera and Thecamoebian Indicators. Cambridge University Press, Cambridge, p. 192.
Scott, D.B., Schafer, C.T., Medioli, F.S., 1980. Eastern Canadian estuarine foraminifera; a framework for comparison. J. Foraminifer. Res. 10, 205–234.
Scott, D.B., Collins, E.S., Duggan, J., Asioli, A., Saito, T., Hasegawa, S., 1996. Pacific Rim marsh foraminiferal distributions: implications for sea-level studies. J. Coast. Res. 12, 850–861.
Sen Gupta, B.K.S., 1999. Foraminifera in marginal marine environments. In: Sen Gupta, B.K.S. (Ed.), Modern Foraminifera. Springer, Netherlands, pp. 141–159.
Setty, M.G.A.P., 1976. The relative sensitivity of benthonic foraminifera in the polluted marine environment of Cola Bay, Goa. In: Proceedings of the Sixth Indian Colloquium of Micropaleontology and Stratigraphy, pp. 225–234.
Smith, C.S., Heggie, D.T., 2003. Benthic Nutrient Fluxes in Smiths Lake. Geoscience Australia, NSW. Record 2003/16.
Southall, K.E., Gehrels, W.R., Hayward, B.W., 2006. Foraminifera in a New Zealand salt marsh and their suitability as sea-level indicators. Mar. Micropaleontol. 60, 167–179.
Stretch, D., Parkinson, M., 2006. The breaching of sand barriers at Perched, Temporary Open/Closed estuaries – a model study. Coast. Eng. J. 48, 13–30.
Strotz, L., 2003. Holocene foraminifera from Tuross estuary and coila Lake, south coast, new South Wales: a preliminary study. Proc. Linn. Soc. N. S. W. 124, 163–182.
Strotz, L.C., 2012. Foraminiferal fauna and biotopes of a barrier estuary system: St Georges Basin, New South Wales, Australia. J. Foraminifer. Res. 42, 369–382.
Suzuki, M.S., Ovalle, A.R.C., Pereira, E.A., 1998. Effects of sand bar openings on some limnological variables in a hypertrophic tropical coastal lagoon of Brazil. Hydrobiologia 368, 111–122.
Teske, P., Wooldridge, T., 2001. A comparison of the macrobenthic faunas of permanently open and temporarily open/closed South African estuaries. Hydrobiologia 464, 227–243.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer, New York, p. 495.
Wang, P., Chappell, J., 2001. Foraminifera as Holocene environmental indicators in the South Alligator River, northern Australia. Quat. Int. 83, 47–62.
Webb, Mckeon and Associates, 2001. Smiths Lake Estuary Management Study and Management Plan. Report for Great Lakes Council. www.greatlakes.nsw.gov.au/files/c25b4e3c.../Smiths_Lakes_EMP.pdf.
Webb, Mckeon and Associates, 2008. Smiths Lake Flood Study. Report for Great Lakes Council. http://www.greatlakes.nsw.gov.au/files/a332515b-d72f-45a0-9be8-9d2600d1e610/Smiths_Lake_Flood_Study.pdf.
Webster, I.T., Harris, G.P., 2004. Anthropogenic impacts on the ecosystems of coastal lagoons: modelling fundamental biogeochemical processes and management implications. Mar. Freshw. Res. 55, 67–78.
Whitfield, A.K., Elliott, M., Basset, A., Blaber, S.J.M., West, R.J., 2012. Paradigms in estuarine ecology – a review of the Remane diagram with a suggested revised model for estuaries. Estuar. Coast. Shelf Sci. 97, 78–90.
Woodroffe, S.A., Horton, B.P., Larcombe, P.E., Whittaker, J.E., 2005. Intertidal mangrove foraminifera from the central Great Barrier Reef shelf, Australia: implications for sea level reconstruction. J. Foraminifer. Res. 35, 259–270.
Yassini, I., Jones, B.G., 1989. Estuarine foraminiferal communities in Lake Illawarra, NSW. Proc. Linn. Soc. N. S. W. 110, 229–266.
Yassini, I., Jones, B.G., 1995. Recent Foraminifera and Ostracoda from Estuarine and Shelf Environments on the Southeastern Coast of Australia. University of Wollongong Press, Wollongong, p. 484.