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# What evidence exists for alternative ecological regimes in salinising wetlands?

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## SUMMARY

1. Land clearing in Australia's southwest has led to widespread salinisation of aquatic ecosystems. Four different ecological regimes (clear, submerged macrophyte-dominated; clear, benthic microbial community-dominated; turbid, phytoplankton-dominated; and turbid, sediment-dominated) have previously been identified in the salinising wetlands of this region.
2. Monitoring data from seven saline wetlands over an 18-month period were used to evaluate whether a continuum, simple threshold or alternative regimes conceptual model (*sensu* Hydrobiologia, 200/201, 1990, 367; Hydrobiologia, 200/201, 1990, 475) most appropriately represented transitions between these ecological regimes. We also aimed to identify whether factors other than salinity played a major role in defining ecological regimes or causing shifts between them.
3. Ordination of biological variables revealed a separation of benthic microbial community-dominated from submerged macrophyte-dominated sites and times. The mean salinities of these two groups were very similar, suggesting that a salinity threshold was not responsible for benthic microbial versus macrophyte dominance. No other environmental variable was found to have a strong, direct influence on the groupings.
4. The dynamics of regime change in saline wetlands appear not to be driven by any single variable, but by the combined effects of salinity and water regime on species life histories and competitive abilities. Macrophytes were powerful competitors, able to germinate and establish under a range of salinities, turbidities and water depths, and were favoured by seasonal drying.
5. Data from the seven wetlands indicated that the continuum, simple threshold and alternative regimes conceptual models did not appropriately represent transitions between ecological regimes in seasonally drying wetlands. Macrophyte and benthic microbial regimes occurred at overlapping salinity levels, excluding both the continuum and threshold models, and the regular occurrence of drying appeared to preclude the alternative regimes model. Drying prevented the development of strong positive feedback mechanisms, which might otherwise have maintained the benthic microbial community-dominated regime. We hypothesise that an alternative regimes model might still be valid for salinising ecosystems holding permanent water.

*Keywords:* benthic microbes, regime shift, salinity, submerged macrophytes, water regime

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## Introduction

Land clearing in the agricultural zone of Australia's southwest has led to widespread salinisation of flowing and standing waters (Davis *et al.*, 2003; Halse, Ruprecht & Pinder, 2003). Recently, attempts have

been made to characterise the salinity-driven ecological changes occurring in wetlands using the paradigm of multiple stable equilibria (Davis *et al.*, 2003). Four different equilibria, viewed as alternative ecological regimes, have been identified in the seasonally drying salinised wetlands of Australia's southwest: (i) clear water dominated by submerged aquatic macrophytes; (ii) clear water dominated by benthic microbial communities; (iii) turbid water dominated by phytoplankton; and (iv) turbid water dominated by sediment (Davis *et al.*, 2003; Strehlow *et al.*, 2005). The criteria used to define each regime are given in Table 1. Davis *et al.* (2003) predicted shifts from (i) to (ii) driven by increased salinity, and from (i) to (iii) and (ii) to (iii) driven by increased nutrient loading. Regime (i) is the desirable regime or management goal for the salinised seasonally drying wetlands of Australia's southwest as it is most similar to the historic condition of these wetlands, and performs a more diverse range of ecological functions than regimes (ii)–(iv) (Sim, Chambers & Davis, in press a; Sim, Davis & Chambers, in press b).

The salinising wetlands of southwestern Australia differ from European brackish coastal lakes (as described in Bales *et al.*, 1993; Jeppesen *et al.*, 1994, 1998; Moss, 1994) in their freshwater origins, inland location and importantly, their ability to support high abundances of large-bodied planktivorous grazers including cladocerans (Strehlow *et al.*, 2005). The occurrence of large numbers of halotolerant-grazing zooplankton appears to allow the development of the clear water (macrophyte or benthic microbial-dominated) regimes described above (Strehlow *et al.*, 2005), even under conditions of nutrient enrichment. In European brackish wetlands, the suppression of these large grazers (particularly cladocerans) by salinity keeps nutrient-enriched saline waters highly turbid, even when macrophytes are abundant (Jeppesen *et al.*, 1994; Moss, 1994). This contrasts with the widely documented association between

macrophytes and clear water that has been observed in freshwater shallow lakes (e.g. Beklioglu & Moss, 1996; Blindow, Hargeby & Andersson, 2002). The existence of saline, clear water regimes in Australian salinising wetlands suggests that aspects of the ecological dynamics of these systems may parallel freshwater lakes more closely than those of their brackish European counterparts.

It is not yet clear whether the alternative regimes model or a different model is the most appropriate representation of salinity-driven ecological dynamics in salinised Australian wetlands. We have used monitoring data from seven saline wetlands to evaluate three different conceptual models that may represent salinity-driven regime shifts [from (i) to (ii) and vice versa] in salinised wetlands. These are the 'continuum', 'simple threshold' and alternative regimes models (Fig. 1) (described in more detail in Sim, Davis & Chambers, 2006). Predictions of ecosystem behaviour under each model are presented in Table 2. To assess the relevance of each model, we need to understand whether the thresholds arising from experimental work on salinity tolerances (Sim *et al.*, in press a,b) accurately represent changes in the field, whether regime shifts appear to occur equally in both directions, whether transitional regimes exist and whether there appear to be positive feedback mechanisms operating. We also aim to identify whether salinity plays the major role in defining ecological regimes or causing shifts between them, or alternatively, whether other physicochemical or biotic factors can be identified as drivers.

## Methods

### Study sites

Regular field sampling was conducted at seven sites; two naturally saline coastal wetlands near Perth (Lake Coogee and Lake Mount Brown), four secondarily

**Table 1** Criteria defining the four ecological regimes of salinised wetlands (Strehlow *et al.*, 2005)

| Ecological regime                                       | Turbidity (NTU) | Chlorophyll <i>a</i> ( $\mu\text{g L}^{-1}$ ) | Cover of submerged macrophytes (%) | Cover of benthic microbial communities (%) |
|---|-----------------|---|------------------------------------|--|
| (i) Clear water, macrophyte-dominated                   | <10             | <30   | >50                                |  |
| (ii) Clear water, benthic microbial community-dominated | <10             | <30   |                                    | >50  |
| (iii) Turbid water, phytoplankton-dominated             | >10             | >30   | <50                                | <50  |
| (iv) Turbid water, sediment-dominated                   | >10             | <30   | <50                                | <50  |

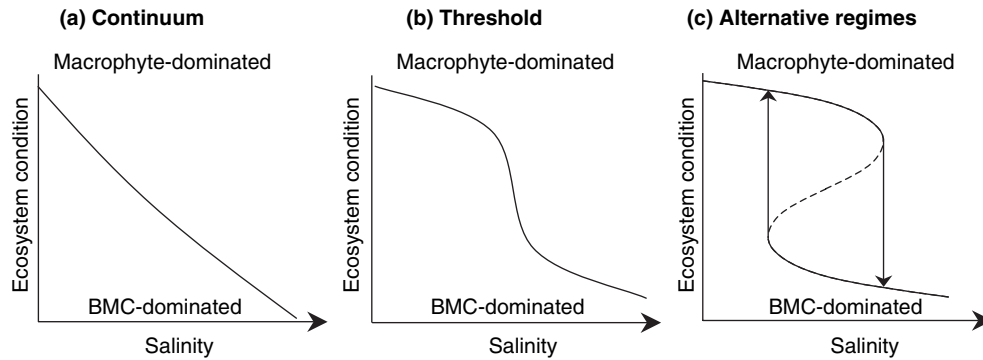


Fig. 1 Three possible pathways along which the shift from a macrophyte-dominated to a benthic microbial community (BMC)-dominated regime might occur in a secondarily salinised wetland system (adapted from Scheffer *et al.*, 2001; Scheffer & Carpenter, 2003).

(anthropogenically) salinised wetlands (Lake Mears, Little White Lake, Rushy Swamp and Meeking Lake) and one secondarily salinised palaeochannel (Arthur River Flats) in the Western Australian 'wheatbelt'. These sites encompassed a range of wetland types and levels of salinisation, and as they were typical of systems in the region, most of the secondarily saline sites were affected by more than one degrading factor, such as clearing, nutrient enrichment or grazing. A summary of the location, type, size and tenure of each of the sites is given in Table 3.

This dataset was recorded over a comparatively short monitoring period (18 months from September 2002 to March 2004), over two drier than average years, which would have influenced the hydrology and salinity characteristics recorded. Watertables would have been relatively low, with less wetland permanency than usual and possibly also higher salinities. Under different conditions these systems may have stayed wet longer, allowing a greater possibility for change between regimes than was evident in this study.

#### Field sampling

Three permanent sampling sites were sampled every 4–6 weeks at each wetland. Sites were sampled for water quality, macrophyte biomass and benthic microbial biomass when wet, but only for benthic microbial biomass when dry.

**Water quality.** When water was present in the wetland, a suite of physicochemical parameters were recorded including: pH, salinity (using a TPS WP-81 pH/salinity/conductivity meter and a portable

salinity refractometer, Vista Series Instruments, A366ATC); turbidity (using a Hach 2100P portable turbidimeter, Hach Company, Colorado, U.S.A.); gilvin (water filtered through 0.2  $\mu\text{m}$  filters and kept in the dark until absorbance was measured at 440 nm), chlorophyll *a*, *b*, *c* (known volume of water filtered using Whatman GF/C filters in the field, then kept on ice for transport to the laboratory) and water depth. Raw absorbances were converted to absorbance coefficients for gilvin by multiplying by  $2.303 \times 100$  (Kirk, 1994). Chlorophyll samples were processed by the Marine and Freshwater Research Laboratory at Murdoch University (NATA accredited). Chlorophylls were extracted by grinding in 90% aqueous ethanol (Clesceri, Greenberg & Eaton, 1999). Absorbances of photosynthetic pigments were determined spectrophotometrically at 750, 630, 664 and 647 nm. Concentrations were calculated using the equations of Clesceri *et al.* (1999). Chlorophyll concentrations that fell below the detection limit ( $0.1 \mu\text{g L}^{-1}$ ) were assumed to be zero for the purposes of data analyses.

Water depth was taken at three permanent sampling sites around each wetland. These records do not provide the absolute maximum depth of the wetland but were comparable between sampling occasions.

**Macrophyte biomass.** When aquatic macrophytes were present and large enough to be harvested (>10 cm tall), aboveground biomass was sampled using grass shears to remove plants at ground level. Relative density was assessed visually and three representative subsamples harvested at each site, to a total area of approximately  $0.07 \text{ m}^2$  (representing three shearing arcs). This process was repeated at each of the three

**Table 2** Predictions for saline wetland ecosystem responses to salinity change under each of three conceptual models (Fig. 1)

| Factor   | Continuum model   | Simple threshold model  | Alternative regimes model   |
|--|---|---|---|
| Relationship between salinity change and regime shifts | Change in community dominance directly proportional to salinity change<br><br>No threshold salinity concentration needs to be crossed for regime to change<br><i>Macrophyte loss and benthic microbial community increase are gradual as salinity increases (and vice versa)</i>  | Regime shift at threshold salinity<br><br>No hysteresis effects evident (shift back can occur at same salinity)<br><i>Macrophyte-dominated below threshold salinity and benthic microbial community-dominance above. Sudden switch between dominance at salinity threshold (approximately 50 ppt)</i>   | Regime shifts at salinity extremes or at intermediate salinities with additional perturbation<br><br>Hysteresis effects evident<br><br><i>Sudden switch between macrophyte and benthic microbial community dominance when salinity reaches an extreme (high or low salinity) or the system is perturbed at intermediate salinities (&lt;15 to approximately 50 ppt)</i> |
| Persistence of transitional regimes                    | Transitional regimes able to persist<br><i>Macrophytes and benthic microbial communities can be co-dominant over a range of salinities and over several months</i><br><br>Changes in ecological resilience are not necessary for a shift to occur<br>Weakening of ecosystem resilience may change the slope of model, but not its shape | Transitional regimes highly transient<br><i>Macrophytes and benthic microbial communities rarely co-dominant and only for very short periods</i><br><br>Changes in ecological resilience are not necessary for a shift to occur<br>Weakening of ecosystem resilience may change threshold salinity, but not the shape of model                          | Transitional regimes highly transient<br><i>Macrophytes and benthic microbial communities rarely co-dominant and only for very short periods</i><br><br>Weakening of ecological resilience important for regime shifts<br>Shifts at intermediate salinities cannot occur without external perturbation  |
| Importance of ecological resilience to regime shifts   | Biotic changes driven largely by salinity increases or decreases (salinity tolerance)<br><i>Macrophyte and benthic microbial community dominance respond primarily to salinity level</i>  | Biotic changes driven largely by salinity increases or decreases (salinity tolerance)<br><i>Macrophyte and benthic microbial community dominance respond primarily to threshold salinity level (50 ppt)</i>   | Changes in resilience may undermine a particular 'equilibrium'<br><i>Macrophyte or benthic microbial community dominance can be maintained over a range of intermediate salinity levels (&lt;15 to approximately 50 ppt)</i>  |
| Existence of self-stabilising mechanisms               | No strong feedback or self-sustaining mechanisms<br><br><i>Once salinity starts to increase, a change in macrophyte and benthic microbial community dominance occurs</i>  | Some weak feedback mechanisms at salinity extremes but likely to break down when threshold salinity reached<br><br><i>Change in macrophyte or benthic microbial community dominance may be minimal until threshold (50 ppt) is reached</i>  | Strong feedback or self-stabilising mechanisms<br><br><i>Very little change in macrophyte or benthic microbial community dominance over a wide range of intermediate salinities (&lt;15 to approximately 50 ppt) (without perturbation)</i>   |
| Viability of recolonisation                            | Persistence of some organisms from each dominant community at intermediate salinities<br><br>Recolonisation relatively rapid<br><br><i>Both types of organisms are able to persist and reproduce at intermediate salinities (&lt;15 to approximately 50 ppt)</i>  | No persistence of organisms from alternative dominant community once threshold is crossed<br><br>Speed of recolonisation dependent on availability of viable propagules from the seedbank or nearby wetland<br><br><i>Once threshold is reached (50 ppt), most/all living organisms from previous regime are no longer able to persist or reproduce</i> | No persistence of organisms from alternative dominant community once regime shift occurs<br><br>Speed of recolonisation dependent on availability of viable propagules from the seedbank or nearby wetland<br><br><i>Once regime shift occurs, most/all living organisms from previous regime are no longer able to persist or reproduce</i>                            |

Proposed threshold salinities (>50 ppt threshold for shift from submerged macrophyte to benthic microbial community dominated, <15 ppt threshold for reverse switch) from Sim et al., in press a,b. Italicised text indicates details specific to regime shifts in saline wetlands.

Table 3 Study site locations and details

| Wetland name       | Location                          | Latitude, longitude       | Type   | Size (ha) | Tenure   |
|--------------------|-----------------------------------|---------------------------|--|-----------|--|
| Lake Coogee        | Near Coogee, southwest of Perth   | 32°08.401'S, 115°46.738'E | Medium-sized, permanent wetland (possibly groundwater fed) with seasonal fluctuations in water level | 60.4      | City of Cockburn   |
| Lake Mears         | Near Brookton                     | 32°13.842'S, 117°21.566'E | Large, open, periodically inundated. Maximum depth 2.4 m   | 208       | Private and Department of Conservation and Land Management |
| Little White Lake  | Near Narrogin                     | 33°00.640'S, 117°26.456'E | Medium-sized, seasonal wetland   | 64        | Department of Conservation and Land Management             |
| Arthur River Flats | Near Highbury                     | 33°04.651'S, 117°16.614'E | Seasonally inundated shallow palaeochannel   | –         | Department of Conservation and Land Management             |
| Lake Mount Brown   | Near Henderson southwest of Perth | 33°10.368'S, 115°47.446'E | Small, seasonal wetland  | 5.3       | Department of Conservation and Land Management             |
| Meeking Lake       | North of Darkan                   | 33°14.732'S, 116°47.058'E | Medium-sized, seasonal wetland   | 25        | Private  |
| Rushy Swamp        | Near Woodanilling                 | 33°32.420'S, 117°16.142'E | Medium-sized, seasonal wetland   | 12.5      | Private  |

permanent sampling sites at each wetland. If macrophytes were too small to be harvested, their presence only was recorded.

Macrophyte samples were refrigerated after collection, and debris, sediment and invertebrates removed from them by washing and hand-picking before drying for 24 h at 105 °C. Dry samples were weighed to the nearest 0.01 g. Macrophyte beds usually comprised two or three species (Table 4), but species were not separated before drying.

Biomass (g dry weight m<sup>-2</sup>) was expressed in categories on a scale of natural logarithms (Table 5). Due to the large spread of values in the data, a linear scale was inappropriate (too many categories would have been required). The use of categories allowed an estimate of biomass to be made for occasions when plants were too small for harvesting and when there were missing data (December 2003). When plants were too small for harvesting they always fell into the first category.

Macrophyte biomass was standardised across sites by adjusting all values to a percentage of the maximum biomass at each site within each wetting and drying cycle. This accounted for between-site variation in biomass and for the effects of year-to-year differences in rainfall.

*Macrophyte % cover.* Percentage cover of submerged macrophytes (whole lake) was determined using aerial photographs where available (usually every 2 months), together with ground-truthing at each four to six weekly sampling event. Ground-truthing consisted of visual surveys of the lake bed during each sampling trip to confirm the presence of macrophyte stands or bare sediment. Data were expressed as categories: 0 = 0%; 20 = 1–20%; 40 = 21–40%; 60 = 41–60%; 80 = 61–80%; and 100 = 81–100%. Similarly to macrophyte biomass, the use of categories allowed an estimate of percentage cover to be made for occasions on which aerial photographs were not available. These estimates were made using the preceding and subsequent aerial photographs for the site.

*Benthic microbial biomass.* If a benthic microbial community was deemed to be present (visual assessment of colour and cohesiveness), the estimated depth of the benthic layer and levels of benthic chlorophyll and phaeophytin were measured using sediment cores (40 mm diameter). If the benthic layer was cohesive,

Table 4 Species of macrophytes found at field sites and relative abundances

| Wetland            | <i>Ruppia polycarpa</i><br>R. Mason           | <i>Ruppia megacarpa</i><br>R. Mason | <i>Lepilaena preissii</i><br>(Lehm.) F. Muell | <i>Lamprothamnium macrospogon</i><br>(A. Braun) Ophel | <i>Lamprothamnium cf. succinctum</i><br>(A. Braun in Ascherson) Wood | <i>Lamprothamnium sp.</i><br>(undescribed) |
|--------------------|---|-------------------------------------|---|---|--|--|
| Lake Coogee        | Few plants only, probably <i>R. polycarpa</i> | -                                   | -   | -   | -  | -  |
| Lake Mears         | -   | Present in clumps                   | -   | -   | Dominant   | -  |
| Little White Lake  | Sparse  | -                                   | Co-dominant                                   | -   | Co-dominant  | -  |
| Arthur River Flats | -   | -                                   | Few plants only                               | -   | -  | -  |
| Lake Mt Brown      | Dominant                                      | -                                   | Not flowering (not positive ID)               | -   | -  | Co-dominant                                |
| Meeking Lake       | Dominant                                      | -                                   | Present                                       | Co-dominant   | -  | -  |
| Rushy Swamp        | Present                                       | -                                   | Present                                       | Dominant  | -  | -  |

Table 5 Above-ground submerged macrophyte biomass categories (scale is natural logarithms)

| Biomass category | Range of biomass values included (g DW m <sup>-2</sup> ) |
|------------------|--|
| 0                | 0  |
| 2.72             | 0–2.72   |
| 7.39             | 2.73–7.39  |
| 20.09            | 7.40–20.09   |
| 54.60            | 20.10–54.60  |
| 148.41           | 54.61–148.41   |
| 403.43           | 148.42–403.43  |
| 1096.63          | 403.44–1096.63   |
| 2980.96          | 1096.64–2980.96  |

the top part of the core (benthic microbial community above the sediment) was cut off and placed in a vial (depth of layer recorded); if flocculent, the top part of the layer was poured into a vial and the volume recorded. The nature of the benthic microbial community varied, but was usually comprised of diatoms, non-filamentous green algae or non-filamentous cyanobacteria.

Similarly to water column photosynthetic pigments, sediment pigments were extracted using the acetone method by the Marine and Freshwater Research Laboratory at Murdoch University (Clesceri *et al.*, 1999). Pigment concentrations that fell below the detection limit (0.1 mg m<sup>-3</sup>) were assumed to be zero for the purposes of data analyses.

Similarly to macrophyte biomass, benthic microbial biomass (mg m<sup>-3</sup> of benthic chlorophyll *a*) was standardised across sites by adjusting all values to a percentage of the maximum biomass at each site within one wetting and drying cycle.

*Benthic microbial community % cover.* Percentage cover of benthic microbial community (whole lake) was determined using visual estimates at each four to six weekly sampling event. Data were expressed as categories: 0 = 0%; 33.3 = 1–33.3%; 66.7 = 33.4–66.7%; and 100 = 66.8–100%. Benthic microbial communities were not reliably detectable using aerial photographs. The patchiness of benthic microbial communities meant that cover could only be assessed with reasonable accuracy in broad categories.

*Statistical analyses*

*Classification and ordination.* Multivariate analyses performed in PRIMER (Clarke & Gorley, 2001) were used

to classify the data into groups, based either on biological abundance and biomass (standardised macrophyte biomass; macrophyte % cover; benthic microbial community % cover; depth of benthic microbial community; standardised benthic microbial community chlorophyll *a*; and water column chlorophyll *a*, *b* and *c*) or on environmental parameters (pH; salinity; turbidity; depth and gilvin).

A subset of the collected data was used, representing 60 date/site combinations when sites held water. Each data point was the mean of the values from the three sampling sites within each wetland. Some measures (e.g. benthic chlorophyll) were also recorded at times when the wetlands were dry, but these data could not be used, as multivariate analyses require a complete set of data for each date/site combination.

Biological data (mean values for each date/site combination) were used to generate a Bray–Curtis similarity matrix. Hierarchical classification and ordination by non-metric multi-dimensional scaling (NMDS) were performed on the data to examine groupings based on biomass. Values of individual biological and environmental variables were overlaid onto the NMDS of biological data using bubble plots (where larger bubbles represent larger values of each variable) to allow a visual assessment of the relationship between the multivariate biological data and univariate biological or environmental measures (Clarke & Warwick, 2001).

Correlation-based principal components analysis (PCA) is considered to be the most appropriate method of ordinating environmental data that is measured at different scales (Clarke & Warwick, 2001). However, to undertake a formal analysis of correlations between biological and environmental data (BIO-ENV), NMDS must be used for both datasets. Therefore, environmental data were  $\log_{10}(x + 1)$  transformed and a similarity matrix based on Euclidean distances was generated. Clarke & Warwick (2001) suggest that there is little practical difference between an NMDS and a PCA plot if they are both run on a small number of variables and both use Euclidean distance as their dissimilarity measure.

## Results

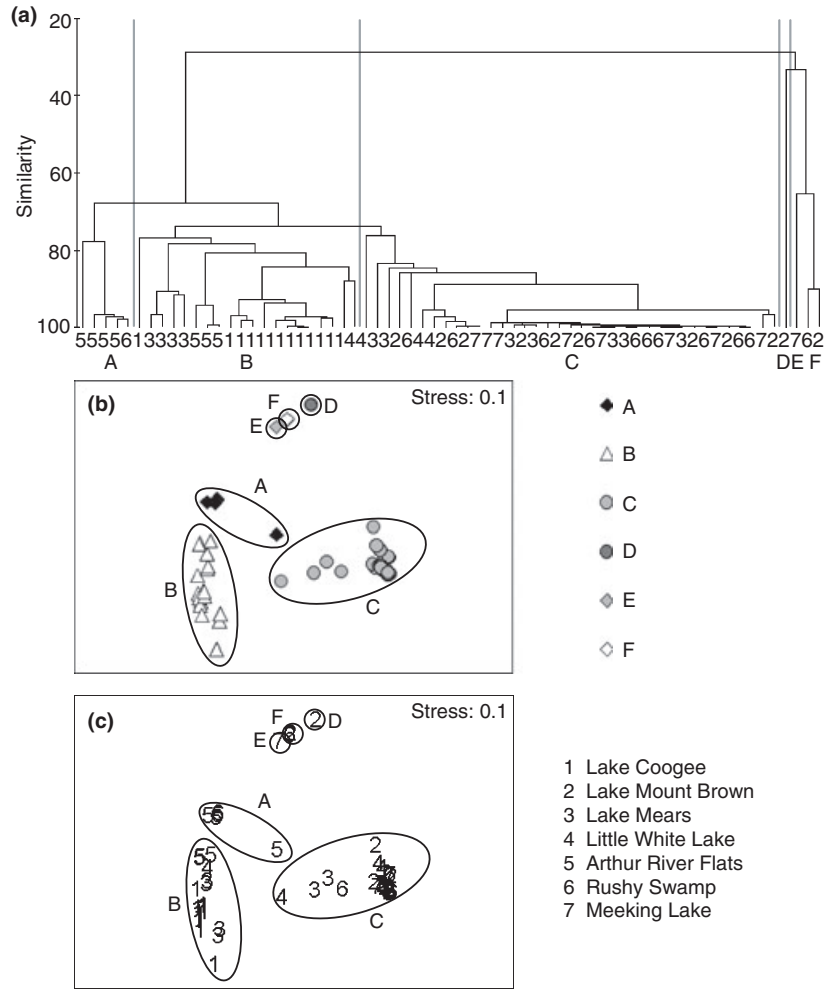
Hierarchical clustering of the biological dataset generated six main cluster groups sharing at least

75% similarity (Fig. 2a) and these groups were superimposed onto an ordination of the same data (Fig. 2b). The biological cluster groups comprised: A – Arthur River Flats on four occasions (Autumn–Winter 2003) and Rushy Swamp on one occasion (Autumn 2003); B – Lake Coogee, Lake Mears, Little White Lake and Arthur River Flats on most sampling occasions; C – Lake Mount Brown, Meeking Lake and Rushy Swamp on most occasions (all seasons) and the remaining occasions for Lake Mears and Little White Lake (Spring 2003); D – Lake Mount Brown on one occasion when it was filling (Autumn 2003); E – Meeking Lake on one occasion when it was drying (Summer 2003); and F – Rushy Swamp and Lake Mount Brown each on one occasion when they were drying (Summer 2003 and 2004) (Fig. 2c).

Bubble plots of the biological variables (Fig. 3) showed a strong association of benthic microbial community biomass and cover with biological cluster group B (Fig. 3e,f) and of macrophyte biomass and cover with biological cluster group C (Fig. 3g,h). Biological cluster group B appears to represent the ‘benthic microbial community-dominated’ regime and biological cluster group C represent the ‘macrophyte-dominated’ regime, with groups A, D, E and F representing abiotic (sediment-dominated) or transitional stages (usually filling or drying). Several wetlands moved between regimes over the 18-month sampling period and most exhibited transitional stages. A few of the site/times that fell in biological cluster group B when benthic microbial community biomass was low (but cover was often high) were dominated by phytoplankton (Fig. 3a–c,e,f).

Fig. 4 shows the association of environmental variables with the biological ordination and highlights where the separation of biological cluster groups may be due to differences in these variables. The mean salinities of biological cluster groups B and C were very similar (Fig. 4c), suggesting that a salinity threshold is not responsible for separating benthic microbial community and macrophyte dominance within these site/times. This overlap in salinities at which each community was dominant also suggests that ecological regime change does not occur along a continuum. Salinities were higher in the abiotic and transitional biological cluster groups (A, D, E, F), which were also associated with low water levels (Fig. 4c,d). The macrophyte-dominated biological cluster group C had the highest mean pH, the lowest





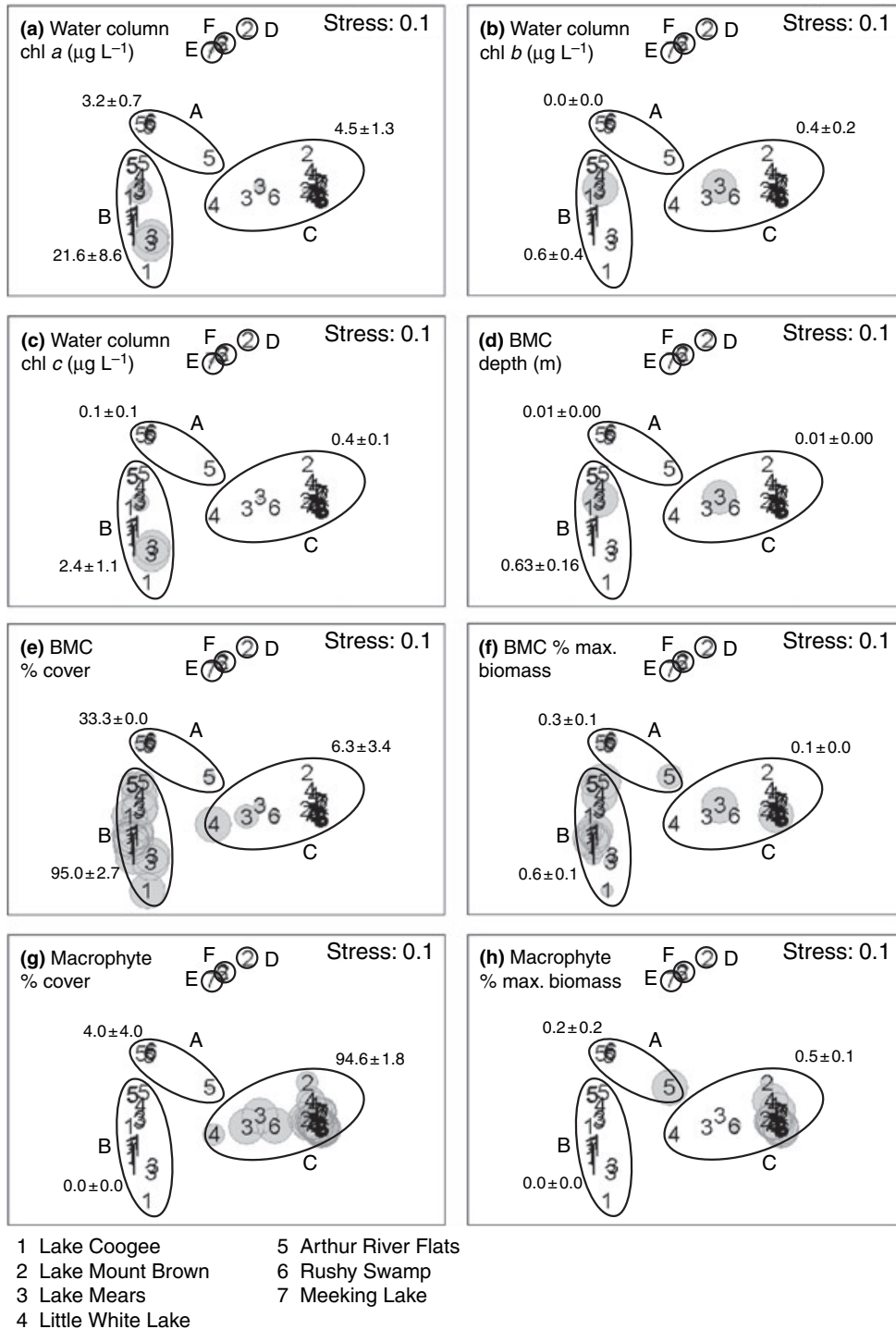
**Fig. 2** Two-dimensional non-metric multidimensional scaling (NMDS) ordination plots and hierarchical cluster diagram based on the biological dataset: (a) hierarchical cluster diagram (single linkage); (b) NMDS showing cluster groupings based on hierarchical clustering ( $\geq 75\%$  similarity); and (c) NMDS showing sites. Cluster groups are circled.

turbidity and the highest mean water depth (Fig. 4a,e,d). Fig. 5 confirms the overlap in salinity levels between biological cluster groups B and C and shows that a threshold between the macrophyte and benthic microbial community-dominated regimes does not exist at 30, 40 or 50 ppt.

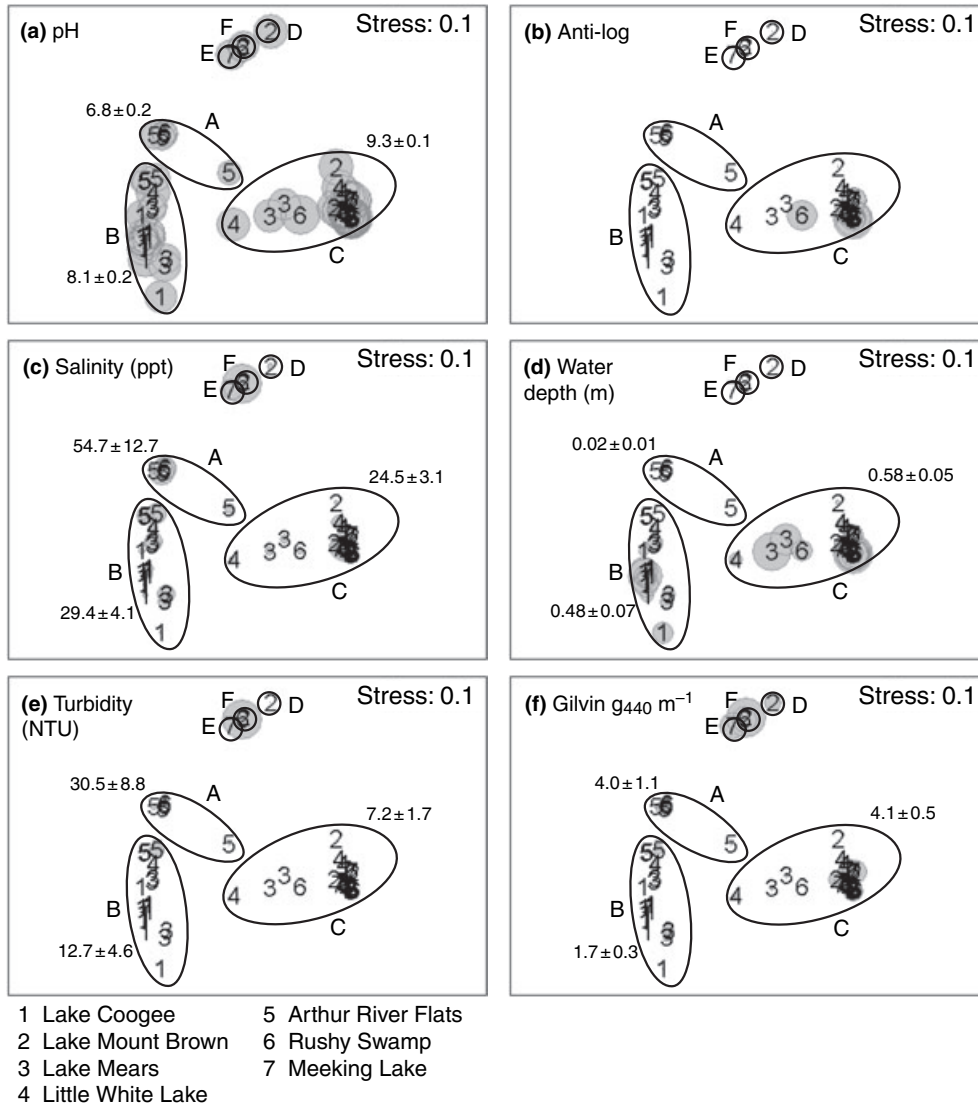
Ranked correlations between the biological similarity matrix and the environmental dataset (using the BIO-ENV procedure, Clarke & Warwick, 2001) revealed that no environmental variable (or combination thereof) strongly influenced the groupings of the biological site/times (Table 6). These low correlations were reflected by the scatter of high and low environmental values across the bubble plots (Fig. 4). The variable with the strongest correlation with the biological similarity matrix was pH ( $\rho_w = 0.361$ , Table 6). The relationship of pH with biological cluster groups was not evident in Fig. 4a due to its expression on a logarithmic scale. However, when pH

was plotted as anti-logs, the highest values can be seen tightly clustered within biological cluster group C, where macrophyte biomass were also high (Figs 3g & 4b).

Ordination of the environmental dataset (Fig. 6) revealed no distinct clustering into environmental cluster groups, but a clear divide between one side of the plot (most of biological cluster groups B and C) and the other side (abiotic and transitional site/times). Strong environmental gradients were evident (Fig. 7), with the ordination apparently driven most strongly by salinity, depth and to a lesser degree by pH (Fig. 7b–d). All the abiotic or transitional site/times, including the outliers from biological cluster group B were characterised by low water levels, and in many cases, also by high salinities. The biological cluster group B outliers were all from Arthur River Flats, the driest site sampled. Both the strongly biotic biological cluster groups (B and C) ranged over a wide range of



**Fig. 3** Bubble plots showing the association of biological variables with the biological dataset. Larger bubbles indicate higher values of each variable. Plots depict: (a) water column chlorophyll *a*; (b) water column chlorophyll *b*; (c) water column chlorophyll *c*; (d) depth of benthic microbial community; (e) % cover of benthic microbial community; (f) % of maximum benthic microbial community biomass (calculated for each wetland and wetting–drying cycle); (g) % cover of submerged macrophytes; and (h) % of maximum submerged macrophyte biomass (calculated for each wetland and wetting–drying cycle). Biological cluster groups are circled. Numbers on each plot are mean values  $\pm$  SE.

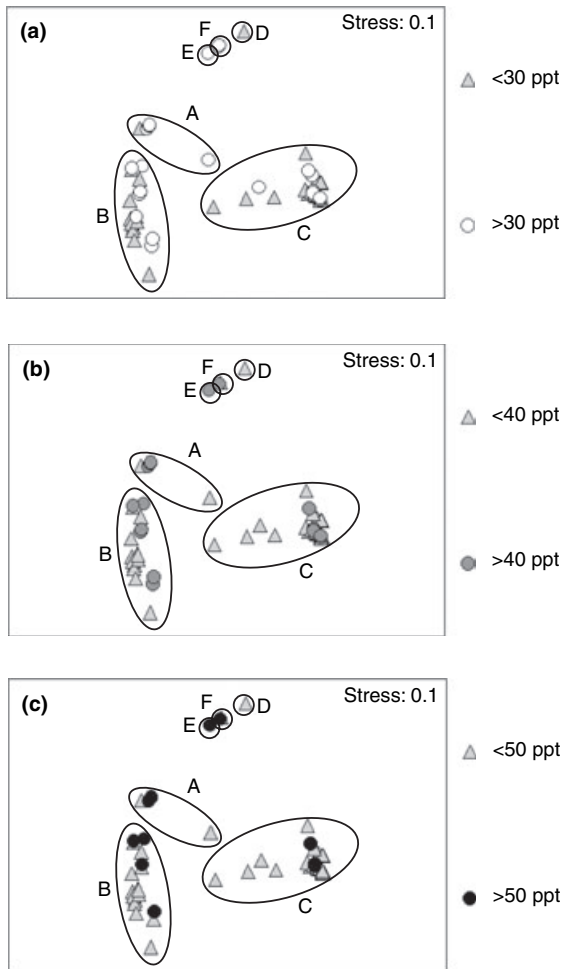


**Fig. 4** Bubble plots showing the association of environmental variables with the biological dataset. Larger bubbles indicate higher values of each variable. Plots depict: (a) pH; (b) anti-log pH; (c) salinity; (d) water depth; (e) turbidity; and (f) gilvin. Biological cluster groups are circled. Numbers on each plot are mean values  $\pm$  SE.

environmental variables, especially salinity. Interestingly, biological cluster group C (macrophytes) covered a wider range of salinities (both higher and lower) than biological cluster group B (benthic microbial communities) (Fig. 7c).

The temporal changes in salinity and depth were caused by seasonal fluctuations in water level at each of the wetlands, making season an important driver of shifts between biological cluster groups (Fig. 8) and therefore also between ecological regimes. These effects of season were felt most strongly at those wetlands that dried seasonally and which experienced large temporal fluctuations in water levels. Permanent

Lake Coogee remained benthic microbial community-dominated over time, only moving a little within biological cluster group B as water level and salinity changed across the seasons (Fig. 8a). When first sampled in September 2002, Lake Mears was highly saline (308 ppt) and benthic microbial community-dominated (biological cluster group B) (Fig. 8b). When it re-flooded in March 2003, when salinities dropped (40 ppt), turbidity rose (23 NTU) and phytoplankton became dominant. Salinity dropped further in August 2003 (31 ppt) and the lake shifted to macrophyte domination (biological cluster group C) in September–October 2003 (Fig. 8b). All subsequent



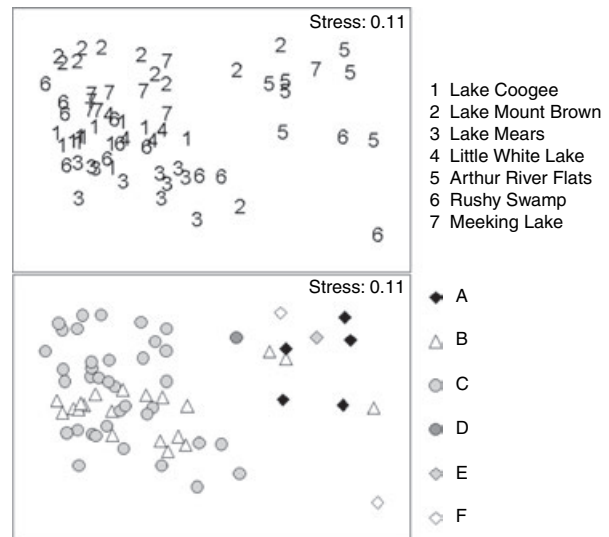
**Fig. 5** Biological non-metric multidimensional scaling (NMDS) plot showing sites classified by salinity level: (a) greater or less than 30 ppt; (b) greater or less than 40 ppt; and (c) greater or less than 50 ppt. The submerged macrophyte community is likely to have a restricted ability to establish and persist at >50 ppt (Sim *et al.*, in press a). Biological cluster groups are circled.

site/times for Lake Mears occurred within biological cluster group C. Little White Lake showed a very similar pattern of movement to Lake Mears, moving rapidly from benthic microbial community-dominated in April–May 2003 (130–192 ppt) to macrophyte-dominated by September when salinity had remained at 27–28 ppt for over a month (Fig. 8c). Arthur River Flats started in biological cluster group A when water levels were low (depth <0.01 m, salinity 79 ppt) and moved into biological cluster group B as the water rose slightly (depth <0.02 m, salinity 65.5 ppt) (Fig. 8d).

There were two occasions on which both macrophytes and a benthic microbial community covered

**Table 6** Results of the BioEnv correlation analysis (Spearman ranked correlation of biological similarity matrix with the environmental dataset)

| Selections                               | Correlation $\rho_w$ |
|--|----------------------|
| pH                                       | 0.361                |
| pH, water depth, gilvin                  | 0.285                |
| Water depth, gilvin                      | 0.28                 |
| pH, turbidity, water depth, gilvin       | 0.26                 |
| Turbidity, water depth, gilvin           | 0.258                |
| pH, salinity, water depth, gilvin        | 0.258                |
| Salinity, water depth, gilvin            | 0.255                |
| All                                      | 0.236                |
| Salinity, turbidity, water depth, gilvin | 0.234                |
| pH, water depth                          | 0.224                |
| pH, turbidity, water depth               | 0.22                 |
| Turbidity, water depth                   | 0.216                |
| Water depth                              | 0.208                |
| pH, salinity, water depth                | 0.205                |
| Salinity, water depth                    | 0.202                |
| pH, salinity, turbidity, water depth     | 0.197                |
| Salinity, turbidity, water depth         | 0.194                |
| pH, turbidity, gilvin                    | 0.193                |
| Turbidity, gilvin                        | 0.188                |
| pH, gilvin                               | 0.162                |



**Fig. 6** Two-dimensional non-metric multidimensional scaling (NMDS) ordination plots based on the environmental dataset: (a) showing sites; and (b) showing biological cluster groupings ( $\geq 75\%$  similarity).

>50% of a wetland; once at Lake Mears and once at Little White Lake, both in September 2003, at a salinity of 27 ppt. By October, the cover of macrophytes at both lakes had increased further and the benthic microbial community had declined,

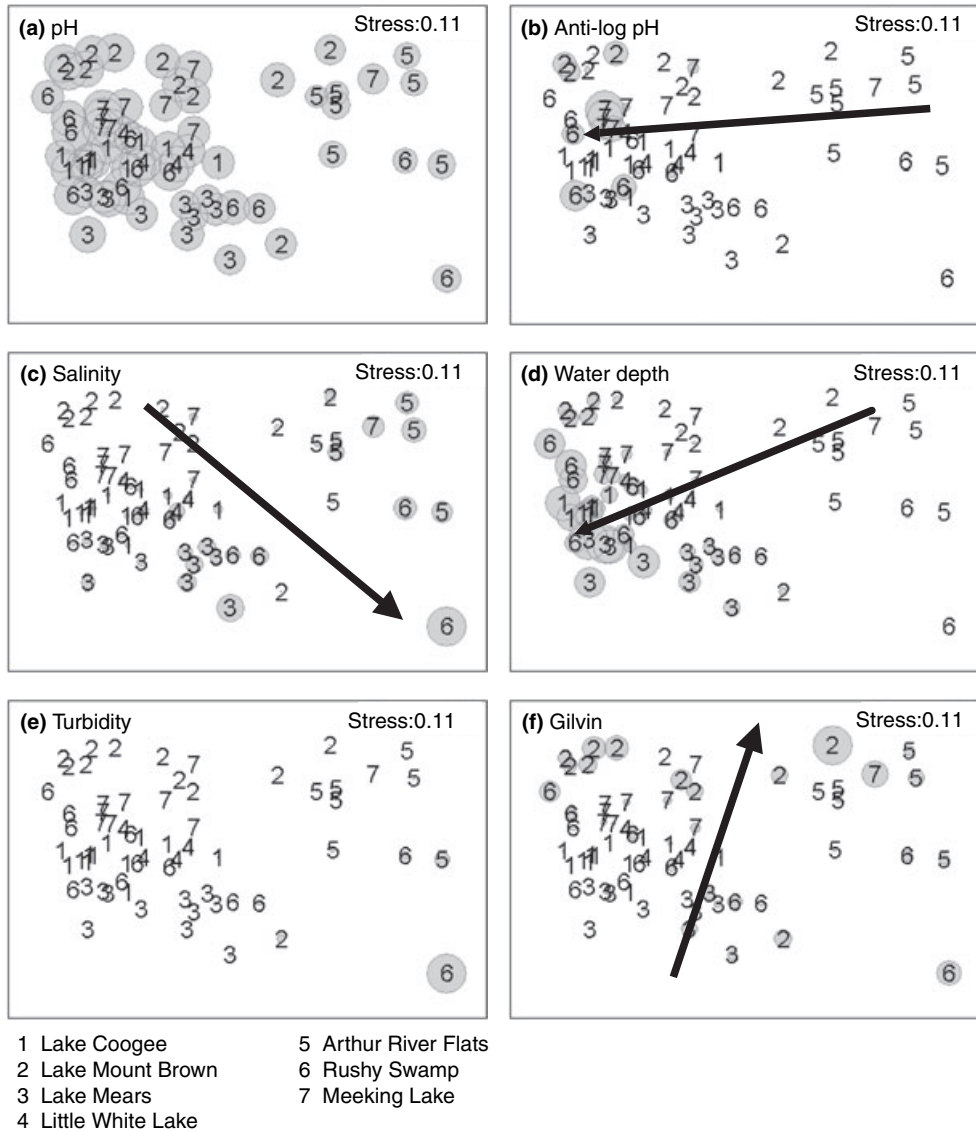
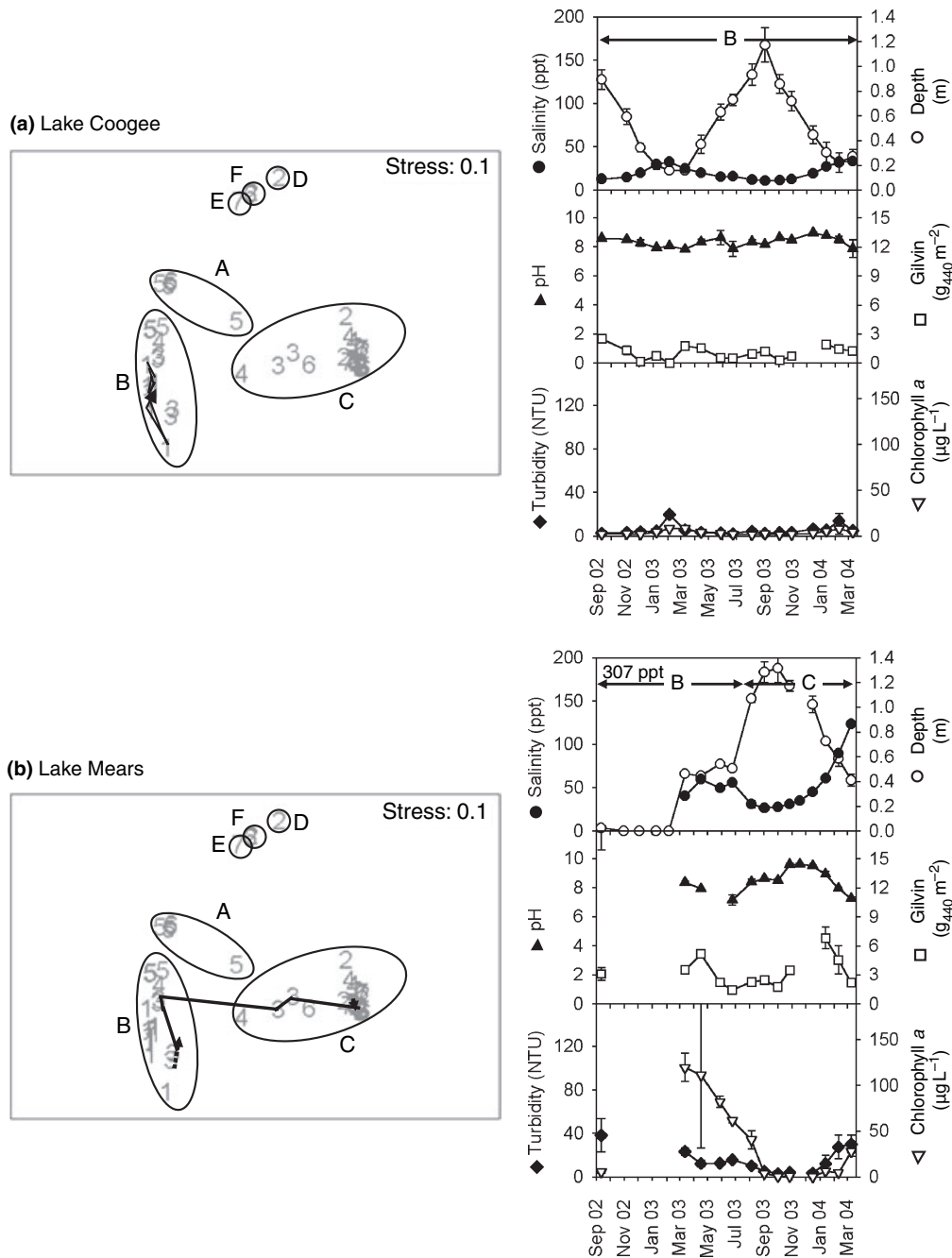


Fig. 7 Bubble plots showing the association of environmental variables with the environmental dataset. Plots depict: (a) pH; (b) anti-log pH; (c) salinity; (d) water depth; (e) turbidity; and (f) gilvin. Larger bubbles indicate higher values of each variable. Arrows indicate gradient of increase for selected variables.

although salinities had increased slightly (Fig. 8b,c). At Lake Mears, phytoplankton were co-dominant with benthic microbial communities from March to late June 2003 and were co-dominant with macrophytes in August 2003.

Lake Mount Brown dried soon after it was first sampled in 2002 (Fig. 8e). When re-wetting occurred in April 2003, salinity was higher (22 ppt), depth lower and turbidity higher than just prior to drying and it formed part of an outlying (transitional) biological cluster group D. It moved back to biological cluster group C (macrophyte-dominated)

on the next sampling occasion as the water level rose, salinity dropped (12 ppt) and macrophytes first became large enough for biomass samples (Fig. 8e). Drying at the end of the season caused it to become transitional once more (Fig. 8e). Meeking Lake and Rushy Swamp showed similar patterns to each other, with rapid movement away from other members of biological cluster group C (clear, macrophyte-dominated) to outlying biological cluster groups E and F, respectively, when drying (Fig. 8f,g). These shifts were associated with decreases in water level, increases in salinity level (to 69

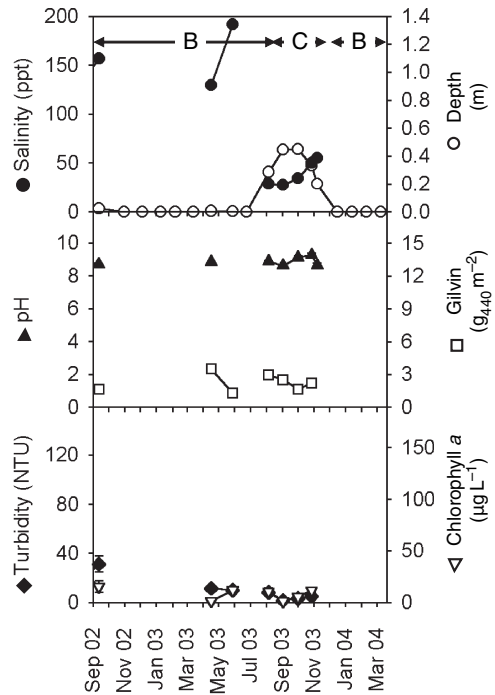
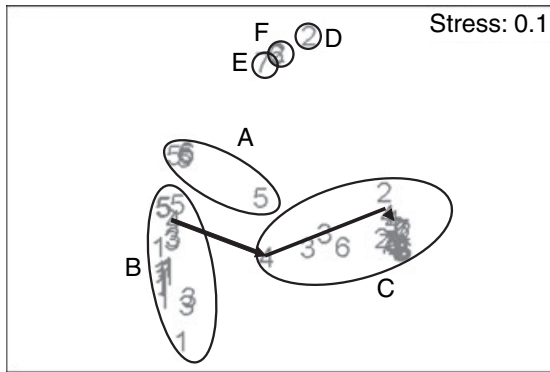


**Fig. 8** ‘Movement’ of wetlands across the biological non-metric multidimensional scaling (NMSD) plot over the 2002–03 (dashed line) and 2003–04 (solid line) seasons and corresponding time series data for salinity, depth, pH, gilvin, turbidity and water column chlorophyll *a* ( $\mu g L^{-1}$ ). Biological cluster groups are circled. Arrows and letters on time series plots indicate times when the wetland fell into each biological cluster group A–F.

and 125 ppt respectively), increases in turbidity and chlorophyll *a* concentrations and the death of submerged macrophytes at both sites (Fig. 8f,g). When macrophytes were present, these sites showed a high degree of similarity (Fig. 3g,h). The most

divergent site/time was Rushy Swamp when it first filled in May 2003 (salinity 73 ppt, turbidity 60 ppt) and formed part of biological cluster group A (Fig. 8g), a group dominated by Arthur River Flats site/times.

(c) Little White Lake



(d) Arthur River Flats

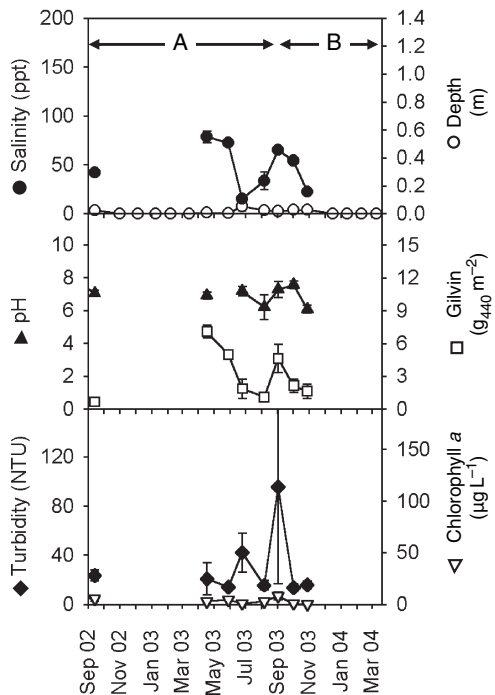
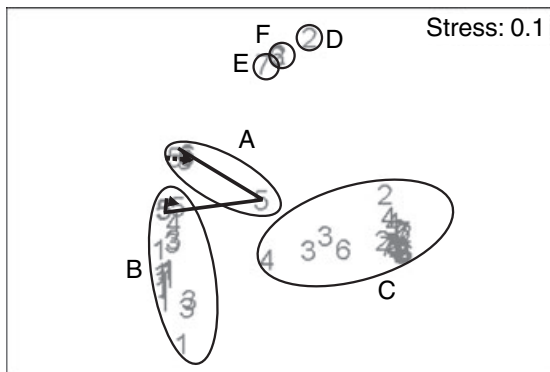


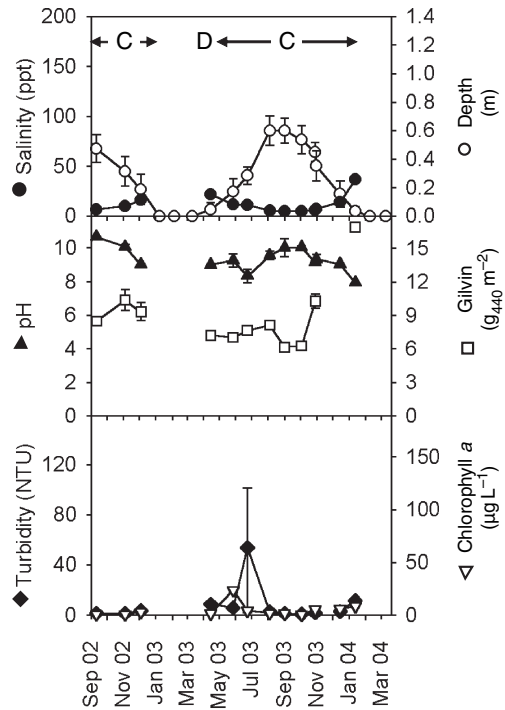
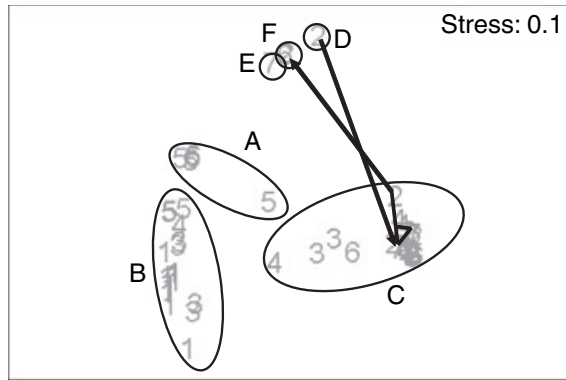
Fig. 8 (Continued)

**Discussion**

Either submerged macrophytes or benthic microbes dominated all seven wetlands on most occasions

when water was present during the 18-month sampling period from September 2002 to March 2004. Dominance of one group usually precluded dominance of the other, despite the fact that the salinities

(e) Lake Mount Brown



(f) Meeking Lake

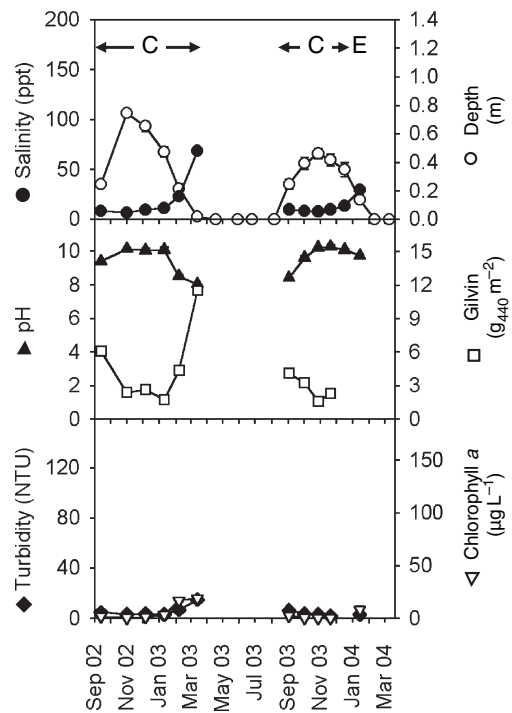
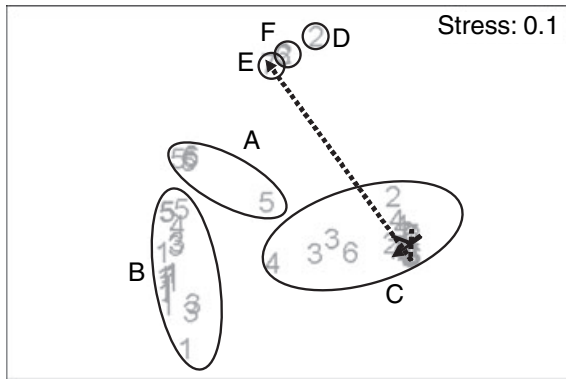


Fig. 8 (Continued)

characterising these two ecological regimes clearly overlapped (Fig. 3). When salinity increased or decreased gradually, there was no corresponding

(proportional) change in either benthic microbial community or macrophyte biomass as predicted by the continuum model, and conversely, biomass often



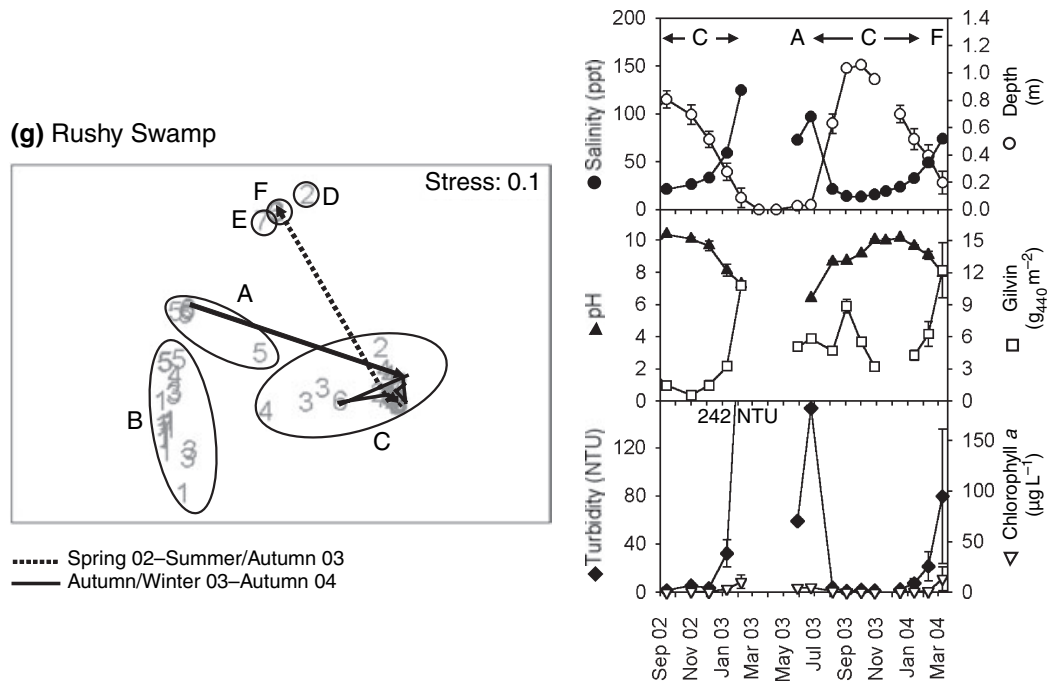


Fig. 8 (Continued)

continued to change when salinity remained relatively stable (Figs 3 & 4). Furthermore, there was no clear threshold salinity at which macrophyte and benthic microbial community dominance switched, even when a possible time lag after reaching this salinity was taken into account (Fig. 8). These results indicated that neither the continuum nor the simple threshold model (Fig. 1) accurately represented ecological regime shifts in these wetlands.

If the continuum model were supported, we would expect to find macrophytes dominant at lower salinities (<50 ppt, Sim *et al.*, in press a) and benthic microbial communities dominant at higher salinities (>50 ppt), with a range of transitional regimes between these (Sim *et al.*, 2006). According to this model, benthic microbial communities should not have become dominant at lower salinities than macrophytes (Fig. 8) and there should have been a range of intermediate salinities at which the two regimes were co-dominant.

If the simple threshold model were supported, we would again have expected macrophytes (only) to be dominant at low salinities and benthic microbial communities (only) at high salinities, but this time with an unstable transitional regime around the threshold salinity (Sim *et al.*, in press a). However, the data indicates that both benthic microbial communities and

macrophytes were able to persist and reproduce within the same salinity range (Fig. 3), contradicting the threshold model. Even if the salinity threshold for loss of the macrophyte community was higher than 50 ppt (explaining why macrophyte communities persisted at <90 ppt), to validate the threshold model, the switch in both directions would have to occur at the same salinity. Instead, benthic microbial communities were able to remain dominant at relatively low salinities ( $\geq 12$  ppt in the field) suggesting that their dominance over intermediate salinities is not restricted by a minimum salinity.

Importantly, however, exclusion of the continuum and threshold models does not automatically mean that the alternative regimes model explained our dataset. The paradigm of alternative ('stable') regimes has begun to be commonly applied in the restoration literature, with widespread acceptance that these types of system behaviours are more common than previously believed (Peterson, Allen & Holling, 1998; Suding, Gross & Houseman, 2004). However, recently, authors have also cautioned against over-ready acceptance of the alternative equilibria concept when limited empirical evidence is available (Scheffer & Carpenter, 2003; Schröder, Persson & De Roos, 2005).

The occurrence of the two ecological regimes at overlapping salinities is not enough to demonstrate that they comprise alternative equilibria. Likewise, the transience of transitional regimes (when benthic microbial community and macrophytes were co-dominant) is far from conclusive evidence for a switch from one 'basin of attraction' to another (Scheffer & Carpenter, 2003). Furthermore, the alternative regimes model predicts that an ecosystem will require external perturbation to cause a regime shift (away from either equilibrium state) at intermediate level of the driving variable (salinity) (Table 2), which does not appear to have occurred at either Lake Mears or Little White Lake when moving from benthic microbial community to macrophyte dominance. Instead, the shift away from the benthic microbial community-dominated regime appears simply to have occurred when water was present for long enough, and at low enough salinities, for germination to occur (Fig. 8). The benthic microbial communities then declined due to physical break-up by emerging macrophytes (L. Sim, personal observations, Sim *et al.*, in press b) and presumably also the eventual shading of the substrate. This evidence suggests that the benthic microbial community-dominated regime is not a very stable equilibrium.

There were no recorded transitions from macrophyte to benthic microbial community dominance except where drying first ended the macrophyte regime (Fig. 8). It appears that once macrophytes have established in seasonally drying wetlands, a salinity-driven shift away from their dominance will not occur within one wetting–drying cycle, even if salinities reach up to 90 ppt. Furthermore, since high salinities usually occur just before drying (Fig. 8) there may be insufficient time for a (high) salinity-driven regime shift to occur in these systems. It is possible that drying is also necessary for conditions to again become suitable for the establishment of benthic microbial communities, since when macrophytes senesce in these wetlands, the dead and dying plants cover the benthos, forming a relatively thick layer of decaying organic matter (L. Sim, personal observations), making it more difficult for a benthic microbial community to establish even if water is present and salinities remain high.

In order for the benthic microbial community and macrophyte-dominated regimes to truly constitute alternative equilibria, both of them would require self-stabilising mechanisms and resilience against pertur-

bations that might cause them to lose their dominance. Ecological resilience is a measure of the amount of change/force required to shift a system from one 'stability domain' or persistent ecological regime to another (Peterson *et al.*, 1998). A measure of ecological resilience takes into account the existence of factors that help to stabilise an ecosystem, such as the presence of multiple species that share similar functional roles (Peterson *et al.*, 1998). If one of these species is lost, the system is still able to maintain the same ecological function, due to functional redundancy. There is an acceptance that lower biodiversity leads to lower resilience for this reason; there is a smaller suite of species to compensate if one group is lost through a disturbance (Peterson *et al.*, 1998).

In the shift from freshwater to salt-tolerant species dominance, wetland ecosystems show considerable resilience; the individual species change, but most of their functional roles in habitat provision, primary production and nutrient cycling are retained. However, the resultant salt-tolerant macrophyte community tends to be species-poor, therefore reducing the ability of the system to compensate for further species losses. The remaining species offset this problem by having very wide tolerance ranges for salinity, light and other physicochemical variables (Brock, 1982; García & Chivas, 2004; Sim *et al.*, in press a) and through their ability to rapidly exploit favourable (if brief) hydrological conditions (Brock & Lane, 1983; Brock *et al.*, 2003), meaning that they are not easily lost from a system.

The resilience of the benthic microbial community-dominated regime appears to be much lower, not because species diversity is too low or because the functions of the microbes do not overlap sufficiently, but because the benthic microbial community has a low resistance to physical disturbance and is easily outcompeted by a superior competitor (submerged macrophytes) (Sim *et al.*, in press b). As a community, the benthic microbial community has wide tolerance limits, but weak competitive power. It therefore requires other conditions to be favourable (e.g. hydrological regime at Lake Coogee) to allow it to maintain dominance.

In this way, the existence of self-stabilising or positive feedback mechanisms directly impact on the resilience of a particular ecological regime. There are well-documented self-stabilising mechanisms that promote submerged macrophyte persistence and

dominance, including their roles in providing refuges for phytoplankton grazers, reducing sediment resuspension and removing nutrients from the water column (Beklioglu & Moss, 1996) and these appear to act over a wide range of salinity levels in Australian salinising wetlands. Abiotic positive feedbacks also promote the macrophyte-dominated regime, including seasonal drying, which both stimulates germination and prevents benthic microbial communities from becoming well established. In permanent systems, the benthic microbial community growth form has the potential for strong self-stabilising mechanisms which could prevent macrophyte establishment; for example it can persist in the form of an unstable (e.g. flocculent) layer, which undermines the physical stability of submerged plants (e.g. at Lake Coogee) or can form a thick, laminated physical barrier between the sediment and water column (Burke & Knott, 1997). In the latter case, sealing-off the sediment can effectively cause a lake to become 'perched', promoting evapoconcentration and making the salinities too high for macrophytes to tolerate (Burke & Knott, 1997). However, in seasonally drying systems, benthic microbial communities are unable to persist for long enough (at intermediate salinities) to facilitate either of these types of mechanisms. Drying consolidates the sediments (Bjornsson, Ostendorf & Recknagel, 2003) and kills the microbial biomass that has been building while sediments were wet (Qiu & McComb, 1996; Baldwin & Mitchell, 2000).

The comparative ecological resilience of these two regimes means that resilience of the macrophyte-dominant regime must be reduced (perturbation is required) to facilitate a shift towards benthic microbial communities, but that the benthic microbial community-dominant regime already has low resilience, allowing shifts away to occur more easily. If benthic microbial communities and macrophytes could be called alternative regimes, it appears that they are not equally 'stable'.

All three of the conceptual models we have considered here assume that salinity is the primary driver of ecological regime shifts in salinising wetlands. However, in the highly disturbed southwestern Australian agricultural zone, salinity is unlikely to be the only environmental variable with importance for the initiation and persistence of regimes. Once a wetland has become salinised, the sensitive freshwater biota are lost (Halse *et al.*, 2003) leaving a

relatively tolerant biota, which are able to persist at a range of salinities (Kay *et al.*, 2001; Sim *et al.*, in press a,b). This means that other factors are likely to be influential within the 'intermediate' ranges of salinity that all these organisms can tolerate. However, we did not find strong relationships between any of the additional physicochemical variables we measured (pH, water depth, turbidity and gilvin, Table 6) and the formation or persistence of ecological regimes (Table 6, Fig. 8). One important condition that we did not measure was trophic status, however, we believe that nutrients were unlikely to be highly influential in determining the dominance of submerged macrophytes versus benthic microbial communities. Both of these two regimes optimally require clear water conditions and are likely to be outcompeted by a phytoplankton-dominated regime under high nutrient loadings. It is, however, clear from our data that several aspects of hydrology other than water depth, particularly water persistence and the timing of drying, strongly interacted with salinity to influence ecological dynamics. This suggests that any model incorporating only a single driver is unlikely to be appropriate when considering seasonally drying saline wetlands.

## Conclusions

The dynamics of regime change in Australian seasonally drying salinising wetlands appear to be driven by the combined effects of salinity and water regime on species life histories and on the ability of different groups to compete effectively with each other. Salinity sets the boundaries within which a macrophyte community can establish and persist (Sim *et al.*, in press a), enabling microbes to hold dominance at the very high salinities beyond this range (Bauld, 1981; Kushner, 1993). Within the salinity limits of macrophyte tolerance, this group were powerful competitors, able to germinate and establish under a range of salinities, turbidities and water depths. In addition, regular drying facilitated their ongoing dominance. At all sites where water was present for at least 4–5 months and which dried annually or biennially, macrophytes became dominant, regardless of the previous dominant regime.

A conceptual model representing regime changes in salinising wetlands must incorporate the roles of both salinity and water regime in ecosystem dynamics. As

such, the alternative regimes model does not appear to be an appropriate model for seasonally drying wetlands, since the regular occurrence of drying appears to prevent the development of strong positive feedback mechanisms which might maintain the benthic microbial community-dominated regime. It is possible that an alternative regimes model might be valid for permanent saline ecosystems; in this case, positive feedback mechanisms for benthic microbial community dominance are likely to be much stronger, allowing this regime to constitute a true alternative to macrophyte dominance.

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