Ecosystem states of the Lower Lakes: A revised ecosystem response model

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1 Introduction

Lakes Albert and Alexandrina form part of the coastal lagoon complex at the terminal end of the Murray-Darling Basin (Figure 1). The River Murray enters in the north-east corner of Lake Alexandrina, near the town of Wellington, and provides the major source of freshwater inflow to the larger of the two lakes (Phillips & Mueller 2006). Lake Albert is a terminal lake lying to the south east of Lake Alexandrina, and receives fresh water primarily from Lake Alexandrina through the Narrung Narrows. Other significant, but smaller, freshwater inputs include rainfall on the lakes surface, groundwater discharge, and tributary flows (Phillips & Mueller 2006).

The Lower Lakes form part of the ecologically-significant Coorong, Lower Lakes, and Murray Mouth (CLLAMM) region that is listed under the Ramsar Convention on Wetlands of International Importance (DEH 2000). This globally, nationally, and regionally unique ecosystem supports a diverse range of ecological communities (Phillips and Muller 2006). It contains a unique mosaic of 23 wetland types, ranging from freshwater lakes into the estuarine environments of the Coorong, providing habitats for nationally-threatened species including the Orange Bellied Parrot, the Southern Mount Lofty Ranges Emu Wren, the Murray hardyhead and the Murray Cod (Phillips and Muller 2006). It also contains (in part) the critically endangered 'Swamps of the Fleurieu Peninsula', as well as threatened Gahnia sedgeland ecosystems (Phillips and Muller 2006). The Lakes also support significant numbers of wetland-dependent migratory bird species, with 49 species that rely on wetland at critical life stages, such as migratory stop-over for breeding habitat or refuge during times of drought (Phillips and Muller 2006). In addition, 20 species of fish utilise the site at critical stages of their life cycle including seven diadromous species and 12 estuarine species that spawn or have large populations and any freshwater species that spawn or recruit within the wetland (Phillips and Muller 2006). The Lakes have significant cultural, economic and recreational values, with sizeable local tourism and commercial fishing industries, nearby agriculture and are the spiritual home of an indigenous Australian community, the Ngarrindjeri nation.

However, Lakes Albert and Alexandrina form part of a highly-regulated system. The construction of locks and weirs to maintain water levels throughout the system impeded water flow, where floods and flows downstream are "less frequent, less extensive, less variable, and of altered duration and seasonality" (Phillips and Mueller 2006; p. 209). The water regime is further affected by extraction (including water pumps, channels, and bores), as well as constant barrage operations that serve to separate the typically fresh and estuarine to saline waters of the Lakes and Coorong, respectively. Between 2001 and 2010, dredging occurred continuously at the Murray Mouth as a result of sand

and silt deposition, maintaining hydrological connectivity between the Coorong and Southern Ocean (Phillips and Mueller 2006). Until recently, the region experienced a severe decade-long drought (2001-10),with lake water levels falling to levels previously unrecorded (-1.5 m AHD in Lake Alexandrina), exposing large tracts of acid sulfate soils and resulting in widespread decline in ecological condition. Since 2010, however, sufficient freshwater inflows have been received to recover lake levels to within the normal operating range of +0.65 to +0.85 m AHD, allowing for ecological recovery of the region to commence.

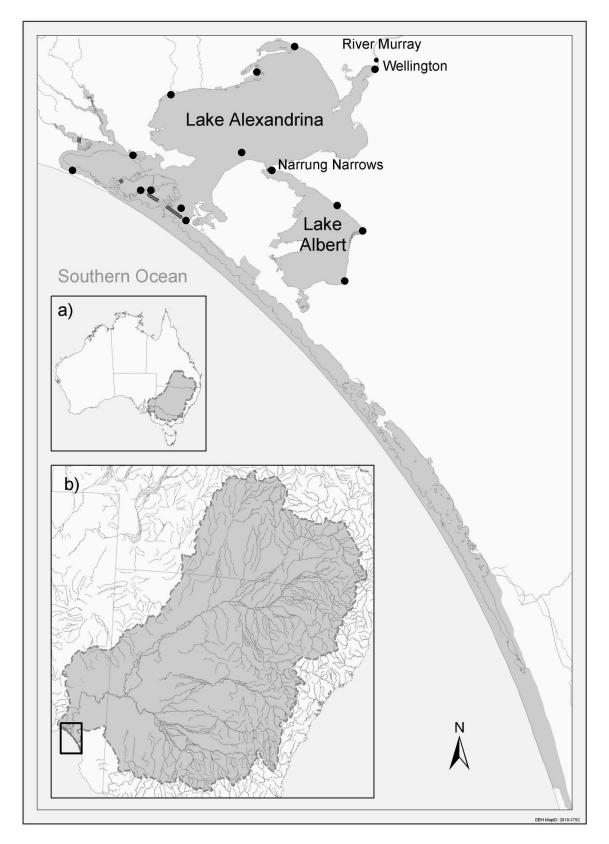


Figure 1. Map showing the Coorong, Lower Lakes, and Murray Mouth region, including Lake Alexandrina, Lake Albert, Narrung Narrows, Wellington, and the Murray River. The dark shading on the main map represents the Ramsar Convention boundaries, whilst dark shading in in-set maps represents the Murray-Darling Basin. There are a number of potential 'levers' used in the management of the system which affect ecosystem condition. These levers include: environmental flows of fresh water, either from the River Murray or the Eastern Mount Lofty Ranges; barrage operations controlling the flow of water between the Lower Lakes and the Coorong, including the operation of fishways; the creation or removal of so-called 'bunds' or barriers at Narrung and Clayton to allow for small-scale control of water levels; and various other local engineering solutions, such as pumping and dredging options. These, combined with climatic forcing factors, determine the ecological condition of the Lower Lakes, and identified 'water benefits' of the region, such as a viable fishery, tourism, cultural values, and sustained waterbird populations.

To develop an ecosystem-level understanding of the Lower Lakes, an ecosystem response model was developed by utilising existing information (see Lester and Fairweather 2009 for more detail on basic methodology and model development) to allow for a range of alternative conditions to be modelled in the future and to highlight gaps in the current understanding of the Lakes ecosystem. The model is explicit in both space and time and allows the prediction of the responses of the ecosystem to the identified system drivers, including climactic forcing and management options. Fundamentally, the ecosystem state model is a statistical model, where existing data for the region have been analysed and modelled to identify associations and relationships between the groups of biota that occur together in space and time within the system and the environmental conditions at the time.

This report is structured as a traditional scientific report. The methods section introduces data collation, identifying preliminary states, differentiating between preliminary states using environmental variables, and the characterisation of the ecosystem states. The results section then presents the ecosystem state model itself, and describes the biota and physico-chemical condition of each state, and how they can be mapped in both space and time. This section may be of most interest to those interested in the outcome of the modelling, rather than the development process, *per se*. Finally, we provide a discussion highlighting the implications of the results presented, limitations associated with the current model, and conclusions arising from the development of the ecosystem state model.

2 Methods

2.1 Data Collection

As many data as were available were compiled for the Lower Lakes region. Data sources included the monitoring and research data that have been collected by state or federal agencies, or research institutes in the region. The data that were collated, and the provenance of each, are listed in Table 1. Data were collected for 15 sites (Figure 1) for the period of 2002 to 2013 at an annual time-step in order to maximise the amount of data that could be included.

Data were divided into a biological data set and an environmental (i.e. physico-chemical) data set. The biological data set consisted of bird abundances as an average number sighted per site and aquatic vegetation abundances at each site (Table 1). The environmental data set included measured water levels, depths and salinities (electrical conductivity; EC) across Lakes Alexandrina and Albert, flow over the barrages, the modelled daily flow available from the MSN-Bigmod hydrological model (Close and Sharma 2005) and Surface Water Resource of the Eastern Mount Lofty Ranges (Alcorn 2010, Alcorn et al. 2008), meteorological data and measured water quality parameters, including the concentration of nutrients, pH, turbidity and dissolved oxygen (Table 2). In addition, distance parameters (i.e. distance to the River Murray, distance to freshwater source), bathymetric data (e.g. average and maximum depth 1 km from the shoreline) and prevailing coastline direction were estimated using Google Earth (Table 2). Discounted annual average flow was also estimated using the average annual flow data divided by the distance to the River Murray (Table 2). For the environmental data set, a range of parameters were calculated for each variable, including the maxima, minima and variability, particularly for water level characteristics, as means are not always best-correlated with changes in ecological character (Gaines and Denny 1993).

Category	Metrics included	Variable	Units	Provenance	Notes
Birds	Average	Species	Individuals within a R = 800 m	DEWNR (O'Connor	Monitored bird abundances
		abundance	semi-circle from a point location	et al. 2013;	undertaken for DEWNR by David Dadd
			(area = 0.5 [π x 8 x 0.8] = 1 km ⁻²)	O'Connor and	were averaged from monthly data for
				Rogers 2013)	each site-year.
Vegetation	Average	Species	Cover/abundance score ranging	SARDI (Gehrig et al.	Vegetation monitoring undertaken as
		abundance	from 1 to 5 (where 1 <5%,	2012)	part of the Lower Lakes Vegetation
			2 = 6-25%, 3 = 26-50%, 4 = 51-		Condition Monitoring program.
			75% and 5 >75%) across three		
			quadrats (each 1 x 3 m) spaced 1		
			m apart on a transect		
			perpendicular to the shore.		

Table 1. Biological variables included as part of the input data set and their provenance.

Table 2. Environmental variables included as part of the input data set and their provenance.

Category	Metrics included	Variables	Units	Provenance	Notes
Geographical	raphical Average Waterbody, Distance to freshwater source , Distance to River Murray, Prevailing coastline direction		km, cardinal directions	Google Earth	Sites were located using GPS points from the biological and water quality & quantity data set sources.
Meteorological	Average minimum, average maximum, maximum, minimum	Temperature	C	ВОМ	Data from 12 weather stations were used for all meteorological variables: Goolwa Council Depot, Strathalbyn, Goolwa Barrage, Hindmarsh Island, Langhorne Creek, Meningie, Milang, Murray Bridge, Narrung, Wellington, Milang (Nav.) & Strathalbyn Racecourse. Where relevant, values were averaged for each site using monthly data.
	Average	Relative Humidity	%	BOM	Measured at 9 am & 3 pm daily. Averages were of twice-daily values for each site
	Average	Precipitation	mm day ⁻¹	BOM	Averages were of daily values for each site
Water quantity	Average	Midpoint bathymetric depth and deepest bathymetric depth in site	m	DEWNR	Constant bathymetric depth across the site- years, estimated from values in Nature Maps (Lower Lakes and Upper Coorong Bathymetry data set) for each site. Midpoint represented the bathymetric depth taken in the middle of the site area and deepest was the deepest bathymetry within the site region. Nature Maps is an interactive online mapping site

Category	Metrics included	Variables	Units	Provenance	Notes
					maintained by DEWNR which includes a range of GIS data sets for natural resource management*.
	Average, average minimum, average maximum, average variability	Average lake level across the site (constant across all sites within each year)	m AHD	DEWNR	Data from the surface water archive** for daily mean lake level. The Surface Water Archive includes online maps and data provided by DEWNR. Constant refers to the average lake level across all the sites for each year (i.e. lake levels are the same across the sites but levels differ in years).
Water quality	Average , maximum, minimum and variability	Electrical conductivity	μS cm ⁻¹	DEWNR & EPA	A composite EC value was calculated as the average from the two data sets. EPA values were from periodic sampling and DEWNR values were a daily mean from telemetry data.
	Average	Temperature	°C	EPA & DEWNR	A composite temperature value was calculated as the average from the two data sets. EPA values were from periodic sampling and DEWNR were the daily mean
	Average	Dissolved oxygen	mg L ⁻¹	EPA	Averages were calculated for each site across the periodic readings available
	Average soluble phosphate and total Kjeldahl nitrogen	Soluble phosphate, total Kjeldahl nitrogen, oxidised nitrogen	mg L ⁻¹	EPA	Averages were calculated for each site across the periodic readings available

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Category	Metrics included	Variables	Units	Provenance	Notes
	Average	рН	pH units	DEWNR & EPA	A composite pH value was calculated as the average from the two data sets. EPA values were from periodic sampling and DEWNR were the daily mean
	Average	Alkalinity	mg L-1	EPA	Averages were calculated for each site across the periodic readings available
	Average	Turbidity	NTU		Averages were calculated for each site across the periodic readings available
	Average	Chlorophyll <i>a</i> & <i>b</i> concentrations	μg L ⁻¹		Averages were calculated for each site across the periodic readings available
Hydrology	Average, minimum, maximum	Daily flow, daily flow from previous year, total annual flow, total annual flow from previous year	ML day ⁻¹ , GL annum ⁻¹	MDBA	Modelled data produced by MSM-BigMod for Wellington (Close and Sharma, 2005)
	Average, minimum, maximum	Daily flow, daily flow from previous year, total annual flow, total annual flow from previous year	ML day ⁻¹ , ML annum ⁻¹	DEWNR	Modelled flow for the tributaries entering the Lower Lakes. Surface Water Resource of the Eastern Mount Lofty Ranges and includes data estimates on watercourse extractions (Alcorn 2010, Alcorn et al. 2008)

*Nature Map data were accessed from www.naturemaps.sa.gov.au/maps/viewer.aspx?site=NatureMaps

**Surface Water Archive data were accessed from www.waterconnect.sa.gov.au/Systems/SWD/SitePages/Home.aspx

2.2 Identifying preliminary states

Cluster analysis was used to identify preliminary groups of cases that had similar biotic assemblages. Only cases that included a complete set of biological data were able to be clustered (i.e. missing values were removed, n = 76). The cluster analyses used a complete-linkage algorithm and a SIMPROF test to identify clusters which were statistically distinct (Clarke & Gorley 2006). These analyses were undertaken in PRIMER v.6. The cluster analysis for the combined biological data identified four distinct clusters. ANOSIM analyses were used to check that the clusters were biologically-distinct from one another and clusters that were not significantly different were combined and re-checked. This resulted in three biologically distinct clusters which were considered the preliminary states for the purposes of CART analyses.

2.3 Differentiating between preliminary states using environmental variables

Classification tree analyses were used to identify environmental variables that differentiated between the preliminary states. These analyses were undertaken in CART 7.0 (Steinberg and Golovnya 2007) using 178 available environmental variables as potential predictive variables. Water quality variables where there were many missing cases were excluded from this step. Twoing splitting was used, with the One Standard Error rule (Breiman et al. 1984), and only cases for which a preliminary state was identified were included in the analysis. Cross-validation occurred with two folds, as this was the size of the cluster with the smallest number of cases. The minimum number of cases allowed was set to five for a parent node and two for a child node. To penalize variables with missing values, β was set to 0.6 (Steinberg and Golovnya 2007).

A five-node tree at a relative cost of learn cost of 0.125 (test cost of 0.597) was produced with a learn prediction success of 80% and a test prediction success of 75%. The predictive capacity of various parameters (e.g. minima, maxima, means) and the more complete set of parameters (including lagged variables and variances, for example) made it difficult to identify in advance which variables were likely to be inter-correlated, so all were included and correlations amongst predictive variables were determined *post hoc*. Where two significant ($\alpha = 0.05$) predictor variables were identified in the CART model that were significantly correlated, the variable explaining the smaller proportion of the variance was excluded and the model re-run, until there were no significant correlations among the identified predictive variables for the model.

2.4 Confirm the distinctness of the ecosystem states

In order to ensure that the terminal nodes identified represented biologically-distinct ecosystem states, the biological assemblages associated with each (birds and vegetation) were tested for distinctness using ANOSIM analyses (in PRIMER v.6) on the biological data set. Where evidence existed that the cases grouped into a terminal node did constitute a biologically-distinct community (by having a significant difference in pair-wise comparisons with each other preliminary state, with some consideration given to the sample sizes), those terminal nodes were considered distinct. Where ANOSIM analysis indicated that terminal nodes were not significantly different, those two terminal nodes were combined and the analyses were re-run. This resulted in the combination of two terminal nodes, leaving a model with four terminal nodes, with three ecosystem states for the region (i.e. one state appears at two separate nodes).

2.5 Characterisation of the ecosystem states

Each of the three identified ecosystem states was then characterised based on the biological community they supported and the environmental conditions under which they occurred. SIMPER analyses (in PRIMER v.6) were used to identify species which were characteristic of each of the ecosystem states, or species which distinguished between the states. Taxa that had a dissimilarity to standard deviation ratio greater than 1 (Clarke and Gorley 2006) were considered reliable indicators of differentiating between sites and were considering characteristic at that site. The average, minima, maxima and variance of environmental variables and species were calculated in Excel using pivot tables to compare across states.

3 Results

3.1 An ecosystem state model for the Lower Lakes

The final ecosystem state model for the Lower Lakes identified three distinct ecosystem states (Figure 2). The splitting variables were average chlorophyll *a* concentration (μ g L⁻¹), bathymetry 1 km, average nitrate and nitrite concentration, measured as the concentration of nitrogen (mg L⁻¹) and average precipitation at Langhorne Creek (mm day⁻¹). The three-node model correctly classified 80% of the cases in the original data file and 75% of cases under cross-validation.

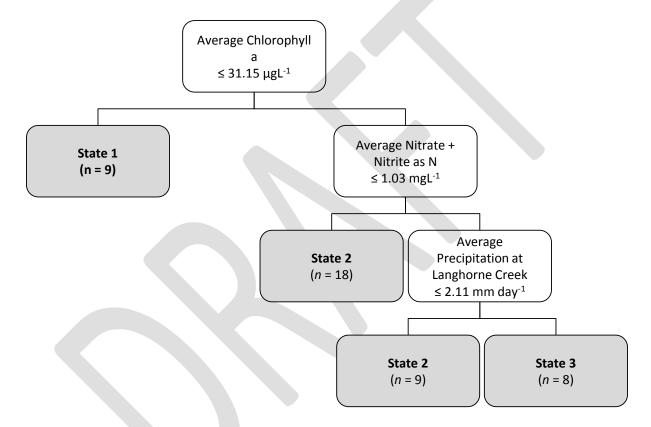


Figure 2. Ecosystem states model for the Lower Lakes as whole. The states are presented as a logic tree, where each box should be read as a logic statement. For a given site-year, if the condition in the box is true, the tree should be followed to the left-hand side. If the condition is false, the tree proceeds to the right, until a shaded terminal node is reached. This terminal node determines which state the Lower Lakes is in at any given location and time, based on its environmental characteristics. *N* represents the number of samples (i.e. site-years) which were characterised within each terminal node. Note that there are two pathways (or sets of environmental conditions) that lead to State 2, but that the biota present are not different for those two pathways.

3.2 Characterising each of the ecosystem states

Each of the three ecosystem states have been described in terms of their biological and environmental characteristics. The cases which were characterised into each of the ecosystem states are shown in Table 3. The environmental parameters and biological species abundances that characterise amongst the three ecosystem states are shown in Tables 4 and 5, respectively.

Table 3. Summary of the cases (i.e. site-years) characterised into each of the ecosystem states with sites listed as columns, years as rows and the ecosystem state for each site in each year listed by number in the body of the table. Cells for State 2 and 3 have been shaded light and dark (respectively) grey to help show the patterns in ecosystem states at each site across the years.

	Year											
Site	'02	'03	'04	'05	' 06	'07	'08	'09	'10	'11	'12	'13
Beacon 90	2	2	1	1	1	2	2	2	1	1	1	2
Clayton	2	2	1	1	1	2	2	2	2	2	1	1
Dog Lake/Tolderol	2	2	1	1	1	2	2	2	3	2	1	1
Ewe Island	2	2	1	1	1	2	2	2	2	2	1	1
Goolwa Barrage	2	3	1	1	1	2	2	2	3	3	1	1
Meningie	2	2	1	1	1	2	2	2	3	3	3	3
Milang	2	3	1	1	1	2	2	2	3	3	3	3
Mundoo	2	2	1	1	1	2	2	2	2	2	1	1
Narrung	2	2	1	1	1	2	2	2	2	2	1	1
Pelican Point	2	3	1	1	1	2	2	2	3	3	1	1
Poltalloch	2	2	1	1	1	2	2	2	2	3	1	1
Tauwitcherie	2	3	1	1	1	2	2	2	3	3	1	1
Top Lake Alexandrina	2	2	1	1	1	2	2	2	3	3	1	1
Waltowa	2	2	1	1	1	2	2	2	2	3	3	3
Wellington	2	3	1	1	1	2	2	2	3	3	1	2

State 1:

All sites were in this state in the years between 2004 and 2006, at most sites in 2012 and 2013 and at Beacon 90 in 2010 and 2011. This state is characterised as having moderate precipitation (1.06 mm day⁻¹) recorded at Hindmarsh Island. This state has low flows from the various tributaries into the region, with low daily flows from the River Murray (average 4380 ML day⁻¹), low daily flows from the previous year for the Angas (average 16 ML annum⁻¹) and Finniss (average 60 ML annum⁻¹) Rivers, low total flows for the current year for the River Murray (average 1,400 GL annum⁻¹), and low

total flows for the previous year for the Murray (average 1,503 GL annum⁻¹), Angas (average 5850 ML annum⁻¹) and Finniss (average 21,986 ML annum⁻¹) Rivers. Despite the low flows, there is moderate lake variability (0.56 m annum⁻¹) in this state. Water quality characteristics include low chlorophyll *a* concentrations (average 25.85 µg L⁻¹), chlorophyll *b* concentrations (average 3.18 µg L⁻¹), nutrient concentrations (TKN average 1.32 mg L⁻¹ and maximum 2.01 mg L⁻¹), low alkalinity (minimum 47.66 mg L⁻¹, average 102.51 mg L⁻¹, maximum 168.86 mg L⁻¹) and conductivity (minimum 336 µS cm⁻¹, average 1585 µS cm⁻¹, maximum µS cm⁻¹) but high silica concentrations (average 7.6 mg L⁻¹).

Characteristic vegetation of this state include high cover of kikuya (*Pennisetum clandestinum*, cover score = 0.77), water fern extent (*Azolla filiculoides*, cover score = 0.60), annual beard-grass (*Polypogon monspeliensis*, cover score = 0.25) and common reed (*Phragmites australis*, cover score = 2.06), and a high extent of open water (cover score = 4.08) habitat. This state supported high numbers of riparian birds (i.e. Eurasian coot *Fulica atra* 103 individuals on average and purple swamphen *Porphyrio porphyrio*, 10 individuals), moderate to high numbers of many piscivorous birds (e.g. little black cormorant *Phalacrocorax sulcirostris*, 33 individuals and whiskered tern *Chlidonias* hybrid, 49 individuals, great cormorant *Phalacrocorax carbo*, 32 individuals, pied cormorant *Phalacrocorax varius*, individuals 33 and silver gull *Chroicocephalus novaehollandiae*, 35 individuals), high numbers of some shorebirds (sharp-tailed sandpiper *Calidris acuminate*, 233 individuals, red-necked stint *Calidris ruficollis*, 222 individuals and straw-necked ibis *Threskiornis spinicollis*, 50 individuals) but low or moderate numbers of other shorebird species. Finally, there tended to be high numbers of many waterfowl (e.g. grey teal *Anas gracilis*, 211 individuals and black swan *Cygnus atratus*, 50 individuals).

State 2:

All sites in the Lower Lakes were in State 2 during 2002 and between 2007 and 2009. This state was also observed at some sites in 2003, 2010, 2011 and 2013. This state is characterised as having low precipitation (average 0.93 mm day⁻¹) recorded at Murray Bridge. High flows from many of the tributaries in the previous year characterise this site, with high daily flows from the previous year in the Bremer (31 ML day⁻¹), Finniss (88 ML day⁻¹) and Tookayerta (49 ML day⁻¹) tributaries. High total flow from the previous year from Finniss River (30,602 ML annum⁻¹) and Tookayerta Creek (17,985 ML annum⁻¹) was also characteristic, as was total moderate daily flows form the River Murray (5956 ML day⁻¹). High lake level variability (0.89 m annum⁻¹) is also characteristic of this state. State 2 has high chlorophyll *a* concentration (61.59 µg L⁻¹), potentially high nutrient concentrations (TKN average 2.63 mg L⁻¹ and maximum 4.05 mg L⁻¹), high alkalinity (minimum 131.50

mg L⁻¹, average 178.64 mg L⁻¹, maximum 223.26 mg L⁻¹) and conductivity (minimum 5166 μ S cm⁻¹, average 8096 μ S cm⁻¹, 3189 maximum μ S cm⁻¹), as well as a lower maximum pH (8.80) than other states.

The vegetation in this state can be characterised with a lower abundance of couch (*Paspalum distichum*, cover score =0.99) and annual beard-grass (*Polypogon monspeliensis*, cover score = 0.38), and a high extent of bare sediment (cover score = 2.83) and a low extent of open water (cover score = 0.87) habitats. Riparian bird abundances were high in this State (i.e. Eurasian coot *Fulica atra*, 96 individuals and purple swamphen *Porphyrio porphyrio*, 106 individuals). There are moderate to high numbers of many piscivorous birds (e.g. pied cormorant *Phalacrocorax varius*, 62 individuals, great cormorant *Phalacrocorax carbo*, 48 individuals, silver gull *Chroicocephalus novaehollandiae*, 42 individuals, whiskered tern *Chlidonias* hybrid, 38 and Australian pelican *Pelecanus conspicillatus*, 34 individuals, sharp-tailed sandpiper *Calidris acuminate*, 114 individuals, and yellow-billed spoonbill *Platalea flavipes*, 6 individuals) and high numbers of many waterfowl (e.g. Cape Barren goose *Cereopsis novaehollandiae*, 32 individuals, Australasian shoveler (*Anas rhynchotis*, 17 individuals, and grey teal *Anas gracilis*, 161 individuals).

State 3:

Ecosystem State 3 occurred at sites only following an occurrence of State 2. State 3 can be characterised as having high precipitation recorded at both Hindmarsh Island (average 1.27 mm day⁻¹) and Murray Bridge (average 1.21 mm day⁻¹). High flows characterise this site, including much higher average daily flows (26,910 ML day⁻¹) and total annual flow (5,987 GL annum⁻¹) from the River Murray when compared with other states. High average daily flows from the previous year from the Angas (20.34 ML day⁻¹), and Finniss (81.10 ML day⁻¹) tributaries but low daily flows from the previous year from the previous year from Bremer (23.74 ML day⁻¹) and Tookayerta (44.50 ML day⁻¹) are also characteristic of this state. Lake level variability is low (average 0.39 m annum⁻¹) in this state. Water quality characteristics for this state are often intermediate between States 1 and 2, including for chlorophyll *a* concentrations (45.88 μ g L⁻¹), alkalinity (minimum 99.47 mg L⁻¹ and average 156.57 mg L⁻¹), conductivity (average 3467 μ S cm⁻¹) and pH (maximum 8.95). Silica concentrations are higher in this state (average 3.74 mg L⁻¹) than State 2.

This state has the greatest extent of bare sediment (cover score = 2.50) and open water (cover score = 3.75) habitats. The extent of couch is highest in this state (*Paspalum distichum*, cover score = 1.37) and the common reed extent is intermediate (*Phragmites australis*, cover score = 1.32). This state

supports comparatively lower abundances of birds compared to States 1 and 2, with low abundances of all feeding guilds. The exceptions to this are high numbers of some piscovores (i.e. silver gull *Chroicocephalus novaehollandiae*, 62 individuals and great cormorant *Phalacrocorax carbo*, 41 individuals) and water fowl (i.e. Australian shelduck *Tadorna tadornoides*, 175 individuals and Pacific black duck *Anas superciliosa*, 27 individuals). Table 4. Summary of the environmental characteristics of the Lower Lakes ecosystem states. Note: Parameters included are based on the results of SIMPER analyses outlining the variables that drove the similarities within states and the differences between states. Water quality variables were analysed in a separate SIMPER analysis because of the limited number of cases available. Average values represent those from non-normalised and untransformed environmental data. NA denotes that the variable did not appear for that particular state in the SIMPER output. SD indicates standard deviation.

				Ecosy	stem	State			
		1			2			3	
Parameter	Average		SD	Average		SD	Average		SD
Meteorological									
Precipitation at Hindmarsh Island (mm day-1)	1.06	±	0.26		NA		1.27	±	0.15
Precipitation at Murray Bridge (mm day ⁻¹)		NA		0.93	±	0.19	1.21	±	0.14
Water Quantity									
Lake level variability (m)	0.56	±	0.24	0.89	±	0.71	0.39	±	0.32
Daily Flow River Murray (ML d ⁻¹)	4380	±	7176	5956	±	12060	26910	±	20759
Daily Flow Prev Year Angas EOS With Losses (ML d ⁻¹)	16.02	±	8.08		NA		20.34	±	13.16
Daily Flow Prev Year Bremer EOS With Losses (ML d ⁻¹)		NA		31.33	±	25.25	23.74	±	19.27
Daily Flow Prev Year Finniss EOS (ML d ⁻¹)	60.23	±	27.44	83.78	±	36.19	81.10	±	46.71
Daily Flow Prev Year Tookayerta EOS (ML d ⁻¹)		NA		49.23	±	9.33	44.50	±	9.35
Total Flow River Murray (ML annum ⁻¹)	1400010	±	1342289		NA		5987225	±	3027628
Total Flow Prev Year Angas EOS With Losses (ML annum ⁻¹)	5850	±	2950		NA		7443	±	4819
Total Flow Prev Year River Murray (ML annum ⁻¹)	1503670	±	635525		NA		2446998	±	2188776
Total Flow Prev Year Finniss EOS (ML annum ⁻¹)	21986	±	10024	30602	±	13209	29674	±	17110
Total Flow Prev Year Tookayerta EOS (ML annum ⁻¹)		NA		17985	±	3397	16277	±	3437
Water Quality									
Alkalinity (mg L ⁻¹ of CaCO3) - average	102.51	±	32.90	178.64	±	76.80	156.57	±	65.73
Alkalinity (mg L ⁻¹ of CaCO3) - maximum	168.86	±	63.46	223.26	±	72.76		NA	

		Ecosystem State								
				2		3				
Parameter	Average		SD	Average		SD	Average		SD	
Alkalinity (mg L ⁻¹ of CaCO3) - minimum	47.66	±	21.34	131.50	±	87.89	99.47	±	54.74	
Chlorophyll <i>a</i> (µg L⁻¹) - average	25.84	±	4.16	61.59	±	20.96	45.88	±	11.86	
Chlorophyll <i>b</i> (µg L ⁻¹) - average	3.18	±	0.36		NA		4.61	±	1.10	
Conductivity (25°C μS cm ⁻¹) - average	1585	±	1411	5166	±	4080	3467	±	2979	
Conductivity (25°C µS cm ⁻¹) - maximum	3177	±	3205	8096	±	6543		NA		
Conductivity (25°C µS cm ⁻¹) - minimum	335.87	±	157.91	3189	±	3174		NA		
pH - average	8.42	±	0.20		NA		8.54	±	0.18	
pH - maximum	8.98	±	0.15	8.80	±	0.22	8.95	NA	0.22	
Silica (reactive) (mg L ⁻¹) - average		NA		1.63	±	0.94	3.74	±	2.32	
Silica (reactive) (mg L ⁻¹) - maximum	7.60	±	3.99	3.44	±	2.79		NA		
TKN as Nitrogen (mg L ⁻¹) - average	1.32	±	0.10	2.63	±	1.09		NA		
TKN as Nitrogen (mg L ⁻¹) - maximum	2.01	±	0.46	4.05	±	1.63		NA		

Table 5. Summary of the biological characteristics of the Lower Lakes ecosystem states. Note: Biota included are based on results of SIMPER analyses outlining the species that drove the similarities within states and the differences between states. SIMPER analyses were done on the bird and vegetation abundances both separately and combined.

Birds (average abundance)Anas castaneaChestnut teal9.6613.8Anas gracilisGrey teal210.74160.8Anas rhynchotisAustralasian shoveler13.2916.8Anas superciliosaPacific black duck26.2024.0Ardea albaGreat egret1.792.4Aythya australisHardhead17.3623.9Calidris acuminataSharp-tailed sandpiper233.16113.9Calidris ruficollisRed-necked stint221.97199.5Cereopsis novaehollandiaeCape barren goose23.0432.2Charadrius ruficapillusRed-capped plover5.7110.7Chlidonias hybridaWhiskered tern49.0337.7Chroicocephalus novaehollandiaeSilver gull34.6141.8Cygnus atratusBlack swan49.8336.1Egretta novaehollandiaeWhite-faced heron2.192.8					
Species	Common Name	1	2	3	
Birds (average abundance)					
Anas castanea	Chestnut teal	9.66	13.87	8.77	
Anas gracilis	Grey teal	210.74	160.82	97.02	
Anas rhynchotis	Australasian shoveler	13.29	16.83	8.58	
Anas superciliosa	Pacific black duck	26.20	24.02	27.44	
Ardea alba	Great egret	1.79	2.41	2.55	
Aythya australis	Hardhead	17.36	23.90	12.26	
Calidris acuminata	Sharp-tailed sandpiper	233.16	113.99	123.95	
Calidris ruficollis	Red-necked stint	221.97	199.57	145.57	
Cereopsis novaehollandiae	Cape barren goose	23.04	32.27	21.31	
Charadrius ruficapillus	Red-capped plover	5.71	10.73	7.98	
Chlidonias hybrida	Whiskered tern	49.03	37.76	26.40	
Chroicocephalus novaehollandiae	Silver gull	34.61	41.88	62.25	
Cygnus atratus	Black swan	49.83	36.17	14.07	
Egretta novaehollandiae	White-faced heron	2.19	2.88	2.44	
Fulica atra	Eurasian coot	103.03	95.80	25.59	
Himantopus himantopus	Black-winged stilt	23.81	15.12	17.85	
Hydroprogne caspia	Caspian tern	10.88	7.22	11.88	
Microcarbo melanoleucos	Little pied cormorant	3.46	9.69	3.11	
Pelecanus conspicillatus	Australian pelican	27.14	33.91	19.00	
Phalacrocorax carbo	Great cormorant	32.32	47.89	41.13	
Phalacrocorax sulcirostris	Little black cormorant	33.43	20.68	19.10	
Phalacrocorax varius	Pied cormorant	32.85	61.51	23.97	
Platalea flavipes	Yellow-billed spoonbill	4.30	5.53	4.58	
Platalea regia	Royal spoonbill	5.53	14.64	5.47	
Podiceps cristatus	Great crested grebe	19.28	10.74	4.08	
Porphyrio porphyrio	Purple swamphen	10.39	15.75	1.00	
Tadorna tadornoides	Australian shelduck	80.82	97.87	175.01	
Thalasseus bergii	Crested tern	19.97	15.20	11.94	
Threskiornis molucca	Australian white ibis	5.86	7.12	6.98	
Threskiornis spinicollis	Straw-necked Ibis	50.37	24.70	14.52	
Tringa nebularia	Common greenshank	3.78	4.11	2.29	
Vanellus miles	Masked lapwing	11.24	8.87	7.37	
Vegetation (cover/abundance score)				
Azolla filiculoides	Water fern	0.60	0.12	NA	
Bare		0.83	2.83	2.50	
		4.08			

		Ecosystem State					
Species	Common Name	1	2	3			
Paspalum distichum	Couch	1.87	0.99	1.37			
Pennisetum clandestinum	Kikuya	0.77	0.63	0.86			
Phragmites australis	Common reed	2.06	1.22	1.32			
Polypogon monspeliensis	Annual beard-grass	0.25	0.38	NA			

4 Discussion

This research project was designed to update and refine a preliminary ecosystem states model for the Lower Lakes that was developed in 2011. At the time, there were eleven identified ecosystem states that were often defined by their location (e.g. by the distance to a given source of freshwater) which made them invariant in time. As a result, while the model did provide interesting characterisation of the spatial differences in Lakes, it was less useful for exploring the impact of management actions on the various components of the ecosystem.

In this refined model, there were three identified ecosystem states. The ecosystem states were identified based on the chlorophyll *a* concentrations, nutrient concentrations (particularly of nitrate and nitrite) and precipitation rates in the region. These splitting variables are quite different from those identified for the ecosystem states of the Coorong, where flows, water levels and salinities were the predominant drivers of the identified ecosystem states (Lester and Fairweather, 2009). The splitting variables identified here likely also indicate the importance of water quality and water level in the Lakes in determining the biota present. Re-suspension via wind or wave action may also play a role in regulating the nutrient concentrations, so may be important as well.

The model described here has an excellent ability to categorise site-years that fall within the training portion of the data (correctly classifying 80% of cases), and also performed well under cross-validation, correctly classifying 75% of cases in the validation portion of the data. The misclassified cases were spread across the three groups, and suggest that no single state was more likely to be classified incorrectly than the others. Such a finding may be a result of a gradation of ecological condition within the system. For example, there appears to be a clear sequence from State 1 to 3 and then State 2 in many sites, suggesting that they may act as a continuum as a result of ongoing changes in the environmental condition of the region (e.g. poor conditions may tend to be followed by a large flow event that inundates edge habitats, temporarily resulting in habitat loss, but followed by recolonisation and regeneration of those habitats as waters recede).

The first of the states, State 1, was characterised by relatively low flows, but also low nutrient concentrations. The state supported high coverage of riparian vegetation and high bird abundances. This was particularly true for waterfowl and piscivorous birds as well as some shorebirds. The prevalence of piscivorous birds suggests that there may have been plentiful fish assemblages nearby to support the predators in those regions. State 2 was characterised by lower water quality than other states. It also tended to have more bare sediment and less vegetation. Interestingly, the decline in water quality did not necessarily appear to coincide with low tributary flows. Despite this lower water quality, the state still supported good numbers of birds, including piscivores, again suggesting that fish were present nearby. Likewise, the presence of shorebirds may indicate that there were sufficient food resources for them nearby, such as benthic invertebrates or vegetation shoots or propagules. Finally, State 3 appeared to be something of a transition state. The state was characterised by intermediate water quality and high flows but low bird numbers and large tracts of water and bare sediment. Such a combination may indicate a disturbance in the region associated with flows. For example, flows may lead to high lakes levels which in turn down out edge habitats and make it difficult for birds and vegetation to survive in the short term.

This second iteration at producing an ecosystem response model for the Lower Lakes identifies many fewer ecosystem states than the first iteration. This may be partly as a result of differences in the biotic data set that has been included, but also due to differences in the Lakes ecosystem following the recovery of the region from drought. The original model included a number of states that were defined by their geographic location only. This was a significant limitation of that model, as there was no potential for those states to alter with the environmental condition of the Lakes, making it of limited value from a management perspective. This iteration of the model rectifies that issue, in that all states are determined based on the suite of environmental conditions that occur at any point in time, the majority of which are susceptible to management actions via levers such as lake-level manipulations. This means that the model is a much more useful tool from the perspective of assessing the potential impact of management actions on Lower Lakes ecosystems.

When characterising the various site-years into ecosystem states using the refined model presented here and based on the environmental conditions at the time, it was apparent that many sites tended to be in the same state in a given year, rather than there being a diverse mix of states at any point in time (see Table 2). Thus, states tend to be uniform across the system in time, suggesting that there was more variability in time in the assemblages present than in space, at least for vegetation and birds. Such a pattern may be a function of the types of data that were able to be included (e.g. a similar pattern may not have appeared if fish and/or invertebrates had been able to be included). Thus, some caution is needed in assuming that this pattern is general for the entire Lakes ecosystem. As a result of this pattern, it is unlikely that this model is appropriate for use in taking decisions regarding small-scale changes, particularly regarding heterogeneous habitats around the lakes, but it may be more relevant for large-scale decisions regarding flows into the region and water levels and their likely impact on the decision variables.

The environmental data set that was available for the development of this model was one of the reasons for the improvement in the utility of the model from the first iteration. Significant resources have been devoted to the collection of data regarding water levels, water quality, physical characteristics (e.g. bathymetry) and meteorological conditions of the region, and this has occurred consistently, and repeatedly, in space and time particularly in recent years. The collection of such data are invaluable to the types of research undertaken here, to develop a tool for synthesising the condition of the region over long time scales. Continued collection of such data should be a high priority for the ongoing management of the region.

The development of this ecosystem states model for the Lower Lakes was, however, hampered by the lack of consistency in the timing and location of both the environmental (particularly between 2002 and 2007) and biotic sampling around the Lakes. Data on the fish assemblages, in particular, would have added significantly to the model, given their importance in the Ramsar-listing of the region and as a goal for the management of the region. While fish data are available, both as a result of the commercial fishery and also due to research organisations and programs such as The Living Murray, these were not able to be included in the model. Commercial fisheries data for the region are only resolved to identify catches at the lake level (i.e. Lake Alexandrina or Lake Albert), so were not at a fine enough spatial resolution to be of value in differentiating among sites within Lakes, despite the high temporal resolution. Research data tended to focus on specific areas within the Lakes also (e.g. the barrages and fishways) or were collected for small numbers of years. This lack of

consistency (or limited resolution) in space and time was unsuitable for the type of model developed here. In addition to fish, it was also not possible to include data collected on macroinvertebrate assemblages for similar reasons, which again would have been of value in developing a truly ecosystem-scale model. A re-alignment of all biotic monitoring schedule within the Lower Lakes to focus on sites routinely sampled for vegetation and birds at similar intervals, for example, would greatly enhance the value of all monitoring data sets. Such a move would enable comprehensive comparisons across the biotic groups within the region and enable decisions to be taken based on their impact on the Lakes ecosystem as a whole, rather than focusing on individual, isolated groups.

In conclusion, the refined ecosystem states model for the Lower Lakes identified three ecosystem states, based on the water quality (specifically cholorphyll *a* and nitrogen concentrations) and rainfall in the region. The states appear to occur in a relatively regular sequence, with State 3 being a transitional state between State 1 and State 2. There was little spatial heterogeneity in the occurrence of ecosystem states, suggesting that the model may be more appropriate for use in large-scale planning, rather than for small-scale, within-Lake interventions. The model did, however, perform well at describing the dataset available. While it will need to be independently validated at a later date, following the collection of additional data, this model could be used with some degree of confidence in the interim to assist in taking decisions relating to the flows and water levels present within the Lower Lakes ecosystem.

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